Plant macrofossil analysis of Holocene alluvium, with special reference to the Lower Thames Basin

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Abstract

Alluvium is an important archaeological and palaeoenvironmental resource in lowland Britain. The research presented here develops plant macrofossil analysis of alluvial facies, with special emphasis on the depositional and natural environments of the Lower Thames Basin. Plant macrofossil analysis is a poorly developed area of alluvial research, usually limited to superficial description of the fossils seen in section, or detailed analysis of a narrow suite of remains. A comprehensive, quantitative method of macrofossil analysis using counts and cover abundance scores is developed. Identification criteria for several groups of macrofossils are presented, including leaves, rootlets and epidermis.

Potential macrofossil incorporation was investigated at eight wetland and alluvial sites, including saltmarsh, wet woodland and herb fen environments. Macrofossil collections were compared to extant vegetation and subject to multivariate analysis. The results showed that macrofossil assemblages produce spatially and temporally precise data of plant presences, although spatial and temporal fidelity varies in different depositional environments and between plant taxa. Vegetation dominants were favoured in the assemblages of all classes of macrofossils, with bulky Monocotyledons and Therophytes favourably preserved and sparsely distributed taxa, such as rosette plants, less well favoured. The depositional environment and position in relation to environmental gradients were also found to affect macrofossil composition. Multiple approaches to macrofossil analysis using a wide range of macrofossils were found to produce improved interpretations. The value of different macrofossil classes and occurrences of the major observed taxa in alluvial sediments are discussed.

The method was applied to samples from the Medway River at Chatham. Vegetation history, hydrology and traces of human disturbance are discussed from 7000BP to 2000BP. Analysis showed a gradual increase in human disturbance over time, development of a distinctive human-influenced upper salt marsh flora from 3000BP and supports the trend across southern Britain for a change in hydrology by the same period.

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1 Introduction

Alluvium has been deposited in many rivers and estuaries in the Lower Thames Basin (referred to from here as the 'Lower Thames') during the Holocene. As river valleys and estuaries are the only spatially extensive sedimentary basins in southeast England in which long sedimentary sequences have been deposited, alluvium is a particularly important source of data for regional archaeological and palaeoenvironmental studies. Alluvium has provided data for the study of Holocene environmental patterns and processes at micro-, macro- and mega-spatial scales in the region (*sensu* Delcourt *et al.* 1983), including terrestrial ecological change (Scaife and Burrin 1987; Greig 1992a, 1992b; Thomas 1996), Holocene river hydrology (Burrin and Scaife 1984) and relative sea-level change (Devoy 1979). Archaeological research over 150 years has demonstrated that alluvial environments were the site of direct human activity throughout the Holocene, with finds including settlements, boats, artefacts, trackways and platforms (see review of Bates and Barham 1995). They also preserve important traces of life in adjacent terrestrial locations that for millennia have been important centres of population, industry and trade. High sediment accumulation rates and maintained anaerobic conditions have led to the preservation of organic archaeological materials that would otherwise perish.

Interpretation of human activity and reconstruction of patterns of environmental change in and adjacent to alluvial environments has best been achieved through the systematic integration of palaeoenvironmental and archaeological data. This approach has a long history (e.g. Bulleid and Gray 1911, 1917; Reid 1917, Clifford 1936, Swinnerton 1931, Godwin 1960) and has been an explicit part of several recent research programmes in wholly or partially alluviated areas (Coles 1987; Van de Noort and Davies 1993; Cowell and Innes 1994; Wilkinson and Murphy 1995). Such systematic programmes have been largely absent from the Lower Thames, with the exception of the Blackwater Estuary Project, and most studies have been associated with individual rescue archaeology works, the reports from which are dispersed in unpublished archives or obscure local publications.

Although alluvium is a regionally important source of information, its use as a basis for reconstructions of environments in time and space is complicated by its mode of deposition. Channel, channel bank, overbank and marsh environments are differentially affected by tides, floods and autogenic processes and may derive fossil and sediment

inputs from both allochthonous and autochthonous sources. Deposition is also often discontinuous and may vary in rate and direction, with sediments subjected to episodes of erosion. Sediments may, therefore, contain widely varying concentrations of fossils differing with spatial and temporal fidelities (*sensu* Kidwell and Flessa 1995) and sequences may be incomplete, with important transitional sections missing. This has partially led to the restricted use of alluvial fossil assemblages for palaeoenvironmental investigations, especially those from clastic sediments. A further problem is that alluvial environments are spatially heterogenous with many sub-environments that have differing sedimentological and fossil characteristics existing at the same point in time. Changes in sediments and fossils may simply reflect local changes and the linkage of facies changes to larger environmental variables is often difficult to prove.

Among the fossil groups preserved in alluvium are plant macrofossils. This group includes all plant structures visible to the naked eye, such as seeds, wood, roots, rhizomes, stem and leaf fragments (Dickson 1970; Birks and Birks 1980). Macrofossil preservation in alluvium is often excellent owing to the anaerobic environment of many sediments. However, analysis of plant macrofossil assemblages is one of the more neglected areas of alluvial research. Descriptions are often limited to the partial identification of fibres, stems and leaves visible in superficial examination of strata (e.g. Waller 1994) or the recording of gross macrofossil groups in stratigraphic descriptions such as those based on the Troels-Smith system (Aaby and Berglund 1986). These records primarily contribute to the identification of depositional environments and, in some cases, the type of vegetation extant during sediment accumulation. Mostly, only loose structural vegetation groups are referred to (e.g. carr, reedbeds, sedge beds) which may be of limited use for investigating detailed ecological variables and environmental parameters. As in most areas of palaeoenvironmental study, macrofossil analysis has become an adjunct to palynology when detailed vegetation reconstructions are required. When used, completed macrofossil analyses are usually restricted to the identification and quantification of a limited range of macrofossils, usually only seeds and fruits. Many classes of remains are not included in analysis or are subject to only cursory examination and rarely if ever subject to quantification and quantitative analysis.

Macrofossils have the potential to make a greater contribution to the investigation of alluvial facies than has previously been the case by allowing greater differentiation of otherwise indistinguishable depositional environments and acting as a

source for spatially precise vegetation information, useful for detailed palaeoecological investigations and contextualising archaeological finds. This potential is due to the heterogeneity of macrofossil assemblages, the limited dispersability of many plant parts in sedimentary environments and the potentially high level of taxonomic identification.

Macrofossils in general are deposited close to the site of plant growth (Collinson 1983; Field 1992) and therefore provide spatially precise information about former vegetation. Such information is important if detailed palaeoecological data are to be gained and if the physical context of archaeological sites is to be understood, a vital element in any interpretation. Alluvial ecosystems have been modified or destroyed by human activity in the last five centuries and palaeoecological information may be the only way to investigate many elements of 'natural' alluvial ecosystems. Macrofossil analysis also provides the potential for much more detailed identifications of ecosystem elements as many macrofossils can be identified to genus and species level, unlike many pollen types.

Identification of vegetation types at a sample point and identification of local vegetation responses is important in determining local and more widespread changes in environmental conditions. Macrofossil assemblage analysis also has the potential to contribute to the identification of the depositional environment. Macrofossil assemblages consist of groups of plant structures (e.g. roots, stems, leaves) and tissues (e.g. cuticles, wood) as well as taxa and, therefore, may be described in structural as well as taxonomic terms. These properties are potentially useful in differentiating depositional environments when differentiation through other means may be impossible, a common problem in alluvial sequences in the Lower Thames.

Although a potentially useful source of information, detailed macrofossil analysis suffers from several problems that limit its application in alluvial investigations. Many come from the general lack of research in macrofossil analysis in Holocene studies and the complexity of macrofossil assemblages as a dataset. Macrofossil assemblages are highly heterogeneous, consisting of many different plant parts. Although some groups of macrofossils, including seeds and fruits and mosses, have been subject to detailed, if intermittent, identification work, many classes of remains have few published identification manuals. Similarly, recording and quantification have been little developed and taphonomic information about macrofossil assemblage formation processes in comparable environments is lacking, making interpretation difficult. An additional

problem in macrofossil analysis of alluvium is access for sampling. Extensive exposures of sediments are rare in many areas of southeast England and it is still unclear whether coring and monolith sampling is adequate for macrofossil collection and the sample sizes that are adequate for different levels of macrofossil-based information.

The objective of the research presented in this thesis is to develop, test and evaluate analytical approaches to plant macrofossils from alluvial facies, specifically targeted at the southeast region of England. It aims to:

I. Develop recording and identification techniques for analysis of macrofossil assemblages, establishing identification criteria where they are lacking;

II. Investigate plant macrofossil assemblage formation processes through actualistic research (*sensu* Kidwell 1986) in modern alluvial environments to determine:

   A. the potential of different alluvial depositional sub-environments to incorporate plant macrofossils;

   B. the quantitative and qualitative properties of macrofossil assemblages preserved in alluvial depositional sub-environments;

   C. the spatial and temporal resolution of information about vegetation structure and floristics provided by different classes of macrofossils and whole macrofossil assemblages preserved in different alluvial depositional sub-environments;

   D. the effects of sample size on the information attainable through macrofossil analysis in different alluvial depositional sub-environments.

III. Evaluate the approach developed through application of an integrated analysis to macrofossil assemblages recovered from a Holocene alluvial sequence in which palaeoenvironmental and archaeological material is preserved.

The following chapters provide background information to the research, details of the methods, sites used and results obtained, and also evaluates these results. Chapter 2 considers the value of alluvium as a resource for archaeology and palaeoecology in the Lower Thames and includes a brief consideration of rivers and estuaries as sedimentary and biological systems. A review of plant macrofossil analysis is also presented, concentrating especially on the applications of plant macrofossil research in alluvial depositional environments and plant macrofossil taphonomy in those environments.

Chapter 3 presents the methods used to generate macrofossil data. It includes a classification of macrofossils, criteria for the identification of previously difficult macrofossil groups and a discussion of the method of macrofossil quantification used in the subsequent chapters. Much of the work in this chapter aims to develop a usable analytical method and the broad range of subjects covered by it means that some had to be treated in a cursory manner.

Chapter 4 details observations of macrofossil accumulation and representation in a range of modern depositional environments including tidal mudflats, saltmarshes and freshwater swamps, reedbeds, herb fens and wet woodlands. Data collected from these observations have provided a basis for discussing macrofossil taphonomy and evaluating the spatial and temporal resolution of information derived from macrofossil assemblages in different depositional environments. The focus was mainly on non-seed macrofossil assemblages, although seed concentrations and profiles were investigated for most of the sites. The observations are also used to determine the suitability of different macrofossil categories and groups of macrofossils to investigate ecological and environmental parameters such as salinity gradients, vegetation structure and vegetation floristics.

Chapter 5 presents the analysis of a group of plant macrofossil assemblages from sediments sampled during the construction of the Medway Tunnel in Chatham, Kent. Sediment accumulation was initiated at *ca* 7000 BP at the site and subsequent alluviation preserved Mesolithic, Neolithic, Bronze Age, Iron Age and Romano-British archaeological features and artefacts within a complex series of alluvial facies. Plant macrofossil analysis aimed to contribute to the definition of depositional environments, reconstruction of local and regional palaeoenvironments and act as a basis for evaluating the efficacy of the developed macrofossil methodology.

Chapter 6 discusses and evaluates the research. Deficiencies and strengths of the work are discussed and the potential contribution of plant macrofossil analysis to alluvial archaeology and palaeoenvironmental investigations in the region and elsewhere is also evaluated. Chapter 7 provides conclusions of the work. The text has four appendices containing the identification criteria of reference specimens and supporting photographic plates.

2 Plant macrofossil analysis in archaeological and palaeoenvironmental investigations of Holocene alluvium, with special reference to the Lower Thames Basin

2.1 Nature and distribution of Holocene alluvium

Alluvium is sediment deposited along river courses in fluvial, estuarine and terrestrial environments (Bates and Barham 1995). Thick deposits accumulated during the Holocene in the rivers of the Lower Thames Basin grading into coastal sediments. The River Thames is the major river of the region which, with its tributaries, drains the Thames Basin, sections of the surrounding Downs and the north Weald (Figure 4.1). To the north of the Thames lie the southern Essex rivers of the Colne, Crouch and Blackwater and to the southeast the River Medway, the main northern conduit of water from the Kentish Weald.

In this text the definition is used to denote all of the sediments that may be deposited in the diverse environments of river-estuarine systems. The following discussion also refers to sites that would usually be considered as 'coastal' as opposed to riverine in genesis. This reflects the blurred boundaries between sedimentation processes and outcomes in these environments. It also reflects the complexity of Holocene alluvial sediment sequences that contain riverine, estuarine and coastal sediments and, therefore, the wide range of methods that their analysis requires. Many of the sites can be considered within alluvial archaeology and inter-tidal archaeology. The following has been derived from numerous sources, but draws heavily on Reading (1978), Dyer (1979), Reineck and Singh (1980), Lewin (1981), Richards (1982), Pethick (1984), Collinson (1986), and Allen (2000).

Holocene sediments have been grouped together on the Thames as the Tilbury Formation (Bridgland 1995), but this grouping belies an inherent complexity. The Tilbury Formation includes a great variety of sediments dominated by inter-tidal muds and organic rich muds and peats, forming a characteristic alternating pattern of peat bands and inorganic units in several rivers. The number and thickness of peat beds varies with location, up to five being identified at Tilbury (Devoy 1979, 1982). Holocene sediments fill the inherited Pleistocene landscape to a height of approximately 5m ordnance datum (OD) reaching depths, depending on the underlying topography, of between -5m OD in central London (Devoy 1979) and approximately -15m OD in the

north Kent Marshes and Medway floodplains (Skempton 1995; Bates *et al.* 1995). The areal extent of alluviated areas is considerable in the region, forming a broad band along the Thames of up to 4.5km wide.

2.2 Rivers and estuaries as sedimentary basins

Rivers are the major agents of terrestrial erosion and transportation, carrying water and sediment from the land to the sea. They form a continuum with estuaries in which freshwater discharge mixes with saline water flowing into a river mouth due to tidal action. Rivers and estuaries are connected but the environments of each are dominated by different hydrological and sedimentation processes. They also contain a range of depositional and erosional environments in which different landforms are generated, inhabited by a diverse biota and represented in the stratigraphic record by a wide range of sedimentary facies.

2.2.1 Hydrological factors

Rivers form as the result of the flow of excess water into channels that conduct water to the sea and entrain, transport and deposit sediment. The main upstream controls on water supply, sediment supply and catchment are the basin physiography, climate, geology, vegetation, soils and land-use. Base-level, the level to which water flows as the result of gravity, sets the downstream control and is set locally by the presence of erosion-resistant rocks and ultimately by the sea at the river-mouth (Leopold *et al.* 1964).

The initial quantity of water available to a river is a balance between precipitation and evapotranspiration (determined by climate) and the capacity of soils and rocks to absorb the water (Richards 1982) enhanced by the presence of vegetation. Water enters into rivers as the result of:

a) Infiltration excess overland flow, when precipitation exceeds the soil's capacity to absorb it;
b) Saturation overland flow caused by the emergence of groundwater at the surface;
c) Subsurface (base) flow when water flows through the soil and rocks.

Discharge, the quantity of water passing a given point in a river channel, varies over the year, usually in a regular cycle. Porous base rocks, such as chalk in the Lower Thames, can absorb rainfall and release it slowly, decreasing peak discharge (Ward 1981). Water velocity is a function of discharge, basin-slope, gravity and the composition of the riverbank, an important factor in determining the resistance of the riverbanks to erosion and channel transformation. Floodplain water levels are affected by the periodicity of flooding, groundwater levels, precipitation and permeability of the substrate, perched water tables forming where clay-silt substrates impede groundwater drainage (Brown 1997).

Estuarine hydrology is dominated by the diurnal tidal cycle. Rising tides cause water to be forced up river valleys, the distance being determined by tidal range, basin shape and river discharge. Estuaries in southeast England are macro-tidal, having a tidal range of 4m, and tidal incursion dominates river discharge. Maximum velocities are reached at mid-tide, minimum velocities being reached at high and low tide. Tides influence landforms through direct inundation and the ponding of river discharge behind the tidal wave. Wind waves are relatively unimportant except in storms, when, like secondary currents caused by mixing of fresh and saline water, they can introduce marine sediments to the system.

2.2.2 Sedimentation

Sediment enters rivers as a result of erosion of rocks in the catchment, the introduction of windblown silt or erosion of the riverbank itself (Lewin 1981). The quantity of sediment entering the river, sediment yield, is determined by precipitation, soil resistance, basin topography and plant cover. The size and type of particles entering the system is limited by those available in the catchment, those in the Lower Thames being dominated by clays and silts carried in suspension. Minerogenic sediment enters estuaries from river discharge and marine sources carried by the tide, especially secondary currents. Most estuarine sediments are thought to come from river discharge, especially in the higher reaches. Plant matter is introduced by plant growth at the site and from detrital inputs from river discharge, tides and wind.

The size of sediment particles carried in a water column (competence) and the total quantity of sediment carried by a river (capacity) are dependent on water flow velocity (Brown 1997). Entrainment of a particle in the water column requires the

attainment of a threshold velocity and sediment transport requires these to be maintained. Higher flow velocities entrain and transport larger particles, those of between 0.25mm and 1mm being the most easily entrained.

Sediment load is divided into:

a) Dissolved load of particles in solution;

b) Suspended or wash load consisting of small particles carried in suspension;

c) Bed load of large particles that roll along the riverbed.

Suspended load is limited by the quantity of sediment supplied by the catchment and bed-load is dependent on the capacity of the river (Brown 1997). Deposition occurs when threshold velocities required to keep a particle in suspension are no longer met. The speed at which particles settle out of suspension is determined by the surface-area to volume ratio. Clay and silt size particles have high values and move slowly through the water column. These particle sizes require slack water for deposition, although settling times and sedimentation rates for clay particles can be increased in saline water if they form aggregates (flocs). Floc formation is vital for estuarine sedimentation as without it most fine-grained sediment would stay in suspension. Vegetation, especially on saltmarshes and floodplains, increases sedimentation rates by slowing water velocity, acting as sites for sediment deposition (Brown 1997; Brown and Brookes 1997) and by causing currents to form that can trap sediments and enhance deposition.

Re-working of sediments commonly occurs in river channels, floodplains and estuarine marshes. A particle may be stored several times on its journey through alluvial system. Estimates of particle mean residence time are 48 years for channel environments and 4000 years for floodplains (Brown 1997).

2.2.3 Morphology

Rivers and estuaries both contain channels, through which water is conducted, and low lying areas surrounding the channel where sediment may be deposited, in rivers the floodplain and in estuaries mudflats and saltmarshes. Although estuarine and riverine systems are superficially similar, channel morphology and landforms are controlled by different processes.

River channel form, confined by basin shape, adjusts to discharge and sediment loads supplied by the catchment. It is also influenced by bank stability, dependent on the

bank composition and vegetation (Brown *et al.* 1995). Channel depth, width and bedforms respond to changes in catchment conditions to provide a stable conduit through which sediment and water are transported.

Floodplains form along the banks of aggrading rivers and are major sites of sediment deposition. Sediment is mainly derived from regular flooding, but also colluviation, wind and as a result of the accumulation of organic matter in basins. Sediment accumulation rates vary widely within individual floodplains and are determined at any one point by the distance from the channel, microtopography, water depth, vegetation and flow capacity (Brown and Brookes 1997). Sedimentation rates are highest in the still waters of abandoned channels and backswamps.

Several systems of river classification have been devised on the basis of channel form, floodplain form and sedimentation processes. High energy braided rivers (high-energy with unstable banks) are the typical form found in upland areas of Britain. Anastomosing rivers (multiple channels with stable banks) although rare today (Brown 1995) may have been the dominant form in some European rivers during the Holocene (Brown and Keough 1992). Meandering rivers are the main form in lowland Britain and are characterised by low energy water flow, silty cohesive banks stabilised by vegetation (Smith 1976) and often the presence of extensive floodplains. Waterflow is confined to a single channel, sediment being scoured from the concave bank and deposited in point bars and shoals. Channel movement is usually confined to a narrow belt of the floodplain (*contra* Leopold and Wolman 1964).

Estuaries bridge the transition between riverine and tidal sedimentation and consist of a channel, through which river discharge and tides are conducted, flanked by creek-dissected mudflats that may develop saltmarshes (for a review of saltmarsh morphology see Allen 2000). Estuary shape is determined by the inherited basin shape, tidal characteristics, sediment loading and river discharge. Mudflats develop above the mid-tide point, at which tidal velocity slows and sediment is deposited as critical settling thresholds are passed. Sediment accumulation rates are highest where tidal standstill is longest, usually in the middle zone of the mudflat, forming a characteristic profile. Particle size tends to decrease landwards and sand can accumulate from suspension at the break in slope at the channel margin, where tidal energy is first dissipated.

Saltmarshes are vegetated areas developed on the higher reaches of mudflats. They are less regularly flooded than mudflats, often only at spring tides, although some

lower reaches are still within the daily tidal reach. Vegetation growth encourages sediment deposition leading to increased isolation from tidal deposition. Creeks dissect the saltmarsh and mudflats and act as conduits for tidal water, having a similar form to river and estuary channels. Marsh building is dependant on the balance of sediment supply, erosion and autocompaction and its limits are determined by tide heights (Allen 2000).

2.2.4 Riverine and estuarine plant ecology

2.2.4.1 Environmental influences

Hydrology is the most significant ecological influence on riverine and estuarine ecology, especially tide and flood depth, water-table height, drainage, flow depth and velocity as well as water chemistry, especially salinity, pH, nutrient status and quantity of dissolved minerals (Chapman 1974, 1977; Adam 1990). The floodplains and rivers of the Lower Thames are mainly eutrophic to mesotrophic systems with alkaline waters. Soil structure and aeration is also important for plant root growth and is more developed in less regularly flooded environments. Distribution of organisms is also dependent on species dispersal and competitive strategies. In some cases ecology may be dominated by plant species first able to colonise a particular wetland or soil, affecting subsequent vegetation structure, floristics and possibilities for vegetation change (Walker 1970). Plant distribution and reproductive success is also influenced by the distribution of herbivores and detritovores.

2.2.4.2 Rivers

Relatively few plants can persist in medium to fast flowing water (e.g. *Glyceria fluitans*) and aquatic vegetation in river channels is usually restricted to areas of slow moving water at the channel margins. In deep-water, floating and submerged vegetation are mixed with emergent deep-water taxa. In shallower water other emergent taxa are found (e.g. *Alisma plantago-aquatica*; *Sparganium* spp.) and more complex groups of species dominate the water margin. Stable banks and levees may have a dense covering of herbs and tree species such as alder (*Almus glutinosa)*.

Floodplains support a complex mosaic of vegetation associations. Extensive swamps, wet-woodlands (carr/fen-carr) and open herb fens can develop where groundwater levels are high. Deep backswamps and oxbow lakes may support aquatic

vegetation. Herbaceous vegetation is dominated by bulky monocotyledons (e.g. *Phragmites australis*) usually forming dense mono- or oligo-specific stands with a sparse understorey of other species, important for defining NVC groups.

Wet-woodlands develop in wetter and drier areas of floodplains where standing water is only present seasonally as high-water levels prevents seedling establishment (Grime *et al.* 1988), although trees may colonise sedge hummocks in swamps (Walker 1970). Vegetation structure is complex with canopy, understorey, groundstorey, epiphytic and climbing elements and includes Bryophytes (mosses and liverworts), ferns and higher vascular plants. Taxa typical of dryland environments (e.g. *Fraxinus excelsior*) can be important vegetation elements, especially in drier parts of wet-woodlands or when growing as epiphytes, especially some ferns.

Open herb-dominated fens are rare and most are the product of intensive management including grazing and mowing for thatching materials. In natural conditions, areas with high groundwater levels but no standing water are quickly colonised by wet-tolerant trees. In comparison to species-poor swamp communities, managed herb-fens are some of the most floristically diverse habitats in Britain. Drier areas of floodplains with high nitrogen availability may promote local growth of taxa such as *Urtica dioica*, while isolation from groundwater may encourage growth of calcifuge taxa such as species of *Sphagnum* moss.

2.2.4.3 Estuaries

Few vascular plants are able to survive permanently below low-tide mark, with the exception of eelgrass (*Zostera* sp.). The main vegetated landforms in estuaries are saltmarshes, stretching from the low-tide to high-spring tide mark (Chapman 1974, 1977; Adam 1990). Saltmarshes are zoned ecological communities, vegetation composition varying with local conditions and microtopography. Plant communities are dominated by Angiosperms, with annual plants dominating pioneer communities. Shrubs and herbaceous perennials dominate most other environments. Bryophytes are only rarely present at the upper saltmarsh margins.

Vegetation survey has distinguished twenty-eight saltmarsh communities (Burd 1989) that can be grouped according to the period of time that they are submerged by tides, although zonation is far from simple because of saltmarsh morphology. Creek dissection and erosion, mixed with inherited morphology mean that tidal penetration,

especially in the upper marshes need not be a direct reflection of distance from the channel (Korber-Grohne 1992).

Pioneer communities can survive regular tidal inundation and invade mudflats, playing an important part in stabilising marsh surfaces and encouraging sedimentation and terrestrialisation. Recent spread of cord-grass (*Spartina anglica*) has severely restricted other pioneer communities (Adam 1990). Vegetation in the regularly inundated low- to mid-saltmarsh zone is dominated by grasses (e.g. *Puccinellia* sp.) and shrubs (*Atriplex portulacoides*) mixed with patches of other species, some reaching local dominance. In the upper saltmarsh, only infrequently inundated by tides, vegetation is dominated by a dense growth of grasses and rushes. Strandline communities develop along the higher parts of marshes that are only weakly influenced by saline water, including dense swards of couch grass (*Elytrigia repens*). Swamps may also develop in natural depressions and abandoned channels. Transitions from saltmarsh to terrestrial and freshwater have largely been destroyed in Britain, but where present, they contain a mixture of upper saltmarsh and freshwater wetland taxa (Burd 1984; Adam 1990).

2.2.5 Depositional environments, erosional environments and facies

Channel, channel bank and overbank (floodplain/mudflat) environments are open to varied sedimentation and fossil inputs from both autochthonous (local) and allochthonous (non-local) sources. The sum of sedimentary and fossil characteristics, or facies (Reading 1978; Reineck and Singh 1980), is used as a basis for interpreting palaeohydrology, palaeovegetation and other palaeoenvironmental variables.

2.2.5.1 Rivers

Channels are represented by erosive surfaces and characteristic sediments such as channel lag, channel bars and point bars. Channel lag is the coarser sediment fraction on the channel bed. Point-bars form on the convex side of river meanders and are the main site of in-channel sedimentation in meandering rivers. They form as the result of discontinuous lateral sedimentation and have a cross-bedded structure with coarser particle sizes fining-upwards from basal lag. Bars also form in channels as the result of point-bar dissection, deposition of sediment by secondary currents and where tributaries meet the main channel.

The channel edge in many rivers is a bench formed by bank erosion or sedimentation onto a point bar or riverbank (Brown 1997). Levees also form in some rivers, although are absent from most British rivers. These wedge-shaped raised mounds form during floods as flow velocity falls causing sedimentation of larger particles at the channel edge. Channel banks often have dense vegetation cover, the roots of which can destroy the cross-bedded sedimentary structures.

Overbank environments, including floodplains and abandoned channels, are the main sites of alluvial sediment deposition in lowland Britain. Floodplain sediments accrete vertically and are usually fine-grained organic-rich muds. Vegetation growth can be extensive over floodplains and swamps form where standing-water is present for much of the year, including abandoned channels (oxbow lakes). These areas act as settling basins for suspended load sediments in floodwater and contain finely laminated sediments, unless disturbed by root penetration, and large quantities of organic matter.

2.2.5.2 Estuaries

Sedimentation varies in individual estuaries, although overall patterns are discernible (Evans 1953). Tidal channels and creeks are the main conduits for tidal waters, with sediments in larger creeks containing larger particle sizes. Basal channel lag, consisting of poorly sorted, large sized particles, is overlain in aggrading beds and shoals (channel bars) by interdigitated silt and sand laminations deposited in the alternating currents of the tidal cycle. Lateral point bar deposition also occurs in some tidal channels and creeks as they migrate across mudflats.

Particle size in tidal flat sediments, as with floodplains, decreases away from the channel, although it is not always constant and depends on sediment availability. In the classic model of Evans (1965), based on the Wash, sand flats grade into the lower mudflats and then inner sand flats above the break in slope at the channel edge. Sand flats are not always extensively developed in the estuaries of the southeast England because of a lack of sand in the catchment. The lower intertidal zone, inner mudflats and saltmarshes consist of fine-grained muds, although bioturbation by vegetation on saltmarshes and invertebrates on mudflats effectively destroys any sedimentary structures (Edwards and Frey 1977). Abandoned channels and low-lying areas at the landward edge of the marsh act as settling basins and, like their counterpart in river systems, become filled with laminated fine-grained sediment rich in organic matter.

2.3 Plant macrofossil analysis

2.3.1 Plant macrofossils in geology and archaeology

Plant macrofossils are the remains of plants preserved in sediments that are visible to the naked eye (Dickson 1970; Watts 1978; Birks and Birks 1980; Mannion 1986). They are preserved through the geological column (White 1994; Stewart 1996), Holocene macrofossils usually being preserved in environments with maintained high groundwater levels such as peat bogs, lakes and rivers. Most plant structures are included in this fossil category with the exception of microspores (including pollen), silicified cells (phytoliths) and diatoms. Complete intact plants are uncommon in the fossil record and macrofossil assemblages usually consist of complete or fragmented structural elements (e.g. leaves, roots).

In the nineteenth and early twentieth centuries, plant macrofossils provided the sole source of geobotanical data (e.g. Heer 1862; Bennie 1894; Geikie 1865-1867; Lewis 1905; Reid 1913). Many early records were limited to verbal descriptions of the macrofossils visible in exposures, and detailed macrofossil studies were rare, usually only recording species lists. Macrofossil analysis declined in importance in Holocene investigations from the 1920s with the development of quantitative palynology, although continued to be important in pre-Holocene geology (e.g. Gastaldo and Ferguson 1998).

Renewed interest in plant macrofossil analysis in recent decades can be attributed to the increased biological detail required for palaeoecological and archaeological investigations (West 1978) and the realisation that palynology is complementary to plant macrofossil analysis, rather than providing an alternative to it (e.g. Birks and Mathewes 1978; Birks 1993). Over the period, advances have occurred in all aspects of the subject, the most important being the development of quantitative analysis and taphonomy. The following properties have been attributed to plant macrofossil assemblages as a result of methodological and taphonomic research:

1) Macrofossil assemblages are incomplete transformations of vegetation data selected as a result of the operation of intrinsic and extrinsic biological, physical and chemical processes.
2) Plant macrofossils are derived from a diverse group of plant structures, each with its own dispersal properties and relationship to accreting sediment surfaces. Some, such as seeds and fruits, accumulate at the sediment surface, having the potential to

provide information about contemporary vegetation and environments (Birks and Birks 1980). Others, such as rhizomes and roots, accumulate below the source plant, providing information about plant growth subsequent to sediment accumulation (Godwin 1960). Assemblages, therefore, contain macrofossils of different spatial and temporal fidelities (*sensu* Kidwell and Flessa 1995).

3) Plant macrofossils are often distributed over short distances in sedimentary environments and, therefore, reflect the flora and conditions close to the site of deposition.
4) Plant macrofossils are distributed non-uniformly, even over small spatial scales (Birks 1980; Mannion 1986). Assemblage composition can vary even within the same environment (Greatrex 1983) making interpretation on the basis of a single sample potentially unreliable (Birks and Mathewes 1978; Birks and Birks 1980; Mannion 1986; Wasylikowa 1986).
5) Macrofossils, especially seeds and fruits, usually achieve low concentrations in sediments. Large sediment samples, therefore, are required to provide a representative sample of macrofossils suitable for quantitative analysis (Watts 1978; Birks and Birks 1980; Mannion 1986). Where cores are used, the requirement for large sediment samples decreases analytical resolution and in many cases precludes analysis.
6) Plant macrofossils, especially seeds and fruits, are often identifiable to genus or species level (Watts 1978; Birks and Birks 1980; Mannion 1986). Plant macrofossil analysis, therefore, has the potential to provide taxonomically detailed reconstructions of past vegetation and also to provide data for palaeocological studies of individual species.
7) Plant macrofossils are produced by taxa which may not produce distinguishable pollen (e.g. *Phragmites australis*), adding detail to palaeovegetation reconstructions (Watts 1978; Birks and Birks 1980; Mannion 1986).

2.3.2 Methods and techniques

2.3.2.1 Plant macrofossils in facies descriptions

Early macrofossil investigations (nineteenth century) usually recorded only the presence of macrofossils in facies descriptions. Informal notation (e.g. Reid 1913; Travis 1927; Godwin 1960) has largely been replaced by more formal systems such as the Troels-Smith system (Troels-Smith 1944; Aaby and Berglund 1986) and later improvements

(e.g. Barber 1981; Waller 1994; Wilkinson and Murphy 1995). These systems record the relative proportion or dominance of macrofossil groups (e.g. wood, vegetative remains) in sediments. The Troels-Smith system uses latinised terms to record sediment components. Its application is practically difficult, highly subjective and requires distinction of facies elements and the conditions in which the materials formed, confusing description and interpretation. These problems have led to the use of more site-specific descriptive schemes (Walker 1970; Waller 1994; Wilkinson and Murphy 1995).

2.3.2.2 Sampling and recovery

Detailed macrofossil analysis, in which specimens are identified and quantified, requires the extraction of intact macrofossils from sediments. Analysis of all preserved macrofossils in an exposure or core is impractical and unnecessary and sampling methods are employed to recover a representative sub-set (sample population) of the total macrofossils present in a sedimentary unit (the population). Plant macrofossil assemblages are not easy to sample as they include a range of fossil sizes present in variable concentrations in different sediments that may be adjacent in alluvial strata. In practice, large macrofossils (e.g. trees) are described *in situ*, plotted and sampled for identification purposes. Smaller macrofossils, present in larger concentrations, are collected in whole sediment samples and extracted in the laboratory.

Sampling and recovery methods affect the sampled macrofossil population and therefore the type, temporal resolution, spatial resolution and reliability of information from assemblage analysis. For most ecological and environmental questions over Holocene and archaeological time-scales, maximum temporal and spatial resolution of data is required. Samples that cross stratigraphic boundaries mix temporally and possibly environmentally distinct fossils. Large homogenised 'bulk-samples' from individual strata mix fossils from different episodes of deposition within a unit. Both reduce the usefulness of macrofossil assemblages and should be avoided. Sample method and size are often limited by the type of investigation. Sections allow optimum sampling access and large samples may be collected with stratigraphic precision. Samples from borehole investigations (e.g. Devoy 1979) are limited by the size of the coring device.

There are no agreed guidelines for sediment sample volume, although West has suggested that the samples should collect at least 50 identifiable seeds and fruits (West 1978). Ultimately the sample size does affect the precision and usefulness of any data set,

although this need not negate the value of smaller sample sizes if the problems inherent in their interpretation is recognised (Jones 1991). Although empirical and *a priori* limits have been set for minimum sample sizes (West *ibid.*; Van der Veen and Fieller 1982 respectively), the most widely adopted and pragmatic method of sampling is to collect a standard volume of sediment. A sample size of 100cm^3 has been suggested for seed and fruit analysis (Birks and Birks 1980) and is widely employed. A sample size of 4 cm^3 has been used for macrofossil cover abundance analysis of ombrotrophic peats (Barber *et al.* 1994; Hughes *et al.* 2000) and samples of a minimum of 10 litres in size have been suggested for archaeological sites (Association for Environmental Archaeology guidelines). Pre-determined sample sizes may collect an inadequate sample of macrofossils or too many for practical analysis, although they provide a basis for comparison of fossil presences as sample size is directly related to taxon diversity (Gee and Giller 1991). One method of determining how representative a sample is, is to construct a cumulative sample profile in which the macrofossils from larger and larger volumes of sediment are plotted (e.g. Fasham and Monk 1978). Samples are shown to be representative when stable values are reached.

Recovery methods typically involve separation by sieving of macrofossils from the sediment in which they are preserved (Dickson 1970; Kenward *et al.* 1980). Sieve size is a vital determinant of which macrofossils are selected for analysis, 125 μm ensuring recovery of even the smallest seeds. Loose sediments such as sands and gravels require minimal pre-treatment (e.g. soaking in water) before sieving, unlike cohesive peats, clays and silts. Excavation of larger macrofossils from peat is followed by soaking, usually in dilute Potassium or Sodium Hydroxide (KOH or NaOH) (Dickson 1970). Compacted clays and silts require deflocculation, the most commonly used being dilute Hydrogen Peroxide (H_2O_2), although like KOH and NaOH, this can destroy organic matter. An alternative is phosphate-based deflocculants (e.g. Calgon), although these are environmentally damaging. After sieving, macrofossils are stored in moist conditions as drying usually causes shrinkage, distortion and physical damage. Distilled water with small amounts of ethanol, formalin or preservatives are suitable storage media.

2.3.2.3 Identification

In contrast to taxonomic botany, where complete plants are present, palaeobotany identifies taxa from fragmentary structures. Fossil specimens are identified (given a

structural and/or taxonomic status) by comparison to verified modern plant reference specimens or published identification criteria. Identification makes the uniformitarian assumption that identification features have changed minimally between the period in which the fossil specimen lived and the present day. For Holocene time-scales such assumptions are acceptable, at least for taxonomic ranks above genus, and for most species. Fossils are assigned to a taxonomic rank only if features thought to be taxonomically distinctive are preserved. In recent decades earlier confidence in the accuracy of macrofossil identification (e.g. Reid and Reid 1908) has been tempered by a realisation that some diagnostic features vary widely within species and genera (Dickson 1970) and higher rank identification of some fossils is impossible.

Most macrofossil analyses include identification of seeds, bracts and seed-like structures using morphological characteristics (i.e. shape, size, presence of characteristic surface structures etc.). Many seed manuals describing identification features are available (e.g. Beijerinck 1947; Mclure 1957; Bergerren 1961, 1981; Korber-Grohne 1964; Schermann 1967; Katz *et al.* 1969) and several papers provide guidelines and bibliographies of relevant publications (e.g. Dickson 1970; Mannion 1986a; Nesbitt and Greig 1989). Megaspores, sporangia and related structures of the ferns and their allies have been described in several texts (Stace 1991; Hutchinson and Thomas 1997).

Vegetative and woody macrofossils are less commonly subject to systematic analysis, with the exception of the Bryophyta (mosses and liverworts). Moss identification uses morphological and anatomical criteria (i.e. the range and distribution of vascular and other tissues in the specimen), with reference to modern specimens and published descriptions. As mosses are often preserved whole or in large, intact pieces, modern floras are suitable for identification (e.g. Smith 1978, 1990; Watson 1955).

Macro-algae are also possibly identifiable, although are rarely encountered in macrofossil assemblages. Morphological and anatomical descriptions of several classes of Algae are available (Burrows 1991; Fletcher 1987; Dixon and Irvine 1977; Moore 1986), although the only algal remains likely to be encountered are Characeae oospores (see Horn af Rantzien 1959; Dickson 1970).

Identification criteria for the vegetative and woody structures of the higher vascular plants are fragmentary and often in dispersed publications. The Anatomy of the Monoctyledon (AoM) (e.g. Metcalfe 1960, 1971) and Anatomy of the Dicotyledon (AoD) series (Metcalfe and Chalk 1950, 1979) provide the most comprehensive

anatomical details, but is patchy in its coverage of genera and species and some commonly preserved fossils (e.g. rootlets). Identification criteria have been published for the stem wood (Schweingruber 1990) and the root wood (Cutler *et al.* 1987) of European arboreal taxa. Vegetative tissues are less well published. Photographs and drawings are available for some of the most common plant fragments, such as *Phragmites australis* rhizomes (e.g. Katz *et al.* 1974; Grosse-Brauckmann 1976). Descriptions of rhizome epidermal, stelar and cortical anatomy are given in the AoD/AoM series and Hather (1993). Relatively few studies of root anatomy have been published (Fahn 1990) and are usually dispersed in autospecific accounts (e.g. Arber 1925), although an account of external root anatomy of sometaxa has been published by Katz *et al.* (1974).

Vegetative aerial stems can be identified from morphology, transverse sections and epidermal features. They are again covered partially at family and genus level in the AoD/AoM series with higher level accounts scattered in botanical and palaeobotanical texts (e.g. Gifford and Foster 1989; Bell 1992; Johnson 1933; Bower 1923, 1926, 1928; Stace 1991). Some leaves, if preserved whole (e.g. Filicophyta and some Dicotyledonae) can be identified by comparison to standard floras (e.g. Stace 1991; Jermy and Camus 1991). Identification is more difficult if the leaves are fragmented or display limited morphological variability (e.g. in many Monocotyledons). In these cases, identification depends on the use of anatomical characters. Although leaf identification criteria are established (e.g. Hickey and Wolfe 1975; Dilcher 1974; Hickey 1979; Pole 1991), descriptions of specific groups are dispersed (e.g. Grosse-Brauckmann 1976; Bhambie 1965; Chiu-Yu Chu 1974; Van Cotthem 1970b, 1973; Sen and Hennipman 1981; Hill 1900; Conard 1905; Jones 1955; Mitchell 1971; Ancibor 1979) and identification criteria for many taxa are simply lacking.

Several other potential groups of fossils are encountered in plant macrofossil assemblages including petioles, abscission layers from petiole and twig bases, stipules, thorns and prickles. Again, descriptive criteria have been established for these structures (e.g. papers in Metcalfe and Chalk 1979), but detailed descriptions of relevant British taxa have yet to appear. Stipules of some taxa have been illustrated (Lubbock 1908; Meikle 1984). A comprehensive description of the buds and bud-scales of British taxa has been published by Tomlinson (1985).

2.3.2.4. Recording and presentation of macrofossil assemblages

Quantification has been one the major methodological advances in macrofossil analysis in the post-war period. Macrofossil quantification is difficult because macrofossil assemblages consist of heterogenous remains derived from many plant structures (West 1978; Faegri and Iversen 1989), some of which cannot easily be quantified. This heterogeneity has led to separate recording and analysis of the various types of plant macrofossils.

Seeds are the only discrete and usually complete structural elements commonly preserved in macrofossil assemblages (West 1978) and are usually counted (e.g. Caseldine *et al.* 1988; Wilkinson and Murphy 1988; Regnell *et al.* 1995). This property has made them one of the main *foci* of plant macrofossil research (West 1978). Counts of fragmented vegetative and woody remains are a dubious basis for interpretation as they reflect taphonomic processes as much as changes in environmental variables, although they have been used (e.g. Kelly and Osbourne 1964). They have more commonly been quantified by use of relative abundance or ranking systems (e.g. Conolly *et al.* 1950; Jessen *et al.* 1959; Walker and Walker 1961; Watts and Winter 1966; Barber 1981; Hall 1984; Newnham *et. al.* 1995). Ranking systems do not conform to any comparative standard making inter-sample comparisons difficult (Rodwell 1991a, general introduction).

Volumetric measurements and estimates have also been used for vegetative macrofossils (Jannsen *et. al.* 1975; Van Geel *et. al.* 1980; Havinga and Von den Berg van Saparoea 1992), as have specific recording systems for particular types of macrofossil (e.g. Janssens 1983). The most recently devised method was that of using cover abundances for estimating the macrofossil composition of peat samples (Barber *et al.* 1994; Hughes *et al.* 2000).

Macrofossil data have been displayed as tables or macrofossil diagrams. Tables provide the most complete recording system (e.g. Behre 1986; Caseldine 1988; Greig 1992a) but are clumsy and of limited use as analytical tools (Watts and Winter 1966). A more visually appealing approach is to generate plant macrofossil diagrams, multiple histograms showing the abidance of taxa at each stratigraphic level (e.g. Walker and Walker 1961; Birks and Mathewes 1978; Caseldine *et al.* 1988; Birks 1993). These diagrams are concise and allow easier visual intra- and inter-sample comparisons. Macrofossil diagrams have been constructed for absolute counts, percentages (Watts and

Winter 1966; Lambrick and Robinson 1988), concentrations (Van Geel *et al.* 1980; Baker 1993 *et al.*; Birks 1993), presence data (Birks and Birks 1980, Chapter 5), ranking scores (Beckett 1978a and b, 1979), volumetric measurements (Havinga and Von den Berg van Saparoea 1992), cover abundances (Barber *et al.* 1994) and influx diagrams (Birks and Mathewes 1978). They can then be divided into assemblage zones by eye or by using computer programmes, boundaries indicating major changes in assemblage composition. Pie charts are also a useful form of presentation and have been used for indicator species salinity data (Behre 1986).

2.3.2.5. Data Analysis

Most early macrofossil analyses compared (and many still do) quantitative and non-quantitative data to environmental variables by eye. More recently, numerical methods have been developed. They have been used inductively to clarify patterns in macrofossil data via internal sample composition using correlation co-efficients, cluster analysis, correspondence analysis and principal components analysis (Barber *et al.* 1994), especially in archaeology (Shennan 1988; Baxter 1994) and deductively to compare data to *a priori* categories by canonical variant analysis (Jones 1991). Cluster analysis can be used for diagram zonation and is mainly used in palynology. Other methods include ubiquity (presence) analysis and the use of various ecological indices (Hubbard and Clapham 1992), the former particularly useful for interpreting vegetation change (Ogden *et al.* 1993).

While providing convenient methods of ordering and investigating patterns in datasets, the results of numerical analysis have to be interpreted by the palaeoecologist. The main advantage of these methods is that they can independently determine the relationship of complex datasets that may not be apparent by other means. The main drawback is that each method operates under assumptions about the dataset that may distort relationships between samples or sample variables and give importance to patterns that have no environmental or ecological significance. In practice, few macrofossil studies have attempted to employ numerical analysis, preferring to continue with the 'eyeballing' method. An exception is in the analysis of ombrotrophic peats where detrended correspondence analysis has been used (Barber *et al.* 1994) and in archaeology on charred archaeological plant remains (e.g. Van der Veen 1992).

2.3.3. An interpretative framework

Plant macrofossil analysis, as with other geological disciplines, has developed a more formal theoretical framework in the last fifty years schematised in Figure 2.1. The basic unit of analysis in Holocene palaeoenvironmental investigations is usually the assemblage defined as 'an accumulation of plant parts, derived from one or several individuals, that is entombed within a volume of sediment laid down under essentially the same conditions' (Spicer 1989, 100). Macrofossil analysis aims to use the presence and relative abundance of taxa preserved in plant macrofossil assemblages as a basis for the interpretation of past vegetation ecology and environmental conditions.

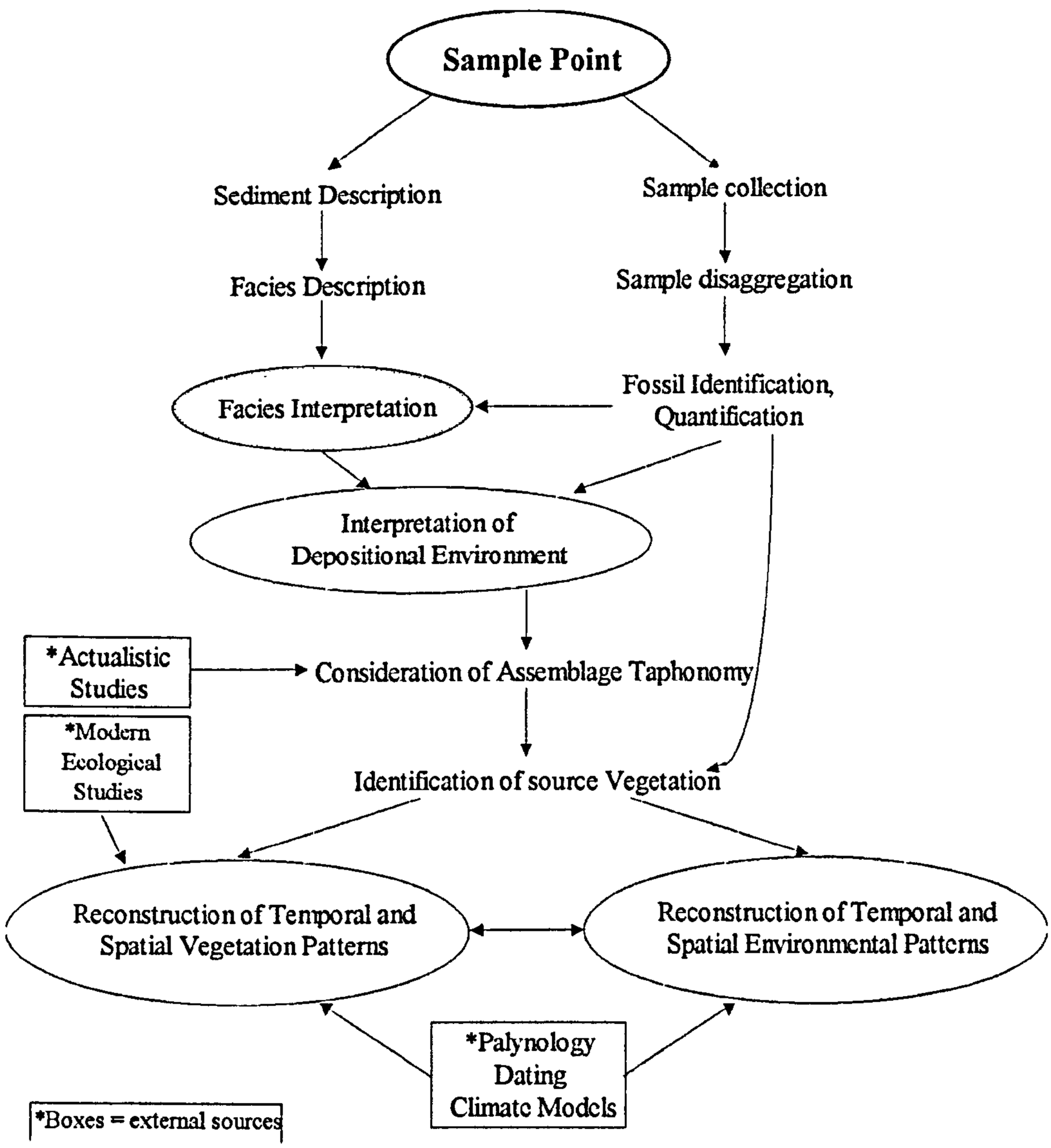


Figure 2.1 Framework of Plant Macrofossil analysis.

Methodological uniformitarianism is a cornerstone of interpretation (Birks and Birks 1980). However, the usefulness of modern reference data for the interpretation of past phenomena depends on the stability of these phenomena over time (Spicer 1989). Interpretation usually involves comparing macrofossil data to those from modern ecological and environmental observations, including autecological (e.g. papers in the Biological Flora of the British Isles such as McVean 1953 and Conway 1942; Grime *et al.* 1988) and community scale studies (e.g. Rodwell 1991a, 1991b, 1992, 1995). Palaeoecological accounts occasionally focus on the ecology of individual taxa (Brown 1988; Chambers and Elliot 1989). More commonly generalised vegetation descriptions are attempted as a basis of floral, ecological and environmental reconstructions (Gee and Giller 1991).

Macrofossil assemblages are not pristine representations of past vegetation. They are death assemblages (thanatocenoses) of fossils preserved selectively as the result of past biological, physical and chemical processes (Evans 1992). Death assemblages may vary in relation to the living assemblage in terms of the range of taxa preserved and the relative proportion of those taxa in the assemblage (Birks and Birks 1980; Gee and Giller 1991). The formation processes affecting the fossil assemblages, or taphonomy, have to be considered if the reliability of fossil data is to be evaluated. Other sources of palaeoenvironmental data, especially sedimentology and palynology, contribute to broader interpretations.

2.3.4. Taphonomy

Taphonomy bridges the gap between modern vegetation studies and the ancient vegetation represented in macrofossil assemblages. The subject was first discussed and named by Efremov as 'the study of the transition (in all its details) of organic remains from the biosphere to lithosphere' (cited in Spicer 1989). It has been redefined more broadly in recent years as 'the study of the process of preservation and how it affects information in the fossil record' (Behrensmeyer and Kidwell 1985) and has been divided into several sub-disciplines (Figure 2.2). Taphonomy has been studied at a theoretical level (Gifford 1981; Wilson 1988; Kidwell 1986; Kidwell and Flessa 1995) and through 'actualistic' studies in which contemporary processes affecting potential fossil incorporation and preservation in sediments are observed. Actualistic studies include:

a) laboratory observations of the behaviour of individual plant structures in sedimentary environments (e.g. Ferguson 1985; Spicer 1989);
b) direct observations of potential fossil assemblages in modern depositional environments as a means of understanding the processes and outcome of those processes on the fossil representation of living communities (e.g. Collinson 1982; Field 1992).

Plant macrofossil taphonomy has been discussed in most detail by workers on Tertiary and older floras (e.g. Scheihing and Pfefferkorn 1984; Spicer and Greek 1986; Wnuk and Pfefferkorn 1987; Spicer 1989; Gastaldo and Huc 1992), although it has also been studied in a Quaternary context (Field 1992) and the results of many studies have a wide temporal application. Taphonomy has also drawn on studies of seedbanks (e.g. Milton 1939; Thompson and Grime 1979; Papers in Fenner 1992), seed dispersal (Praeger 1913; Ridley 1937; Salisbury 1975, 1976b) and leaf litter turnover (Nykvist 1959, 1961, 1962), although seedbank studies often record only viable seeds and so have to be treated cautiously (Collinson 1983).

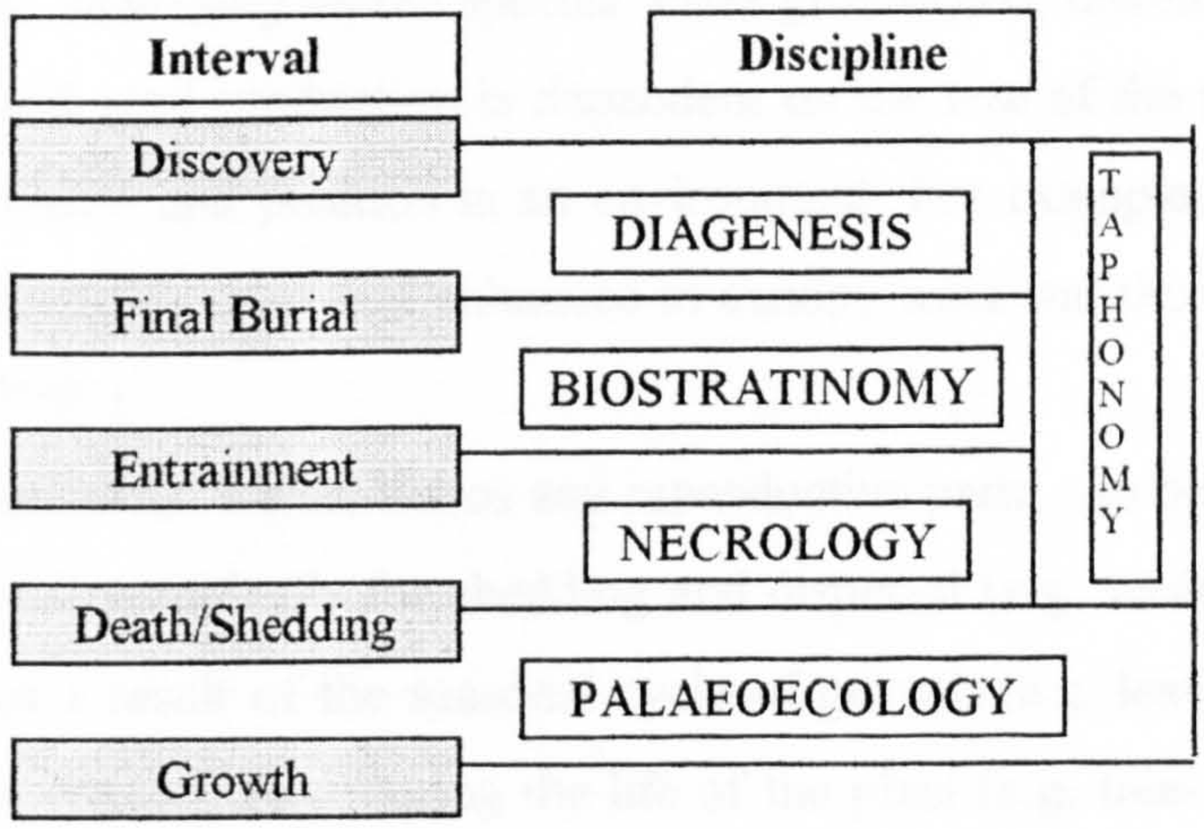


Figure 2.2 The relationship of palaeoecology and the component disciplines of taphonomy based upon the time interval of the organism(s) under study (Based on Lawrence 1968).

2.3.4.1. Biological considerations

Communities consist of mosaics of vegetation associations in which the diversity and abundance of species vary. The chances of a plant's structures being preserved in fossil assemblages depends on its proximity to depositional basins (Gee and Giller 1991),

turnover rates and life-habit as to its abundance. Taxa with dense structures, short lifespans, living in dense communities in active depositional environments will be preferentially preserved. Although there may be spatial variability in community composition, many often have core species, present in all sub-communities and patches, which are thought usually to be preserved in abundance (Gee and Giller 1991; Kidwell and Flessa 1995). Unfortunately these species may provide the least specific ecological data, having the widest range of tolerances (Kidwell and Flessa 1995).

2.3.4.2. Necrology

Necrology is the study of the production and shedding of plant parts (Gastaldo 1988). The potential for plant fossil incorporation in sediments is dependent, in the first instance, on the dispersal properties of each plant structure and its chances of becoming exposed to sedimentary processes. Plants are fixed in one position during life, producing and shedding organs according to the species life-cycle (Spicer 1989), both above and below ground. They are composed of several structures, each having one or more primary functions, depending on the species. Plant growth and, therefore, the quantity of leaf, stem, root and seed production is dependent on the size of the plant, the nutrients available to it, climate and position in an environment. For example, leaf production is depressed in understorey trees and enhanced in canopy trees and those growing in open sites (Galstaldo 1989).

Aerial plant parts, stems, leaves and reproductive parts, can be divided into those which are produced specifically for shedding and dispersal (e.g. seeds and fruits); those which are shed as a result of the seasonal cycle of growth (e.g. leaves and herbaceous stems); and those which persist during the life of the plant (e.g. tree-trunks). Structures produced for deliberate dispersal are often thickened and have evolved to resist decay and predation. Leaves and herbaceous stems are disposable structures and decay under normal circumstances (Spicer 1989).

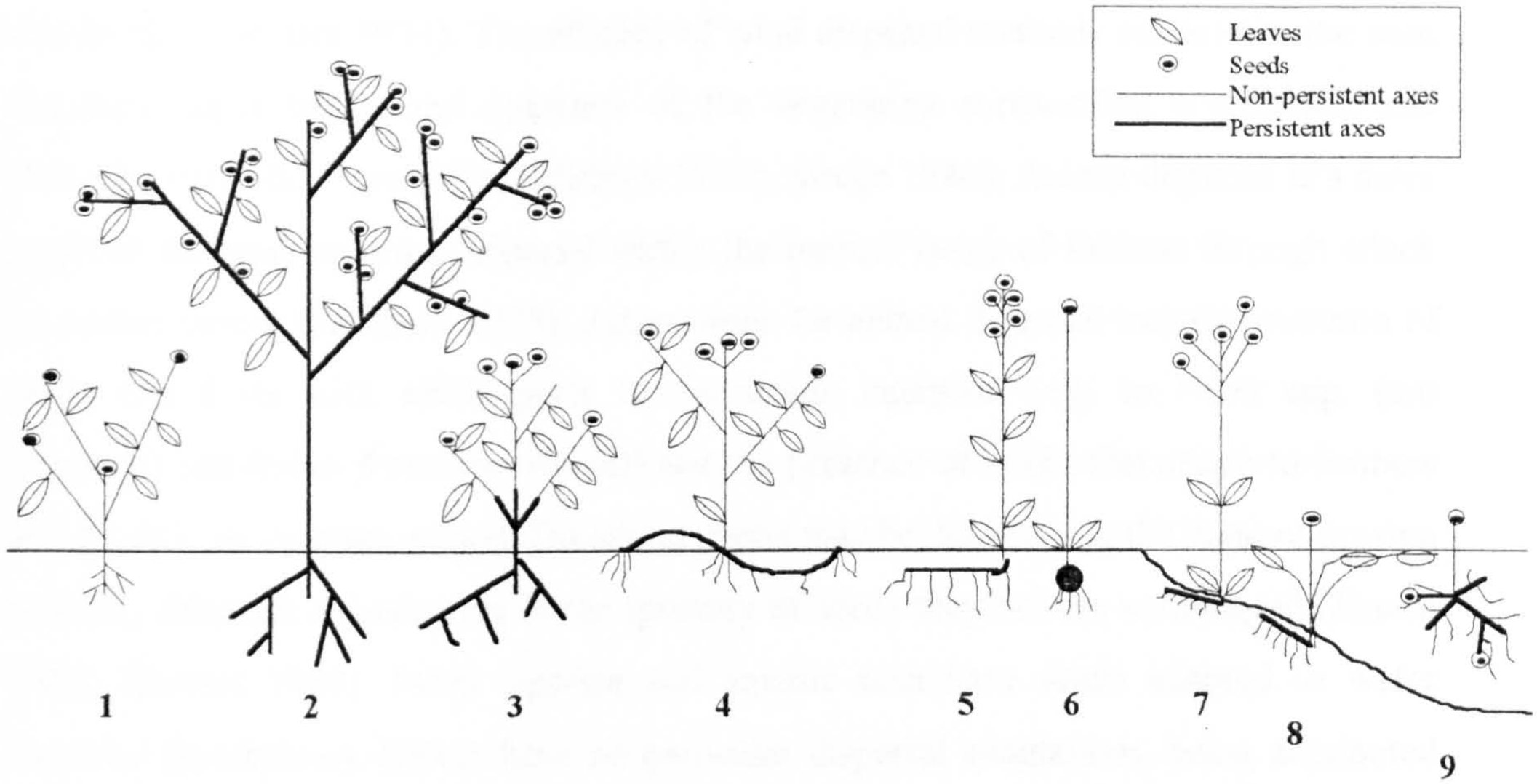
Macrofossil assemblages also include sub-aerial structures such as roots and rhizomes which hold the plant in position and provide a means of vegetative propagation. These organs are less susceptible to movement from the growing point of the plant and so are more likely to be incorporated in accreting sediments, although they do penetrate sediments deposited earlier than the accreting surface. Movement of these structures is only likely if sediments of which they are a part are eroded away.

With the exception of traumatic loss caused by storms, the quantity and range of plant structures shed, the periodicity of shedding and the extent of subterranean growth is dependant upon the plants life-cycle and regenerative strategy. A useful framework for considering this is Raunkiaers life-form classification which orders plants on the strategy employed to overcome the unfavourable season (see Figure 2.3). Trees and shrubs (phanerophytes and chaemophytes) shed leaves and seeds annually in temperate areas while retaining the woody stem during the lifecycle. Perennial herbs (geophytes, hemicryptophytes or helophytes), such as the common reed (*Phragmites australis*) shed seed and the entire aerial portion of the plant annually, producing a large quantity of leaf and stem detritus while retaining a living rhizome and root mass below the ground. Annuals (Therophytes) reproduce by seed and usually have ephemeral stem, leaf and root structures.

Many plants retain both sexual and asexual means of propagation, utilising each in different circumstances. Seed production allows plants that would otherwise reproduce vegetatively in stable conditions to overcome periods of environmental instability and colonise exposed new habitats (Salisbury 1976a; Willson 1992). The allocation of energy to seed production depends on environmental conditions (Bazzaz and Ackerly 1992) and can be negligible if a plant mainly spreads by vegetative reproduction, as in *Phragmites australis* (Grime *et al.* 1988). For example, seed production is enhanced in some shade-tolerant species, such as *Epilobium angustifolium* and *Circaea lutetiana,* if light levels are increased (Salisbury 1976b). Therophytes rely entirely on seed production and often produce many thousands of seeds, up to 75,000 per plant in the case of *Chenopodium album*. Seed production also varies with the type of seed dispersal mechanism adopted, larger numbers being produced in taxa that use wind dispersal (Salisbury 1976b).

The timing and method of shedding aerial plant parts is important for the chance of entrainment in depositional systems. Seed and leaf shed have been studied in most detail, aerial stems less so. The periodicity of woody stem production is much lower than leaves and seeds, although in herbaceous plants stem production also follows a yearly cycle. As stems usually die and decay *in situ* they have a low potential for incorporation in sediments. Tree trunks and branches are also less readily shed than herbaceous stems, leaves and seeds, although branch fall can be common in some species (e.g. in *Fagus sylvatica*) and tree trunks can be introduced into sedimentary basins by erosion and

catastrophic storm damage (Gastaldo *et al.* 1989). Leaf shed from deciduous trees in the temperate zone is a synchronous event, whereas leaf fall from coniferous and evergreen taxa occurs during the year (Spicer 1989).



Life Form	Features	Example
1. Therophyte	Pass unfavourable season as seeds	*Chenopodium album*
2. Phanerophyte	Woody plants with buds more than 25cm above ground	*Quercus robur*
3. Chamaephyte	Woody or herbaceous plants with buds less than 25cm above ground	*Empetrum nigrum*
4. Hemicryptophyte	Herbs with buds at soil level	*Potentilla anserina*
5. Geophyte	Herbs with buds below soil level (on rhizomes/roots)	*Orchis* sp.
6. Geophyte	Herbs with buds below soil level (bulbs/corms)	*Hyancinthoides non-scripta*
7. Helophyte	Marsh plants	*Carex acutiformis*
8. Hydrophyte	Water plants (with basal rhizome/root)	*Sagittaria sagittifolia*
9. Hydrophyte	Water plants (free floating)	*Lemna truscula*

Figure 2.3 Raunkaier's life-form classification

Plant structures have different dispersal potentials once shed from the parent plant, depending on the species and local environmental factors. Dispersal properties determine the distance from the parent plant a structure may travel and, therefore, its potential for sediment entrainment. Heavy structures, such as branches and tree-trunks, are unlikely to be dispersed, in the first instance, far from the site of growth (although see Gastaldo *et al.* 1989), as are herbaceous stems which die and decay *in situ*.

Seeds and fruits have evolved into a variety of forms to enhance dispersal depending on the survival strategy of the parent plant. Adaptations to wind dispersal include the development of feathery and wing-like structures (e.g. Asteraceae and Aceraceae) and production of an easily dispersed 'dust' of tiny seeds (e.g. Orchidaceae, *Juncus* spp.) (Ridley 1934). The efficacy of wind dispersal methods varies with the seed structure, plant height and openness of the vegetation surrounding it (Sheldon and Burrows 1973; Burrows 1973; Salisbury 1976b; Green 1980). Animal dispersal is a more targeted strategy, ensuring dispersal within the narrow range of habitats through which an animal moves (Salisbury 1975). Adaptations for animal dispersal include provision of seeds and fruits with edible parts to encourage ingestion (e.g. in *Viola* spp. (ant dispersal) and *Rubus fruticosus* (birds)) and the presence of hooks that attach to feathers and fur (e.g. in *Arctium minus*). Grassland plants may be dispersed in the dung of grazing animals, although animals vary in the quantity of seeds they excrete undamaged (Janzen 1982; Herrera 1984). Many riparian and aquatic taxa have seeds adapted to water dispersal (see below). Others have no particular dispersal adaptations, being distributed by a mixture of water, air and animal transport (e.g. *Chenopodium*). All dispersal methods have benefits and costs to the source plant. Wind transport is the least efficient and discriminatory method, although seeds are distributed in many habitats (Salisbury 1975). Water transport and animal transport is more efficient, the vectors limiting dispersal to environments the plant is more likely to tolerate (*ibid.*).

Efficacy of leaf dispersal depends on leaf-weight per unit area and environmental factors (Ferguson 1985); therefore species vary widely in their dispersal potential. Smaller, lighter leaves and those that do not abscise readily (e.g. *Fagus sylvatica*) have the greatest potential for movement (*ibid.*; Spicer 1989). Leaves have been shown to move only a short distance from the parent tree in temperate and tropical forests. Several studies show that leaf assemblages accurately reflected canopy composition above the sampling point, although the main biomass producers can be over-represented (Ferguson 1985; Spicer 1989; Burnham *et al.* 1992; Burnham 1994).

Vegetation structure exerts an effect on aerial dispersal. Dense and tall vegetation can reduce wind velocities and the quantity of plant detritus transported. Vegetation, for example the presence of high groundcover, can also causes a barrier which can physically hinder leaf and seed movement (Salisbury 1975; Spicer 1989). Tall vegetation along lakes and riverbanks can be an almost impenetrable barrier reducing the transport of

plant matter into sedimentary environments (Birks 1973; Spicer 1989). Conversely, in poorly vegetated open environments such as periglacial tundra, wind can transport plant remains over considerable distances (Glaser 1981).

Plant detritus and seeds are an important source of energy in many ecosystems and are decayed and preyed upon by bacteria, fungi, invertebrates, and vertebrates often working in association (Edwards and Heath 1963). Periodic or continuous shedding of plant organs causes a 'rain' of plant detritus which is available for incorporation into sedimentary systems, but continuously destroyed by detritovores and predators. Seasonal shedding of plant parts can produce surges of plant litter; however, breeding cycles can be timed to take advantage of them (Spicer 1989). Surges of detritus caused by storm damage can overload detritovores and be important contributors to the fossil record, providing complete and temporally precise macrofloral assemblages (*ibid.*).

The effect of decay processes on macrofossils is dependent on:

1) plant chemistry (Ferguson 1985);
2) environmental chemistry (Nykvist 1959b);
3) the extent of physical breakdown of detritus on exposure to decay organisms (Nykvist 1962);
4) the range of organisms in the environment (Edwards and Heath 1963).

Leaves are subjected to an initial phase of rapid physical and chemical breakdown (Nykvist 1959a and b; Witkamp and Olsen 1963; Witkamp 1966; Spicer 1989), after which the effect of decay processes depends on the chemical environment. In anaerobic environments decay ceases, whereas in aerobic environments massive continued tissue loss occurs (*ibid.*). Decomposition rates do, however, vary between species, the waxy leaves of pine (*Pinus sylvestris*) being very resistant (Nykvist 1959b) and broadleaf taxa less so (Nykvist 1959a, 1961, 1962). Seeds are also heavily predated, especially near the source plant (Thompson 1992), although resistant seed coats increase the chances of survival. Detritovores and predators on seeds and leaves often target single species and concentrate near to the prey plant and it has been found that assemblages of potential leaf fossils in some aquatic environments consist only of allochthonous species, the remains of local species being totally recycled (Spicer 1989).

2.3.4.3. Biostratinomy

Sedimentary processes further select the plant fragments incorporated into macrofossil assemblages and the study of these processes is biostratinomy (Gastaldo 1988). Plant structures are incorporated in sediments as the result of:

1) gradual accumulation due to deposition in sedimentary environments;
2) 'event' sedimentation (*ibid.*) in which large bodies of sediment and plant tissue are deposited at once, as in catastrophic flooding or mudslides;
3) penetration into sediments of plant structures during normal growth (e.g. roots and rhizomes).

The rate and scale of these processes varies in different environments, but most plant material in Holocene alluvial sediments derives from 1) and 3).

Once in the sedimentary system, plant detritus varies in how it responds to water depending on the species, structural component and structural completeness (Spicer 1989). Environmental controls also exert an effect, including water velocity and turbulence, the latter causing plant detritus to sink more rapidly (*ibid.*). Plant parts can be transported floating at the surface, as suspended load and as bed load (Field 1992). Floating matter has the potential to travel farthest in rivers and is easily stranded on shore surfaces, although this may increase susceptibility to predation. Floating rafts may also be affected by wind movement (Guppy 1894; Spicer 1989), whereas suspended and bed load movement is solely dependent on water velocity.

Seeds vary in their ability to float (e.g. Praeger 1913; Ridley 1930), depending on the reproductive strategy of the species. Adaptations to water dispersal include development of low specific gravity, air pockets, hairs or other structures which increase surface area (Howe and Smallwood 1982). Floating increases the distance over which seeds are dispersed but slows down incorporation into sediments and increases the chances of predation. Leaves initially float in water, sinking as they become waterlogged. Floating times vary between species, undamaged thick leaves floating longest, and thin leaves sinking most rapidly (Ferguson 1985). Wood may float for several years before sinking, leaving it prone to decay and mechanical damage.

Plant matter provides a major source of nutrients in aquatic environments and is heavily predated in the water column (Petersen and Cummins 1974). Biological decay is

affected by nutrient status, water chemistry and temperature (Kaushik and Hynes 1971) and combined with predation and mechanical damage in the water column, causes massive loss of plant matter from the sedimentary record. Even toughened structures, such as seeds and fruits, are damaged and differentially destroyed as a result of abrasion, crushing and enhanced decay by movements in waters moving at high-velocity, assemblages from bedload being particularly affected (Gee *et al.* 1997; Huber and Ferguson 1998). Low velocity movement only causes minor damage to most seed surfaces, suggesting that good preservation is a good indicator of local origins (Huber and Ferguson 1998).

Deposition of plant matter occurs when the settling velocity is reached due to density increasing as it becomes waterlogged and/or as water speeds decrease. Leaf settling behaviour depends on leaf structure, with major differences between leaves from broad-leaved and coniferous trees (Spicer 1989). Movement through the water column can damage fragile plant structures, although the effect is dependent on water velocity and the extent of macrofossil decomposition (Ferguson 1985). Deposition is aided by riverbed roughness and enhanced in areas of slow water movement (Spicer 1989). Bankside vegetation can physically trap or prevent the penetration of plant particles. Deposition reaches a peak during slack-water in diurnal tidal cycles and during peak river discharges (Holyoak 1984). Distribution of macrofossils in sediments has been found to be uneven (Greatrex 1983; Watts 1978), with water movement and physical barriers causing concentration effects.

Plant parts are either buried *in situ* at the place in which the parent plant grows (autochthonous deposition), or are carried into the sediment from elsewhere as a result of various dispersal processes (allochthonous deposition) (Gastaldo 1988). The quantity of allochthonous and autochthonous inputs depends on the openess of the environments to transport agents as well as the rate and type of dispersal processes in operation (Spicer 1989). Environments subject to limited water movement and high local water levels such as fens, swamps and bogs provide conditions in which plant material can be incorporated and preserved at the point of growth. Other, more open, depositional environments such as channel and channel bank environments in both rivers and estuaries may have considerable allochthonous inputs.

2.3.4.4. Diagenesis

Diagenesis studies the processes affecting fossils once incorporated into sediments, including compression, mineral replacement and selective loss (Gastaldo 1988). Mineral replacement is less important over Holocene time-scales but preserves many earlier fossils. In Holocene and many Quaternary sediments, macrofossils are preserved by the maintenance of anaerobic environments. Sandy substrates are prone to percolation by oxygen-rich waters that encourage biological decay. Silts and clays accumulated in rivers and lakes hold water well and have a limited oxygen supply (Gastaldo 1988), encouraging preservation if groundwater levels are high or if there is a perched water table (Brown 1997). Changes from anaerobic to aerobic conditions caused by drainage can cause rapid decay of all organic remains as demonstrated in several archaeological projects (e.g. French and Taylor 1985), although similar processes may have occurred naturally in some sediments during periods of sea-level regression. Estuaries are sites of intense biological activity (Reineck and Sing 1980) and potential fossils can be lost through nutrient cycling.

2.3.4.5. Actualistic research

Data from studies of potential macrofossil assemblages in modern depositional environments have been used to evaluate the usefulness of macrofossil data from fossil assemblages deposited in similar environments. Many studies focus on determining how macrofossil assemblages reflect the depositional environment rather than specific ecological parameters (although see Burnham 1994). Studies have been completed for glacial environments (Van der Valk and Davis 1976; Glaser 1981; Holyoak 1984), lakes (Birks 1973; Rich 1993), woodlands (Burnham 1989, 1994; Burnham *et al.* 1992), pastures, grasslands (Chippendale and Milton 1934; Major and Pyott 1966) and mires (Greatrex 1983). Coverage of environments and plant macrofossil groups is uneven (Evans 1992) and studies have often focused solely on one type of plant macrofossil and/or depositional environment. European studies have mainly focused on seeds and fruits, American studies on leaves, although some more wide-ranging analyses have been attempted (Scheihing and Pfefferkorn 1984; Gastaldo and Huc 1992).

Several studies of small freshwater rivers and tidally influenced deltas have provided some information about plant macrofossil taphonomy in alluvial systems and have demonstrated that there are repeated recognisable patterns of macrofossil

preservation in depositional sub-environments, although in many cases they cannot be used as a direct analogue to northern European environments.

Incorporation of surface accumulations of macrofossils on channel edge and bank surfaces depends on the rate and type of sedimentation, with some environments preserving discontinuous patches of leaves, twigs and seeds (Scheihing and Pfefferkorn 1984) and others beds of macrofossils within laminated sediments (Gastaldo and Huc 1992). Point-bars are the main site of in-channel deposition with a mixture of seeds, comminuted leaves and wood fragments deposited at floodstage (Scheihing and Pfefferkorn 1984; Field 1992). Other channel environments have little potential for incorporation of identifiable macrofossils because of constant re-working by currents (Galstado and Huc 1992).

Macrofossils in channel bank and channel deposits are mainly derived from bankside or levee vegetation (Collinson 1983; Scheihing and Pfefferkorn 1984; Gastaldo 1984; Gastaldo and Huc 1992; Field 1992), although terrestrial and more distant aquatic taxa are represented (Collinson 1983; Field 1992). Field (1992) noted regular patterns of over and under-representation of the seeds of some taxa, for example *Plantago major* and *Prunella vulgaris* respectively, depending on the mode of dispersal, although several, including *Urtica dioica* and *Epilobium hirsutum*, reached abundances approaching those in local vegetation communities. Channel sediments also have a high potential for the incorporation of plant matter re-worked from older deposits, with re-working possibly accounting for many rootlets and woody clasts (Gastaldo and Huc 1992).

Natural levees are composed of relatively coarse material which does not hold water and are subject to fluctuating water-levels (Gastaldo 1988) leading to destruction of macrofossils and preservation of only compression fossils and root casts (Scheihing and Pfefferkorn 1983; Gastaldo 1989). Crevasse splays, caused by the breaching of levees, have a higher chance of incorporating plant macrofossils, in some cases covering and preserving whole, intact beds of leaf litter (Gastaldo 1989).

Fluvial backswamps, oxbow lakes and marshes are the main locations for macrofossil incorporation in alluvial systems. Vegetation prevents dispersal of levee and channel-edge macrofossils into backswamps (Gastaldo and Huc 1992) and macrofossil assemblages mainly reflect the local flora. Leaves are only preserved when water levels are permanently high and sedimentation is rapid (Scheihing and Pfefferkorn 1984;

Gastaldo 1989). Oxbow lakes are the main sites for preservation of leaves and other delicate macrofossils mainly derived from vegetation fringing the basin (Gastaldo 1987; Gastaldo *et al.* 1989). Comparisons of macrofossil and vegetation abundance have demonstrated that ultra-local canopy and groundcover dominants are over-represented and that assemblages are unreliable for characterising larger vegetation associations (Greatrex 1984; Scheihing and Pfefferkorn 1984; Gastaldo 1989; Burnham 1992).

Plant litter entering tidally dominated environments is prone to extensive mechanical fragmentation caused by daily tidal movement and high biological turnover. Preservation is dependent on how open the specific depositional environment is to tidal influence, although most macrofossils again derive from local plants. Channel sediments contain well preserved macrofossils only if sedimentation is rapid (Scheihing and Pfefferkorn 1984), more usually being comminuted into tiny unidentifiable fragments (Gastaldo and Huc 1992). Point-bars can incorporate plant beds as in fluvial channels (ibid.) and marshes preserve root structures but relatively little aerial plant matter, much of which is removed by tidal action (Gastaldo 1989). All environments that are tidally inundated are prone to allochthonous inputs, some of which may derive from considerable distances (Cappers 1993), although marshes with dense vegetation may effectively shut out allochthonous water-borne inputs.

2.3.4.6. Temporal and spatial averaging

Time-averaging is the mixing of fossils from different generations within a community or different environments into potentially misleading fossil assemblages (Kidwell and Flessa 1995). Time-averaging varies between different alluvial environments, being more extreme in those with slowly accumulating sediments (*ibid.*) that are open to allochthonous inputs and/or have *in situ* vegetation growth. Channel, channel edge and mudflat sediments may be most affected by allochthonous inputs, although marshes and wooded fens may be disturbed by the penetration of roots and, in the latter case, falling branches. Time-averaging can also be accompanied by 'spatial-averaging' where representatives of spatially distant communities are mixed in fossil assemblages. In environments influenced by water-flow, such as tides and floods, the source biota may be at great distances from the site of deposition. This can be useful if catchment vegetation or ecologies are under investigation, and if extra-local inputs can be distinguished, for example on the basis of habitat requirements. Taphonomic studies have helped to refine

our understanding of fossil recruitment and some estimates of the distance some fossils have been made (Evans 1992; Waller 1994, Table 6.1; Brown 1997).

2.3.4.7. Implications

Taphonomic studies have demonstrated that plant macrofossil assemblages do not directly represent standing vegetation and should be treated as 'death assemblages', the composition of which is a result of:

1) the life form of the source organism(s);
2) the habitat in which it/they lived (including the presence of detritovores etc.);
3) proximity of the organism to a depositional sedimentary environment;
4) the dispersal properties of individual plant parts;
5) the sedimentary environment in which the fossils accumulated;
6) post-depositional history, including water-level changes and sediment re-working.

Plant macrofossil assemblages at best form partial records of past vegetation. Patterning reflects environmental and sedimentological selection processes as much as biological phenomena and affects both the spatial and temporal resolution of interpretations of fossil data. Actualistic studies also show that taphonomic patterning can be understood, at least partially, although the ecological resolution of assemblages in many environments has yet to be fully investigated (Kidwell and Flessa 1995). In alluvial environments, macrofossil incorporation can vary widely between different depositional sub-environments and appreciation of assemblage taphonomy is required if any meaningful information is to be gained from macrofossil analysis. This means that investigation of long-scale temporal and spatial patterns requires comparison between assemblages deposited in similar environments or as a result of similar 'taphonomic modes' (Behrensmeyer and Hook 1992)

2.4. Palaeoenvironmental and palaeoecological applications

2.4.1. Interpreting alluvium in space and time

Analysis of sedimentary and biological data is used to reconstruct alluvial environments and investigate the global, regional and local variables that influence their development.

Independent variables, external to the fluvial system, include basin physiography and geology, climate, sea-level, base-level, anthropogenic disturbance and tectonic factors (see references at the beginning of this chapter; Burrin 1983). Dependant variables, emergent from the interaction of external variables, include discharge, sediment load, sediment type and flow velocity (*ibid.*). Resolution of these variables, especially at the level of temporal resolution required in archaeological and Holocene studies, is complicated by the following factors:

A) Alluvial sedimentation is discontinuous. Erosion and hiatuses in sedimentation may create gaps in the sedimentary record and spatial discontinuity in sedimentation means that secure correlation of sediments from similar heights in different parts of an exposure may not be possible.

B) Dating of episodes of sedimentation is difficult. Absolute methods rely on the presence of fossils that may be re-worked, intrusive (i.e. roots and rhizomes) or contain hard-water error. Apparently synchronous events, such as episodes of peat deposition (e.g. Devoy 1979) may be time-transgressive and should not be considered chronostratigraphic markers.

C) Sediment deposition occurs laterally and vertically and sediment accumulation rates are variable.

D) Similar sedimentary profiles and structures may be produced in different depositional environments, especially when fine-grained sediments are deposited and bioturbated.

E) Bioturbation by root penetration and animal burrowing on saltmarshes, fens and carrs destroys sedimentary structures and mixes diachronous deposits.

F) Different depositional environments incorporate variable and unpredictable quantities of allochthonous and autochthonous fossils.

G) Local processes may dominate sedimentation and ecology, masking the effects of global and regional scale variables, such as climate.

H) Exposures of alluvium are often small, reducing the potential for identification of sedimentary structures and landforms, potentially leading to the collection of unrepresentative fossil samples.

2.4.2. Channel and floodplain development

Reconstruction of former channel dimensions and channel networks is difficult because river movement and re-working obliterates traces of channel sediments and cuts. Presence of channel lag and bar facies may point to in-channel deposition and levee facies may indicate former channel margins. Changes in floodplain sedimentation and vegetation can also be used to infer channel processes and changes in the catchment. Reconstruction of channel and floodplain morphology and development has been attempted using inductive formal models (e.g. Leopold and Wolman 1970). More recently deductive approaches have been attempted (Richards 1982) that aim to explain river development within a broader understanding of catchment history, including human impact (Richards 1982; Burrin 1983). Plant macrofossil analysis has mainly contributed to these models by providing local vegetation reconstructions (e.g. Brown and Keough 1992).

2.4.3. Palaeohydrology

Palaeohydrology is the study of past water composition and movement. Sedimentological information and historical records can contribute to reconstructions of flood regimes and channel dimensions can be used to calculate palaeodischarge (Brown 1997). Fossils can act as indicators of past hydrological conditions, although, because alluvial environments are open to allochthonous and autochthonous inputs, careful consideration of fossil taphonomy is required to ensure the spatial and temporal fidelity of the assemblages. The most commonly used fossils include diatoms (Batterbee 1988), used to identify the penetration of the tidal wedge up the river Thames (Milne *et al.* 1986). Palynology has also produced important information about floodplain and channel biota (Devoy 1979; Burrin and Scaife 1984; Scaife and Burrin 1992; Waller 1994; Brown 1997).

Plant macrofossil analysis has mostly contributed to palaeohydrological investigations of lake and bog development (e.g. Godwin 1959; Walker and Walker 1961; Nenwnham *et al.* 1995). Multi-disciplinary studies of alluvial sequences have also included macrofossil analysis to identify saline-freshwater transitions (e.g. Devoy 1979; Waller 1994). Various other studies have used macrofossil analysis to reconstruct water quality (Baker *et al.* 1995), river and basin histories (Godwin 1955; Caseldine *et al.* 1988; Housley 1995) and the environmental context of archaeological finds (e.g.

Clapham and Godwin 1948; Beckett 1978a and b, 1979; Hillman 1981; Wilkinson and Murphy 1988, 1995). Studies of alluvium have shown that groundwater levels have risen over much of southern England as a result of anthropogenic disturbance (Bell 1982; Scaife and Burrin 1987; Lambrick and Robinson 1984) from at least 3000BC.

2.4.4. Palaeoecology and vegetation history

Vegetation history aims to reconstruct the distribution and development of major vegetation associations over space and time and has long been a major focus of Quaternary palaeobotany. Palaeoecology aims to reconstruct the distribution *and* interaction of organisms within their environment in space and time by analysis of death assemblages (Birks and Birks 1980). Palaeoecology, therefore, operates at a more detailed scale of analysis, is concerned with elements of the whole ecosystem rather than its plant component solely, and requires a multi-disciplinary approach. Both subjects contribute towards the interpretation of alluvial environments, the determination of the potential for and influence of human activity and the interpretation of wider environmental conditions and long-term change (Brown 1997).

Underlying palaeoecology and vegetation history is uniformitarianism, the concept that modern environments and biota can be used as a basis for interpreting the same phenomena in the past (Birks and Birk 1980). Alluvial sedimentation processes are thought to have varied little over recent millennia, although the full suite of causal factors affecting alluviation cannot be assumed to be operating today (Brown and Keough 1992). Biological tolerances and processes are also assumed to have changed little over Holocene timescales, although some modern ecological studies suggest that plant species may be prone to rapid evolution (Adam 1990). It remains a possibility that modern organisms with identical morphology to fossil specimens may have evolved different ecological tolerances and competitive strategies and it is almost certain, given the impact of human activity, that community structure has changed.

Distributions of taxa are made on the basis of their presences in fossil assemblages. Environmental conditions can also be reconstructed using modern observations to identify indictor species, assumed to have unchanging associations with particular environmental conditions (Figure 2.4). More refined ecological and environmental investigations require community-level reconstructions, a task complicated by taphonomic processes (see above). Reference is usually made to modern

ecological studies (see section 2.3.3). These accounts, however, only classify extant vegetation, providing a restricted and anthropogenically influenced reference flora, and other vegetation combinations would have existed in the past. Direct application of formal classification schemes have to be applied with caution (Greig 1992a) and it is usually difficult as the ecological indices used to classify vegetation are not directly comparable to those describing parameters in palaeoecological datasets. Most vegetation classifications use cover abundance measurements as a basis for classification. Experimental observations have suggested that relative pollen frequencies, modified to account for differential production and dispersal, equate well with vegetation cover abundance figures and that absolute pollen counts are useful indicators of relative plant biomass. No similarly detailed information is available for plant macrofossils.

Concepts such as succession and zonation are commonly employed in palaeoecological interpretations. Saltmarshes are zoned communities and modern vegetation zones have been used as a basis for interpreting macrofloras from alluvial and archaeological sediments (Hillman 1981; Behre 1986; Korbe-Grohne 1992). The 'verlandungs' series or hydrosere is an autogenic element to sediment deposition which has also to be considered in interpretations of floodplain lakes and backswamps (Birks and Birks 1980, Behre 1986). Fen-woodland successions in lowland settings have been modelled by Walker (1970) and recently re-evaluated by Waller *et al.* (1999). The latter showed alder carr woodland does not necessarily have to be a seral community in coastal wetlands, succeeded by ombrotorphic bog, but may, under conditions of rising sea-level, be a sustainable community in its own right. This examples serves to show the potentially dynamic nature of Holocene vegetation in alluvial environments and cautions the rigid application of autogenic models to past vegetation.

Most palaeoecological investigations describe past communities, environmental conditions and palaeoecological data, and rarely have the resolution to explain the processes occurring within communities (Gee and Giller 1992). Successful, detailed palaeoecological investigations are rare (e.g. Walker 1970; Barber 1980; Waller *et al.* 1999). Palaeoecological investigations of alluvium have often been part of investigations into sea-level and broader environmental change (e.g. Devoy 1979; Waller 1994; Scaife and Burrin 1987). Important contributions to regional and local vegetation histories have, however, resulted from these studies (e.g. Greig's use of Devoy's data in Greig 1992b) and many have included some level of plant macrofossil analysis. Site-specific

vegetation histories have also been forthcoming from archaeological investigations (see Somerset Levels Papers and Severn Estuary Levels Research Committee annual reports; Greig 1992a, b; Thomas and Rackham 1996). Ecological questions partly addressed by studies of alluvium include the development of grasslands in Britain and Europe (Greig 1988; Lambrick and Robinson 1988), the impact of European colonisation of America (Baker *et al.* 1993), ecology of the Somerset Levels (Godwin 1960; Caseldine 1988; Housley 1995), the ecology of the floodplains of Central Britain (Brown 1988) and the history of alder expansion (Chambers and Elliot 1989).

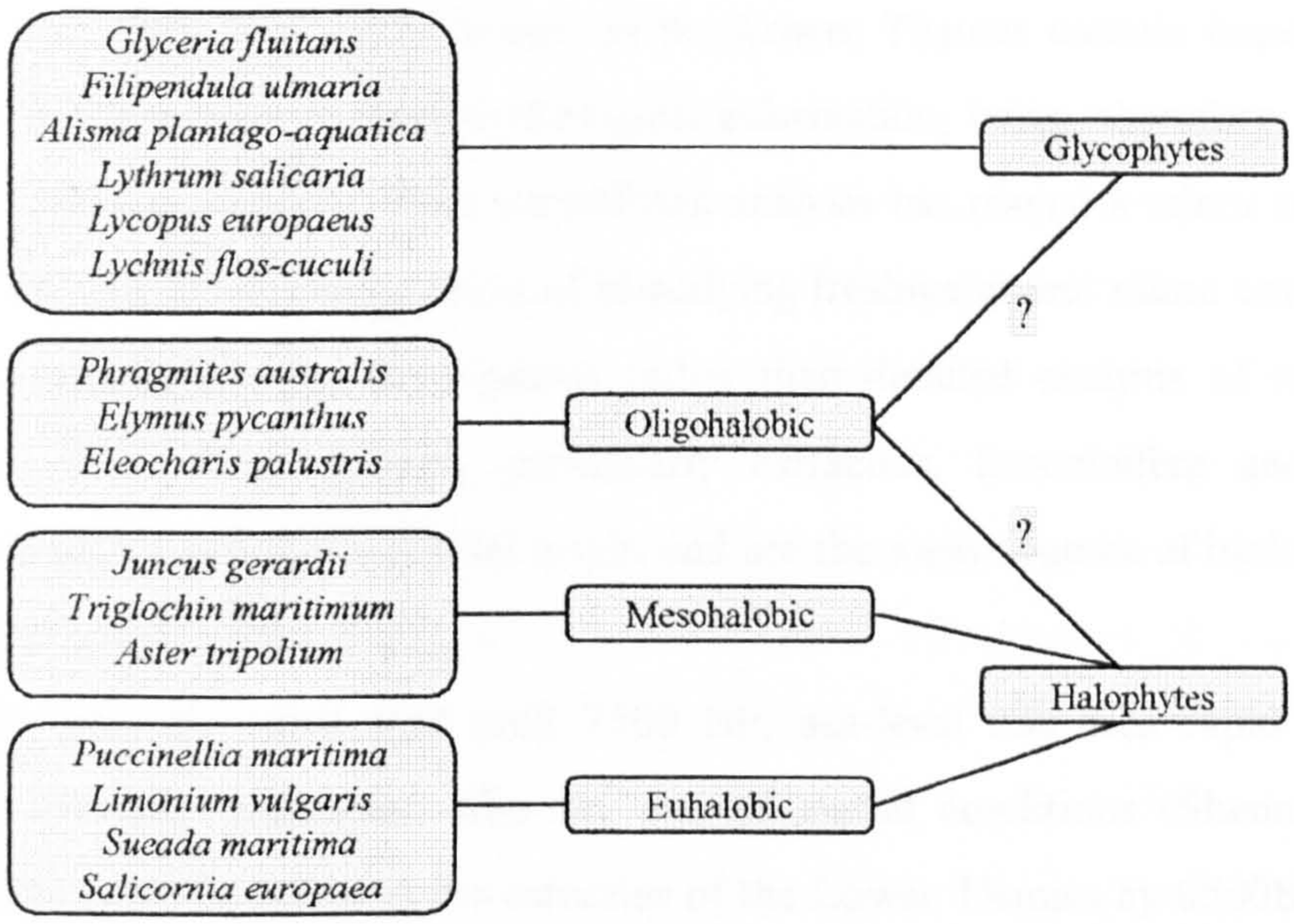


Figure 2.4 Freshwater (glycophytic) and saltwater (halophytic) indicator species, including those of strong (euhalobic), medium (mesohalobic) and weak (oligohalobic) salinity (based on Behre 1986 Table 1)

2.4.5. Local terrestrial environmental change

Macrofossil assemblages in lakes have commonly been used as a basis for interpretation of larger landscape vegetation and environmental changes (e.g. Watts and Winter 1966; Birks 1993). Studies of alluvium have contributed to the interpretation of terrestrial environmental change and land-use patterns through vegetation reconstructions and studies of floodplain formation processes. Increased accumulation of sediments in several basins can be interpreted as the result of landscape clearance from at least the Bronze Age, if not earlier, as a result of soil breakdown, increased sediment supply and runoff (Bell 1982; Burrin and Scaife 1984; Burrin 1983; Scaife and Burrin 1987, 1992;

Lambrick and Robinson 1984; Brown 1997). Vegetation studies of dryland biota have also been completed via analysis of pollen and macrofossils from alluvial sediments (e.g. Grieg 1992a 1992b; Thomas and Rackham 1996). These reconstructions have been particularly important in the Lower Thames Basin where other sedimentary basins are lacking.

2.4.6 Relative sea-level change

Sea-level research aims to identify the heights of sea-level at dated points in the past and to use these sea-level reference points to construct regional sea-level curves (Devoy 1979; Shennan 1987). Alluvial sediments in the Lower Thames contain important sea-level reference points and regional hydrological information, being, therefore, important sources for sea-level research. Plant macrofossil analysis has played a minor role in sea-level investigations, usually as a means of identifying freshwater and saline environments via broad Troels-Smith type descriptions rather than detailed analysis of macrofossil assemblages. Other fossil groups, particularly ostracods, foraminifera and diatoms provide more useful indicators of tidal height and are the main sources of biological data for sea-level research (Allen 2000).

Most accounts agree that until 7500 BP, sea-level rise was rapid following eustatic and isostatic adjustment after the end of glacial conditions (Shennan 1987). Marine influence can be traced in the estuaries of the Lower Thames by 8500BP (Devoy 1979) when sea-level is estimated at -25.5m O.D.. Further sea-level rise has continued and prompted alluviation along the rivers of the Lower Thames Basin, tectonic movement being an increasingly important factor (Shennan 1989). Alluviation in many of the region's valleys contains alternating bands of silt/clay and peat deposited in estuarine and freshwater environments respectively. Traditionally regressive contacts (silt/clay to peat deposition) and transgressive contacts (peat to silt/clay deposition) have been assumed to represent lowering and rising sea-level, the contact point corresponding to the mean high watermark of spring tides (MHWST), or average highest tidal level (Devoy 1979; Behre 1986). Devoy suggested that these alternating phases of sedimentation were synchronous over the region. Episodes of peat deposition were named Tilbury I-V, the major phases of which occurred between 7000 BP and 6600 BP, 5000 BP and 3900 BP, 2800 BP and 2600 BP and at approximately 1700 BP. Intervening episodes were named Thames I-V.

Subsequent work has confirmed broad correlation of episodes of peat deposition in the Lower Thames (Tyers 1988; Long 1995). In Essex the sequence differs from that described by Devoy, although there are some striking parallels. Early Holocene peat development was lacking, with that between 5000BP and 4000 BP corresponding to the Tilbury III regression. Another phase, between 1600BP and 1400BP, corresponds to Tilbury V (Greensmith and Tucker 1971; Wilkinson and Murphy 1988, 1995). A similar record is seen on the Medway River (Evans 1953). Post-Roman sea-level rise was limited (Skempton 1995) but has led to the flooding of islands and lower estuary marshes on the Medway (Evans 1953).

The identification of Thames and Tilbury phases as chronologically distinct has, however, been criticised, as alluvial sedimentation is time-transgressive (Kidson and Heyworth 1982; Rackham 1994) and correlation of strata from widely spaced cores does not account for differential compaction rates that distort recorded contact levels (Skempton 1995). It has also been suggested that transgressive and regressive contacts do not necessarily directly correspond to sea-level rise and fall and should only be used to show sea-level tendencies. Even the theory behind using these contacts to interpret sea-level change has been questioned because of the complex causative factors behind alluvial sedimentation. It has been pointed out that peat can form during marine transgressions if local groundwater conditions allow and sea-level rise is locally slow (Kidson and Heyworth 1973; Heyworth and Kidson 1982; Haggart 1995; Waller *et al.* 1999). Reconstructions of MHWST have been superseded by identification of relative mean sea-level (RMSL) (Allen 2000). The generally accepted trends for Holocene RMSL in Britain show rapid rise up until *ca* 6000BP, followed by a slowing rate of rise until *ca* 3500BP. After a period of more rapid rise until *ca* 2000BP, RMSL rise decreased again and several authors have commentated on the problems in using the shallow, homogenous sediment record of the last two millennia to reconstruct general trends (Waller *et al.* 1999; Allen 2000).

2.4.7. Climate change

Local factors dominate alluvial sedimentology and ecology, masking more subtle climatic changes. Only large-scale climatic signals register unambiguously in the alluvial stratigraphical record, for example the identification of arctic as opposed to temperate floras (Reid 1949). Most investigations of climate using plant macrofossil analysis have

been applied to lake and bog sediments over Late-Glacial/Holocene transitions (e.g. Reid *ibid.*; Godwin 1959; Jessen *et al.* 1959; Watts and Winter1966; Birks and Mathewes 1978; Van Geel *et al.* 1980; Hall 1984; Birks 1993; Hughes *et al.* 2000). Investigations of Holocene climatic change have most successfully been applied to peat bogs such as the analysis of Bolton Fell Moss where bog surface responses were correlated with climatic fluctuations (Barber 1981; Barber *et al.* 1994). In a recent investigation of sediments at Walland Marsh, Kent, ombrotrophic peat growth has been attributed to increasing precipitation at approximately 2700BP, the boundary of the Sub-Boreal/Sub-Atlantic transition (Waller *et al.* 1999). The investigators noted that fen woodland development could only be adequately investigated through the detailed analysis of macrofossil data, highlighting the deficiencies in current approaches to macrofossil analysis in coastal margins.

2.5 The archaeology of alluvium

2.5.1 Alluvium as an archaeological resource

Archaeological finds have been recovered from lowland wetlands, including alluvium, for over a century (see Bates and Barham 1995); however, its full archaeological significance has only been recognised in recent decades (e.g. Needham and Macklin 1992), partly through the work of several research projects. These include the Severn Estuary and Somerset Levels (Coles 1987; Bell and Neumann 1997); Fenland (Waller 1994); Humber Wetlands (Van de Noort and Davies 1993); North-West wetlands and coast (Cowell and Innes 1994; Huddart *et al.* 1999); Thames Archaeological Survey (in Milne *et al.* 1997); and Essex Rivers projects (Wilkinson and Murphy 1995), as well as a variety of other excavations (e.g. Allen *et al.* 1997; Cowie and Eastman 1997a and b). The archaeological importance of alluvium can be summarised as follows:

I. *Preservation of materials.* Anoxic conditions caused by waterlogging provide suitable conditions for the preservation of organic materials, such as wood, leather and cloth, that usually decay.
II. *Local context.* Archaeological sites and artefacts are often preserved alongside the remains of the environments in which they were used, providing the potential for detailed reconstructions of the context of human activity that is impossible on many dryland sites.

III. *Catchment and regional-scale information.* Alluvium incorporates fossils from non-local as well as local habitats that provide a basis for the reconstruction of vegetation (e.g. Grieg 1992) and human effects on terrestrial landscapes (e.g. Fairbairn 1998).

IV. *Extinct landscapes.* Alluvium preserves some former wetland landscapes *in situ*, providing the only direct source for understanding landscapes that are extinct or greatly altered as a result of drainage and land reclamation. These landscapes are not only unique in biological and geological terms, but also archaeologically, as in the Severn Estuary Levels, where landscapes distinct from adjacent terrestrial landscapes and those of the Somerset Levels have been uncovered (Bell Neumann 1997).

V. *Burial of terrestrial landscapes.* Alluvium has sealed former terrestrial landscapes along many rivers preserving sites and artefacts *in situ*. These include Mesolithic flint spreads (Jacobi 1982; Lambrick and Robinson 1988; Wilkinson and Murphy 1995); Neolithic occupation sites (Murphy 1988; Greig 1992a); Iron Age herding structures (Bell 1993; Bell and Neumann 1997); ceramic manufactories (Evans 1953) and entire suites of multi-phase sites (Allen *et al.* 1997; Bell and Neumann 1997).

Ironically, alluvium also provides as many problems for the archaeologist as potential. The main problem is the limited visibility of archaeological sites and structures which, combined with high water-tables, can make identification and excavation of archaeological horizons and features difficult (Barham and Bates 1995; Allen *et al.* 1997; Bates and Bates 2000). These problems are at their most extreme in the deep stratified seidments of the Lower Thames, although a variety of coring and monitoring strategies have been used to circumvent the problem, with some success (Milne *et al.* 1997; Bates and Bates 2000). Furthermore, the management of the archaeological and palaeoenvironmental resource in alluviated areas is complex. Many hold nature reserves of endangered biota and straddle the edges of important communications routes. Therefore, access to the alluvial environments is controlled by multiple authorities with statutory powers of control, including nature conservancy bodies (e.g. English Nature) and Port authorities (e.g. the Port of London Authority) (see Milne *et al.* 1997).

2.5.2 Preserved sites, artefacts and structures

Several classes of archaeological sites and artefacts are preserved in alluvium:

I. *Settlements and domestic structures.* Permanent settlements in alluvial wetlands are rare, bu, have provided detailed insights into past societies as a result of the preservation of organic materials. Examples from Europe include the Iron age wurten of the northern European coast and Mesolithic settlements in Germany and Denmark (Andersen 1987; Gramsch 1991). In Britain, the Meare and Glastonbury 'Lake villages', built in a freshwater lagoon, preserved a similar range of artefacts and environmental data (Bullied and Gray 1911, 1917, 1949; Coles and Minnitt 1995). Settlements were more commonly situated at wetland margins preserved by later alluvial deposition, as for example at Starr Carr (Mellars and Dark 1998), the Essex estuaries (Wilkinson and Murphy 1995), the Severn Levels (Bell and Neumann 1997), and Runneymede (Needham 1991).

II. *Trackways and Causeways.* Wooden trackways have been found in several alluviated areas in Britain and across Europe demonstrating the presence and maintenance of communication routes through wetlands from the Neolithic to the Iron Age. Many have been found in the Somerset Levels over the last fifty years (Clapham and Godwin 1949; Coles 1987) and more recently in the nearby Gwent Levels (Bell 1997). Similar structures have recently been excavated in the Lower floodplain of the Thames river (Meddens 1996) at Rainham (Meddens and Beasley 1990), Beckton (Meddens 1993), Barking (Chew 1994), Bramcote Green (Thomas and Rackham 1996) and Erith (J. Sidell pers. com.).

III. *Platforms and Enclosures.* Enclosures, platforms and post-settings have been excavated in several sites, including Flag Fen, Etton causewayed enclosure (Pryor 1998) and Yarnton on the Middle where a Later Neolithic excarnation enclosure was found on a former island (Tim Allen pers. com.).

IV. *Boats and jetties.* Alluvium has preserved many boats and jetties such as the famous sequence on the Humber (McGrail 1981) and the recently excavated Bronze-Age sewn plank boat at Dover. Prehistoric jetties are known from the Thames at Yarnton (T. Allen pers. com.) and on the Severn (Bell and Neumann 1997). More substantial structures are known from the Roman (Yule 1988) and Post-Medieval periods (Cowie and Eastman 1997b).

V. *Human remains.* Most human remains in alluvium are isolated bones, such as the skulls and long-bones frequently recovered from the Thames, possibly deposited during burial or other rites (Needham 1987; Parker-Pearson 1993).

VI. *Remains of extractive industries.* Remains of extractive industries, such as fishing and salt-making, are found along many river valleys and estuaries. Fishtraps dating from Saxon times are known along the Thames (Cowie and Eastman 1997a), among other rivers (e.g. Gobold and Turner 1994), and salterns have been found in several lowland basins (Swinnerton 1931; Wilkinson and Murphy 1995).

VII. *Artefacts.* Artefacts are preserved in alluvium both as stray finds and in association with structures. They include oars, flint scatters, bronze objects (Needham 1987), wooden figurines (Coles 1990) and even agricultural equipment (Tim Allen pers. com.).

VIII. *Modified trees.* Waterlogged remains of managed trees from the Neolithic have been preserved as at Skipsea Withow Mere (Gilbertson 1984) and Etton causewayed enclosure (Pryor 1998), providing important evidence for the antiquity of woodland management.

2.5.3 Rivers, floodplains, estuaries and saltmarshes in the human past

Whether directly utilised, or simply present at the margins of dry-land, wetlands have had a place in human experience through the Holocene for:

A) *Settlement.* Settlements were rarely sited on active floodplains and marshes and were more placed near the wetland edge, opening the resources of wetland, aquatic and terrestrial resources to inhabitants and providing good communications routes. In recent centuries infilling of floodplains has occurred widely in urban centres on river margins as, for example, in Southwark, London, where Post-Medieval land reclamation buried the former landscape of wetlands and sand eyots (Yule 1988).

B) *Resource extraction.* Wetlands are particularly rich ecosystems providing animal, plant and mineral resources. Management of reedbeds may have been as early as the Mesolithic at Starr Carr, Yorkshire (J. Hather 1998; see also Brown 1986) and wet woodland management is known from the Neolithic onwards (Gilbertson 1984). In recent centuries, management of alder in East Anglia fuelled industry, and reed beds were intensively managed for roofing. Wetland animal resources, including birds and fish have also been exploited (e.g. Coles and Minnitt 1995). Grazing of animals on natural wet pastures and saltmarshes has a long history, although in recent centuries it

has become more common to graze animals on drained marshes. Salt extraction is known from the Roman period onwards.

C) *Communications routes and boundaries.* Trackways, boats, jetties and oars, as well as historical texts record the use of rivers and estuaries as trade and communications routes for millennia. The exchange and spread of different suites of material culture would have been facilitated by such movement; therefore, we can situate rivers and estuaries centrally in processes of spread. Rivers also provide natural boundaries that have been adopted as social boundaries in many areas. The Thames for example has been a boundary since at least the Iron Age (Allen *et al.* 1997).

D) *Social and ritual activities.* Rivers and wetlands had an explicit social and ritual significance in prehistory. The deposition of numerous bronze artefacts and bodies into the Thames during the Bronze Age (e.g. Allen *et al.* 1997) has been used to suggest that it was an important place of burial (Parker Pearson 1993), a tradition that may have started in the Later Neolithic, as attested by the Yarnton mortuary enclosure (Tim Allen pers. com.). Trackways and jetties may have facilitated movement through and to the wetlands for burials and the delivery of offerings, as well as being used for resource extraction and communications. These records, and later evidence from proto-historic sources (Green 1992), suggest that alluvial environments had utilitarian and social significance simultaneously for prehistoric communities and that functionalist interpretations are inadequate if their place in the human past is to be accurately reconstructed (cf. Allen *et al.* 1997; Milne *et al.* 1997).

2.5.4 Human-wetland interactions in the Lower Thames

Sea-level, climatic and vegetation changes over the Holocene have constantly affected the distribution, characteristics and potential of alluvial systems for human exploitation, just as human action has affected alluvial systems themselves. The study of human behaviour and alluvial environmental change is, therefore, intimately linked, although this should not imply a deterministic relationship.

Glacial retreat at the end of the Devensian led to rapid inundation of the North Sea Plain, or 'Doggerland' (Coles 1998), and continued through the early Holocene, eventually filling the Strait of Dover by *ca* 8000BP (Bridgland 1995). Tidal incursion into the lower sections of river valleys caused changes in alluvial hydrology, sedimentology and ecology until sea-level rise slowed by the mid-Holocene. Mesolithic

gatherer-hunter groups may have widely exploited the rich resources available in both the terrestrial/wetland ecotone ahead of the tidal advance and the extensive estuaries beyond, although continuous changes in alluvial environments must have caused constant re-adjustment of subsistence practice and territorial boundaries. Direct evidence for Mesolithic exploitation of alluvial environments is sparse but includes several flint scatters on the floodplain edge of the Thames (Lambrick and Robinson 1988), Medway (Jacobi 1982) and Essex rivers (Wilkinson and Murphy 1995). As with later prehistoric and early historical periods, Mesolithic wetland exploitation was extractive, utilising natural productivity, and involved minimal disturbance of natural processes. Management would have affected vegetation structure if some species (e.g. reed or alder) were tended at the expense of others, but there was no intervention in hydrological processes.

Potential for exploitation and settlement was, however, strongly influenced by environmental responses to sea-level change which, judging by stratigraphic changes in the region's alluvial sequences, were complex. Tidal inundation may have led to the abandonment of the Essex coast by Mesolithic communities (Wilkinson and Murphy 1995) and floodplain formation in the Middle and Upper Thames during the Bronze Age disturbed a wide area (Allen *et al.* 1997). Widespread peat development between *ca* 5000 BP and *ca* 4000 BP in the region is associated with Neolithic settlement expansion onto some floodplains (Wilkinson and Murphy 1995). By the Bronze Age there is also evidence of widespread human presence on the floodplain peatlands of the Thames (e.g. Meddens 1996; Thomas and Rackham 1996), possibly for resource extraction and ceremonial reasons. Romano-British settlement expanded onto the floodplain of the river Crouch, Essex, during a later phase of sea-level regression between 1600BP and 1400BP (Wilkinson and Murphy 1995), an event that also allowed industrial expansion onto the marshes of the Lower Medway estuary (Evans 1953). Medieval sea-level rise, however, caused abandonment and flooding of these areas (*ibid.*).

Human communities have also exerted direct and indirect influence on river systems. Deforestation and arable farming causes increased runoff, erosion, discharge and sediment supply and was a major influence on alluvial systems in the Thames and Weald from at least the Bronze Age (Lambrick and Robinson 1984), if not the Mesolithic (Burrin and Scaife 1984; Scaife and Burrin 1987; Waller and Hamilton 2000). A permanent rise in the water table of the Upper Thames (dated to 3000BP) was followed by alluviation from the Iron Age as clearance became more extensive (Lambrick

and Robinson 1984). By the end of the Iron Age much of the Lower Thames was cleared (Greig 1992b; Thomas and Rackham 1996); however, it is uncertain the extent to which human activity affected its tidal environments.

More direct intervention in alluvial environments in the Lower Thames can be dated from the Roman period construction of revetments along the Thames and reclamation of parts of Southwark (Yule 1988). Drainage of marshes for grazing ('innage') may also have its beginnings at this time, although this may have been earlier (Lambrick and Robinson 1988; Brown 1997). Innage became widespread during the Medieval period, recorded from the ninth century on the Medway (Evans 1953) and on the Thames by the fourteenth century (Skempton 1995). Late Medieval and post-Medieval periods have witnessed considerable increases in settlement expansion, industrialisation, drainage, development of river canalisation and construction of tidal defences. These innovations led to widespread disturbance of natural sedimentation, hydrology and ecosystems leading to the almost total destruction of natural riverine and estuarine environments in the region and elsewhere (see Sheail and Wells 1983). River valleys today form important hubs of development, floodplains in particular being sites of extensive, if flood-prone construction for industrial and residential purposes.

2.6 Plant macrofossil analysis of alluvial facies: potential and problems

Plant macrofossils are preserved widely in alluvium, in both clastic and organic facies and have contributed to the investigation of many archaeological and environmental issues. Most commonly, macrofossils have contributed to investigations via Troels-Smith type descriptions acting as a basis for interpretation of the depositional environment. Detailed quantitative analyses have mainly used seed and fruit assemblages as a basis for vegetation and wider environmental reconstructions. Therefore, alluvial plant macrofossil analysis is split between generalised analysis of whole macrofossil assemblages and detailed analysis of one constituent element. While this approach provides useful information, it does not fully exploit the potential of macrofossil analysis of alluvial facies. Detailed analysis of all macrofossil components provides another means of analysis that has the potential to provide more accurate vegetation reconstructions and descriptors of alluvial depositional environments.

Concentration of detailed analysis on seeds and fruits is pragmatic but it inevitably draws analysis towards those sediments where these remains are well

represented, by no means all of the fossil record. As seeds and fruits are not produced universally by plants, they also only provide a partial picture of the palaeoflora. Seeds and fruits are also commonly transported over substantial distances, unlike most vegetative and woody remains; therefore, a holistic macrofossil analysis provides the potential for greater spatial detail in vegetation reconstructions. It also provides the potential to investigate vegetation in several ways. The usual route to interpretation uses the taxa identified in seed and fruit assemblages as a basis for floristic and structural interpretations. Utilising different structural groups of macrofossils (e.g. wood, vegetative remains) provides the potential for direct structural analysis of vegetation.

Descriptions of whole plant macrofossil assemblages, beyond Troels-Smith type descriptions, also provide the potential for contributing towards more accurate identifications of depositional environments. This would be particularly important in estuarine facies that in the Lower Thames Basin are composed of structureless fine-grained sediments precluding differentiation. Improved determination of depositional environment is also important for vegetation reconstructions, considering the complexity of alluvial taphonomy, and would improve the resolution of reconstructions of sea-level and past river and estuary morphology, information that is crucial for further understanding of low-lying wetlands (see Waller *et al.* 1999, 1440).

Several obstacles prevent applying such an holistic approach to macrofossil analysis:

1) Provision of rigorous, comparable quantified descriptions of heterogenous macrofossil assemblages is difficult.
2) Published identification criteria for stem, leaf and rootlet remains are lacking and it is uncertain to what level they are identifiable.
3) It is unknown how the sampling limitations that constrain deep alluvial investigations affect ecological and environmental data produced by macrofossil analysis.
4) Actualistic studies for many alluvial depositional environments from temperate ecosystems are lacking and those available often miss out vegetative and woody macrofossils; therefore, the spatial and temporal fidelity of macrofossil assemblages in these environments is, at best, partially known.

3 Laboratory methods

3.1 Classification

The plant kingdom contains three major groups of plants: the Algae, Bryophyta (mosses and liverworts), and the Tracheophyta (the vascular plants). The latter includes the ferns and allied plants (Filicophyta, Lycophyta and Sphenophyta), conifers (Gymnospermatophyta) and seed plants (Angiospermatophyta). Structures from members of each of the groups are potentially preserved in alluvium. Figure 3.1 shows the phylogenetic relationships of the main contributors to macrofossil assemblages in British environments. The range of structures and taxa in alluvial macrofossil assemblages is, therefore, very broad. As a first step in the production of a dataset from a macrofossil assemblage, a macrofossil classification was developed (Table 3.1). This was used to divide macrofossil assemblages into broad, structurally equivalent 'macrofossil classes'. This was necessary because:

a) It renders a complex and initially bewildering range of macrofossils into logical and recognisable groups for practical analysis
b) It provided groups of structures of similar morphology and, in many cases, anatomy, that require similar identification techniques
c) It provides a basis for comparison of the quantity and diversity of macrofossil classes present in samples

Macrofossils can be divided into several major divisions: aerial structures, underground structures, dispersal and reproductive structures and a general division (Table 3.1). The moss division has been isolated because of the distinctiveness and peculiarity of its structures. Therefore, the non-moss divisions include structures primarily from the Tracheophyta, the ecological dominants and the main contributors of macrofossils to alluvial sediments and the most morphologically and anatomically diverse plant group. The divisions include macrofossil classes that are structurally coherent groups of broad potential taxonomic inclusion, such as 'aerial stems', rootlets and various reproductive and attendant structures. The plant components included in each group are shown on Table 3.1 and are discussed below. Some component groups have been defined within the classes to denote easily distinguished plant structural groups (e.g. Moncotyledonae type structures) that may have ecological or structural significance. The classes also contain macrofossils that are treated in a similar analytical

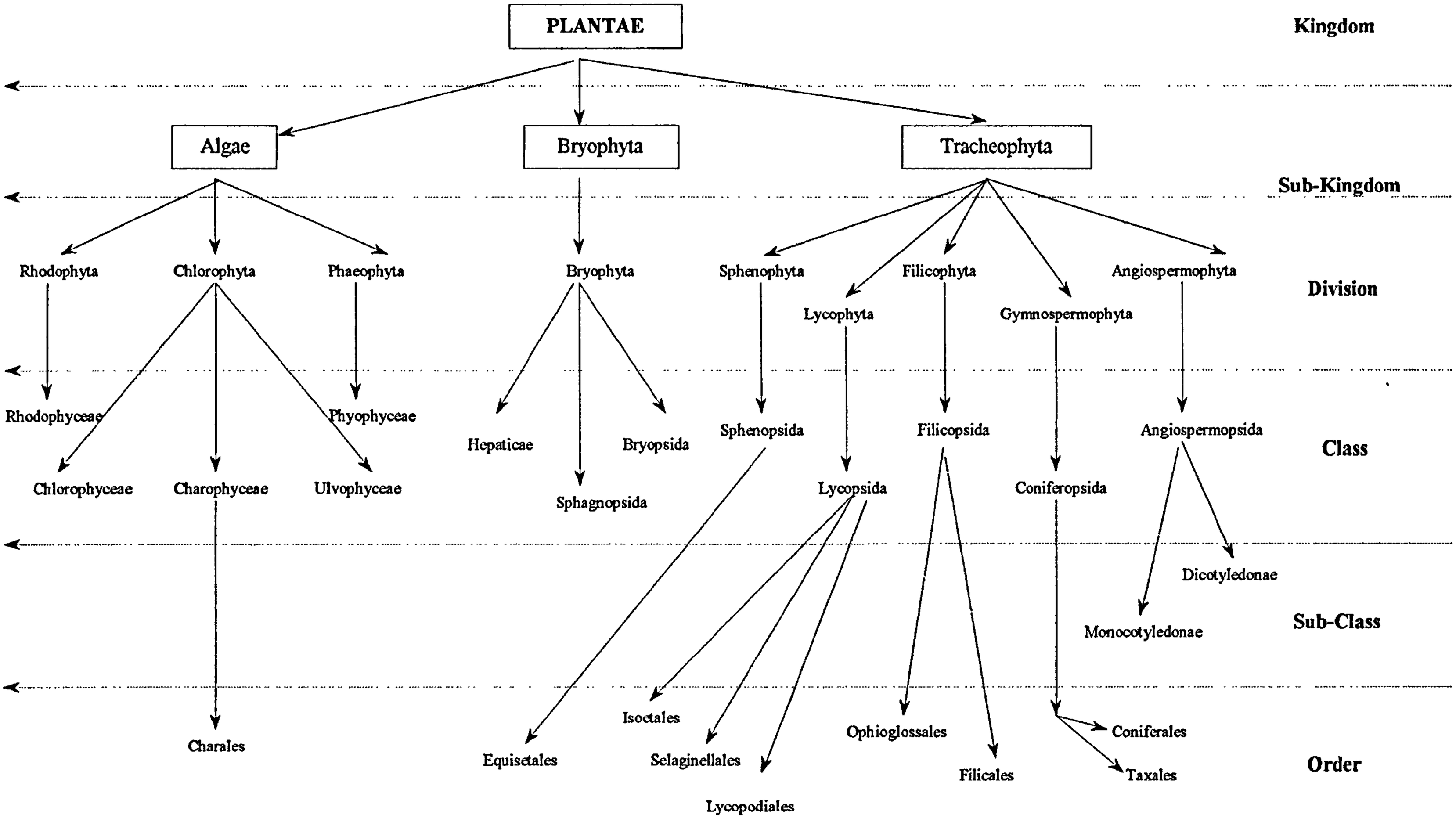


Figure 3.1 Phylogenetic relationships of the higher ranks of the plant kingdom showing the major taxa native to the British Flora (the general structure and classification of the Tracheophyta follows Bell 1992 and that of the Bryophyta follows A. J. E. Smith 1978, 1990)

Macrofossil division	Macrofossil class	Plant component	Source plant taxa
Moss	Moss	Moss plants	Bryophyta
		Moss Stems	Bryophyta
		Moss leaves	Bryophyta
		Moss capsules	Bryophyta
Aerial structures	Woody stems	Bark	Some Dicotyledonae and all Gymnospermatophyta
		Twigs	Some Dicotyledonae and all Gymnospermatophyta
		Branch sections	Some Dicotyledonae and all Gymnospermatophyta
	Non-woody aerial stems	Monocotyledonae type	Moncotyledonae
		Sphenophyte type	Sphenophyta
		Dicotyledonae type	Dicotyledonae
	Buds and bud-scales	Buds	Woody Dicotyledonae and Gymnospermatophyta
		Bud scales	Woody Dicotyledonae and Gymnospermatophyta
	Leaves	Monocot type leaves	Monocotyledonae and a few Dicoytledonae
		Reticulate leaves	Dicotyledonae and few Monocotyledonae
		Needle leaves	Gymnospermophyta and some Dicotyledonae
		Rachis	Filicales
		Petioles	Some Dicotyledonae
		Abscission surfaces	Some Dicotyledonae
	Other	Stipules	Some Dicotyledonae
		Thorns	Some Dicotyledonae
		Prickles	Some Dicotyledonae
		Scales	Filicophyta and some Angiospermatophyta
Underground structures	Non-woody underground stems	Rhizomes and similar structures	All Tracheophyta
		Underground Monocot type stems	Moncotyledonae
	Roots	Rootlets	All Tracheophyta
		Woody roots	Some Dicotyledonae and all Gymnospermatophyta
Dispersal and reproduction	Spores and sporangia	Sporangia	Filicophyta
		Oospores	Charophyta
		Megaspores	Lycophyta
		Indusia	Some Filicales
	Seeds and fruits	Indehiscent Seeds/Fruits	Gymnospermatophyta and Angiospermatophyta
		Dehiscent Fruit fragments	Angiospermatophyta
		Bracts and similar structures	Gymnospermatophyta and Angiospermatophyta
General	Tissues	Epidermis and cuticle	All Tracheophyta
		Vascular strands	All Tracheophyta
		Wood fragments	Some Dicotyledonae and all Gymnospermatophyta
		Unidentifiable vegetative tissue	All Tracheophyta
	Indeterminate	Unidentifiable organic matter (UOM)	All taxa

Table 3.1 Plant macrofossil groups and source plant taxa

manner, providing a basis for determining the extent of coverage of published identification criteria (see section 3.2). Some of the terminology uses 'types' to denote a morphological class that is usually dominated by one taxon but may include some others.

3.1.1 Moss and liverwort (Bryophyta) macrofossils

Simple Bryophyta have a multi-layered thallus, although identification is unlikely if the structure is fragmented because they lack stomata and complex epidermal structures. Only whole plant sections or large fragments are likely to be identified. The more ecologically important leafy Bryophyta are distinctive, having morphologically and anatomically distinguishable leaves, stems, gametangia and capsules. The stems are simple, undifferentiated, small (<2mm width in most cases) and have leaf insertion points lacking in the distinctive leaf traces and abscission surfaces seen in the Tracheophyta. The leaves have no differentiated epidermis, mesopyhll or vascular tissues and the lamina consists of a single layer of cells. Leaf cells are conspicuous, even under low-powered microscopy, the arrangement often varying across the leaf surface. A central rib and marginal serrations are present in many taxa. Sphagnopsida leaves have a distinctive structure. The capsules consist of a cylindrical structure carried on a stem-like structure (seta) with distinctive aperture morphology. All potential macrofossils from the leafy Bryophyta are unique in form and whole sections, denuded stems, leaves and capsules are commonly preserved in alluvium.

3.1.2 Aerial structures

This division includes stem and leaf structures that are positioned above the ground surface and are primarily concerned with support and photosynthesis.

3.1.2.1 Woody stems

This category includes the perennial woody stems of trees and shrubs, including the trunks, branches and twigs of trees and shrubs, and the woody stems of chaemophytes such as *Sarcocornia perennis*. The structures consist of an elongated axis composed of wood (see below) with an outer covering of bark. Bark is a toughened, dense, multiple layered structure, although the bark on waterlogged specimens often loses the phellogen and phelloderm, because of differential decay, and becomes a loose sac of phellum around the wood. Detached fragments are common and often retain the reflective outer

coating seen on live trees and shrubs. This and the less regular, very dense cellular structure allows easy separation from wood. Tree-trunks and large branches form important and recognisable elements of peat-beds. Smaller woody stem structures, such as twigs and small shoot axes, often retain the traces of nodes and abscission surfaces. Moderate sized branches, if denuded of bark, may be confused with woody roots.

3.1.2.2 Non-woody aerial stems

Fossils in this group consist of an elongated axis of vegetative tissue surrounded by an epidermis or non-woody periderm. Longitudinal grooves, veins or nodes may also be apparent. It includes stems from all of the main Tracheophyta Divisions. Many aerial stems, especially in the Monocotyledonae, retain stomata on the epidermis, have recognisable leaf traces and lack rootlet growth. Stems have steles composed of multiple vascular strands, distinguishing them from herbaceous roots that have a single stele.

Two main sub-groups of stem-types can be distinguished. The Monocotyledonae type are often cylindrical with obvious parallel longitudinal veins or grooves, highly regular longitudinally arranged rectangular epidermal cells, and nodes that run around the circumference of the stem, where present. The Sphenophyta type is similar to the Monocotyledonae type, having hollow cylindrical stems and regular longitudinal files of cells. Longitudinal ridges are well developed in this group and the characteristic leaf sheaths, ridged branchlets or distinctive stomata should allow easy differentiation from similar types. The Dicotyledonae type is difficult to generalise but has no obvious parallel venation, a variety of cross-sectional shapes, conspicuous crescent or oval nodes and a variety of epidermal types. Differential decay of the unstrengthened cortex in non-woody stems can reduce the axis to a loose epidermal sac surrounding the stele.

3.1.2.3 Buds and Bud scales

Bud-scales are leaf-like scales protecting the leaf meristems in Gymnospermophyta and Angiospermophyta taxa and are especially toughened in trees and shrubs. Individual scales are thicker than equivalent sized leaves. They also have a broad basal attachment scar and a variety of surface features, venation patterns and marginal forms. They are found individually or as whole buds and are potentially important macrofossils of tree and shrub species.

3.1.2.4 Leaves

Tracheophyta leaves are preserved whole, or more usually fragmented. Unlike the simple, undifferentiated leaves of the Bryophyta, those of the Tracheophyta are complex structures with differentiation into mesophyll, vascular bundles and epidermis, all commonly surviving in waterlogged alluvium.

Several leaf sub-groups are distinguishable. Filicales leaves consist of laminar structures with dichotomously branching veins, complex epidermis and a highly dissected form. The leaves are sub-divided into ranks of 'leaflets' termed pinnae and pinnules, depending on the degree of dissection. Needle leaves are elongated cylindrical structures with a thick waxy cuticle and usually only a single vein apparent. The group includes the leaves of the Gymnospermophyta and some Dicotyledonae groups including the heathers (Ericaceae).

Most leaves of the Angiospermatophyta are included in the final two sub-groups. The reticulate type includes laminar leaves with a net-like venation pattern and complex epidermis. This type derives almost exclusively from the Dicotyledonae, although some Monocotyledonae (e.g. *Sagittaria* sp.) and Filicophyta (e.g. *Ophioglossum* sp.) may be superficially similar. Monoctyledonae type leaves have longitudinally parallel veins and a regular patterned epidermis. Most taxa in this group are Monocotyledonae, although some Dicotyledonae taxa are superficially similar (e.g. *Plantago* sp.).

Other leaf elements may form potential macrofossils. Filicales pinnule and pinnae segments are held by a stem-like structure, the rachis. This is difficult to distinguish using gross morphology, unless leaflets are attached and may, without anatomical inspection be included erroneously in the stem class. Petioles are the leaf stalks of the Angiospermatophyta. They are often preserved attached to leaves, but are also preserved detached. They consist of an elongated axis of cortex, vasculature and epidermis that has a well-defined abscission surface at the proximal end. Abscission surfaces are a thickened pad of tissue that seals the leaf attachment point when leaves are shed from a plant. They are preserved on petioles and as detached individual macrofossils of semi-circular or crescent shape through which the remains of leaf veins protrude. The morphology and number of vascular strands is potentially diagnostic.

3.1.2.5 Other

Several other plant structures are potentially preserved in alluvium. Only the most common have been defined here.

3.1.2.5.1 Stipules

Stipules are small leaf-like structures found at the base of, and often continuous with, leaves in many Dicotyledonae taxa. Some (e.g. those of *Salix* spp.) are commonly preserved in alluvium and may be identified on the basis of morphology.

3.1.2.5.2 Thorns

Thorns are short, narrowly lanceolate, pointed wooden structures developed from a modified branch as seen, for example, in *Prunus spinosa*. They have a thin periderm, often several nodes along the surface and are woody.

3.1.2.5.3 Prickles

Prickles are thickened epidermal outgrowths usually with a broad, elliptical base and curved point, as seen on the stem and leaf surface of taxa such as *Rosa* spp. (rose) and *Rubus fruticosus* agg. (bramble). They may survive as discrete structures or on stem sections.

3.1.2.5.4 Scales

This group contains a diverse range of vegetative structures attached to aerial and underground stems and especially rachis sections in the Filicophyta, although they are unlikely to be preserved in a distinguishable form.

3.1.3 Underground structures

This division includes the subterranean structures primarily functioning as support, anchorage, in water and mineral absorption and vegetative reproduction.

3.1.3.1 Non-woody underground stems

Non-woody underground stem structures include rhizomes, corms and tubers and horizontal structures, such as stolons, that are at the ground surface. These structures have the form of an elongated axis with nodes, roots and often leaf-like scales at the nodes, especially in the Moncotyledonae. The epidermis or periderm lacks stomata. Two sub-groups have been defined for these structures:

1) The Monocotyledonae type has nodes that extend around the whole circumference of the stem, may have obvious parallel longitudinal veins or ridges and often bear scale leaves or scale-leaf scars.
2) A generalised 'rhizome and other group' includes similar structures, lacking the parallel venation of the above group and in general being less-regular.

3.1.3.2 Rootlets

Non-woody rootlets are often preserved in abundance in waterlogged sediments. Decay and compression usually removes the cortex and collapses the structure. Fossils are, therefore, reduced to an elongated epidermal sac, with or without the swollen apical root-cap, surrounding a dark, wire-like single stele. The discrete, single-stranded stele distinguishes larger roots from underground stem structures. Stomata and trichomes (modified hairs) are absent from the epidermis, although many taxa have root hairs or 'cube-like' projections visible using low-powered microscopy. Large storage roots are unlikely to be preserved whole in waterlogged conditions as the cortex is likely to decay and the peridermal sac and vascular core is unlikely to stay intact. Woody roots are often preserved in waterlogged sediments and are produced by trees and shrubs. Woody roots lack the nodes and abscission surfaces of woody stems.

3.1.4 Dispersal and reproductive structures

This division includes the structures used in sexual reproduction and the dispersal of embryos, and also some of the more advanced spore-producing organs, spores and the attendant structures such as bracts. The combination of seeds, fruits and spores is artificial, but convenient as they have a similar form.

3.1.4.1 Spores and sporangia

Large visible spores are produced by a small number of the lower-vascular plants and the complex algae. They are used to disperse the gametophytes in taxa with alternating generations. They are produced in structures called sporangia that are more commonly preserved in macrofossil assemblages. Large, spirally ridged, seed-like oospores are produced by the alga Characeae, members of the Charales order (Figure 3.1), and are common in alluvial macrofossil assemblages. Megaspores are produced by several of the Lycophyta, including *Selaginella* spp. and *Isoetes* spp.. These spheroid structures

are visible to the naked eye (*ca* 0.5mm diameter) and are important for species identification (see Stace 1991).

Characteristic sporangia are produced by several taxa. Those of the Filicophyta are among the most commonly preserved in alluvium, especially those of *Osmunda* spp., and the indistinguishable sporangia of other Filicales taxa. The Sphenophyta have characteristic compound strobili consisting of many structures called sporangiophores (a type of sporangia). Lycophyta sporangia are leaf-like structures called sporophylls that are again carried in compound cone-like structures. Leaf-like indusia are also produced in the Filicophyta. These are vegetative covers that protect the sporangia and are often detached in taxa such as *Dryopteris*, being commonly preserved in some alluvium.

3.1.4.2 Seeds and fruits

3.1.4.2.1 Seeds and similar structures

Seeds develop from the fertilised ovule in the Gymnospermophyta and Angiospermophyta and vary widely in size and form. All, however, have a toughened outer layer of cells and contain a single embryonic plant. Fruit structures are derived from the carpel that surrounds the ovule in the Angispermophyta and often contain multiple seeds. They include indehiscent fruit structures that fuse to the seed (i.e. Ranunculaceae achenes) that are recognisable as discrete, individual structures, usually with a toughened exterior and often elaborate sculpting. This group contains structures with a huge range of morphological variability. Dehiscent fruit structures act as a container or dispersal mechanism and release the seeds when ripe, such as the legume pod of the Fabaceae. Fragments of these structures may also be found in sediments.

3.1.4.2.2 Bracts and similar structures

A number of structures are derived from modified leaves and are associated with seed and fruit production in the Angiospermatophyta and Gymnospermatophyta. These include the bract-scales of the Gymnospermatophyta, as well as the bracts, scales and perianth segments of the Angiospermophyta. Most are small leaf-like structures with obvious veins. Perianth segments (petals and sepals) are unlikely to be preserved detached in waterlogged alluvial sediments, although bracts and scales are commonly found.

3.1.5 General

This division includes fossil types that may derive from several of the groups above.

3.1.5.1 Tissues

3.1.5.1.1 Epidermis and cuticles

Tracheophyta structures are composed of highly differentiated groups of tissues that may become detached from each other as a result of decay processes. Some of the more commonly preserved types of tissue includes epidermis and cuticle. Epidermis is a compound structure consisting of toughened cells and a waxy cuticle that forms the outermost covering of the plant body. Cuticle may become detached and often preserves anatomical and morphological features, especially when well developed, as in the leaves of holly (*Ilex aquifolium*). Epidermal and cuticle macrofossils derive from a potentially wide range of primary plant structures including stems, leaves and roots.

3.1.5.1.2 Vascular strands

Individual vascular strands, or more properly steles, are often preserved in macrofossil assemblages, especially those of roots that have a highly thickened endodermis. They are distinguishable as 'wire-like' narrow, elongated cylindrical structures with a dark, toughened surface (the endodermis) and derive from many Tracheophyta, especially the Angiospermatophyta.

3.1.5.1.3 Wood

Wood fragments are often preserved and have a characteristic anatomical structure of regularly arranged longitudinal and radial cells that are distinctive even when fragments are small. Wood potentially derives from both stem and root structures.

3.1.5.1.4 Unidentifiable vegetative/herbaceous matter

This group includes fragments of plant tissue that are clearly non-woody, but defy higher level classification.

3.1.5.2 Indeterminate

Many macrofossils are indeterminate, being fragmented or decayed to a point where diagnostic criteria are obliterated. Unidentifiable organic matter (UOM) is a 'catch-all' group that includes fragments that defy any other classification.

3.2 Identification

Published plant macrofossil identification criteria have been reviewed in section 2.3.2.3. This research showed that there were gaps in the range of published identification criteria for several macrofossil classes and many taxa important in British alluvial macrofossil assemblages, especially:

1) Non-woody roots;
2) Tracheophyta leaves including:
    a) Sphenophyta leaf sheaths,
    b) Filicophyta pinnae and pinnules,
    c) Dicotyledonae leaves,
    d) Some Monocotyledonae leaves;
3) Epidermis and cuticles of many groups, with the exception of some Monocotyledonae.

Research was undertaken to expand the range of macrofossils that could be included in alluvial assemblage analysis by:

a) Compiling morphological and anatomical information from the literature;
b) Preparing and describing reference specimens for selected taxa.

This section presents the results of that research.

3.2.1 Selected Taxa

From the outset it was realised that the description of the leaves, epidermis and roots of all the taxa that potentially grow in British alluvial habitats could not be achieved in a project of this size. A reduced number of the most abundant and dominant taxa in British alluvial habitats was selected for inclusion in the research, mainly on the basis of ecological accounts and fieldwork experience. Other important ecological taxa that may grow adjacent to alluvial habitats were added to this list, as were some to allow intra- and inter-family and genus comparison. The aim was not to provide a comprehensive account of the potential macrofossils in the above classes, but rather to

Division	Family	Species	Structure identified
Sphenophyta	Equisetaceae	*Equisetum arvense*	Epidermis
		Equisetum fluviatile	Epidermis and root
		Equisetum variegatum	Epidermis
Filicophyta	Ophioglossaceae	*Ophioglossum vulgatum*	Pinnae
	Osmundaceae	*Osmunda regalis*	Pinnae and root
	Hymenophyllaceae	*Hymenophyllum tunbridgense*	Pinnae
	Polypodiaceae	*Polypodium interjectum*	Pinnae
		Polypodium cambricum	Pinnae
	Dennstaedtiaceae	*Pteridium aquilinum*	Pinnae
	Thelypteridaceae	*Oreopteris limbosperma*	Pinnae
		Thelypteris palustris	Pinnae and root
	Aspleniaceae	*Asplenium trichomanes*	Pinnae
		Asplenium marinum	Pinnae
		Asplenium ceterach	Pinnae
		Asplenium ruta-muraria	Pinnae
	Woodsiaceae	*Athyrium felix-femina*	Pinnae
	Dryopteridaceae	*Polystichum setiferum*	Pinnae
		Dryopteris dilitata	Pinnae and root
		Dryopteris felix-mas	Pinnae
	Blechnaceae	*Blechnum spicant*	Pinnae
Dicotyledonae	Ranunculaceae	*Anemone nemorosa*	Leaf
		Caltha palustris	Leaf
		Clematis vitalba	Leaf
		Ranunculus acris	Leaf
		Ranunculus ficaria	Leaf
		Ranunculus flammula	Leaf
		Ranunculus repens	Leaf
		Ranunculus sceleratus	Leaf
		Ranunculus sub-genus *Batrachium*	Leaf
	Papaveraceae	*Glaucium flavum*	Leaf
	Ulmaceae	*Ulmus glabra*	Leaf
	Cannabaceae	*Humulus lupulus*	Leaf
	Urticaceae	*Urtica dioica*	Leaf and root
	Myricaceae	*Myrica gale*	Leaf
	Fagaceae	*Fagus sylvatica*	Leaf
		Quercus petraea	Leaf
		Quercus robur	Leaf
	Betulaceae	*Alnus glutinosa*	Leaf
		Betula pendula	Leaf
		Carpinus betulus	Leaf
		Corylus avellana	Leaf
	Chenopodiaceae	*Atriplex portulacoides*	Leaf and root
		Atriplex prostrata	Leaf
		Salicornia europaea agg.	Leaf and root
		Sarcocornia perennis	Leaf and root
		Suaeda maritima	Leaf and root
	Caryophyllaceae	*Cerastium fontanum*	Leaf
		Spergularia media	Leaf
		Stellaria media	Leaf
	Polygonaceae	*Persicaria hydropiper*	Leaf
		Persicaria maculosa	Leaf and root
		Rumex acetosella	Leaf
		Rumex hydrolapathum	Leaf
	Plumbaginaceae	*Limonium* sp.	Leaf and root
	Tiliaceae	*Tilia cordata*	Leaf
	Malvaceae	*Althaea officinalis*	Leaf
	Violaceae	*Viola* sp.	Leaf
	Salicaceae	*Populus nigra*	Leaf
		Populus tremula	Leaf
		Salix cinerea	Leaf
	Brassicaceae	*Cardamine* sp.	Leaf
		Cochlearia anglica	Leaf
		Rorippa islandica	Leaf
	Primulaceae	*Lysimachia vulgaris*	Leaf and root
	Rosaceae	*Crataegus monogyna*	Leaf
		Filipendula vulgaris	Leaf
		Geum rivale	Leaf
		Potentilla erecta	Leaf
		Prunus spinosa	Leaf

Table 3.2 Taxa and structures included in the identification work

Division	Family	Species	Structure identified
Dicotyledonae (cont)	Rosaceae (cont.)	*Rosa* sp.	Leaf
		Rubus fruticosus agg.	Leaf
		Sorbus aucuparia	Leaf
	Fabaceae	*Lathyrus palustris*	Leaf
		Lotus uliginosus	Leaf
	Haloragaceae	*Myriophyllum spicatum*	Root
	Lythraceae	*Lythrum salicaria*	Leaf and root
	Onagraceae	*Epilobium hirsutum*	Leaf and root
	Cornaceae	*Cornus sanguinea*	Leaf
	Rhamnaceae	*Rhamnus cathartica*	Leaf
	Aceraceae	*Acer campestre*	Leaf
	Araliaceae	*Hedera helix*	Leaf
	Apiaceae	*Apium graveolens*	Leaf
		Apium nodiflorum	Leaf
		Hydroctyle vulgaris	Leaf
		Peucedanum palustre	Leaf
	Solananceae	*Solanum dulcamara*	Root
	Convolvulaceae	*Calystegia sepium*	Leaf and root
	Menyanthaceae	*Menyanthes trifoliata*	Leaf and root
	Boraginaceae	*Myosotis scorpioides*	Leaf and root
		Veronica beccabunga	Leaf and root
	Lamiaceae	*Lamium album*	Leaf
		Lycopus europaeus	Leaf and root
		Stachys palustris	Leaf and root
	Plantaginaceae	*Plantago coronopus*	Leaf
		Plantago maritima	Leaf and root
	Oleaceae	*Fraxinus excelsior*	Leaf
	Scrophulariaceae	*Scrophularia nodosa*	Leaf
	Rubiaceae	*Galium palustre*	Leaf and root
		Galium odoratum	Leaf
	Caprifoliaceae	*Lonicera periclymenum*	Leaf
		Sambucus nigra	Leaf
		Viburnum opulus	Leaf
	Asteraceae	*Artemisia maritima*	Leaf
		Aster tripolium	Root
		Bidens cernua	Leaf
		Cirsium palustre	Leaf and root
		Eupatorium cannabinum	Leaf
Monocotyledonae	Butomaceae	*Butomus umbellatus*	Leaf and epidermis
	Alismataceae	*Alisma plantago-aquatica*	Leaf and root
		Sagittaria sagittifolia	Leaf
	Hydrocharitaceae	*Hydrocharis morsus-ranae*	Leaf
	Juncaginaceae	*Triglochin maritimum*	Leaf and root
	Potamogetonaceae	*Potamogeton lucens*	Leaf
	Juncaceae	*Juncus acutiflorus*	Root
		Juncus acutus	Leaf and epidermis
		Juncus effusus	Root
		Juncus gerardii	Root
		Luzula sp.	Leaf, epidermis and root
	Cyperaceae	*Bolboschoenus maritimus*	Leaf, epidermis and root
		Carex riparia	Leaf, epidermis and root
		Carex remota	Leaf
		Cladium mariscus	Leaf and epidermis
		Eleocharis palustris	Leaf, epidermis and root
		Schoenus nigricans	Leaf
		Scirpus lacustris	Leaf, epidermis and root
	Poaceae	*Elytrigia repens*	Root
		Glyceria maxima	Root
		Phalaris arundinacea	Leaf and Root
		Phragmites australis	Leaf and Root
		Puccinellia maritima	Root
	Sparganiaceae	*Sparganium erectum*	Leaf, epidermis and root
	Typhaceae	*Typha angustifolia*	Leaf, epidermis and root
		Typha latifolia	Root
	Iridaceae	*Iris pseudacorus*	Leaf, epidermis and root

Table 3.2 (cont.) Taxa and structures included in the identification work

provide a working reference collection with an acceptable level of taxonomic coverage. All major Genera, Families, Orders and Sub-Classes were included.

The taxa and elements of those taxa included in this research are shown in Table 3.2. Leaves and epidermis were included from both sub-genera of the Sphenophyta and all major Filicophyta families and wetland taxa found in lowland Britain. The Dicotyledonae species were restricted to taxa with thickened leaves that were more likely to be preserved in alluvial sediments, especially arboreal dominant species, and important herbs repeatedly recorded during fieldwork. The leaf and epidermal characteristics of many of the important Monocotyledonae have been published elsewhere (e.g. Gross-Braukmann 1976) and only a limited number of taxa were included to improve this author's familiarity with them. Gymnospermatophyta leaves, those of the Lycophyta and some Dicotyledonae taxa (e.g. Nymphaceae) were not included as they were adequately covered elsewhere (see section 2.3.2.3).

Rootlets were analysed from only 34 taxa. It was quickly established that there was limited variability in the surface morphology of the taxa (see below). The research was, therefore, limited to verifying and extending where possible existing published work on the subject (e.g. Katz *et al.* 1969, 1974).

3.2.2 Reference specimen preparation

3.2.2.1 Specimen collection and pre-treatment

Leaves, stems and roots were collected during fieldwork visits with permission from the management authorities at each site. Leaves were collected whole and complete sections of root systems were gathered where possible. Leaves and non-succulent stems were pressed at the time of collection. Succulent stems, leaves and roots were sealed in plastic bags in the field and preserved later in formalin, acetic acid, alcohol (FAA) solution (Berlyn and Miksche 1976). Additional specimens were supplied by the collections of the Institute of Archaeology.

Only undamaged leaves and root sections were used as reference specimens. Whole leaf-mount reference slides were made where possible, although in some cases especially large specimens (e.g. *Nuphar lutea*) were sampled. Samples included basal and main lamina sections, main ranks of veins and leaf margins. Samples of root were used from the root apex (e.g. including root cap) and mid-section of each rootlet. Entire pinnae were prepared where possible from the Filicophyta. Central leaf and stem sections were mounted from the stems and leaves of the Monocotyledonae and

Sphenophyta and cylindrical structures were bisected longitudinally before treatment (i.e. *Juncus* spp. leaves).

Structures preserved in FAA were rinsed in several washes of 50% industrial methylated spirits (IMS) before further processing took place. Dried leaves from the herbarium were rehydrated before use. Several methods were tried. A combined method of clearing and rehydration had samples boiled in 5% sodium hydroxide (Loquin and Langeron 1978). This was found to cause incomplete rehydration and often destroyed delicate structures and tissues before rehydration was complete. A 0.5% solution of cold tri-sodium phosphate, used to rehydrate desiccated archaeological remains (Tim Holden pers. com.), was effective, although full rehydration took several days, if not weeks. The most effective method was found to be boiling sections of whole structures in distilled water. This was rapid, had minimal detrimental effect on the specimens and used a cheap and environmentally neutral substance.

3.2.2.2 Clearing

Clearing was required before specimen staining and mounting. Many clearing agents were recommended in the literature including lactic acid and chromic acid solutions (Tomlinson 1984). Lactic acid was rejected after trials with whole specimens showed that it was ineffectual unless heated. It, and several other methods, was found to be unsafe, and the large number of preparations meant that the method was also prohibitively expensive. Chromic acid was rejected as it is highly poisonous and causes a major disposal problem. The technique applied involved heating the specimens just below 100°C in 5% sodium hydroxide (NaOH) solution until the leaves or other specimens became translucent. When this point was reached the specimens were removed from the clearing solution and gently rinsed in running water for up to three minutes and then rinsed in three changes of distilled water. Boiling during this stage was avoided. This method proved to be effective, safe under laboratory conditions, relatively inexpensive and used chemicals that were both easily obtained and disposed of.

Preparation of whole leaf mounts required close attention as clearing times varied considerably between the different species. Thin leaves, such as those of *Lycopus europaeus* and *Calystegia sepium*, required immersion for 2-4 minutes, while thicker leaves, such as those of *Ulmus glabra* could take up to 40 minutes. Similarly, thickened, large roots similarly took a longer time to clear, while the cut edges of leaf sections

allowed rapid movement of clearing agents into the specimens and decreased clearing times.

After sodium hydroxide treatment, specimens were immersed in a 5% solution of sodium hypochlorite (bleach) to complete the clearing process. Over-bleaching was avoided as it can cause specimens to become opaque (Johansen 1940). As a rule the specimens could be removed before bleaching was fully completed as the process continued for several minutes until the bleach was neutralised or rinsed off. Removal of the bleach was essential and a particularly difficult task taking up to five changes of distilled water after prolonged rinsing. A weak solution of acetic acid was used to neutralise the bleach in very large or tough specimens where water percolation was slow. After clearing and rinsing the leaves were transferred to a 50% IMS solution until required.

3.2.2.3 Staining and mounting methods

Mounting and staining methods were used to provide the maximum quantity of information for comparison to ancient specimens. The only practical method of identification in most cases for waterlogged remains is through plan view identification of surfaces via transmitted and epi-illuminating microscopy. Sectioning, with the exception of wood and some large thickened stems, is difficult, time-consuming and impractical for everyday analysis of rootlets and soft, herbaceous stem fragments.

Roots were mounted unstained in temporary slides in 50% glycerol after clearing and were sealed with nail varnish (Tomlinson 1984). This allowed detailed analysis of the surface features on slides that lasted for at least one year and could be rehydrated easily if they dried out. Sectioning of multiple root specimens embedded in a plastic, metyl-methachlorate, was tested. While it proved possible to obtain useful sections, it was expensive and time-consuming and provided only very limited information that added little to the identification of any specimens.

Whole leaves and leaf sections provided a more difficult preparatory task. Leaf architecture, form and epidermal anatomy were the main criteria used for identification. Initial observation of the proposed identification features in the first cleared specimens indicated that many characters would be invisible unless stained. For example, in unstained thick specimens the mesophyll diffused light to the point that epidermal characters were invisible. The procedure for staining is shown in Figure 3.2. Several stains were tried including single-stain preparations of Safranin 0 (e.g. Dilcher 1974),

light green, and Delafields Haematoxylin. The most useful method was found to be a duel staining technique using Safranin 0 and Delafields Haematoxylin (Theobold *et al.* 1979). Safranin preferentially stains lignified tissues in the veins, while the Haematoxylin stained the cellulose. Various immersion times were experimented with and showed that the results varied with the taxon. On several occasions destaining of the Safranin was required or specimens became useless as the Haematoxylin overstained. Calcium carbonate was also added to the Haematoxylin to enhance the stain (Johansen 1940).

Specimens in 50% Industrial Methylated Spirit (IMS)
⇩
15:1 water:Safranin 0 stain in 70% IMS
⇩
Rinsed in 70% IMS
⇩
Delafields Haematoxylin with $CaC0_3$ added to enhance stain
⇩
Rinsed in 70% IMS
⇩
Dehydrated in alcohol series from 70%→90%→100% IMS
⇩
Leaves soaked in two changes of xylene
⇩
Mounted in DPX mountant

Figure 3.2 Staining and mounting procedure

DPX, a xylene based mountant, was used as a permanent mountant for the leaves. Prior to mounting, the leaves were taken through an alcohol series to 100% solution and then soaked in two changes of xylene to remove the alcohol. The leaves were then mounted in DPX on 1mm and 2mm glass slides, the larger slides for whole leaf mounts being cut by hand. Drying times varied widely for the slides as did success of slide making. Whole leaf mounts often required the coverslips to be weighed down as the leaf-veins forced the coverslip to move, introducing air bubbles to the specimen. In many cases air-bubbles could not be stopped from entering the slides. Slides were made with both abaxial and adaxial epidermal surfaces uppermost.

3.2.2.4 Recording methods

Slides were analysed on a transmitted-light microscope using normal and polarised light operating at between 20x and 1000x magnification. Black and white photographs were taken using a 35mm camera with a green filter to enhance the contrast. Illustrations were also made where useful. Description used standard, published criteria where

published and developed them where not, using *pro-forma* sheets. Standard criteria for morphological description of roots have not been previously published. Using the observations made during this research and general plant morphology texts, the criteria in Table 3.3 were isolated. Roots are particularly difficult structures to describe as they are very simple with few structural elements. They also vary in size and proportion throughout the root system, making criteria based on size useless. The criteria in Table 3.3 are robust and are based on features that are present or absent, rather than being based on sizes, and are, therefore, more suitable for morphological and anatomical description (Theobald *et al.* 1979).

Character	Source
Leaf Orientation	See Hickey 1979
Organisation	See Hickey 1979
Shape	See Hickey 1979
Texture	See Hickey 1979
Form of leaf Margin	See Hickey 1979
Texture	See Hickey 1979
Gland Position	See Hickey 1979
Petiole	See Hickey 1979
Venation	See Hickey 1979/Pole 1991
Tooth architecture	See Hickey 1979
Stomatal complex	Dilcher 1974; Van Cotthem 1970a, 1973
Stomatal features	Dilcher 1974; Van Cotthem 1970a, 1973
Description of Indumentum (hairs)	See Theobald *et al.* 1979
Description of individual trichome morphology	See Theobald *et al.* 1979
Description of trichome anatomy	See Theobald *et al.* 1979
Description of trichome complement	See Theobald *et al.* 1979
Epidermis description	See Dilcher 1974
Presence of crystals in mesophyll or veins	

Table 3.4 Descriptive characters for leaves and epidermis

The standard criteria for leaf and epidermal features are summarised in Table 3.4. The terminology for leaf shape, texture, margin form, tooth architecture and petiole follows Hickey (1979). Characters I to VI follow the modified leaf architecture criteria of Pole (1991). Initially descriptions of leaf architecture were made using the characters summarised in Hickey (1979). This terminology was found to be difficult to apply, very subjective and of dubious value for comparative purposes. The major problem was defining vein orders, the basis of the whole system. The alternative modified system developed by Pole was found to be easier to apply and also of more use for potentially fragmented remains as it provides descriptions of segments of the leaf lamina found in macrofossil assemblages. Terminology for areolation and veinlet shape was derived from Hickey, while an additional feature was added to describe the crystals often found

A. Root type		a) Branched b) Radial unbranched
B. General appearance		Verbal description
C. Epidermal layers	1. Number	a) One b) State number c) Uncertain
	2. Variability	a) a) Upper epidermal cells vary in shape b) b) Lower epidermal cells vary in shape c) Upper epidermal cells vary in size d) Lower epidermal cells vary in size e) Upper layer cells larger than lower layer f) Lower layer cells larger than upper layer g) Cells similar
D. Epidermal cells	1. Arrangement	a) Linear with regular cells b) Linear with variable cells c) Random
	2. Cell shape	a) Rectangular b) Square c) Isodyametric d) Other (describe)
	3. Anticlinal cell wall shape	a) Straight b) Rounded c) Undulate
	4. End wall shape	a) Squared b) Rounded c) Oblique d) Irregular
	5. Cell appearance	a) Swollen b) Not swollen
E. Root hairs	1. Root type	a) Cylindrical b) Flattened
	2. Root hair density	a) Absent b) Occasional (less than 1:30 ratio with epidermal cells) c) Sparse (between 1:30 and 1:15 ratio with epidermal cells) d) Dense (greater than 1:15 ratio with epidermal cells)
	3. Cell shape	a) As other epidermal cells b) Cell differing in shape to background epidermis
	4. Base	a) Swollen b) Not swollen
	5. Length	a) Long (greater than twice rootlet width) b) Short (less than twice rootlet width)
	6. Distribution	a) Irregular covering b) Regular covering c) In zones or files
F. Other features	1. Outgrowths on epidermis	a) Absent b) Occasional (less than 1:30 ratio with epidermal cells) c) Sparse (between 1:30 and 1:15 ratio with epidermal cells) d) Dense (greater than 1:15 ratio with epidermal cells)
	2. Other (specify)	Specify

Table 3.3 Descriptive characters for non-woody roots

in leaf bundle sheaths. Epidermal cell descriptions follow Dilcher (1974). Trichome description follows Theobald *et al.* (1979) and the nomenclature for stomatal description uses a combination of schemes (Dilcher 1974; Van Cotthem 1970a, 1973). Full descriptions were recorded for the leaves of the Dicotyledonae, Filicophyta and broad-leaved Monocotyledonae, while only the epidermis sections were recorded for narrow-leafed Monocotyledonae and the Sphenophyta.

3.2.3 Identification criteria

3.2.3.1 Rootlets

Details of the morphology of the roots of the 46 taxa included in the study are shown in Appendix 1. Only a limited amount of morphological and anatomical variation was recorded for the roots included in the study, perhaps unsurprising considering how anatomically and morphologically conservative roots are. Up to three layers of cells were recorded in surface view, although in some specimens only the uppermost layer was discernible and the number of epidermal layers could not be ascertained. The epidermal cell layers often varied in size and/or shape, commonly with an upper layer of small, highly regular rectangular cells covering a more variable lower layer of larger cells.

Eight root types have been distinguished (Table 3.5), each with variable taxonomic resolution. These types are provisional because only relatively few taxa were included in the study. Some criteria proved difficult to determine, such as the number and variation in epidermal layers in surface view. It was also observed that root morphology often varied considerably on individual root sections, especially the size of the epidermal cells and the density of hairs. Size criteria were unreliable and only those based on the presence or density of specific features were considered to be useful. It should be noted, however, that the most important diagnostic features were usually discernible on most root sections.

The Equisteaceae formed a distinctive group, as did the Filicophyta, although the latter were distinguished as much by overall appearance as epidermal anatomy that was inconsistent. Flattened root hairs were noted in both of the lower vascular plant groups and may be an important character. Within the few taxa analysed *Thelypteris palustris* roots had distinctive undulate cell margins. It is uncertain if the epidermis of the many Filicophyta would survive preservation processes. It proved to be fragile and susceptible to destruction during clearing, the clearing chemicals weakening and eventually rupturing the epidermis and cortex leaving only the thick stele.

Root Type	Taxa	Distinguishing features
1) Equisetaceae	*Equisetum*	Fibrous radial roots; regular longitudinal rows of rectangular cells with rows of regularly spaced square cells carrying flattened root hairs.
2) Filicales	Filicales	Wiry, branched, brown roots with wide steles; epidermis cells in longitudinal rows of irregular, elongated cells carrying flattened root hairs.
3) Juncaceae	*Juncus* spp. and *Luzula* spp.	Fleshy radial roots; regular rows of rectangular epidermal cells with dense concentration of hairs on square cells that have swollen hair bases. In some sections the hair cells and epidermal cells alternate.
4) Cyperaceae	Cyperaceae	Fleshy radial roots; regular rows of rectangular cells with or without hairs on rectangular cells with or without swollen bases; main feature is the presence of cubic projections on the epidermal surface.
5) Type 1a	Many Dicotyledonae	Fleshy or fine branched roots; epidermis of regular, rectangular cells with sparse to dense hairs without swollen base on normal cells.
6) *Lycopus* spp. Type	*Lycopus europaeus*	Fine branched roots; epidermis of regular rows of alternating square and rectangular cells with rounded walls; no hairs noted.
7) Type 1b	Poaceae, *Iris* spp., *Alisma* spp., *Cirsium* spp., *Urtica* spp. etc.	Fleshy or fine radial roots; epidermis of regular, rectangular cells without hairs or any projections.
8) Type 2	*Sparganium* spp., *Typha* spp.	Fleshy radial roots; rounded square (+/– swollen) epidermal cells in regular rows without root hairs or projections.

Table 3.5. Provisional root types

The two most distinctive root types were those of Juncaceae and Cyperaceae taxa. Sections of Juncaceae root were packed with dense hairs with a characteristic swollen base. Hair density varied in different sections of the same root, although the observed specimens were always dense (under the definitions above). Young hairs were often noted as short projections similar to papillae, especially around the root cap. The Cyperaceae type was characterised by the presence of cubic projections on the epidermis surface. These are seemingly unique to the Cyperaceae and were present in all of the analysed taxa on all sections of the roots. Hairs were also present in many Cyperaceae, usually with a characteristically swollen base. The presence of hairs did, however, vary considerably within and between taxa, and some sections, especially near the root tip, lacked them.

The *Lycopus* type roots had a distinctive arrangement of epidermal cells in which rounded rectangular and square cells alternated in regular longitudinal files. This was the only type that was distinctive at the species level. During the analysis of modern surface sediment samples *Atriplex* roots were distinguished. This was purely on the

basis of colour, the *Atriplex* roots having strongly coloured yellow cells, a trait unlikely to be preserved in fossil material and one which did not survive the clearing process. The occurrence of such a specific root type suggests that others may exist in the many taxa that were not included in the survey, especially among the Dicotyledonae.

The final root types were not confined to any particular taxon. Type 1 roots consisted of featureless roots with a regular arrangement of rectangular epidermal cells. Hairs, if present, were on normal epidermal cells and lacked swollen bases. A distinction has been made between hairy and non-hairy types, the non-hairy category including the important Poaceae group and many Monocotyledonae. Type 2 roots had clearly different epidermal cells of rounded to square shape arranged in regular longitudinal rows. This type was only seen in *Sparganium* sp. and *Typha* sp., the latter having clearly swollen epidermal cells that projected from the root surface.

The work presented here has formalised root descriptions, providing a basis for more systematic comparison between taxa and has clarified the usefulness of some earlier work (e.g. Katz *et al.* 1974). It has also confirmed that root-types with broad taxonomic, ecological and structural implications can be distinguished on the basis of easily viewed features preserved in macrofossil material (see Chapter 5). While some variation is seen within the groups, specific criteria for identifying many families, genera and species are not yet available, and in many cases are unlikely to be so. The *Lycopus* spp. type shows that identifications may be possible in some genera or even higher, and further investigation of more Dicotyledonae taxa may prove useful.

3.2.3.2 Sphenophyta leaf sheaths and epidermis

The main distinctive identification features for the genus are the presence of silica bodies and deposits over the epidermis, distinctive stomata, cell and stomatal arrangement and number of ridges and teeth on stems, branches and leaf-sheaths. Ridge numbers and teeth shape have been described in several volumes (Jermy and Camus 1991; Hutchinson and Thomas 1997). Features of the epidermal anatomy were found to be consistent on samples of epidermis from the main stem, branches and leaf-sheaths. The epidermal cells were arranged in regular longitudinal files and were rectangular with finely undulate margins. Stomata are arranged in multiple longitudinal files in the troughs between ridges, the number of which depends on the width of the trough. The stomata are unique, the guard cells being covered by two subsidiary cells separated by an aperture. Striations are visible on the stomatal apparatus in surface view, although

these are in fact on the base of the subsidiary cells (Kaufmann *et al.* 1971). The leaf-sheaths have distinctive areas of irregular cells at the base of each serration.

Equisetum is divided into two sub-genera, each having distinctive stomatal characters and type of silicification. Sub-genus *Hippochaete* includes *E. hyemale*, *E. ramosissimum* and *E. variegatum* (Plates 22 and 23) in the British flora and is characterised by:

- Stomata sunk in crypts, normal epidermal cells form the surface aperture over subsidiary and guard cells.
- Silica is distributed over the surface of the epidermis in 'candle-wax' like deposits. There is a lack of discrete silica knobs, teeth or rosettes.
- Stomatal strips arranged in ladder-like formation.
- Apertures formed by the epidermal cells that are transversely orientated.

E. variegatum has only a single line of stomata in each trough and thick wax-like deposits of silica on the surface which often obscures the with epidermal cells (possibly also *E. hyemale* shows these characteristics). *E. variegatum* and *E. hyemale* have a distinctive ladder like appearance with a dumbbell-shaped aperture at the tip of the swelling over the stomatal crypt. The whole aperture is in fact not dumbbell-shaped, only the section at the top of the swelling over the pit is. *E. ramosissimum* has fewer surface deposits of silica, fewer dumbbell-like apertures and stomata arranged in files of up to 4 wide (Chatterjee 1964; Pant and Kidvai 1968).

Sub-genus *Equisetum* includes *E. fluviatile*, *E. arvense* (Plates 20 and 21), *E. sylvaticum*, *E. pratense*, *E. palustre*, *E. telmateia*. The epidermis is characterised by the following:

- Stomatal subsidiary cells at the surface, lacking overlying epidermal cells. Stomata are hidden and only pits are visible.
- Stomatal subsidiary cells (over guard cells) are covered with discrete silica knobs. These are large at the edges of subsidiary cells and form rosettes of several knobs on normal epidermal surfaces. There is no overall covering as in *Hippochaete.*
- Stomata are arranged in multiseriate longitudinal files.

- Apertures at the surface are longitudinally aligned, often with a line of silica teeth.

E. arvense has siliceous teeth on the stomatal aperture edges and knobs over the surface (Kaufmann *et al.* 1971). *E. fluviatile* was found to have similar aperture teeth but far fewer siliceous knobs occur on the stomatal and epidermal surface.

As *E. palustre*, *E. fluviatile* and *E.* hyemale are common wetland plants there is good reason to believe that fossils of Equisetaceae will be found in alluvium. The epidermal patterns in the Equisetaceae are so distinctive that even small fragments are identifiable to genus and sub-genus level. Species-level identification probably requires large stem fragments, preferably with leaf-sheaths, but is possible if suitable smaller fragments are preserved.

3.2.3.3 Filicophyta leaves and epidermis

The main identification features for the group are the pinnule or pinnae segment morphology, venation pattern, sporangium and indusium form and arrangement, stomatal complex and types of glands and trichomes. Detailed descriptions of Filicophyta leaf morphology have been published by Jermy and Camus (1991), Hutchinson and Thomas (1997) and Bower (1923, 1926 and 1928). In all cases these texts deal only with the gross morphology (leaf shape, form and arrangement of sporangia and indusia). Epidermal anatomy has been covered sporadically for few taxa (e.g. Van Cottem 1970b, 1973).

The identification features are listed in Table 3.6. A specimen of the fertile blade of *Ophioglossum vulgatum* from the order Ophioglossales was prepared (Plate 24 – 25). It differed from the Filicales (see below) by not having a dichotomous branching venation system and by having simple, lanceolate-ovate blades. The venation varied along the axis, being parallel at the base and splitting into three orders or branched, interconnected veinlets on the blade itself. Cells in the basal area were elongated sub-rectangular with straight walls, irregular end walls and anomyocytic stomata. Similar stomata were recorded on the blade within a matrix of irregularly shaped, isodyametric cells with undulate margins. The marginal cells of the blade were similar to those at the base and no trichomes were found on the specimen.

The Filicales specimens all had branching dichotomous venation on a dissected frond (Plates 26 – 46). The shape of the pinnae/pinnules was of vital importance,

Species	Blade/pinnule/ pinna shape	Base	Pinnule margins	Main epidermal cell shape	Venation	Stomatal types	Indusia	Trichomes. (see Figure 3.7)
Ophioglossum vulgatum	Blade: broad ovate-lanceolate	Cuneate	Entire	Linear sub-rectangular to undulate iso.	Closed freely branching	Anomyocytic	NA	Absent
Osmunda regalis	Oblong-lanceolate	Sessile lobed	Entire sinuous	Undulate iso.	Open dichotomous	Anomyocytic	Absent	Absent
Hymenophyllum tunbrigense	Elliptic-oblong	Symmetrical	Serrate	5-6 sided with thickenings	Dichotomous	None observed	Pocket	Absent
Polypodium interjectum	Linear	Symmetrical	Weakly serrate	Undulate iso.	Open dichotomous	Polocytic + staurocytic	Absent	Ab lamina 1 Sori 2
Polypodium cambricum	Linear	Symmetrical	Sharply serrate	Undulate iso.	Open dichotomous	Polocytic + staurocytic	Absent	Absent
Pteridium aquilinum	Lanceolate	Symmetrical	Entire sinuous	Undulate iso.	Open dichotomous	Polocytic + occ. Anomyocytic	Marginal	Veins 3
Thelypteris palustris	Oblong-ovate	Symmetrical	Inrolled sinuous	Undulate iso.	Open dichotomous	Polocytic + occ. Anomyocytic	Irregular dentate	Veins 2 Ab lamina 4
Oreopteris limbosperma	Oblong-ovate	Symmetrical	Entire sinuous	Undulate iso.	Open dichotomous	Polocytic + occ. Anomyocytic	Reniform	Ab ad lamina 2 Ab lamina 5
Phyllitis scolopendrium	Lanceolate	Cordate	Entire sinuous	Undulate iso.	Open dichotomous	Polocytic + occ. Anomyocytic	Linear	Ab lamina 3a 6
Asplenium ruta-muraria	Suborbicular/oval	Cuneate	Minutely serrate	Undulate iso.	Open dichotomous	Polocytic + occ. Anomyocytic	Linear	Absent
Asplenium trichomanes	Oblong	Decurrent	Weakly serrate	Undulate iso.	Open dichotomous	Polocytic	Linear	Absent
Asplenium ceterach	Ovate/oblong	Decurrent	Entire sinuous	Undulate iso.	Closed dichotomous	Polocytic + occ. Anomyocytic	Absent	Absent
Asplenium marinum	Oblong/ovate	Asymmetrical +- lobed	Weakly serrate	Undulate iso.	Open dichotomous	Polocytic + occ. Anomyocytic	Linear	Absent
Athyrium felix-femina	Oblong/ oblong-lanceolate	Sessile	Serrate/ pinnately lobed	Undulate iso.	Open dichotomous	Polocytic + occ. Anomyocytic	Linear	Absent
Polystichum setiferum	Ovate	Sessile lobed	Deeply serrate	Undulate iso.	Open dichotomous	Stuarocytic + anomyocytic + occ. Polocytic	Peltate	Veins and ab lamina 3& 6
Dryopteris felix-mas	Oblong	Decurrent	Weakly serrate	Undulate iso.	Open dichotomous	Polocytic + occ. Stuarocytic	Reniform	Absent
Dryopteris dilitata	Oblong-ovate/ oblong lanceolate	Decurrent/ sessile	Serrate	Undulate iso.	Open dichotomous	Polocytic + occ. Stuarocytic	Reniform; +- glandular	Veins 3, 8 Ab lamina 7
Blechnum spicant	Linear-oblong	Sessile	Entire sinuous	Undulate iso.	Open dichotomous	Polocytic + anomyocytic	Linear	Absent

Table 3.6 Summary of leaf and epidermal identification features in the Filicophyta
Abbreviations: +- = may or many not have feature; iso. = isodyametric; occ. = occasional; ab. = abaxial surface; ad = adaxial; NA = not found or applicable. For terminology see references in text)

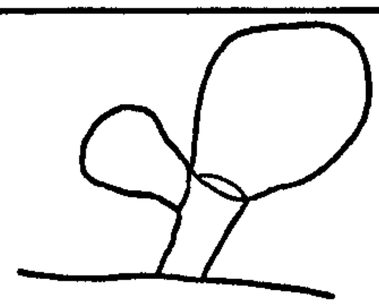
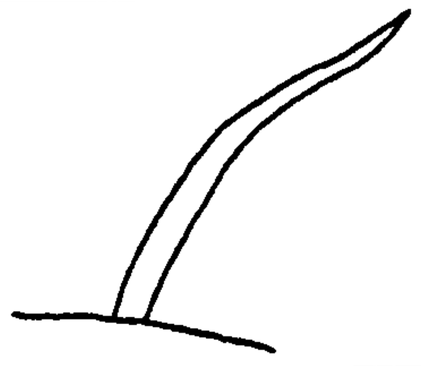
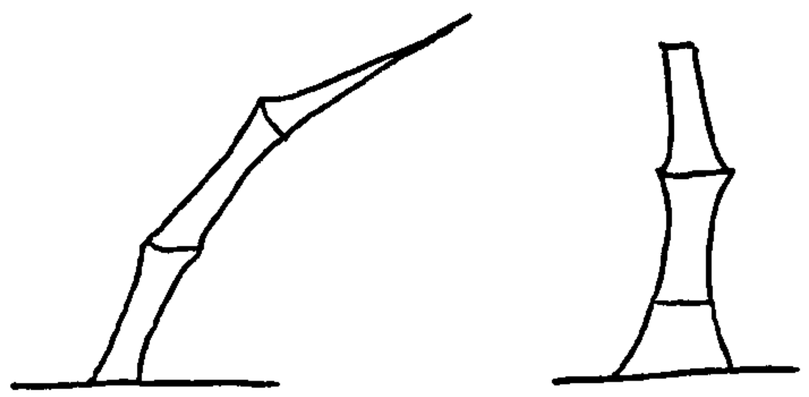
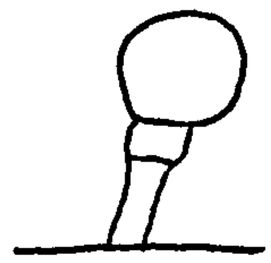
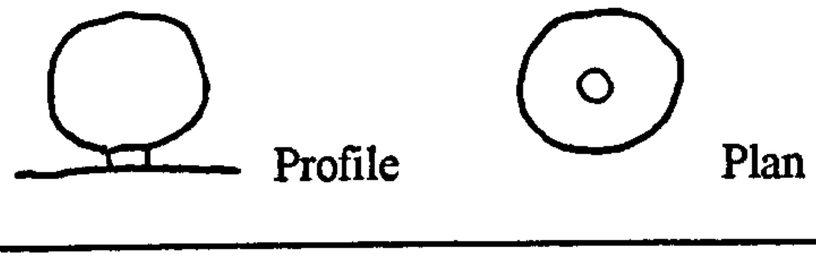
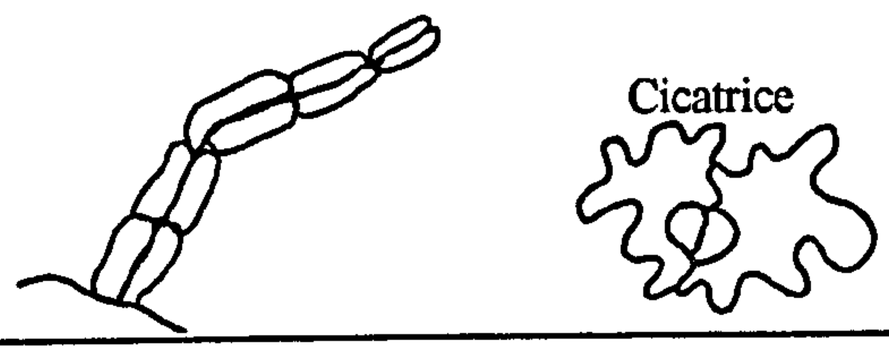
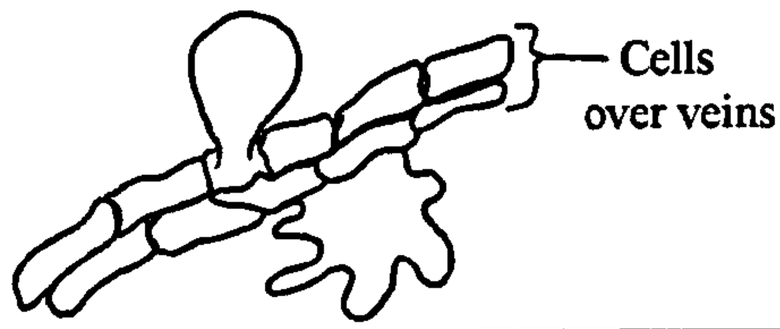
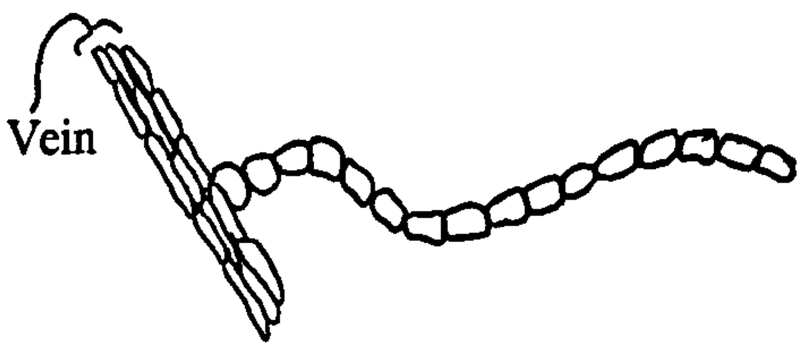
Type 1	Glandular uniseriate, multicellular branched (e.g. *Polypodium interjectum*)	
Type 2	Non-glandular unicellular, uniseriate hair with attenuated apex. (e.g. *Polypodium interjectum*)	
Type 3 **3b**	Non-glandular uniseriate, multicellular hair with attenuated apex. (e.g. *Pteridium aquilinum*) As above with swollen base	
Type 4	Stalked gland; multicellular, uniseriate base with spherical gland (e.g. *Thelypteris palustris*)	
Type 5	Unicellular spherical gland (e.g. *Oreopteris limbosperma*)	
Type 6	Non-glandular biseriate, multicellular hair (e.g. *Phyllitis scolopendrium*)	
Type 7	Unicellular uniseriate gland (e.g. *Dryopteris dilitata*)	
Type 8	Uniseriate, multicellular, non-glandular hair with short cells and no attenuated apex (e.g. *Dryopteris dilitata*)	

Table 3.7 Filicophyta trichome types

especially the level of dissection of the leaf margin and the presence of marginal serrations. Indusia and sori were also of some importance, especially their shape, although it is unlikely that these structures would remain attached to the pinnae/pinnules (e.g. *Dryopteris* species which tend to shed indusia on spore ripening). Epidermal anatomy was similar in many of the species, the cells being irregular in shape with deeply undulate margins. Cells over the veins and along the margins tended to be sub-rectangular, had limited development of undulations and were aligned to the vein/margin. Most taxa had polocytic stomata, although staurocyctic and anomyocytic types were not uncommon and were the dominant types in the case of *Polystichum setiferum*. Stomata were usually grouped on the abaxial lamina between the veins and were aligned to the main veins of the lamina segment. Trichomes were present in some species (see Tables 3.6 and 3.7).

Rachis epidermal peels were collected from *Dryopteris dilitata, Thelypteris palustris, Osmunda regalis* and *Pteridium aquilinum.* All were similar with the epidermis having elongated sub-rectangular cells with oblique/irregular end walls and occasional anomyocytic stomata. The cells had no clear undulations, but had irregular cell walls at x400 magnification, appearing to have a discontinuous outline at low magnification.

Potential Filicophyta leaf macrofossils are distinctive, especially in the Filicales. Class identification is likely, even if only tiny fragments of lamina or epidermis were preserved. Family, genus and/or species-level identification is possible if fragments have margins in-tact and retain stomata and trichomes, although it should be noted that the range of taxa described here was far less than complete and species-level identifications made on the basis of trichome complement would be tentative. *Osmunda* spp. and taxa with robust unique features, such as the marginal indusium of *Pteridium aquilinum*, would be identifiable even if highly fragmented. Fragments of rachis are unlikely to be distinguished on the basis of epidermal anatomy, although isolated scales and indusia have distinctive morphology and anatomy.

3.2.3.4 Dicotyledonae leaves

Appendix 2 holds the records of leaf architecture and epidermal anatomy for the species included in this survey (see also Plates 47 – 193), the main details of which are summarised in Table 3.8. The records matched well with the patterns and trends recorded in Hickey and Wolfe and also the fragmentary accounts found in Metcalfe and

Chalk, although the stomatal and venation patterns varied below family level. The species' accounts provided here are a significant addition to those available for the extant British flora and include the main tree species, many shrubs and representatives of most families and many genera contributing to lowland vegetation. Some taxa were not fully described but scanned briefly to compare characteristics with those of the family or other species in the genus. In all cases the comparisons showed very similar if not identical patterns of characters. These taxa included *Symphytum officinale, Galium odoratum, Lamium purpureum, Stachys nigra* and *Primula vulgaris.*

It is clear from the results that Dictoyledonae leaves are identifiable to a high level of taxonomic resolution, perhaps even at the species level if all of the main groups of identification criteria are preserved in ancient specimens. It should be noted that the species included here are only a selection from the British flora and identifications at the higher ranks (genus, species) based only on the information contained here could not be absolutely certain.

Beyond the overall morphology, other important discriminatory criteria included the primary venation pattern (*sensu* Pole 1991), lower order venation, presence and development of vein looping, marginal tooth type, stomatal complex and trichome complement (types summarised in Table 3.9). Individual characters were also important, such as:

- the presence of large spines (e.g. *Cirsium* spp.);
- crystals in the vein bundle sheaths (many of the Fagaceae);
- crystals in the mesophyll (e.g. *Galium palustre*);
- hydathodes (e.g. *Caltha* spp.);
- spherical glands on several halophytes (e.g. *Atriplex portulacoides*);
- cystoliths in *Urtica dioica;*
- stomatal crypts and aperture shapes (e.g. *Spergularia* sp. and the other analysed Caryophyllaceae).

Some characters were found in many taxa (e.g. stomatal types), but combinations of different traits were in many cases highly diagnostic. Clearing was needed to see many features, some, such as areolation development and tooth type being difficult to ascertain. Venation could also be irregular and several examples of mixtures of the

Table 3.8a Summary of the main features of the leaf architecture and epidermis in selected angiosperm taxa Magnoliflorae and Caryopllifloraе

Sub-class	Order	Family	Species	Primary Venation	Higher order Venation	Non-primary looping?	Tooth type	Stomata	Trichomes
Magnoliflorae	Ranuncullales	Ranunculaceae	*Caltha palustris*	Craspedodromous	Random	Absent	Chloranthoid	Anomyocytic	Absent
			Anemone nemorosa	Craspedodromous	Random	Absent	Chloranthoid	Anomyocytic	1,2
			Clematis vitalba	Brochidodromous	Random	Some secondary	None	Anomyocitic	3
			Ranunculus acris	?	?	?	?	Anomyocytic	3
			Ranunculus repens	?	?	?	?	Anomyocytic	3
			Ranunculus sceleratus	Craspedodromous	Random	Absent	Chloranthoid	Anomyocytic	1
			Ranunculus flammula	Craspedodromous	Random	Absent	Chloranthoid	Anomyocytic	Absent
			Ranunculus ficaria	Craspedodromous	Random	Absent	Chloranthoid	Anomyocytic	2
			sub-genus *Batrachium*	?	?	Absent	Absent	Absent	4 at leaf apex
	Papaverales	Papaveraceae	*Glaucium flavum*	Craspedodromous	Random	Absent	Absent	Anomyocytic	5&6
	Urticales	Ulmaceae	*Ulmus glabra*	Craspedodromous	Regular percurrent	Absent	Urticoid	Anomyocytic	Dense 1,2,3,6
		Cannabaceae	*Humulus lupulus*	Craspedodromous	Regular percurrent	Absent	Urticoid	Anomyocytic	1, 7,8,9
		Urticaceae	*Urtica dioica*	Craspedodromous	Regular percurrent	Absent	Urticoid	Anomyocytic	1, 2, 3, 3a
	Myricales	Myricaceae	*Myrica gale*	Craspedodromous mixed	Regular cascade	Narrow marginal	Urticoid	Anomyocytic	Dense 3,10, 11, 12
	Fagales	Fagaceae	*Fagus sylvatica*	Eucamptodromous	Regular percurrent	Narrow marginal	Absent	Anomyocytic	1, 13
			Quercus robur	Craspedodromous + fimbrial	Regular percurrent	Marginal	Absent	Anomyocytic	1, 2, 14, 15
			Quercus petraea	Craspedodromous + fimbrial	Regular percurrent	Narrow marginal	Absent	Anomyocytic	Dense 1, 14,15, 16
		Betulaceae	*Alnus glutinosa*	Craspedodromous	Regular percurrent	Poor laminar	Urticoid	Anomyocytic	Dense 3, 7, 12,
			Betula pendula	Craspedodromous	Regular percurrent	Poor laminar	Urticoid	Anomyocytic	Dense 1, 3, 7
			Carpinus betulus	Craspedodromous	Regular percurrent	Poor laminar	Urticoid	Anomyocytic	Dense 1, 7, 17
			Corylus avellana	Craspedodromous	Regular percurrent	Poor laminar	Urticoid	Anomyocytic	Dense 2, 3
Caryophyllifloraе	Caryophyllales	Chenopodiaceae	*Atriplex prostrata*	Craspedodromous	Ramifying looped	Some secondary	Theoid	Paracytic	6
			Atriplex portulacoides	Brochiododromous	Regular Cascade	Narrow marginal	Absent	Paracytic	6
			Suaeda maritima	Brochiododromous	Indistinct	Well developed	Absent	Paracytic	Absent
			Salicornia europaea agg.	NA	?	?	?	Paracytic	Absent
			Sarcocronia perrenis	NA	?	?	?	Paracytic	Absent
		Caryophyllaceae	*Cerastium fontana*	Brochiododromous	Cascade	Some secondary	Absent	Diacytic-stau-para	dense 18
			Spergularia media	Brochiododromous	Indistinct	Absent	Absent	Diacytic	Absent
			Stellaria media	Brochiododromous	Cascade	Absent	Absent	Diacytic-stau-para	1
	Polygonales	Polygonaceae	*Persicaria hydropiper*	Eucamptodromous	Cascade	Narrow marginal	Absent	Paracytic-ano	Marginal 19
			Persicaria maculosa	Eucamptodromous	Cascade	Basal loops	Absent	Aniso-ano-para	Laminar 19
			Rumex acetosella	Eucamptodromous	Casacde	Developed loop zone	Absent	Paracytic-ano	Dense 17
			Rumex hydrolapathum	Eucamptodromous	Cascade	Broad marginal zone	Absent	Anomyocytic-para	Absent
	Plumbaginales	Plumbaganiaceae	*Limonium* sp.	Eucamptodromous	Cascade	Broad marginal zone	Absent	Anisocytic	small 6

Table 3.8b Summary of the main features of the leaf architecture and epidermis in selected angiosperm taxa - Dilleniflorae and Rosiflorae

Sub-class	Order	Family	Species	Primary Venation	Secondary Venation	Non-primary looping?	Tooth type	Stomata	Trichomes
Dilleniflorae	Malvales	Tiliaceae	*Tilia cordata*	Craspedodromous	Strongly percurrent	Basal, poorly developed	Malvoid	Anomyocytic	Absent
		Malvaceae	*Althaea officinalis*	Craspedodromous	Regular casacade	Basal, poorly developed	Malvoid	Anomyocytic	20 dense
	Violales	Violaceae	*Viola* sp.	Externodromous	Regular percurrent	Basal, poorly developed	Violoid	Anomyocytic-para	Absent
	Salicales	Salicaceae	*Salix cinerea*	Externodromous	Regular percurrent	Marginal weak	Salicoid	Paracytic	2, 3
			Populus nigra	Externodromous	Regular percurrent	Narrow marginal	Salicoid	Paracytic	3
			Populus tremula	Externodromous	Regular percurrent	Narrow marginal	Salicoid	Paracytic	Sparse 3 (long type)
	Capparales	Brassicaceae	*Cardamine* sp.	Externodromous	Casacde	Marginal	Absent	Anisocytic	4 marginal
			Cochlearia anglica	Eucamptodromous	Reticulate	Weak marginal	Absent	Anisocytic	Absent
			Rorippa islandica	Craspedodromous	Cascade	Absent	Salicoid	Anisocytic	Absent
	Primulales	Primulaceae	*Lysimachia vulgaris*	Eucamptodromous	Cascade	Absent	Absent	Anomyocytic	Dense 13, 21
Rosiflorae	Rosales	Rosaceae	*Crataegus monogyna*	Craspedodromous mixed	Mixed percurrent	Well developed marginal	Rosoid	Anomyocytic	1
			Filipendula vulgaris	Craspedodromous	Strongly percurrent	Absent	Rosoid	Anomyocytic	Dense 1,;4 - marginal
			Geum rivale	Craspedodromous	Strongly cascade	Basal +-poorly developed	Rosoid	Anomyocytic	Dense 22
			Prunus spinosa	Externodromous	Strongly percurrent	Well developed	Rosoid	Anomyocytic	4 margin; 1, 23
			Rubus fruticosus agg.	Craspedodromous	Percurrent	Absent	Rosoid	Anomyocytic	3, 17
			Rosa sp.	Craspedodromous mixed	Percurrent-casacde	Well developed marginal	Rosoid	Anomyocytic	3, 17
			Sorbus acuparia	Craspedodromous mixed	Percurrent-cascade	Poor basal and marginal	Rosoid	Anomyocytic	3
	Fabales	Fabaceae	*Lathyrus palustris*	Externodromous	Cascade	Well developed laminar	Absent	Anomyocytic	Absent
			Lotus uliginosus	Externodromous	Cascade	Well developed laminar	Absent	Anomyocytic	Absent
	Myrtales	Lythraceae	*Lythrum salicaria*	Brochiodromous	Percurrent	Occasional	Absent	Anisoyctic	Dense 1; 4
		Onagraceae	*Epilobium hirsutum*	Externodromous	Cascade-percurrent	Narrow marginal	Cunonioid	Anomyocytic	Dense long 1
	Cornales	Cornaceae	*Cornus sanguinea*	Eucamptodromous	Percurrent	Developed at base	Absent	Anomyocytic	1; 24
	Rhamnales	Rhamnaceae	*Rhamnus cathartica*	Eucamptodromous	Percurrent	Well developed laminar	Cunonioid	Anomyocytic	Absent
	Sapindales	Aceraceae	*Acer campestre*	Craspedodromous mixed	Cascade	Basal and narrow margin	Absent	Anomyocytic	17, 25
	Apiales	Araliaceae	*Hedera helix*	Eucamptodromous	Cascade	Well developed	Cunonioid	Paracytic	Absent
		Apiaceae	*Apium graveolens*	Craspedodromous mixed	Cascade	Poorly developed	Cunonioid	Anomyocytic	Absent
			Apium nodiflorum	Craspedodromous	Casacde	Marginal	Cunonioid	Anomyocytic	Absent
			Hydrocotyle vulgaris	Craspedodromous	Cascade	Basal	Cunonioid	Paracytic	Absent
			Peucedanum palustre	Eucamptodromous	Indistinct	Marginal?	?	Anomyocytic	Absent

Table 3.8c Summary of the main features of the leaf architecture and epidermis in selected angiosperm taxa - Asteriflorae

Sub-class	Order	Family	Species	Primary Venation	Secondary Venation	Non-primary Looping?	Tooth type	Stomata	Trichomes
Asteriflorae	Solanales	Convolvulaceae	*Calystegia sepium*	Exterodromous	Percurrent/Casacde	Well developed marginal	Absent	Paracytic	25?27?
		Menyanthaceae	*Menyanthes trifoliata*	Exterodromous	Percurrent/Casacde	Well developed	Cunonioid	Anomyocytic	Absent
	Lamiales	Boraginaceae	*Myosotis scorpioides*	Brochiodromous	Cascade	Well developed	Absent	Anomyocytic	26 dense
			Veronica beccabunga	Exterodromous	Cascade	Well developed	Cunonioid	Anomyocytic	3?
		Lamiaceae	*Lamium album*	Exterodromous	Cascade	Well developed	Cunoniod	Diacytic	Dense 27; 2
			Lycopus europaeus	Craspedodromous mixed	Percurrent	Well developed	Cunonioid	Diacytic	1, 4, variable 6
			Stachys palustris	Exterodromous	Cascade	Well developed margina	Cunonioid	Diacytic	Dense 27; 2
	Plantaginales	Plantaginaceae	*Plantago maritima*	Exterodromous	Cascade-percurrent	Well developed marginal	Absent	Diacytic	Absent
			Plantago coronpus	Brochiodromous	Cascade	Well developed marginal	Cunonioid	Diacyitc	28 marginal
	Scrophulariales	Oleaceae	*Fraxinus excelsior*	Eucamptodromous mixed	Cascade	Well developed	Cunonioid	Anomyocytic	3?
		Scrophulariaceae	*Scrophularia nodosa*	Eucamptodromous mixed	Percurrent-cascade	Well developed marginal	Cunonioid	Anomyocytic	Dense 29
	Rubiales	Rubiaceae	*Galium palustre*	Eucamptodromous mixed	Cascade	Well developed	Absent	Paracytic	4 Marginal
	Dipsacales	Caprifoliaceae	*Galium odoratum*	Eucamptodromous mixed	Cascade	Well developed	Absent	Paracytic	?
			Lonicera periclymenum	Eucamptodromous	Percurrent-cascade	Well developed	Absent	Anomyocytic	3 & 3a
			Sambucus nigra	Eucamptodromous	Strongly percurrent	Well deveoped regular	Cunonioid	Anomyocytic	4
			Viburnum opulus	Eucamptodromous mixed	Percurrent-casacde	Well developed	Cunonioid	Anomyocytic	Dense 3
	Asterales	Asteraceae	*Artemisia maritima*	Brochiodormous	Absent	Whole venation system	Absent	Anomyocytic	Sparse 3
			Eupatorium cannabinum	Eucamptodromous	Cascade	Well developed marginal	Cunonioid	Paracytic + anomyo	Dense 27; sparse 11
			Cirsium palustre	Eucamptodromous	Percurrent	Uncertain	Absent	Aniso + paracytic	30

Table 3.9 Trichome types recorded in the Dicotyledonae

Type	Plate	Description
1	68 – 69	Simple, unicellular hairs with wide base and no special cicatrice. Variable length, often long.
2	49, 91	Short glandular unicellular trichomes with rounded apex.
3	48, 62, 66	Simple, unicellular non-glandular hairs with a cicatrice of radially aligned cells. Variable length.
3a	67	As 3 with hair set on a pedestal of epidermal cells
4	145	Simple uniseriate barb-hairs with a sharp cirved point +- radial cicatrice. Variable length.
5	57, 58	Large multicellular glandular hairs. Base 1-2 cells supporting uni-bi-seriate hair with rounded apex. Radial cicatrice.
6	61, 173	Stalked gland. Short stalk supporting spherical head of 1-4cells.
7	64, 86	Peltate glandular scales. Base 1+ cells glandular with flattened, multicellular disc-like head.
8	127	Stalked gland. Long unicellular base and wide bi-cellular head.
9	63	Non-glandular 2-armed branched trichome with wide central support on large pillar of epidermal cells.
10	68	Large unicellular spherical gland on short unicellular stalk.
11		Small spherical unicellular gland.
12	128	Multicellular uniseriate simple pointed hairs on radial cicatrice.
13		Multicellular uniseriate glandular hairs with swollen apex on radial cicatrice.
14	75	Stellate 2-5 armed trichomes with unicellular arms.
15	75	Multicellular, uniseriate hairs with swollen glandular basal cell.
16	76	Glandular hair with uniseriate multicellular base of 1-4 cells and bi-seriate multicellular head.
17	155	Stalked gland with long basall cells (1-2 cells) carrying a spherical multicellular gland.
18	99	Non-glandular uniseriate multicellular hair with wide radial cicatrice. Basal cell wider than rest and cylindrical with striations. Hair cells long swollen at junctions.
19	100	Simple, multicellular, multiseriate hairs. Cells long and arranged longitudinally on a bunched cicatrice.
20	115, 116	Stellate trichome of 5+ long cells.
21		Stalked gland. Base unicellular and long carrying a unicellular small spherical gland.
22	133	Bicellular, uniseriate simple hair on radial cicatrice. Apical cell has swollen base and septae noted + surface wrinkles.
23	103	Short multiseriate multicellular spherical glands.
24	149	Unicellular simple 2-armed hair supported on a narrow central support and cicatrice of bunched-radial cells. Arms pointed and opposite.
25		Unicellular simple hair with swollen wide-hexagonal base on a radial cicatrice and wrinkled surface
26	165	Unicellular simple hair with very wide base and radial cicatrice. septate with papillae over surface.
27	194, 195	Multicellular, uniseriate hairs with 2+ cells on a hexagonal baseal cell and cicatrice of radial cells.
28	176	As 27 but glandular.
29	180	Uniseriate multicellular hairs composed of alternating wide and narrow cells with an apical spherical gland. Base a radial cicatrice.
30	192	Large uniseriate multicellular glandular hairs with swollen basal cells, radial cicatrice and carrying an apical spherical gland.

types described by Pole were recorded. Venation was also distorted in deeply lobed and serrated leaves.

The Magnoliflorae consisted of two distinctive groups of taxa. All of the taxa analysed from the Ranunculales and Papaverales had irregular higher order venation patterns, whereas taxa in the Myricales and Fagales had regular higher order venation patterns. In other Sub-Classes a higher incidence of looped primary venation and regular higher order venation becomes more common and external systems of vein loops become more developed. The tooth types described by Hickey and Wolfe were consistent in most cases and were often easily distinguishable. The anomyocytic stomatal complex was the most widespread, occurring in many taxa distributed throughout the Sub-Classes. Other types were more restricted in distribution, especially the diacytic types found only in the Caryophylliflorae and Asteriflorae and anisocytic types found in the Caryophylliflorae, Dilleniflorae and Asteriflorae. The trichome types were often very specific, for example the peltate multicellular form (type 7) which was only recorded in *Humulus lupulus, Almus glutinosa* and *Betula pendula.* Areolation, marginal venation, variability in abaxial and adaxial epidermis and the type of veinlets present were useful, with trichome type, at the sub-family level.

While a combination of factors could be used in whole specimens to identify unknown leaves, the level of identification attainable in fossil material is dependent on the level of fragmentation. Most Dicotyledonae leaf material in waterlogged alluvium is highly fragmented. Fragments have a wide range of potential for identification and only some morphological and anatomical elements may be preserved. Fragments containing complete sections of the margin, the lamina with part of the venation and intact epidermis are potentially identifiable to genus or even species level. Fragments without intact margins have much lower identification potential because some characters are present in a wide variety of taxa. Epidermis or cuticle fragments similarly have limited identification potential, although family level identifications may be made and higher levels if trichomes and some marginal features are preserved. Another complication in identification is exemplified in taxa where variation in features, such as marginal teeth, is seen along the leaf axis (e.g. marginal teeth in *Sambucus* spp.). Trichomes provide vital information, but are easily detached, although peltate trichomes (Type 7) were preserved in the ancient specimens analysed in Chapter 5. Cicatrice configuration is preserved on the epidermis even when the trichome becomes detached. Unfortunately this feature itself varies relatively little, although some taxa have hairs with persistent

unique bases (e.g. trichome type 27) and the density of cicatrices would indicate the distribution of hairs over the leaf surface.

One limitation of the research was the number of leaves that could be analysed of each taxon. One to three specimens were usually prepared and provided in abaxial and adaxial view. Where multiple specimens were prepared (e.g. *Betula* spp.), the characteristics were found to be consistent. As mentioned above, the criteria also matched those, where present, in published texts. Although the work presented here is large and was time-consuming, the range of taxa and specimens was narrow. There remains the possibility that greater variability in leaf anatomy and morphology is present in many of the taxa than described herein. A recent investigation of *Quercus petraea* leaves showed differences in trichome complement and shape between leaves from different parts of a single plant (Kurschner 1997). Immature *Alnus glutinosa* leaves were also found to have a lack of trichomes and limited epidermal development in this study. Some of these differences would preclude identification and distinction of plant macrofossil leaves, although it is uncertain the extent to which it would affect taxonomic assignment.

3.2.3.5 Monocotyledonae leaves and epidermis

Epidermal characters are described and/or illustrated in Grosse-Braukmann (1976), Katz *et al.* (1977) and the Anatomy of the Monocotyledons series. The survey described here:

1. gathered information from published texts;
2. developed a standard range of descriptive criteria to facilitate systematic taxonomic comparison;
3. described many of the same taxa plus those which were missed or only partly covered that are of relevance to this project;
4. provided a series of photographs of the taxa.

The results are provided in full in Appendix 3 (see also Plates 194 – 215). Six broad groupings of taxa could be distinguished in the Monocotyledonae on the basis of leaf shape, stomatal complex and epidermal cell shape and configuration (Table 3.10). Groups 1 - 3 have distinctive lobed subsidiary cells with the stomata, in sharp contrast to the Cyperales group which have paracytic stomata in which the subsidiary cells are folded over the stomtatal apparatus (narrow type) or which closely follow the guard cell

edges. Group 6 includes the major Monocotyledonae families in the British flora and are all characterised by an epidermis composed of longitudinal files of cells with files of paracytic stomata.

Table 3.10 Monocotyledonae grouped on the basis of leaf architecture and epidermal anatomy

Group/Family	Leaf shape	Venation	Epidermal cells	Stomatal complex
1. *Butomus umbellatus*	Linear	Parallelodromous	Straight edged regular	Paracytic lobed
2. Alismataceae	Laminar	Parallelodromous	Straight edged irregular	Paracytic lobed
3. *Hydrocharis morsus-ranae*	Laminar	Parallelodromous	Undulate irregular	Paracytic lobed
4. *Triglochin* type	Linear	Hyphodromous	Undulate irregular	Anomyocytic
5. *Potamogeton* type	Laminar	Parallelodromous	Straight edged square in files	Absent
6. Cyperales type	Linear	Parallel	Undulate or straight walled cells in regular longitudinal files	Paracytic
6a. Juncaceae	Linear	Parallel	Straight-walled rectangular in files	Paracytic narrow
b. Cyperaceae	Linear	Parallel	Undulate-walled rectangular cells in longitudinal files	Paracytic narrow
c. Poaceae	Linear	Parallel	Undulate walled rectangular cells alternating with rounded square cells in longitudinal files.	Paracytic narrow
d. Sparganiaceae	Linear	Parallel	Straight walled rectangular to square cells in longitudinal files	Paracytic some hexacytic?
e. Typhaceae	Linear	Parallel	Straight-walled rectangular cells in longitudinal files	Paracytic narrow
f. Iridaceae	Linear	Parallel	Straight walled elongated hexagonal cells in longitudinal files	Paracytic in crypts

The families within group 6 are also relatively easily distinguished, although genus and species level identification is not possible using these characters alone and requires the preservation of hairs, spines and other features noted in the species descriptions. Within the Poaceae little variation was noted between the taxa included in the project, although *Phragmites australis* has distinctive prickle hairs at the leaf margin. Within the Cyperaceae *Cladium mariscus* has stomata sunken in crypts and also large spines along the leaf edge. *Schoenus nigricans* has small cells between the stomatal apparatus and subsidiary cells and, like several other taxa, has small prickles along the leaf margin. Silica bodies and papillae are seen widely in and on the epidermal cells of the Cyperaceae, the form and number possibly having taxonomic significance. No trends were noted in the observations to support these findings and in the analysis of macrofossils in Chapter 5 neither was apparent on Cyperaceae epidermis, suggesting that these features may not be preserved.

Large fragments of leaf or epidermis may be distinguishable at the family, or in some cases genus level. Small fragments of the epidermis from groups 1-4 may be confused with some Dicotyledonae taxa. It seems unlikely that the Group 5 or 6

epidermis types would be similarly confused as they have a regular structure often with unique narrow-type paracytic stomata. In most cases the family types in group 6 would be distinguishable even in small fragments. One point of confusion may be caused if stem epidermis or epidermis from underground organs was encountered. Grosse-Braukmann and Katz et al. have described some of these tissues, and similar epidermal structure was noted to that on the leaves, with the exception that the stomata were absent in epidermis from underground organs. The potential for identification of the epidermis from these organs to family level seems to be less certain than with the epidermis of the leaves and aerial stems.

3.2.4 Limitations and implications

The identification work presented here has consolidated and expanded earlier identification work and brought the identification criteria within a systematic recording system. The root work can be used as it stands in Table 3.5. Leaf and epidermal criteria have been split into several tables. Table 3.11 provides generalised criteria to distinguish the main epidermis and leaf types.

Class/Order	Venation	Epidermal cells	Trichomes	Stomata
Sphenophyta	Parallel	Rectangular cells with undulate margins in regular longitudinal files. Silica deposits.	Absent	Anomyocytic with striations and silica deposits in longitudinal files.
Ophioglossales	Reticulate	Polyhedral straight-walled, no specific alignment.	Absent	Anomyocytic
Filicales	Dichotomous	Irregular cells with deeply undulate walls in no specific alignment; Rectangular cells over veins.	Restricted types present mainly on margins and veins, but also across lamina in some taxa.	Mainly polocytic with some anomyocytic and staurocytic. Arranged in groups on lamina orientated to veins.
Dicotyledonae	Reticulate	Variable shape straight to undulate without specific alignment.	Present and often dense in many taxa. Many types.	Variable. Arranged in groups on lamina orientated to veins.
Monocotyledonae	Parallel with some perpendicular transverse veins.	Mostly square or rectangular with straight walls in regular longitudinal rows. Some with undulate cells and less regular.	Restricted range of types present at margins in some taxa. Rarely papillae on lamina.	Mostly paracytic, arranged in longitudinal rows or groups.

Table 3.11 Main distinguishing features of epidermis and leaves at Class/Order level

The work on roots, leaves and epidermis has demonstrated that identifications with taxonomic implications can be provided for even highly fragmented vegetative macrofossils. Even taking into account the restricted range of taxa included in this survey, there is good reason to believe that family and genus level identifications are possible for much plant material. Higher level identifications require large, well preserved fragments (in the absence of unique features). The features used in this part of the research are observable with standard laboratory bench equipment and are easily prepared. The implication of this work is that identifications of vegetative macrofossil remains have the potential to provide information of ecological and palaeoenvironmental significance. This information, however, may be of a general nature and may not provide the level of detail required for NVC or phytosociological classificatory groups, but may be possible at the family or genus level, or using structural type groupings (e.g. life-form analysis).

3.3 Quantification and recording

Going beyond a species list to record accurately and quantify the taxa and types of plant macrofossils present in sediments is complicated by the inherent heterogeneity of macrofossil assemblages. The most common methods include simple counts, volumetric methods and DAFOR type estimates of abundance. Each has its own limitations that will now be outlined.

Counting is the most accurate method of quantification for plant macrofossils that are preserved as discrete units, such as seeds and fruits. Counting is, however, an inappropriate method of quantification for vegetative and woody macrofossils where counts reflect fragmentation as much as abundance. One possible method of accounting for fragmentation is to divide the sample into different size fractions and then count within those fractions, as happens in wood charcoal analysis. A trial of this method with waterlogged macrofossil assemblages failed because it was impossible to separate accurately the assemblages using sieves into size fractions due to water tension. Sieving also damaged the more delicate macrofossils.

Volumetric measurements were the most intellectually appealing form of recording for vegetative and woody macrofossils. Many of the macrofossils included in this investigation were typically small (between 0.5 mm and 10 mm in diameter). Division of the macrofossils from a sample into groups was simply found to take too long to be practical. Another theoretical problem is the effect of differential water

absorption by macrofossils when released from compaction by sieving in water, the only practical method of macrofossil extraction. Volumetric measurements of macrofossil assemblages would be affected by differential water absorption, even if they were possible, making any measurements problematic.

DAFOR estimates use relative abundance scales and are among the most widely employed methods of quantification for vegetative and woody macrofossils. They are useful as a means of preparing rapid abundance information. The method was, however, ultimately rejected because it is highly subjective and uses no standard reference, making of dubious value the comparison of macrofossil abundances from different samples and sediments (see General introduction to Rodwell 1991a for a discussion of the problems in using DAFOR quantification in vegetation recording).

3.3.1 The cover abundance method

The method of quantification used for the following investigations is a modified form of the cover abundance method described by Barber *et al.* (1994) for macrofossil analysis of ombrotrophic peat. This method was devised primarily for rapid analysis of moss and other vegetative assemblages from ombrotrophic peats and in its pure form provides a means of absolute comparison between macrofossil abundances. As with the cover abundance method of vegetation description, it uses as an abundance measure the area covered by macrofossils within a series of sample quadrats. Samples of a standardised size are disaggregated in a specific volume of liquid and then spread out in a container to form a 'monolayer' over which sample quadrats are recorded using a 10 x 10 grid graticule at 10x magnification on a binocular dissecting microscope (Barber *et al.* 1994). This monolayer is a single sheet of macrofossils with minimum overlap. The area within each quadrat covered by each class of macrofossil is recorded and the final cover abundance figures are an average of fifteen quadrat counts per sample. Cover abundance figures for vegetative and woody macrofossils are accompanied by the counts of seeds and other countable items. This method was found to produce repeatable results used as a basis for numerical analysis via detrended correspondence analysis to interpret bog surface wetness as a proxy for climatic signals (Barber *et al.* 1994).

3.3.2 Tests

The cover abundance method was tested on vegetative macrofossils from modern surface samples of both peat and silt-rich sediments. The most thorough tests were completed on an organic-rich silt sample (04/116). Macrofossils were recovered in a 125 μm sieve after disaggregation using 10 litres of water. The recovered macrofossils were placed in a container forming a monolayer from which the cover abundance was recorded. Fifteen full trial runs were recorded, each value being the mean of fifteen individual quadrat counts (Table 3.12). Figure 3.3 shows the typical pattern of cumulative mean values that developed in the trials. The early values varied, sometimes considerably, but eventually became constant.

Although a similar pattern of representation was noted in all fifteen trials, there was variability in the mean values, although the variability was limited. Variability can be attributed to observer-error and the practical difficulty in forming the macrofossil 'monolayer'. Overlapping of plant fragments in the dish could not be eliminated. This caused distortions in the area covered by any class of plant macrofossils and hence alters the probability of the fragments being recorded. A further problem was the presence of non-macrofossil material and gaps in the monolayer. These were recorded as 'void' on the record sheets and calculated out of the final mean values.

Although the method was easy to use after some practice, the taxonomic identification of macrofossils proved more difficult. Identification required using higher levels of magnification than achievable on a standard dissecting microscope. Identification required removal of the fragments from the sample dish, after the cover abundance was recorded, and use of transmitted light microscopy. The identification could then be assigned and the record added to the record sheet.

3.3.3 Comparability of cover abundance values

The cover abundance method was devised for ombrogenous peats where all of the material was allochthonous and mainly composed of plant tissues. In such sediments, therefore, the percentage cover abundance values can be directly equated with the absolute quantity of plant material in a sample. Variations in macrofossil abundance between samples reflect the changes in the abundance of that class of macrofossils, rather than reflecting the changes in another macrofossil type, as with relative (e.g. percentage) methods of quantification.

A major drawback with application of the method to alluvial sediments is the variability in macrofossil content and often the presence of substantial quantities of inorganic material that was removed during sieving. Although cover abundance values could be generated for any sample, several further points emerged from tests of the method:

1. dishes of different sizes had to be used to contain different samples, altering the probability of macrofossils being incorporated in a quadrat ;
2. cover abundance values from samples in which non-plant matter was present are relative, showing the internal composition of macrofossils in a sample;
3. cover abundance values from these samples are not absolute, so a value in one sample does not correspond directly to the value in another sample.

Prolonged use of the method suggested that, while the differing dish size may have theoretically affected cover abundance values, stable values were in fact produced, even when the total macrofossil volume was extremely low. A more serious deficiency was the lack of comparability between values. To circumvent this problem the loss-on-ignition (LOI) figures, representing the bulk organic content, have been used as a means of providing a standardising factor to allow some measure of inter-sample comparison. The method of LOI used is that described by Gale and Hoare (1991, 262 - 264). Mean cover abundance was re-calculated for the organic content of the sample using the following formula to provide mean cover abundance (C) per unit of organic content (O):

$$CO^2 = C/100 \times O$$

Using LOI in this way is not totally satisfactory. The method itself is prone to errors caused by small changes in organic content over space. LOI figures also represent the total quantity of organic matter present in the sample. This includes macroscopic animal fragments and microscopic particles of plant and animal detritus. It has been assumed that the formers contribution to the samples was minimal, as it is when the method is used in geology (Gale and Hoare 1991, 262). For alluvial peats, the assumption that there is no allochthonous inorganic content cannot be sustained, because backswamps and fens are often flooded, providing a vector for possible allochthonous sediment inputs. CO^2 has, therefore been used for all sediment types.

	Cover abundances for Macrofossil groups					
Trial observation	Poaceae Stem	Poaceae Leaf	Type 1 root	Monocot Leaf	Herb undiff.	Seeds
1	26.9	13.7	8.7	2.1	47.6	1
2	27.3	14.9	7.4	2.1	47.3	1
3	30.8	12.9	8.6	1.1	45.6	1
4	29.6	15.4	8.4	1	45.7	1.9
5	30.2	15.4	6.6	1	46.1	0.7
6	30.5	16.4	6.9	0.8	44.4	1
7	28.7	15.2	8.8	0.7	46.5	0.1
8	27.9	14.5	7.9	1	49.7	1
9	30.1	12.3	6.6	0.6	49.7	0.7
10	27.4	14.3	7.1	0.9	51.2	1
11	28.7	13.2	7.8	2	46.7	1.6
12	30.2	15.7	9	1.3	44.6	0.6
13	27.4	16.3	7.6	1.1	48.4	1
14	28.1	15.3	8.2	0.7	49.7	1.5
15	29.3	17.4	6.9	1.3	50.1	1.3
Maximum Value	30.8	17.4	9	2.1	51.2	1.9
Minimum Value	26.9	12.3	6.6	0.6	44.4	0.1
Mean	28.8	14.9	7.7	1.2	47.6	1.0
Standard deviation	1.4	1.4	0.9	0.509	2.1	0.4

Table 3.12 Cover abundances for trial sample 04/116

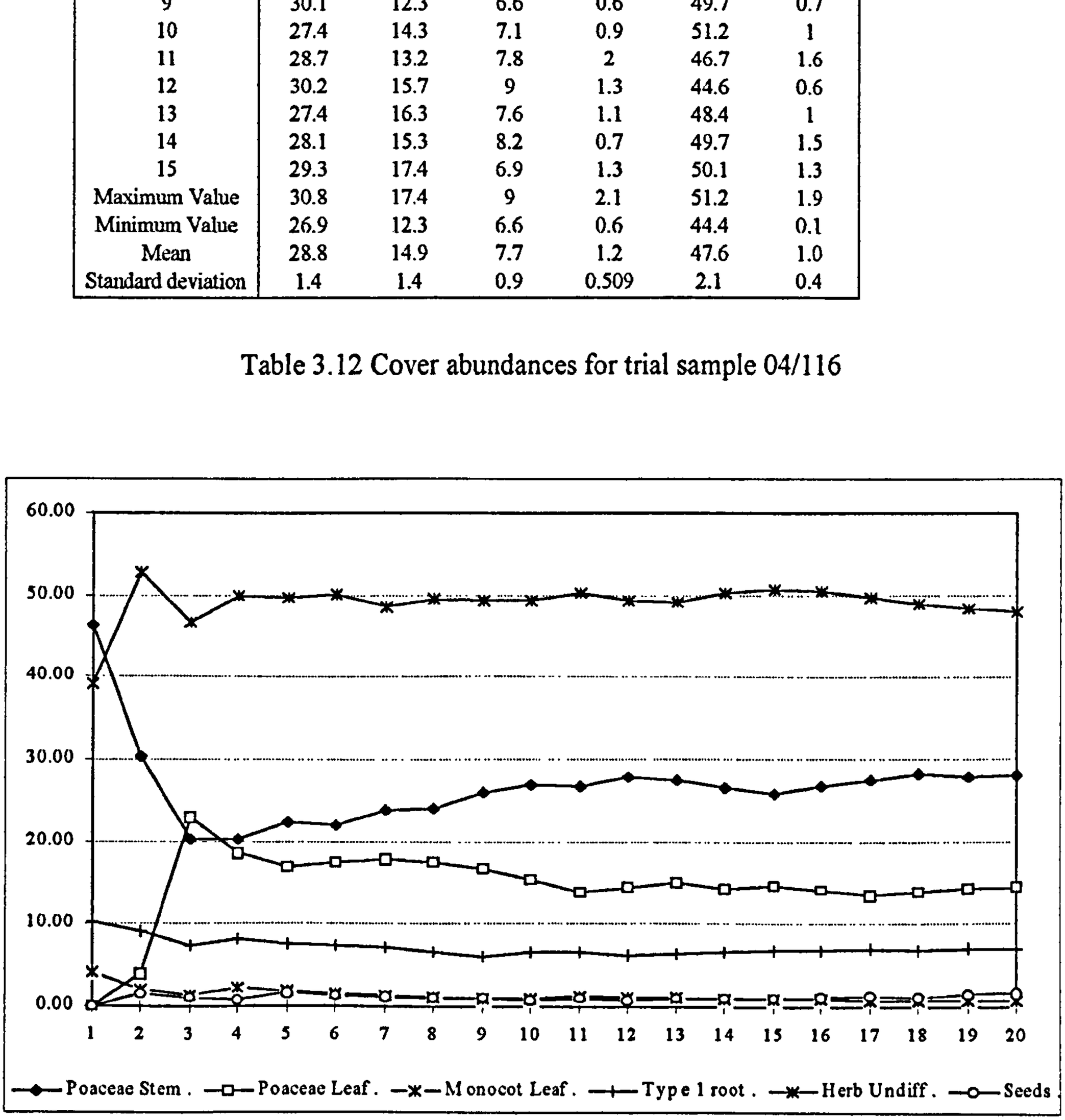


Figure 3.3 Sample 04/116 Cover Abundance Trial 8

3.3.4 Evaluation

Testing over several weeks showed that, while the method provided a practicable means of determining macrofossil abundance, the obtained values were subject to a measure of variability caused by observer and methodological errors. Inexperience and unfamiliarity with the procedures caused some of the observer error, especially in early trials. This was overcome by repeated application of the procedure. The methodological errors, inherent in the method, were less easily removed. Raw cover abundance figures, with void values removed, provided moderately accurate, repeatable values. Major elements of the macrofossil assemblages were accurately distinguished from minor elements (of less than 3% cover abundance). The variability in values, however, suggests that values lower than 3% cover abundance are not reliably distinguished. Small values are, therefore, essentially of identical value. Interestingly, although the minutiae of the samples are quantitatively indistinguishable, if ranked, the main elements remained stable in the trials. The use of LOI as a standardising factor means that comparative absolute comparisons of abundance are available. The LOI figures do, however, contain further errors and using them in this way multiplies those inherent in the cover abundance method itself.

The method provides a means of establishing the composition of the vegetative and woody macrofossils in a sample and comparing it to others, although the precise cover abundance figures could not be used to separate samples in which the plant macrofossil values varied little. It was considered adequate for the purposes of this research. Ultimately, while imperfect, the cover abundance method provided the most practical method of macrofossil recording tested during this research and a useful basis for interpretation as long as its limitations are recognised.

The method can be compared to a DOMIN type recording system used in vegetation recording in which the approximate percentage cover is more important than the precise figure. As with DOMIN recording systems for standing vegetation, the cover abundance method is also practical to employ and the errors are understandable. It also has considerable advantages over other methods. While it is flawed, the flaws were found not to invalidate the method as long as small changes in values are not given too much interpretative significance. As with the use of cover abundance methods in vegetation mapping, questions can be asked about the suitability of estimates based on the areas of two-dimensional space covered to describe complex three-dimensional

forms. In this case the method favoured macrofossils that are flattened, such as leaves, and, in terms of volume and mass, underrepresented twigs and other cylindrical forms.

4 Investigation of plant macrofossil taphonomy in modern alluvial environments

Plant macrofossil taphonomy was investigated at a number of active alluvial sedimentary environments. The primary means of investigation involved the comparison of the macrofossils present in surface sediment samples to the standing vegetation, supplemented by sediment descriptions and observations of plant part shedding. Estuarine depositional environments, especially saltmarshes, were the main focus of study because little published information is available about macrofossil taphonomy in those environments.

4.1 Site selection

The initial aim of the research was to sample complete estuarine sedimentary systems. Preliminary research and field investigations confirmed, however, that most alluvial environments in the region have been enclosed in flood defences and drained for use in agriculture and construction, a pattern of destruction seen throughout the British Isles and Northern Europe (Brown 1997). As elsewhere, only fragments of these once extensive systems survive intact, most managed as nature reserves, and many transitional environments no longer exist or are very rare (e.g. Burd 1989). This re-directed research towards taking samples from a number of sites where a limited range of depositional environments were active, but which, when grouped together, provided a representative range of alluvial environments in existence today in the region.

Enquiries to English Nature regional offices and relevant publications (e.g. Ratcliffe 1977) located a number of suitable nature reserves in Southeast England. These included a handful of suitable tidally influenced environments, but lacked extensive upper saltmarshes and freshwater wetlands. Reserves in East Anglia extended the list. This area was chosen for inclusion in the project as it has the largest extent of both saltmarsh and freshwater fen environments in the British Isles and, like Southeast England, has a marked continentality to its climate. Fifteen sites were visited and from these eight were selected for inclusion in the project (Table 4.1; Figure 4.1).

Intact sections of saltmarsh environments were preserved under active tidal influence at Burham Marsh, Snape Saltings, Angel Marsh, Stonemarsh and Borstal Marsh. At all sites, with the exception of Snape Saltings, flood defences truncated the transitional zone between the saltmarsh and terrestrial/freshwater habitats. Sampled freshwater environments were more disturbed than the tidal environments. All were

isolated from regular flooding and were managed to maintain the vegetation composition. All three freshwater sites were habitat fragments, analogous to areas of floodplain wetland influenced by groundwater but isolated from flood inputs. They were included in the project mainly to provide additional information about non-seed and fruit assemblage composition that was lacking in other studies where the focus was on seed assemblages.

Site	*Location*	*Owner/Manager*	*Environments*
01 Bure Marsh	River Bure, Norfolk.	English Nature	Fen-wood on floodplain, especially managed and unmanaged alder wood
03 Hickling Broad	River Thurn, Norfolk	Norfolk Naturalists Trust.	Herb fen on floodplain.
04 Burham Marsh	River Medway, Kent	Kent Trust for Nature Conservation.	Mature tidal reedswamp
07 Snape Saltings	River Alde, Suffolk	Suffolk Wildlife Trust	Middle-upper saltmarsh, including marsh, abandoned channel and saltpan
09 Stonemarsh	Hamford Water, Essex	English Nature	Low-middle saltmarsh, mudflats and creek system
13 Angel Marsh Walberswick	River Blyth, Suffolk	Crown Estate / English Nature	Low-middle and upper saltmarsh, creeks, mudflats, tidal reedswamp
14 Wicken Fen	Cambridgeshire Fens	National Trust	Wooded fen
15 Borstal Marsh	River Medway, Kent	Kent County Council	Low-mid saltmarsh and mudflats

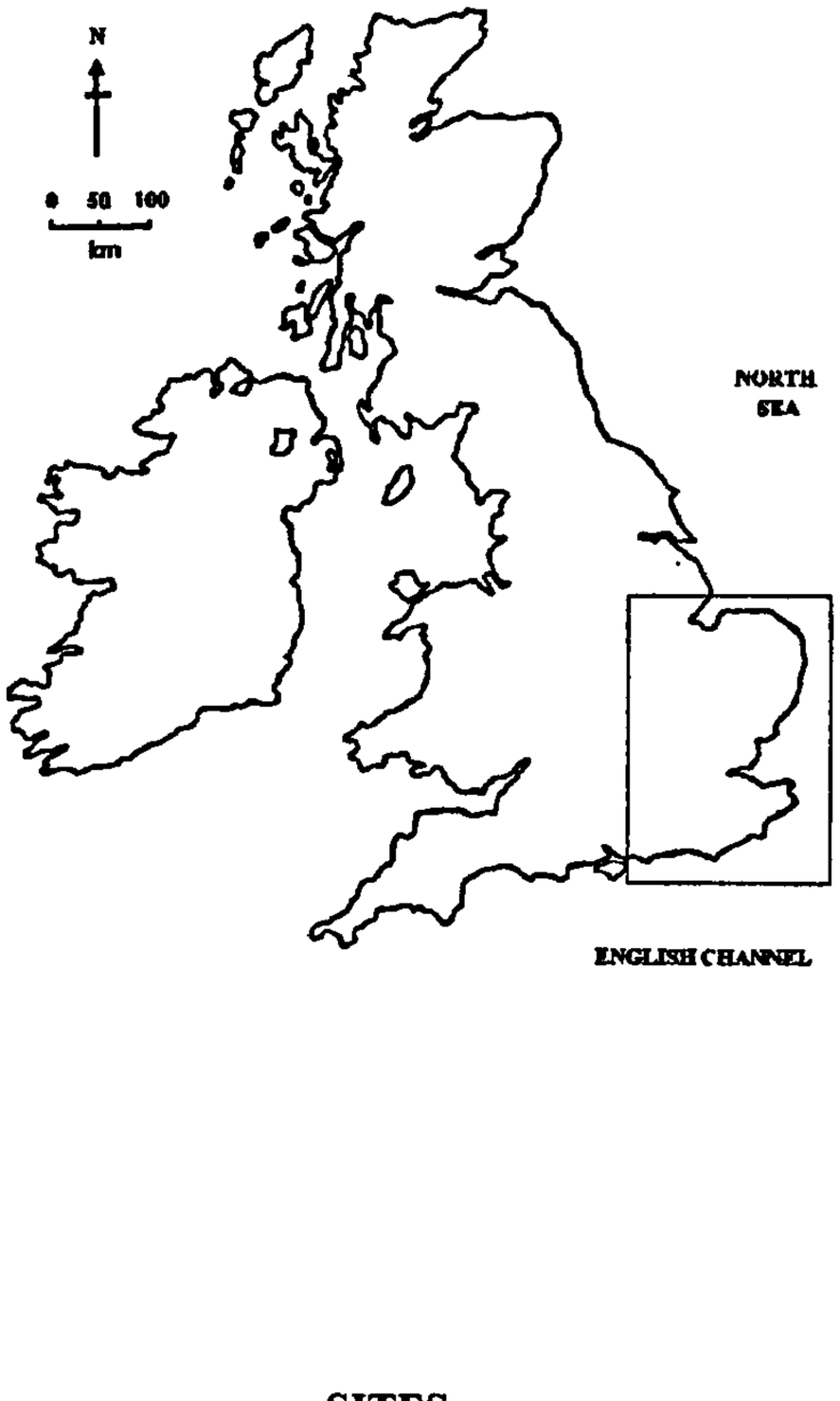
Table 4.1 Sites included in the project

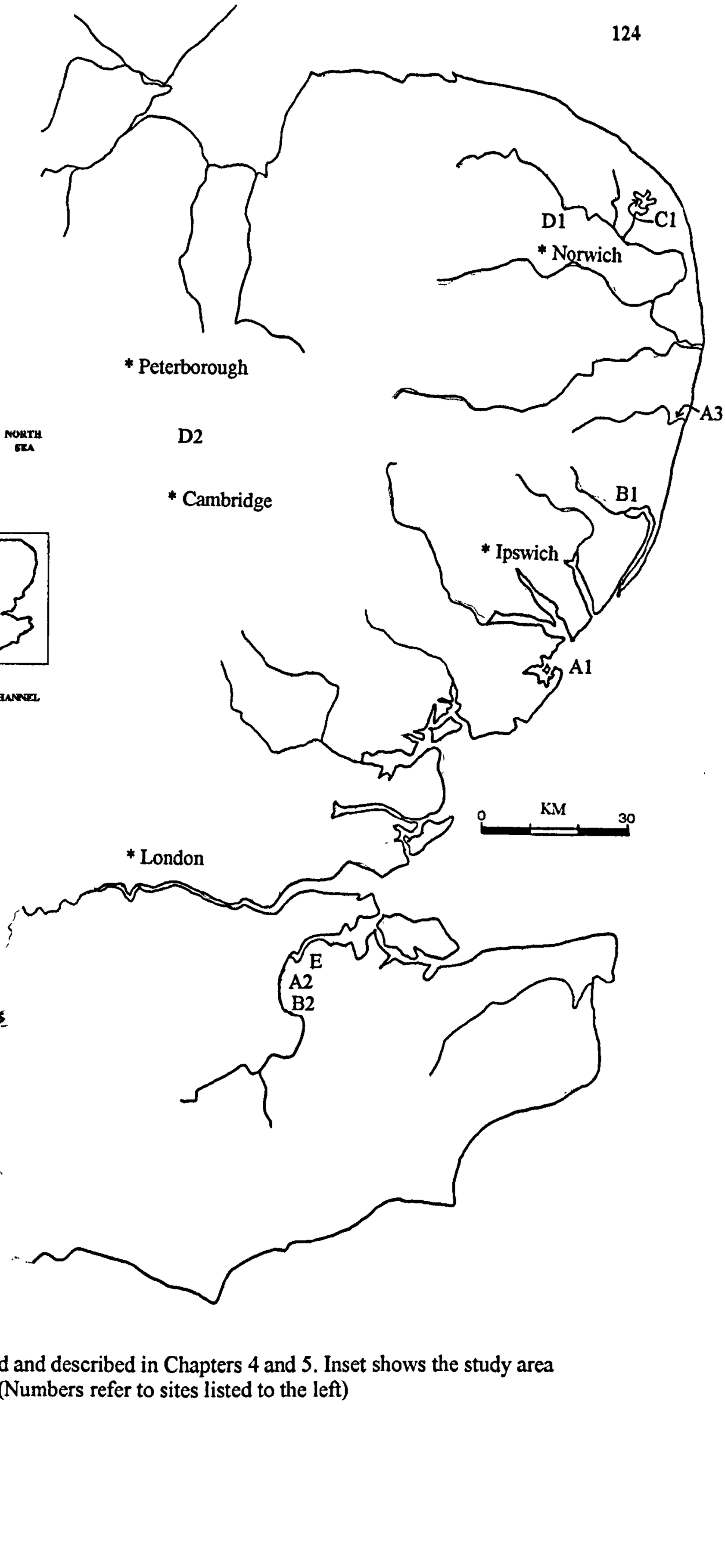
4.2 Field and laboratory methods

4.2.1 Sample point selection

In zoned environments (e.g. saltmarshes) samples were collected along transects chosen to cross major environmental and vegetation gradients, including marsh-channel transitions. In the fen woodlands and marshes, where the habitat was a mosaic with no obvious unidirectional environmental gradients, samples were collected from the main sub-environments (e.g. tree base, marsh surface) and major vegetation communities. Some sections of saltmarshes were also sampled in this way to incorporate vegetation types not included within the main transects.

The sites were assigned numbers during initial fieldwork (see Table 4.1). Added to these were sample area and sample numbers, so each sample could be located accurately. For example, at Snape Saltings a group of samples at the saltmarsh edge were





SITES

A Low to mid-saltmarshes
1 Stonemarsh
2 Bortsal Marsh
3 Angel Marsh, Walberswick

B Mid to upper-saltmarshes
1 Snape Saltings
2 Burham Marsh

C Herb fens
1 Hickling Broad

D Wet woodlands
1 Bure Marshes
2 Wicken Fen

E Medway Tunnel Site

Figure 4.1 Sites sampled and described in Chapters 4 and 5. Inset shows the study area (Numbers refer to sites listed to the left)

assigned area number 01; therefore the first sample from this area was 07/01/01. Samples in transects were assigned numbers in a series; therefore, the first sample in the Angel Marsh transect is identified by the number 13/1. Block samples were given three digit numbers, the first being the block sample number; therefore, sample 3 from Snape Block 1 would be written 07/103.

4.2.2 Sediment sampling

Surface sediment samples were collected from sample points along transects and in mosaic vegetation. Sample sizes were standardised as much as possible to allow direct comparison of sample composition within and between sites. Only consolidated sediment was collected in the surface samples. Loose surface litter was described in the sample area prior to its removal and collection of the sediment beneath. Samples were measured and cut using a sharp knife, excavated with a trowel and placed in labelled bags. Large blocks were excavated using a spade. All samples were double-sealed in plastic and refrigerated at 4°C until analysed.

Samples were collected in two visits to the sites. In the first visit, large block samples were collected for description and sub-sampling in the laboratory. These large sediment blocks were of a minimum depth of 20cm and had a surface area of *ca* 30cm x 30cm. The surface of the blocks was divided into a grid 12.5cm^3, 25cm^3 and 50cm^3 sub-samples (surface area of 2.5cm x 2.5cm, 2.5cm x 5cm and 5cm x 5cm respectively and depth of 2cm). These samples were collected to:

a) Allow analysis of the variability of macrofossil incorporation into sediments across a known surface area;
b) Provide a basis for determining an adequate sample size for seed and non-seed macrofossil assemblages (following Fasham and Monk 1978) in the wide variety of depositional environments studied;
c) Provide a basis for comparing the effects of sample size on macrofossil assemblage composition.

Samples of 50cm^3 were also collected down the block profile to allow investigation of changes in macrofossil preservation with depth. Sediment characteristics, distribution and variation in the preservation of macrofossils were also recorded across the block surface and down the profile.

The size of samples collected along transects and in mosaic vegetation was determined by the initial investigations of the block sample used to establish the minimum sample size that would provide a representative sample of the macrofossils. A minimum sample of 100 identifiable seeds was aimed for, as well as stable profiles on cumulative percentage diagrams of seed and non-seed macrofossils (following Fasham and Monk 1978). Although $50cm^3$ samples would, in several cases, have provided adequate samples of the most abundant seed types, in the event samples of $200cm^3$ (10cm x 10cm x 2cm depth) were collected. This proved to be a suitable size for collection of adequate seed assemblages and allowed direct comparison between samples from different sites, although the size was too large for the accurate measurement of cover abundance values. Cover abundance was measured using $50cm^3$ sub-samples of the larger samples, divided at the time of collection. Small samples of $50cm^3$ or less were also collected with the macrofossil samples for LOI tests.

4.2.3 Sediment description

Sediments were described in the field or as soon as the samples reached the laboratory within days of collection. Colour was described using Munsell soil colour charts. Sediment composition was initially described using the 'Troels-Smith' terminology (Aaby and Berglund 1986). Texture was described with reference to the Udden-Wentworth system of grain size terminology (Tucker 1982) and the touch tests described in Gardiner and Dackombe (1983). Sorting, sediment strength, bedding and nomenclature for sand, silt and clay mixtures followed the systems outlined in Gardiner and Dackombe.

4.2.4 Vegetation recording

The vegetation community within which the sample point lay was described using the DOMIN cover abundance values and vegetation sample sizes as described by the National Vegetation Classification (NVC) (e.g. Rodwell 1991a). The community types referenced in the text (e.g. SM8 annual *Salicornia* community) follow Rodwell (1991a, 1991b 1992, 1995) and Burd (1989). The distance of the closest representative of each taxon to the sample point was recorded, along with general observations about the proximity of other vegetation types to the sample point.

4.2.5 Laboratory preparation, description and analysis of macrofossils

Macrofossils were collected from the samples and described using the methods outlined in section 3.3. It should be noted that seeds, bracts and other countable macrofossils (including Filicales sporangia in some cases) are referred to in the text as 'seeds' when discussing general trends in macrofossil preservation. All of the other material, usually described using the cover abundance method, is referred to as 'non-seed' macrofossils. Not all of the collected samples were analysed, as reflected by the discontinuous numbering. A 125 μm mesh sieve was used to collect the macrofossils and, for some compacted silts, pre-treatment using a deflocculant was required. After sieving, the retained macrofossils were sealed in labelled plastic bags in a solution of 70% Industrial Methylated Spirits (IMS).

It was initially hoped to identify woody remains as well as vegetative macrofossils; however, this was not possible because of identification problems, poor preservation and, eventually, time pressure. Most of the wood in the samples was badly degraded and below the size required for identification. Larger fragments were often spongy and difficult to section. The only woody components identified were twigs that retained identifiable buds.

Correspondence analysis (CA) was used as an exploratory technique. CA groups samples along the major axes of variability on the basis of the quantitative sample composition and provides summary statistics to describe how different macrofossil groups contribute to those axes (Shennan 1988; Baxter 1994). Sample points and macrofossil points can be plotted on two-dimensional diagrams. These provide a visual means of determining how the samples compare in terms of macrofossil composition and which macrofossils account for the differences. Known environmental gradients or phenomena can be then compared to the patterns of variability expressed in the diagrams and accompanying statistics.

Canonical correspondence analysis (CCA) was used to ordinate axes of variation in the macrofossil data to the cover abundance records of standing vegetation. The method allows explanatory variables, in this case standing vegetation data, to be correlated with the macrofossil records from each sample, providing a means of determining how well the abundance of macrofossils reflects the abundance of source taxa in the standing vegetation.

To summarise, the plots produced by these two methods provide a means of:

a) describing statistically macrofossil assemblages in the sediments at a particular sample point;
b) describing the variability in macrofossil assemblages between sample points in a site or sites;
c) providing visual plots that allow easier interpretation of the variability in sample composition;
d) determining how well macrofossils correlate with values for standing vegetation cover abundance.

CANOCO for Windows 4.0 was used for all data analysis (Ter Braak 1999), CANODRAW 3.1 and CANOPOST for Windows 1.0 to plot the ordination diagrams. Standardised seed concentrations per $100cm^3$ of sediment were used in the analysis. Modified cover abundance (CO^2) values were used for the non-seed data. Statistical analysis required standardisation of data and the merging of separate types of macrofossil that were derived from the same fruit (e.g. caryopses and whole spikelets of the Poaceae taxa). The specific combination of seed and non-seed data used in each plot is discussed in the appropriate section. Various transformations, reductions and consolidations of the data were also tested. Square root transformations of the data were used in the analyses and rare species were down-weighted. These procedures reduced the distortions on the analysis caused by the high-abundance of macrofossils of few taxa in the samples and the effects of rare species respectively. Any variable present in less than 10% of the samples in the sample set was also removed, to reduce the influence of single macrofossil occurrences further. CANOCO uses abbreviations for samples and species identified in both the standing vegetation and the macrofossil assemblages. These are listed in Tables 4.2 and 4.3 respectively.

Additional indices were calculated including the total seed concentration and species concentration (seeds and species per cm^3 sediment). The proportion of seeds produced by plants recorded within set distances of the sample point was also calculated, as was the proportion of species represented in the sample sets.

The CANOCO diagrams in the text contain three separate types of data. Sample points are open circles with a number or numbers next to them (O). Macrofossil points are filled circles with a six letter abbreviation in normal font (e.g. • phg stm). These points are present on both the CA and CCA plots. Additionally the CCA plots have

arrows originating from the origin of the two diagram axes that show how the scores for standing vegetation elements correlate to the axes in the ordination. Arrow length indicates the strength of the correlation. The abbreviated names of the taxa represented by each arrow are shown in bold font (e.g. ↑ **opn grn**). Boxes and arrows have been added to many diagrams to show the position of data labels when the diagram was crowded. These arrows are distinguishable from the data arrows because they do not start at the origin. Note that the first axis is shown horizontal and the second vertical.

4.2.6 Sediment tests

Bulk organic content was calculated for all samples using the LOI method described by Gale and Hoare (1991), modified to using a temperature of 550°C maintained for 2 hours. This shorter time was found to be sufficient to remove all organic matter (S. Mellalieu pers. comm.) and also provided a measurement of % water content by mass.

Abbreviation	Species	Abbreviation	Species
alt off	*Althaea officinalis*	lys vul	*Lysimachia vulgaris*
ast tri	*Aster tripolium*	mol cae	*Molinia caerulea*
atx prt	*Atriplex portulacoides*	opn grn	Open
atx prs	*Atriplex prostrata*	peu pal	*Peucedanum palustre*
bol mar	*Bolboscheonus maritimus*	phl aru	*Phalaris arundinacea*
mos ind	Bryophyta	phg aus	*Phragmites australis*
cal sep	*Calystegia sepium*	pln mar	*Plantago maritima*
aln can	Canopy *Alnus glutinosa*	puc mar	*Puccinellia* sp.
bet can	Canopy *Betula pubescens*	rib nig	*Ribes nigrum*
frn can	Canopy *Frangula almus*	rub fru	*Rubus fruticosus* agg.
frx can	Canopy *Fraxinus excelsior*	rux crp	*Rumex crispus*
slx can	Canopy *Salix cinerea*	rux hyd	*Rumex hydrolapathum*
crx app	*Carex appropinquinta*	sal eur	*Salicornia sp.*
crx pan	*Carex paniculata*	sar per	*Sarcocornia perennis*
crx pen	*Carex pendula*	sol dul	*Solanum dulcamara*
crx rem	*Carex remota*	spt ang	*Spartina anglica*
crx rip	*Carex riparia*	spg med	*Spergularia media*
cld mar	*Cladium mariscus*	sua mar	*Suaeda maritima*
coc ang	*Cochlearia anglica*	thy pal	*Thelypteris palustris*
ely rep	*Elytrigium repens*	trg mar	*Triglochin maritimum*
eup can	*Eupatorium cannabimum*	typ ang	*Typha angustifolia*
fes rub	*Festuca rubra*	ace can	Understorey *Acer pseudoplatanus*
fil ulm	*Filipendula ulmaria*	bet und	Understorey *Betula pubescens*
gal pal	*Galium palustre* agg.	crt und	Understorey *Crataegus monogyna*
glx mar	*Glaux maritima*	frn und	Understorey *Frangula alnus*
irs psu	*Iris pseudacorus*	frx und	Understorey *Fraxinus excelsior*
jun ger	*Juncus gerardii*	aln und	Understory *Alnus glutinosa*
jun mar	*Juncus maritimus*	slx und	Understory *Salix cinerea*
jun sub	*Juncus subnodulosus*	ros und	Undetstorey *Rosa* sp.
lim spp	*Limonium* sp.	urt dio	*Urtica dioica*
lyc eur	*Lycopus europaeus*	val dio	*Valeriana dioica*

Table 4.2 Canoco abbreviations for standing vegetation elements

Abbrev.	Species	Macrofossil
ajg sed	*Ajuga* sp.	Seed
ali sed	*Alisma* sp.	Seed
aln brc	*Alnus glutinosa*	Bracteole
aln bud	*Alnus glutinosa*	Buds and budscales
aln con	*Alnus glutinosa*	Cone
aln lef	*Alnus glutinosa*	Leaf
aln sed	*Alnus glutinosa*	Seed
alt sed	*Althaea officionalis*	Seed
ang sed	cf. *Angelica officionalis*	Fruit
aph sed	*Aphanes arvensis*	Seed
api sed	*Apium* sp.	Fruit
arc sed	*Arctium* sp.	Fruit
ast sed	*Aster tripolium*	Seed
atp epd	*Atriplex portulacoides*	Epidermis
atp lef	*Atriplex portulacoides*	Leaf
atp rot	*Atriplex portulacoides*	Root
atp sed	*Atriplex portulacoides*	Seed
atp stm	*Atriplex portulacoides*	Stem
atx abs	*Atriplex portulacoides*	Abscission surface
atx lef	*Atriplex* sp.	Leaf
atx rhz	*Atriplex* sp.	Rhizome
atx rot	*Atriplex* sp.	Non-woody root
atx sed	*Atriplex* sp.	Seed
atx stm	*Atriplex* sp.	Stem
bet brc	*Betula* sp.	Bract
bet bsc	*Betula* sp.	Bud-scale
bet con	*Betula* sp.	Cone bract
bet lef	*Betula* sp.	Leaf
bet sed	*Betula* sp.	Seed
bid sed	*Bidens cernua*	Seed
bol sed	*Bolboschoenus maritimus*	Seed
bol stm	*Bolboschoenus maritimus*	Stem
btl lef	*Betulaceae*	Leaf
cal sed	*Callitriche*	Seed
cap sed	*Caltha palustris*	Seed
chn epd	cf. *Chenopodiaceae*	Epidermis
chn sed	*Chenopodium* sp.	Seed
chr oos	*Characeae*	Oospore
cic sed	*Cicuta virosa*	Seed
cir sed	*Cirsium* cf. *palustre*	Fruit
cld lef	*Cladium mariscus*	Leaf
cld rhz	*Cladium mariscus*	Rhizome
cld sed	*Cladium mariscus*	Seed
cld stm,	*Cladium mariscus*	Stem
coc sed	*Cochlearia* sp.	Seed
cra bsc	*Corylus avellana*	Budscale
cra sed	*Corylus avellana*	Nutshell
crn sed	*Cornus sanguinea*	Seed
crt sed	*Crataegus* sp.	Fruit
crx sed	*Carex* sp.	Seed
cxd sed	*Carex* cf. *diandra*	Fruit
cxp sed	*Carex paniculata*	Fruit
cxr sed	*Carex remota*	Fruit
cxu sed	*Carex* cf. *pendula*	Fruit
cyp epd	*Cyperaceae*	Epidermis
cyp lef	*Cyperaceae*	Leaf
cyp rhz	*Cyperaceae*	Rhizome
cyp rot	*Cyperaceae*	Non-woody root
cyp stm	*Cyperaceae*	Stem
cys cap	*Calystegia sepium*	Capsule
cys lef	*Calystegia sepium*	Leaf
cys rhz	*Calystegia sepium*	Rhizome
cys sed	*Calystegia sepium*	Seed
dic lef	*Dicotyledon*	Leaf
dic stm	*Dicotyledon*	Stem
dry pin	*Dryopteris dilitata*	Pinnule
ele sed	*Eleocharis* sp.	Seed
elg sed	*Elogiton fluitans*	Seed
ely sed	*Elytrigia sp.*	Seed
eph sed	*Epilobium hirsutum*	Seed
epl sed	*Epilobium* sp.	Seed
eup sed	*Eupatorium cannabinum*	Fruit
fes sed	*Festuca rubra*	Seed
fil rot	*Filicales*	Rootlet
fil sed	*Filipendula ulmaria*	Fruit
fil spg	*Filicales*	Sporangia
frn sed	*Frangula alnus*	Seed
frx bsc	*Fraxinus excelsior*	Budscale
frx lef	*Fraxinus excelsior*	Leaf
gap sed	*Galium palustre*	Fruit
glx lef	*Glaux maritima*	Leaf
glx sed	*Glaux maritima*	Seed
gly sed	*Glyceria fluitans*/spp.	Fruit
hrb stm	*Indeterminate*	Herb stem
hyd sed	*Hydrocotyle vulgaris*	Seed
hyp sed	*Hypericum perforatum*	Seed
ind abs	Indeterminate	Abscission surface
ind brk	Indeterminate	Bark
ind chr	Indeterminate	Charcoal
ind epd	Indeterminate	Epidermis
ind hrb	Indeterminate	Herbaceous matter
ind ind	Indeterminate	Indeterminate
ind mos	Indeterminate	Moss
ind per	Indeterminate	Periderm
ind rhz	Indeterminate	Rhizome
ind rot	Indeterminate	Root
ind stm	Indeterminate	Stem
ind twg	Indeterminate	Twig
ind wod	Indeterminate	Wood
ind wrt	Indeterminate	Woody root
irs rhz	*Iris pseudacorus*	Rhizome
irs sed	*Iris pseudacorus*	Sed
jef sed	*Juncus effusus* type	Seed
jna sed	*Juncus acutus* type	Seed
jnb sed	*Juncus bufonius*	Seed
jng sed	*Juncus gerardii*	Seed
jum sed	*Juncus maritimus*	Seed
jun epd	*Juncus* sp.	Epidermis
jun rhz	*Juncus* sp.	Rhizome
jun rot	*Juncus* sp.	Root
jun sed	*Juncus* sp.	Seed
jun stm	*Juncus* sp.	Stem
jus sed	*Juncus subnodulosus*	Seed
lem sed	*Lemna* sp.	Fruit
lim sed	*Limonium* sp.	Seed/capsule
lyc sed	*Lycopus europaeus*	Seed
lys sed	*Lysimachia vulgaris*	Seed
men sed	*Mentha* sp.	Fruit
min rot	*Indeterminate*	Mineralised root
mol sed	*Molinia caerulea*	Fruit
mon lef	*Monocot*	Leaf
mon rhz	*Moncotyledon*	Rhizome
mon stm	*Monocot*	Stem
oen sed	*Oenanthe* spp.	Sed
peu sed	*Peucedanum palustre*	Seed
phg lef	*Phragmites australis*	Leaf
phg rhz	*Phragmites australis*	Rhizome
phg sed	*Phragmites australis*	Seed
phg spk	*Phragmites australis*	Spikelet
phg stm	*Phragmites australis*	Stem
pla sed	*Polygonum aviculare*	Seed
plj sed	*Plantago major*	Seed
plm sed	*Plantago maritima*	Seed
poa epd	*Poaceae*	Epidermis
poa lef	*Poaceae*	Leaf
poa rhz	*Poaceae*	Rhizome
poa stm	*Poaceae*	Stem
pot sed	*Potamogeton* sp.	Seed
prm sed	*Persicaria maculosa*	Seed
prn bsc	*Prunus* sp.	Budscale
prs sed	*Prunus spinosa/padus*	Seed
pta sed	*Potentilla anserina*	Seed
ptd pin	*Pteridium aquilinum*	Pinnule
puc rhz	*Puccinellia* sp.	Rhizome
puc sed	*Puccinellia* sp.	Seed
puc stm	*Puccinellia* sp.	Stem
que bsc	*Quercus* sp.	Bud scale
que lef	*Quercus* sp.	Leaf
rac sed	*Ranunculus acris*	Fruit
ras sed	*Ranunculus sceleratus*	Seed
rbf sed	*Rubus fruticosus*	Seed
ros bsc	*Rosaceae*	Budscale
rub sed	*Rubus idaeus*	Seed
ruc sed	*Rumex conglomeratus*	Fruit
ruh sed	*Rumex hydrolapathum*	Fruit
ruo sed	*Rumex obtusifolius*	Fruit
rup sed	*Rumex crispus*	Fruit
rux brc	*Rumex* sp.	Bract
rux sed	*Rumex* sp.	Seed
sag sed	*Sagina* spp.	Seed
sal epd	*Salicornia*	Epidermis
sal sed	*Salicornia* spp.	Seed
sal stm	*Salicornia*	Stem
sam sed	*Sambucus nigra*	Seed
slx bsc	*Salix* sp.	Budscale
slx cap	*Salix* sp.	Capsule
slx lef	*Salix* sp.	Leaf
slx sed	*Salix* sp.	Seed
slx stp	*Salix* sp.	Stipule
slx twg	*Salix* sp.	Twig
smv sed	*Samolus valerandi*	Seed
sol sed	*Solanum dulcamara*	Seed
son sed	*Sonchus palustris*	Fruit
spa sed	*Sparganium* sp.	Sed
spg sed	*Spergularia media*	Seed
sph lef	*Sphagnum* sp.	Leaf
spt sed	*Spartina*	Seed
ssy sed	*Scirpus sylvaticus*	Seed
stg sed	*Stellaria graminea*	Seed
stl sed	*Stellaria* sp.	Seed
stp sed	*Stellaria palustre*	Seed
sue lef	*Suaeda*	Leaf
sue sed	*Suaeda* sp.	Seed
thm sed	*Thymus* spp.	Seed
thy pin	*Thelypteris palustris*	Pinnule
tri sed	*Triglochin maritimum*	Seed
ty1 rot	Type 1	Root
ty2 rot	Type 2	Root
typ epd	*Typha* sp.	Epidermis
typ sed	*Typha* sp.	Seed
urt sed	*Urtica dioica*	Seed
val sed	*Valerianella officinalis*	Seed

Table 4.3 CANOCO abbreviations for macrofossil data

4.3 Stonemarsh

4.3.1 Location and topography

Stonemarsh (grid reference: TM 255 252) lies at the eastern end of Hamford Water 3km north of Walton-on-the-Naze, Essex, sheltered within a sand/shingle spit (Figures 4.2). The marsh does not lie on an estuary and so freshwater discharge is minimal. It was still included in the research because no other extensive, undisturbed, mature, creek-dissected lower saltmarsh was identified in estuaries visited during the preliminary fieldwork.

4.3.2 Vegetation and surface litter

Samples were collected from an aggrading creek-bed supporting a mosaic of mudflats and pioneer vegetation grading into lower-mid saltmarsh communities (Table 4.4, Figure 4.2). Pioneer vegetation consisted mainly of SM8 annual *Salicornia* community growing along creek edges and point-bars. This graded into SM10 transitional vegetation dominated by *Suaeda maritima, Salicornia* spp., *Aster tripolium, Puccinellia maritima* and *Spartina anglica.* Higher areas on the saltmarsh supported a mosaic of SM13 *Puccinellia maritima* community, SM13 *Limonium* sub-community and SM14 *Atriplex portulacoides* community. The latter also dominated the higher areas of saltmarsh to the east and west of the sample site.

Plant litter was sparse on all examined surfaces. The mudflats were generally devoid of surface litter, although a few stem fragments and leaves were occasionally present. Pioneer stands of vegetation contained only sparse stems of dead pioneer taxa such as *Salicornia* spp. and *Suaeda maritima.* Surface litter increased markedly in the more dense vegetation, dominated by stem and leaf matter, especially stems of the Poaceae taxa and the aerial parts of *Atriplex portulacoides.*

4.3.3 Sampling

Seven 200cm^3 samples from across the sample site were analysed, along with 14 samples from Block 3. Block 3 was collected from a point par at the eastern edge of the site and had a sparse surface growth of *Salicornia* spp.. Samples were analysed from the mudflats (Samples 09/01/01, 09/01/02) and creek edges (09/01/06) at the south of the site. Others were analysed from pioneer vegetation (Block 3, 09/01/07 and 09/01/08), transitional vegetation (09/01/09) and the low-saltmarsh vegetation to the north (09/01/13).

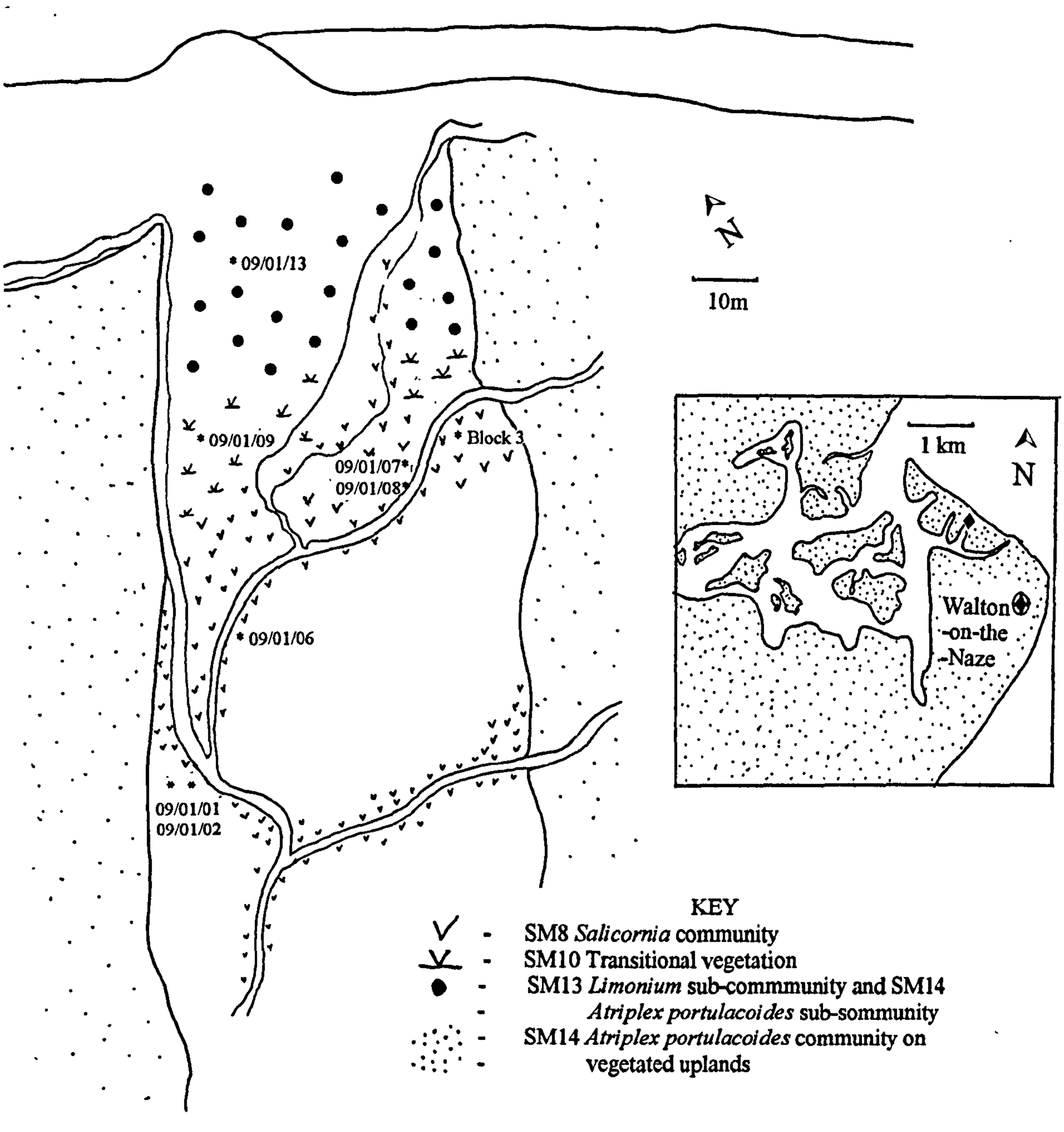


Figure 4.2 Map of Stonemarsh showing sample points. Inset shows location of sample area (marked ♦)

Sample	09\01\01	09\01\02	09\01\06	09\01\07	09\01\08	09\01\09	09\01\13	Block 3
Distance	0m	0m/17mE	20m	48m/32mE	48m/32mE	55m	86m	60m/40mE
Troels-Smith	Ag4As+Gmin+Dh+	Ag4As+Gmin+Dh+	Ag2As1Gmin1	Ag3Dh1Gmin+As+	Ag3Dh1Gmin+As+	Ag3As1Dh+Gmin+	Ag3As1Dh+Gmin+	As3Ag1
Colour	10YR4/3	10YR4/4	10YR4/3	5Y 4/2	2.5Y 3/2	2.5Y 4/2	10YR 4/3	10YR 4/3
% Water	37.72	36.45	27.4	44.72	43.19	44.35	45.04	48.3
% organic	11.42	11.36	6.66	14.51	14.99	15.59	14.24	13.9
Cover Abundance								
Aster tripolium						1		1
Atriplex portulacoides							7	
Limonium sp.							5	
Puccinellia sp.				4	4	6	5	
Salicornia sp.			4	8	8	7	5	9
Sarcocornia perennis							2	
Spartina anglica						2		
Spergularia media							3	
Suaeda maritima				4	4	5		1
Open	10	10	9					
Distance of nearest example								
Aster tripolium			10-50m			<0.5m		
Atriplex portulacoides	5-10m	5-10m	5-10m			5-50m	<0.5	
Limonium sp.			5-10m			5-50m	0.5-2m	2-5m
Puccinellia sp.						<0.5m	0.5-2m	
Salicornia sp.	0.5-2m	0.5-2m	0.5-2m	<0.5m	<0.5m	<0.5m		<0.5m
Sarcocornia perennis							0.5-2m	
Spergularia media							<0.5m	
Suaeda maritma	10 – 50m	10 – 50m	2-5m	<0.5m	<0.5m	<0.5m	5-10m	5-10m

Table 4.4 Stonemarsh standing vegetation, sediment and distance data

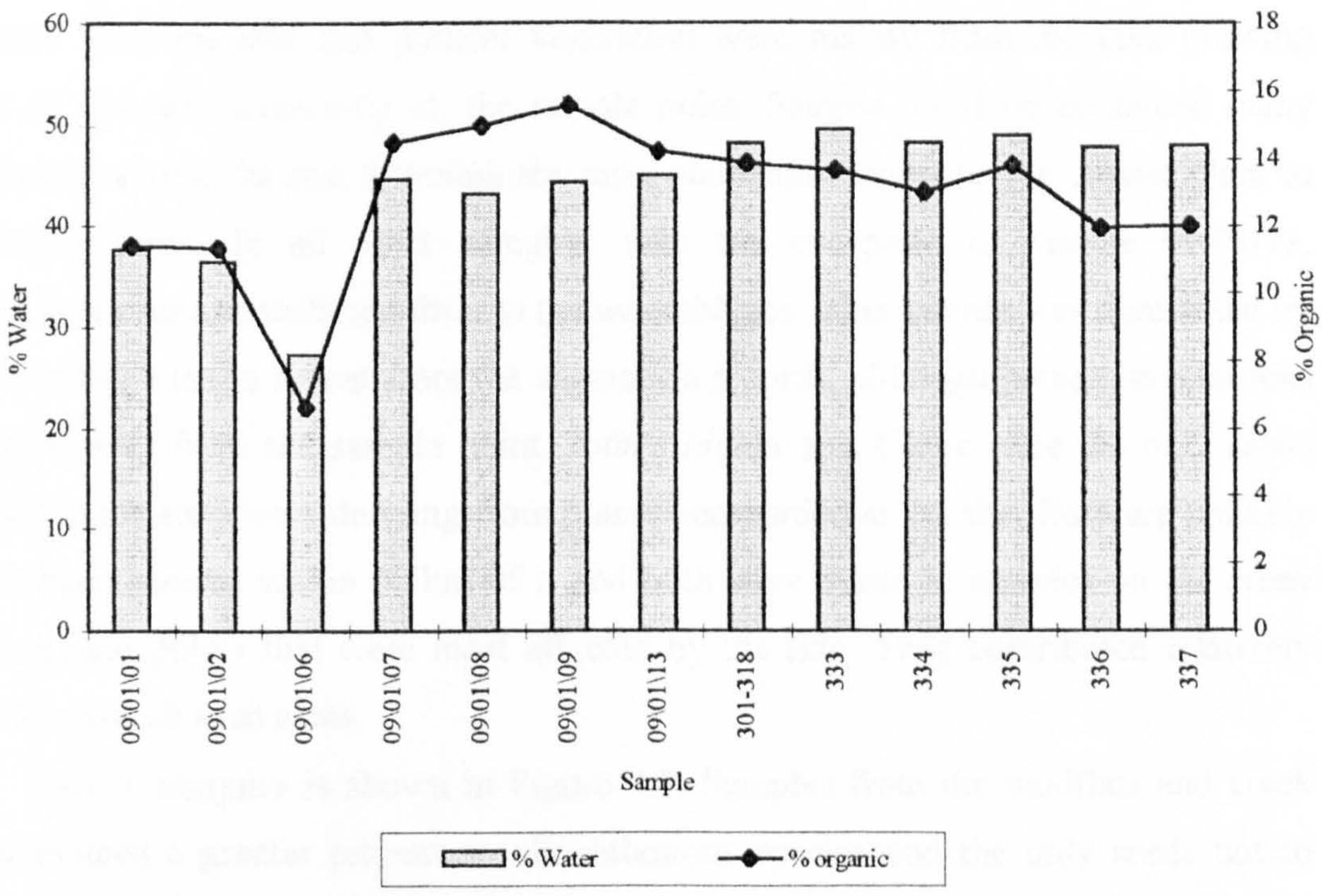
	Sample	09\01\01	09\01\02	09\01\06	09\01\07	09\01\08	09\01\09	09\01\13	301	302	303	304	307	314	315	316	318	333	334	335	336	337
	Sample Size	200	200	200	200	200	200	200	50	12.5	12.5	25	25	50	50	12.5	25	50	50	50	50	50
Taxon	Position	Surface	Surface	Surface	Surface	Surface	Surface	Surface	0	0	0	0	0	0	0	0	0	2-4cm	4-6cm	6-8cm	8-10cm	10-12cm
1 Seeds and Fruits	Component																					
Aster tripolium	Seed			1																		
Carex sp.	Seed			1																		
Limonium sp.	Calyx			1				5														1
Puccinellia sp.	Seed						7	21														
Rubus idaeus	Seed		2	2																		
Salicornia sp.	Seed	23	14	32	123	87	90	24	23	8	9	9	11	21	19	9	11	12	7	7	4	6
Spergularia media	Seed							14														
Suaeda sp.	Seed	2	1	17	4	3	32	94											1	1		
Poaceae	Spikelet	1																				
Indet.	Seed			1																		
2 Vegetative remains																						
Atriplex portulacoides	Leaf							6														
Atriplex portulacoides	Root	1	2					8														
Salicornia sp.	Stem			6	20	28			5	16	5	8	15	10	11	4	10		3	20	12	2
Salicornia sp.	Epidermis														4							
Suaeda sp.	Leaf	2	8	8	4	4	3															
Poaceae	Epidermis	2	4				1			5												
Poaceae	Stem				5		35	13	7	4	14	2		8	2				2			
Type 1	Root	23	32	13	10	13	28	59	56	48	55	55	55	46	56	57	38	72	81	17	42	58
Indeterminate	Wood	2	1						3	3		6	4	4	8	8	10	4	2	32	20	15
Indeterminate	Wood root								8	8	4	4	3	8	4	12	6	1				
Indeterminate	Herb matter	70	53	71	41	47	25	11	21	16	20	21	17	20	11	17	30	21	12	27	20	23
Indeterminate	Stem				20	8																
Indeterminate	Epidermis			2				3			2	4	6	4	4	2	6	2	2	4	6	2
Indeterminate	Rhizome						8															
3. Derived Indices.																						
Number of Seeds		26	17	55	127	90	129	158	23	8	9	9	11	21	19	9	11	12	8	8	4	7
Number of Species		3	3	7	2	2	3	5	1	1	1	1	1	1	1	1	1	1	2	2	1	2
Seeds concentration		0.130	0.085	0.275	0.635	0.450	0.645	0.790	0.460	0.640	0.720	0.360	0.440	0.420	0.380	0.720	0.440	0.240	0.160	0.160	0.080	0.140
Species concentration		0.015	0.015	0.035	0.01	0.01	0.015	0.025	0.02	0.08	0.08	0.04	0.04	0.02	0.02	0.08	0.04	0.02	0.04	0.04	0.02	0.04

Table 4.5 Stonemarsh plant macrofossil data and derived indices

4.3.4 Sediments

Sediments at the site were silt-clay mixtures with variable quantities of medium to coarse sand and organic matter (Table 4.4). Sand was found in greater quantities in mudflat and creek edge sediments and was almost absent in the saltmarsh sediments. Organic percentage values were low, between 10% and 16% (Table 4.4; Figure 4.3). Low values were attained for the mudflats and pioneer vegetation stands. Sample 09/01/06 returned the lowest organic and water content figures, perhaps as a result of increased oxygenation and drainage at the creek edge. Values increased in the more heavily vegetated marshes, as did the water content of the sediments. Both are probably correlated as the roots and other organic matter would be a major reservoir of water.

Figure 4.3 Stonemarsh Organic Content and % water by weight



4.3.5 Incorporation, sources and preservation of macrofossils

Macrofossils were preserved in all of the samples (Table 4.5), although some samples contained little classifiable material and few identifiable seeds. Non-seed macrofossil assemblages were dominated by rootlets, unidentifiable non-woody matter and aerial stem remains, especially of *Salicornia* spp.. Leaf remains were sparse, though some leaf fragments and epidermis fragments of *Suaeda* sp. and *Atriplex portulacoides* were

preserved. The assemblages from samples on the mudflats and in pioneer *Salicornia* vegetation included substantial quantities of apparently allochthonous plant matter. This included wood fragments and vegetative Poaceae remains, probably introduced to the sample sites by tides and wind. The samples in Block 3 contained many woody root remains, almost certainly of *Atriplex portulacoides* derived from eroded sediments. Much of the plant matter in the mudflat samples was highly comminuted, although large fragments were occasionally present.

Seed abundance in the 200cm^3 samples varied between 17 and 158, with species numbers varying between 2 and 5 species per sample (Figure 4.4). Seed abundance and concentration were higher in the sediments from the more highly vegetated, tidally isolated areas, seed concentration being comparable to other similar depositional environments. The species concentration figures obtained from the creek edge sample (09/01/06) were higher than those of other 200cm^3 samples from the site (Figure 4.5).

Most seeds were from plants present within 5m of the sample point (Figure 4.6), and those from mudflat and pioneer vegetation were mainly from the taxa growing closest to, but not necessarily at, the sample point. Sample 09/01/06 contained many taxa present across the site, although the most abundant taxon was the closest plant to the sample point. In all other samples, with the exception of sample 09/01/13, allochthonous taxa contributed little to the assemblages. This sample was dominated by *Suaeda* seeds, a taxon absent from the vegetation records, although present several tens of metres away from the sample point. *Rubus idaeus* and *Carex* were the only seeds recorded in the sediments deriving from plants unrecorded at the site. Both are unlikely to have been present within 0.5km of it and both were found in samples on the creek edges, sample points that were most affected by the tide. They contributed relatively few to the overall seed sums.

Sample ubiquity is shown in Figure 4.7. Samples from the mudflats and creek edge contained a greater proportion allochthonous species and the only seeds not to have derived from recorded vegetation. Seed assemblages in the vegetated sample points were dominated by autochthonous taxa and contained 60-80% of the taxa in the standing vegetation. The theropyhtes *Salicornia, Suaeda* and *Spergularia* were favoured, with *Puccinellia* commonly being absent. The best representation of species was in sample 09/01/13 where 80% of the taxa were present. Identified taxa in the non-seed assemblages from the mudflat samples were all allochthonous, although all were recorded in the nearby marsh vegetation. The creek edge sample contained

Figure 4.4 Stonemarsh seed and species abundance data

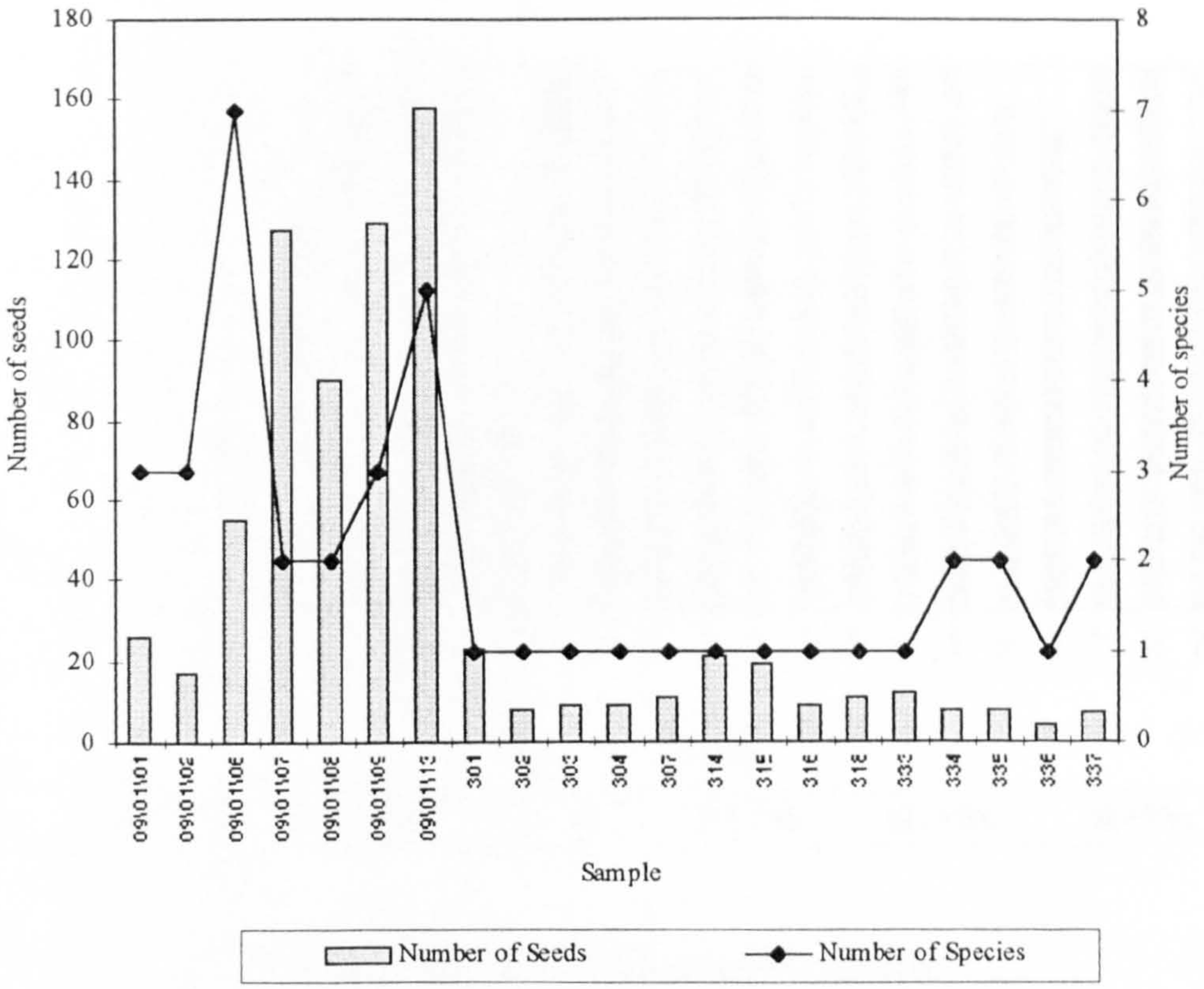


Figure 4.5 Stonemarsh seed and species concentration

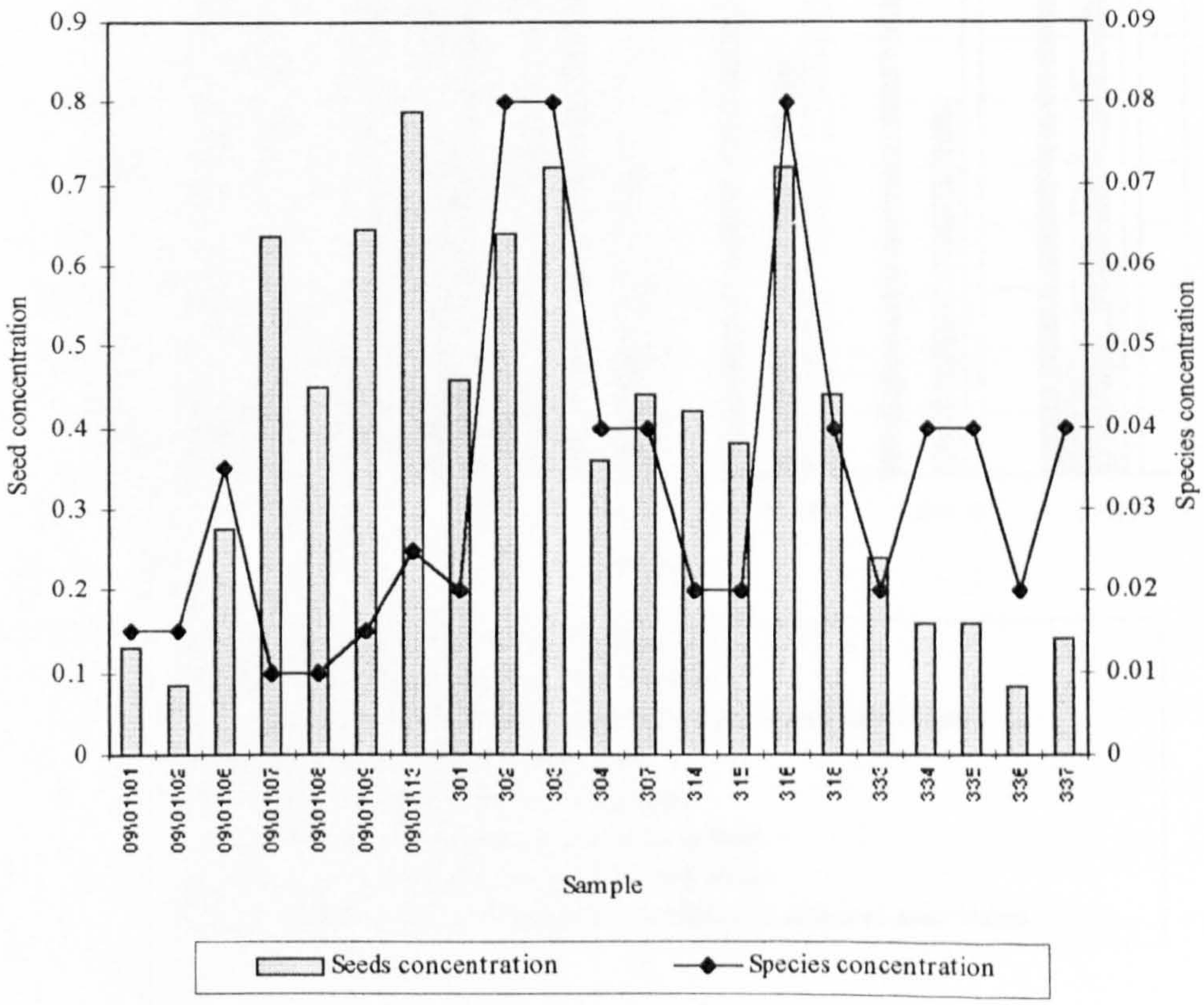


Figure 4.6 Stonemarsh: Percentage of seeds from plants at set distances from sample points

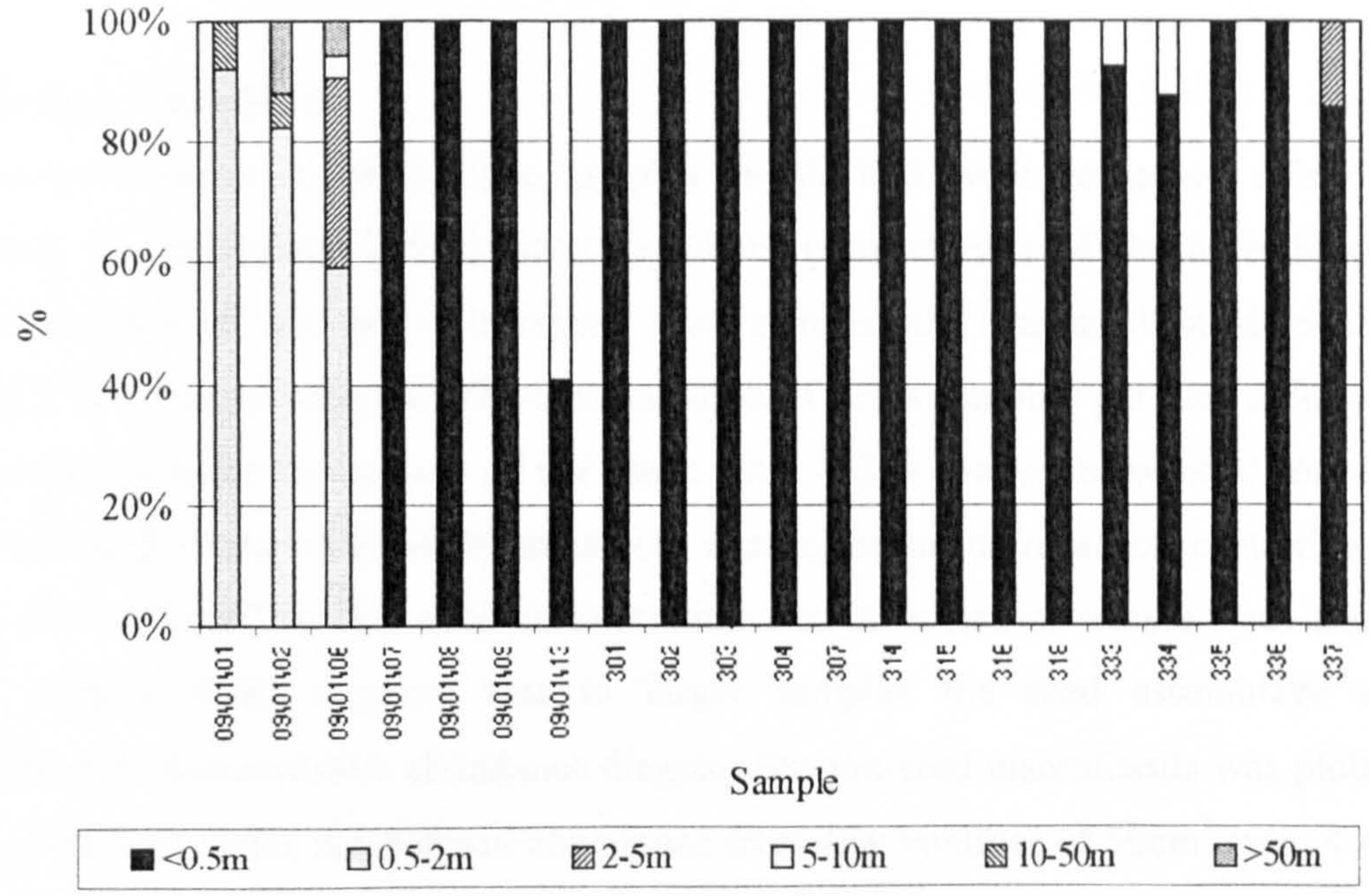
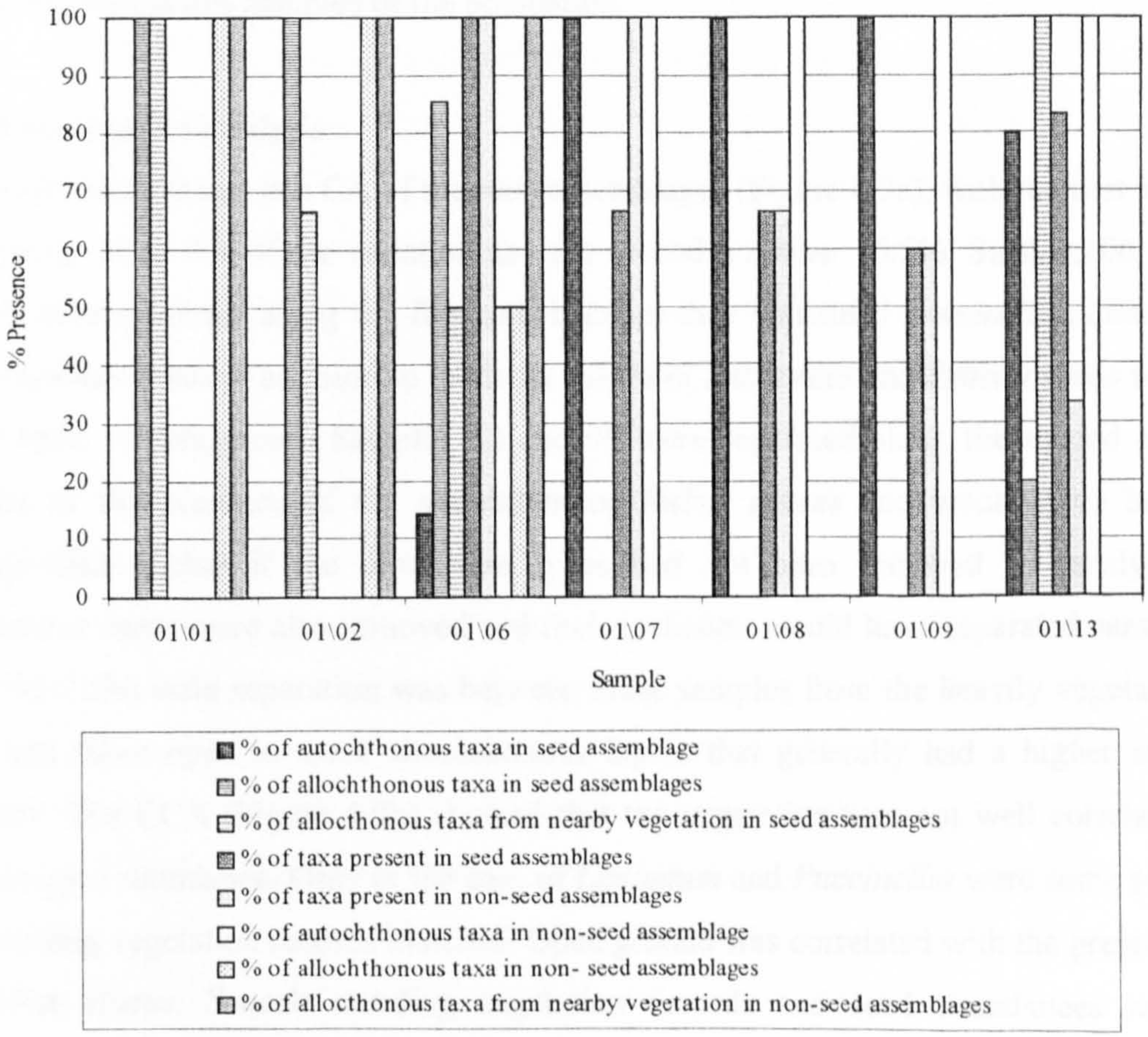


Figure 4.7 Stonemarsh area 01 sample ubiquity data



allochthonous and autochthonous taxa. Non-seed assemblages from the vegetated marshes contained only autochthonous taxa, although 33% - 67% of the taxa were absent from the non-seed assemblages in samples 8, 9 and 13.

4.3.6 Sample size effects

Seed assemblages from all surface samples in Block 3 were composed solely of *Salicornia* sp., providing little information about representivity of the assemblages. Seed abundance of this taxon increased with sample size, the smallest abundance coming from 12.5cm^3 samples. The concentration of seeds (number per cm^3 sediment) in the samples from the surface of the block (301 – 318) varied between 0.360 and 0.790, although those from the 50cm sample were close to the mean concentration of 0.436. This and the fact that seed concentration also stabilised at sample sizes above 50cm^3 (Figure 4.8a) suggests that in larger samples the seed assemblage are representative. A cumulative abundance diagram for non-seed macrofossils was plotted and showed very stable macrofossil abundance from low volumes of 50cm^3 (Fig. 4.8b) and achieved similar relative abundance from 25cm^3. Variation in the assemblages was within the observation errors of the recording method and the assemblages are thought to form representative samples of the population.

4.3.7 Quantitative analysis

Variability was limited in a CA of the seed assemblages (Figure 4.9a), with the first axis accounting for 64.4% of the variation and the second a further 16.5%. Samples 06, 09 and 13 were separated along the first axis because they contained *Puccinellia, Suaeda* and *Limonium* seeds in addition to the large values of *Salicornia* and *Suaeda* seeds seen in the main sample group. Samples 02 and 06 were separated along the second axis because of the presence of the allochthonous *Rubus idaeus* and would have been distinguished further if the other rare types had not been removed for analysis. *Spergularia* seeds were also removed and their inclusion would have separated sample 13 further. The main separation was between those samples from the heavily vegetated areas and those open to more allochthonous inputs that generally had a higher seed diversity. The CCA (Figure 4.9b) showed that the vegetation was not well correlated with the seed abundance. Only in the case of *Limonium* and *Puccinellia* were some seed and standing vegetation records matched. Open ground was correlated with the presence of *Rubus idaeus. Suaeda* standing vegetation records and seed abundances were

particularly badly correlated. *Salicornia* seeds were well dispersed and present when often a minor or missing vegetation element, however, larger sample composition was usually associated with local stands of the vegetation.

CA of non-seed macrofossils (Fig. 4.10a) produced a large homogenous cluster of samples from the block, with the other samples separated along the first and second axes in groups approximating to the environmental position. The eigenvalues were low for this analysis, among the lowest of the whole project, showing a small statistical difference in the non-seed cover abundance values. *Atriplex portulacoides* components, *Suaeda* leaves, *Poaceae* components, indeterminate stem and rhizome were the main positive components of the first axis. The non-block samples contained larger quantities of these remains, with the block samples distinguished by the larger quantity of rootlets and woody components. Mudflat samples 01 and 02 contained a mixed assemblage of non-seed macrofossils, with small quantities of rootlets. Larger quantities of stem material and *Suaeda* leaves separated the creek edge sample 6 and the pioneer vegetation in samples 07 and 08. The transitional sample 9 contained large quantities of Poaceae stem components and rhizomes, both deriving from the local sward of *Puccinellia*. Sample 13 was well separated by the presence of *Atriplex portulacoides* leaves and roots. The block samples were separated from the others by the high values of indeterminate matter, especially the wood and epidermis fragments.

CCA of the assemblages (Figure 4.10b) showed a correlation between *Salicornia* presence and stem remains (including epidermis). *Atriplex portulacoides* presence was also well correlated with the preservation of leaves of the species. *Puccinellia* and *Spartina* were only correlated with macrofossil equivalents (Poaceae stem and epidermis) in the areas where the taxon was abundant. *Suaeda* was poorly correlated with the presence of its leaves.

A CA of the combined data (Figure 4.11a) split the samples into groups corresponding to mudflat, pioneer vegetation, transitional vegetation and marsh environments. Again the eigenvalues were low showing that the sample composition varied little. Samples from the Block were clustered near the axis on the negative side of the first axis with high values of indeterminate matter, wood and *Salicornia* components. The other samples were separated by the presence of large quantities of specific macrofossils, such as *Puccinellia* seeds, *Atriplex portulacoides* components and *Suaeda* leaves. Samples 01, 02, 06, 07 and 08 were only separated along the second axis on the basis of the lower counts, among others, of the rootlets and well dispersed items

Figure 4.8a Stonemarsh cumulative seed concentration for Block 3

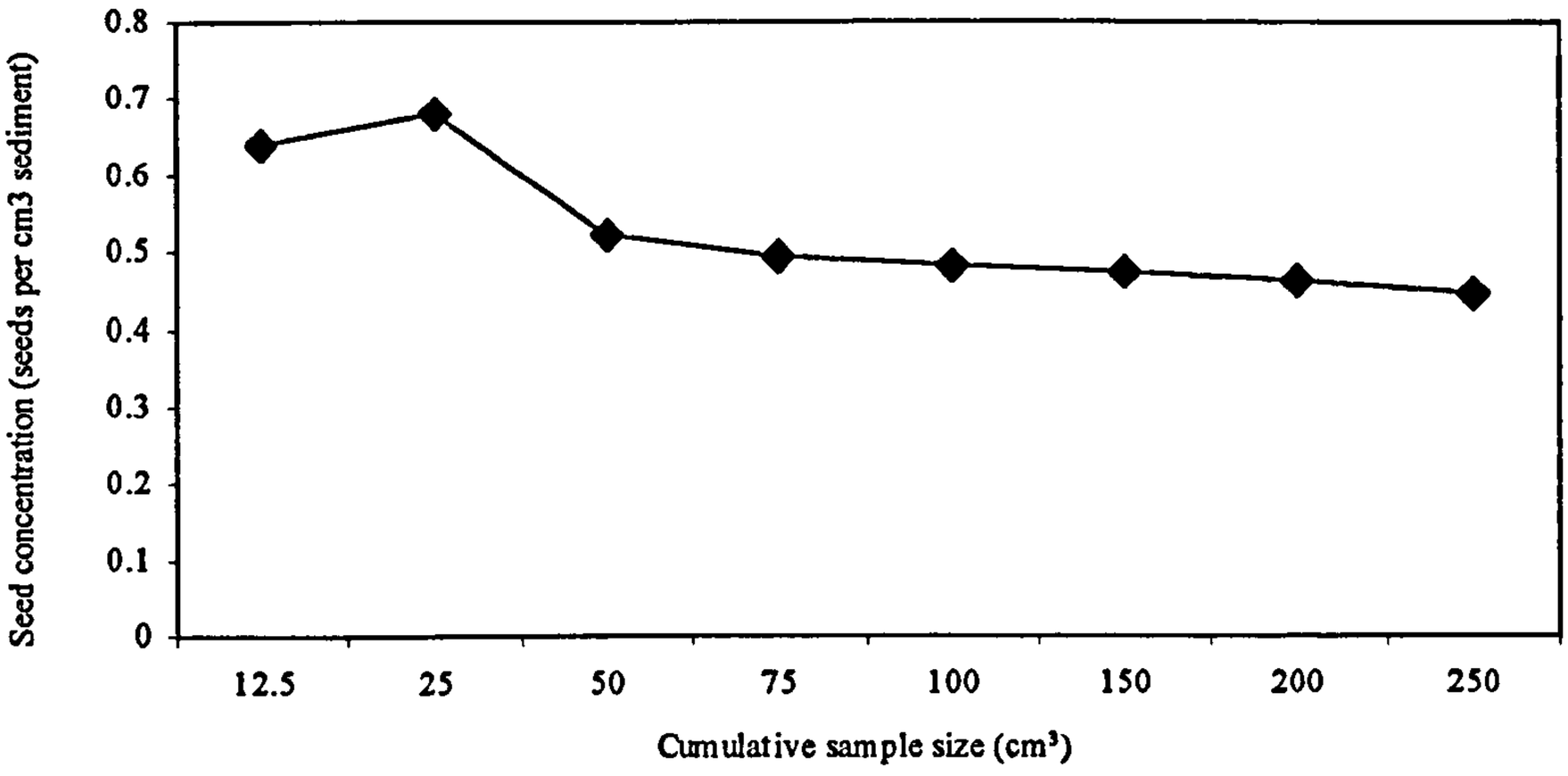


Figure 4.8b Stonemarsh: Cumulative percentage plots for major non-seed elements

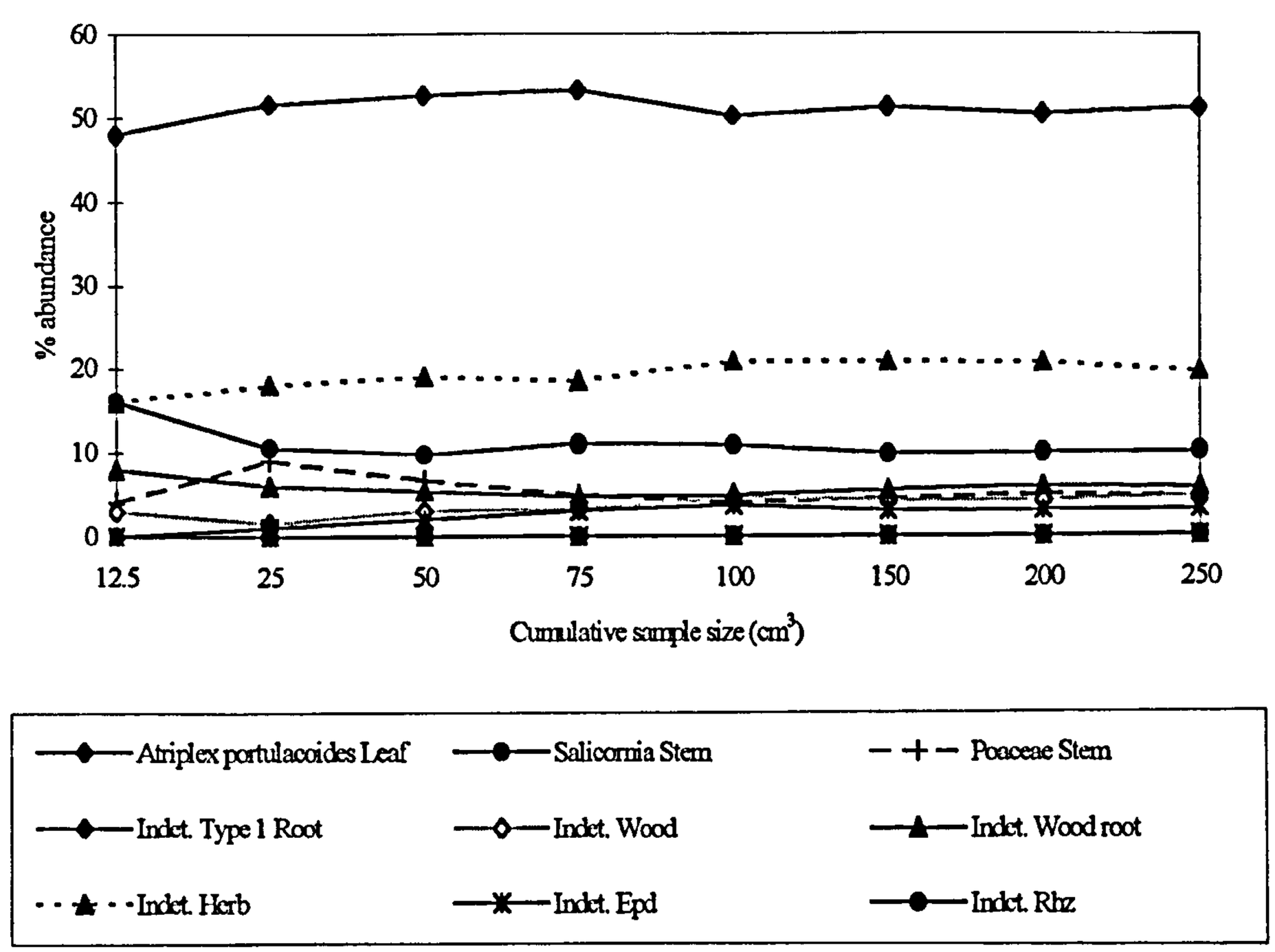


Figure 4.9a Correspondence analysis of seed data from Stonemarsh

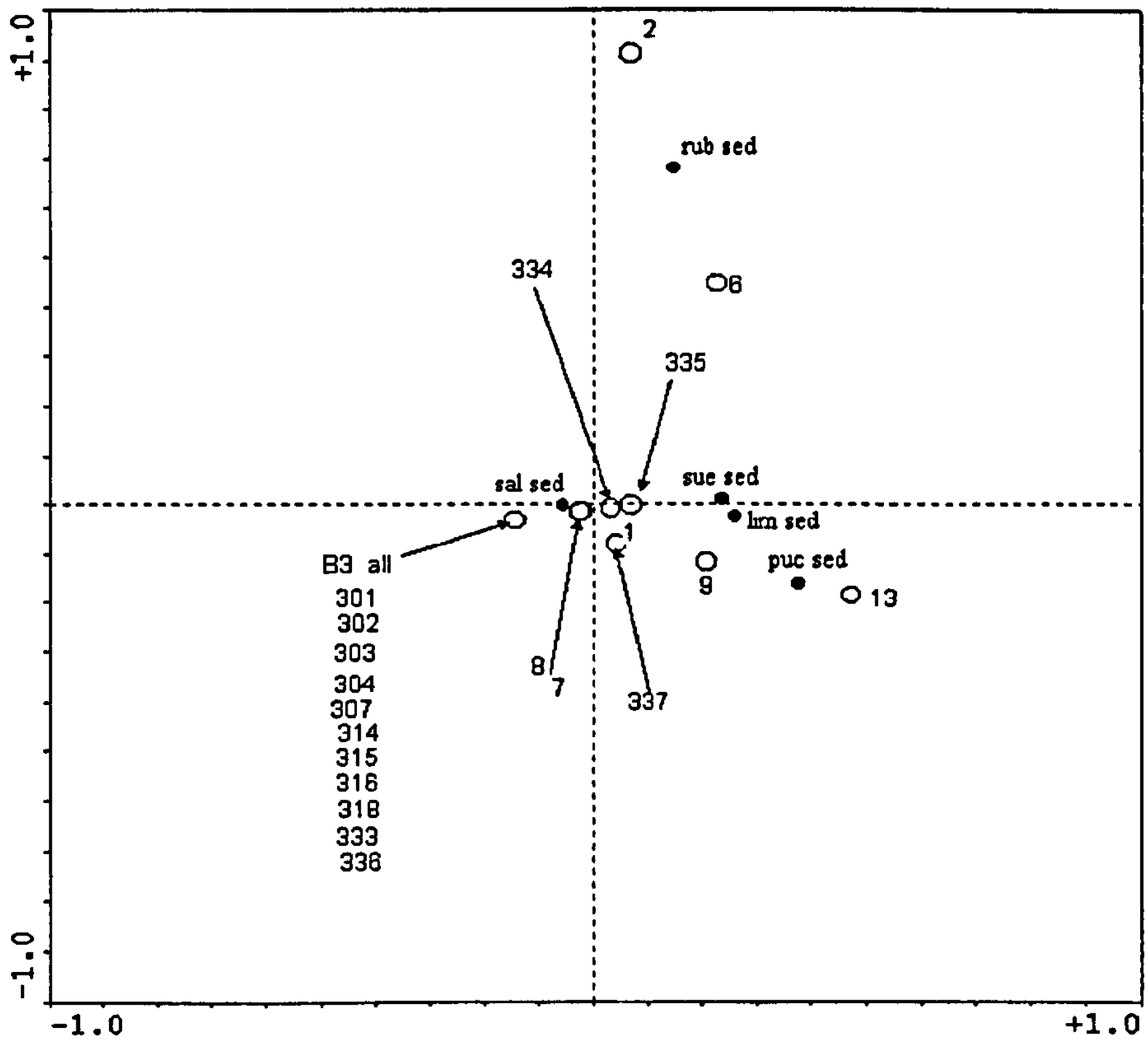


Figure 4.9b Canonical correspondence analysis of seed data from Stonemarsh

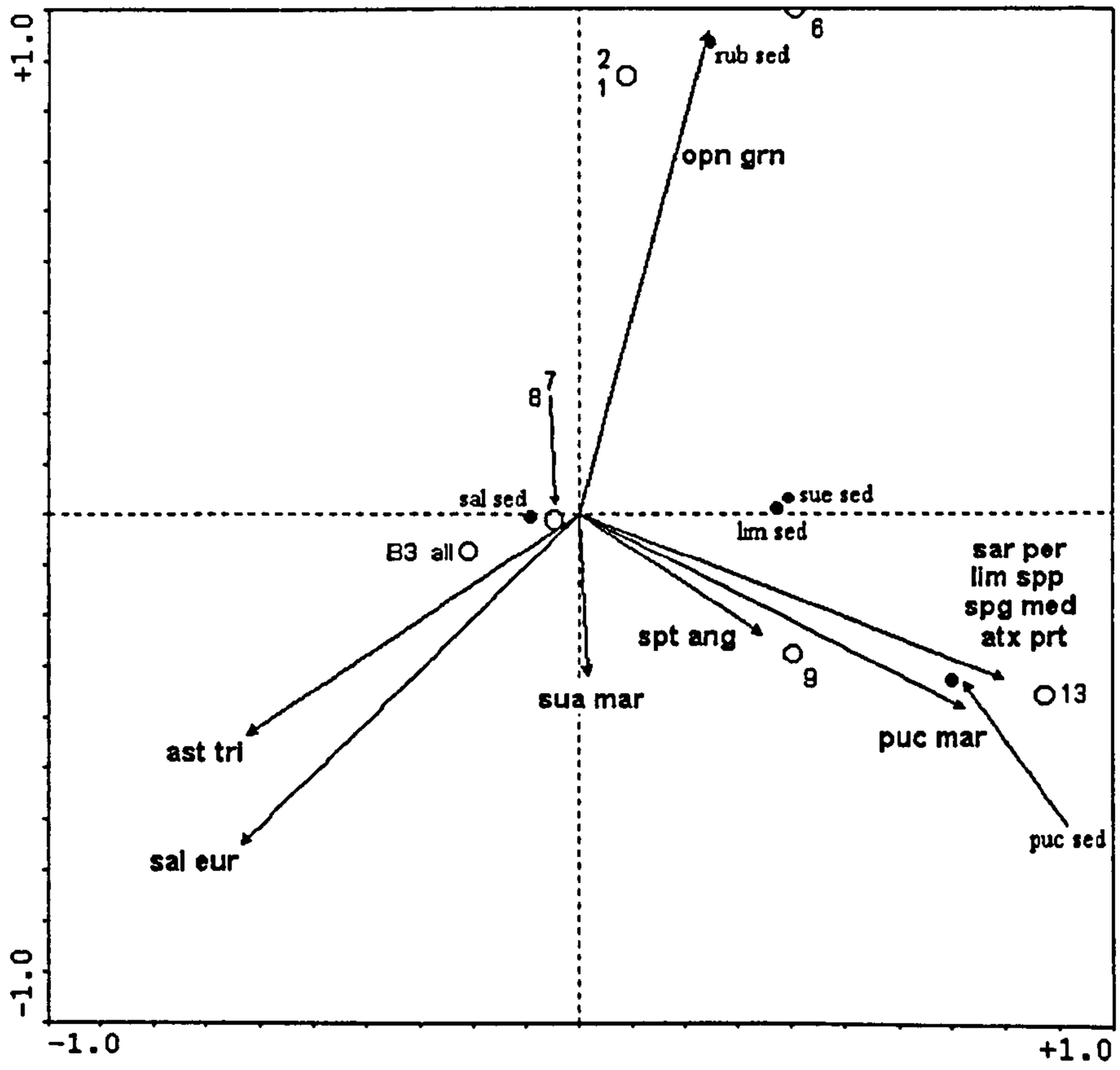


Figure 4.10a Correspondence analysis of non-seed data from Stonemarsh

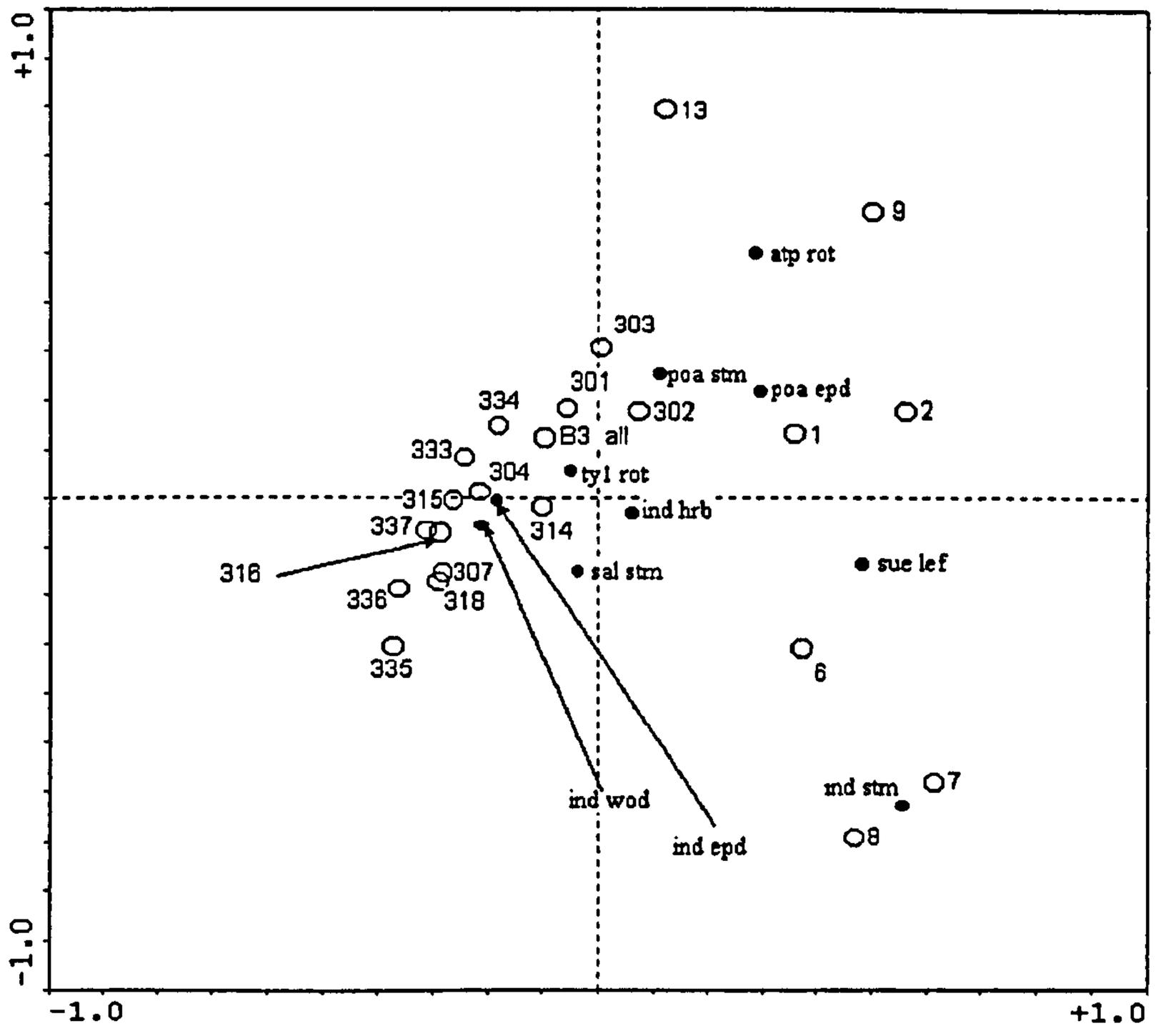


Figure 4.10b Canonical correspondence analysis of non-seed data from Stonemarsh

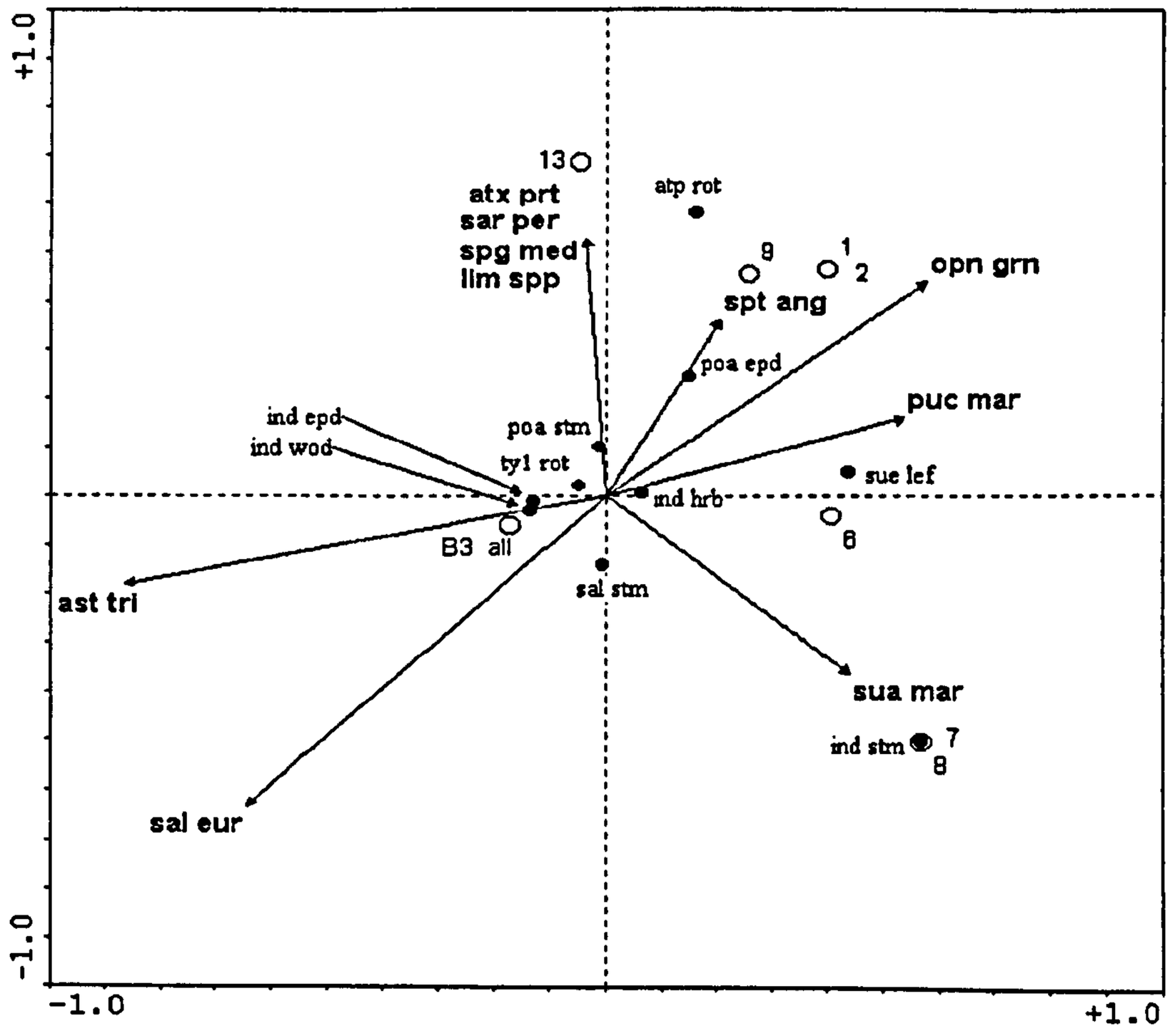


Figure 4.11a Correspondence analysis of seed and non-seed data from Stonemarsh

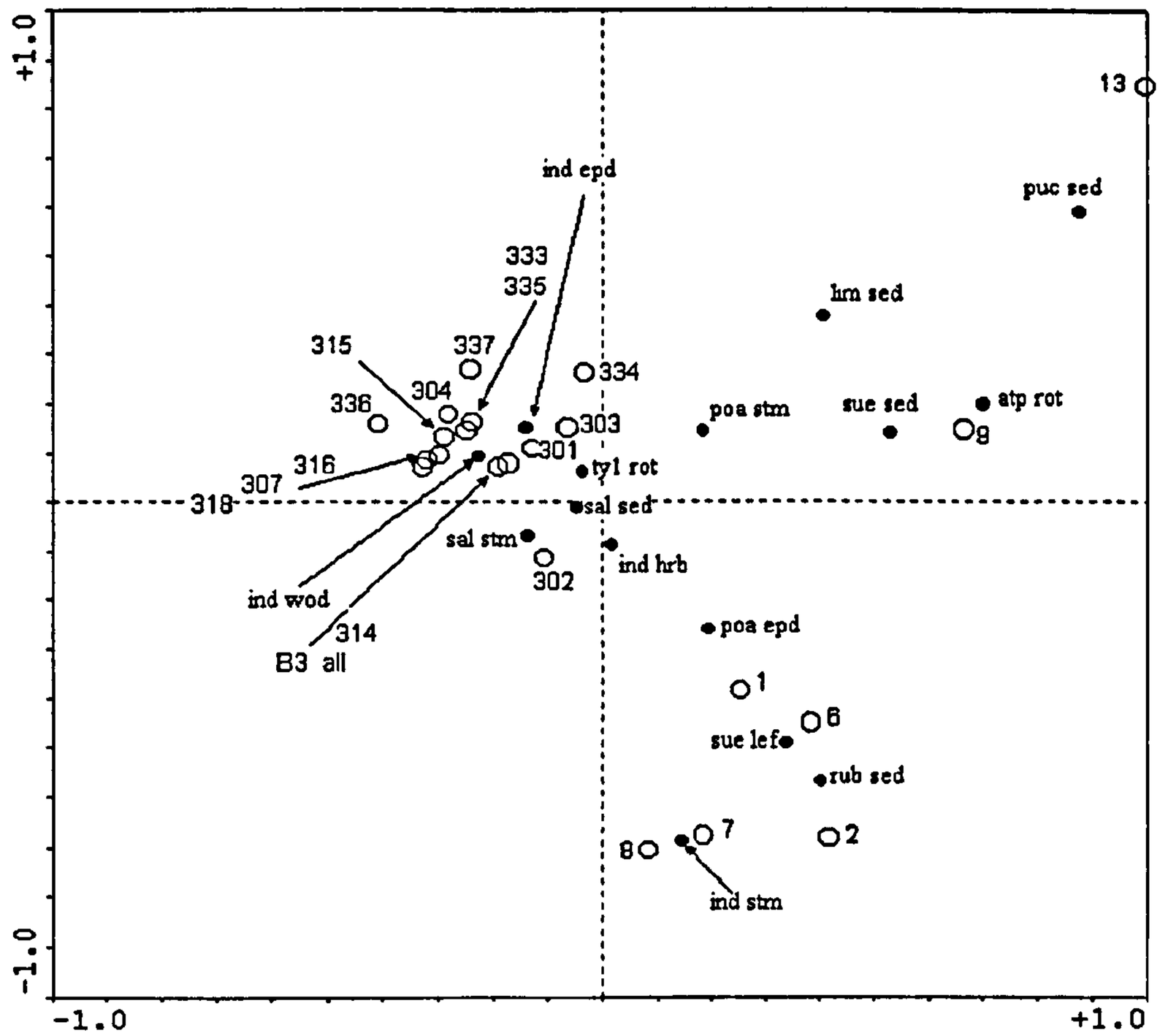
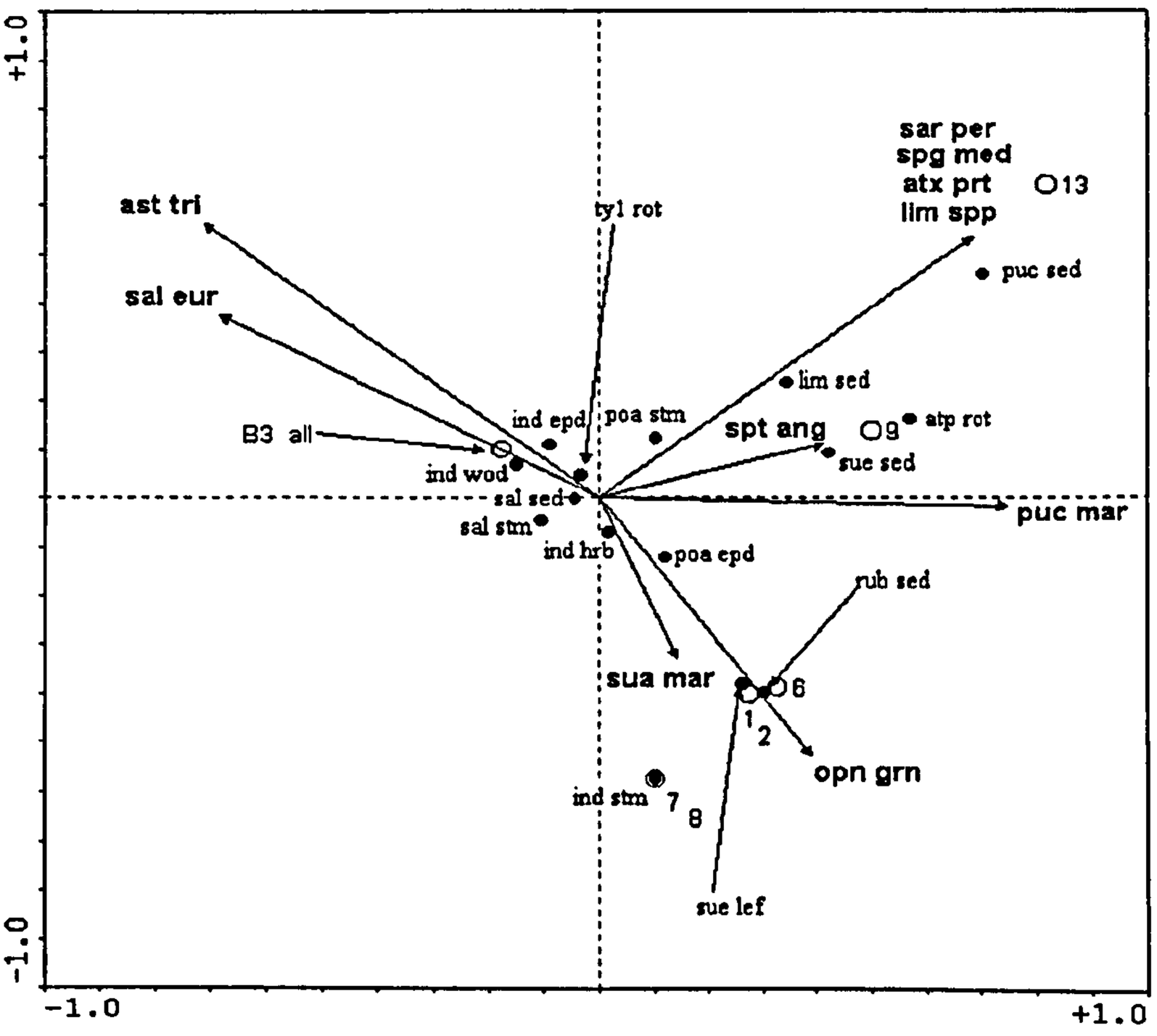


Figure 4.11b Canonical correspondence analysis of seed and non-seed data from Stonemarsh



such as *Rubus* seeds and *Suaeda* leaves and the presence of eroded stem material in samples 07 and 08. All of these are indicative of exposure to greater tidal exposure and that is the main environmental difference picked out by the quantitative analysis.

Several macrofossil components showed a reasonable correlation with standing vegetation occurrences in a CCA (Figure 4.11b). These included *Salicornia* stems and leaves, *Atriplex portulacoides* rootlets and *Puccinellia* seeds. *Suaeda* seeds were poorly correlated with presence of the species in the vegetation. Had they been included in the analysis, the seeds of *Spergularia* and leaves of *Atriplex portulacoides* would have been highly correlated with the vegetation records.

4.3.8 Differences in depositional environment

There were broad differences between samples from the different depositional environments. Those from the mudflats and creek edge contained the lowest overall quantities of macrofossils, often containing heterogenous assemblages of poorly preserved remains. These assemblages contained the highest proportion of unidentifiable matter, although all of the samples contained substantial values. The creek edge sample contained large quantities of seeds, with allochthonous as well as local taxa likely to be represented. The vegetated areas of the saltmarsh contained progressively larger quantities of plant remains, especially well preserved rootlets, stems and leaves. Seed concentrations also were higher in the vegetated areas. Much of the variability between the vegetated areas was due to the characteristics of the taxa in the standing vegetation.

4.3.9 Vegetation representation

Seed presence and abundance neither directly nor accurately reflected the presence nor abundance of taxa in the standing vegetation at most sample locations. In most cases, however, the seeds of plants dominant in the local vegetation were the most ubiquitous seeds in the sample set and usually dominated sample composition. One problem at this site was the low incorporation rates. Sample size was small and only 3 samples passed the target of 100 seeds used as a minimum figure for a representative assemblage. The conclusions drawn here do, therefore, have to be taken with the proviso that the samples may be unrepresentative. In the mudflat and block samples the seed assemblages were usually dominated by important elements of the nearby vegetation. The seed assemblage from 09/01/06 on the creek edge consisted of a cross-section of the taxa

present across the marsh and included several allochthonous taxa. Samples 07 and 08 contained similar assemblages, lacking *Puccinellia,* which was present in the vegetation. *Puccinellia* seeds were only present where the plant was a major vegetation element, although it was under-represented in transitional sample 09, a sample dominated by therophyte seeds. Several taxa were not represented in the macrofossil assemblages in 09/01/09 and 09/01/13, including the dominant, *Atriplex portulacoides,* in the latter. Most other absent species were usually minor vegetation components.

Salicornia was usually over-represented and was widely dispersed across the sample area, even in the absence of the plant, although large quantities of the plants seeds were only present where the plant grew. *Suaeda* was similarly widely spread but present in smaller quantities, apart from sample 13 which it dominated, although there was little sign of the plant locally. These species are therophytes, reproducing by seed alone. The over-representation and wide dispersal of these taxa may, therefore, reflect abundant seed production and successful seed dispersal mechanisms in the intertidal zone. Taxa which reproduce by both vegetative growth and seed, including the geophytes (e.g. *Puccinellia*) and Chaemophytes (e.g. *Atriplex portulacoides*), were usually underrepresented in seed assemblages as were the perennial Dicotyledonous herbs, especially *Aster*.

Non-seed macrofossil abundance also proved to be a poor indicator of the abundance of plants in the local vegetation, although the most abundant local taxa often featured prominently in the macrofossil assemblages. An exception was *Atriplex portulacoides* which, even when locally dominant, was a minor macrofossil component. *Atriplex* was best represented by its roots and leaves. *Salicornia* stem remains tended to be abundant when that taxon was present in the local vegetation. *Suaeda* leaves were the only preserved non-seed macrofossil of the taxon and were found even where the taxon did not grow, showing that the macrofossils are well dispersed. Poaceae stem and epidermis remains were only abundant when taxa from the family (e.g. *Puccinellia*) were present locally. The best-represented taxa in the non-seed assemblages were the geophytes with widely spreading stem and root systems. Again Dicotyledonous herbs and the lone Chaemophyte were under-represented, as were the Therophytes.

The block samples contained only *Salicornia* seeds and the only large assemblages of woody material on the site, the latter almost certainly from *Atriplex* vegetation lying adjacent to the site. The unusual composition may be a result of the differential effects of sedimentation processes on the point bar, with the buoyant and

durable woody components being the only allochthonous macrofossils to be able to endure the constant water-movement and drying of the bar with tidal movement.

4.3.10 Sub-surface samples from sediment blocks

Sub surface sediment samples from block 3 (samples 333 - 337) showed increasing quantities of unidentifiable material and lower stem and rootlet abundance with depth, probably reflecting the earlier open mudflat environment. Seed assemblages were similar to those on the surface mainly containing the seeds of *Salicornia*, although lower samples included occasional other taxa. Seed abundance stayed static and species abundance was slightly higher in the lower samples. The seed and species concentration figures were among the lowest in the site. All of this supports the idea that the block shows increasing terrestriality towards the top of the profile and that recent developments at the site through sediment accumulation and vegetation invasion caused the differences between the surface and lower samples.

4.4 Borstal Marsh

4.4.1 Location and topography

Borstal Marsh lies on the River Medway near Rochester, Kent (grid reference: TQ 730673) (Figures 4.12a and b) on an aggrading reach of the river beneath a low chalk cliff. It includes a transition from mudflats through pioneer vegetation to low and mid-saltmarsh communities. The surface is inundated daily by the tide, although inundation of the upper reaches is restricted to spring tides only. A dry, non-saline ridge at the landward edge of the marsh supports non-halophytic plants, including *Taraxacum* spp. and various terrestrial grasses. A creek system is only slightly developed and the marsh sloped gently towards the waters-edge from the base of the dry ridge. The site is a close analogue to the Medway Tunnel floodplain site discussed in Chapter 5.

4.4.2 Vegetation and surface litter

Mudflats exposed at the river-edge (from ca. 70m) were colonised at a distance of 60m from the cliff by a sparse SM6 *Spartina anglica* and SM11/12 *Aster tripolium* communities with extensive patches of bare open ground (Table 4.6). SM10 Transitional saltmarsh vegetation at 50m was succeeded by dense SM13 *Puccinellia maritima* community sward from 40m. *Puccinellia maritima* was mixed with *Atriplex portulacoides* and occasional plants of *Triglochin maritimum*. SM11/12 *Aster tripolium*

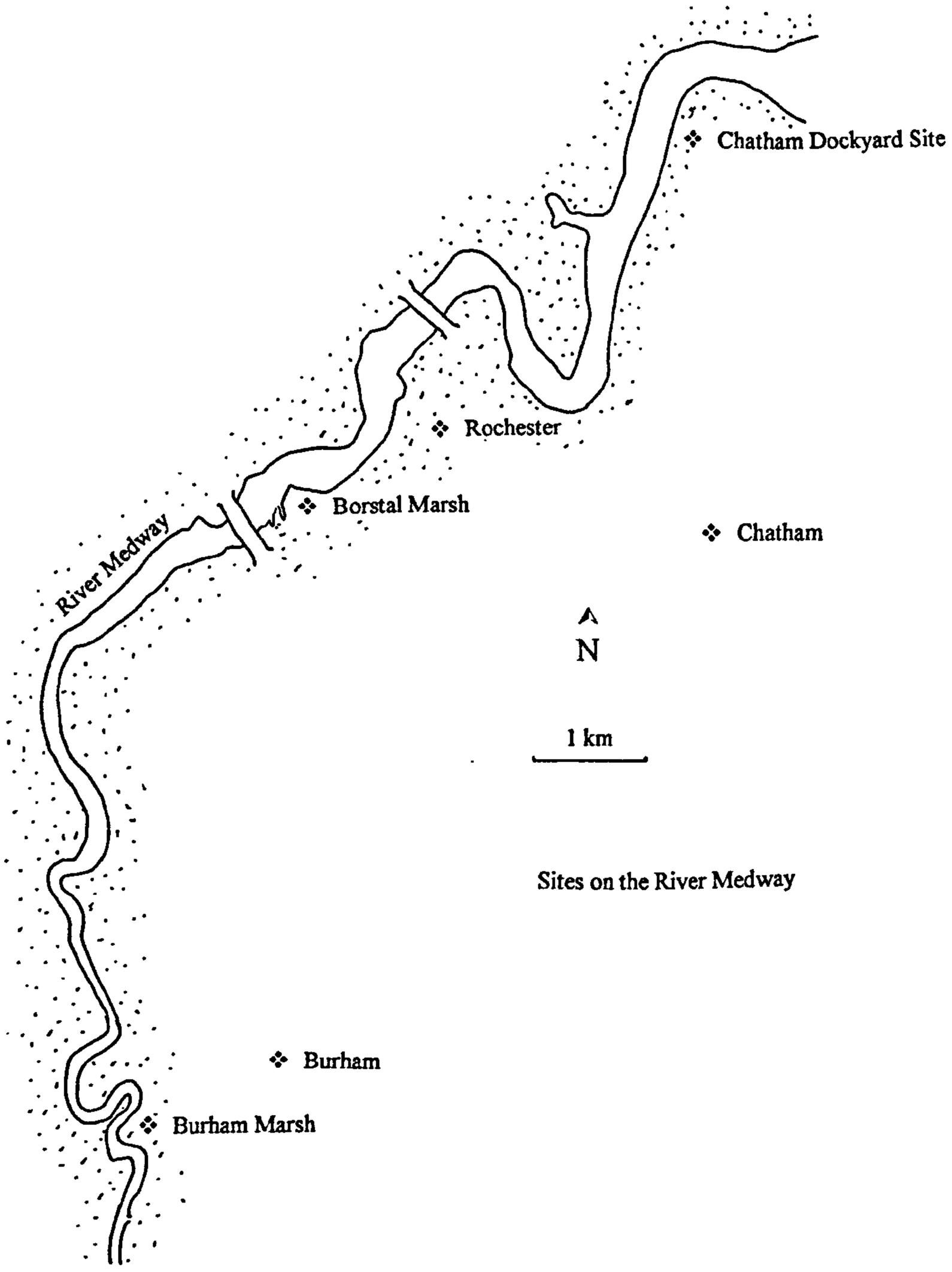


Figure 4.12a Sites on the River Medway

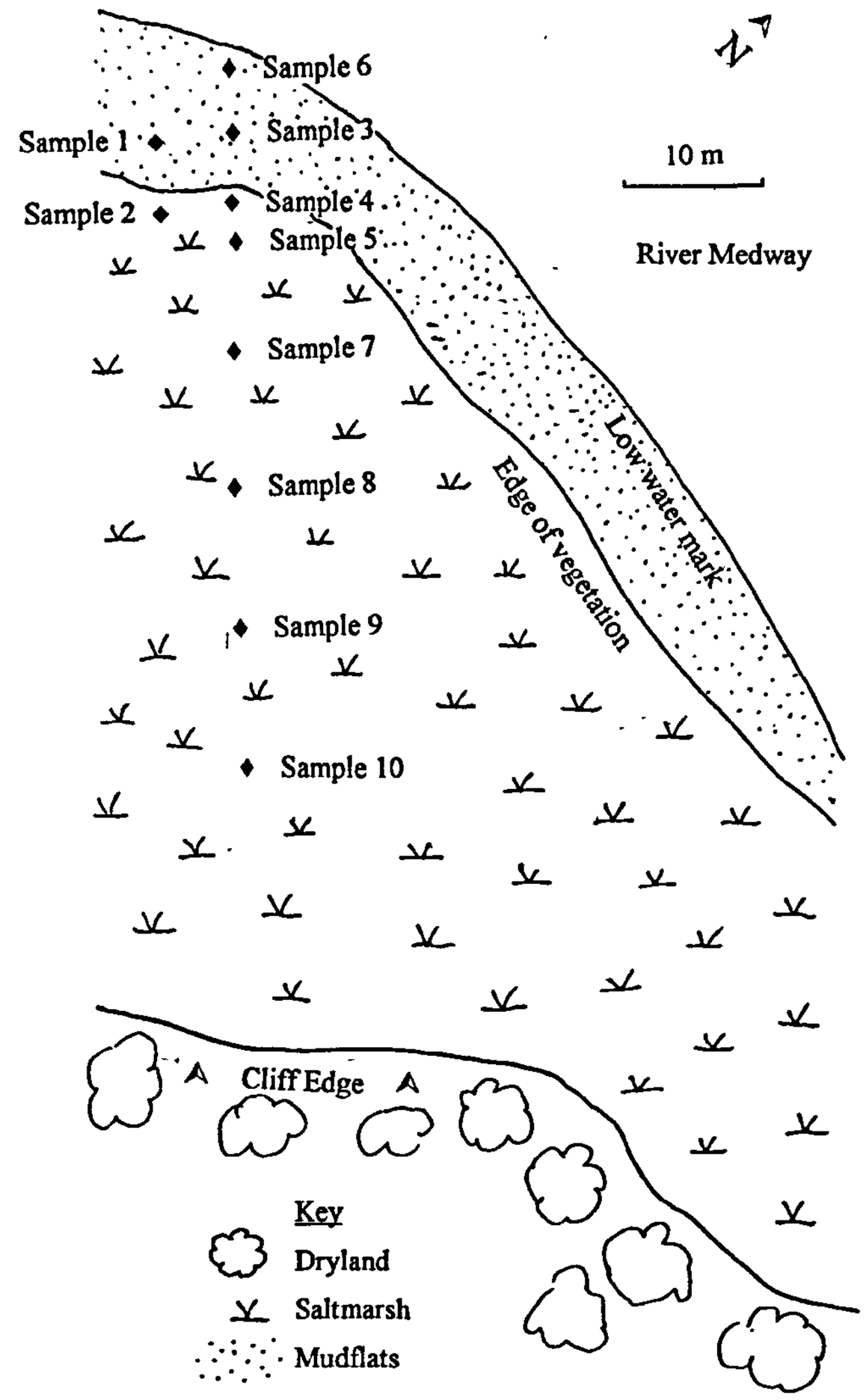


Figure 4.12b Borstal marsh sample points

Distance from dryland	70	65	60	58	50	40	30	20	65/5s	60/5s
Sample	1	2	3	4	5	6	7	8	9	10
Troels-Smith	Ag3As1	Ag3As1	Ag3As1	Ag3As1Dh+	Ag2As2Dh+	Ag2As1Th1	Ag2As1Th1	Ag2As1Th1	Ag3As1	Ag3As1
Sediment Description	Clay-Silt	Clay-Silt	Clay-Silt	Clay-Silt	Rooted Clay-Silt	Rooted Clay-Silt	Rooted Clay-Silt	Rooted Clay-Silt	Clay-Silt	Clay-Silt
Colour	2.5Y4\3	2.5Y4\2	2.5Y4\3	2.5Y4\3	2.5Y4\2	2.5Y4\3	2.5Y4\2	2.5Y4\3	2.5Y4\3	2.5Y4\2
% water	54.75	54.45	52.91	53.83	53.27	59.5	64.64	71.42	55.74	51.73
%organic	14.02	14.24	24.57	14.46	15.9	19.2	22.07	26.03	14.7	13.48
%inorganic	85.98	85.76	75.43	85.54	84.1	80.8	77.93	73.97	85.3	86.52
Cover Abundance										
Aster tripolium			7	9	3	4	4	4		
Atriplex prostrata						4	4	4		
Puccinellia maritima					9	9	9	9		
Spartina anglica			7							8
Triglochin maritimum						4				
Open ground	10	10	4	5					10	7
Distance of nearest plant of species										
Aster tripolium			<0.5m		<0.5-2m	0.5-2m	0.5-2m	0.5-2m	5-10m	
Atriplex sp.						0.5-2m	0.5-2m	0.5-2m		
Puccinellia sp.						0.5-2m	0.5-2m	0.5-2m		
Puccinellia sp.										
Salicornia sp.	10-50m			10-50m						
Spartina sp.			<0.5m		10-50m	10-50m	10-50m			
Suaeda sp.			10-50m				10-50m	10-50m		
Triglochin maritimum					5-10m	<0.5m			10-50m	

Table 4.6 Borstal Marsh Standing Vegetation and Distance information

	Sample	1	2	3	4	5	6	7	8	9	10
	Sample size	200	200	200	200	200	200	200	200	200	200
	Distance	70	65	60	58	50	40	30	20	65/5s	60/5s
Taxon	**Component**										
Seeds etc.											
1. Local taxa.											
Aster tripolium	Fruit			1		34	41	4	13	11	
Atriplex sp.	Seed						2	3	7		
Puccinellia sp.	Fruit						2	75	112		
Puccinellia sp.	Spikelet								14		
Salicornia sp.	Seed	4				5					
Spartina	Fruit			7		11	5	9			
Suaeda sp.	Seed			4		1		9	3		
Triglochin maritimum	Seed						11			5	
2.Other taxa.											
Alnus glutinosa	Seed	2			3					1	1
Callitriche sp.	Seed									1	
Juncus acutus type	Seed	1			1					5	
Juncus bufonius	Seed									1	2
Polygonum aviculare	Seed										1
Sagina sp.	Seed										1
Urtica dioica	Seed		2						1	1	
Lemna minor	Leaves	23			4		2		2	27	13
Poaceae	Ligule	2							1		2
Salix sp.	Stipule									3	2
Indet.	Moss leaf										1
Non-seed macrofossils											
cf. Chenopodiaceae	Epidermis									0.73	
Cyperaceae	Rootlets		0.2	0.2						1.53	0.99
Poaceae	Epidermis	9.25		2.4	1.56	9.8	2.81	3.2	1.67	5.93	0.94
Poaceae	Leaf		1.12	0.87		10.8				6.53	
Poaceae	Stem	7.03		2.53	42.1	4.8	5.1		1.4	3.13	4.59
Poaceae	Rhizome					15.6	55.36	51.87	62.07		
Type 1	Rootlets	2.82	3.28	2.8	1.83	51.47	35.54	44.53	34.2	2.2	2.99
Quercus sp.	Leaf	0.12									
Salix sp.	Leaf			1.8							
Sphagnum sp.	Leaf			1							
Dicotyledon	Leaf	0.51					0.6				0.4
Indet	Stem		4.35	30.67							5.94
Indet	Wood									2.67	
Indet	Indet.	80.29	91.04	58.73	51.8	6.07				77.27	84.14
Indet	Periderm				1.15	1.47					
Indet.	Epidermis				0.75						
Various	seeds	0.1					0.6	0.4	0.7		
Derived indices											
Seed abundance		7	2	12	9	46	61	100	150	25	5
Species abundance		3	1	3	3	3	5	5	5	7	4
Seed concentration		0.035	0.010	0.060	0.045	0.230	0.305	0.500	0.750	0.125	0.025
Species concentration		0.015	0.005	0.015	0.015	0.015	0.025	0.025	0.025	0.035	0.020

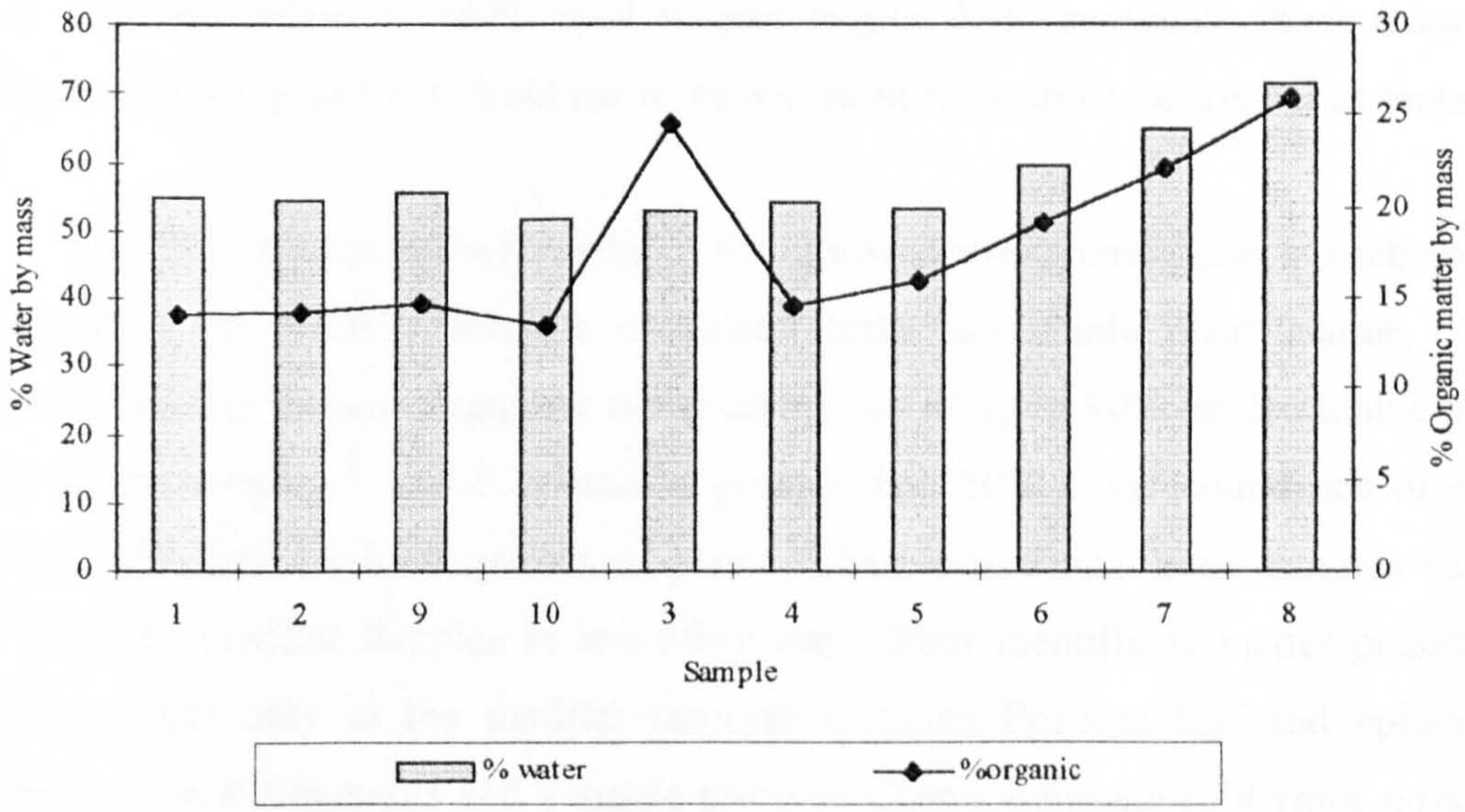
Table 4.7 Borstal Marsh plant macrofossil data and derived indices

vegetation was recorded in the landward depression. Vegetation on the cliff was tended parkland dominated by trees and shrubs, including *Quercus robur, Prunus spinosa, Fraxinus excelsior* and *Acer pseudoplatanus*.

4.4.3 Sampling

Samples of 200cm^3 volume were collected along a transect from the mudflats to the cliff base at approximately 10m intervals (samples 1 – 8), although samples were collected at closer intervals when the vegetation changed (Figure 4.12b). Samples 1 and 2 were from the mudflats at the river edge, with samples 3 and 4 from the transitional vegetation and samples 5-8 from dense marsh vegetation. A second pair of samples from the mudflat/pioneer vegetation were collected to the south of the main transect (samples 9 and 10). No samples were collected from 20 - 0m from the cliff because of considerable disturbance (caused by vehicles) at the cliff-edge and the lack of macrofossils in the aerobic soils of the ridge at the cliff base.

Figure 4.13 Borstal Marsh % Organic and water content



4.4.4 Sediments

Sediments were all fine-grained silt-mud mixtures and lacked sand components (Table 4.6). Sediments lying between 50m and the river-edge contained little obvious plant content, while those lying between 50m and the cliff base contained rootlets, often forming dense root mats. The paucity of incorporated organic matter is reflected in the loss-on-ignition figures (Fig. 4.13), all of which were below 30%, with those on the

mudflats being as low as 15%. A peak in the LOI figure for sample 3 may be caused by the presence of the roots of a locally dense sward of *Spartina*. The increase towards the cliff is the result of the presence of plants with extensive, dense root systems. Sediment water levels also increased towards the cliff base, being uniform in the mudflat samples.

4.4.5 Incorporation, sources and preservation of macrofossils

Macrofossils were preserved in variable quantities across the site (Table 4.7). The mudflat and transitional samples (1-4, 9-10) contained small quantities of poorly preserved and unidentifiable material and small seed densities. Seed abundance increased markedly towards the cliff edge (Table 4.6), although seed density/concentration remained below 0.8 seeds per unit sediment, similar to the riverward end of the Snape transect (see below). The species concentration was low at the mudflat fringe (0.015 or below (Figure 4.14)), rising to 0.035, again at the lower end of the range seen at Snape. The seeds in samples on the mudflats were largely from species absent in the area (Figure 4.15), indicating the influence of tidal processes on seed assemblage composition. The landward samples contained seed assemblages composed mainly of local seeds from plants within 5m of the sample point or on the marsh. The population of seeds used to plot Figure 4.15, especially those from the mudflats, was small and the conclusions drawn from them must be treated as tentative only.

Non-seed macrofossil assemblages also showed strong tendencies at each end of the transect. The mudflat samples contained little identifiable plant matter, cover abundance figures for some samples being composed of up to 90% unidentifiable plant matter. Only samples 5 and 6 contained greater than 20% cover abundance of stem material, reflecting the local growth of plants. These transitional zone samples varied little from the mudflat samples in any other way. Other identifiable matter present in small quantities only in the mudflat samples included Poaceae leaf and epidermis fragments, rootlet fragments and a single piece of Chenopodiaceae epidermis, possibly from nearby *Salicornia* and *Suaeda* stands. Fragments of *Quercus* and *Salix* leaves were also identified in the mudflat samples, along with the only wood in the sample set. Assemblages from the landward samples contained larger, less fragmented macrofossils than those from the mudflats. Most plant material in the marsh samples (5-8) was classifiable, if not identifiable. Rootlets and stem/stolon sections from Poaceae taxa, presumably *Puccinellia*, dominated assemblages.

Figure 4.14 Borstal Marsh seed and species concentration data

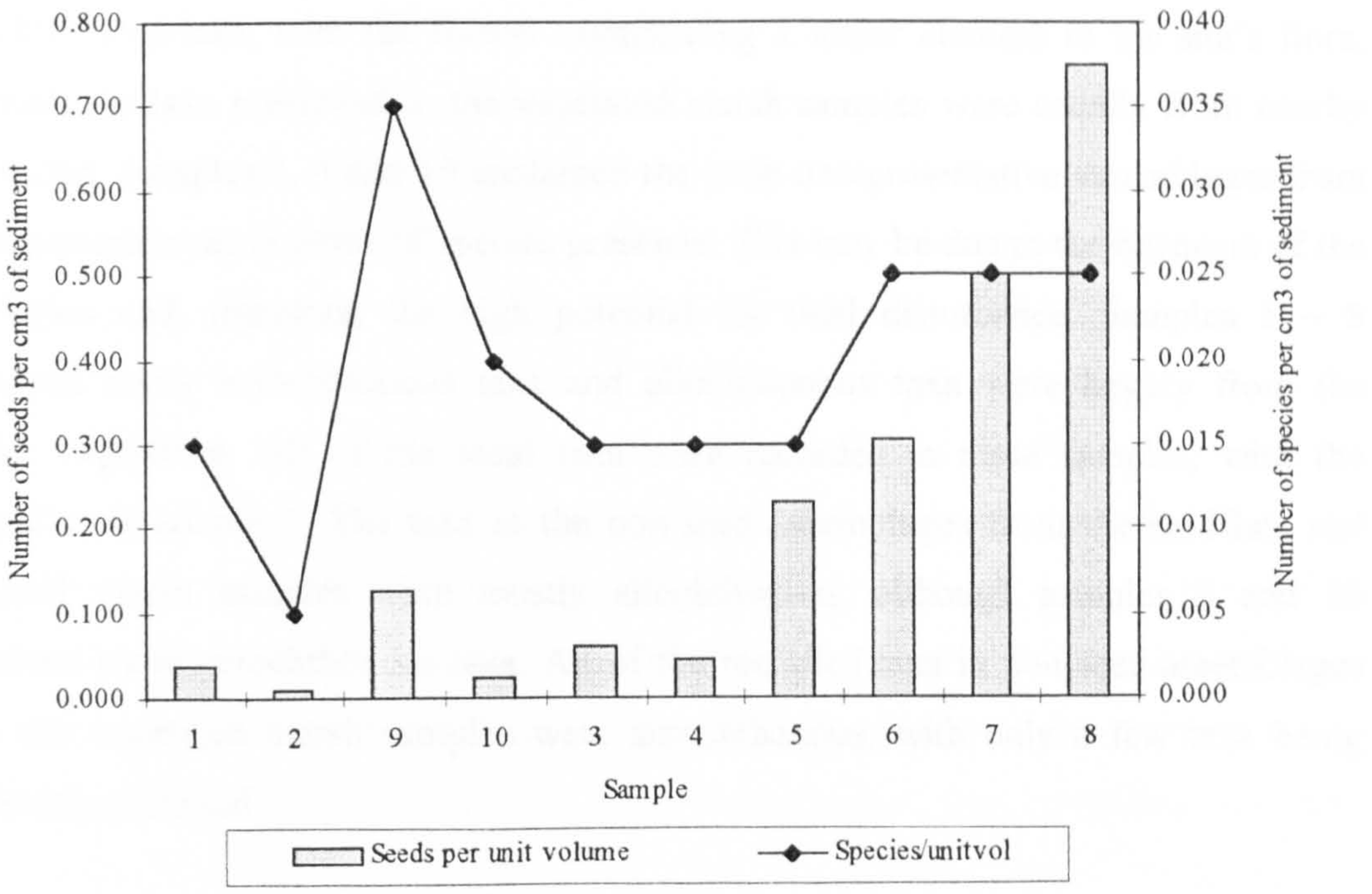
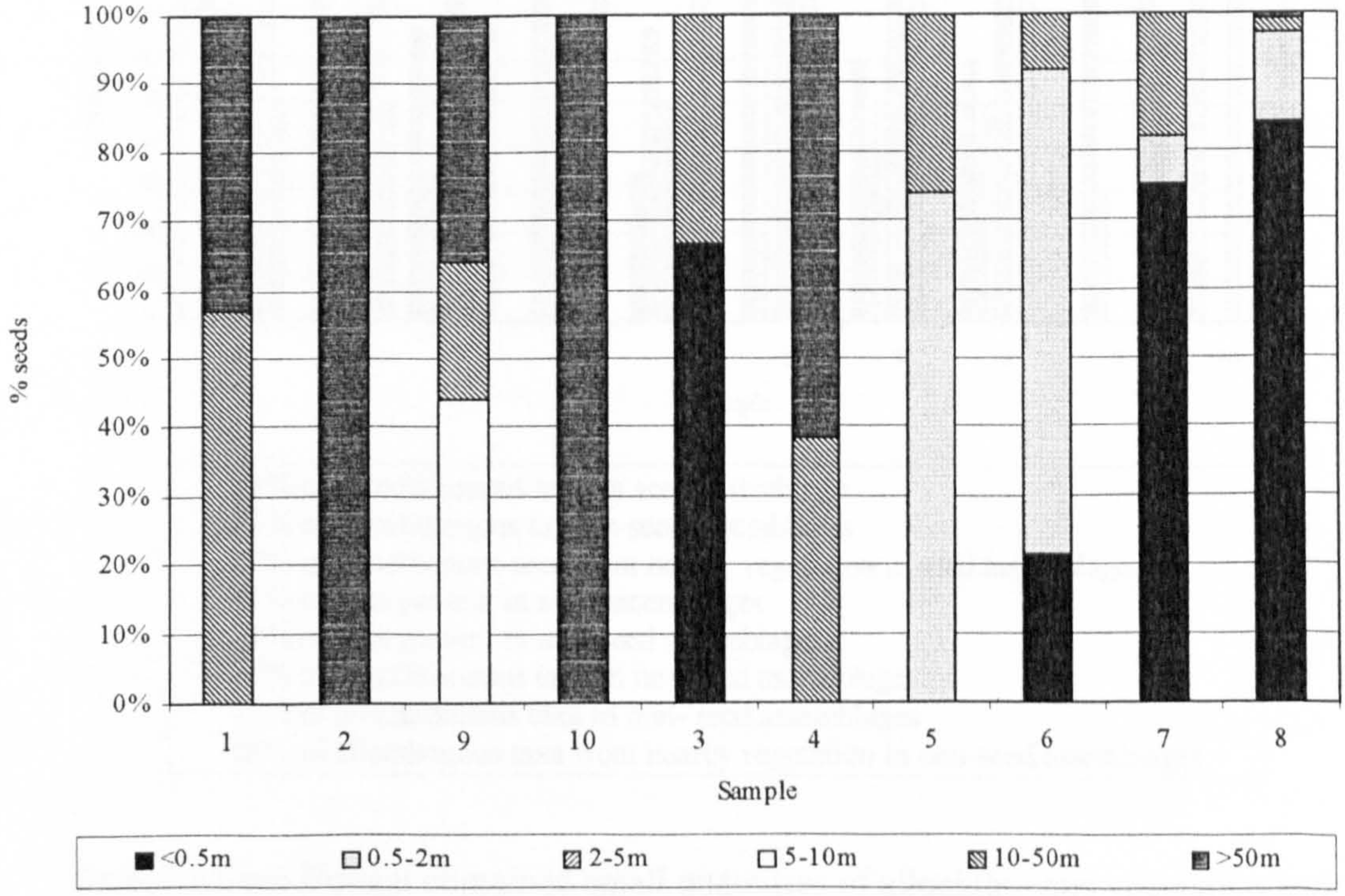
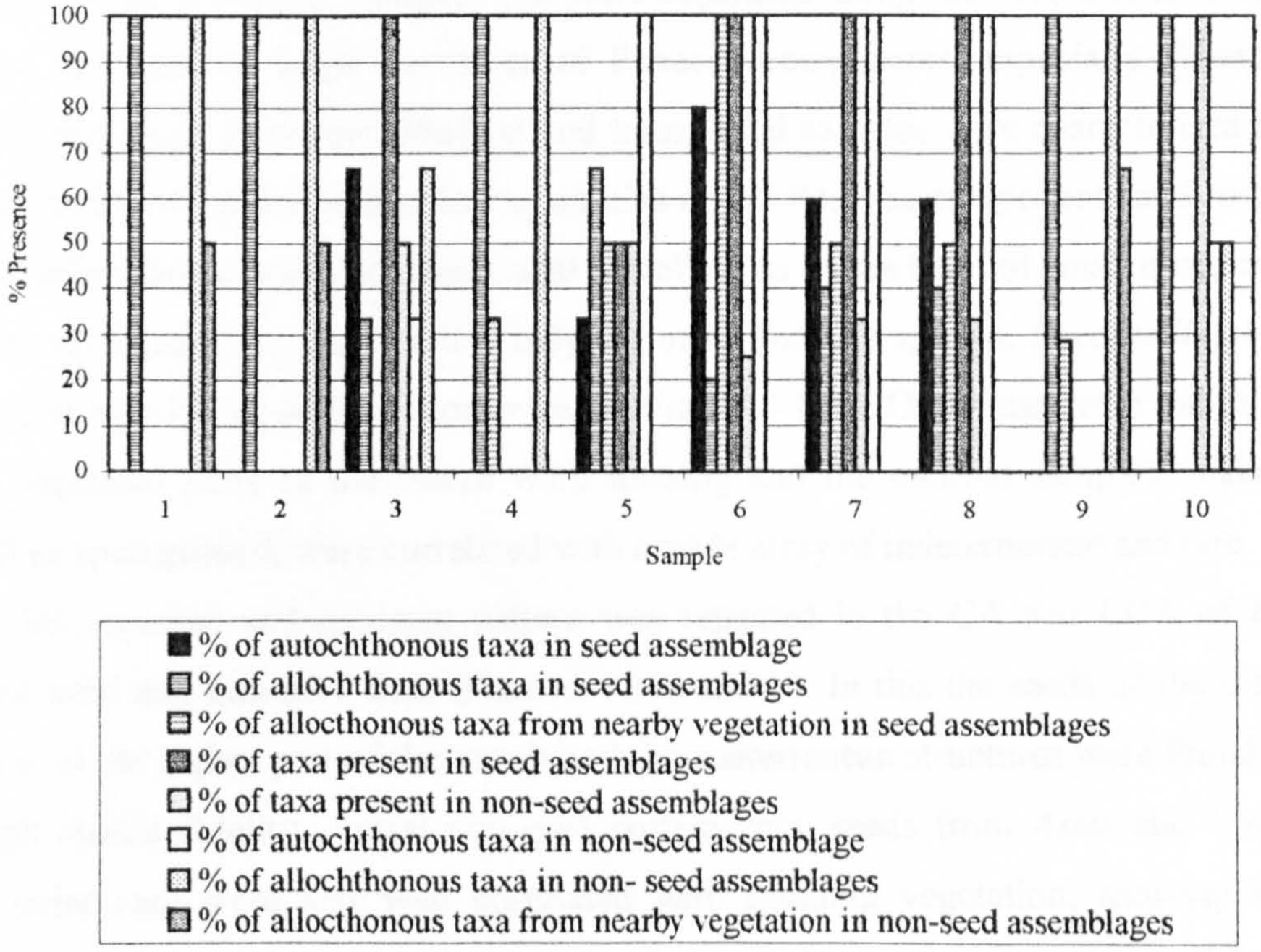


Figure 4.15 Borstal Marsh: Percentage of seeds at set distances from the sample points



Mudflat samples 1, 2 and 9 contained seed assemblages with allochthonous species only, mainly from taxa not recorded in the vegetation near to the sample sites (Figure 4.16). The other samples contained a mixture of allochthonous and autochthonous taxa, with the former contributing a major element to the site's flora, although the taxa preserved in the vegetated marsh samples were usually from nearby vegetation. Samples 3, 4 and 10 contained the most unrepresentative assemblages from the vegetated areas in terms of species presence. This may be due to the openness of the vegetation and, therefore, the high potential for tidal disturbance. Samples 5 – 8 contained many autochthonous taxa and allochthonous taxa were largely from the nearby vegetation. All of the local taxa were recorded in these samples, with the exception of sample 5. The taxa in the non-seed assemblages from the mudflats and marginal marsh samples were mostly allochthonous, although samples 3 and 10 contained some autochthonous taxa. All of the recorded taxa in non-seed assemblages from the vegetated marsh samples were autochthonous, with only a few taxa being commonly recorded.

Figure 4.16 Borstal Marsh Sample Ubiquity Data



Samples from Borstal contained small quantities of allochthonous vegetative and woody remains as well as allochthonous seed and fruit remains. Among the

allochthonous remains were many plants of *Lemna minor*. The large allochthonous component, and these finds in particular, is directly attributable to tidal influence. There was little evidence of any input from the cliff top.

4.4.6 Quantitative analysis

Many of the seed assemblages contained few seeds and only two the minimum 100 seeds necessary for analysis. The CA results, are then, highly suspect (Figure 4.17a). The eigenvalues were low, as with all of the analyses and the samples were split into two broad groups along the first axis. Samples from the mudflats and open environments were separated on the presence of a wide range of allochthonous taxa. Only samples 3, 5, 6, 7 and 8 were found to have high values of seeds derived from allochthonous taxa. Samples 5 and 6 were separated from the rest on the basis of the presence of *Aster* seeds. CCA (4.17b) showed that only *Puccinellia* and *Atriplex prostrata* seeds were correlated to occurrences in the standing vegetation. Open ground, in this case in the mudflat and open vegetation samples, was correlated with the allochthonous taxa scores.

CA of the non-seed macrofossils produced a split that was closer to a visual division of the data (4.18a). Samples 5-8 were separated along the first axis from the others on the basis of large quantities of Poaceae components, especially rhizome fragments, and Type 1 rootlets. Mudflat and transitional samples were characterised by a wide diversity of inclusions and low quantities of the Poaceae components and roots. Division within the mudflat and transitional samples was on the basis of small quantities of rare components. CCA showed that only the main Poaceae species, *Puccinellia*, was correlated at all with macrofossil components (Figure 4.18b). Other taxa from the most heavily vegetated parts of the marsh were missing and the mudflat samples, mainly recorded as open ground, were correlated with a wide array of indeterminate and rare.

This repeated and coherent pattern was repeated in the CA and CCA of the combined seed and non-seed data (Figures 4.19a and b). In this the seeds of the main dominants at the higher part of the marsh and the subterranean structures were found to have high spatial fidelity. Aerial non-seed components, seeds from *Aster* and lower sample point taxa were less well correlated with standing vegetation, showing the influence of tidal movement on the macrofossil record. The coherent division of these depauperate macrofossil assemblages by quantitative methods was surprising and suggests that even low abundance data may of interpretative value.

Figure 4.17a Correspondence analysis of seed data from Borstal Marsh

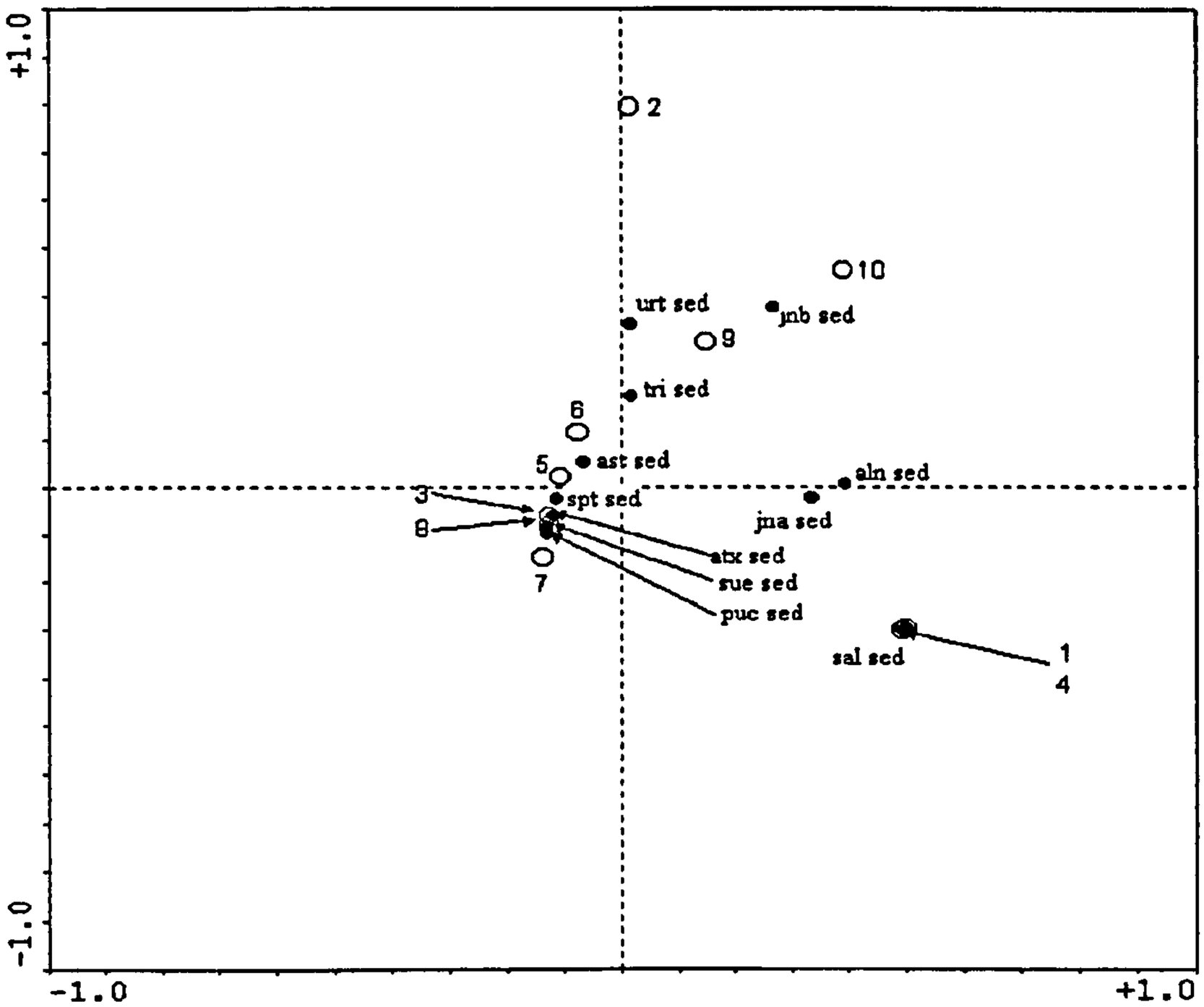


Figure 4.17b Canonical correspondence analysis of seed data from Borstal Marsh

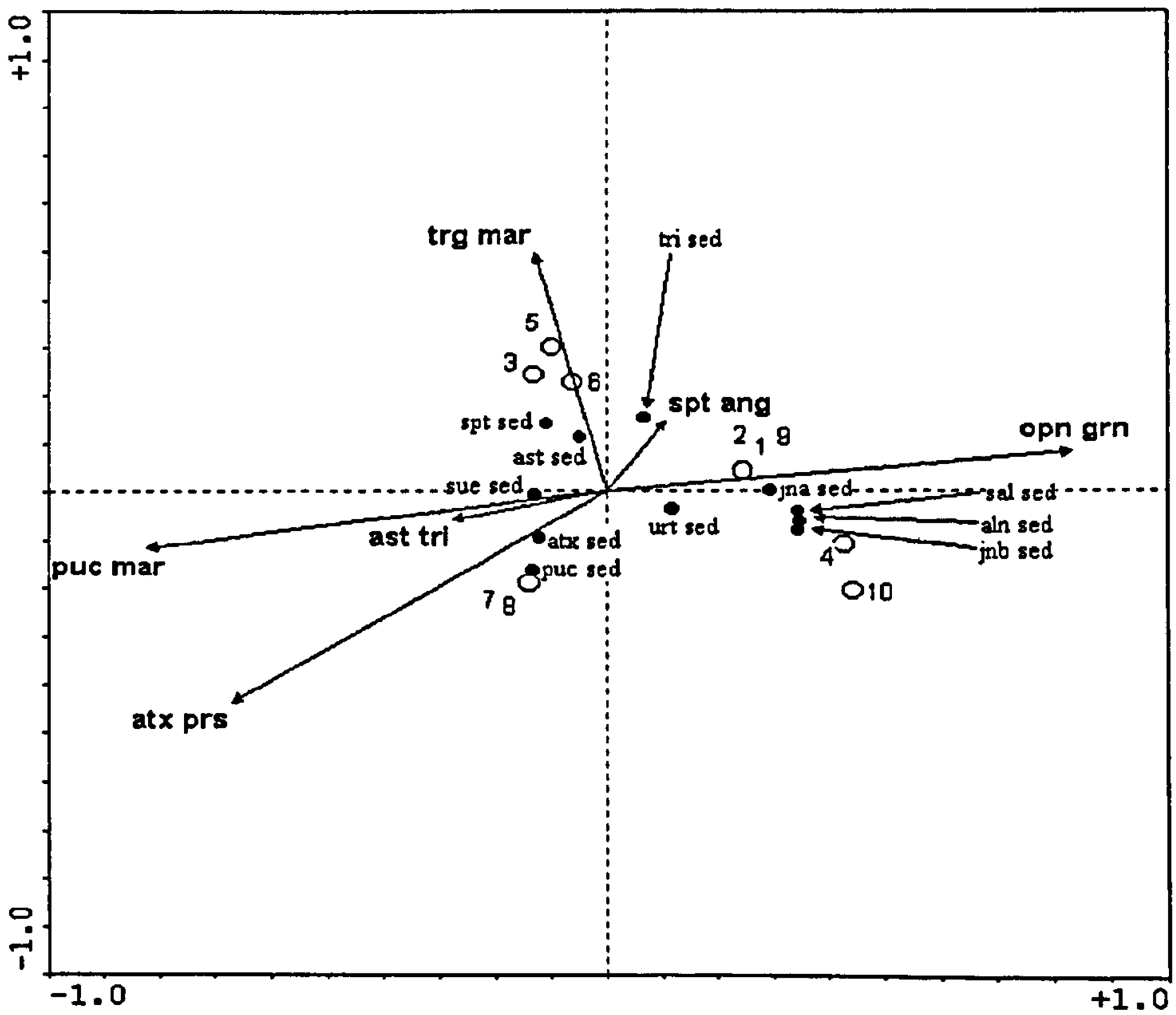


Figure 4.18a Correspondence analysis of non-seed data from Borstal Marsh

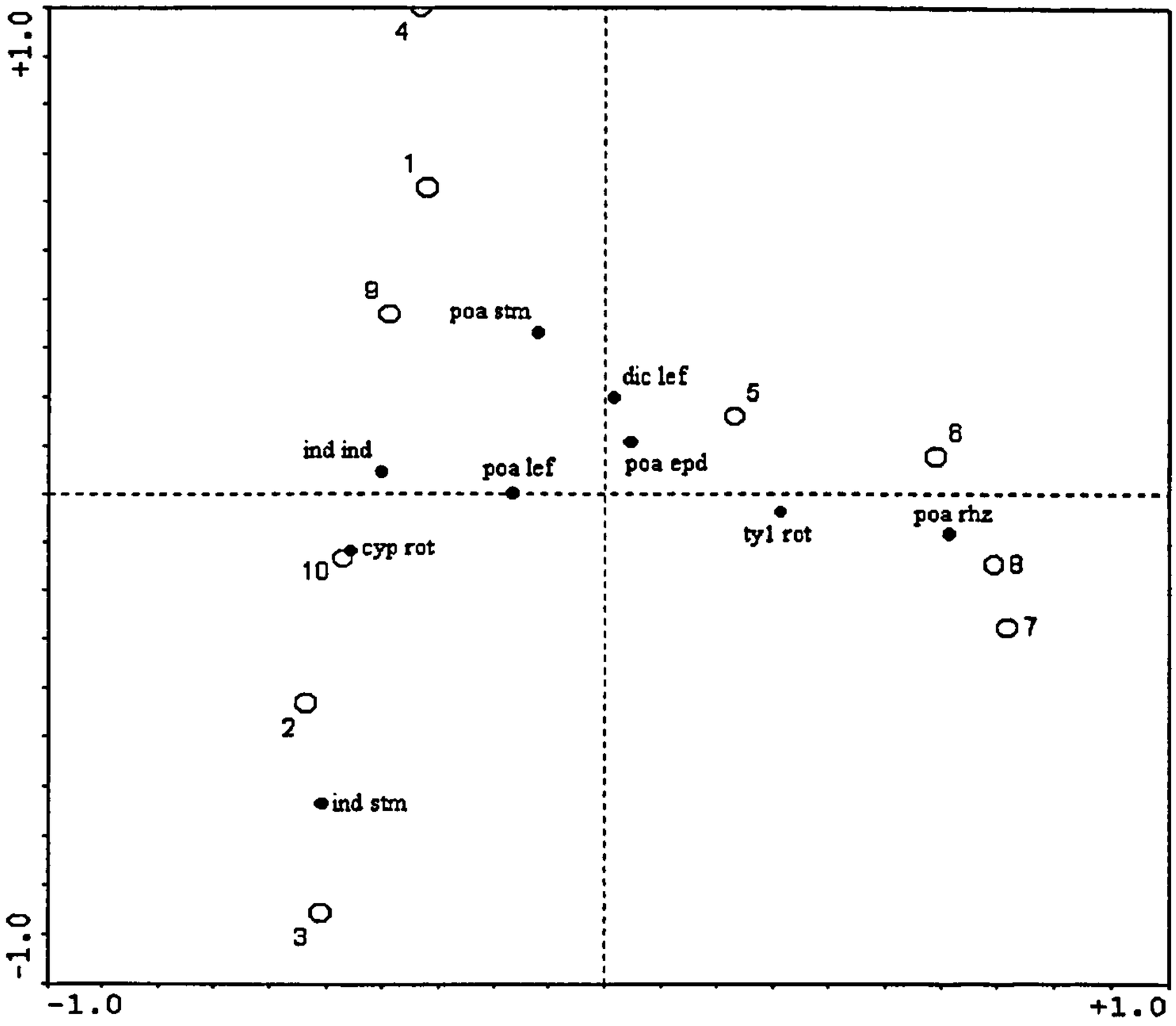


Figure 4.18b Canonical correspondence analysis of non-seed data from Borstal Marsh

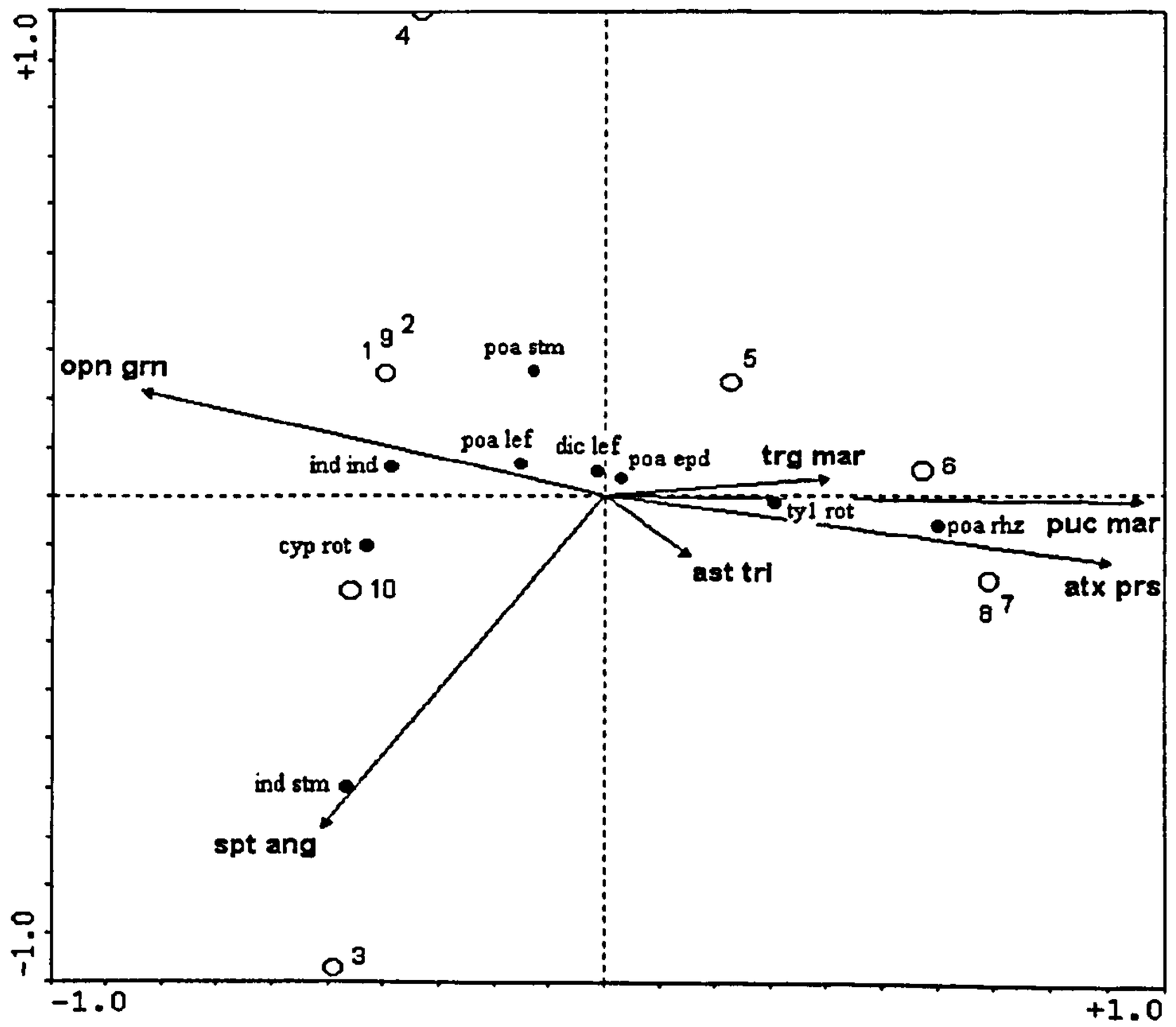


Figure 4.19a Correspondence analysis of seed and non-seed data from Borstal Marsh

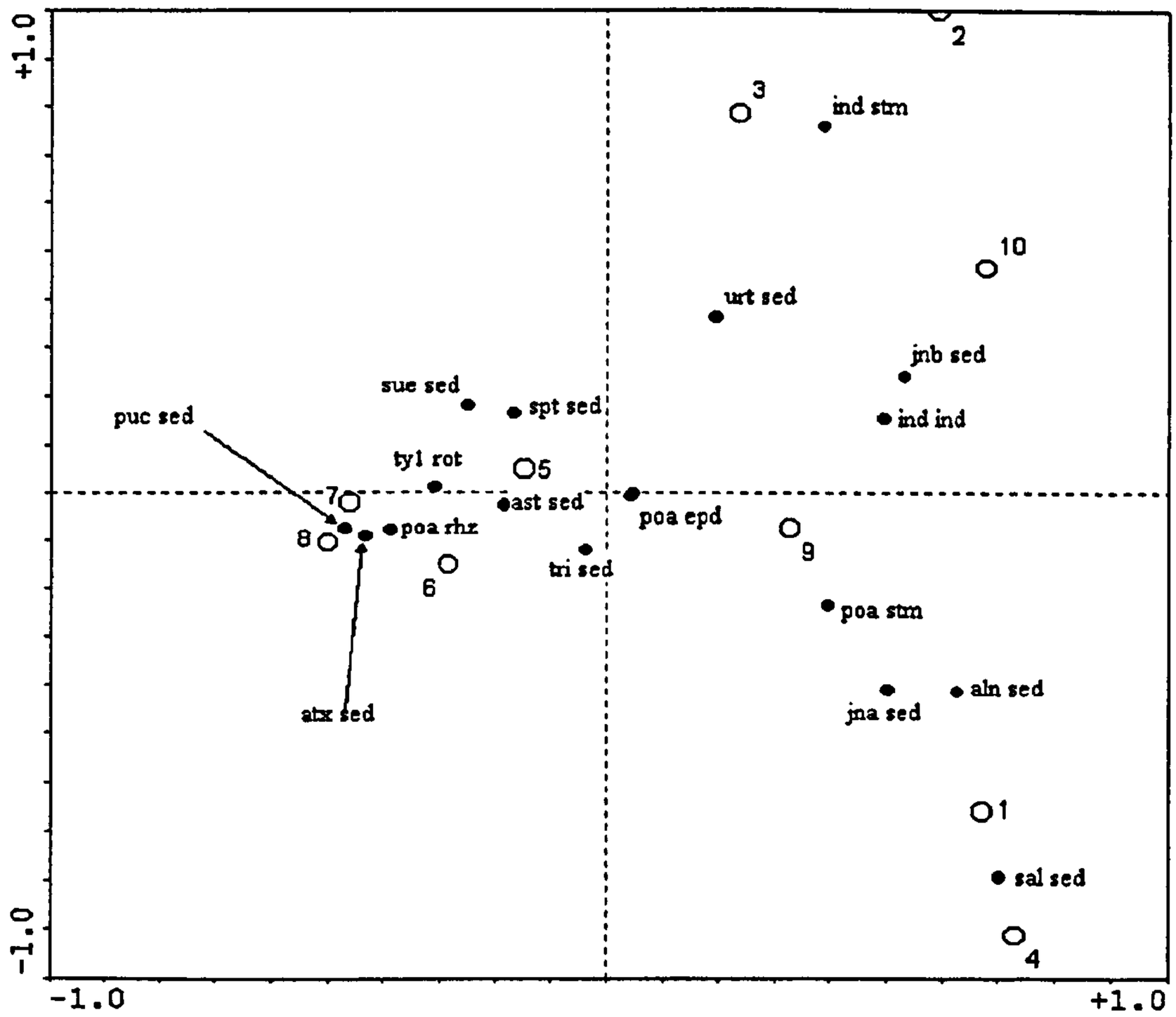
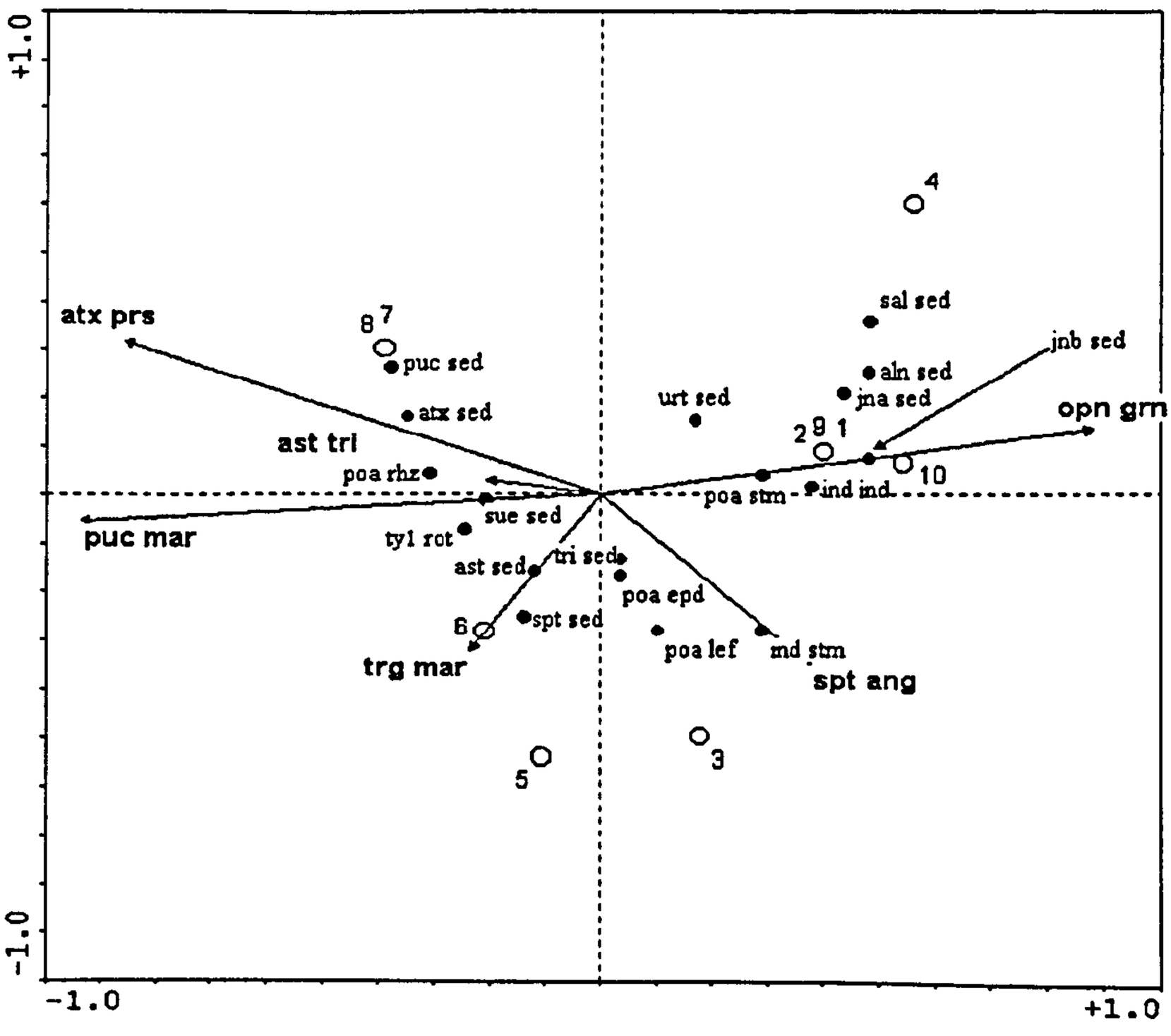


Figure 4.19b Canonical correspondence analysis of seed and non-seed data from Borstal Marsh



4.4.7 Vegetation representation

Seed assemblages recovered from many of the samples were depauperate and, with the exception of samples 5 - 8, were possibly unrepresentative of the seeds present in the sediments. Ordination and interpretation of seed abundance in samples 1-4 and 9-10 is difficult because of the small quantities of seeds incorporated. There was no definite association between vegetation and seed abundance in the transitional samples (3 and 4) and the only characteristic of the samples was the preservation of a wide range of taxa and fossil types. The seeds of *Puccinellia*, with smaller quantities of *Aster*, *Spartina* and *Suaeda* dominated samples 7 and 8. The latter two species were not found at the sample point, but were present in vegetation 10m distant. In these samples the taxon dominant in the vegetation was also dominant in the seed assemblages, although the other local taxa, *Aster tripolium* and *Atriplex portulacoides* were absent or under-represented.

Only the most landward samples contained seed assemblages showing some similarity to the standing vegetation. The considerable tidal influence is the main reason for the distorted picture of the vegetation in the seed assemblages further towards the river. Seed assemblages from nearer the river were less and less reliable, containing many allochthonous taxa from several habitats.

Identified non-seed macrofossils from samples at the river-edge provided little information about local vegetation. Much of the material was unidentifiable. Even the large pieces of plant matter incorporated in the samples were usually unidentifiable or derived from aerial litter of nearby, but non-local vegetation. Possible indicators of low vegetation cover abundance or lack of vegetation altogether are plant macrofossil fragmentation, general low macrofossil incorporation and low rootlet abundance. The dominant *Aster tripolium* was not identified in the non-seed assemblages and the small fragments of Dicotyledonae leaf in the river-edge samples were allochthonous. Remains of the local vegetation dominant *Puccinellia* dominated the landward sample assemblages, although the macrofossils were only identifiable to family level. The landward samples show a bias towards the preservation of taxa with dense root systems and extensive horizontal stem networks. Other perennial herbs, such as *Aster tripolium*, were not identifiable in the non-seed macrofossil assemblages at all.

4.5 Angel Marsh, Walberswick

4.5.1 Location and topography

Angel Marsh lies on the southern bank of the River Blyth near Blythburgh, Suffolk (grid reference: TM 458752). It includes a wide swathe of unvegetated mudflats grading into low- to middle saltmarsh and reedbeds (Figures 4.20). Low flood defences at the edge of heath and pine-woodland to the south and west truncate the marsh vegetation. The marshes are well developed and dissected by creek systems that become increasingly complex towards the main river channel. Measurements using a dumpy-level showed that the marsh surface varies in height by only 20cm over a distance of 240m. Creek bottoms and mudflats were 30-40cm lower than the main marsh surface.

4.5.2 Vegetation and surface litter

Vegetation is zoned from reedbeds at the landward edge through several low-middle saltmarsh communities and pioneer vegetation at the saltmarsh edge (Tables 4.8 and 4.9). The landward edge of the marsh is fringed by a dense stand of S4 *Phragmites australis* swamp community, standing up to 2.5m high in many places. *Phragmites* was also actively colonising mudflats and creek-edges. Towards the river *Atriplex portulacoides* formed an increasingly dense understorey to the *Phragmites* which thinned and became shorter. At the edge of the main reed stand *Juncus gerardii* was common. A thick deposit of *Phragmites* detritus was present at the reedbed edge in several places (sampled in Transect 2), which was formed by tidal action.

Beyond the reedbeds lay a mosaic of low-middle saltmarsh communities. Dominant among these were the SM13 *Puccinellia maritima* community, SM14 *Atriplex portulacoides* community and SM16 *Festuca rubra Juncus gerardii* sub-community. Of more restricted distribution were patches of SM13 *Puccinellia maritima, Limonium* sub-community, SM9 *Suaeda maritima* community, SM8 *Salicornia* community and SM6 *Spartina anglica* community, the latter being more common nearer to the mudflat edge. Several other species, including *Plantago maritima, Triglochin maritima, Glaux maritima, Aster tripolium* and *Sarcocornia perennis*, were distributed throughout the dominant taxa. Marginal vegetation on the dryland fringing the marsh included *Almus, Quercus,* and *Pinus* woodland and pasture. *Almus glutinosa* and *Rubus fruticosus* agg. seedlings were recorded growing in the peaty *Phragmites* detritus at the landward edge, although there was no evidence for the persistence of either species in the marsh.

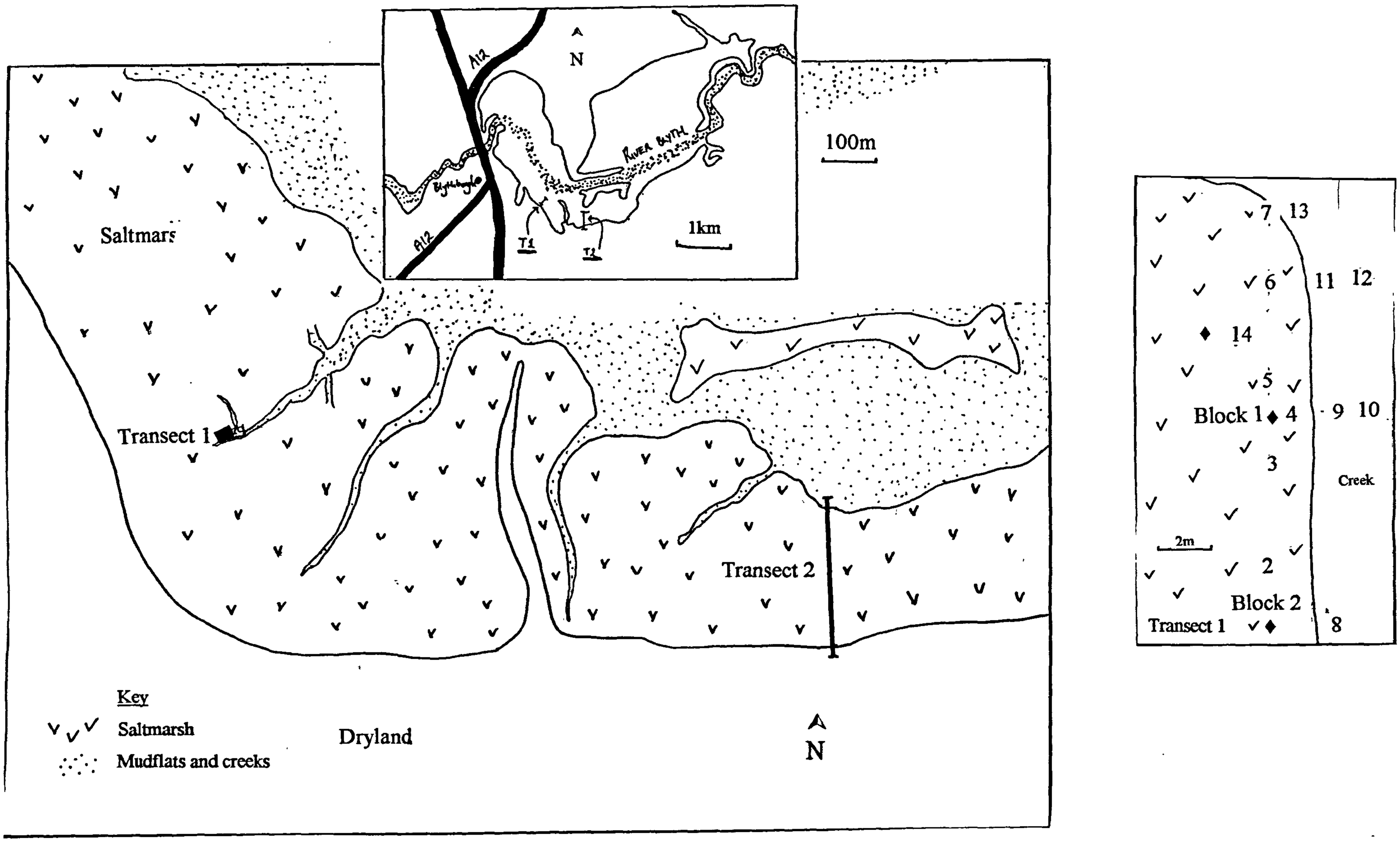


Figure 4.20 Angel Marsh, Walberswick. Location map (inset) and location of sample transects. Box shows sample points along Transect 1

Sample	Block 2	2	3	4	Block 1	5	14	6	7	8	9	10	11	12	13
Distance from origin	0	2	6	8	8	9.5	11/2.5north	13	16	0/2south	8/2.5south	8/3.5south	13/2south	13/3.5south	16/1south
Troels-Smith	Ag3As1Dh+	Ag3As1Dh+	Ag4Dh+	Ag4Dh+	Ag3As1Dh+	Ag4Dh+	Ag3Dh1	Ag4DH+	Ag4Dh+	Ag4Dh+	Ag4Dh+	Ag4Dh+	Ag4Dh+	Ag4Dh+	Ag4Dh+
Colour	10YR4/2	10YR4/3	10YR4/3	10YR3/2	10YR3/2	10YR4/3	10YR4/3	10YR4/3	10YR4/2	10YR4/2	10YR4/3	10YR4/3	10YR4/3	10YR4/3	10YR4/3
% water	44.71*	51.75	53.71	50.01	47.35*	47.9	64.93	51.17	44.35	59.98	57.44	60.37	57.54	60.54	60.27
%organic	16.26*	16.53	17.08	16.81	17.16*	15.34	19.49	16.25	15.55	13.81	14.03	13.25	12.87	12.43	13.92
Cover Abundance															
Aster tripolium			2	2	4	2	4	2							
Atriplex portulacoides		9	8	8	9	8		5	10						
Limonium sp.								2							
Phragmites australis	10	9	5							7					
Puccinellia maritima			4	4	4	4		8	4						
Sarcocornia perennis															
Spartina maritima							4								
Suaeda maritima			2	4	2	4	9	2							
Open ground				4		4				8	10	10	10	10	10
Distances to nearest plant															
Aster tripolium	5-10m		0.5-2m	0.5-2m	0.5-2m	<0.5m	0.5-2m		<0.5m						0.5-2m
Atriplex portulacoides	2-5m	2-5m	<0.5m	<0.5m	<0.5		2-5m	<0.5m							2-5m
Juncus gerardii												10-50m			
Limonium sp.													2-5m		
Phragmites australis	<0.5	<0.5	<0.5	2-5m						<0.5	2-5m	2-5m	5-10m	5-10m	0.5-2m
Puccinellia sp.	5-10m	5-10m			0.5-2m	0.5-2m	2-5m	<0.5	0.5-2m						
Spartina anglica	10-50m					2-5m				10-50m					
Spergularia media														>50m	
Suaeda maritma	5-10m	5-10m	0.5-2		0.5-2m										
Triglochin maritium	10-50m			10-50m											

Table 4.8 Angel Marsh standing vegetation, sediment and distance data: Transect 1

Samples Collected	23	24	25	26	27	28	29	30	31	32	33	34	35	36	37	38
Distance from dryland	20	60	70	80	100	110	120	140	160	180	200	220	240	246	248	248
Troels-Smith	Th2 Sh2	Sh2Th2	Th2Ag1Sh1	Th2Ag1Sh1	Ag3Dh1	Ag3Th1	Ag3Dh2	Ag2Dh2	Ag3Dh1	Ag3Dh1	Ag3Dh1	Ag3Dh1	Ag3Dh1	Ag3Dh1	Ag4Dh+	Ag4Dh+
Colour	10YR2/1	10YR2/2	10YR3/4	10YR3/4	10YR2/2	7.5YR3/2	10YR3/2	10YR2/2	10YR3/2	10YR4/3	10YR3/2	10YR4/3	10YR4/3	10YR3/2	10YR4/2	10YR3/2
% water	87.02%	83.08	78.32	82.17	71.68	74.84	73.47	74.81	76.11	80.66	69.31	61.92	47.45	42.6	58.81	54.18
%organic	66.38	43.94	43.27	41.81	32.09	34.53	30.04	26.65	25.68	29.72	20.83	11.97	12.34	12.69	11.18	10.99
Cover Abundance																
Aster tripolium										2		4	9	2		
Atriplex portulacoides		7	8	8				2		4	2					
Juncus gerardii				5		8	5									
Limonium sp.							8	2		2			2			
Phragmites australis	10	9	9	8		4										
Puccinellia maritima						5	4	10	10	9	9	8		9		
Sarcocornia perennis						5	2	2								
Spartina maritima									4	3	3	2	5	5		
Suaeda maritima							4	2		2	5	5		2		
Open ground					10*										10	10
Distances to nearest plant																
Aster tripolium													<0.5m		2-5m	
Atriplex portulacoides		<0.5		<0.5m		10-50m		0.5-2m		<0.5m	0.5-2m	10-50m	10-50m			
Cochlearia				10-50m		10-50m									10-50m	
Juncus gerardii			5-10m	<0.5m	2-5m	<0.5m		10-50m	10-50m				5-10m	5-10m		
Limonium sp.							<0.5m									
Phragmites australis	<0.5m	<0.5	<0.5	<0.5m	2-5m											
Puccinellia sp.						<0.5m	0.5-2m	<0.5m	<0.5m	<0.5m	<0.5m	<0.5m	<0.5m	<0.5m		
Salicornia/Sarcocornia							0.5-2m					5-10m	5-10m	<0.5m		
Spartina anglica								0.5m								
Spergularia media						10-50m										
Suaeda maritma								0.5-2m								

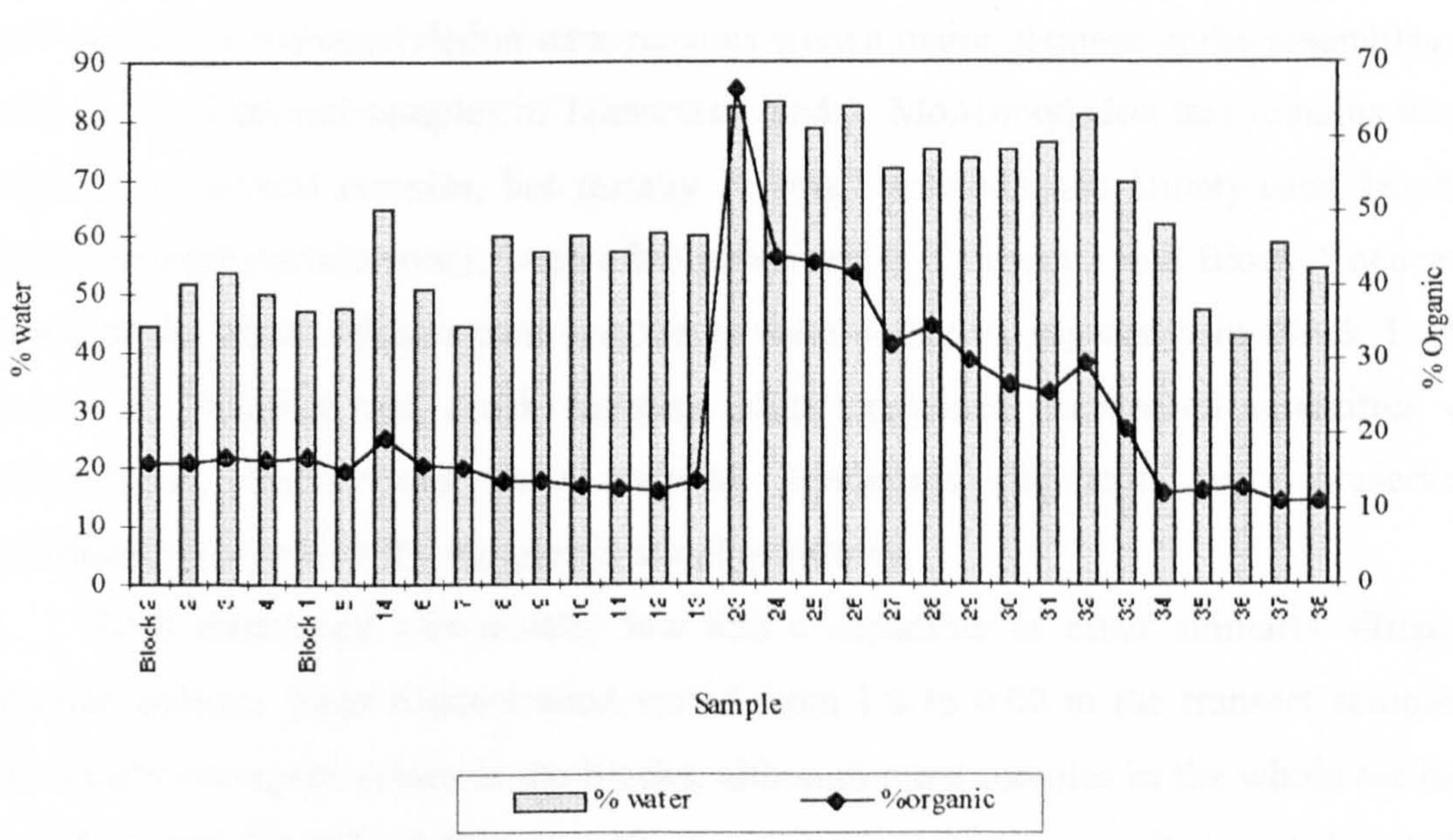
Table 4.9 Angel Marsh standing vegetation, sediment and distance data: Transect 1

Litter in the reedbeds was dominated by *Phragmites* stem and leaf remains. Litter was sparser in the saltmarsh, mainly consisting of Monocotyledon stem material and leaves of the local dominants, especially *Atriplex portulacoides*. Aerial parts of many of the perennial Dicotyledon herbs and Monocotyledon rosette plants were observed to decay rapidly *in situ* without being shed. The mudflats and creek bottoms contained little surface debris, usually only occasional stem fragments.

4.5.3 Sampling

Samples were collected from two transects. Transect 1 was at the western end of the marsh and included a transition from reedbed through to low-mid saltmarsh, terminating at the marsh edge. Samples of 200cm^3 were collected along the transect and across it into the adjacent creek (Figure 4.20). Blocks 1 and 2 were collected from a stand of *Atriplex portulacoides* and the adjacent reedbed respectively. Samples of 200cm^3 were collected along Transect 2 from the flood defences across the transitional reedbed zone through various saltmarsh zones to the marsh edge and mudflats.

Figure 4.21 Angel Marsh organic content and % water



4.5.4 Sediments

Silt-clay mixtures with varying amounts of incorporated detritus (Table 4.8 and 4.9) were observed across the site. The exception was at the very southernmost edge of the reedbeds (Transect 2) where a thick herb peat had developed consisting of *Phragmites* stem, leaf and rootlets in a matrix of silt and degraded *Substantia humosa*. A sample

from this peat (23) consisted of 65% organic matter in comparison to most other sediments with values of 10-30% (Figure 4.21). Organic incorporation decreased across the marshes from the reedbeds in Transect 2 with the lowest values seen in the creeks and mudflats. There was little variation in the organic values from Transect 1, although values decreased slightly in the creek edge. Water content was highest in the organic-rich sediments and those from the creeks.

4.5.5 Incorporation, sources and preservation of macrofossils

Macrofossils were preserved throughout the sample set (Table 4.10 – 4.13). The most abundant assemblages were preserved under *Phragmites* stands in each transect area, with progressive reduction in macrofossil incorporation towards the marsh edges. Macrofossils were often highly degraded. Creek and mudflat samples contained few plant remains that were badly preserved and fragmented in comparison to the saltmarsh samples.

Floodplain samples from Block 2 and Transects 1 and 2 contained abundant rootlets, including those of *Atriplex portulacoides*, recognisable in these samples, but unlikely to be so in ancient material. Woody roots of the species were also preserved in small quantities. Monocotyledon stem remains were a major element of the assemblages in Block 1 and several samples in Transects 1 and 2. Monocotyledon leaf remains were preserved in several samples, but usually in small amounts and Dicotyledon leaves, mainly *Atriplex portulacoides*, were often preserved in Transect 1 and Block 1 beneath growth of the plant. *Atriplex* stem fragments were common, especially in Block 1 and Transect 1. Mudflat and creek samples often contained substantial quantities of unidentifiable, comminuted plant material. Epidermis fragments were preserved sporadically throughout the samples in small quantities.

Seed abundance was usually low and comparable to other similarly situated estuarine habitats. Seed concentration varied from 1.8 to 0.02 in the transect samples, with widely divergent values in the blocks, although most samples in the whole set had values between 0.2 and 0.9 (Figure 4.22). Species concentration usually was below 0.10 seeds per unit sediment, although values were much higher and more variable in the small, unreliable Block samples. Lowest seed incorporation rates were in the mudflat and creek samples. The highest transect values were from the section of marsh in which abundant seed producers *Juncus gerardii* were found.

Most seeds were from plants found within 2-5m of the sample point in the vegetated marshes (Figure 4.23). Allochthonous seeds formed 0-20% of the floodplain sample seed assemblages, but were often more numerous in mudflat and creek samples as were seeds unrecorded in the local vegetation. In both transects the proportion of seeds derived from taxa between at least 5 and 50+m distance increased towards the marsh edge. Block 2 contained allochthonous seeds from several taxa, but they were minor components being swamped by the seeds of the local dominant *Phragmites*. Most of the non-seed macrofossils were from the marsh, although a fragment of *Alnus* leaf and several *Lemna* plants were found in some samples. These fragments were always sparse and were present even in the high marsh, showing the depth of tidal penetration.

Sample ubiquity data is shown in Figure 4.24 a and b. Seed assemblages contained a large proportion of allochthonous taxa, although many were from local vegetation. A large number of taxa were present in small abundance that grew outside the marsh. Local taxa were dominant in the creek and mudflat seed assemblages. Many taxa were missing from the seed assemblages, especially in the more open saltmarsh vegetation, and a greater proportion of taxa were absent from the samples near the marsh edges. Non-seed material was mostly derived from autochthonous taxa. Mudflat, creek and saltmarsh edge samples were the exception, although most preserved taxa were present in nearby vegetation. These latter properties can be attributed to the effects of tidal movement. As with other sites, the non-seed assemblages were dominated by the remains of the most abundant local taxon and many taxa were missing, especially the Dicotyledon herbs. As with the seeds the proportion of missing taxa tended to increase towards the marsh edge and in the creek and mudflat samples.

4.5.6 Sample size effects

As in other sites, seed and species abundance increased with sample size, although the trend was not uniform and both the seed and species abundance ranges overlapped. Cumulative macrofossil abundance for the main identified taxa tended to stabilise at sample volumes of $50cm^3$ and above (Figures 4.25). The seed data for Block 1 varied most, although by $50cm^3$ the main species were present and in correct rank order. Non-seed data in both sites was stable when both whole assemblages were plotted and after removal of the most abundant taxa were removed (Figure 4.26). As with other sites, larger samples included more of the less common taxa, but even small samples correctly identified the most abundant taxa.

	Sample	2	3	4	5	6	7	8	9	10	11	12	13	14
	Position	2	6	8	9 5	13	16	0/2n	8/2.5n	8/3.5n	13e2n	13e3.5n	16e1s	11e2.5n
Taxon	**Component**													
1. Seeds and fruits														
A. Local taxa														
Aster tripolium	Fruit		1	11									1	7
Atriplex portulacoides	Fruit	2	27	9	29	5	8						2	3
Juncus gerardii	Seed									6				
Juncus sp.	Seed									2				
Limonium sp.	Capsule										2			
Phragmites australis	Fruit	224	11	33						9				
Phragmites australis	Spikelet	51						51	11	46	39	48		
Puccinellia sp.	Fruit	18			11	27	15						20	35
Spartina sp.	Fruit				1			4						
Spergularia media	Seed											3		
Suaeda maritima	Fruit	3	3											
Triglochin maritimum	Fruit			7										
B. Other taxa.														
Alnus glutinosa	Seed						2		1			1		
Betula sp.	Fruit				2	1								
Lycopus europaea	Fruit	2								1				
Quercus sp.	Bud-scale					2								
Ranunculus sceleratus	Fruit	1								1				
Typha sp.	Fruit								3					
2 Non-seed														
Atriplex portulacoides	Stem									8.29				
Atriplex portulacoides	Rootlet	11.14	70.31	63.19	21.58	62.73	78.38			8 59	10	13.41		82.87
Phragmites australis	Stem	75.57	5.92		0.67			3.12						
Phragmites australis	Leaf	1.74						93 2						
Poaceae	Stem				3.94	6 31	1.97		0 85	14.45	5.98	19.26	17.31	4.27
Poaceae	Leaf													
Poaceae	Epidermis	0.54	1.21		0.67	0.89	2 66	0.67					3.22	1.4
Poaceae	Rhizome													10.2
Type 1	Rootlet	1.28	5 81	7.2	4.17	26.35	3.95	2.34	29.41	8	20.73	3.2	43.17	1.2
Indet.	Rhizome											0.24		
Indet.	Epidermis								5.66	10.43	3.8			
Indet.	Stem									0 47				
Indet.	Indet.	6.31	4 4		2.46				38 82	13.98	15.77	24 88	3.11	
Various	Seeds		0.76		1.64	0.59		0.67	0.94	1.3		1 65	0.22	0.07
3. Derived Indices														
Seed abundance		301	42	60	43	35	25	55	15	65	41	52	23	45
Species abundance		6	4	4	4	3	3	2	3	4	2	3	3	3
Seed concentration		1.505	0.21	0.3	0 215	0.175	0.125	0.275	0.075	0.325	0.205	0.26	0 115	0.225
Species concentration		0 03	0.02	0.02	0 02	0.015	0.015	0 01	0.015	0.02	0.01	0.015	0.015	0.015

Table 4.10 Angel Marsh plant macrofossil data and derived indices: Transect 1

Taxon	Component	Sample	104	105	106	108	109	110	111	112	113	114	115	133	134	135	136	137
		Sample Size	50	25	12.5	12.5	50	12.5	12.5	25	50	25	25	50	50	50	50	50
1 Seeds etc																		
Alnus glutinosa	Seed		1										1		1			
Aster tripolium	Seed						1	2		1	3	2					1	
Atriplex portulacoides	Seed		7	1	1	1	2	8	1	3	4	5	3		1	1	1	
Atriplex sp.	Seed		2				2											
Suaeda maritima	Seed		2			2	4	1	1				1					2
Puccinellia sp.	Fruit		3	1		1	3		7		1	1			2	5	2	1
2 Non-seed																		
Poaceae	Epidermis		1.85	0.28	1.27	4.33	0.6	3.08	0.67	0.28	0.27	3.53	0.99	0.54	0.75		0.27	0.6
Poaceae	Stem																	
Poaceae	Leaf																	
Puccinellia sp.	Rhizome			2.5	6.8	5	2.27								1.83			
Puccinellia sp.	Stem		9.09	8.54			4.13	14.54	16.81	6.94	1.9	7.27	4.11	8.56	5.56	2.51	6.23	1.8
Atriplex portulacoides	Stem						14.07		0.84					5.19	9.29	8.46	13.2	
Atriplex portulacoides	Leaf		0.81		2		1.67	0.67		1.67		1.67	0.28			3.52	4.22	1
Atriplex portulacoides	Horiz. Stem		51.37	21.04	19.6	38.33		6.43	28.89	25	43.74	50	28.94	6.87	2.71			4.33
Atriplex portulacoides	Rootlet		30.45	55.14	64.27	38.53	40.8	67.69	48.24	53.4	46.26	32.67	57.94	56.4	64.52	70.62	53.35	79.8
Type 1	Rootlet		5.91	7.36	4.4	9.73	36.2	7.44	6.55	9.79	4.29	4.73	4.26	22.44	13.36	12.86	21.38	8.13
Various	Seeds		0.52	0.14		0.27		0.13		0.41		0.13	0.85					0.2
Indet.	Indet.																	
Indet.	Periderm			5	1.67	3.8	0.27			2.5	3.54		0.99		1.97	2.03	1.34	1.6
3 Derived indices																		
Seed abundance			15	2	1	4	12	11	9	4	8	8	5	0	4	6	4	3
Species abundance			4	2	1	3	3	3	3	2	3	3	3	0	3	1	3	2
Seed concentration			0.3	0.08	0.08	0.32	0.24	0.88	0.72	0.16	0.16	0.32	0.2	0	0.08	0.12	0.08	0.06
Species concentration			0.08	0.08	0.08	0.24	0.06	0.24	0.24	0.08	0.06	0.12	0.12	0	0.06	0.02	0.06	0.04

Table 4.11 Angel Marsh plant macrofossil data and derived indices: Block 1

	Sample	205	207	208	209	211	212	214	222	223	224	233	234	235	236	237
	Sample size	12.5	25	50	12.5	25	50	12.5	12 5	25	50	50	50	50	50	50
Taxon	Component															
1 Seeds etc.																
Alnus glutinosa	Seed		2	4			7	3		3	6					
Aphanes arvensis	Seed										1					
Anthemis cotula	Fruit											1				
Atriplex portulacoides	Seed	3	2	4		3			1			6	4			1
Atriplex sp.	Seed	1	5	1		3	3	3	2	2	4			2		
Aster tripolium	Seed										2					
Betula sp.	Seed		1					1			1					1
Carex sp.	Fruit			2	1		1	1								
*Chenopodium*sp.	Seed										5					
Epilobium sp.	Fruit											1				
Lemna sp.	Leaf		1	1												
Lycopus europaeus	Seed										1					
Phragmites australis	Fruit	14	82	137	48	49	22	18	8	34	108	17	12	4		4
Poaceae	Fruit				1											
Puccinellia sp.	Fruit													1	3	
Ranunculus sceleratus	Fruit			1		1										
Rumex sp.	Fruit			1		1		1								
Spartina sp.	Fruit	2									3				1	
Suaeda maritima	Seed	2	2			1	2	1	1	2	3	1				
Triglochin maritima	Seed			1								1				
Urtica dioica	Seed				1	1										
2. Non-seed																
Phragmites australis	Stem	83.59	85.46	90.53	87.37	76.98	73.79	84.26	87.08	85.65	89.79	60.27	15	6.19	15.99	10.79
Phragmites australis	Leaf	4 61	5.57	3.8	7.82	8.26	10.92	8.87	4.42	7.62	6 78		0.33		1.16	2.16
Phragmites australis	Rhizome					6.71	6.7							6.73	11 62	7.65
Poaceae	Epidermis	0.35	1.77	2 07	2.41	2 89	4.75		0.8			0.4	6.87	6.26	5.67	0.97
Type 1	Non-woody root	8.94	4.42	1.33	1.43	0.54	2.48	0.55	4.22	0.2	0.34	1.21		0.2		
Atriplex portulacoides	Stem	0.91		1.67		3 09						0.67	13.6	1.55	2.87	5.36
Atriplex portulacoides	Leaf	0.84	0.68			0 81			1.34						0.34	
Atriplex portulacoides	Epidermis							0.41		0.27		1.75				
Atriplex portulacoides	Non-woody root							4.54		5.71	1 81	33.74	61.07	78 94	60.08	70.42
Lemna sp.	Leaf		0.2	0.2												
Indet.	Periderm		1.56		0.47		0.67		1.81			1.68	2.67		2.05	2.64
3. Derived indices																
Seed abundance		22	94	151	51	59	35	28	12	41	134	27	16	7	4	6
Species abundance		4	5	6	3	6	5	7	3	4	6	6	2	3	2	3
Seed concentration		1.76	3.76	3 02	4.08	2.36	0.7	2.24	0.96	1.64	2 68	0.54	0.32	0.14	0 08	0.12
Species concentration		0.32	0.2	0.12	0 24	0.24	0.1	0.56	0.24	0.16	0 12	0.12	0.04	0.06	0.04	0 06

Table 4.12 Angel Marsh plant macrofossil data and derived indices: Block 2

Taxon	Sample	23	24	25	26	27	28	29	30	31	32	33	34	35	36	37	38
	Distance	20m	60	70	80	100	110	120	140	160	180	200	220	240	246	248	248
1. Seeds and fruits	**Component**																
Atriplex portulacoides	Seed		2		7		27		8		9	20	19	14			
Aster tripolium	Seed								1					7		1	
Atriplex sp.	Seed													13			
Cochlearia sp.	Seed				1		22									2	
Juncus gerardii	Seed			101	15	129	73		15	13				5	25		
Juncus sp.	Seed						9										
Limonium sp.	Calyx							9									
Phragmites australis	Seed	23	348		27	23											
Phragmites australis	Spikelet			49	52	8											
Puccinellia sp.	Spikelet						28			9	25	14	6	31	2		
Puccinellia sp.	Seed							8	62	56	33	73	69				
Poaceae sp.	Seed					2											
Salicornia sp.	Seed							31	11				16	6	12		
Spergularia media	Seed						10										
Suaeda maritima	Seed								7								
Alnus glutinosa	Seed													2			
Betula sp.	Seed	1	1	2	1									1			2
Quercus sp.	Bud scale	1															
Rubus fruticosus agg	Seed	1															
2. Vegetative remains																	
Alnus glutinosa	Leaf						0.2										
Atriplex portulacoides	Leaf			0.27	2.56									29.52			
Atriplex portulacoides	Stem			3.96	2.36	2 67	2.2	1 48	2.6					1 68	2.18		
Atriplex portulacoides	Epidermis			0 94								0 8					
Atriplex portulacoides	Rootlet			17.58	63.39	50			1.6			2.13		41 2	57.55		
Juncus sp.	Stem				3.1		82.73	8.89	17.27	17.73	4.33	7.2	24.4	2.64	6 68		
Juncus type	Rootlet						1.8	21.77								14.44	38.77
Phragmites australis	Leaf	6.71	2.75			0 53											
Phragmites australis	Stem		30.47		11.04	22.53											
Poaceae	Stem	57.99	1 81	15.17			3 4										
Poaceae	Leaf			5.44					5.27								
Poaceae	Epidermis	0.94			3.5	7.87		2.09		2.6	0.53	2.6	2 07	2.08			5.33
Poaceae	Rhizome				2.42						35.33						
Type1	Rootlet	31.74	64.63	51.28	11.24	8.4	7.6	59.84	72.6	78.2	57.73	81.33	67	21.68	33.1		38.37
Dicotyledon	Leaf	0 81						5.93	0.4						0.49		
Indeterminate	Rootlet			0.3													
Indeterminate	Epidermis															12.78	
Indeterminate	Charcoal	1.54															
Indeterminate	Indeterminate	0.27		4.3		8	1.6			0.8	2.07	5.93	6.53			72.78	17.53
3. Derived Indices																	
Seed abundance		25	351	152	103	162	169	48	104	78	67	107	110	79	39	3	2
Species abundance		3	2	3	4	2	5	3	6	2	2	2	3	7	3	2	1
Seed concentration		0.125	1.755	0.76	0.515	0 81	0.845	0.24	0.52	0.39	0.335	0.535	0.55	0.395	0.195	0.015	0.01
Species concentration		0.015	0.01	0 015	0 02	0.01	0.025	0 015	0 03	0.01	0 01	0 01	0.015	0.035	0.015	0 01	0.005

Table 4.13 Angel Marsh plant macrofossil data and derived indices: Transect 2

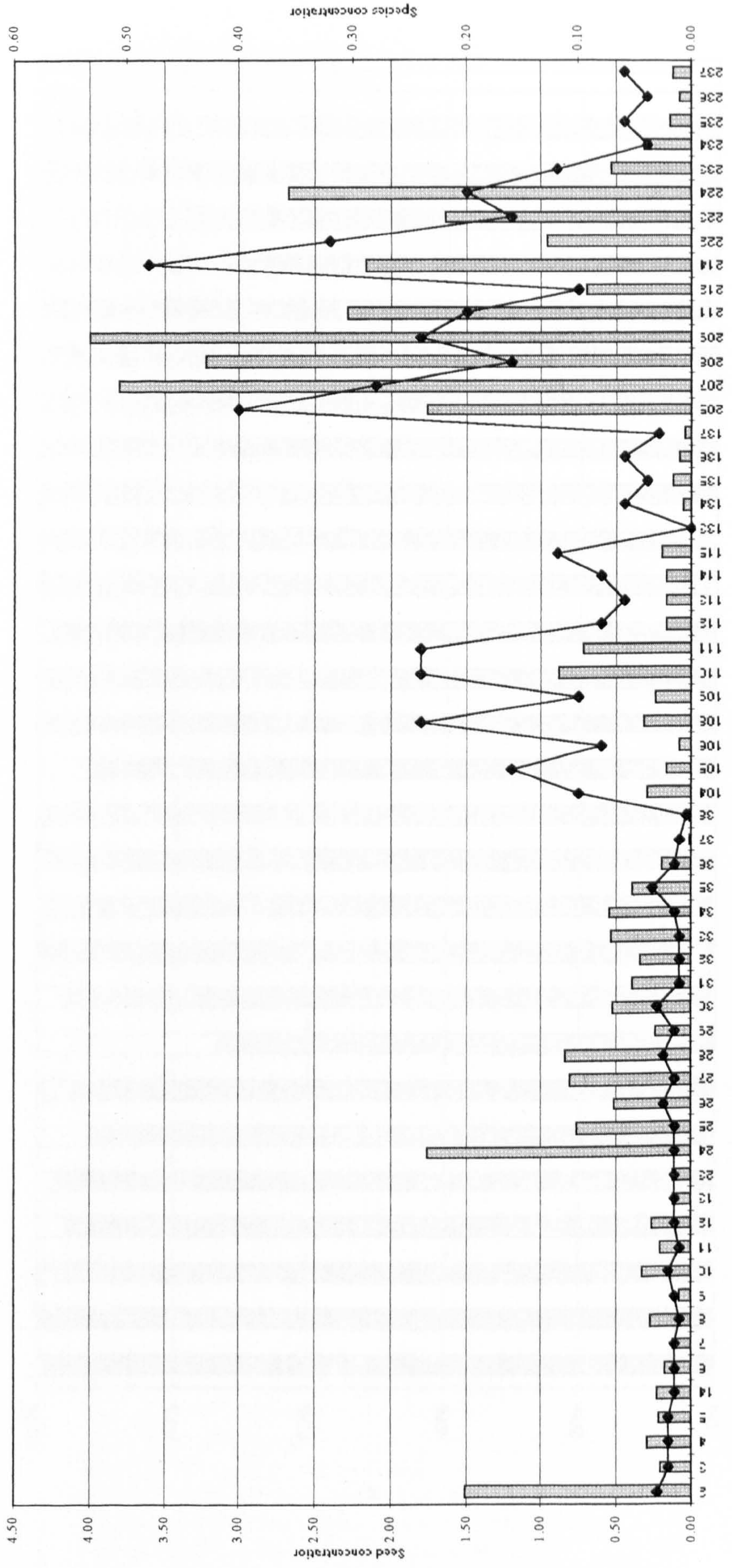


Figure 4.22 Angel Marsh seed and species concentration data

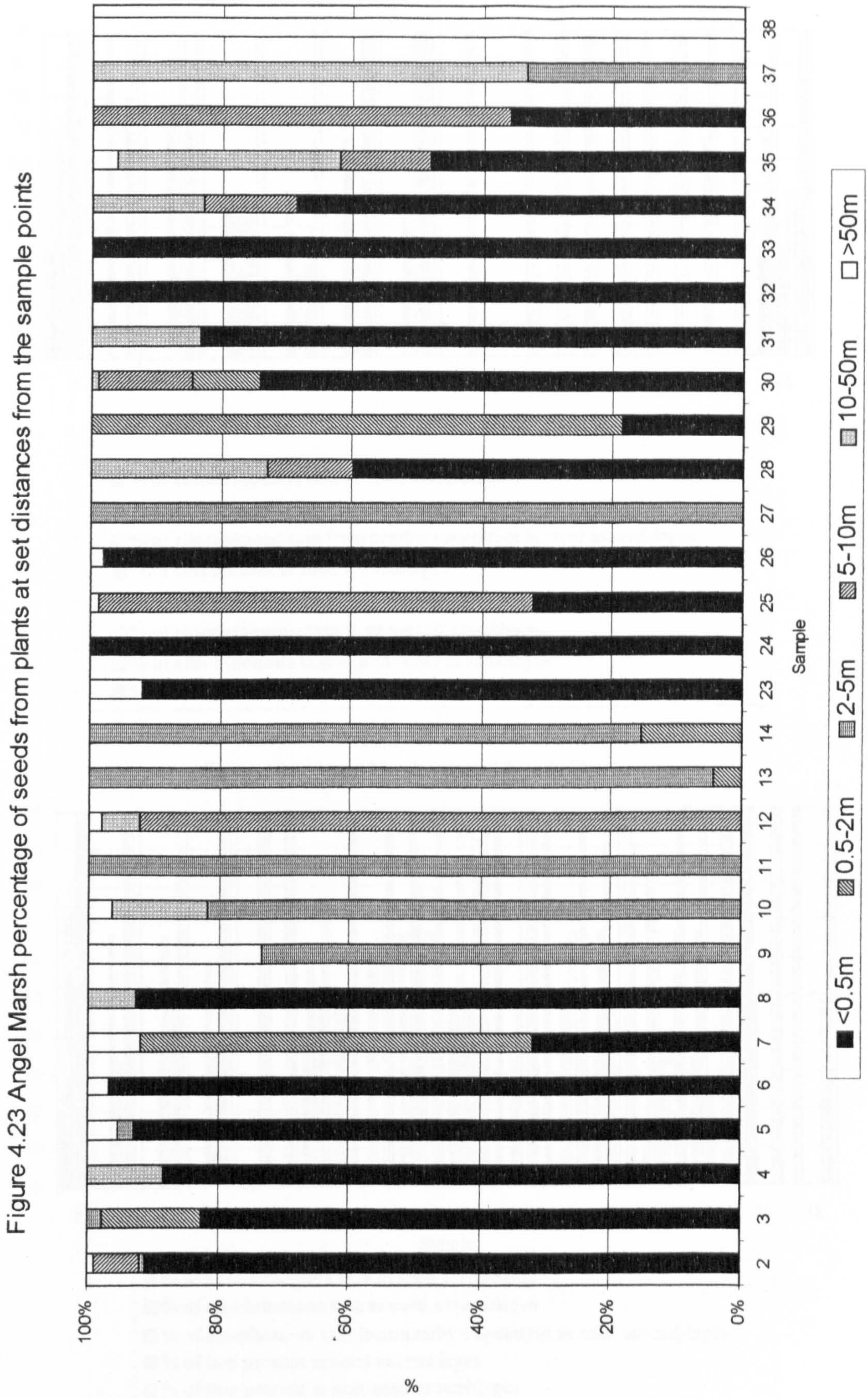


Figure 4.23 Angel Marsh percentage of seeds from plants at set distances from the sample points
Sample
%
100%
80%
60%
40%
20%
0%
2 3 4 5 6 7 8 9 10 11 12 13 14 23 24 25 26 27 28 29 30 31 32 33 34 35 36 37 38
<0.5m
0.5-2m
2-5m
5-10m
>50m

Figure 4.24a Angel Marsh Sample Ubiquity Data

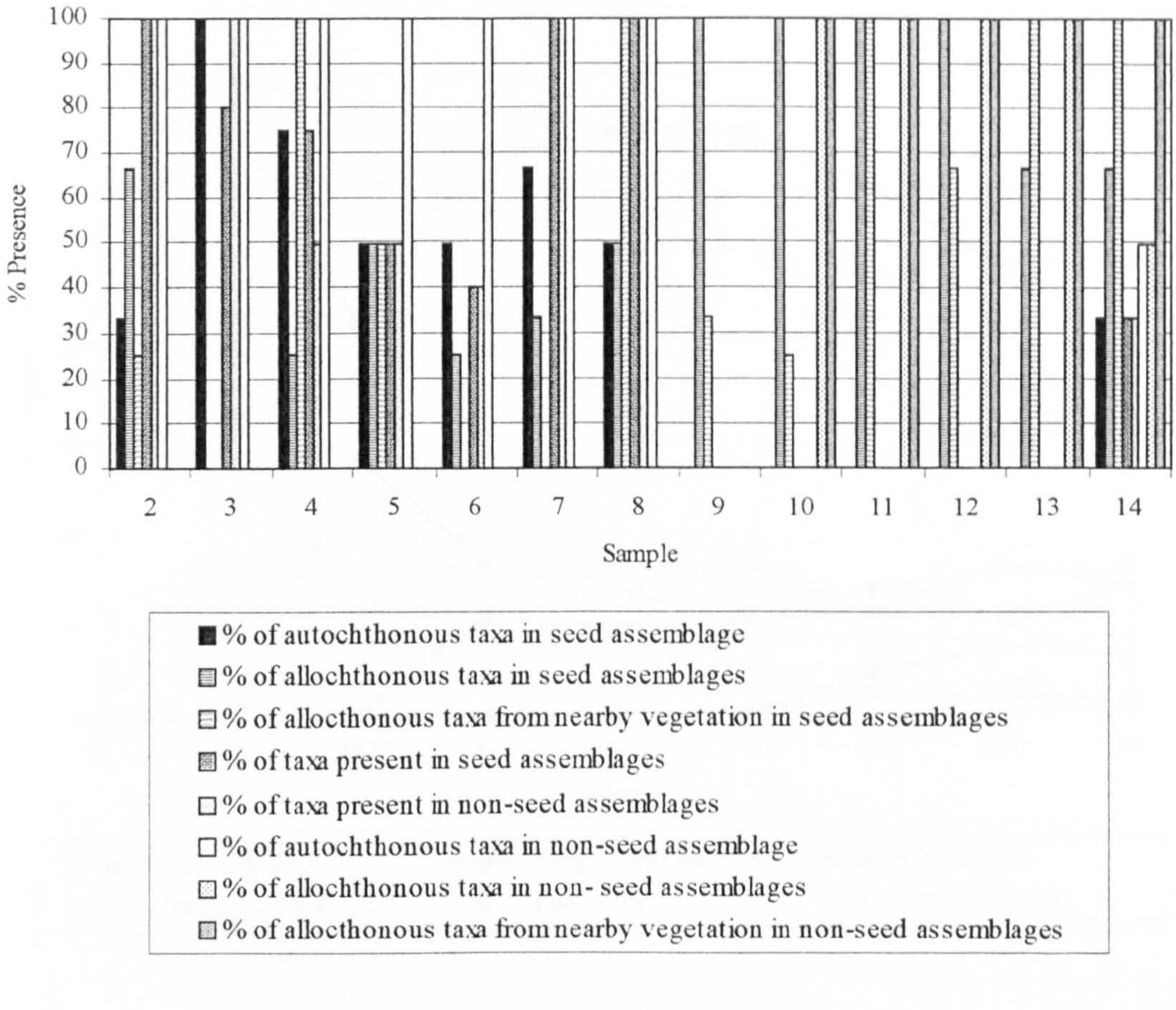


Figure 4.24b Angel Marsh Sample Ubiquity Data

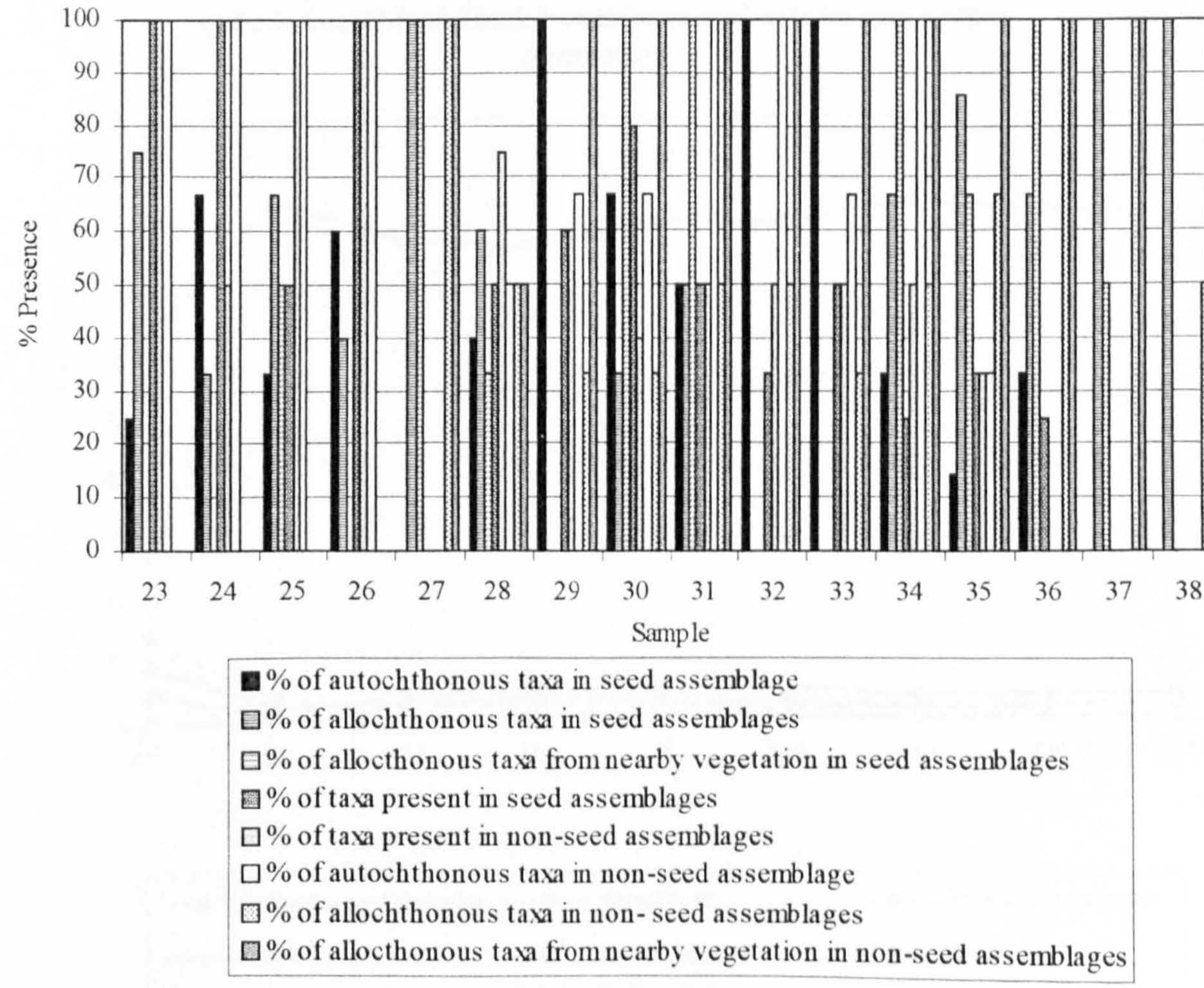


Fig 4.25a Angel Marsh Block 1: Cumulative percentage seed data for main sample components

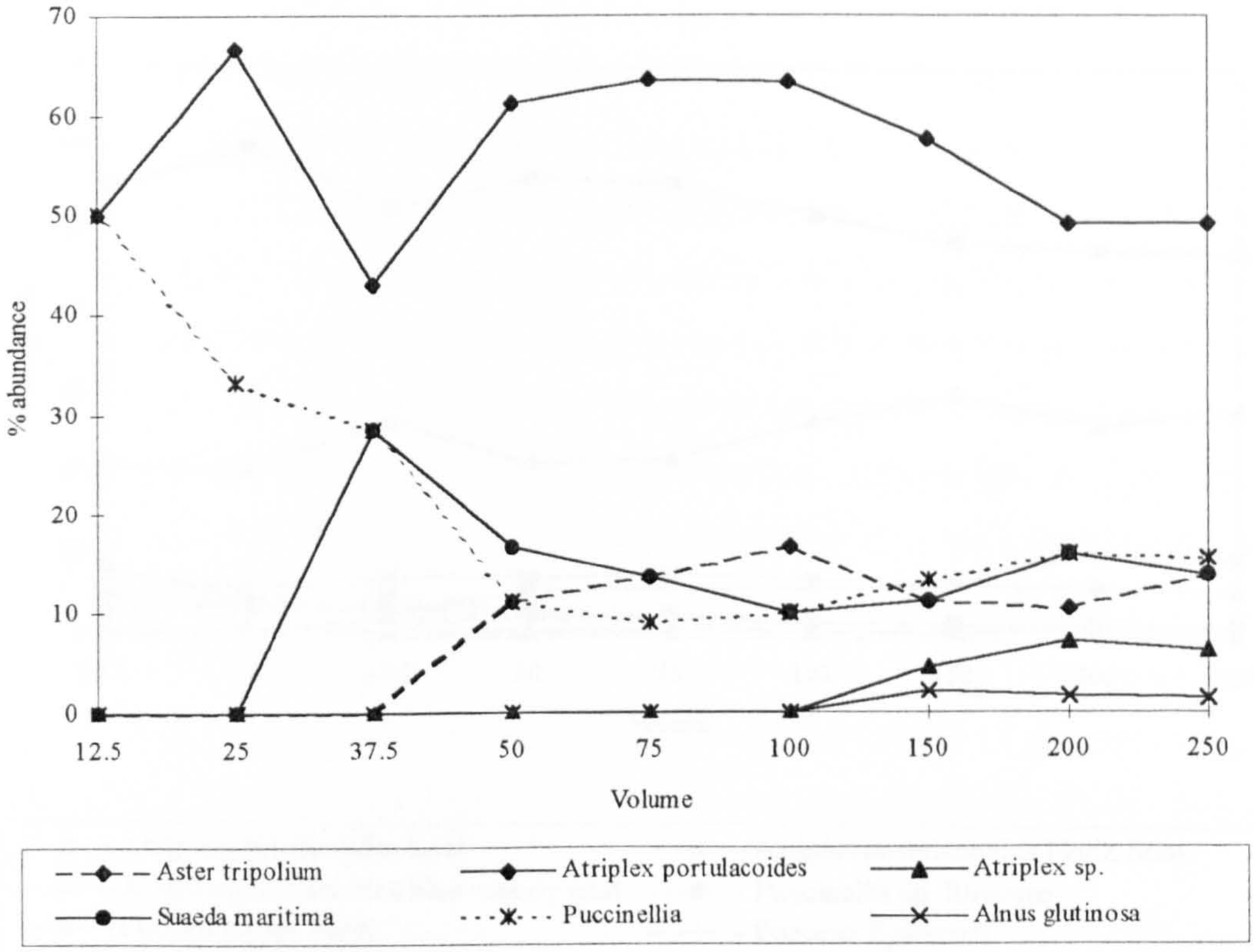


Fig 4.25b Angel March Block 2: cumulative seed data for main sample components

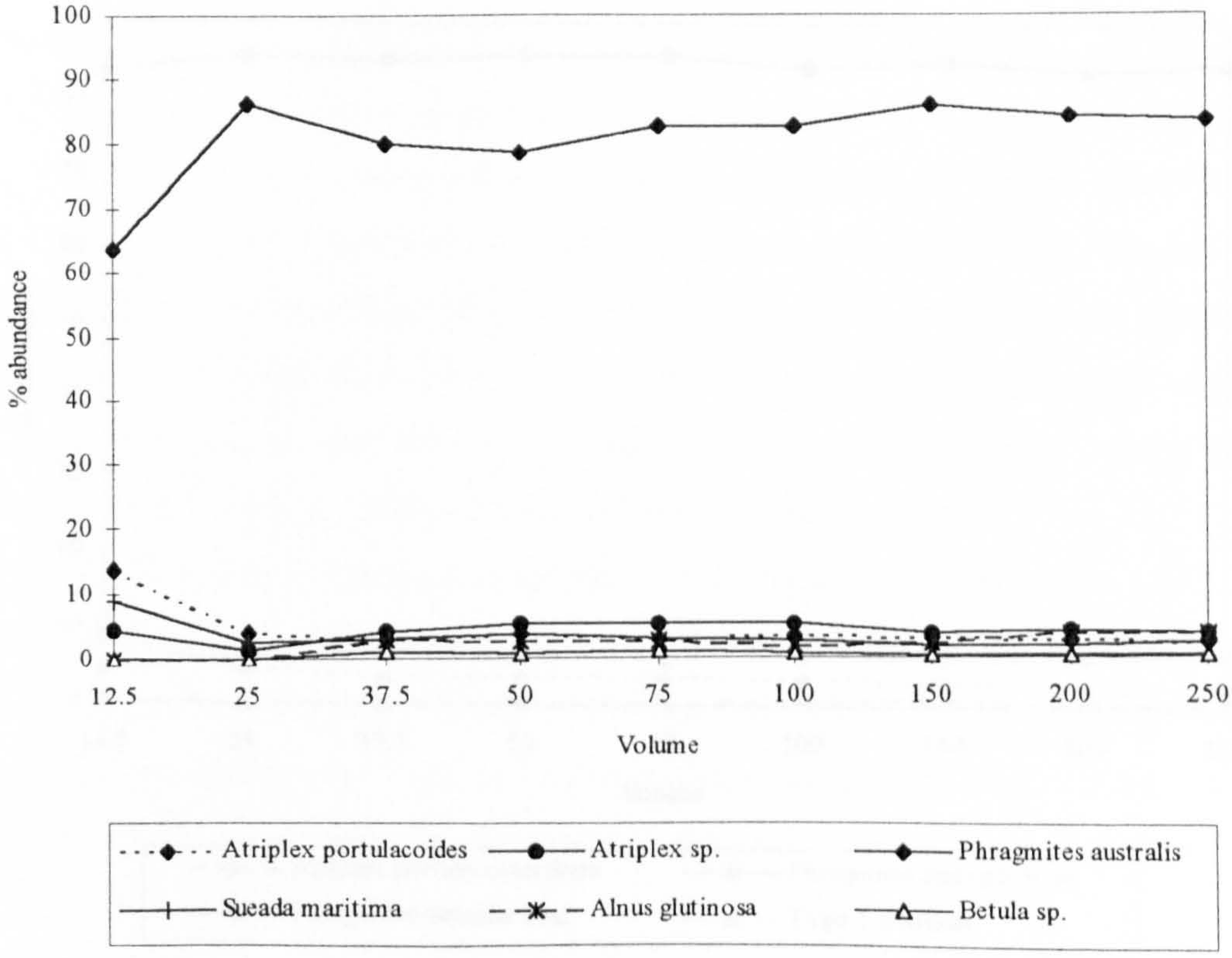


Fig 4.26a Angel Marsh Block 1: Cumulative non-seed abundances main sample components

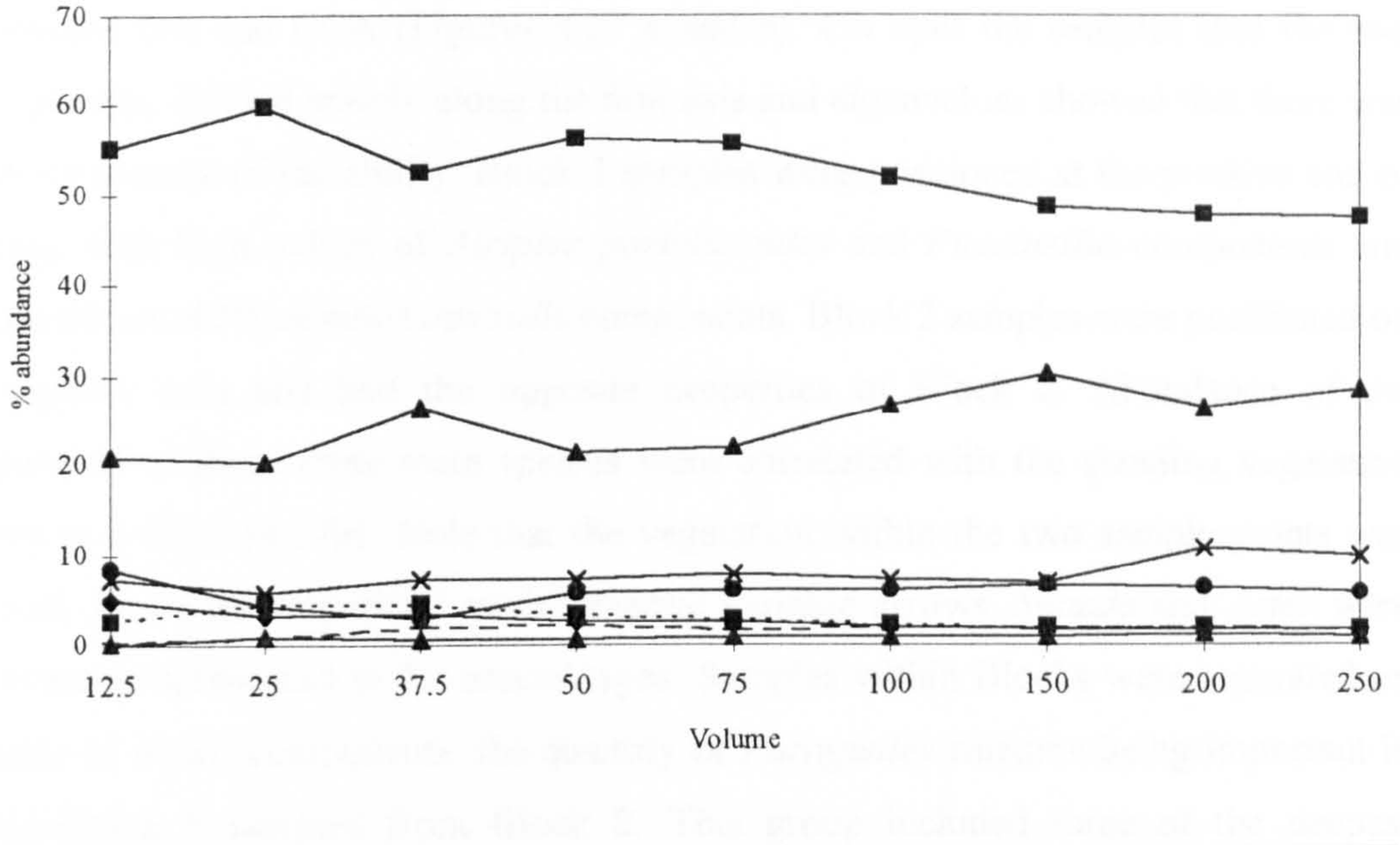
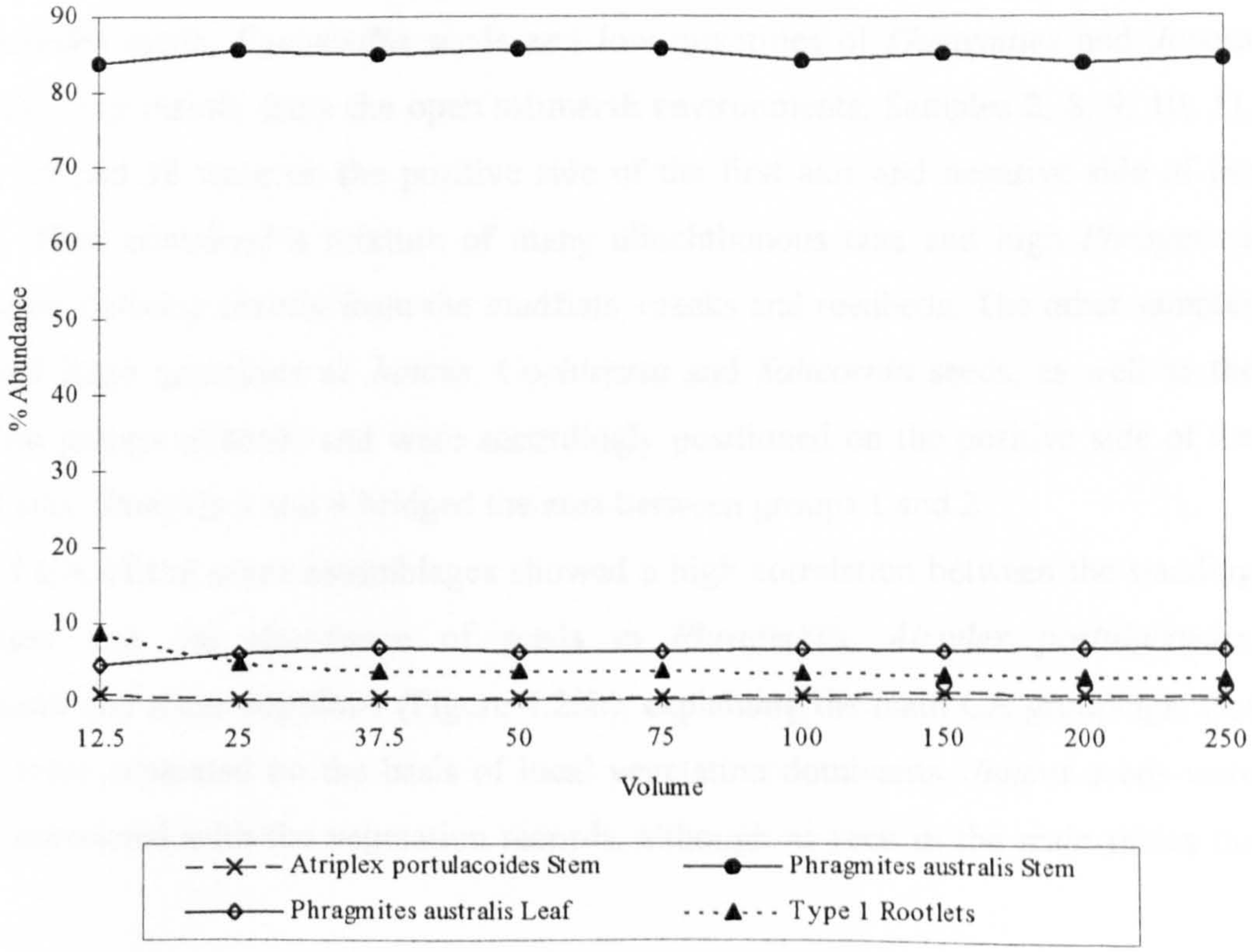


Fig 4.26b Angel Marsh Block 2: Cumulative non-seed abundances of main sample components



4.5.7. Quantitative analysis

An initial CA of all samples showed that the Block samples skewed the analysis to a degree that it was uninformative. The Block samples data were removed and subject to a combined CA and CCA (Figures 4.27 a and b). CA split the samples into the two Block groups, divided mainly along the first axis and eigenvalues showed that there was moderate amount of variability. Block 1 samples were positioned at the positive end of the axis, with high values of *Atriplex portulacoides* and *Puccinellia* components and low quantities of *Phragmites australis* components. Block 2 samples were positioned on the negative axis and had the opposite properties of Block 2. Abundance of the components of these three main species were correlated with the standing vegetation records in a CCA (4.27b). Note that the vegetation within the two sample points was identical, hence the horizontal environmental variable arrows. *Suaeda* and *Aster* were inaccurately represented in the assemblages. Samples within Blocks were separated on the basis of minor components, the quantity of *Phragmites* rhizome being important in distinguishing 5 samples from Block 2. This group included three of the deepest samples from the Block.

CA of the seed assemblages split the samples into four main groupings (Figure 4.28a), although variability in the samples was small. Seeds of *Juncus, Phragmites* and *Atriplex* were the main contributors to the variability. Samples 5, 6, 7, 13, 14, 32, 33, 34 35 and 38 were grouped with high negative values along the first axis and negative values on the second. These samples contained large quantities of *Atriplex portulacoides* seeds, *Puccinellia* seeds and low quantities of *Phragmites* and *Juncus* seeds, deriving mainly from the open saltmarsh environments. Samples 2, 8, 9, 10, 11, 12, 23, 24 and 38 were on the positive side of the first axis and negative side of the second. They contained a mixture of many allochthonous taxa and high *Phragmites* abundance, deriving mainly from the mudflats, creeks and reedbeds. The other samples contained large quantities of *Juncus, Cochlearia* and *Salicornia* seeds, as well as the other two groups of seeds and were accordingly positioned on the positive side of the second axis. Samples 3 and 4 bridged the area between groups 1 and 2.

CCA of the seeds assemblages showed a high correlation between the standing vegetation and the abundance of seeds in *Phragmites, Atriplex portulacoides, Puccinellia* and *Aster tripolium* (Figure 4.28b), explaining the main CA groupings, that largely were separated on the basis of local vegetation dominants. *Juncus* seeds were largely correlated with the vegetation records, although as seen in the main tables the

seeds were well distributed, usually only in small numbers. *Salicornia* and *Suaeda* seeds were poorly correlated to the standing vegetation records. In the CA the mudflat and creek samples were spread across the plot, although the sample composition usually showed affinities with samples from nearby or similar vegetation as that bordering the creek/mudflat sample points.

CA of non-seed macrofossils (Figure 4.29a) split the samples into three broad groups. Samples 28, 29, 30, 31, 32, 33, 34, 37 and 38 were separated because they contained large quantities of *Juncus* components mixed with quantities of Poaceae components. Samples 2, 8, 23 and 24 were dominated by *Phragmites* components, sample 8, from the creek invaded by *Phragmites* preserving a large quantity of leaf material. Samples on the negative side of the second axis contained few of the components mentioned above and were dominated by indeterminate macrofossils and those of *Atriplex portulacoides*. This latter group was roughly divided into mudflat/creek samples and those from *Atriplex portulacoides* vegetation. As suggested here there was a strong correlation between the main macrofossil categories and the standing vegetation, as shown in the CCA results (Figure 4.29b). *Atriplex portulacoides*, *Phragmites* and *Juncus* components were strongly correlated with standing vegetation records, with indeterminate categories correlated with the open ground of mudflats and creeks.

Results of combined CA (Figure 4.30a) and CCA (Figure 4.30b) of the seed and non-seed assemblages were confused, but broadly consistent with the groups and trends already talked about above. It was notable that the samples from the mudflats in Transect 2 correlated with some of the allochthonous elements. Overall there was a strong presence of the main three taxa in the vegetation and poor representation of the others, with the exception of *Puccinellia*. High abundance of seed and non-seed macrofossils of these taxa was generally consistent with local presence of the species in the vegetation. *Puccinellia* was difficult to discern on the basis of non-seed presence but showed a strong correlation between high seed abundance and local presence.

4.5.8 Vegetation representation

In both the seed and non-seed assemblages the main dominant taxa on the marshes, namely *Phragmites*, *Atriplex portulacoides*, *Juncus gerardii* and *Puccinellia*, were the main contributors to the macrofossil assemblages at the sample points. Macrofossil assemblages provided accurate information about the local dominants. The visibility of

Figure 4.27a Angel Marsh canonical correspondence analysis of combined seed and non-seed data from block sample

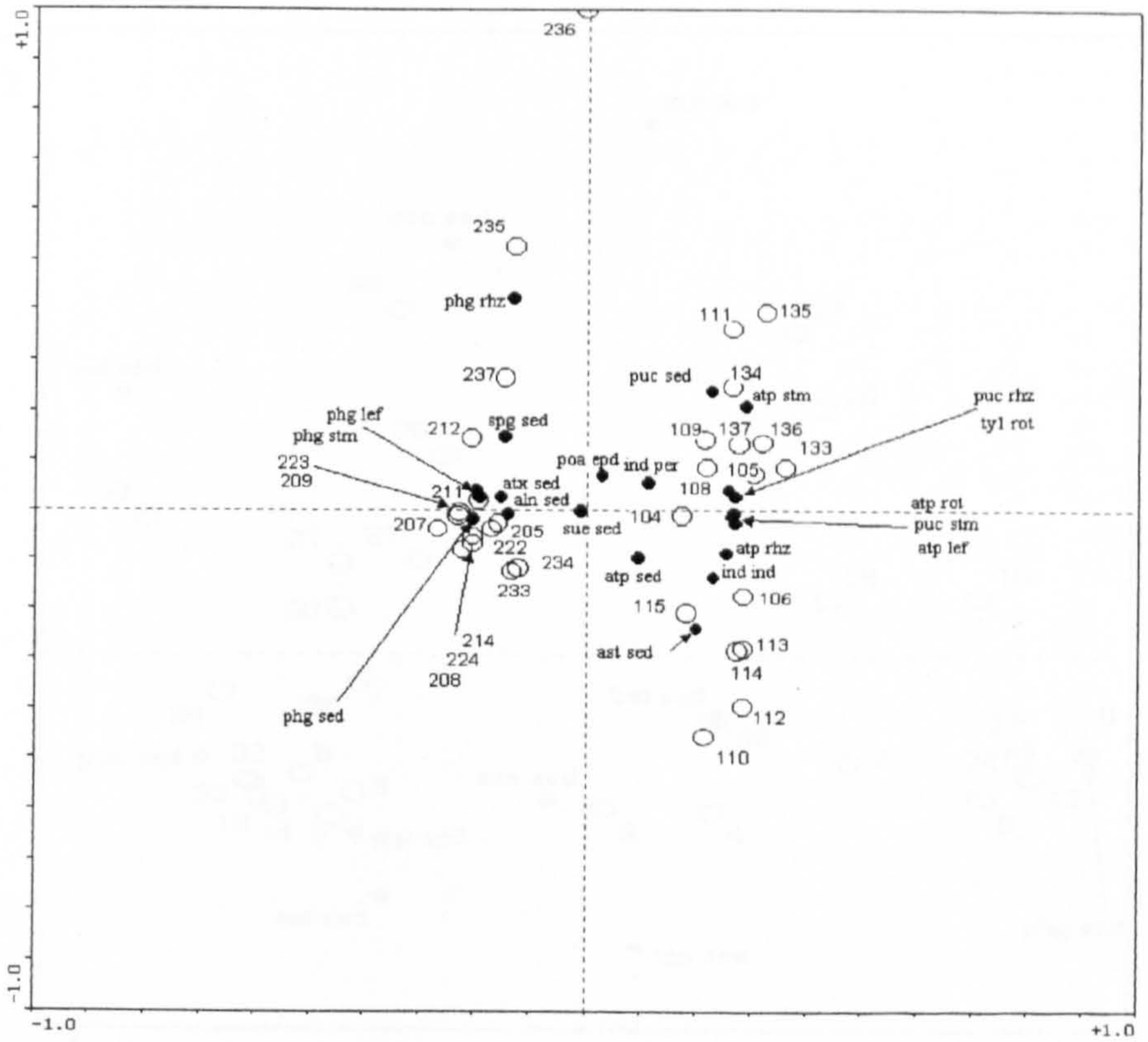


Figure 4.27b Angel Marsh canonical correspondence analysis of combined seed and non-seed data from block sample

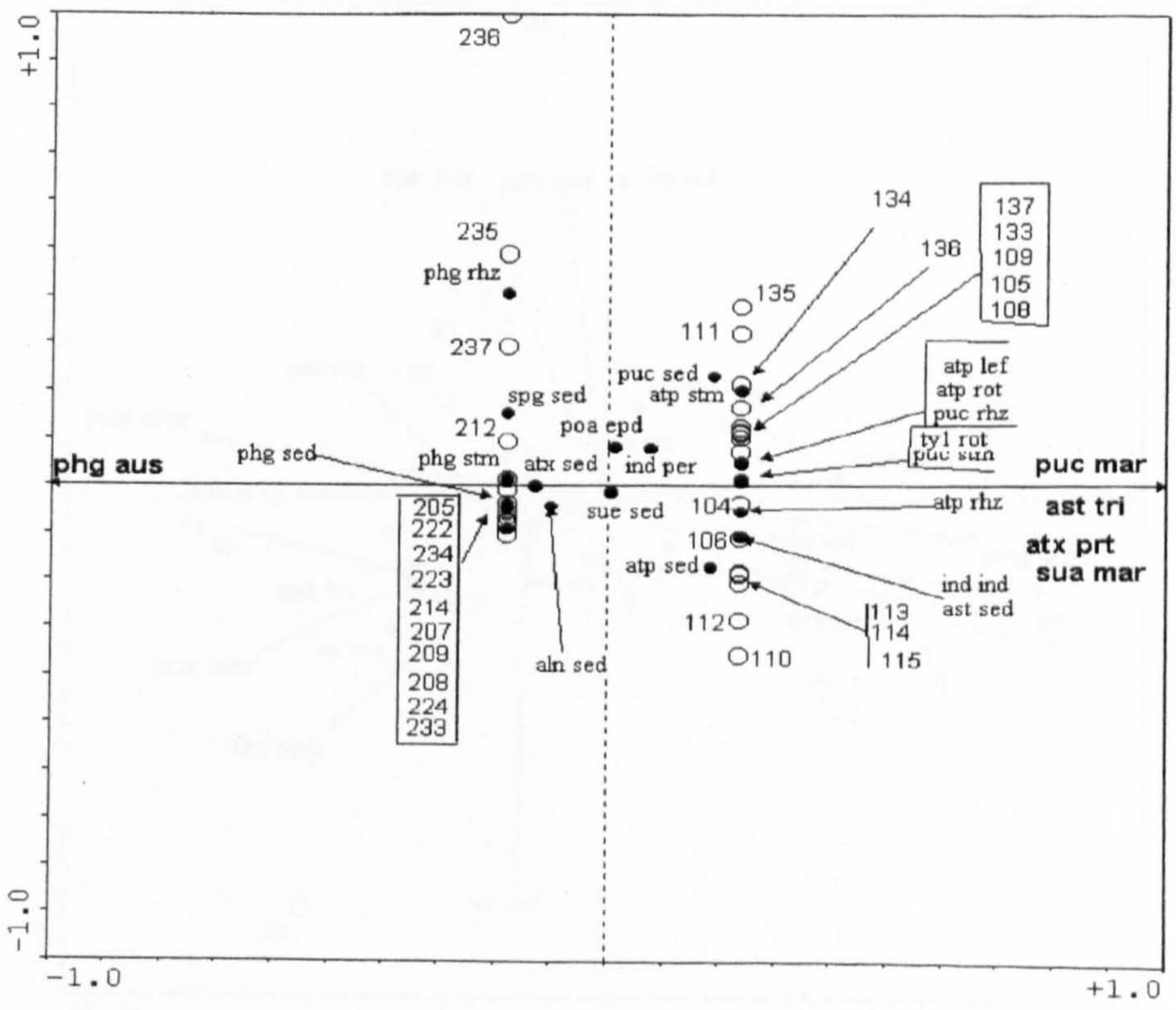


Figure 4.28a Correspondence analysis of seed data from Transect samples at Angel Marsh

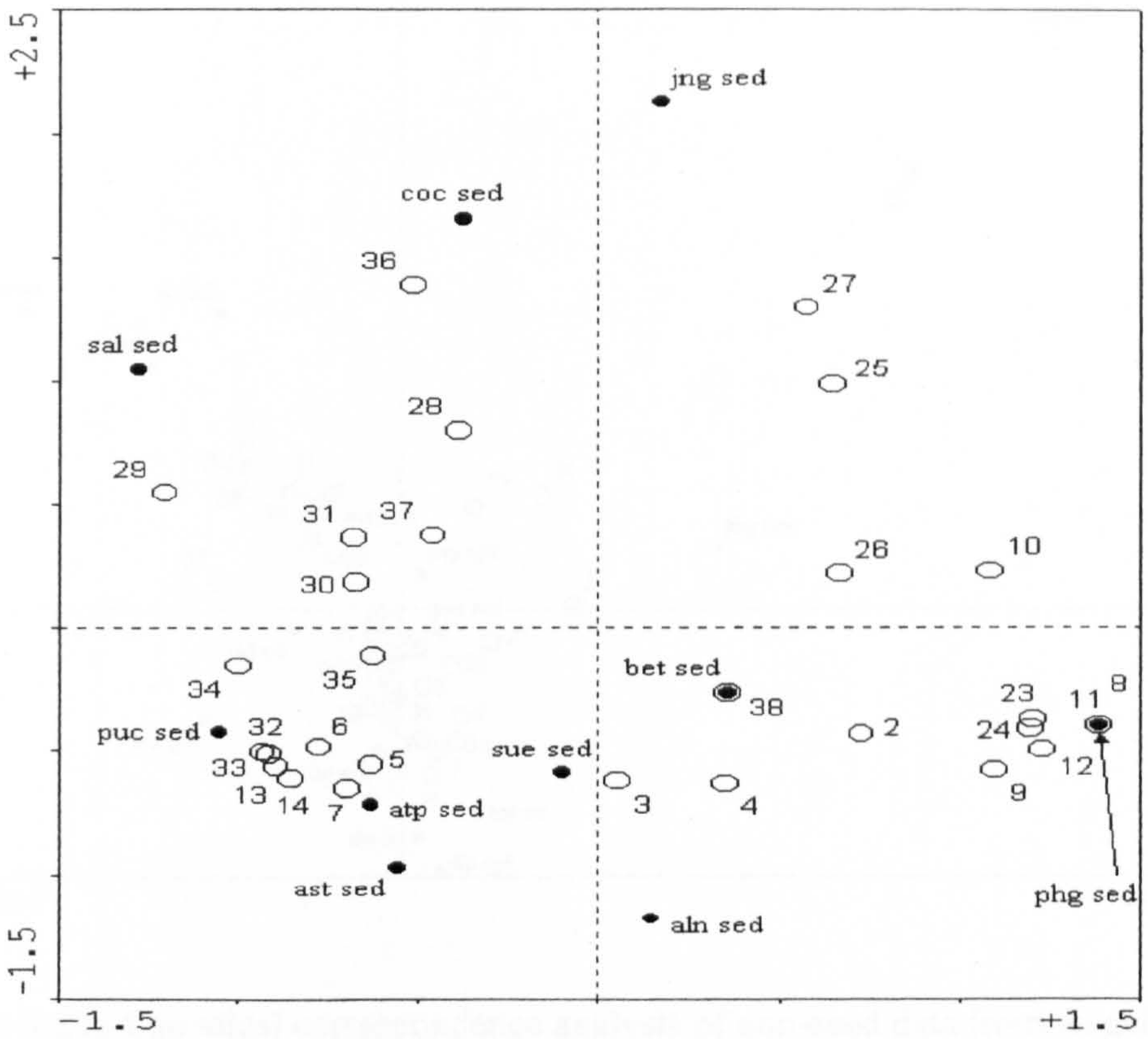


Figure 4.28b Canonical correspondence analysis of seed data from Angel Marsh

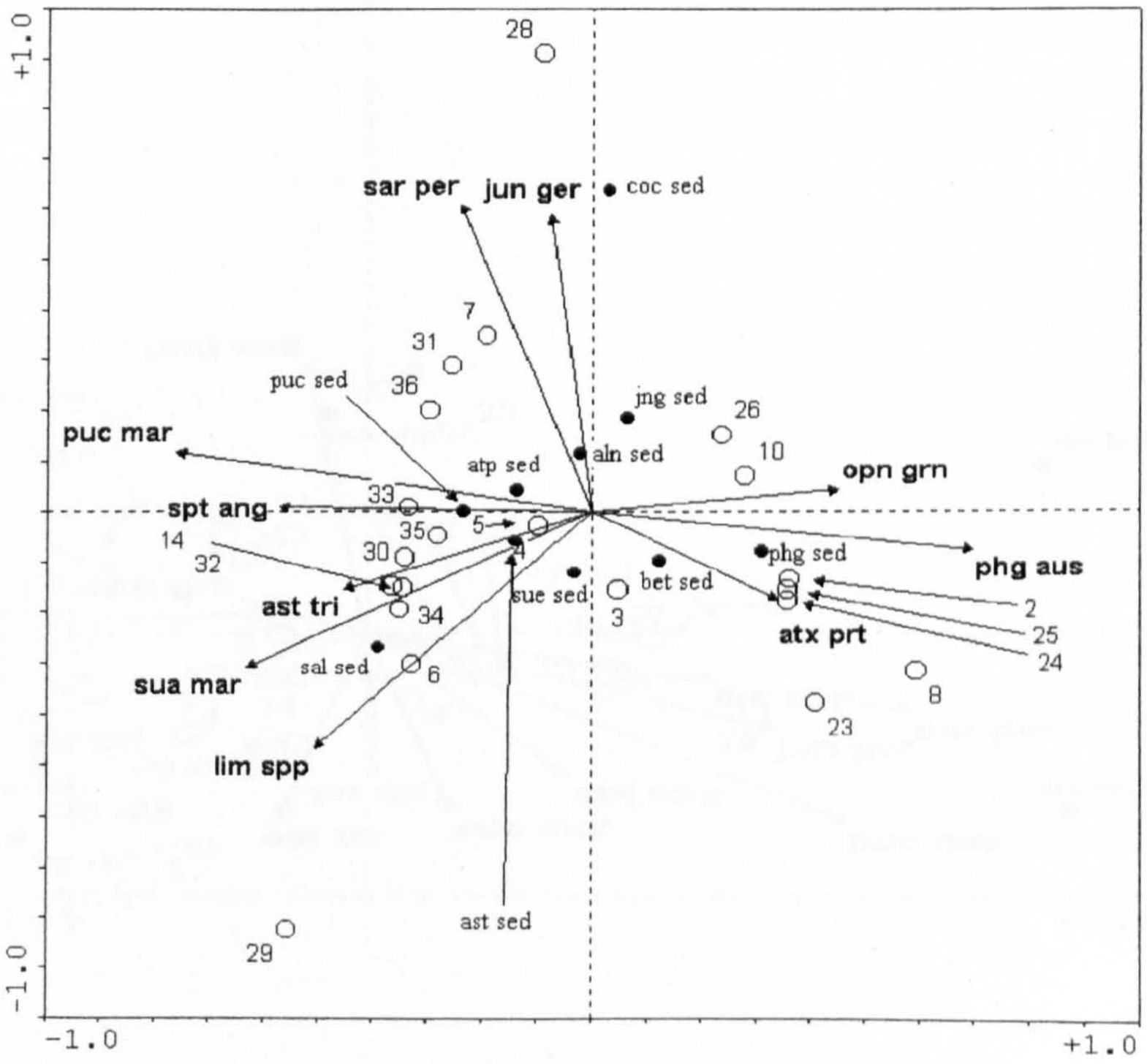


Figure 4.29a Correspondence analysis of non-seed data from Angel Marsh

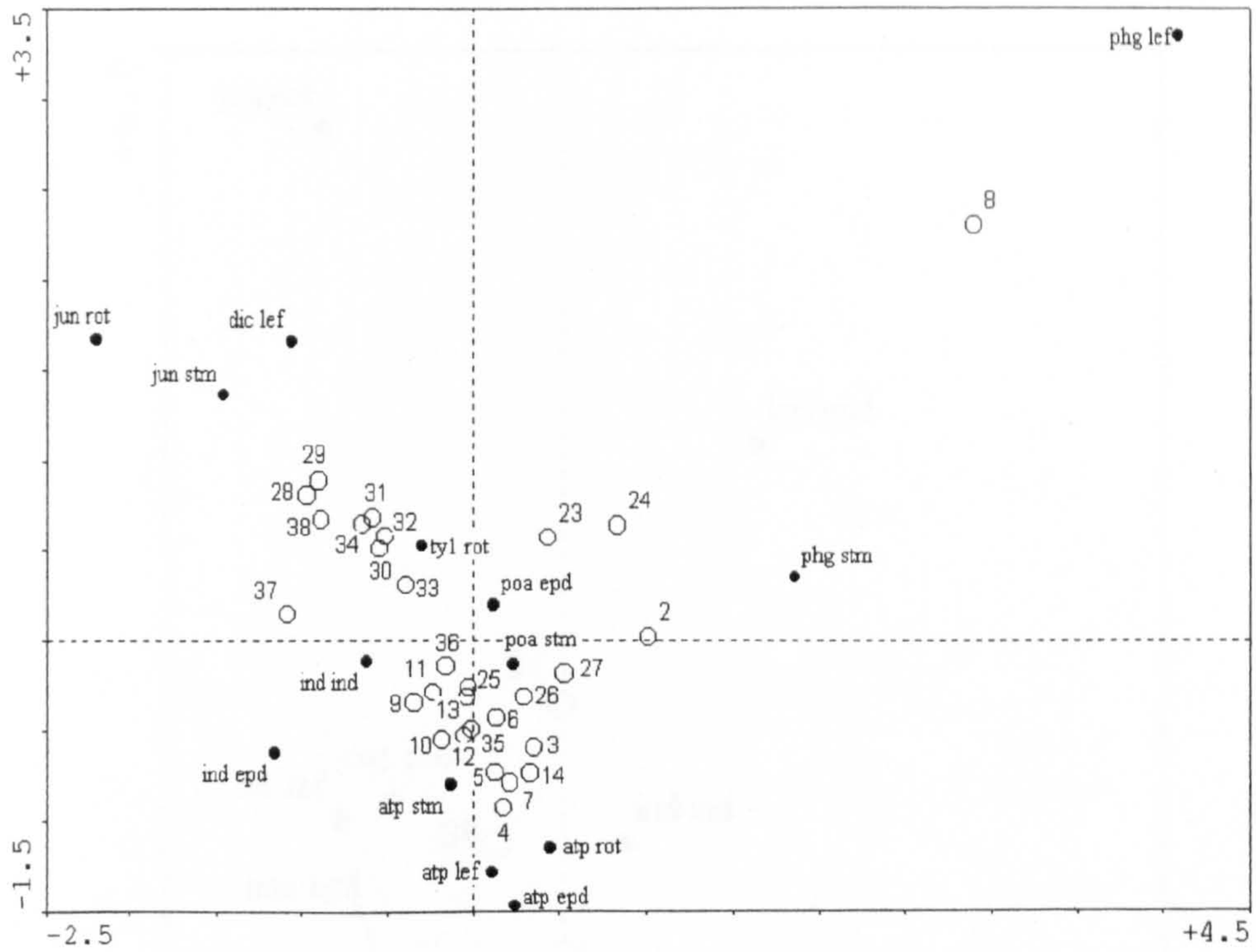


Figure 4.29b Canonical correspondence analysis of non-seed data from Angel Marsh

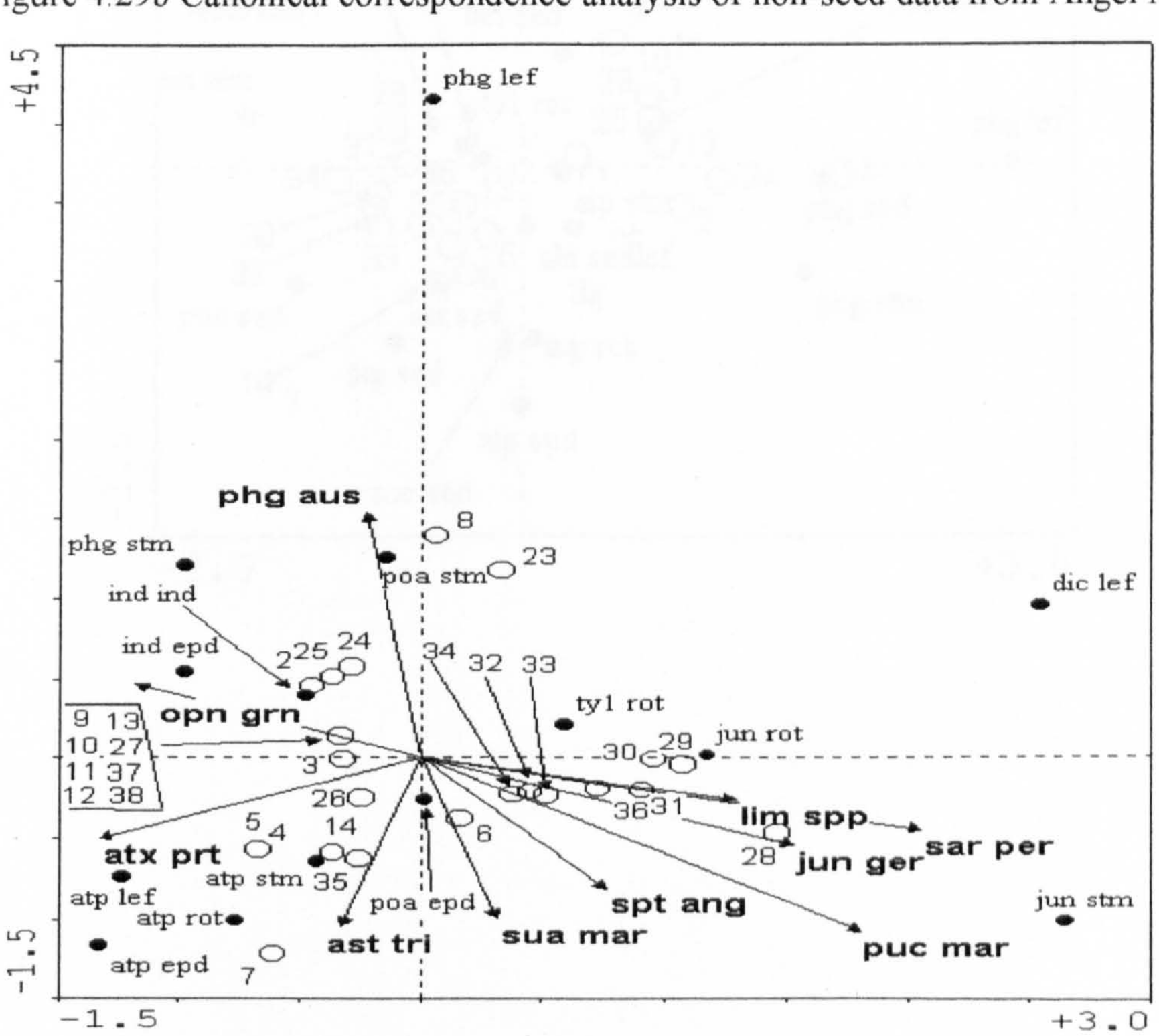


Figure 4.30a Correspondence analysis of seed and non-seed data from Angel Marsh

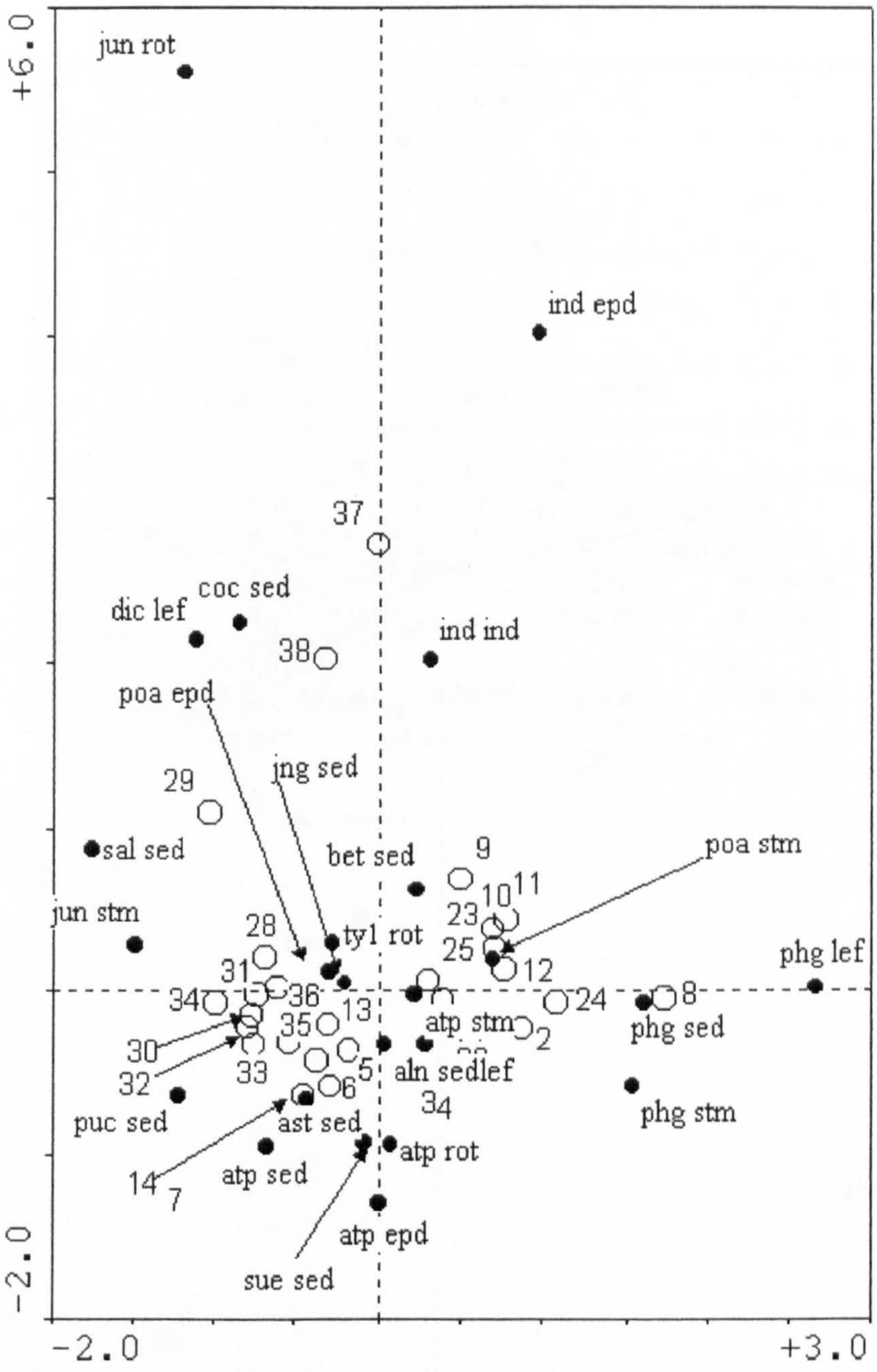
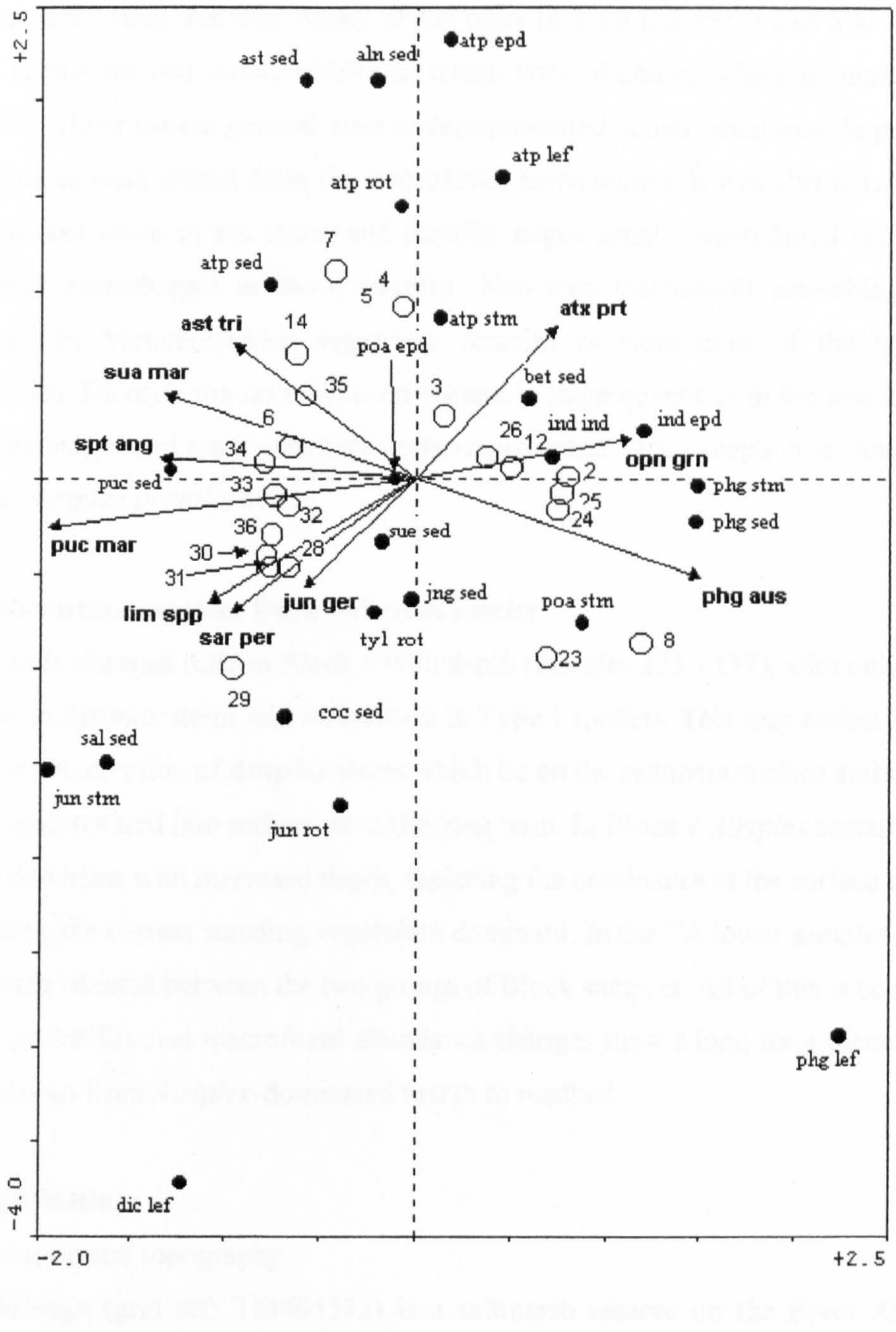


Figure 4.30b Canonical correspondence analysis of seed and non-seed data from Angel Marsh



these taxa depended on the level of identification and, in the case of *Puccinellia* and *Juncus gerardii*, this was only possible to the family level. *Atriplex portulacoides* was mainly represented by fruits, seeds (only identifiable to genus level), leaves, woody roots and aerial stem material. Many of the other taxa on the marsh had low visibility, such as *Limonium* and *Aster*, neither of which were abundant where dominant in the vegetation. Minor taxa in general were underrepresented at individual sample points and in many cases were absent from the macrofossil assemblages. It was also noted that the dominant taxa close to the creek and mudflat edges usually contributed most to the macrofossil assemblages in those samples. Non-seed macrofossil assemblages were dominated by Monocotyledon vegetative remains as were most of the vegetation communities. Dicotyledon taxa were not present in large quantities in the seed and non-seed assemblages and were generally under-represented. One exception at this site was the shrub *Atriplex portulacoides*.

4.5.9 Sub-surface samples from sediment blocks

Macrofossils changed little in Block 1 with depth (samples 133 - 137), with only small decreases in *Atriplex* stems and an increase in Type 1 rootlets. This may reflect the long-term preservation of *Atriplex* stems which lie on the sediment surface and may not become incorporated into sediments in the long term. In Block 2 *Atriplex* remains become dominant with increased depth, replacing the dominance at the surface of *Phragmites*, the current standing vegetation dominant. In the CA lower samples in the blocks were situated between the two groups of Block samples. All of this is consistent with the possibility that macrofossil abundance changes show a long-term succession in the vegetation from *Atriplex*-dominated marsh to reedbed.

4.6 Snape Saltings

4.6.1 Location and topography

Snape Saltings (grid ref: TM403573) is a saltmarsh reserve on the River Alde near Snape, Suffolk (Figure 4.31). The reserve consists of 16.7 acres of protected saltmarsh contiguous with grazing marsh, abandoned farmland and extensive mudflats. The marsh consists of a creek-dissected tidal floodplain supporting herbaceous upper saltmarsh and transitional terrestrial vegetation with lower saltmarsh communities towards the river edge. The marsh topography was complex, with the surface sloping gently from the dryland edge up to a distance of 210m. Beyond this the surface sloped gently towards

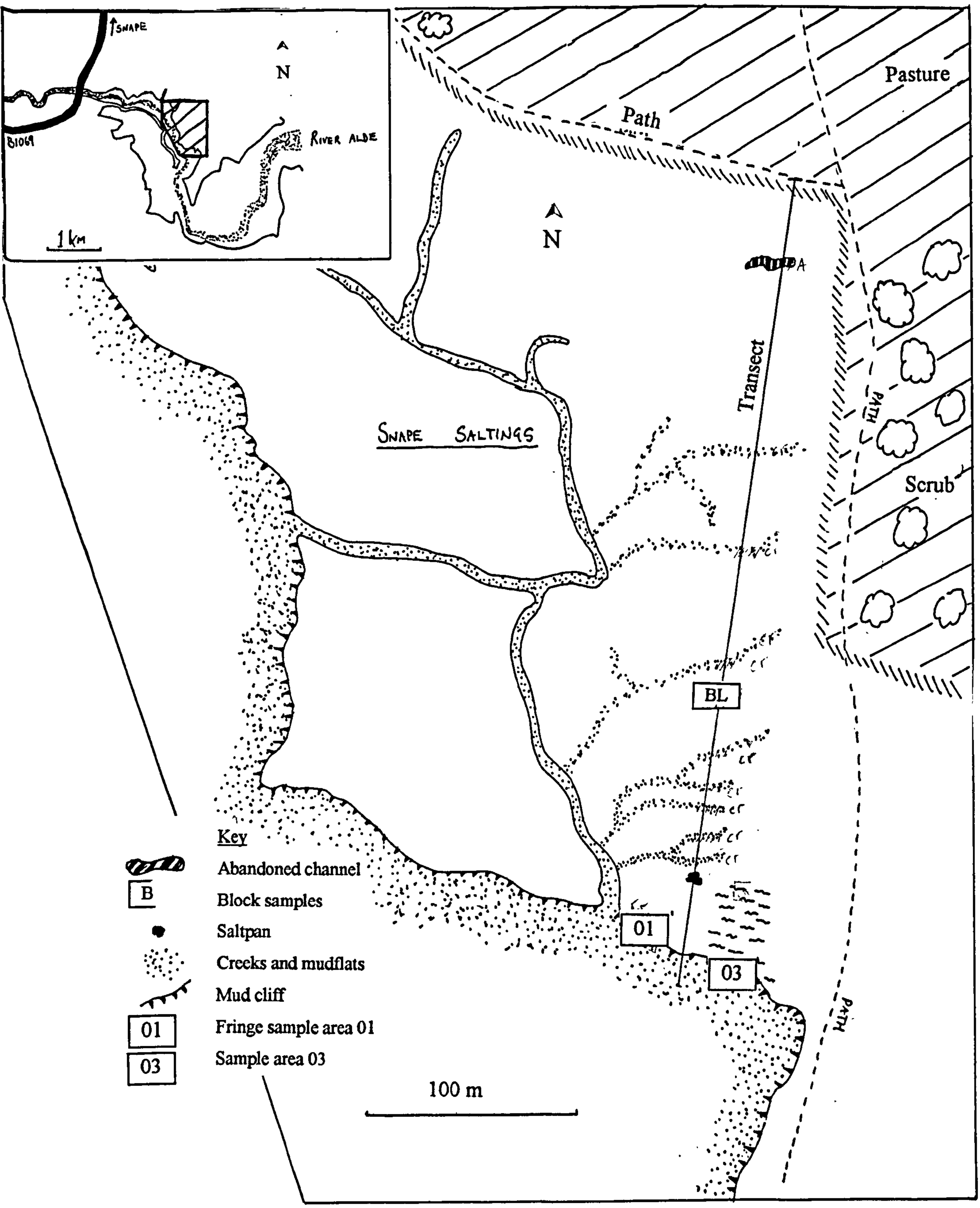


Figure 4.31 Snape Saltings location map (inset) and sample point information

the river. In total the marsh surface varied in height by only 25cm over approximately 360m distance. Superimposed on this general pattern were localised changes caused by erosion and deposition.

An eroding mud cliff, 68cm in height, separated the marsh from the mudflats to the south and west. Low sand hills, partly cultivated, partly covered in gorse and birch-scrub, enclosed the northern and eastern sides of the site. Regular tidal inundation of the marsh was evidenced by the presence of a strandline of detritus high in the marsh. Creeks were eroded below the level of the marsh, usually 50-60cm below the marsh surface and 10-20cm above the river mudflat level.

4.6.2 Vegetation and surface litter

Vegetation at the site was a dense, low-growing mosaic of grass and rush-dominated plant communities (Hughes 1994) (Table 4.14a - b). Vegetation on the higher northern and eastern marsh was dominated by SM16 *Festuca rubra* and SM24 *Elytrigia pycanthus* communities. On the northern section of the marsh, where a peaty substrate had formed, was a stand of SM16 *Juncus gerardii* community in which *Glaux maritima*, *Triglochin maritimum* and *Plantago maritima* were important elements, with often sparse plant coverage and considerable areas of open ground.

Vegetation in the south of the marsh was dominated by the *Puccinellia maritima* sub-communities of SM16 and SM24 mixed with extensive patches of the *Juncus gerardii* sub-community of SM16. Local stands of SM10 transitional low saltmarsh (*Puccinellia* dominated) were found along the southern area of the marsh punctuated by dense patches of SM14 *Atriplex portulacoides* community. Extensive areas of S4 *Phragmites australis* saltmarsh were found in some areas of higher ground towards the river margin and formed dense colonising vegetation on mudflats higher in the river.

Stands of marsh dominants contained occasional plants of species such as *Triglochin maritimum*, *Aster tripolium*, *Glaux maritima*, *Plantago maritima* and *Atriplex portulacoides*. *Atriplex prostrata* was co-dominant in some stands, commonly with *Puccinellia maritima* and *Elytrigia pycanthus*. *Althaea officinalis* and *Sonchus palustris* were noted at the marsh margins. Vegetation was typically more variable at creek margins and the cliff edge, where taxa such as *Atriplex portulacoides* were more dominant, possibly because of more frequent inundation and higher soil salinity. Salt-pans were noted towards the southern end of the marsh. One abandoned creek was

recorded at the northern edge of the site containing 25cm of standing water and tufts of *Juncus maritimus* and *Bolboschoenus maritimus*.

Surface litter was sparse across the marsh. Most litter consisted of Poaceae and *Juncus* stem and leaf material in a sparse continuous mat. Branch sections and occasional fruits were found below *Atriplex portulacoides* stands, although the ground surface there was generally free of litter, possibly because of the lively invertebrate fauna. Only on creek beds and in the bottom of the abandoned channel was any conspicuous accumulation of litter recorded. In both environments litter was discontinuous, occasionally accumulating in dense mats on point-bars and the lag of the creek bed. Mudflats contained little obvious surface litter.

4.6.3 Sampling

Block samples and surface samples were collected along a transect from the northern flood defence bank to the mudflats at the river margin (Fig. 4.31). Analysis of the block samples suggested that while a 50cm^3 sample would provide a general view of macrofossil incorporation at the site, more detailed and reliable information would be collected in 200cm^3 samples. An additional cluster of samples were collected from the marsh edge ('fringe area' 01) to investigate the more complex vegetation at that location. In addition a pair of samples were analysed from the mudflats adjacent to the *Phragmites* stand (area 03).

The sample suite included sediments from all of the major vegetation associations at the site and all depositional environments, including the marsh surface, creeks, saltpans, abandoned channels and mudflats (see 'environment' entry in Table 4.14). It was initially hoped to extend the transect across the mudflat to the edge of the main river channel; however, this proved to be logistically impossible and dangerous because of the mudflat topography and tidal regime of the river. Block 1 sampled a mixed stand of *Juncus gerardii* and *Festuca rubra*. Block 3 sampled a stand of *Elytrigia pycanthus*. Both block samples were aligned to the main transect.

4.6.4 Sediments

Sediments across the site were mainly organic rich silt-clay mixtures. Finely laminated soft sediments were found in the mudflats and creeks, with highly bioturbated firm and hard sediments seen across the marsh surface. Dense root mats penetrated the marsh sediments and contributed to often high organic content values (Figure 4.32). There was

Distance from dryland	35	43	55	75	90	105	120	135	138.5	149	160	170	180	189	190	200
Environment	M	A	M	M	M	M	M	M	C	M	M	M	M	C	E	M
Sample	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16
% water	73.2	74.57	80.84	74.91	77.2	74.29	69.27	56.12	77.01	70.23	60.08	68.16	59.85	66.95	61.35	67.13
%organic	48.57	45.13	54.31	45.6	37.61	38.25	35.14	14.74	19.73	36.29	25.32	31.64	28.47	19.84	23.6	30.98
Cover abundance																
Aster tripolium	6	4	2	5	2	2	4	2		2	4	2	2		4	2
Atriplex prostrata				3		5		5			4	5	5		5	4
Bolboscheomus maritimus		6														
Elytrigium repens	6					2	3	9		2	9	5	9		9	
Festuca rubra					3											
Glaux maritima	2			5			2			2		2				
Juncus gerardii	5		5			8	8			10		8				10
Juncus maritimus		2														
Plantago maritima			5	4	8											
Triglochin maritimum	5		5				6			2						
Open/unvegetated area		8	6		5				10					10		
Distance from nearest plant																
Aster tripolium	<0.5m	0.5-2m	0.5-2m	<0.5m	0.5-2m	0.5-2m	<0.5m			0.5-2m						
Atriplex sp.	10-50m	10-50m		0.5-2m	5-10m	0.5-2m		<0.5m		5-10m	<0.5m	<0.5m	<0.5m	0.5-2m	<0.5m	0.5-2m
Bolboschoenus maritimus		<0.5m														
Elytrigia sp.	<0.5m	2-5m	10-50m	10-50m	5-10m	0.5-2m	0.5-2m	<0.5m	2-5m	0.5-2m	<0.5m	<0.5m	<0.5m	0.5-2m	<0.5m	5-10m
Glaux maritima	0.5-2m	0.5-2m			5-10m	5-10m	0.5-2m							5-10m	5-10m	
Juncus gerardii	<0.5m	2-5m	<0.5m	10-50m	10-50m	<0.5m	<0.5m		5-10m	<0.5m		<0.5m		5-10m	5-10m	<0.5m
Limonium sp.					10-50m		10-50m									
Plantago maritima		2-5m	<0.5m	0.5-2m	<0.5m	5-10m	5-10m	5-10m	5-10m							
Suaeda maritima																>50m
Triglochin maritimum	<0.5m	5-10m	<0.5m	5-10m	<0.5m	5-10m	<0.5m			0.5-2m		5-10m				10-50m

Table 4.14a Snape Saltings standing vegetation, sediment and distance data

Distance from dryland	210	220	230	241.9	260	270	280	284	290	291	300	300.7	310	310.6	320	324.5	330	336
Environment	M	M	M	C	M	M	M	C	M	M	E	C	E	C	M	C	M	C
Sample	17	Block3	Block 1	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32
% water	59.62	65.79	70.12	73.05	69.04	71	58.98	70.93	57.37	56.2	54.39	66.44	54.66	70.93	53.37	63.91	59.34	69.75
%organic	25.3	39.01	31.56	26.16	28.24	31.72	21.65	20.09	20.11	20.33	16.89	28.69	19.98	17.17	13.3	15.79	39.85	17.41
Cover abundance																		
Aster tripolium	2	2	1		2	2	2		2				2		1		2	
Atriplex portulacoides										10	9		8		10			
Atriplex prostrata	4	4			2	2	2				4		4		2		2	
Elytrigium repens	10										7							
Festuca rubra		8	2										6		3		7	
Glaux maritima		1			2	2	2											
Juncus gerardii		5	9		10	10	10										7	
Plantago maritima		1	4															
Puccinellia maritima			2						10	4								
Triglochin maritimum					2	2	2											
Open/unvegetated area				10				10				10		10		10		10
Distance from nearest plant																		
Aster tripolium		0.5-2m	0.5-2m	2-5m	0.5-2m			2-5m		0.5-2m		5-10m		0.5-2m	<0.5m	2-5m	0.5-2m	
Atriplex sp.	0.5-2m	<0.5m	5-10m	2-5m		0.5-2m			0.5-2m	2-5m		0.5-2m	<0.5			0.5-2m	0.5-2m	2-5m
Atriplex portulacoides								5-10m		<0.5m	<0.5m		<0.5		<0.5m	0.5-2m	0.5-2m	2-5m
Elytrigia sp.	<0.5m				10-50m						<0.5m	0.5-2m						
Festuca rubra		<0.5m	0.5-2m		10-50m	10-50m								0.5-2m		0.5-2m		
Glaux maritima	5-10m	0.5-2m	0.5-2m	0.5-2m				2-5m										
Juncus gerardii	5-10m	<0.5m	<0.5m	<0.5m	<0.5m	<0.5m	<0.5m	2-5m			10-50m	10-50m		10-50m		0.5-2m	<0.5m	
Limonium sp.									>50m									
Plantago maritima			<0.5m	10-50m									10-50m					
Puccinellia sp.		5-10m	0.5-2m	10-50m			5-10m	5-10m										
Triglochin maritimum	10-50m		10-50m					2-5m						10-50m		10-50m		

Table 4.14b Snape Saltings standing vegetation, sediment and distance data

Distance from dryland	346	349	350/15	360	364	366	372	372	370	370	370	370	390	390
Environment	M	P	M	M	M	U	U	U	M	M	M	M	U	U
Sample	33	34	35	36	37	38	07\01\01	07\01\02	07\01\03	07\01\05	07\01\07	07\01\09	07\03\01	07\01\02
% water	62.1	66	57.98	54.07	47.69	69.93	57.1	54.62	54.36	51.29	52.56	58.36	61.31	53.83
%organic	18.7	18.4	16.75	16.96	16.36	13.27	14.98	14.84	16.27	16.47	16.75	18.62	15.3	14.02
Cover abundance														
Aster tripolium	2			4	5				4		5	1		
Atriplex portulacoides					2					9				
Atriplex prostrata	5			4								2		
Bolboscheonus maritimus									1					
Cochlearia anglica											1			
Festuca rubra									6					
Glaux maritima									1					
Juncus gerardii	9								7	3	7	8		
Phragmites australis			10											
Plantago maritima									4		4	2		
Puccinellia maritima				8	8				2	3	5	7		
Spergularia media									1		5			
Suaeda maritima	2			3	5									
Triglochin maritimum										2				
Open/unvegetated area		10	4	5		10								
Distance from nearest plant														
Aster tripolium					<0.5m					0.5-2m		0.5-2m		
Atriplex sp.	<0.5m		2-5m					2-5m						
Atriplex portulacoides		0.5-2m									0.5-2m	2-5m	2-5m	
Bolboschoenus maritimus														
Cochlearia sp.							2-5m		2-5m	0.5-2m	<0.5m	<0.5m		
Festuca rubra										2-5m	2-5m	2-5m		
Glaux maritima							2-5m							
Juncus gerardii	<0.5m		5-10m			5-10m	2-5m	2-5m	<0.5m			<0.5m		
Phragmites australis			<0.5m				10-50m						2-5m	2-5m
Plantago maritima												0.5-2m		
Suaeda maritima				0.5-2m	<0.5m	2-5m								
Triglochin maritimum							5-10m		2-5m	0.5-2m		2-5m		

Table 4.14c Snape Saltings standing vegetation, sediment and distance data

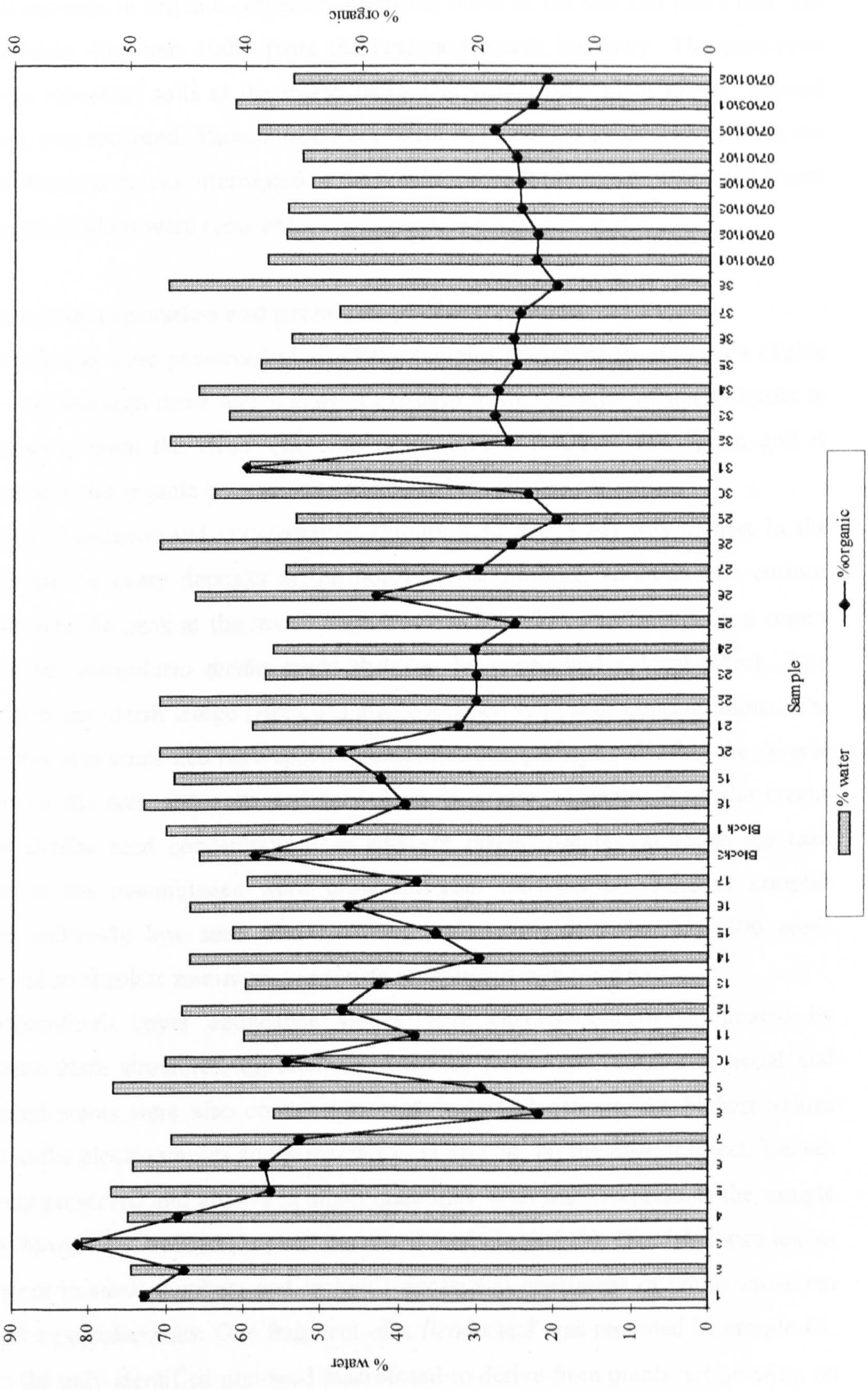


Figure 4.32 Snape Saltings organic content and % water

an overall increase in organic content towards the north of the site and peaty soil was formed between 40m and 100m from the landward marsh boundary. The peat-zone merged into terrestrial soils at the marsh margin in which little plant matter, beyond living roots, was recorded. Though organic content in general increased away from the river edge, the pattern was interrupted in the creeks, where both much higher and lower organic content values were recorded.

4.6.5 Sources, incorporation and preservation of macrofossils

Plant macrofossils were preserved in all of the samples recovered from the site (Table 4.15 – 4.18), although there was a general increase in the quantity of macrofossils in sediments away from the river. This was noted during sediment description and is demonstrated in the organic content values and seed abundance patterns.

Seed abundance and concentration (Figure 4.33 and 4.34) was highest in the samples from the peaty deposits at the north of the transect, although one curious occurrence was the peak at the marsh edge (sample 38). This was caused by a super-abundance of *Spergularia media* seeds that can be considered a local effect. Two samples from the marsh fringe (Area 01) also contained high seed concentrations. The edge samples also contained high species concentrations, perhaps reflecting the diverse vegetation of the area and enhanced seed deposition rates. Samples from the creeks contained similar seed concentrations to adjacent marsh samples, although the taxa contained in the assemblages were often different (see below). Mudflat samples contained uniformly low seed concentrations and usually less than the 100 seeds suggested as an absolute minimum to provide reliable quantitative data.

Macrofossil cover abundance values were characteristically dominated by subterranean plant structures, especially non-woody roots. The remains of aerial and underground stems were also common at some sample locations, the highest values recorded in the block samples and samples 13, 31 and 34, on the main transect. Leaves were rarely preserved and always in small quantities, with the exception of the sample from the *Phragmites* reedbed (35) and the abandoned channel (2). Dicotyledonae leaves were present in small numbers and included occasional specimens of *Glaux maritima* and *Atriplex portulacoides*. One fragment of a *Betula* leaf was recorded in sample 61. This was the only identified non-seed macrofossil to derive from plants not growing on the marsh. Negligible quantities of woody root and stem remains were recorded, usually only beneath or adjacent to stands of *Atriplex portulacoides*. Unidentifiable plant matter

rarely exceeded 10% of total cover abundance in most marsh samples, although it did reach much higher values in samples from the mudflats and the peaty area at the north of the site.

Most species recorded in the seed and fruit assemblages were present in the marsh vegetation or nearby on surrounding dry land. In all of the samples, 90% or more of the seeds came from plants recorded within 50m of the sample site and most of the seeds had potential source plants within 5m of the sample point (see Figures 4.35a and b). There were three groups of samples in which a large proportion of seeds derived from plants between 5 and 50m away from the sample point (samples 4 - 10, 17 - 20 and 24 – 32). These groups corresponded to the areas dissected by the most extensive creek systems and may represent the areas subject to the most regular input of allochthonous plant matter carried on tides. Creek sediments contained considerable quantities of seeds from beyond the adjacent vegetation. They clearly were important conduits for the distribution of seeds on the marsh.

Allochthonous taxa formed a small proportion of the recovered seed and fruit assemblages and were distinguishable from the local taxa on the basis of environmental tolerances. Allochthonous seeds were usually airborne (e.g. *Betula pendula, Epilobium, Sonchus palustris*), carried by animals (*Rubus fruticosus*) or were adapted to water dispersal (*Alnus glutinosa, Ranunculus sceleratus*). A more detailed picture can be seen in the sample ubiquity data presented in Figure 4.36a and 4.36b. Seed assemblages contained a mixture of allochthonous and autochthonous taxa, with allochthonous taxa often being most common in samples near the edge of the marsh, on mudflats, in creeks and in the upper area of the marsh that contained open vegetation. Otherwise seed assemblages were mainly composed of autochthonous taxa. In most cases the allochthonous taxa were from nearby plants. The proportion of taxa represented in the seed assemblages was typically high, especially in the upper marsh areas, with the proportion of missing taxa increasing nearer the marsh edge. The complex of saltmarsh vegetation sampled in the sample area 01 contained the least taxonomically complete seed assemblages. The non-seed assemblages were very incomplete, with only a limited range of taxa identified in most samples. Allochthonous taxa were rare and in all cases, except sample 34, the allochthonous taxa could be identified in nearby vegetation.

Taxon	Sample	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20
	Sample	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20
	Component																				
1 Seeds etc																					
Aster tripolium	Fruit	79	53	40	26	101	17	12			1								19		
Atriplex sp.	Fruit	30	9		173	122	2	5			43	25	30	15	61	129	24	59	71	39	41
Bolboschoenus maritimus	Nutlet		5																		
Elytrigia sp.	Fruit		1	91	85	13	25	67	188	21	103	93	74	123		99	74	128		9	
Elytrigia sp.	Spikelet	2	9		43	41	16	1	32	3	1		2	40	151	23		13		101	
Festuca rubra	seed																			64	132
Glaux maritima	Seed	36	6			2	1	153							20	22		1	5		
Glaux maritima	Capsule							11													
Juncus gerardii	Capsule		21	2		5	11	3			15		15		17	16	5	61	88		
Juncus gerardii	Seed	123	40	522	27	23	372	102		694	682		61			47	233		9	7	25
Lemonium sp.	Capsule					2		1													
Plantago maritima	Capsule	93	27	131	84	247	2	5	1										72		
Plantago maritima	Seed		17	27		152		11		2									73		
Puccinellia sp.	Fruit																		73		
Puccinellia sp.	Spikelet																				6
Sonchus palustris	Fruit								1												
Suaeda maritima	Fruit																1				
Triglochin maritimus	Seed	374	511	245	189	77	43	512			24		61				11	2			
Betula cf pendula	Fruit	1		1		3	1						2					2	1		
Epilobium sp.	Seed								2												
Juncus sp.	Seed		1																		
Poaceae	Spikelet base		5																		
Rubus fruticosus agg.	Fruit				4																
Indeterminate	Seed/fruit										3										
2 Vegetative/Woody Remains	Component																				0.87
Atriplex portulacoides	Leaf																				7.2
Juncus sp.	Stem		10.73	5.13		22	4.92	16.64					13.09				20		12.8	20	0.8
Juncus sp.	Epidermis										0 81										
Juncus sp.	Rhizome			3.33		0.67													31.78	72.93	87.2
Juncus sp.	Non-woody roots		46.15				89 13	79.01		93.13	92.86		84.75						6.47	5.8	3.27
Poaceae	Stem	5 67	2		24.9				27.98	4	6.06	18.55		80.73	25.87	15	7.13	11	0.8		
Poaceae	Leaf	1.2				6.53			2.98	2.53		2.27		1.2							
Poaceae	Epidermis				2.73										11.8	1.07	1.73	3.8			
Poaceae	Rhizome			0 8					3 2									2.8			
Poaceae	Non-woody roots	57.67	8.99	64.2	48 4	51.4			63 14			64.5		15.47	62.07	82.33	70 87	71.4	43.22		
Type 1	Stem		10																		
Cyperaceae	Epidermis		16.93																		
Cyperaceae	Non-woody roots		4																		
Cyperaceae	Stem						3.38														
Dicotyledon	Leaf			9 07				0.59		0.27	0.27		1.89								
Monocotyledon	Seeds	0.73	0.4		0.3	1	2.57	3.39	0.43	0.07			0.27	0.27	0.27	1.6	0.27	1	1.13	1.27	0.67
Various	Woody Stem			2																	
Indeterminate	Indet	34.73		8 93	23.67	18.4		0.36	2.27			14 69		2.33					3 8		
Indeterminate																					
3 Derived indices																					
Total No. Seeds/Fruits		738	705	1059	631	788	490	883	224	720	872	118	245	178	249	336	348	266	411	220	204
No. Species		8	10	6	7	9	8	8	4	3	6	2	5	2	4	4	5	6	7	4	4
Seeds/cm3 sediment		3 69	3.525	5 295	3.155	3.94	2.45	4.415	1.12	3.6	4.36	0.59	1.225	0 89	1.245	1 68	1.74	1.33	2.055	1.1	1.02
Species/cm3 sediment		0.04	0.05	0 03	0.035	0.045	0.04	0.04	0 02	0.015	0.03	0.01	0.025	0.01	0.02	0 02	0.025	0.03	0.035	0 02	0.02

Table 4.15a Snape Saltings Transect macrofossil data and derived indices

Taxon	Component	Sample	21	22	23	24	25	26	27	28	29	30	31	32	33	34	35	36	37	38
1 Seeds etc.																				
Aster tripolium	Fruit			2		3		1		5	1	2	2						3	
Atriplex sp.	Fruit				34	2	26	91	39			15	39	50	27		10			
Atriplex portulacoides	Fruit			21		26	2		16		10	2	1			10				
Elytrigia sp.	Fruit						32													
Elytrigia sp.	Spikelet						29	8												
Festuca rubra	seed									3		1	31							
Glaux maritima	Seed			32					1											
Juncus gerardii	Capsule												2		15		3			
Juncus gerardii	Seed		67	27			49	12		118		15								17
Limonium sp.	Capsule				1			2												
Phragmites australis	Fruit																21			
Plantago maritima	Seed								4											
Puccinellia sp.	Fruit		168	130	306	112	55	44	111	124	109	89	102	131	98	87	109	120	87	36
Puccinellia sp.	Spikelet		19		10	9		36			25	14			5					
Spergularia media	Seed									1								8	411	
Suaeda maritima	Fruit																	5	6	11
Triglochin maritimus	Seed			11						5		9								
Betula cf. *pendula*	Fruit				1		6			2							1	11	6	
Betula cf. *pendula*	Bract												1						2	
Epilobium sp.	Seed													1			2			
Rubus fruticosus agg.	Fruit			1																
Rumex cf. *crispus*	Fruit&bract											1								
2 Non-seed macrofossils																				
Atriplex portulacoides	Stem							38	2.53											
Atriplex portulacoides	Leaf					4.07	1.16		2.47	0.54	1.6									
Atriplex portulacoides	Epidermis					0.93			3.53											0.28
Atriplex portulacoides	Non-woody roots					58.07	58.05		33.53	45 84	72.4	1.73						16.8	4.97	
cf. *Betula* sp.	Lead															1.53				
Juncus sp.	Stem		52							2.29	2.73		22.53		54.2					
Juncus sp.	Epidermis		2.13							0.7					5.33	10.53				
Juncus sp.	Rhizome																			
Juncus sp.	Non-woody roots		45.67	14.69				7.133				7.4	25.3		39.87					
Phragmites australis	Stem																37.33			
Poaceae	Stem			11	19.53	6 67	20.2	8 67	23 2	11.33	8.6	12	21.53						15.58	3.88
Poaceae	Leaf																3.53			
Poaceae	Epidermis			7.27	3		3.55	15.2		5.19	1.87	8.2					4.27	1.73	4.35	3.88
Poaceae	Rhizome									0.94										
Type 1	Non-woody roots			58.78	74.07	29.67	14.51	21.4	33.87	30.56	12.13	59.2	25 4	62.6		40 07	54.13	78	75.88	68.83
Mococtyledon	Stem													10.4				2.73		
Various	Seeds		0.4	0.27	1 4	0 6	1.98		0 87	1.07	0 67	0.27	0.8		0.6	0.13	0.73	0.73	1.22	1.27
Indeterminate	Stem															47.73				
Indeterminate	Epidermis									1.48			4 27	25.47						7.07
Indeterminate	Non-woody roots							42.8						1.53						
Indeterminate	Herb.			8																
Indeterminate	Indet				2		0.55					11.2								13.56
3 Derived indices																				
Seed abundance			254	224	352	152	199	194	171	258	145	148	178	182	145	97	146	144	515	64
Species abundance			2	7	4	4	6	6	5	7	3	8	6	3	3	2	6	4	6	3
Seed concentration			1.27	1 12	1.76	0.76	0 995	0 97	0.855	1.29	0.725	0.74	0 89	0.91	0.725	0.485	0.73	0.72	2.575	0.32
Species concentration			0.01	0 035	0.02	0.02	0 03	0 03	0 025	0 035	0.015	0.04	0.03	0.015	0.015	0 01	0.03	0.02	0 03	0.015

Table 4.15b Snape Saltings Transect macrofossil data and derived indices

Taxon	Sample	07\01\01	07\01\02	07\01\03	07\01\05	07\01\07	07\01\09	07\03\01	07\03\02
Seeds and Fruits	**Component**								
1. Seeds etc.									
Aster tripolium	Seed				3		1		
Atriplex portulacoides	Seed					2	1	1	
Atriplex sp.	Seed		1				16		
Cochlearia sp.	Seed	1		39	402	16	18		
Elytrigia sp.	Seed								
Festuca cf. *rubra*	Seed				8	2	2		
Glaux maritima	Seed	1							
Juncus gerardii	Seed	6	2	1			6		
Phragmites australis	Spikelet	1						22	21
Plantago maritima	Seed						17		
Plantago maritima	Capsule						3		
Puccinellia sp.	Seed	2	3	25	31	26	239		
Puccinellia sp.	Spikelet			4	3		3		
Spergularia media	Seed		1		23				
Triglochin maritimus	Seed	1		1	2		2		
Almus glutinosa	Seed					1		1	
Betula cf. *pendula*	Seed	1			2	3	3		
Betula spp.	Seed	1							1
Callitriche sp.	Seed								1
Epilobium sp.	Seed								
Glyceria sp.	Seed								
Lycopus europaeus	Seed					1			
Ranunculus sceleratus	Seed							1	
Rumex sp.	Seed					1		1	
Rubus type	Seed								1
Sonchus palustris	Seed								
Stellaria media	Seed						1		
Urtica dioica	Seed					1		1	2
Indeterminate	Seed							1	
2. Non-seed macrofossils									
Atriplex portulacoides	Stem						0.67		
Atriplex portulacoides	Leaf					3.04			
Atriplex portulacoides	Rootlet	1			82.67				
Suaeda sp.	Leaf					0.26			
Juncus sp.	Sten				0.33				
Juncus sp.	Rhizome					1.78	2.87		
Juncus sp.	Rootlet	1	4	30.2		66.89	22.47		
Phragmites australis	Stem							1	8
Poaceae	Stem			7	3.67	6.28	11	16	15
Poaceae	Epidermis	2		1.73	1.93	1.72	1	2	4
Poaceae	Rhizome					7.93			
Type 1	Rootlet	20	26	47.87	10.07	8	53.47	15	12
Moncotyledon	Stem		1	3.87		2.64			
Moncotyledon	Leaf		1				4.4		
Moncotyledon	Rhizome			2.53					
Rubus type	Spine								4
Dicotyledonae	Leaf								1
Indeterminate	Epidermis						1.27		
Indeterminate	Woody Root			5.8					
Indeterminate	-	75	68					66	56
3 Derived indices									
Total No. Seeds/Fruits		14	7	70	474	55	312	28	26
No. Species		7	4	4	7	11	11	7	3
Seeds/cm3 sediment		0.07	0.035	0.35	2.37	0.275	1.56	0.14	0.13
Species/cm3 sediment		0.035	0.02	0.02	0.035	0.055	0.055	0.035	0.015

Table 4.16 Snape Saltings area 01 and 03 macrofossil data and derived indices

	Sample	111	112	114	116	118	119	120	122	131	132	133	134	135	136
Taxon	**Size**	50	12.5	25	12.5	25	50	12.5	25	50	50	50	50	50	50
1 Seeds etc.	**Component**														
Aster tripolium	fruit	4		1	1	4	1			8	7				1
Atriplex sp.	fruit				1		9					4	8		
Festuca cf. *rubra*	spikelet	6	7	4	2	1	8		5	7	3	2	6		3
Glaux maritima	seed	21	12	14	11	15	28	8	19	26	20	18		5	16
Glaux maritima	leaves						6			3	2			1	
Juncus gerardii	seed	18	8	9		3	13		16	2	2	8	23	62	33
Plantago maritima	seed														5
Puccinellia sp.	fruit	1		3			1		2			1			
Triglochin maritimum	seed	7		2		12	9	3	5	6	7	2	4	1	3
Betula cf. *pendula*	fruit		1		1										
Sonchus palustris	fruit		1					1		1					
Epilobium sp.	seed									1					
2 Non-seed macrofossils															
Glaux maritima	Leaves						0.2			0.53	0.47			0.4	
Juncus sp.	Stem	2.45		9.96		9.73	1.93	2.46		3.27	9.93				
Juncus sp.	Epidermis	0.7	1.16		2.27	1.2	1.67	0.41	0.6	0.67	1.27	1	1.13	0.87	4
Juncus sp.	Rhizome	15.77	11.97	0.88	9.53	11.13	12.27	6.3	12.2	14.87	17.8	15.87	17.8	7.2	4.2
Juncus sp.	Rootlets	74.56	81.35	70.5	84	74.3	80.53	86.65	77.73	78.53	66.6	77.4	77.33	85.73	88.2
Juncus sp.	Leaf			7.17											
Poaceae	Rhizome								4.13						
Type 1	Rootlets	6.52	5.52		3.87	3.6	3.4	3.7	4.93	1.73	3.27	5	3.73	4.4	3.33
Indeterminate	Rhizome			3.66											
Indeterminate	Seeds				0.33			0.48	0.4	0.4	0.67	0.73			0.27
Indeterminate	Herb stem			7.84											
Indeterminate	Indet.													1.4	
3 Derived Indices															
Seed abundance		57	29	33	16	35	69	12	47	51	39	35	41	68	61
Species abundance		6	5	6	5	5	7	3	5	7	5	6	4	4	6
Seed concentration		1.14	2.32	1.32	1.28	1.4	1.38	0.96	1.88	1.02	0.78	0.7	0.82	1.36	1.22
Species concentration		0.12	0.4	0.24	0.4	0.2	0.14	0.24	0.2	0.14	0.1	0.12	0.08	0.08	0.12

Table 4.17 Snape Saltings Block 1 macrofossil data and derived indices

Taxon	Sample	301	302	305	311	312	313	314	315	316	333	334	335	336
	Size	50	25	50	12.5	25	50	12.5	12.5	25	50	50	50	50
1 Seeds etc.	**Component**													
Aster tripolium	fruit			2			1					1		
Atriplex sp.	fruit	36	19	41	13	22	39	16	9	17	32	27	16	22
Festuca cf. *rubra*	fruit	15	11	18	6	12	2	5	3	7	10	7		14
Festuca cf. *rubra*	spikelet						4				1			
Glaux maritima	seed	7	2	8			12			2	6	5	18	7
Juncus gerardii	seed	2	5	3	3		7	2	1			7	4	9
Puccinellia sp.	fruit	3	1	2	2	4	4	6	3	6				
Betula cf. *pendula*	fruit								1		2			
Glyceria sp.	fruit									1				
Ranunculus sceleratus	fruit						1							
2 Non-seed macrofosssils														
Juncus sp.	Rootlet			2.8	1.53	3.99	1.44	0.4	1.63	2.13	2.93	79.5	65.5	59
Juncus sp.	rhizome											11.79	7.33	21.7
Poaceae	stem	20.76	10.54	21.2	20.01	7.91	15.56	3.24	6.85	5.23	1.27		1.47	2.67
Poaceae	epidermis	0.99	4.2	0.6	5.96	1.86	1.64			1.1	0.93			
Poaceae	rhizome	8.52	29.06	12.4	11.67	14.93	15.08	8.02	19.8	19.67	16.67			
Type 1	Rootlet	67.7	52.03	60.53	58.26	68.61	65.52	86.85	68.14	69.81	77.13	15.21	25.5	15.1
Indeterminate	Periderm	1.06	1.19	1.13	0.68	2	0.21	1.01	0.2		0.8			
Indeterminate	Epidermis		0.28						2.03			0.64		1.53
3 Derived indices														
Seed abundance		63	38	74	24	38	70	29	17	33	51	47	38	52
Species abundance		5	5	6	4	3	7	4	5	5	4	5	3	4
Seed concentration		1.26	1.52	1.48	1.92	1.52	1.4	2.32	1.36	1.32	1.02	0.94	0.76	1.04
Species concentration		0.1	0.2	0.12	0.32	0.12	0.14	0.32	0.4	0.2	0.08	0.1	0.06	0.08

Table 4.18 Snape Saltings Block 3 macrofossil data and derived indices

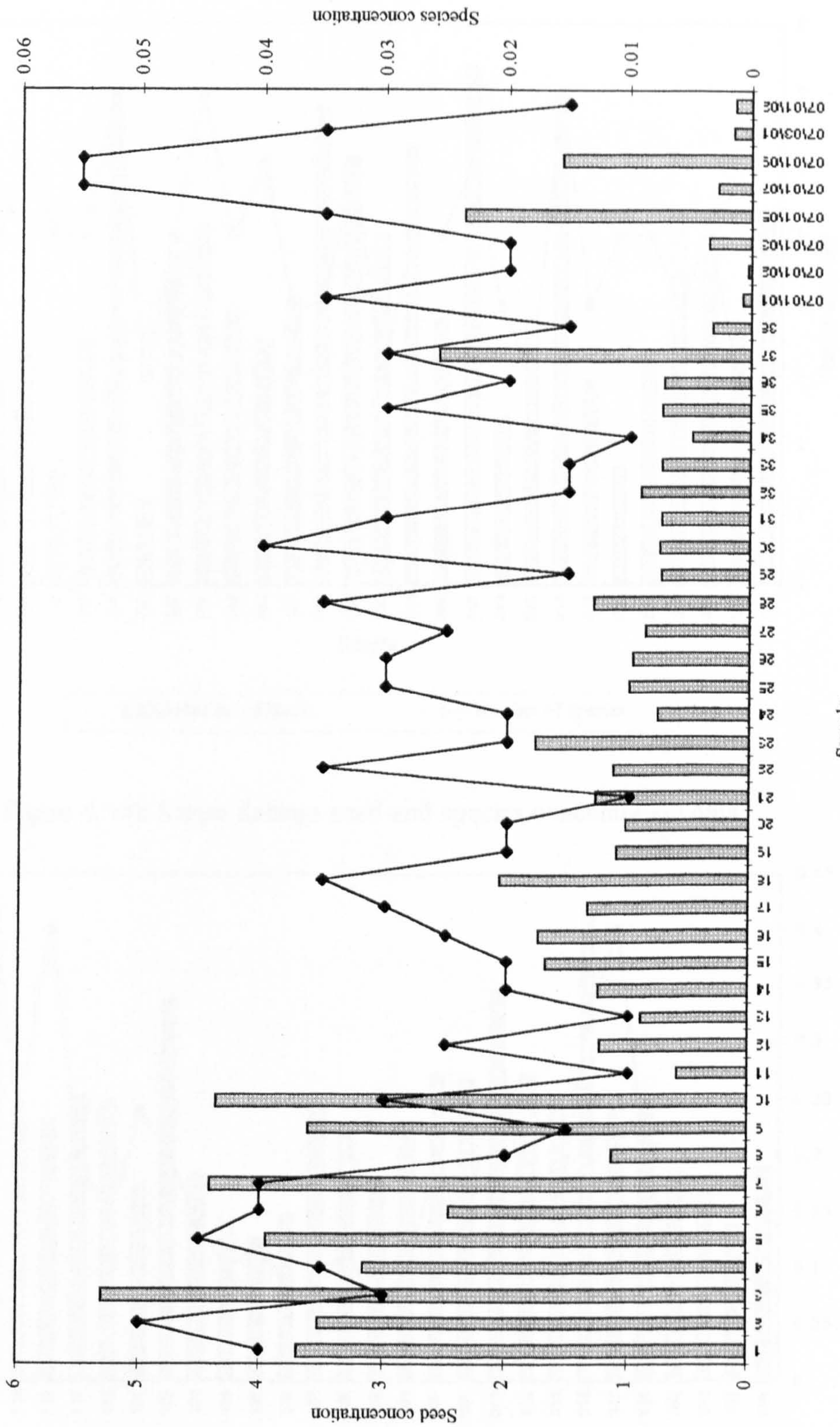


Figure 4.33 Seed and species concentration data

Figure 4.34a Snape Saltings seed and species abundance data

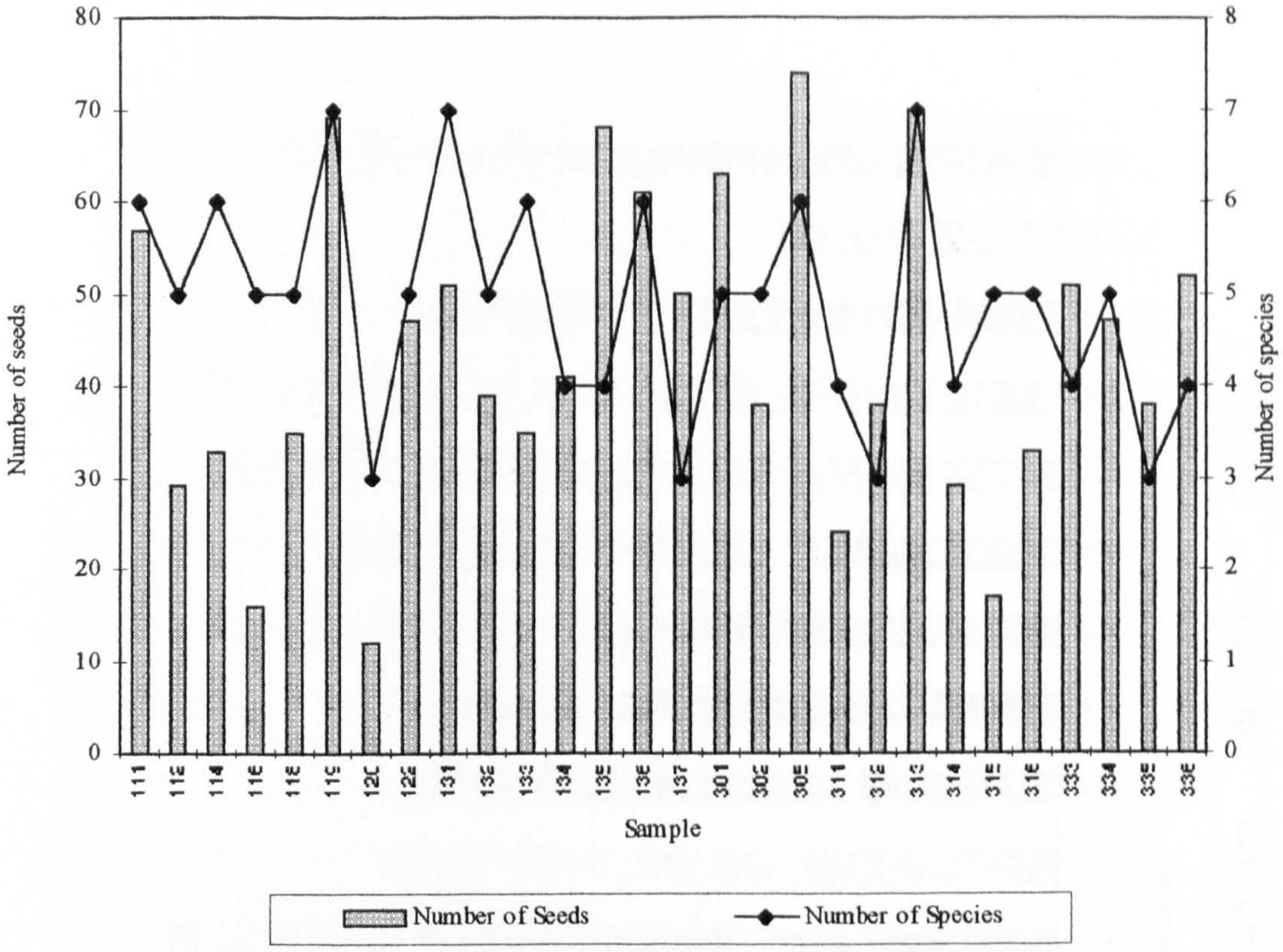
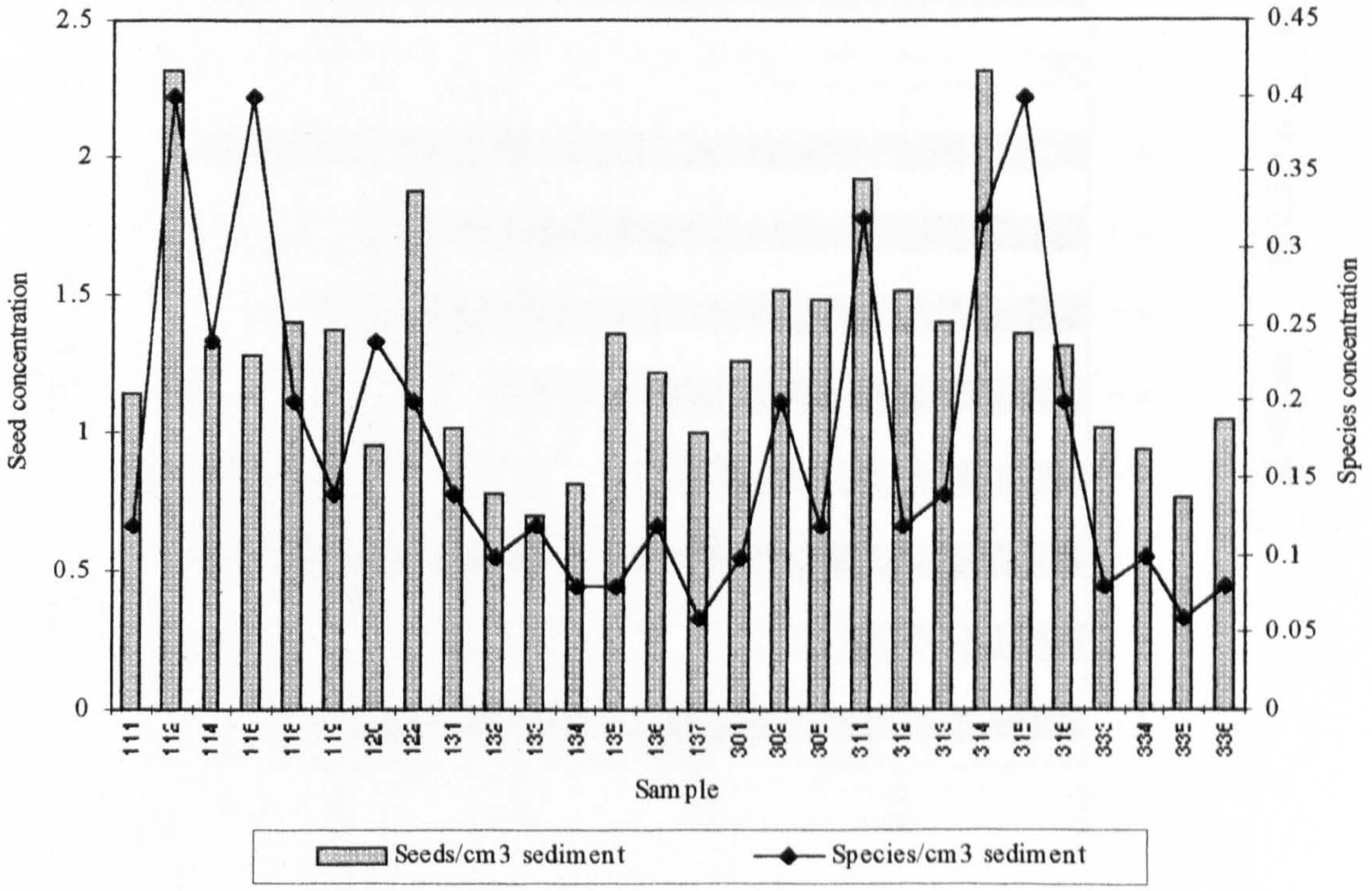


Figure 4.34b Snape Saltings seed and species concentration data



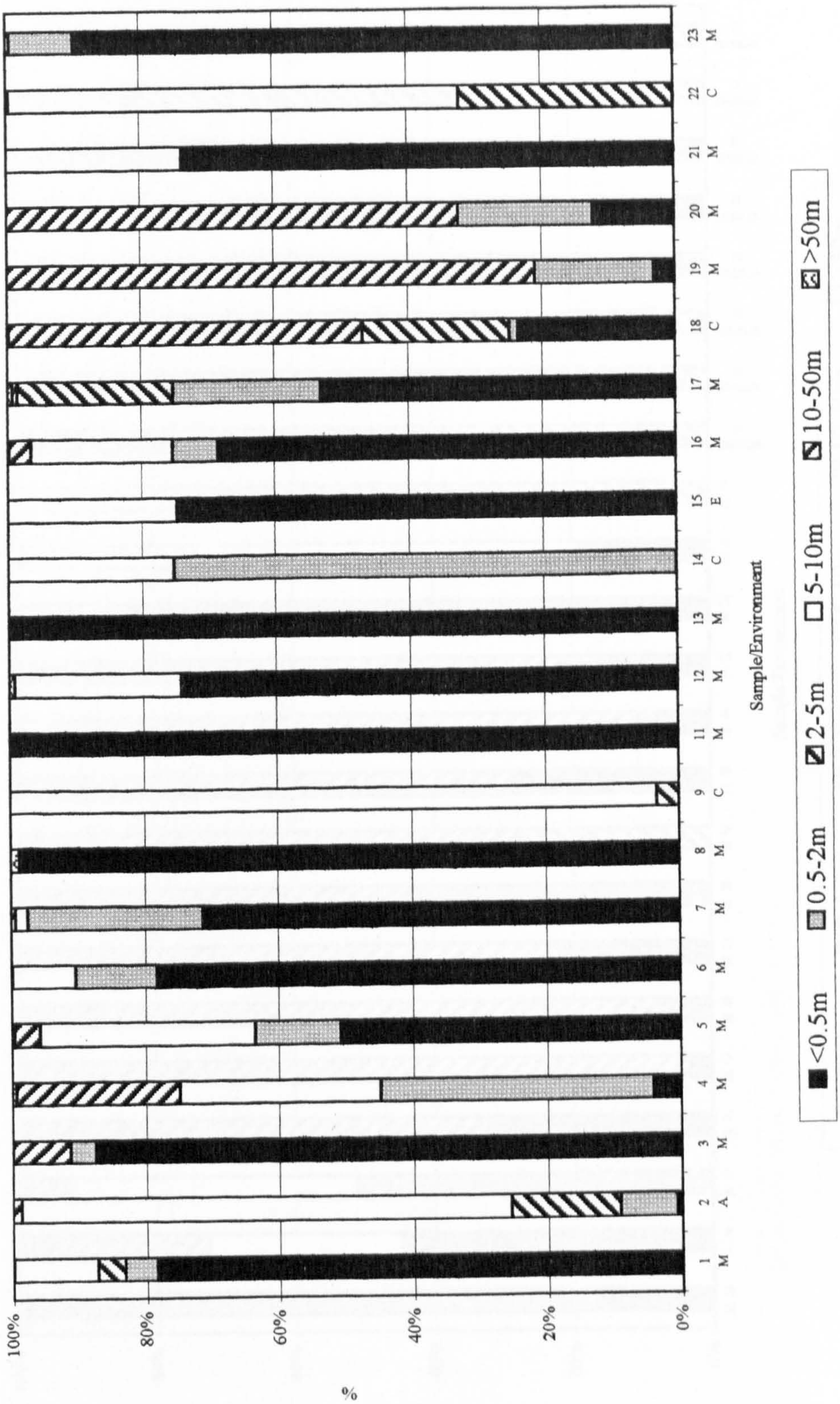


Figure 4.35a Snape Saltings: Percentage of seeds from sample points on set distances from sample points

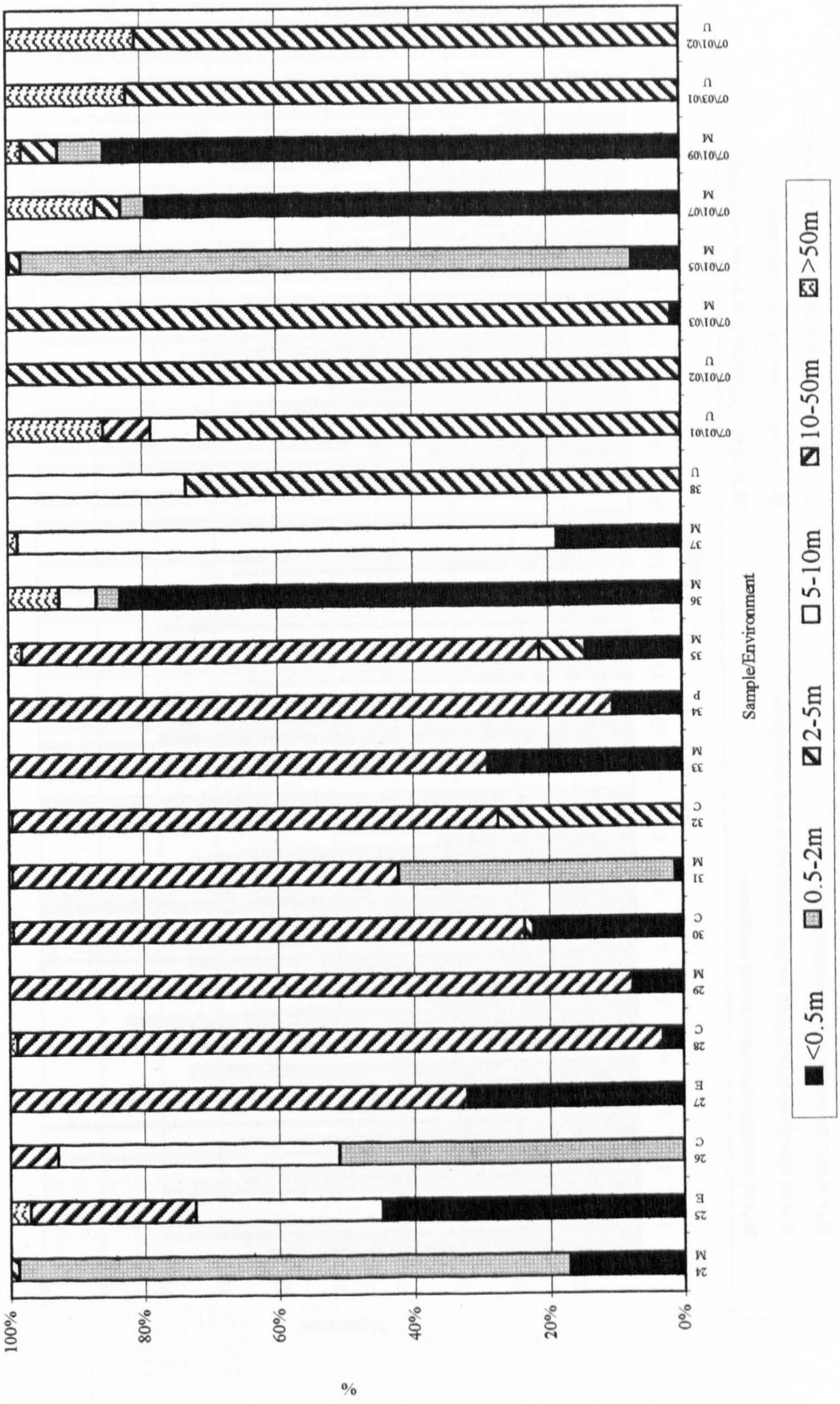


Figure 4.35b Snape Saltings: Percentage of seeds from set distances from sample points

Figure 4.36a Snape Saltings sample ubiquity data

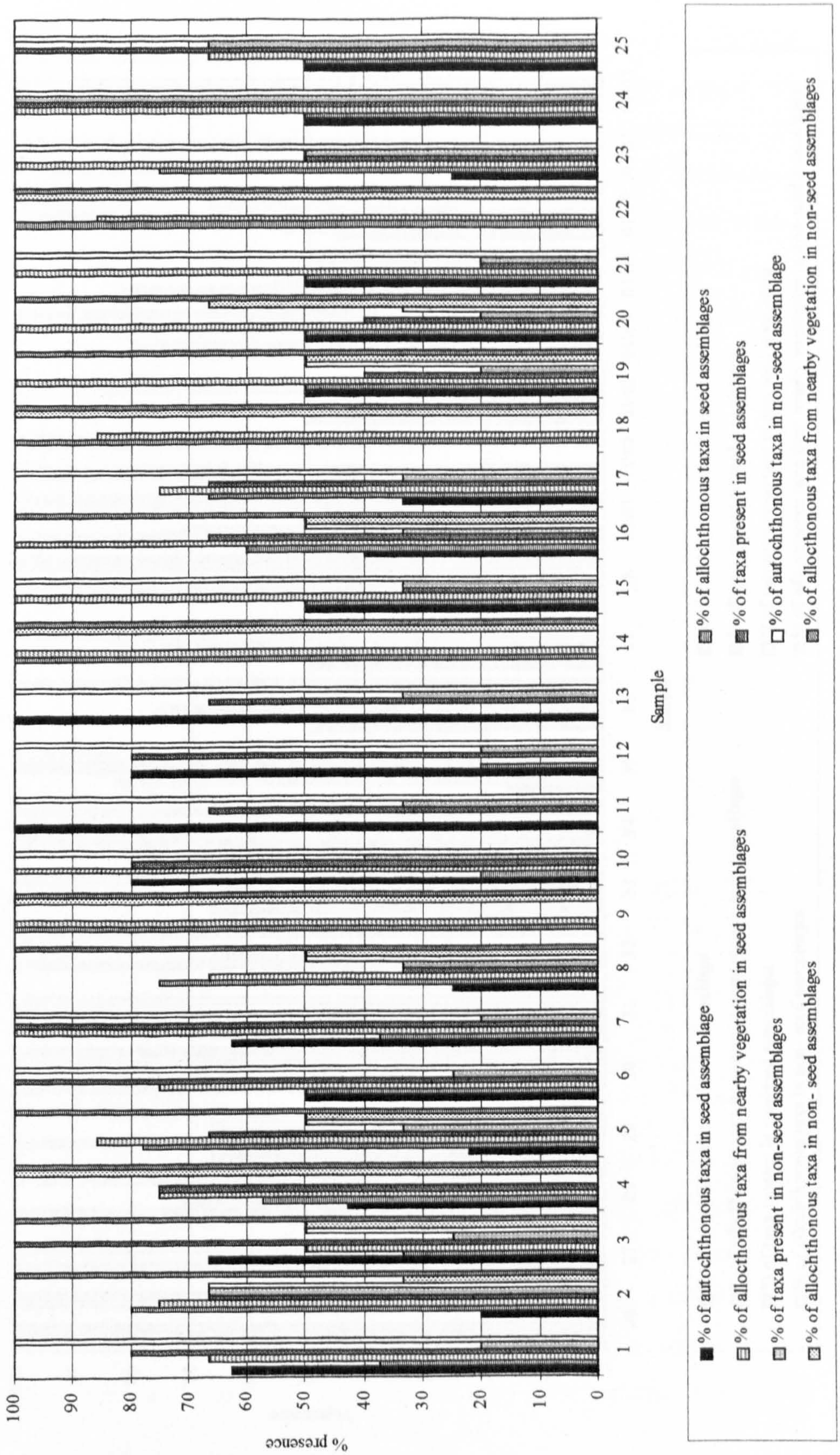
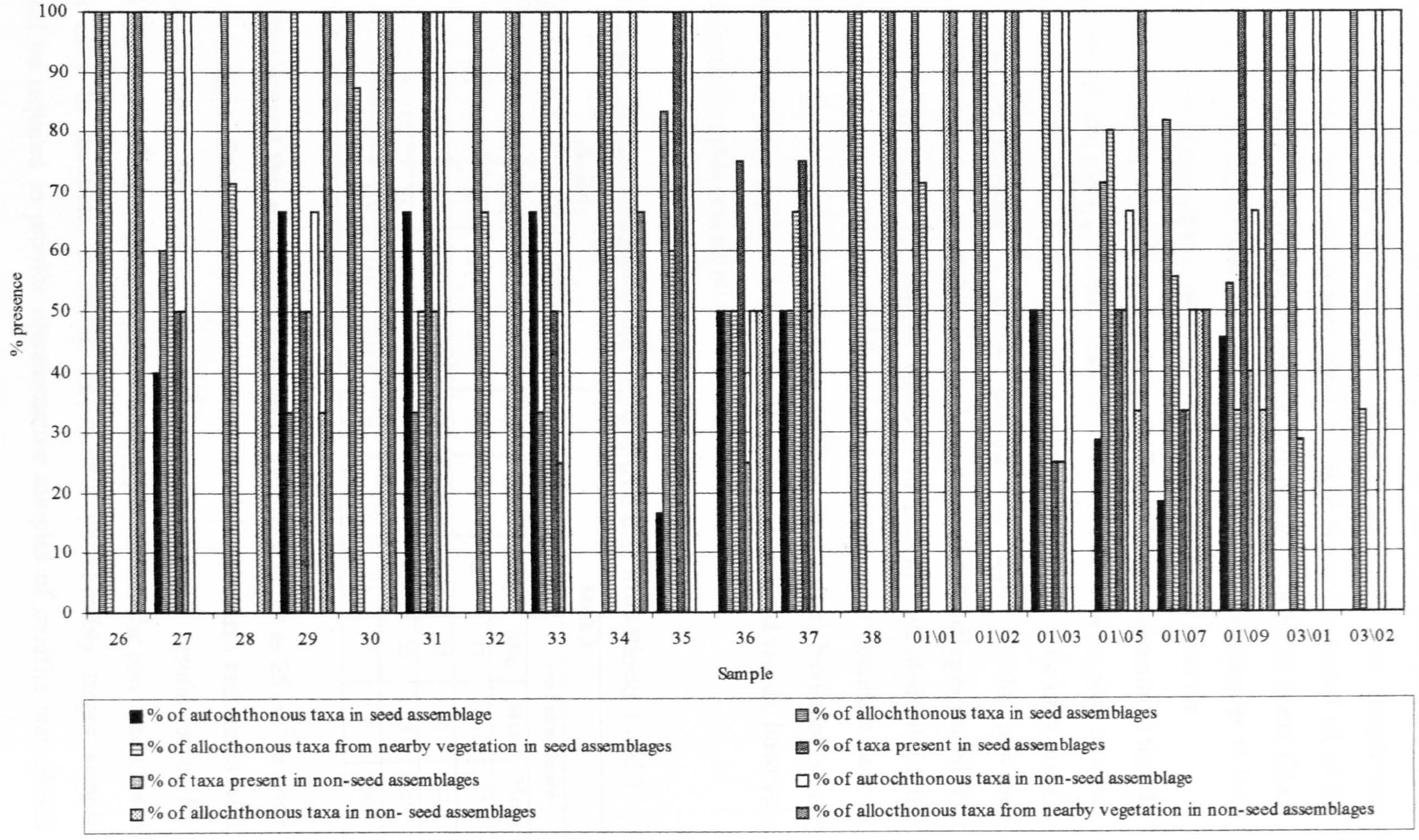


Figure 4.36b Snape Saltings sample ubqiuity data



4.6.6 Sample size effects

Plant macrofossil assemblages from different sample sizes varied in each of the blocks. Both the number of species and the abundance of seeds increased with sample size (Figure 4.34; Table 4.19); however, in each block a single taxon dominated all of the surface sample assemblages, irrespective of sample size (*Atriplex* in block 3 and *Glaux maritima* in Block 1). The main variation between the different sized samples in both blocks was the presence of taxa of low seed abundance such as *Betula pendula*.

Cumulative percentage seed diagrams (Fig. 4.37 and 4.38) demonstrated that the proportion of seeds of the most abundant taxa in the seed assemblages was constant from volumes of 25cm^2 to 50 cm^2 and upwards. Less common seeds were only present as larger volumes accumulated. A similar pattern was noted in the non-seed assemblages in both blocks, although the non-seed macrofossil assemblages varied less than the seeds. In both blocks cumulative volumes of 200cm^2 included all of the identified taxa while sample volumes of 50 cm^2 included the most abundant taxa in correct rank order, but missed out rare taxa of low abundance. Non-seed cover abundance values were more stable at lower sample volumes than seed values; however, the larger cumulative samples contained more of the rare taxa.

Table 4.19 Snape Saltings: Comparison of seed and fruit data from Blocks 1 and 3

	Block 1						Block 3					
	Number of species			Seed abundance			Number of species			Seed abundance		
Sample	Min	Max	Mean	Min	Max	Mean	Min	Max	Mean	Min	Max	Mean
12.5cm^2	4	6	4.7	6	21	14.3	3	5	3.7	12	16	14.3
25cm^2	4	6	4.7	6	33	18	3	5	4.3	21	24	22.7
50cm^2	3	7	5.4	19	36	28.5	3	6	4.7	32	33	29
200cm^2	9	10	9.5	113	138	125.5	*	*	9	*	*	165

These data suggest that even small samples of as little volume as 25 cm^2 provide a representative sample of the most abundant macrofossils in saltmarsh sediments with low incorporation rates. Samples of 50 cm^2 provide a more certain basis for interpretation and 200 cm^2 for representation of rare types. Given the low macrofossil incorporation rates in mudflats, it seems certain that considerably larger sample volumes would be required to provide representative samples of mudflat macrofossil populations.

Figure 4.37a SnapeSaltings Block 1 cumulative seed data for major taxa

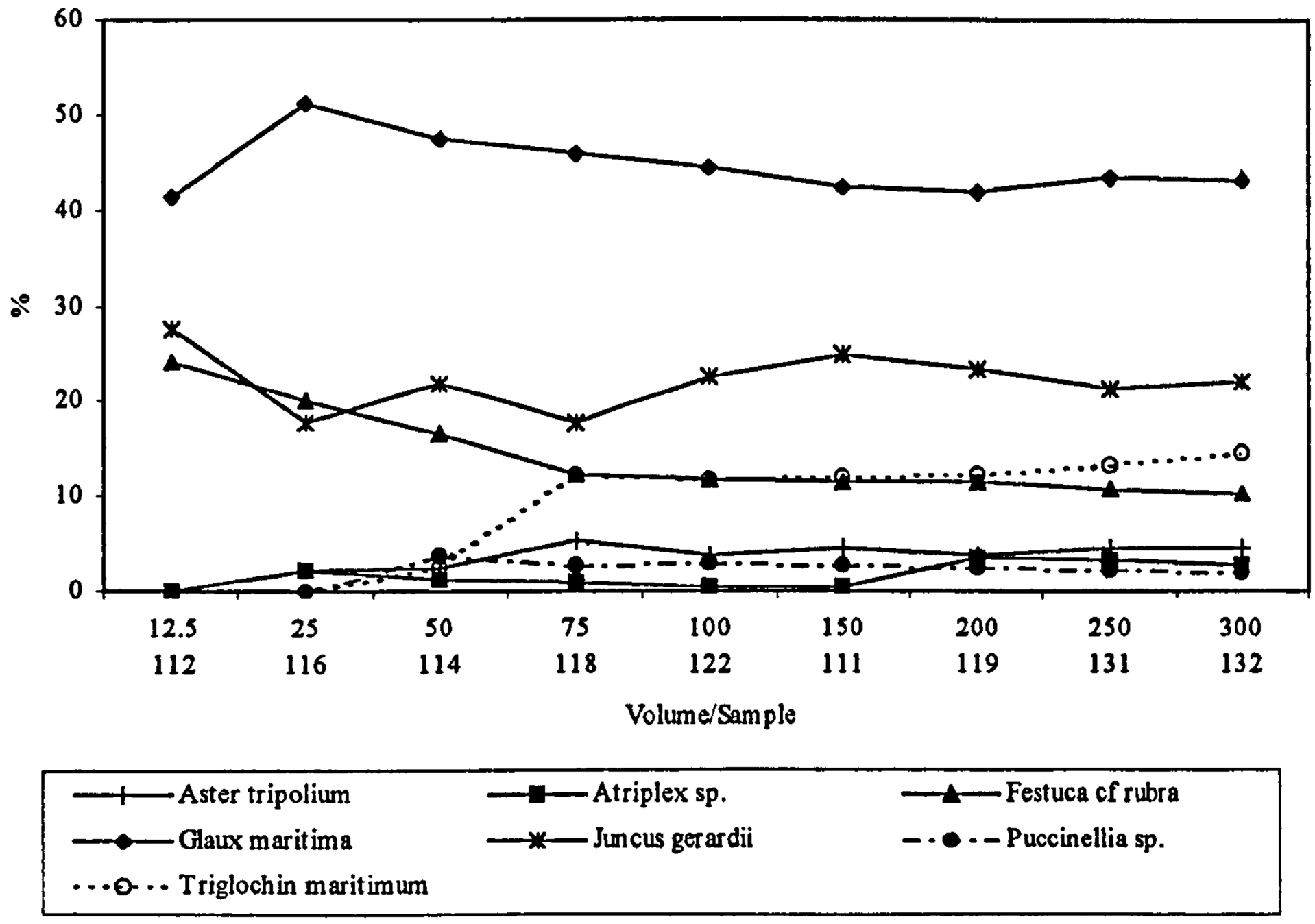


Figure 4.37b Snape Saltings Block 3 cumulative seed data for major taxa

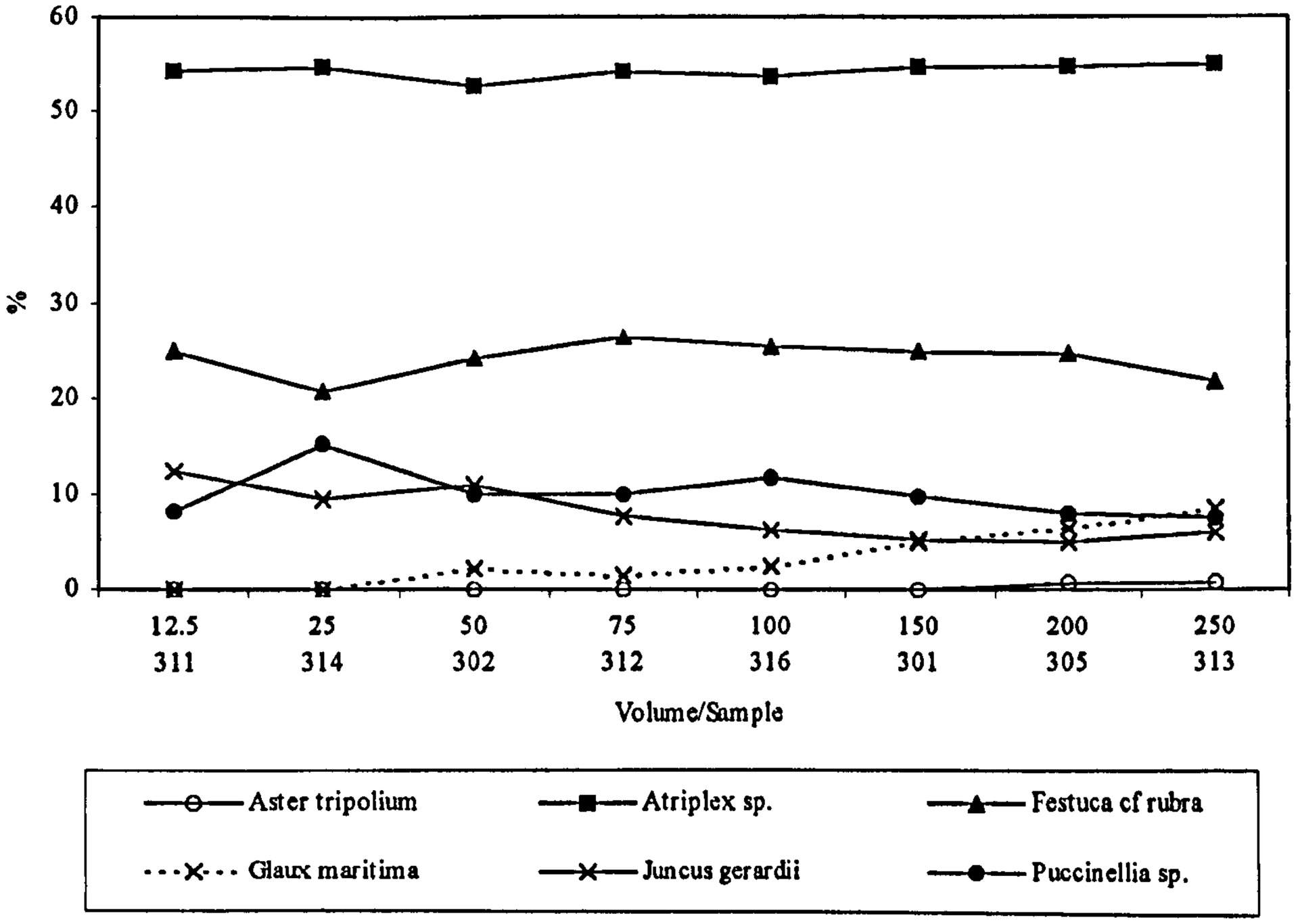


Figure 4.38a Snape Saltings Block 1 non-seed cumulative data for major taxa

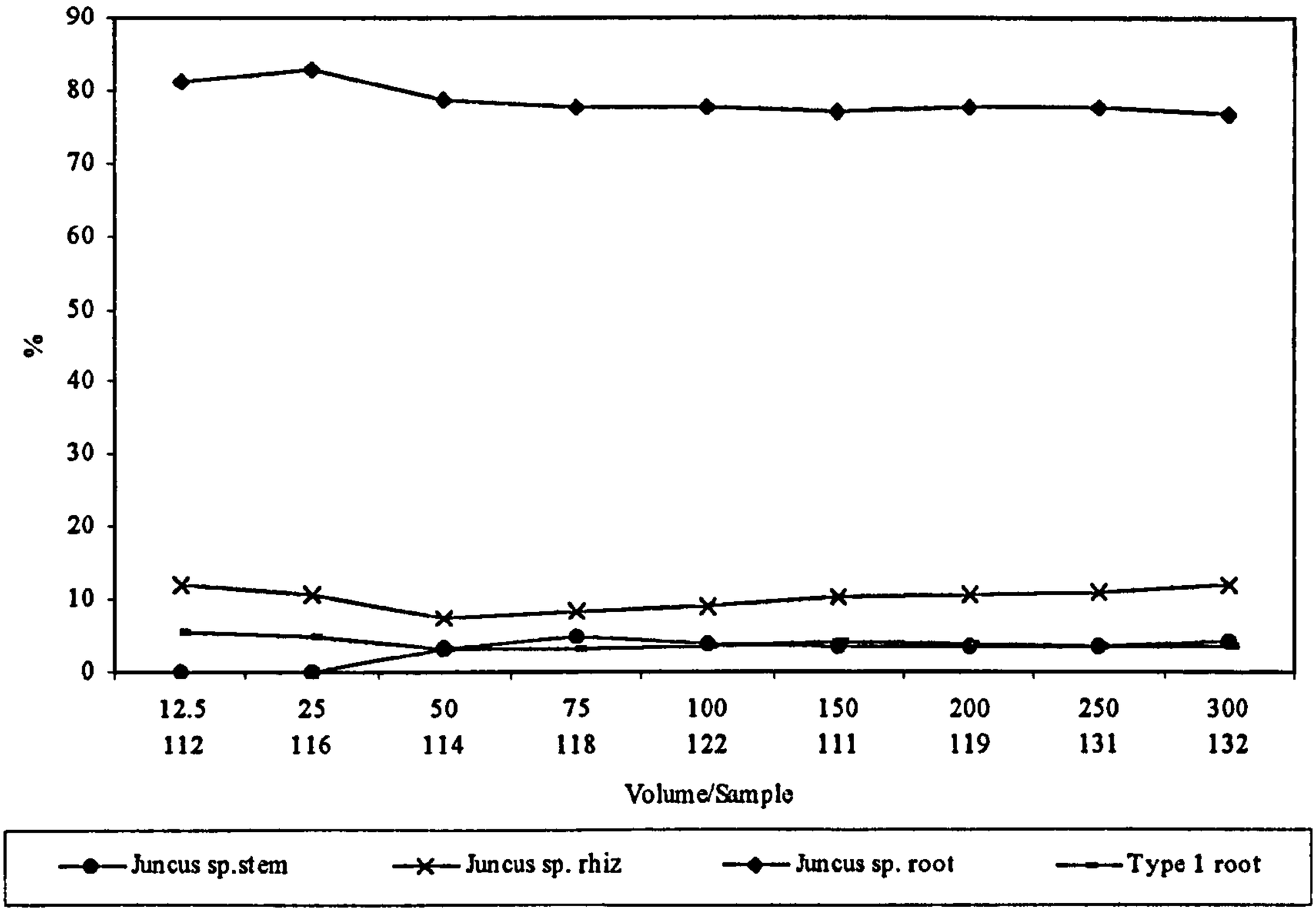
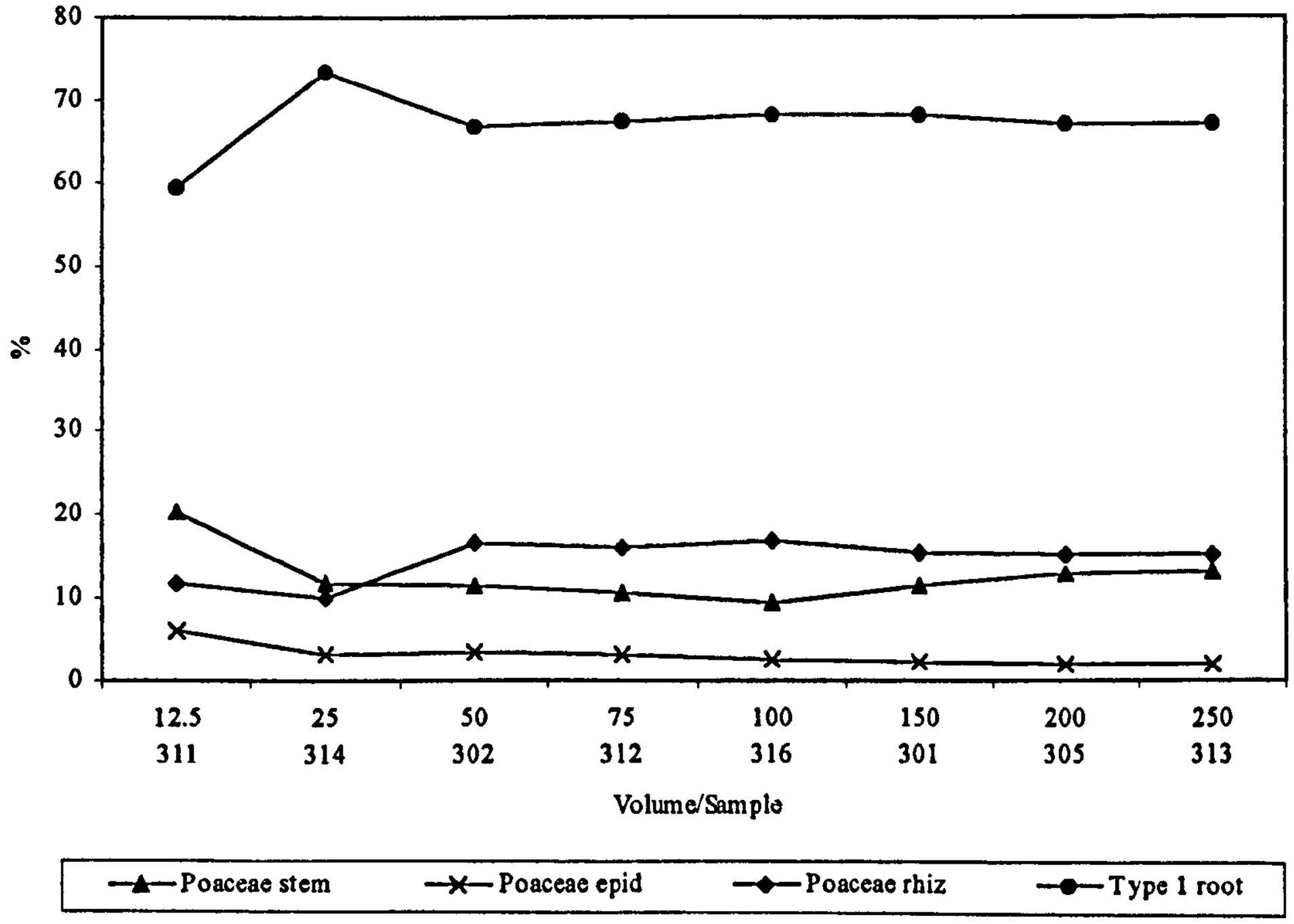


Figure 4.38b Snape Saltings Block 3 cumulative non-seed data for major taxa



4.6.7 Quantitative analysis

An initial CA of all samples showed that the Block samples skewed the analysis to such a degree that it was uninformative. The Block samples data were removed and subject to CA and CCA on combined seed and non-seed data (Figures 4.39 a and b)

CA split the samples into two groups corresponding to the Blocks along the first axis, with differences within each Block sample group seen along the second axis. There was little overlap in the sample points for the two sample groups, with the exception of the points for some Block 3 depth samples. Block 1 samples were distinguished by the presence of large quantities of *Juncus* components, including seed and non-seed elements. The samples were separated along the second axis by the presence of large quantities of *Juncus gerardii* seeds and subterranean components (positive axis) and by the presence of allochthonous taxa (negative axis). Increasing quantities of *Juncus gerardii* seeds with depth may simply indicate increasing compaction and concentration with depth. *Glaux maritima* seeds and *Juncus* rootlets, *Glaux* leaves and *Triglochin* seeds were the most commonly shared of the macrofossils in the Block. Macrofossil assemblages in Block 3 were very similar, with only the quantities of *Betula* seeds providing a major source of variation along the second axis. Interestingly the lowermost samples from the Block (335-336) were in a transitional position between the two sample groups, reflecting the change in composition with depth towards a greater quantity of *Juncus* components.

CCA (Figure 4.39b) showed higher abundance quantities of *Juncus gerardii, Atriplex prostrata* and *Festuca rubra* macrofossils correlated well with standing vegetation abundance. Seeds of other taxa were not well correlated with the standing vegetation, being well dispersed or, perhaps, incorporated in such small quantities as to be unreliable. Poaceae components were recorded mainly in Block 3, where *Festuca* was a dominant, and were rarer in Block 1. This result shows that mainly the dominants are recorded in macrofossil assemblages, with incorporation more sporadic and proportionately small where a species is a minor vegetation component. Interestingly *Glaux* leaves were found to be uncorrelated with the records of the plant in the vegetation, suggesting that the leaves are as mobile as the seeds.

Variation in the first two axes of the seed CA for Transect samples was limited (Figure 4.40a). A main group of samples was clustered around the axis, split into two broad groups. To the negative side of the first axis were samples from the northern section of the saltmarsh typically containing large quantities *Elytrigia, Juncus, Plantago*

maritima, Triglochin maritimum and *Aster tripolium* seeds. To the positive side of the first axis were samples from the southern end of the marsh, including those from Area 01 and 03. The main determinant here was the presence of *Puccinellia, Festuca, Spergularia, Atriplex* and *Betula* seeds. *Phragmites* seeds separated samples from Area 03 and the creek/mudflat samples tended to be spread among the two groups, mainly in a similar place to those from nearby marsh vegetation. CCA of the seed assemblages showed high correlation between standing vegetation cover abundance of dominant taxa and seed abundance in many samples (Figure 4.40b). *Juncus gerardii, Puccinellia, Plantago maritimus, Glaux maritimus* and *Elytrigia* showed high correlation where they were dominant in the vegetation.

CA of the non-seed data split the samples into several groups (Figure 4.41a). Samples with large quantities of *Juncus* components were grouped on the positive part of the first axis. These were opposed to samples containing large quantities of Poaceae components, *Atriplex* components and indeterminate components. Samples with large quantities of *Atriplex* components were separated along the second axis. Mudflat samples were grouped together containing large quantities of indeterminate matter. CCA of the non-seed material showed that standing vegetation of *Juncus* and *Atriplex* was well correlated with the appropriate components in the samples (Figure 4.41b). Most of the Dicotyledons were not represented at all and the Poaceae taxa were well correlated with the standing vegetation. The open ground samples (mudflats) were well correlated with the quantities of indeterminate matter.

Combined seed and non-seed data CA (Figure 4.42a) split the samples into three broad groups. The upper marsh samples from the north of the site (1 – 19) were grouped to the negative side of the first axis with those from the lower marsh to the positive side. The former group contained higher abundances of *Juncus* components, *Elytrigia* seeds and the seeds of herbaceous Dicotyledon and rosette plants (e.g. *Glaux maritima* and *Triglochin*). The second group contained higher abundances of the other Poaceae components, most *Atriplex portulacoides* components and the *Betula* seeds. The mudflat and marsh edge samples were separated along the second axis, mainly because of the presence of indeterminate matter and a variety of site-specific seeds. Creek samples were distributed throughout the other marsh samples. In most cases the seeds CCA (Figure 4.42b) confirmed the general trend seen in separate seed and non-seed plots that the presence of the main vegetation dominants correlated well with the presence of appropriate macrofossils.

Figure 4.39 a Correspondence analysis of seed and non-seed data from Snape Saltings Blocks

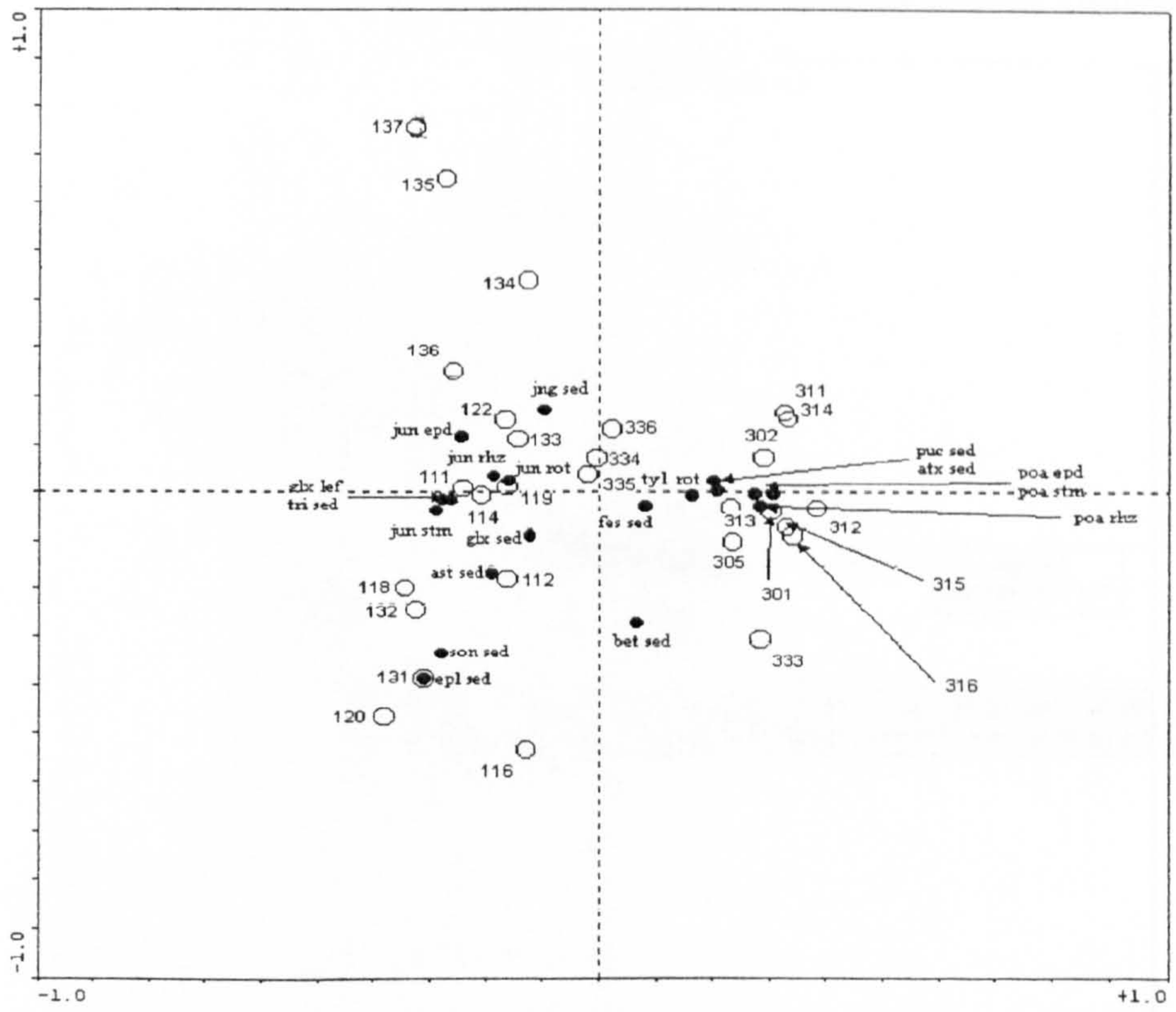


Figure 4.39 b Canonical correspondence analysis of seed and non-seed data from Snape Saltings Blocks

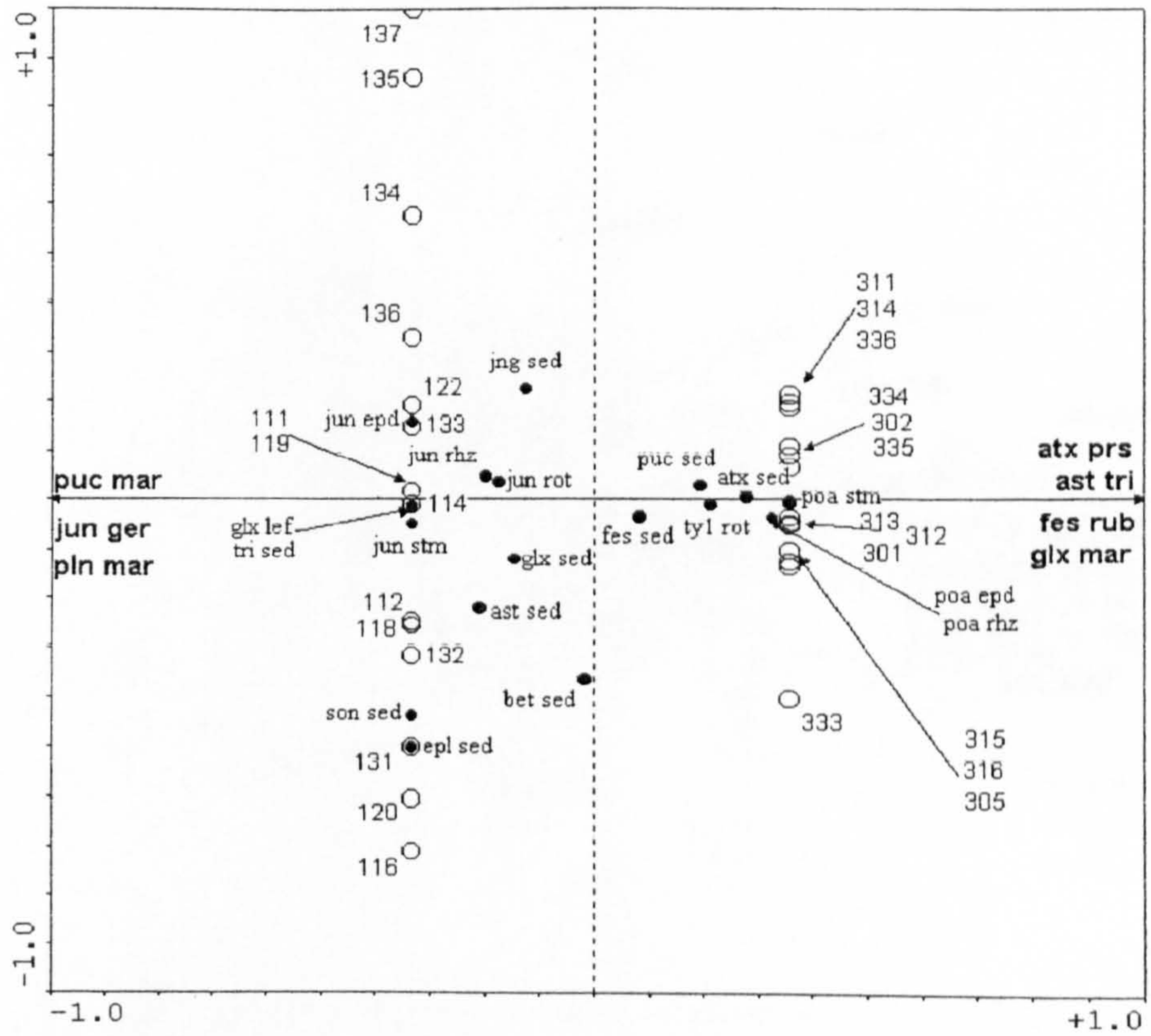


Figure 4.40a Correspondence analysis of seed data from Snape Saltings Transect

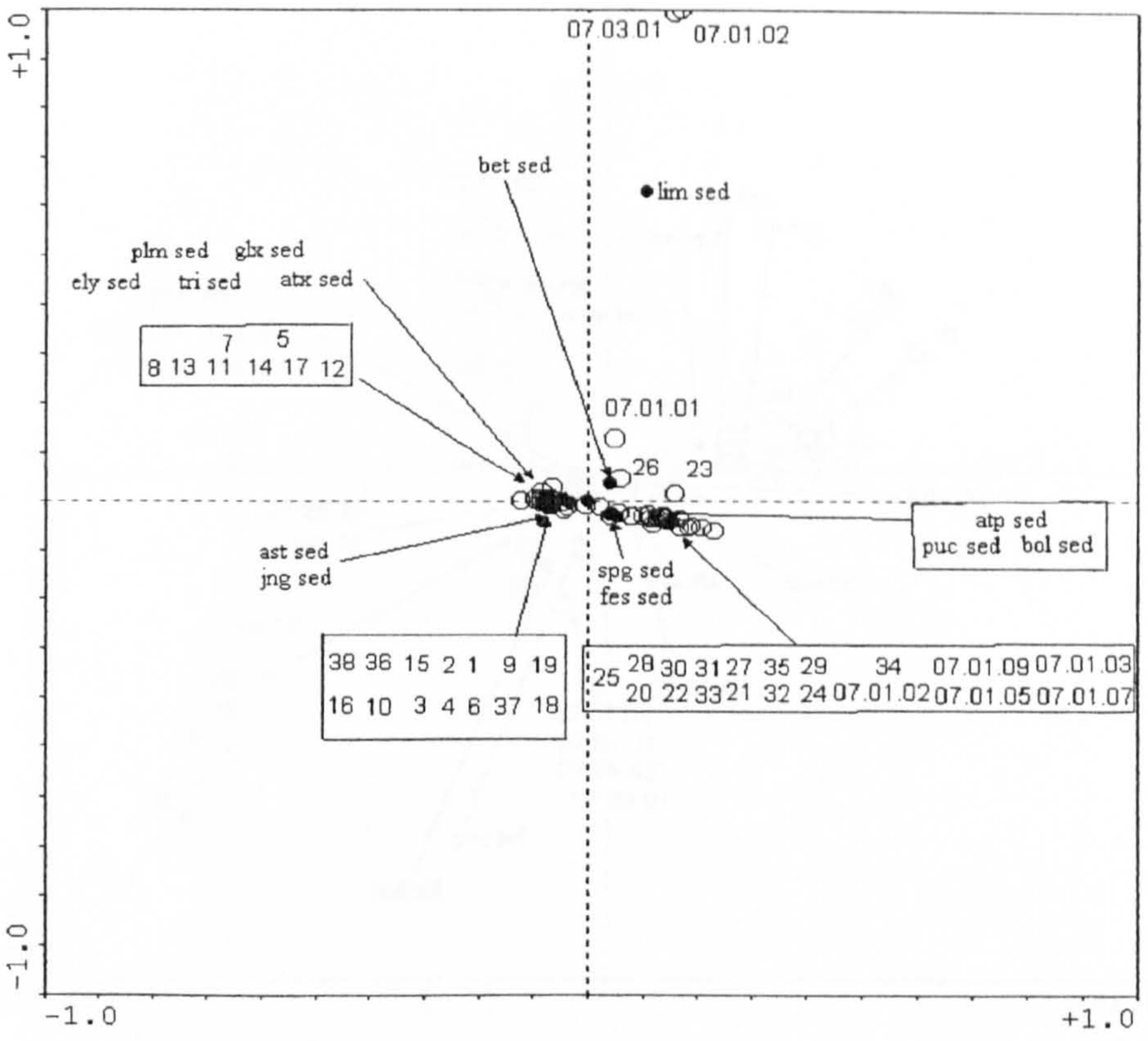


Figure 4.40 b Canonical correspondence analysis of seed data from Snape Saltings Transect

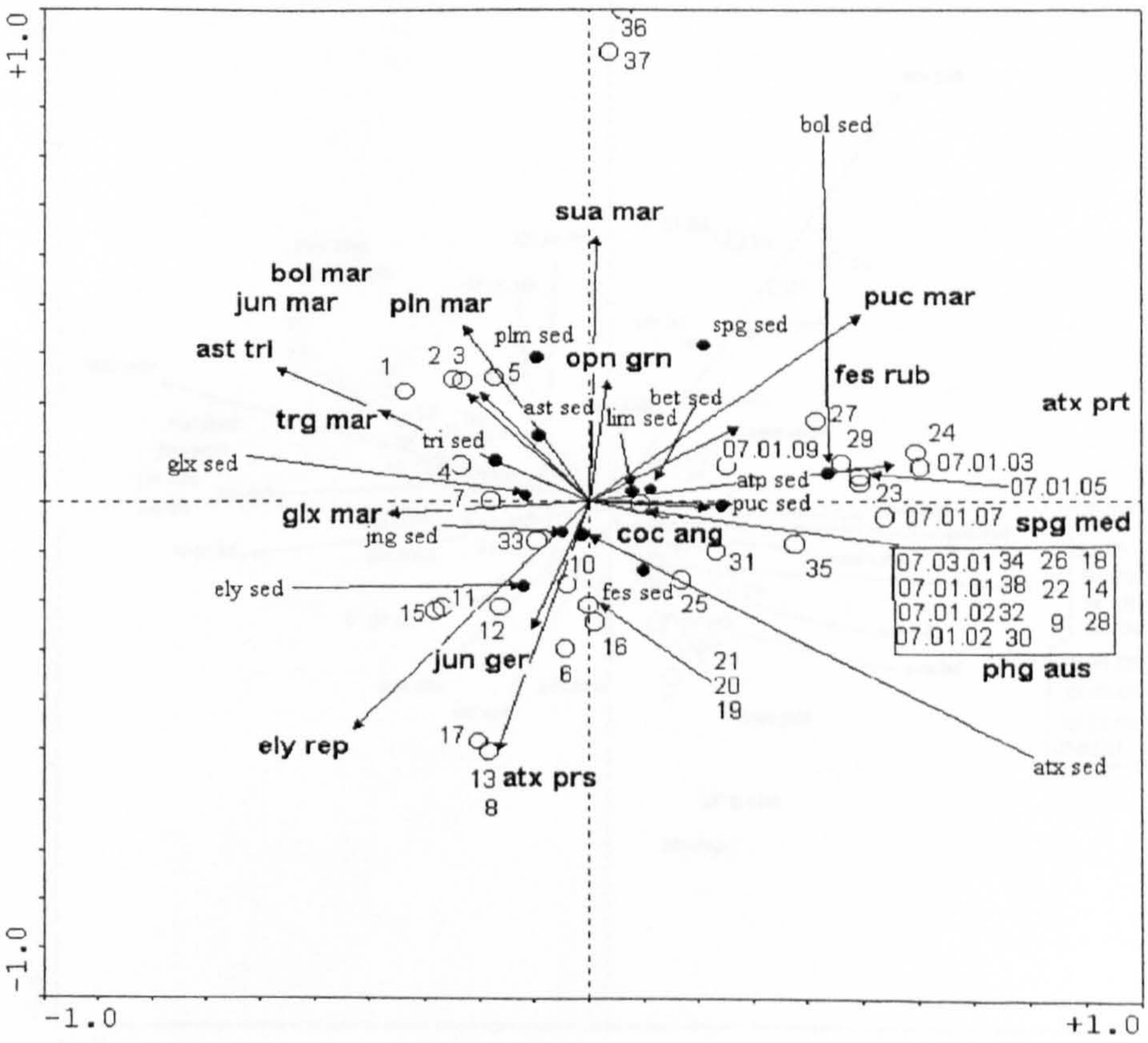


Figure 4.41 a Correspondence analysis of non-seed data from Snape Saltings Transect

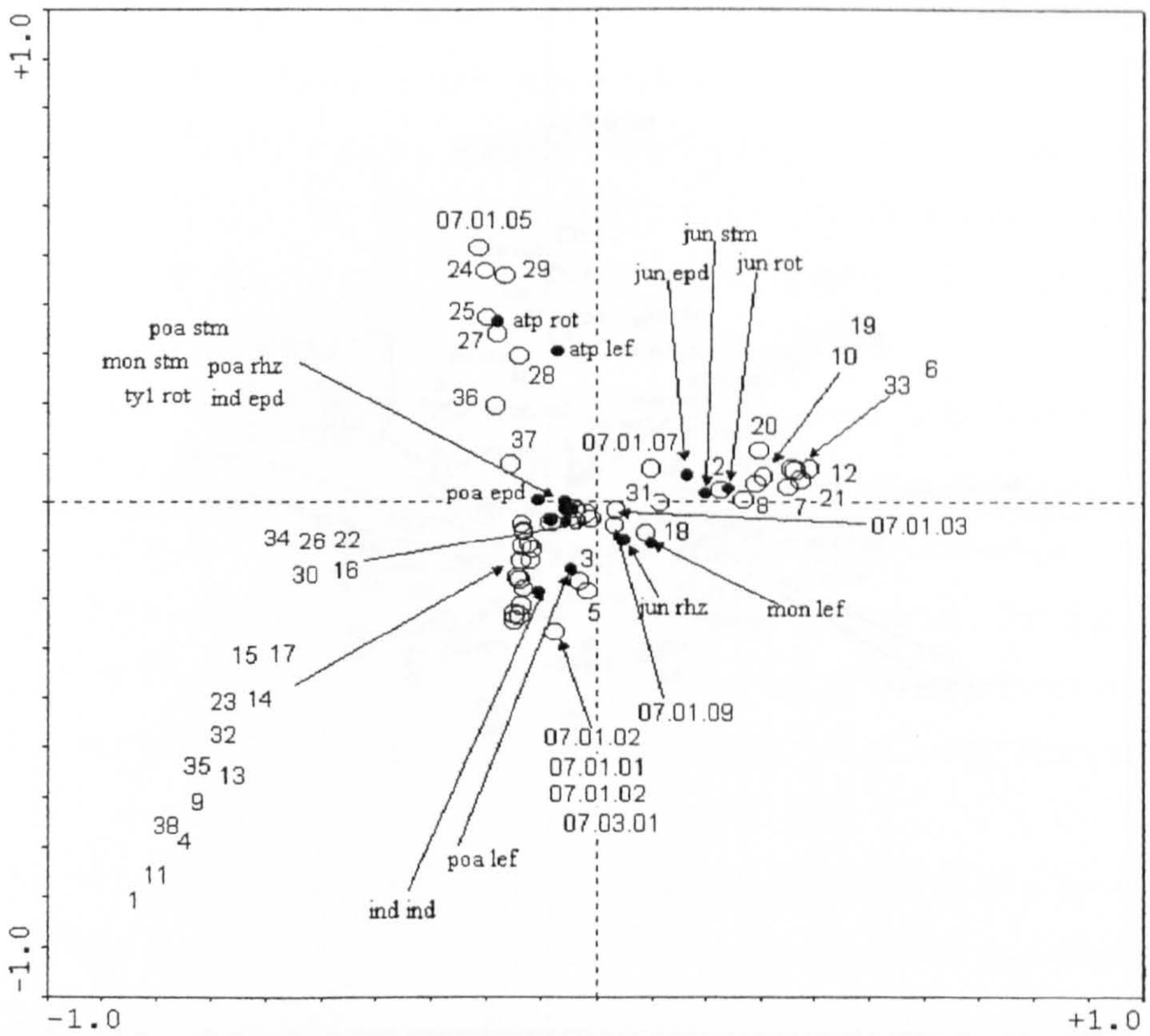


Figure 4.41 b Canonical correspondence analysis of non-seed data from Snape Saltings Transect

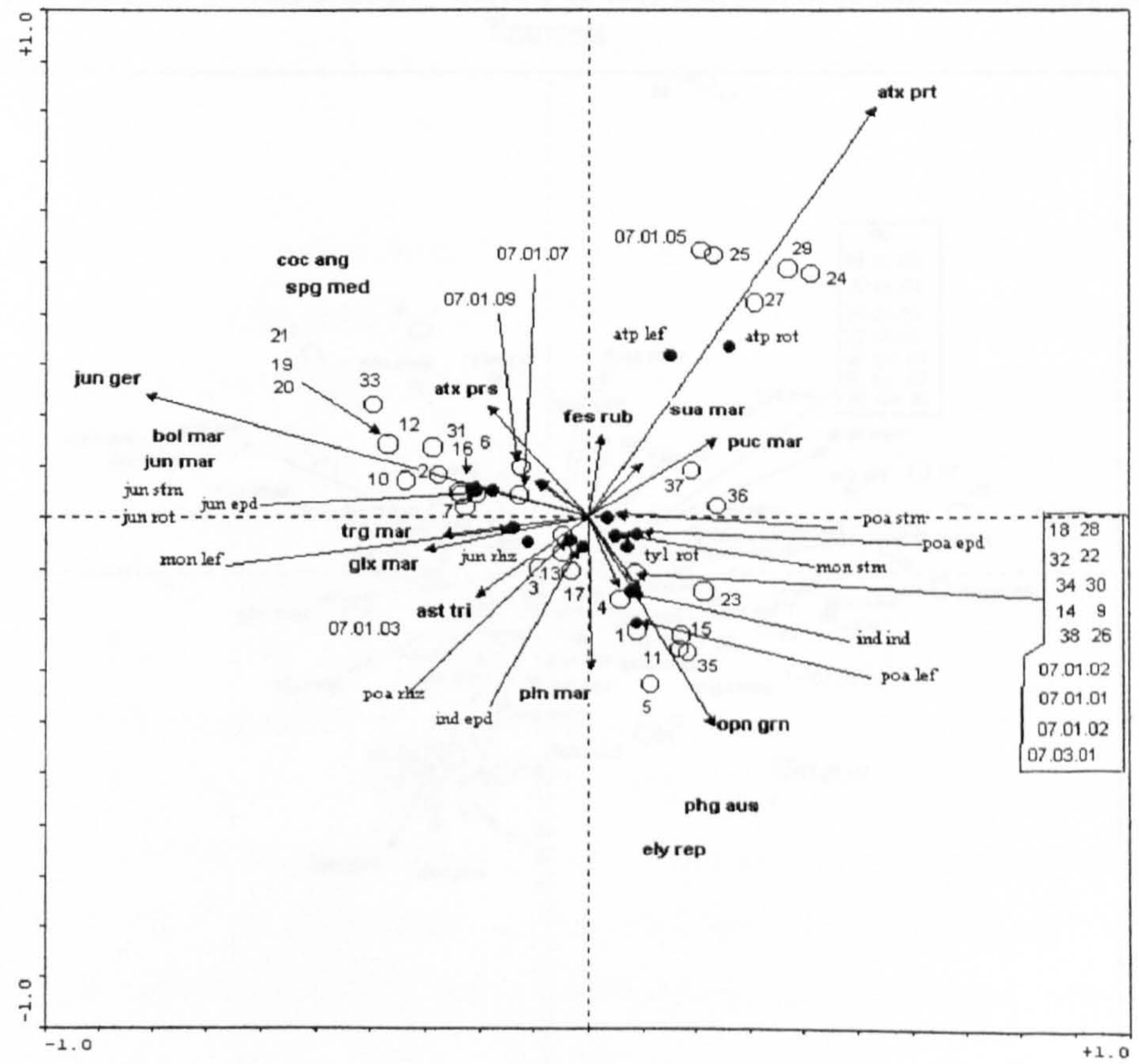


Figure 4.42 a Correspondence analysis of seed and non-seed data from Snape Saltings Transect

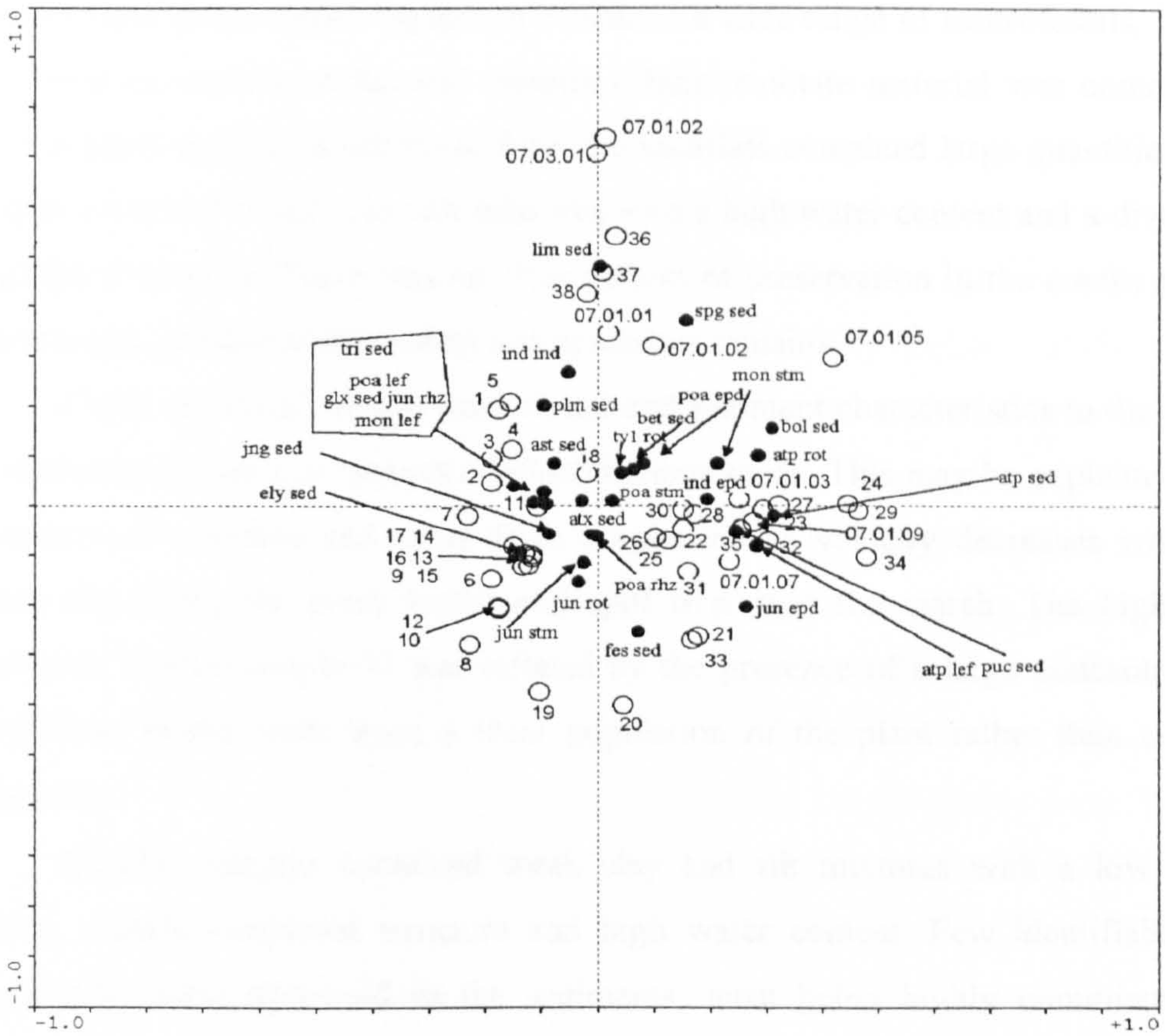
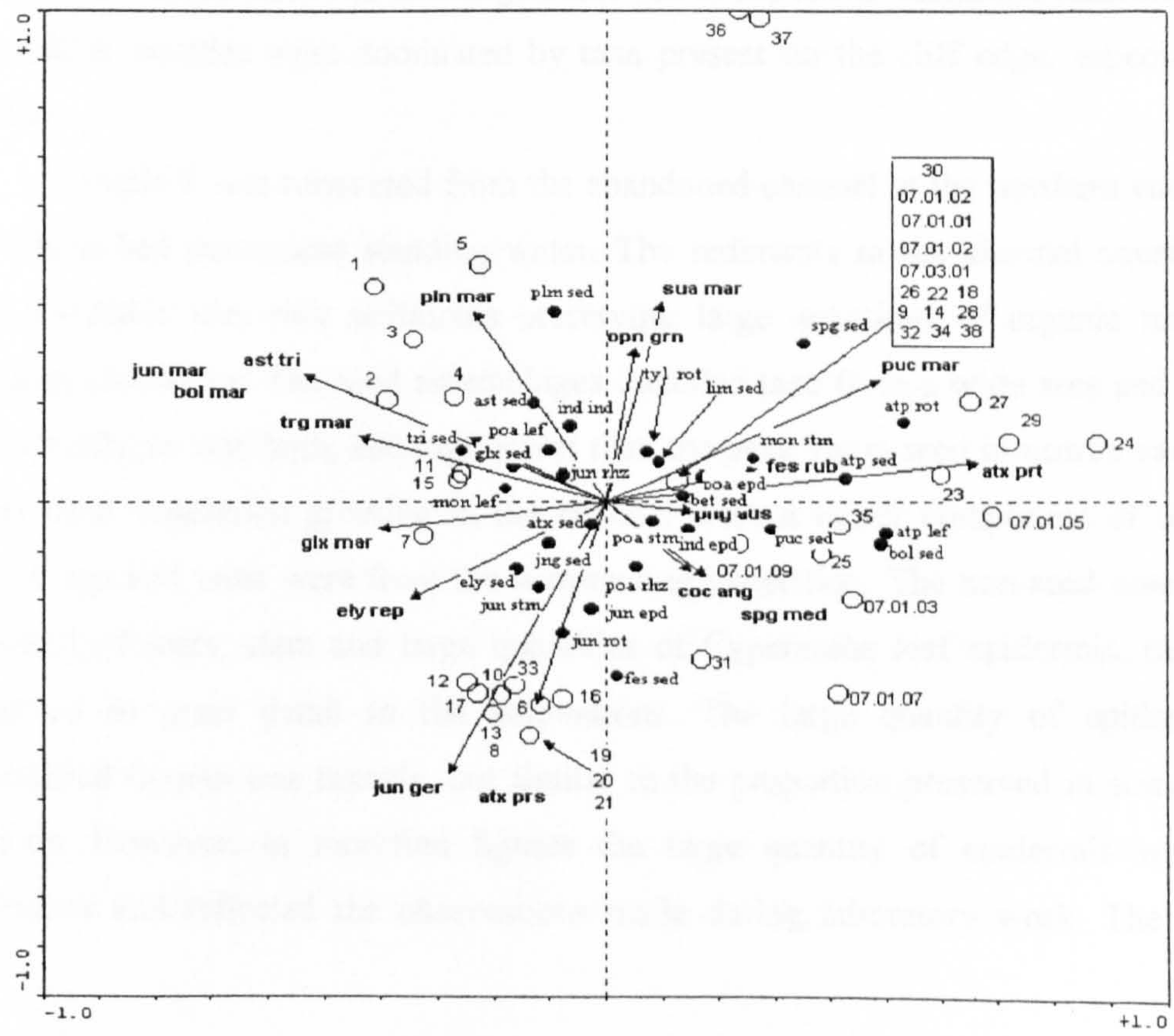


Figure 4.42b Canonical correspondence analysis of seed and non-seed data from Snape Saltings Transect



4.6.8 Differences in depositional environment

Samples from dense marsh vegetation contained a wide range of macrofossils, but were dominated by rootlets, stems and rhizomes. Indeterminate material was common, but only the peaty sediments and those from the mudflats contained large quantities. Creek samples consisted of soft clay-silt mixtures with a high water content and a diversity of macrofossil remains. There was no clear pattern of preservation in the creeks although some samples contained more stem and epidermis remains.

Creek edges had similar macrofossil and sediment characteristics to the marshes but contained higher percentages of allochthonous seeds. This may be explained by the deposition of sediment and seeds from suspension as velocity decreases when tidal waters rise above the creek banks and spill over into the marsh. The higher seed abundance in cliff sample 37 was inflated by the presence of a large concentration of *Spergularia media* seeds from a local population of the plant rather than enhanced deposition.

Mudflat samples contained weak clay and silt mixtures with a low organic content, weakly laminated structure and high water content. Few identifiable plant macrofossils were preserved in the sediments, most being highly comminuted and decayed. The samples also had uniformly low seed concentrations. Macrofossils in the mudflat samples were a mix of allochthonous matter carried in by the tides and those in sediment collapsed from the cliff edge some 1m to the north. Identified macrofossils in all mudflat samples were dominated by taxa present on the cliff edge, especially the Poaceae.

Sample 2 was recovered from the abandoned channel at the northern end of the site which had permanent standing water. The sediments in the channel consisted of soft, laminated clay-rich sediments preserving large quantities of organic matter in reducing conditions. The seed assemblages included taxa from a wide area and overall seed abundance was high, although lower than the peak value seed in nearby sample 3. Seeds from vegetation growing in the channel were a minor component of the seed assemblage and most were from the surrounding vegetation. The non-seed assemblage consisted of roots, stem and large quantities of Cyperaceae leaf epidermis, the latter preserved in great detail in the laminations. The large quantity of epidermis in unmodified figures was notable, but similar to the proportion preserved in some creek samples. However, in modified figures the large quantity of epidermis was very distinctive and reflected the observations made during laboratory work. The sample

grouped with the creek samples in the CA and formed the most extreme end of the first axis of variation.

Sample 34 was collected from a saltpan, a depression that lacked standing vegetation. The sediments were similar to the surrounding marshes consisting of firm clay-silt mixtures. The main distinguishing macrofossil characteristic of this sample was the presence of large quantities of aerial stem that littered the sediment surface. This was picked out in the CA (Figure 4.42a) and was presumably from collapsed surrounding vegetation and airborne litter. The stem material was uniformly badly preserved, but its presence may be due to a combination of low decay caused by high salinity and enhanced sedimentation rates into the hollow. Seed density was typically low for this section of the marsh and all of the macrofossils could be accounted for by the plants growing within 5m of the sample point. This sample included a single fragment of *Betula* leaf, the only fragment of definite allochthonous non-seed plant matter identified at the site. Incorporation of airborne allochthonous plant litter may have been encouraged in the saltpan by the presence of open vegetation.

4.6.9 Vegetation representation

Although there was a degree of correlation between the seed assemblages and standing vegetation in many samples, macrofossil assemblages preserved only a proportion of the taxa present. In most cases the taxa that dominated the seed assemblages were dominant or co-dominant in the standing vegetation. Many of the minor taxa were not preserved and in several samples, species of high abundance were only minor vegetation components. These included *Atriplex* seeds in Block 3, *Cochlearia anglica* and *Spergularia media* seeds in samples from near the saltmarsh edge, and the presence of seeds that were absent from the vegetation (e.g. *Glaux maritima* seeds in Block 3). Reconstruction of vegetation using the seeds was not a simple case of directly converting macrofossil abundance into standing vegetation values. The spatial fidelity of many of the samples was high, providing a generalised view of the vegetation over a wide area and conflating taxa from the saltmarsh vegetation mosaic. Again, taxa that used seeds as a major means of dispersal (e.g. *Glaux*, *Plantago*, *Triglochin*) were over-represented and had lower spatial fidelity than some other taxa (e.g. *Elytrigia*).

There were distinctive patterns of representation among most abundant species in the macrofossil assemblages. Among the most widely dispersed seeds and fruits were those of *Puccinellia* which were spread across the southern end of the site, irrespective

of the presence of the plant in the local vegetation. While the seeds were well distributed, the highest abundance was found in the areas where the plant was dominant or co-dominant in the vegetation. *Aster tripolium* was one of the taxa represented by sparse seeds in sediments across the marsh. It was the commonest taxon to be lacking from seed and fruit assemblages where present in standing vegetation. Seed abundance varied widely and it was also common in samples without nearby plants. The fruits of the plant are aerially dispersed and the pattern of incorporation is consistent with the observations by Salisbury of the wide potential dispersal, but low survival rate, of aerially dispersed seeds (Salisbury 1975, 1976b). The data presented here suggest that this dispersal behaviour is reflected in the sedimentary record.

Most of the *Atriplex* seeds can be assumed to have derived from *Atriplex prostrata* which was also found across the marsh. These seeds were found in many samples at some distance from the closest possible parent. The seeds of the plant were clearly over-represented. This species is one of the few therophytes on the marsh and reproduces entirely through seed production, enhancing its chances of incorporation in sediments.

Glaux maritima seeds were often present in sediments at some distance from recorded plant specimens, although again higher abundance was recorded where the plant was found locally. One exception was in Block 1, where the species was the dominant seed type, yet absent in the vegetation. This may be due to the presence of a nearby stand of the species that was low growing and easily overlooked.

Triglochin maritimum seeds were mainly found in large abundance at or near where the plant was a major element in the vegetation in the northern area of the site. In those areas the seeds were well spread. Elsewhere on the marsh the seeds of this species were found in creek sediments and the plant was not recorded in the local vegetation. The seeds were also found in several of the samples from the fringe area. This distribution may indicate that the seeds are well dispersed by water.

Among the more reliable seed distributions was that of *Plantago maritima*, the seeds of which were found only in samples from sites where the plant grew or at sample points near the point where *Plantago* was a major vegetation element at the north of the site. This was one of the few taxa in which the seed abundance was close to that of the standing vegetation. Only in Block 1 was the species under-represented, although it was a minor vegetation element.

Juncus gerardii seeds were also distributed at, or near sample points at which the species grew. Large seed abundance (when converted to DOMIN scale, reaching values of 6-10 of the total seed content) almost invariably indicated the presence of dense swards of the plant close to or at the sample point. Smaller abundance was less reliable, and in the case of Block 1 and samples from the saltmarsh fringe, the plant was present in the vegetation and absent in the seed assemblages. *Juncus* capsules were more often preserved at, or near standing *Juncus* plants and the seeds of the plants were commonly incorporated in creek sediments at some distance from extant specimens. The presence of *Juncus* seeds in the creek samples suggests that seeds were dispersed far in water.

Festuca rubra was fragmentarily represented in the seed assemblages, possibly because its reproductive strategy is mainly via vegetative means. The plant is also known to have a non-persistent seedbank (Grime *et al.* 1988). Its presence in sediment samples may be a more reliable guide to its presence in the local vegetation than other Poaceae, including *Puccinellia*.

Non-seed macrofossil abundance corresponded well with the abundance of taxa in the standing vegetation, although in most cases vegetative remains were identifiable only at the family or genus level. Most of the vegetation units sampled in the study were dominated by a single species and the vegetative macrofossils of the dominant taxa were similarly dominant in the assemblages. The major problem with the non-seed material was the limited extent of identification, namely to type or family. Only the most abundant and bulky vegetation dominants were represented in the assemblages and the non-seed data provided spatially and highly accurate but taxonomically imprecise information.

Juncus gerardii was mixed with Poaceae taxa in several samples. Table 4.20 compares the standing vegetation and macrofossil abundance figures for Poaceae taxa and *Juncus* converted to DOMIN scale, assuming that Type 1 roots are equivalent to those of the Poaceae. Where the vegetation is dominated by a single taxon with only minor quantities of other taxa, the dominant was recorded but the minor taxon was usually not. Where co-dominance is seen, both taxa achieve high root abundance figures, although when converted to DOMIN figures the relative cover abundance in standing vegetation was not necessarily maintained. A similar pattern was noted in the fringe samples.

Table 4.20 Snape Saltings: Comparison of root cover abundance and corresponding vegetation data

Sample	1	6	7	10	12	16	01/03	01/05	01/07	01/09
Juncus gerardii CA	5	8	8	10	8	8	7	3	7	8
Juncus type root CA	0	9	8	10	9	8	6	9	8	5
Elytrigia spp. CA	6	2	3	2	5	0	0	0	0	0
Puccinellia spp. CA	0	0	0	0	0	0	2	3	5	7
Festuca rubra CA	0	0	0	0	0	0	6	0	0	0
Type 1 Root	9	0	0	0	0	0	7	5	5	8

While the subterranean structures often accurately represented the dominant surface taxa, aerial structures were less consistent with the surface vegetation. For example, aerial sections of *Atriplex portulacoides* were recorded in samples near to a pure stand of this vegetation in the saltmarsh fringe area (Area 01), however, none was recorded in the area dominated by the taxon. It should also be noted that in assemblages of both subterranean and aerial structures, preservation favoured taxa with high biomass, cover abundance and which were well distributed. More sparsely distributed plants such as *Triglochin* were less likely to have recognisable remains incorporated in the small samples collected in this research.

A combined CA and CCA of both seed and non-seed data showed that the assemblages were loosely grouped according to the main dominant in the assemblages in the case of taxa such as *Juncus*, *Puccinellia* and *Atriplex portulacoides*. Correlation between macrofossil abundance and standing vegetation was usually high for these taxa, although samples from creek edges and closer to the river tended to be less reliable. Taxa were differentially represented by macrofossil components, with the more sparsely distributed taxa, such as *Triglochin*, represented mainly by seeds. On the other hand, the Poaceae and *Juncus gerardii* were well represented by both seed and non-seed remains, although the seeds were required to identify the genus and species of plant in each case.

Overall, the bulky Monocotyledons that dominated many of the vegetation units were best represented while the Dicotyledon taxa that punctuated them were not. The only woody vegetation in the marsh, namely stands of *Atriplex portulacoides*, was sporadically represented. Aerial components of this species were under-represented and were the main means of distinguishing it in the samples. Poor preservation of *Atriplex portulacoides*, a distinctive and structurally different plant, may be in part explained by its growth habit. Unlike other communities, the plant grows in an open, loose bush and is home to dense populations of invertebrates that may remove any detritus.

4.6.10 Sub-surface samples from sediment blocks

Contiguous 50cm^3 samples were analysed down the profile in Blocks 1 and 3. Macrofossils in samples from Block 1 were consistent with the surface; however, the lower samples in Block 3 showed a major change from Poaceae to *Juncus* components with increased depth (Figure 4.39a). The change in taxa is consistent with succession in the saltmarsh community from *Juncus gerardii* to *Festuca rubra* dominated marsh and may signify increasing terrestrialistaion. The stratigraphic change is abrupt, although the quantity of roots of *Juncus* increases and *Juncus* stem material reduces prior to the dominance by Poaceae components. This may indicate a reduction in sedimentation prior to the changes in the vegetation. The abruptness of change is startling and suggests that either community change is abrupt without intermediate community form, or that periods of transition are not discernible in the fossil record. The example is interesting as it indicates that transitions in vegetation in slowly accumulating sediment are not obliterated by subsequent vegetative growth by taxa with dense root systems.

4.7 Burham Marsh

4.7.1 Location and topography

Burham Marsh lies on the eastern bank of the River Medway near Rochester, Kent (grid reference: TQ 713617). The site consists of a floodplain reedbed, some 400m in width, bounded by a flood defence levee to the east and a mud cliff at the rivers edge to the west (Fig. 4.43) with weak creek development. Mudflats 110cm below the marsh surface sloped into the river from the base of the mud cliff. The landward edge of the marsh was only flooded during high spring tides.

4.7.2 Vegetation and surface litter

Vegetation at the site (Table 4.21-4.22) was dominated by a tall, dense S4 *Phragmites australis* swamp community. Although the site was tidal, inundation was of low enough duration to allow the growth of several species more suited to freshwater habitats. Among the *Phragmites* were found variable quantities of *Atriplex prostrata, Calystegia sepium* and, at the landward edge of the marsh, occasional plants of *Sonchus asper, Epilobium hirsutum* and *Althaea officinalis*. Towards the river edge S4d *Phragmites australis-Atriplex prostrata* sub-community dominated with occasional plants of *Rumex crispus, Oenanthe* sp., *Althaea officionalis* and *Sonchus asper*. In this community shorter, thin *Phragmites australis* stems formed an upper storey of vegetation with *Atriplex prostrata* beneath. In some areas the *Phragmites* thinned until only a few

lodged culms remained in a mass of dense, tangled *Atriplex prostrata*. To the north of the main reedbed stand was an unclassifiable stand dominated by *Epilobium hirsutum* with smaller quantities of *Phragmites australis*, *Althaea officionalis* and *Calystegia sepium*. This community may be an S4 variant or a variant of S25 or S26 tall herb fens. Along the river margin were occasional isolated stands of S21 *Scirpus maritimus* swamp community, forming stable islands of vegetation within the mudflats. The cliff edge was host to dense *Phragmites* stands with occasional plants of *Aster tripolium* and *Atriplex portulacoides*.

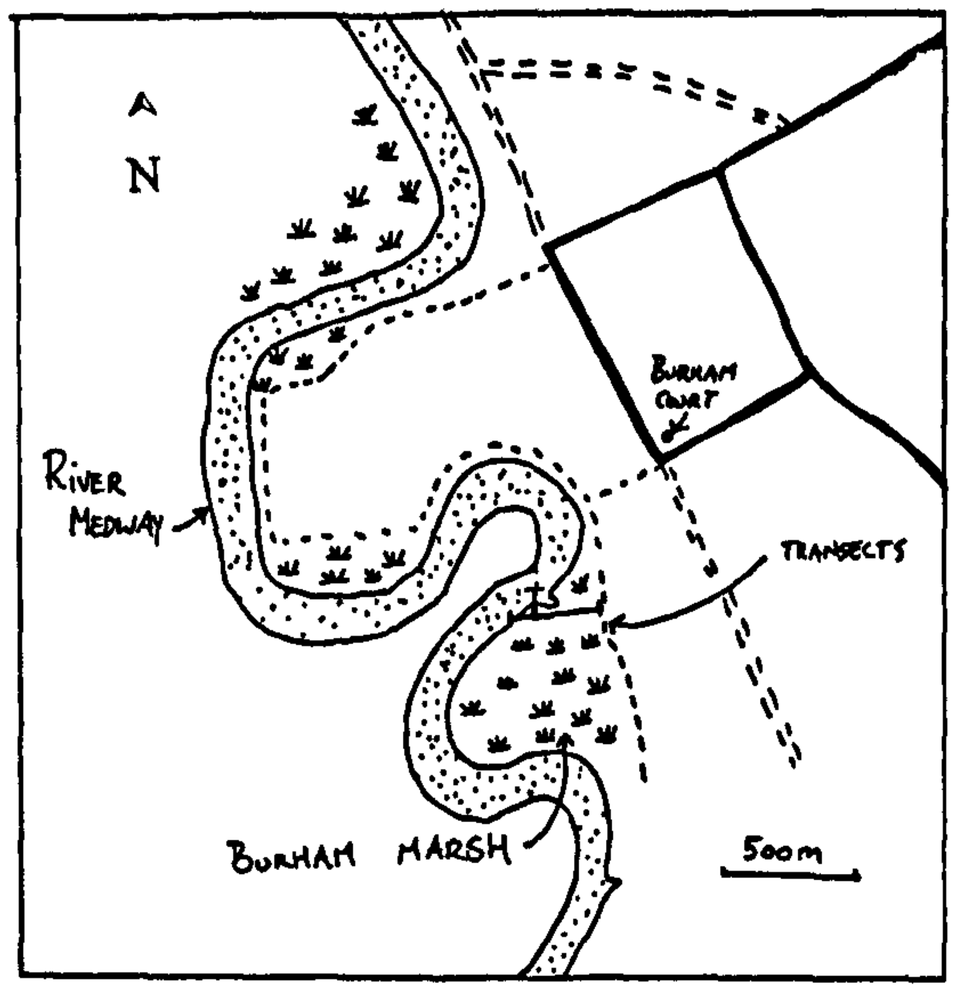
Litter over the whole site was dominated by *Phragmites* stem and leaf remains. Towards the landward edge of the marsh the debris formed a 1cm thick layer over the sediment surface. The layer thinned towards the marsh edge, but persisted even when the *Phragmites* thinned and *Atriplex* became dense. *Atriplex prostrata* litter was common in the litter layer beneath vegetation dominated by it. Litter thinned noticeably towards the cliff edge and was sparse over the mudflats at the river edge.

4.7.3 Sampling

Samples were collected along two transects at the northern end of the main reedbed, both on the aggrading side of the meander bend (Figure 4.43). Samples 1 – 16 formed an east-west transect ran from the flood defences to the mud-cliff. Samples 17-28 formed a south-north transect taken perpendicularly from the 100m point on the east-west transect to the river bank on the north of the meander bend. Blocks were collected from the reedbed near the flood defences (Block 1) and from the *Phragmites-Atriplex* sub-community (Block 2) at the 100m point on the east-west transect. 200cm^3 samples were collected at approximately 10m points along the transect, although those in the south-north transect were usually collected more closely together, especially near the cliff edge.

4.7.4 Sediments

Sediments were dominated by grey, organic-rich silts (Table 4.21) incorporating greater quantities of organic matter towards the landward edge (Figure 4.44). One value in the south-north transect approached 60% organic content and may have been caused by experimental error or due to the presence of a local organic debris concentration. Samples at the river-edge contained more conspicuous quantities of sand-sized particles and the mudflat samples contained almost sterile silts.



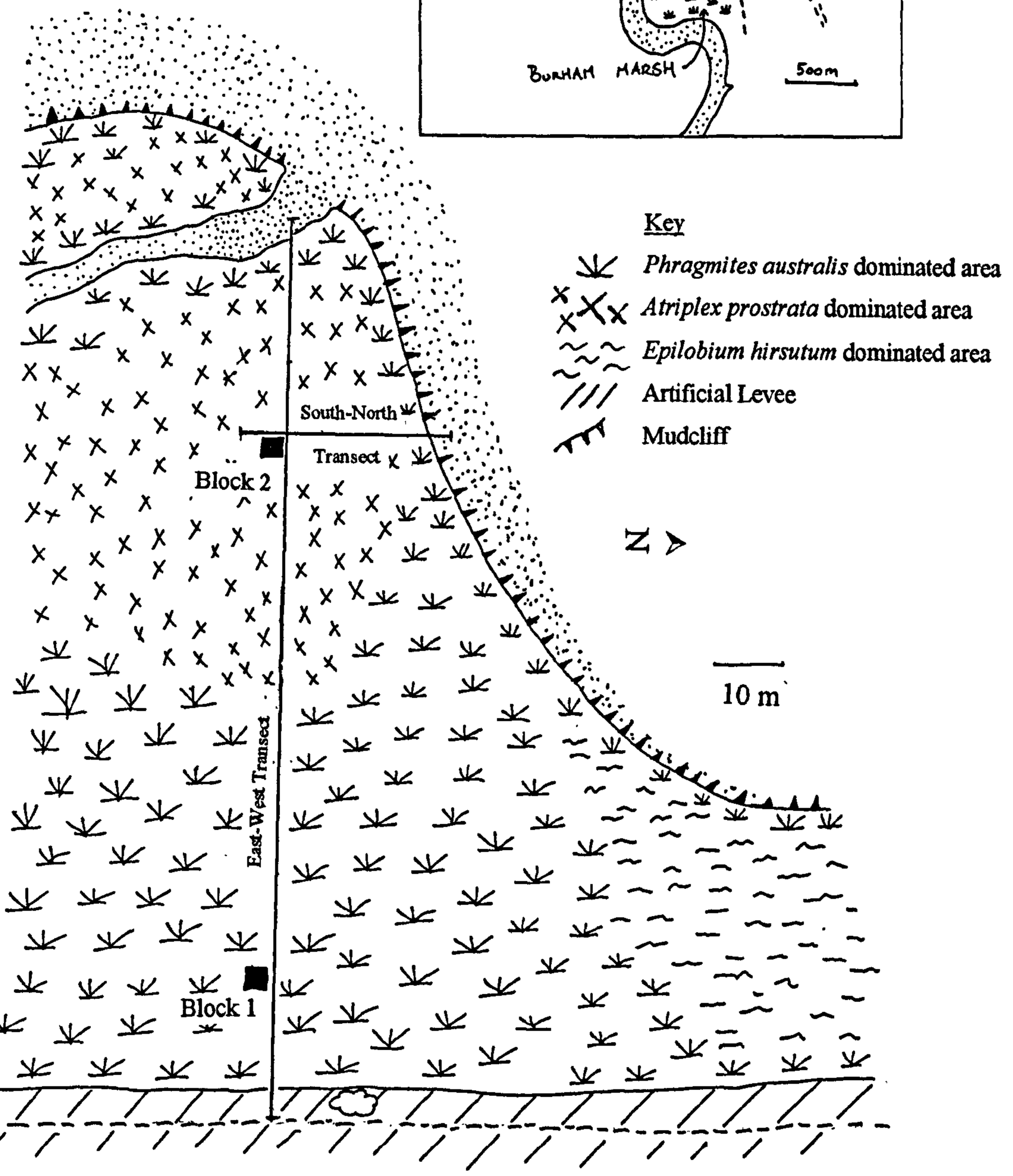


Figure 4.43 Burham Marsh location map (inset) and sample points

Site/Location	T1.	Block 1	T1.	T1.	T1.	T1.	T1.	T1.	T1.	T1.	T1.	T1.	Block 2	T1.	T1.	T1.	T1.	T1.
Environment*	PM	PM	PM	PM	PM	PM	PM	AM	AM	PM	PM	AM	AM	AM	AM	E	E	C
Distance from dryland	10	15	20	30	40	45	50	60	70	80	90	93.5	100	100	125	126.5	128	129
Sample	1	*	2	3	4	5	6	7	8	9	10	11	*	12	13	14	15	16
Troels-Smith Description	Ag3Dh1	Ag3Dh1	Ag3Dh1	Ag3Dh1	Ag3Dh1	Ag3Dh1	Ag3Dh1	Ag3Dh1	Ag3Dh1	Ag3Dh1	Ag3Dh1	Ag3Dh1	Ag3Dh1	Ag3Dh1	Ag4Dh+	Ag4Dh+	Ag4Dh+	Ag4Dh+
Colour	10YR4/2	10YR3/1	2.5Y4/3	2.5Y4/3	2.5Y4/3	2.5Y3/3	2.5Y4/3	2.5Y3/3	2.5Y3/3	2.5Y3/3	2.5Y3/2	2.5Y4/2	2.5Y4/2	2.5Y4/2	2.5Y3/2	2.5Y3/2	2.5Y4/2	2.5Y4/2
% water	69.26	65.25	59.38	55.64	58.88	52.55	55.05	55.4	50.79	50.72	47.49	45.77	47.91	45.85	46.68	48.33	58.84	59.16
%organic	31.07	23.48	23.31	24.4	25.38	27.01	22.46	23.4	20.09	20.87	20	19.38	18.7	19.05	17.68	15.81	15.77	14.85
Cover Abundance																		
Althaea officionalis				4	3	4												
Aster tripolium																		2
Atriplex prostrata			3	4		3		9	9	9	6	10	10	8	7			
Calystegia sepium	3	4	4	5	6	4	4	4	4	4	5	4	4	5	5	4		
Phragmites australis	10	10	10	9	10	10	10	8	8	8	10	5	5	8	8	10	9	9
Solanum dulcamara															5			
Distance to nearest plant																		
Althaea officionalis		10-50m																
Atriplex sp.	5-10m	5-10m	0.5-2m	<0.5m	5-10m	0.5-2m	2-5m	<0.5m	<0.5m	<0.5m	<0.5m	<0.5m	<0.5m	<0.5m	<0.5m	2-5m	2-5m	
Calystegia sepium		<0.5m	<0.5m	<0.5m					<0.5m	<0.5m	<0.5m	<0.5m	<0.5m					
Phragmites australis	<0.5m	<0.5m	<0.5m	<0.5m	<0.5m	<0.5m	<0.5m	<0.5m	<0.5m	<0.5m	<0.5m	<0.5m	<0.5m	<0.5m	<0.5m	<0.5m	<0.5m	<0.5m
Rumex crispus																		10-50m
Almus glutinosa																	>50m	
Apiaceae indet.											10-50m	10-50m		10-50m				
Cirsium cf. palustre	10-50m		10-50m							>50m			>50m					
Epilobium hirsutum	10-50m	10-50m	10-50m	10-50m					10-50m	10-50m	10-50m	10-50m	10-50m					
Oenanthe aquitalis		>50m										10-50m	10-50m	10-50m	5-10m	5-10m	5-10m	
Polygonum aviculare													>50m		>50m			
Solanum dulcamara											10-50m		10-50m		<0.5m			

Table 4.21 Burham Marsh East-West Transect (T1) and Block sample standing vegetation, sediment and distance data
(*Key for environment: PM = *Phragmites* dominated marsh; AM = *Atriplex* dominated marsh; E = Marsh edge; C = Creek)

Site/Location	T2	T2	T2	T2	T2	T2	T2	T2	T2	T2	T2	T2
Distance from dryland	110/7s	100/8s	100/5n	100/10n	100/15n	100/16.5n	100/17.5n	100/18n	100/19n	100/20n	100/21n	100/21.5n
Environment	AM	PM	AM	AM	AM	AM	E	E	E	E	E	U
Sample	17	18	19	20	21	22	23	24	25	26	27	28
Troels-Smith Description	Ag3Dh1	Ag3Dh1	Ag3Dh1	Ag3Dh1	Ag3Dh1	Ag3Dh1	Ag4Th+	Ag4Th+	Ag4Th+	Ag4Th+	Ag4Th+	Ag4Th+
Colour	2.5Y4/2	2.5Y4/2	2.5Y4/2	2.5Y4/2	2.5Y4/2	2.5Y4/2	2.5Y4/2	2.5Y4/2	2.5Y4/2	2.5Y4/2	2.5Y4/2	2.5Y4/2
% water	50.29	49.21	50.15	47.1	44.83	52.33	54.47	56.32	58.68	57.76	59.04	61.12
%organic	58.81	20.12	23.55	33.87	18.5	18.38	16.76	15.5	16.22	15.78	15.63	14.95
Cover Abundance												
Aster tripolium											4	
Atriplex prostrata	8	4	8	8	8	8			8	8	8	
Calystegia sepium	5	5	5	5	4	6	5		6	6	6	
Phragmites australis	8	10	8	8	6	4	10	10	4	4	4	
Rumex crispus			1									
Open ground												10
Distance to nearest plant												
Althaea officionalis						10-50m		10-50m				
Atriplex sp.	<0.5m	<0.5m	<0.5m	<0.5m	<0.5m	<0.5m	0.5-2m	0.5-2m	<0.5m		<0.5m	0.5-2m
Calystegia sepium	<0.5m	<0.5m	<0.5m		<0.5m							
Phragmites australis	<0.5m	<0.5m	<0.5m	<0.5m	<0.5m	<0.5m	<0.5m	<0.5m	<0.5m	<0.5m	<0.5m	
Rumex crispus		2-5m		2-5m							10-50m	
Cochlearia sp.								>50m				
Epilobium hirsutum			10-50m									
Oenanthe aquitalis		10-50m		10-50m	10-50m	10-50m		10-50m		10-50m		
Solanum dulcamara			10-50m									

Table 4.22 Burham Marsh South-North Transect (T2) sample standing vegetation, sediment and distance data
(*Key for environment: PM = *Phragmites* dominated marsh; AM = *Atriplex* dominated marsh; E = Marsh edge; U = Unvegetated mudflat)

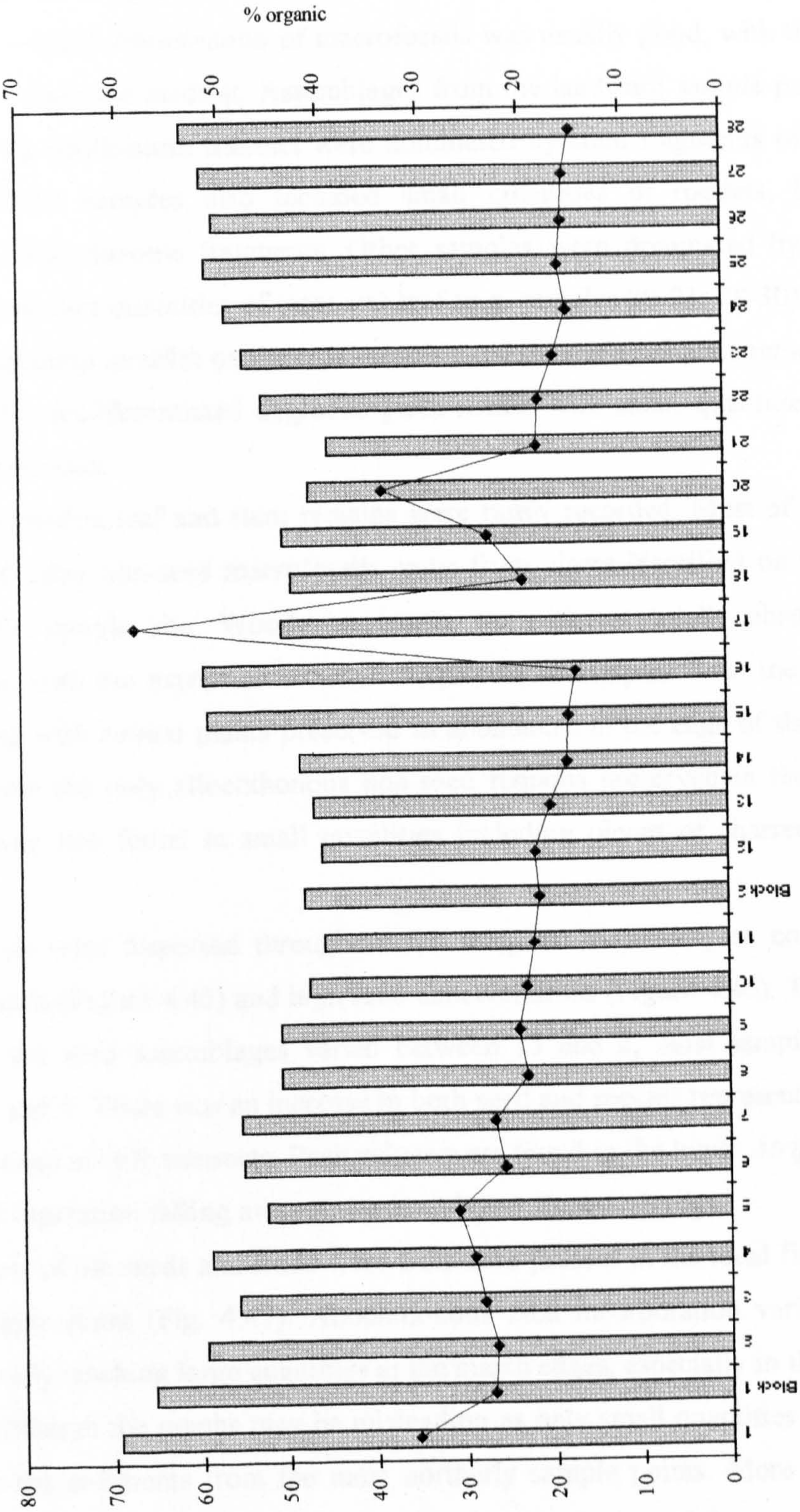


Figure 4.44 Burham Marsh % Organic and % water

Figure 4.44 Burham Marsh organic content and % water

4.7.5 Sources, incorporation and preservation of macrofossils

Plant macrofossils were preserved in abundance throughout the sample set with the exception of the sample 28, collected from the mudflat on the south-north transect (Table 4.23 – 4.26). Preservation of macrofossils was usually good, with the exception of sample 24 from the mudflat. Assemblages from the landward sample points and the cliff-top in the south-north transect were dominated by stem fragments of *Phragmites australis*. These samples also included small quantities of rootlets, leaf (mainly *Phragmites*) and rhizome fragments. Other samples were dominated by non-woody rootlets and smaller quantities of stem and leaf (e.g. samples 20-23; 28-30). Sample 24, from the aggrading mudflat on the south-north transect, has a unique composition being dominated by undifferentiated degraded plant matter with small quantities of rootlets and other structures.

Dicotyledon leaf and stem remains were rarely recorded. Most of the non-seed remains and other non-seed macrofossils came from plants identified on the marsh or close to the sample site. Woody structures were almost totally absent from the assemblages with the exception of small fragments in samples from the marsh edge. These, along with *Lemna* plants preserved in abundance at the edge of the south-north transect, were the only allochthonous non-seed remains preserved in the sample set. Charcoal was also found in small quantities including pieces of charred *Phragmites* stem.

Seeds were dispersed throughout the samples. Most samples contained more than 100 seeds (Figure 4.45) and high seed concentrations (Figure 4.46). The number of species in the seed assemblages varied between 15 and 2, most samples containing between 2 and 4. There was an increase in both seed and species representation towards the marsh edge in both transects. Peak values were found in the lower *Atriplex prostrata* dominated vegetation falling away towards and over the marsh edge.

Most of the seeds and fruits were from taxa present in the local flora within 5m of the sample point (Fig. 4.47). Allochthonous seed incorporation varied across the transects, only reaching large quantities at the marsh edges, especially in the south-north transect, although the graphs may be misleading as only small quantities of seeds were present in the sediments from the most northerly sample points. More allochthonous seeds were also recorded in samples from the landward edge of the east-west transect, most deriving from vegetation on the levee and being easily transported aerially dispersed seeds.

1. Seeds etc.		Sample	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16
Althaea officinalis	Seed					2												
Atriplex sp.	Seed		7	76	57	85	77	182	172	272	108	594	445	751	61	30	8	
Calystegia sepium	Seed									6	2	11						
Calystegia sepium	Capsule												1	5				
Phragmites australis	Fruit		54	49	111	61	138	130	126	165	106	53			43	19	26	
Phragmites australis	Spikelet		133	128	82	95	56	49	173	119	22		18	68	5		7	35
Rumex crispus	Fruit																	
Alnus glutinosa	Seed																4	1
cf. *Angelica officinalis*	Fruit																	
Anthriscus sylvestris	Fruit																	
Apiaceae indet.	Fruit											3	1	2				
Apium sp.	Fruit																	
Arctium sp.	Fruit													1				
Cirsium cf. *palustre*	Fruit		1	1							1							
Corylus avellana	Nutshell											2						
Epilobium hirsutum	Seed		2	3	3					1	1	2	1					
Galeopsis tetrahit	Seed														1			
Glyceria fluitans	Fruit		1															
Lemna sp.	Leaf												1		34	12	97	0
Lycopus europaeus	Seed														1			31
Oenanthe aquatalis	Fruit												1	2	6	1	1	
Poaceae indet.	Fruit			1								1						
Polygonum aviculare	Fruit														1			
Prunus type	Bud-scale															2		
Rumex sp.	Fruit									3			1				1	
Solanum dulcamara	Seed											1			4			
2. Non-seed macrofossils																		
Atriplex sp.	Leaf													0 47				
Atriplex sp.	Non-woody root									3.6	3.2	7.67	8.16	11	10.53	3.33	1.47	
Calystegia sepium	Leaf			0.27									0.27	0.27				
Calystegia sepium	Rhizome				1.4													
Cyperaceae	Non-woody root																	
Lemna sp.	Leaf														2.47		0.93	1.14
Phragmites australis	Stem		75.2	84.87	86.73	86	91.41	87.4	89.07	85.13	85	85.73	84 83	71.2	30.07	4.27	5.12	1.85
Phragmites australis	Leaf		8.33		1.4	1	0.8	1.13	0.27	2.27			0.54	7.27	5.8	2.2	5.28	11.51
Phragmites australis	Rhizome					1.6												5.98
Poaceae	Epidermis		6.53	1.33	2.4	2.2	3.13	3	0.53	1.8	3 8	1.87	3.27	1.27		1.33		
Type 1	Non-woody root		9.2	1 07	7.3	8.3	4.66	7 67	7.27	5.73	6.67	2.93	1.22	1.93	36.87	87.73	83.32	
Dicotyledonae	Leaf													0.6	7.33		0.39	60.9
Indet.	Twig														4.8		2.56	
Indet.	Periderm															0.6		
Indet.	Charcoal		0.67					0.8	1.07	0.8								
Various	Seeds		0.07	0.73	0.73	0.87			1.8		1.3	1.8	1.7	2.4	0.13	0.53	0.93	
Indet.	Indet.			1.07										3.6	2			1.49
3. Derived Indices																		
Seed abundance			198	258	253	243	271	361	471	566	240	666	468	829	118	52	47	67
Species abundance			5	4	3	3	2	2	2	4	5	7	8	5	7	3	3	2
Seed concentration			0.99	1.29	1.27	1.22	1.36	1.81	2.36	2.83	1.20	3.33	2.34	4.15	0.59	0.26	0.24	0.34
Species concentration			0.03	0.02	0 02	0.02	0.01	0.01	0.01	0.02	0.03	0.04	0.04	0.03	0.04	0.02	0.02	0.01

Table 4.23 Burham Marsh East-West Transect sample macrofossil data

I. Seeds etc		**Sample**	17	18	19	20	21	22	23	24	25	26	27	28
Althaea officinalis	Seed							8		4				
Atriplex sp.	Seed		601	2046	746	520	673	698	113	12	42		3	4
Atriplex sp.	Bract		23		11	12	23	26	13		6			
Calystegia sepium	Seed		20	2			2							
Calystegia sepium	Capsule		11		8									
Phragmites australis	Fruit		72	100	47	79	22	166				15		
Phragmites australis	Spikelet			28	13	37	41	25	49	25	31		44	
Rumex crispus	Fruit			9		6							1	
Alnus glutinosa	Seed			1	1		17	46	36	3	7	22	7	
cf. *Angelica officinalis*	Fruit								1					
Apium sp.	Fruit								1					
Betula sp.	Seed					2		1		5		2		3
Carex sp.	Fruit							1						
Cochlearia sp.	Seed									1				
Crataegus sp.	Fruit							1						
Epilobium hirsutum	Seed				3									
Lemna sp.	Leaf						146	278	799	213	745	731	182	29
Lycopus europeaus	Seed					2	15	26			5	3	7	
Oenanthe aquitalis	Fruit		1	5		7	13	2		19		6		
Persicaria maculosa	Fruit					1								
Polygonum aviculare	Fruit									1				
Ranunculus acris	Fruit							1						
Ranunculus sceleratus	Fruit						1				1			
Rubus fruticosus	Fruit							2					1	
Rumex conglomeratus	Fruit							1						
Rumex obtusifolius	Fruit										1	1		
Rumex sp.	Fruit					31	2	2		2			1	1
Sambucus nigra	Seed							2	1			1		
Solanum dulcamara	Seed				1									
Sonchus palustris	Fruit							1						
Urtica dioica	Fruit						1							
2. Non-seed macrofossils														
Atriplex sp.	Rootlet		7.33	8 63	5	11.67	23.93	5.53						
Atriplex sp.	Stem												16.49	
Bolboschoenus maritimus	Stem								2.39				7.53	
Calystegia sepium	Leaf		1.27											
Cyperaceae	Rootlet												49.54	7.11
Cyperaceae	Epidermis													0 94
Lemna sp.	Leaf						0.93	2	6.13	4.2	8.39	0.61		1.61
Phragmites australis	Stem		79 27	78.59	84.47	73.67	66.87	71.6	67.73	40.56	31.76	20.92	13.72	5.23
Phragmites australis	Leaf			1.93	2	5.27	2.6	8.33	6.81	3.11		9.17	5.44	7.92
Phragmites australis	Rhizome											4.14		
Poaceae	Epidermis			1.52	1.4	1.93	1.27		3 88		2.51	0 61	1.34	
Type 1	Rootlet		1 2	2 9	3.13	4.2	2.6	7.27	9 87	35.66	55.91	53 6	5.52	3.22
Dicotyledonae	Leaf													3.22
Indet.	Twig							3.33	2.39	1.94				
Indet.	Epidermis			2.56		2 6	0.33							
3. Derived Indices														
Seed abundance			728	2191	830	697	810	1009	214	72	93	50	64	8
Species abundance			5	6	5	8	9	15	6	8	7	7	6	3
Seed concentration			3 64	10 955	4.15	3.485	4 05	5.045	1.07	0 36	0.465	0 25	0.32	0.04
Species concentration			0 025	0 03	0.025	0.04	0.045	0.075	0.03	0.04	0.035	0.035	0.03	0 015

Table 4.24 Burham Marsh South-North Transect sample macrofossil data

Taxon	Sample	103	104	111	112	114	115	116	118	120	137	138	139
	Sample Size	50	50	25	25	12.5	25	12.5	50	25	50	50	50
1. Seeds etc.	**Component**												
Althaea officinalis	Fruit		2									1	
Atriplex sp.	Fruit	127	194	62	18	27	72	47	67	44	11	19	31
Calystegia sepium	Seed	4	1				2		1				
Phragmites australis	Fruit	21	43	16	7	13	19	2	29	6	2	10	4
Betula sp.	Fruit						2	2					1
Cornus sanguinea	Fruit	1											
Epilobium hirsutum	Fruit		4			1			3		1		
Lemna sp.	Leaves											1	
Oenanthe aquaticum	Fruit		1										
2. Non-seed data													
Phragmites australis	Stem	71.73	65.6	79.33	67.93	85.13	68.73	74.53	66.87	73.87	51.48	54.27	62.6
Phragmites australis	Leaf	14.4	11.6	3.55	13.87	1.53	10.4	19	17.87	15.2	13.56	4.53	4.6
Phragmites australis	Rhizome				6.13		10.2		1.33		4.7	7.07	2.53
Poaceae	Epidermis	1.73	1.87	4.55	2.8	2	3.8	2.67	3.93	0.73	25.91	3.6	3.47
Type 1	Rootlet	10.73	18.07	10.5	8.53	10.6	5	3.6	9	8.87	25.9	29.53	21.6
Indet.	Epidermis	0.4										0.67	1.33
Indet.	Rootlet	0.87	1.47		0.53				1		0.67		3.87
Various	Seeds	0.13	1	1.54	0.2	0.73	1.67	0.2		0.87		0.33	
Indet.	Charcoal		0.4	0.5			0.2			0.47			
3. Derived Indices													
Seed abundance		153	245	78	25	41	95	120	100	50	14	31	36
Species abundance		4	6	2	5	3	4	3	4	2	3	4	3
Seed concentration		3.06	4.9	3.12	1	3.28	3.8	9.6	2	2	0.28	0.62	0.72
Species concentration		0.08	0.12	0.08	0.2	0.24	0.16	0.24	0.08	0.08	0.06	0.08	0.06

Table 4.25 Burham Marsh Block 1 sample macrofossil data

Taxon	Sample	201	202	203	204	209	210	211	212	218	219	220	221
	Sample Size	25	12.5	50	50	50	50	50	50	50	12.5	25	12.5
	Component												
1 Seeds etc.													
Atriplex sp.	Seed	162	60	43	244	237	272	237	253	332	54	85	193
Calystegia sepium	Seed				1								
Phragmites australis	Fruit		1		12	8	3	3	21	8			9
Betula sp.	Seed					2							
Cirsium palustre	Fruit					1	1						
cf. *Elytrigia* sp.	Fruit							2					
Epilobium hirsutum	Fruit	11	4		84	87	116	139	69	136	2	3	67
Oenanthe aquatica	Seed				1	1	1	1	3	7			6
Poaceae	Fruit									3			
Polygonum aviculare agg.	Fruit											1	
Solanum dulcamara	Seed				1				1	1			2
Sonchus palustris	Fruit		1						1				
2 Vegetative remains													
Atriplex sp.	Epidermis			6.73		0.35				3.67			
Atriplex sp.	Rhizome					3.17							
Atriplex type	Rootlet	16.65	4	28.93	6.98	10.22	9.25	5.93	4.16	6.4	29.2	12.35	11.24
Phragmites australis	Stem	67.55	58.07	48.86	84.52	77.62	79.14	85.4	85.47	83.2	57.74	74.09	80.87
Phragmites australis	Leaf		1.87		0.76		3.25		0.39				
Poaceae	Epidermis	3.42		3.17	2.7	3.35	1.85	2.73	3.85	2.93	7.07	2.36	1.81
Indet.	Epidermis	5.15						2.4	0.63			5.25	1.47
Type 1	Rootlet	3.18	33.13	10.03	1.8	1.59	1.63	1.33	1.41	1.27	2.54	2.36	1.07
Indet.	Charcoal				0.21								0.13
Indet.	Stem						1.78						
3 Derived Indices													
Seed abundance		173	66	43	343	336	393	379	348	487	56	89	277
Species abundance		2	4	1	6	6	5	4	6	6	2	3	5
Seed concentration		6.92	5.28	0.86	6.86	6.72	7.86	7.58	6.96	9.74	4.48	3.56	22.16
Species concentration		0.01	0.02	0.01	0.03	0.03	0.03	0.02	0.03	0.03	0.01	0.02	0.03

Table 4.26 Burham Marsh Block 2 sample macrofossil data

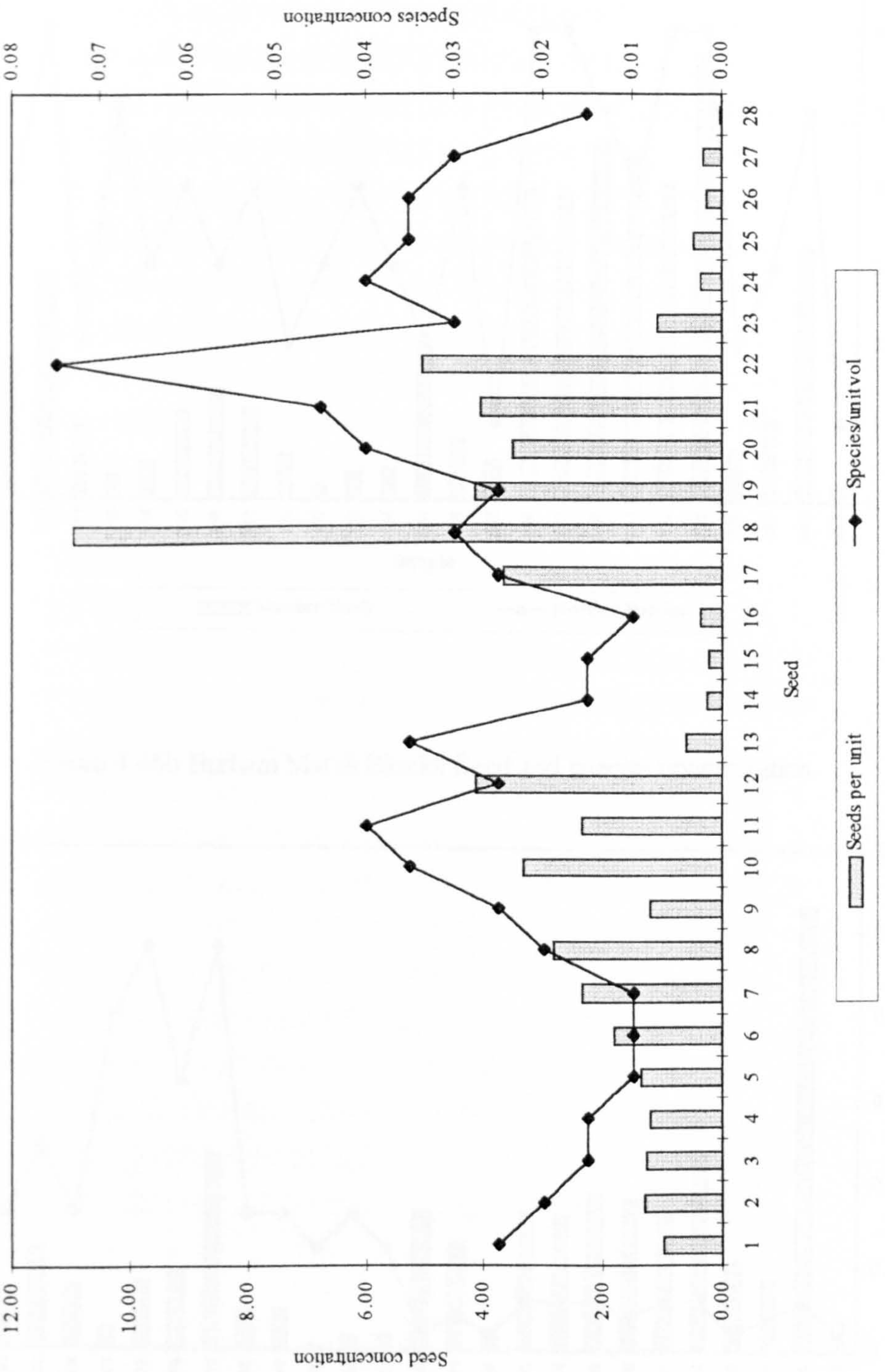


Figure 4.45 Burham Marsh seed and species concentration

Figure 4.46a Burham Marsh Block seed and species abundance

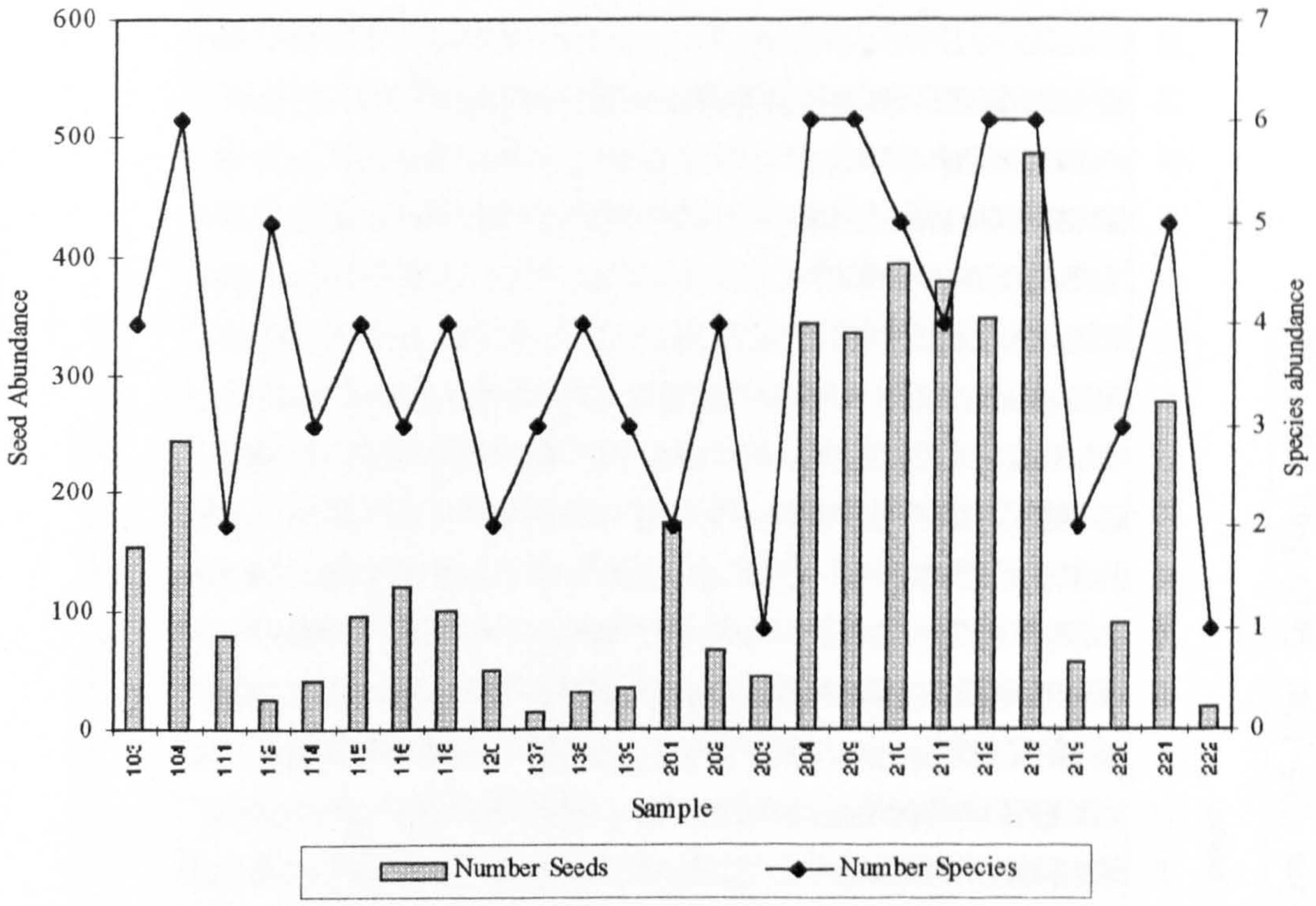


Figure 4.46b Burham Marsh Blocks Seed and species concentration

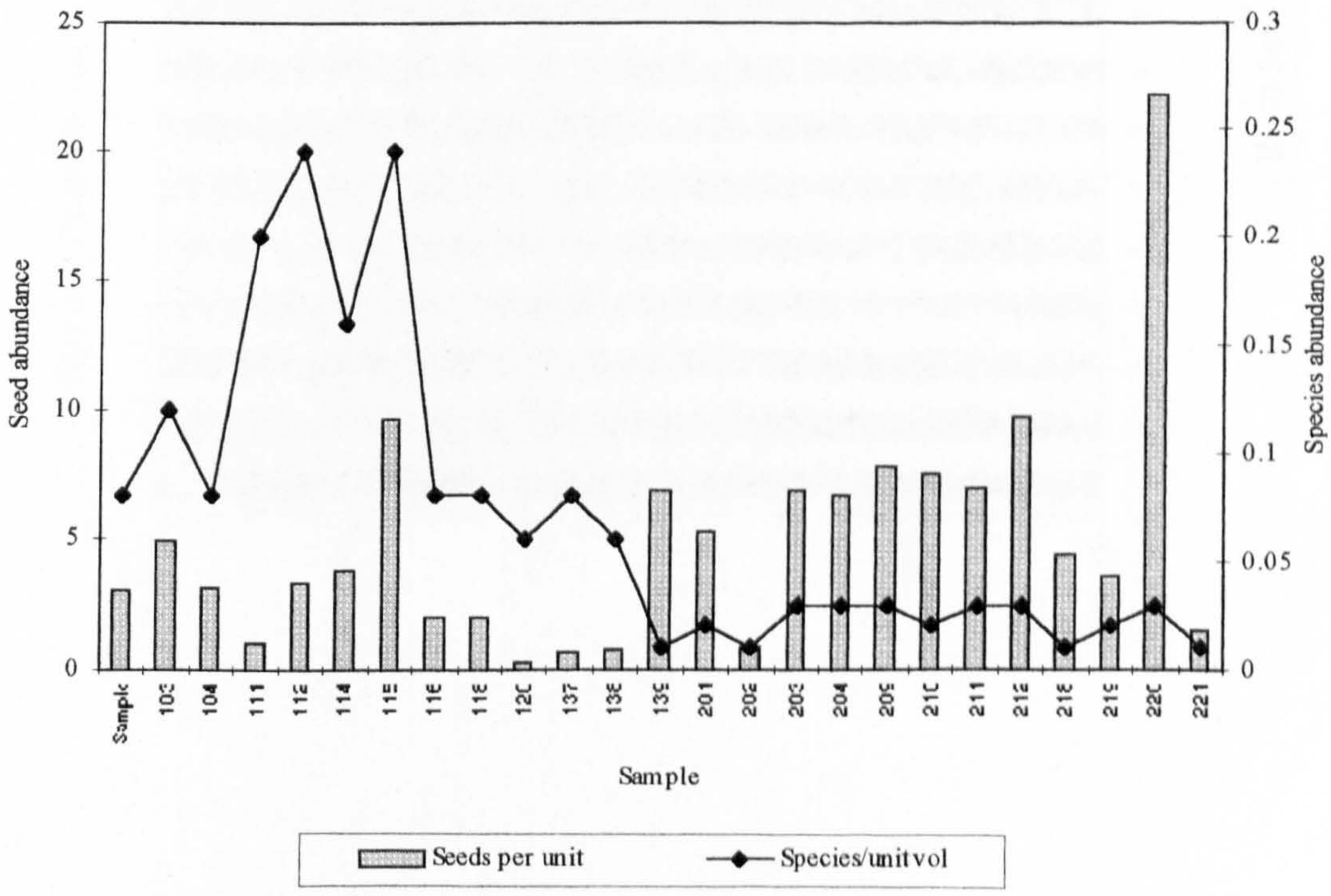


Figure 4.47 Burham Marsh Percentage of seeds from set distances from the sample point

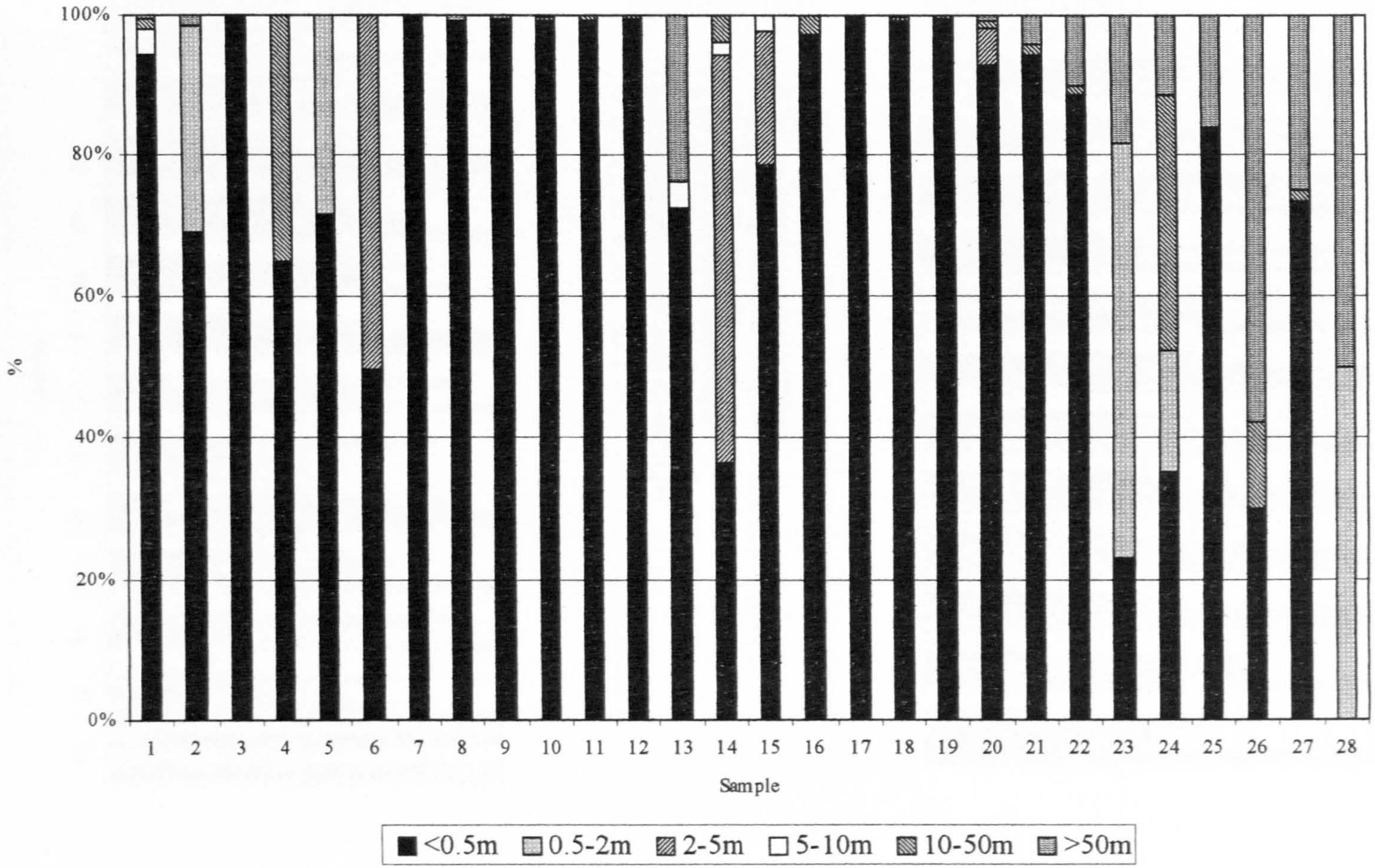


Figure 4.48a Burham Marsh Ubqiuity data

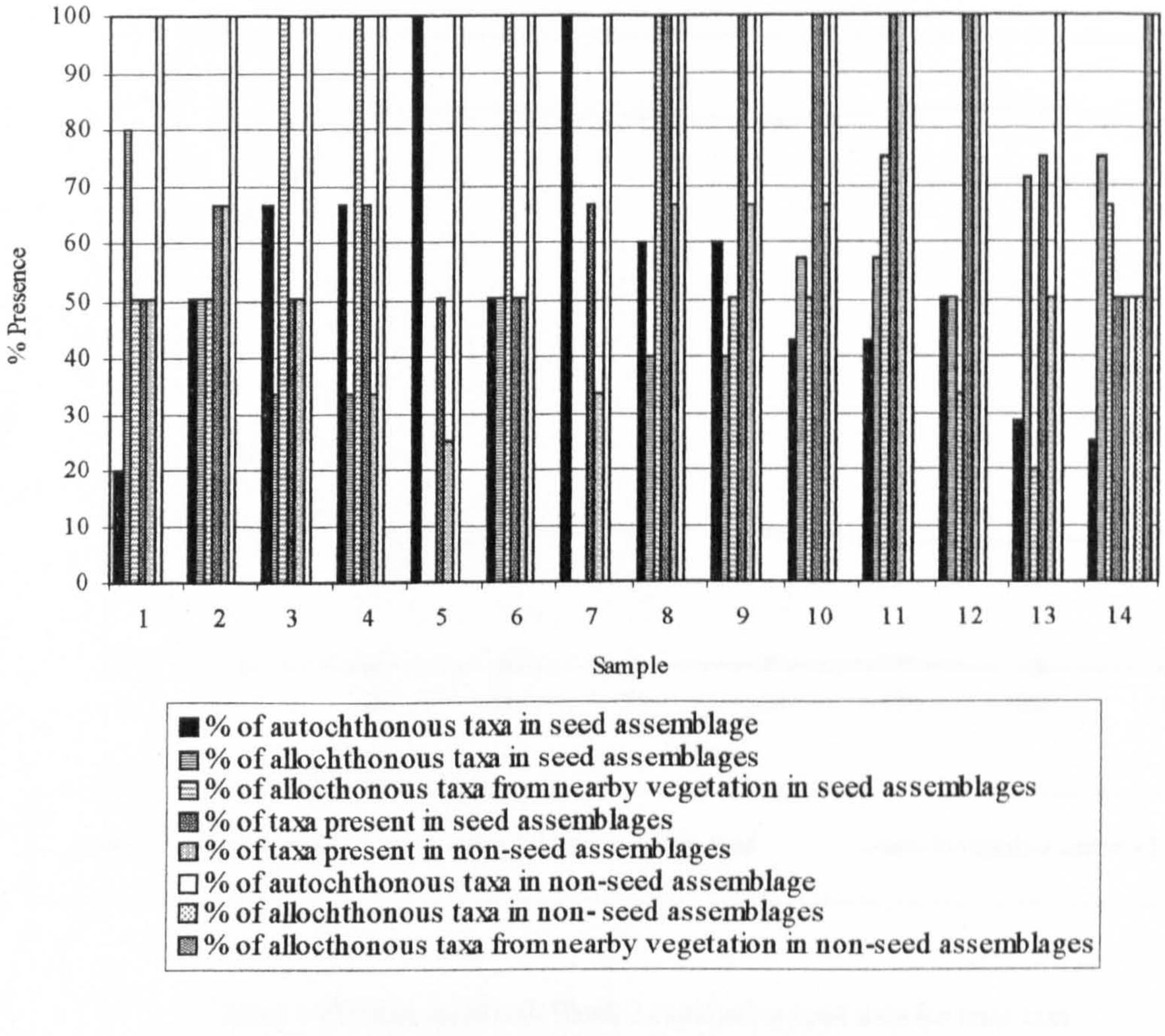


Figure 4.48b Burham Marsh Sample Ubiquity Data

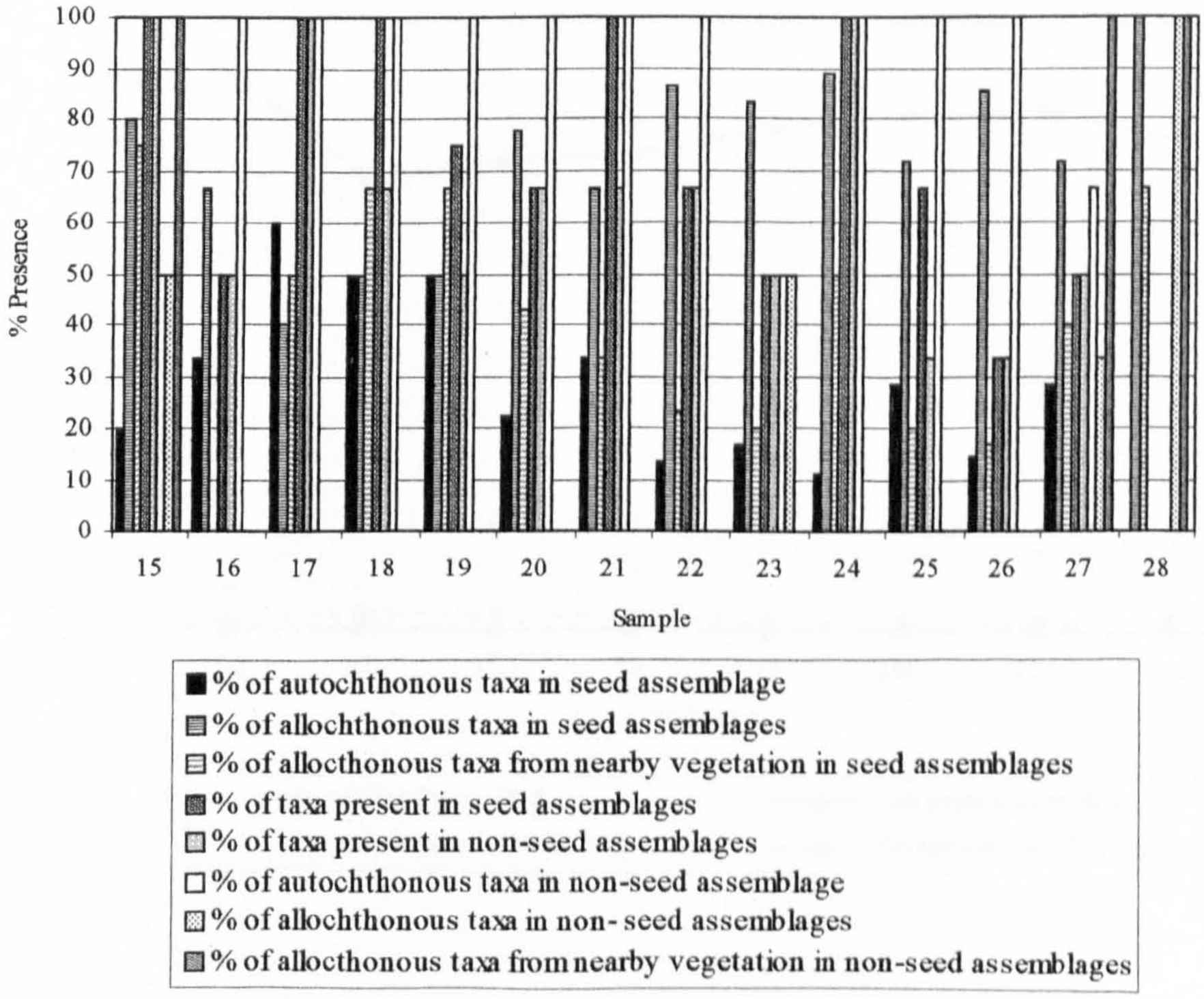


Figure 4.49a Burham Marsh Block 1 Cumulative seed data for main taxa

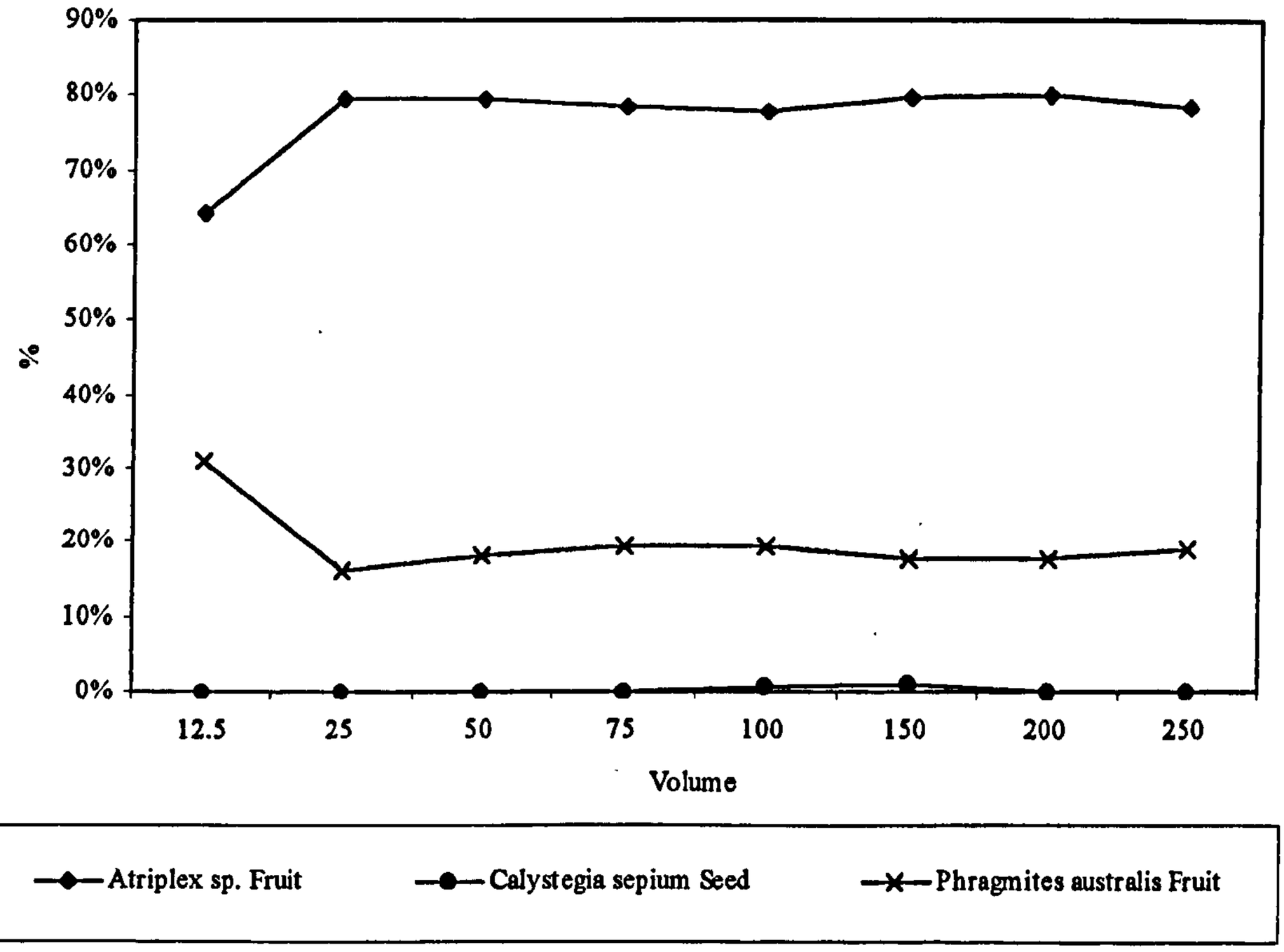


Figure 4.49b Burham Marsh Block 3 cumulative seed data for main taxa

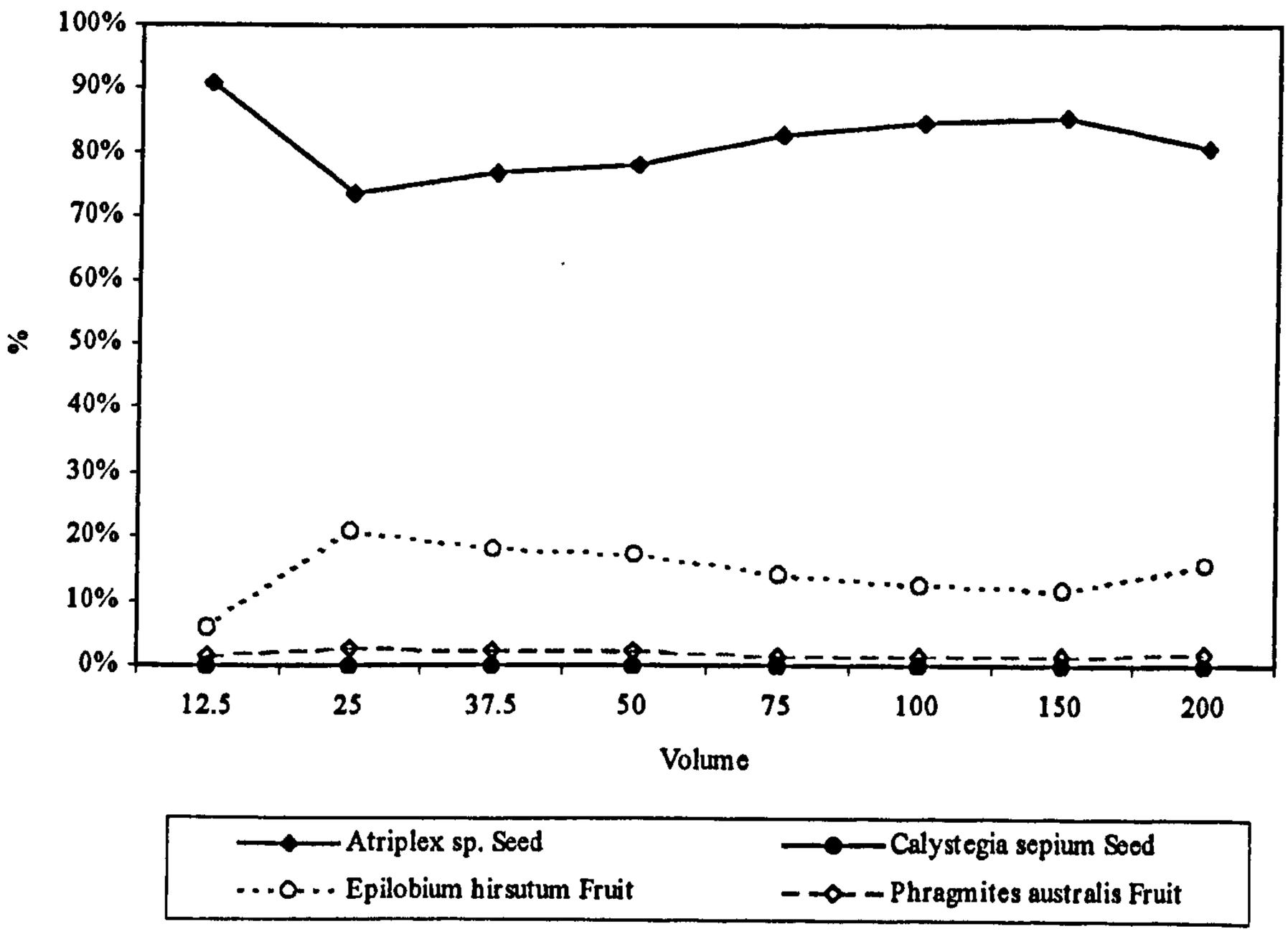


Figure 4.50a Burham Marsh Block 1 cumulative non-seed data for main taxa

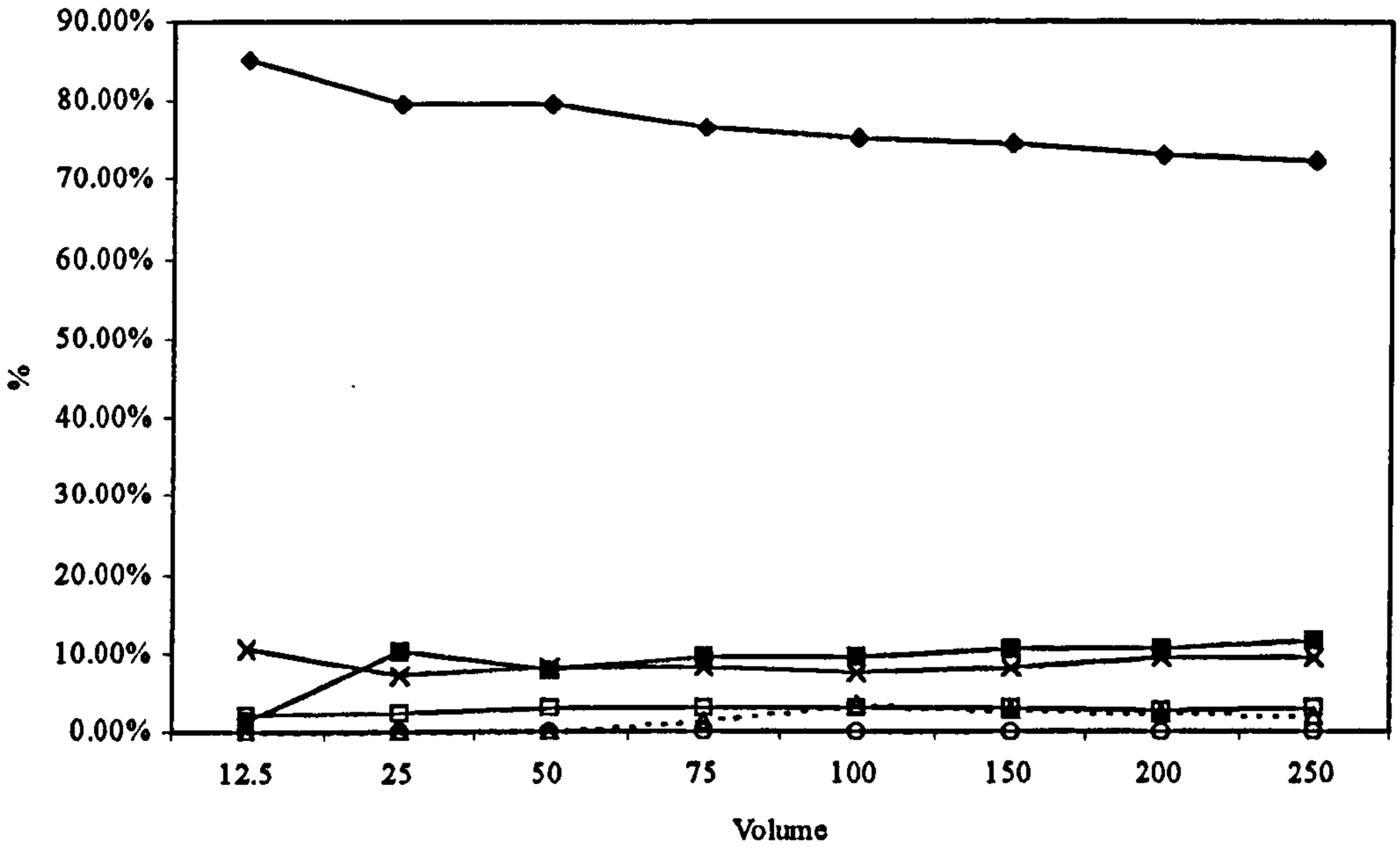
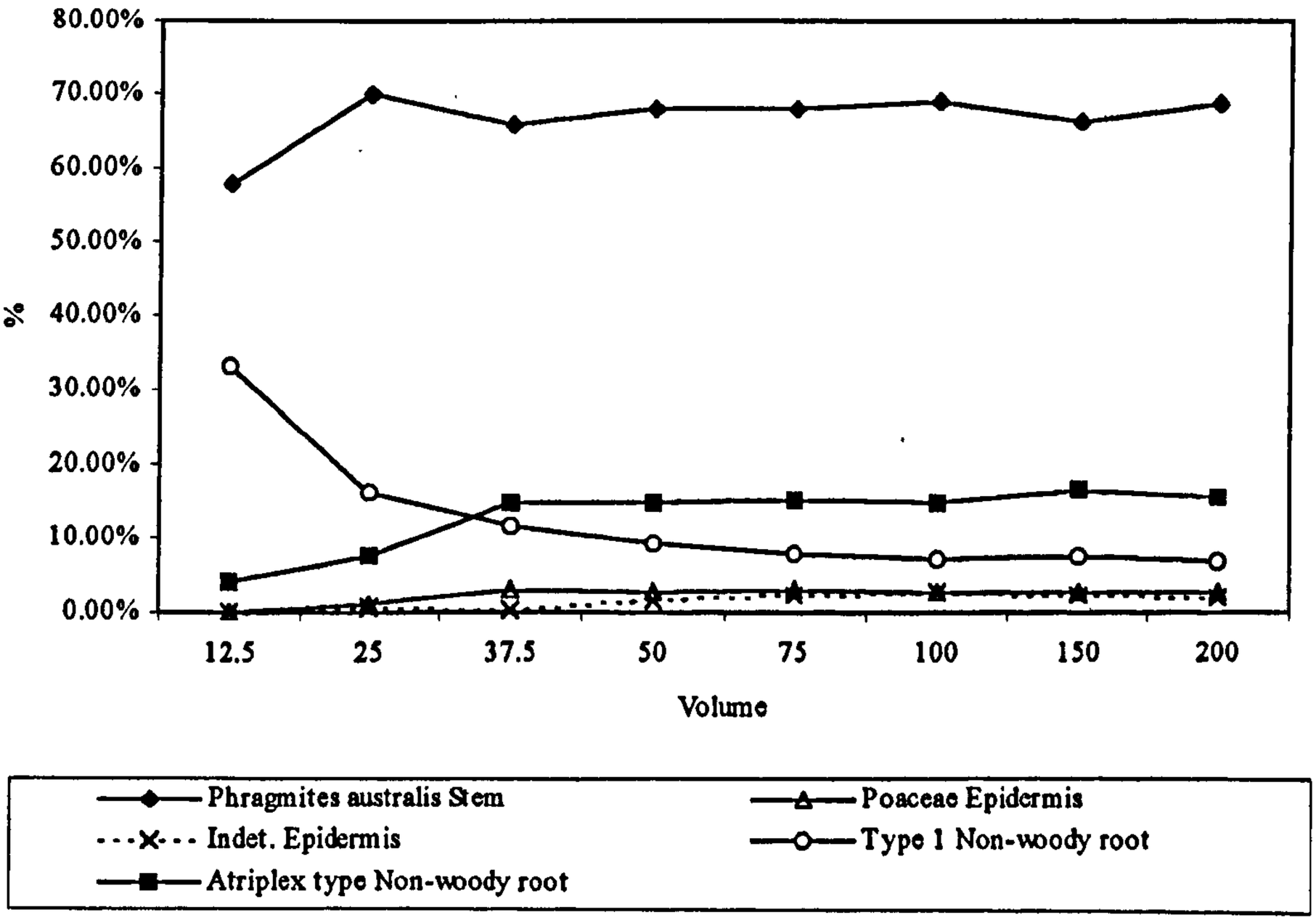


Figure 4.50b Burham Marsh Block 3 cumulative non- seed data for main taxa



Sample ubiquity data are shown in Figure 4.48. Both allochthonous and autochthonous seed taxa contributed to the seed assemblages, allochthonous taxa representing a large proportion of the taxa in samples from the landward edge of the sample transect and towards the saltmarsh edge. Many of the allochthonous taxa were found in the local vegetation, with *Atriplex* seeds being most commonly found where it did not grow. The quantity of taxa unrecorded in the marsh increased markedly at the edges of the dense reedbed vegetation, especially along the raised levee at the river edge. It was common for considerable numbers of taxa to be absent, especially *Calystegia* and *Althaea*. Samples from the vegetation where these taxa grow commonly had 50% of the local taxa missing from the assemblages. Few taxa were represented in the non-seed assemblages, with most of the samples containing only autochthonous taxa. Fifty percent or more of the local taxa were commonly missing from the non-seed assemblages. Only in three cases, all being samples from near the end of transects, were allochthonous taxa represented in the non-seed assemblages. Most of these were recorded in the nearby vegetation. Both the seed and non-seed taxa in the mudflat sample were mostly found in nearby vegetation.

4.7.6 Sample size effects

In both blocks the cumulative percentage abundance figures for seed and non-seed data were surprisingly stable (Figures 4.49 - 4.50). In each case the abundance of the main species varied in sample sizes of $25cm^3$ or less. However, the rank order and abundance of the main macrofossil types were apparent by $50cm^3$ and varied little as sample sizes increased. Larger sample sizes included progressively more species, but these were always minor components. The number of species and overall species abundance increased with larger sample sizes in both blocks.

4.7.7 Quantitative analysis

As in earlier analyses the Block samples were removed and analysed separately to prevent the large number of sample points from a limited sample area and of varying size affecting the Transect samples. CA of the combined seed and non-seed Block data (Figure 4.51a) showed that the ubiquitous *Atriplex* seeds and *Phragmites* stem remains were equally shared by the samples. The main split was in the higher quantities of *Atriplex* components present in Block 2 and wide range of seeds, and the presence of

Phragmites components in larger quantities in Block 1. The CCA (Figure 4.51b) showed that these differences correlated with the presence of the appropriate source plant in the standing vegetation. Depth samples in Block 1 were separated by the presence of higher abundance of *Phragmites* rhizome and indeterminate epidermis.

CA of the Transect seed assemblages (Figure 4.52a) showed that most samples could not be split easily on the basis of macrofossil composition. Even so two main groups could be distinguished. The first, mainly the higher marsh seeds isolated from the river, on the negative side of the first axis contained large quantities of *Epilobium* and *Atriplex* seeds. A second group on the positive side of the first axis contained samples with a large allochthonous component and included all of the marsh edge samples. The main separation of the first group along the second axis was made on the basis of those with large quantities of *Atriplex* seeds and those with larger quantities of *Phragmites* seeds. The division in the second group was mainly on the basis of varying quantities of allochthonous seeds. CCA of the seed assemblages (Figure 4.52b) showed that only *Atriplex* seeds were correlated with *Atriplex* in the standing vegetation. Correlation between seed data and standing vegetation was poor in general and both analyses suggest that seed rain at the site was a poor means of identifying the local flora, being a palimpsest of the site flora as a whole.

CA of the non-seed assemblages (Figure 4.53a) again showed limited differences between the samples. *Phragmites* stem remains were ubiquitous in the samples. A rough division was made between the samples at the negative side of the axis with other *Phragmites* components and those on the positive side that contained *Atriplex* and other components. Indeterminate matter was found in the double positive quadrant of the diagram and separated out some outliers. CCA of the non-seed assemblages showed that *Phragmites* rhizome and leaf remains were better correlated with standing vegetation values than the stem remains, although correlation was poor (Figure 4.53b). *Atriplex* was only represented by rootlets, but correlation with rootlets was strong. Many taxa were poorly visible, especially the climbers (*Calystegia* and *Solanum*) and their remains were of such low ubiquity that they were absent from the plots. Consultation of the tables showed that *Calystegia* non-seed remains were usually only found at the points where the plant grew. Open ground was correlated with indeterminate matter, in this case being mudflat sample 28.

CA of combined seed and non-seed data (Figure 4.54a) split the Transect samples into three rough groupings, similar to those in the plots above. Samples

containing large quantities of *Atriplex* components were grouped to the negative side of the first axis and positive side of the second. Samples with higher quantities of *Phragmites* remains were grouped to the negative side of both axes. There was, however, no clear distinction and the distributions overlapped. To the positive side of the first axis were samples containing higher quantities of allochthonous matter and *Phragmites* leaf and rhizome remains. The CCA (Figure 4.54b) showed that *Phragmites* stem and seed remains were better correlated with high standing cover abundance values than other elements and that *Atriplex* elements, especially the rootlets, were also slightly correlated with high standing vegetation values. The second group was correlated mainly with open ground and contained the samples from mudflats, cliff edge and more open areas in the marsh open to allochthonous inputs. Quantitative analysis did split the samples into rough groups, although it cannot be emphasised enough that the split was poor and that there was considerable overlap between samples and no clear association between cover abundance and macrofossil abundance.

4.7.8 Differences in depositional environment

Samples from the floodplain (1-12 and 17-20) were dominated by remains of *Phragmites* stems, contained low species concentrations, mainly autochthonous seeds and generally high seed abundance. Seed abundance, species abundance and organic content varied on the floodplain; however, they were usually still separable from values from other depositional environments. Samples from the other environments had lower organic content and contained a greater proportion of allochthonous seeds. Species abundance was generally lower in mudflat (sample 28) and channel samples (15, 16), but higher in the levee samples (13-14; 21-27) than the floodplain samples. The levee and channel samples tended to have lower quantities of *Phragmites* stem and were dominated by rootlets, also containing many allochthonous remains, including *Lemna* plants, and larger quantities of unidentifiable material. The latter reflects differing sedimentary processes, most clearly the action of tides causing removal of surface detritus, introduction of allochthonous matter and enhanced sedimentation. The single mudflat sample contained mainly unidentifiable matter and was very different to the other depositional environments. The seed abundance was low and may, therefore, be unrepresentative, although the sample was similar to others from similar sites.

Figure 4.51a Burham Marsh correspondence analysis of Block sample seed and non-seed data

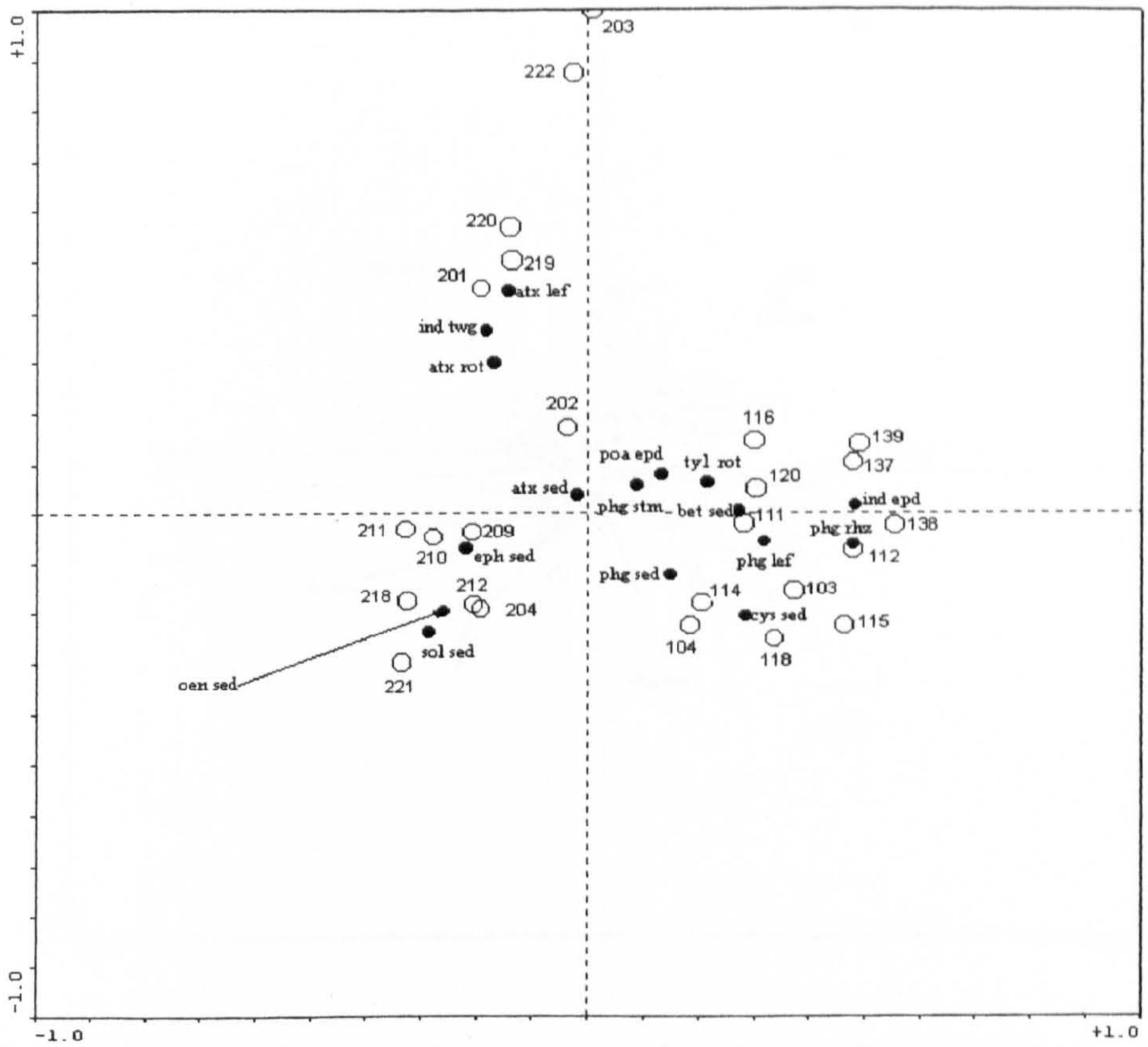


Figure 4.51b Burham Marsh canonical correspondence analysis of Block samples seed and non-seed data

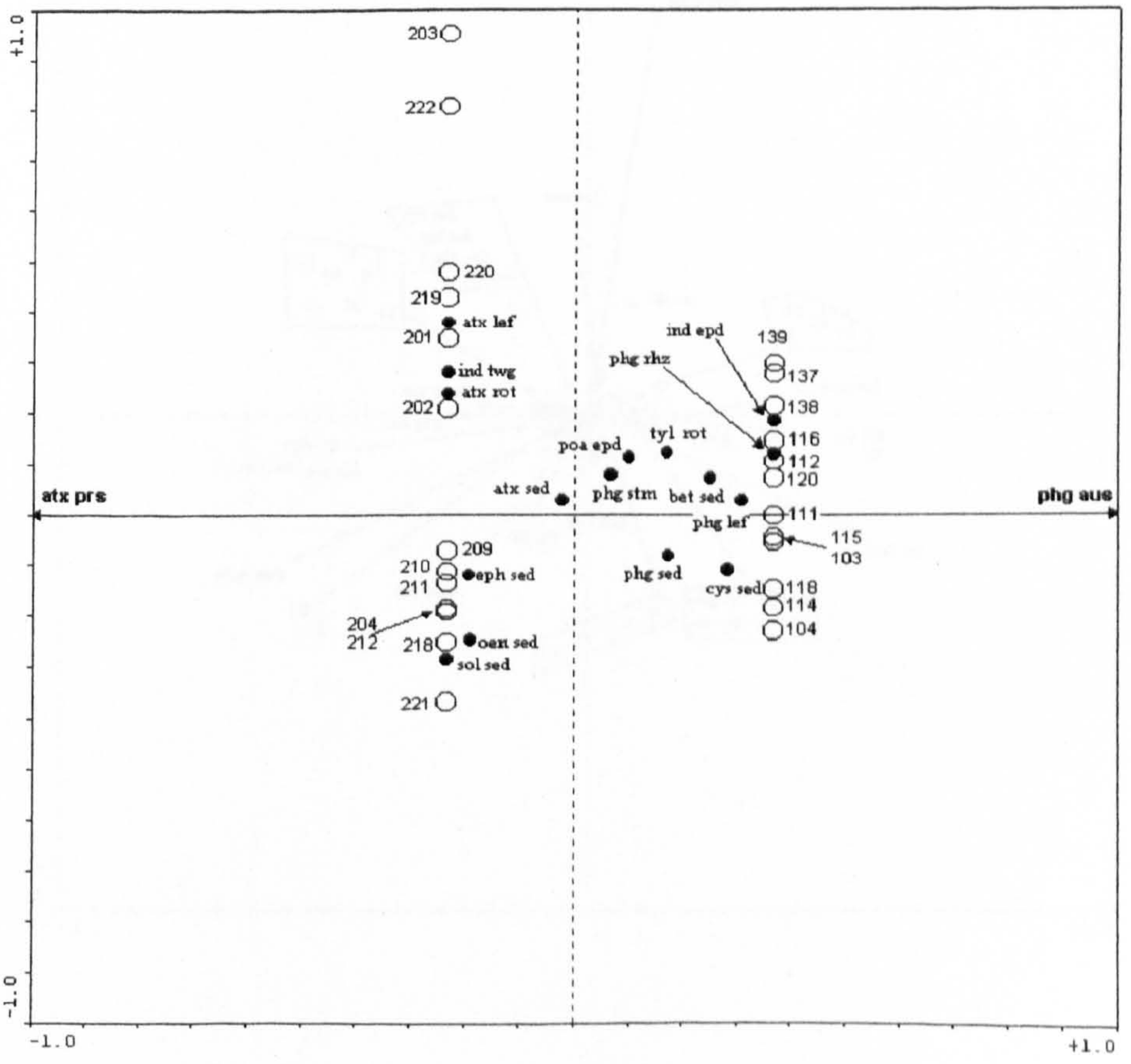


Figure 4.52a Burham Marsh correspondence analysis of Transect sample seed data

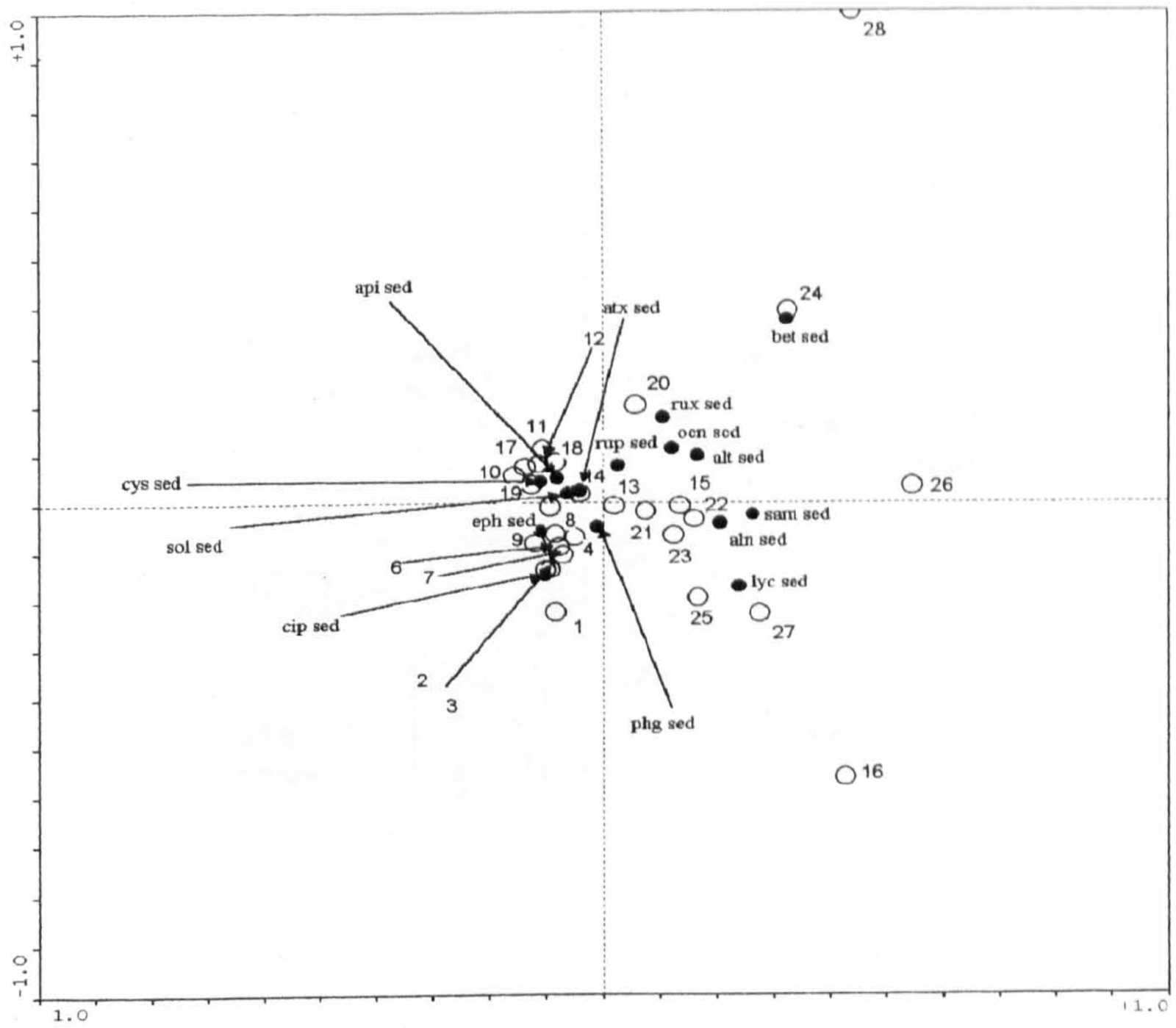


Figure 4.52b Burham Marsh canonical correspondence analysis of Transect sample seed data

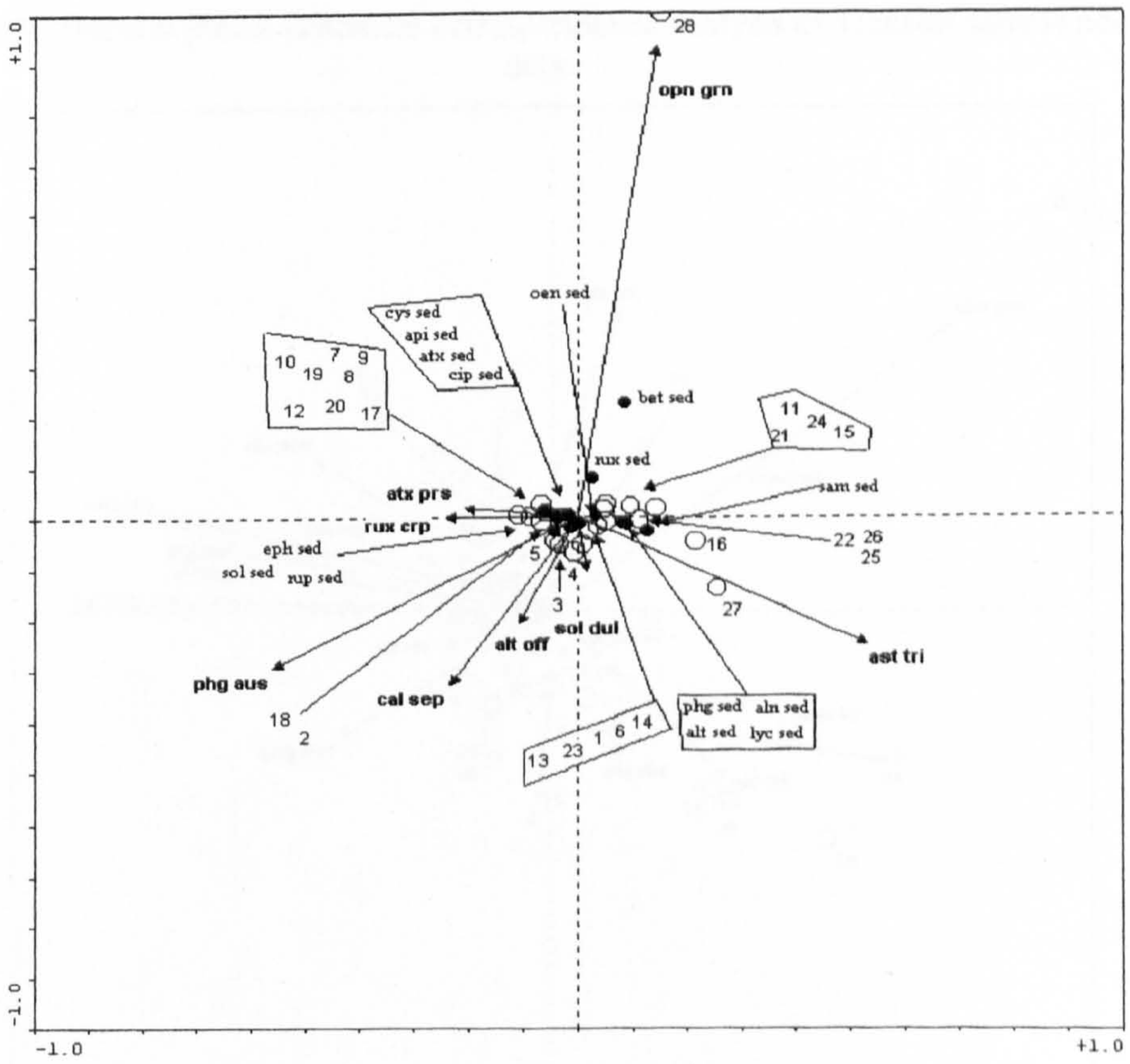


Figure 4.53a Burham Marsh correspondence analysis of Transect sample non-seed data

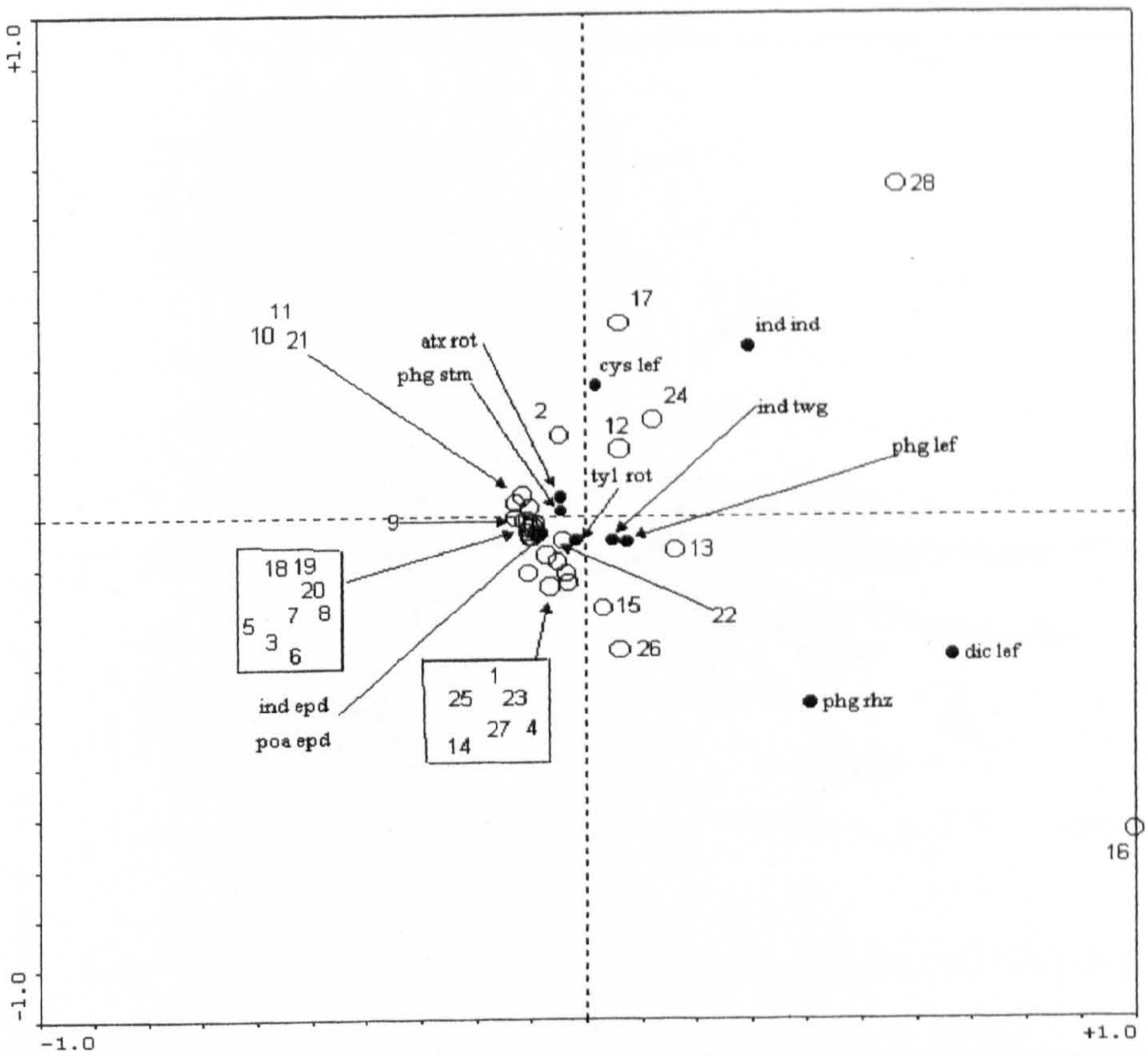


Figure 4.53b Burham Marsh canonical correspondence analysis of Transect sample non-seed data

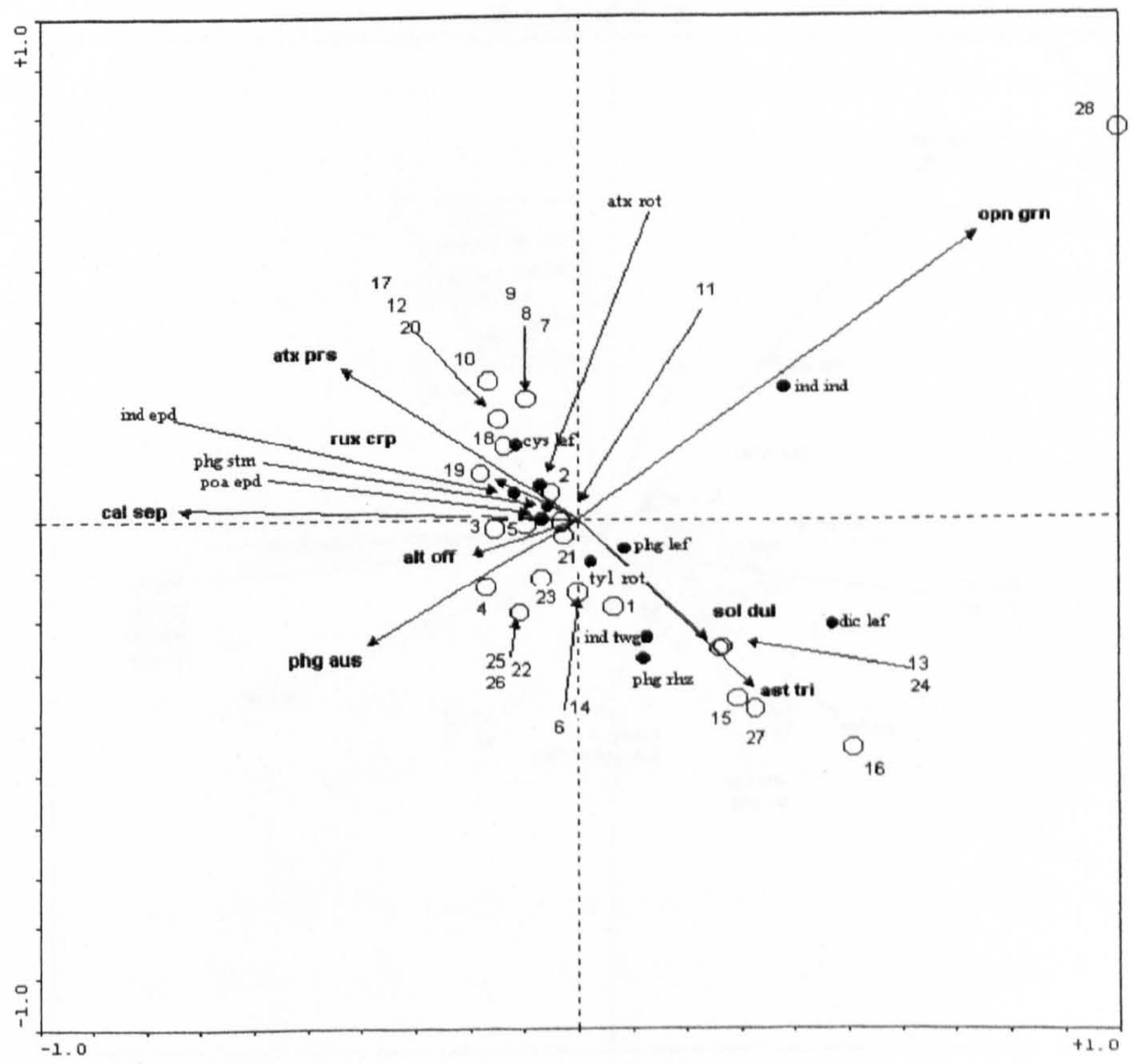


Figure 4.54a Burham Marsh correspondence analysis of Transect sample seed and non-seed data

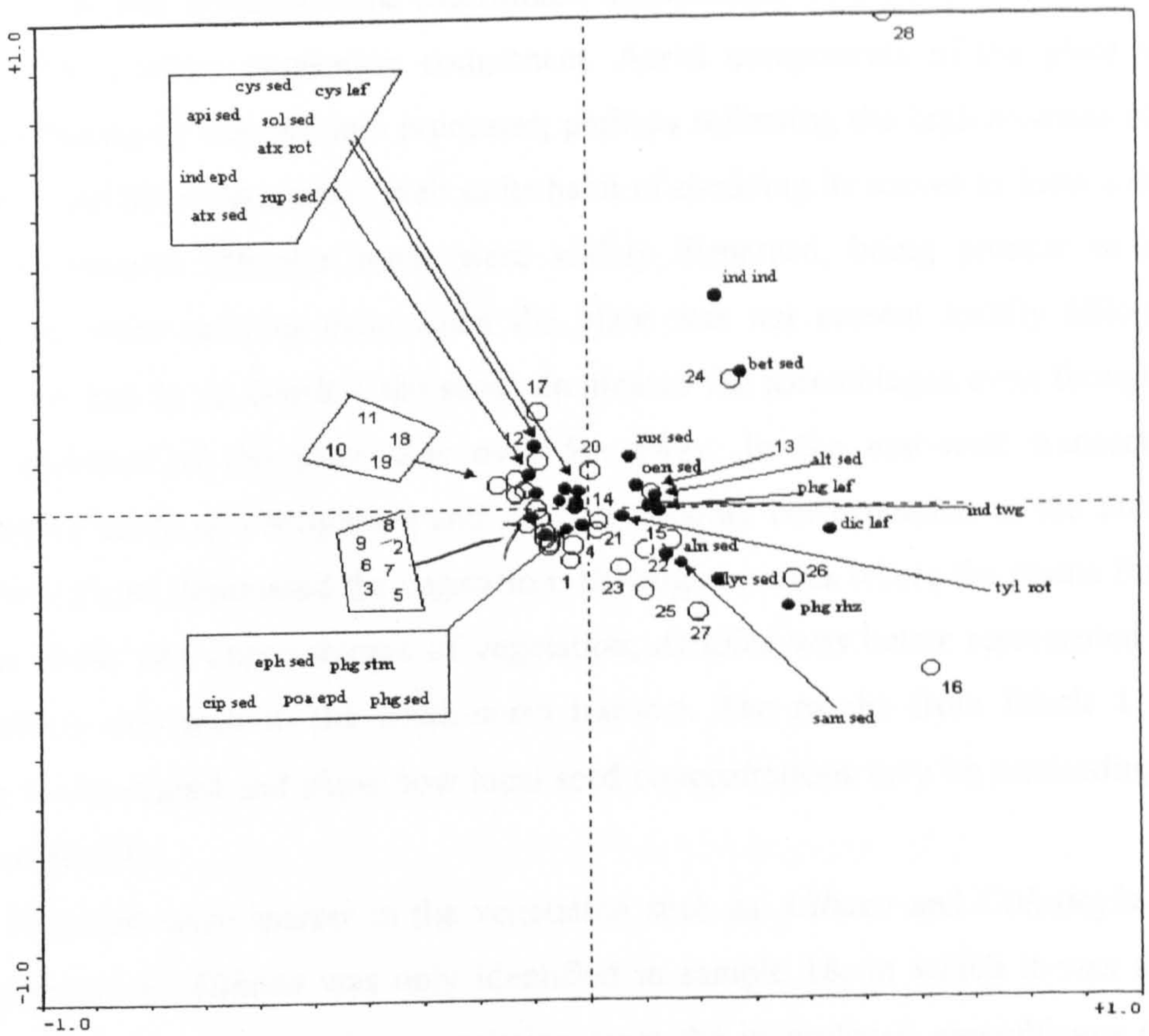
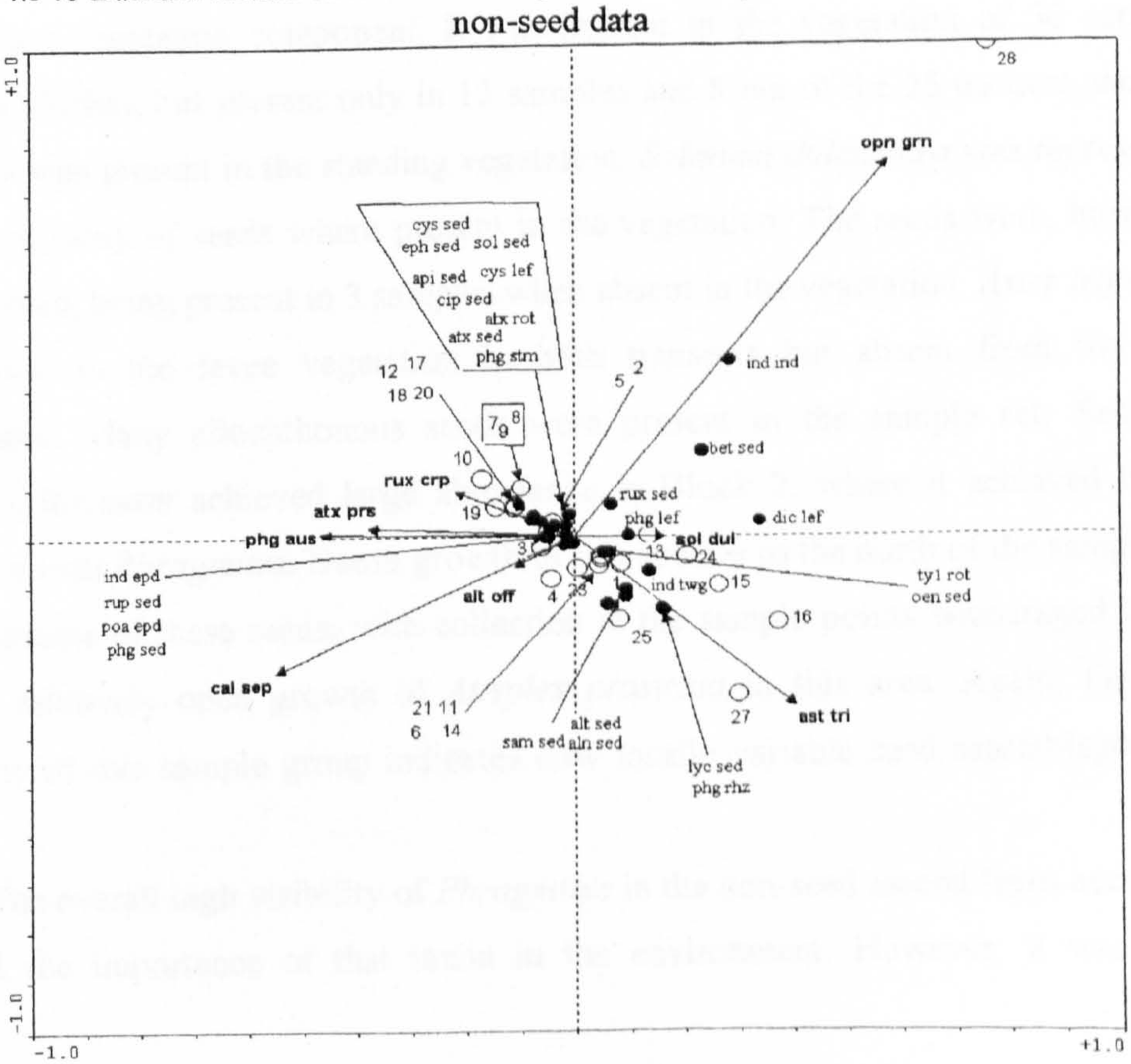


Figure 4.54b Burham Marsh canonical correspondence analysis of Transect sample seed and non-seed data



4.7.9 Vegetation representation

Phragmites remains dominated the macrofossil assemblages across the site, even when the plant was a minor vegetation component. Aerial components of the plant were favourably biased by depositional processes, perhaps reflecting the high biomass of the plant above and below ground as well as its habit of shedding its leaves to form a dense mat in the autumn. *Atriplex* seeds were widely dispersed, being present in large quantities in some samples even when the plant was not present locally (Block 1; samples 1, 4 and 5). In Block 1 the seeds dominated the assemblages even though the nearest specimen of the plant was over 5m away. In the east-west transect the proportion of seeds of *Phragmites* and *Atriplex* roughly corresponded to the areas in which these plants dominated the vegetation, although in areas where the plants formed dominant lower and upper storeys of vegetation, *Atriplex* was better represented. The same pattern was seen in the south-north transect. The results from Block 1 were aberrant in this regard and show how local seed concentrations may be misleading and vary considerably.

Taxa that were sparser in the vegetation such as *Althaea* and *Calystegia* were under-represented. *Althaea* was only identified in sample 18, in which it was absent from the surface vegetation. It was missing from the macrofossil assemblages of the three samples in the east-west transect when present in the vegetation. *Calystegia* was an important vegetation component. It was present in the vegetation of 50 samples (including blocks), but present only in 13 samples and 8 out of the 25 transect samples in which it was present in the standing vegetation. *Solanum dulcamara* was represented by a tiny quantity of seeds where present in the vegetation. The seeds were, however, widely spread, being present in 3 samples when absent in the vegetation. *Aster tripolium* was present in the levee vegetation in both transects but absent from the seed assemblages. Many allochthonous seeds were present in the sample set. Seeds of *Epilobium hirsutum* achieved large abundance in Block 2, where it achieved higher abundance than *Phragmites*. Dense growth of this species to the north of the sample site was the source of these seeds, with collection at the sample points encouraged by the low and relatively open growth of *Atriplex prostrata* in this area. Again, the local peculiarity of this sample group indicates how locally variable seed assemblages may be.

The overall high visibility of *Phragmites* in the non-seed assemblages accurately reflected the importance of that taxon in the environment. However, it was over-

represented, even in Block 2 where it was a minor vegetation component. The real changes in vegetation were more accurately reflected by the change in root types, *Atriplex* type roots being more common in Block 2 and where the taxon was present in the vegetation. *Atriplex* rootlets were still a minor component of the assemblages in each case and so the relative quantity of rootlets was still no guide to the importance in the surface vegetation. It should be noted that the rootlets of *Atriplex* are unlikely to be identifiable in ancient macrofossil assemblages, so this important indicator of the local growth of the plant is unlikely to be available in palaeoenvironmental studies. *Lemna* leaves are similarly unlikely to be preserved in a recognisable form.

Leaf remains of all of the Dicotyledons were rare, although fragments of *Calystegia* leaf and *Atriplex* were occasionally identified. *Calystegia* was poorly represented and minor taxa such as *Althaea* were absent from the non-seed assemblages. Allochthonous stem and rootlet remains (Cyperaceae type), probably from *Bolboschoenus maritimus*, were identified in samples from the mudflat and levee samples in the south-north transect, 4m away from a local growth of the plant.

To summarise, the vegetation was mostly reedbeds dominated by Monocotyledon geophytes with common climbers (*Calystegia*) and an understorey of annual herbs and occasional geophyte perennial herbs. The Monocotyledon element of the vegetation was well represented in both seed and non-seed elements of the macrofossil assemblages, although local growth of the annual herb *Atriplex* tended to swamp *Phragmites* seed abundance. Macrofossils of the climbers *Calystegia* and *Solanum* were sporadic and under-represented, while the occasional perennial herbs in the vegetation were almost invisible. They were usually only represented by seeds that could not be distinguished from allochthonous inputs in terms of quantity or environmental tolerances. This pattern of representation is similar to other similar sites.

4.7.10 Sub-surface samples from sediment blocks

Sub-surface samples from Block 1 (137-139) contained lower seed abundance and larger quantities of rootlets, but were otherwise comparable to similarly sized surface samples (Tables 4.25 and 4.26). In Block 2, the depth samples were similar to the 50cm^3 surface samples, although they contained smaller quantities of *Atriplex* rootlets, possibly indicating recent vegetation change. In all respects, the derived seed indices of sub-surface samples in both blocks were similar.

Table 4.27 Burham Marsh: Sub-surface sample sediment data from Blocks 1 and 3

	Block 1		Block 2	
Depth	**% water**	**% organic**	**% water**	**% organic**
0-2	65.5	24.8	48	17.8
2-4	65.79	24.12	49.03	19.57
4-6	66.04	23.31	49.47	19.86
6-8	66.76	25.14	48.48	20.05
8-10	62.15	20.28	49.75	21.14
10-12	-	-	48.36	26.52

Depth sediment data for both blocks is shown in Table 4.27. Water content showed no trends with depth and varied positively and negatively from the surface mean figure. Organic content figures in Block 2 increased with depth, indicating slower sediment accumulation rates, decreased decay or increased sediment compaction with depth. No similar trend was observable in Block 1 where penetration by dense *Phragmites* rhizomes may have locally influenced the organic figures.

4.8 Hickling Broad

4.8.1 Location and topography

Hickling Broad is a complex of herb and wooded fens, pools, reedbeds, mowed fens and grazing marshes surrounding the eponymous Broad on the River Thurne 2km northeast of Potter Heigham, Norfolk (grid reference: TG 423218). Herb fens lying outside the flood levee and still subject to periodic flooding were the main focus of interest in this study (Figure 4.55). With the exception of one mown area of *Cladium mariscus* (site 5) the sampled areas showed no evidence of recent disturbance, although the vegetation of the whole area is the result of long-term management and is unlikely to represent natural formations.

4.8.2 Vegetation and surface litter

Sample area 02 contained a mosaic of S4 *Phragmites australis* swamp community and S24 *Phragmites australis - Peucedanum palustre* tall herb fen community variants (Table 4.28). The latter vegetation was very diverse and included *Iris pseudacorus, Peucedanum palustre, Valeriana dioica, Typha angustifolia, Juncus subnodulosus, Eupatorium cannabinum, Cladium mariscus, Filipendula ulmaria, Galium palustre, Lysimachia vulgaris* and *Solanum dulcamara.* Site 5 was located in an area of mown S2 *Cladium mariscus* swamp community and was relatively species poor. Areas 06 and 07 were further variants of S24 *Phragmites australis - Peucedanum palustre* tall herb fen.

Lysimachia vulgaris was especially common on site 06 and *Rumex hydrolapathum* on 07. Area 08 was an isolated stand of S25 *Phragmites australis-Eupatorium cannabinum* tall herb fen with a *Juncus subnodulosus* understorey.

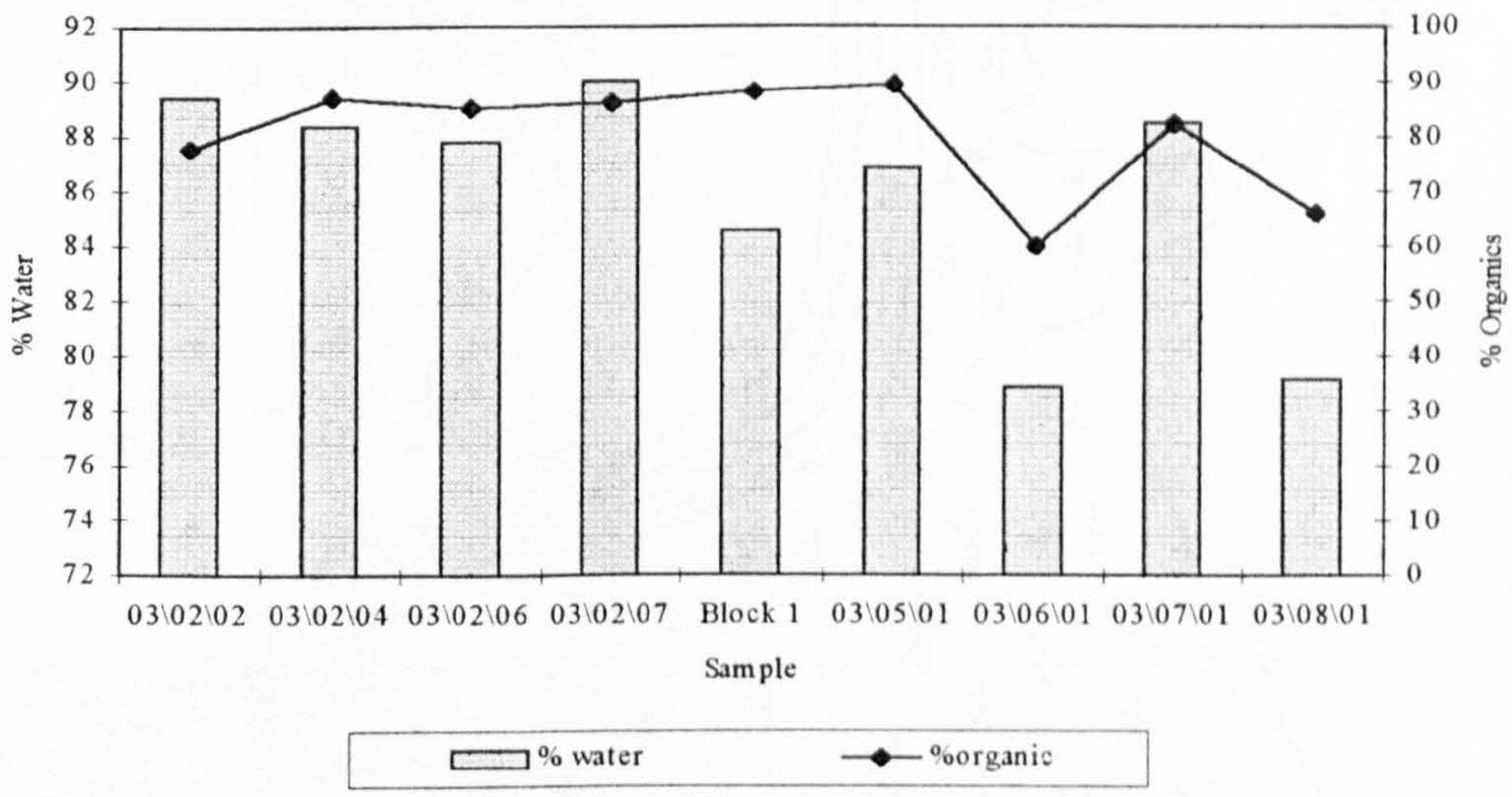
Surface litter mainly contained fragments of aerial debris from the local Monocotyledon dominant. In areas 06 - 08 large quantities of Dicotyledon leaf debris were also noted, although Monocotyledon debris was still dominant.

4.8.3 Sampling

Samples were collected from 5 sample areas. Block 1 and four 200cm^3 surface samples were analysed from area 02, the mosaic of *Phragmites* swamp and species-rich herb fen. Single 200cm^3 surface samples were also collected from the other four areas.

4.8.4 Sediments

Figure 4.56 Hickling Broad Organic and water content



Sediments in all sample areas were humified herbaceous peats (Table 4.28.) in which the degree of humification and quantity of silt varied. Some of the sediments were clearly open to silt inputs from flooding of the Broad, especially at sites 06 and 08. Sample point 02 in area 02 also contained silts, being near an inlet in the broad-edge. Samples from area 05 and 08 were particularly humified and much of the plant matter was decayed. All of the sampled sediments were penetrated by rootlets and often contained large fragments of rhizome and stem material. Water and organic content was high in all samples, water percentages ranging from 78% to 90% and the organic content ranging from 60% to 90% (Figure 4.56).

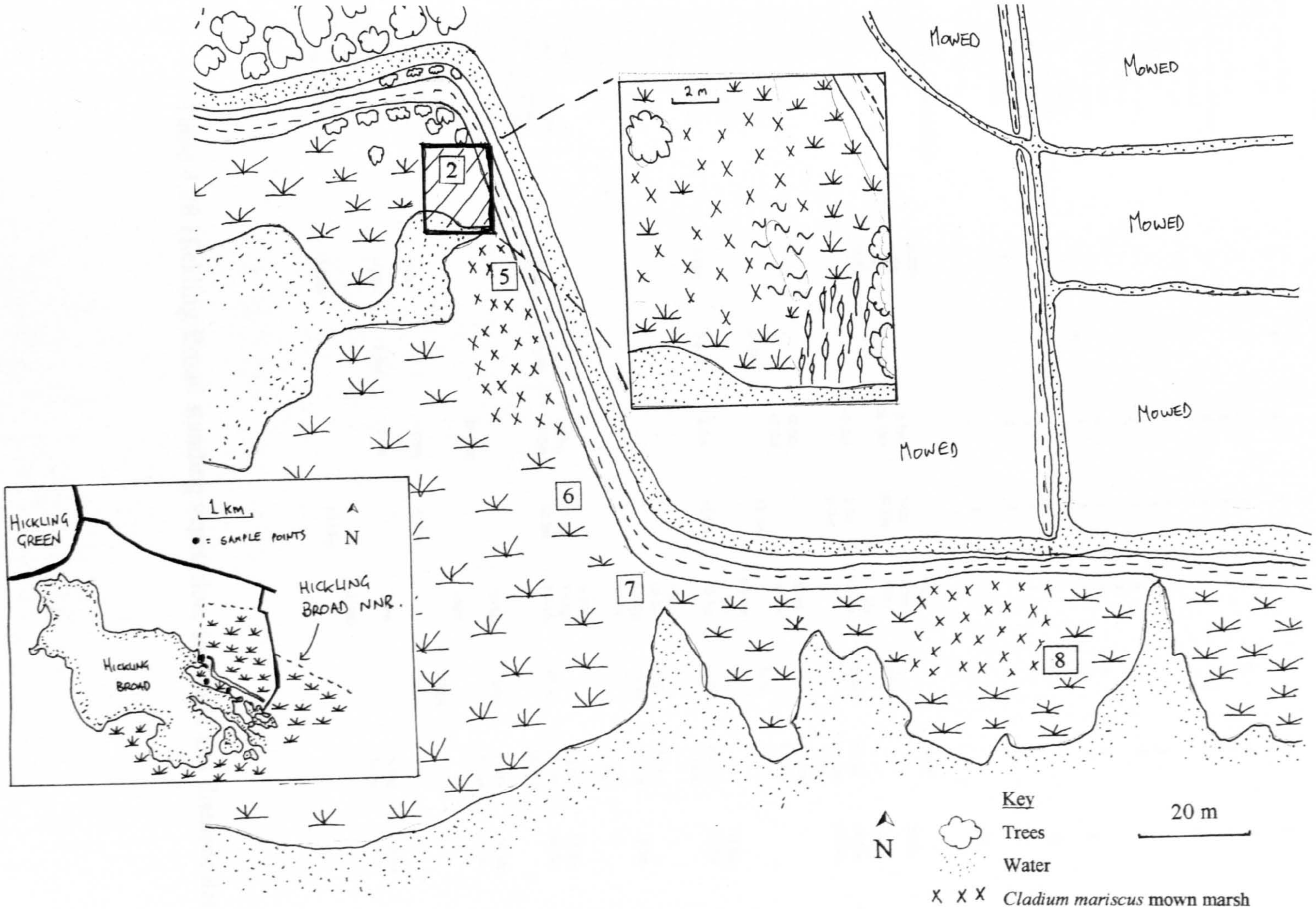


Figure 4.55 Hickling Broad location map (inset) and sample points. Box shows detail of vegetation at sample area 02. Numbers in boxes refer to other sample areas

Sediment Description	03\02\02 Th2Sh1Ag1	03\02\04 Th2Sh2Ag+	03\02\06 Sh3Th1Ag+	03\02\07 Sh3Th1Ag+	Block 1 Sh2Th2Ag+	03\05\01 Sh3Th1Ag+	03\06\01 Sh2Th1Ag1	03\07\01 Sh2Th2Ag+	03\08\01 Sh2Th1Ag1
Colour	10YR2/2	10YR2/2	10YR2/2	10YR2/1	10YR2/2	7.5YR2.5/2	10YR2/2	10YR2/2	10YR2/1
% water	89.43	88.39	87.8	90.02	84 57	86.83	78.83	88.47	79.15
%organic	77.7	87.24	85.1	86.27	88.31	89.56	60.18	82.33	66.34
Cover Abundance									
Calystegia sepium	7	3	4	5	3	4	3	4	4
Carex riparia							2		1
Cladium mariscus			5	7	5	9	4	5	2
Eupatorium cannabinum			5	2	4		1	1	8
Filipendula ulmaria			6	2	1		1		
Galium palustre agg.	3			3				2	
Iris pseudacorus				1	4			1	
Juncus subnodulosus				4	5		5		2
Lysimachia vulgaris			2	1	5		8	4	
Lycopus europaeus					3				
Peucedanum palustre			4	2	4	1	1		
Phragmites australis	7	10	5	6	4	5	4	6	4
Rubus fruticosus agg.									5
Rumex hydrolapathum				2	4			6	
Solanum dulcamara	3		2	2	1				
Typha angustifolia	5		4	5				5	
Urtica dioica									1
Valeriana dioica				3				2	
Distance from nearest plant									
Alnus glutinosa	10-50m				>50m		>50m		
Apium sp.	2-5m		2-5m	2-5m	2-5m			2-5m	
Betula sp.	5-10m	5-10m	10-50m	10-50m	>50m	>50m			
Calystegia sepium	<0.5m				0.5-2m			<0.5m	
Cladium mariscus			<0.5m	2-5m	0 5-2m	<0.5m	<0.5m	<0.5m	0.5-2m
Carex sp.				2-5m			0.5-2m	0.5-2m	
Epilobium sp.							>50m		
Eupatorium cannabinum	5-10m		<0.5m		<0 5m		0.5-2m		<0.5m
Filipendula ulmaria			<0.5m		<0.5m		0.5-2m		
Galium palustre agg.		5-10m		<0 5m		2-5m			
Hydrocotyle vulgaris					0 5-2m				0.5-2m
Iris pseudacorus					2-5m	2-5m		<0 5m	
Juncus subnodulosus	5-10m	5-10m	2-5m	<0.5m	<0.5m	5-10m	0 5-2m	5-10m	0.5-2m
cf. *Lathyrus* sp.							>50m		
Luzula sp.					>50m				
Lycopus europaeus					<0.5m	2-5m	5-10m		
Lysimachia vulgaris					0.5-2m	<0.5m	<0.5m	<0 5m	
Lythrum salicaria					2-5m				
Mentha sp.							2-5m		
Oenanthe sp.					>50m				
Peucedanum palustre			<0.5m	0 5-2m	<0 5m		0.5-2m	0.5-2m	
Phragmites australis	<0 5m	<0.5m	<0.5m	<0.5m	0.5-2m	<0.5m	0.5-2m	<0.5m	0.5-2m
Ranunculus acris type							10-50m		
Rubus fruticosus agg.									<0.5m
Rumex hydrolapathum					<0.5m	5-10m	5-10m	<0.5m	10-50m
Salix sp.			10-50m				5-10m	2-5m	10-50m
Samolus valerandi					>50m				0 5-2m
Schoenoplectus lacustris						>50m			
Solanum dulcamara	<0.5m		<0.5m	<0.5m					
Sonchus sp.			>50						
Typha sp.	<0 5m	2-5m	2-5m		2-5m		5-10m	<0.5m	10-50m
Urtica dioica							5-10m	<0.5m	0.5-2m
Valeriana dioica					5-10m				
Chenopodium sp	5-10m			10-50m					

Table 4.28 Hickling Broad standing vegetation, sediment and distance data

Taxon	Sample	105	108	114	115	116	132	133	03\02\02	03\02\04	03\02\06	03\02\07	03\05\01	03\06\01	03\07\01	03\08\01
	Size (cm³)	50	12.5	25	25	50	12.5	50	200	200	200	200	200	200	200	200
1. Seeds etc.																
Alnus glutinosa	Fruit	1				1								1		
Apium sp.	Fruit	7	4	9	6	3	1		3		1	45			6	
Betula sp.	Fruit	71	23	19	15	27	17	6	55	40	21	8	4			
Betula sp.	Catkin Scale	3	2	1		1			2	4	1					
Betula sp.	Cone								1							
Calystegia sepium	Seed	2													1	
Calystegia sepium	Capsule								4							
Cladium mariscus	Fruit	21	13	41	34	44	31	8			44	6	286	14	193	37
Carex sp.	Seed											1		3		
Epilobium sp.	Fruit													1		
Eupatorium cannabinum	Fruit	8	5	8	4	10	3	11	3		126			43	124	137
Filipendula ulmaria	Fruit	6	2	1			2				1			3		
Galium palustre agg.	Fruit									1		3	3			
Hydrocotyle vulgaris	Fruit	1					1									4
Iris pseudacorus	Seed	1	4	1									1		5	
Juncus subnodulosus	Seed	234	87	163	178	282	98	156	64	194	124	278		203	2	11
Juncus sp.	Capsule			3	4	18	23	1				25	1	19		
cf. *Lathyrus* sp.	Seed													1		
Luzula sp.	Seed							4								
Lycopus europaeus	Fruit	2		1									3	1		
Lysimachia vulgaris	Seed	4	2		1	1	1	9						19	2	
Lythrum salicaria	Seed	1														
Mentha sp.	Fruit													3		
Oenanthe sp.	Fruit			1												
Peucedanum palustre	Fruit	6		2	2	3	2	3			5	4		2	2	
Phragmites australis	Fruit	93	12	9	24	32	24	6	113	119	75	30	9	2	8	2
Ranunculus acris type	Fruit													1		
Rubus fruticosus agg.	Fruit															17
Rubus type	Spine															2
Rumex hydrolapathum	Fruit	3	23	12	5	25	7	3							120	
Rumex hydrolapathum	Bract			10	2	11	13	1							3	1
Rumex sp.	Fruit	10	13	18	15	16	15						1	1		1
Salix sp.	Seed										31			19	17	17
Salix sp.	Stipule															1
Samolus valerandi	Seed		1		1			23								7
Schoenoplectus lacustris	Fruit												2			
Solanum dulcamara	Seed								4		22	9				
Sonchus sp.	Fruit										1					
Typha sp.	Fruit	3		1	3	2	3		13	3	3			3	23	1
Urtica dioica	Seed													2		1
Valeriana dioica	Fruit	5	1	1	1	2	1								3	
Chenopodium sp.	Fruit								1			2				
Indet.	Seed/Fruit	1		1											3	

Table 4.29a Hickling Broad seed macrofossil data

	Sample	105	108	114	115	116	132	133	03\02\02	03\02\04	03\02\06	03\02\07	03\05\01	03\06\01	03\07\01	03\08\01
	Size	50	12.5	25	25	50	12.5	50	200	200	200	200	200	200	200	200
Taxon	**Component**															
2. Non-seed macrofossils																
Phragmites australis	Stem								37 23	26.42		5 6	8.38		9.13	
Phragmites australis	Leaf					0 8			4.99	11.01	0.8	4.22	2.2		8.53	
Phragmites australis	Rhizome								4 32	7.63						
Poaceae	Epidermis			3 87		0.4	0.2									
Poaceae	Stem					2.67										
Type 1	Non-woody root			22.73	14 07	14.73	23.33	8.27	35.45	27.59	32 05	2.1	19.12	26.15	23.83	13 61
Cladium mariscus	Stem		4								7.33	4.21	4.97			
Cladium mariscus	Leaf					4						6.37				
Cladium mariscus	Rhizome	5.33						23.6								
Cyperaceae	Stem	17.67									4 12		10.18			
Cyperaceae	Leaf	2			4 4		1.8	6.4				3.1	5.14		1.69	
Cyperaceae	Epidermis	8 6	2.6	0 67	6.33	4 27	7.47	3 8			1.4	2.25	3.31			
Cyperaceae	Non-woody root			14.67	34 53	44 6	25.6	46.67			21.2	36.12	35.45		43.68	45.06
Typha sp.	Epidermis	0.4		0 8			0 8									
Type 2	Non-woody root	10.93	10 6						3.1							
Juncus sp.	Stem	1.53		2.27		1.33						8 01		2.7		
Juncus sp.	Epidermis				1.73									2.27		
Juncus sp.	Non-woody root	29.2	48 07				0 27					17.89		33.98		
Iris pseudacorus	Rhizome			11.2							4.4					
Monocot.	Stem	1.53		2 8	7.73	5 73	5.6	3			7.98	7.35	1.11	2.25		
Betula sp.	Leaf									2.3						
cf. *Eupatorium* sp.	Leaf															2.17
cf. *Lysimachia* sp.	Leaf													1.98		
Rumex sp.	Leaf	0.33														
Dicotyledonae	Leaf			1.4		1 67	2.33				4.33					1.36
Indet.	Epidermis	0.4				1.47										1.31
Indet.	Rhizome			4	3	1 73								5.35		
Indet.	Stem			16.4												
Various	Seeds	1 93	5.13	2.53	0 67	2.2	3.2	1.4						0.12		1.22
Indet.	Indet.	20.13	29 6	16.68	27.53	14 4	29 4	7.08	14.91	25.05	16.39	12.18	10 15	25.2	13.14	35.27
3. Derived indices																
Seed abundance	-	487	210	297	294	461	219	223	263	361	455	411	310	341	512	239
Species abundance	-	19	12	14	12	12	13	9	9	5	12	10	10	18	14	11
Seed concentration	-	9.74	16.8	11.88	11.76	9 22	17.52	4 46	1.315	1.805	2.275	2.055	1.55	1.705	2.56	1.195
Species concentration	-	0.38	0.24	0.28	0.24	0.24	0.26	0.18	0.045	0.025	0.06	0.05	0 05	0.09	0.07	0.055

Table 4.29b Hickling Broad non-seed macrofossil data and derived indices

Figure 4.57 Hickling Broad seed cumulative concentration data for main taxa

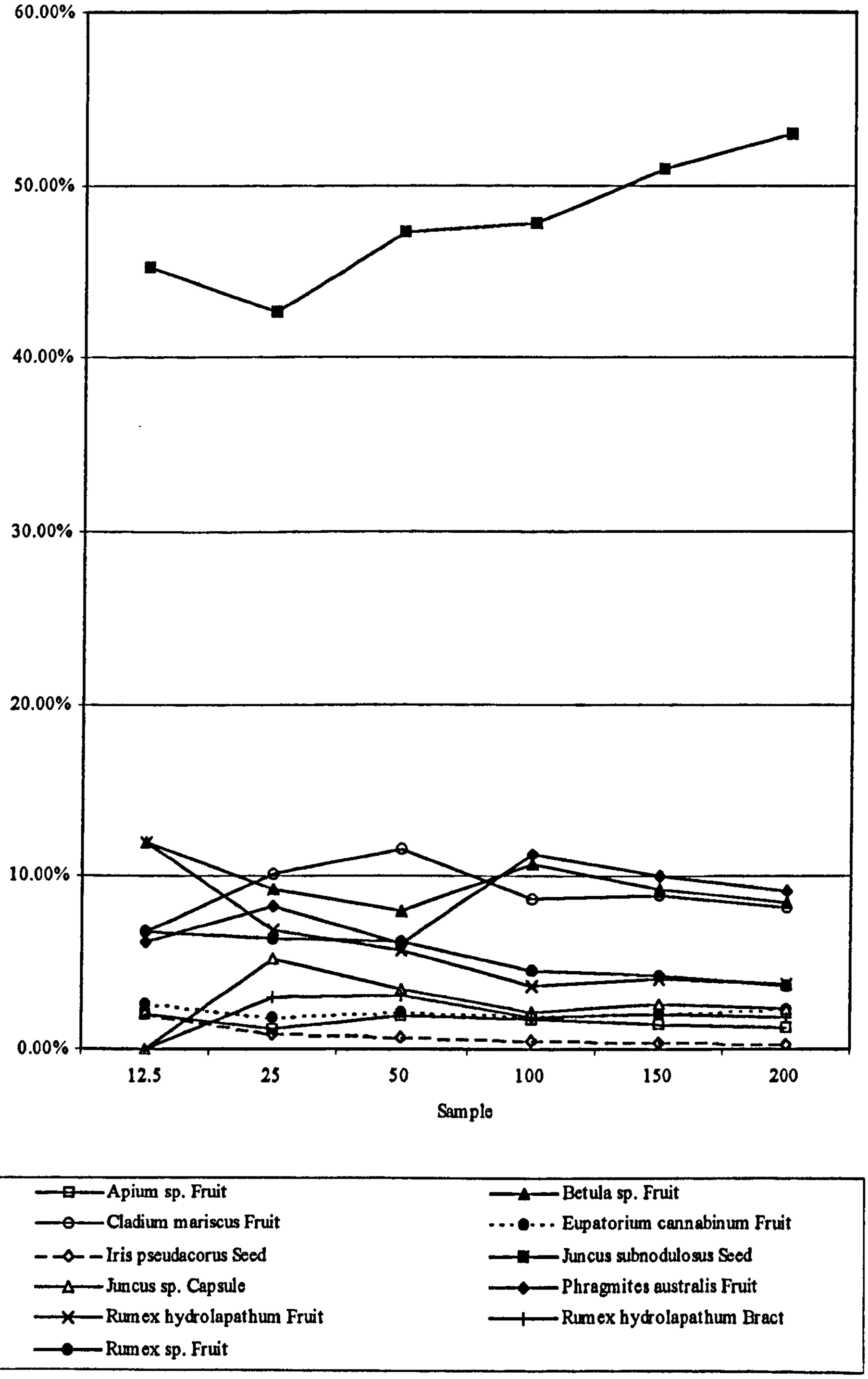


Figure 4.58 Hickling Broad Block 1 cumulative non-seed data

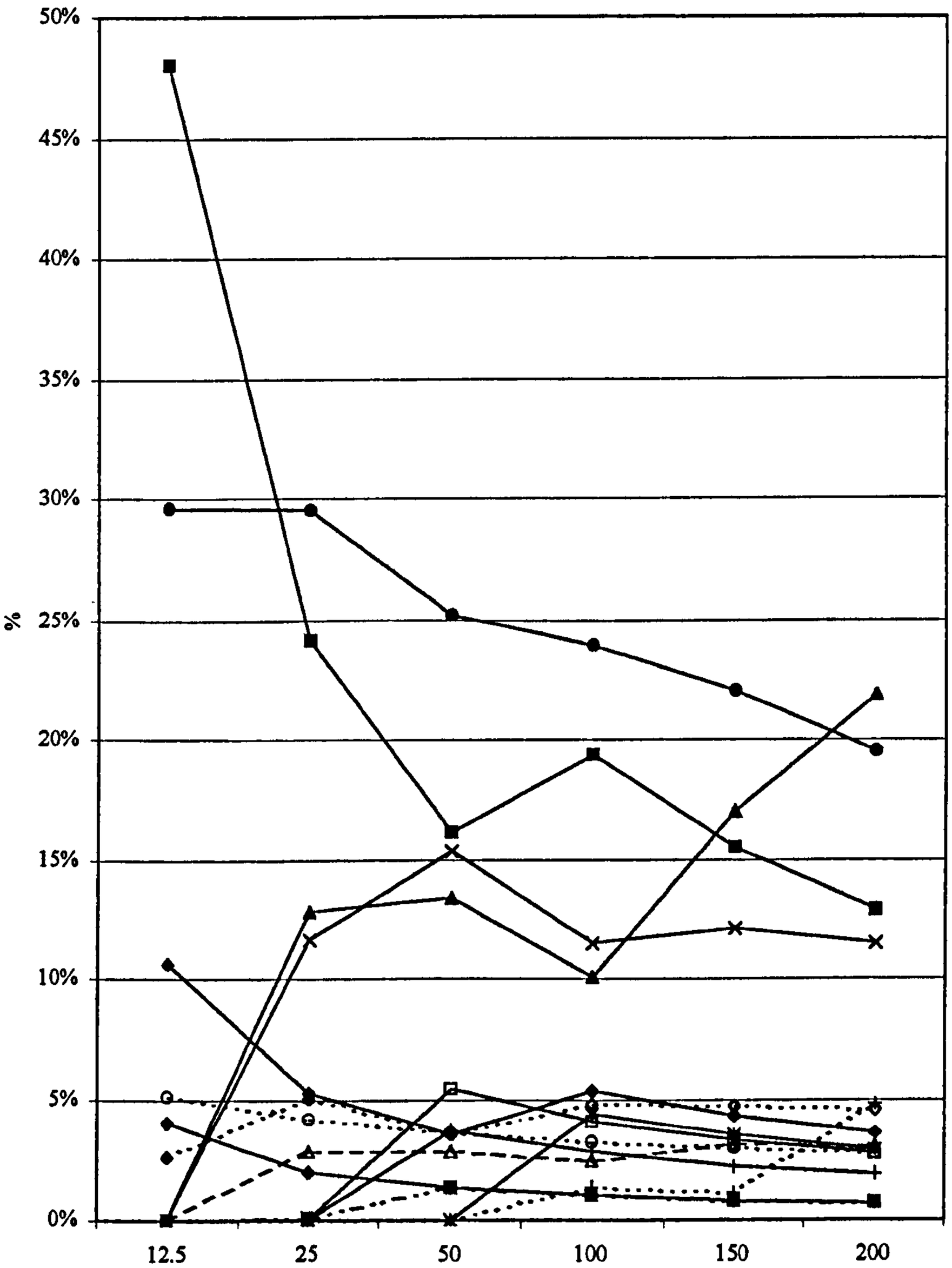


Figure 4.59a Hickling Broad Seed and Species abundance

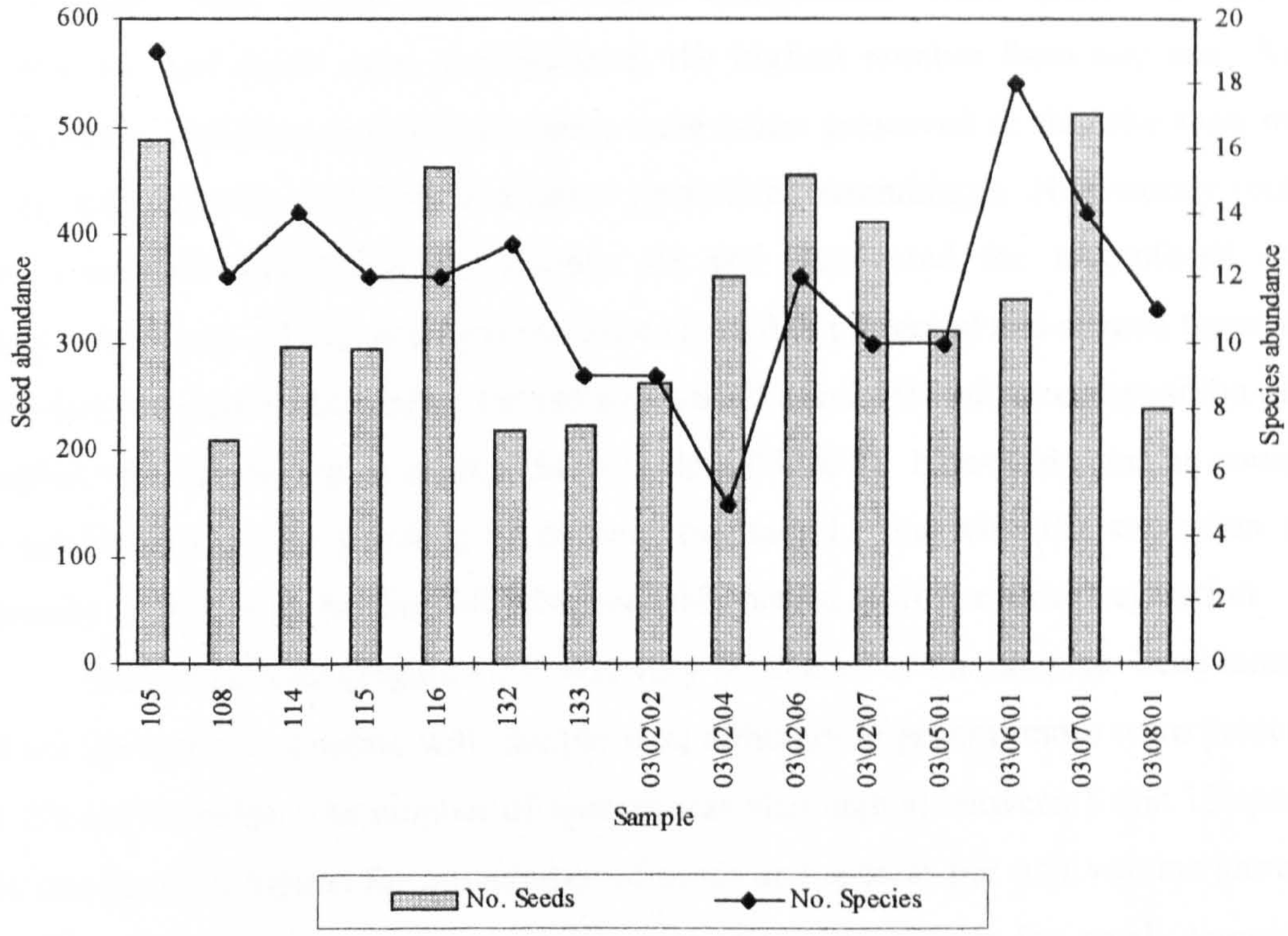
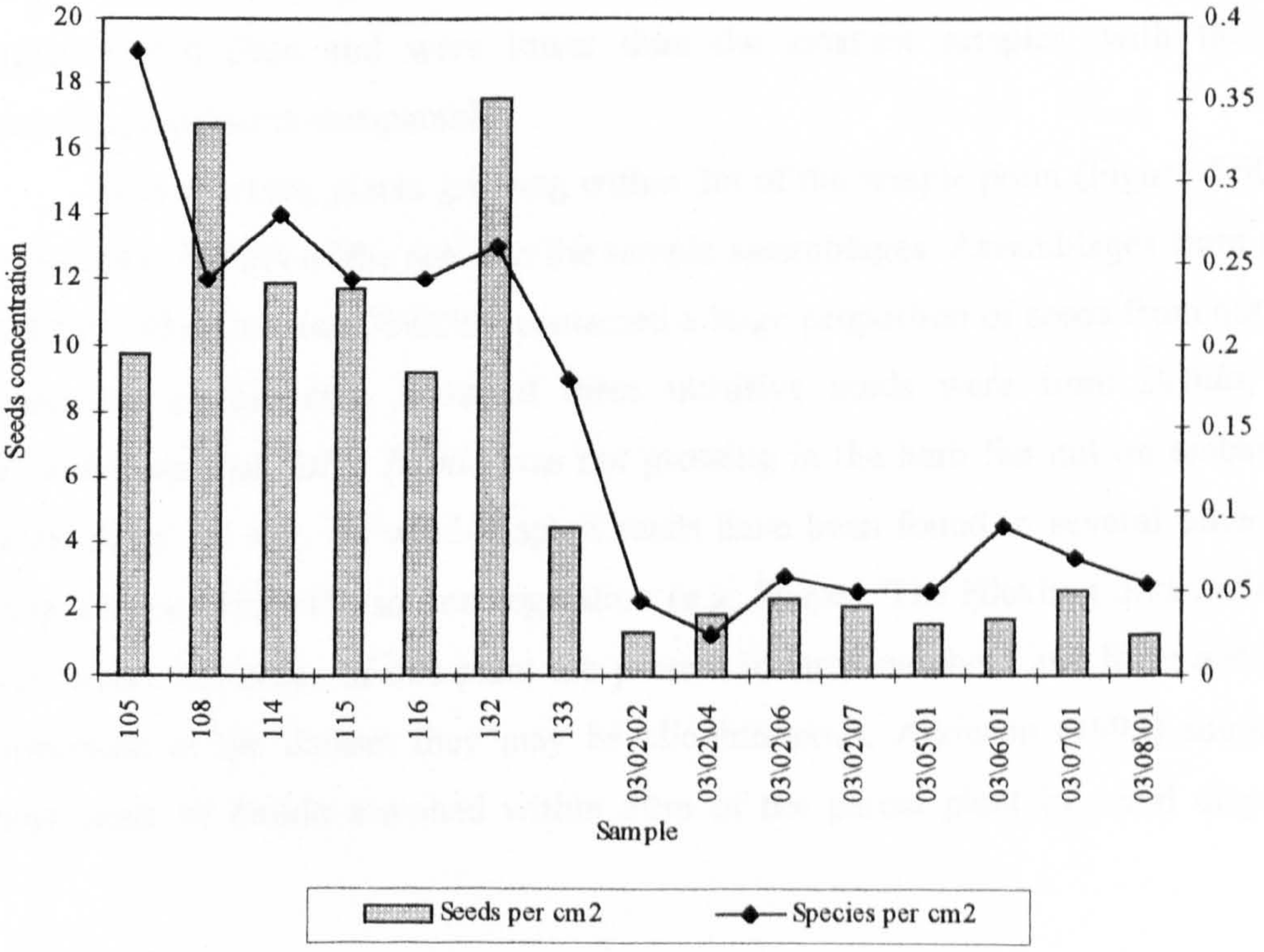


Figure 4.59b Hickling Broad Seed and Species Concentration



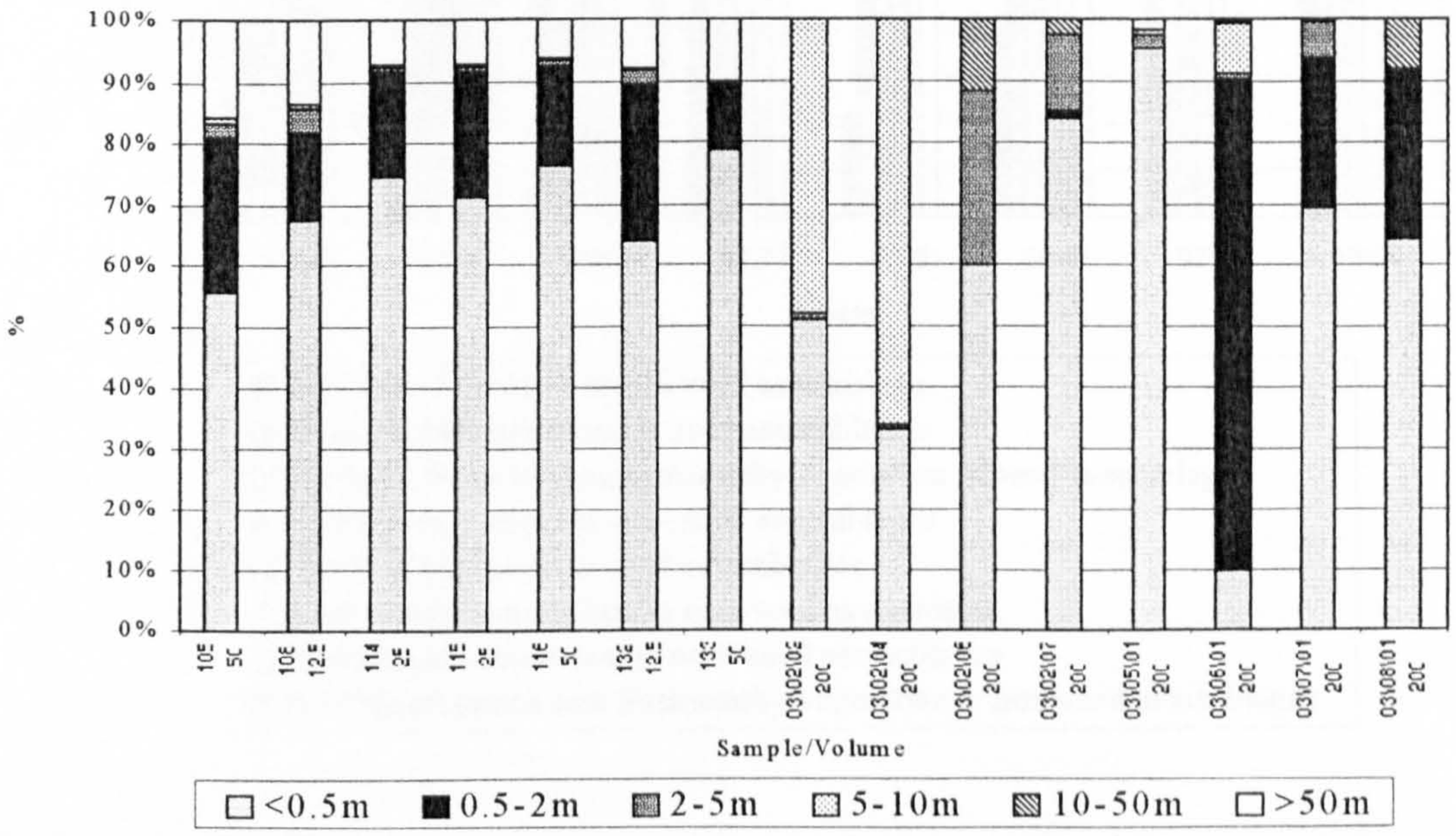
Rich, diverse assemblages of both seed and non-seed macrofossils were preserved throughout the sample set (Table 4.29 a and b). Although the peat was subject to much humification, both seeds and less tough components were preserved. Several Dicotyledon leaf types were distinguished, the highest number from any site. Aerial components, including leaves and stems, were better preserved at this site than many others, although they still formed a minor part of the assemblages. Non-woody rootlets were preserved throughout the sample set and dominated the macrofossil cover abundance values. Rhizome fragments were also often preserved and several types were identified. Unidentifiable matter formed between 7% and 35% of the composition of the samples, the highest figure coming from sample 03/08/01. Non-seed remains could all be supplied by plants growing at or near the sample site with the exception of a fragment of *Betula* sp. leaf in 03/02/04, probably blown in from nearby vegetation.

Seed abundance (Figure 4.59) was very high in all of the samples. Seed numbers did not necessarily correlate with sample size, although in general more were present in the 200cm^3 samples. The number of species was also high at between 8 and 19 species. The comparative figures for the number of seeds and species per unit volume show the variability in seed preservation and incorporation. The figures for small samples in Block 1 (samples 105 - 133) may support the notion that in this environment seeds were generally well dispersed from the parent plant but tended to accumulate in pockets and were not evenly distributed over the sediment surface. The figures for the 200cm^3 samples were at the higher end of the range for the whole project. Seed concentration figures varied little and were lower than the smallest samples, with the species concentrations being comparable.

In most cases, plants growing within 2m of the sample point (Figure 4.60) could account for 70-90% of the seeds in the sample assemblages. Assemblages from samples 03\02\04, 03\02\06 and 03\02\07 contained a large proportion of seeds from outside the immediate sample area. Most of these intrusive seeds were from *Betula*, *Juncus subnodulosus* and *Salix*. *Betula* was not growing in the herb fen but on embankments overlooking the site. Its wind-adapted seeds have been found in several other sites at some distance from the source vegetation (e.g. Snape). The Hickling data indicate that even where the seeds of this plant are present in large numbers and form a substantial proportion of the dataset they may be allochthonous. Atkinson (1992) suggests that most seeds of *Betula* are shed within 50m of the parent plant by wind dispersal. In

circumstances where some local taxa set relatively little seed (e.g. *Phragmites* in this case), *Betula* seeds may be over-represented. *Salix* seeds seem to have similar dispersal properties, the nearest plants being some 50m away. *Juncus subnodulosus* seeds are thought to be buoyant (Richards and Clapham 1941) and the large allochthonous assemblages in samples 03/02/02 and 03/02/04 probably floated to the sample sites from vegetation sampled by Block 1 and sample 03/02/07. Some seeds from *Hydrocotyle vulgaris* and *Apium* were probably from plants growing in the local vegetation but were missed in the vegetation survey. Two seeds of *Alnus glutinosa* were recorded in samples 105 and 03/06/01, presumably from trees growing nearby which have floated into the herb fen.

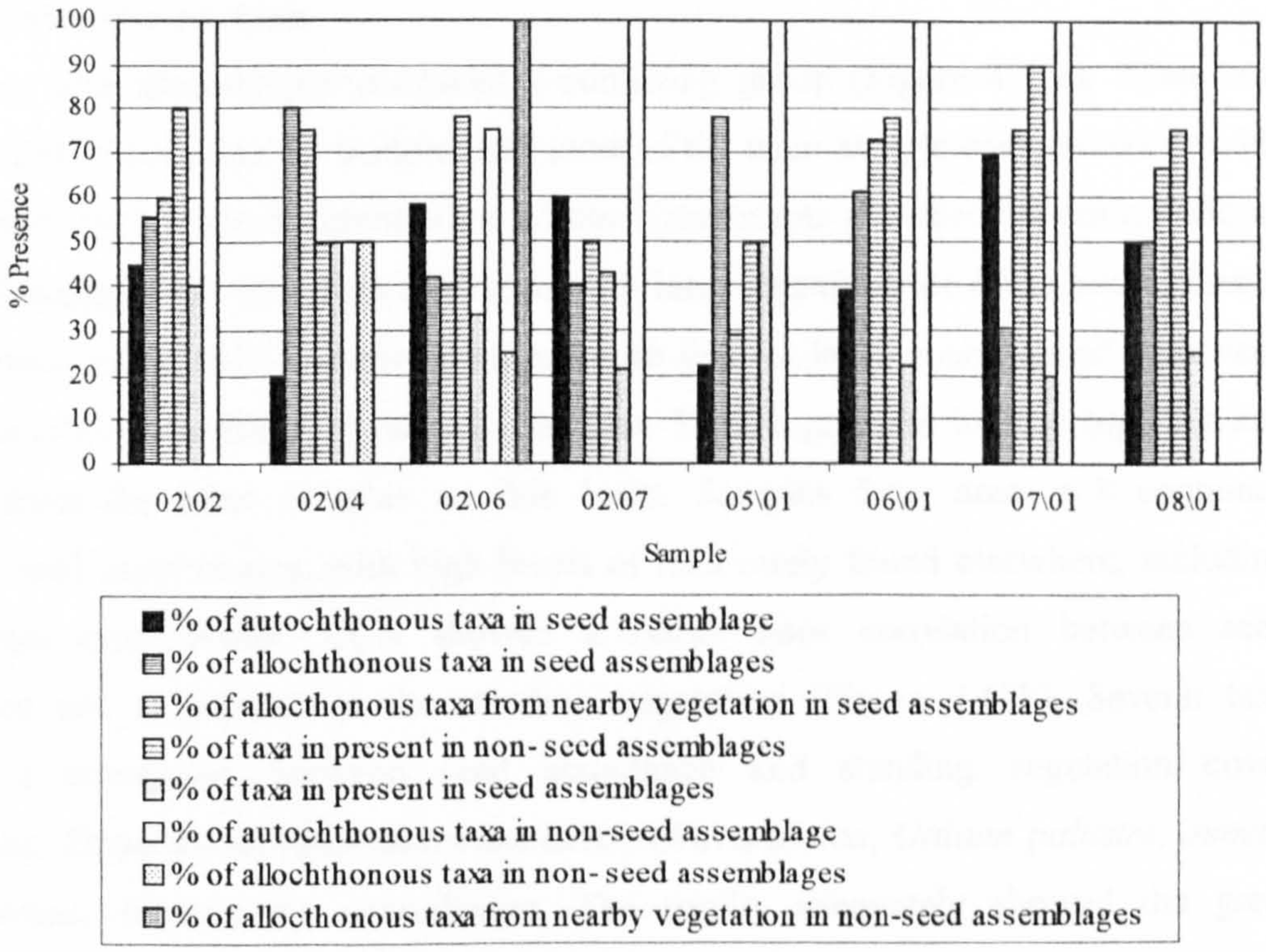
Figure 4.60 Hickling Broad seeds frm set distances from the sample point



Sample ubiquity data are shown in Figure 4.61. The seed assemblages were diverse and contained a considerable number of allochthonous taxa, although most were found near to the sample point. The seeds of arboreal taxa were commonly present and while going some hundreds of metres away, were not present in close proximity to the sites. None of the seed assemblages contained all of the taxa in the standing vegetation with between 10% and 50% of the taxa absent. The 50% figure was from sample 02/04,

collected from vegetation containing only *Phragmites* and *Calystegia*. The proportion of taxa missing from the vegetation represents the dispersal behaviour of this latter taxon that was generally poorly represented in seed assemblages. The non-seed assemblages contained largely autochthonous taxa and those containing allochthonous elements were largely present in nearby vegetation. The proportion of taxa represented in the non-seed assemblages was very low, and only in the samples with low vegetation diversity were larger proportions of the taxa represented.

Figure 4.61 Hickling Broad Sample Ubiquity Data



4.8.6 Sample size effects

The sample set is small but work on macrofossil representation in the block sample suggests that representative macrofossil samples were present. Cumulative percentage abundance diagrams were prepared for samples from Block 1 (Figure 4.57 and 4.58). Figures for the non-seed cover abundance values showed a similar pattern to elsewhere with the percentage abundance stable by 200cm^3 and varying little for most components at volumes of above 50cm^3. The picture was not as stable as in some other blocks, with the figure for Cyperaceae rootlets rising from 100cm^3 and obviously depressing other values, especially those of *Juncus* type rootlets. The difference is outside the range of errors for the cover abundance method. This variability may be explained in part by the

diversity of the standing vegetation. During excavation of the block it was noted that the stems and bases of many different taxa were present over a very small area, much more than in any other block excavated so far. Root abundance may vary correspondingly. The seed assemblages were dominated by *Juncus subnodulosus*, but followed a similar pattern to the cover abundance values, stabilising by 100cm^3 (Figure 4.57). The data suggest that while the samples provide a rich source of information, the sheer diversity in species and macrofossils may make samples from rich herb-fen environments more variable than other environments.

4.8.7 Quantitative analysis

CA of the seed assemblages produced a confusing group (Figure 4.62a). There was essentially little to divide the samples and most of the main sample components provide a weak basis for sample differentiation. Minor components provided the main dividing factors. Samples were split between those with large quantities of *Phragmites*, *Juncus subnodulosus* and *Cladium* seeds and those with few, or large quantities of other seed types. Samples from Block 1, area 2 and area 5 were grouped loosely together and divided from the other samples on this basis. Samples from areas 6-8 contained different seed assemblages, with high levels of taxa rarely found elsewhere, including *Eupatorium cannabinum*. CCA showed a rather poor correlation between seed abundance and abundance in the standing vegetation (Figure 4.62b). Several taxa showed a correlation between seed abundance and standing vegetation cover abundance. These included *Cladium mariscus, Urtica dioica, Galium palustre, Juncus subnodulosus, Eupatorium cannabinum*. The results adequately showed the great overlap in the distribution of the seeds of many taxa in the assemblages.

CA of the non-seed assemblages split the samples into four main groups (Figure 4.63a). Samples 03/02/02 and 03/02/04 were well separated from the others on the basis of the presence of *Phragmites* components and Type 1 roots. Samples 105, 108, 03/02/07 and 03/06/01 were separated on the basis of the presence of *Juncus* rootlets, and some *Cladium*/Cyperaceae components. A third group of samples was split from the others on the basis of the presence of a number of components, including *Iris* rhizomes and Cyperaceae components. This included many of the samples from the Block, 03/06/01 and 03/08/01. Samples 03/05/01 and 03/05/01 formed an intermediate group between groups 1 and 3. The CA was confused and illustrates the high spatial variability in macrofossil assemblages, reflecting the high floristic variability in the

vegetation. It should be noted that individual occurrences of macrofossils were removed from the CA data, taking away the individual records of *Rumex hydrolapathum*, *Eupatorium cannabinum* and *Lysimachia vulgaris* leaves from samples 105, 03/08/01 and 03/06/01 respectively. Inclusion would have separated all three samples from the rest of the group.

CCA of the non-seed data showed a good correlation between the macrofossils of *Phragmites* and the presence of it in the vegetation (Figure 4.63b). Correlation between the presence of the main other dominants and standing vegetation was variable, although Cyperaceae components, especially the rootlets, were moderately well correlated with taxa of that family, especially *Cladium mariscus*. *Juncus* components, especially the rootlets, were also well correlated with occurrences of *Juncus subnodulosus*. Other taxa, including *Iris pseudacorus*, *Eupatorium* and *Lysimachia*, had occasional occurrences of non-seed remains where they were present in large quantities in the standing vegetation. Many species were absent from the non-seed records.

Combined CA of the seed and non-seed data (Figures 4.64a) split the samples into similar groups as above and showed that there was a moderate correlation between seed and non-seed data occurrences. The non-seed data improved the division of samples made on the basis of seed occurrences. The CCA (Figure 4.64b) showed that broad correlations were present between the macrofossils and standing vegetation of some taxa. The data were, however, confusing and no straightforward interpretation was possible of the data. Non-seed macrofossils were more spatially accurate than the seed data, but were much less easily interpreted than in other sites.

4.8.8 Vegetation representation

Most samples contained the seeds of 70%-90% of the species recorded in the local standing vegetation. Representation was better in the 200cm^3 samples in which only one or two of the species in the vegetation were missing as opposed to 3 to 4 taxa in the smaller samples. Most of the taxa present in the samples were of local origin, although the nearby tree species often contributed significant, but allochthonous, quantities of seeds to the assemblages.

Some trends in the representation of taxa were noted in the seed abundance and when the presence of taxa in samples were compared (Table 4.30). *Calystegia sepium*, *Iris pseudacorus* and *Galium palustre* were usually under-represented in all samples, suggesting low seed productivity and dispersal. *Solanum dulcamra* and *Filipendula*

Figure 4.62a Hickling Broad correspondence analysis of seed data

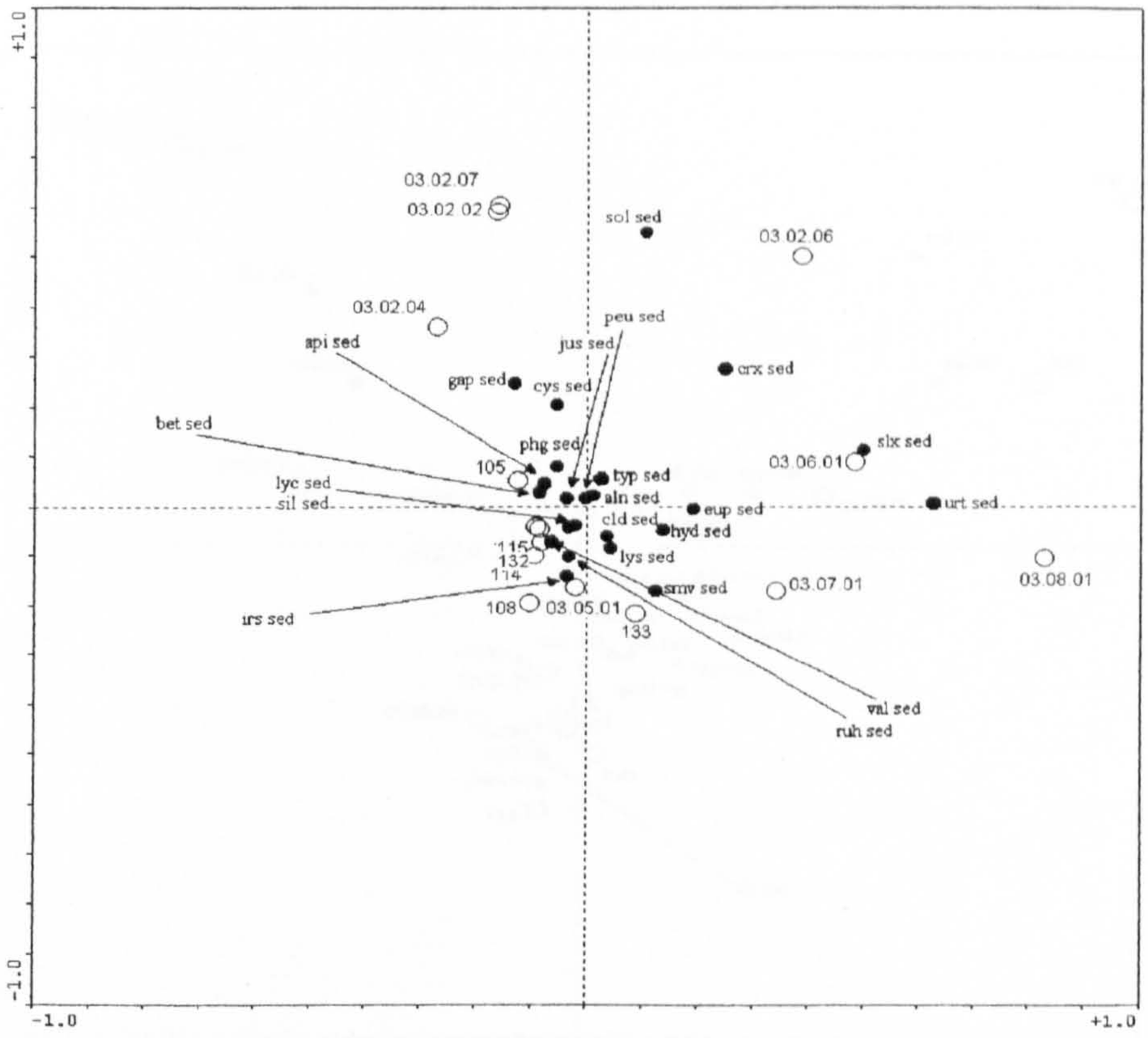


Figure 4.62b Hickling Broad canonical correspondence analysis of seed data

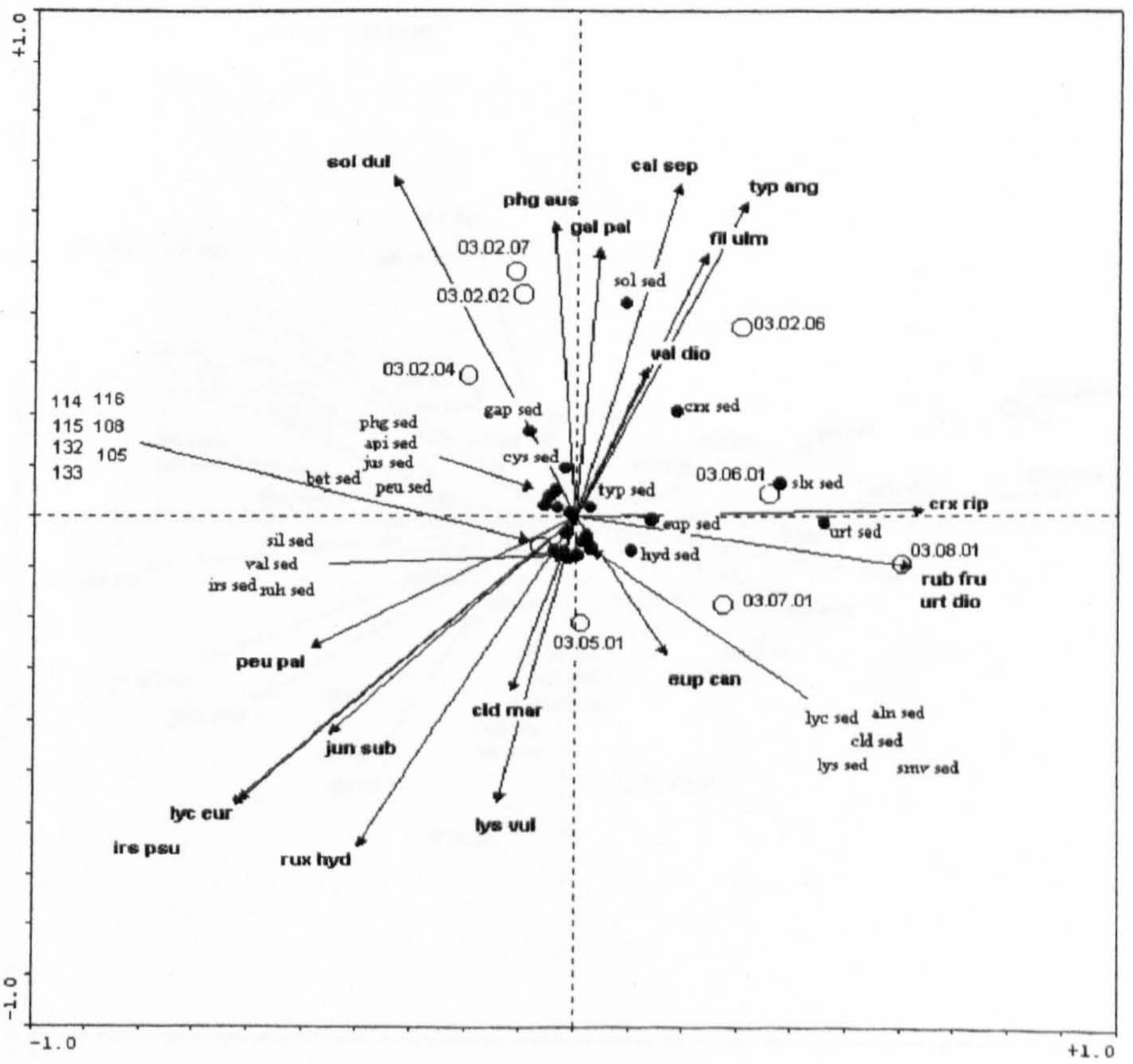


Figure 4.63a Hickling Broad correspondence analysis of non-seed data

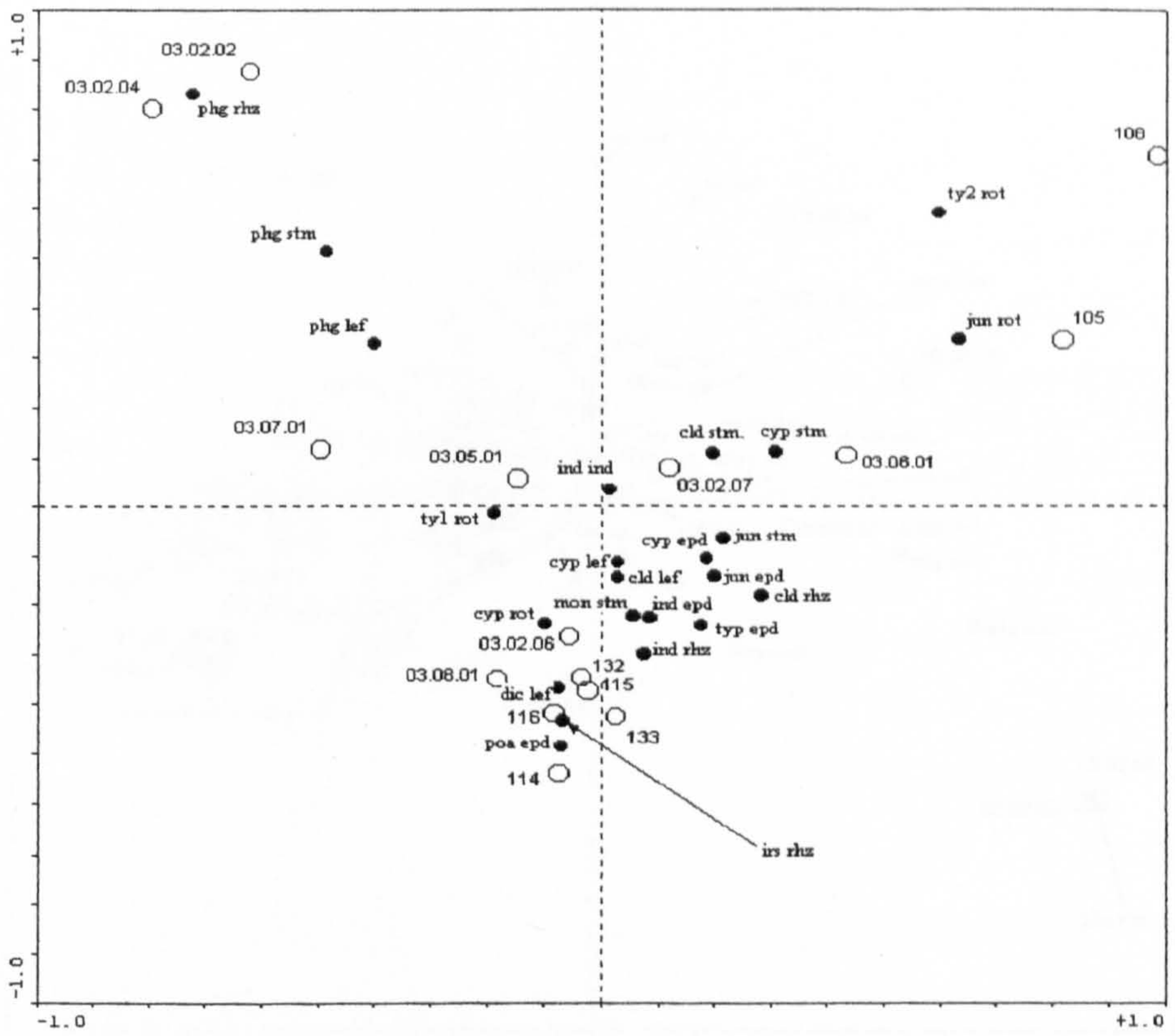


Figure 4.63b Hickling Broad canonical correspondence analysis of non-seed data

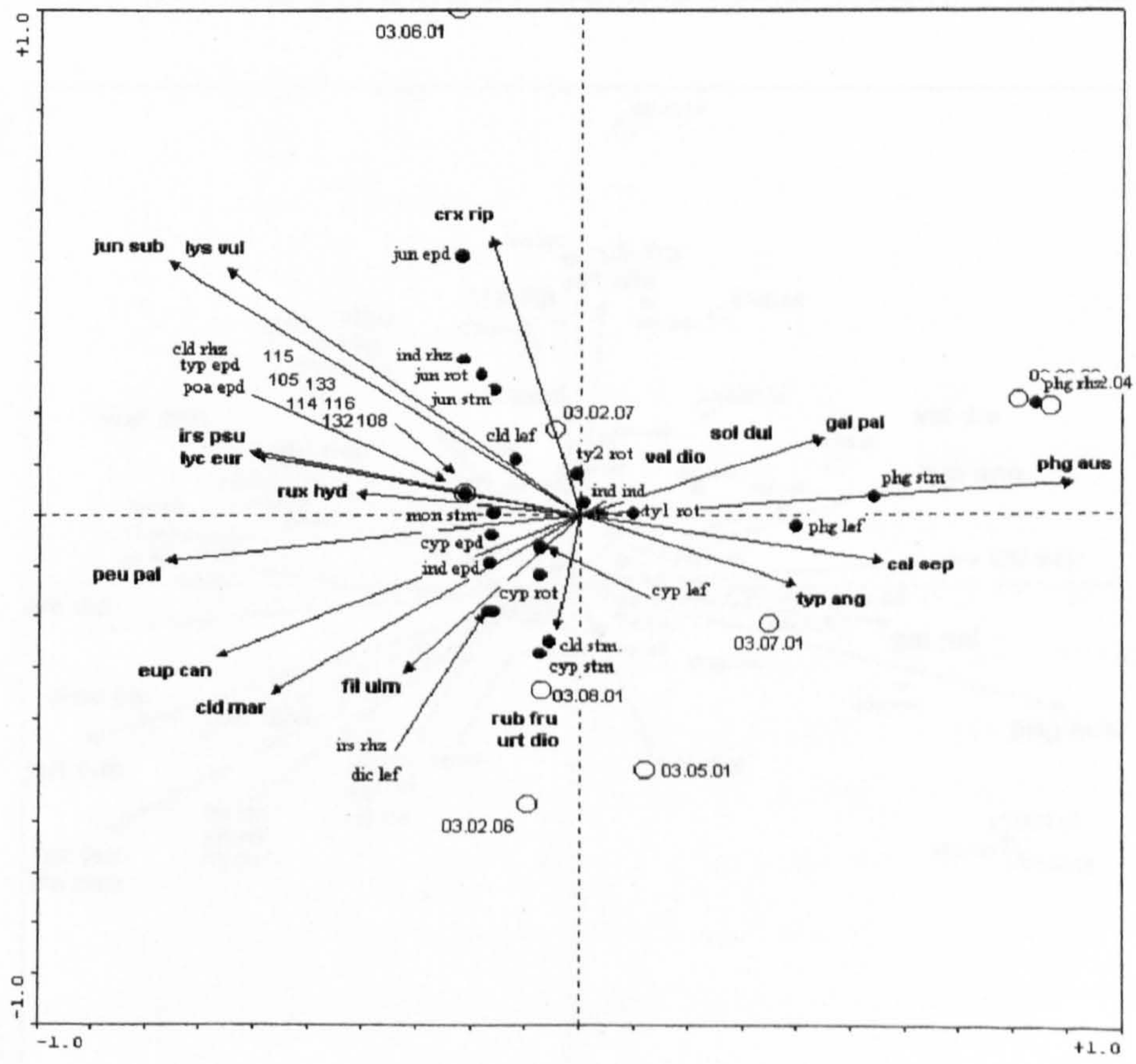


Figure 4.64a Hickling Broad correspondence analysis of seed and non-seed data

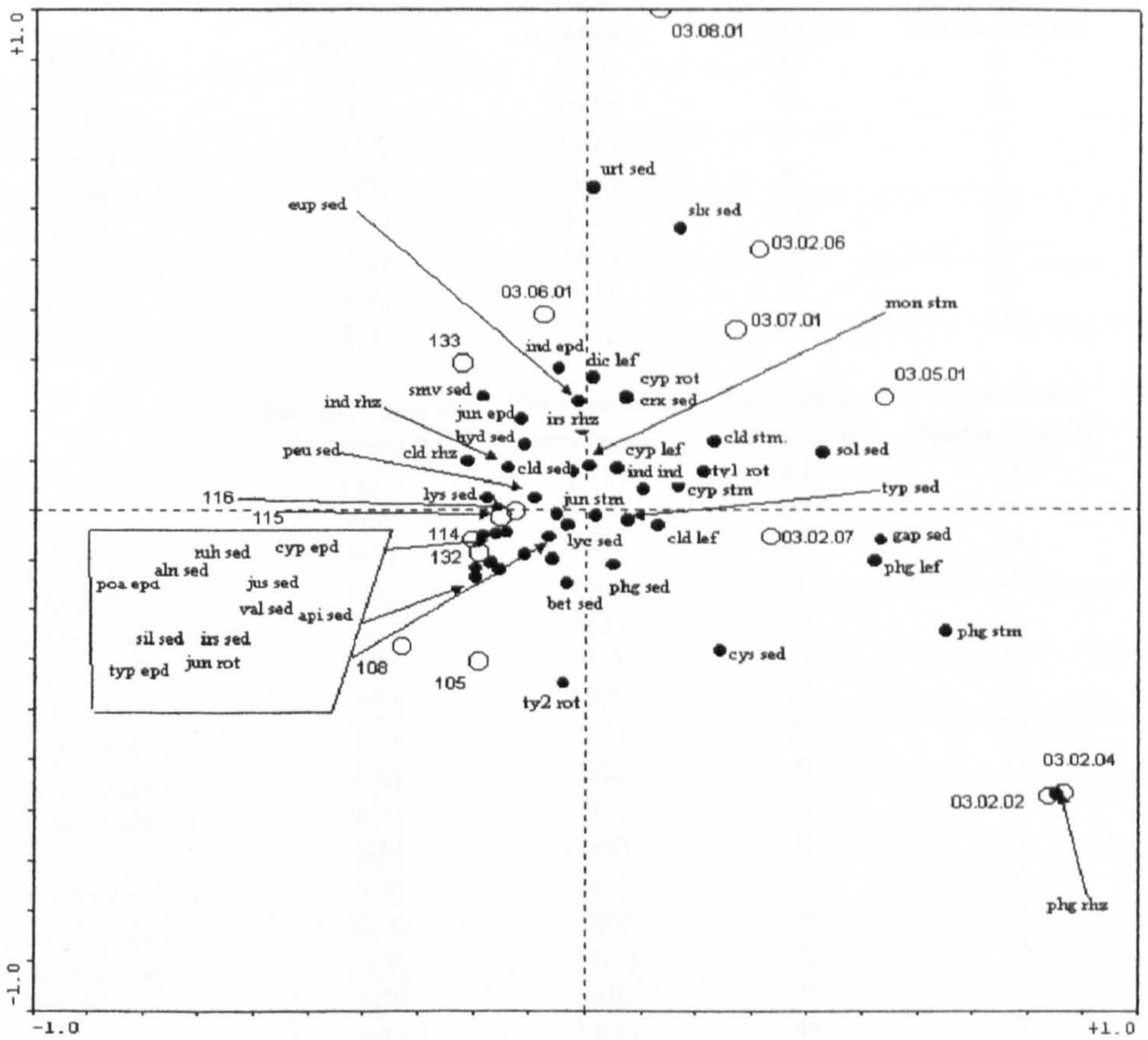
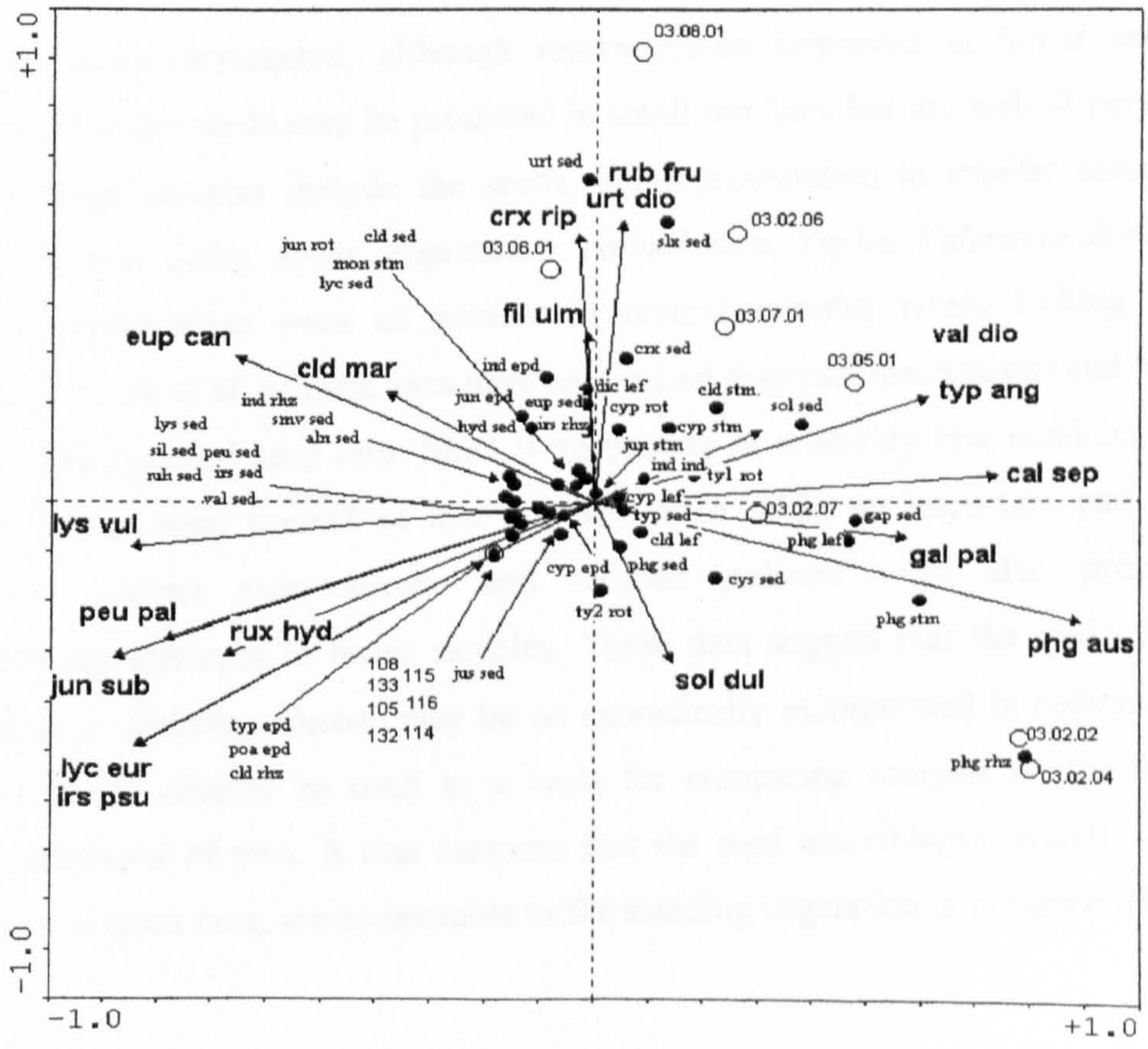


Figure 4.64b Hickling Broad canonical correspondence analysis of seed and non-seed data



Taxon	Absent when in Vegetation	Present in vegetation	% absence all samples	% absence 200cm samples
Solanum dulcamara	7(0)	10(3)	70	0
Calystegia sepium	11(5)	15(8)	73	63
Peucedanum palustre	1(0)	11(4)	9	0
Lysimachia vulgaris	1(0)	11(4)	9	0
Iris pseudacorus	5(1)	8(2)	63	50
Filipendula ulmaria	3(0)	10(2)	30	0
Galium palustre	2(2)	3(3)	67	67
Carex riparia	1(1)	1(1)	100	100

	Present when not in vegetation	Not present in vegetation	% presence all samples	% presence 200cm samples
Betula sp.	12(5)	15(8)	80	63
Salix sp.	4(4)	15(8)	27	50
Alnus glutinosa	4(1)	15(8)	27	13
Cladium mariscus	0(0)	0(0)	0	0
Eupatorium cannabinum	0(1)	3(3)	33	33
Filipendula ulmaria	0(0)	5(5)	0	0
Galium palustre	3(3)	13(6)	23	50
Juncus subnodulosus	1(1)	5(5)	20	20
Lysimachia vulgaris	0(0)	0(0)	0	0
Peucedanum palustre	4(4)	1(1)	25	25
Rubus sp.	0(0)	0(0)	0	0
Rumex hydrolapathum	3(3)	6(6)	50	50
Solanum dulcamara	0(0)	0(0)	0	0
Typha angustifolia	8(3)	11(4)	73	75
Urtica dioica	0(0)	0(0)	0	0
Valeriana dioica	6(0)	13(6)	46	0

Table 4.30 Representation of taxa in the samples from Hickling Broad

were also under-represented, although representation improved in larger samples, suggesting that the seeds may be produced in small numbers but are well dispersed. In this case large samples include the seeds, but representation in smaller samples is sporadic. *Betula*, *Salix*, *Alnus*, *Eupatorium cannabinum*, *Typha*, *Valeriana dioica* and *Rumex hydrolapathum* were all present in several samples where lacking in the vegetation. Seeds of all of these taxa have specialised dispersal mechanisms and seem to have a well-dispersed seed rain. Most were present in relatively low numbers, some, such as *Typha* were present in low numbers even when an important part of the vegetation. *Juncus subnodulosus* and *Galium palustre* were also present as allochthonous elements in fewer samples. These data suggest that the seeds of some taxa, such as *Galium palustre*, may be so sporadically incorporated in sediments that they could not reliably be used as a basis for comparing samples on the basis of presence/absence of taxa. It also suggests that the seed assemblages overall, with the exception of some taxa, are comparable to the standing vegetation in presence terms.

CCA showed that the vegetation composition could not be directly interpreted from seed abundance, although large abundance of seeds of a particular taxon (e.g. >50%) was usually indicative of substantial local presence. An exception here was *J. subnodulosus*, which was over-represented throughout. In areas 05, 07 and 08 the dominance of the seed assemblages by *Cladium mariscus*, *Rumex hydrolapathum* and *Eupatorium cannabinum* did reflect a local dominance in the vegetation of these taxa. *Phragmites* was only present in large numbers where it was dominant in the vegetation (03/02/02, 03/02/04 and 03/01/01). A local presence of taxa that contributed few seeds to the seed sum and are apparently poorly dispersed, such as *Lysimachia*, may be indicated by percentage presence of 5% to 6% in the seed assemblages.

Incorporation of the remains of bulky Monocotyledonous taxa was favoured in the non-seed assemblages with taxa such as *Cladium mariscus*, *Phragmites australis* and *Juncus* well represented. In most sampled areas these taxa were important, but not necessarily dominant taxa in the standing vegetation. Dicotyledon taxa were poorly represented, usually only discernible by the presence of occasional leaf fragments. These were only incorporated where large quantities of litter were being produced by a locally dominant Dicotyledon taxon (samples 03/06/01, 03/07/01 and 03/08/01). Many of the rootlets of these taxa would be in the indeterminate or Type 1 root group and so indistinguishable from those of Poaceae taxa. The bias towards the Monocotyledons reflects the growth habit of the taxa present in the sampled areas that tend to produce large quantities of adventitious rootlets on extensive rhizome or stolon systems. They also produce large quantities of leaf litter and stems that often have long subterranean sections more prone to preservation.

Climbers *Calystegia sepium* and *Galium palustre* were present in all of the sampled vegetation stands, but present only in 6 out of the 15 samples. *Calystegia* was especially under-represented, a pattern seen also at Burham marsh.

The assemblages of Monoctyledon remains only accurately reflected the abundance of taxa in the surface vegetation when it was dominated by a single taxon. Samples 02/02 and 02/04 were from areas rich in *Phragmites* and included large quantities of stem and leaf material. *Typha angustifolia* was badly preserved, although *Juncus* vegetative remains were more indicative of a local presence than the well dispersed seeds. *Cladium* was preserved well even when forming a minor vegetation component, and there was little difference in the total quantity of incorporated *Cladium*

remains between 03/05/01 and some of the smaller samples from the blocks. *Iris* was only represented by a rhizome fragment in one of the samples in which it was preserved.

Rubus fruticosus was the only shrubby plant present in the sampled vegetation at site 03/08/01. Both the spines and seeds of the plant were found in that sample alone and represented 8% (= DOMIN cover abundance 4) of the seed assemblage, less than the cover abundance of the taxon in the standing vegetation (DOMIN cover abundance 5). Tree seeds were over-represented in all of the samples, being present in all of the samples, even though tree species were absent from the sampled standing vegetation. In 03/02/02 they represented 22% of the seed assemblage. These data must question the suitability of tree seed assemblages to provide accurate information about local tree cover, although the presence of the seeds does accurately reflect the presence of trees nearby which were mainly *Betula*, *Salix* and *Almus*, the latter at some distance from the site.

4.9 Wet woodlands at Bure Marshes and Wicken Fen

Two wet woodland sites, Bure Marshes and Wicken Fen, were sampled during fieldwork. Both sites were heavily influenced by human activity; however, they provided some of the best and most accessible wet-woodlands prospected during preliminary fieldwork. Both sites contained managed woodland 'panels' in which varying management regimes were enacted and the water levels were managed using ditches, canals and sluices. Sampled wet woodland sites have been treated together in this section because each panel is in effect a separate environment.

4.9.1 Location and topography

Bure Marsh (grid reference: TG 335170) lies between the villages of Woodbastwick and Horning on the River Bure, Norfolk (Figure 4.65). It contains a mosaic of managed fen habitats including alder and birch carr, willow swamp, reedbeds, mowed *Cladium* marsh and grazing marsh. The site is isolated today from the waters of the Bure by flood defences and is dissected by narrow access canals. Groundwater flooding provides the main hydrological influence on sedimentation and ecology and much of the site is permanently wet with standing water in the winter. Wicken Fen (grid reference: TL533705) is a managed fen remnant 14km northeast of Cambridge (Figure 4.66). A mixture of carr, reedbeds, sedge and litter fields is actively maintained in one of the oldest nature reserves in Britain.

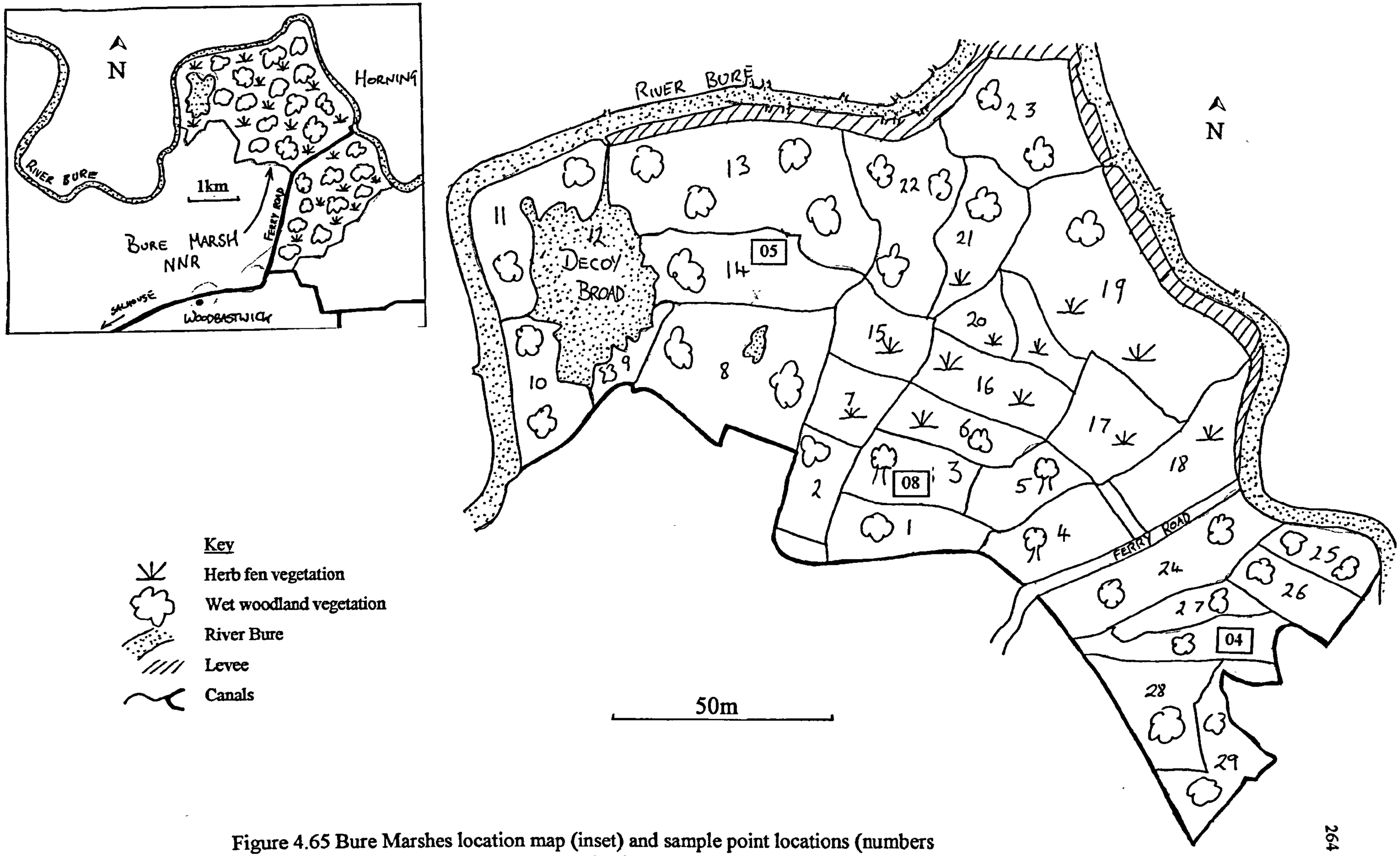


Figure 4.65 Bure Marshes location map (inset) and sample point locations (numbers in boxes). NB the numbers in the map outside boxes are the management panel numbers.

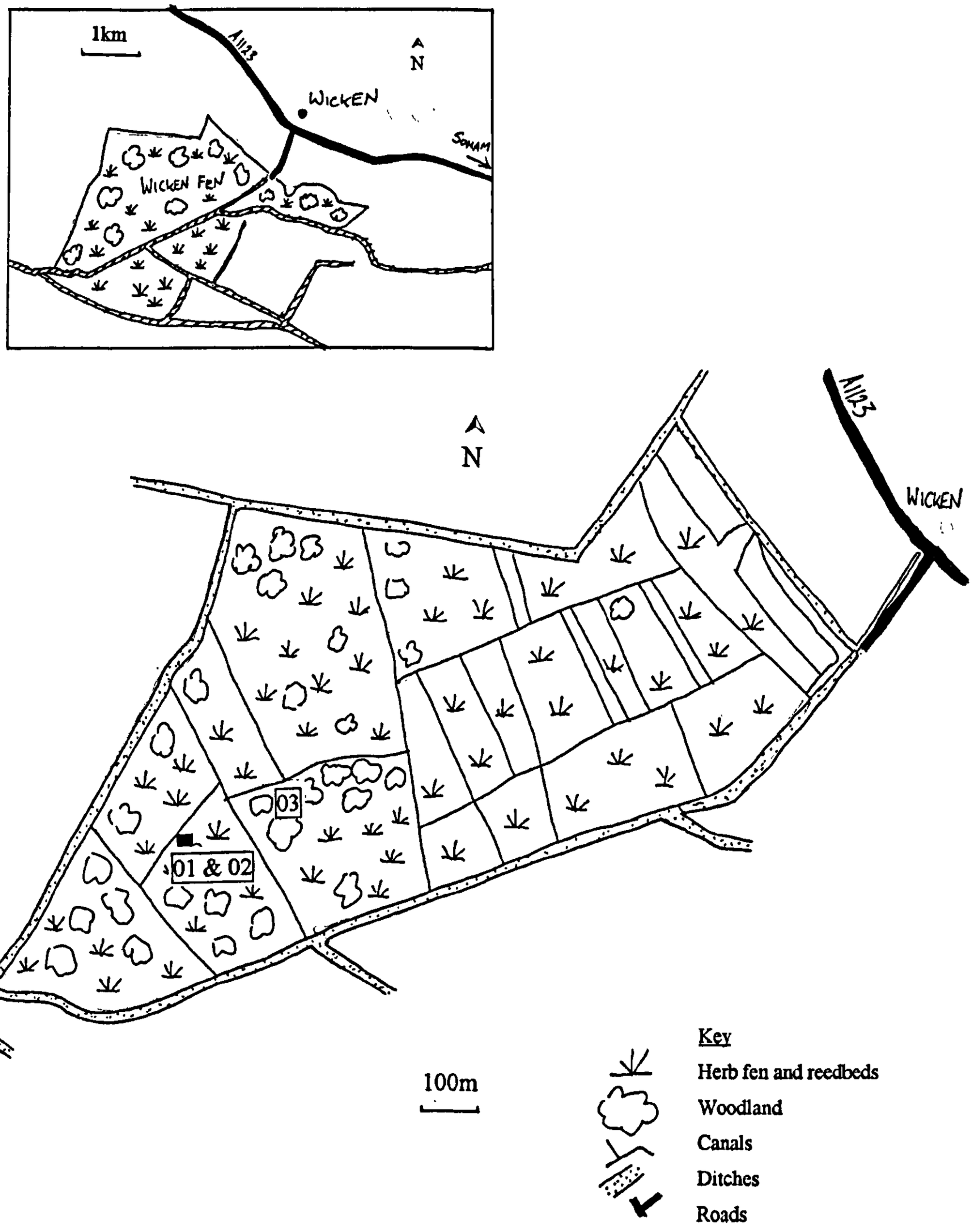


Figure 4.66 Wicken Fen location map (inset) and sample points (numbers in boxes)

4.9.2 Vegetation and surface litter

At Bure Marshes the wooded vegetation is mainly coppiced W5 *Alnus glutinosa-Carex paniculata* woodland (Table 4.31). Much of the sampled vegetation was in the W5 *Lysimachia vulgaris* sub-community, although extensive patches of W5 *Phragmites australis* sub-community were also recorded. In all sampled areas *Alnus glutinosa* formed an important element of the canopy and dominated at sites 04 and 05. Area 05 contained uncoppiced alder scrub. *Salix cinerea* and *Betula pubescens* also achieved local dominance in some stands and dominated sample site 08. In drier areas occasional specimens of *Fraxinus excelsior*, *Sambucus nigra* and *Crataegus monogyna* were recorded. The ground flora was typically dominated by sedges, including *Carex paniculata*, *Carex appropinquinta* and, locally, *Carex riparia*. Ferns, especially *Dryopteris diliatata* and *Athyrium felix-femina* were abundant on the raised, dry tree stumps and *Thelypteris palustris* dominated the ground storey of some panels. *Osmunda regalis*, *Phragmites australis* and *Iris pseudacorus* also attained extensive local ground cover. Climbers such as *Lonicera periclymenum* and *Humulus lupulus* were not uncommon. Mosses were abundant, especially *Eurynchium praelongum*.

At Wicken fen the sampled wooded areas were mainly in the W2 *Salix cinerea-Betula pubescens-Phragmites australis* community. Areas 01 and 02 were situated in a closed canopy woodland dominated by *Betula pubescens* with an understorey of *Frangula almus* and sparse *Salix cinerea*, *Rosa* and *Crataegus monogyna*. The groundstorey under the woodland (01) had a sparse flora of *Molinia caerulea*, *Phragmites australis* and *Eupatorium cannabinum*. Area 02 was a glade within the *Betula-Frangula* woodland dominated by *Molinia caerulea* and *Phragmites australis*. The ground flora in areas 01 and 02 contained some *Sphagna* and had similarities to W2b *Sphagnum* sub-community. The canopy in area 03 was dominated by *Salix cinerea* in which there was moderate abundance of *Frangula almus* and a ground flora dominated by *Thelypteris palustris* and *Urtica dioica*.

The litter layer at Bure was sparse and consisted mainly of tree leaves and twigs, both usually partially decayed. Much loose litter was apparently incorporated directly into the peat surface. Where *Carex paniculata* and other monocotyledonous plants were dominant, sparse mats of fallen stem and leaf remains were present. Peat quality varied between the permanently wet patches of ground in between the trees and that formed on the dry tree bases. The latter was densely packed and contained more dried leaf remains while the former was soft with visible leaf fragments.

Site	Bure	Bure	Bure	Bure	Bure	Bure	Bure	Wicken	Wicken	Wicken
Site\Sample	04\block1	04\03	04\09	05\02	05\06	08\01	08\03	01\01	02\01	03\01
Sediment Description	Sh3Th1Tl+	Sh2Th2Tl+	Sh3Th1Tl+	Sh4Th+Tl+	Sh3Th1Tl+	Sh4Th+Tl+	Sh4Th+Tl+	Sh3Th1Tl+	Sh3Th1Th+	Sh3Th1Th+
Colour	10YR2/2	10YR2/1	10YR2/2	10YR2/1	10YR2/1	10YR2/1	10YR2/1	10YR 3/2	10YR 2/1	10YR 2/1
% water	88.54%	79.54%	83.78%	81.62%	80.11%	82.58%	83.67%	59.44	63.41	65.17
%organic	88.70%	90.41%	89.20%	88 37%	88.95%	88.37%	88.49%	78.1	80.27	84.07
Cover Abundance										
Canopy *Alnus glutinosa*	9	9	9	9	9	6	6			
Canopy *Betula pubescens*						6	6	8	8	
Canopy *Frangula alnus*										5
Canopy *Fraxinus excelsior*	2	2	2							
Canopy *Salix cinerea*	4	4	4			8	8			9
Understorey *Acer pseudoplatanus*						1	1			
Understory *Alnus glutinosa*	1	1	1	4	4	1	1			
Understorey *Betula pubescens*	1	1	1			1	1	7	4	
Understorey *Frangula alnus*								6	6	
Understorey *Fraxinus excelsior*				4	4	1	1			
Understorey *Crataegus monogyna*				1	1			1		
Understorey *Rosa* sp.								1		
Understory *Salix cinerea*				4	4			4	4	
Calystegia sepium								1		
Carex appropinquinta	1									
Carex paniculata	7	8	6	8	8					
Carex pendula						4	4			
Carex remota		5				5	5			
Dryopteris dilitata		3								
Eupatorium cannabinum								3	1	1
Filipendula ulmaria	1			1	1					
Galium palustre agg.		2				2	2		2	
Iris pseudacorus	2	4	7	4	4					2
Lycopus europaeus	1									
Molinia caerulea								2	8	
Phragmites australis		1	3					1	6	3
Phalaris arundinacea										1
Ribes nigrum		2		6	6	5	5			
Rubus fruticosus agg.								5	3	
Solanum dulcamara	2	2	2	2	2	2	2			1
Thelypteris palustris				4	4	7	7			5
Urtica dioica	2	2		2	2			1	4	5
Bryophyta						5	5	5	5	6
Open ground	5	4								
Distance to nearest plant										
Alnus glutinosa	<0.5m		<0.5m	<0.5m	<0.5m	<0.5m	<0.5m		>50m	
Betula sp.	2-5m	2-5m	2-5m	>50m	>50m	<0.5m	<0.5m	<0.5m	2-5m	10-50m
Salix sp.	2-5m	2-5m	<0.5m	2-5m	2-5m	<0.5m	<0.5m	2-5m	2-5m	<0.5m
Frangula alnus										<0.5m
Fraxinus excelsior		5-10m		5-10m	2-5m					
Angelica sylvestris	>50m								>50m	
Apera sp.						>50m				
Apium sp.				>50m						
Callitriche stagnalis	>50m									
Carex cf. *diandra*	10-50m		>50m							
Carex remota	0 5-2m		0 5-2m			<0.5m	0.5-2m			
Carex paniculata	<0.5m	0.5-2m	<0 5m	<0.5m	<0.5m					
Carex cf. *pendula*						2-5m	2-5m			
Characeae								>50m	>50m	
Cirsium palustris	10-50m					10-50m				
Dryopteris dilitata	0.5-2m	0.5-2m								
Epilobium sp.	>50m							>50m		10-50m
Eupatorium cannabinum	>50m			2-5m				2-5m		2-10m
Filicales	<0.5m	0.5-2m	0.5-2m	2-5m	<0.5m	<0.5m				<0.5m
Filipendula ulmaria				0.5-2m	5-10m	>50m				
Galium palustre	0.5-2m								0.5-2m	
Iris pseudacorus			<0.5m	2-5m	<0 5m					
Juncus effusus type	10-50m	>50m		10-50m	10-50m		>50m			
Lemna sp.	10-50m									
Lycopus europaeus	0 5-2m		5-10m							
Mentha sp.			5-10m		5-10m	>50m	>50m			
Molinia caerulea									<0.5m	
Phragmites australis	5-10m								<0.5m	0.5-2m
Rubus fruticosus agg.	>50m									
Sambucus nigra								10-50m		
Solanum dulcamara	0.5-2m			<0.5m						0.5-2m
Stellaria palustre			2-5m							
Thelypteris palustris										<0.5m
Urtica dioica			0.5-2m	<0.5m	2-5m	10-50m		2-5m		0.5-2m
Bryophyta	<0.5m	<0.5m	<0.5m	<0.5m	<0.5m	<0.5m	<0.5m	<0.5m	<0 5m	<0 5m

Table 4.31 Wet woodland standing vegetation, sediment and distance data

Litter was more conspicuous on the drier surface at Wicken Fen and generally reflected the local vegetation. At site 01 the litter was dominated by *Betula* leaves, branch and twig debris. Grass culms and mosses were sparsely distributed. At 02 peat between the *Molinia* tussocks was covered by a thick layer of grass stem and leaf detritus. *Betula* and *Salix* leaves were sparsely present throughout the litter layer. Mosses grew over the litter layer and did not appear to become incorporated within it. At site 03 the litter layer was again thick and consisted mainly of *Salix* leaves mixed with twig and branch wood, occasional grass culms and *Thelypteris* pinnae.

4.9.3 Sampling

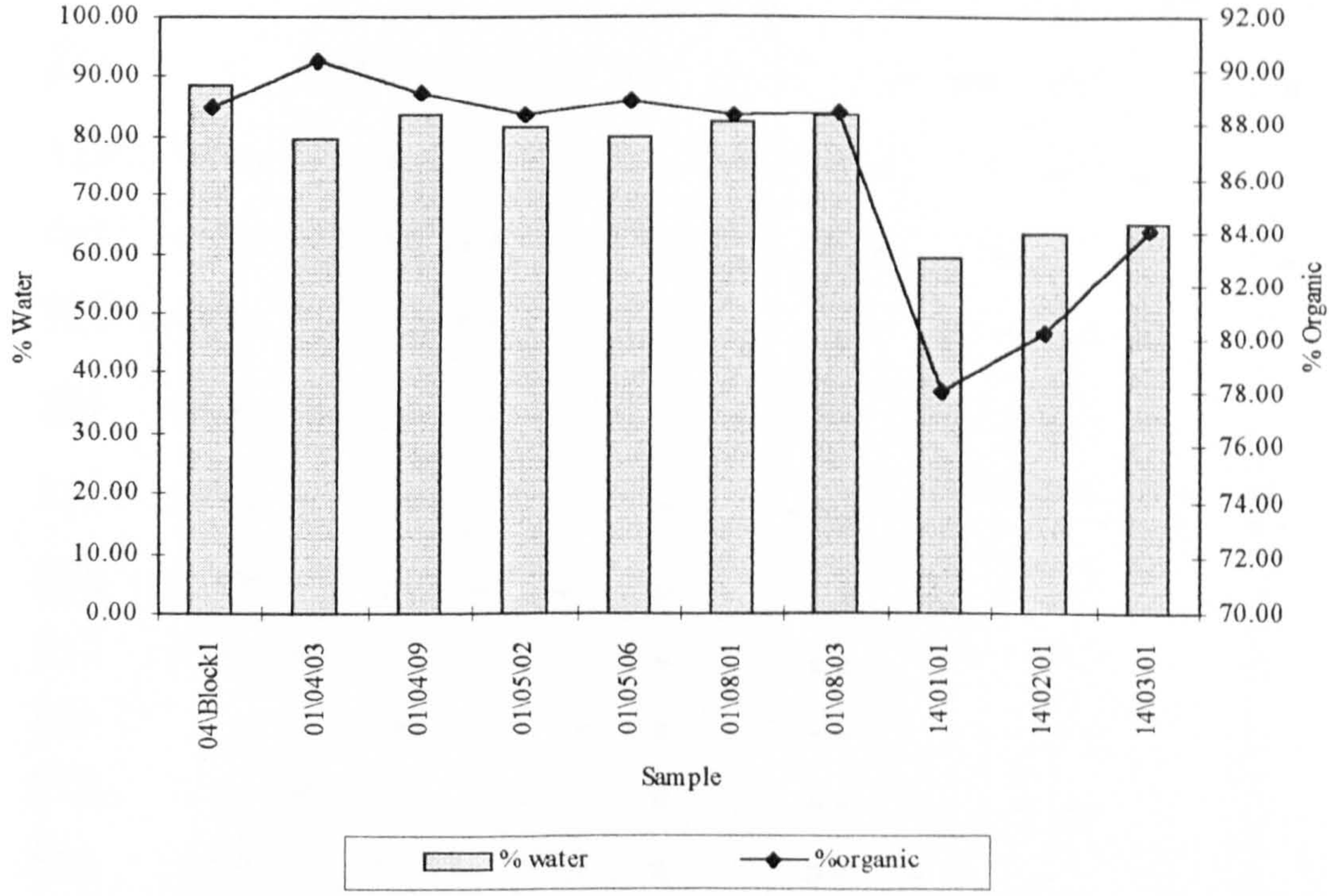
One block and two 200cm^3 samples were analysed from sample area 04, a stand of closed canopy coppiced W5 *Alnus-C. paniculata* woodland *Lysimachia vulgaris* sub-community with an extensive ground storey of *Carex paniculata.* The block was collected from the fen surface in the most extensive type of groundstorey vegetation. Sample 04/03 was from the raised peat on a tree base and sample 04/09 was from an area dominated by *Iris pseudacorus.* Two 200cm^3 samples were analysed from area 05, an area of unmanaged alder carr, with a young canopy and similar ground flora to that of 04. Two samples were also analysed from area 08, dominated by *Betula pubescens* and *Salix cinerea,* with smaller quantities of *Alnus* and having a ground flora rich in *Thelypteris palustris* and sparse *Phragmites australis.* Three 200cm^3 samples were analysed from Wicken Fen, one from each of the sample sites.

4.9.4 Sediments

The sediment in all sampled areas was a humified, dark peat of varying quality. At Bure marshes the peat in all of the sites was soft, permeated by rootlets and penetrated by twigs and branches. Troels-Smith descriptions were dominated by *Substantia humosa* (Sh) with only small quantities of recognisable plant tissue (Table 4.30). The sediments at the site typically contained up to 88% water, the lowest figures from dry peat on a tree bole (Figure 4.67). Percentage organic content was also very high at between 87% and 90%. Peat at Wicken Fen was typically much drier than that in Bure. In area 01 the peat was dry, humified and had little visible structure. Peat from area 02 was a well preserved fibrous peat in which plant fibres, especially stem, leaf and root remains were visible. Area 03 contained a woody peat, with obvious wood fragments and twigs. All of the peat samples had a water content of 59% - 65% and an organic content of 78% -

82%. This was lower than Bure marshes and may indicate a greater degree of decay at the site, reflecting perhaps the effects of de-watering that has only recently been slowed down.

Figure 4.67 Bure Marsh and Wicken Fen Organic and water data



4.9.5 Sources, incorporation and preservation of macrofossils

Plant macrofossils were preserved in abundance in all of the samples (Table 4.32 a and b), although degraded plant matter (UOM or *Substantia humosa* in the Troels-Smith descriptions) was common in all of the samples. Much of this substance was unidentifiable, but in samples from Bure Marshes it was found to be composed of degraded wood fibres. The macrofossil assemblages were diverse and incorporated a wide variety of seeds, buds, vegetative material and woody structures. Most of the material was autochthonous with only a few seeds and fruits deriving from non-recorded taxa.

Seed concentrations varied in the 200cm^3 samples between 1.3 and 4.88 seeds per unit of sediment (Figure 4.68b), with the concentrations of all countable macrofossils (including bracts and bud-scales) being between 1.39 and 7.87. Seed abundance and concentration figures for Wicken Fen samples were higher than those for

	Site	Bure	Bure	Bure	Bure	Bure	Bure	Bure	Bure	Bure	Bure	Bure	Bure	Bure	Bure	Bure	Wicken	Wicken	Wicken
	Sample	101	102	103	104	120	121	122	124	126	04\03	04\09	05\02	05\06	08\01	08\03	01\01	02\01	03\01
	Sample Size	50	50	50	50	25	25	12.5	25	12.5	200	200	200	200	200	200	200	200	200
Taxon	Component																		
1. Seeds, fruits etc.																			
Alnus glutinosa	Bracteole			9	6	2				4	16	11	87	62	4	14			
Alnus glutinosa	Cone		2	3	1		1			1	2	8	73	9	5	3		3	
Alnus glutinosa	Seeds	9	33	32	14	13	2	3		4	157	97	200	204	24	46			
Alnus glutinosa	Bud-scale	1	3	6	4	6	2	1	1	3	12	27	7	8	8	8		9	
Alnus glutinosa	Buds				1						1								
Betula sp.	Seed	1	25	6	4	8		4		2	3	13	53	38	87	89	736	724	392
Betula sp.	Bract			1		2	1						6	9	26	19	492	356	
Betula sp.	Cone Bract																237	31	
Betula sp.	Bud-scale						2			2					19	21	222	184	
Salix sp.	Seed	13	7	7	8				4		67	53	145	104	286	247		24	231
Salix sp.	Capsule											22							
Salix sp.	Stipule		1											3	6				
Salix sp.	Budscale										2		1	2	2	7			161
Crataegus sp.	Stone																2		
Frangula alnus	Seed																		7
Fraxinus excelsior	Budscale										2								
Rubus fruticosus agg.	Fruit		2			1			3							1			
Sambucus sp.	Seed																3		
Rubus type	Spine		2	4	1	1													
Filicales	Sporangia	54	33	66	152	4	15	13	18	3	12	50			6				
Angelica sylvestris	Fruit				1													3	
Apera sp.	Fruit														6				
Apium sp.	Fruit												2						
Callitriche stagnalis	Fruit					1													
Carex cf. *diandra*	Fruit		3		2	5						4							
Carex remota	Fruit	18	54	53	2	20	23	2	4	13		39			2	5			
Carex paniculata	Fruit	11	14	24	3	7	1	6	3	10	20	8	5						
Carex cf. *pendula*	Fruit														3	7			
Characeae	Oospore																7	26	
Cirsium palustris	Fruit						1												
Epilobium sp.	Fruit		2												1		21		12
Eupatorium cannabinum	Fruit		1														39		36
Filipendula ulmaria	Fruit												1	2	1				
Galium palustre	Fruit	1						1										4	
Juncus effusus type	Seed		2	3		2	1				1		11	1		1			
Lemna sp.	Fruit		1					1											
Lycopus europaeus	Fruit		1	1		4		1				4							
Mentha sp.	Fruit											1		1	3	3			
Molinia coerulea	Fruit																	192	
Phragmites australis	Fruit	1		1														2	
Poaceae indet	Fruit			1															
Solanum dulcamara	Seed		1	2															15
Stellaria palustre	Seed											3							
Urtica dioica	Seed											1			1		36		23
Indet.	Seed					1													

Table 4.32a Wet Woodland sample seed macrofossil data

		Site	Bure	Bure	Bure	Bure	Bure	Bure	Bure	Bure	Bure	Bure	Bure	Bure	Bure	Bure	Bure	Wicken	Wicken	Wicken
		Sample	101	102	103	104	120	121	122	124	126	04\03	04\09	05\02	05\06	08\01	08\03	01\01	02\01	03\01
2. Non-seed remains		Sample Size	50	50	50	50	25	25	12.5	25	12.5	200	200	200	200	200	200	200	200	200
Alnus glutinosa	Leaf		1.47		1.93	5.87	0.67	0.2	3.2			3 61	4.07	1.56	5.3					
Betula sp.	Leaf															7 87		2.74	4.21	
Betula sp.	Budscale																	4.32	2.56	
Fraxinus excelsior	Leaf										0.27				0.12					
Salix sp.	Leaf			1.4	1.33	2.55	0 8	0 47			1.2						0.3			20.23
Salix sp.	Twigs																			4.63
Salix sp.	Budscale																			3.75
Dryopteris dilatata	Pinnule			2.67	1.13							2 87								
Filicales	Rootlet											18.1				1.7				12.51
Thelypteris palustris	Pinnule																			1.36
Cyperaceae	Leaf		3 2	4.87	7.6	8.73	1.27	3 47	12 5	0.27	1.73	0 73	8.2	8 11	2.44	0.2				
Cyperaceae	Rootlet		14 1	10.7	7.47	5.93	9	6.8	7.4	17.1	9.47		5.3	1.52	2.12	5.1				
Cyperaceae	Rhizome		8.13		2.4	1			5.67	6.4	1.67				9.4					
Cyperaceae	Epidermis			1.67																
Cyperaceae	Stem											1.67								
Iris pseudacorus	Rhizome												22.7							
Phragmites australis	Stem																		11	9.35
Poaceae	Stem																		18 85	
Poaceae	Rhizome																		10.12	
Type I	Rootlet																	10.81	13.6	10 1
Dicotyledonae	Leaf				1.14	2.12						1.52		4 33		7.13		10.57		
Indet.	Wood		5.67	19.8	20.3	7.27	3.67	6 4	2.8	5.73	2.6	2.27	4 87	18 6	23.2	23.6	17.7	18.39		7.81
Indet.	Twig		6.33	8.2	11.5	5.33	6	16.1	9 67	4.2	6.2	10.1	9 87	8.3		25.1	7	12.11	5.37	10.18
Indet.	Bark		5.4	8.73	1 67	12 9	2.33	4 87	3 67	18.6	3	2	3.8		3.62	1.27	7.67			
Indet.	Wood root		8.33	3.27	1.67	2.07	1.53	3 47	0.27	2.2	2.8	4.27	0.4			0.53	23.2			
Indet.	Epidermis		1.47	11.7	0.53	0.47			0.2										17.15	
Indet.	Rootlet		11		3.2	4.2	5.13	1 67	10.7	12.9	6.33	13.3	6.33	8.11	16 6		9.93	4.98		4.23
Indet.	Moss			1.53								0.67					1.13	0.76		
Indet.	Indet.		32.5	25.4	37.8	21.1	67.7	54 8	43.3	28 8	62.9	31.2	34.2	38.9	32.6	25 6	27.5	32.13	14.92	13 83
3. Derived indices																				
Seeds and other abundance			108	181	209	193	69	45	31	32	37	278	314	583	430	455	435	1573	1365	716
Seeds only abundance			108	179	196	186	65	43	31	32	32	260	273	417	350	420	399	844	975	716
Species abundance			8	14	11	8	10	7	8	6	5	6	11	7	6	11	8	7	8	7
Seeds+other concentration			2.16	3.62	4.18	3 86	2.76	1.8	2 48	1.28	2.96	1.39	1.57	2.915	2.15	2.275	2.175	7.865	6 825	3.58
Seeds only concentration			2.16	3.58	3 92	3.72	2.6	1.72	2 48	1.28	2.56	1.3	1.365	2.085	1.75	2.1	1.995	4.22	4.875	3.58
Species concentration			0.16	0.28	0.22	0.16	0 4	0.28	0 64	0.24	0.4	0.03	0 055	0.035	0.03	0.055	0.04	0.035	0.04	0.035

Table 4.32b Wet Woodland sample non-seed macrofossil data and derived indices

Figure 4.68a Seed, seed and bract and species abundance

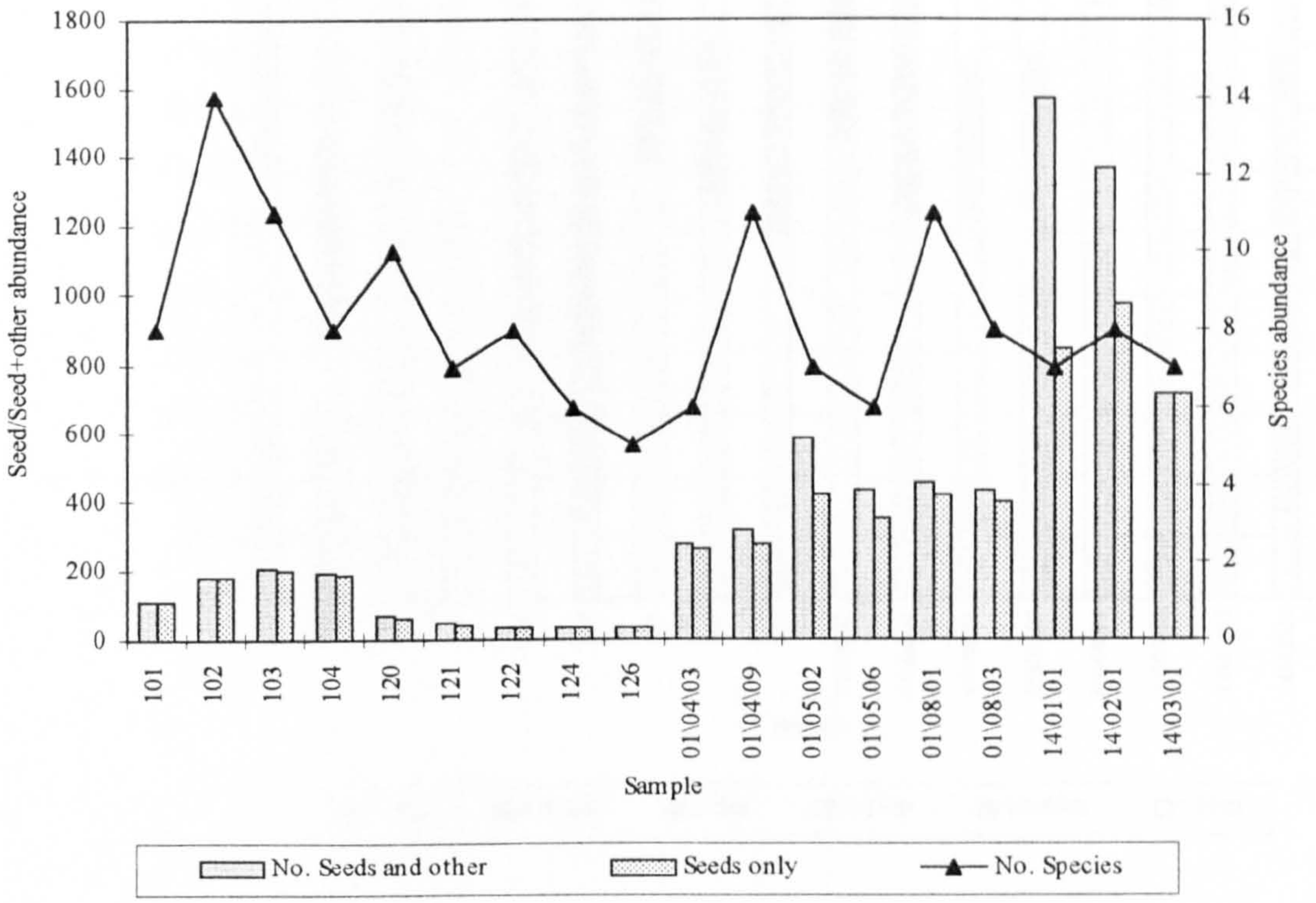


Figure 4.68b Bure and Wicken Marshes Seed, seed and bract and species concentration

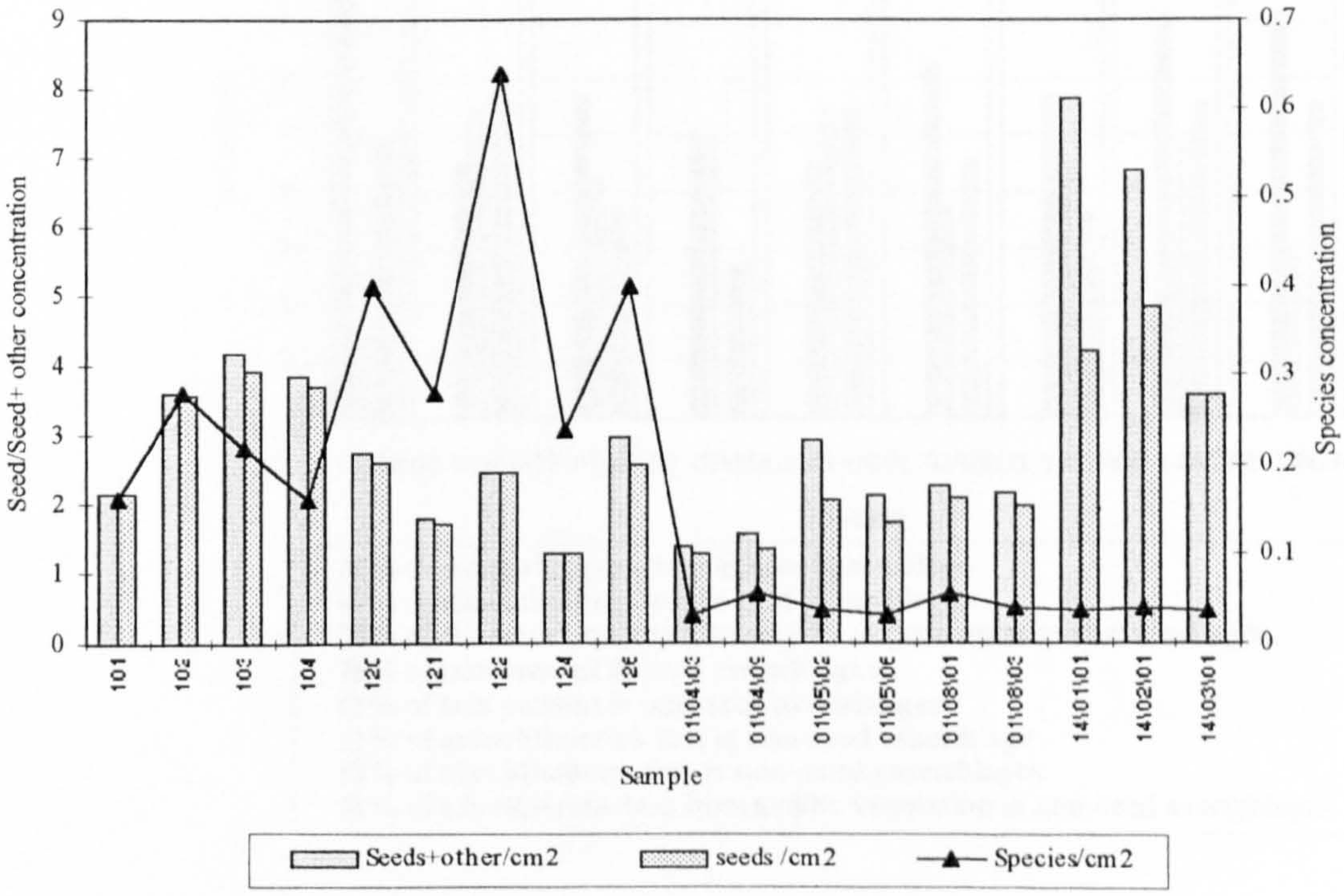


Figure 4.69 Bure/Wicken seeds from set distances

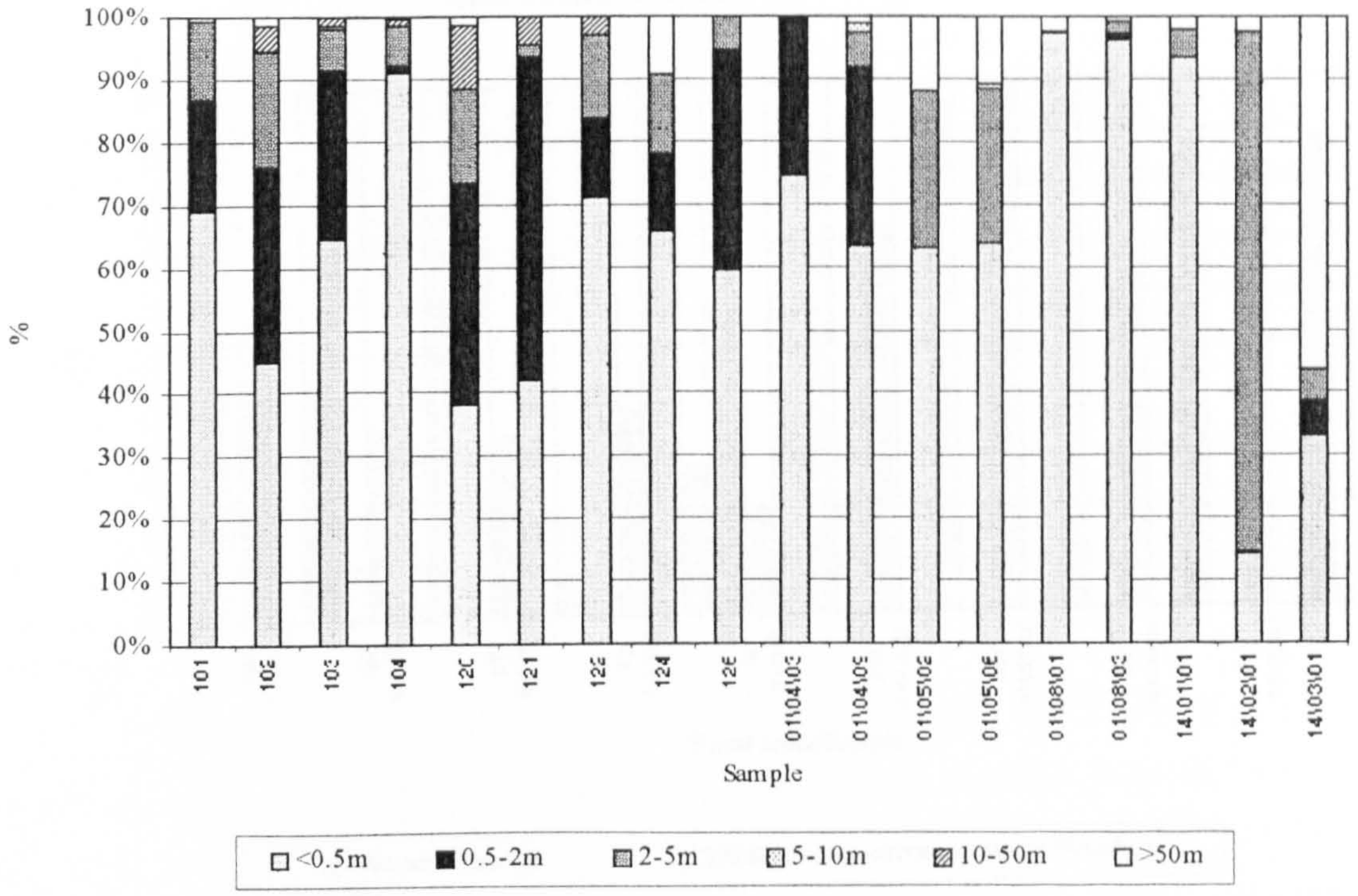


Figure 4.71 Wet Woodland Sample Ubiquity Data

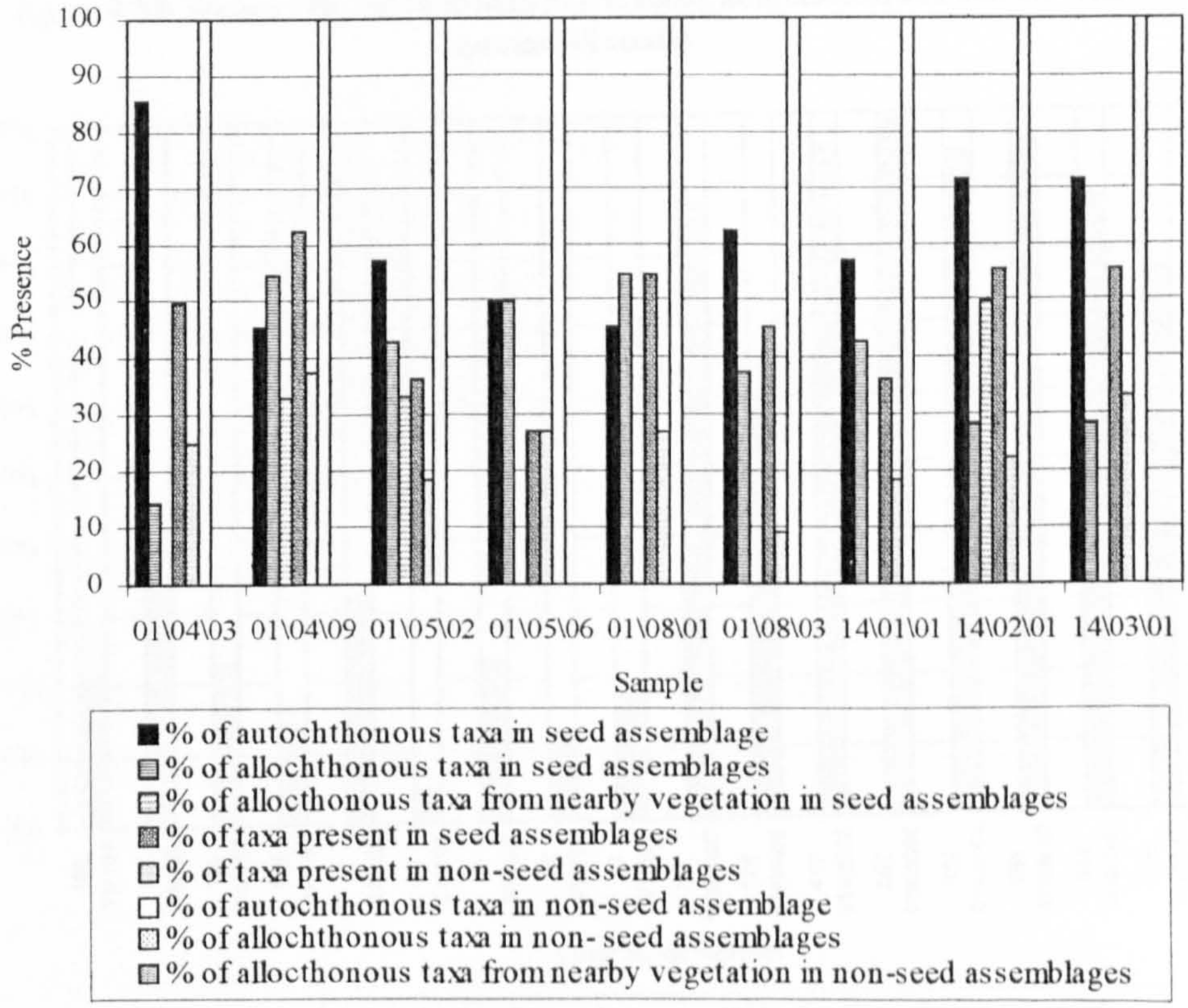


Figure 4.70a WIcken Fen and Bure Marshes: % Arboreal and Non-Arboreal taxa (minus Filicales) in seed assemblages

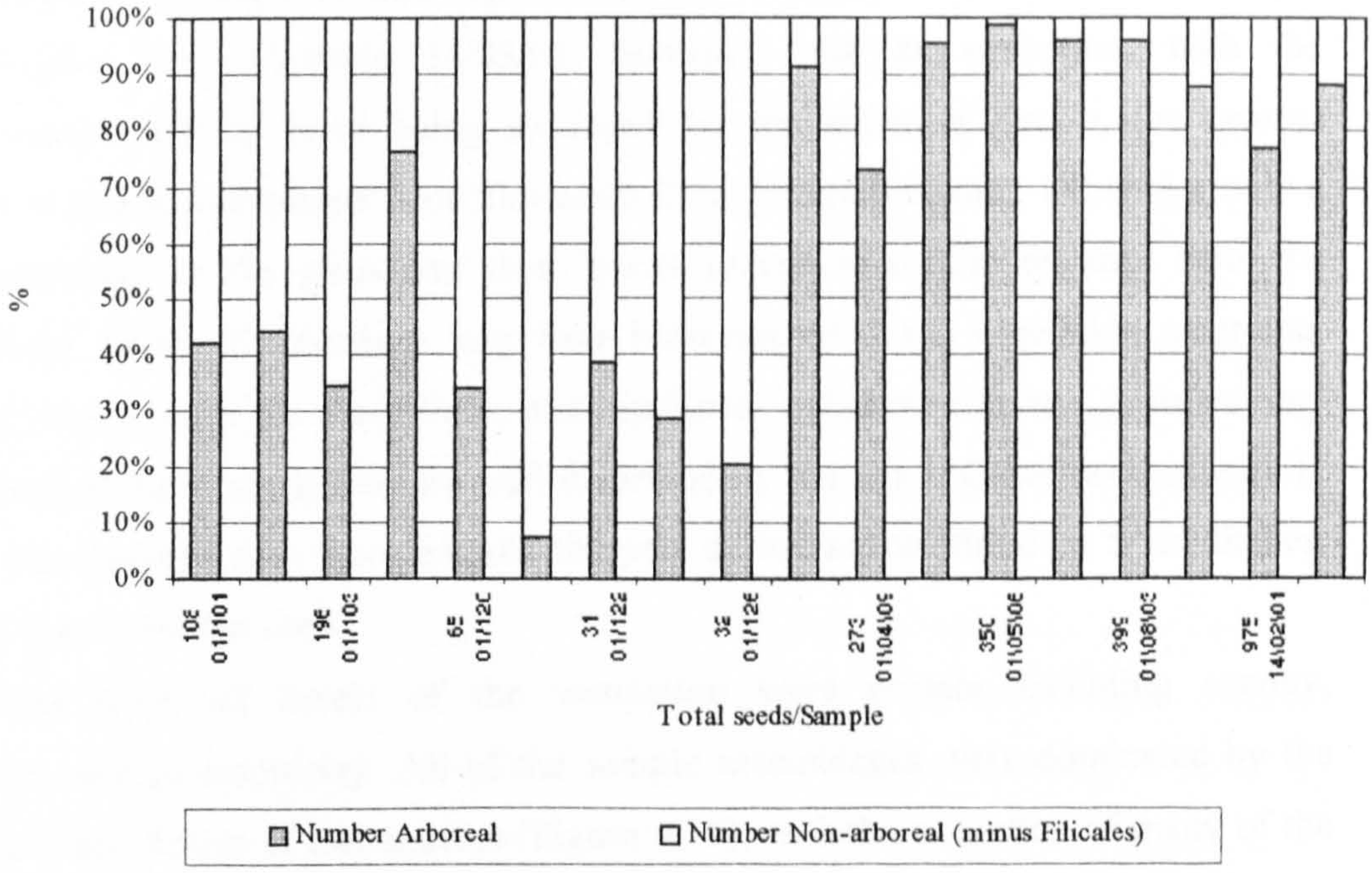
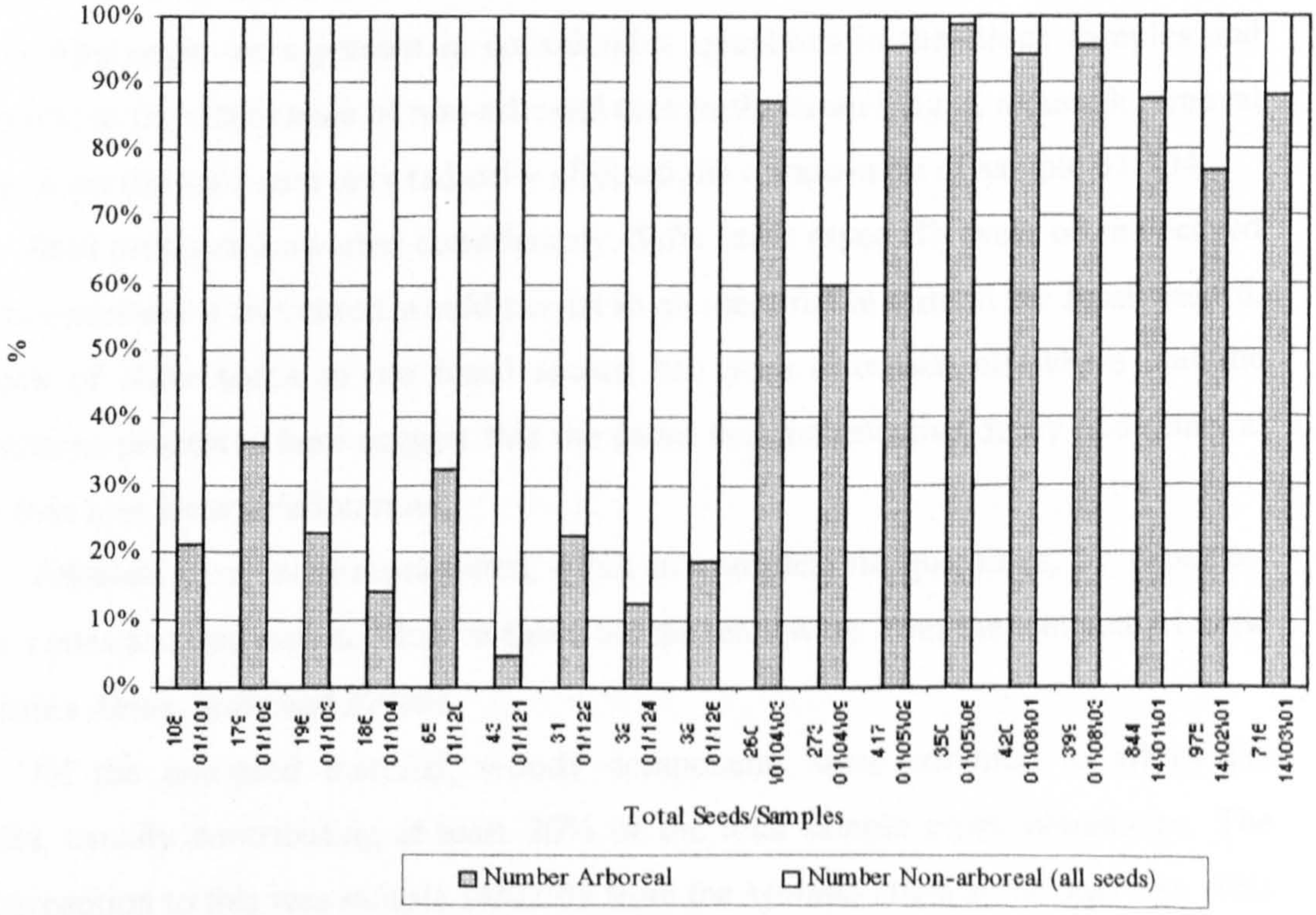


Figure 4.70b Wicken Fen and Bure Marshes % seeds from arboreal and non-arboreal species (all seeds)



Bure, perhaps reflecting the concentration effect of higher rates of decay in the sediments. Species indices were similar.

Seeds and fruits in the assemblages were largely autochthonous, with 80% to 90% of seeds in the samples deriving from plants recorded within 5m of the sample points (Figure 4.69). Sample 14/03/01, however, was an exception, with the autochthonous seeds of *Salix* being swamped by the seeds of *Betula*, the nearest specimen of which was greater than 50m away from the sample point. Otherwise only a minor percentage of the seeds was from plants greater than 50m distance from the sample point. Some of these taxa may have been missed in the vegetation recording, especially those such as *Callitriche* and *Stellaria palustre. Cirsium palustre* and *Epilobium* both have seeds that are well dispersed by the wind. Other taxa, especially those of the aquatics, may have entered the peat during annual flooding from ditches, canals and pools on the sites.

Taxa from all levels of the vegetation were present including canopy, understorey and groundstorey. All of the sample assemblages were dominated by the seeds, fruits and bracts of tree species (Figure 4.70), with the exception of many of the Block samples. This discrepancy may reflect local concentration effects. Of the arboreal taxa, canopy species dominated the assemblages, with the understorey taxa only occasionally contributing to the assemblages. Filicophyta were represented by sporangia that were unevenly distributed and prone to form local concentrations (e.g. sample 01/104). Sporangia were present in considerable quantities in the Block samples and contributed to the dominance of non-arboreal taxa in the assemblages, although removal of them from the seed sum only radically affected the composition of sample 01/104.

Seed preservation varied considerably. *Salix* seeds especially were often decayed and it is uncertain if this taxon would persist in an identifiable state in the fossil record. The lack of *Salix* seeds in the fossil record has been discussed elsewhere and the observations presented here suggest that the cause may be selective decay and removal rather than low incorporation rates.

Arboreal taxa were represented, often in considerable quantities, by capsules, bracts, cones and bud-scales. Most of these components were from the wetland arboreal dominants *Alnus, Salix* and *Betula.*

Of the non-seed material, woody components were common in all of the samples, usually contributing at least 20% of the total sample cover abundance. The main exception to this was sample 14/02/01 from the *Molinia* stand at Wicken Fen. This

sample was dominated by non-woody components and only twigs were recorded, showing how the litter and vegetation at the sample point may exclude some materials. Wood in general was highly degraded and of a size below that required for identification. Bark and twig remains were also common. Most of the wood was from aerial structures. Branch and twig sections commonly penetrated the soft peat at Bure marshes and were found to penetrate the block sample for up to 20cm. While aerial wood is a major contributor to the peat the observations from Bure suggest that much decays rapidly at the peat surface and only the twig and branch wood that penetrated the peat surface was in good condition. These observations suggest that well preserved wood from similar sedimentary facies may not be contemporary with the peat in which it is preserved but with later peat growth, the wood surviving only because it penetrated the peat surface.

Leaves were commonly preserved in the samples, especially those of the arboreal dominants, although only in sample 14/03/01 were they major sample components. In this sample, the dense *Salix* leaf litter was well preserved, possibly because of high groundwater levels. At both sites leaf litter formed continuous and thick surface cover. Leaf remains actually incorporated into the peat were usually, but not always, highly fragmented. Individual fragments were often partially decayed and small fragments of detached veins were not uncommon. Leaf identification was successful in many cases, especially where margins were preserved.

Understorey and minor canopy taxa were absent with the exception of two fragments of *Fraxinus* leaf. The absence of *Frangula* leaves was interesting considering that it was an important floristic component at Wicken Fen. During reference specimen preparation the leaves of this taxon were found to be very fragile and rapidly disintegrate in NaOH. This contrasted sharply to most other arboreal taxa which could successfully and easily be cleared using this method without undue damage to the leaf structure. This suggests that *Frangula* leaves may be selectively decayed.

Filicophyta pinnules were occasionally preserved, although preservation was uneven and fern species were most commonly preserved as unidentifiable sporangia. Monocotyledon leaves and stems were common components, with Poaceae and Cyperaceae remains dominant, reflecting the dominance of the taxa in the groundstorey vegetation. Rhizomes were also commonly preserved and rootlets were the most common subterranean plant structures in all of the samples, especially Cyperaceae type. Large quantities of rootlets were unidentifiable, having lost the upper epidermis. In

contrast to the ubiquity of moss species in most sub-environments in the marshes, moss remains were present in few samples.

Sample ubiquity data are shown in Figure 4.71. Seed assemblages contained mainly autochthonous taxa, although several from Bure Marshes contained many allochthonous taxa. Incidentally, these were usually present in low abundance. A smaller proportion of allochthonous taxa were present in nearby vegetation in these samples and a considerable proportion of taxa were missing from the assemblages, typically 40% to 60%. The non-seed assemblages consisted entirely of autochthonous taxa and contained far fewer taxa than the seed assemblages. As with the seed assemblages the autochthonous taxa present in the non-seed assemblages were generally the most abundant in the vegetation.

4.9.6 Sample size effects

Cumulative cover abundance values for the Block samples from Bure Marshes were very stable, even at low volumes, although the figures were swamped by unidentified matter, usually accounting for approximately 50% of the cover abundance values (Figure 4.72). More variation was recorded in the samples when cumulative abundances were re-calculated without unidentifiable matter, although the percentage values and rank order were stable at and above 200cm^3. Cumulative seed, fruit and similar component macrofossil data showed a similar pattern, although the figures were more affected by unreliable local concentrations of some components, for example Filicales sporangia. The canopy and groundstorey components were separated. The canopy components showed little variation in percentage abundance and rank order from 50cm^3 upwards, the main variation being in *Alnus* bracteoles. The groundstorey components were more variable, mainly because of the variation in Filicales sporangia; however, the pattern of rank order was stable by 150cm^3.

4.9.7 Quantitative analysis

CA of the seed assemblages (Figure 4.73a) showed the main influences on the sample set were *Betula* components (positive on the first axis and negative on the second), *Salix* components (positive first axis and positive second axis), *Alnus* and *Carex* (negative first axis and clustered near the origin on the second). The samples from Bure Marshes, with the exception of those from area 08, were grouped to the negative side of the first axis. Much of the variability between the Bure Marsh samples from the Block, Areas 4

and 5 were split mainly by the quantity of different bract, bud-scale and cone components and *Salix* seeds. Samples from area 08 contained many *Betula* and *Salix* seeds, being dominated by the latter. CCA (Figure 4.73b) showed that *Alnus, Betula, Carex* and *Salix* macrofossil abundance were correlated broadly with standing vegetation abundance. *Betula* cone, budscale and bract abundances were better correlated with the local presence of the species than the seeds. *Salix* components were also correlated with the standing vegetation; however, the best arboreal correlation was with *Alnus* remains. Only the *Carex* seeds of the groundstorey vegetation had high correlation with standing vegetation, with *Carex paniculata* having the best correlation. Fern sporangia abundance was shown to have no direct correlation with standing vegetation abundance.

CA of the non-seed assemblages (Figure 4.74a) split the samples into a loose group of samples from Bure Marshes with the samples from Wicken Fen having high positive values along the first axis. The main influences on that axis were *Betula* leaf and bud-scales, *Phragmites* stems and rootlets. The Bure Marshes samples were clustered along the negative side of the fist axis, the main influences being the presence of Cyperaceae components and *Alnus* leaves. CCA (Figure 4.74b) showed that most of non-seed remains showed a close correlation between macrofossil abundance, including leaves, stems and rootlets, and standing vegetation cover abundance in the main Dicotyledon arboreal elements, Monocotyledons and ferns. Of the main arboreal taxa *Alnus* had the poorest correlation between leaves and standing vegetation. Several taxa were missing from the assemblages.

Combined CA (Figure 4.75a) showed the influence of seed and non-seed macrofossils from the main arboreal and groundstorey dominants that were often present in coherent groups in the same sector of the diagrams. The patterning shows that coherent, site-specific macrofossil assemblages are formed in wet woodlands. The CCA plot (Figure 4.75b) confirmed that different groups of macrofossils were broadly correlated with standing vegetation cover abundance values of the appropriate taxa. Taxa such as *Iris, Eupatorium cannabinum, Lycopus europaeus* and *Solanum dulcamara* were largely under-represented or mis-represented. Woody components were poorly correlated to any one taxon, although were more strongly correlated with *Alnus* records. This may reflect the higher water levels and better preservation in the alder-dominated wet woodland sites. Wicken samples had higher rootlet values, perhaps reflecting higher compaction rates and density of vegetation growth at the site.

Figure 4.72a Bure Marshes Block 1 seed cumulative data of main taxa

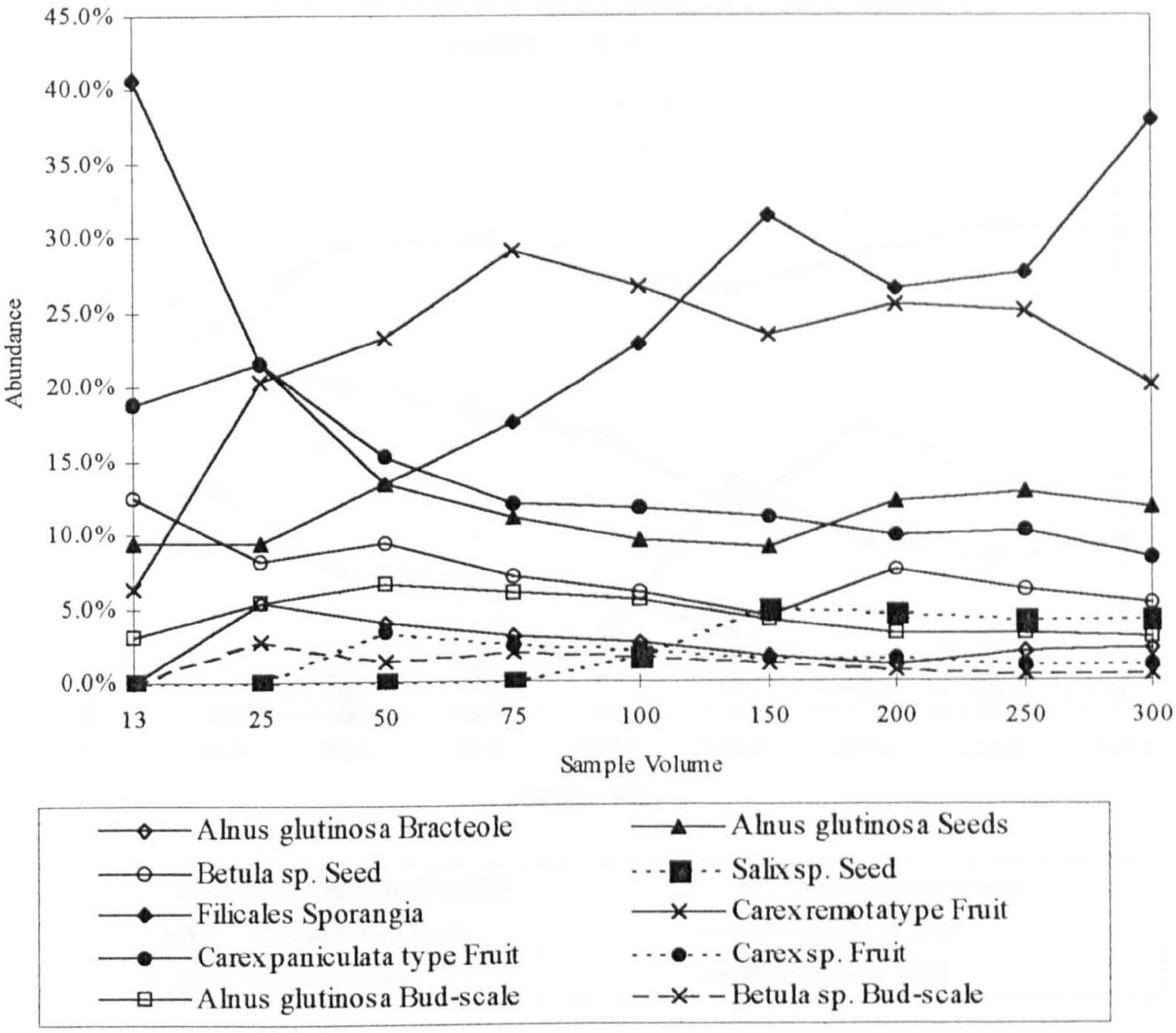


Figure 4.72b Bure Marsh Block 1 cumulative non-seed data for main taxa without Indeterminate matter

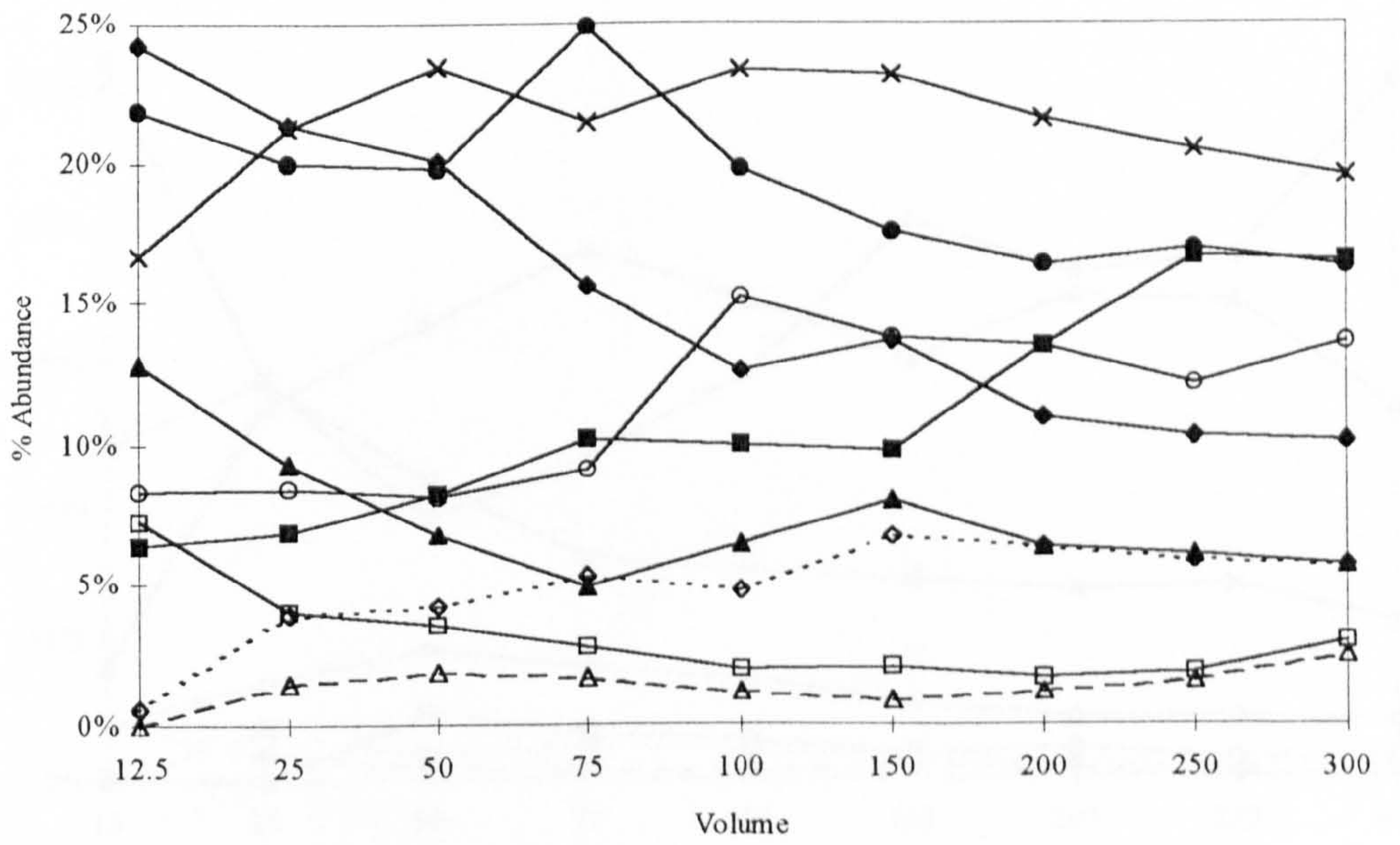


Figure 4.72c Bure Marsh Block 1cumulative seed abundance diagram for canopy elements

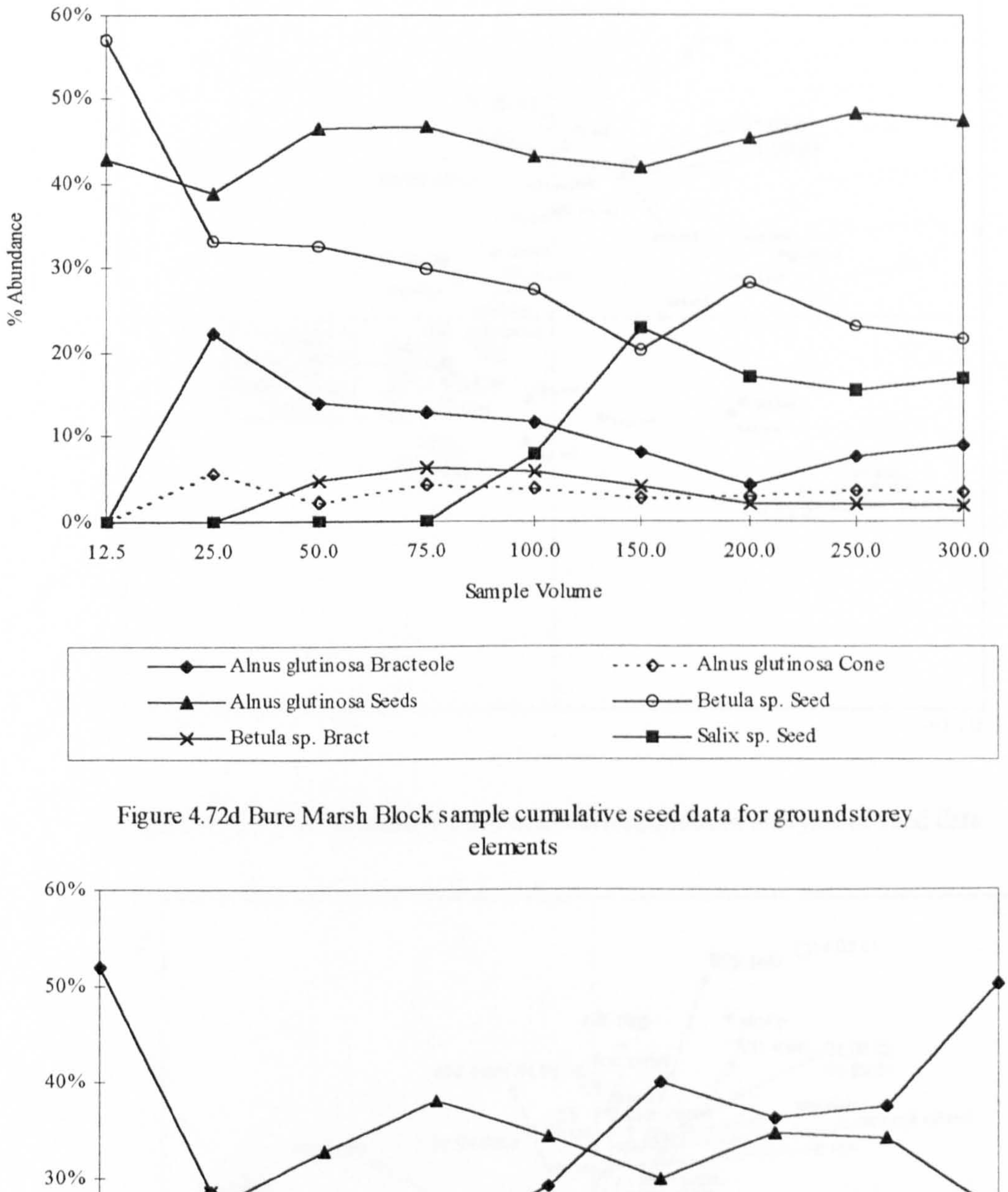


Figure 4.72d Bure Marsh Block sample cumulative seed data for groundstorey elements

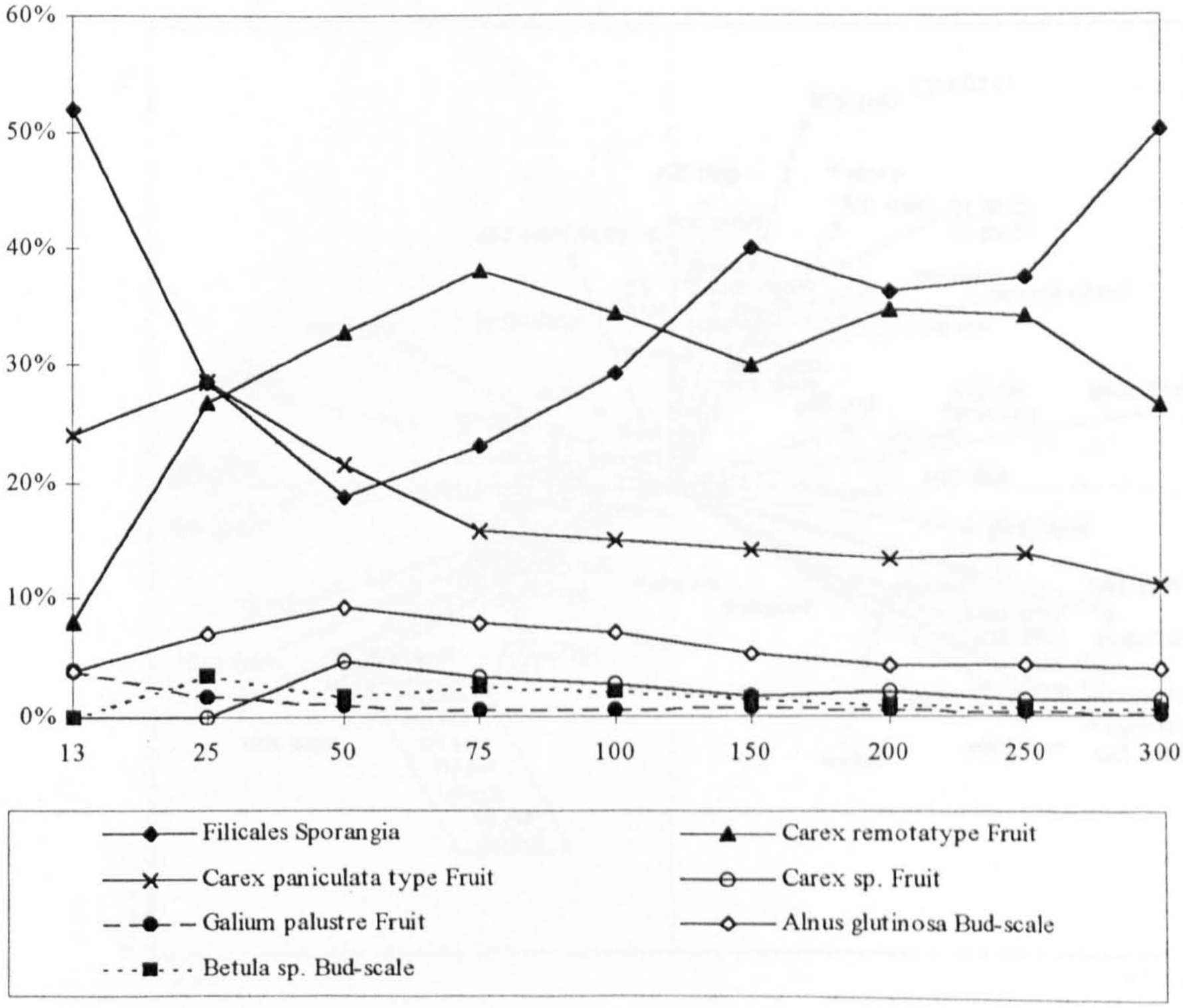


Figure 4.73a Wet Woodland correspondence analysis of seed data

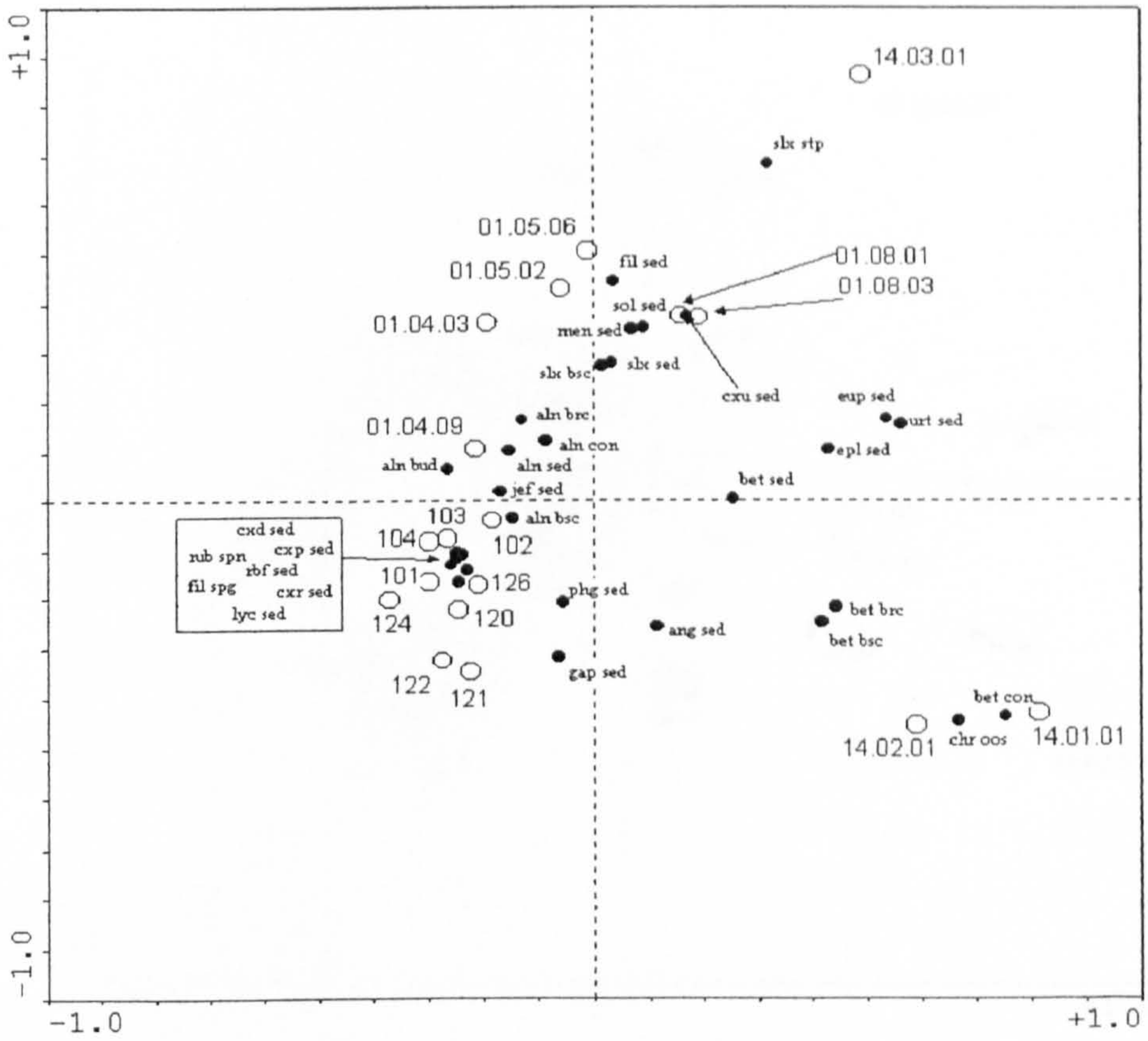


Figure 4.73b Wet Woodland canonical correspondence analysis of seed data

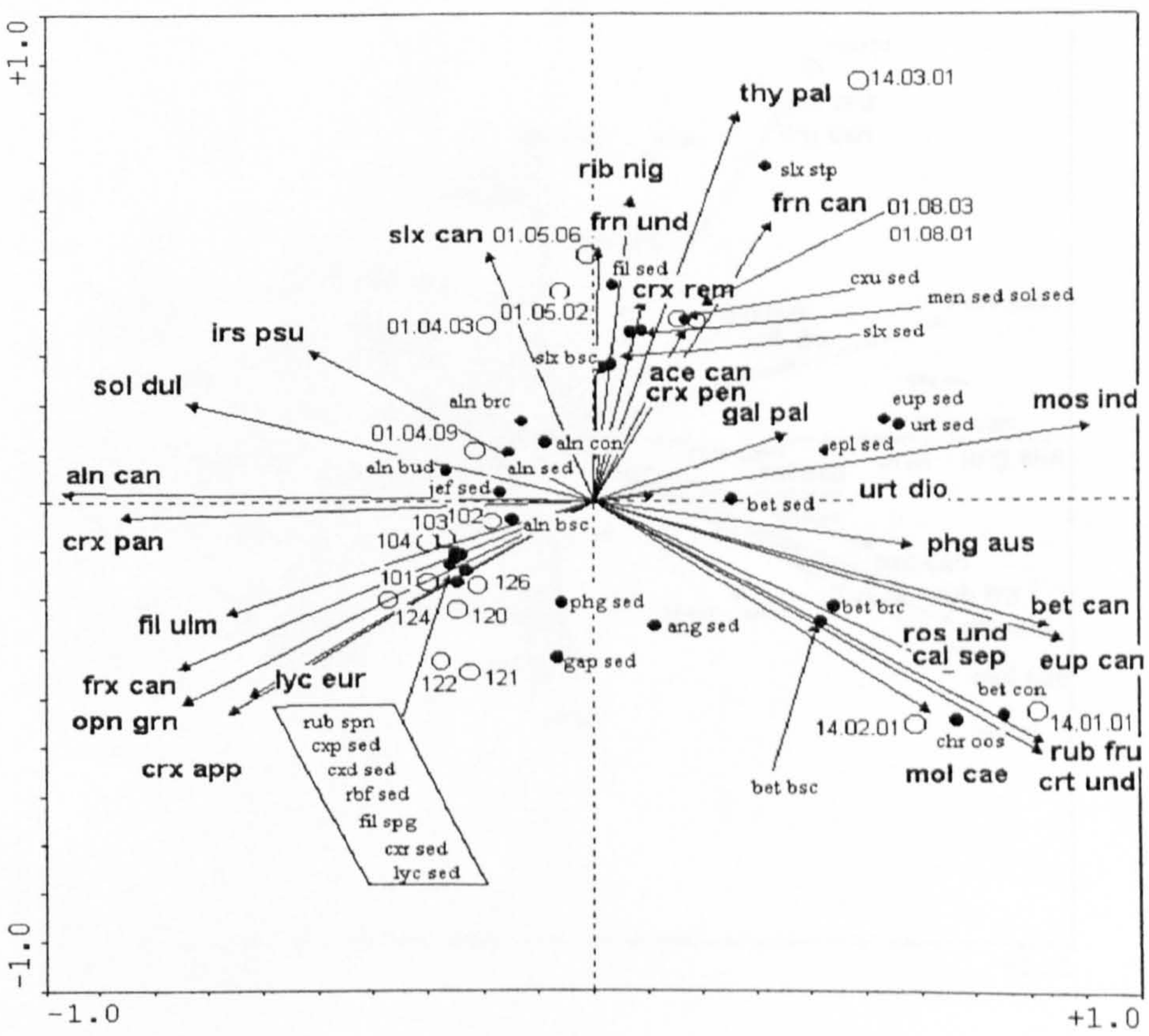


Figure 4.74a Wet Woodland correspondence analysis of non-seed data

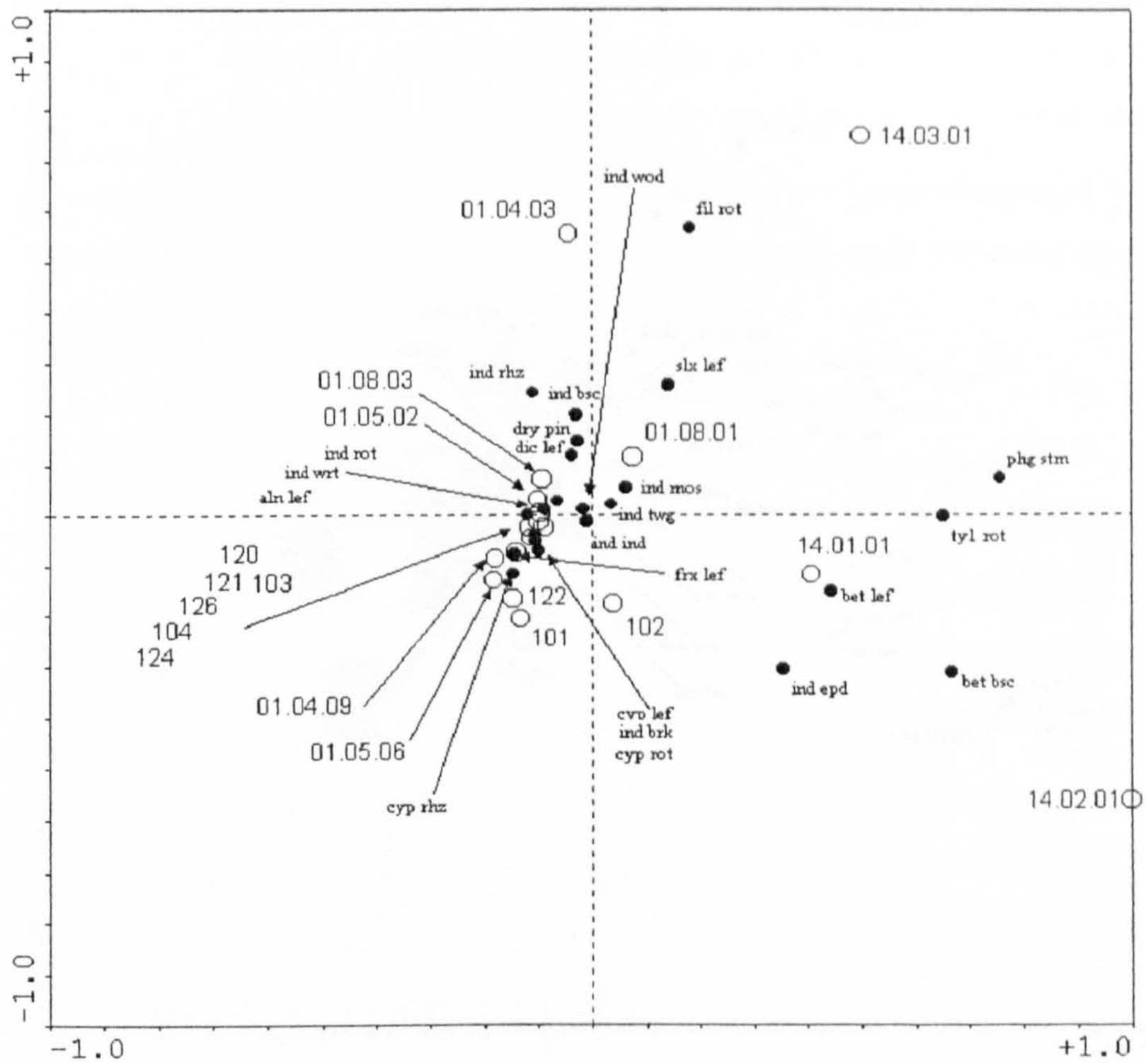


Figure 4.74b Wet Woodland canonical correspondence analysis of non-seed data

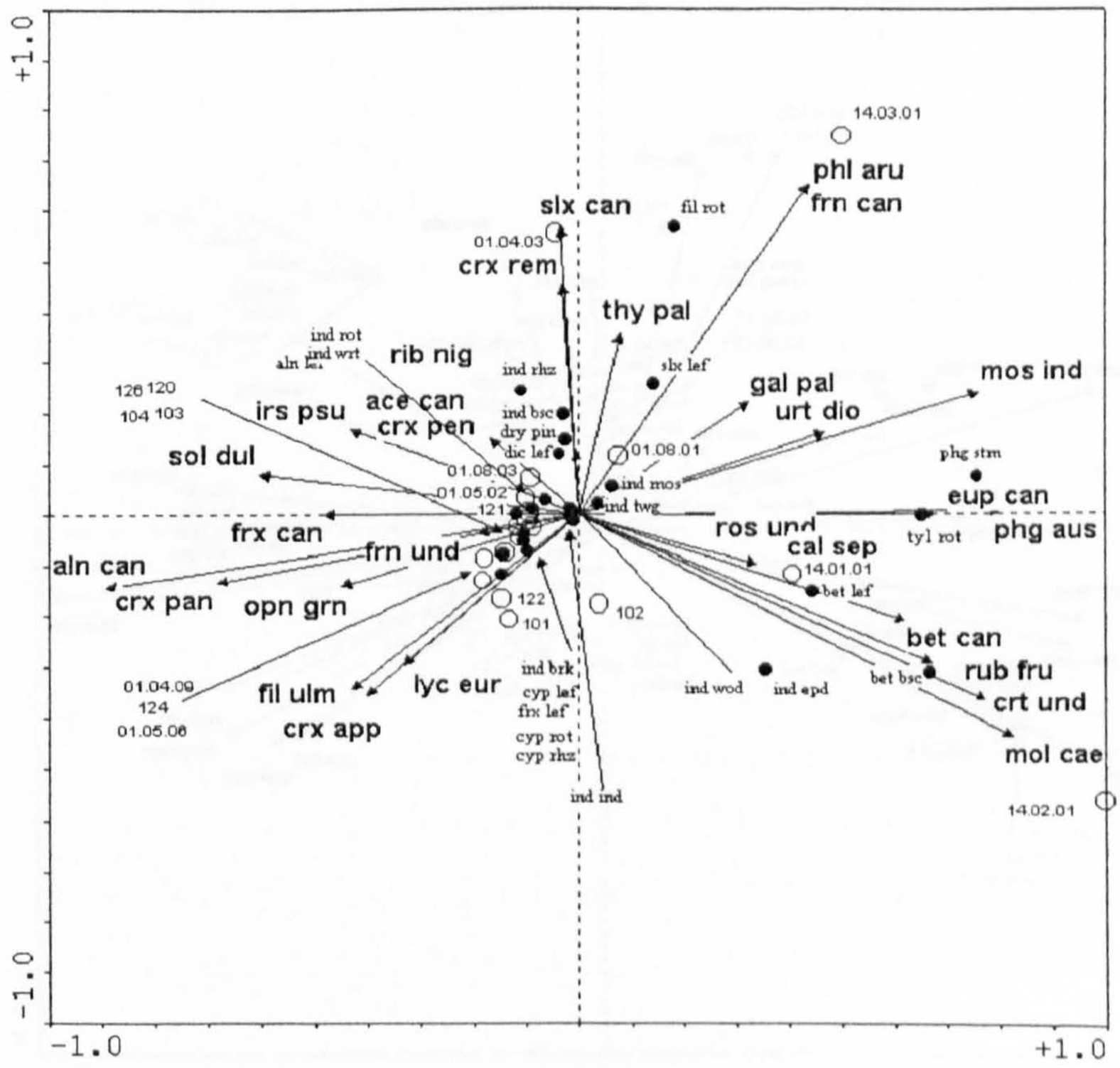


Figure 4.75a Wet Woodland correspondence analysis of seed and non-seed data

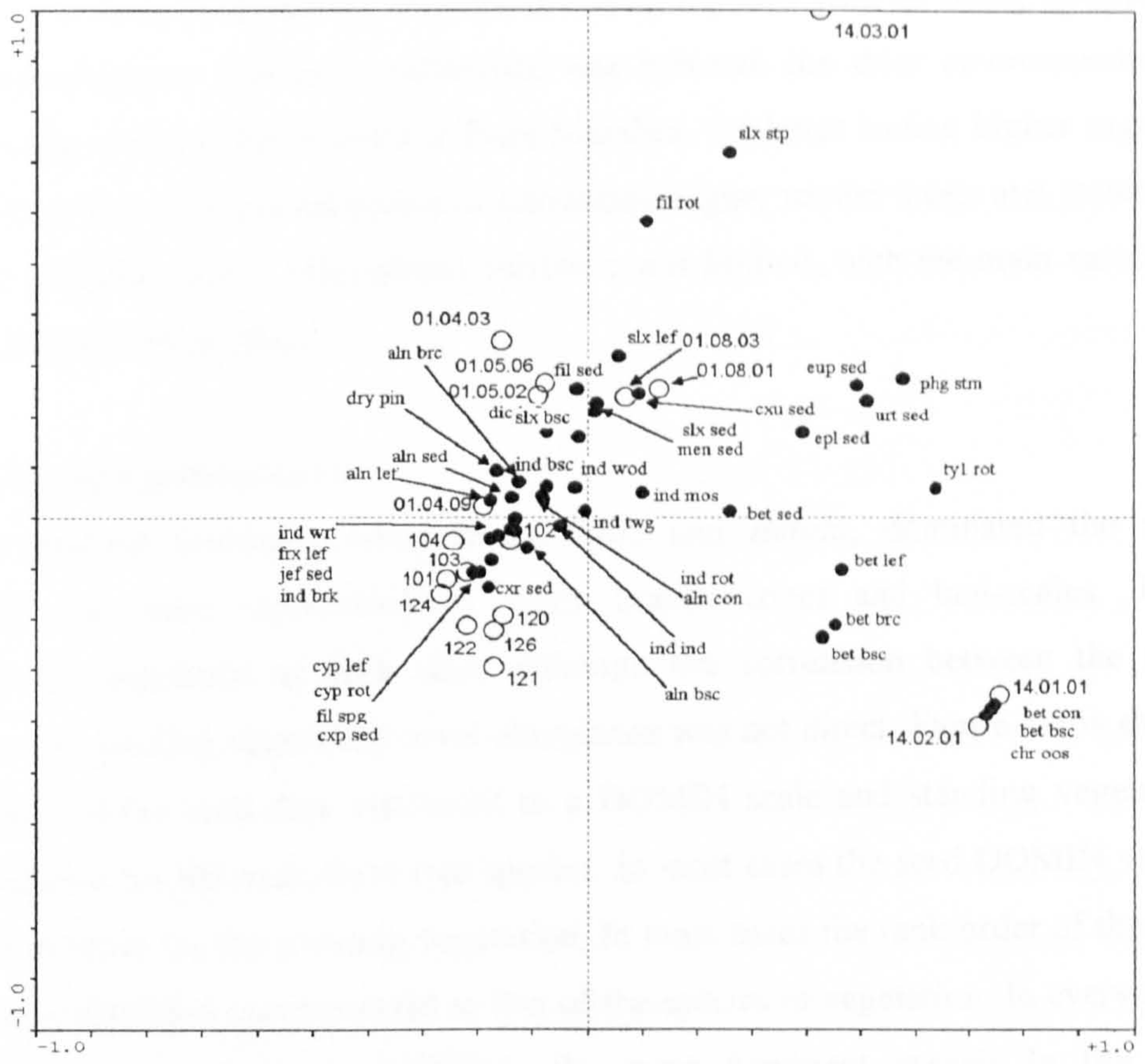
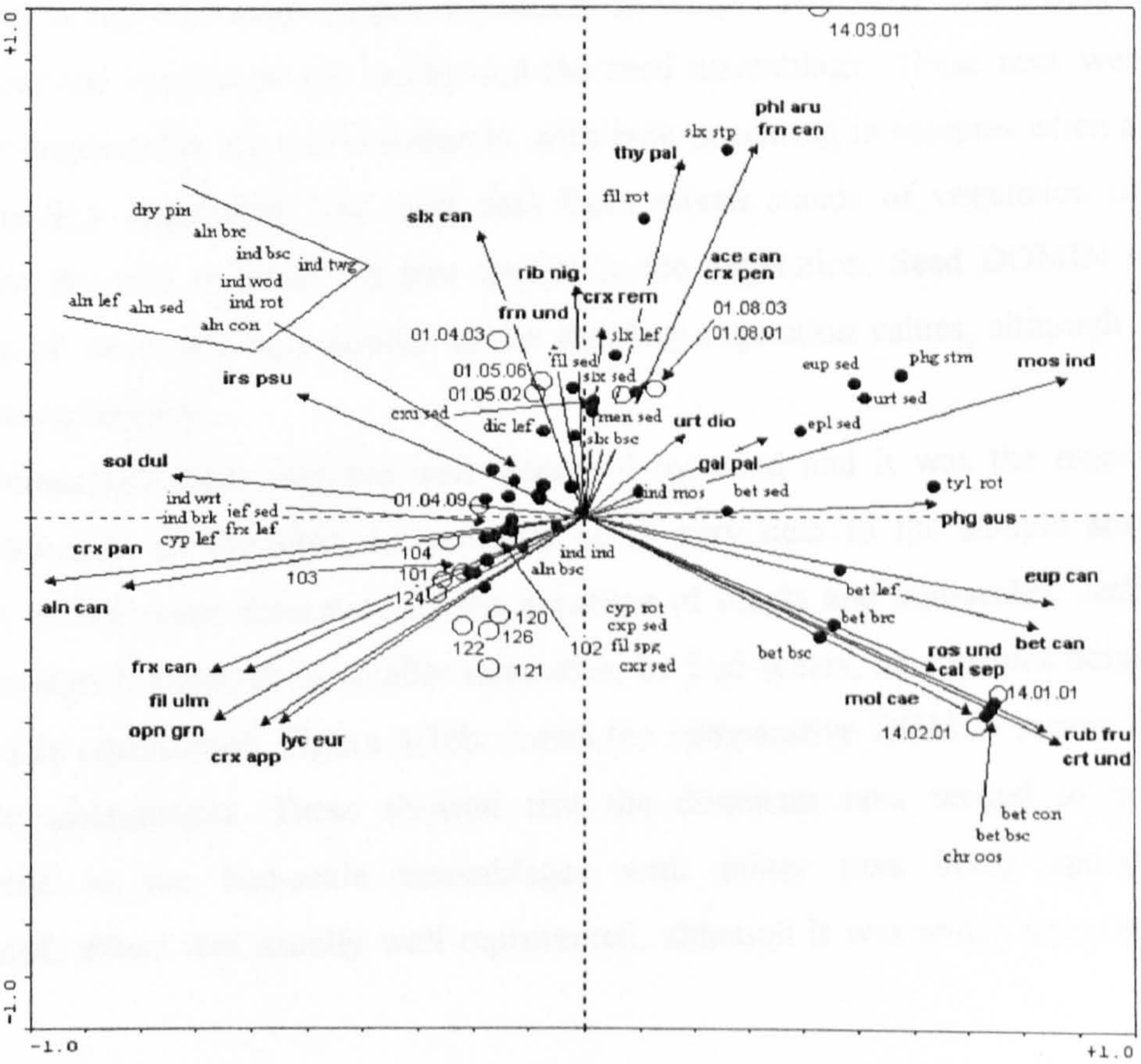


Figure 4.75b Wet Woodland canonical correspondence analysis of seed and non-seed data



4.9.8 Differences in depositional environment

There were only minor differences between the sample points with all being floodplain peatland environments. The main difference was between the drier environments at Wicken and the wetter environments at Bure Marshes, the latter having higher organic content and the former increased seed concentrations, higher rootlet levels and generally worse level of preservation. Macrofossil variation was limited, with the main variation being in sediment composition.

4.9.9 Vegetation representation

The main arboreal dominant taxa, *Alnus*, *Salix* and *Betula*, dominated the seed assemblages and were represented by many bracts, cones and bud-scales. They dominated the vegetation at both sites, although the correlation between the seed abundance and standing vegetation cover abundance was not direct. Figure 4.76a shows a comparison of the seed data converted to a DOMIN scale and standing vegetation cover abundance for the main three tree species. In most cases the seed DOMIN values were close to those for the standing vegetation. In most cases the rank order of the taxa in the seed assemblages corresponded to that of the species in vegetation. In every case, with the exception of sample 14\03\01, the most dominant species in the seed assemblage was the vegetation dominant. *Salix* and *Betula* were often slightly over-represented in the seed assemblages, especially in sample 14\03\01, where *Betula* was absent from the vegetation but dominated the seed assemblage. These taxa were the most well dispersed in the wet woodlands, with both appearing in samples when absent in the standing vegetation. The seed data from mixed stands of vegetation usually maintained the rank order of the tree species in the vegetation. Seed DOMIN values from area 08 were strikingly similar to the standing vegetation values, although *Alnus* was under-represented.

Betula has seeds that are well dispersed by wind and it was the most over-represented seed on the sites. Its presence at or very near to the sample site was, however, shown more accurately by the presence of bracts and bud-scales. *Salix* was also represented, although in smaller quantities, by bud-scales, its capsules being only occasionally represented. Figure 4.76b shows the comparative DOMIN scores for the bud-scale assemblages. These showed that the dominant taxa tended to be well represented in the bud-scale assemblages with minor taxa being sporadically represented. *Alnus* was usually well represented, although it was under-represented in

14\02\01, with *Betula* over-represented and *Salix* being under-represented in vegetation where they were dominant or co-dominant elements. Comparative DOMIN scores for Betulaceae bract/cone abundance and standing vegetation have been presented in Figure 4.76c. The bracts and catkin scales were usually found only near trees of the species, with the exception of *Betula* catkin scales in 01\05\02 and 01\05\06. *Betula* was commonly over-represented in mixed vegetation, although there was a surprising similarity between the cover abundance and seed DOMIN data. These data suggest that the seed, bract and bud-scale data are important for determining the composition of woodland cover and each has different spatial fidelity and representative value.

Tree-leaves were the most commonly preserved of the non-Monocotyledon taxa. The local arboreal dominants were the greatest contributors to the leaf assemblages and they usually accurately reflected the dominance of taxa in the vegetation, although some of the Block samples contained more *Salix* than *Almus* leaves. *Salix* leaves were well preserved in sample 14\03\01 and were generally tougher than the other arboreal wetland dominants. *Betula* leaves were present only in samples from areas where the plant was dominant. As with the seeds and fruits, preservation of the dominant species is more likely than the preservation of minor canopy components, although some major canopy elements may be totally missed (for example *Salix* in site 08). As with the seeds and fruits, local concentrations of leaf mats, seen during the fieldwork, may distort the picture of the flora obtainable from analysis of leaf remains. The only identified twigs of *Salix* in sample 03 accurately reflect the dominance of this taxon in the canopy (the twigs were identified on the basis of bud morphology).

Minor arboreal components in the canopy and understorey, including *Crataegus, Acer pseudoplatanus, Fraxinus excelsior* and *Frangula almus* were poorly represented in the seed assemblages. Though the latter was almost a co-dominant in site 14\03, it was represented by only a single seed and was absent from the leaf assemblages. These taxa often appeared only as isolated shrubs, being absent from the seed assemblages as a result of the supression of fruiting by shade (*Crataegus, Fraxinus, Sambucus* (Grime *et al.* 1988)), immaturity, or because they produce seeds that fail to contribute to persistent seedbanks (e.g. *Acer pseudoplatanus* (Grime *et al.* 1988)). Sparsely recorded shrubby and climbing woody plants, *Rosa* sp. and *Rubus fruticosus*, were also under-represented, only the latter contributing to the seed assemblages although not in sediments near stands of the species. These seeds and those of *Sambucus* probably entered the sediments via bird droppings.

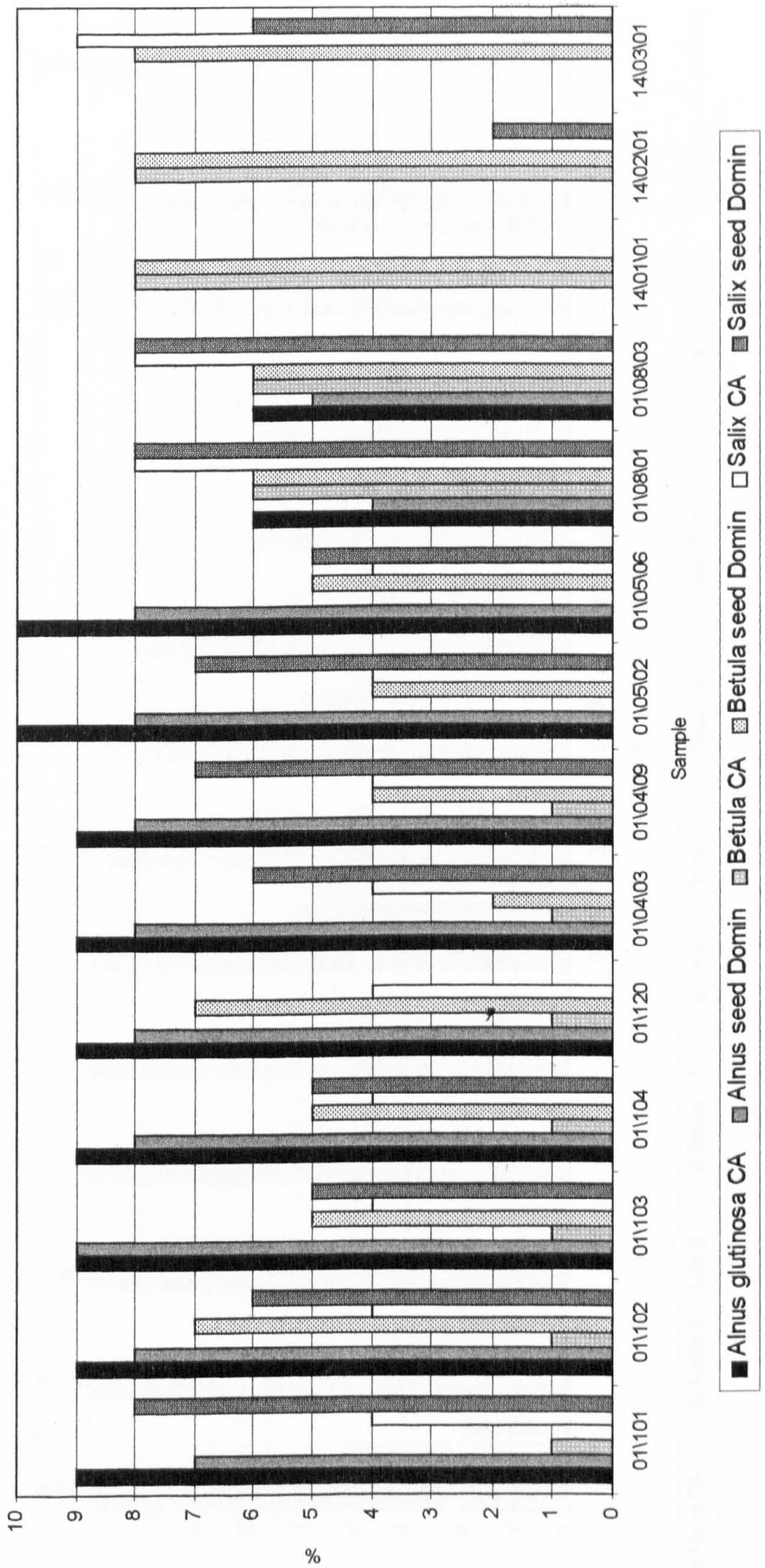


Figure 4.76a Comparative DOMIN scores of standing vegetation cover abundance (CA) and seed data for the main arboreal taxa

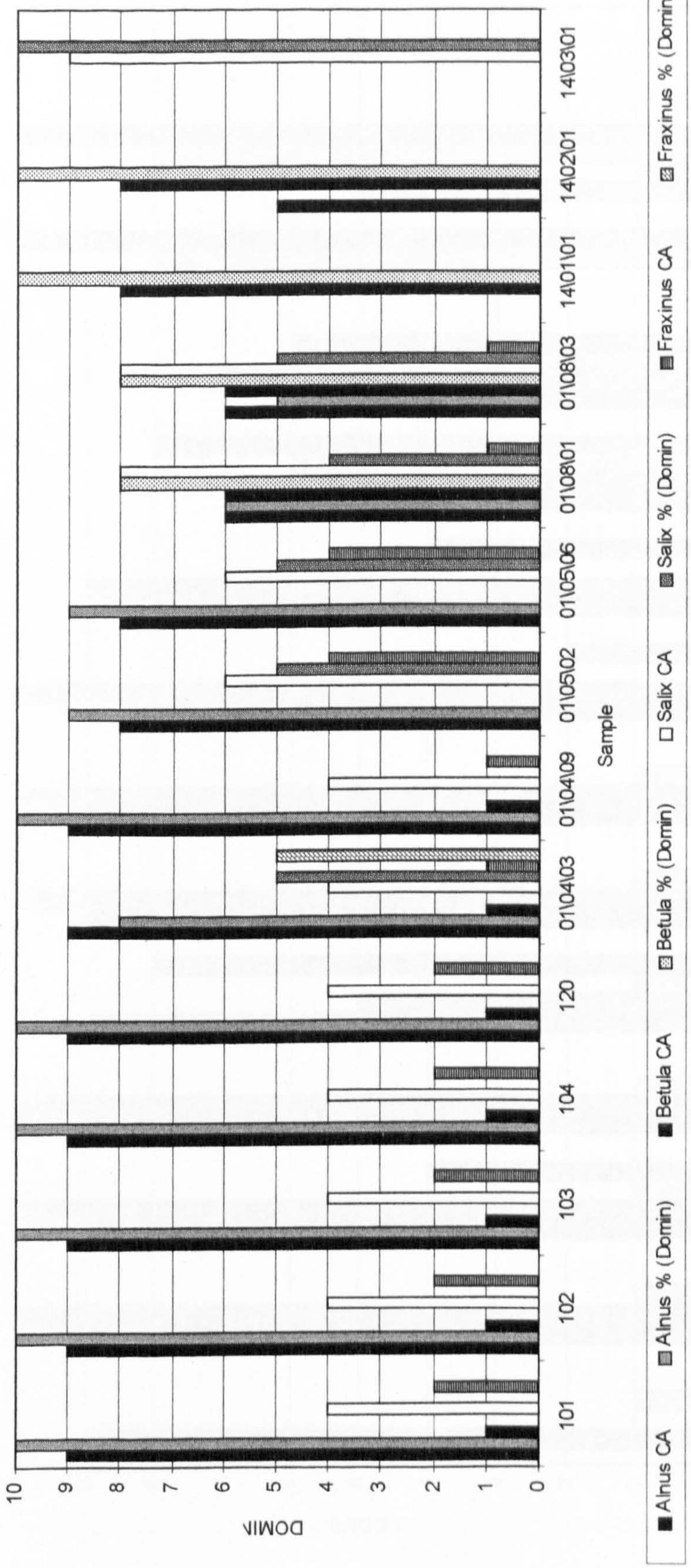


Figure 4.76b Comparative DOMIN scores of standing vegetation cover abundance (CA) and bud-scale data for the main arboreal taxa

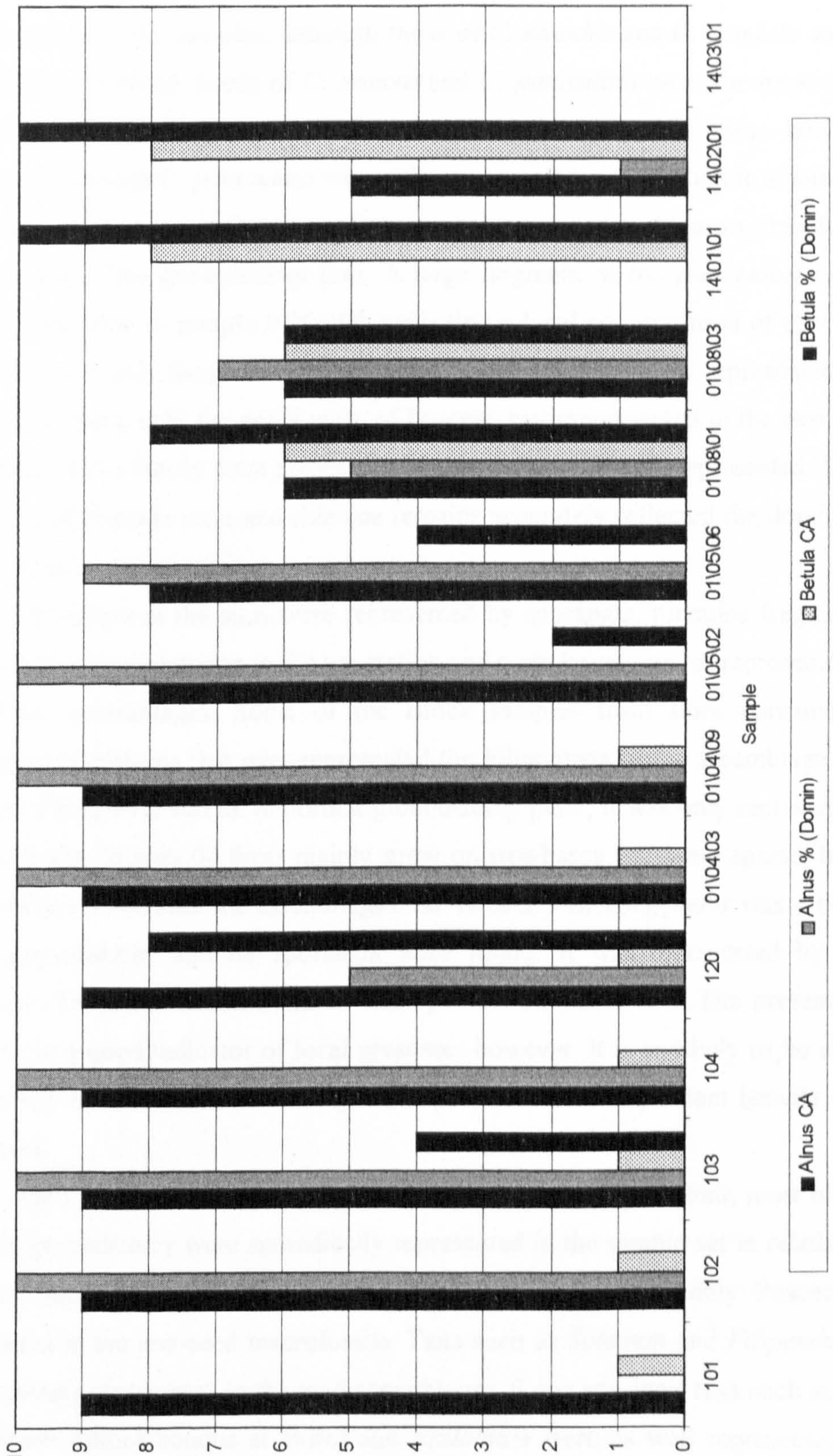


Figure 4.76c Comparative DOMIN scores of standing vegetation cover abundance (CA) and bract data for the Betulaceae arboreal taxa

Only the most abundant groundstorey taxa were well represented in the macrofossil assemblages. In the case of Bure Marsh, the groundstorey component was dominated by seeds of the Carices. Seed types corresponding to the four *Carex* species were identified in the samples, although those of *C. diandra* and *C. pendula* were only sporadically preserved. Seeds of *C. remota* and *C. paniculata* were the most common seeds in samples from site 04. This reflected a dominance of these taxa in the vegetation, although *C. paniculata* was under-represented even though it dominated the vegetation. Cyperaceae leaf, stem and root remains were also the most abundant non-seed material of the groundstorey taxa. A large fragment of *Iris pseudacorus* rhizome was also identified in sample 01\04\09, reflecting a local concentration of this species. At Wicken Fen, only the groundstorey flora at 14\02 was accurately represented. Of the groundstorey taxa, only the aerial parts of Poaceae were represented in the two samples where taxa of this family were present. In 03 the stems were over-represented. In 01 the abundance of Poaceae stem and rhizome remains accurately reflected the dominance of Poaceae taxa in the vegetation.

Filicophyta at the sites were represented by sporangia, pinnules fragments and rootlets. They were common in the vegetation and were largely under-represented in the macrofossil assemblages. Some of the Block samples from Bure contained large sporangia assemblages that over-represented the Filicophyta in the assemblage. In area 08 where *Thelypteris* was an important groundstorey plant, it was only represented by a few sporangia. In area 04 ferns mainly grew on tree-bases and were sparse; however, the sproangia dominated the assemblages. At Wicken Fen *Thelypteris* was a dominant in the groundstorey and no sporangia were found. It was represented by pinnule fragments. The preservation of ferns was sporadic and uncertain. The presence of its remains are a good indicator of local presence; however, it is as likely to be absent as represented in macrofossil assemblages and preservation is dependant heavily on local conditions.

Apart from the fern sporangia and fruits of *Carex* and *Molinia*, most other taxa from the groundstorey were sporadically represented in the sample set in relatively low numbers. Most of these taxa were represented as seeds, with only Poaceae being represented in the non-seed macrofossils. Taxa such as *Solanum* and *Filipendula* were not accurately represented in the seed assemblages. Some non-local taxa such as *Juncus*, *Eupatorium (*allochthonous at Bure) and *Epilobium* were as well represented, if not more so, than the local taxa. The latter are aerially dispersed and, therefore, are more

likely to be incorporated in non-local sediments. *Eupatorium* was present at Wicken Fen and over-represented. Shading may again be important for suppressing the flowering of some local taxa, such as *Filipendula*, that may rely more on vegetative reproduction for perennation in wet woodland than sexual reproduction (Grime *et al.* 1988).

Overall, the macrofossil assemblages in the wet-woodland sites were dominated by the remains of the arboreal dominants, with moderately accurate representation of the woodland canopy in the seed, bract, bud-scale and leaf assemblages. Minor canopy elements were occasionally represented but where present, were spatially accurate and no allochthonous arboreal elements reached the sites. Groundstorey macrofossils were again dominated by the bulky local dominants, especially the bulky Monocotyledons. The diversity of the groundstorey flora was best described by the seed assemblages, although the non-seed macrofossils were useful for determining major, local, ground-flora elements. The ferns and Dicotyledons were, as at several other sites, under-represented or poorly represented when dominants or minor elements. Using the macrofossil data the reconstruction offered for the Bure Marsh sites would be of closed-canopy wet woodland (denoted by arboreal taxa and lack of light-demanding species) with a ground flora of tussocky sedges and occasional ferns and mosses. This would be correct for sites 04 and 05 but would miss the important ground-layer of ferns in site 08. The reconstruction at Wicken Fen would be of wet-woodlands, with site 02 having dense Poaceae growth. Overall the reconstructions would be accurate, although the minutae of the vegetation would be missing. It is also probable that the seeds of *Salix* would be missing if the assemblages were preserved for any length of time. Therefore, the presence of this taxon would be represented mainly by capsules, leaves and bud-scales. This would mean that *Salix* would be less visible and interpretation of itsgs presence would require the identification of non-seed components.

4.9.10 Sub-surface samples from sediment blocks

Organic content decreased and the water content increased slightly with increasing depth in Block 1 (Table 4.33). In each case the difference between the depth samples and surface samples was between 1% and 5%, increasing with depth. The differences in water with depth are as expected, as in the absence of flooding at the peat surface increased evaporation would reduce water levels. The decreasing organic content may reflect continued decay of the organic matter in the peat after deposition.

Table 4.33 Bure Marsh: sedimentological data from depth samples from Block 1

	Block 1	
	% Organic	% Water
0-2cm	c. 90%	c. 85%
2-4cm	88.36%	85.05%
4-6cm	85.53%	85.21%
6-8cm	85.19%	85.13%
8-10cm	86.10%	86.50%
10-12cm	85.79%	86.08%

4.10 Synthesis

Analysis of the macrofossils collected from the eight sites showed that there were broad coherent patterns of macrofossil incorporation in the various sampled depositional environments. Broad generalisations about the spatial and temporal fidelity of those assemblages could also be made. The data provided important information about the usefulness of different classes of macrofossils, the visibility of different species in macrofossil assemblages and the fidelity of macrofossils of those species. The broad patterns of macrofossil preservation and fidelity will now be discussed. Although every effort was made to gain access to the broadest range of depositional environments and sediments, comprehensive cover was impossible and the deficiencies of the data set are recognised. To supplement the insights produced by data analysis, this section also includes a series of models of macrofossil incorporation and fidelity for some environments that were poorly sampled or are absent from the sample set. It also includes some predictive theoretical discussion of macrofossil changes over time, made primarily on the basis of the Block sample observations.

4.10.1 Macrofossil characterisation of different depositional environments

4.10.1.1 Saltmarsh environments

Mudflat sub-environments were sampled in both upper and lower saltmarsh sites at several locations along rivers and marshes. Mudflat sediments were typically soft, fine-grained sediments with some visible structure, often laminations. They had a low overall organic content and, therefore, a low plant macrofossil content. Macrofossil assemblages at all of the sites were composed of poorly preserved fragments of non-seed material and low concentrations of seeds. The macrofossil properties are the result of constant sediment re-working by tides, the openness of the sediments to tidal and aerial inputs and the high level of biological activity on the mudflats causing physical, chemical and biological breakdown of plant matter introduced from a wide area and number of habitats.

Organic content was typically between 11% and 15% by mass, with the figures being significantly below the values for adjacent vegetated marsh sub-environments. Greater organic values were also usually recorded at positions more isolated from tidal flow and closer to land. This was seen at Angel Marsh (compare values for mudflat samples in Transects 1 and 2) and also when comparing mudflat samples from Borstal Marsh and Burham Marshes, although the differences in values there were slight. The composition of macrofossil assemblages was typically diverse in the mudflat samples, with many classes of macrofossil represented. Unidentifiable plant matter typically dominated the assemblages and was often a major influence in the correspondence analyses. Fragment size was often small, although the constant tidal action introduced a number of large plant fragments in several samples. It seems probable that extensive beds of such macrofossils may be potentially incorporated in mudflat sediments should storms or changing depositional conditions deposit large packets of sediments. Seed assemblages were usually taxonomically diverse, deriving from many sources, and were present in low numbers. Unlike many other seed assemblages dominated by a single or small number of taxa, those from the mudflats contained relatively small numbers of seeds from a wide range of taxa.

Vegetated saltmarsh sub-environments were the most thoroughly sampled. In general the marsh sediments were much firmer, compacted and had a higher organic content than other saltmarsh sub-environments. This was seen in the differences in LOI figures, water content figures and physical sediment properties. Vegetated saltmarsh sub-environments sampled during the project covered a wide range of locations and habitats from low-saltmarsh at the edge of mudflats to upper saltmarsh grading into terrestrial habitats.

Non-seed material was typically dominated by non-woody components, even when the chaemophyte *Atriplex portulacoides* was present. Rootlets and other subterranean structures usually dominated macrofossil assemblages in saltmarsh sub-environments, reflecting the dense vegetation that typically covered the marsh surface. There was some evidence, especially over transitions at Borstal Marsh and Stonemarsh, that rootlet content and organic content increased with surface vegetation cover.

Aerial components were preserved in variable quantities, with the stems of grass taxa, especially *Phragmites*, being well represented. Preservation of these taxa can be attributed to the form of the plants. In many taxa stems that display aerial stem

morphology originate from buried rhizomes and may be classified as aerial, although are in fact beneath the sediment surface. Leaves were usually not preserved in any quantity, although those of *Atriplex portulacoides* were preserved at several sample points, as were those of *Glaux maritima*, *Atriplex prostrata* and some of the Monocotyledon dominants. Only in the case of one marsh sample from Angel Marsh did leaves form a dominant element, in that case beneath a stand of *Atriplex portulacoides*. Although sediments remained moist for much of the year and so were in theory able to preserve macrofossils, the active detritovore communities and other agents of biological decay clearly removed much of the aerial plant matter before its incorporation into the sediments. This effect was evidently suppressed in some of the more terrestrial reedbeds at the tidally isolated ends of marsh transects at Burham and Angel Marshes, where the massive autumnal deposition of leaf litter by *Phragmites* caused at least some leaf incorporation of that plant.

Upper saltmarsh sediments contained increasing quantities of organic matter if soil moisture levels were maintained towards dry land. This was the extreme end of a trend seen across saltmarshes, where organic content increased with decreasing tidal influence and higher elevation. This was evident at all of the sites, although Snape Saltings showed the most extreme patterning. In some areas of the site with high groundwater levels caused by terrestrial water inputs in a water-retaining matrix, a saltmarsh peat developed. In other areas of the site, where the sediments were isolated from water, no macrofossils were preserved at all and an oxygen-rich clay-loam soil developed.

Vegetated saltmarshes contained a much higher seed abundance than mudflat samples and again, there was a general trend of increasing seed abundance with elevation and isolation from tidal influence. This was especially noticeable at Snape Saltings, although it was complicated by local production and concentration effects. Local concentration effects can be seen at Burham Marsh, where some of the assemblages contained a high abundance of allochthonous aerially distributed seeds, concentrated perhaps because of the combination of wind direction and vegetation structure. Species diversity was also often high, especially at the marsh margins where allochthonous taxa from tidal and terrestrial sources could easily enter the marsh. Although diversity was often high, a single taxon or very few taxa commonly dominated the assemblages and most of the taxa were often represented by very few seeds.

Creek sediments were sampled at several sites, mainly in lower saltmarsh settings. Sediments contained the usual mixture of fine-grained particles and had a high water content. Organic percentage figures were usually lower than samples from adjacent vegetated saltmarsh, although figures were higher than those from mudflats. This trend is illustrated well by comparisons between the samples from saltmarsh and creek in Transect 1 at Angel Marsh. The pattern was more complex at Snape Saltings, where sediments were found to contain packets of macrofossil material from overhanging vegetation, inflating the organic values of some samples.

Macrofossil assemblages in creek sediments were usually sparse and consisted of a mixture of macrofossil components. Preservation was better than in mudflats, although in most cases large quantities of indeterminate matter were preserved, usually greater than that in saltmarsh sediments. Aerial components were preserved in larger quantities in creeks than saltmarsh sediments, with stem and leaf remains common and epidermis fragments also preserved in some quantity. The enhanced preservation of epidermis and aerial components is due to the high permanent water content of the sediments, and tidal flow may be the cause of the high indeterminate matter content.

There was a noticeable difference between the preservation at Angel Marsh and Snape. At Snape, the non-seed assemblages were highly variable and often varied little from the surrounding marshes. At Angel Marsh, unidentified matter, epidermis and leaf fragments, as well as large quantities of stem, dominated the assemblages. Sample 8, collected from the creek-end within the colonisation zone of the *Phragmites* reedbed, contained mainly leaves whereas stem remains dominated the samples from the saltmarsh. The differences in assemblage composition can be explained by the nature of the creeks. Those at Snape were narrow, enclosed and had dense overhanging vegetation contributing to the sediments. At Angel Marsh, the samples were taken from a wide and deep creek that had no overhanging vegetation. Situation and character of the local vegetation clearly played a role in determining the macrofossil characteristics of creek sediments and some, especially in upper saltmarshes, may be indistinguishable from the vegetated saltmarsh sediments.

Seed assemblages were usually composed primarily of seeds from vegetation growing near to the sample point. They were similar to the assemblages from saltmarsh sediments, usually being dominated by a single taxon and having similar abundance and

diversity. In some of the Snape samples the overall seed diversity was higher. However, this trend is uncertain.

Creeks are the main sites of water movement into vegetated saltmarshes and as such are exposed to powerful erosive forces, though high sediment water levels enhance the potential for preservation of soft tissues and aerial components. It is uncertain whether any of the described material in the samples would be preserved under stable conditions as the sediments and the macrofossils they contain are continuously re-worked. Only when active sedimentation occurs, because of increasing tidal heights or isolation of the creek from tidal influence, would the material be likely to be preserved.

Creek point-bar sediments were sampled at Stonemarsh in Block 3. The bar was covered with sparse *Salicornia* vegetation. It consisted of similar sediments to those of the surrounding mudflats, but had a higher organic content, presumably directly reflecting the quantity of surface vegetation at the site. The macrofossil assemblages contained relatively high seed concentrations, many roots and a diverse array of other classes of macrofossils. Stems of *Salicornia* were well represented, as in other pioneer vegetation areas, and wood fragments were well represented. The overall macrofossil profile was between that of the mudflats and the lower saltmarsh, with enhanced preservation of stems and some soft tissues.

Sample 09/01/06 from the creek edge at Stonemarsh contained a little organic matter, probably as a result of the raised position of the sediments and the oxygen-rich atmosphere. The macrofossil assemblages contained high levels of unidentifiable matter, as with the surrounding mudflats, but a very diverse seed assemblage. This latter characteristic may be a result of seeds settling out of suspension as the tidal waters rise above the creek edge and lose energy (see Field 1992). Evidence from Snape and Burham suggests that seed assemblages from the saltmarsh edge may also be affected in this way. The non-seed macrofossil assemblages were similar to the adjacent environments, whether pioneer marshes, mudflats or saltmarsh. The long-term survival of any macrofossils in these sub-environments is doubtful. The aerobic environment suggests that even though the surface sediments contain seeds and macrofossils it is probable that in the longer term decay would drastically affect the assemblages.

A single sample at Snape was collected from a saltpan (sample 34) that carried no standing vegetation and which was strewn with numerous stems and litter. The recorded sediment characteristics and seed assemblage were similar to those from surrounding

vegetated areas. The non-seed macrofossil assemblage was similar to others on the marsh, although it included large quantities of decayed stem and epidermis fragments. Enhanced preservation of these macrofossils is presumably encouraged by the hyper-saline conditions, which may depress biological decay processes. It seems unlikely that this specific environment would be distinguishable on the basis of macrofossil composition.

Snape was also the location of a single sample from an abandoned channel sub-environment (sample 2), a channel permanently filled with water. The channel was filled with finely laminated, fine-grained sediments. The main difference between the macrofossil assemblage from sample 2 and the surrounding marshes was the presence of a large quantity of Cyperaceae epidermis in the sediment laminations. The quantity of epidermis far exceeded the values seen in any other sample when raw and when converted to CO^2 values. The seed assemblage was also very diverse with seed abundance well spread throughout the different taxa.

4.10.1.2 Freshwater environments

A limited number of freshwater sub-environments was sampled, namely wet-woodland floor, wet-woodland tree-base and herb-fen environments. All are variants of floodplain vegetation and there were no opportunities to collect channel, bank and backswamp sediments from intact environments. The main variability was in the dryness and nature of vegetation cover at the sites. All of the sediments were peaty, having a high organic content and low allochthonous plant and inorganic sediment input. As discussed in the introductory section to this chapter, the best way of viewing the data presented here is to see the freshwater wetland fragments as representative of isolated floodplain mires with a permanently high water-table.

The wet-woodland floor was sampled at Bure and Wicken Fen at four different sites. All of the samples contained large quantities of woody components including wood fragments, twigs and bark. Seeds and bud-scales were common, as were the bracts and capsules of the different wet-woodland species. Dicotyledon leaves were preserved in variable quantities, depending on the wetness of the sediments. The best leaf assemblages were recovered from the wet woodland floor at Bure, especially in the very wet conditions of sample 01/04/09, and the wet *Salix* swamp at Wicken Fen (site 03). At the latter, leaf preservation was enhanced by the toughness of the *Salix* leaves. Drier

conditions at Wicken Fen site 01 did not allow large-scale leaf preservation. Monocotyledon leaves, rhizomes, stems and roots were preserved throughout.

The open clearing at Wicken Fen site 02 was clearly distinguished by the quantity of Monocotyledon components and reduced quantities of woody matter. The surface mat of vegetation at the site effectively prevented overhanging woody vegetation from contributing wood to the sediments. The tree-stump sample (01/04/03) was distinguished by the presence of large quantities of Filicales components, a plant that grew at the site in some density, and the presence of many woody roots. This suggests that increased values of woody rootlets may indicate closer proximity to growing trees.

Rootlets, stem, leaf and other vegetative components dominated the herb fen sediments from Hickling Broad. Seed abundance and diversity, as at Bure and Wicken, were high in all of the samples. The contribution that different herbaceous components made to the samples was dependent on the physical characteristics of the species in the local vegetation. The samples were, however, very distinctive from the wet-woodland samples, even when the components of some arboreal species were present.

4.10.1.3 Transitions

Transitions between depositional environments were not easy to sample. This was due in part to the truncation of many environments by human disturbance and the fact that many environments have no smooth transitions between them, as for instance the division between mudflat and saltmarsh at Snape. The division between saltmarsh and mudflat was often defined by a low mud-cliff, an erosive feature. At Borstal Marsh and Stonemarsh, smooth transitions between mudflats and saltmarshes were sampled. In both sites the mudflats contained organic-poor sediments with badly preserved and heterogeneous macrofossil assemblages in which much of the preserved material was unidentifiable. Increasing vegetation cover marked the transition to saltmarsh. Increasing organic content and a marked change in macrofossil content accompanied this change. Larger, better-preserved macrofossil fragments were recovered and both root and seed abundance increased. The change in content was abrupt and spatially precise and the subsequent changes in vegetation density were marked by a gradual increase in organic content, sediment compaction and rootlet density towards dry land.

The transition from saltmarsh to freshwater environment or terrestrial habitat was not well observed in the project, mainly because of habitat destruction and truncation.

Upper saltmarsh habitats at Burham and Angel Marsh (Transect 2) saw the invasion of dense *Phragmites* beds in each case truncated by flood defences. The soils at both sites became progressively more organic rich and peaty. At Snape, a peat was developed at the northern end of the site, where tidal incursion was limited and groundwater was permanently high, possibly because of the presence of a spring-line at the junction between the sandy hills to the north and the clay of the saltmarsh. The peat began abruptly and graded into a loamy soil with no observable macrofossils to the north and east. There seemed to be a definite barrier between the preservation of macrofossils and their destruction by soil formation processes and oxidation.

The Snape evidence shows the importance of topography, geology and hydrology in determining the potential for macrofossil preservation. The saltmarsh samples showed limited macrofossil variability, with the exception of those caused by local vegetation differences, and sedimentation over the whole surface probably reacts rapidly to changing tidal regimes and sedimentation because of the lack of relief. At the northern end of the site this response was affected by local hydrology that has a sedimentary, biological and plant macrofossil response.

4.10.1.4 Interpreting facies changes in time and space

Plant macrofossil assemblages from both saltmarsh and freshwater sedimentary depositional environments had characteristic profiles. The range of depositional environments available for sampling was determined by the limited distribution and survival of in tact suitable environments. The range of sampled environments is partial, with freshwater riverine and floodplain depositional environments being badly represented. Saltmarsh environments, especially from vegetated saltmarsh sub-environments, were well covered. Though the sample set is partial, the information gained provides a basis for determining the usefulness of complete macrofossil profiles and individual macrofossil properties for interpreting sedimentary facies changes in terms of past depositional environments.

Macrofossil assemblages showed strong tendencies in the various depositional sub-environments, suggesting that past depositional environments may be reconstructed in some detail from ancient macrofossil assemblages. Mudflat and vegetated saltmarsh environments produced markedly different assemblages that were distinctive even over gradual transitions between the two. Macrofossil characteristics, in this case the overall

preservation of macrofossil classes, are therefore useful as a means of differentiating between some major depositional environments. Macrofossil characteristics from abandoned channel and creek environments were distinct from the others, although without detailed description of the sediment characters could be confused with each other. Salt pan, creek and marsh edges are largely indistinguishable from the surrounding environments, with seed characteristics being especially important for determining differences. It is possible that unsampled vegetation associations could produce similar seed concentrations and diversity characteristics. The sampled freshwater environments were also distinct.

Spatial variability within depositional environments was reflected to some extent in vegetated saltmarshes and fen woodlands. Only in the case of saltmarshes were whole transitions sampled. They displayed a gradual change in sediment and macrofossil properties. Local vegetation and environmental characteristics, however, also affected this pattern. Saltmarshes are broadly zoned, but also have a mosaic character with extreme changes in environmental gradients being reflected in the vegetation and macrofossil assemblages. Broad 'upper', 'lower' and 'transitional' macrofossil assemblage types are distinguishable. However, their usefulness in interpreting broader patterns of environmental change is dependent on the topography of the basin. Each basin also had a characteristic range of organic contents, reflecting the incorporation potential of organic matter within the specific set of biological and sedimentary conditions, especially sedimentation rate. This has important implications for the interpretation of macrofossil records, especially when modified by organic content (i.e. CO^2 values). Similar environments may, in different catchments or at different times, give different absolute values, while maintaining similar relative macrofossil values.

Observations from the sampled sites showed the saltmarsh, and to a lesser extent freshwater wetland surface, to be a complex entity with many sedimentary responses to the various environmental stimuli affecting each section of the marsh. Topography was in general of limited relief, though differences in height between vegetated marsh and mudflat could be large. The variability in height and deposition is one of the main problems in correlating cores and sections from different sections of alluvial sediment stacks.

While spatial patterns were, to some extent, reflected in the macrofossil assemblages, it would be too simplistic to assume that these modern surface patterns

could be transposed directly to the fossil record. Disturbance of strata by subsequent events and biological activity may have a pronounced effect on the macrofossil assemblages in a sediment body. Destruction of the macrofossil load would occur with the lowering of the water table and operation of soil formation processes in an oxygenated environment.

Growth of some kinds of vegetation may also disturb and alter the macrofossil content of sediment at a location, the effect, to some extent, being dependent on the speed of sedimentation. Disturbance would be minimal when mudflats replaced vegetated marshes, although this circumstance would also provide the opportunity for erosion of the marsh surface and physical destruction of the sediments. Replacement of mudflats by saltmarsh would cause disturbance of the mudflat sediments by saltmarsh plant roots, but the effect would be minimised by high sedimentation rates. The block samples from Angel Marsh and Snape showed some changes in macrofossil assemblages that were consistent with expected seral changes in upper marshes. Changes in vegetation structure, consistent with changes in sediment-water state, are, therefore, reflected in macrofossil assemblages. The transition from saltmarsh to freshwater mires has the potential for major disturbance to the macrofossil record, especially if arboreal taxa are established. The establishment of rhizomatous Monocotyledons would introduce plant matter of a later date deep into earlier sediments meaning that the use of rhizome remains as a basis for palaeoenvironmental information has to be evaluated carefully. Periods of brief saltmarsh occurrence, or periods with low sedimentation rates, could be obliterated by later growth of dense vegetation. Only the traces of saltmarsh taxa in the macrofossil assemblages would provide a route for the identification of such an episode.

Freshwater floodplain transitions from open herb-fen to wet woodland would involve the establishment of trees with the rapid generation of leaf and wood litter. The penetration of branches and twigs from the arboreal canopy and, presumably, fallen trunks, would have the potential to alter the macrofossil traces of herb-fens. As many of the herb-fen taxa are present in wet woodlands, the definition of herb-fen environments may be reliant on the presence of large quantities of the seeds of light-intolerant taxa. Trees may also sink into peat and underlying strata. The growth of herb-fens and swamps over former wet-woodlands, perhaps killed by rising water-levels, may also merge into the wet-woodland peat. Wood would still be present in the herb-fen peat in patches from tree-stumps and branches on the sediment surface, although the seeds and

bracts of arboreal taxa would be missing. Rapid change from wet-woodland to herb-fen and/or saltmarsh may provide a sedimentary record of highly fragmented sediments that would merge together when superficially observed, and require detailed analysis to distinguish them. This argument suggests that there are good reasons for the domination of the lowland Holocene alluvial sedimentary record by relatively few facies types and macrofossil assemblages. It also suggests that the less detailed macrofossil descriptions of alluvial facies using such systems as the Troels-Smith classification are simply inadequate in disentangling the complex merging of macrofossil assemblages that characterises alluvial environments over time

There were considerable differences in water content and compaction of the sediments at the various sample points. Those at Bure Marsh were extremely soft. Drying and consolidation would have reduced the sediment volume considerably. A similar effect would have been seen in mudflat, abandoned channel and creek sediments. The differential compaction rates add another problem to the correlation of sediments from different environments in alluvial habitats. They also pose some troubling questions about reconstructing wet-woodlands, especially using apparently contemporaneous tree-stumps and macrofossil flora in the surrounding peat. Correlation clearly cannot be taken for granted on the basis of height, and independent methods may be required to assure the correct association of tree-stumps and other macrofossils.

4.10.2 Vegetation reconstruction

4.10.2.1 Spatial fidelity of macrofossil assemblages

Macrofossil assemblages in most of the sampled environments were dominated by seed and non-seed macrofossils from nearby vegetation and showed considerable spatial fidelity. Seeds were by far the most mobile macrofossils; however, in all but the most mobile environments, seed assemblages were dominated by taxa present within 50m, if not 2m, of the sample point.

Seeds in the sampled wet woodland and herb-fen sites were unsurprisingly, given the closed hydrology, mainly from local sources, although occasional unrecorded taxa were noted (e.g. *Angelica* at Bure Marsh site 04 and *Hydrocotyle* at Hickling site 02). The unrecorded taxa were usually taxa with seeds adapted to aerial dispersal, water dispersal or were from small plants that may have been missed in the vegetation survey. The main intrusive seeds in the herb fen sites were from *Betula* and *Salix*, both adapted

to aerial dispersal and produced in large quantities by mature trees. *Alnus* seeds were also well dispersed and found at points distant from standing trees. However, they were not found in such high abundance and as regularly as allochthonous elements as *Betula*.

As with the sampled freshwater environments, seed assemblages in the saltmarsh environments contained some allochthonous taxa, but were dominated by seeds of local plants growing within 0.5m to 50m of the sample point. The local component easily swamped the non-local, although some saltmarsh plants such as *Aster tripolium*, *Atriplex prostrata* and *Puccinellia* produced seeds that were well dispersed and would not be easily distinguished from the seeds of local species. Seeds of non-marsh plants were usually easily identified by their environmental tolerances and included species adapted to aerial or water dispersal such as *Sonchus palustris*, *Lycopus europaeus* and *Alnus glutinosa*. Samples from the marsh edge of Burham Marsh contained the greatest concentration of allochthonous macrofossils, especially of seeds adapted to aerial and water dispersal, including *Epilobium hirsutum* and *Oenanthe aquatilis*. The depauperate seed assemblages in the mudflat and transitional samples from Borstal Marsh also contained mainly allochthonous species, although seed numbers were small and the assemblages may be unrepresentative of the sampled sediments. Other mudflat sediments contained seeds mainly drawn from local saltmarsh vegetation. This is shown at Snape where the mudflat samples contained the seeds of taxa growing at the adjacent cliff edge.

Non-seed macrofossils were almost uniformly autochthonous. Exceptions occurred in the mudflat samples at Borstal and other sites, although much of the macrofossil debris in mudflats came from the nearby marsh itself. At Snape a fragment of *Betula* leaf from the open vegetation of the saltpan (sample 34) was the only identifiable allochthonous non-seed macrofossil. In the herb fens and wet woodlands, all of the non-seed macrofossils were locally derived, including aerial components such as leaves. Leaves were identified in the wet woodland samples from trees as much as 50m distant and it is clear that some movement of leaves does occur even in these closed environments

Subterranean structures, such as roots and rhizomes, have the greatest spatial fidelity as they anchor the plant to the sediment and, unlike aerial structures are rarely moved during life or after shedding. The exception is in mudflats and other re-deposited sediments lacking vegetation growth, as roots and rhizomes in these sediments will have derived from eroded sediments elsewhere. The spatial fidelity of these structures is so

extreme that in fen vegetation containing many species (e.g. at Hickling Broad) the root and rhizome content varied widely even in a restricted area (e.g. Block 1). The samples of these structures are likely to reflect only ultra-local conditions (i.e. actually at the point of sampling). Relevance for the wider vegetation depends on the structure of the vegetation involved and may be limited if the vegetation is heterogenous and more useful if the vegetation consists of homogenous stands.

Although influenced by tidal processes, it appears that many saltmarsh environments are largely closed to allochthonous macrofossil inputs. The most satisfactory explanation is that the dense vegetation effectively prevents allochthonous debris from entering on the tides. Vegetation may slow down tidal velocity below macrofossil settling velocity and physically prevent larger macrofossils from penetrating far into the marsh. This combined effect would cause allochthonous macrofossils to accumulate at the marsh edge, as seen at Burham. It also would leave much of the allochthonous matter within tidal influence and so leave it exposed to re-working and erosion. The vegetation would also effectively prevent the entrainment of marsh detritus into the tide, or, if entrained, the detritus from being carried from the marsh. In marshes with extensive creek systems, tidal waters may lose so much velocity by the time they reach the upper marsh that macrofossils are deposited in the creek or at the creek edges.

4.10.2.2 Temporal fidelity of macrofossil assemblages

The temporal fidelity of macrofossils is, perhaps, more variable than the spatial fidelity and varies with the environmental conditions. Temporal fidelity is partially dependent on sediment accumulation rates. Low sediment accumulation rates would increase temporal averaging of assemblages and reduce the temporal fidelity. Rapid sediment accumulation rates would increase the temporal fidelity. As a general rule, deposition in mudflats, abandoned channels and lower saltmarshes would produce macrofossil assemblages of higher temporal fidelity than upper saltmarshes and peat-forming environments.

Seeds and other aerial components are incorporated into the sediment surface at the time of growth. Penetration of the sediment is minimal, suggesting that the temporal fidelity of these remains is high. However, the quantity of remains incorporated is of course changed by the period of time macrofossils are moving in the sub-aerial environment. Seeds are toughened and will survive sub-aerial decay processes for a

longer period than leaves and exposed herbaceous stems, which require rapid incorporation into sediment if they are to persist in the fossil record.

Subterranean structures, including roots and rhizomes, have good spatial fidelity. Temporal fidelity is, however, less assured as roots and rhizomes fulfil the support function by ramifying through sediment into deposits accumulated before the period in which the plant lived. The depth to which plant roots penetrate depends on the species of plant concerned. For example *Phragmites* rhizomes and the adventitous roots they carry penetrate deeply into the soil for many centimetres, perhaps, metres. *Puccinellia* rootlets emerge from the stem base of stolons at the sediment surface, as do the rootlets from rhizomes of *Juncus gerardii* and *Iris pseudacorus*. These latter plants form dense surface root and rhizome/stolon mats and, if identified, would provide a temporally precise record of growth at a site. Evidence for change in root concentrations at Snape (Block 3) and Angel Marsh (Block 2) indicate that rootlet analysis may accurately reflect vegetation changes in some taxa. With taxa such as *Phragmites*, the presence of leaves and stem sections may be more representative of the presence of the taxon at a point in time and rootlet/rhizome records would have to be treated with caution.

As discussed above, the temporal fidelity of some plant remains and whole sections of peat may be compromised in peat-forming wet woodlands because of the penetration of canopy elements, especially branches and twigs, into the peat surface. While the problems of penetration and differential compaction may affect woody components, it is uncertain if other aerial and subterranean structures are affected. It is likely that branch falls and trunk falls will push macrofossils on the surface into the peat. The time averaging effect of slow sediment accumulation rates, root disturbance and, in the case of wet woodlands, wood intrusion, may obliterate all vestiges of some vegetation communities, environments and episodes of change. This problem will potentially affect upper saltmarshes as well as peat-forming environments. Only careful observation of macrofossil abundance from close-interval samples may locate the remnants of the obliterated phases of sedimentation.

4.10.2.3 Taxonomic fidelity of macrofossil assemblages

The potential for macrofossil identification varied considerably within and between depositional environments with the level of decay and fragmentation The latter in particular, was important in reducing the identification potential of leaves and cuticles.

The worst preservation was in the tidally scoured mudflats, creeks and creek edges. The best macrofossil preservation was found in the abandoned channel at Snape (sample 2) and creek terminal at Angel Marsh, where many fragments of epidermis were preserved in exquisite detail. Preservation in the vegetated marshes and fens varied, but was usually good, with leaves commonly preserved in the latter. Leaf and herbaceous preservation in the drier fen-woodlands was often poor.

The level of identification of different macrofossil classes was variable. As expected, genus and species level identifications were only usually possible for seeds, fruits, bracts and bud-scales. Other macrofossil groups were far less easily and precisely identified. Rootlets were often identified only to a type that had varying levels of taxonomic precision. Stem and rhizome fragments were identified using morphology or surface anatomy at sub-class, family, genus or type level. Stems and leaves of the Monocotyledon taxa were the most commonly identified and the identification methods applied did not allow identification of the few recovered Dicotyledon stems. Dicotyledon leaves were identified to a range of levels, with some well-preserved specimens identifiable to genus level. Fragmentation and epidermal decay often precluded identification, and taxa with toughened leaves were favoured.

Identification of the non-seed macrofossils was limited by the preservation of the remains and the information available to provide secure identifications, as well as the anatomical and morphological properties of the plant structures themselves. Some macrofossils, such as leaf and rhizome fragments, simply did not contain enough morphological and anatomical variability to be identified. Level of identification was also limited by the methods used and improved results for roots, rhizomes and stems may have been attained if embedding and cross sectioning had proved feasible for routine identification work. It was, however, too time-consuming and expensive. Also, while the identification work presented in Chapter 3 provided a baseline for identification of the macrofossils, comprehensive coverage of the British Flora was not possible.

The identified macrofossil assemblage in each sample consisted of a range of macrofossils identified to different taxonomic levels. This limited the usefulness of the assemblages for reconstructing precise vegetation composition in floristic terms. Structural reconstruction was possible, but floristic reconstruction relied heavily on the use of seeds and other identifiable components. The differences in identification also

meant that one species could be represented by several groups of macrofossils, causing over or under-representation of species depending on the depositional environment.

4.10.2.4 Taxon presence

Remains of the most abundant taxa in the recorded vegetation were usually the most ubiquitous in the samples and also dominated sample abundance. Dominant taxa in the vegetation were usually present in one form or another in the macrofossil assemblages. Therophytes and other plants that produce numerous seeds were the most commonly encountered and were widely spread in several sites contributing to the allochthonous component of the assemblages. Taxa of limited cover abundance in standing vegetation were often unrepresented. Taxa representation in the samples was usually good, especially the seed and fruit assemblages. Samples from closed vegetation in areas subject to limited air and water movement contained the highest proportion of autochthonous taxa and many samples from these situations contained most of the taxa in the standing vegetation. Non-seed macrofossils were highly autochthonous and rarely contained any material from outside the recorded marsh vegetation.

Seed assemblages tended to represent a wider range of taxa than the non-seed assemblages, although this reflects the lower potential for identification of the non-seed macrofossils as much as actual presence. The seed assemblages also usually incorporated more allochthonous taxa than the non-seed assemblages and therefore in ubiquity terms, they provided a less reliable source of data, although the seed assemblages were always of a higher taxonomic resolution. Many of the allochthonous taxa in all of the samples and both seed and non-seed assemblages, even those from mudflats, were usually from vegetation growing near to the sample point. Higher quantities of allochthonous taxa were usually found in samples with regular tidal influence. Creeks, mudflats and samples near the vegetated saltmarsh edges contained the largest proportion of allochthonous taxa.

Overall, the macrofossil assemblages provided a good census of the range of taxa growing at any sample point, with seed assemblages providing a more detailed taxonomically detailed, but less spatially reliable picture than the non-seed material. The more complex vegetation with high floristic diversity was relatively less well represented. This may be due to a combination of the high spatial heterogeneity of the vegetation and macrofossil rain and the presence of many taxa of small cover abundance and limited

seed production. Even so, the taxa present were environmentally specific. Many of the allochthonous taxa were present in small numbers and local taxa tended to be present in large numbers and dominated the assemblages, although some taxa did not conform to these rules. This observation suggests that while presence is a useful characteristic, its use in isolation limits the potential interpretation of macrofossil data. High abundance usually indicated correctly that a taxon was present at or near the sampling point. This does not mean that quantitative macrofossil assemblage descriptions can be directly interpreted as indicating the relative abundance of major vegetation elements. It does, however, with a consideration of specific taxon macrofossil characteristics, provide a means of evaluating the reliability of taxon in an assemblage as a source of local vegetation information.

4.10.2.5 The quantitative reconstruction of vegetation using macrofossil data

As discussed above, the macrofossil assemblages in all environments derived overwhelmingly from vegetation at or near the sample points. The abundance of taxa in macrofossil assemblages in the surface samples rarely, however, correlated exactly with the abundance of taxa in the standing vegetation. The most dominant taxa in the local vegetation repeatedly contributed the bulk of both seed and non-seed macrofossils to the assemblages and it can accurately be said that the most abundant taxa in the assemblages were usually vegetation dominants or co-dominants. Mudflat and creek assemblages were the least representative of local standing vegetation, while samples from the vegetated marshes and fens varied in fidelity. The usefulness of abundance as an indicator of the abundance of a taxon in an assemblage was determined by:

1. The taphonomic characteristics of the depositional environment in which the sediments accumulated;
2. The dispersal potential and spatial fidelity of the particular macrofossil, determined partly by the species;
3. Productivity of the species in the source vegetation;
4. The toughness of the macrofossil in a given environment;
5. The potential for identification of the macrofossils;

Seed assemblages tended to be dominated by the local dominants, typically woody or herbaceous perennial plants, with therophytes also being well represented. The

seeds of the latter, and taxa adapted to aerial and water dispersal, were commonly preserved in abundance even when not present at the sample site. This was especially the case at Burham Marsh where seeds of the therophyte *Atriplex prostrata* and the aerially dispersed *Epilobium hirsutum* were dominant in several samples when absent from the vegetation. Seed dispersal over large distances was noted even in the relatively closed wet woodland habitats. The various dispersal mechanisms caused mixing of seeds from numerous taxa over wide areas of the sampled habitats, especially in the saltmarshes. Broad upper and lower saltmarsh zones could be distinguished at Snape Saltings, the most thoroughly investigated site, on the basis of seed assemblage data. Distribution of this seed rain was, however, uneven, as shown by the variable abundance in the Block samples. Seed abundance data, therefore, usually reflected the productivity, dispersability and survivability of a seed type in a particular habitat.

As well as perennial dominants, local therophytes, especially those of high cover abundance were also contributors to the seed assemblages, although the seeds were usually well dispersed and only large concentrations verified a local presence. In saltmarshes, these latter annual plants (e.g. *Atriplex prostrata*, *Salicornia europaea* agg. and *Suaeda maritima*) were almost absent in the non-seed macrofossil assemblages, as were many of the broad-leaved perennial Dicotyledon herbs (e.g. *Plantago maritima* and *Aster tripolium*). Dicotyledon herbs were usually only represented as seeds. In several cases, the seeds of Monocotyledon saltmarsh dominants were absent or under-represented in assemblages. *Festuca rubra* was almost always under-represented and it was common for *Elytrigia* and *Puccinellia* to be under-represented. This may reflect the preferred reproductive strategy of these taxa in established saltmarsh environments. The standing vegetation cover abundance figures for the samples from Snape Saltings have been compared to the DOMIN figures of the seed and fruit assemblages as a proportion of all of the seeds and only the local seeds. The figures make sober reading and confirm that while major taxa are usually incorporated in seed assemblages, there is considerable mixing, and direct interpretation of abundance data is an inadequate means of reconstructing the floristic detail of standing vegetation.

In the freshwater environments a similar overall pattern of representation was apparent. The major canopy elements were well represented in the seed and fruit assemblages from wet-woodlands, although minor canopy taxa (e.g. *Fraxinus excelsior*) and shrubby understorey taxa (e.g. *Crataegus monogyna*) were often absent. This may

be due to the suppression of fruiting in these taxa by the presence of dark conditions. Most of the dominant groundstorey taxa were also present, although minor components may have been missed, again probably as a result of suppressed or low seed production. Dominants of the herb fen environments also dominated the seed assemblages. Interestingly the samples from Hickling also contained many taxa that were not recorded in the standing vegetation, especially *Juncus subnodulosus*, a taxon present in some areas, the seeds of which were well dispersed in large quantities. It is possible that these taxa were missed in the vegetation survey. However, there was evidence of a considerable movement of seeds in the fen environment, presumably by water dispersal, and it is possible that these taxa were growing in other areas of the site. The vegetation at the fen sites was usually complex and locally variable. The local dominants were usually well represented. However, most of the minor taxa were incorporated only sporadically and while the abundance, when present, was an accurate reflection of a taxon's importance in the vegetation, incorporation and, therefore, representation of minor vegetation elements was sporadic. Some taxa that were generally under-represented, such as *Lysimachia*, were evident in relatively large numbers when present as a vegetation dominant although they were swamped by other taxa. Presence of large quantities of the seeds of this taxon, as with other under-represented taxa such as *Atriplex portulacoides, Calystegia* and *Aster*, are indicative of much greater presence in the standing vegetation than a bare reading of the abundance may suggest.

Non-seed macrofossil assemblages incorporated only a proportion of the taxa present in standing vegetation, usually the canopy or groundstorey vegetation dominants. Bulky Monocotyledons with massive stem and leaf production and dense root/rhizome systems were favoured in the assemblages. Where these taxa dominated the vegetation, the identified macrofossils accurately reflected the dominance. However, in more complex vegetation, many elements, especially perennial Dicotyledon herbs, were absent. The non-seed assemblages reflected accurately the dominance of the local Monocotyledon dominants, but the abundance could not be used to interpret directly the cover abundance of a taxon in the standing vegetation. Where the root and other macrofossil DOMIN figures were compared for Snape Saltings, the correlation between presence, especially when a plant was dominant, was good. The presence and abundance of a plant, especially as roots and rhizomes, was dependent on the chances of a sample collecting it, and for taxa with limited or fragmented distributions, sampling of the non-

seed material was unlikely. Many taxa were also not distinguishable in the non-seed assemblages - for example, the leaves of grass species and many of the root types. Some non-seed components, especially some Monocotyledon stems, were mobile in saltmarsh environments. Super-abundance of one taxon was often found: for example, the leaves of *Atriplex portulacoides* or many of the root/rhizome counts. This is unsurprising considering the type of growth of many species.

Non-seed assemblages from the more floristically diverse fen environments showed a similar pattern with local dominants well represented. Canopy elements were only partly represented in the leaf and bud-scale assemblages from the wet-woodlands and incorporation of leaves especially was sporadic. Again, leaf abundance was usually an inaccurate means of determining the actual abundance of taxa in the vegetation, although the most abundant leaf types did derive from vegetation dominants. Dominant groundstorey vegetation and taxa in the herb-fens were present in the non-seed assemblages, including the leaf assemblages, where accumulated. Minor components tended to be absent and the non-seed assemblages commonly incorporated leaves of many taxa, including the Dicotyledon herbs. The presence of a moderate abundance of leaves in the samples is perhaps more important in distinguishing the presence and local dominance of a plant than the actual abundance figure in comparison to others.

Multivariate analysis of the samples showed the main trends in representation and the suitability of macrofossil abundance as a means of reconstructing standing vegetation in the different environments. Non-seed macrofossil abundance was found to correlate more closely with vegetation stands in saltmarsh environments. Seed assemblages were much more variable in saltmarshes and rarely corresponded with vegetation parameters at all. This was demonstrated repeatedly in CCA of the surface sample macrofossil records and standing vegetation data. A confused spread of points across the CCA axes for seed assemblages was replaced by a more coherent range of sample clusters corresponding to vegetation parameters when non-seed macrofossils were considered. The exception was with the seeds of many Dicotyledon herbs (e.g. *Triglochin maritimum*) that corresponded well with standing plant distribution and abundance. However, the low level of identification of most non-seed macrofossils precludes even genus-level identification of the surface vegetation. While this was less of a problem in the modern observations, it will cause a greater element of uncertainty in ancient records.

Conversely, the seed assemblages from herb fens and wet-woodlands provided

the most coherent comparison to standing vegetation in the CCA, and CA clusters were more coherent than the non-seed macrofossils. This perhaps reflects, in the case of the herb fens, the problems of comparing records of vegetation homogenised within quadrat samples with macrofossil records from tightly bounded surface samples. In this environment, and that of wet-woodlands, the dispersal powers of seeds were useful in providing a local mixed picture at the sample point that reflected the wider vegetation. This is useful in closed environments with obviously limited movement of plant structures.

Quantitative analysis of macrofossil assemblages does provide useful data, although only some assemblage components correlated with the standing vegetation abundance. The data presented here do, however, suggest that use of quantitative seed and non-seed data together provides the most reliable and useful basis for macrofossil interpretation, providing at least some potential for representation of most plant taxa and life-form groups.

4.10.2.6 Alluvial macrofossil assemblages as a basis for vegetation reconstruction

Plant macrofossil assemblages are complex entities consisting of a range of plant components that all have a variable chance of inclusion in sediments depending on the physical and dispersal properties of the species and the characteristics of the depositional environment. Analysis of macrofossils from alluvial surface samples in this project has demonstrated that, with some exceptions, most assemblages contain macrofossils from vegetation standing at, or near the sample point. In most situations, autochthonous taxa were the most ubiquitous and abundant. Macrofossil abundance is useful for determining local dominants, if not the more detailed elements of vegetation floristics. Some of these details may be teased out of the data with a consideration of the taphonomic characteristics of particular taxa in particular depositional environments.

Where allochthonous taxa were present, many derived from vegetation outside the particular sampled vegetation formation, but within the relevant environment. Allochthonous taxa from beyond the environment tended to be present in small numbers and were minor assemblage components. Most allochthonous inputs in estuarine settings could be identified on the basis of environmental preference and generally contributed little to the overall macrofossil assemblages. They provided an incomplete, yet potentially useful, census of some of the more productive and well dispersed seeds of taxa in the

area, perhaps useful for sensing new plant presences in some Holocene settings. Allochthonous taxa were less distinguishable in fen environments, and again, were usually a minimal input.

In environments without standing vegetation, namely mudflats and creeks, the macroflora was mainly derived from nearby vegetation, although this varied with the openness of the environment. Most of the creeks sampled in this project were reasonably closed and those from nearer open channels may contain more allochthonous inputs. Similarly one would expect mudflat sediments to contain more allochthonous matter from a progressively wider catchment nearer to the permanent river channel and away from the saltmarsh, or nearer to the sea, with increasing tidal influence.

Autochthonous taxa in the assemblages provided a valid and potentially useful means of reconstructing vegetation, although dominants were usually favoured in the assemblages and interpretation of the assemblages was less simple than directly transferring macrofossil abundance to standing vegetation abundance. While the results of quantitative analysis of whole assemblages was mixed, a similar pattern of representation was noted in many sites, that is that the most abundant seed types/taxa in assemblages usually included important local vegetation components. Minor taxa were commonly absent and different macrofossil classes sampled different vegetation elements. Seed assemblages were the most useful in taxonomic terms and tended to sample a broader range of taxa and structural groups, especially the often well dispersed rosette plants that were absent in the non-seed assemblages. The non-seed assemblages were biased towards the more productive and well spread plants. Most of the structural elements of the vegetation were usually present, although only if the taxa were used as representatives of a structural group. Complete representative suites of macrofossil classes were not usually preserved.

Detailed reconstruction of the vegetation was not possible beyond stating whether taxa were major or minor vegetation elements. Quantified NVC-type vegetation reconstructions would not be reliable if based on a direct transfer of macrofossil abundance to standing vegetation abundance. Major components are, however, reliably identified in most environments, although samples from the edges of marshes were less reliable. Identification problems limited the taxonomic resolution of all of the assemblages, especially the non-seed material, adding to the obstacles barring detailed and precise vegetation reconstructions. It seems unlikely that many of these problems

would be overcome and it seems unlikely that more precise non-seed macrofossil profiles could be attained.

A broader type of vegetation reconstruction is attainable using macrofossil analysis of alluvial sediments. Both seed and non-seed assemblages are required for this as they provide complementary information about standing vegetation. The data they provided was found to be complimentary and interpretations made using one type of macrofossil were re-enforced by analysis of others. Vegetation is a complex three-dimensional phenomenon and the samples inevitably come from a small spatial area. Seed-shadows from individual plants overlap and are affected by environmental and taxon-specific characteristics. Non-seed macrofossils are usually highly local in derivation. Use of both types of data provides the best picture of past vegetation. A multi-disciplinary research approach is also required using a combination of species abundance, species presence, sedimentology, macrofossil class analysis and studies of macrofossil dispersal and reproductive behaviour to provide the most complete interpretation of macrofossil assemblages. Sedimentary data are also vital to ensure that some environments can be distinguished. These observations are consistent with work of Tertiary floras (Gastaldo and Ferguson 1998). Only the most basic sediment descriptions were attempted in this project and it seems likely that other parameters, such as magnetic susceptibility and particle size analysis may provide useful data for improving interpretations.

A broad interpretation of macrofossil data in terms of dominant and minor taxa in the assemblages may not only be the most attainable, but also more relevant for the main research questions addressed by palaeoenvironmental analysis than NVC-style reconstructions. Broad upper and lower saltmarsh zones were identifiable using the euhalobic, mesohalobic and oligohalobic classification discussed in chapter 2. The data from Snape split the site into two broad zones that correlated with the main vegetation patterns and zonation of the site. Macrofossil assemblages tended to include taxa from the upper or lower saltmarsh zones as well as the local taxa. If only ultra-local taxa had been included, some assemblages would have been difficult to place on the saltmarsh. The homogenisation of assemblages in the different zones actually overcomes the parochial nature of many of the assemblages and the nondescript vegetation they represent. This type of classification is useful when trying to locate and track tidal heights. Broad changes in wet-woodlands would also be identifiable in this way.

Although spatial trends in macrofossil abundance and presence are understandable, some degree of temporal averaging will cause merging of assemblages from different periods. Mostly non-seed data would be affected by such mixing, especially subterranean components. One possible way to check information would be to use seed characteristics as a gauge of temporal mixing of non-seed material.

4.10.3 The usefulness of different types of macrofossils

Moss remains were not systematically identified in the standing vegetation nor were they identified in the macrofossil assemblages. Only in the wet-woodland sites were they present in considerable numbers, forming a dense cover in some open areas and commonly forming epiphytic communities on trees. Moss macrofossils were rarely recovered in macrofossil assemblages, although where they were preserved they commonly were in good condition and may have been identifiable to a high taxonomic level. They clearly provide a means of identifying another component of the vegetation but seem to be rarely and unevenly incorporated into alluvial sediments.

Woody stems and stem components were preserved in the wet-woodland samples and also in some of the samples in saltmarshes where *Atriplex portulacoides* grew. Wood was usually only preserved in any quantity where arboreal or woody taxa were present in the vegetation. In the wet-woodlands the peat was often composed mainly of degraded wood and indeterminate matter. Much of the wood in these samples could not confidently be assigned on the basis of structure to stem or root wood. However, given the high canopy turnover, most probably comes from the stem structures. It was clear at Bure Marsh that woody litter was a major contributor to the assemblages, but decay was pronounced and only rarely were large wood fragments preserved. Branches and twigs penetrated the peat and it seems likely that wood preserved in an identifiable state may be intrusive, only surviving when it penetrated soft peat. Otherwise, wood decayed at the peat surface to a point where it is unidentifiable. This observation must bring up a question about the temporal fidelity of identifiable wood in peat samples, although it should be said that wood seems to have a high spatial fidelity. Wood fragments were preserved in some mudflat samples, but only as isolated rounded 'pebbles'. The preservation of *Atriplex portulacoides* wood in saltmarsh sediments was variable and woody components were only sporadically preserved beneath *Atriplex* stands.

Woody roots were preserved at several sites, with the greatest abundance in samples from near tree-bases. They offer a means of identifying local tree presence but poor identification potential restricts the usefulness of the remains. Bark was a common component in all of the samples where arboreal species were present. It was not identified and may well be unidentifiable. Bark fragments were not found widely distributed in the mudflats and channel samples, although its toughness may suggest that it has the potential to be entrained for long periods in rivers and channels.

Non-woody aerial stems were preserved in both saltmarsh and fen environments. Identification was generally to family or genus level and most of the remains were autochthonous. In saltmarsh samples it was uncertain whether many of the Monocotyledon remains were from aerial stems or stolons. Monocotyledon stems were commonly preserved, whereas Dicotyledon and Filicophyta stems were much rarer. This reflects the mode of growth of the different plants. Many of the stems of the Monocotyledon taxa grow from beneath the sediment surface and often collapsed onto the sediment surface, so had a greater chance of incorporation in sediments. Dicotyledon and Filicophyta stems tended to grow from the sediment surface and the stems usually decayed *in situ*. The Monocotyledons tended also to grow in dense stands with multiple tillers producing a vast quantity of stem material that had a greater chance of incorporation in sediment. Most of the stem remains were autochthonous, although incorporation was sporadic. The remains, therefore, provided a spatially sensitive, but taxonomically insensitive source of data. Identification may well improve with more research: however, an outstanding problem will remain the temporal averaging caused by the penetration of sediments by rhizomes and emergent stems. In mudflat and transitional samples the stems of the pioneer taxa *Salicornia* and *Suaeda* were commonly preserved and provide an important resource for determining the environment.

Buds and bud-scales were preserved mainly in the wet-woodland sites and large assemblages were only preserved where arboreal taxa were present. Large quantities of the bud-scales of a taxon were a good indicator of a taxon's presence. They occasionally appeared in estuarine sediments, usually as single scales, and from local taxa in riverine fringe vegetation. Buds are produced at the surface and are likely to be temporally sensitive, unless penetrating sediments on twigs. They provide a useful and durable source of data and are important for confirming the presence of arboreal taxa and determining the dominants in wet-woodland vegetation. In some cases they were the

only macrofossil trace of minor canopy elements and understorey taxa. The estuarine data also show that they may be useful for providing evidence of the presence of some taxa in river catchments.

Leaves were a common find in samples, although they were rarely preserved in large quantities. Leaf preservation was highly dependent on the environment and rapidity of sediment cover. The Monocotyledon taxa were favoured again, probably because of their high productivity. Most leaves wither and decay on the plants in the case of the Monocotyledons and herbaceous Dicotyledons. It was noticeable that among the most commonly preserved leaves were those of *Phragmites*, a plant that grows in dense stands and sheds its leaves. Monocotyledon leaves were usually less commonly preserved than stems. Dicotyledon leaves were rarely preserved, with the exception of *Suaeda* and *Atriplex portulacoides* in the saltmarshes, the arboreal dominants in the wet-woodlands and some of the dominants in the fens. *Suaeda* and *Atriplex portulacoides* produced easily detached tough leaves that were evidently more likely to become entrained in the sediment column. The arboreal dominants in the wet-woodlands produced vast quantities of leaves, most of which are destroyed. The quantity of Dicotyledon leaves was often small in the peat samples and the drier environments at Wicken Fen had limited leaf incorporation. The leaf assemblages in the wet-woodland sites preserved mainly the dominant taxa, with only a few co-dominants and minor arboreal species preserved. Leaf incorporation was, nevertheless, sporadic and the utilised sampling method did not provide assemblages that could be reliably used to give a total census of standing vegetation and the details of arboreal taxon abundance.

The herb-fen samples only contained Dicotyledon leaves when taxa were present in large numbers. Identification was heavily dependent on fragmentation and surface erosion. Many fragments could not be identified. Those that were provide a useful identification tool and where present in large numbers, also indicate favourable high-water conditions and an anaerobic environment at the time of deposition. Leaf beds were not seen at the sampled environments, although they were observed in a ditch at Minsmere Marsh in Suffolk. Identification may be improved by further research, although improvements in technique cannot circumvent the problems of the innate fragility of leaves.

Petioles and rachis fragments were rarely preserved. Abscission surfaces were preserved in many habitats, although they are not easily identifiable. They do not provide a useful source of data in relation to other classes of material discussed here.

A range of other aerial non-seed macrofossils was potentially present including stipules, thorns, prickles and scales. Scales seen on Filicophyta rachis were absent from the assemblages. Prickles and spines were rarely preserved and are only identifiable to type. Stipules were preserved in wet-woodland samples from *Salix*. They were only preserved where *Salix* provided dense cover and usually in small numbers. As with bud-scales, they are mobile and were found in one estuarine sediment sample. Apart from providing some additional presence data, all of these macrofossil types were unimportant in the interpretations.

Non-woody underground stems again were mainly preserved by Monocotyledon taxa and usually only family- and genus-level identifications could be assigned. Dicotyledon remains were scarce, perhaps reflecting the sparseness of the taxa in the sampled vegetation. When present, Dicotyledon rhizomes proved difficult to identify, although identification could have been improved with further technical work and the quantity of anatomical data present in the literature suggests that this is possible. These remains provide spatially precise data and were of some importance for ascertaining the local presence of taxa. Underground structures do, however, have a lower spatial fidelity than other remains. Taxa varied in the depth of penetration, with some of the saltmarsh grasses having shallow rhizome mats, while taxa such as *Phragmites* had rhizomes that could penetrate several metres of sediment.

Rootlets proved to be one of the most ubiquitous and difficult macrofossils to identify. They were often featureless and many had lost important surface features. The ubiquity of this class of material and the potential taxonomic information attainable through even low-level identification suggests that they are a vital element of macrofossil analysis. When taxa could be distinguished, there was usually a strong correlation between the standing vegetation and the roots, although they were so local that they did often not include minor taxa or taxa that were absent from the exact sample location. Identification was a problem and is unlikely to become more refined as the features for identification are absent. Sectioning would produce important basic information (i.e. Monocotyledon versus Dicotyledon). However, systematic sectioning is not thought to be feasible. In most cases the rootlets ramified through sediment but were usually

concentrated near the sediment surface and for most taxa the majority of roots will be accurately represented near to the sediment surface. Several of the block samples picked up changes in the rootlet load that corresponded to other macrofossil changes and predicted vegetation changes, suggesting that root abundance is temporally precise.

Spores and sporangia were only produced by Filicophyta in the sampled habitats, although several Characeae oospores were preserved in samples, suggesting that these macrofossils may be carried far on floodwaters. Indusia were not recorded. Huge quantities of sporangia were produced in many situations and they had to be treated separately from the seed sums to prevent swamping. Incorporation was, however, sporadic and some sites with Filicophyta growth produced none. The presence of sporangia tended to indicate a local presence of fern; however, identification was always at a low level. Vegetative remains of ferns proved to be poorly visible and the sporangia provided a useful, if taxonomically limited means of verifying fern presence.

Seed and fruit assemblages were one of the most important elements of macrofossil analysis. A wide range of taxa and structures was preserved, including seeds, capsules and bracts. All were useful, with bracts providing additional and more reliable evidence of the local presence of tree species. Seed and fruit assemblages provided the most taxonomically high-level information with varying spatial fidelity depending on species. Abundance and presence data were also vital for interpretation. Seed and fruit elements have been discussed at great length so far elsewhere and no further pronouncements on them is necessary.

Of the detached individual tissues, epidermis fragments were among the most commonly encountered. They were highly identifiable and most abundantly preserved in the still, anaerobic sediments of the abandoned creek at Snape. As such they provide, with the sedimentology, a useful means of identifying similar environments.

Unidentifiable matter was a constantly present class of remains and was divided into obvious herbaceous matter and that which could not be assigned to any particular plant structure. Both classes of remains increased in abundance in creeks and mudflats, where environmental conditions were detrimental to macrofossil survival. Large quantities of herbaceous plant fragments were an accurate indicator of the presence of large quantities of herbaceous taxa in the vegetation, just as wood fragments were an indicator of the presence of tree species. Surprisingly then, the quantity of these

seemingly unprepossessing remains provides useful, if broad-scale, data about the vegetation and depositional environment.

4.10.4. Autotaphonomy of species

Macrofossil data from the sampled sites has produced a range of information about the representation of several taxa in alluvial macrofossil assemblages in a range of environments. As with the information about macrofossil assemblages as a source of data about past vegetation and depositional environments, the following is based on relatively few samples and few sites. The reliability of the information as a basis for interpretation varies for each species, especially for those in freshwater habitats. Repeated patterns of representation for some taxa, especially from the saltmarshes, do, however, suggest that these generalisations may be of interpretative use.

4.10.4.1 Tree species

The remains of tree species were widely distributed in the samples, small quantities being incorporated in many of the estuarine samples and dominating the macrofossils incorporated in the wet-woodlands.

Alnus glutinosa was only found growing at the sample points at Bure Marshes and Wicken Fen. Its seeds, cones and bud-scales were usually preserved where the taxa were present in the standing vegetation and were the main seed components when the taxon was dominant in the canopy. The seeds were also well dispersed, being adapted to water dispersal, and were found in many samples from saltmarshes and mudflats. Eighty percent of the seed occurrences were found where there was no vegetation (Figure 4.77a and Table 4.34). Bracteoles, cones and bud-scales were more spatially confined and provide a more reliable source of presence data for the tree. Leaves were identified at Bure Marshes and were often well preserved, although samples only contained the remains where the taxon was a major canopy dominant and the leaves were absent from drier wet-woodland sites.

The seeds of *Betula* were one of the most ubiquitous seed types encountered in the project and were some of the most well dispersed, being found in many samples (87% of occurrences) where it was not present in the vegetation. Where the tree was present in the vegetation its seeds were usually preserved along with cone bracts. The seed was commonly over-represented, being produced in massive numbers and preserved

Taxon	Number of samples in which taxon present in standing vegetation	Number of samples in which taxon present in seed assemblage	% of samples in which seeds present in assemblage and standing vegetation	% of samples in which seeds present where vegetation is absent
Acer pseudoplatanus	2	0	0	0
Alnus glutinosa	6	30	100	80
Althaea officinalis	3	1	33	0
Angelica sp	0	2	0	100
Anthriscus sylvestris	0	1	0	100
Apium sp.	0	7	0	100
Arctium sp.	0	1	0	100
Aster tripolium	46	33	46	36
Atriplex portulacoides	19	27	84	41
Atriplex prostrata	41	53	88	32
Betula pubescens	6	46	100	87
Bolboschoenus maritimus	2	1	50	0
Callitriche sp.	0	2	0	100
Calystegia sepium	33	11	33	0
Carex appropinquinta	0	0	0	0
Carex paniculata	4	3	75	0
Carex pendula	2	0	0	0
Carex remota	3	3	67	33
Carex riparia	2	0	0	0
Carex sp.	3	5	67	60
Characeae	0	2	0	100
Chenopodium sp	0	2	0	100
Cirsium palustris	0	4	0	100
Cladium mariscus	6	6	100	0
Cochlearia anglica	1	9	100	89
Corylus avellana	0	1	0	100
Crataegus monogyna	3	2	33	50
Epilobium sp	0	15	0	100
Elytrigium repens	11	20	100	45
Eupatorium cannabinum	8	8	75	25
Festuca rubra	5	8	20	88
Filipendula ulmaria	4	3	75	0
Frangula alnus	3	1	33	0
Fraxinus excelsior	6	1	17	0
Galium palustre agg.	7	4	29	50
Glaux maritima	9	12	22	83
Glyceria sp.	0	1	0	100
Hydrocotyle vulgaris	0	1	0	100
Iris pseudacorus	7	2	14	50
Juncus gerardii	19	40	84	60
Juncus maritimus	1	0	0	0
Juncus subnodulosus	3	7	100	57
Juncus other	0	9	0	100
Lathyrus sp.	0	1	0	100
Limonium sp.	6	4	33	50
Lycopus europaeaus	0	12	0	100
Lysimachia vulgaris	4	2	50	0
Mentha sp.	0	5	0	100
Molinia caerulea	2	1	50	0
Oenanthe spp.	0	12	0	100
Peucedanum palustre	4	4	75	25
Phalaris arundinacea	1	0	0	0
Phragmites australis	49	53	92	15
Plantago maritima	6	12	67	67
Polygonum/Persicaria spp.	0	4	0	100
Puccinellia sp.	29	44	79	48
Ranunculus acris	0	3	0	100
Ranunculus sceleratus	0	6	0	100
Rosa sp.	1	0	0	0
Rubus sp	4	10	25	90
Rumex crispus	1	3	0	100
Rumex hydrolapathum	2	2	50	50
Rumex spp.	0	11	0	100
Sagina sp.	0	1	0	100
Salicornia/Sarcocornia sp.	8	14	88	50
Salix sp.	9	12	89	33
Sambucus nigra	0	1	0	100
Samolus valerandi	0	1	0	100
Schoenoplectus lacustris	0	1	0	100
Solanum dulcamara	11	7	45	29
Sonchus palustris	0	4	0	100
Spartina anglica	9	6	11	83
Spergularia media	3	6	33	83
Stellaria spp.	0	2	0	100
Suaeda maritima	17	18	41	61
Triglochin maritimum	9	20	67	70
Typha angustifolia	4	7	75	57
Urtica dioica	8	11	38	73
Valeriana dioica	1	2	100	50

Table 4.34 Ubiquity data for taxa identified in the standing vegetation at sample sites

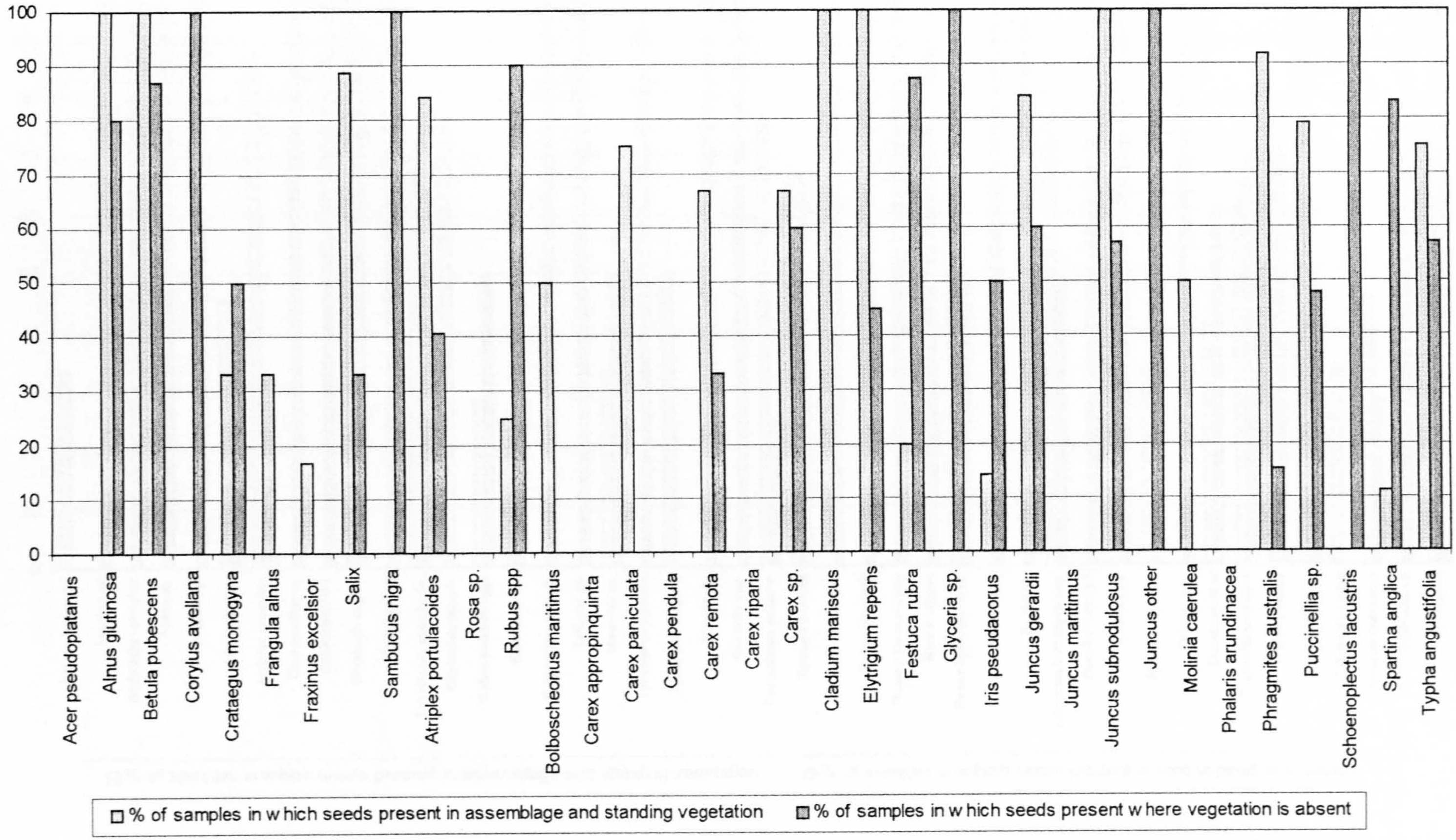


Figure 4.77a Comparative ubiquity data of seeds from Arboreal and bulky Monocotyledon taxa present in modern sediment samples

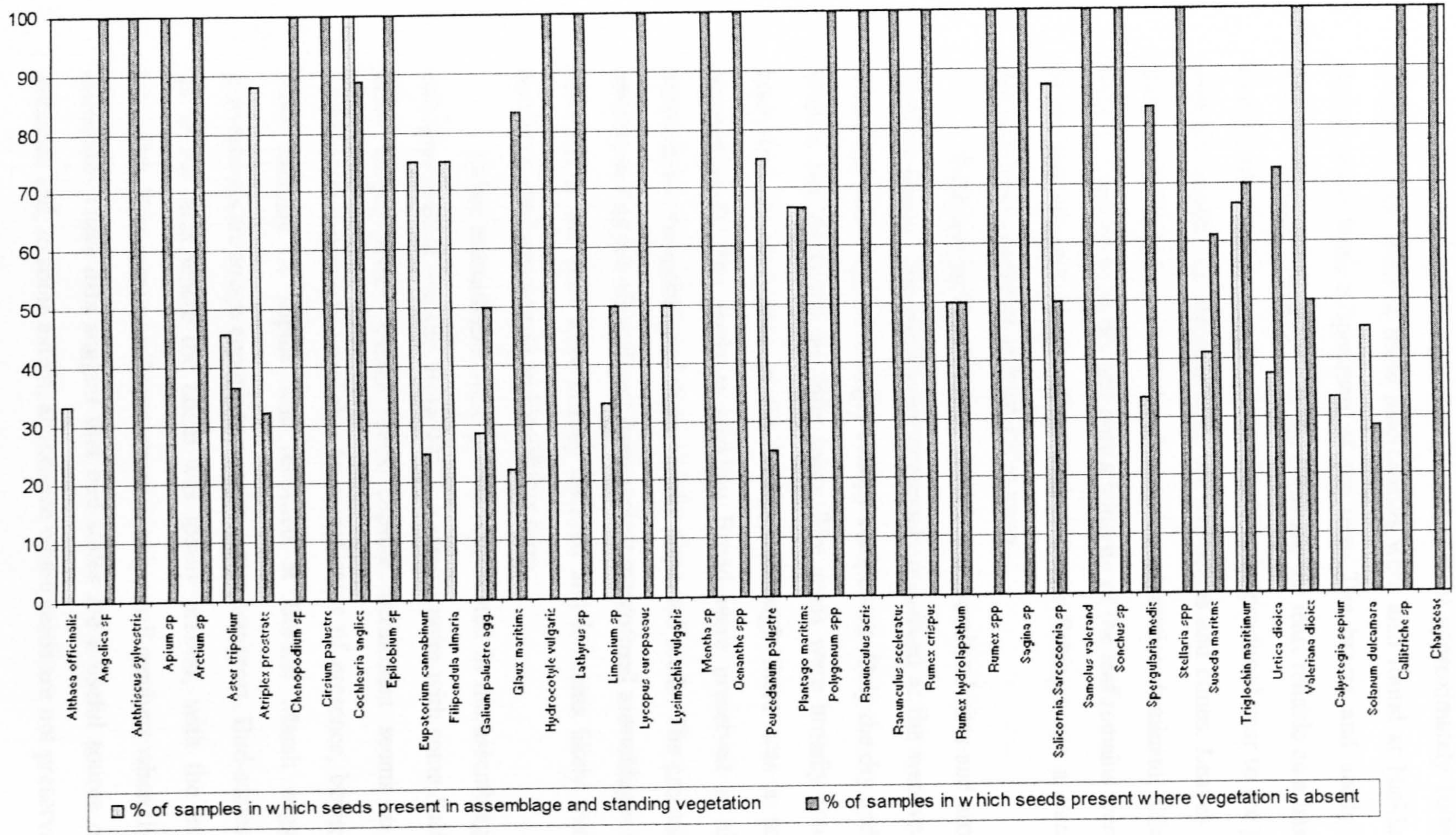


Figure 4.77b Comparative ubiquity data for seeds of herbaceous Dicotyledon and Monocotyledon rosette vegetation elements present in modern sediment samples

near standing vegetation. Cones and bud-scales were only preserved in large quantities where the tree was an important canopy element. The case of site 01/05 is interesting as both seeds and bracts were present in the macrofossil assemblages but the taxon was not recorded nearby in the vegetation (it was present approximately 100m distant from the sample point). Both of these macrofossils were also found at Hickling Broad, tens of metres away from a specimen of the tree. The bracts and seeds are clearly easily distributed on the winds. While the seeds are the least reliable as a basis for determining local presence of the tree, bracts are likely to be produced near to the plant and the most spatially reliable macrofossils were the bud-scales and cones. Leaves were preserved at Bure and Wicken Fen where the plant was a vegetation dominant, although sediments at both sites tended to be dry and only a minority of the leaf remains were identifiable. One of the few allochthonous leaf remains at Snape Saltings was a *Betula* leaf fragment, deriving from vegetation at least 150m away.

Salix species were present at both wet woodland sites and around the fringes of Hickling Broad. The seeds were commonly preserved at the wet-woodland sites, even where the taxon was not a major canopy component. Only the dry and isolated site 01 at Wicken Fen contained no *Salix* seeds. The seeds were broadly produced in numbers equivalent to abundance in the canopy, although there was a tendency for over-representation. The seeds at Hickling Broad were preserved in small numbers but demonstrate the mobility of these aerially dispersed seeds. The presence of seeds was of interest as they are often absent from ancient macrofossil assemblages. Many of the seeds recorded at the sites were heavily decayed and it seems likely that most would not survive in the long-term in an identifiable form.

Other macrofossils were poorly represented in the assemblages. Capsules were only preserved at one site, Bure 04/09, a sample point with some *Salix*, but far less than other sample points. Unlike seeds, capsule recruitment seems to be unpredictable. Stipules were similarly unreliable as an indicator of presence, being preserved in only three samples. A stipule was recorded at Borstal Marsh suggesting that these macrofossils are tough enough to survive water transport. Bud-scales were preserved in all of the sites where the taxon was locally present, with the exception of sample 01/04/09. They were usually preserved in only small numbers when the taxon was a non-dominant. These data suggest that bud-scales are a useful source of data about *Salix* presence and, to some extent, abundance where seeds are not preserved. *Salix* leaves are

easily identified and tough and were one of the more well-represented leaf types. They were preserved in large numbers at Wicken Fen site 03, where it formed dense shrubby growth. Leaf incorporation in other sites, where the taxon was a minor canopy element, was sporadic. In ancient deposits, as with other taxa, large leaf assemblages almost certainly indicate local presence.

Minor arboreal taxa were poorly represented in the assemblages. *Frangula almus* was present at Wicken Fen and was almost absent from the macrofossil assemblages, a few seeds being the only trace of the species in one sample out of three. Compared to the abundance of *Salix* macrofossils the taxon was hugely under-represented. The leaves of this and *Rhammus cathartica* were found to be very fragile during leaf reference slide work and it seems unlikely that, in the absence of standing water, leaves would be preserved in ancient macrofossil assemblages. *Acer* was a minor component and absent from the macrofossil assemblages and *Fraxinus*, a common minor element at Bure Marshes, was only represented by two bud-scales and two leaf finds. The latter finds show the importance of non-seed data for sensing minor arboreal components and also show that the chances of incorporation of macrofossils from a species is increased with greater productivity and standing cover abundance. *Crataegus* was a minor element at Bure Marshes and was recorded in one sample. The seeds were also preserved in several estuarine sediment samples, as was a specimen of *Corylus avellana*. The presence of these with a *Sambucus* seed and several bud-scales in estuarine sediments show that river sediments are a useful source of qualitative data about species presence in a catchment.

4.10.4.2 Shrubs and sub-shrubs

Atriplex portulacoides was present as a vegetation dominant at several saltmarsh sites. Its macrofossils were preserved in many of the samples where it grew, although the seeds were often sparsely incorporated and were also found in many samples where the plant was absent. The rootlets were the most reliable indicator of its presence. However, these are unlikely to be preserved in an identifiable form in ancient sediments as the main distinguishing character was colour. Woody elements and leaves were also regularly preserved, although their presence was much less consistent than the seeds and roots. Woody components especially were under-represented. However, leaves were more commonly incoporated. At Stonemarsh and the Snape Fringe area, stands of *Atriplex portulacoides* was represented by very few macrofossils and no seeds. At these sites the

leaves were important for determining the local presence of the plant and without leaf identification it would be less visible.

Rubus fruticosus was in the standing vegetation only at Wicken Fen and Hickling Broad, in environments with dry and humified peat. It was represented in the seed assemblages by its characteristic fruits and prickles that are most likely to have derived from the taxon. Seeds were often preserved in samples where the plant was not in the vegetation, always in small numbers. The most likely source of these widespread seeds is bird droppings. Only at Hickling Broad where the plant was growing at sample point 07/01 were seeds present in large numbers. Prickles were also preserved in the sample. The prickles identified in several samples may have derived from several taxa. However, *Rubus fruticosus* is the most likely source. Its presence in several samples from Bure Marshes may indicate that the plant was present, growing on the dry tree-stumps, but was unrecorded during fieldwork.

4.10.4.3 Bulky Monocotyledons

Phragmites australis was an important component of vegetation in saltmarsh fen and wet-woodland habitats. Its macrofossils were commonly preserved where it was a vegetation dominant, especially in the reedbeds that fringed many saltmarshes. Stems were the most abundant of the macrofossils in the sample set, leaves also being commonly preserved, although in much smaller numbers. Rhizome fragments were also commonly recovered. Preservation was favoured where dense stands of the taxon were present and its dominance in assemblages usually reflected a real dominance on the ground. In the wet-woodlands, a sparse reed-cover was commonly present but macrofossils of the plant were rarely incorporated. Only seeds were preserved and these were present usually in small quantities. Seeds were commonly preserved in the saltmarsh and fen environments alongside vegetative remains. They were rarely allochthonous components and were always recorded in small numbers. *Phragmites* was commonly over-represented in seed assemblages, its vegetative remains being preserved in proportion to its abundance in comparison to other similar taxa (e.g. the Carices), but being over-represented in comparison to Dicotyledon and hemicryptophyte Monocotyledons. Its preservation was favoured by the growth cycle, its stems originating below the sediment surface and leaves being shed in autumn forming a dense mat that enhanced the prospect of leaf incorporation in sediments.

Several saltmarsh grasses were present in the standing vegetation, namely *Festuca rubra, Elytrigia pycanthus* and *Puccinellia* spp. The main means of distinguishing the species was by use of the seed assemblages. *Festuca rubra* was under-represented in most of the samples and absent from many where it was in the standing vegetation. *Puccinellia* and *Elytrigia* seeds were present in most of the samples where the taxon was present in the vegetation, although *Puccinellia* was absent from 20% of the samples where it grew. The seeds of these taxa were widely dispersed and abundance was not necessarily an accurate reflection of the local presence of the taxon. Rhizome, stem and leaf remains of these taxa were also present, although many were identified using the knowledge of the standing vegetation, rather than microscopic criteria. In ancient material, such a method would be impossible and a family or sub-family level identification would only be attainable. Seed data, therefore provide a useful means of identification of the taxa, but the data are of variable spatial accuracy.

Several other grasses were present in the sampled vegetation and in general the presence of Poaceae vegetative remains was a reliable means of establishing the presence of grass taxa. The dense growth of *Molinia* at Wicken Fen site 02 was reflected in the vegetative remains and in the high abundance of *Molinia* seeds. Although few samples were analysed, it seems that the spatial resolution of the grass seed data in fens and wet-woodlands may be much higher.

Carex species were present at the wet-woodland and fen sample sites. Nutlets of this genus are notoriously difficult to identify, and the vegetative remains, where present, were only identifiable to family level. *Carex* seeds were in most of the samples where present in the standing vegetation. However, coverage was sporadic and samples from several sites lacked seeds when it was present in the vegetation, especially at Bure Marshes sites 5 and 8. This may reflect the suppression of seed production under dense tree canopies. The species identified in the assemblages should be regarded as 'types' and could be identified at that level because of knowledge of the standing vegetation. The dominant *Carex* species did not necessarily dominate the seed assemblages and *Carex remota* was repeatedly over-represented in relation to the seeds of the dominant *Carex paniculata*. Overall seed production was actually very low, but *Carex* species regularly and accurately dominated the seed assemblages of wet-woodlands where they were the dominant taxon. *Carex* vegetative material was present at most of the sample points where it was preserved. Roots were preferentially preserved over leaf and stem

material; however, in some samples the non-seed material was missing. *Carex* was well represented in macrofossil assemblages, although accurate species level identification was not possible. The Cyperaceae level identifications made here for the non-seed material could also probably be improved.

Cladium mariscus was in the standing vegetation at most of the sample points at Hickling Broad. The seeds were only found in samples where there was standing vegetation and the lack of seeds in samples 03/02/02 and 04 suggests that the seeds are not widely dispersed in fen environments. The seed abundance could not be related directly to standing vegetation abundance and *Cladium* was usually well represented in relation to other Monocotyledons and better represented than most Dicotyledons. Stems and leaf remains were sparsely preserved where the plant was preserved in large quantities. However, only half of the samples contained vegetative macrofossils. Roots would have been included in the Cyperaceae category and these roots were present in all of the samples where *Cladium* was present. *Cladium* was most adequately represented by its seeds, which appeared to be rarely spread beyond the local area of the plant and are tough, ensuring preservation.

Juncus gerardii was present at Snape and Angel Marshes and its macrofossils were commonly preserved in the samples. The most ubiquitous macrofossils were the seeds, present in many samples where it is in the standing vegetation and also well distributed across adjacent areas of the saltmarsh. High abundance of seeds was usually an indicator of the local presence of the taxon, but large abundance was also found in creeks and some marsh samples where the taxon was absent. The seed rain was more variable and better correlated with the standing vegetation at Snape. Many samples at Angel Marsh contained seeds where the plant was absent in the sample point vegetation. Capsules were better correlated to standing vegetation presence than the seeds. Stem and rootlet remains were commonly preserved in the samples although the stem remains were regularly found at locations where the species did not grow. Stems are therefore unreliable as indicators of the local presence of the plant. Rootlets were well correlated with the standing vegetation of the plant, although in some stands where the plant was present the roots were absent. Again, more movement in the stem and rootlet material was seen in Angel Marsh as a whole and also in the creek and mudflat sediments.

Juncus subnodulosus seeds were commonly distributed throughout the samples at Hickling, even when it was absent in the standing vegetation. The seeds, as with *J.*

gerardii are evidently easily distributed in alluvial environments and abundance was not an adequate means of determining the local presence of the plant. Capsules were only preserved where the plant was present in the standing vegetation, as were the vegetative components, mainly roots with occasional stem fragments. These remains were preserved only when the plant was a major vegetation element. The non-seed material was only identifiable at genus level and again the seeds provide the only means of determining the species.

The remains of *Iris pseudacorus* were sparse and underrepresented, seeds being only occasionally incorporated into sediments when the plant was growing at the site. Seeds were commonly preserved when the vegetation was absent and the seeds were clearly well distributed in fen environments. Rhizome fragments were preserved in several samples, being the only indication at Bure site 04/09 of the presence of this groundstorey dominant. Rhizomes at Hickling were found where the plant was no longer a live element of the vegetation. The plant was present nearby and evidently its thick rhizomes are persistent in fen sediments.

Typha was only present in the vegetation at Hickling Broad, where it was co-dominant at one site and present in the diverse vegetation at several others. The seeds of the plant were largely preserved in small numbers, although the sample from the co-dominant vegetation had 17 specimens. Seventy percent of the samples from sites with *Typha* in the vegetation contained seeds, with seeds being found in several samples where the plant was not present. In fen environments, the presence of large quantities of seeds will be a reliable guide of taxon presence. However, the seeds are well dispersed and preferably other remains would be identified. Non-seed material was present in several samples, including the characteristic roots, always where the plant was growing in the standing vegetation. Roots and epidermis fragments were distinctive and occasionally identified. Only where the vegetation contained *Typha* as a co-dominant were all types of identified macrofossil present. Where *Typha* was a minor vegetation element, incorporation of non-seed macrofossils was uncertain.

4.10.4.4 Perennial Dicotyledon herbs and Monocotyledon rosette plants

Perennial Dicotyledon herbs and Monocotyledon rosette plants were only represented by seeds in samples from the saltmarsh sites, with the exception of *Glaux maritima*. They were important elements of saltmarsh communities; However, the plants were usually

well distributed and not favoured for inclusion in surface samples of a small area. Rhizomes and leaves would only be included in the samples if they covered the exact point of growth. The more abundant, extensive and denser growths of bulky Monocotyledons were more likely to be incorporated in the samples.

Althaea seeds were present at Burham Marsh but only in a small number of samples at which the plant was growing and always in small numbers. The plant was a minor vegetation component, but was still under-represented. *Aster* was a common saltmarsh element at all of the sites. Only in the upper saltmarsh samples at Snape was it preserved in any quantity. The seed assemblages of *Aster* were unreliable as a source of information, being present in as many samples where it was a local plant as where it was absent (Table 33; Figure 4.77b). *Limonium* was under-represented, only a few whole flowers being preserved in the samples. *Cochlearia* seeds were present at Snape and Angel Marsh, although the plant was rare in the vegetation. Only in the saltmarsh fringe (area 01) at Snape were the seeds common, the highest abundance correlating with the presence of the plant in the vegetation. The seeds were unreliable as a means of identifying local plants, except in huge numbers.

Plantago maritima was present at Snape where its seeds were as likely to be present whether the plant was present in the vegetation or not. Capsules were preserved as well as seeds. The seeds of *Plantago* were well dispersed over a wide area where present. A 'rogue' concentration of seeds was present in sample 18 from a creek near an outpost of the vegetation sampled by the blocks. The presence of these seeds, with the overall pattern of representation, shows how well adapted to dispersal the seeds are. *Triglochin maritimum* seeds were also well dispersed in the upper area of the saltmarsh at Snape, where large concentrations of seeds were preserved. Seeds were preserved in most of the sample points where the plant was present in the vegetation. However, many other samples contained, sometimes large, quantities of seeds. *Triglochin* seeds were evidently well dispersed in saltmarshes and are unreliable as a source of spatially precise data, although again they were dispersed in the zone of the saltmarsh where the species was present. A similar pattern was seen in the records for *Glaux maritima*. This species was represented by seeds and leaves, both of which were highly mobile and widely spread over the upper zone of the saltmarsh where the plant was growing. Leaves of *Glaux* were unlike the other plants discussed in this section, being arranged along the stem axes and easily detached. Clearly, leaves only have a potential for deposition in

slow and stable sedimentary conditions if they are detachable and can be entrained in the sediment column.

Representation of this class of plants from mainly freshwater habitats was variable, mainly being restricted to occasional leaf fragments along with the seeds and fruits. The lack of leafy material in peats is due to the habit of many plants to decay *in situ*. Only where large concentrations of these taxa are present were the remains of aerial parts preserved in mires. The roots and rhizomes were rarely encountered and the roots were largely indistinguishable, carrying few or no identification features.

Epilobium seeds were present in many samples, especially from Burham where it was the dominant taxon in one of the block samples. All of the seeds were allochthonous, and while the plant did grow in abundance near to the Burham transects, it was 100m plus distant. The seeds of this genus are produced in abundance and are aerially dispersed. Large concentrations of the seeds would indicate its presence near to the site; however, it is not a reliable indicator of a local presence.

Lycopus europaeus was another common allochthonous seed type, being present in the vegetation of only one sample. Only a few seeds were incorporated at that sample point, reflecting perhaps its low productivity and high dispersal potential. The seeds are adapted for water dispersal and were found in several samples at Burham, even though the plant was absent, presumably as a result of tidal input. Macrofossils of the plant are not a reliable indicator of its presence in most settings, even the relatively low-movement fens.

Filipendula ulmaria seeds were present in small numbers usually only near vegetation with the taxon in it. They were absent from several samples where the plant grew. The seeds are evidently not well dispersed and presence is a reliable indicator of the plant in closed fen environments.

Galium paustre was a sparse but regular element of fen and wet woodland vegetation. It was only represented by seeds, and was absent from many samples where it was present in the vegetation and present in samples where it was not (Figure 4.77b; Table 4.33). The seed assemblages were always depauperate and it was an unreliable source of information about the precise vegetation at the point of sampling, although as with most seed types was recorded only in its habitat type.

Lysimachia was only present at Hickling Broad where it was a regular vegetation element. It was under-represented in the seed assemblages, being preserved in

small numbers and being present in only 50% of the samples in which the plant was present. The seeds were fragile and may be prone to decay. Leaves were only present where the plant was a dominant taxon and identification was uncertain. This plant is under-represented in macrofossil assemblages and small quantities of seed may be used to indicate considerable vegetation cover abundance.

Eupatorium cannabinum seeds were present in several samples in the wet woodlands and fens, the plant itself being a common component of both types of vegetation, especially on drier peats. Leaves of the plant were only preserved at Hickling, where large fragments were present in the peat beneath a dense stand of the plant. Otherwise, only seeds were preserved, and surprisingly, given its mode of dispersal, most of these were in samples from vegetation with the plant in it. The allochthonous specimens were preserved in small numbers and while small numbers were also present in the wet-woodland samples where the plant was extant, the autochthonous assemblages at Hickling contained large numbers of specimens. The seeds of the plant are aerially dispersed and so will turn up as occasional allochthonous inputs; however, large quantities almost certainly indicate accurately the presence of the plant at the sample site.

Peucedanum palustre was present at Hickling Broad and seeds were present in many of the samples where it was in the vegetation. The seeds were always preserved in small numbers and are mobile, making the seeds an unreliable indicator of exact sample point presence, although a good indicator of nearby presence. *Rumex hydrolapathum* seeds were similar, being well dispersed where identifiable in the marshes. Some fragments of *Rumex* leaf were preserved in the peat where the taxon was present. The seeds of *Valeriana dioica* were preserved in only one sample where the plant grew and other specimens were present in non-fen habitats suggesting that the plant is well dispersed, but occurrences in fen deposits may indicate the local presence of the plant.

Urtica dioica was present in only a few sample points as a part of the standing vegetation; however, its seeds were quite commonly encountered in all environments. Large abundances of seeds were not a good guide to its local presence and are overall a poor indicator of its presence.

4.10.4.5 Therophytes

Atriplex prostrata was a major component of the vegetation at Burham Marsh and a minor component in some areas of Snape. The seeds of the species were not

distinguishable from others in the genus. However, the large number of seeds of the genus were undoubtedly from the species at both sites. The seeds were present in often huge numbers where the plant was growing, but several samples at Burham contained its seeds in large numbers when the nearest example of the plant was several metres distant. As with other therophytes, the seeds are over-represented in macrofossil assemblages and are highly mobile. Rootlets were commonly preserved where the taxon was densely growing at Burham, but were absent in samples from areas of sparse growth at Snape. Leaves and stems were occasionally preserved, always at the point of plant growth, but were a sparse and unreliable source of data.

Salicornia was present in many of the saltmarsh sites. Only its seeds and stems were preserved, the seeds being indistinguishable from those of *Sarcocornia*. The seeds were well dispersed over saltmarshes, although they were usually found at the site of plant growth, often in large numbers. Many samples without growth of the plant contained the seeds, especially from mudflats adjacent to areas where the plant was extant. At Borstal and Angel Marshes, where the plant was present sparsely at some distance from the sample locations, the seeds were present in small numbers in numerous samples. The seeds are, therefore, well adapted to water dispersal and while a large abundance would suggest nearby growth, it may not be relied upon to indicate growth at the sample location. The stems were preserved near to the plants and in some abundance beneath the growing plants, and fragments of epidermis were also common. As with the seeds, however, the stems are mobile in saltmarsh environments, especially pioneer stands of vegetation and mudflats.

Suaeda maritima was present in the lower saltmarsh sites and again its seeds were well dispersed across saltmarshes. Less than half the samples from vegetation containing the plant contained seeds, although large assemblages tended to be accumulated where the plant was growing. The leaves of the taxon were present over a wide area at Stonemarsh and, as with *Salicornia*, presence showed nearby growth of the plant but not necessarily at the sample point.

Spergularia media was present in two sample points; however, the seeds were widely dispersed and were commonly present where the plant did not grow. The super-abundance of seeds in sample 61 at Snape may be an edge effect, or the seeds may have derived from nearby vegetation. The example shows, however, that the abundance of this therophyte is no guide to its abundance at a sampling point.

4.10.4.6 Climbers

Two climbers were common in brackish saltmarsh environments and freshwater fens, *Solanum dulcamara* and *Calystegia sepium*. Both taxa were under-represented, with *Solanum* only represented by seeds. Less than 50% of the samples underlying vegetation with the taxon in it contained seeds and always in small numbers. Its seeds were well dispersed at Burham, where it was mainly recorded, and there was no quantitative difference between the allochthonous and autochthonous assemblages. *Calystegia* was also massively under-represented with seeds present in only 30% of the samples where the plant was present in the vegetation. In no case were its seeds found as allochthonous elements and while presence of its seeds and capsules would be a reliable indicator of its presence in vegetation, absence may be due to taphonomic factors. The under-representation of seeds is due, as with *Solanum*, to low production, but also the fact that the seeds were fragile and tended to collapse and fragment after dispersal. *Calystegia* also contributed capsules and leaf fragments to the assemblages, but again, only where the plant was present in the immediate vegetation. *Calystegia* was a major vegetation element and is unlikely to be represented in the seed assemblages, making vegetative elements a potentially important source of information.

5. Plant macrofossil analysis of alluvial facies from the River Medway, Chatham, Kent

5.1. The site

Between 1993 and 1995 Canterbury Archaeological Trust and the Geoarchaeological Service Facility (GSF) of the Institute of Archaeology, UCL undertook monitoring, evaluation, excavation and sampling exercises for Kent County Council (KCC) at the construction site of the Medway Road Tunnel, Chatham, Kent (Figure 4.1). The works were part of the mitigation strategy negotiated between KCC and the Highways Agency to evaluate the damage caused to a deep deposit of Holocene alluvium uncovered at the site (Pine *et al.* 1994; Allen *et al.* 1995). The project also aimed to provide a record of the alluvium and the archaeological features it contained. Of particular interest was the excavation of the eastern approach to the Tunnel, an area of 45,000 m^2, where Holocene sediments filled the former floodplain to a depth of 13m and sealed Pleistocene gravels and a chalk bluff, the latter to the east of the site (Figures 5.1 and 5.2). Sediments consisted of peat and organic silt units intercalated with deposits of sand and silt. Archaeological remains were found within the sediments detailing activity from the Mesolithic (*ca* 7000 BP) to Roman periods. Plant macrofossils were preserved throughout the strata (Fairbairn in Pine *et al.* 1994) and, with other types of biological material, provided an unparalleled record of Holocene vegetation and environmental change in the Medway valley.

The analysis of the macrofossil record from the site is detailed here and aimed to fulfil the following objectives:

1. To act as a source for vegetation reconstructions providing:
    a) Palaeohydrological information (water qualities, height etc.);
    b) Palaeoecological data about specific communities, including:
        i) Floristic information,
        ii) Structural information,
        iii) Information about spatial and diachronous vegetation patterns,
2. To contribute to interpretations of the depositional environments in which sediments accumulated at the site;

3. Using 1 and 2 Above, to contribute to the reconstruction of the long-term sequences of environmental and vegetation change over the mid- to late-Holocene and contribute to the understanding of:

   a) Long-term vegetation development, especially the reaction of littoral vegetation to sea-level and other changes;

   b) Sea-level changes and changes in the river catchment;

   c) Human impact and influence on environment and vegetation;

   d) The local human environment and availability of resources to human communities;

   e) Phases of human occupation at the location.

The sample set also provided the opportunity to apply and evaluate the macrofossil analytical methods discussed above on a real sedimentary example in which a characteristically diverse range of sediments, archaeological deposits and practical problems were encountered.

5.2 Stratigraphy and archaeological evidence

The sampled sediments spanned a depth of between *ca.* -9.90m Ordnance Datum (OD) and *ca.* +2.50m OD (Figures 5.1 and 5.2). Access to the sediments was restricted by the method of construction which involved the cutting of steps and emplacement of sheet piling to prevent collapse of the excavation walls. Much of the recording of the sediments was in the form of descriptions of the cleaned step and bank surfaces. A series of boreholes was used to obtain sediment from areas concealed by the piling and to provide a more controlled spatial sequence across the site. Sections were also cut into the excavation bank at prescribed points to investigate in detail the main sedimentary contacts. They also provided an opportunity for sampling. The sections were determined as much by engineering concerns as archaeological concerns and the distribution was uneven, being biased towards the upper horizons. A facies sequence was constructed using the sum of borehole and section data and is shown in Figure 5.2.

The earliest geology recorded at the site is a chalk outcrop forming the bedrock at the eastern end of the site. Pleistocene gravels formed the earliest deposit uncovered

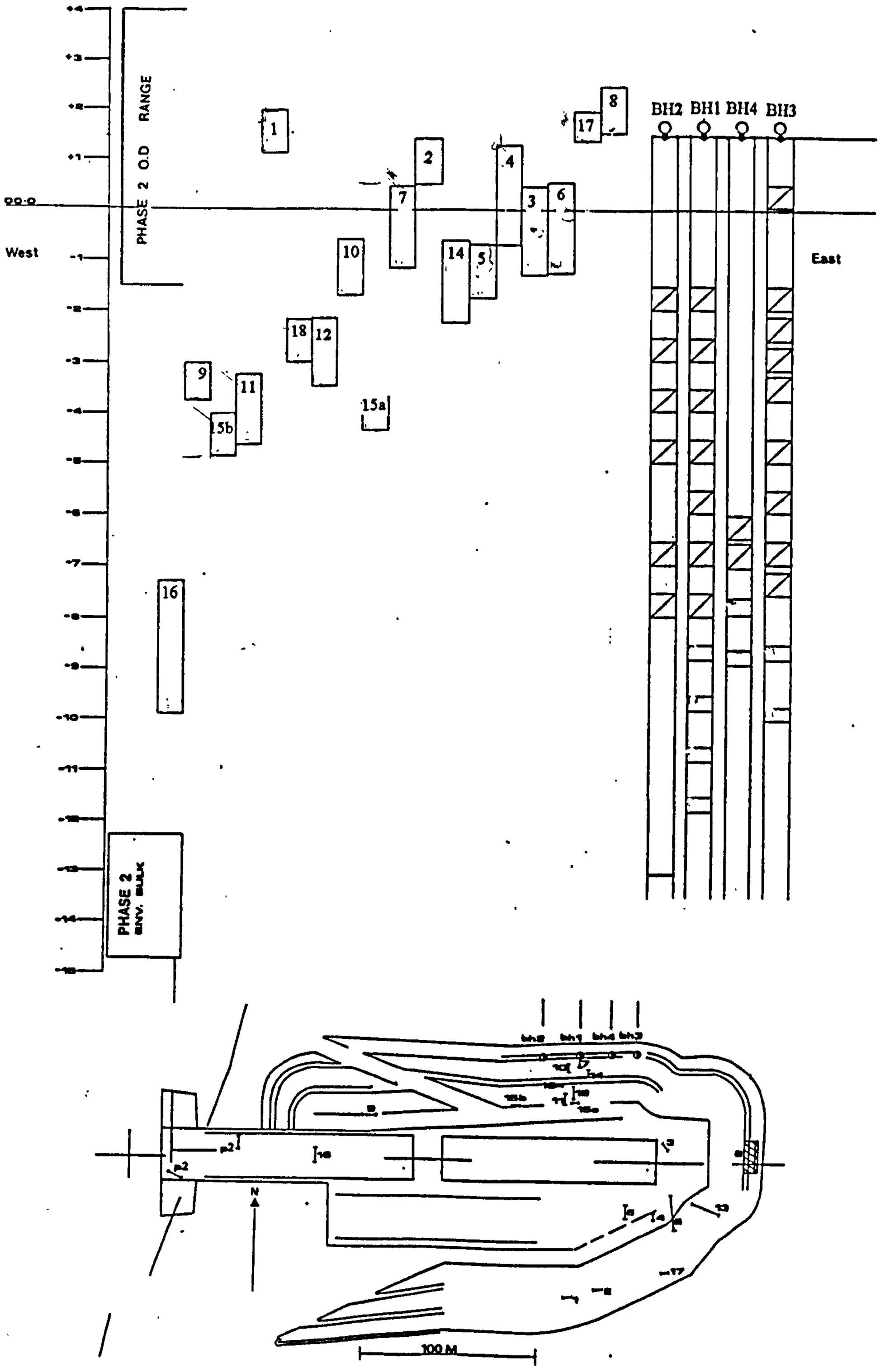


Figure 5.1 Plan and section of the Medway Tunnel site showing locations of sections from the Phase 1 works (After Pine *et al.* 1994). Scale to the left is in metres OD; BH/bh = borehole location; p2 = phase 2 works

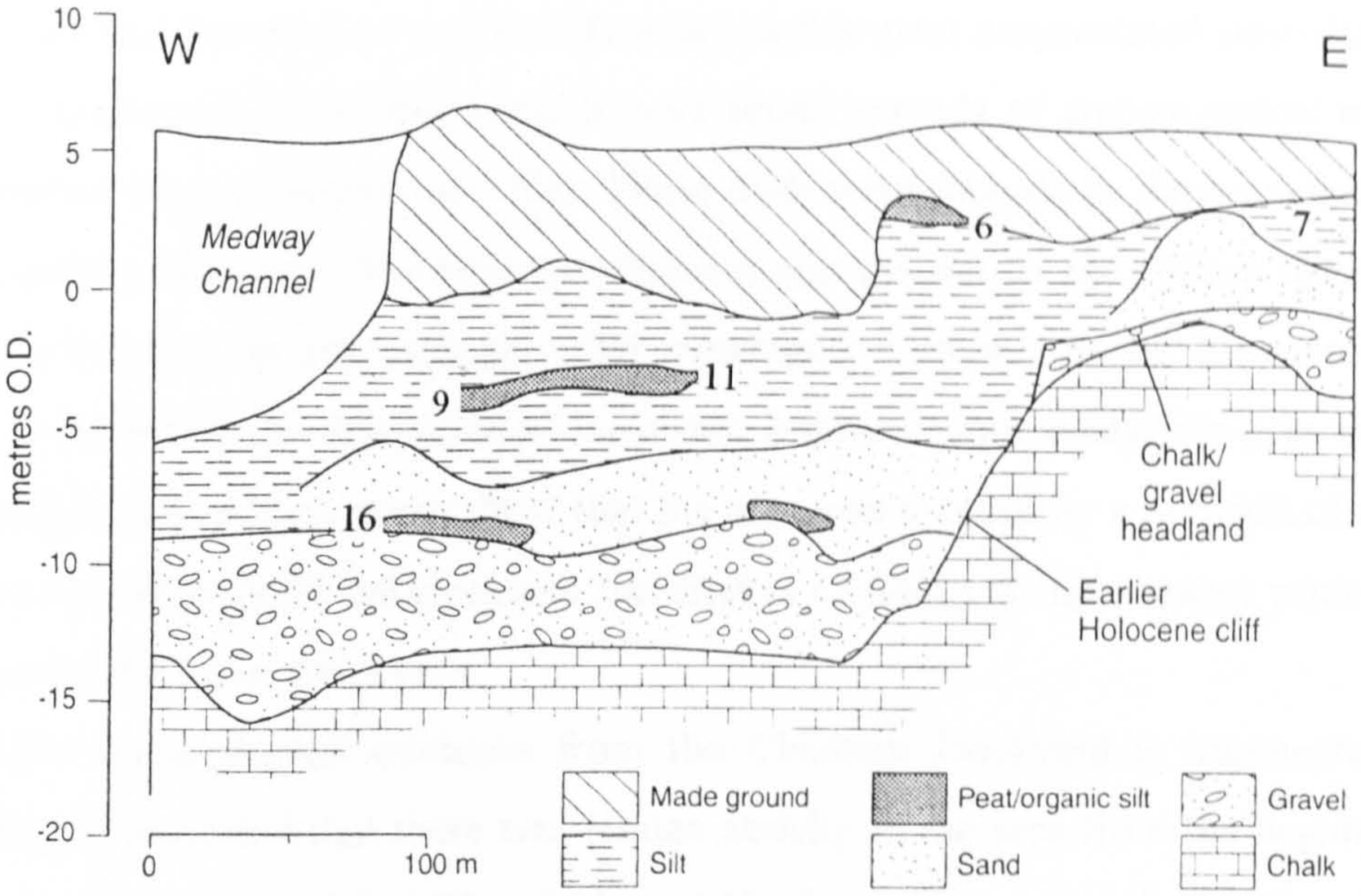


Figure 5.2 Schematic profile of the sediments at the Medway Tunnel site with relevant sections numbered (after Bates and Bates 2000)

in the deepest part of the tunnel excavation (hereafter the 'floodplain') and also formed a thin deposit atop the chalk outcrop (hereafter the 'clifftop'). The upper surface of the floodplain gravel terrace lay at approx. -9.90m OD. The higher clifftop gravels and sands included an ovate Palaeolithic handaxe, probably redeposited at the site, but indicative of Pleistocene human activity in the area.

The earliest Holocene sediments were confined to the floodplain and were found above *ca* -9.90m OD. Sands with gradually increasing organic content were described between -9.90m and *ca* -9.70m. Increasing organic content was accompanied by increasing content of silts and clays dated to *ca* 6900 BP. A flint blade (Mesolithic type) and abundant charcoal were collected from between -9.40m and -9.50m, indicating the presence of Mesolithic populations in the area. Above this point, the fine-grained, bedded, organic-rich sediments were found giving way at *ca* –8.80m OD to alternating beds of sand and sandy silts containing few visible plant remains.

A primarily clastic deposit is recorded up to *ca* -4.00m at which point a widespread episode of peat deposition occurred across the site. This has been dated to *ca* 4800 BP, a date consistent with the find of a Neolithic-type flint blade in the peat bed (Section 15). The peat unit varied in thickness and character over the site. It included woody and herbaceous patches, varying locally. Above the peat bed was a band of fine-

grained silts that extended to *ca* 0m OD where a thin peat accumulated post-dating *ca* 3000BP. Above and below this horizon were found spreads of archaeological material and individual finds of pottery and flint. These finds were thought to derive mainly from clifftop settlement activity. Permanent settlement was present on the clifftop by the Iron Age. This came to an end with the tidal inundation sometime in the Romano-British period, as shown by the deposition of laminated sediments and sandy-silts over the site. By the eighteenth century, maps show that the area was crossed by a network of ditches and walls, probably flood defences and the ditches of tidal grazing marshes prior to the expansion of the Royal Dockyard.

The archaeological evidence from the Chatham Dockyard is fragmentary but compelling. It indicated that there was human activity in the area from the beginning of Holocene sedimentation. Most Mesolithic and Neolithic finds are single artefacts in fine-grained sediments and sands, the presence of which cannot simply be explained by natural processes. Mesolithic activity was sparse and probably derived from short-term occupation as part of a seasonal round of activity or less-structured foraging and/or hunting expeditions. Sparse activity from the Neolithic and Bronze Age is evidenced on the floodplain and clifftop, by stray finds of flints on the former and the presence of ditches with charcoal-rich fills on the latter. The nature of the clifftop settlement during this period is uncertain, but both a domestic and/or ceremonial function could be suggested. The evidence was so poor as to prevent confirmation or refutation of either possibility. The charcoal-rich fills were dated to between *ca* 3800 BP and *ca* 3500 BP (Allen *et al.* 1995). The presence of ditches may indicate that the site was subject to local flooding and/or high groundwater at the time of use. In the Iron Age and Romano-British period a settlement was established on the clifftop. Accumulation of sediments containing plant remains in low-lying areas and hollows on the clifftop indicate that high groundwater levels were sustained during the period.

The sequence at the site was almost totally destroyed by construction work. Environmental samples and evidence were recovered from non-contiguous sections that, nevertheless, sample the whole 13m sequence, often at several synchronous points. Archaeological excavation was limited and poorly funded, but it provided tantalising evidence of a long history of human use of and movement over the floodplain and the adjacent chalk outcrop. Much of the evidence is ephemeral: individual finds and limited spreads of artefacts and charcoal in unpromising floodplain sediments, with limited

excavation of ditch segments and truncated features on the chalk cliff. Only the later settlement provides extensive evidence of a permanent, human presence. The evidence does, however, suggest the use of the river margin, the marshes and mudflats that existed at the site for millennia. This record is consistent with the evidence from several river margins and floodplains including the Thames, Essex Rivers and Severn Estuary. The chalk cliff would have projected above the surrounding land for several millennia and commanded a view over the river and surrounding wetlands. Use of this feature may have changed over the period that it was above the floodplain and permanent settlement can only be verified from the Iron-Age and Romano-British periods. Some ceremonial use and temporary settlement should not be ruled out for other periods.

5.3 Materials and Methods

5.3.1 Sample framework

Samples were selected from sections exposed in the Phase I and Phase III works (Pine *et al.* 1994; Allen *et al.* 1995). They included bulk samples, samples from monoliths and specially collected intact sediment blocks. The sample set was selected to investigate the macrofossil record in the main organic units identified during fieldwork, the regressive and transgressive transitions between clastic and organic sedimentation and areas in which human occupation or activity was recorded. The whole project focused mainly on the episodes of organic sedimentation, using the philosophy that the peaty horizons represented potential stable land-surfaces that could be used as activity areas (Allen *et al.* 1995). While some non-peat producing environments may also provide stable surfaces, the sample set provided a useful sub-set of the sediments on the site and focused attention on the main sedimentary transitions.

5.3.1.1 Phase I Section 16

This was the deepest section recorded at the site. It included a sand unit overlying the Pleistocene gravel, over which a sequence of laminated silt-clays developed, followed by intercalated sands and silts. Assessment showed that the silt-clays contained rich plant remain assemblages, including tree leaves (Fairbairn in Pine *et al.* 1994). Samples were analysed from Monoliths 1, 2, 4, 6 and blocks 1 to 10, covering depths from -7.38 to -9.90m OD. The top of the basal sand at -9.75m was dated to 6930+- 70BP (see Allen *et al.* 1995) and a flint blade, abundant charcoal and fire-cracked flint were collected from

Monolith 9 at between -9.40m and -9.50m corresponding to Plant Macrofossil Block 6 (Pine *et al.* 1994, 46-47). The main aims in studying plant material from this section were to determine the environment of Mesolithic activity and also the environmental, vegetation and hydrological changes that occurred during the first phases of Holocene sedimentation

5.3.1.2 Phase I Section 9

This section sampled the peat lying at -3.50m. All of the samples were collected from a block stack between -3.00 and -4.00m. Samples covered the main transitions between clastic and organic sedimentation. The peat was humified through most of the profile with discrete lenses of silt and fine sand noted at several levels. Small patches of laminated sediment with leaf layers were also preserved at several points. The peat at -3.50m OD was dated to 4820+-70BP (Allen *et al.* 1995) and correlates with the organic unit sampled in Section 11 (see below) and Section 15, the latter which contained a Neolithic flint blade (Allen *et al.* 1995).

5.3.1.3 Phase I Section 11

Section 11 sampled a non-woody organic lens that correlated in height with Section 9. Nine samples from Monolith 2 were included in the analysis covering the regressive contact from clastic to organic sedimentation and providing data to compare with the woody peat in Section 9. No radiocarbon dates are available for this section but estimates of between *ca* 4500 and 5000 BP have been made.

5.3.1.4 Phase I Section 6

Section 6 sampled the herbaceous peat at between -0.87m and +0.11m OD. The date on the basis of pottery finds is Late Bronze Age and archaeological material including flint, pottery and charcoal were abundant in this area below the peat. Samples from Monoliths 3 and 5 were analysed, Monolith 3 covering the regressive transition from silt to peat with Monolith 5 covering the transgressive contact.

5.3.1.5 Phase III Trench 7

The samples analysed in this Trench were contemporary with the period of Iron-Age occupation on the cliff-top (Allen *et al.* 1995). Plant macrofossil Block 1 was subject to full analysis. Samples from Block 2, extracted from the same stratum, were scanned and found to contain identical macrofossil assemblages, so analysis was not continued and restricted to Block 1. The samples cover the heights from +1.25m to +1.09 m and are from an organic/peaty silt in a depression overlying Pleistocene sediment. The main focus of interest was the local environment of the settlement, especially the hydrology of the former cliff-top at this point.

5.3.1.6 Phase III Trench 6

The charcoal from four samples used in radiocarbon dating were checked before submission to the dating laboratory for the presence of charred seeds and fruits and were found to contain identifiable remains. This analysis was brief but provided additional data from site contexts about plant use at the sites.

5.3.2 Sampling

Bulk sampling homogenises the plant remains from any one stratum, lowering the temporal resolution of the resultant analysis. For this reason intact strata were sampled from monolith tins or blocks wherever possible, providing macrofossils from exact depths and providing a detailed sample set in which precise relative positions were known. The sample size was standardised at approximately 50 cm^3, being extracted as blocks 5cm x 5cm in area and 2cm in depth from the large sediment blocks and monoliths. This size was selected because the seed concentration was found to be adequate in exploratory work and the quantity of non-seed material was not too large to be analysed. Compaction of sediments evidently increased the concentration of macrofossils in ancient sediments compared to the uncompacted sediments sampled in modern alluvial environments. Sample intervals varied from 2cm to 8 cm depending on the nature of the sediment and sediment availability, as some monoliths had been extensively sampled for several types of palaeoenvironmental investigation.

5.3.3 Sample preparation

Sub-samples were described on the basis of visual appearance using Troels-Smith terminology and then were wet-sieved on a 125µm mesh. Some samples were pre-treated using a deflocculant (Calgon) and left to soak for periods of between one day and three weeks before sieving. The retained residue was stored in 70% industrial methylated spirit (IMS) prior to analysis to prevent decay.

5.3.4 Recording and identification

Seeds were counted and non-seed material was recorded using the cover abundance method described in Chapter 3. The Dicotyledon leaves proved difficult to identify and only in several cases in Section 16 were convincing and thorough identifications possible. The methods and identification criteria outlined in Chapter 3 and the manuals discussed in Chapter 2 were used for identification of the macrofossils. Identification of seeds was confirmed using the seed reference collections of the Institute of Archaeology, University College London. Identification was carried out using a dissecting microscope of up to 50x magnification and a transmitted light microscope of up to x1000 magnification, the latter for non-seed material and small seeds, such as those of *Juncus* spp.. Bud-scales were cleared with a 2% solution of bleach and identified using a high-powered dissecting microscope with reference to Tomlinson (1985).

5.4 Results

5.4.1 Range of preserved macrofossils

The identified macrofossils from the samples are presented in Tables 5.1, 5.3, 5.5, 5.7 and 5.9. Seeds, fruits, endocarps and bracts of a large number of species were identified in the samples from wet woodland, herbaceous fen, aquatic, saltmarsh, dry woodland, grassland and ruderal habitats. Seed preservation was typically good and most specimens retained testae intact, allowing genus- and species-level identification in many cases. Only in some of the sand and silt units were seeds badly preserved, especially in Sections 11 and 16. Sporangia and oospores from Filicales and Characeae species were also recorded, although higher level identification was not attempted for these species.

Preservation of non-seed macrofossils varied in the sample set. Sandy units and most of those in the upper part of the sequence sampled in Section 16 were highly fragmented. Vegetative remains dominated the assemblages, with the exception of the

woody peat in Section 9. Preservation in the peat units varied, the best-preserved vegetative remains coming from sections 6 and 11.

The organic silt in Section 16 contained beds of very well preserved Dicotyledon leaf fragments and Monocotyledon vegetative tissues. Leaves from several taxa were identified including *Alnus glutinosa, Salix* sp., *Quercus* sp. and Poaceae. Only fragments of these leaves with unambiguous preserved features were recorded as deriving from those taxa. Among useful characteristics in the tree leaves were the trichomes and margins of *Alnus*, venation, stomatal apparatus and margin of *Salix* and the trichomes, venation, shape and fimbrial vein in *Quercus*. Surprisingly, trichomes were commonly preserved on some of the ancient leaf fragments, although damage was common and preservation was best on lamina near the central veins, a relatively sheltered part of the leaf. Poaceae leaves and epidermal fragments were commonly preserved, with those of *Phragmites* being identified in several samples. *Phragmites* stem and rhizome fragments were also identified in several of the sections, among a larger assemblage of Poaceae remains identified only to the family level.

Other herbaceous stem and leaf remains included pinnules from an indeterminate fern and *Pteridium aquilinum*, the latter readily identifiable by the marginal indusium (see Chapter 3). Epidermis fragments from Poaceae, Cyperaceae and *Juncus* spp. were identified, although most fragments were small and lacked hairs and crystals. Higher level identifications were, therefore, difficult and epidermis could have come from either aerial stem or leaves. Cyperaceae and *Juncus*-type rootlets were found in many contexts with unidentifiable Types 1 and 2 also present, the former being common. Budscales were identified from six arboreal taxa and analysis proved to be simple and rapid. Clearing using sodium hydroxide and bleach followed by multiple washes of distilled water was possible on the slide. Many scales remained unidentifiable.

Many other non-seed remains were identified only as a macrofossil class, including moss, wood, bark, twig and woody root remains. Mineralised root casts were present in the basal sand of Section 16. These appeared as obvious vertical channels during Block sample preparation work and proved to be sediment-filled root casts. Unidentifiable matter and unidentifiable vegetative remains were common and often contributed a major component to many samples, especially the peat units and the samples from Section 16. Thorns were occasionally preserved, although they were unidentifiable. One interesting category of finds were the anthers seen in several samples.

These were the only floral elements (as opposed to seed/fruit/bract remains) identified in the assemblages.

Charred remains were preserved in samples from Section 16, Section 6 and samples from Phase III Trench 6. Those from the floodplain sections included well preserved cereal awn and culm fragments in Section 6 and hazelnut shell and sloe endocarp fragments from Section 16. These were present in tiny quantities; however, wood charcoal fragments were common in many of the samples from the earliest episodes of deposition at the site. The remains were well preserved, probably because of stable waterlogging in the sediments. A number of charred plant remains were collected from the drainage ditches around the Iron Age and Romano-British settlement sampled in Phase III Trench 6. Although the assemblages were of low abundance, a surprising diversity of taxa was identified, including spelt and macaroni wheat chaff, barley and oat grains and the seeds of several weedy taxa including knotweed and goosefoot (Table 5.11).

5.4.2 Phase I, Section 16

5.4.2.1 Identified taxa (Table 5.1)

Woody components were preserved in small quantities throughout the samples from this section. In the basal sands only unidentifiable fragments were distinguishable and may have derived from stem or root tissues. Twiggy material was preserved in the upper part of the sand unit with twigs and wood fragments being more abundant and constantly present above -9.36m. Samples between -8.90 and -9.36m OD had a distinctive composition, containing a large quantity of bedded fragmentary Dicotyledon leaves, among them *Alnus*, *Salix* and *Quercus*, which were preserved in large quantities and even dominated the cover abundance values in some samples. Alder was well represented; however, oak leaves were also common and dominated one sample assemblage. Although many Dicotyledon leaves were identified, much of the preserved leaf material was beyond identification. Above and below these depths, Dicotyledon leaf fragments were sparse and poorly preserved, only rarely being identifiable. *Pteridium aquilinum* pinnules were present in one sample.

Mineralised roots were present throughout the basal sand, waterlogged herbaceous roots becoming abundant between -9.36m and -8.90m OD. Most rootlets were in the indeterminate Type 1 group, probably deriving from a Poaceae species such

Monolith	M1	M1	M1	M1	M1	M1	M1	M2	M2	M2	M2	M2	M4
Monolith Depth (cm)	0-2*	6-8*	10-12*	18-20	24-26	30-32	38-40	10-12*	24-26	30-32	36-38	42-44	0-2*
Depth O.D. (m)	-7.28	-7.34	-7.38	-7.46	-7.52	-7.58	-7.66	-7.75	-7.89	-7.95	-8.01	-8.07	-8.14
Taxon/component	Ag2Gmi2	Gmin3Ag1	Ag2Gmin2	Gmin3Ag1	Ag2Gmin2	Gmin3Ag1	Ag3Gmin1	Gmin3Ag1Dmol+	As2Gmin2	As2Gmin2	Ag3Gmin1	Ag3Gmin1	Ag3Gmin1
1. Wetland Trees.													
Alnus glutinosa cone												1	
Alnus glutinosa seed	1	3	2	2		6	1	0(1)	15	3	3	6	16
Alnus glutinosa bract		1	1			2			2			2	6
Alnus glutinosa budscale								1	3				1
2. Submerged/Float. Aquatics													
Alisma/Baldellia sp. seed							1		1			1	
Alismataceae seed embryo				1							1		
Callitriche cf. *stagnalis* seed	1	2			1				1		1	1	1
Characeae oospore	2	1	1(1)	7	5	2	1	1	2	3	2	1	
Nymphaea alba seed	1												
Potamogeton sp. seed						2			1				
Ranunculus sub-g. *Batrachium* seed											1		
Zannichellia palustris seed							1			1			
3. Emergent aquatics.													
*Typha sp.*seed	1	6	5	6	8	4	3	6	4	3	5	3	1
4. Open riparian/marsh/mire													
Apium cf. *nodiflorum* seed													
Bidens cernua seed					1								
Caltha palustris seed													
Carex sp trigonous seed					1					1		1	3
Carex sp biconves seed			1			1					1		
Carex sp. fruit													1
Eupatorium cannabinum seed		1							1		1	1	1
Juncus bufonus seed		1											
Juncus sp. seed		1	4		4	17			2	4			2
Lycopus europaeus seed												2	
Oenanthe sp. seed													1
Phalaris arundinacea seed													
Phragmites australis seed			1		2	2			1		1	1	5
Ranunculus sceleratus seed						1			3	1		1	
Samolus valerandi seed						2		1				3	
Solanum dulcamara seed				1	1			1			1		3
Stellaria palustris seed													
Thalictrum sp. seed										1			
Urtica dioica seed		1	1	1		3			1		2		6
5. Shaded marsh/mire													
Scirpus sylvaticus				1					8			3	
6. Saltmarsh.													
Bolboschoenus maritimus seed						2					1		4
Glaux maritimus seed											1		
Festuca rubra seed				2	3								
Juncus gerardii seed					1		1						
Juncus maritimus seed	2	4		8	3		4		4		8	2	
Puccinellia sp. Seed											1	3	
Salicornia sp. Seed	8	4	5	3	2	6	3		1		1	6	1
cf. *Salicornia* sp. Seed			1										
Suaeda maritima seed													
*Triglochin sp.*seed	1	1	1			4(1)				1		2	

Table 5.1 Medway Tunnel Section 16 macrofossil records

Monolith	M1	M1	M1	M1	M1	M1	M1	M2	M2	M2	M2	M2	M4
Monolith Depth (cm)	**0-2***	**6-8***	**10-12***	**18-20**	**24-26**	**30-32**	**38-40**	**10-12***	**24-26**	**30-32**	**36-38**	**42-44**	**0-2***
7. Dryland trees/shrubs													
Betula sp. bract	1							1	1				
Betula sp. budscale								2					
Corylus avellana nutshell													
Prunus spinosa/padus sp. stone													
Quercus sp. *budscale*			2			3			3	8			7
Rosaceae cf. *Prunus budscale*													
Rubus fruticosus agg. Seed													
Sambucus nigra seed		1											1
8. Ferns.													
Filicales sporangia								0(1)			3		
9. Grassland.													
Filipendula ulmaria seed													
Poa annua/Phleum pratense seed												1	
Ranunculus acris type seed										1			1
10. Arable and disturbed.													
cf. *Valerianella locusta* seed										1			
12. Indeterminate.													
Apiaceae seed													
Asteraceae seed													
Atriplex sp. seed									1				
Chenopodiaceae seed													
Euphorbia sp. seed				1									
Mentha sp. seed		3		1	2	2		1		2		2	
Poaceae seed	1		1			4		1					2
Poaceae spikelet										1			
Potentilla sp. seed												1	
Rumex sp. seed													1
Solanaceae seed								1					
Sonchus sp. seed													2
Sagina sp. seed	1												
cf. *Viola* sp. seed		1								1			
indeterminate seed						6		1		3			
Indeterminate budscale		1							3				

Table 5.1 Medway Tunnel Section 16 macrofossil records (cont.)

Monolith	M1	M1	M1	M1	M1	M1	M1	M2	M2	M2	M2	M2	M4
Monolith Depth (cm)	**0-2***	**6-8***	**10-12***	**18-20**	**24-26**	**30-32**	**38-40**	**10-12***	**24-26**	**30-32**	**36-38**	**42-44**	**0-2***
Taxon/component													
Cyperaceae type root			1 (1)							1(1)			
Phragmites australis stem												2	12
Phragmites australis leaf				3									20
Poaceae stem			2 (1)									8	17
Poaceae leaf	7 (2)	9 (3)		2	5 (2)	2 (1)	1(1)	1(1)	3(1)	4(2)	1 (1)	4 (2)	1
Poaceae epidermis						1 (1)							
Poaceae rhizome scale								1(1)					
Pteridium aquilinum pinnule													
Alnus glutinosa leaf						1 (1)							
Salix sp. Leaf						2 (1)		1(1)					
Dicotyledon leaf	1 (1)	6 (2)	2 (1)	4 (1)		2 (1)	2 (1)	1(1)	4(1)	6(2)	2 (1)	5 (3)	2 (1)
Dicotyledonae Rhizome		4 (1)											
Monocotyledon stem		6 (2)		1 (1)	5 (1)		14(5)				7 (3)		
Type 1 root			2 (1)					1(1)		1(1)			
Indeterminate Rootlet	20 (6)	6 (2)	1 (1)	15 (5)	10 (3)	1 (1)	5 (2)	1(1)	7(2)	2 (1)	10(4)	15(7)	
Woody Root													1(1)
Indet. Epidermis			1 (1)										3 (2)
Wood	15 (5)	28 (8)	8 (2)	9 (3)	21 (6)	17 (5)	19 (7)	18(6)	28(8)	14 (5)	16 (6)	20(10)	
Twig													
Bark	1 (1)	1 (1)		1 (1)	4 (1)	1 (1)	3 (1)		5(1)		3 (1)	3 (1)	
Budscale		1 (1)	1 (1)				1 (1)		1(1)			1(1)	
Seed	1 (1)	1 (1)	1 (1)	1 (1)	1 (1)		2 (1)	1(1)	1(1)		1 (1)	1(1)	
Sphagnum sp.	3 (1)	3 (1)					3 (1)		4(2)		2(1)		
Moss indet			1 (1)		1 (1)		1 (1)	1(1)		1(1)			
Charcoal	1 (1)	1 (1)	5 (2)	1 (1)	3 (1)	4 (1)	8 (3)	2 (1)		2(1)	1(1)	1(1)	1(1)
Indeterminate Vegetative matter			12 (4)			11(3)		16(5)		26(11)			
Unidentifiable Organic Matter	55(17)	37(11)	67(20)	62(19)	51(15)	59(18)	45(17)	59(18)	51(15)	45(18)	60(24)	43(21)	43(26)

	M1	M1	M1	M1	M1	M1	M1	M2	M2	M2	M2	M2	M4
Sample No.	**0-2***	**6-8***	**10-12***	**18-20**	**24-26**	**30-32**	**38-40**	**10-12***	**24-26**	**30-32**	**36-38**	**42-44**	**0-2***
Seed Abundance	20	32	25	34	34	65	15	17	58	35	34	44	66
Species diversity	9	13	9	12	13	15	8	9	17	15	17	19	18
Seed concentration	0.4	0.64	0.5	0.68	0.68	1.3	0.3	0.34	1.16	0.7	0.68	0.88	1.32
Species concentration	0.18	0.26	0.18	0.24	0.26	0.3	0.16	0.18	0.34	0.3	0.34	0.38	0.36

Table 5.1 Medway Tunnel Section 16 macrofossil records (cont.). Numbers in brackets refer to CO^2 figures

Monolith	M4	M4	M4*	M4	M4	M4	M4	M4	M6	M6	M6
Monolith Depth (cm)	10-12*	16-18	20- 22	24-26	30-32	34-36	40-42	46-48	4-6*	14-16	25-26
Depth O.D. (m)	-8.24	-8.30	-8.34	-8.38	-8 44	-8.48	-8.54	-8.60	-8 64	-8.74	-8.85
Taxon/component	Ag3Gmin1	Ag3As1Gmin+	Ag3Gmin1	Ag3Gmin1	Ag3As1Gmin+	Ag3As1Gmin+	Ag3As1Gmin+	Ag3As1Gmin+	Ag3As1Gmin+	Ag3As1Dh+	Ag2As2Dh+
1. Wetland Trees.											
Alnus glutinosa cone	1	1	3	2							1
Alnus glutinosa seed	14	7	11	6	2(2)	9	3	2	1		51
Alnus glutinosa bract	6		6	7	4	5		1			34
Alnus glutinosa budscale			5		1	3	2				7
2. Submerged/Float. Aquatics											
Alisma/Baldellia sp. Seed	1										33
Alismataceae seed embryo	3	1	1		3						1
Callitriche cf. *stagnalis* seed	2	1	1	1		1		1			48
Characeae oospore											
Nymphoea alba seed											
Potamogeton sp. seed											
Ranunculus sub-g. *Batrachium* seed											
Zannichellia palustris seed											
3. Emergent aquatics.											
*Typha sp.*seed	1	2		3	3		3	1		1	
4. Open riparian/marsh/mire											
Apium cf. *nodiflorum* seed		2				1					1
Bidens cernua seed											
Caltha palustris seed											4
Carex sp trigonous seed	1(3)		7	1	1(1)	2	2				
Carex sp biconves seed	2		3								
Carex sp. fruit		1	2		1						
Eupatorium cannabinum seed	1(2)		1					1			
Juncus bufonius seed											
Juncus sp. seed	1		1	1	1			4			
Lycopus europaeus seed			1								
Oenanthe sp. seed	6		1	1	1						
Phalaris arundinacea seed						2					
Phragmites australis seed		4		3		4	8	2		2	3
Ranunculus sceleratus seed	2	2	1							2	132
Samolus valerandi seed		1		1							
Solanum dulcamara seed		1				1					
Stellaria palustris seed					1						
Thalictrum sp. seed											
Urtica dioica seed	2	1	1		4						
5. Shaded marsh/mire											
Scirpus sylvaticus		7		1		1	4				
6. Saltmarsh.											
Bolboschoenus maritimus seed	7	5	10		1	14			1		
Glaux maritimus seed											
Festuca rubra seed		1									
Juncus gerardii seed											
Juncus maritimus seed		3									
Puccinellia sp. seed	2										
Salicornia sp. seed	6(1)	1	1	1		2				1	
cf. *Salicornia* sp. seed											
Suaeda maritima seed						1					
Triglochin sp seed			2					1			

Table 5.1 Medway Tunnel Section 16 macrofossil records (cont.)

Monolith	M4	M4	M4*	M4	M4	M4	M4	M4	M6	M6	M6
Monolith Depth (cm)	**10-12***	**16-18**	**20- 22**	**24-26**	**30-32**	**34-36**	**40-42**	**46-48**	**4-6***	**14-16**	**25-26**
7. Dryland trees/shrubs											
Betula sp. bract											
Betula sp. budscale											
Corylus avellana nutshell	2		1								
Prunus spinosa/padus sp. stone	1										
Quercus sp. *budscale*	1	6	3	1	10				1		
Rosaceae cf. *Prunus budscale*	1		1								1
Rubus fruticosus agg. seed		1									
*Sambucus nigra*seed						1					
8. Ferns.											
Filicales sporangia								3			
9. Grassland.											
Filipendula ulmaria seed			1								
Poa annua/Phleum pratense seed											
Ranunculus acris type seed	4			1							
10. Arable and disturbed.											
cf. *Valerianella locusta* seed											
12. Indeterminate.											
Apiaceae seed		1	1								
Asteraceae seed	1								1		
Atriplex sp. seed	1										
Chenopodiaceae seed	1		3								
Euphorbia sp. seed											
Mentha sp. seed	2		5								
Poaceae seed	6	2	6		4			4		2	
Poaceae spikelet	2										
Potentilla sp. seed											
Rumex sp. seed	1			1							
Solanaceae seed											
Sonchus sp. seed											
Sagina sp. seed											
cf. *Viola* sp. seed											
indeterminate seed	23		10	2	3			3	1	2	2
Indeterminate budscale		4				2					

Table 5.1 Medway Tunnel Section 16 macrofossil records (cont.)

Monolith	M4	M4	M4*	M4	M4	M4	M4	M4	M6	M6	M6
Monolith Depth (cm)	10-12*	16-18	20- 22	24-26	30-32	34-36	40-42	46-48	4-6*	14-16	25-26
Taxon/component											
Cyperaceae type root	1(1)								2(2)	21	2(2)
Phragmites australis stem	21	2				1				2	
Phragmites australis leaf	16									4	
Poaceae stem	12	10				14		8(11)			
Poaceae leaf	5	5(4)	16(12)	5(7)		9(11)	10(13)	6(9)	1(1)	4	
Poaceae epidermis	1(1)		2(2)					1(1)		9(9)	
Poaceae rhizome scale											
Pteridium aquilinum pinnule		1(1)									
Alnus glutinosa leaf											
Salix sp. Leaf	1(1)							2(3)			
Dicotyledon leaf	1(1)	2(1)	1(1)	1(1)		1(1)	2(2)				4(4)
Dicotyledonae Rhizome			32(26)				2(2)				
Monocotyledon stem				23(28)	4(5)		14(18)				
Type 1 root	2(1)		2(2)					3(5)	6(6)	42(44)	4(4)
Indeterminate Rootlet		5(4)		6(7)	3(3)	11(13)	3(4)		1(1)	7(8)	2(2)
Woody Root	2(1)	1(1)	2(2)								1(1)
Indet. Epidermis											
Wood		8 (5)		13(16)	12(13)	13(15)	14(18)		27(27)	1(1)	32(35)
Twig	2(1)	1(1)		3(3)		3(3)	2(3)				
Bark		2 (2)		7(8)		7(8)	9(11)				
Budscale	1(1)	1(1)		1(1)			1(1)				1(1)
Seed	1(1)	1(1)	2(1)	1(1)		1(1)			1(1)	1(1)	2(2)
Sphagnum sp.		2(1)			1(1)						
Moss indet						1(1)					
Charcoal	1(1)	1(1)	1(1)		2(2)	1(1)	1(1)	1(1)	1(1)		4(5)
Indeterminate Vegetative matter					20(22)		32(42)	40(57)	23(23)	9(10)	
Unidentifiable Organic Matter	35(19)	63(44)	45(36)	41(49)	60(65)	40(48)	11(15)	38(53)	28(28)	1(1)	43(47)
	M4	M4	M4	M4	M4	M4	M4	M4	M6	M6	M6
Sample No.	10-12*	16-18	20- 22	24-26	30-32	34-36	40-42	46-48	4-6*	14-16	25-26
Seed Abundance	96	55	89	33	37	49	22	23	5	10	318
Species diversity	21	18	21	13	10	12	5	8	4	6	8
Seed concentration	1.92	1.1	1.78	0.66	0.74	0.98	0.44	0.46	0.1	0.2	6.36
Species concentration	0.42	0.36	0.42	0.26	0.2	0.24	0.1	0.16	0.08	0.12	0.16

Table 5.1 Medway Tunnel Section 16 macrofossil records (cont.) Numbers in brackets refer to CO^2 figures

Sample	16050	16051*	16053	16054	16049	16043	16035	16039	16033*	16025	16026	16027	16028
Block Depth (cm)	0-2.	2-4.	6-8.	8-10.	18-20	26-28	30 -32	38-40	46-48	50-52	52-54	54-56	56-58
Depth O.D. (m)	-8 90	-8.92	-8.96	-8 98	-9.08	-9.16	-9 20	-9.28	-9.36	-9.40	-9.42	-9.44	-9.46
Taxon/component	As3Ag1	Ag2As2Dh+	Ag2As2Dh+	Ag2As2Dh+	Ag2As2Dh+	Ag2As2Dh+	Ag2As2Dh+	Ag3As1Dl1Dh1	Ag3As1Dl1Dh1	Ag2As1Gmin1Dl1Dh1	Ag3Gmin1Dh+	Ag3Gmin1Dh+	Gmin2Ag2Gmaj+
1. Wetland Trees.													
Alnus glutinosa cone	6	1	3	5	1	11	6	12	5				
Alnus glutinosa seed	51	67	32	34	45	123	53	66	36				
Alnus glutinosa bract	18	26	49	33	15	90	115	117	43				
Alnus glutinosa budscale		2	26	23	12	3	39	28	12				
Alnus glutinosa bud				1	1	1	1	4					
Salix sp. bud				5			1						
2. Submerged/Float. aquatics													
Alisma sp.			1	2	1		1						
Alismataceae seed	3				1	5	2						
Alismataceae seed embryo	9		2	2		2	2		1				
Callitriche cf. stagnalis	18	15	522	309	25	211	408	61	2				
3. Emergent Aquatics.													
Glyceria sp.						1							
Typha sp.	1						1						
4. Open mire/marsh.													
Angelica sylvestris				1									
Caltha palustris	2				1	2		3					
Carex sp biconvex seed	1				2				4	1			
Carex sp. trigonous seed	1							1					
Cirsium palustris seed			1	1	2								
Eupatorium cannabinum	4	1				1	1		4	8		3	
Lycopus europaeus	1		1		1		1	4	3				
Oenanthe sp.	2				1				1				
Phragmites australis	16			11	4			5	5				
Ranunculus sceleratus		7	392	298	148	41	63	73					
Samolus valerandi	2										1		
Solanum dulcamara	2				1	1		1		1			
Stachys palustris								2					
Urtica dioica											3	3	
Valeriana dioica					1			3					
Filipendula ulmaria	1			1				1					
7. Dryland trees/shrubs.													
Sambucus nigra										4	2	1	2
Prunus spinosa	1			1									
Prunus spinosa/padus sp.	1					1	1						
Quercus sp. budscale			1				2						
Rosaceae (cf. *Prunus*) bud			4										
Rosaceae (cf. *Prunus*) budscale				2	1	2		4	4				
8. Ferns.													
Filicales		10		1	1	3	4		2				
9. Grassland.													
Ranunculus acris type						1	1						
10. Arable and disturbed.													
Galeopsis tetrahit								1	0				
11. Wayside and wasteland.													
Rumex cf. crispus bract							1						
Rumex crispus type seed							1						
Rumex crispus fruit			1										

Table 5.1 Medway Tunnel Section 16 macrofossil records (cont.)

Sample	16050	16051*	16053	16054	16049	16043	16035	16039	16033*	16025	16026	16027	16028
12. Indeterminate.													
Apiaceae					1								
Asteraceae indet.						1							
Chenopodium sp.										1			
Mentha sp.								3	25	1			
Poaceae	15					3	1	0	0				
Poaceae spikelet													
Rumex sp.	1												
Rumex sp. bract							1						
Sonchus sp.	2												
Stachys sp.								3					
Indeterminate seed	7	2	4	4	12	2	4	2	8				
Indeterminate budscale											1		
13. Charred remains.													
Corylus avellana nutshell											1		
Prunus sp. endocarp										1			
B Non-seed macrofossils													
Cyperaceae type rootlet													
Phragmites australis stem	6 (9)	4 (5)		2 (3)				1 (1)	6 (15)	1 (1)			
Phragmites australis leaf	14 (21)	9 (14)		3 (4)	8 (11)	2 (4)	1 (1)	1 (2)	18 (42)	2 (2)	9 (6)	3 (2)	1 (1)
Phragmites australis Rhizome					2 (3)						8 (6)		
Phragmites australis rhizome scale													
Poaceae epidermis													
Monocotyledon Leaf													
Alnus leaf			5 (9)	3 (4)	12 (17)	4 (7)	8 (13)						
Quercus leaf			1 (2)		4 (6)		1 (2)		1 (2)				
Salix leaf			1 (2)			4 (7)	14 (22)		1 (2)				
Dicotyledon leaf	1 (1)	5 (7)	18 (31)	12 (15)	52 (75)	19 (32)	14 (22)	37 (62)					
Wood	4 (7)	7 (11)	12 (21)	3 (4)	3 (4)	7 (12)	10 (16)	7 (12)	2 (4)			3 (2)	
Twig	1 (1)	5 (7)	1 (2)	1 (1)	2 (3)	15 (26)	4 (6)	11 (19)		1 (1)			2 (1)
Bark		2 (3)			3 (4)	5 (9)	3 (4)	2 (4)	5 (11)		2 (1)		
Type 1 rootlet	58 (87)	55 (82)	48 (82)	64 (80)	9 (13)	22 (38)	28 (45)	21 (35)	39 (93)	13 (12)	14 (10)	8 (5)	71 (42)
Type 2 rootlet										52 (47)	34 (24)	20 (12)	
Herb root indet.	9 (14)		2 (2)								3 (2)	8 (5)	
Woody Root							2 (3)						2 (1)
Mineralised root/rhizome													
Herb stem							1 (1)						
Budscale		1 (1)	1 (2)	1 (1)		1 (2)	1 (1)	2 (3)					
Seed	1 (1)	1 (1)	3 (5)	3 (4)	1 (1)	2 (4)	1 (2)	3 (5)	2 (6)	1 (1)			1 (1)
Moss indet			1 (2)	1 (1)									
Charcoal								1 (1)	1 (1)	7 (6)	10 (7)	5 (3)	2 (1)
Indet. Vegetative matter												35 (21)	
Intet. Plant Matter	7 (11)	12	11	9 (11)	7 (10)	17 (30)	15 (23)	13 (22)	26 (63)	24 (21)	20 (14)	18 (11)	22 (13)
Sample No.	16050	16051*	16053	16054	16049	16043	16035	16039	16033*	16025	16026	16027	16028
Seed Abundance	165	131	1039	734	277	505	710	394	155	17	8	7	2
Species diversity	17	5	9	13	15	13	13	15	11	6	3	3	1
Seed concentration	3.3	2.62	20.78	14.68	5.54	10.1	14.2	7.88	3.1	0.34	0.16	0.14	0.04
Species concentration	0.34	0.1	0.18	0.26	0.3	0.26	0.26	0.3	0.22	0.12	0.06	0.06	0.02

Table 5.1 Medway Tunnel Section 16 macrofossil records (cont.) Numbers in brackets refer to CO^2 figures

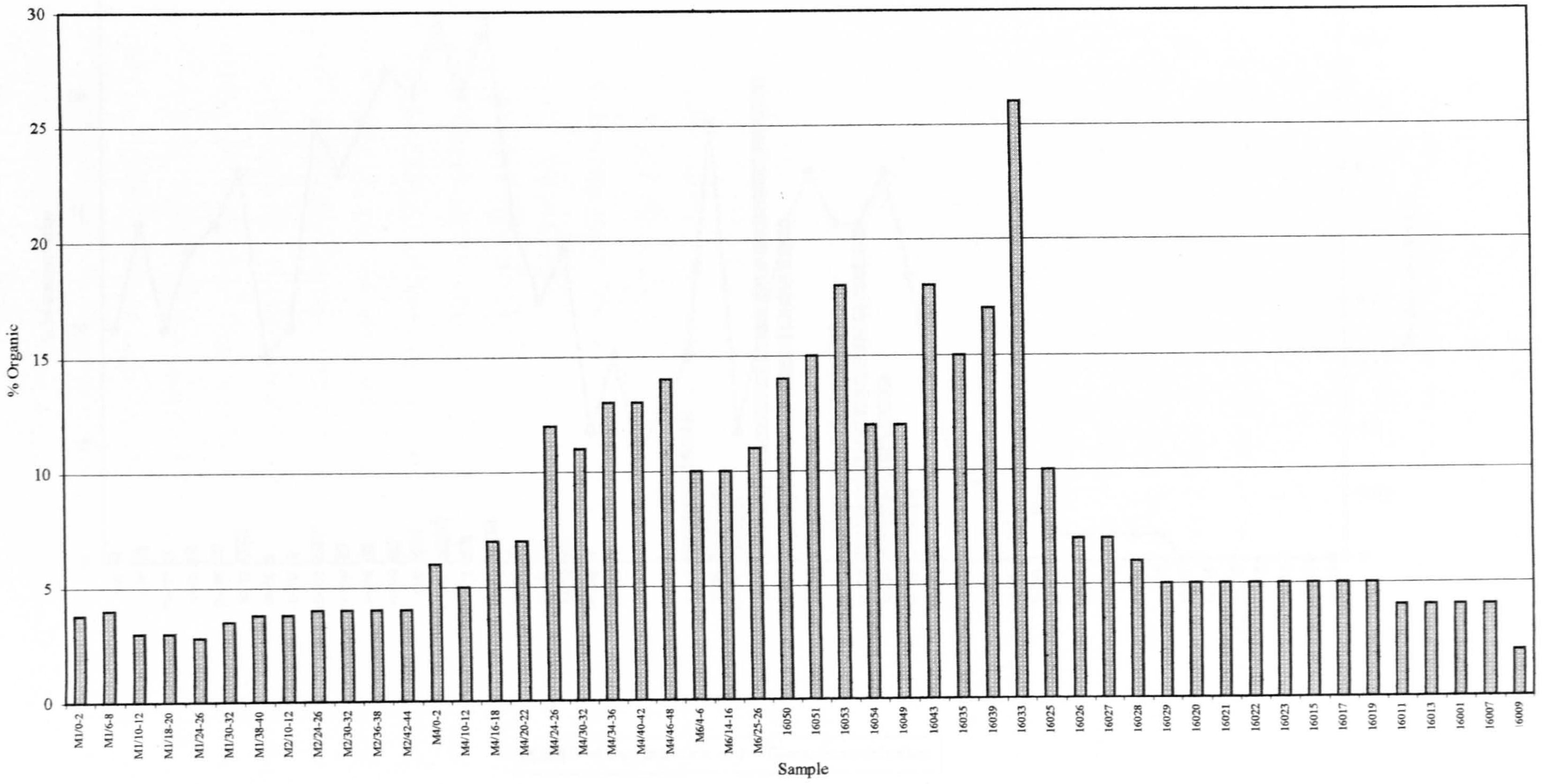
Sample	16029	16020	16021	16022	16023	16015	16017	16019	16011	16013	16001	16007	16009
Block Depth (cm)	58-60	60-62	62-64	64-66	66-68	70-72	74-76	78-80	82-84	86-88	90-92	94-96	98-100
Depth O.D. (m)	-9.48	-9.50	-9.52	-9.54	-9.56	-9.60	-9.64	-9.68	-9.72	-9.76	-9.80	-9 84	-9 88
Taxon/component	Gmin2Ag2Gmaj+	Gmin2Ag2As+	Gmin2Ag2As+	Gmin2Ag2As+	Gmin2Ag2As+	Gmin2Ag2Dh+	Ag2Gmin1As1h+	Gmin2Ag2Dh+	Gmin2Ag2Dh+	Gmin2Ag2Dh+	Gmin2Ag2Dh+	Gmin2Ag2Dh+	Gmin2Ag2Dh+
1. Wetland Trees.													
Alnus glutinosa cone													
Alnus glutinosa seed													
Alnus glutinosa bract													
Alnus glutinosa budscale													
Alnus glutinosa bud													
Salix sp. bud													
2. Submerged/Float. aquatics													
Alisma sp.													
Alismataceae seed													
Alismataceae seed embryo													
Callitriche cf. *stagnalis*													
3. Emergent Aquatics.													
Glyceria sp.													
Typha sp.													
4. Open mire/marsh.													
Angelica sylvestris													
Caltha palustris													
Carex sp biconvex seed													
Carex sp. trigonous seed													
Cirsium palustre seed													
Eupatorium cannabinum	2												
Lycopus europoeus													
Oenanthe sp.													
Phragmites australis													
Ranunculus sceleratus													
Samolus valerandi													
Solanum dulcamara													
Stachys palustris													
Urtica dioica	2												
Valeriana dioica													
Filipendula ulmaria													
7. Dryland trees/shrubs.													
Sambucus nigra		1	2	1	1	1							
Prunus spinosa													
Prunus spinosa/padus sp.													
Quercus sp. budscale													
Rosaceae (cf. *Prunus*) bud													
Rosaceae (cf. *Prunus*) budscale													
8. Ferns.													
Filicales													
9. Grassland.													
Ranunculus acris type													
10. Arable and disturbed.													
Galeopsis tetrahit													
11. Wayside and waste land.													
Rumex cf crispus bract													
Rumex crispus type seed													
Rumex crispus fruit													

Table 5.1 Medway Tunnel Section 16 macrofossil records (cont.)

Sample	16029	16020	16021	16022	16023	16015	16017	16019	16011	16013	16001	16007	16009
12. Indeterminate.													
Apiaceae													
Asteraceae indet.													
Chenopodium sp.													
Mentha sp.													
Poaceae													
Poaceae spikelet													
Rumex sp.													
Rumex sp. bract													
Sonchus sp.													
Stachys sp.													
Indeterminate seed													
Indeterminate budscale													
Indeterminate anthers													
13. Charred remains.													
Corylus avellana nutshell													
Prunus sp. endocarp													
B Non-seed macrofossils													
Cyperaceae type rootlet				1 (1)									
Monocoytledon Leaf	1 (1)												
Phragmites australis leaf											3 (1)	13 (3)	
Phragmites australis Rhizome	1 (1)				22 (11)								
Phragmites australis thizome scale							4 (2)						
Phragmites australis stem													
Poaceae epidermis	3 (2)				4 (2)		7 (4)						
Alnus leaf													
Quercus leaf													
Salix leaf													
Dicotyledon leaf													
Wood	1 (1)			11 (5)	1 (1)	10 (5)	11 (5)	28 (14)					
Twig												19 (4)	10 (2)
Bark					1 (1)	1 (1)							
Type 1 rootlet	24 (13)						8 (4)						
Type 2 rootlet							1 (1)						
Herb root indet.		23 (12)	47 (23)	22 (11)	13 (6)	12 (6)		2 (1)	40 (16)	13 (5)	33 (13)	19 (4)	
Woody Root													
Mineralised root/rhizome		17 (9)	7 (4)		9 (4)	15 (8)	33 (17)	42 (21)	21 (9)	32 (13)	6 (2)	4 (1)	51 (10)
Herb stem													
Budscale													
Seed		4 (2)	1 (1)			1 (1)							
Moss indet													
Charcoal	1 (1)	26 (13)	7 (4)	22 (11)	5 (2)	16 (8)	8 (4)	4 (2)	2 (1)	4 (2)	16 (7)	14 (3)	1 (1)
Indet. Vegetative matter	29 (16)		11 (6)			10 (5)							9 (2)
Intet. Plant Matter	40 (22)	30 (15)	26 (13)	44 (22)	45 (22)	32 (16)	30 (15)	23 (12)	36 (14)	52 (21)	42 (17)	31 (6)	30 (6)
Sample No.	16029	16020	16021	16022	16023	16015	16017	16019	16011	16013	16001	16007	16009
Seed Abundance	4	1	2	1	1	1	0	0	0	0	0	0	0
Species diversity	2	1	1	1	1	1	0	0	0	0	0	0	0
Seed concentration	0.08	0 02	0 04	0.02	0 02	0 02	0	0	0	0	0	0	0
Species concentration	0 04	0 02	0.02	0.02	0 02	0 02	0	0	0	0	0	0	0

Table 5.1 Medway Tunnel Section 16 macrofossil records (cont.) Numbers in brackets refer to CO^2 figures

Figure 5.3 Medway Tunnel Section 16 LOI figures



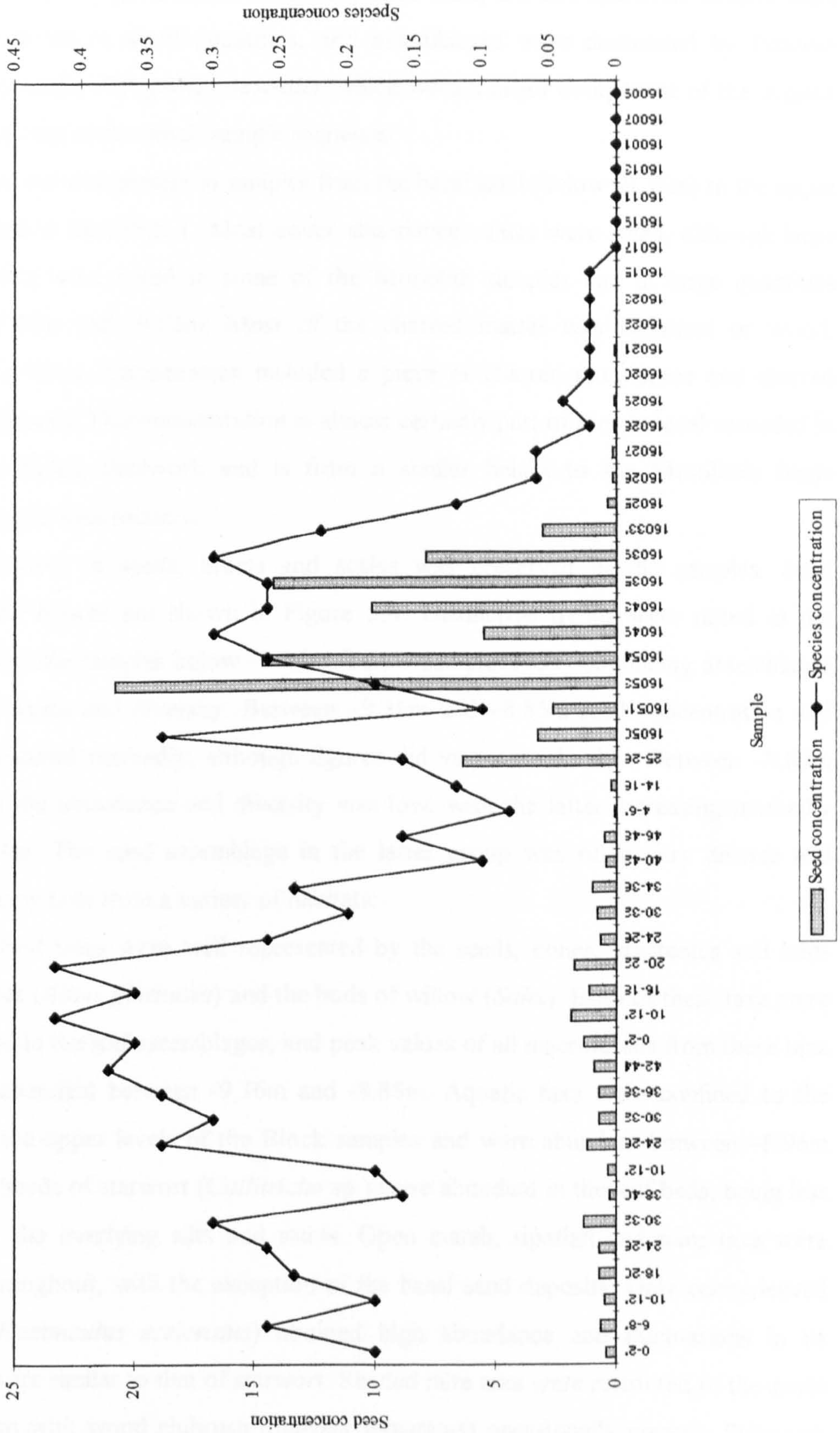


Figure 5.4 Medway Tunnel Section 16 seed and species concentration

as common reed (*Phragmites australis*). Cyperaceae rootlets were also identified in a limited range of samples, especially in the samples from Monolith 6 at the junction of the organic-rich and inorganic strata. Monocotyledon stem, leaf and epidermis remains were usually preserved in small quantities, and assemblages were dominated by Poaceae remains, especially *Phragmites australis*, which were a major component of the organic section at the top of the block sample sequence.

Charcoal was present in samples from the basal sand (below -9.36m) to the upper units sampled in Monolith 1. Most cover abundance values were small, although large concentrations were noted in some of the Monolith samples and in large quantities between -9.40m and -9.60m. Most of the charred matter was indistinct or wood, although the latter concentration included a piece of charred plum-stone and charred hazelnut fragment. This concentration is almost certainly part of the charcoal recorded in the section during fieldwork and is from a similar height to the Mesolithic blade discussed in previous sections.

A variety of seeds, bracts and scales was preserved in the samples. Seed concentration figures are shown in Figure 5.4. Distinctive trends were noted in the assemblages, with samples below –9.36m (below sample16033) containing assemblages of low abundance and diversity. Between –9.36m and –8.85m seed concentration and diversity increased markedly, although figures did vary considerably. Between –8.85m and –8.54m the abundance and diversity was low, with the latter increasing markedly above –8.54m. The seed assemblage in the latter group was often very diverse and contained many taxa from a variety of habitats.

Wetland trees were well represented by the seeds, cones, bracteoles and bud-scales of alder (*Alnus glutinosa*) and the buds of willow (*Salix*). Both of these taxa were also recorded in the leaf assemblages, and peak values of all macrofossils from these taxa were most abundant between -9.36m and -8.85m. Aquatic taxa were confined to the strata from the upper levels of the Block samples and were abundant between –8.96m and 9.20m. Seeds of starwort (*Callitriche* sp.) were abundant in the leaf beds, being less abundant in the overlying silts and sands. Open marsh, riparian and mire taxa were abundant throughout, with the exception of the basal sand deposits. Only celery-leaved buttercup (*Ranunculus sceleratus*) attained high abundance and fluctuations in its abundance were similar to that of starwort. Shaded mire taxa were restricted to the sands above -8.85m with wood clubrush (*Scirpus sylvaticus*) occasionally present. Saltmarsh

taxa were preserved above -8.74m, the lowest specimens being a *Salicornia* seed. Above that an increasing number and diversity of saltmarsh taxa were preserved in mixtures with freshwater aquatic and terrestrial taxa.

Dryland trees and shrubs were well represented in the assemblages of seeds and buds, including oak (*Quercus*), birch (*Betula*) and hazel (*Corylus*) as well as scrub taxa including elder (*Sambucus*), sloe (*Prunus spinosa*) and bramble (*Rubus fruticosus*). Elder was one of the only seed types to be preserved in the basal sand and the other tree and shrub species were distributed throughout the higher sediments. *Quercus* was also present in the leaf assemblages. Bud-scales were present throughout the sample set, often appearing in large numbers, especially in the samples between –9.36m and –8.85m OD. In fact, they were well represented as a whole in most of the samples, even when overall seed and bud abundance was low. Grassland, wayside and agricultural indicators were sparsely represented and those taxa identified from these habitat groups may have derived from natural marsh or riparian floras.

5.4.2.2 Analysis

Correspondence analysis results are shown in Figures 5.5 and 5.6. There was considerable overlap in sample composition and there was no simple pattern of variability.

CA of the combined seed and non-seed data (Figure 5.5) divided the samples into four broad groups. The variability shown on the diagram accounted for only 34% of that in the sample set, showing the weakness of the quantitative analysis. Variability along the first and second axes was similar at 19% and 15% respectively. The saltmarsh taxa, indeterminate components and those from the Monocotyledons were the main influences along the positive side of the first axis, with the alder and other arboreal elements and many aquatic seeds, including *Ranunculus sceleratus* and the Alismataceae. The second axis opposed many of the aquatic and saltmarsh seeds with the Dicotyledon leaves, many of the arboreal seeds, mineralised roots and most of the indeterminate categories. The major split was between the samples from the central part of the sequence (samples 16033 to the lowest sample in M6) and the rest. The latter contained the lowest quantity of plant matter and the former contained abundant macrofossils. The only samples in this group to show any quantitative variation from the main group were samples 16033 and 16050, both on the fringes of the main sample group and characterised by a lack of

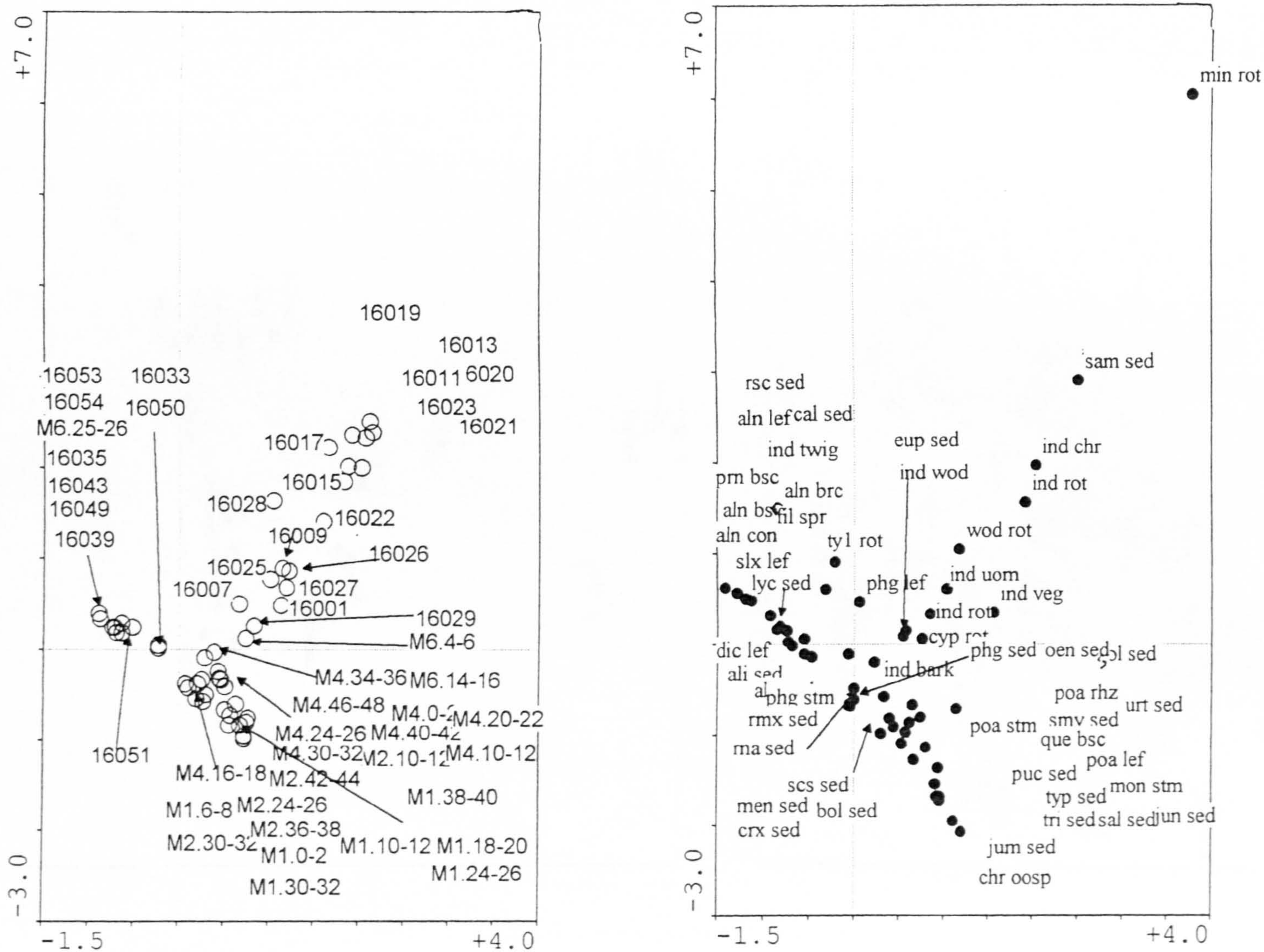
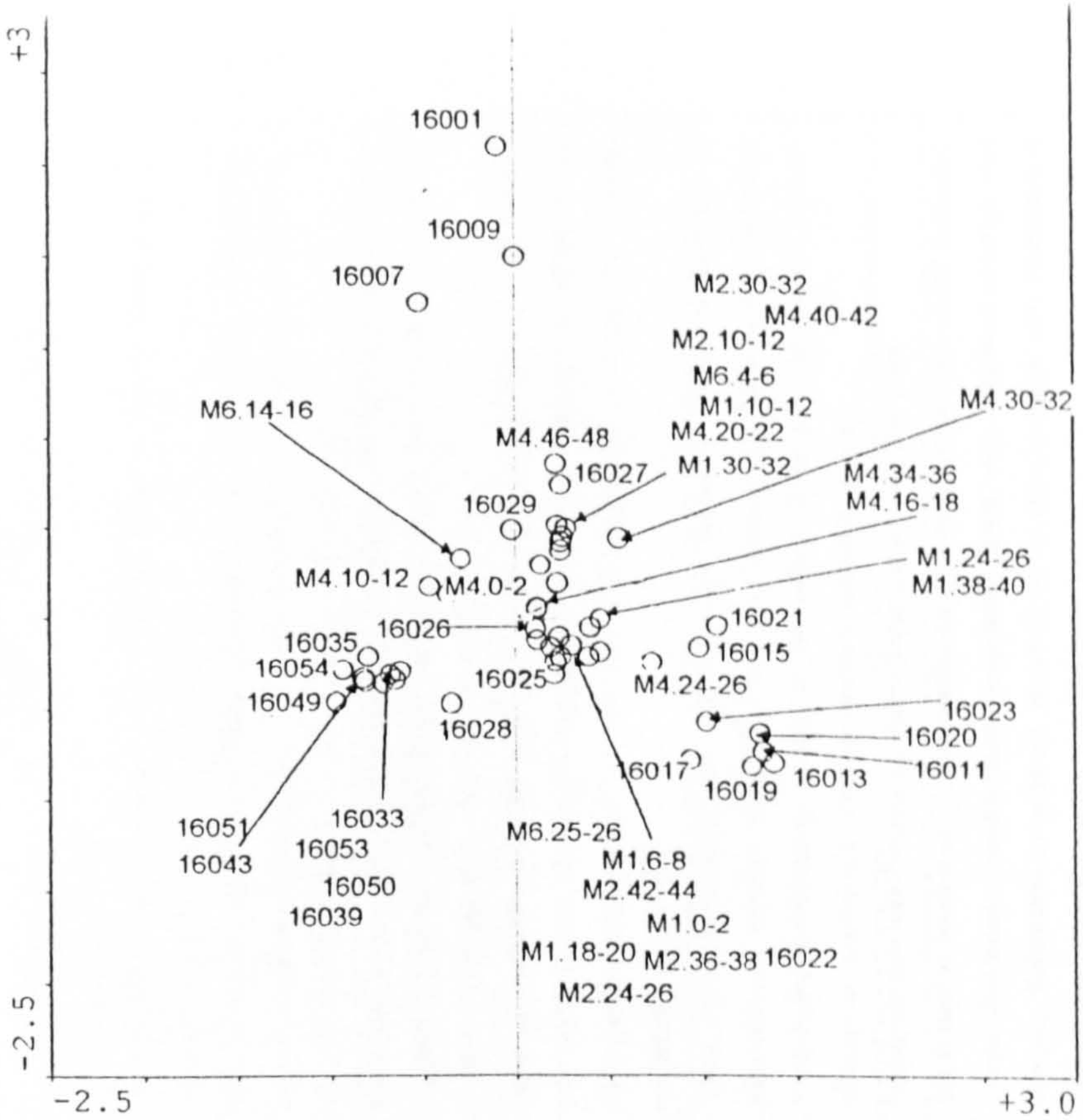


Figure 5.5 Medway Tunnel Section 16 correspondence analysis of all macrofossil data
(NB the diagrams have been presented like this because a single diagram was too crowded



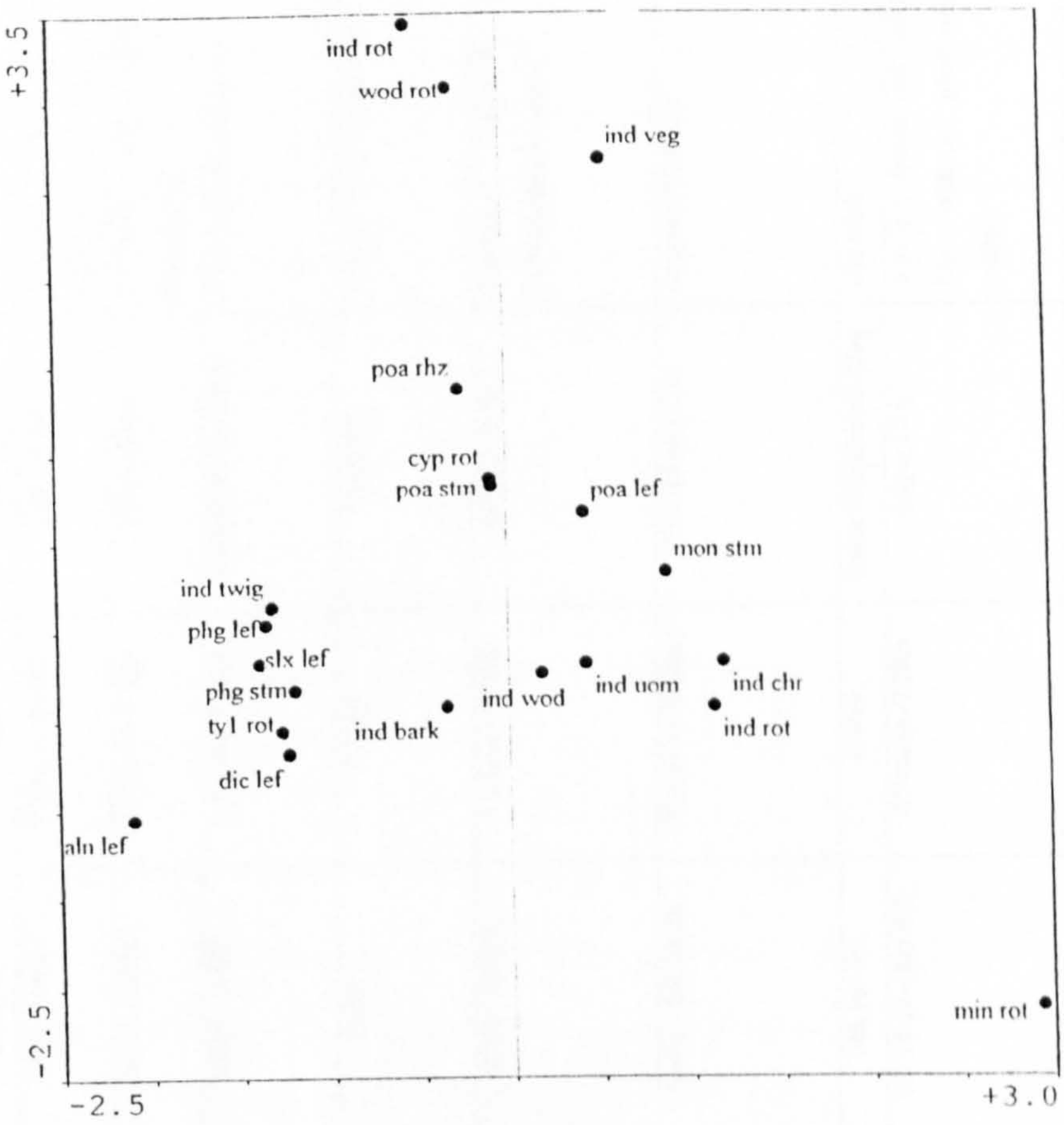


Figure 5.6 Medway Tunnel Section 16 correspondence analysis of non-seed macrofossil data (NB the diagrams have been presented like this because a single diagram was too crowded)

Group	Samples	Depth	Unit Name	Sediment	Macrofossil characters
A	16009 –16001	-9.88m to -9.80m	Basal Sand	Silt-Sand with occasional mineralised macrofossils	Few plant macrofossils in a sandy matrix. Macrofossils mainly roots and rhizomes with much indeterminate matter
B	16013 – 16020	-9.76m to -9.50m	Upper Sand	Silt-Sand with occasional macrofossils	Few macrofossils in the samples, mainly roots and rhizomes with increasing quantities higher in the profile. Few seeds, only *Sambucus*.
C	16029 – 16025	-9.48m to -9.40m	Transitional Sand/Silt	Silt-sand and Sand-Silts	Better preserved and more abundant macrofossils in a sand/silt matrix. This group crosses a sedimentary boundary. More seeds, mainly herbaceous riparian and marsh taxa. Macrofossils mainly vegetative, especially Moncotyledon remains
D	16033	-9.36m	Basal Silt	Organic Clay-Silt mixture	Much higher macrofossil abundance and preservation of much herbaceous matter, especially *Phragmites* stems and herb rootlets, including those of the Cyperaceae. Seeds diverse and dominated by *Alnus* and riparian/marsh taxa
E	16039 - 16053	-9.28m to -8.96m	Organic Silts	Laminated Clay-Silt with bedded plant remains	Abundant macrofossils in fine matrix, dominated by vegetative remains of tree leaves and wood. Leaves are bedded and preserved in large fragments or whole. Much Monocotyledon type matter and abundant seed assemblages dominated by arboreal, aquatic and riparian taxa.
F	16051 - M6 25-26	-8.92m to -8.85m	Transitional Clay	Organic Silt-Clays	Many fewer tree leaves and mostly poorly preserved. Better preservation of Monoctyledon material, especially *Phragmites* remains and lower wood abundance. Much higher indeterminate material in M6 sample. Seeds vary between the samples, although the species in all three are similar to the lower samples.
G	M6 14 - 16	-8.74m	Upper Transitional Clay	Clay-Silt	Mainly rootlets with Poaceae vegetative fragments and very few seeds
H	M6 14-16 - M1 0-2	-8.74m to -7.28m	Upper Clay	Silt/Clay Sands and Silt/Sand Clays with few plant remains visible	Much smaller abundance of macrofossils, mostly pororly preserved in small fargments. Larger abundance of indeterminate components, lower seed abundance and high seed diversity. Saline taxa are apparent, especially in the upper samples. Low abundance of Dicotyledon leaves and mainly Monocotyledon remains

Table 5.2 Medway Tunnel Section 16 sample groups

Dicotyledon leaves. The samples from beyond this group were split into two groups along the second axis, the upper group containing most of the lower Block samples and the lower (negative side of the second axis) containing the Monolith samples. The main split was in the quantity of mineralised and indeterminate remains and in the representation of saltmarsh taxa in the lower group.

A further CA was performed on only the non-seed data, because the seed assemblages were small and potentially unrepresentative (Figure 5.6). The division between the samples was very similar, although the lowest samples were much better divided along the second axis from the sample group and the samples from the lower Blocks and the Monoliths were less well separated. The central Block sample group (samples above 16033) were well separated, although the lowest M6 sample was merged with the other Monolith samples. This suggests that this sample mainly varies in terms of its seed assemblage from the other Monolith samples. It also shows that the sample is not only transitional in position between the central sample group and the Monoliths, but is also transitional in composition. This analysis separated the samples from between 16029 and 16025 that had a very mixed composition.

Quantitative analysis only weakly divided the samples, although the divisions were consistent with the main sedimentary changes. A combination of these results with consideration of the sediments allowed separation of the samples into eight groups (Table 5.2).

5.4.2.3 Interpretation

The macrofossils in Groups A and B are probably intrusive and derive from the penetration of roots and rhizomes into the sediments from later vegetation growth. The plant macrofossil preservation and sediments would be consistent with deposition in natural levee or channel bank environments in which the accumulating surface is above groundwater levels. Anaerobic conditions reduce the potential for macrofossil preservation and mineralisation of root casts has been recorded in modern analogue environments (Scheihing and Pfefferkorn 1984). The general increase in finer particles and organic preservation towards the top of this group can be explained by the combination of reducing energy in the depositional system and the onset of permanent higher water levels at the site.

The few seeds and fruits are likely to be autochthonous, although they are of little interpretative value being from elder (*Sambucus nigra*), a taxon that produces very tough seeds that are both preferentially preserved and well dispersed. Charcoal concentrations in the upper sand unit are most likely explained as the result of human activity, coming from a similar level to that of the worked flint. The finds include a sloe stone and hazelnut shell fragments and were from a section of the strata that contained a considerable quantity of charcoal. These finds are few, but again support the interpretation of local Mesolithic activity. The finds may have derived from riverbank campsites beneath the chalk bluff and the charred plant remains may suggest the local exploitation of woodland resources, a pattern common in this period (Zvelebil 1994). The status of the charred potential foods is uncertain, and similar remains could be generated by clearance activity.

Group C samples straddle the divide between the sterile sands at the base of the site and the organic-rich silts above. Samples 16029 and 16028 are from the uppermost sand unit that changes rather abruptly into the sand-silts sampled in 16025 – 16027. These samples formed a loose grouping on the CA plots. Organic incorporation was much higher in the sand-silt samples that the silt-sands, although it was still much lower than the Basal Silt and Organic Silt units above. 16029 and 16028 were notable for being the lowest samples with high rootlet values and preservation of larger macrofossil fragments. These and the other samples in the group contained the seeds of a range of riparian and marsh taxa and the preservation of rootlets suggests the presence of a marsh at the site. The only identifiable vegetative remains were those of *Phragmites* suggesting that the plant was a local vegetation component at the time. The seeds are few in number but all are from plants of freshwater wetlands and river banks. Most are mobile and so may have derived from a wide area, reducing the spatial precision of the information attainable from the assemblages. The low numbers also mean that the assemblages may not be representative. Presence of *Sambucus* may again be misleading. Although the seeds of freshwater taxa were preserved in modern saltmarsh sediments, the seed rain at most sites was overwhelmingly dominated by saltmarsh taxa and the quantity of incorporated allochthonous seeds, even in mobile environments, was minimal. Applying this argument to open freshwater environments, none of which was found in the modern sites, would suggest that the interpretation of a freshwater environment is secure.

Sample 16033 had a unique composition and sediment profile, having the highest LOI figure (Figure 5.3) and containing mainly vegetative macrofossils, especially rootlets and the leaves and stems of *Phragmites*. The seed assemblage was similar to that immediately above, containing many tree species with a mixture of riparian taxa, although unlike those it lacked the seeds of numerous aquatic taxa. The presence of *Phragmites* vegetative remains in such abundance, especially the leaves that form a mat at the sediment surface, and the high rootlet count suggest that the site was home to a reed-bed or swamp. Good preservation of roots and *Phragmites* leaves attests to high sediment water levels during the period of deposition. Wood, bud and bark remains in the sample suggest the growth of *Alnus* and perhaps other trees at the site or on slightly higher ground next to the cliff. Although many of the seeds of the identified taxa are well dispersed, the abundance of freshwater taxa and lack of saltmarsh in this depositional environment suggests that the site was home to a reedbed with associated freshwater herbs. The abundance of *Mentha* seeds suggests that the plant may have been locally abundant. The local growth of *Alnus* is a new feature in this sample and is suggested by the large number of bracts, cones and buds. Interestingly, the seed concentration in the samples from Groups C and D was low, and while the overall characteristics of the seed assemblage in sample 16033 is similar to those above it, the concentration is lower overall and when comparing the same species. This may indicate a decreasing sedimentation rate.

Sample Group E were the most distinctive on the site, consisting of leaf beds, abundant rootlets, abundant aquatic seeds, high wood and wetland tree representation and a good overall preservation of vegetative remains. The seed assemblages in the group were dominated by the seeds of *Callitriche stagnalis* and *Ranunculus sceleratus*, the former an aquatic and the latter characteristic of muddy banks. The vast quantities of seeds preserved in the sediments suggests that the area supported populations of both taxa. *R. sceleratus* cannot survive in permanently inundated areas and thus its presence conflicts with the presence of *Callitriche*, the laminated sediments and the bedded leaves, all support the suggestion of local standing water. Preservation of such large quantities of tree leaves indicates that the remains were covered with sediment rapidly, were not broken up by fast-moving water or extensive vegetation growth at the site of deposition and that waterlogging was maintained permanently from the point of deposition onwards. The presence of considerable surface water is beyond doubt at the sample

point, and while not necessarily continuous, would have been visible as pools throughout the year. The balance of data suggests that *R. sceleratus* seeds may be allochthonous, deriving from nearby raised banks, or that the landscape was undulating with different plants occupying the slightly differing topography. The clastic nature of the sediments indicates that there were external inputs, probably from overbank flooding or overland water flows, that were deposited into the site. Many seeds in the assemblages were probably allochthonous. However, the most abundant are unlikely to be so and the physical environment indicated by the sediments and leaf preservation would be favourable for growth of the identified species.

The riparian taxa may have been derived from the local flora or, with many having well dispersed seeds, may have grown further up the river catchment. The presence of vegetative Monocotyledon remains suggests local non-arboreal vegetation, probably *Phragmites*, represented in the leaf assemblages but represented only rarely in the seed assemblages. A wide variety of tree and shrub taxa was present in both the seed and leaf assemblages, their remains deriving from vegetation growing at the site or from overhanging vegetation living on the still exposed areas of the riverbank, levee or on the chalk cliff. *Alnus* is the most visible species and the presence of buds, scales and leaves are an unequivocal indicator of local growth. The twigs are also an indictor of local arboreal growth and some fallen *Alnus* trunks also support this interpretation. The other taxa are, in this low-energy environment, likely to have also been present at the site, either in the swampy conditions of the marsh (*Salix*) or along the drier fringes (*Quercus* and *Prunus*).

The macrofossils and sediments in Group E are unique in my experience and provide a potentially non-analogue environment. The presence of continuous standing water is intriguing and suggests the presence of a widespread backswamp. The leaf beds were not continuous in the sediments and appeared as patches among more homogenised sediments. These sediments may be the indicator of the undulating landscape suggested above. The environment seems to have been entirely freshwater. The site may have contained standing *Alnus* forming a partially closed canopy. If the modern data are accurate and shade does suppress seed production in *Phragmites*, the presence of very few seeds and vegetative remains may indicate that the site was shaded. An alternative is that the woodland vegetation formed a fringe along the drier riverbank. One of the curious characteristics of this facies is the long period of its deposition and the apparent

contradiction of high sediment input, lack of peat formation, apparent dominance of woodland vegetation and the high visibility of aquatics. The pattern of sedimentation within the longer sequence does not conform to any established Northern temperate model of channel infill or backswamp development. The depth of sediments indicates that the environment persisted for some time and that high water and sedimentation kept pace with each other.

Sample Group F lies above the laminated clay-silts and contained samples with similar composition to those below, but with a much lower abundance of less well preserved leaves, a higher abundance of *Phragmites* components and a depression in *Ranunculus sceleratus* seeds. Remains from arboreal taxa continued throughout the period of deposition, indicating the maintenance of tree-cover at or near the site. An increase in the diversity of the samples is notable here and the sediments were not laminated, being more homogenised. These changes are consistent with the development of a more reed-rich environment and a reduction in standing water, although there was still high groundwater. *R. sceleratus* is not successful in closed vegetation and the disappearance of this species adds further support to the idea of the development of reed vegetation. The lack of leaves and aerial tree-remains may reflect the change in depositional environment rather than the vegetation at the site, and the tree canopy may have remained intact, at least partially.

Sample composition changed radically above –8.74m, with a marked decrease in the overall quantity of preserved plant macrofossils, a decrease in fragment size and a continuation of the low seed abundance. A single sample at –8.74m contained a few seeds, was dominated by rootlets, contained *Phragmites* vegetative remains and a relatively small quantity of seeds. The assemblage is consistent with deposition in a marsh habitat or within tidal mudflats at a marsh fringe. The presence of rootlets in such large quantities would suggest local vegetation growth. The seed and non-seed assemblages included reed, reed canary grass and *Typha* seeds. Also present was a seed of *Salicornia* indicating tidal influence and the presence of saltmarsh vegetation in the catchment. The deposition would be consistent with a tidal reedbed, the freshwater taxa coming from tidal or aerial dispersal.

Above –8.64m OD the samples were characterised by an increasing abundance and diversity of macrofossils, including many more halophytes, and a decrease in organic incorporation. The sediments consisted of alternate bands of clay and sand-rich units.

The overall preservation in all of the samples was poor, the non-seed remains being especially degraded. The assemblages are consistent with deposition in mudflats and a high biological turnover causing physical erosion of the plants entering the sediments mixed with high diversity and low overall macrofossil abundance. The mixture of freshwater and saline taxa in these samples confirms that the area at this time was under estuarine sedimentation conditions. The seed and fruit assemblages include both autochthonous and allochthonous taxa and so provide a sample of the vegetation along the river and in the surrounding dryland. Wet woodlands, or fringing arboreal vegetation, is well represented as are the riparian and marsh floras and representatives of each are present throughout the period of deposition. Most of the dryland taxa are trees and shrubs, with occasional open ground taxa possibly from glades of grassland on heavy, low-lying land. In comparison to the dryland taxa identified in samples higher up the sequence, the predominance of trees and shrubs may indicate that the area was still wooded throughout the period of sediment accumulation.

The environmental and vegetation sequence in Section 16 can be summarised as follows:

1) Deposition in a levee or riverbank environment at *ca* 6900 BP. Local vegetation unknown. Human activity with exploitation of woodland plant resources. Slowing depositional conditions towards the top of Group B.
2) Slowing water movement at the site and development of a freshwater wetland with reeds.
3) Inundation of the site as water-levels at the site increase. Invasion of the site by wet-woodland taxa and deposition of sediment in an environment in which there was often standing water allowing the preservation of leaves. Open vegetation in muddy conditions nearby. Perhaps the presence of a backswamp.
4) Transition to more open conditions and/or loss of standing water. Development of reed vegetation and crowding out of *Ranunculus sceleratus*.
5) Development of reedbed vegetation, loss of arboreal taxa at the site, although maintained nearby. Onset of tidal conditions.
6) Estuarine conditions persist with continuing deposition of sediment in mudflats with fringing saltmarsh. A developed freshwater riparian flora persists upstream and wooded conditions continue on land around the sample site.

5.4.3 Section 9

5.4.3.1 Macrofossil preservation (Table 5.3)

With the exception of samples 9035 and 9037, woody remains were dominant in the assemblages, although they were commonly poorly preserved and highly fragmented. Vegetative remains were very abundant, especially rootlets, although many were unidentifiable. Cyperaceae types were preserved as were Type 1 roots. Cyperaceae, *Phragmites* and Poaceae type stems and leaves were identified, the former only in the lowest two samples. Dicotyledon leaves, including *Alnus* fragments were preserved, although many remained unidentified.

Seed assemblages were dominated by seeds, bracts, cones and bracteoles of Alder (*Alnus glutinosa*) and fern sporangia, both confined mainly to the peat samples. A willow budscale was also identified in the peat unit. Freshwater taxa included aquatic species such as starwort (*Callitriche stagnalis*). Wetland and riparian taxa included bittersweet (*Solanum dulcamara*) identified only in the non-peat units. Other taxa included reed (*Phragmites australis*) and brooklime (*Samolus valerandi*). Seablite (*Suaeda maritima*) was identified in the sample immediately below the peat unit in association with *Scirpus maritimus*. Dryland remains included tree and shrub species, such as oak (*Quercus*) and birch (*Betula* sp.) identified in some abundance in the peat as bud-scales. The only herbaceous dryland taxon in the samples was great plantain (*Plantago major*). The overall seed and species concentrations are shown in Figure 5.7. The highest values were from the peat samples 9014 and 9018, with the two lowest peat samples having intermediate values between those from the upper peat and the basal silt (9035 and 9037). The values in 9014 and 9018 were inflated by the vast quantity of Filicales sporangia present in the assemblages. However, the pattern was similar when these macrofossils were removed from the seed sum.

5.4.3.2 Analysis

A CA of the combined seed and non-seed data is shown in Figure 5.8. The samples were split into three broad groups, most of the separation being along the first axis. At the positive end of the axis were samples 9035 and 9037, the main components of variation being the Cyperaceae and *Phragmites* remains, the saltmarsh seeds and the type 1 rootlets. The peat samples were grouped at or towards the negative end, the main influences being the woodland and woody components. In between the two main groups

Sample No.	9003	9014	9018	9026	9031	9035	9037
Troels-Smith	Th1Tl1Sh1Ag1	Th1Tl1Sh1Ag1	Th1Tl1Sh1Ag1	Th2Sh1Ag1 Tl+	Sh2Th1Ag1	As3Ag1Dh+G min+	As3Ag1Dh+G min+
Block Depth	4-6cm	26-28cm	34-36cm	50-52cm	60-61cm	65-67cm	69-71cm
Depth O.D. (m)	-3.14	-3.36	-3.44	-3.60	-3.70	-3.75	-3.79
Taxon/component							
1. Wetland trees.							
Alnus glutinosa seed	43	127	153	164	7		
Alnus glutinosa bracteole		31	111	25	11		
Alnus glutinosa cones	6	7	7	5	2		
Alnus glutinosa budscale		6		10			
Salix sp. budscale				1			
2. Submerged and floating aquatics.							
Callitriche stagnalis seed		62		1			
cf. *Cicuta virosa* seed		7		2			
Menyanthes trifoliata seed	1						
3. Emergent aquatics.							
Typha sp. seed					4		
4. Herb. riparian, mire and marsh: open							
Caltha palustris seed			3				
Carex sp. seed	1	1	7	5			
Eupatorium cannabinum seed	1	1		1		2	
Lychnis flos-cuculi seed		1					
Phragmites australis seed	2	4	3	3		5	
Ranunculus sceleratus seed		5					
Samolus valerandi seed		60					
Solanum dulcamara seed	17					10	1
Urtica dioica seed		6	102	42	18		
6. Saltmarsh taxa.							
Suaeda sp. seed						6	
Bolboschoenus maritimus seed						4	7
7. Dryland trees, shrubs and woody taxa							
Betula sp, budscale		2		2			
Rosaceae budscale		3					
Rubus fruticosus seed	10	5					
Quercus sp. budscale		47		2			
Taxus baccata seed	1						
8. Ferns.							
Filicales sporangia		824	900	120	120		
11. Wayside and wasteland.							
Plantago major seed		1					
12. Indeterminate.							
Apiaceae seed			1			9	3
Chenopodium/Atriplex sp. seed			1				1
Mentha sp. seed					2		
Polygonum sp. seed		1			1		
Rumex sp. seed		1					
Stellaria sp. seed			1				
indet. seed	3	23	6	10	3	5	1
indet budscale		14					

Sample No.	9003	9014	9018	9026	9031	9035	9037
B. Non-seed macrofossils							
Cyperaceae stem						6	3
Cyperaceae Type roots						67	61
Phragmites australis Stem					10		6
Phragmites australis Leaf	35	8	2	9	17	7	11
cf. *Phragmites australis* rhizome						6	
Poaceae leaf							
cf *Alnus glutinosa* leaf		1		1			
Dicot. leaf	1	2					
Wood	29	33	28	28	29		1
Twigs	3	11	7	14			
Bark	13	11	12	2	1		
Moncotyleon rhizome						4	
Rootlets Type 1						8	16
Indeterminate roots	17	29	47	35	43		
Woody roots		3	2	1			
Seeds	2	2	1			1	
Thorn							
Buds/scales		1	1				
Moss							
Indet. vegetative matter							
Indet plant matter						2	1

Sample No.	9003	9014	9018	9026	9031	9035	9037
Seed Abundance	82	1201	1288	383	165	36	12
Seed abundance minus Filicales	82	377	388	263	45	36	12
Species diversity	8	17	9	10	5	6	4
Seed concentration	1 64	24 02	25.76	7.66	3.3	0.72	0.24
Seed concentration minus Filicales	1.64	7.54	7.76	5.26	0 9	0.72	0.24
Species concentration	0.16	0.34	0.18	0.2	0.1	0.12	0.08

Table 5.3 Medway Tunnel Section 9 macrofossil records

Figure 5.7 Medway Tunnel Section 9 seed and species concentration

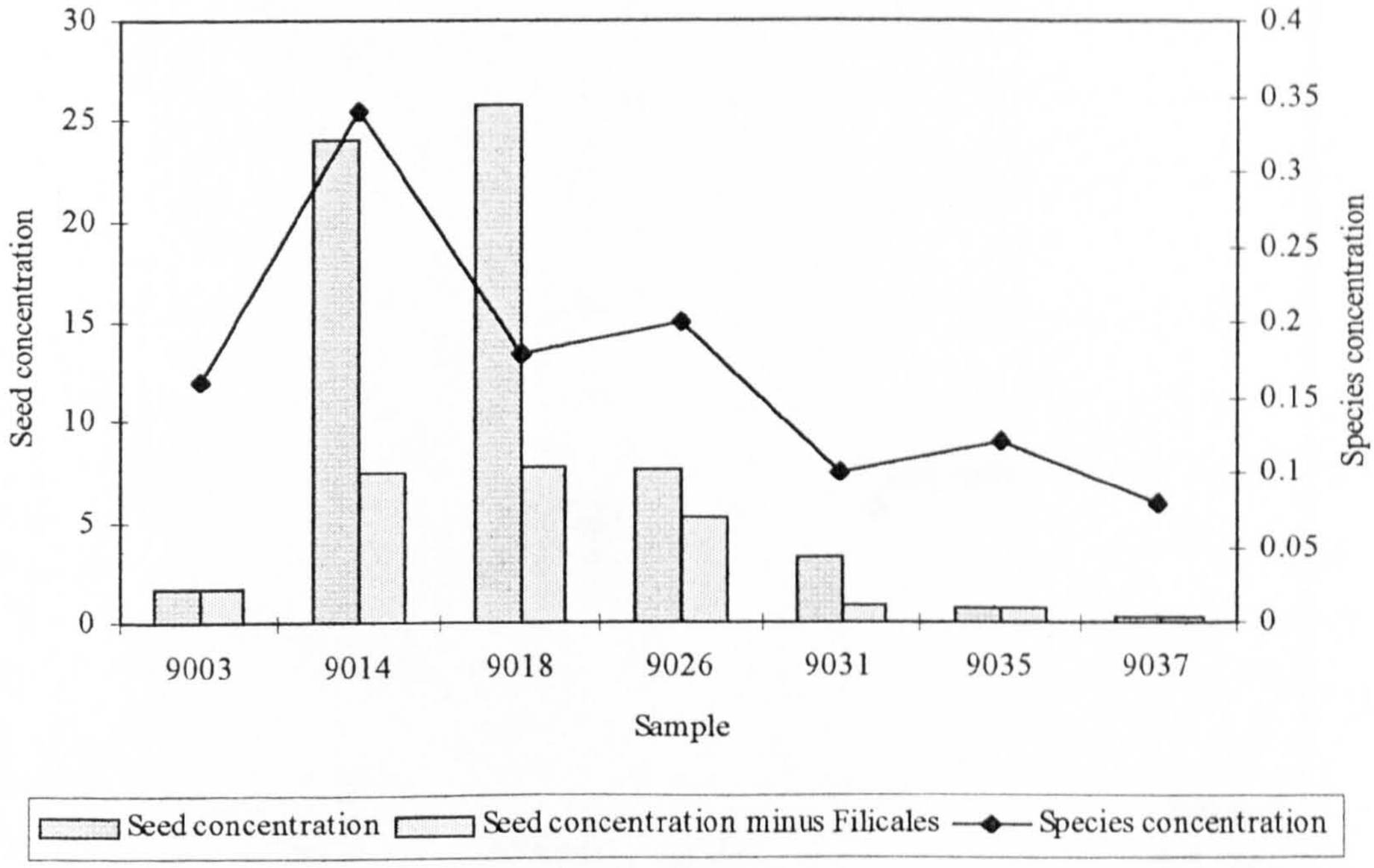
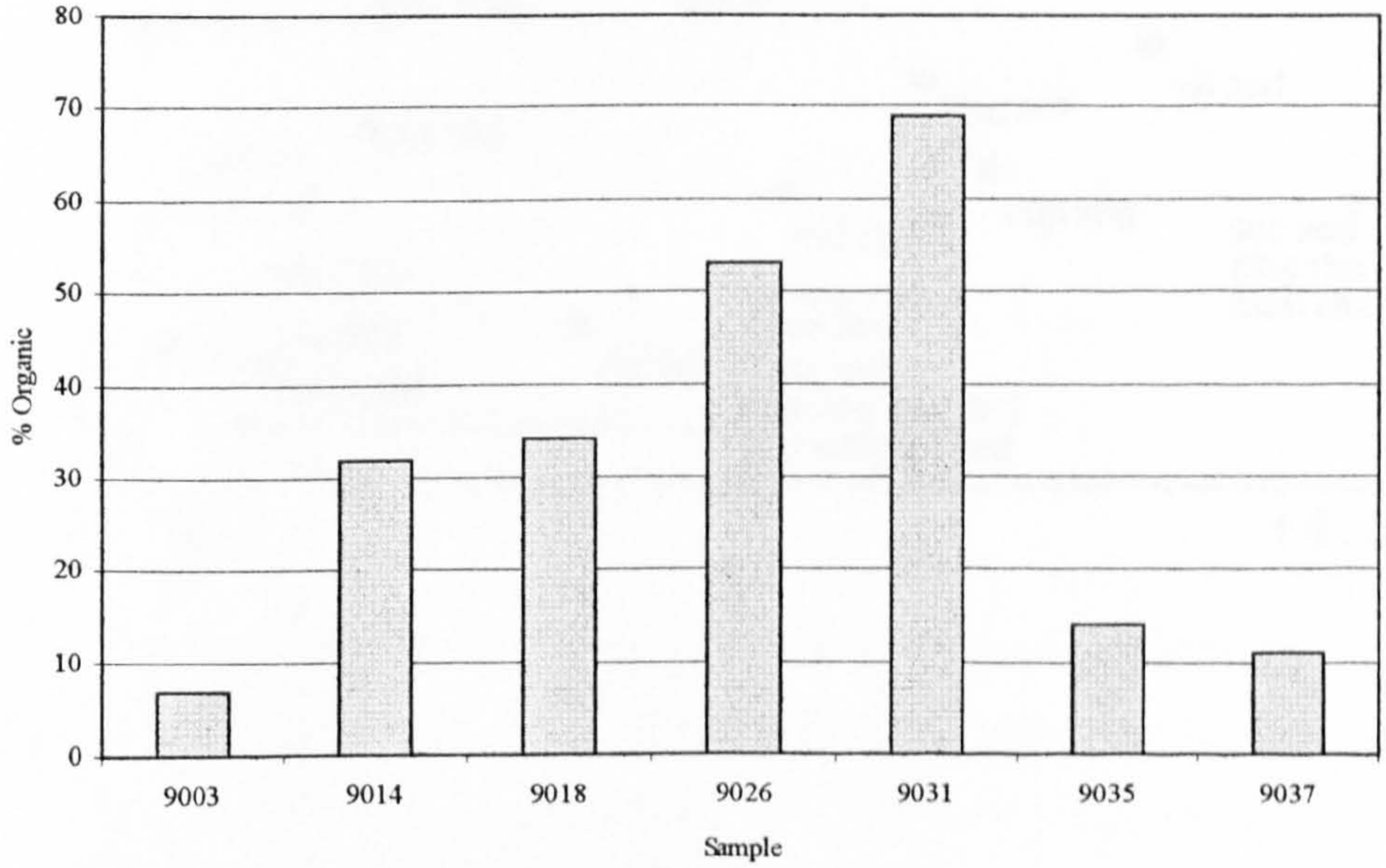


Figure 5.9 Medway Tunnel Section 9 LOI data



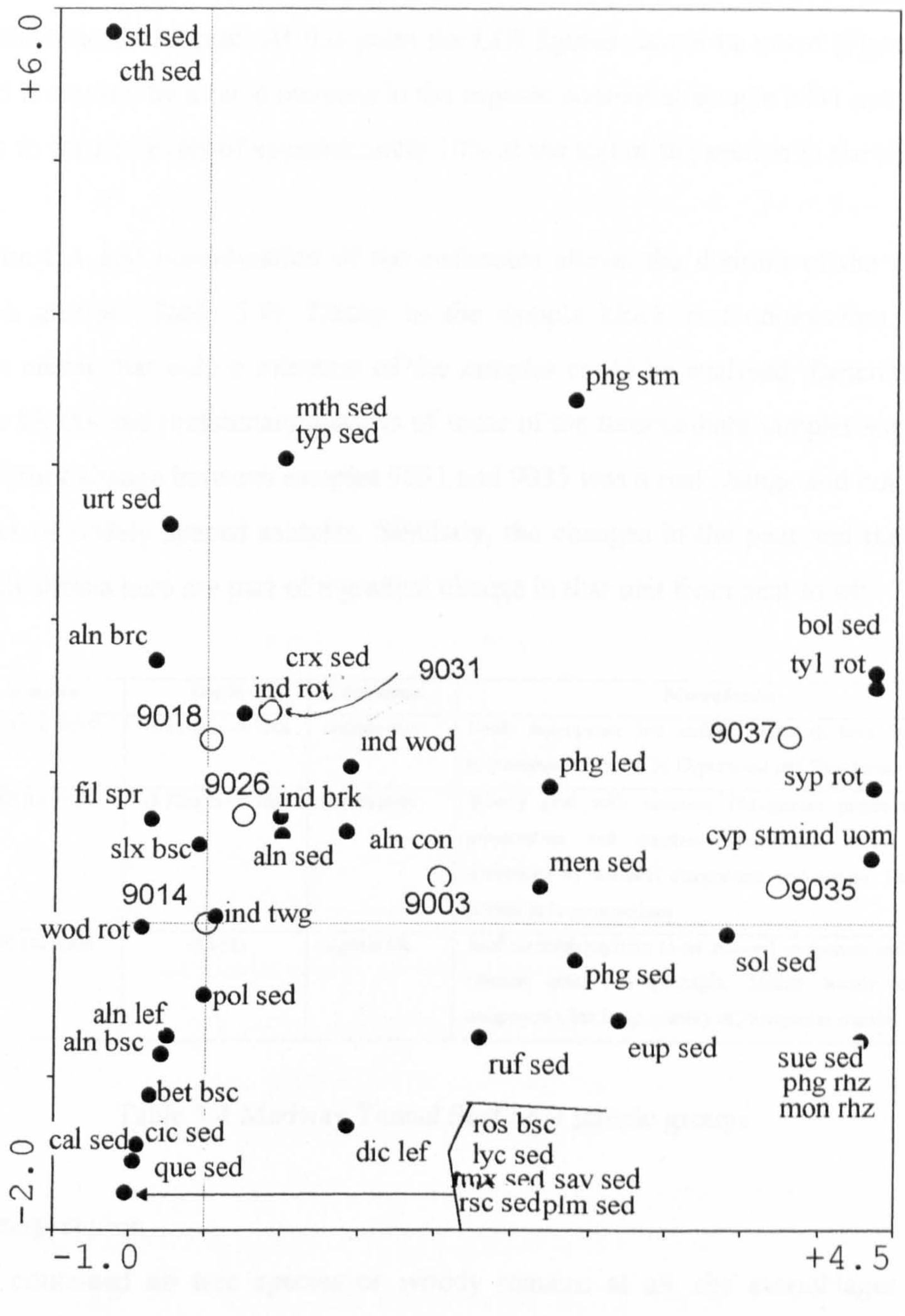


Figure 5.8 Medway Tunnel Section 9 CA of all macrofossil data

was sample 9003 from the organic-rich silts in the upper part of the section. Interestingly samples 9014, 9018, 9026 and 9031 are arranged in correct order along the first axis showing an increase in the positive components and decrease in the negative components towards the base of the peat. At this point the LOI figures should be noted (Figure 5.9). The trend is marked by a rapid increase in the organic content at sample 9031 and slow reduction to former levels of approximately 10% at the top of the section in the silty peat of 9003.

The CA and consideration of the sediments allows the division of the samples into three groups (Table 5.4). Decay in the sample block and compaction of the sediments meant that only a selection of the samples could be analysed. Description of the whole blocks and preliminary analysis of some of the intermediate samples suggested that the abrupt change between samples 9031 and 9035 was a real change and not simply an artefact of widely spaced samples. Similarly, the changes in the peat and the upper organic silt shown here are part of a gradual change in that unit from peat to silt.

Group	Samples	Depth	Sediment	Macrofossils
A	9035 to 9037	-3.81m to –3.75m	organic clay	Seeds depauperate but include saltmarsh taxa. Non-seed herbaceous dominated by Cyperaceae and *Phargmites*
B	9031to 9014	-3.72m to –3.36m	woody peat	Woody peat with constant *Phragmites* presence. Poor preservation and constant Dicotyledon leaves. Seeds dominated by arboreal components and *Urtica*. Sporangia present in large quantities
C	9003 to 9006	-3.14m	organic silt	Seed assemblages have lower arboreal component and mainly riparian taxa. No sporangia. Mainly woody non-seed components, but large quantity of *Phragmites* remains

Table 5.4 Medway Tunnel Section 9 sample groups

5.4.3.3 Interpretation

Group A contained no tree species or woody remains at all, the assemblages being dominated by Poaceae leaf fragments and Cyperaceae rootlets. Preservation was good and suggests deposition in an environment with high water levels. The finds are consistent with the deposition of macrofossils in a vegetated marsh, possibly dominated by clubrush (*Scirpus maritimus*) and reed (*Phragmites australis*), both of which were found in the sediments and the latter in the vegetative remains. The presence of *Scirpus maritimus* and the seeds of seablite (*Suaeda*) indicate that the environment was tidal.

The transition from organic silt dominated by herbaceous remains to woody peat was rapid. A preliminary analysis of the samples between 9031 and 9035 showed that the samples were dominated by *Phragmites* vegetative remains. In Group B the mixture of arboreal, *Phragmites* and various herbs, including Filicales species is consistent with deposition in a closed canopy wet-woodland with a mixed groundstorey of sedges, reeds and ferns intermixed with Dicotyledon herbs. The lack of Cyperaceae vegetative remains would suggest that sedges were not the major groundstorey element. The presence of the budscales of dryland trees, especially *Quercus*, would indicate the close proximity of these species. These could only persist on high ground or dry areas of the mire. Nettle seeds (*Urtica dioica*) were ubiquitous in these samples and are consistent with the presence of drying and decay in the peat. This is also supported by the poor state of the wood and vegetative tissues.

The high silt content in the samples from Group B suggests a constant input of sediment from low-energy floodwaters and some of the seeds are almost certainly from this source. An increase in sediment input towards the top of the peat is shown in the LOI figures and the diverse assemblage of seeds in sample 9014 may be consistent with increased floodwater influence. An alternative interpretation is that the canopy of the wet woodland was beginning to open up with higher water levels allowing ragged robin (*Lychnis flos-cuculi*), celery-leaved buttercup (*Ranunculus sceleratus*) and brooklime (*Samolus valerandi*) to flower and set seed.

The single sample of Group C showed a decrease in the number of alder seeds and fruits and woody components and a relative rise in *Phragmites* remains, although overall macrofossil incorporation was lower in this sample than in those below it. This may be due to higher sedimentation rates. It is uncertain if the wood present in this sample is from trees growing at the time of sedimentation or derived from the decaying trunks and branches of the earlier flora. The presence of *Plantago major* and a wider variety of tree species may be due to increased allochthonous inputs from flood inundation. This final sample in the stack continues the overall trend to increased clastic sedimentation and possibly a more open flora, in which the seeds and fruits of the tree species decline. The uppermost samples indicate increasing inundation of an open marshy habitat dominated by herbaceous taxa, including reed. Groups B and C contained no saltmarsh taxa and the whole upper sequence represents a sequence of freshwater environments.

The sequence of events can be summarised as follows:

1) Deposition in an estuarine marsh environment on the floodplain or riverbank with rapid sedimentation and high water levels. Mixed *Scirpus* and *Phragmites* vegetation giving way to *Phragmites* dominated marsh.
2) Rapid development of an alder carr with lowering water levels, isolation of the area from tidal influence and greater influence of groundwater on sedimentation and vegetation. Freshwater conditions persist and a closed canopy alder woodland is established by *ca* 4800 BP. The mire has a mixture of pools as shown by aquatic taxa and dry areas in which otherwise dryland trees and nitrophilous *Urtica* are established.
3) Increasing sediment inputs are caused by continued rises in the water-table and flooding, causing increased allochthonous inputs and/or opening of the canopy. Eventual development of a herbaceous wetland, possibly a reedbed, and opening of the tree cover.

5.4.4 Section 11

5.4.4.1 Macrofossil preservation (Table 5.5)

Woody remains, including twigs, bark and wood fragments, were restricted to the upper three samples in section 11, especially the highest sample where they were associated with tree seeds and bracts. The lowest samples contained little plant matter and there was a general increase in the overall quantity of macrofossil remains upward through the profile as reflected in the LOI figures (Figure 5.10). Rootlets were preserved throughout the sediments, with the silts containing abundant Cyperaceae rootlets. Monocotyledon stem fragments, rhizome fragments and leaves were recorded sporadically in the silts and small fragments of leaves from Betulaceae species were present in both silts and peats.

Seed abundance was highest in sample 11001. The peat samples contained a variable seed concentration, with 11001 and 11003 having considerably higher seed/sporangia concentrations than the silt samples (Figure 5.11). These samples also contained much higher species concentrations than the silts. Numerous seeds, bracteoles, bracts and budscales of *Alnus* were preserved in the uppermost peat sample. This sample also contained, as with the other two peat samples, a large assemblage of freshwater aquatic and marsh taxa. Saltmarsh taxa were mainly confined to the lower sediments, with sea clubrush (*Bolboschoenus maritimus*) the most numerous taxon in the lower

Taxon/Component	Sample	11001	11002	11003	11004	11005	11006	11007	11008	11009
	Troles Smith Description	Sh3Ag1	Sh3Ag1Th+	Sh3Ag1Th+	Sh3Ag1Th+	As3Ag1Dh+	As2Ag2Dh+	As2Ag2Dh+	As2Ag2Dh+	As3Ag1Dh+
	Colour	10YR2/1	10YR2/1	10YR2/1	10YR2/1	5Y3/1	5Y4/1	5Y4/1	5Y4/1	5Y4/1
	Monolith Depth	3cm	9cm	15cm	18cm	23cm	31cm	39cm	42cm	45cm
	Depth O.D. (m)	-3 56	-3.63	-3.69	-3 72	-3.77	-3 84	-3 93	-3.95	-3.99
		28.00	30	34	35	7	5	4.3	4.1	3.5
A. Seeds, Fruits and buds										
1. Wetland Trees.										
Alnus glutinosa cone		9								
Alnus glutinosa seed		22		1					1	
Alnus glutinosa bracteole		57								
Alnus glutinosa bud scales		11								
2. Submerged and floating aquatics										
Alisma/Baldellia sp. seed		10								
Alismataceae seed embryo		14								
Callitriche cf. *stagnalis* seed		42	2	1						
Characeae oospore		113								
Lemna sp. seed			3	2						
3. Emergent aquatics.										
Glyceria sp. seed		4								
Typha sp. seed			12	23					1	
4. Herb. riparian, marsh and mire: open.										
Apium cf. *inundatum* seed				2						
Bidens cernua seed		3								
Carex sp. trigonous seed				10	6					
Eupatorium cannabinum seed						2				
Juncus acutiflorus seed		38	2							
Juncus bufonius seed		51								
Juncus sp. seed		12								
Phragmites australis seed		12		27	15		1			
cf. *Phragmites australis* spikelet		6								
Solanum dulcamara seed		5								
Urtica dioica seed		20	13	3						
6. Saltmarsh.										
Bolboschoenus maritimus seed		4		2		16	31	38	21	16
Triglochin maritimus seed							1			
7. Dryland trees, shrubs and woody taxa.										
Rubus fruticosus agg. seed		4								

Table 5.5 Medway Tunnel Section 11 macrofossil data

Taxon/Component	Sample	11001	11002	11003	11004	11005	11006	11007	11008	11009
8. Ferns.										
Filicales sporangia		823	725	58						
9. Grassland.										
Potentilla anserina seed				17						
Ranunculus acris type seed				7						
12. Indeterminate.										
Atriplex sp. seed						2				
Poaceae indet. seed					5					
Anthers		8								
Indeterminate seeds		15					1			
B. Vegetative macrofossils										
Betulaceae leaf fragments		4			1					
Cyperaceae epidermis									1	
Cyperaceae type roots							10	26	25	20
cf *Phragmites australis* leaf							18	11		
Phragmites australis stem			6		2	1	3	5	18	11
Poaceae epidermis		1	22	11	20	38	1	5	9	2
Monocotyledon Rhizome										1
Type 1 rootlet (smooth)		2	22	38	21	26	41	7	11	12
Type 2 rootlet						3				8
Wood Fragments		18	13	6						
Bark		16	9	1						
Twig		1								
Woody root		1		1						
Moss		1	2							
Seeds		2	2		1	1	2	16	1	1
Indeterminate Vegetative Tissue		13	24	43	54	30	24	30	36	45
Unidentifiable Organic Matter		43								
Charcoal			1		1	1				

Sample	11001	11002	11003	11004	11005	11006	11007	11008	11009
Seed Abundance	1283	757	153	26	20	34	38	23	16
Seed abundance minus Filicales	460	32	95	26	20	34	38	23	16
Species diversity	14	6	12	2	3	3	1	3	1
Seed concentration	25.66	15.14	3.06	0.52	0.4	0 68	0.76	0.46	0.32
Seed concentration minus Filicales	9.2	0.64	1.9	0.52	0.4	0.68	0.76	0 46	0.32
Species concentration	0.28	0.12	0.24	0.04	0.06	0.06	0.02	0.06	0.02

Table 5.5 Medway Tunnel Section 11 macrofossil data (cont.)

Figure 5.10 Medway Tunnel Section 11 LOI data

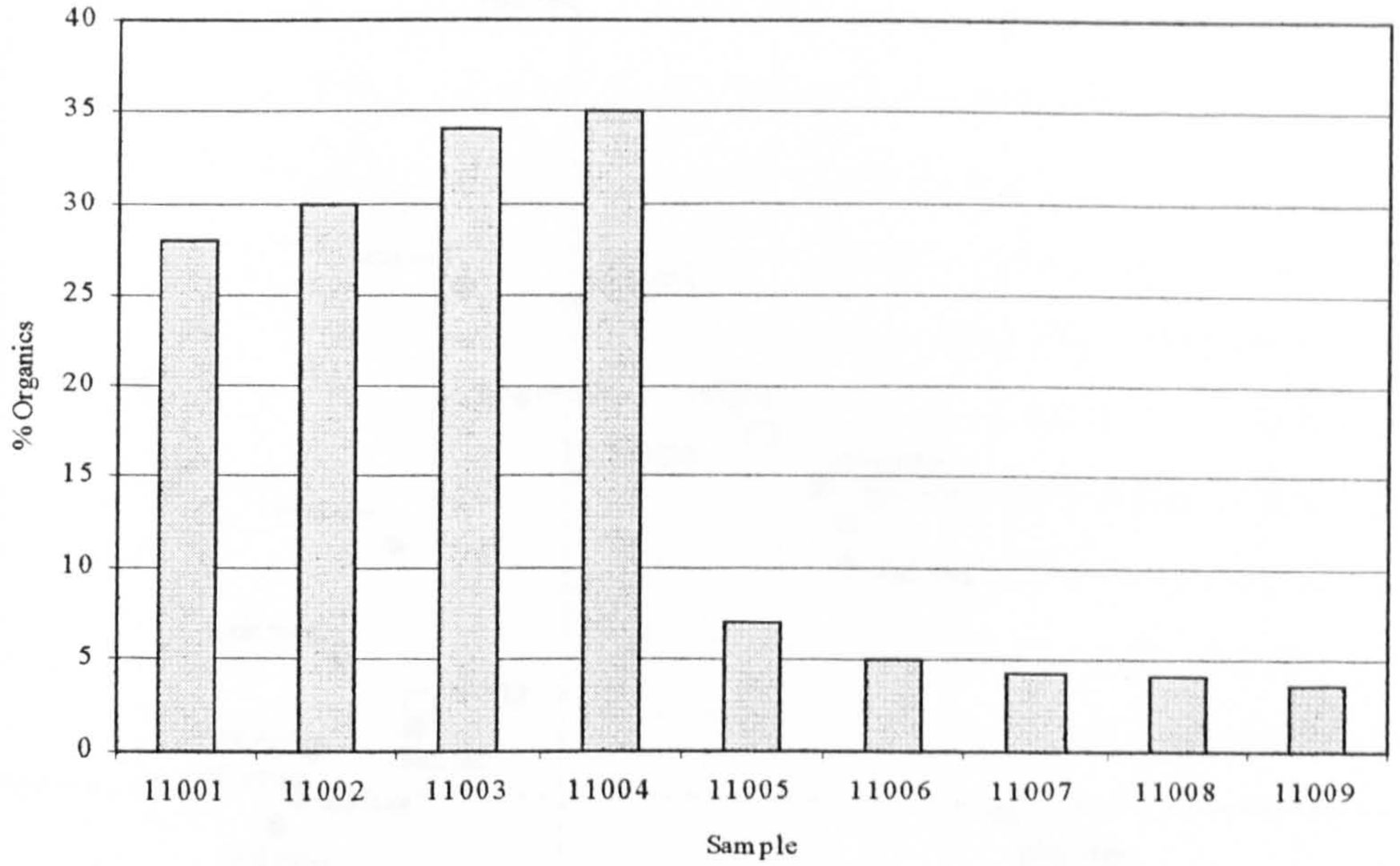
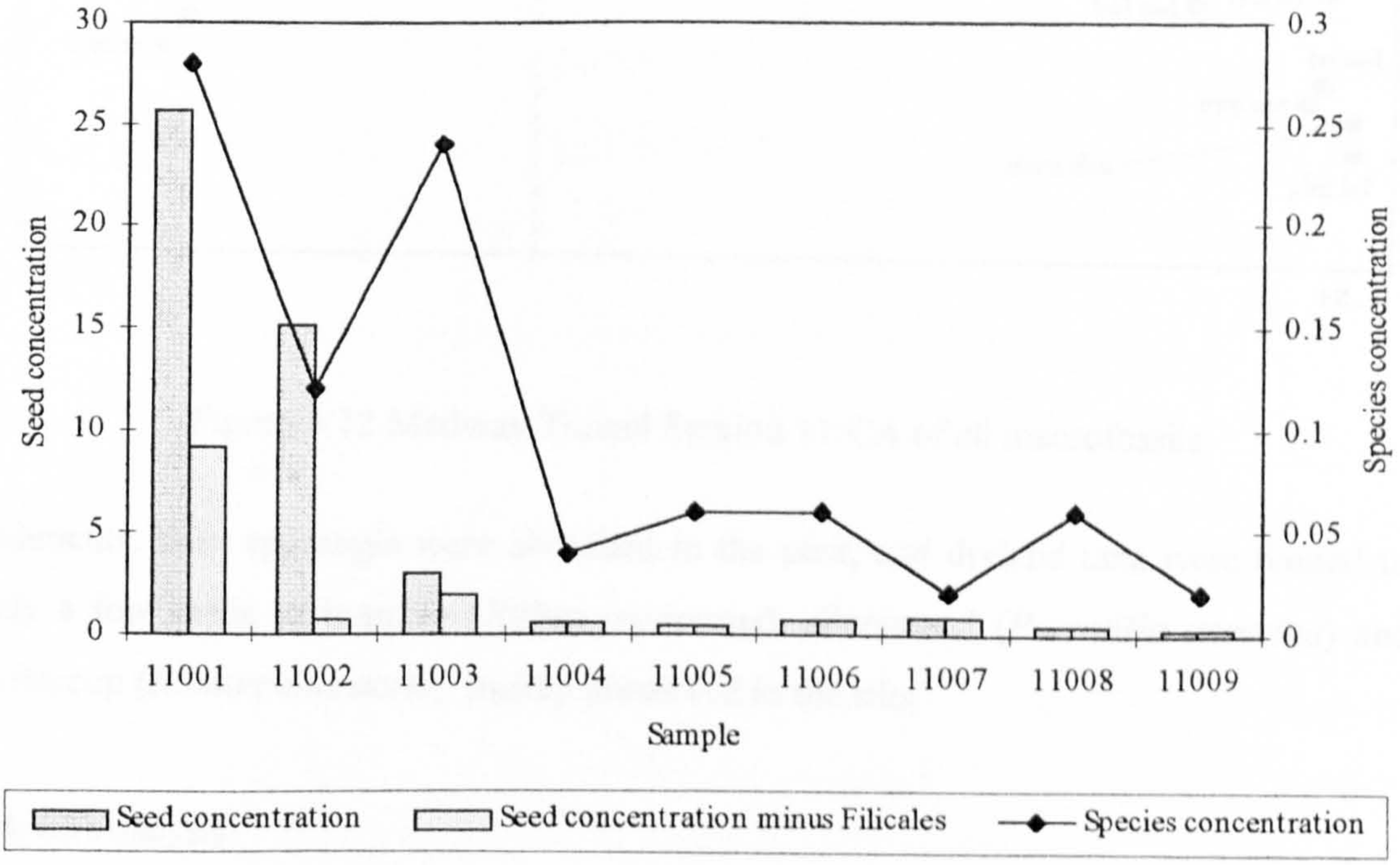


Figure 5.11 Medway Tunnel Section 11 seed and species concentration



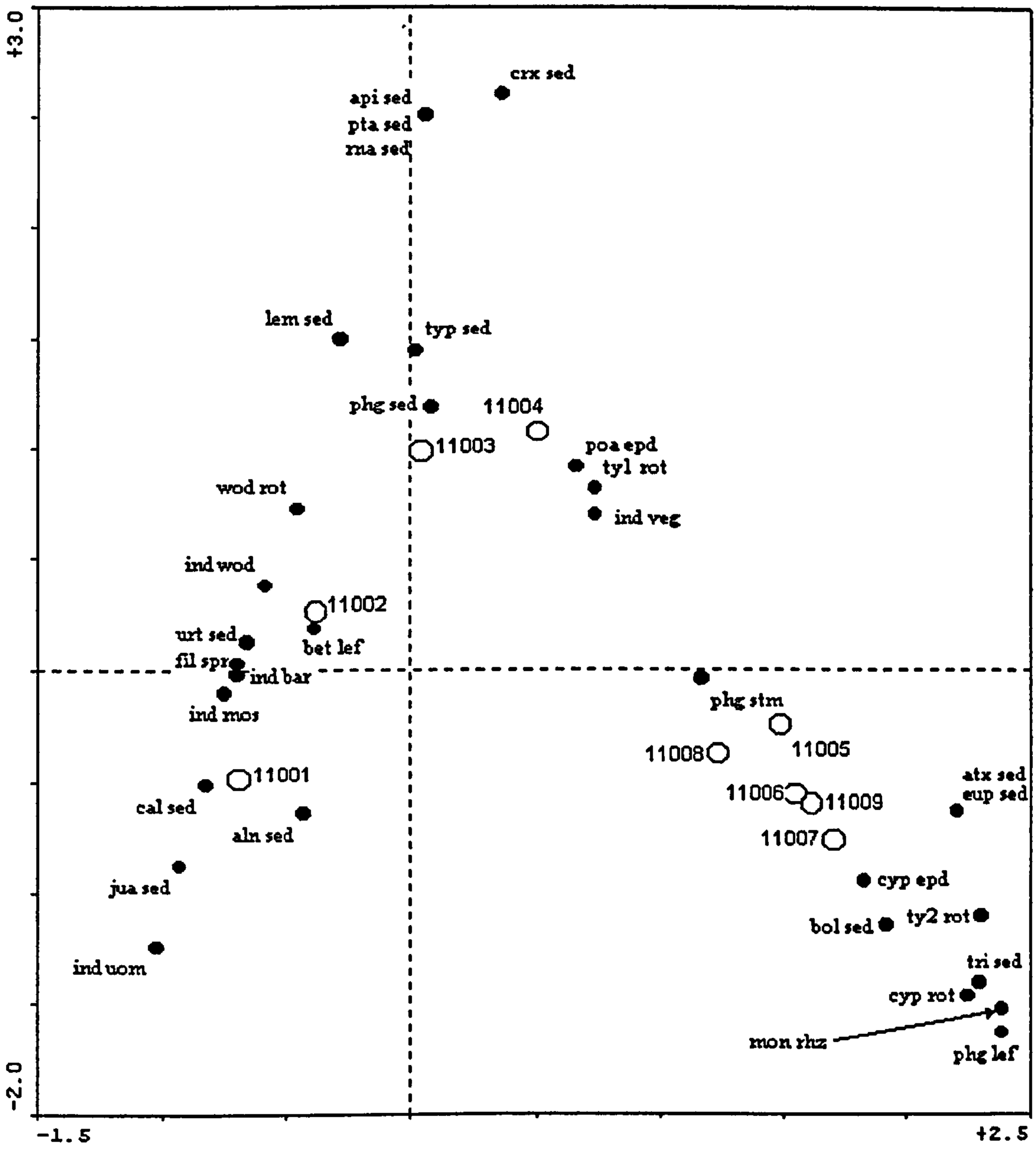


Figure 5.12 Medway Tunnel Section 11 CA of all macrofossils

sediments. Fern sporangia were abundant in the peat, and dryland taxa were limited to only a few seeds of bramble (*Rubus fruticosus*), silverweed (*Potentilla anserina*) and buttercup (*Ranunculus acris*), mainly preserved in the silts.

5.4.4.2 Analysis

CA of the assemblages split the samples into four groups on the basis of macrofossil composition. Axis 1 accounted for much of the variation in the sample set although, as with the other palaeoenvironmental sample sets in this analysis, the eigenvalues

(representing overall variance) were low. Samples 11005 – 11009 were grouped at the positive end of the first axis with high values of *Phragmites* components, Cyperaceae components and *Bolboschoenus* seeds among other characteristics (Figure 5.12). Opposed to this was sample 11001, which had low values of the above and preserved large quantities of *Almus* components, unidentifiable matter, Betulaceae leaf fragments and woody components. In between these were samples 11002 to 11004, which contained variable quantities of the major components on the first axis, 11002 being similar to 11001 but being separated along the second axis and having higher values of *Phragmites* seeds, *Phragmites* stems, rootlets and Poaceae epidermis. 11003 was similar to 11002, differing in its high rootlet concentration and indeterminate vegetative matter. 11004 contained no wood and was dominated by rootlets and decayed vegetative matter, lying between the composition of the silt samples and the higher peat samples.

The samples can be divided on the basis of macrofossil composition into four groups (Table 5.6).

Group	Samples	Depth	Sediment	Macrofossils
A	11005 - 11009	-3.99m to -3.77m	Silt-Clays	Low seed abundance and diversity with saltmarsh taxa. Cyperaceae and Poaceae vegetative remains dominant and no woody components
B	11004	-3.74m to -3.72m	Organic silt	Seed concentration low, mainly *Phragmites* seeds. Most non-seed matter vegetative remains, epidermis and rootlets
C	11002 - 11003	-3.71m to –3.63m	Silty Peat	Variable seed concentrations. High organic content with many roots and vegetative remains, including Poaceae/*Phragmites*
D	11001	-3.58 to –3.56	Silty Peat	High seed concentration with trees and herbs. Wood content high with much decayed matter and vegetative remains

Table 5.6 Medway Tunnel Section 11 macrofossil groups

5.4.4.3 Interpretation

In sample group A, the presence of well preserved vegetative tissues indicates deposition in an environment with maintained high water-levels at the sampling point. The presence of sea clubrush (*Bolboschoenus maritimus*) and *Triglochin* suggest that the deposits were accumulated in an estuarine environment and presence of Cyperaceae rootlets suggests that the plants grew locally. Occasional seeds of *Almus* and *Typha* may have been introduced to the site by tides as both taxa are very well dispersed by water (Collinson 1983; Field 1992). The presence of *Phragmites* components suggests that reeds also grew at the site. It is difficult to be sure of local plant growth and the deposits

may have been accumulated in a mudflat adjacent to a stand of established marsh vegetation, similar results having been found at Snape Saltings (Chapter 4). The lack of Cyperaceae components in sample 11005 and presence of Poaceae taxa may suggest that the site was home to a stand of *Phragmites* or other grass-dominated habitats and that the *Bolboschoemus* was no longer locally dominant.

Sample 11004, forming group B, is notable for the presence of greater quantities of freshwater wetland plants, larger quantities of rootlets, a lack of sedge rootlets, an increase in quantities of Poaceae epidermis and larger quantities of vegetative tissues. A marsh flora growing at the site seems likely, especially with the presence of much higher quantities of organic matter in general and rootlets in particular. Sediment changes may suggest that sediment accumulation rates had slowed down. *Phragmites* is the only obvious candidate for a vegetation dominant, although it may be over-represented in sediments. The lack of saltmarsh taxa may suggest that the environment became closed to tidal inputs, although conversely it may be a result of the small sample size.

In group C, woody components were preserved for the first time in the sequence, although in small quantities, suggesting the presence of a wet-woodland environment nearby, possibly in the area sampled by section 9. Both the abundance and diversity of the freshwater wetland and aquatic taxa increased. Sea-clubrush seeds were present in sample 11003 in small numbers, possibly indicating occasional tidal flooding or aerial input. The latter is the most likely, probably from a nearby stand of the taxon. The local vegetation was probably that of an open freshwater marsh, with taxa such as *Phragmites*, *Typha*, *Carex* and *Urtica*. The abundant and well preserved epidermis in these samples may suggest that water-levels were often high in the marsh and sedimentation rapid.

The uppermost sample 11001 contained evidence of a nearby fen woodland with *Alnus* seeds, bracts and budscales being present and wood, including twigs, forming a major sample element. Aquatic taxa were also present in large numbers, as in Section 16, and it is possible that permanent standing water was present at the sample point. The abundance of wood suggests that the sample point supported tree-cover during the period of deposition, although the seed flora suggests that the local vegetation was diverse. A similar vegetation to that in Group E in Section 16 is suggested, with the seeds of several taxa being possibly allochthonous.

Human activity was not particularly marked in the sample set, although the presence of charcoal flecks in samples 11002, 11004 and 11005 may indicate burning

activity in the catchment. The presence of grassland taxa in 11003 may indicate that open grassland was present on the non-calcareous soils in the local area.

The sequence can be summarised as follows:

1) Deposition in or adjacent to saltmarsh with clubrush and reed components.
2) Similar conditions as above but a local dominance of reed and loss of *Bolboschoenus*. Increasing organic preservation suggesting possible decreasing sedimentation rates. Both consistent with isolation from tidal influence.
3) Development of an open freshwater marsh at between *ca* 4500 BP and 5000 BP, possibly a reedbed, with high groundwater levels. Riverborne and possibly tidally borne seeds enter the sediments. Development of wet-woodland vegetation nearby.
4) Isolation from flooding but maintained high groundwater influence causing peat formation. Colonisation of the peat by alder and formation of an open fen-carr woodland with standing water in pools and a reed-like groundstorey.

5.4.5 Section 6

5.4.5.1 Macrofossil preservation (Table 5.7)

Woody tissues were almost totally absent from the sample set and the assemblages of vegetative tissue consisted mostly of herbaceous rootlets, epidermis, Monocotyledon leaf fragments and humified vegetative matter. The main difference between the silts and peats was the higher rootlet abundance in the latter. Cyperaceae, Juncaceae and Type 1 rootlets dominated the assemblages, with Type 2 roots also being present in several samples. Preservation was good in the samples, although much of the vegetative matter was highly fragmented. The good epidermal preservation suggests that the sediments rarely dried out since deposition. Organic content was low with the exception of the samples from the peat (Figure 5.13).

Seed assemblages were abundant and dominated riparian/wetland taxa, especially the *Juncus* types. Identification of *Juncus* was limited to distinction of *J.gerardii* and *J. maritimus*, *J. bufonius* and *J. articulatus* types following Korbe-Grohne (1964). Seed and species concentrations are shown in Figure 5.14. The peak values of seed abundance were found in samples 6505, 6018 and 6016, all samples adjacent to episodes of peat deposition. Seed concentrations were very high, distorted by the large quantities of *Juncus* seeds. Species concentration was high in all of the samples and the assemblages were very diverse. The highest values were found in the peat samples.

Wetland taxa included celery-leaved buttercup (*Ranunculus sceleratus*) and toad-rush (*Juncus bufonius*), both of which inhabit muddy riverbanks, the latter also inhabiting disturbed environments. Other taxa such as marsh pennywort (*Hydrocotyle vulgaris*) and lesser spearwort (*Ranunculus flammula*) were found only in the peat. Aquatic taxa were distributed throughout the samples but were concentrated in the peat. They included starwort (*Callitriche stagnalis*) and spikerush (*Eleocharis palustris/uniglumis*). Few wet-woodland trees were represented, the seeds of (*Almus*) and a single budscale of willow (*Salix*) being the only identified macrofossils. The shaded marsh taxa figwort (*Scrophularia nodosa*) and wood-clubrush (*Scirpus sylvaticus*) were present in the peat unit. The seeds of saltmarsh taxa were again present throughout the samples. Saltmarsh rush (*Juncus gerardii*) and sea rush (*Juncus maritimus*) seeds were abundant and concentrated in the organic silts, accompanied by seablite (*Suaeda maritima*), sea-arrowgrass (*Triglochin maritimum*), scurvy-grass (*Cochlearia* sp.), sea milkwort (*Glaux maritima*) and seagrass (*Puccinellia* sp.), all in fewer numbers and located only in the silts.

Dryland taxa were well represented and included trees and shrubs, the seeds and buds of which were most abundant in the silts around the peat. The pinnules of bracken (*Pteridium aquilinum*) were preserved throughout the samples as were fern sporangia. Grassland, wayside and arable taxa were present in very small numbers and charcoal was similarly represented. Of some note was the presence of charred cereal awns, culm fragments and rush seeds in sample 6501, which also contained metal slags and small fragments of pottery.

5.4.5.2 Analysis

CA of the samples showed limited variation and split the samples from the two monoliths along the first axis (Figure 5.15). Samples from Monolith 3 (prefixed with 600-) were found at the positive end of the first axis in a tight group with high positive values of Cyperaceae rootlets among many other positive influences. The exception was sample 6020, found grouped near 6506, the peat sample from Monolith 5. This and the other samples from Monolith 5 were spread across the negative side of the axis, being separated by the occurrence of many minor components. The peat samples were also distinguished by the greater quantity of seeds otherwise rare in the samples, especially *Hydrocotyle* and *Samolus*. The main negative influences on the first axis were the *Juncus*

	Monolith	5	5	5	5	5	5	3	3	3	3	3	3	3
	Monolith Depth	4-6cm	12-14cm	20-22cm	28-30cm	36-38cm	46-48cm	10-12cm	14-16cm	18-20cm	26-28cm	34-36cm	38-40cm	46-48cm
	Depth O.D. (m)	0 06	-0.02	-0.09	-0.18	-0.26	-0.36	-0.50	-0.54	-0 58	-0.60	-0.66	-0.74	-0.86
	Troels-Smith Description	Ag3As1Dh+	Ag3As1Dh+	Ag2As2Dh+	Ag2As2Dh+	Ag2Sh1As1Dh+	Sh3As1Th+	Sh2Ag2Th+Gmin+	Ag2As1Sh1Th+Gmin+	Ag2As1Sh1Th+Gmin+	Ag2As1Th1	Ag2As2Th+	Ag2As2Th+	Ag2As2Th+
Taxon	Sample	6501	6502	6503	6504	6505	6506	6020	6018	6016	6012	6008	6006	6002
A. Seeds, Fruits and buds														
1. Wetland trees.														
Alnus glutinosa seed			1				8							
Salix sp. bud-scale									1					
2. Submerged and floating aquatics														
Alisma sp. seed								1						
Alismataceae seed embryo				1		3	8	2	1					
Berula erecta seed								1						
Callitriche stagnalis seed		3	17	6	5	11		16	7	2	1	3	3	3
Ranunculus sub genus *Batrachium* seed		3	2			6	10							
3. Emergent aquatics.														
Eleocharis palustris/uniglumis seed			7	16	9	10	14	3						
Eleogiton fluitans seed					1				1					
Glyceria maxima seed			5	4	4									
Sparganium sp. seed								2	1					
Typha sp. seed						1	4							
4. Open riparian, marsh and mire														
Apium inundatum seed							2	1						
Bidens cernua seed							10							
Carex flat buff seed			3	9	8	24	22	7	17	9				1
Carex sp. brown biconvex seed						5		2						
Carex sect. Paniculatae seed					3	6	72	42	1					
Carex sp. trigonous seed							6	1		3	1	3	3	1
Epilobium hirsutum seed			1											
Eupatorium cannabinum seed				2		4	2							
Hydrocotyle vulgaris seed							22	11	1					
Juncus articulatus type seed	5	93	90	99	100	52	34	53			9			
Juncus bufonius seed	9	93	185	142	55	58	5	13		50	36	16	38	40
Juncus sp. seed	38	19	11	35	14	26		4						
Lycopus europaeus seed						14	2					1		
Phragmites australis seed	5	2		3										
Poa palustris seed		7	4											
Poaceae indet. Seed	7							2						
Poaceae indet. spikelet base		1												
Potentilla palustris seed								1						
Ranunculus sceleratus seed	2	18	22	29	29	60	9	5	8	1	8	12	13	
Rumex cf. *maritimus* seed	3													
Sagina cf. *nodosa* seed		2		1				7						
Samolus valerandi seed	2							61	61		1	4	1	3
Solanum cf. *dulcamara* seed							2							
Urtica dioica seed	2			4	4			1				1	1	
5. Shaded riparian, marsh and mire														
Scirpus sylvaticus seed								2						
Scrophularia nodosa seed							2							

Table 5.7 Medway Tunnel Section 6 macrofossil records

	Monolith	5	5	5	5	5	5	3	3	3	3	3	3	3
	Monolith Depth	4-6cm	12-14cm	20-22cm	28-30cm	36-38cm	46-48cm	10-12cm	14-16cm	18-20cm	26-28cm	34-36cm	38-40cm	46-48cm
6. Saltmarsh.														
Cochlearia sp. seed											2			
Glaux maritimus seed												2	3	1
Juncus gerardii seed		40	67	113	135	1142	212	187	810	1446	450	552	540	38
Juncus maritimus seed		17	13	413	183	162	96	37	2	25	13	40	13	13
Puccinellia cf. *maritima* seed											1			1
Bolboschoenus maritimus seed		5	37	23	40	45	122	90	6	9	2	7	4	3
Suaeda maritima seed		2								2				
Triglochin maritimus seed		12												
7. Dryland trees, shrubs etc														
Corylus avellana nutshell												1		1
Corylus avellana bud-scale												3		4
Betula sp. seed		2												
Betula sp. catkin scale			1											
Quercus sp. bud-scale			2										7	3
Sambucus sp. diaspore		2												
Rubus fruticosus agg. seed					1		4						2	
8. Ferns.														
Pteridium aquilinum pinnule		2	1	1	1		2	05						
Filicales sporangia		3	56			3		41	76	27				
9. Grassland.														
Ajuga reptans seed							2							1
Hypericum perforatum seed				3	1	11	28	6						
Potentilla anserina seed				3		3	4	7	1					
Ranunculus acris type seed		6	1	1										
Stellaria cf. *graminaeus* seed		2			1			1						
10. Arable and disturbed ground.														
Aphanes arvensis seed			1	3		1		1						
Papaver dubium/rhoeas seed		4												
Polygonum aviculare seed			1											
11. Wayside and waste land.														
Plantago major seed									2					1
12. Indeterminate.														
Atriplex sp. seed			1							1				
Mentha sp. seed			1	4	1	19	40	12	8	2				
Rumex sp. seed				1	1									
Sonchus sp. seed		2												
Stellaria sp. seed					1									
Indeterminate seeds				3			8				2			
13. Charred seeds etc.														
Juncus sp. seed		2												
Cerealia awn		2												
Cerealia culm		2												

Table 5.7 Medway Tunnel Section 6 macrofossil records (cont.)

Monolith	5	5	5	5	5	5	3	3	3	3	3	3	3
Monolith Depth	4-6cm	12-14cm	20-22cm	28-30cm	36-38cm	46-48cm	10-12cm	14-16cm	18-20cm	26-28cm	34-36cm	38-40cm	46-48cm
B. Vegetative & woody macrofossils													
Betulaceae indet leaf fragment													1
Cyperaceae type roots		12		20			54	50	44	68	85	73	38
Juncus stem										2			
Juncus type roots		55	63	34	25	8		8	14				19
cf *Phragmites australis* leaf	2			1	3	5			16	2		6	
Phragmites australis stem	1	2		2	2		4						
Poaceae epidermis		2		1			7	14					10
Poaceae rhizome				2				1	2	2	2	3	
Type 1 rootlet	18	12	17	14	59	75	21	25	14	17	8	18	6
Type 2 rootlet						4	2				2		
Hypnum sp. leaf				1									
Moss	1		1				2	1					
Filicales rachis	3												
Twig		1											1
Indeterminate Vegetative Tissue	58	12	19	15	9	10	6		10	11	1	1	22
Indeterminate Plant Matter	17	2		9					1				
Charcoal	1	1	1		1		1			1	1	1	1
Derived indices													
Sample	6501	6502	6503	6504	6505	6506	6020	6018	6016	6012	6008	6006	6002
Seed Abundance	189	458	923	713	1663	917	599	1074	1587	522	644	630	130
Species diversity	23	24	21	22	21	27	30	19	12	11	13	12	15
Seed concentration	3.780	9.153	18.462	14.256	33.260	18.340	11.970	21.480	31.740	10.440	12.880	12.600	2.600
Species concentration	0.460	0.480	0.420	0.440	0.420	0.540	0.600	0.380	0.240	0.220	0.260	0.240	0.300

Table 5.7 Medway Tunnel Section 6 macrofossil records (cont.)

Figure 5.13 Medway Tunnel Section 6 LOI data

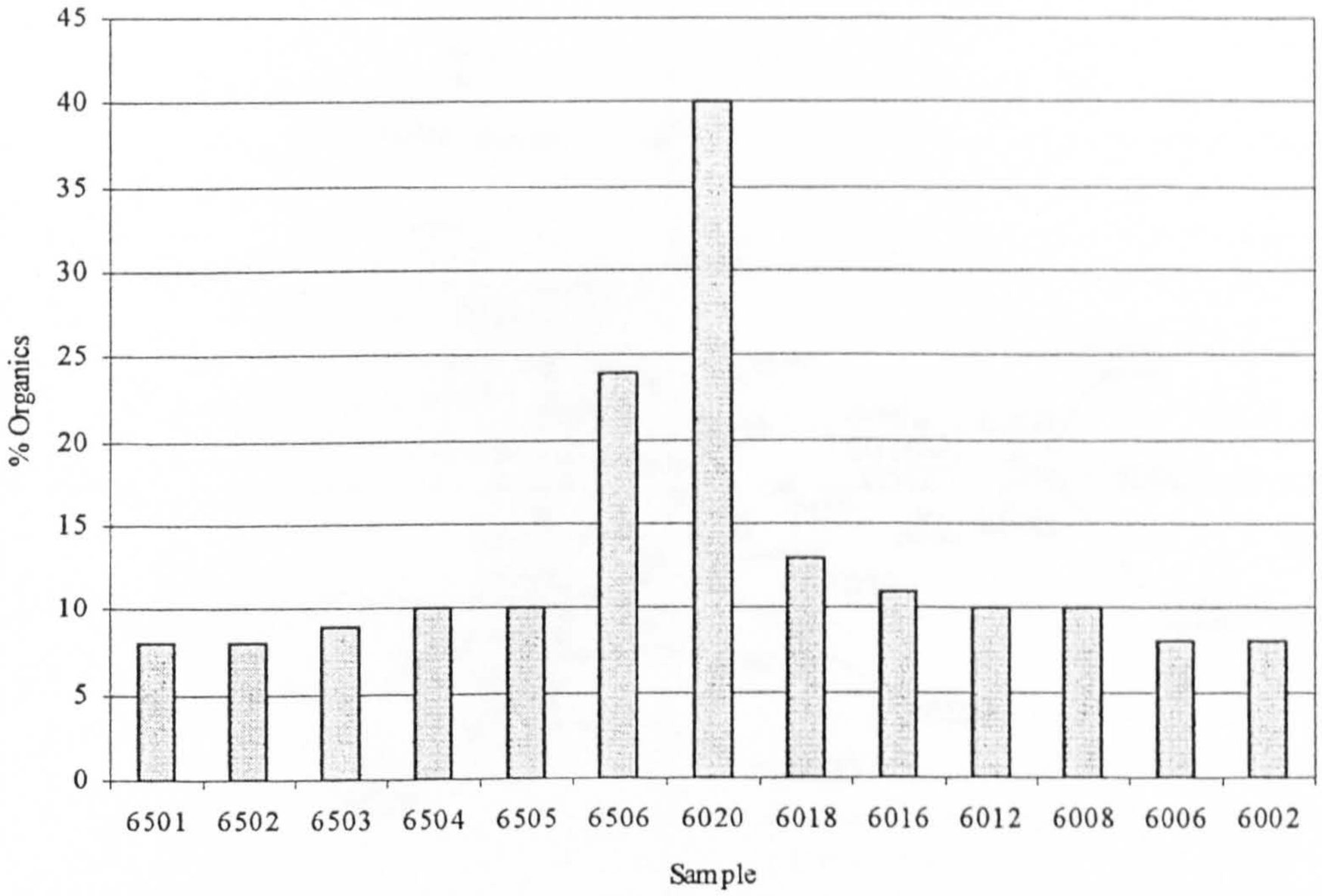
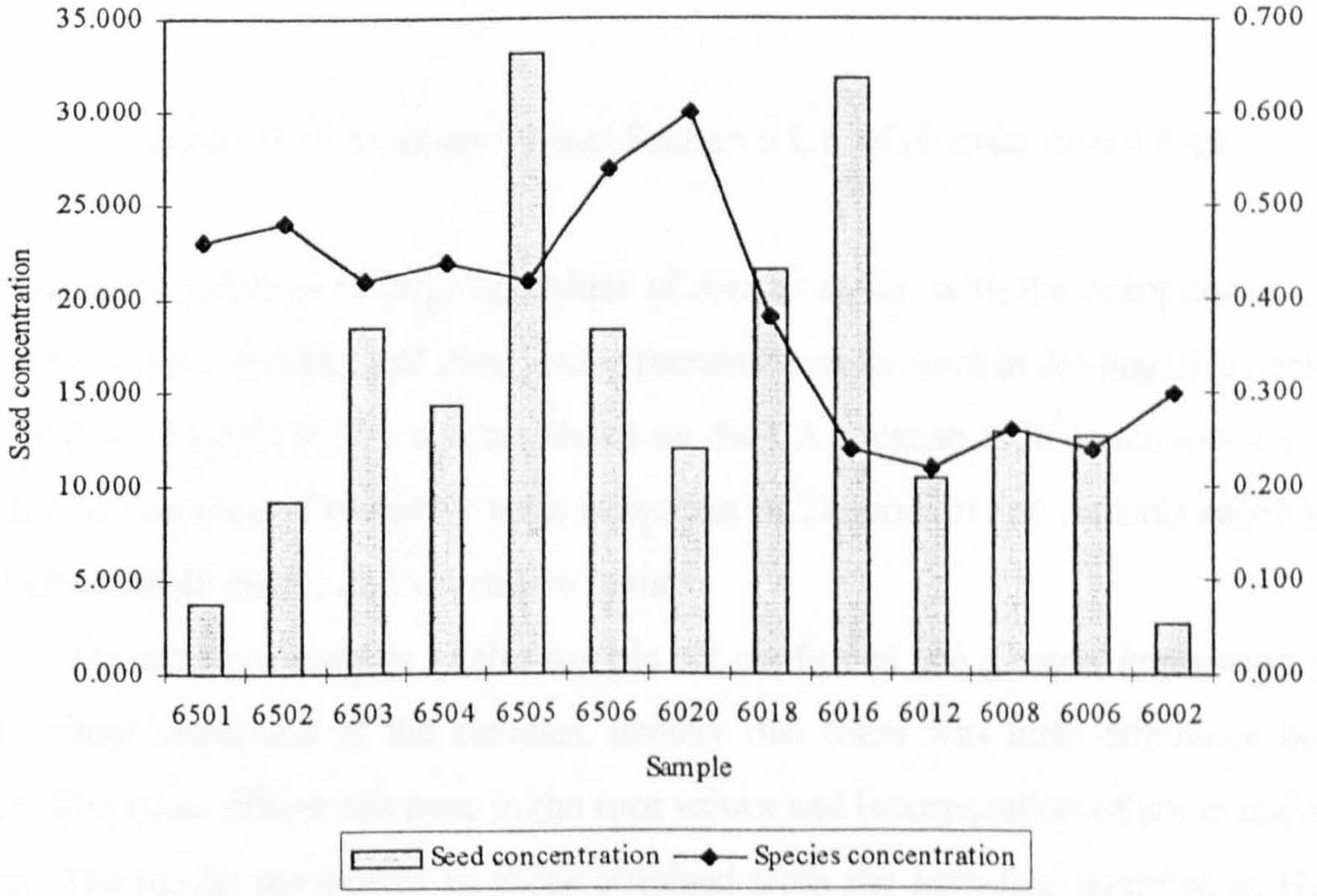


Figure 5.14 Medway Tunnel Section 6 Seed and Species concentration



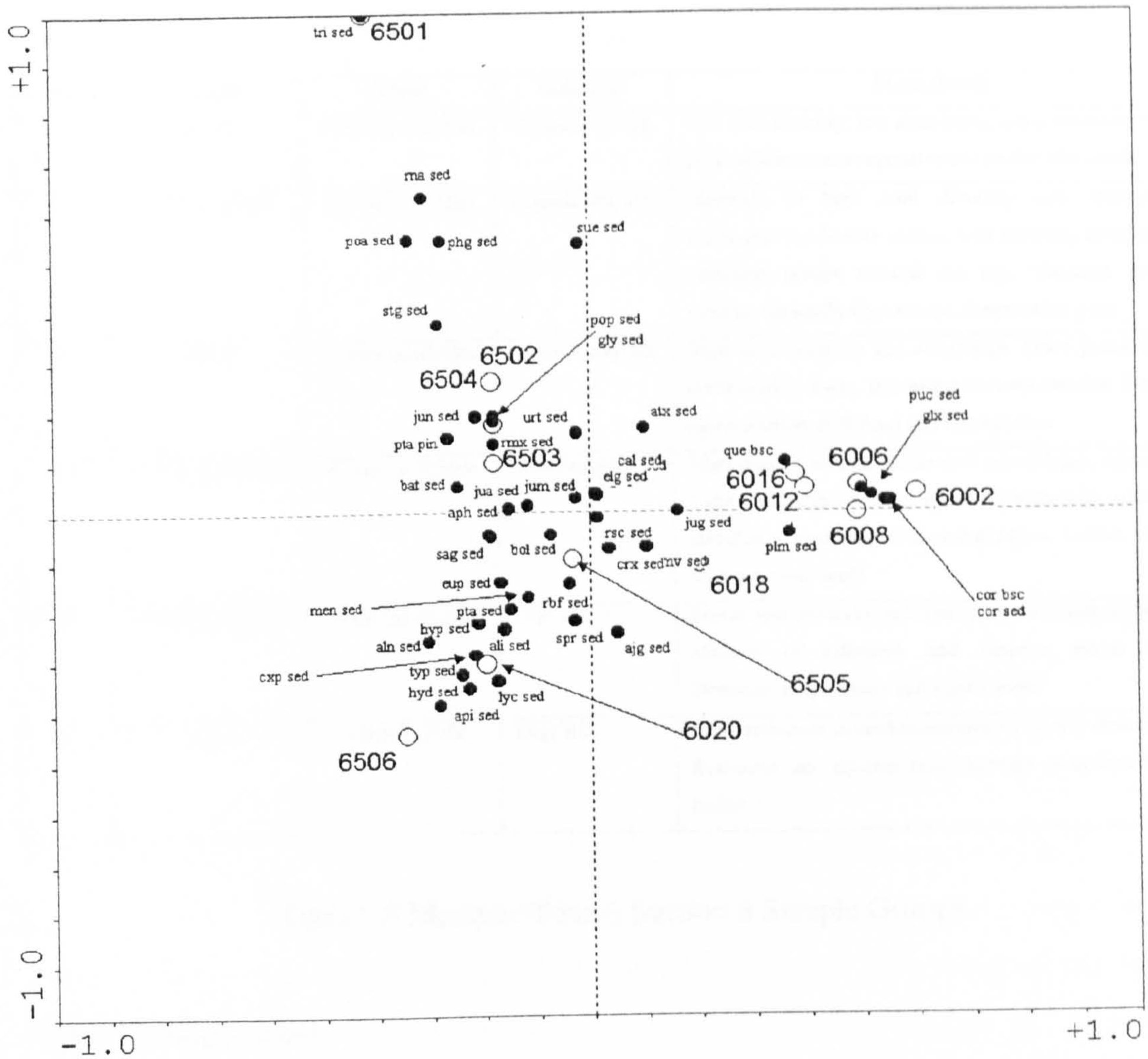


Figure 5.15 Medway Tunnel Section 6 CA of all macrofossil data

roots and the presence of large quantities of *Juncus* seeds, with the exception of *Juncus gerardii*. Type 1 rootlets and *Phragmites* remains were present in the negative section of the diagram. Sample 06501 was separated on the CA because of its much lower range of seeds and presence of relatively large quantities of *Triglochin* and *Suaeda* seeds as well as unidentifiable matter and vegetative remains.

Quantitative analysis of this sample set confirmed the general impression gained from visual inspection of the samples, namely that there was little difference between them. The main differences were in the root values and incorporation of some major seed types. The results are similar to those obtained from the herb-fens sampled at Hickling Broad, being species-rich and difficult to classify and separate using quantitative methods. Consideration of the quantitative data and the sediment information has led to the splitting of samples into 5 groups (Table 5.8)

Group	Samples	Height	Sediment	Macrofossils
A	06002	-0.88m to –0.86m	Organic clay-silt	Low seed diversity, low abundance, many saltmarsh taxa. High indeterminate vegetative and rootlet abundance.
B	06006 to 06016	-0.76m to -0.58m	Organic clay silt	Moderate to high seed diversity and abundance. Dominated by *Juncus* species with reducing diversity of saltmarsh species towards the top. Non-seed mainly rootlets, especially Cyperaceae. Preservation good.
C	06018	-0.56m to -0.54m	Organic clay-silt	High seed diversity and abundance. Good preservation dominated by roots. Increasing Poaceae remains. Greater representation of dryland and riparian taxa
D	06020 and 06506	-0.52m to -0.36m	Silt/Clay peat	High organic content, dense root assemblages, especially Type 1 and Cyperaceae. Highest diversity with moderate abundance, especially of freshwater taxa. Lowest values of *Juncus* spp. seeds
E	06505 to 06502	-0.28m to -0.02m	Clay-silt	Lower seed diversity and lower, but still high diversity. Mixture of saltmarsh and riparian marsh taxa. Domination by *Juncus* and Type 1 roots
F	06501	0.04m to 0.06	Clay-silt	Great reduction in seed abundance and lower diversity of freshwater and riparian taxa. Increase in unidentifiable matter.

Table 5.8 Medway Tunnel Section 6 Sample Groups

5.4.5.3 Interpretation

The seed flora and the abundant herbaceous rootlets present throughout the sample set indicate the maintenance of open, marshy vegetation cover, including plants from the sedge and rush families. Tree and shrub species were present only as seeds, fruits and budscales, suggesting that there was no extensive local wet woodland.

Sample Groups A and B show strong representation of saltmarsh taxa. An increase in the abundance of all taxa and an overall increase in macrofossil incorporation mainly distinguished Group B. Cyperaceae roots, and Juncaceae types in samples 06002 and 06016, suggest the local growth of these taxa and both are well represented in the seed assemblages. The overwhelming dominance of the seeds of saltmarsh taxa, especially *Juncus gerardii*, suggests the presence of this species in the vegetation, with local stands of *Bolboschoenus*, the only Cyperaceae likely to be able to withstand the salinity. *Suaeda* and *Salicornia* seeds are well dispersed and the presence of so few in the samples may suggest that they were not a local plant. The presence of *Puccinellia* seeds may be more spatially reliable, suggesting with the *Juncus*, the presence of a local middle to upper saltmarsh habitat. *Bolboschoenus* is a common plant of rarely flooded upper

marsh swamps. The sequence in group B may show a transition from upper saltmarsh to marginal/upper swamp. Many of the other seeds are easily dispersed wetland taxa suggesting the input from tides and nearby vegetation on land. The numbers of bud-scales of *Quercus* in particular may suggest local stands of the tree. Throughout group B the diversity of freshwater taxa reduced, suggesting possible isolation of the sediment from tidal action.

Group C consisted of a single sample (06018) and had a transitional composition with an increased organic content, large seed abundance and higher diversity than the lower samples. Rootlet concentrations increased in the sample and Poaceae epidermis was well preserved, suggesting deposition in high water conditions. The assemblage still is indicative of saltmarsh deposition. However, the presence of *Samolus* seeds and large quantities of Filicales sporangia suggests the close proximity of terrestrial habitats or freshwater wetlands, although the former is found along the banks of estuaries.

The peat samples of Group D have an intriguing mixture of freshwater and saltmarsh taxa. The entry of some seeds to the deposits can be seen as being due to tidal or flood input, however, the high abundance of many taxa suggest the presence at or near the sample point of many. The fact that the seeds are well preserved and suffer a minimum of surface erosion also argue for limited water transport (cf. Huber and Ferguson 1998). A major change between the two peat samples is the change in root abundance from Cyperaceae dominants in 06020 to *Juncus* and Type 1 in 06506. This may in part be explained by the spatial separation (3m) of the monoliths. The seed flora does not show a correlated change paralleling that of the roots. This may be due to root penetration and the seed flora may provide a more temporally reliable indicator of the local flora. Both samples are dominated by similar taxa, especially *Carex* spp., *Bolboschoenus maritimis*, *Juncus* spp. and a wide range of other wetland taxa. The seed flora suggests the local presence of a transitional freshwater/upper saltmarsh swamp, dominated by *Carex* spp., *Bolboschoenus* and a wide range of Monocotyledon and Dicotyledon herbs. The presence of Type 2 rootlets may suggest the local presence of *Typha* or *Sparganium* spp., also common upper saltmarsh taxon. Others include *Samolus valerandi*, *Eleocharis* and *Eleogiton fluitans*, all consistent with a freshwater to brackish transitional swampy environment. The identification of this flora is important as analagous floras are not present today in the Lower Thames. The range of aquatics, emergents, Monocotyledons and Dicotyledon herbs suggests the presence of a variety of

sub-environments locally, including swamp, pools, channels and drier marshes. This flora is indicative of considerable groundwater influence and could be due to increases in runoff or river discharge under conditions of lowering/stable sea-level. The presence of saltmarsh rush seeds in the peat is of some interest and may indicate the input of seeds via the wind, as rush seeds can be dispersed in this way (Ridley 1939). Much lower abundances of this taxon were found in the peat samples in comparison to the silts, perhaps supporting this thesis.

Group E samples see a reduction in the diversity of the assemblages and a return to dominance of *Juncus* spp. seeds. The dominance of *Juncus* rootlets suggests the actual presence of the plant at the site, as does the presence of *Phragmites* remains. This change suggests a return of greater tidal influence, perhaps with a flora similar to that of the preceding upper-marsh swamp, but with a reduction in the less salt-tolerant species. One would expect an increase in seed types with greater tidal influence and this does not happen. The final sample group was distinguished by a further reduction in freshwater taxa, an increase in saltmarsh taxa and an increase in unidentifiable material. This is all consistent with further increasing saline influence. The reduction in root abundance may suggest the onset of more open conditions and perhaps even the presence of a mudflat environment.

Human disturbance indicators are represented in many of the samples, with charcoal present throughout the sample set and charred remains in sample 06501. Other indicators come from the waterlogged seed flora, with both non-calcareous grassland and ruderal taxa present. *Pteridium aquilinum* remains are also ubiquitous and may indicate the presence of infested pasture or arable land nearby. The charred remains at the top of the sample column also indicate human activity at or near the site as the cereal awn was very well preserved, with its morphology preserved in detail. It is unlikely that this detail would have been preserved if the awn had been transported in the river, suggesting a local origin. The most likely incorporation route is from the dumping of hearth debris nearby. Much of this evidence is in the upper samples from Monolith 5. This may suggest that human activity at the site was minimal before the period of peat deposition; however, it may simply reflect the closer proximity of that monolith to the shore.

The sequence can be summarised as follows:

1) Deposition of sediment in an upper saltmarsh subject to limited tidal intrusion dominated by *Bolboschoenus* and *Juncus gerardii*.
2) Continued presence of *Juncus gerardii* saltmarsh at the site and freshwater marshes nearby. Isolation of the site from regular tidal inundation.
3) Further reduction of tidal influence and/or increasing runoff and groundwater levels. Onset of peat accumulation at *ca* 3000 BP in an open transitional brackish swamp dominated by sedges, club-rush and a wide range of Dicotyledon herbs. Shrubs and trees persisted on dryland nearby, although open terrestrial environments are also probable. Near to the site a *Juncus gerardii* saltmarsh persisted, its seeds being blown into the site.
4) Return of upper saltmarsh at the sample site and increasing tidal influence. Increasing evidence of human activity
5) Further tidal influence with the development of saltmarsh flora and perhaps the development of mudflats.

5.4.6 Trench 7

5.4.6.1 Macrofossil preservation

Seed assemblages were abundant and diverse (Table 5.9; Figure 5.16), with the basal sample (37014) containing a large quantity of seeds, mainly *Juncus*. The other samples had much lower seed concentrations, but they were still very high. Species diversity increased up the profile. Freshwater marsh and riverbank taxa were common in the seed assemblages, including several sedges (*Carex* sp.), toad rush (*Juncus bufonius*), rushes (*Juncus articulatus*) and celery-leaved buttercup (*Ranunculus sceleratus*). Other less ubiquitous taxa included marsh cinquefoil (*Potentilla palustris*), nettle (*Urtica dioica*) and brooklime (*Samolus valerandi*). Nettle may also have derived from disturbed nitrophilous conditions and is often associated with human activity. Saltmarsh taxa were also well represented, saltmarsh rush (*Juncus gerardii*) being the most abundant taxon in the sample set and present in all of the samples. Sea rush (*Juncus maritimus*), sea club-rush (*Bolboschoenus maritimus*) and spikerush (*Eleocharis palustris*) were also common, with sea milkwort (*Glaux maritima*) and scurvy-grass (*Cochlearia* sp.) present in only a few samples. Other aquatics were sporadically preserved and included lesser-marshwort (*Apium inundatum*) and water-crowfoot (*Ranunculus* sub-genus

Sample		37001	37002	37003	37004	37005	37013	37006	37008	37014
Troels-Smith		As3Ag1	As3Ag1,	Ag2Sh1As1	As3Ag1	As3Ag1Sh+Th +	Sh2Ag2Th+	As2Ag2Th+	As2Sh1Ag1Th+	As2Sh1Ag1Th+
Color		10YR5/1	10YR5/1	10YR3/1	10YR5/1	10YR3/1	10YR2/1	10YR3/1	10YR3/2	10YR3/2
Block Depth		0-2cm	2-4.5cm	4.5-6cm	6-8cm	8-10cm	10-11.5cm	11.5-12cm	14-16cm	16-17cm
Taxon/Component	Depth O.D. (m)	1.25	1.23	1.20	1 19	1.17	1.15	1.13	1.11	1.09
A. Seeds and Fruits										
2. Submerged and floating aquatics.										
Apium cf. *inundatum* seed		2	1							
Ranunculus sub-genus *Batrachium* seed		1					6	2		
3. Emergent aquatics.										
Eleocharis uniglumis/palustris seed		13	24	25	1	1	8			
Typha sp. seed										1
4. Open riparian, mire and marsh										
Carex sp. flat buff seed		6	2		1	4	21	5		
Carex sp. trigonous seed			1	6				2	1	
Juncus articulatus type seed		125	210	191			57	7	25	
Juncus bufonius seed		125	369	102	609	372	40	53		
Juncus sp. seed							1		14	420
Potentilla cf. *palustris* seed		2								
Ranunculus sceleratus seed		57	30	20	4	12	18	57	2	2
Urtica dioica seed		1								
Samolus valerandi seed				15			32			
6. Saltmarsh.										
Cochlearia sp. seed									1	5
Glaux maritima seed		1		11	11					
Juncus gerardii seed		738	148	285	352	284	113	367	951	4617
Juncus maritimus seed		10	43	280		16			10	
Bolboschoenus maritimus seed		15	3	8	2	6	6	3		
7. Dryland trees, shrubs etc.										
Rubus fruticosus agg. seed		1	4				3			
8. Ferns.										
Filicales sporangia			9							
9. Grassland.										
Hypericum cf. *perforatum* seed					1					
Potentilla anserina seed			1	4	8	4	3	2		
Thymus praecox/puligioides seed					1		21			
11. Wayside and wasteland.										
Plantago major seed			1	6	1	1	57	18		
12. Indeterminate.										
Apium sp. seed				3						
Mentha sp. seed			1		1	2	3			
Poaceae sp. seed			1							
Viola sp. seed								2		
Cyperaceae seed						1				
Chenopodium sp. seed								2		
B. Non-seed macrofossils										
Cyperaceae stem		1								
Cyperaceae epidermis		4					1			
Cyperaceae type rootlet		15				8	8	4	7	
Juncaceae epidermis		1								
Juncus sp. type rootlet		15	26	18	22	24	17	37	22	25
Type 1 root			9	9	7	8	8	8	15	12
Dicotyledon leaf								1	1	
Indeterminate rootlet		45	51	62	44	39	51	33	29	25
Indeterminate epidermis			1		1					4
Indeterminate Moss		1	1	1	1	1	1	1	1	
Charcoal		1		1						2
Indeterminate herbaceous matter		16	13	10	25	18	14	16	24	30
Unidentifiable Organic Matter						1		1	1	
Seed Abundance		1097	848	956	992	703	389	520	1005	5048
Species diversity		14	15	13	12	10	15	12	7	5
Seed concentration		21.94	16.96	19.12	19.84	14.06	7.78	10.4	20.1	100 96
Species concentration		0 28	0.3	0.26	0.24	0 2	0.3	0.24	0.14	0.1

Table 5.9 Medway Tunnel Trench 7 macrofossil records

Figure 5.16 Medway Tunnel Trench 7 seed and species concentration

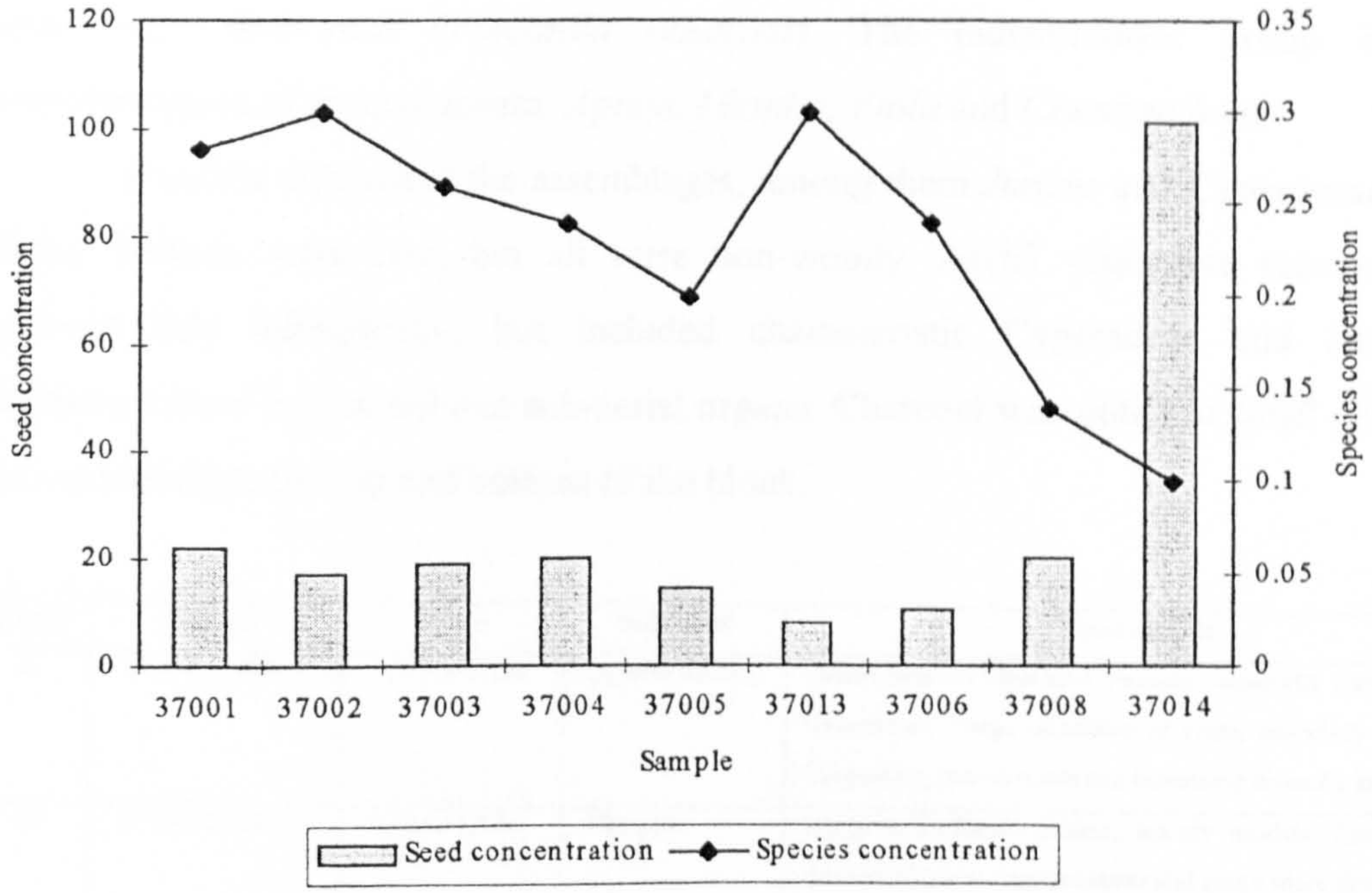
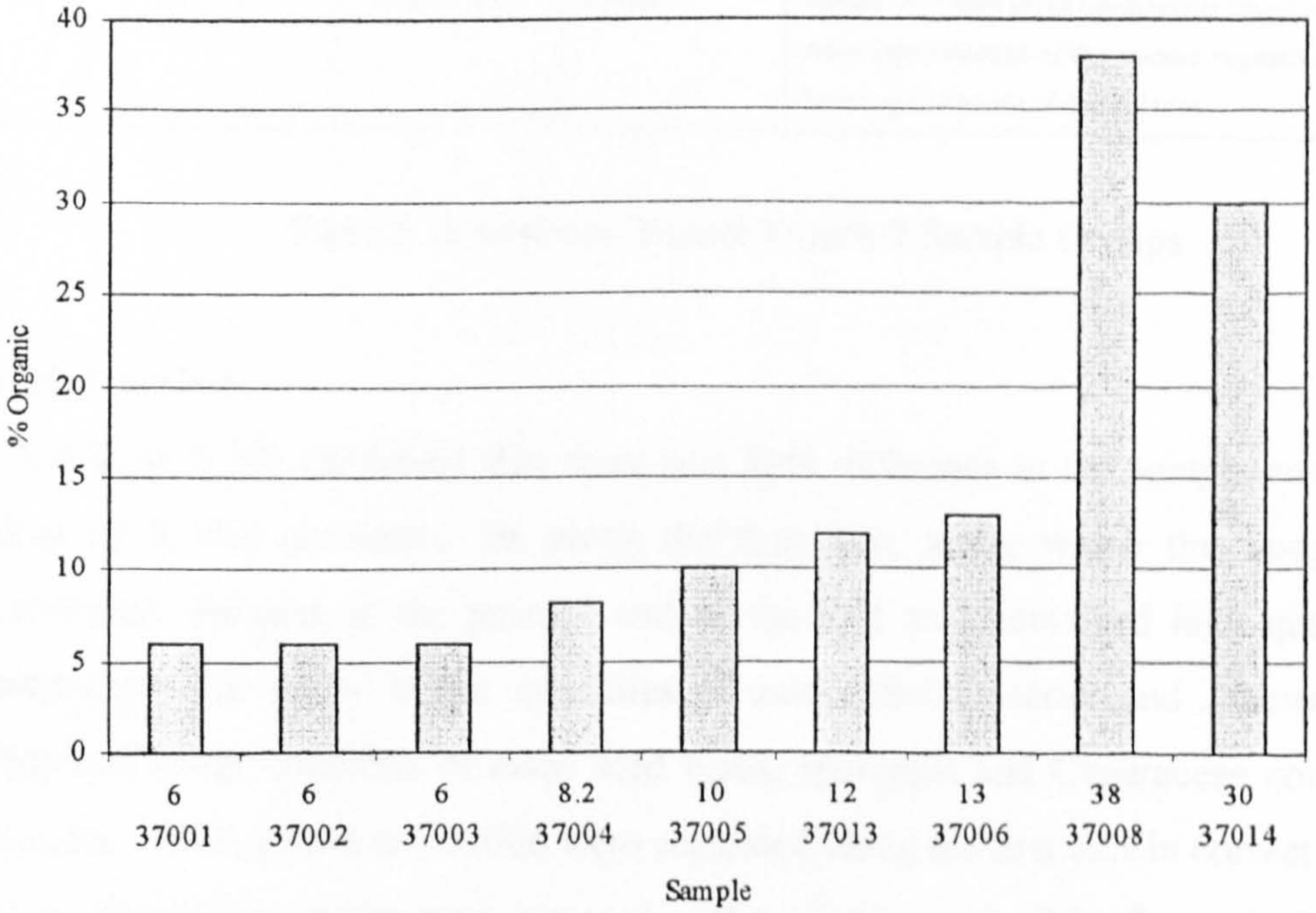


Figure 5.17 Medway Tunnel Trench 7 LOI data



Batrachium). Dryland taxa were present in only small numbers but included the indicator of chalk grassland, wild thyme (*Thymus praecox*), and one of non-calcareous open conditions, silverweed (*Potentilla anserina*). The indeterminate group included representatives of several genera: *Apium, Mentha, Viola* and *Chenopodium.*

Rootlets dominated the assemblages, among them *Juncus* and Cyperaceae types. Other remains were rare, but all were non-woody. Aerial vegetative remains were present only infrequently, but included characteristic Cyperaceae and Juncaceae epidermis from both aerial and sub-aerial organs. Charcoal was noted in small quantities in samples from the top and bottom of the block.

Group	Sample	Depth	Sediment	Macrofossils
A	37014 to 37008	1.07 to1.11m	Organic silt-clay	Dominance of vegetative remains, especially *Juncus* and Cyperaceae. Large quantities of roots, especially *Juncus*. Decreasing *Juncus* seeds and increasing diversity in 37006
B	37006 to 37013	1.11 to 1.15m	Silty peat	Large macrofossils content, mainly rootlets. Seeds more diverse with low *Juncus* counts and many more dryland and freshwater wetland taxa
C	37005 to 37002	1.115 to 1.23m	Silt-clay	Continued dominance of rootlets, especially *Juncus*, but otherwise similar to that below. Diverse seed assemblages with many dryland taxa, but domination of *Juncus* species and higher visibility of saltmarsh taxa
D	37001	1.23 to 1.25	Silt-clay	Similar to Group D but much higher abundance of *Juncus*, better representation of Cyperaceae vegetative remains and lower representation of dryland taxa.

Table 5.10 Medway Tunnel Trench 7 Sample Groups

5.4.6.2 Analysis

CA (Figure 5.18) confirmed that there was little difference in the sample composition. Most of it was accounted for along the first axis, along which the samples were distributed. Samples at the positive end of the first axis contained high quantities of *Juncus gerardii* seeds, higher quantities of unidentifiable matter and *Juncus* rootlets. They had lower quantities of many seed types, sporangia and Cyperaceae components. Samples 37014, 37008 and 37006 were separated along the first axis in correct sequence order. The other samples were grouped at the negative end of the first axis, having the opposite values to those noted for the positive end. All of these samples contained a wider range of macrofossils, especially the seed flora. Only 37013 was separated from this group, mainly on the basis of the greater abundance and diversity of Cyperaceae

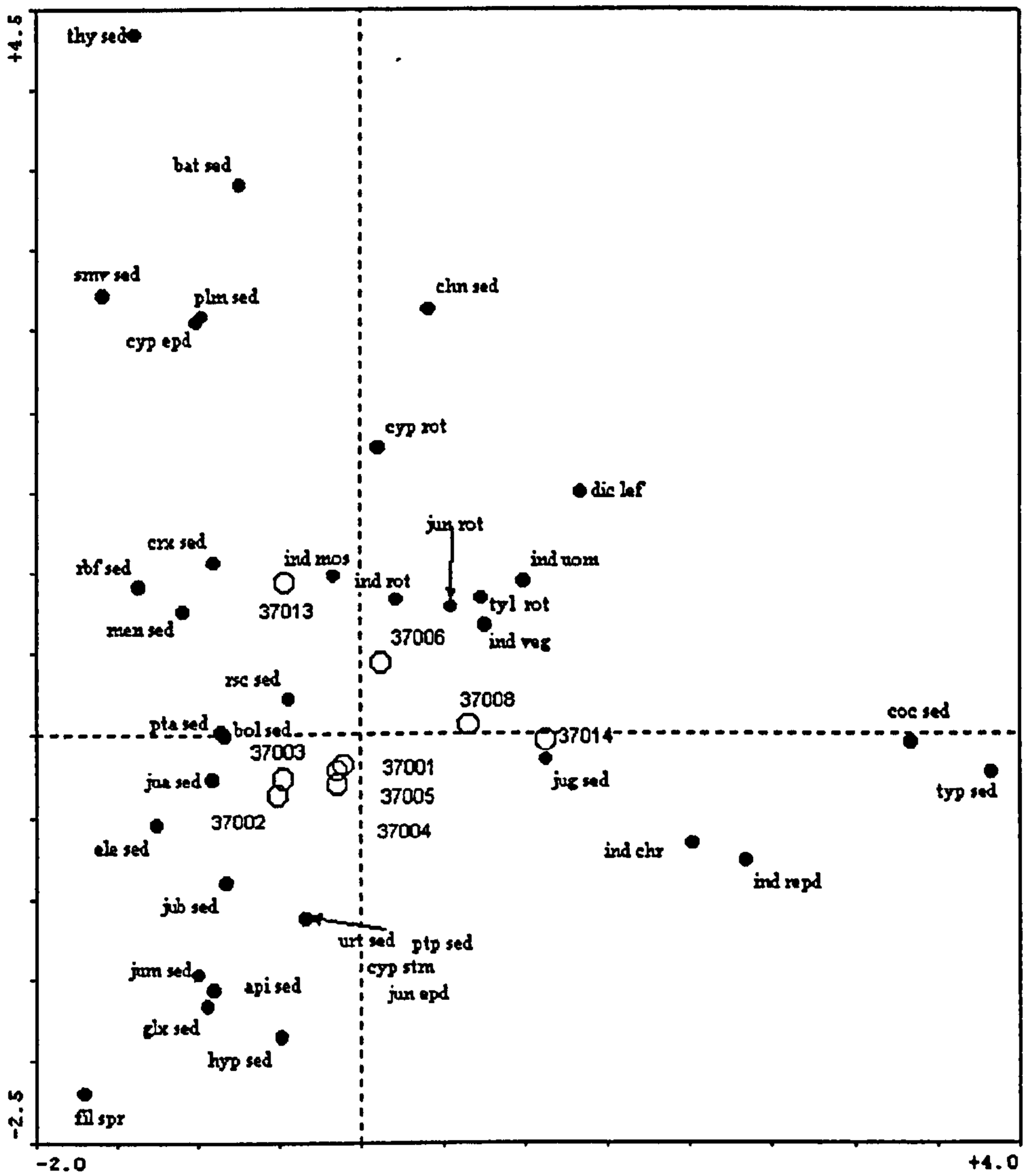


Figure 5.18 Medway Tunnel Trench 7 CA of all macrofossil data

components and the addition of several seed types. This analysis separated four broad groups of samples that may have interpretative significance (Table 5.10).

5.4.6.3 Interpretation

The vegetative component of the sample varied little throughout the block and is consistent with a dense open marshland flora, dominated by grasses (Poaceae), sedges (Cyperaceae) and rushes (Juncaceae). The dense rootlet mat that the sediment contained can only have derived from vegetation growth at the sample site. Trees and shrubs were not present, with the seeds of bramble (*Rubus fruticosus*) probably entering the site via water transport bird excrement.

Taxonomic identification of vegetative tissues is limited to family level and more precise habitat information from plant macrofossil relies on the seed and fruit assemblages. The seed flora is consistent with the vegetative remains. The samples of Group A had the highest organic content and were dominated by rootlets, especially of *Juncus*. The seed assemblages were dominated by saltmarsh taxa, mainly saltmarsh rush (*Juncus gerardii*) mixed with smaller quantities of sea rush (*Juncus maritimus*) and scurvy-grass (*Cochlearia*). Non-saltmarsh taxa were present in small numbers and all of those present have seeds that are widely dispersed (Field 1992; Praeger 1913). The overwhelming domination of the assemblage by saltmarsh components indicates that at the time of deposition the site held a *Juncus gerardii* upper saltmarsh flora or a swampy habitat with this taxon nearby.

Group B samples were similar in composition to Group A, although they contained a much greater diversity of seed taxa and the Cyperaceae components that appeared in 37008 are common. The organic content of the samples was much lower than Group A and the organic content decreased above this point (Figure 5.18). Decreasing *Juncus gerardii* values may suggest that the plant was less common at the site. However, this is uncertain as it may simply be a local seed concentration effect. The mixture of taxa is reminiscent of those in Section 6 and may indicate the presence of a local upper marsh swamp in the depression that the silts filled. The lower organic content suggests that sediment input may have increased to the site as a result of increased runoff drainage into the depression, flooding, or increased tidal incursion over the site. The presence of dryland taxa begins in these samples and continues through Group C.

The samples of Group C have a similar macrofossil composition with the exception of the change in numerical dominance of the samples from saltmarsh to freshwater taxa, especially toad-rush (*Juncus bufonius*). The presence of this taxon suggests that the area contained disturbed vegetation. The continued presence of saline indicators suggests that the basin itself contained saltmarsh vegetation or was open to inputs from the tide. The freshwater taxa may have derived from nearby transitional marshes as the samples come from a depression, the site acting as a basin for the deposition of macrofossils from elsewhere.

The sample from Group D contained the seeds of saltmarsh rushes and Cyperaceae taxa, the latter also represented in the vegetative remain assemblages. The main difference between this sample and the one below is the lack of dryland taxa.

Otherwise the samples contain more taxa typical of upper saltmarsh swamps. The changes may simply indicate the isolation of the basin from tidal or runoff flows and local development of a transitional saline/freshwater flora.

Studies of modern seed rain (Chapter 4) showed that the interpretation of seed abundance of well dispersed taxa, such as the *Juncus* species is difficult, although high abundance usually means that the taxon grew close to the site. This work also suggests that seeds would, at most, be subject to local re-distribution in the low energy environment in which the sediment accumulated. If this is accepted, these taxa must have derived from the local flora. Given this, the mixture of seed types present here is confusing and mutually exclusive at one site. The most likely explanation is that the local vegetation was largely saline, with the other taxa coming from tidal and wind inputs from the complex of transitional and freshwater communities that may have lived on higher ground around the depression. The plant communities may have been strongly affected by human interference and, perhaps, grazing. The differences in quantitative macrofossil characters may be due to changes in tidal and runoff inputs, with the local flora changing little during the period of deposition. The apparent isolation from tidal inputs may indicate a period of relative sea-level stillstand and development of a transitional flora.

Represented dryland taxa include thyme (*Thymus praecox*) and silverweed (*Potentilla anserina*), the former a chalk grassland indicator and the latter indicative of non-calcareous, damp open habitats and grassland, although it may also grow in upper saltmarsh transitions (Burd 1984; Adam 1990). These suggest the presence of chalk grassland in the local environments during this period of deposition, a new occurrence at the site and continuing the overall trend of increasing evidence of terrestrial environmental modification at the site as a whole.

The sequence of events can be reconstructed as follows:

1) Initial deposition in a basin supporting *Juncus gerardii* saltmarsh flora, high groundwater levels but no standing water. Occasional seeds from surrounding marsh vegetation introduced as the result of low-energy tidal incursion and/or deposition by air currents. Saline conditions persist throughout the period.
2) Opening of the basin to more allochthonous water-borne seeds and fruits from taxa with floating seeds through increased tidal activity or flooding.
3) Reduction in dryland inputs possibly because of a reduction of tidal influence and development of a transitional flora.

4) Human disturbance and modified landscapes represented through much of the sequence

5.4.7 Trench 6

A small number of samples rich in Charcoal from the Romano British settlement at the site were sieved and subject to a brief analysis. The finds are shown in Table 5.11. The non-charcoal component was small, but contained a large number of taxa. Cultivars included free-threshing and glume wheats, domestic barley and oat, although the latter may not be domestic. Both wheat chaff and grains were identified suggesting that some crop processing or use of crop by-products (e.g. for animal feed) occurred at the site. The crop species are typical for the period. The non-cultivated remains were few but included common weedy species such as goosefoot (*Chenopodium*) and knotweed (*Polygonum aviculare*). Culm fragments, possibly from burnt straw or hay, were present and the dock seed may have derived from burnt local weeds or again animal fodder.

			Sample	P3 CS1A	P3 CS1B	P3 CS2A	P3 SB1
Taxon	**English Name**	**Component**					
Avena sp.	Oat	Grain Fragment		1			
Hordeum vulgare	Barley	Grain Fragment		1			
Triticum cf. *turgidum*type	Rivet wheat	Rachis Internode				1	
Triticum cf. *spelta*	Spelt wheat	Glume Base				1	
Triticum cf. *spelta*	Spelt Wheat	Spikelet Forks					2
Triticum sp.	Wheat	Spikelet Forks					1
Triticum sp.	Wheat	Glume Base		1		4	17
Cerealia spp.	Cereal	Grain Fragments		4		1	
Chenopodium spp.	Goosefoot	Seed			3	4	5
Poaceae	Grass	Seed		1	1		1
Poaceae	Grass	Culm Fragments				36	8
Polygonum cf. *aviculare*	Knotweed	Seed		1			
Rumex sp.	Dock	Seed				1	
Indeterminate		Seed		2	3	1	6
Indeterminate		Soft Fruit				1	
Indeterminate		Leaf				1	
Indeterminate		Parenchyma Fragments		5	1	3	8

Table 5.11 Medway Tunnel Phase III charred plant macrofossil records

The small and possibly unrepresentative samples allow little to be said about the details of life at the site. Crops may have been grown on drier ground away from the surrounding estuary or traded into the site. There is no direct evidence of saltmarsh

exploitation; however, the area would have provided a rich grazing resource. Some of the taxa commonly identified in the seed assemblages, especially *Potentilla anserina* are common in disturbed grazing at the edge of saltmarshes (Adam 1990) and the dense sward of herbs on the marsh would have provided attractive grazing for cattle. The abundance of *Juncus bufonius* further supports the presence of local disturbed wetland conditions. The non-analogue nature of the seed assemblages from Sections 6, 11 and Trench 7 have been noted above. Site habitation is contemporary with Trench 7, in which chalk grassland and a range of disturbed habitats are present. It is possible that grazing at the upper edges of the saltmarsh may be responsible for the strange mixture of species and evidence for disturbance. The open herbaceous environments contained a large diversity of species, one that is unlikely to have occurred naturally in a low-energy alluvial system. It is possible that the mixture was encouraged by grazing of cattle and, in the drier areas, sheep, on the biologically productive salts. Going further, one could speculate that the presence of chalk grassland, slight though it is, may point to the use of grazing land in a wide range of environments, accompanying arable production nearby, or importation of grain from elsewhere. The evidence is slight, and suggests that the site was part of a diverse local agricultural economy during the Romano-British occupation that utilised the rivers resources alongside that of terrestrial environments.

5.5 Major research themes

5.5.1 Vegetation cover

Macrofossil analysis provided information about the vegetation on and near the sample sites, including both floodplain/estuarine environments and those of the surrounding terrestrial ecosystems.

5.5.1.1 River and riverbank vegetation

Vegetation along the river varied between woodland, fen and saltmarsh in response to changes in hydrology and sedimentation regime accompanying environmental changes in the river catchment. The earliest flora identified was freshwater and included a canopy of alder on the riverbanks, succumbing to rising water-levels and the formation of reedbeds. Estuarine conditions are reflected early in the sequence with mixtures of freshwater riverbank, aquatic and saltmarsh taxa. Marine deposition dominates much of the rest of

the sequence above this point, interspersed with episodes of deposition of peats and organic silts in freshwater and transitional saline/freshwater habitats.

The first transition to tidal conditions (Section 16) seems to be gradual with the death of trees at the site and development of a reedbed, as would be expected. There is no evidence, however, of the development of the type of transitional species-rich upper-marsh swamps that characterise later deposits. Most macrofossil assemblages above the onset of tidal influence in Section 16 are more characteristic of tidal-flat environments than those of vegetated saltmarshes, although the presence of abundant rootlets and some aerial material may indicate the growth of marshes nearby. The continued influx of freshwater riparian and aquatic species indicates that a diverse river flora persisted in freshwater areas upstream of the site.

The leaf-beds in Section 16 are found nowhere else on the site and seem to have been deposited in a habitat of tree cover with many open pools and stands of mixed riparian vegetation. The depth of similar sediments suggests that this floodplain environment persisted for some time and it is possible that the unusual combination of elements, at least in comparison to modern vegetation, is due to the reaction to continuous disturbance caused by increasing water levels. The vegetation changes in Sections 9 and 11 are easily explained in terms of local hydrological change (see below) and relatively simple brackish/saltmarsh vegetation formations are suggested in the seed and non-seed floras. The range of taxa found in the wet-woodland units suggests rather diverse vegetation associations, including drier and wetter patches, and a mixture of canopy and groundstorey elements. The vegetation was much more diverse than modern observed wet woodlands and shows the limitations of modern observations in informing us about past ecosystems. This is unsurprising, considering that all of the wet-woodlands present in Britain today are heavily managed and have been for centuries. The open-fen flora of Section 11 is relatively simple and contains mostly open-marsh freshwater and brackish taxa. It may represent a natural transitional saline-freshwater/terrestrial transition.

The simple vegetation of Section 11 is in contrast to the range of open, marshy species, many apparently local to the sampling site, seen in Section 6 and Trench 7. The combination of freshwater and saline-tolerant taxa cannot easily be explained in terms of allochthonous tidal inputs of freshwater taxa to an upper saltmarsh, although some seeds probably entered the site from such vectors. In both sections the flora is similar to that

reported in transitional upper-saltmarsh swamps, rarely surviving in Britain today (Burd 1984; Adam 1990). The change from clastic to organic sedimentation in Section 6 can be seen as a response to a change in balance from tidal to groundwater dominated hydrology, although the flora suggests that saline influence was still present, albeit diminished.

The complexity of the flora may have been further enhanced by human disturbance or disturbance by grazing animals. The evidence from both sites is of a complex of vegetation not seen in the region today, reflecting local hydrology and disturbance on an extensive floodplain in which the complex interplay of tides and groundwater mixed with human disturbance determined local vegetation character. The truncation of the floodplains and saltmarshes, stability of the rivers because of slower increases in sea-level rise and human control have restricted the range of such communities in the modern day. The Section 6 'peat' is a saltmarsh peat, coming from a transitional terrestrialising zone. The reversion to clastic sedimentation is a result of changing hydrology and may indicate the swinging of the hydrological balance once more towards tidal inputs, although the vegetation change may have been limited, with only those salt-intolerant taxa, such as *Hydrocotyle*, being removed. This period of saltmarsh peat accumulation was brief and the lack of arboreal invasion suggests that water-levels continued to rise during the period and that it was a transitional environment.

5.5.1.2 Terrestrial vegetation

Evidence for dryland vegetation in the plant macrofossil assemblages was limited, but some long-term changes were noticeable, supported by trends in the preliminary pollen analysis of the site (Branch 1994). Evidence from section 16 was restricted to the tidal deposits above the bedded leaves in which allochthonous seeds and fruits were preserved. Most of the identified taxa were of woodland or scrub origin, with few open country species present. These included common components of natural glades and woodland edges and, in one case, open wetland (*Filipendula ulmaria*). Few indicators of dryland vegetation were preserved in sediments from sections 11 and 9, with the environments in both being closed to allochthonous inputs. *Potentilla anserina* and *Ranunculus acris* in sample 11003 are indicative of open plant communities on non-calcareous soils and may indicate the presence of mesotrophic grassland. Again, these

taxa may have a natural origin, or may have grown in the saltmarsh transition and firm conclusions concerning the nature of the dryland vegetation cannot be offered.

Evidence from section 6 is more compelling, with dryland tree taxa being almost absent and indicators of both open non-calcareous grassland and arable/disturbed habitats being preserved. Bracken indicates the presence of weedy arable land or rank grassland, both human created and particularly susceptible to bracken infestation. In Trench 7 the chalk grassland indicator *Thymus* sp. was preserved. Chalk grassland has recently been identified in Dover, contemporary with the deposition of the Dover Bronze Age Boat (Fairbairn 1998). The Medway and Dover evidence suggests that a similar trend to open country occurred in Kent as elsewhere in the river valleys of southern England (e.g. Lambrick and Robinson 1988; Greig 1988; Greig 1992b). There was no evidence in the lower sections for the presence of open chalk grassland in the Mesolithic as seen in Sussex (Scaife 1987; Waller and Hamilton 2000), although this may reflect the selective nature of allochthonous macrofossil incorporation

5.5.1.3 Vegetation change and stability

The overall picture of river-edge and floodplain vegetation during the period of deposition is one of constant adjustment to the changing hydrological conditions at the site. There were clearly major shifts in the hydrology of the basin linked to both river discharge, sea-level changes and local runoff. The most pronounced changes in the river vegetation are found in Section 16, with the initial period of tidal influence. This whole episode can be explained as an effect of river-adjustment to rising sea-level. A major fluctuation in hydrology is seen in Section 9, where tidal sediments are replaced by freshwater deposits. It suggests that this latter episode does reflect a major episode of sea-level stillstand or decline. Higher sections show fluctuations, but nothing on such a scale and all are potentially explained as occurring within a trend of rising sea-level. The upper sections can be seen to represent episodes of deposition a stable environment and may be explained in terms of local variation in vegetation and sedimentation expected over a wide floodplain with a rising sea-level.

The absence of arboreal littoral vegetation in the upper sections is of interest. The lack of vegetation may be due to the sample position, as arboreal macrofossils are unlikely to intrude far into herbaceous communities; however, the abundance of *Alnus* pollen is also low in the upper sections (Branch and Lowe in Pine *et al.* 1994). The

littoral area was inhabited by a mixed herbaceous community. As discussed above, this may have been at least in part influenced by grazing, this preventing *Alnus* establishment on suitable substrates at the marsh edge. The lack of *Alnus* may have reduced transpiration loss of water from damp soils and helped to increase the height of the local groundwater table. This and the increased runoff caused by local deforestation may have helped to form the correct hydrological conditions, specifically high freshwater input, that sustained the complex marginal vegetation.

Human impact is apparent on dryland. Although evidence is slim, the plant macrofossil record indicates the existence of woodland cover on dry land and along both riverbanks and floodplain at *ca* 6900BP. There is tentative evidence for the existence of open grassland communities at *ca* 4800BP (Section 11) and definitely by *ca* 3000BP (Section 6) where some of the remains are consistent with the presence of open communities, non-calcareous grassland and arable disturbance. The overall change in macrofossil presence suggests that woodland cover reduced in later periods. Tree and scrub species are still represented in the assemblages, but the landscape was more open than previously. Chalk, and possibly mesotrophic grassland, may have developed by the period of Iron Age and Roman settlement, although estimation of tree cover is not possible using macrofossil evidence. Over the period of deposition, the dryland flora underwent major changes almost certainly connected with human activity, locally and/or within the river catchment.

5.5.2 Changes in depositional environment and hydrology

Overall macrofossil preservation and the quantified taxonomic data have helped in the determination of extant depositional environments at the sample points and suggest the influence of a complex of hydrological influences on facies formation and standing vegetation. The leaf beds in Section 16 had a unique composition for the site. Leaf beds are rarely preserved in alluvial sediments and indicate quiet water conditions, with minimal *in situ* vegetation growth and maintained groundwater levels. The persistence of these features suggests that deposition under similar conditions persisted for some time. High standing water levels suggest impeded drainage of groundwater because of high river-levels. High river levels in this context would be best explained by the effects of rising sea-level on peak flood heights. Sedimentation would normally rapidly fill any basin in which standing water was present. The continued deposition in this environment

indicates a long period of rising sea-level in which the groundwater levels were maintained. The eventual beginning of saline influence at the site indicates the point at which the tidal head reached Chatham and at which tides became the predominant hydrological influence.

Sections 9 and 11 show a rather dramatic change from clastic sedimentation in tidal environments to organic sedimentation in freshwater environments. Organic sedimentation is accompanied by immediate alder colonisation in section 9 and by a more gradual change in Section 11 to a herb-dominated open fen environment only later invaded by fen woodland. The most adequate explanation for this difference in response rate is the difference in local hydrology. Section 9 is much closer to the modern river bed than Section 11. Assuming that the river channel was in a similar place as today, this suggests the formation of an open swamp to the rear of the *Alnus* woodland that occupied the river edge, possibly on a former bank or levee. High groundwater levels fed by runoff from the chalk cliff and perched on the impermeable lower silt substrate may have sustained the swamp. Only later, after the infilling of the local basin, were conditions dry enough to allow invasion of alder growth at that site.

The transition from marine to freshwater influence is apparently rapid at both sites and the usual interpretation would cite it as a response to falling sea-level, freshwater vegetation invading sediments that are no longer inundated by the tides. Groundwater and floodwater levels are the main control on hydrology and sediment development. In the case of Sections 9 and 11, the rapid change to freshwater conditions would be consistent with reduction in tidal influence, although groundwater levels must have been high for peat development to be instituted. A less likely scenario is that peat development was the result of high river bank formation, possibly because of a change in sediment load, isolating the area from the river. This latter interpretation suffers from a lack of direct evidence. A further alternative is that groundwater influence increased in the margins of the floodplain, occupied in the lower parts of Section 9, by an upper saltmarsh swamp. While this interpretation would be sustainable for marginal areas, it seems unlikely that it could explain such massive peat formation and wet-woodland presence over such a large area seen at this point. The idea of a sea-level rise slowing or stillstand, coinciding with higher groundwater levels and runoff, may be the most plausible explanation. It seems unlikely that, given the shape of the Medway River Basin

at this point, that groundwater and river discharge would be able to overcome the influence of tides continuing to rise rapidly.

Further changes in Section 9, especially the gradual increase in freshwater levels and death of the tree canopy, suggest increasing water-levels at the site. This would be consistent with of continuing rising groundwater levels. High groundwater levels may be linked to increasing precipitation or clearance of woodland in the surrounding catchment. That groundwater levels were at least maintained seems to be shown by the continued presence of a freshwater flora. Alder growth at the site seems also to have persisted, although there is some evidence for a more open canopy.

The higher sections are indicative of fluctuations in the hydrology that are best explained as sedimentation responses to changing groundwater levels in an overall trend of rising sea-levels. Change from primarily clastic to organic sedimentation in Section 6 is rapid and the seed rain is best interpreted as the result of slight modifications in an open, diverse, herbaceous upper-saltmarsh swamp flora caused by increasing runoff and groundwater levels. A reduction in tidal influence would be expected to cause the invasion of the site by less salt tolerant taxa, reduction or elimination of salt-tolerant taxa, worsening preservation and rapid invasion of the site by fen woodland. Increasing groundwater may be associated with local deforestation or climatic changes. In Trench 7 the reduction in organic content up the profile may be a result of higher sedimentation rate, caused perhaps by increased tidal influence. This may be the on-site indicator of the widely seen post-Roman increase in rates of sea-level rise. Slight fluctuations in the macrofossil assemblages higher in the sequence may be linked to a temporary reduction in tidal influence in a brackish swampy environment.

5.5.3 Human activity and disturbance

Direct evidence of human disturbance and use of the area is scant in the described assemblages and associated deposits, although it is compelling. Direct use of the floodplain, or its margin, is seen in Section 16, where the riverbank sediments preserved traces of Mesolithic occupation. Food preparation is hinted at and it is beyond doubt that the river would have provided a rich suite of both animal and plant resources for local gatherer-hunter groups. The open vegetation of the riverbank, at this point a stable sand, would have also provided an easily traversed surface and perhaps an important communications route. Charcoal is preserved throughout the sediments above the leaf-

beds in Section 16. Its most likely source in British ecosystems is human-generated fires, for sustenance or clearance activity, but almost certainly linked to human activity. The onset of estuarine conditions would have increased the resource value of the area considerably, with tidal flats and shallows being home to many fish and birds and a vast range of microhabitats opening up for the local population in the river/estuary/dryland ecotone.

Later prehistoric sites on estuaries, such as the Glastonbury Lake Village (Coles and Minnit 1995), have demonstrated the attraction of such areas for human communities and the full exploitation of the many resources that they offered. It is likely that the Medway Estuary provided just such a rich habitat for much of later prehistory. The constant change in environments caused by rising sea-level and changes in the terrestrial landscape would have provided a suite of ever-changing, but abundant resources. The constant presence of humans in the area supports the contention that the floodplain and surrounding areas provided an attractive resource base and place to live throughout the period of the Holocene in which sediments accumulated at the site.

There are few indicators of human activity in Sections 9 and 11, with the exception of possible grassland taxa. The presence of a flint blade in the peat suggests that forays were being made into the wetlands in the Neolithic, possibly from the Neolithic and Bronze Age occupation, some signs of which were fund on the chalk cliff. The wetlands represented by the peat beds would have represented potentially useful, but difficult habitats to access. The swampy conditions in the upper part of Section 9 would have been impassable for much of the year making access to the river difficult.

In Section 6, of broad Iron Age date, definite human impact on the landscape can be suggested. The presence of cereal awns and straw in charred form indicates, with quantities of charcoal and associated cultural material, that the local inhabitants were dumping the refuse from fires in the river. The presence of cereals confirms local cultivation at this point. Evidence of grassland, which could only have persisted with human intervention through maintaining grazing or by cutting (Greig 1988), demonstrates a marked human impact on the local flora, even at the upper end of the saltmarsh. It shows the existence of an open landscape by this point, as opposed to the natural wooded landscape represented in Section 16, with impact on clay and other non-calcareous soils in the area. By the period of deposition of sediment in Trench 7, chalk grassland also became established.

Indirect evidence of human impact can be suggested for the hydrological changes in Section 6. Iron Age clearances were widespread and the evidence from the Medway may suggest an expansion of local clearance and grazing during the period. The later increase in groundwater seen in Section 9 may also have been influenced by terrestrial landscape changes and may indicate local or catchment-scale clearances. If so, this would follow a pattern noted elsewhere in southern Britain for clearance in the third millennium (e.g. Burrin and Scaife 1984; Scaife and Burrin 1992).

One area of interest highlighted in the original project design was the identification of 'activity surfaces', that is areas that are accessible to humans. In the initial site reports these were identified with the periods of peat deposition. The evidence from the plant macrofossil analysis suggests that access was not easy in any of the periods of organic deposition and that the association of peat with accessibility is spurious. Many of the sandy-silt deposits in Section 16 would have been far more accessible that the wet swamps that characterise much of the analysed sediment. The floodplain would have only provided secure footing in some marginal habitats where dense root networks and moderate groundwater levels were present.

5.5.4 Usefulness of Method

Application of the plant macrofossil analytical method to the sediments from the Medway Tunnel site was successful, but not without problems. Samples from the compacted, and on occasion dried sediments, were difficult to disaggregate adequately and macrofossil extraction could be difficult. Some damage was inevitably caused to the macrofossils, potentially reducing the quantity of vegetative remains identified. Samples from Section 9 were particularly difficult to recover. Identification proved to be successful, with the leaves in Section 16 being particularly well preserved. Fragmentation was high in many of the sediments and no non-arboreal Dicotyledon leaves or other aerial components were identified. Some were present, though decay was so advanced and anatomical structures often so obscure that secure identification was not possible. Monocotyledon preservation was better and the identification easier and more successful as seen in the modern sites (Chapter 4).

The cover abundance method was found to be sometimes difficult to apply and the compounded errors in the method and conversion to CO^2 figures do raise questions about the results. It should be noted that the figures have been used with caution and

only major changes in macrofossil abundance have been given any interpretative weight. More importance was given to the presence of large versus small quantities of macrofossils, than tiny changes in actual figures to several decimal places. The results usually agreed with the subjective impression gained by 'eyeballing'. However, the systematic methods of sample analysis often brought to attention groups of macrofossils that were overlooked or under-identified. The use of the relative, raw cover abundance figures was useful in checking patterns and identifying the effects of changes in sedimentation rate, and perhaps more systematic use of these figures in analysis would be useful. Experiments with CA and CCA plots during the initial stages of analysis did, however, suggest that there were limited differences between plots made using cover abundance and CO^2 values. The cover abundance method is gradually becoming established in ombrotrophic peat sequences (Barber *et al.* 1994) and the research presented here suggests that wider application is possible.

Results of quantitative analysis were coherent and some of the patterns were also consistent with those seen in the modern sediments, although many of the sediments were from non-analogue environments. The method did produce useful results and while the significance of quantitative data has to be carefully considered, the abundance data and the wide suite of classes of macrofossils present allowed for more secure interpretations of past vegetation and environment. The quantification of macrofossil classes itself provided useful data and was significant in identifying particular environmental conditions, such as the presence of standing water in Section 16. The comparability of samples from the modern and ancient sediments has to be questioned. Much smaller sample sizes were required to provide useful data in the Medway Tunnel sites, a result of greater compaction of those sediments. A greater time-depth is likely to be present in the same 2cm depth as in those of modern sediments. This does not preclude the comparison of these data sets but does open up the possibility of different time-concentration effects producing non-analogue assemblages.

6 Discussion

Plant macrofossil analysis of Holocene alluvial sediments has typically focused on a narrow suite of remains, especially seeds and fruits, and has suffered from a lack of understanding of the formation processes of macrofossil assemblages in temperate environments. The work presented in the preceding chapters has, given certain provisos, successfully extended the analytical methods available to alluvial macrofossil researchers. Analysis of waterlogged macrofossils from alluvium is, however, a difficult technical task. Quantification and identification are problematical because of the nature of the source material and the lack of accessible systematic accounts of identification criteria. The range of taxa included in the identification work in Chapter 3 is limited, being tailored to the taxa and types of remains expected in the range of environments extant in the modern alluvial sites. Further development of the range of taxa is required if secure identifications are to be made and a wider range of macrofossils and facies is to be analysed. The work presented here does, however, provide a core reference collection and includes most of the key taxa to be expected in Holocene alluvial facies at genus or family level. Additionally, organs at different stages of growth and from multiple populations would improve the reference source further.

The quantitative methods used here for recording non-seed macrofossils have substantial in-built errors. Conversion of non-seed cover abundance from percentages to facilitate comparison between samples incurs more errors. In spite of this, the figures produced were still useful and similarities between the values generated for modern and ancient sediments supports the notion that they are of use. Non-seed cover abundance values provide information lying between the rather generalised Troels-Smith type descriptions from sections and cores and full identification and quantification of every single macrofossil, a possibility that is practically infeasible. It is interesting to note the difference between the detailed macrofossil abundance values and Troels-Smith figures. The latter showed limited variability and were of little interpretative value, showing only gross macrofossil changes that were useful at a general level only, and missed much of the subtlety in the macrofossil assemblages.

A note of caution has to be sounded, however, as small variations in macrofossil abundance should not be given too much interpretative weight. The converted cover abundance figures (CO^2) provide a means of comparing non-seed abundance between samples. It is also important to look at the raw cover abundance and converted figures

to see whether changes in macrofossil abundance are due to overall differences in macrofossil influx or whether they reflect changes in surface vegetation.

Seeds and other countable remains were used to calculate seed and species concentration data. Meaningful trends were found in these indices in the modern data and they were used to some effect in the Medway Tunnel analysis. Further indices could have been generated and used and in the early stages of analysis Shannon-Weiner and Menhinicks diversity indices were calculated for several sites. The results have not been included here because of reasons of space, although interesting trends were noted. The use of a wider range of data manipulations is a potentially fruitful source of investigation, as has been shown in the analysis of leaf incorporation in backswamp facies (Gastaldo *et al.* 1989). These indices complement standard analytical procedures, providing a different range of analytical tools that help to refine interpretations based on taxonomic quantification. The range of indices calculated in this project has been limited and rather obvious. Others linked to specific environmental parameters could be generated, as suggested by Hubbard and Clapham (1992).

One part of the method beyond the normal remit of archaeobotanists is the use of LOI figures to calibrate CO^2 figures. Organic percentage figures also provided an independent source of data that showed coherent variation in response to environmental gradients. Textural data also provided vital interpretative data. The dependence of the method on LOI figures shows the need for a broad approach to macrofossil analysis if meaningful interpretations are to be provided. If one rule of thumb could be suggested for a broad-scale macrofossil analysis, it is the need for flexibility in the approach adopted to cope with the innate complexity of the assemblages. Alluvial plant macrofossils are best studied as part of an interdisciplinary, facies-based approach and while individual analysis provides useful data, other sources are required to realise full interpretative potential. Furthermore, analysis of a range of macrofossils, including seed and non-seed classes, provides a much stronger base for interpretation than analysis of any one class of macrofossils in isolation. Only a combination of datasets would provide the means to distinguish creek sediments in upper saltmarshes, for example, if possible at all.

Two sets of properties were useful in the interpretation of macrofossil assemblages, namely quantitative and presence data about macrofossil classes (leaves, stems, etc.) and the quantitative taxonomic data (e.g. *x* quantity of leaves of *n* species). Both properties were mutually re-inforcing in the interpretation. The former provided

detail about the depositional environment and the structure of the vegetation, while the latter provided more detail for each of these and the detailed floristic properties of the vegetation. Both sets of data were important for providing an accurate interpretation. There is some potential for abandoning taxonomic cover abundance identifications and simply recording macrofossil classes as a basis for interpretation. This would form a rapid means of assessing the non-seed data and would furnish basic environmental and structural interpretations, although the floristic depth of the interpretation would be limited.

A fragmentation index was not developed in the research, although this was tried in the early stages. An attempt was made to provide a universal recording system in which fragmentation, macrofossil classes and taxonomic properties were recorded. This proved beyond the competence of the investigator. In the event, fragmentation was described verbally. Development of a simple comparative fragmentation index would be useful. Coherent patterns of fragmentation were noted in the estuarine sediments suggesting that it is a useful and meaningful interpretative parameter. Fragmentation alone would have provided a reliable means of identifying mudflat samples and those from transitional mudflat-saltmarsh habitats. Murphy and Wiltshire (1994) have developed a preservation index that may provide a useful template for a general macrofossil fragmentation index. It is useful in that it scores individual macrofossil groups and so recognises the heterogeneity of the assemblages. Use and development of this system was not attempted, but would be a useful additional interpretive tool.

The actualistic taphonomic research presented here (Chapter 4) supports work from alluvial habitats elsewhere in the world, showing that the macrofossil record can be understood and can provide a basis for environmental and vegetation interpretation. The observations of modern macrofossil accumulation in estuarine and floodplain habitats provided useful analogue data for interpreting ancient macrofossil assemblages. General trends in incorporation in similar depositional environments were observed, and repeated trends in the preservation of the parts of different taxa were also noted (Chapter 4).

British researchers have been the main investigators of seed incorporation, although few studies have been made in comparative environments. Even so, some parallels with the trends seen in this work are present. Most workers were in agreement that in most habitats seeds are derived from near the sample point if not from vegetation growing at it (Greatrex 1983; Collinson 1983; Field 1992). Field (1992) noted the

presence of aerially dispersed seeds in many samples as allochthonous elements, especially *Typha* sp., an observation supported here. *Epilobium* spp., a common allochthonous find in the sites studied here, has been found as an allochthonous component at several sites (Greatrex 1983; Field 1992). Collinson (1983) noted the widespread dispersal of the seeds of aquatic species. Few were recorded in the estuarine sediments suggesting that perhaps dispersal is limited in distance and seeds from freshwater aquatics are unlikely to enter estuarine sediments in traceable quantities.

Interestingly Greatrex (*ibid.*) found *Carex* spp. to be over-represented, whereas in all of the modern sites in this research it was either present in approximate proportion to its presence, or under-represented. In both of these researches, as well as Field (1992), *Solanum dulcamara* and *Iris pseudacorus* were under-represented in the seed rain, while *Alnus* sp. and *Betula* sp. were commonly widely dispersed and the latter was over-represented. The research presented here agrees with Greatrex's assertion that non-seed components, specifically catkin scales, were a more reliable indicator of local presence than seeds. As well as catkin scales, bud-scales can also be added as a spatially precise indicator, although only if several are preserved in a sample. Greatrex was the only worker to note the dominance of *Phragmites* sp. vegetative remains in peatland dominated by the species, again a contention supported here.

Greatrex noted the uneven distribution of seeds in mire surfaces and the preceding work shows that uneven distribution of seed rain is also common to several estuarine and floodplain habitats, although the severity varies. The mire samples at Hickling Broad showed a particularly strong local distribution pattern. Seed concentrations tended to relate in terms of taxa to the surrounding vegetation and the most abundant taxa were usually important vegetation constituents. Careful reading of the seed data was, however, necessary, as was an understanding of the depositional environment if seed abundance was to be properly interpreted. The seed rain in the saltmarshes was often more homogenised that that of the mires and, while concentration effects were noted, tidal action served to mix the seeds over the marsh surface, severity of mixing depending on sample position.

Workers on pre-Quaternary floras based in the USA, studying mainly arboreal leaf assemblages, have mainly studied non-seed macrofossil incorporation. Again, in most cases the assemblages tend to be composed of macrofossils from nearby vegetation, although increasing quantities of allochthonous matter and overall lower incorporation rates of macrofossils in general have been noted in environments with

greater tidal influence (Burnham 1989; Scheihing and Pfefferkorn 1984; Gastaldo and Huc 1992). Backswamps and floodplain woodlands provide the most spatially accurate assemblages of leaves and most diverse assemblages of remains (Burham 1989; Gastaldo *et al.* 1989; Scheihing and Pfefferkorn 1984; Burnham *et al.* 1994). Unlike some deltaic environments (e.g. Scheihing and Pfefferkorn 1984) those from temperate estuaries sampled here incorporated plant macrofossils across the sediment surface, with incorporation and preservation being poor only in marginal sediments and those in raised, aerobic sediments such as creek edges (see Stonemarsh, Chapter 4).

Heterogeneous vegetation in tropical environments has been found to require more intensive sampling to provide accurate leaf assemblages and accurate mapping (Burnham 1989), with less intensive sampling required in temperate forests (Burnham *et al.* 1994). The level of sampling in the wet-woodlands identified here was limited and while the canopy dominants provided most of the leaf remains, the potential for mis-representation of canopy composition has to be recognised. The small sample sizes used in Holocene studies, in comparison to pre-Quaternary palaeobotany, suggest a potential for unrepresentative datasets. It should be noted, however, that even small samples were found to indicate the canopy dominants accurately (Burnham *et al.* 1994) with such sizes reducing the accuracy of interpretations of minor canopy elements rather than negating the whole interpretation.

This is a pattern seen in most of the modern samples and all of the Block samples analysed in this research and suggests that even small samples have an important role to play in alluvial macrofossil analysis. This is important when considering the small volume available of sediment and related macrofossil sample size in many alluvial investigations. It also opens up the use of borehole investigations as a means of recovering low-precision, but still useful, macrofossil datasets and accurately identifying major vegetation elements and depositional environments. The larger 200 cm^3 samples used as the investigation standard provided adequate macrofossil samples in all except the mudflat samples where samples of 1000 cm^3 or higher would have been required to produce a minimum of 100 identifiable units in many cases. It is debatable whether such large samples would produce useful information and if, in the case of mudflat samples, smaller samples provide as much relevant data as is necessary. Even when large samples with large quantities of seeds could be recovered from such sediments, many of the seeds would be allochthonous and the assemblages so mixed that only the presence of local taxa could be assured. Elsewhere the standard sample

size provided a sample of the dominant taxa and the rare types suitable for quantitative analysis.

Although there is a broad correlation between the results in Chapter 4 and comparative studies in other areas of the world, much of the information provided here is new. The detail of macrofossil incorporation in estuarine environments, especially that of non-seed material, is not available elsewhere. A major trend, even in the dynamic environments of the saltmarsh, is the local source of most macrofossil material. The data from the block samples, albeit limited in quantity, also suggest that even subterranean structures provide temporally precise sources of data, exceptions being some of the deep-rooted taxa such as *Phragmites* sp.. Overall, the level of spatial and temporal resolution of macrofossil analysis is high, although it varies widely between different classes of macrofossils and in different depositional environments. Mudflat and creek environments have the lowest spatial and temporal fidelity, with macrofossil assemblages in creek edges being prone to severe erosion. Mudflat sediments are easily separated from others, although creeks, especially in the upper marshes, may not be so easily distinguished from surrounding sediments. Creeks are erosive features and are unlikely to contribute to the sedimentary record in any quantity, unless they are abandoned, in which case the sediments are discrete. Minor deposits of mud drapes and bars may be deposited during creek action and may not be so easily discernible.

Spatial changes in vegetation and environment over mudflat-saltmarsh transitions and vegetated saltmarsh surfaces were reflected in the modern macrofossil records. Seed and non-seed records proved suitable for distinguishing the spatial variability between upper and middle saltmarsh at Snape Saltings, although exact local vegetation reconstruction, beyond determination of local dominants, was not possible. A major problem that cannot be observed is the obliteration of spatial patterns by later vegetation growth, although again it seems likely that temporal trends are recorded in macrofossil records, albeit in a slightly blurred fashion.

The usefulness of macrofossil results for interpreting broader environmental change, such as sea-level, depends very much on the environment under study and whether clear environmental gradients can be associated with macrofossil abundance. Although saltmarsh environments are zoned in relation to tidal levels, it was clear from the evidence at Snape Saltings and Stonemarsh, the most complete active environments in the project, that zonation at a micro-scale level is complex. Local factors, such as the

penetration of creeks, allowed the formation of islands of apparently lower to middle marsh vegetation, preserved in upper marshes. The position of a stand of vegetation is determined by local factors and in mature marshes local topography may make a confusing association of vegetation communities if viewed at a very small spatial scale. Unfortunately macrofossil samples are essentially samples of vegetation from a small spatial area. In saltmarshes, however, the mixing of the seed rain provides a useful corrective for the skewed picture provided by local incorporation, allowing broad zones to be identified as well as local vegetation dominants, although the non-seed macrofossils are likely to favour Monocotyledon taxa. There is, however, no easily readable direct link between sea-level and local macrofossil incorporation. There is basically a local macrofossil pattern based on local vegetation and sedimentation processes (e.g. creek water penetration) overlain by a larger pattern determined by major flood events and tidal properties.

Macrofossil preservation in transitions to dryland were particularly under-represented, with only one being sampled, namely a truncated transition at Snape Saltings. The increasing influence of groundwater and runoff was visible in the accumulation of peat, although tidal influence was still apparent with growth of some saltmarsh taxa. The odd composition of the environment, with saltmarsh Dicotyledon herbs and large expanses of open peat, suggest that transitional conditions may be locally specific and produce rather odd floristic and structural plant communities. Another problem with the data was that of most of the sites containing stable marshes only Stonemarsh has a dynamic transitional marsh. It seems possible that rapid changes over low-lying marsh surfaces are possible in rapid periods of sea-level adjustment, as in the early Holocene. Non-analogue macrofossil composition should be expected in such scenarios, with sedimentation rates perhaps being enhanced if sea-level rise was rapid. If the vegetation composition were similar to that in recent vegetation associations, similar relative compositions would be expected in samples. Higher sedimentation may also reduce the effect of temporal mixing in such environments.

Although macrofossil analysis provides information of high taxonomic detail, it seems unlikely that in most cases detailed, NVC-like reconstruction of vegetation are attainable. Macrofossils still move and are concentrated locally in sometimes confusing mixtures. Ironically, some of the most difficult macrofossil assemblages to disentangle were those allochthonous assemblages from the fens at Hickling. The implications for palaeoecology are that spatially and temporally accurate records of the ecological

dominants and some other taxa that produce large quantities of seeds or structural remains are attainable. Detailed study of community formation and development, if based on the presence of a small quantity of a particular taxon may not be possible. Some of the sub-divisions in the NVC are based on relatively small floristic changes (e.g. wet woodland sub-communities) and may simply be unidentifiable even in well-preserved assemblages. This should not mask the potential for macrofossil analysis to improve taxonomic resolution greatly in vegetation reconstructions of alluvial environments. The method offers a powerful tool for detailed vegetation mapping, especially important in the determination of the context of human use of such environments.

It became obvious during fieldwork that using observations from modern environments as a basis for interpreting past phenomena is fraught with problems, especially when there has been such obvious human impact on the ecology and dynamics of the environments under study. Even ungrazed, unenclosed environments (e.g. Snape Saltings and Borstal Marsh) could not be guaranteed to be free from human influence, as river control and land-use change has influenced river discharge regimes, sediment loading, groundwater height, runoff rates and surrounding ecology. Rather than providing direct analogues of macrofossil incorporation in past environments, the study presented here provides details of macrofossil incorporation from known plant taxa in sediments deposited under known conditions. The results required careful consideration before being applied to ancient sediments and it was clear that the interpretation of ancient sediments has to be open to considering combinations of macrofossils outside those observed in the modern environments.

Application of the method to the macrofossil assemblages from the Medway Tunnel site (Chapter 5) showed that meaningful results are attainable for ancient sediments. A complex set of facies was sampled at the site and the fragmented nature of the strata meant that while detailed investigation of single sections and transitions was possible, no single profile was available for the site. Macrofossil analysis indicates a complex set of changes in hydrology linked to the balance between tidal influence, determined by sea-level and basin shape, river discharge, groundwater height and runoff, the latter three determined by climatic and catchment controls. The presence of leaf beds is suggestive of swamp-woodland conditions in the lower section of the site and episodes of high water are seen throughout the profile. Much of the evidence higher in the profile is for open upper-saltmarsh swamps and transitional zones that were not

seen in any modern sites. The higher variability in macrofossil composition and facies is in fact what would be expected in natural sedimentation conditions. This evidence adds to the theoretical suggestion that use of modern 'template' analogues is not a suitable means of investigating past environmental phenomena. A better approach is to be aware of the variation in taphonomic influences on macrofossil preservation in specific conditions.

There is also some evidence in the allochthnous sample flora of increasing human impact on the landscape and removal of woodland along the valleys during the period of deposition. This general trend is similar to that seen along many of the river valleys of Europe (Brown 1997) and in the southeast of England. Human activity is also seen directly in the deposits paralleling finds of human use and movement through wetland settings in the region (e.g. Meddens and Beasley 1990; Chew 1993; Meddens 1993; Barham *et al.* 1995; Wilkinson and Murphy 1995; Rackham 1994) and elsewhere from the Mesolithic onwards (Coles 1987; Van de Noort and Davies 1993; Cowell and Innes 1994; Gramsch 1991; Andersen 1987; Bell and Neumann 1997). Human access was a major focus of research in the broader archaeological project of which this work formed a part. The inaccessibility of several 'peatland' environments in the Medway tunnel sequence has been discussed above (Chapter 5) and suggests that blanket pronouncements about the accessibility of environments made on the basis of cursory examination of sediments should be avoided. Saltmarsh environments could have been as accessible or inaccessible as the freshwater and transitional environments. In fact there is evidence from the Severn estuary that saltmarsh habitats were used for grazing in prehistory as they have been in recent times, showing that many alluvial environments have long been exploited by human communities (Bell and Neumann 1997).

The macrofossil interpretation offered here suggests that sea-level rise affected the Medway Tunnel site directly at approximately 7000 BP, after a period of increased flooding and rising groundwater caused by sea-level rise lower in the basin. The wide lower estuary would have provided a large basin in which tidal incursion would have been absorbed over a large area. When the tidal head neared the narrows of Chatham Reach, river discharge may have pooled up behind the highest tidal incursion forming a freshwater pool that flooded a wide area upstream of the tide. This may explain the swamp-like sediments in the Section 16 leaf-beds, sustained by regular and deep flooding. Once the tidal head reached the Chatham Reach, the narrowing of the channel

may have led to rapid tidal incursion far up the valley. The rapid replacement of the swamp environment of Section 16 by active mudflats after a brief period of reedbed development is entirely consistent with this theory. The transition at the top of the leaf beds may, therefore, have been as rapid as the small depth of sediment would suggest.

Only one major sea-level stillstand seems to be suggested, namely at 4800 BP. Peat formation during this period occurred over much of the eastern bank of the Medway at this constricted point in the valley. That this episode of peat deposition could have occurred over such a wide area under conditions of rapid sea-level rise, caused by high groundwater or river discharge (cf. Haggart 1995) seems unlikely. Increased groundwater penetration would have influenced the upper edges of the saltmarsh (cf. Snape Saltings; Section 11); however, it seems unlikely that even the highest discharges could have overcome tidal influence if sea-level was sustained or rising. Channel movement is restricted in the narrows at Chatham, discounting the possibility of isolation of the area from tidal inundation because of channel movement. The only possibility that adequately explains peat formation on such a scale in this setting is a slowing of sea-level rise, or stillstand combined with higher groundwater and runoff. Widespread isolation from tidal influence in this environment would have only required a modest change in conditions.

Higher deposits can be interpreted as the result of changes in catchment conditions within an overall trend of increasing sea-level. A single episode of silty-peat formation in Section 6 can be equated with a period of increased catchment-water runoff at approximately 3000 BP. The peat deposition at 4800 BP corresponds to a wider event seen in the Thames Basin (Devoy 1979; Tyers 1988; Skempton 1995), the Essex rivers (Greensmith and Tucker 1971; Wilkinson and Murphy 1988, 1995) and the lower marshes on the river Medway itself (Evans 1955).

Evidence in Section 6 for increasing runoff or groundwater correlated well with observations elsewhere in the Thames Basin and the southeast as a whole, of changes in hydrology and sedimentation caused by deforestation. Deforestation becomes more clearly registered in the pollen record across Southern Britain in the Bronze Age (Pryor 1988; Moffet *et al.* 1989) when the impact on forest composition and the openness of the landscape became more permanent (Scaife 1987). Large, permanent clearings within woodland became established in some areas, especially on the chalk (Scaife *ibid.*). Alder woodland still dominated the alluvium of the floodplains which were yet to be drained and deforested (e.g. Tyers 1988; Meddens and Beasley 1990; Thomas and

Rackham 1996). The Stour Valley was subject to at least partial clearance by *ca.* 3500 BP (Fairbairn 1998; Lowe *et al.* 1998) and in the Upper Thames some grassland had developed (Lambrick and Robinson 1988), chalk and mesotrophic grassland being well represented at Runnymede along with heath and woodland (Greig 1992a). Deforestation occurred by *ca* 3000 BP near Canterbury at Wingham, Kent and also at Frogholt, near Folkstone, by *ca* 3000 BP (Evans 1975).

These changes in catchment vegetation are similar to those seen elsewhere in the region at around 3000BP, linked to groundwater rise (Lambrick and Robinson 1984), increased runoff (Burrin 1983; Burrin and Scaife 1984; Bell 1982; Scaife and Burrin 1992) or climatic change (Waller *et al.* 1999). The identification of this trend is significant in the Medway valley as so little work has been done in the catchment, but it is not unambiguous and requires support from pollen and other studies to confirm it. Though direct macrofossil evidence of the post-Roman sea-level rise (Evans 1953) was not analysed, the abandonment and inundation of the Romano-British settlement at the site suggests that the trend was seen higher in the valley.

The Medway Tunnel strata show no evidence for the repeated formation of peat layers that typifies tidal sections of the Thames valley. The peat formed by sea-level regression in Section 9 correlates with the Tilbury III regression of Devoy (1979). Other organic episodes correlating with the other Tilbury regressive phases are lacking. This may be due to the position of the sections and the lack of comparative material up and down stream. It may also be caused by a higher rate of subsidence in the Medway Estuary, the sinking bedrock counteracting changes in sea-level. Tilbury I does not overlap temporally with the period of deposition at the site, but is found in the Lower Medway Basin at the Isle of Grain (Devoy 1979). Tilbury II does overlap temporally with the period of deposition, but is not registered in the deposits. This may indicate that the peats identified by Devoy are not responses to a single event, or that the peculiar conditions of Chatham Reach effectively buffered the changes. The later episodes of sea-level regression were not recorded in the strata at all. Later sea-level changes would not have necessarily registered at Chatham as the site would, by 1750 BP and 1000 BP, have been well within the tidal range.

The presence of *Alnus*-dominated woodland formations in Sections 16 and 9 indicates that the plant is capable of withstanding periods of deep water immersion and regenerating over considerable periods of time. This is consistent with the observations of Waller *et al.* (1999) who have questioned the notion that alder carr is a seral

formation in coastal settings. It seems clear that *Alnus* was the dominant arboreal taxon in the wet-woodlands at Chatham, with macrofossil evidence being overwhelming and being supported by pollen data (Branch 1994). Although *Salix* was present in both sources of data, it was usually present only in small numbers and was only visible widely in Section 16 in the macrofossil assemblages. The abundance of leaf and bud-scale remains, as well as seeds of alder and converse lack of *Salix* remains is consistent with alder domination. One exception is the central section of the leaf-bed in Section 16 where *Salix* leaves were dominant. This suggests that *Salix* was locally dominant at the time, perhaps forming a swamp community in deeper water sections of the site. The Section 16 assemblage is consistent with a swamp carr formation. *Salix* was almost absent from Section 9 and the interpretation of this assemblage is of an alder carr or *Alnus*-dominated swamp-carr. Maintenance of these vegetation formations may be due to continuous rises is groundwater levels, dependant on sea-level and catchment changes and *Alnus* is clearly capable of regeneration in such environments for long periods.

7 Conclusion

The research presented herein is wide-ranging and some of the individual elements require further development, especially the leaf and epidermis identification criteria, if they are to become standard elements in the plant macrofossil analysis of alluvial facies. Identification and quantification of heterogenous macrofossil assemblages was difficult. The data provided by the cover abundance method described here have a substantial built-in error, making only major changes in abundance worthy of interpretative value. The analysis of macrofossil assemblages from modern alluvial sediments showed that coherent patterns of macrofossil representation were identifiable and that accurate interpretations of the depositional environment and standing vegetation were possible. Patterns of over- and under-representation of taxa and structures were noted, some of which supported earlier work. Coherent patterns were identified in the analysis of the Medway Tunnel site that have led to important interpretations about the vegetation, the wider environment and long-term trends in sea-level in the Medway valley.

The work suggests that there are no hard and fast rules in macrofossil analysis and interpretation. The heterogenous nature of the assemblages and the complexity of the environments in which they are preserved means simple application of calibration figures to abundance values will not provide meaningful interpretations. Each assemblage has to be considered individually with a consideration of the preceding and following sediment episodes. Macrofossil assemblages are local accumulations that reflect ante- and post-depositional factors. Ultimately the most complete interpretation of macrofossil assemblages is provided by use of standard quantitative data with species and seed concentration figures, presence analysis, sedimentological information, seed concentrations and other derived indices. Modern observations of deposition in analogous environments are essential; however, the limitations of such an approach in a human impacted planet must be considered.

The research presented here provides some answers to questions concerning the usefulness and full exploitation of plant macrofossils in alluvial sediments. Other approaches should be tried and this work provides only an entry point and demonstration of the potential of the approach. In Southeast England as a whole and the Lower Thames Basin in particular, alluvium provides a diminishing but vital archaeological and palaeoenvironmental resource. Alluvium is also common around the coastline of Britain and across Northern Europe, again providing an important resource. Plant macrofossil analysis provides a potentially important means of investigation and

the observations presented here suggest that generalised schemes of recording such as the Troels-Smith system and derivatives (e.g. Waller 1994) are not adequate for understanding the subtlety of local vegetation dynamics. Restricting macrofossil inclusion in palaeoenvironmental investigations to such systems of recording is not good enough and provides a homogenised record that may simplify some of the more subtle signatures challenging established interpretations (e.g. Haggart 1995). Further refinement of investigations of alluvial facies sequences requires the kind of data that macrofossil analysis provides and a more systematic, widespread application of the method as part of inter-disciplinary projects can only improve our understanding of the past.

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