EFFECTS OF INSECT HERBIVORES ON EARLY SUCCESSIONAL HABITATS

by

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ABSTRACT

The majority of studies on insect-plant relationships have concentrated on the influence of various plant factors on the population dynamics of insect herbivores. Although some works have investigated the effects of insect herbivory on single-species plant populations, especially in the field of biological control of weeds, relatively few studies have been concerned with natural plant communities.

The aim of this study was to investigate the effects of insect herbivores on the development and structure of natural plant communities characteristic of an early successional habitat. The dominant herbivore groups encountered were Heteroptera (Miridae), Homoptera (Aphididae, Cicadellidae and Delphacidae) and Coleoptera (Chrysomelidae and Curculionidae).

A two-year detailed survey was made of the flora and invertebrate fauna (mainly insects) associated with Young Fields established from abandoned arable land at Silwood Park, Berkshire. Characteristics of the plant community are assessed in terms of taxonomic composition, species diversity, structure (using spatial and architectural criteria) and biomass. A comparison is made of the developmental and structural attributes of the plant communities between two Young Fields with different histories of land use. The associated invertebrate community is analysed in terms of taxonomic composition, trophic structure and life-history strategies with particular emphasis on the herbivore guild. Certain insect-plant relationships are determined.

A parallel study investigated the effects of insect herbivores on the development and structure of the early successional habitat. This involved the experimental exclusion of insects from comparable sites, protected from rabbits and birds, by regular use of a non-persistent insecticide. From these long-term field studies the influence of insect grazing on the dynamics of early successional plant communities can be ascertained. These findings are discussed in the light of contemporary ecological theory.

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CHAPTER ONE

INSECT HERBIVORES AND NATURAL PLANT COMMUNITIES

1.1 INTRODUCTION

Studies of insect-plant relationships have undergone considerable diversification in recent years. Of particular interest is how host plants may influence the diversity of phytophagous insects in both evolutionary and ecological time. Major plant factors believed to influence insect herbivore diversity include plant chemistry and defence mechanisms (*e.g.* Southwood 1973; Lawton 1976; Levin 1976; Rhoades 1979; Prestidge & McNeill 1982), plant 'apparency' (Feeny 1975,1976), species-area relationships (*e.g.* Southwood 1960; Strong 1974,1979) and plant architecture (*e.g.* Lawton 1978; Southwood *et al* 1979; Stinson & Brown 1983). Although the role of vertebrate grazing in the dynamics of plant populations is well documented (*e.g.* Ellison 1960; Harper 1977; Crawley 1983) considerably less work has focused on the influence that insect herbivores may exert on natural plant communities (see Crawley 1983). This is probably because insect damage to natural plant communities is a rare occurrence (Hairston, Smith & Slobodkin 1960) or else difficult to assess (Bullock 1967).

At Silwood Park a long-term study was initiated in 1977 by Prof T.R.E. Southwood and Dr V.K. Brown to investigate insect-plant relationships along a secondary successional gradient. A recently harrowed field (Young Field, 0-2 years old), an area of mixed grassland with forbs (Old Field, 7-8 years old) and a predominantly birch woodland (around 60 years old) were regularily sampled and were used to represent early, mid and late successional habitats in a secondary succession. Since then these sites have been continued and new Young Fields created. The first publication from this research described certain relationships between insect and plant diversities in succession (Southwood, Brown & Reader 1979). Subsequent publications and present research cover areas such as the relationship between palatability to invertebrates and successional status of the plant (Reader & Southwood 1981), host plant patchiness and its influence on insect population dynamics (Southwood, Brown & Reader 1983) and trophic diversity, niche breadth and generation times of exopterygote insects (Brown & Southwood 1983). Additional research has undertaken detailed ecological examinations of particular insect taxa along the successional gradient and includes studies on Heteroptera (Brown 1982a), leaf-miners (Godfray 1982) and phytophagous Coleoptera (Hyman in prep.).

This thesis investigates the effects of insect herbivory on the development and structure of natural plant communities characteristic of an early successional habitat. Certain preliminary results from this work have already been cited at a recent symposium by Brown (1982b).

The thesis is arranged in seven chapters. This first chapter includes reviews on plant succession and herbivory. Chapter Two describes the materials and methods used. Chapters Three and Four describe the ecological characteristics of the early successional habitat based on field studies carried out in 1980 and 1981. Chapter Three describes the plant community and Chapter Four deals with the insect fauna. A detailed analysis of insect-plant relationships in the early successional habitat is given in Chapter Five. Chapter Six describes a parallel study that investigated the impact of herbivory on the early successional habitat by the experimental exclusion of insects from comparable sites (protected from rabbits and birds) by regular use of a non-persistent insecticide. A summary of the thesis follows Chapter Six.

1.2 PLANT SUCCESSION

1.2.1 Theories of succession

Plant succession refers to vegetation changes in time. Such changes may occur as a primary succession on newly exposed surfaces or as a secondary succession following a disturbance or stress in a plant community that opens up a relatively large space for colonisation. Descriptions of successional change were originally only concerned with the sequence of invasion of plant species (*e.g.* Clements 1916) while later studies tackled other aspects such as biomass, productivity and nutrient cycling (Odum 1969; Ricklefs 1973). This review is only concerned with successional theory on observed plant species sequences of invasion and establishment on a site.

The earliest popular theory of succession was proposed by Clements (1916). His idea was that the species sequence in a succession was governed by a process of 'reaction' whereby later successional species could only establish themselves after habitat preparation by earlier successional species. This implied that certain species modified their environment to make it less suitable for themselves but more fit for new and later colonisers. The end point of the particular succession is reached when the reaction process is arrested and a community of 'climax' species is maintained. This classical theory implies then that there are successional species and climax species. If the climax community is subject to disturbance a secondary succession of these successional species can occur.

Reviews of successional theory may be found in Drury & Nisbet (1973), Horn (1974), Connell & Slatyer (1977) and van Hulst (1978). The Clementsian approach has been criticised in a number of works including Connell (1972) and Drury & Nisbet (1973). More recently, Connell & Slatyer (1977) described three alternative models of succession to account for the observed sequence of species following the initial 'pioneer' or ruderal stage. The models agree in that these earliest colonisers have evolved various life-history characteristics that enable them to quickly establish themselves in newly created unoccupied sites (see Section 1.2.2). Offspring will seldom survive in the presence of their parents or other primary colonisers because they are not adapted to germinating and surviving in occupied sites. The mechanism of species sequence that follows this early successional period is described in the different models. In model 1 ('facilitation') later successional species can only become established and mature after earlier species have suitably modified the conditions. Evidence for this mechanism comes from studies of primary successions such as the virgin colonisation of soils after glacial retreat. Certain heterotrophic successions also fit into the facilitation concept. Model 2 ('tolerance') states that later species will be successful with or without a previous history of site colonisation by earlier successional species. These later species can establish themselves and mature in the presence of other species because they are better competitors. Evidence is lacking for this model. In model 3 ('inhibition') earlier species are resistant to invasion; later species are typically longer-lived and cannot reproduce in the presence of earlier ones and succession can only progress when earlier species become extinct. This model of inhibition is favoured by Connell & Slatyer (1977) who cite supportive evidence, mainly from secondary successions.

If insect herbivores preferentially attacked early successional species rather than late species then there are three possible different outcomes from the three different models. Succession would be decelerated in the facilitation model due to a lowering of the reaction rate. Herbivory would have no effect in the tolerance model because this mechanism proposes that the establishment of later successional species is dependent only on the life-history characteristics of the later species and is not reliant on a previous reaction process. Finally, succession would be accelerated in the inhibition model as damage and mortality to early successionals by grazers would open up gaps in the vegetation for later species to colonise.

The exclusion of insects from these early habitats can provide a testing of the three mechanisms of succession that Connell & Slatyer (1977) put forward. The outcome from this will be considered in the discussion of Chapter Six.

The selection of studies used by Connell & Slatyer (1977) to develop their models has been disputed by McIntosh (1980) on the ground that many were inapplicable. Indeed, more than one succession mechanism may operate at the same time on different species in the same seral community (Hils & Vankat 1982).

1.2.2 Life-history strategies in succession

The life-history strategies of animals and plants are shaped by their environment. Early successional habitats are characteristically ephemeral (or temporary) and have low 'durational stability' (Southwood 1977a,b). As a consequence early successional species have evolved the strategy of exploitation and have been given various labels such as 'fugitive species' (Hutchinson 1951), 'opportunists' (MacArthur 1960) and 'pioneering species' (Wynne-Edwards 1962). Such species (*e.g.* opportunists) have the ability to rapidly colonise new open sites, reproduce rapidly (usually in large numbers) and disperse efficiently in time and space. As succession progresses habitat durational stability increases and the opportunists are replaced by species that are adapted to a more permanent habitat; these are the typical later successional species.

Life-history characteristics along a successional gradient may be equated with the r-K continuum of MacArthur & Wilson (1967). r and K have subsequently been used as a convenient descriptive tool in population ecology. The terms cover the two extremes of early and late/climax communities and originate from the logistic growth equation. Selection in early successional habitats will favour species that have a high reproductive rate at low population levels and short generation times so that r_{max} will be maximised; the regulation of these populations will be mainly density-independent. K-strategists are adapted to more predictable environments and are good competitors and will tend to maintain their populations at or around their carrying-capacity (K); population regulation of these species is chiefly density-dependent (Southwood, May, Hassell & Conway 1974).

1.3 HERBIVORY

1.3.1 Population regulation of herbivores

Discussions and studies on herbivory have led to two opposing schools of thought as to how populations of herbivores are regulated. On one extreme it is argued that herbivore populations are food limited (Murdoch 1966; Ehrlich & Birch 1967; Breedlove & Ehrlich 1972) and regulate the abundance of host plants (Brues 1946). The other view is that since so little of primary production is consumed by herbivores (Wiegert & Evans 1967; Varley 1970; Phillipson 1973; Reichle, Goldstein, van Hook & Dodson 1973) that herbivores are not food limited (Hairston, Smith & Slobodkin 1960; Slobodkin, Smith & Hairston 1967) but are regulated by factors such as natural enemies (Hairston *et al* 1960) or abiotic factors (Andrewartha & Birch 1954). Hairston *et al* (1960) and Slobodkin *et al* (1967) assume that since there is so little evidence of plant population regulation by herbivores or meteorological disasters the abundance of all green plants must be resource limited (*e.g.* nutrients, space, water and light).

As Crawley (1983) emphasises in his comprehensive review of herbivory the world is not always green and herbivore population regulation may occur in these non-green periods when plant food is scarce (in winter or in drought; after fire or flood). This was shown to be the case by Sinclair (1975) who also found that not all green material may be utilised as a food resource since structural or chemical changes occur to render it inedible, indigestible or nutritionally inadequate. These observations prompted Sinclair (1975) to propose a resource-limitation hypothesis for the regulation of herbivore populations.

Evidence from field studies provides firm support for either hypothesis (Crawley 1983). The resource limitation hypothesis is supported by studies of the biological control of weeds in which herbivores become food limited when their numbers build up to levels where plant density is sufficiently reduced. Other studies show that predation (and parasitism) are chief regulatory factors.

1.3.2 Role of herbivory

Herbivory undoubtedly plays an important role in structuring plant communities. The selective pressure of herbivores is believed to have resulted in the evolutionary development of various anti-herbivore defence mechanisms (*e.g.* plant chemistry and morphological traits) found in many present day plant taxa (Southwood 1973; Lawton 1976; Levin 1976; Feeny 1975,1976; Rhoades & Cates 1976; Rhoades 1979; Prestidge & McNeill 1982). Herbivorous animals influence plant community structure by affecting the plant species richness, the relative abundance of plant species and spatial heterogeneity within the community (see reviews by Harper 1977 and Crawley 1983).

1.3.3 Effects of vertebrate grazers

The majority of studies on herbivory have been restricted to vertebrate grazing and then chiefly to mammals (*e.g.* Farrow 1917; Cameron 1935; Baker 1937; Fenton 1940; Gooding 1955; Gillham 1955,1963; Costin & Moore 1960; Duffey, Morris, Sheail, Ward, Wells & Wells 1974; Watt 1981a,b; see also reviews by Harper 1977 and Crawley 1983). Vertebrate grazers exert influences on plant communities by selecting palatable species and grazing preferentially on the most nutritious and rapidly growing parts of plants (Bell 1970; Harper 1977; Crawley 1983). Consequent successional changes in the floristics of the community are usually due the result of altering the competitive balance between plant species (Harper 1977; Crawley 1983). By mechanically damaging the vegetation and depositing dung and urine herbivores may also have important secondary effects on plant communities (Buechner & Dawkins 1961; Hughes 1975; Lock 1972; Harper 1977; Crawley 1983).

The effects of vertebrates on plant succession have been assessed by either intuitive observations or enclosure/exclosure experiments (Harper 1977; Crawley 1983). A major review of the influence of grazing on plant succession of rangelands is given by Ellison (1960). In grassland communities the floral composition and structure reflects a history of the selective pressures of vertebrate grazing (Duffey *et al* 1974). Indeed moderate grazing of these grasslands may maintain a floristically rich and essentially stabilised sub-climax (Tansley & Adamson 1925) or deflected succession (Hope-Simpson 1940). Plant species that are successful in permanent pastures are tolerant to continued herbivore pressures and show various morphological (Baker 1937; Harper 1977; Crawley 1983) and physiological (Harper 1977) adaptations to grazing. Visible effects of vertebrate grazing on plant succession are most evident where a fence line separates areas that have had a long history of different grazing management and the effect is most obvious when grazed and ungrazed areas are compared. The grazed area is usually closely cropped, with mainly graminaceous plants, while the ungrazed area is dominated by shrubs and tall herbs which left long enough would revert to woodland (Crawley 1983). Overgrazing by vertebrate herbivores can have drastic consequences for the botanical composition and quality of grasslands and rangelands by lowering productivity and opening up spaces for invasion or ecological release of non-forage woody plants, undesirable grasses or toxic weeds (Cameron 1935; Ellison 1960; Harper 1977; Crawley 1983). Severe overgrazing can produce accelerated soil erosion on arid lands (Ellison 1960).

1.3.4 Effects of insect grazers

Although some works have investigated the effects of phytophagous insects on single-species populations, especially in the field of biological control of weeds, relatively few studies have been concerned with natural plant communities. This is mainly because insect devastations rarely occur in nature and as a consequence most plant ecologists have tended to ignore the effects of insect grazing in plant community studies. Indeed many authors believe that insect herbivory is by and large an insignificant factor in plant community dynamics (Williams 1954; Hairston *et al* 1960). On the other hand there is a rapidly growing body of evidence that regards insect grazing as a major driving force in the evolution of plant communities and in the maintenance of plant diversity in time and space (Gillet 1962; Ehrlich & Raven 1964; Bullock 1967; Breedlove & Ehrlich 1968,1972; Ehrlich 1970; Janzen 1970; see also reviews by Harper 1977 and Crawley 1983) and in the evolution of anti-herbivore defence mechanisms (Southwood 1973; Lawton 1976; Levin 1976; Feeny 1975,1976; Rhoades & Cates 1976; Rhoades 1979; Prestidge & McNeill 1982). Some researchers even believe that insects regulate the primary productivity of whole ecosystems (Mattson & Addy 1975; Springett 1978). It was indeed this large body of current evidence which prompted the present study.

Studies of the biological control of weeds have shown that insect grazing may result in the reduction of plant populations by more complex mechanisms than mere destruction (Wilson 1954; Huffaker 1952,1962; Holloway & Huffaker 1952; Goeden, Fleschner & Ricker 1967; Weldon, Blackburn & Durdan 1973; Andres & Bennett 1975; see also reviews by Harris 1973; Harper 1977; Whittaker 1979 and Crawley 1983). These studies suggest that even low levels of grazing in the presence of an additional stress, especially competition, may seriously reduce a plant's ability to successfully compete with other plant species. Other studies of natural populations also indicate that the competitive ability of a plant may be undermined by grazing although these works have been restricted to single herbivore species with single plant species or pairs of plant species (Bentley, Whittaker & Malloch 1980). In other similar studies grazing has been studied under controlled conditions (Bentley & Whittaker 1979; Whittaker 1982) or simulated by artificial defoliation (Lee & Bazzaz 1980). Futhermore, in the majority of studies the plant species are usually perennials and the insects monophagous (Brown 1982b).

The ruderal-early stages of the secondary succession represent a period where species of plants and insects have a high turnover rate (Southwood *et al* 1979; Brown & Southwood 1983) and where the insects themselves may reach high levels of abundance (Southwood 1977b). So what effects would occur in early successional habitats where the plant community contains a high proportion of annuals and the insects are mainly polyphagous? The lack of such important research in insect-plant relationships in natural communities has been stressed time and time again by ecologists such as Price (1975), Harper (1977), Whittaker (1979) and Crawley (1983). It is hoped that the present work will throw some light on the subject although it is restricted to early successional plant communities.

CHAPTER TWO

GENERAL MATERIALS AND METHODS

2.1 SILWOOD PARK

Imperial College at Silwood Park, Berkshire is situated in 93ha (230 acres) at 51°21′N and 0°39′ and an elevation of 91m. The grounds lie mainly on sand and gravel of Eocene Bracklesham Beds and Bagshot Sands. The vegetation consists mainly of arable land, acidic grassland and woodland areas (predominantly birch and oak with scattered beech and various exotics). The woodlands were originally part of the old Windsor Forest but are now secondary.

2.2 DESCRIPTION OF STUDY AREAS

Two study areas (each of 405m^2) were established in March, one in 1980 and another in 1981, and are henceforth referred to as Site A and Site D respectively. The two sites lay adjacent to the early successional sites used by Southwood *et al* (1979). Site A was an area of long-standing arable land (Hill Bottom) that had been under rotation of potato, broad bean, wheat and brussel sprouts for many years. Rabbits have been excluded from both areas since 1976. In the autumn, prior to site establishment the following spring, each area was treated with weed-killer to destroy perennial weeds. Preparation in March consisted of shallow ploughing, harrowing and light rolling. The area was then left to recolonise naturally. A site thus prepared is referred to as a Young Field with both ruderal and early successional plant species (see Southwood *et al* 1979 and Stinson & Brown 1983).

The materials and methods given in this chapter are those that were used to assess the characteristics of the early successional habitat as represented by Sites A and D. Results and discussions of this assessment are presented in Chapter Three (plants), Chapter Four (insects) and Chapter Five (insect-plant relationships). A separate materials and methods section is included in Chapter Six where the effects of insect herbivores are considered.

2.3 SAMPLING PROCEDURE

Each site was subdivided into 45 subplots, each 3m x 3m, arranged in a 9 x 5 pattern (Site A) and a 5 + (8 x 5) pattern (Site D). This approach was designed to standardise sampling procedures, minimise errors, speed and simplify the sampling process and enable specific regions of each site to be located with ease (see Southwood 1978 and Southwood *et al* 1979). Samples were then taken from within each subplot. Both sites were 5-6 weeks old at the time of the first sample. Site A was sampled for the first two years (1980 + 1981) and Site D for the first year (1981); observations were continued in early 1982. Green plants and invertebrates were sampled six times during the growing season (at approximately monthly intervals from early May to late October).

2.3.1 Vegetation sampling

Steel sampling pins (point quadrats) were used to describe the plant community. Sample pins were 3mm in diameter and marked in intervals of 2,4,6,8,10 and successive 5cm from soil level. Pin lengths of 75cm were commonly used although 1m pins were sometimes required.

For Site A in 1980, 30 pins were placed at random within each subplot using a linear-frame quadrat carrying 10 pins at one time (*i.e.* three frame placements): this gave a total of 1350 point quadrats on each sampling occasion. A reduced sample was taken in October (10 pins per subplot: a total of 450 pins). Alternate subplots were sampled during 1981 using 10 pins per subplot (a total of 230 pins). For Site D in 1981, 10 pins per subplot were used throughout (a total of 450 pins). The reduction in sampling intensity in both sites was made because it was felt that adequate information would be gained as well as considerably reducing the amount of time spent on data collection.

The use of a linear frame speeds up the sampling process considerably, although a drawback with this method is that pins only sample randomly with respect to placement of the frame itself (Mueller-Dombois & Ellenberg 1974).

2.3.2 Plant biomass

Primary productivity estimates were made during the growing season. Three samples were taken in early June, mid-August and late October using a 25cm x 25cm quadrat thrown randomly within each site. Vegetation was clipped to soil level within each quadrat, separated into species and stored in paper bags.

2.3.3 Seed bank

At the time of site establishment in March, 5 soil cores (10cm diameter) were removed from each site. Samples were placed in shallow seed trays in a temperate greenhouse and watered as necessary. As seedlings emerged they were either identified immediately, or when they had acquired true leaves, and removed. Hanf (1980) was used to assist identification. Periodically the soil was broken up and turned to allow every opportunity for successful germination. The seed bank assessment test was run until no further germination occurred.

2.3.4 Invertebrate sampling

The D-vac suction apparatus was used to remove field-layer invertebrates. Three random samples were taken from within each subplot and samples from subplot pairs were bulked (*i.e.* six sucks): this provided a total of 135 individual and 23 bulked samples. Each individual suck covered an area of $0.096m^2$ and therefore $0.288m^2$ for 1 subplot. A single D-vac suck entailed holding the apparatus in position for 30s followed by a 30s search of the area sampled and any further invertebrates found were added to the sample: these were mainly large specimens of Carabidae and Araneae. Each bulked sample was transferred to a labelled polythene bag and stored in a refrigerator at 4°C prior to sorting.

2.4 DATA RECORDING - PLANTS

2.4.1 Point quadrats

A point quadrat records either a presence (*i.e.* the occurrence of one or more 'plant events') or absence (*i.e.* bare ground) of vegetation. When vegetation was present at a pin the number of touches at each height category was recorded together with the species and structure type. Note that for each pin it is possible to have combinations of species, structure types and height categories. Data were collected using a battery-operated cassette recorder and later transferred via coding sheets to punch cards.

Plant species were identified using Clapham, Tutin & Warburg (1981), Hubbard (1978) and Fitter & Fitter (1980). Plant structures were recorded as in Table 2.1.

2.4.2 Plant biomass

Biomass samples were oven-dried at 70°C for 72h and weighed on a Stanton electrical balance to 0.1g.

2.4.3 Seed bank

The number of individuals of each species was recorded. This was then used to provide an estimate of species richness and diversity of the seed bank.

2.5 DATA RECORDING - INVERTEBRATES

D-vac samples were sorted within 24h of collection. Sorting was facilitated using a special wooden-framed hood with a perspex rear. Invertebrates were collected using a handheld aspirator (or pooter) and stored in 70% ethanol with glycerol prior to identification.

The following insect groups, which are either wholly or partly phytophagous, were identified to species (a few unnamed specimens were assigned a type name) and counted for each sample:-

TABLE 2.1: List of Plant Structures Recorded

Herb Structures		Gramineae Structures	
seedling (2 leaf)		Seedling (1 leaf)	
green stem		sheath	
petiole			
leaf	immature mature	blade	immature mature
flowering stem	immature mature	culm	
flowers	pre-anthesis anthesis post-anthesis	panicle	
ripening/ripe fruits			

TABLE 2.2: Taxonomic Reference List for Invertebrate Groups

TAXA	
Collembola-Sminthuridae	Fjellberg (1980)
Orthoptera	Raage (1965)
Hemiptera-Heteroptera	Leston & Scudder (1956); Southwood (1956); Sands (1957); Southwood & Leston (1959); Southwood & Fewke (1961); Wagner & Weber (1964).
Hemiptera-Homoptera	Le Quesne (1960, 1965, 1969); Le Quesne & Payne (1981).
Thysanoptera	Mound, Morison, Pitkin and Palmer (1976).
Neuroptera	Fraser (1959).
Coleoptera	Fowler (1887-1891); Fowler & Donisthorpe (1913); Reiter (1912, 1916); Joy (1932); Hoffman (1950, 1954 1958; Thompson (1958); Scherf (1964); Freude & Harde (1966); Cox (1976); Freude, Harde & Lohse (1981); Lindroth (1974), Harde (1966)
Araneae	Locket & Millidge (1951); Locket, Millidge & Merrett (1974).

Apterygota	Collembola: Sminthuridae
Exopterygota	Orthoptera
	Hemiptera-Heteroptera
	Hemiptera-Homoptera: excluding aphids
	Thysanoptera
Endopterygota	Coleoptera

Immature stages were usually identified to species, but only to genus when this was impossible. Coleoptera larvae were identified to family only. Homoptera: Aphididae and Lepidoptera larvae were counted but not identified. These identifications (of aphids) were not undertaken because of inherent taxonomic difficulties.

Biomass measurements were also made for each sample. The adult biomass of each species was estimated by taking a mean dry weight measurement of twenty individuals (or as near that figure as possible for rare species). This was accomplished by freeze-drying specimens for 96h and then weighing on a Cahn microbalance to 0.1mg. For immature stages of identified species the biomass of each sample was found by direct measurement of all material in a sample. For aphid biomass, adults and nymphs were weighed together: 8 of the 23 samples were used to provide an estimate, the remainder being left for possible identification at a later date.

Examples of solely predatory groups considered were the Neuroptera and Araneae. For Site A in 1980 all insect predators were identified to species (immature Coleoptera were identified to family), counted and biomass estimates made as for herbivore groups. Spider adults and immatures were combined for biomass measurements. For Site A and Site D in 1981 the spiders were identified to family, counted and biomass estimates made.

A reference list for taxonomy of insects and spiders is given in Table 2.2.

Of the remaining taxa the Diptera and Hymenoptera were excluded from this study (although 5 of the 23 samples were used to provide an estimate of abundance and biomass). This was partly due to the difficulty in identifying the large numbers of individuals caught (*e.g.* >5000 individuals/sample in peak months), but also because of the impracticality in providing a realistic assessment of their role in the invertebrate community: many of these species would undoubtedly be 'tourists' (Moran & Southwood 1982). Similar taxonomic and abundance problems also led to the exclusion of the non-phytophagous exopterygotes from this study.

2.6 DATA SYNTHESIS AND ANALYSIS - PLANTS

2.6.1 Database system for point quadrat data

From the eight variables recorded from sampling pins (*i.e.* site, date, subplot, pin, species, structure, height category, touches) more than 500,000 pieces of information (*i.e.* individual variable values) were obtained. A database was set up to analyse this data using the powerful SIR system (Scientific Information Retrieval, Inc., Illinois, U.S.A.) and currently available as Version 1.1 at Imperial College Computer Centre (ICCC).

The SIR system was chosen because it has excellent variable sorting capabilities for data storage and retrieval. Data storage facilities also include a variety of ways for inputting, modifying, deleting and in general, controlling the contents of the data file. The data retrieval capabilities enable the user to perform both simple and highly complex retrievals in a straightforward way. An additional bonus is that SIR is available for use either interactively or on batch. A full explanation of the SIR system is given in Robinson, Anderson, Cohen and Gadzik (1979) and in the ICCC SIR user's guide (1982).

2.6.2 Defining the database

The Initial Schema Definition command set is provided in Appendix 1 and incorporates a full self-explanatory documentation.

2.6.3 SIR retrieval programs

All major programs are listed in Appendix 2 with full documentation. The complete SIR database status is given in Appendix 3. Main programs used are listed below:-

Overall information

Prog1 : Cover.

Prog5 : Abundance (multiple touches).

Height Category information

Prog10 : Vertical cover.

Prog11 : Species list.

Prog13 : Vertical abundance.

Species information

Prog6a : Number of pins touched by each species and cover.

Prog6b : As for Prog6a but in vertical profile.

Prog7 : Total abundance plus abundance in vertical profile.

Structure information

Prog21 : Structure abundance of individual species overall and in vertical profile.

Prog22 : Structure pins touched and cover of individual species in vertical profile.

Prog24 : Number of pins touched and cover of structures of individual species.

2.6.4 Database backup

A copy of the SIR database used in this study is available on magnetic tape and currently stored in ICCC's tape library. The backup copy contains the Schema Definition Commands, the SIR Program File and the Data File and access may be gained with the author's permission.

2.6.5 Determining measures of abundance and diversity

These are covered in Southwood (1978) and Southwood *et al* (1979). Percentage cover was computed from

(no. of pins touched/total pins used) x 100%.

Abundance was determined by summing pin records of single or multiple touches.

Diversity was determined using William's α. This index is best suited for populations showing a log normal distribution of component species. It will be shown later that rank abundance curves in this study tended towards this distribution. The William's Index was calculated by maximum likelihood using a program available at ICCC.

Plant species (or taxonomic) diversity was assessed using the number of species (S) and the total number of individual pins touched (N). N was computed from

$$N = \Sigma(s_i) \quad 1 \leq i \leq S$$

where s_i is the number of pins touched by species i (from Prog6a).

Plant spatial and architectural diversity (the components of structural diversity) were based on height categories and structures respectively.

The spatial component was assessed by recording the number of pins touched by vegetation (any species, any structure) within each height category. For the diversity statistic,

$$N_h = \Sigma(h_j) \quad 1 \leq j \leq H$$

where h_j is the number of pins with touches at height category j and H is the number of height categories. This provides a measure of the vertical distribution of plant structures (any type) in space (from Prog10).

Architectural diversity was determined using values computed from Prog24. In this study similar structures (*e.g.* mature leaf) of different species were considered architecturally distinct. This leads to a more detailed description of architectural diversity than in earlier work (see Southwood *et al* 1979 and Stinson & Brown 1983). Architectural diversity was computed from

$$N_a = \Sigma(a_k) \quad 1 \leq k \leq A$$

where a_k is the number of pins touched by structure k and A is the number of different structures.

The Berger-Parker Dominance Index (d) was also employed and is simple to calculate (Southwood 1978).

β-diversity was described using Sorensen's Index of Similarity. Both qualitative (I_s) and quantitative (I_w) indices were calculated. For the qualitative index

$$I_s = 2J/(A+B)$$

where J = species present in both samples and A and B = species present in samples A and B respectively. For the quantitative index

$$I_w = 2W/(A+B)$$

where W = sum of the smaller of the two cover values for each species pair that are common to both samples. A and B = sum of all cover values for species in samples A and B respectively.

2.7 DATA SYNTHESIS AND ANALYSIS - INVERTEBRATES

2.7.1 Invertebrate density and biomass

Invertebrate abundance and biomass of each bulked D-vac sample was corrected to $1 m^2$ by multiplying each parameter by a factor of 1.74 (for the 22 samples representing 44 subplots) or 3.48 (for the single sample representing 1 subplot). Mean density of individuals and mean biomass per $metre^2$ was then calculated using the 23 samples with values corrected to $1 m^2$.

2.7.2 Determining diversity

Taxonomic α-diversity and β-diversity were expressed as described in 2.6.5.

CHAPTER THREE

ECOLOGICAL CHARACTERISTICS
OF THE
EARLY SUCCESSIONAL HABITAT: PLANTS

3.1 CHARACTERISTICS OF THE PLANT COMMUNITY

3.1.1 General trends

In Site A seedlings were abundant within several days of site establishment in late March. Plant species were represented primarily by *Spergula arvensis* and *Chenopodium album* with lesser amounts of *Medicago lupulina*, *Trifolium repens*, *Sonchus asper*, *S.oleraceus*, *Polygonum persicaria*, *Capsella bursa-pastoris* and *Poa annua*. These species originated from the seed bank since at the time of site establishment there were no reproducing plants to act as a source of immigrant seed.

Weed cover increased rapidly from 10.81%, just over one month after abandonment in May, and reached a plateau around 90% by mid-July, only nine weeks later. Cover dropped to 68.67% at the end of the season.

During 1980 the site was colonised by 41 species of herbs and 6 species of grasses. Of these primary colonisers twelve species attained a cover value of 5% or more and nine of these species were typically ruderal (Table 3.1): for definition of the term 'ruderal' see Baker (1965), Southwood (1977b) and Southwood *et al* (1979). The early establishment and dominance of *Spergula* was followed by a mid-season flourish of *Medicago*. A second phase of germination occurred in September (mainly of *Crepis capillaris* and *Plantago major*) and by autumn *Holcus lanatus* and *Poa annua* had become increasingly dominant.

Forty-three species were found during the second year (38 herbs and 5 grasses) and plant cover was maintained around 90%. Only five of the original twelve dominant 'pioneer' species attained 5% cover during the season and just three ruderals were significant (Table 3.1). New species found during the second year originated either as first year autumn germinators from the seed bank or as immigrant seed.

Grasses were the dominant component of the flora during the second year. *Poa annua* dominated early in the season and then died back. *Holcus lanatus* rapidly increased and by

TABLE 3.1: Percentage Cover of Dominant Species ($\geqslant$ 5% cover) During the First Two Years of Succession (Site A).

	YEAR 1						YEAR 2					
	May	June	July	Aug	Sept	Oct	May	June	July	Aug	Sept	Oct
Spergula arvensis^r	3.33	49.18	64.74	33.04	9.18	2.67						
Chenopodium album^r	3.63	21.18	23.11	14.37	6.81	6.22						
Veronica persica^r	0	13.63	22.96	5.93	1.70	1.33						
Sonchus asper^r	0	8.59	21.18	11.93	0.89	0						
Medicago lupulina^r	0.30	2.30	30.00	51.70	55.48	23.33	0	18.26	34.78	22.17	12.17	3.48
Trifolium pratense	0	0.30	2.44	6.67	14.00	9.56	0.87	9.56	17.39	18.26	10.00	0
T. repens	0.07	1.11	5.70	3.26	5.11	2.22	7.83	11.30	7.39	12.61	15.22	13.48
Sonchus oleraceus^r	0	6.37	6.00	3.11	0.22	0						
Polygonum persicaria^r	2.22	2.96	7.26	8.74	1.41	0.22						
Capsella bursa-pastoris^r	0	4.81	5.41	1.41	1.56	2.89						
Holcus lanatus	0	0.22	2.44	9.41	12.81	14.44	26.09	28.70	30.00	38.26	54.35	39.13
Poa annua^r	0.07	1.18	1.70	6.67	8.74	19.11	41.74	40.43	10.00	3.91	3.48	6.09
Agrostis capillaris							11.30	10.00	13.91	14.35	17.39	10.00
Crepis capillaris							14.78	23.48	33.48	34.78	22.61	14.39
Plantago major							1.30	3.48	3.48	6.96	2.61	2.17
Cirsium arvense							6.09	2.17	5.65	12.17	9.13	7.83
Tripleurospermum inodorum							0	7.39	18.70	9.10	2.17	0.87
Erigeron canadensis							3.48	4.78	6.96	4.78	7.39	0
Ranunculus repens							0	2.17	0.43	2.61	1.74	6.09
Stellaria media^r							6.96	0.43	0	0	1.74	0
Senecio jacobaea							1.74	4.78	6.52	6.09	3.91	3.04
Lactuca serriola							0.87	2.17	3.48	5.65	6.52	0

r denotes a ruderal species

September had reached over 50% cover. The dominant herbs were *Crepis capillaris*, *Medicago lupulina*, *Trifolium pratense* and *T.repens*. The establishment and spread of small islands (or patches) of vegetatively spreading perennial herbs and grasses during the second year of succession was conspicuous.

3.1.2 Taxonomic composition, species abundance and diversity

3.1.2(a) Taxonomic composition

Plant species richness rose rapidly during the first year to a peak of 39 in mid-August and then declined. The second year vegetation was less rich but more numerically stable and richness again peaked in August, with 29 species (Fig. 3.1).

In terms of colonisation rates, species were initially accumulated extremely rapidly during the first year and after mid-August, just eighteen weeks into the succession, very few new colonisers appeared. A second wave of colonisation occurred throughout the second year (Fig. 3.1). Differences in colonisation rates between the major plant groupings (annual, biennial and perennial herbs and Gramineae) are shown in Fig. 3.2. The early rapid species accumulation during 1980 was due predominantly to the annuals; by early June (just over eight weeks into the succession) 20 annual herb species, representing 77% of the 1980 seasonal total of annual herb species, had become established. By the end of the second year the annuals were heading for extinction. These results from sampling were backed up by field observations. The perennial herbs show a gradual but significant colonisation over the two years. The biennial herbs were gained slowly, mainly from June 1980 to June 1981, and by the end of the second year were almost extinct. The few Gramineae species colonised early in the first year and showed little change thereafter.

Consequent upon differences in colonisation and extinction rates the major plant groupings also differed in their contribution to the species composition of the Young Field vegetation (Fig. 3.3). In 1980 annual herbs dominated, representing 73% of the community in May and falling to 50% in late October. The drop in annual herb species dominance was mainly due to a gradual increase in the species contribution of perennial herbs which rose from 18% in May to 30% by the end of the first year (annuals remaining numerically stable). During the second year the annual herb contribution continued to fall, finally dropping to 30%; this was accompanied by a general rise in the importance of perennial species which represented 50% of the community by the autumn of 1981. Both biennial herbs and grasses had low

Fig. 3.1 Plant species richness with gain and loss rates during the first two years of succession (Site A).

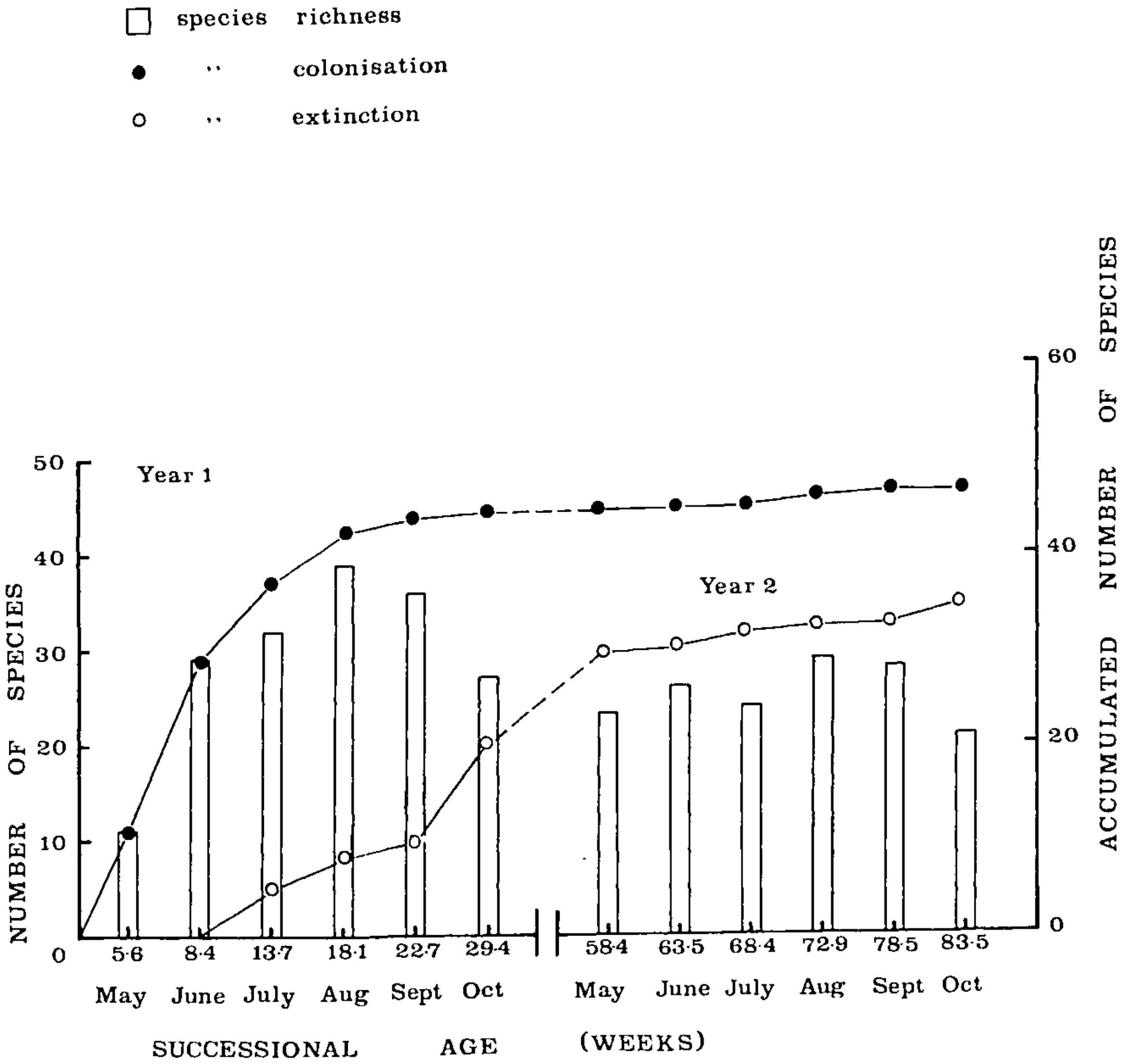

□ species richness
● ,, colonisation
○ ,, extinction
Year 1
Year 2
NUMBER OF SPECIES
0
10
20
30
40
50
ACCUMULATED NUMBER OF SPECIES
0
20
40
60
5·6
8·4
13·7
18·1
22·7
29·4
58·4
63·5
68·4
72·9
78·5
83·5
May
June
July
Aug
Sept
Oct
May
June
July
Aug
Sept
Oct
SUCCESSIONAL AGE (WEEKS)

Fig. 3.2 Species gain and loss rates of the major plant groupings during the first two years of succession (Site A).

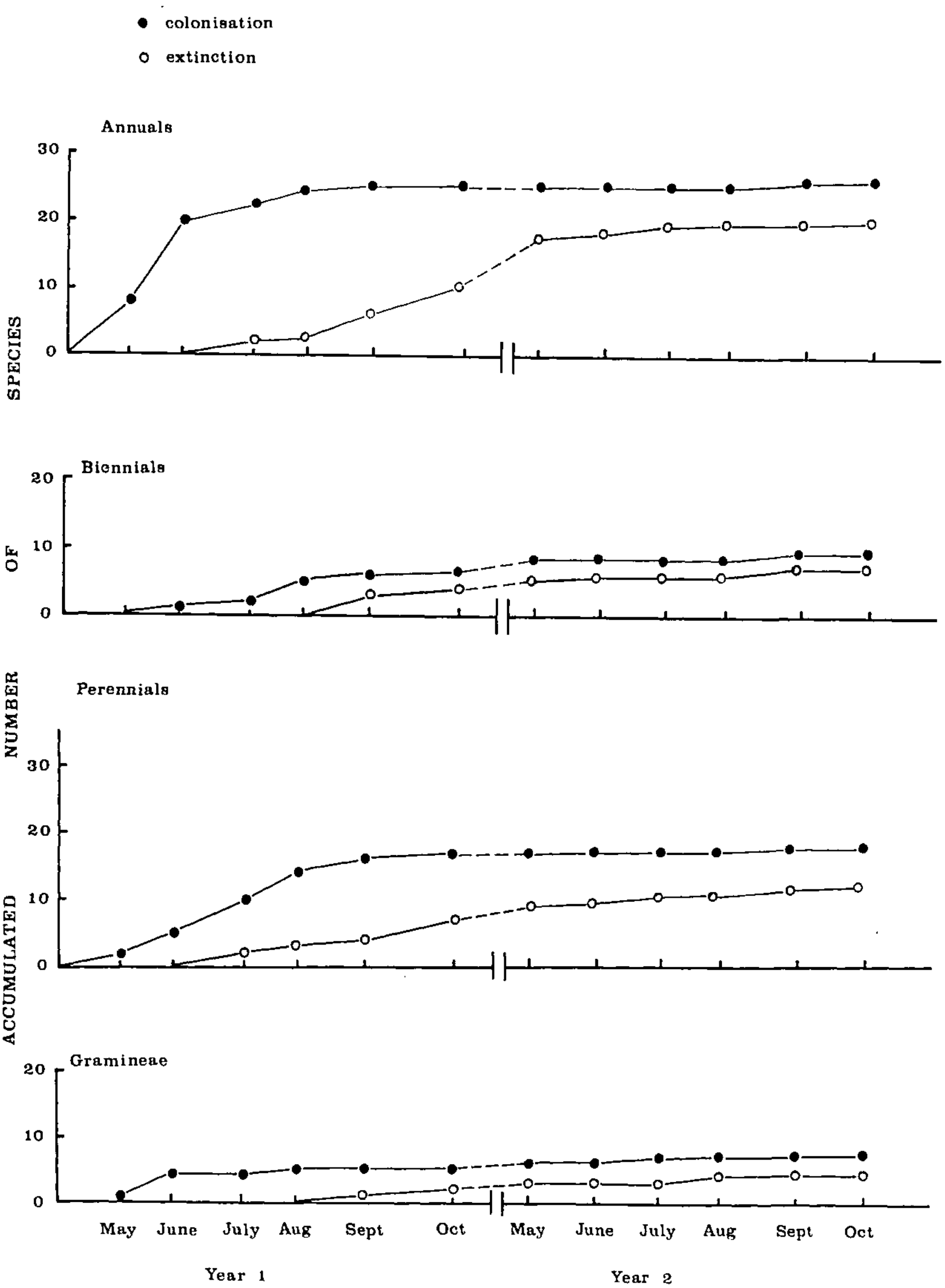
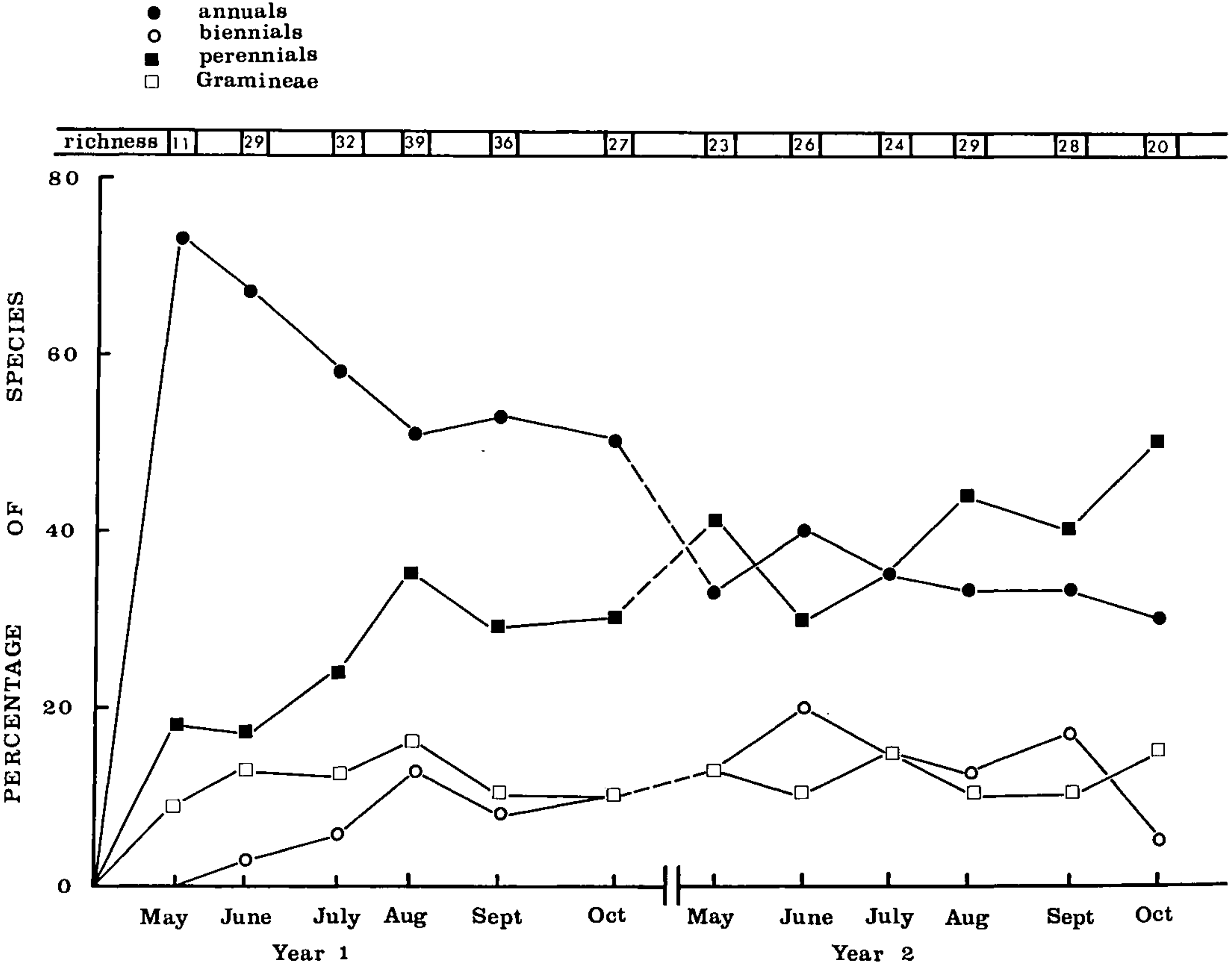

● colonisation
○ extinction
Annuals
Biennials
Perennials
Gramineae
ACCUMULATED NUMBER OF SPECIES
30
20
10
0
20
10
0
30
20
10
0
20
10
0
May
June
July
Aug
Sept
Oct
May
June
July
Aug
Sept
Oct
Year 1
Year 2

Fig. 3.3 Species contributions of the major plant groupings during the first two years of succession (Site A). Total species richness is given along the figure top.


● annuals
○ biennials
■ perennials
□ Gramineae
richness
11
29
32
39
36
27
23
26
24
29
28
20
PERCENTAGE OF SPECIES
80
60
40
20
0
May
June
July
Aug
Sept
Oct
Year 1
May
June
July
Aug
Sept
Oct
Year 2

species richness throughout the first two years of succession and were relatively unimportant in terms of their species contribution to the Young Field community.

Comparisons of plant cover contributions of the major plant groupings are interesting and present rather a different picture to the species contributions (Fig. 3.4). Here the annual and perennial herbs and grasses are important over the two years with the biennials contributing relatively little cover. The three former groups each show two peaks in cover, though at different times. Annual herb cover peaked rapidly in July of the first year (88% cover) and then declined to May of the second year; a second but smaller peak (50% cover) occurred in July 1981, contributed mainly by a final flourish of *Medicago*. By the end of the second year the annual herbs had dropped to under 10% cover. Cover of perennial herbs rose gradually to a peak in September of the first year (24% cover), declined in October and by July-August of the second year had rapidly risen to a second peak (65-70% cover). The most important perennials were *Crepis capillaris*, and two legumes *Trifolium pratense* and *T.repens*. Grass cover rose gradually through 1980 and peaked initially in May-June of the second year (around 70% cover) and again in September. The drop in grass cover after spring was due to die back of *Poa annua* and the increased spread of *Holcus* brought about the second peak in September of 1981.

Successional change in basic taxonomic composition, or species turnover, of the Young Field plant community over the first two years can also be demonstrated in the use of Sorensen's Index of Similarity. There is a very high similarity in species composition between 1980 and 1981 vegetation ($I_s=0.95$) with 42 shared species. However, from an insect's standpoint it is similarity in relative abundance of species that is important and this can be found by using only those species that attained at least 5% cover (as in Table 3.1) in both years; similarity is then much lower ($I_s=0.37$) with just 5 common species.

Accounting for relative abundance yields a more valid interpretation of taxonomic change, within and between years, as can be seen from Table 3.2 where I_s and I_w are both cited for comparison. It is clear that the qualitative I_s approach may be misleading since it will tend to overestimate habitat similarity (Table 3.2a). I_w, on the other hand, indicates that the Young Field has moved quickly along a β-diversity gradient. This is evident from Table 3.2b where Similarity between the first two years began at 3% and by the end of the growing season had reached 34%. The grasses especially show a rise in stability with successional age.

Fig. 3.4 Cover contributions of the major plant groupings during the first two years of succession (Site A).

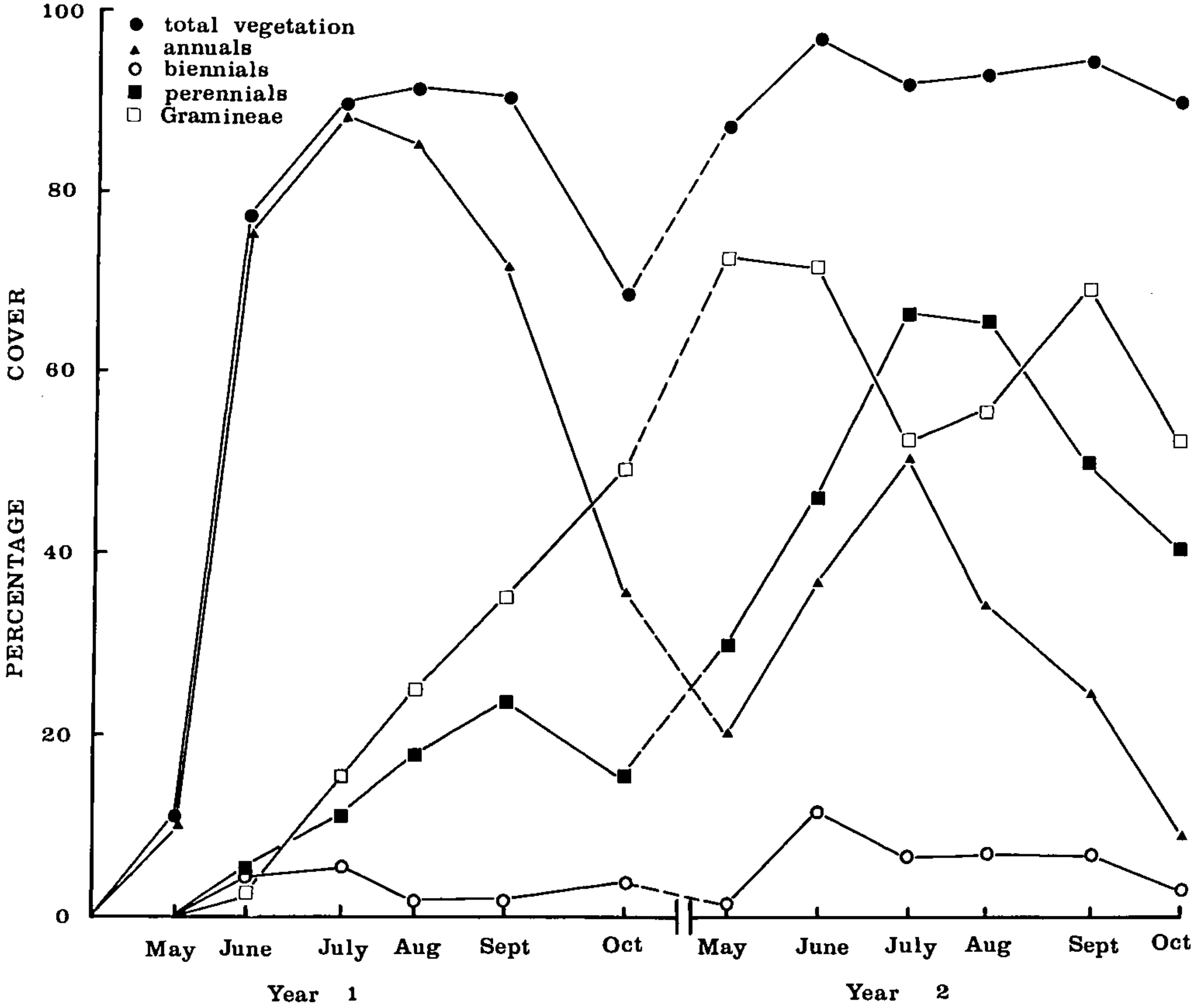

● total vegetation
▲ annuals
○ biennials
■ perennials
□ Gramineae
PERCENTAGE COVER
100
80
60
40
20
0
May
June
July
Aug
Sept
Oct
May
June
July
Aug
Sept
Oct
Year 1
Year 2

TABLE 3.2: Indices of Similarity Between Green Plants in Site A.

a. Over the first two years of succession b. Between the first and second years of succession.

(a)

I_s = upper figure; I_w in italics

	YEAR 1						YEAR 2				
	May - June	June - July	July - Aug	Aug - Sept	Sept - Oct	Oct'80 - May'81	May - June	June - July	July - Aug	Aug - Sept	Sept - Oct
Annuals	0.57 *(0.16)*	0.87 *(0.75)*	0.90 *(0.69)*	0.93 *(0.71)*	0.80 *(0.60)*	0.48 *(0.20)*	0.40 *(0.18)*	0.66 *(0.63)*	0.53 *(0.70)*	0.50 *(0.58)*	0.62 *(0.46)*
Biennials	0 *(0)*	0.66 *(0.51)*	0.66 *(0.59)*	0.57 *(0.92)*	1.00 *(0.93)*	0 *(0)*	0.44 *(0.41)*	0.80 *(0.98)*	0.50 *(0.94)*	0.66 *(0.90)*	0.50 *(0.61)*
Perennials	0.57 *(0.02)*	0.46 *(0.18)*	0.74 *(0.29)*	0.73 *(0.60)*	0.80 *(0.62)*	0.74 *(0.30)*	0.63 *(0.61)*	0.88 *(0.72)*	0.82 *(0.85)*	0.80 *(0.79)*	0.73 *(0.75)*
Gramineae	0.40 *(0.05)*	1.00 *(0.60)*	0.88 *(0.39)*	0.88 *(0.85)*	0.86 *(0.74)*	1.00 *(0.65)*	1.00 *(0.98)*	1.00 *(0.77)*	1.00 *(0.91)*	1.00 *(0.86)*	0.75 *(0.81)*
TOTAL	0.55 *(0.16)*	0.76 *(0.71)*	0.84 *(0.66)*	0.83 *(0.72)*	0.82 *(0.64)*	0.60 *(0.43)*	0.66 *(0.69)*	0.84 *(0.70)*	0.75 *(0.82)*	0.74 *(0.77)*	0.71 *(0.70)*

TABLE 3.2: (Continued)

(b)

	May'80 + May'81	Jun'80 + Jun'81	Jul'80 + Jul'81	Aug'80 + Aug'81	Sept'80 + Sept'81	Oct'80 + Oct'81
Annuals	0.25 *(0.11)*	0.50 *(0.06)*	0.36 *(0.26)*	0.64 *(0.30)*	0.47 *(0.28)*	0.48 *(0.23)*
Biennials	0 *(0)*	0.28 *(0.07)*	0.66 *(0.01)*	0.50 *(0.04)*	0.50 *(0.03)*	0 *(0)*
Perennials	0.33 *(0.04)*	0.43 *(0.11)*	0.70 *(0.26)*	0.83 *(0.34)*	0.78 *(0.42)*	0.63 *(0.18)*
Gramineae	0.40 *(<0.01)*	0.86 *(0.04)*	0.75 *(0.15)*	1.00 *(0.42)*	0.86 *(0.36)*	1.00 *(0.54)*
TOTAL	0.23 *(0.03)*	0.51 *(0.06)*	0.53 *(0.24)*	0.71 *(0.32)*	0.66 *(0.36)*	0.55 *(0.34)*

3.1.2(b) Species abundance and diversity

The rapid change in β-diversity is also demonstrated by values of the dominance index (*d*) for abundance of the six most common species and the major plant groupings (Table 3.3). The grass/forb ratio reflects overall successional changes occurring in the Young Field plant community; as grasses become established and their cover and abundance rises the ratio increases. The implications for the structure of the insect herbivore guild will be expanded in Chapter Five.

The distribution of all species throughout the first two years are described by dominance diversity curves in Fig. 3.5. Equitability (or evenness) of the flora is expressed by the slope of each curve and it is clear from Fig. 3.5a that equitability in the first year rose through May to July, levelled off from July to September and declined in October. During the second year equitability was higher and more stable (Fig. 3.5b).

As might be expected from the general trend shown by these curves the taxonomic diversity of green plants, as expressed by Williams α, increased in the first season and remained fairly stable thereafter. The main contributors to α-diversity were annual and perennial herbs (Table 3.4a).

3.1.2(c) Structural attributes

Spatial (or height) profiles over the two years reflect both seasonal and successional changes in the distribution of plant material in the vertical plane (Fig. 3.6). Seasonal changes are notable for vertical changes in the distribution of plant material (or canopy development) and each year the canopy becomes most evenly layered in August. Successional changes can be detected by comparing spatial profiles of the same months between the two years. Vertical distribution of plant material is more even during the first four months of the second year than over the same period in the first year. The trend towards maximal density at or near ground level in the second year, as shown by the September and October profiles, is mainly due to increased cover of and abundance of the Gramineae, especially *Holcus lanatus*.

Spatial diversity of the vegetation, as expressed by Williams α, follows a similar (but with lower values) pattern to that of plant taxonomic diversity (Table 3.4) although seasonal differences are more pronounced. All four major plant groupings were important in their contributions to total α. Spatial diversity showed a overall increase during the second year.

Seasonal changes in plant community architecture were dramatic, with α-diversity in each year climbing extremely rapidly to a peak in August and then followed by a similarly

TABLE 3.3: Values of the Dominance Index (*d*) for Abundance of Green Plants Over the First Two Years of Succession (Site A). The Berger-Parker Index is underlined

SPECIES	YEAR 1 May	June	July	Aug	Sept	Oct	YEAR 2 May	June	July	Aug	Sept	Oct
Spergula arvensis	0.36	0.59	0.46	0.16	0.05							
Chenopodium album	0.29	0.13	0.09	0.05	0.02	0.05						
Polygonum persicaria	0.17											
Raphanus raphanistrum	0.05		0.20									
Cirsium arvense	0.04									0.05		0.04
Fallopia convolvulus	0.02											
Medicago lupulina	0.02		0.18	0.48	0.48	0.19		0.08	0.18			
Veronica persica		0.07	0.07									
Sonchus asper		0.03	0.06	0.03								
S. oleraceus		0.03										
Capsella bursa-pastoris		0.02										
Trifolium pratense				0.05	0.14	0.12		0.06	0.10	0.10		
Holcus lanatus				0.04	0.09	0.21	0.30	0.27	0.24	0.31	0.48	0.49
Poa annua					0.04	0.19	0.31	0.18				
Agrostis capillaris						0.05	0.10		0.07		0.12	0.11
Tripleurospermum inodorum							0.03		0.09			
Crepis capillaris							0.07	0.11	0.12	0.14	0.07	0.06
Trifolium repens							0.03	0.06		0.06	0.07	0.12
Ranunculus repens										0.04		0.04
Erigeron canadensis											0.04	

(Continued)

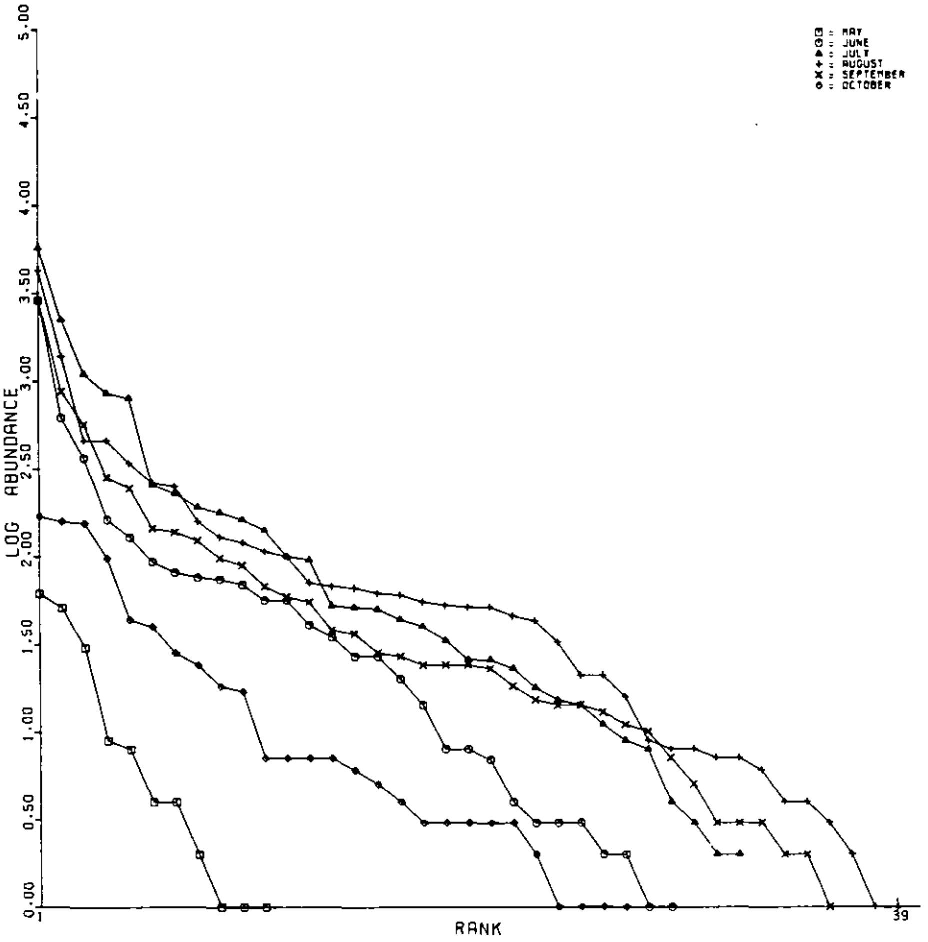
TABLE 3.3: (Continued)

	YEAR 1						YEAR 2					
	May	June	July	Aug	Sept	Oct	May	June	July	Aug	Sept	Oct
MAJOR GROUPINGS												
Annuals	0.94	0.96	0.95	0.84	0.64	0.34	0.14	0.22	0.33	0.17	0.12	0.03
Biennials	-	0.01	0.01	0.01	0.01	0.01	0.01	0.02	0.01	0.03	0.04	0.01
Perennials	0.05	0.02	0.03	0.09	0.20	0.20	0.14	0.26	0.32	0.41	0.23	0.33
Gramineae	0.01	0.01	0.01	0.06	0.15	0.45	0.71	0.50	0.34	0.39	0.61	0.63
Grass/forb ratio (abundance)	0.01	0.01	0.01	0.06	0.18	0.82	2.45	1.00	0.51	0.64	1.56	1.70
" " (cover)	0.01	0.03	0.06	0.28	0.41	1.00	1.50	1.05	0.63	0.71	1.10	1.08

Fig. 3.5 Dominance diversity curves for vegetation during the first two years of succession (Site A).

a. Year 1.
b. Year 2.

PLANT SPECIES ABUNDANCES SITE A 1980


a

PLANT SPECIES ABUNDANCES FOR 1981 SITE A

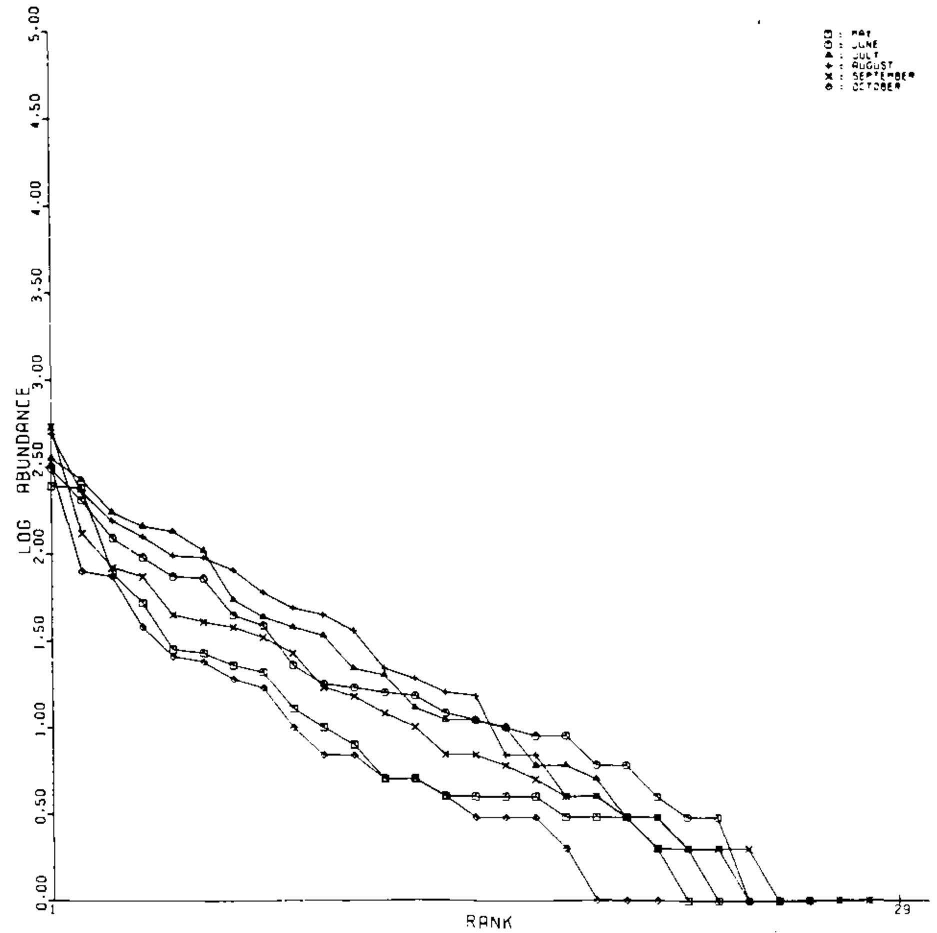

b

TABLE 3.4 : Williams α - Diversity for Green Plants Over the First Two years of Succession (Site A)

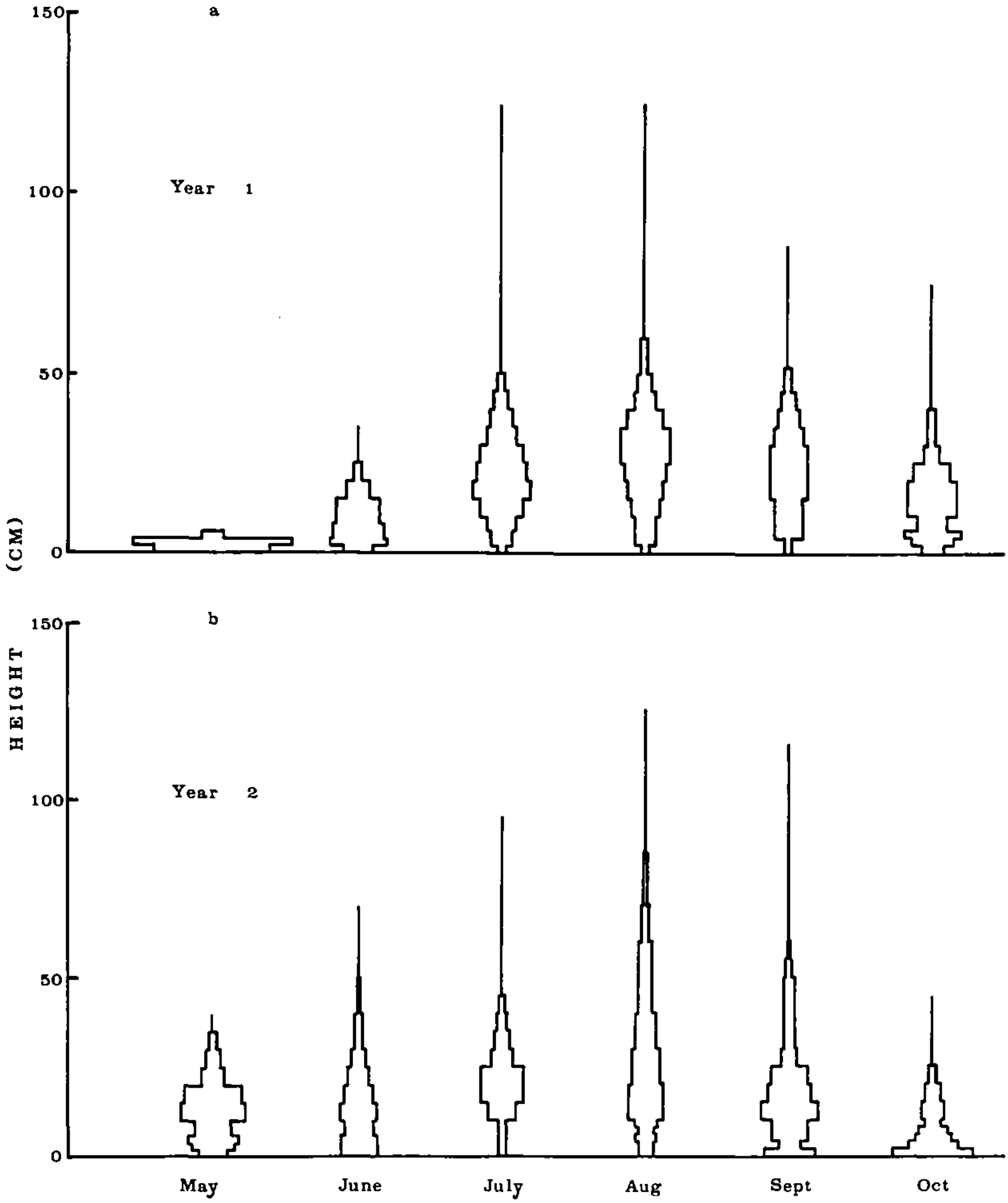
a. Taxonomic α   b. Spatial α   ∞ is from N = 1, s = 1

	YEAR 1						YEAR 2					
(a)	MAY	JUNE	JULY	AUG	SEPT	OCT	MAY	JUNE	JULY	AUG	SEPT	OCT
Annuals	1.8	3.2	2.8	3.3	3.4	3.9	2.7	3.6	2.1	2.8	3.3	3.2
Biennials	-	0.2	0.5	1.2	1.5	2.0	2.0	2.7	1.3	1.2	1.7	0.3
Perennials	0.8	1.2	1.8	2.3	2.1	2.6	3.0	2.2	2.0	3.0	3.0	2.6
Gramineae	∞	1.2	0.9	0.9	0.6	0.5	0.5	0.5	0.8	0.5	0.5	0.6
Total vegetation	2.7	4.9	5.0	6.5	6.2	6.3	5.7	6.1	5.3	6.8	6.7	5.0

	YEAR 1						YEAR 2					
(b)	MAY	JUNE	JULY	AUG	SEPT	OCT	MAY	JUNE	JULY	AUG	SEPT	OCT
Annuals	0.5	1.3	3.8	3.3	3.3	4.4	2.3	4.0	3.3	6.0	7.4	3.1
Biennials	-	1.8	2.4	7.0	1.8	1.5	3.2	4.0	4.5	8.3	4.7	2.0
Perennials	0.8	2.0	3.3	3.7	2.9	3.5	2.6	3.7	4.4	6.2	6.8	2.3
Gramineae	∞	2.3	3.6	3.7	2.7	1.7	1.8	3.5	4.6	6.1	3.4	2.2
Total vegetation	0.5	1.3	3.8	3.2	3.0	3.4	1.7	3.0	3.9	5.1	5.1	2.0

Fig. 3.6 Spatial profiles for vegetation during the first two years of succession (Site A).

a. Year 1.
b. Year 2.


150
a
100
Year 1
50
0
HEIGHT (CM)
150
b
100
Year 2
50
0
May
June
July
Aug
Sept
Oct

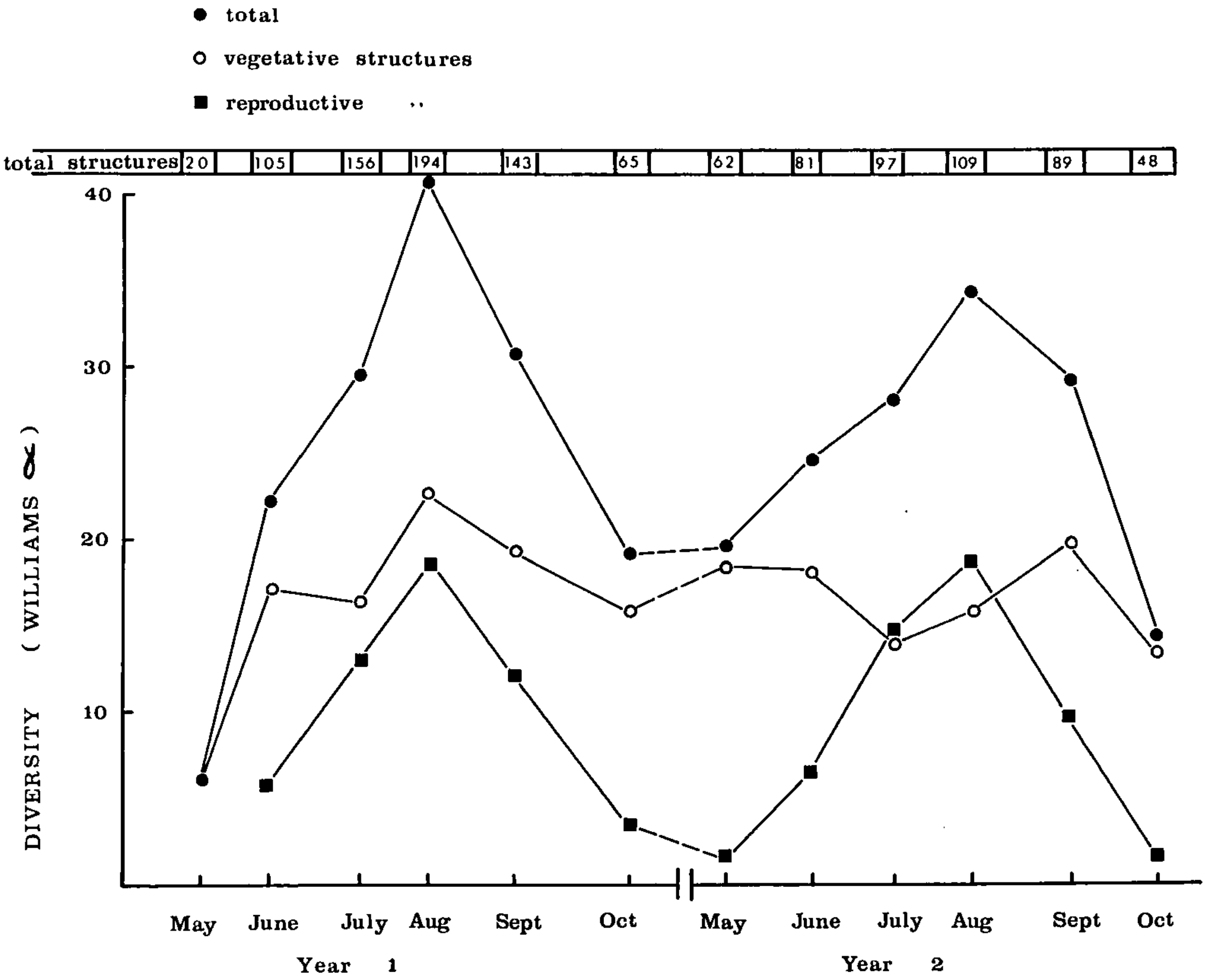
rapid decline towards the end of the growing season (Fig. 3.7). Successional patterns in plant architecture are more clearly detected when the major plant groupings are considered (Fig. 3.8). During the first year annual herbs were the main contributors to total architectural α, with perennial herbs of secondary importance; in 1981 these roles were reversed. Evidence that successional change in plant architecture occurred in the Young Field community is provided by the conspicuous differences in the levels and patterns of α-diversity for annual herb architecture between the two years. In the second year, levels were generally lower and fluctuations reduced compared with the dramatic rise and fall of annual herb architecture in the first year. Both biennial herbs and the Gramineae showed considerably lower architectural diversity over the two years, although the biennials did produce two relatively small peaks in α-diversity.

Further analysis of community architecture may be made by considering the relative importance of vegetative and reproductive structures (Fig. 3.7). Architectural diversity for reproductive structures shows an expected rise and fall in each year; vegetative α for architecture, however, remains at a high but fairly stable level after the initial rise in the ruderal community. The contributors to architectural diversity by vegetative and reproductive structures for the major plant groupings are given in Appendix 4. As expected annual herbs were the main contributors to architectural diversity of both vegetative and reproductive structures during the first year although perennial herbs were rather surprisingly not unimportant. During the second year the annual herbs were again important but the perennial herbs showed a general rise in architectural α, especially for vegetative structures.

3.1.2(d) Biomass

Biomass samples have been combined for each sampling month. The biomass of the four major plant groupings together with the percentage contributions of the six most abundant species are given in Table 3.5. Total biomass of green plants rose during the first year, declined during the winter and then rose and plateaued by mid-August of the second year. Domination by annual herbs during the first year quickly changed to perennial herb-grass domination by early June of the second year and by the end of the season the Gramineae were the most important, with *Holcus lanatus* showing a very high contribution.

Fig. 3.7 Total architectural diversity of green plants, with vegetative and reproductive components, during the first two years of succession (Site A). The total number of structures is given along the figure top.



● total
○ vegetative structures
■ reproductive ,,
total structures
20
105
156
194
143
65
62
81
97
109
89
48
40
30
20
10
DIVERSITY (WILLIAMS α)
May
June
July
Aug
Sept
Oct
May
June
July
Aug
Sept
Oct
Year 1
Year 2

Fig. 3.8 Contributions to community architecture by the major plant groupings during the first two years of succession (Site A).

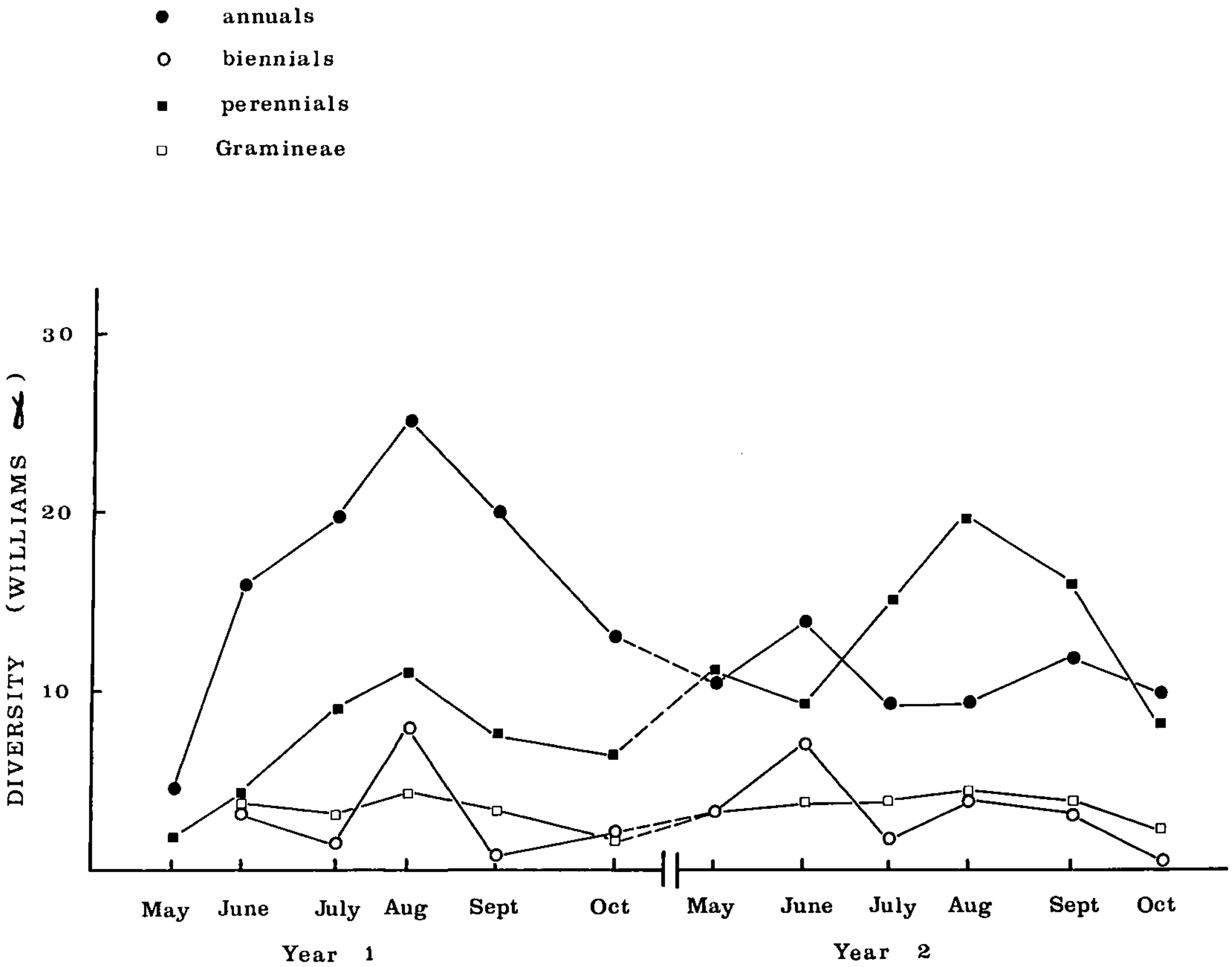

● annuals
○ biennials
■ perennials
□ Gramineae
DIVERSITY (WILLIAMS α)
30
20
10
May
June
July
Aug
Sept
Oct
Year 1
May
June
July
Aug
Sept
Oct
Year 2

TABLE 3.5 : Biomass (gm dry weight) and % contribution values of the major plant groupings and the six most dominant species over two years (Site A) and one year (Site D). Note that only 4 species were present in samples on several occasions.

	SITE A						SITE D		
	YEAR 1			YEAR 2			YEAR 1		
BIOMASS	EARLY JUNE	MID AUGUST	EARLY OCTOBER	EARLY JUNE	MID AUGUST	EARLY OCTOBER	EARLY JUNE	MID AUGUST	EARLY OCTOBER
Annuals	7.00	82.26	53.66	0	11.40	0	4.00	27.25	0
Biennials	0	0	0	0	0	0	0	0	0
Perennials	0	6.85	20.70	25.85	64.45	31.65	7.90	36.20	98.50
Gramineae	0	0	34.80	42.80	42.30	85.00	1.40	12.50	59.75
Total	7.00	89.11	109.16	68.65	118.15	116.65	13.30	75.95	158.25
% Contribution									
Spergula arvensis	73	12	9				30	36	
Chenopodium album	1	9							
Sonchus asper	21	19	5						
Polygonum persicaria	5								
Medicago lupulina		35	26		10				
Sonchus oleraceus		12							
Trifolium pratense		6	17	30	6	16	41	22	44
Tripleurospermum inodorum				8					

Continued..

TABLE 3.5 : (continued)

	SITE A						SITE D		
	YEAR 1			YEAR 2			YEAR 1		
% Contribution	EARLY JUNE	MID AUGUST	EARLY OCTOBER	EARLY JUNE	MID AUGUST	EARLY OCTOBER	EARLY JUNE	MID AUGUST	EARLY OCTOBER
Holcus lanatus			32	29	36	73	10	16	35
Trifolium repens			6			9			2
Poa annua				33					
Crepis capillaris					18			4	3
Cirsium arvense					13				
Plantago major					8				
Hypochaeris radicata						2		5	
Plantago lanceolata							19	17	4
Rumex acetosella									12

3.2 COMPARISON OF TWO YOUNG FIELDS WITH DIFFERENT HISTORIES OF LAND USE

3.2.1 General trends

History of land use is probably the biggest single influence in determining the initial plant species composition of abandoned fields (R.Chancellor, *pers.comm.*). Differences in plant community structure found during the first year between Site A (1980) and Site D (1981) were conspicuous and reflect associated differences in previous land use of the two sites. The annual cultivation of the area within which Site A was established ensured continuous addition to the seed bank and this was reflected in a relatively high species richness of vegetation during the first year following abandonment. Site D, on the other hand, established within a long-standing meadow area, had considerably fewer resources to draw from (Table 3.6) since bare ground had not been exposed for almost two decades and the seed life of the majority of these early successional species is considerably less than that period (R.Chancellor, *pers.comm.*).

General trends in the Young Field plant community of Site D differred from those described for Site A (see 3.1.1). The early dominant pioneer species in Site D were represented primarily by *Spergula arvensis*, *Plantago lanceolata*, *Trifolium pratense* and *Holcus lanatus*. Weed cover also increased extremely rapidly in Site D, from 1.78% in May to a plateau around 95% cover by July. There was no fall off in cover at the end of the season as for Site A in 1980.

Site D was colonised by 31 species of herbs and 3 species of grasses. Of these primary colonisers 10 species attained a cover value of 5% or more (a similar number of species as Site A) (Table 3.7). As for Site A, *Spergula* established early on in the first year and dominated the flora, although, instead of a switch-over in domination to another ruderal herb, perennial legume cover (esp. of *Trifolium pratense*) increased rapidly together with *Holcus lanatus*. These two species dominated the community for the rest of the year with *Plantago lanceolata* and *Crepis capillaris* providing lesser but significant cover for the latter part of the growing season.

TABLE 3.6. Seed Bank results for Site A and Site D. Volume of soil sampled from each site = 785cm^3.

	SITE A	SITE D
Species	Total Number of Seedlings	Total Number of Seedlings
Spergula arvensis	145	82
Raphanus raphanistrum	24	6
Chenopodium album	35	
Polygonum persicaria	15	
P. aviculare	6	
Fallopia convolvulus	9	8
Medicago lupulina	44	
Trifolium pratense	61	30
T. repens	21	9
Sonchus asper	16	2
Capsella bursa-pastoris *	17	11
Veronica persica	33	
Cirsium arvense	3	
Crepis capillaris	7	17
Ranunculus repens	4	
Stellaria media	10	
Agrostis capillaris	23	10
Holcus lanatus	35	47
Poa annua	71	
Plantago lanceolata		24
Rumex acetosella		8

*annual or biennial

	SITE A		SITE D	
Plant groupings	No. species	Number of seedlings	No species	Number of seedlings
Annuals	11	354	5	109
(Biennials)	(1)	(17)	(1)	(11)
Perennials	5	96	5	88
Gramineae	3	129	2	57
Total	19	579	12	254

TABLE 3.7: Percentage cover of dominant species (≥5% cover) during the first year of succession (Site D). r denotes a ruderal species.

	MAY	JUNE	JULY	AUG	SEPT	OCT
Spergula arvensis^r	1.11	30.44	77.78	62.44	5.11	1.11
Plantago lanceolata	0.22	12.22	16.89	28.67	33.78	18.22
Trifolium pratense	-	6.89	28.00	61.56	65.33	76.22
T. repens	-	1.56	3.56	7.56	7.78	7.56
Capsella bursa-pastoris^r	-	3.11	9.56	4.22	0.67	-
Crepis capillaris	-	7.78	8.89	15.56	13.33	3.78
Raphanus raphanistrum^r	-	4.00	6.67	0.89	0.22	-
Rumex acetosella	-	2.22	12.89	8.67	4.67	11.56
Agrostis capillaris	0.22	3.11	2.22	7.78	5.11	1.56
Holcus lanatus	-	7.56	20.67	42.44	59.11	67.11

TABLE 3.8 : Differences in plant species richness, gain and loss rates between two young fields (Site A 1980 and Site D 1981) during the first year of succession. Colonisation and extinction refer to accumulated gains and losses respectively.

MONTH	SPECIES RICHNESS		COLONISATION		EXTINCTION	
SITE D	SITE D	DIFFERENCE TO SITE A	SITE D	DIFFERENCE TO SITE A	SITE D	DIFFERENCE TO SITE A
MAY	4	-7	4	-7	0	0
JUNE	17	-12	17	-12	0	0
JULY	25	-7	26	-11	1	-4
AUG	28	-11	33	-14	5	-3
SEPT	18	-18	35	-15	17	+3
OCT	13	-14	39	-14	26	0

3.2.2.Characteristics of the plant community

3.2.2(a) Taxonomic composition

Plant species richness for Site D in 1981 followed the pattern for Site A in the first year but species numbers and colonisation rates were always much lower (Table 3.8). However, as for Site A in 1980 similar differences in colonisation rates between the major plant groupings occurred with the annual and perennial herbs the dominant colonisers (Fig. 3.9).

Major differences between the two Young Field communities are found when the species and cover contributions of the major plant groupings are considered (Table 3.9). Succession to a perennial herb and grass (primarily *Holcus lanatus*) community progressed faster in Site D where the situation at the end of the season was similar to that found for Site A at the end of the second year.

Differences in β-diversity between the two Young Field communities are also evident as can be seen by Sorensen's Index of Similarity. There is a very high similarity in basic taxonomic composition between Site A and Site D for the first year ($I_s=0.81$) with 33 shared species. However, by taking relative importance of species into account (using only those species with coverage of at least 5%) the similarity is much lower ($I_s=0.45$) with just 5 common species. Additional evidence of a more rapid movement of species along a β-diversity gradient is provided in Table 3.10 where Sorensen's Index has been used quantitatively in the form of I_w.

3.2.2(b) Species abundance and diversity

Table 3.11 provides values of the dominance index (*d*) for abundance of species in Site D for comparison with Table 3.3 for Site A. Both the Gramineae and perennial herbs show a gradual increase in dominance throughout the growing season in Site D with the latter group the most important; this contrasts with Site A in the first year where the grasses were dominating the perennials by October. This difference results in a lower grass/forb ratio for both cover and abundance in Site D.

Species distributions in the form of dominance-diversity curves are given in Fig. 3.10 for Site D and are comparable to the patterns for the first year in Site A. Equitability of species distributions as observed from the diversity curves rose through the season to July and declined in September (*cf* Site A 1980).

Fig. 3.9 Species gain and loss rates of the major plant groupings during the first year of succession (Site D).

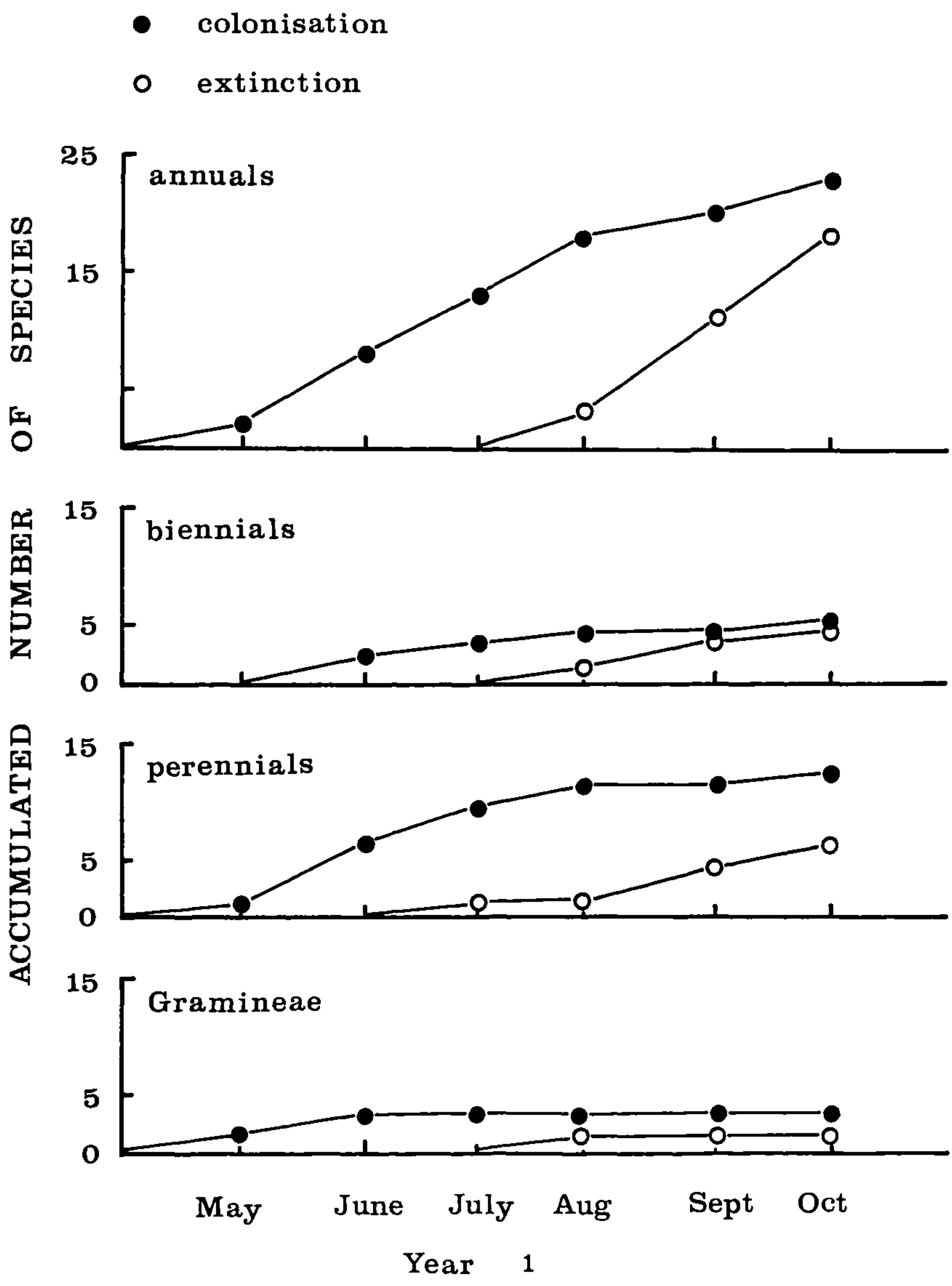

● colonisation
○ extinction
ACCUMULATED NUMBER OF SPECIES
annuals
25
15
biennials
15
5
0
perennials
15
5
0
Gramineae
15
5
0
May
June
July
Aug
Sept
Oct
Year 1

TABLE 3.9 : Comparison of percentage species contributions and percentage cover contributions between two Young Fields (Site A 1980 and Site D 1981) during the first year of succession. Site D = top figure; Site A in italics

a. % Species contributions

b. % Cover contributions

(a)	MAY	JUNE	JULY	AUG	SEPT	OCT
Annuals	50	42	48	50	47	36
	(73)	*(67)*	*(58)*	*(51)*	*(53)*	*(50)*
Biennials	0	10	11	10	15	7
	(0)	*(3)*	*(6)*	*(13)*	*(8)*	*(10)*
Perennials	25	32	30	33	37	43
	(18)	*(17)*	*(24)*	*(35)*	*(29)*	*(30)*
Gramineae	25	16	11	7	10	14
	(9)	*(13)*	*(12)*	*(16)*	*(10)*	*(10)*

(b)	MAY	JUNE	JULY	AUG	SEPT	OCT
Annuals	1	39	83	67	9	2
	(10)	*(75)*	*(88)*	*(86)*	*(71)*	*(35)*
Biennials	0	3	10	7	0.5	0.2
	(0)	*(5)*	*(5)*	*(2)*	*(2)*	*(4)*
Perennials	0.2	27	54	83	86	89
	(1)	*(5)*	*(11)*	*(18)*	*(23)*	*(15)*
Gramineae	0.2	12	23	48	62	68
	(0.07)	*(3)*	*(5)*	*(25)*	*(35)*	*(49)*

TABLE 3.10: Differences in Similarity (I_w) between two Young Fields (Site A 1980 and Site D 1981) during the first year of succession. Site D = top figure; difference from Site A in italics.

	MAY - JUNE	JUNE - JULY	JULY - AUG	AUG - SEPT	SEPT - OCT
Annuals	0.06 *(-0.10)*	0.57 *(-0.18)*	0.81 *(+0.10)*	0.44 *(-0.27)*	0.31 *(-0.29)*
Biennials	0 *(0)*	0.49 *(-0.02)*	0.52 *(-0.07)*	0.18 *(-0.74)*	0 *(-0.93)*
Perennials	0.03 *(+0.01)*	0.74 *(+0.56)*	0.68 *(+0.39)*	0.93 *(+0.33)*	0.82 *(+0.20)*
Gramineae	0.04 *(-0.01)*	0.60 *(0)*	0.62 *(+0.23)*	0.83 *(-0.02)*	0.91 *(+0.17)*
Total	0.04 *(-0.12)*	0.58 *(-0.13)*	0.72 *(+0.06)*	0.76 *(+0.04)*	0.81 *(+0.17)*

TABLE 3.11 Values of the dominance index (d) for abundance of green plants over the first year of succession (Site D).

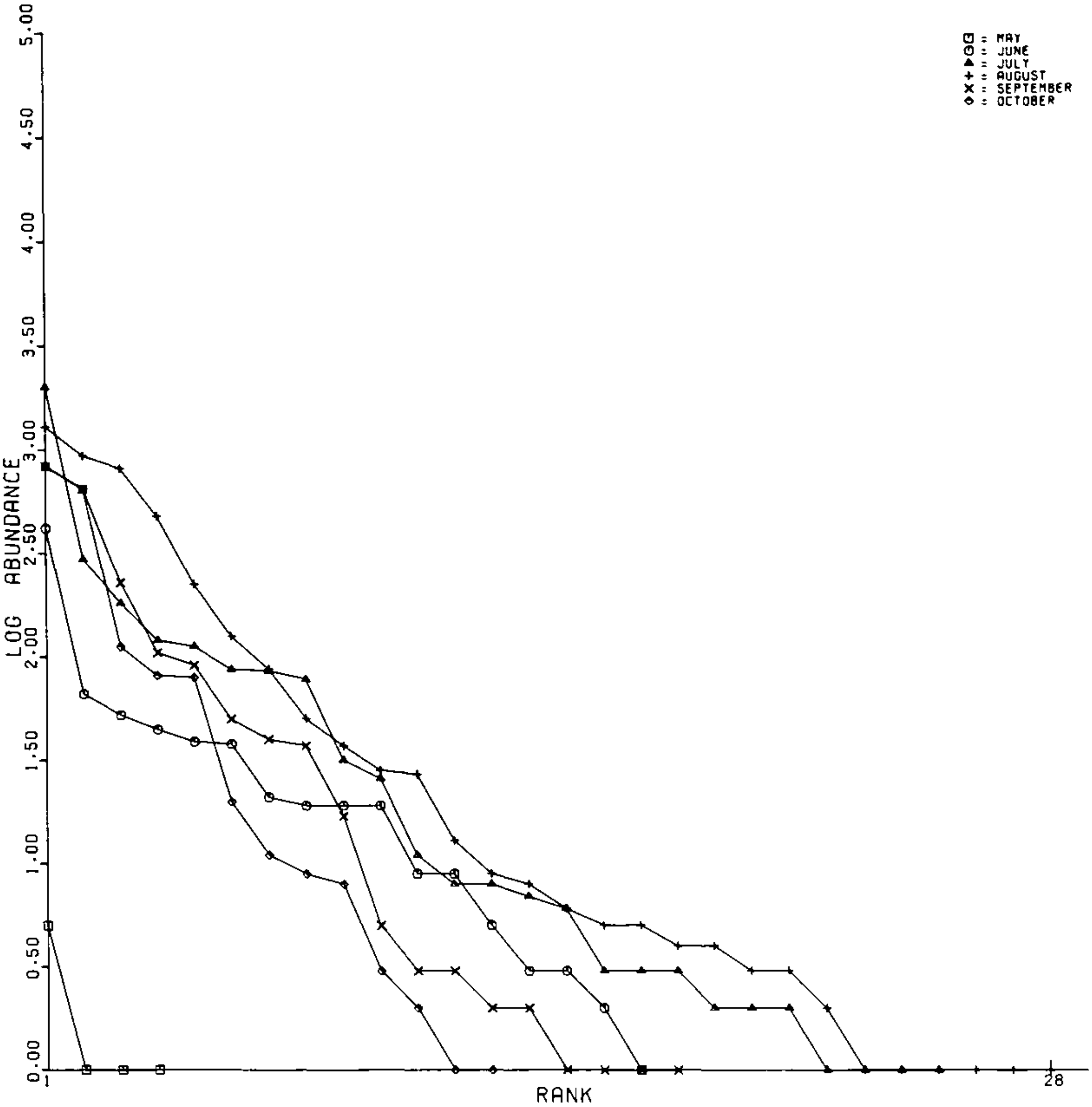
The Berger-Parker Index is underlined:

* = species not occurring in Site A in that month.

	YEAR 1					
SPECIES	MAY	JUNE	JULY	AUG	SEPT	OCT
Spergula arvensis	0.61	0.55	0.65	0.39		
Plantago lanceolata	0.13*	0.08*	0.04	0.07	0.11	0.06
Stellaria media	0.13*					
Agrostis capillaris	0.13*					
Holcus lanatus		0.07	0.06	0.14	0.31	0.36
Crepis capillaris		0.06*		0.04	0.05	0.01
Raphanus raphanistrum		0.05	0.03			
Trifolium pratense		0.05	0.09	0.25	0.40	0.46
Rumex acetosella			0.04*		0.02	0.05
Trifolium repens				0.03	0.04	0.04
MAJOR GROUPINGS						
Annuals	0.75	0.65	0.70	0.42	0.03	0.01
Biennials	-	0.01	<0.01	0.01	<0.01	<0.01
Perennials	0.13	0.23	0.23	0.41	0.63	0.62
Gramineae	0.12	0.11	0.06	0.16	0.33	0.36
Grass/forb ratio (abundance)	0.14	0.11	0.07	0.19	0.49	0.57
" " (cover)	0.14	0.21	0.25	0.50	0.71	0.76

Fig. 3.10 Dominance diversity curves for green plants during the first year of succession (Site D).

PLANT SPECIES ABUNDANCES SITE D 1981



Although the general patterns of taxonomic diversity of green plants in Site D during 1981 were similar, values of α were generally lower than for the first year vegetation in Site A. Again the main contributors to α-diversity were annual and perennial herbs (Table 3.12a).

3.2.2(c) Structural attributes

Spatial profiles for Site D during 1981 resemble a condensed version of the two year profiles for Site A (Fig. 3.11 *cf* Fig. 3.6). The progressive lowering of the height strata where maximal density of plant material occurs is indicative of the contribution of the predominantly low growing and increasingly dominating perennial herbs and grasses (Fig. 3.11).

Values of William's α for spatial diversity of Site D are lower than those found for Site A in the first year (Table 3.12b); all four major plant groupings were again important in their contribution to total α.

Seasonal changes in plant community architecture in Site D were not as extreme as for Site A in the first year; architectural diversity did not increase beyond July as it did for Site A (Fig. 3.12a). The relatively low peak in architectural diversity in Site D was due to a much lower contribution to total architectural diversity by the annual herbs (Fig. 3.12b). Contribution to architectural α by the other major plant groupings were of similar patterns and values to Site A in 1980.

The relative importance of vegetative and reproductive structures is shown in Fig. 3.12c. As for total architecture, values are lower and the seasonal progression of each component is smoother when compared to trends found for Site A. Annual and perennial herbs were the main contributors to vegetative and reproductive α, although perennial herbs were slightly more important than annual herbs for reproductive α (Appendix 4).

3.2.2(d) Biomass

Differences between Site A and Site D for the first year are further emphasised by the reduced importance of annual herbs and the consequently greater contribution to total vegetation biomass by perennial herbs and the Gramineae in Site D (Table 3.5). As for Site A the perennial herb with the greatest contribution to total biomass was *Trifolium pratense* and the most important grass was *Holcus lanatus*.

TABLE 3.12: Comparison of Williams α-diversity for green plants over the first year of succession. Site D = top figure; difference to Site A in italics. a. Taxonomic b. Spatial

(a)	YEAR 1					
	MAY	JUNE	JULY	AUG	SEPT	OCT
Annuals	1.1 *(-0.7)*	1.7 *(-1.5)*	2.5 *(-0.3)*	3.2 *(-0.1)*	3.4 *(0)*	1.4 *(-2.5)*
Biennials	- *(0)*	0.9 *(+0.7)*	0.9 *(+0.4)*	0.7 *(+0.5)*	∞ *(-1.5)*	∞ *(-2.0)*
Perennials	∞ *(-0.8)*	1.3 *(+0.1)*	1.5 *(-0.3)*	1.7 *(-0.6)*	1.1 *(-1.0)*	1.0 *(-1.6)*
Gramineae	∞ *(0)*	0.7 *(-0.5)*	0.6 *(-0.3)*	0.3 *(-0.6)*	0.3 *(-0.3)*	0.3 *(-0.2)*
Total vegetation	3.2 *(-0.5)*	3.6 *(-1.3)*	4.8 *(-0.2)*	5.2 *(-1.3)*	3.2 *(-3.0)*	2.2 *(-3.1)*

(b)	YEAR 1					
	MAY	JUNE	JULY	AUG	SEPT	OCT
Annuals	1.1 *(+0.6)*	1.7 *(+0.4)*	2.6 *(-1.2)*	3.4 *(+0.1)*	4.1 *(+0.8)*	4.2 *(-0.2)*
Biennials	- *(0)*	2.8 *(+1.0)*	6.1 *(+3.7)*	8.7 *(+1.7)*	2.6 *(+0.8)*	∞ *(-1.5)*
Perennials	∞ *(-0.8)*	1.5 *(-0.5)*	3.1 *(-0.2)*	3.3 *(-0.4)*	1.9 *(-1.0)*	2.1 *(-1.4)*
Gramineae	∞ *(0)*	1.6 *(-0.7)*	1.8 *(-1.8)*	2.3 *(-1.4)*	2.8 *(+0.1)*	1.1 *(-0.6)*
Total vegetation	0.9 *(+0.4)*	1.5 *(+0.2)*	2.4 *(-1.4)*	3.2 *(0)*	3.3 *(+0.3)*	2.0 *(-1.4)*

For ∞, n = 1 and s = 1

Fig. 3.11 Spatial profiles for green plants during the first year of succession (Site D).

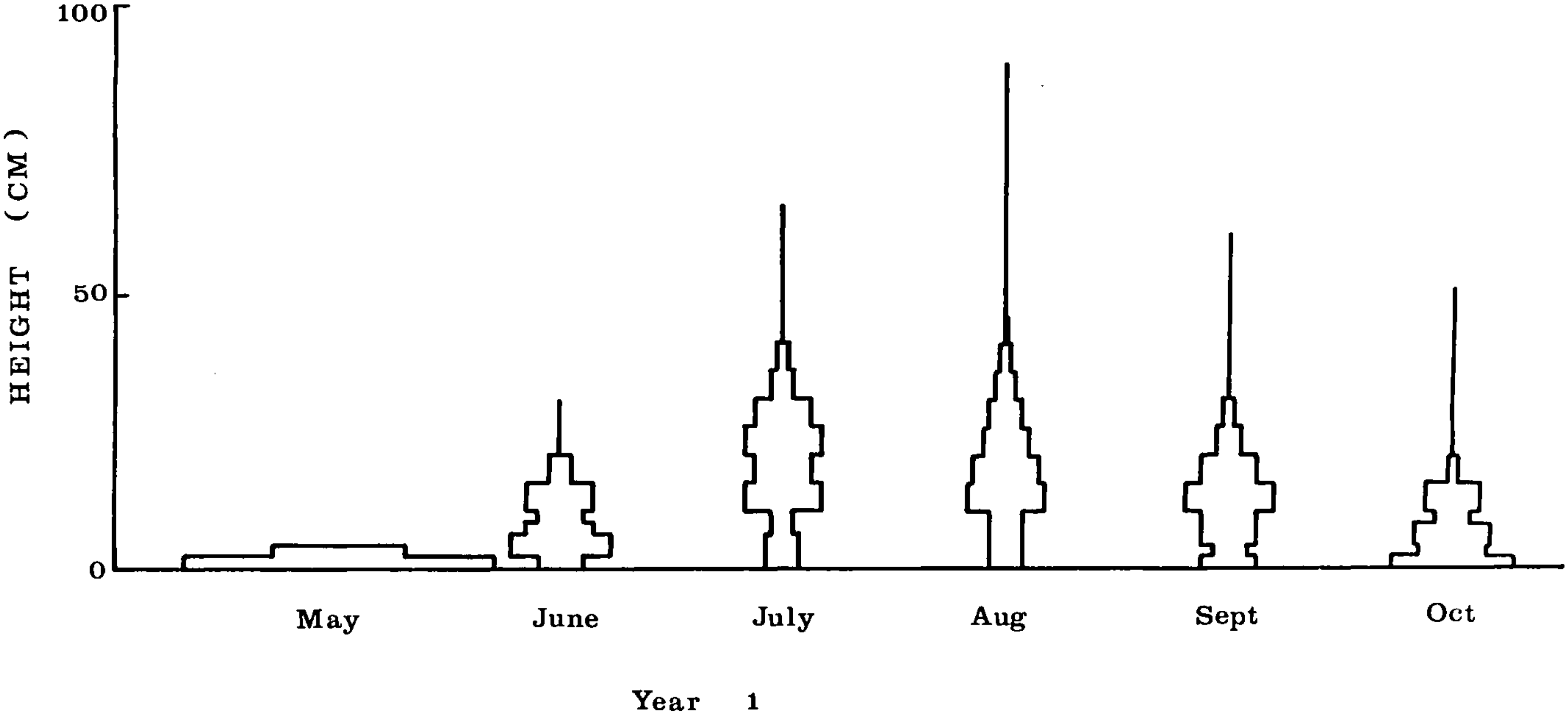
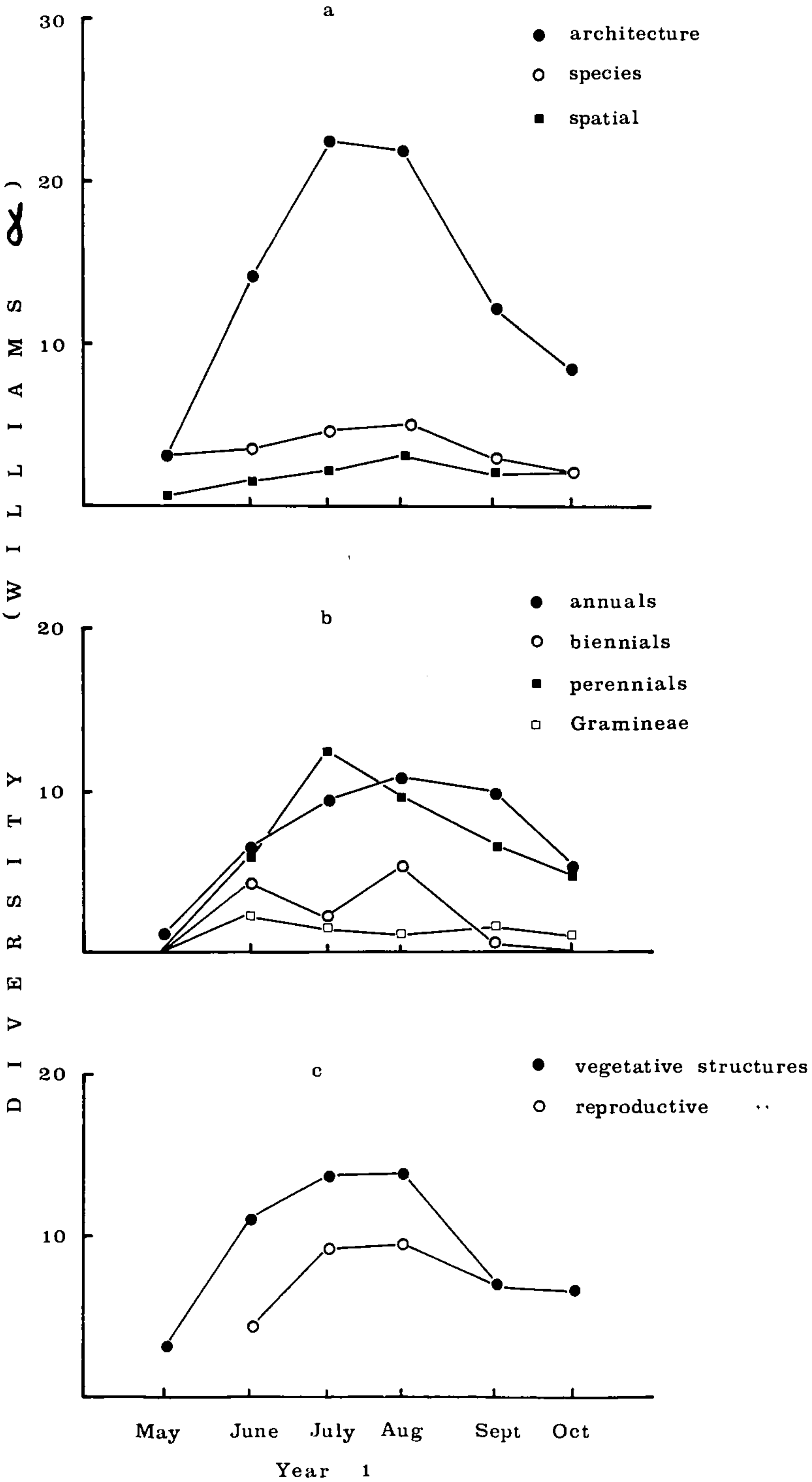

100
50
0
HEIGHT (CM)
May
June
July
Aug
Sept
Oct
Year 1

Fig. 3.12 Changes in plant architecture during the first year of succession (Site D).

a. Total architecture with taxonomic and spatial diversity.
b. Contributions to community architecture by the major plant groupings.
c. Contributions to community architecture by vegetative and reproductive structures.


a
architecture
species
spatial
b
annuals
biennials
perennials
Gramineae
c
vegetative structures
reproductive ··
30
20
10
20
10
20
10
DIVERSITY (WILLIAMS α)
May
June
July
Aug
Sept
Oct
Year 1

3.2.2(e) Seed bank

In contrast to Site A the Site D seed bank was relatively impoverished. The main differences were fewer annual herb species and lower numbers of seedlings of annuals herbs and grasses (Table 3.6).

3.3 DISCUSSION

Sections 3.1 and 3.2 showed that early successional habitats may be easily created by opening up a relatively large area for colonisation by plants. It would not be expected that the mosaic of changes that immediately follow this exposure of bare ground would be identical from one area to another, and the sites in question have certainly shown differences. The more rapid sucession in the Site D plant community is shown by a reduced duration of the ruderal community in terms of percentage cover of annual herbs (Sections 3.2.1 and 3.2.2(a)) as well as the more rapid change in β-diversity of the vegetation (Section 3.2.2(a)). In this case it was evidently due to a reduced seed bank in Site D where there were lower numbers of annual herb species (5 species in Site D compared to 11 species in Site A) which was further reflected by the lower numbers of annual herb seedlings that germinated (109 in Site D compared to 354 in Site A) (see Table 3.6).

In Section 3.2 it was mentioned that the history of land use is undoubtedly of prime importance in determining the initial plant species community of the secondary succession. This statement in itself encompasses many different factors and a review of the subject may be found in Haug (1970). Before the succession begins there are various historical factors that may influence what species will appear, the sequence of species and the relative abundance of species following the creation of the habitat. These factors include the effects of previous land use (*e.g.* cultivation) on organic and moisture content of the soil, the duration and intensity of cultivation, the season of cultivation, the type of crop grown, the crop system and the effects of fertilisation (Haug 1970; R.Chancellor *pers.comm.*). The impoverished Site D community reflected its previous history of a long-standing meadow area whereas frequent exposure through annual cultivation of the Site A arable area produced a richer seed bank and consequently a more diverse and distinctive ruderal community.

Setting aside these fundamental differences between the two plant communities the two

Young Fields exhibited life-history strategies characteristic of early successional species. Such strategies may be equated with the *r-K* continuum (as described in Chapter One, Section 1.2.2) with the early successionals displaying typically *r*-strategy life-history characteristics in Sites A and D. The chief features shown by these pioneers in Site D, and especially Site A, was a rapid germination (or colonisation) immediately following the exposure of bare ground in March of Year 1, rapid rates of growth, reproduction and species turnover and relatively short life-cycles; these properties are essentially characteristic of the main plant grouping in the first year in Sites A and D, the annual herbs. Plant species following the short-lived ruderals in Sites A and D generally displayed more of the features associated with *K*-strategy life cycles. These later species were typically slower growing, longer-lived, vegetatively spreading perennial herbs and grasses that were becoming progressively resistant to the invasion of other species (especially earlier ones). In Sites A and D the establishment of perennials (chiefly *Trifolium pratense*) and the visibly increasing spread of small patches of *Holcus lanatus* severely reduced available space for germination microsites and seedling establishment. Colonisation and establishment of new species in the second year in Site A was therefore severely limited; observations in 1982 indicated that a similar situation had arisen in Site D.

These vegetation processes in this early succession lend support to findings from sites at Silwood Park lying adjacent to Sites A and D by Southwood *et al* (1979). The overall successional trends in species richness in the two Young Fields also agree with patterns of plant species richness observed by Tramer (1975) in a study of the early stages of a secondary succession in an Ohio Old Field. Tramer suggested that the plant species richness pattern expected during the *r-K* continuum should reflect a pattern of colonisation similar to that described for terrestrial arthropods of defaunated islands of red mangrove by Simberloff & Wilson (1969). This latter work showed a period of rapid colonisation followed by a temporary over-saturation of species and, finally, a moderate decline in species richness. Certainly Sites A and D demonstrated an initial period of rapid colonisation and a later decline in species richness, although whether one can summise that the peak species richness, in August of the first year in each site, represents a temporary over-saturation of the system is debateable.

It was shown in Sections 3.1.2(c) and 3.2.2(c) that these early successional trends were accompanied by changes in the structural diversity of the plant community and both the spatial and architectural components were described. Plant community architecture especially showed a dramatic spring-early summer rise followed by a subsequent late summer-autumn fall in each season in Site A and in the single season in Site D. Such seasonal changes in plant architecture have been observed for single plant species by several authors (*e.g.* for wild parsnip, *Pastinaca sativa*, by Thompson 1978 and Berenbaum 1981; for fireweed, *Epilobium angustifolium*, by Addicott 1978 and for bracken, *Pteridium aquilinum*, by Lawton 1978). Although changes in plant community architecture have been described by Southwood *et al* (1979) over a successional gradient (on which this present study represents the early seral stages) I believe that the descriptions of Site A and Site D provide the only detailed accounts of seasonal changes in the architecture of natural plant communites.

The habitat has been described in terms of the length of favourable (*H*) and unfavourable (*L*) periods (Southwood 1977a,b) and indeed is regarded as a template on which evolutionary pressures shape the life-history characteristics of animals and plants (Southwood *et al* 1974; Southwood 1977a). Based on *H* and *L*, the habitat has been further classified in three different types:- the predictable habitat (*i.e.* relatively permanent with low variances of *H* and *L*), the unpredictable habitat (*i.e.* with high variances of *H* and *L*) and the temporary or ephemeral habitat (*i.e.* with a large variance in *H*, although *H* is small, and with a small or insignificant *L*) (Southwood 1977a). For example, the predictable habitat would be associated with later successional stages and the unpredictable habitat with the growth of annuals in semi-arid areas with erratic rainfall. The temporary habitat characterises the early stages of secondary succession (Southwood 1962,1977a,b) and, as described by the successional events in Sites A and D, this especially refers to the ruderal community. One might expect, therefore, that insect herbivore species associated with such habitats of low durational stability would possess certain life-history strategies that enable them to exploit their environment as efficiently as possible. The following chapter will investigate this in detail when the ecological characteristics of the early successional insect fauna are considered.

CHAPTER FOUR

ECOLOGICAL CHARACTERISTICS OF THE EARLY SUCCESSIONAL HABITAT: INVERTEBRATES

4.1 INTRODUCTION

The following three sections of this chapter (4.2-4.4) deal with developmental aspects of the invertebrate community in Site A in terms of taxonomic composition, abundance and biomass, trophic structure and, finally, life history strategies. In a later section (4.5), comparisons with the invertebrate community of the Site D Young Field are drawn in the light of differences found in the development and structure of the two plant communities during the first year following abandonment. Information on the taxonomy, abundance and biomass of the major insect taxa and spiders found during the first two years in Site A is provided in Table 4.1.

The difficulty and impracticality of assessing the role of adult Diptera and Hymenoptera in the insect and spider community, as previously mentioned in Chapter Two, is emphasised in Table 4.2 where the percentage contributions to insect and total insect + spider abundance and biomass in Site A are given. Diptera (>95% were acalypterates) and Hymenoptera (>99% were Parasitica) were both numerically abundant by June and July of the first year. By mid-August the Diptera had become extremely numerous, representing 92% and 91% of insect and total insect + spider abundance respectively and 66% and 64% of insect and total insect + spider biomass respectively. This mid-summer abundance of more than 50000 dipterans was equivalent to just over 4100 individuals/m^2. Although numbers of Diptera and Hymenoptera were lower in the second year their combined contribution to insect and total insect + spider abundance and biomass was still considerable. In addition, the transient relationship of the adults of these taxa to the habitat also made their inclusion undesirable.

TABLE 4.1 : Taxonomy, abundance and biomass information available on insects and spiders in Site A.

Explanation of symbols:
√ = information available
X = information not available
\- = major taxa not found in the second year
* = adults only identified for the first year
** = no immatures found

Additional information:
1. Groups that have been identified include information on immature stages (where present)
2. Specimens of Lepidoptera were all larvae.
3. All abundance and biomass information is for adult and immature stages combined.

	YEAR 1			YEAR 2		
	Species	Abundance	Biomass	Species	Abundance	Biomass
Orthoptera	√	√	√	√	√	√
Hemiptera-Heteroptera	√	√	√	√	√	√
Hemiptera-Homoptera						
Aphididae	X	√	√	X	√	√
Cercopidae	√	√	√	√	√	√
Cicadellidae	√	√	√	√	√	√
Delphacidae	√	√	√	√	√	√
Thysanoptera	√	√	√	-	-	-
Neuroptera	√	√	√	√	√	√
Diptera	X	√	√	X	√	√
Hymenoptera	X	√	√	X	√	√
Lepidoptera	X	√	√	X	√	√
Coleoptera						
Elateridae	X	√	√	X	√	√
Chrysomelidae	√	√	√	√	√	√
Curculionidae	√	√	√	√	√	√
Cantharidae	√	√	√	X	√	√
Carabidae*	√	√	√	X	√	√
Coccinellidae	√	√	√	X	√	√
Staphylinidae	X	√	√	X	√	√
Cryptophagidae**	√	√	√	X	√	√
Lathridiidae**	√	√	√	X	√	√
Histeridae**	√	√	√	X	√	√
Nitidulidae**	√	√	√	X	√	√
Oedemeridae**	√	√	√	X	√	√

Continued...

TABLE 4.1 : (Continued)

	YEAR 1			YEAR 2		
	Species	Abundance	Biomass	Species	Abundance	Biomass
Phalacridae**	✓	✓	✓	X	✓	✓
Silphidae**	✓	✓	✓	X	✓	✓
Araneae*	✓	✓	✓	X	✓	✓

TABLE 4.2: Contributions by Diptera and Hymenoptera to Abundance and Biomass (mgm dry weight) of Insects and Total Insects and Spiders During the First Two Years of Succession (Site A).

a.	Year 1						Year 2					
% of Total insects	May	June	July	Aug	Sept	Oct	May	June	July	Aug	Sept	Oct
Diptera	0	16	18	92	31	9	38	40	11	28	22	12
Hymenoptera	0	15	38	3	5	3						
	(108)	*(806)*	*(4582)*	*(58947)*	*(3665)*	*(1479)*	*(939)*	*(792)*	*(1597)*	*(1396)*	*(976)*	*(533)*
% of Total Insects & Spiders												
Diptera	0	16	17	91	27	6	33	35	10	25	16	7
Hymenoptera	0	14	36	3	4	2						
	(108)	*(1843)*	*(4882)*	*(59278)*	*(4229)*	*(2199)*	*(1097)*	*(898)*	*(1822)*	*(1595)*	*(1330)*	*(960)*

b.	Year 1						Year 2					
% of Total Insects	May	June	July	Aug	Sept	Oct	May	June	July	Aug	Sept	Oct
Diptera	0	20	27	66	14	17	5	13	12	26	18	11
Hymenoptera	0	2	10	3	1	1						
	(138)	*(484)*	*(1198)*	*(4869)*	*(2073)*	*(778)*	*(344)*	*(543)*	*(795)*	*(853)*	*(619)*	*(373)*
% of Total Insects & Spiders												
Diptera	0	20	25	64	11	14	4	12	11	23	13	8
Hymenoptera	0	2	9	3	1	1						
	(138)	*(490)*	*(1286)*	*(5023)*	*(2598)*	*(950)*	*(424)*	*(607)*	*(875)*	*(970)*	*(841)*	*(519)*

a. % contribution to abundance: b. % contribution to biomass. Figures in italics are total abundance or biomass for insects or insects & spiders and represent an area of 12.96m^2 sampled each month.

4.2 TAXONOMIC COMPOSITION, ABUNDANCE AND BIOMASS

Of the exopterygote insects all groups, with the exception of the Aphididae, were identified and are included in subsequent analyses. The endopterygotes are represented by the largest insect order, the Coleoptera. With the exception of the Staphylinidae and carabid beetle larvae all specimens were identified to species. Though larval Lepidoptera were not identified to species, their abundance and biomass is included in certain calculations. The small numbers of Neuroptera are also included.

During the first year of succession Site A was colonised by at least 207 species of insects and spiders in 41 families, with contributions from exopterygote insects (63 spp. in 16 families), endopterygote insects (112 spp. in 14 families) and Araneae (32 spp. in 11 families). However, in the latter case it may be assumed that most immature species would be included in the adult totals. The omission of certain groups obviously reduces the significance of any discussion of relative species contributions of different groups although certain points are worthy of mention. Species richness of identified invertebrate taxa in the first year rose rapidly to a peak in August (112 spp.) and then declined gradually to late October (70 spp.) (Fig. 4.1). In terms of colonisation rates, species were accumulated rapidly during the first year with almost 80% of the total year's species number arriving in a main wave before mid-August (Fig. 4.1). The Coleoptera contributed considerably more to invertebrate species colonisation than either the exopterygote insects or spiders (Fig. 4.2a).

These differences in species accumulations between the major insect and spider groupings during the first year are also reflected in the species composition of the community (Fig. 4.2b). After an initial dominance of endopterygotes the species contributions of the major groupings remained relatively stable by June with the endopterygotes contributing about 50%, the exopterygotes at around 30% and the spiders around 20%. The species richness of the major insect taxa (Table 4.3) shows that the Heteroptera was the most important exopterygote group, as far as number of species is concerned, and the Coleoptera the most important of the endopterygotes (excluding Lepidoptera, Diptera and Hymenoptera). The exclusion of the Aphididae obviously reduced the importance of the Homoptera in their contribution to exopterygote species richness. A credible estimate of peak aphid richness in the first year of about 15 species in mid-summer may be obtained from collections from similar and adjacent Young Field habitats at Silwood Park (from data of Southwood *et al*, *pers.comm.*). This would make the Homoptera approximately equal in importance to the Heteroptera in terms of

Fig. 4.1 Species richness and colonisation rates of insects and spiders during the first year of succession (Site A). Colonisation refers to the accumulated number of species.

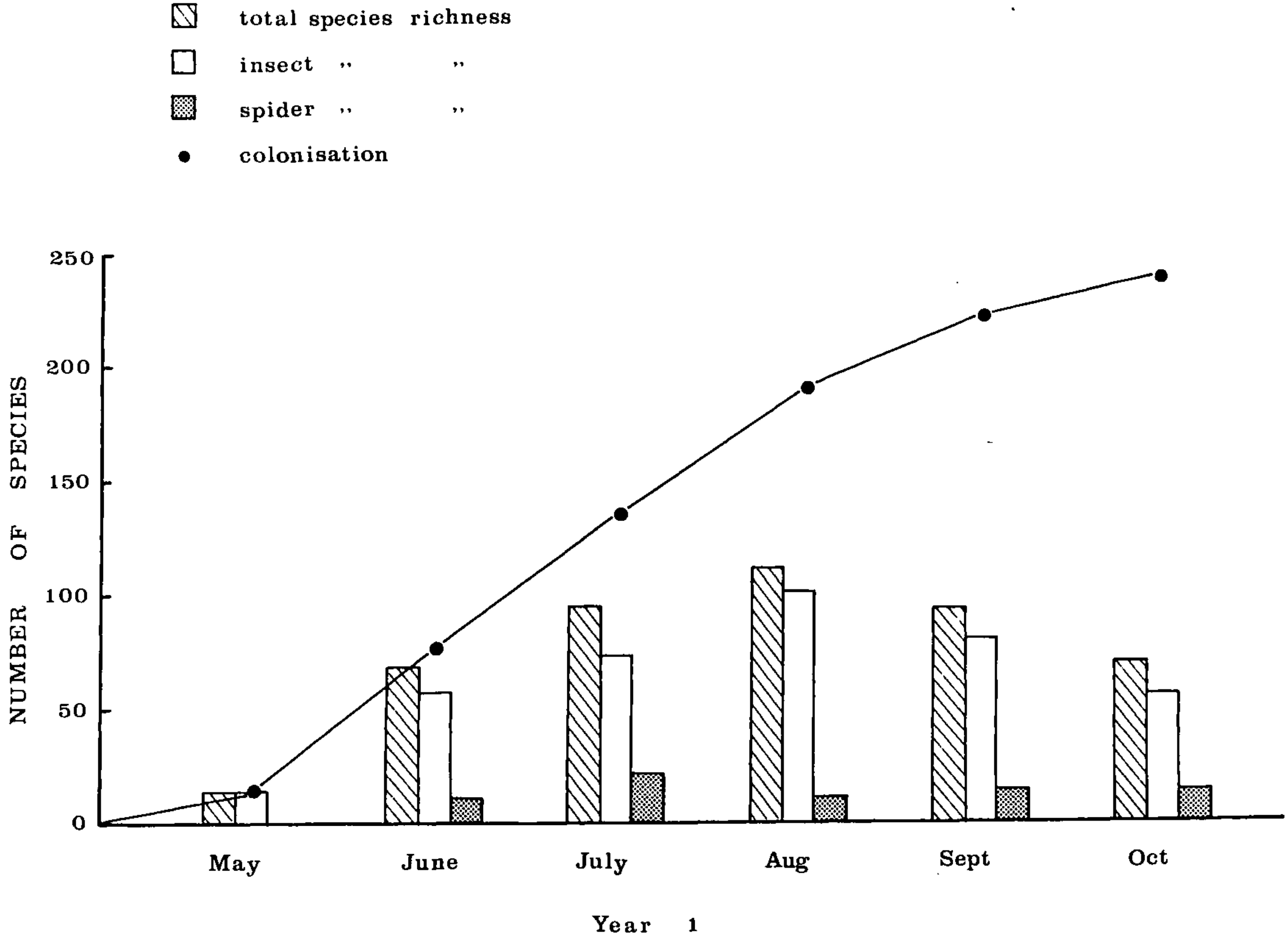

total species richness
insect ,, ,,
spider ,, ,,
colonisation
NUMBER OF SPECIES
250
200
150
100
50
0
May
June
July
Aug
Sept
Oct
Year 1

Fig. 4.2 Colonisation rates and species contributions of major insect taxa and spiders during the first year of succession (Site A).

a. Colonisation rates. Colonisation refers to the accumulated number of species.
b. Species contributions. Total species richness is given along the figure top. Note that Coleoptera was the only group present in May.

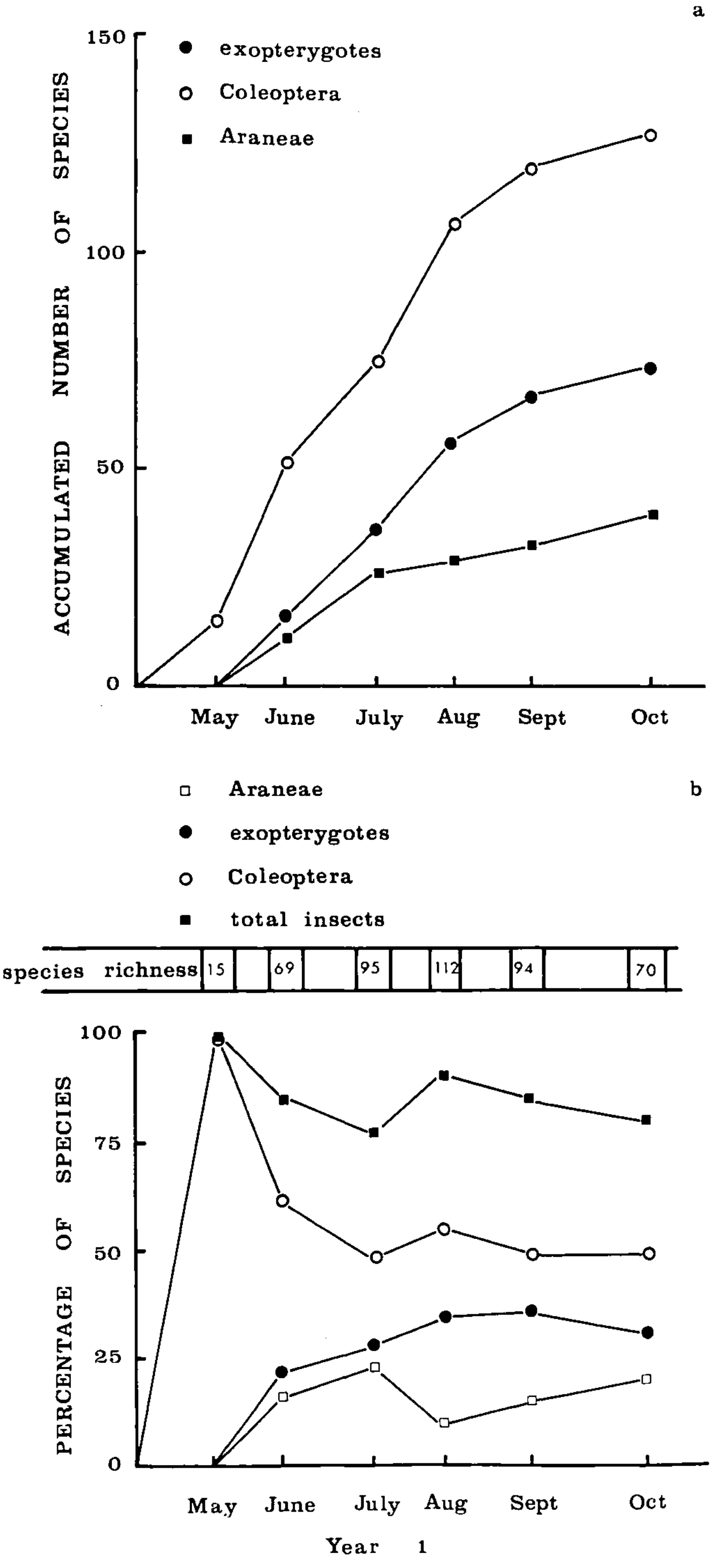

a
ACCUMULATED NUMBER OF SPECIES
0
50
100
150
exopterygotes
Coleoptera
Araneae
May
June
July
Aug
Sept
Oct
b
Araneae
exopterygotes
Coleoptera
total insects
species richness
15
69
95
112
94
70
PERCENTAGE OF SPECIES
0
25
50
75
100
May
June
July
Aug
Sept
Oct
Year 1

TABLE 4.3: Species Richness of Major Invertebrate Taxa in the Young Field Community (Site A) Over the First Year of Succession

	Year 1					
	May	June	July	Aug	Sept	Oct
Orthoptera	0	1	0	1	0	0
Hemiptera-Heteroptera	0	4	13	19	19	11
Hemiptera-Homoptera[1]	0	9	6	11	14	9
Total Hemiptera	0	13	19	30	33	20
Thysanoptera	0	2	7	8	1	2
Total Exopterygotes[1]	0	16	26	39	34	22
Neuroptera	0	0	1	2	0	1
Coleoptera[2]	15	42	45	60	46	33
Araneae[3,4]	0	11	22	11	14	14
Total insects[1,2,4]	15	58	72	101	80	56
Total insects and spiders[1,2,3,4]	15	69	94	112	94	70

1 = excluding Aphididae.
2 = excluding Staphylinidae and Carabidae.
3 = adults only.
4 = excluding Lepidoptera, Diptera and Hymenoptera.

contribution to total exopterygote species richness during the first year of succession. Staphylinid species numbers peaked at around 20-30 species in mid-summer (estimated from samples studied by P.Hammond, *pers.comm.*) and with a few additional beetle species (mainly larval Carabidae) and Lepidoptera species which would not be accounted for in the sampling, the endopterygote contribution (excluding Diptera and Hymenoptera) would be about 100 species in mid-summer. This would produce an approximate total of 280 species of insects and spiders (excluding Diptera and Hymenoptera) colonising the Young Field during the first year, with estimated numbers of 85 spp. of exopterygotes, 160 spp. of endopterygotes and 35 spp. of Araneae. Taking these additional species into account would obviously affect the colonisation curves and the species contributions just described by increasing the percentage contribution of the endopterygote insects to total insect + spider species richness during the first year of succession. Data on species richness and colonisation rates for the second year have focused on the insect herbivore guild and will be presented in Section 4.3.

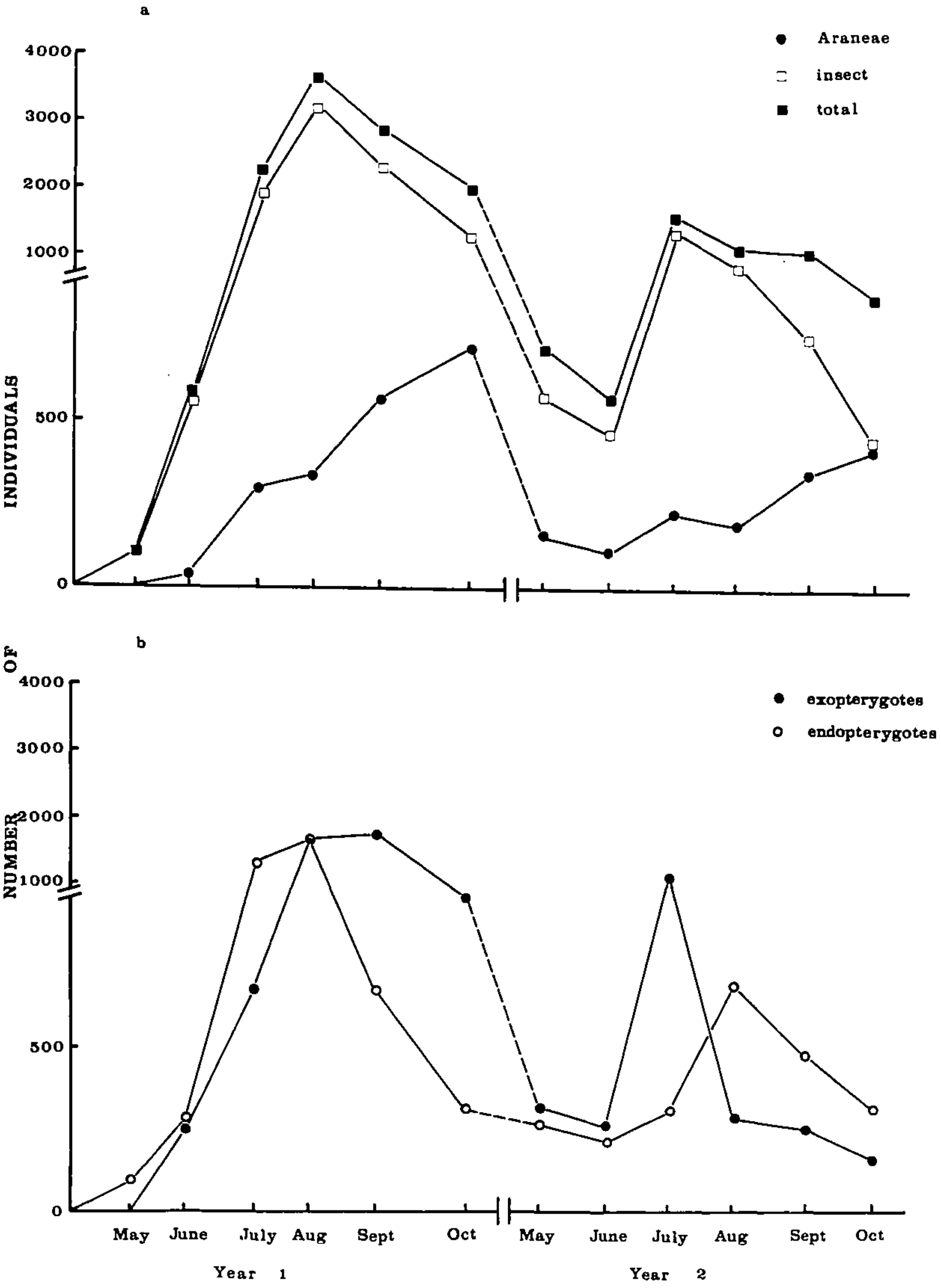
Invertebrate abundance, with insect and spider components (both adult and immature), over the first season is shown in Fig. 4.3a. The abundance of Diptera and Hymenoptera is given in Table 4.2. Invertebrate abundance rose rapidly during the first year to a maximum in August (an abundance equivalent to 270 individuals/m^2) and then quickly declined in the autumn (155 individuals/m^2); a second but reduced peak occurred in July of the second year (125 individuals/m^2) followed by a decline in October (70 individuals/m^2).

The insect abundance followed this general pattern closely, rising rapidly to a maximum level in August (250 individuals/m^2) and declining to October (100 individuals/m^2) in the first year. In the second year abundance was highest at 110 individuals/m^2 in July and then rapidly fell off to around 35 individuals/m^2 at the end of the growing season. On the other hand, spider abundance increased gradually in the first year and reached a maximum level of around 55 individuals/m^2 at the end of the season. Numbers fell off during the winter and then gradually built up throughout the second year, although at the end of the season spider abundance had only reached just over 50% of the peak spider population found in the first year.

The abundance of the two major insect groupings over the first two years is given in Fig. 4.3b. Diptera and Hymenoptera have again been separated from the other insect groups and their abundances have been provided in Table 4.2. Maximum abundance of endopterygotes (*i.e.* Neuroptera, Lepidoptera and Coleoptera) in the first year was reached in July and maintained through August after which there was a rapid decline in numbers, while the

Fig. 4.3 Abundance of insects and spiders during the first two years of succession (Site A). Diptera and Hymenoptera are not included in the figures but their abundances may be found in Table 4.2a.

a. Insect, spider and total abundances.
b. Abundance of exopterygote and endopterygote insects.


a
Araneae
insect
total
4000
3000
2000
1000
500
0
NUMBER OF INDIVIDUALS
b
exopterygotes
endopterygotes
4000
3000
2000
1000
500
0
May
June
July
Aug
Sept
Oct
May
June
July
Aug
Sept
Oct
Year 1
Year 2

exopterygotes peaked one month later and remained numerically stable until September and then declined in October. Patterns of abundance during the second year were quite different with the exopterygotes rising to a similar maximum level to the first year, but earlier, in July, and then rapidly declining. The endopterygotes were less abundant and had a later peak in August, the numbers then gradually declining to the end of the season.

General trends in biomass patterns of the invertebrate community were similar to changes in abundance (Fig. 4.4a and b), with insect biomass very closely following the insect + spider pattern. Spider biomass, however, reached its maximum level in September of both years. Changes in biomass of the two major insect groupings were dramatic during the first year with maximum levels of biomass values reached in August and September in the endopterygotes and exopterygotes respectively. The biomass levels were lower in the second year in each case.

The relative importance of the major insect groups and Araneae, in terms of abundance and biomass, is given in Table 4.4a. The abundance and biomass contributions of Diptera and Hymenoptera to the insect and spider community have already been described (Section 4.1 and Table 4.2) and they have not been included here. The endopterygotes are thus represented by Neuroptera, Lepidoptera and Coleoptera. The insect biomass contributions were generally higher than those for abundance; the reverse being true for the spiders. Percentage contribution to insect + spider abundance and biomass by the Araneae rose through the first year and had reached 36% and 21% of total abundance and biomass respectively at the end of the season. In the second year spider contributions were kept at around 15-20% for both abundance and biomass for the main part of the season and finally rose in the autumn (48% and 30% of abundance and biomass respectively). The Hemiptera were the main contributors to exopterygote abundance and biomass with the Homoptera and Heteroptera switching dominance several times over the two years (Table 4.4b). The Coleoptera together with Diptera and Hymenoptera were the most important endopterygote orders (Table 4.4c). These latter two groups have been included here to give a complete picture of the structure of the endopterygote group.

Fig. 4.4 Biomass of insects and spiders during the first two years of succession (Site A). Diptera and Hymenoptera are not included in the figures but their biomass may be found in Table 4.2b.

a. Insect, spider and total biomass.
b. Biomass of exopterygote and endopterygote insects.

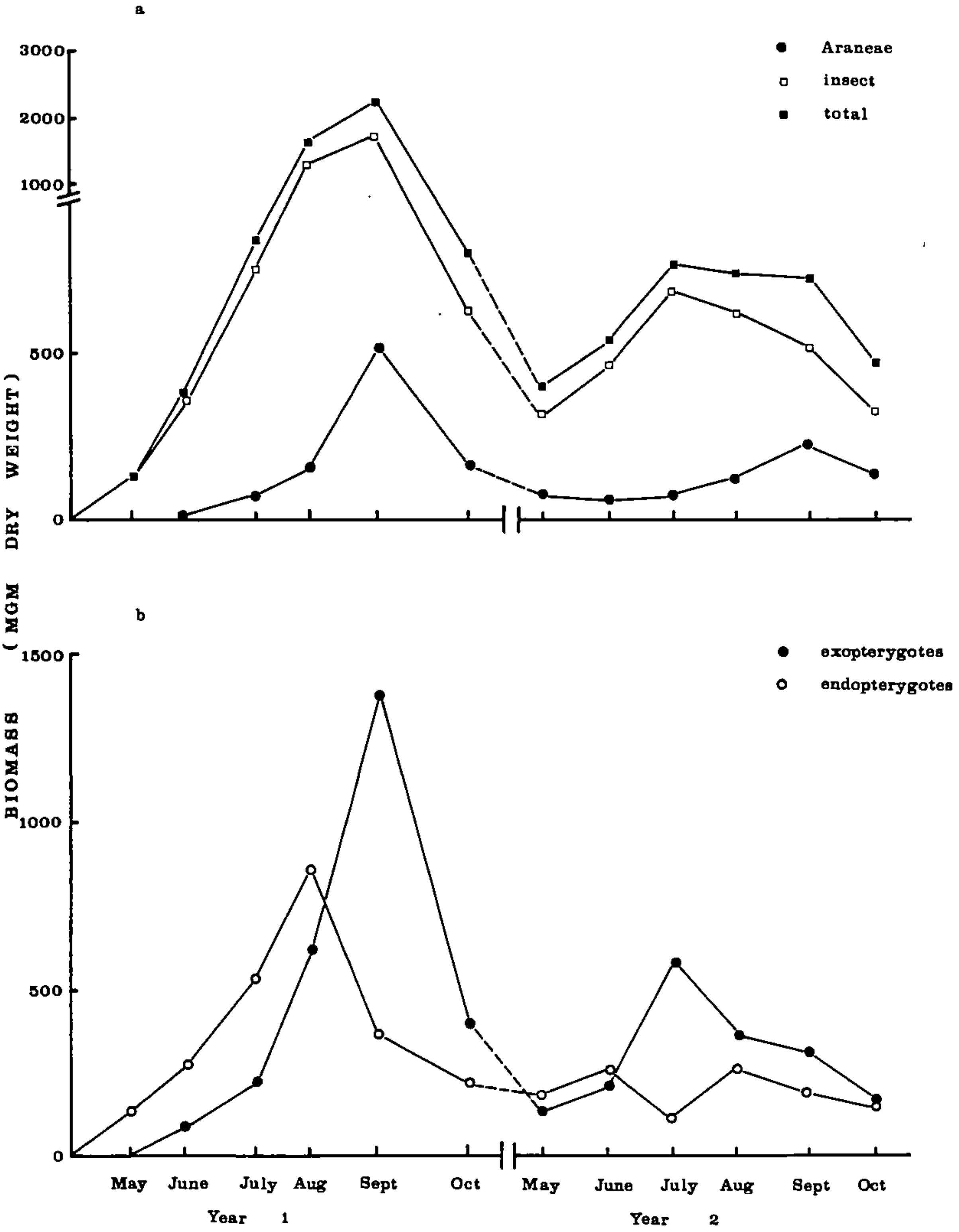

a
3000
2000
1000
500
0
Araneae
insect
total
BIOMASS (MGM DRY WEIGHT)
b
1500
1000
500
0
exopterygotes
endopterygotes
May
June
July
Aug
Sept
Oct
May
June
July
Aug
Sept
Oct
Year 1
Year 2

TABLE 4.4 : Composition of the insect and spider community in terms of abundance and biomass during the first two years of succession (Site A). Abundance contribution = top figure; biomass contribution in italics.

a. % contribution to the insect (excluding Diptera and Hymenoptera) and spider community by major taxa.
b. % contribution to exopterygote abundance and biomass by major insect taxa.
c. % contribution to endopterygote abundance and biomass by major insect taxa. This includes Diptera and Hymenoptera and thus givesa complete picture of the structure of the endopterygoto community.

(a)	YEAR 1						YEAR 2					
	May	June	July	Aug	Sept	Oct	May	June	July	Aug	Sept	Oct
EXOPTERYGOTES	0 *(0)*	45 *(25)*	30 *(26)*	45 *(38)*	58 *(61)*	49 *(51)*	42 *(33)*	46 *(40)*	68 *(75)*	25 *(50)*	24 *(43)*	17 *(39)*
ENDOPTERYGOTES	100 *(100)*	49 *(73)*	57 *(64)*	46 *(53)*	23 *(16)*	15 *(28)*	37 *(47)*	36 *(48)*	18 *(15)*	58 *(35)*	44 *(27)*	35 *(31)*
TOTAL INSECTS	100 *(100)*	94 *(98)*	87 *(90)*	91 *(91)*	81 *(77)*	64 *(79)*	79 *(80)*	82 *(88)*	86 *(90)*	83 *(85)*	68 *(70)*	52 *(70)*
ARANEAE	0 *(0)*	6 *(2)*	13 *(10)*	9 *(9)*	19 *(23)*	36 *(21)*	21 *(20)*	18 *(12)*	14 *(10)*	17 *(15)*	32 *(30)*	48 *(30)*

(b)	YEAR 1						YEAR 2					
EXOPTERYGOTES	May	June	July	Aug	Sept	Oct	May	June	July	Aug	Sept	Oct
ORTHOPTERA	0 *(0)*	<1 *(20)*	0 *(0)*	<1 *(5)*	0 *(0)*	0 *(0)*	0 *(0)*	0 *(0)*	<1 1	<1 8	0 *(0)*	0 *(0)*
HEMIPTERA-HETEROPTERA	0 *(0)*	5 *(8)*	20 *(34)*	36 *(44)*	42 *(73)*	15 *(43)*	12 *(35)*	17 *(35)*	76 *(76)*	47 *(46)*	46 *(58)*	53 *(57)*
HEMIPTERA-HOMOPTERA	0 *(0)*	71 *(71)*	63 *(65)*	56 *(50)*	57 *(26)*	84 *(56)*	88 *(65)*	83 *(65)*	23 *(23)*	52 *(46)*	54 *(42)*	47 *(33)*
TOTAL HEMIPTERA	0 *(0)*	76 *(79)*	83 *(99)*	91 *(94)*	99 *(99)*	99 *(99)*	100 *(100)*	100 *(100)*	99 *(99)*	99 *(92)*	100 *(100)*	100 *(100)*
THYSANOPTERA	0 *(0)*	23 *(<1)*	17 *(<1)*	9 *(<1)*	<1 *(<1)*	<1 *(<1)*	0 *(0)*	0 *(0)*	0 *(0)*	0 *(0)*	0 *(0)*	0 *(0)*

Continued..

TABLE 4.4: (Continued)

(c)

	YEAR 1						YEAR 2					
	May	June	July	Aug	Sept	Oct	May	June	July	Aug	Sept	Oct
ENDOPTERYGOTES												
NEUROPTERA	0 *(0)*	0 *(0)*	<1 *(<1)*	<1 *(<1)*	0 *(0)*	<1 *(<1)*	0 *(0)*	0 *(0)*	0 *(0)*	<1 *(<1)*	0 *(0)*	0 *(0)*
LEPIDOPTERA	0 *(0)*	<1 *(<1)*	<1 *(8)*	<1 *(<1)*	0 *(0)*	<1 *(<1)*	0 *(0)*	<1 *(<1)*	<1 *(<1)*	<1 *(<1)*	0 *(0)*	0 *(0)*
COLEOPTERA	100 *(100)*	53 *(74)*	33 *(47)*	3 *(20)*	34 *(54)*	63 *(61)*	43 *(92)*	40 *(78)*	61 *(53)*	63 *(53)*	70 *(65)*	82 *(79)*
DIPTERA	0 *(0)*	25 *(25)*	21 *(33)*	94 *(76)*	58 *(42)*	27 *(36)*	57 *(8)*	60 *(22)*	38 *(47)*	36 *(46)*	30 *(35)*	18 *(21)*
HYMENOPTERA	0 *(0)*	22 *(<1)*	45 *(12)*	3 *(4)*	8 *(4)*	9 *(2)*						

4.3 TROPHIC STRUCTURE

4.3.1 Introduction

The idea that the term 'guild' should be used to describe a group of species that exploit a common resource was originally encapsulated by Root (1967; see also Root, 1973). The consequences of this definition is to group together species, regardless of their taxonomic composition, that have a significant overlap in their niche requirements. Since then, a number of researchers have recognised the convenience of using the term as a means of describing certain important structural aspects of both vertebrate and invertebrate communities. A discussion on the abuse and misuse of the term 'guild' in ecological studies is provided by Jaksic (1981).

When food is the common resource then a number of 'trophic' guilds may be defined. This may entail either a simple or more elaborate study of the trophic dynamics of the community. For example, a simple breakdown of the insect and spider community would be to have just two guilds, insect herbivores and entomophages (*e.g.* Cole, 1980). If further information concerning these guilds was required then it would be necessary to form sub-groups of these two major guilds. An example of this may be found in Evans & Murdoch (1968), in their study of an Old Field community, where the herbivore guild consisted of leaf- and stem-feeders and flower-feeders and the predators were grouped into insect predators, parasites and other predators. A further elaborate breakdown of trophic groups is described for arboreal invertebrates by Moran & Southwood (1982) and Southwood, Moran & Kennedy (1982) where seven distinct guilds are recognised:- phytophages (subdivided into chewers and sap-suckers), epiphytes, scavengers, predators (subdivided into insect predators and other predators), parasitoids, ants and tourists.

In this study the herbivores are obviously the guild on which most attention is focused and therefore form a major category. In addition, predators are recognised as a distinct group. A third and relatively minor group has been termed 'omnivores'. This group includes species which are reputed in the literature to feed on both plant and animal material and, in addition, the very small number of true scavengers. The latter would of course form a more important group in later successional stages. A full list of insect families falling into each guild is provided in Appendix 5. This section on the trophic structure of the Young Field insect and spider community is only concerned with these three major groupings and their dynamics. In the following section (4.4) the life history strategies of the insect herbivores are presented and the herbivore guild is subsequently subdivided into smaller trophic categories.

4.3.2 Taxonomic composition and species diversity

In a previous section (4.2) estimates of total insect and spider species richness found during the first year were given although certain taxa were omitted. It is not possible to make a complete comparison between the richness of the different guilds for the first year. Nevertheless, data are provided in Table 4.5 which show species richness of the major taxa comprising each guild. The number of species of predators (mainly carabids and spiders) increased considerably in the first year and would have been even larger if the numbers of Staphylinidae (20-30 spp.) had been taken into account.

The species richness of the insect herbivores (excluding aphids and Lepidoptera) over the first two years of succession rose rapidly in the first year and reached 55 species in August (Table 4.5). Herbivore species richness in the second year was more numerically stable, ranging from 34 to 47 species with highest numbers again occurring in August. Both Hemiptera and Coleoptera contributions to the species richness of the herbivore guild in the first year would be slightly biased towards the Hemiptera and about equal in the second year if the Aphididae were accounted for. At any rate, with the exclusion of the aphids (as well as the estimated few species of Lepidoptera), it is clear that insect herbivore species accumulated extremely rapidly, from May to September of the first year, and again, but at a lower rate, throughout the second year (Fig. 4.5). The most important contributors to herbivore species colonisation were the Heteroptera, Homoptera and Coleoptera, the latter group especially so (Fig. 4.5).

It has previously been remarked that the qualitative Index of Similarity (I_s) for comparing the species composition of two communities will tend to overestimate habitat similarity. This is also evident from Table 4.6a where seasonal changes in insect herbivore species composition (I_s), abundance (I_w) and biomass (I_w) are shown. For total herbivores (excluding aphids) the general trend is for a rise in species similarity (I_s) through the first year to 60% at the end of the season. In the second year, following a rise in the spring, species similarity was fairly constant at around 60%. Similarity in numbers of individuals (I_w) was generally considerably lower than corresponding I_s values (Table 4.6a). Seasonal changes in biomass (Table 4.6b) also occurred in the Young Field insect herbivore community. Total I_w values

TABLE 4.5 : Trophic structure of the invertebrate community in terms of species richness during the first two years of succession (Site A)

1 = excludes Aphididae; 2 = excludes carabid larvae and Staphylinidae; 3 = excludes immature spiders
4 = omnivore species numbers only available for Heteroptera in the second year;
- = data not available for predator species in the second year.

	YEAR 1						YEAR 2					
	MAY	JUNE	JULY	AUG	SEPT	OCT	MAY	JUNE	JULY	AUG	SEPT	OCT
Herbivores												
Orthoptera	0	1	0	1	0	0	0	0	2	1	0	0
Hemiptera-Heteroptera	0	4	9	11	12	6	5	6	8	8	9	6
Hemiptera-Homoptera[1]	0	9	6	11	14	9	4	9	11	14	12	10
Total Hemiptera[1]	0	13	15	22	26	15	9	15	19	22	21	16
Thysanoptera	0	2	7	8	1	2	0	0	0	0	0	0
Coleoptera	5	24	14	24	27	19	25	19	15	24	25	24
Total herbivores[1]	5	40	36	55	54	36	34	34	36	47	46	40
Predators												
Hemiptera-Heteroptera	0	0	4	6	6	5	3	5	5	4	4	2
Neuroptera	0	0	1	2	0	1	-	-	-	-	-	-
Coleoptera[2]	9	10	19	24	9	6	-	-	-	-	-	-
Total insect predators[2]	9	10	24	32	15	12	-	-	-	-	-	-
Araneae[3]	0	11	22	11	14	14	-	-	-	-	-	-
Total predators[2,3]	9	21	46	43	29	26	-	-	-	-	-	-

Continued.

TABLE 4.5 : (Continued)

	YEAR 1						YEAR 2					
	MAY	JUNE	JULY	AUG	SEPT	OCT	MAY	JUNE	JULY	AUG	SEPT	OCT
Omnivores												
Hemiptera-Heteroptera[4]	0	0	0	2	1	0	1	1	3	3	2	1
Coleoptera	1	8	12	12	10	8	-	-	-	-	-	-
Total omnivores[4]	1	8	12	14	11	8	-	-	-	-	-	-
TOTAL INSECTS[1,2,4]	15	58	72	101	80	56	-	-	-	-	-	-
TOTAL INSECT + SPIDER[1,2,3]	15	69	94	112	94	70	-	-	-	-	-	-

Fig. 4.5 Colonisation rates of insect herbivore species in major taxa during the first two years of succession (Site A).

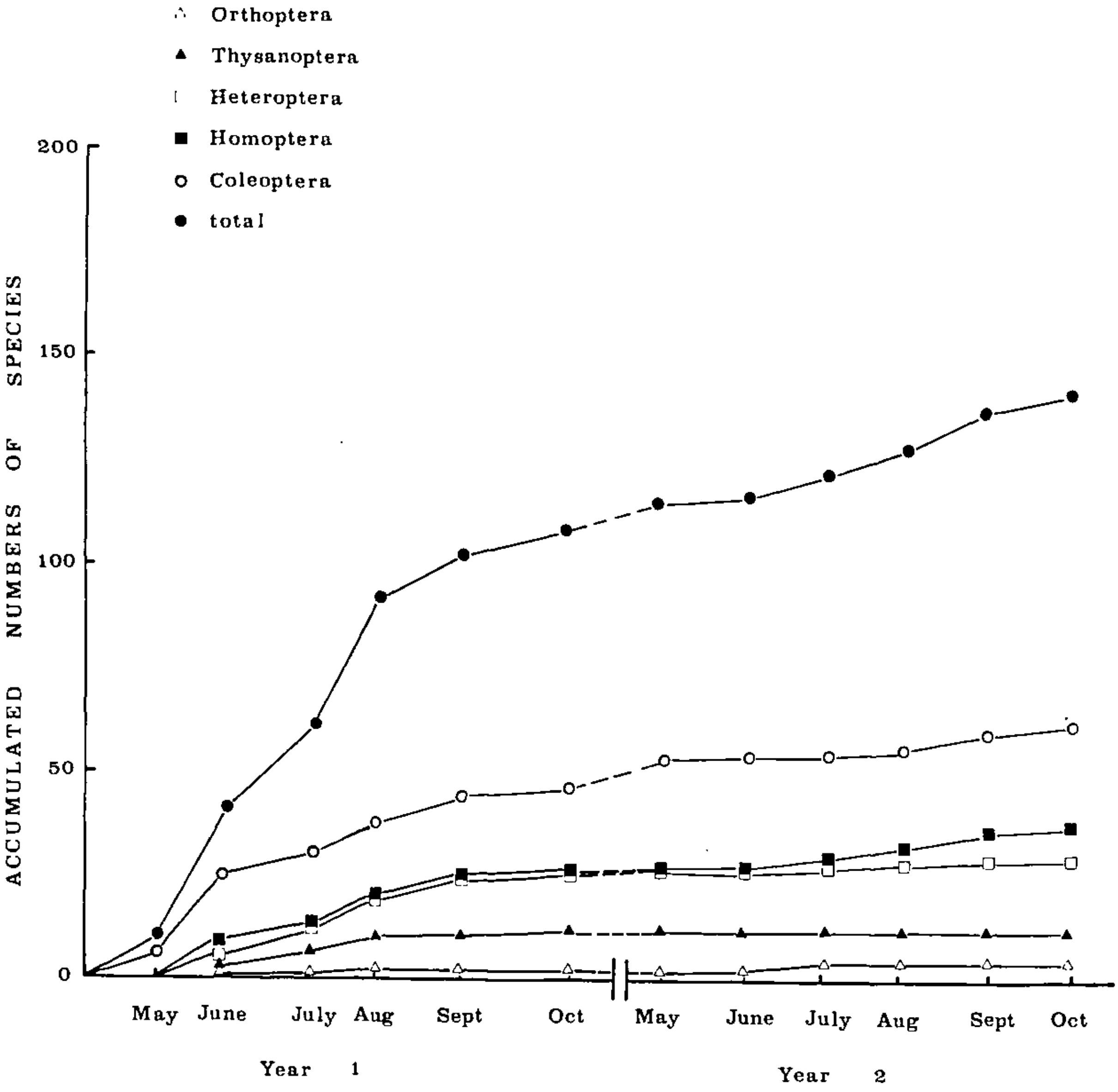

Orthoptera
Thysanoptera
Heteroptera
Homoptera
Coleoptera
total
ACCUMULATED NUMBERS OF SPECIES
200
150
100
50
0
May
June
July
Aug
Sept
Oct
May
June
July
Aug
Sept
Oct
Year 1
Year 2

TABLE 4.6 : Indices of similarity between insect herbivores during the first two years of succession (Site A)

a. Species composition and abundance: I_s value above, I_w value for number of individuals in italics.

b. Biomass : I_w value

(a)	YEAR 1 MAY – JUNE	JUNE – JULY	JULY – AUG	AUG – SEPT	SEPT – OCT	OCT 80 – MAY 81	YEAR 2 MAY – JUNE	JUNE – JULY	JULY – AUG	AUG – SEPT	SEPT – OCT
Orthoptera	0 *(0)*	0 *(0)*	0 *(0)*	0 *(0)*	0 *(0)*	0 *(0)*	0 *(0)*	0 *(0)*	0.66 *(0.50)*	0 *(0)*	0 *(0)*
Hemiptera-Heteroptera	0 *(0)*	0.15 *(0.14)*	0.50 *(0.42)*	0.19 *(0.67)*	0.56 *(0.23)*	0.36 *(0.24)*	0.55 *(0.18)*	0.43 *(0.04)*	0.50 *(0.15)*	0.71 *(0.17)*	0.40 *(0.69)*
Hemiptera-Homoptera	0 *(0)*	0.40 *(0.34)*	0.47 *(0.14)*	0.64 *(0.14)*	0.53 *(0.09)*	0.31 *(0.16)*	0.62 *(0.18)*	0.40 *(0.36)*	0.64 *(0.22)*	0.46 *(0.43)*	0.73 *(0.57)*
Total Hemiptera	0 *(0)*	0.29 *(0.34)*	0.49 *(0.23)*	0.58 *(0.34)*	0.54 *(0.13)*	0.33 *(0.17)*	0.58 *(0.18)*	0.61 *(0.16)*	0.59 *(0.17)*	0.56 *(0.36)*	0.59 *(0.62)*
Thysanoptera	0 *(0)*	0.44 *(0.67)*	0.67 *(0.68)*	0.22 *(0.02)*	0.67 *(0.67)*	0 *(0)*	0 *(0)*	0 *(0)*	0 *(0)*	0 *(0)*	0 *(0)*
Coleoptera	0.28 *(0.10)*	0.47 *(0.32)*	0.47 *(0.34)*	0.67 *(0.38)*	0.65 *(0.65)*	0.41 *(0.20)*	0.64 *(0.29)*	0.71 *(0.58)*	0.67 *(0.44)*	0.69 *(0.68)*	0.69 *(0.55)*
Total herbivores	0.18 *(0.03)*	0.39 *(0.37)*	0.51 *(0.29)*	0.59 *(0.34)*	0.60 *(0.20)*	0.37 *(0.17)*	0.62 *(0.20)*	0.58 *(0.24)*	0.63 *(0.14)*	0.62 *(0.58)*	0.65 *(0.58)*

Continued

TABLE 4.6 : (Continued)

(b)	YEAR 1						YEAR 2				
	MAY - JUNE	JUNE - JULY	JULY - AUG	AUG - SEPT	SEPT - OCT	OCT 80 - MAY 81	MAY - JUNE	JUNE - JULY	JULY - AUG	AUG - SEPT	SEPT - OCT
Orthoptera	0	0	0	0	0	0	0	0	0.05	0	0
Hemiptera-Heteroptera	0	0.22	0.40	0.31	0.17	0.10	0.13	0.11	0.15	0.24	0.55
Hemiptera-Homoptera	0	0.51	0.18	0.22	0.20	0.27	0.41	0.54	0.30	0.51	0.62
Total Hemiptera	0	0.43	0.27	0.28	0.18	0.25	0.36	0.29	0.22	0.44	0.59
Thysanoptera	0	0.80	0.76	0.02	0.73	0	0	0	0	0	0
Coleoptera	0.26	0.39	0.24	0.39	0.80	0.16	0.37	0.53	0.40	0.66	0.59
Total Herbivores	0.14	0.60	0.24	0.31	0.31	0.22	0.37	0.33	0.26	0.54	0.59

for biomass were generally low (around 20-30%) in the first year. In the second season similarity was again relatively low for the first four months and then rose quickly to 59% at the end of the season.

Seasonal changes in species composition, abundance and biomass of the herbivore guild are also accompanied by successional changes. In Table 4.7 Indices of Similarity between the first two years of succession are given for I_s (species similarity), I_w (similarity in the number of individuals of common species) and I_w for biomass similarity of common species. From the I_s values it would appear that the herbivore guild had moved quickly along a β-diversity gradient after just two years of succession. However, if numbers of individuals are taken into account (I_w) (Table 4.7a) then it is clear that β-diversity proceeded at a much lower rate (*i.e.* low values of the Sorensen's Index indicated a rapid turnover of insect herbivore species). The same evidence applies to successional changes in biomass (Table 4.7b).

Values of the Williams Index of α-diversity for main groups of insect herbivores (excluding the Aphididae and Lepidoptera) are given in Table 4.8. The Coleoptera were generally the most diverse group during the first two years of succession and displayed considerable seasonal fluctuations. Where a group of herbivores colonise rapidly, as previously found for the Coleoptera, then relatively high levels of α-diversity, together with accompanying fluctuations, would be expected. Accordingly, a lower colonisation of hemipterans resulted in lower values of α in both years, although diversity of the Hemiptera throughout the second year was higher than that found for the first season.

4.3.3 General trends of abundance and biomass

Pyramids of numbers of individuals of the major trophic guilds (adults and immatures) for the first two years are presented in Fig. 4.6. The pyramid for May of the first year, five weeks after site establishment, is highly predator-biased. This was due to a relatively high abundance of the carabid *Bembidion lampros*, although it should be noted that the total numbers of insects and spiders present were very low at this time (<10 individuals/m^2). For the remainder of the first year, guild structure for abundance varied between 41-64% for herbivores, 25-44% for predators and 4-15% for omnivores. With the exception of the July sample (by this time predatory Staphylinidae and Araneae had built up relatively large populations), the percentage contributions of herbivores, predators and omnivores were fairly stable and after July averaged 61, 31 and 8% respectively. The pattern of guild composition

TABLE 4.7: Indices of similarity between the first two years of succession for insect herbivores (Site A)

a. Insect abundance: I_s value above, I_w value (for number of individuals) in italics.
b. Insect biomass: I_w value

(a)	MAY 80 - MAY 81	JUNE 80 - JUNE 81	JULY 80 - JULY 81	AUG 80 - AUG 81	SEPT 80 - SEPT 81	OCT 80 - OCT 81
Orthoptera	0 *(0)*	0 *(0)*	0 *(0)*	0 *(0)*	0 *(0)*	0 *(0)*
Hemiptera-Heteroptera	0 *(0)*	0.20 *(0.06)*	0.67 *(0.22)*	0.32 *(0.22)*	0.29 *(0.12)*	0.33 *(0.69)*
Hemiptera-Homoptera	0 *(0)*	0.44 *(0.34)*	0.24 *(0.05)*	0.64 *(0.10)*	0.38 *(0.12)*	0.53 *(0.08)*
Total Hemiptera	0 *(0)*	0.36 *(0.32)*	0.41 *(0.15)*	0.50 *(0.14)*	0.34 *(0.12)*	0.45 *(0.17)*
Thysanoptera	0 *(0)*	0 *(0)*	0 *(0)*	0 *(0)*	0 *(0)*	0 *(0)*
Coleoptera	0.13 *(0.10)*	0.23 *(0.07)*	0.28 *(0.06)*	0.38 *(0.06)*	0.67 *(0.19)*	0.56 *(0.24)*
Total herbivores	0.10 *(0.02)*	0.27 *(0.21)*	0.31 *(0.12)*	0.39 *(0.10)*	0.44 *(0.14)*	0.50 *(0.18)*

(b)	MAY 80 - MAY 81	JUNE 80 - JUNE 81	JULY 80 - JULY 81	AUG 80 - AUG 81	SEPT 80 - SEPT 81	OCT 80 - OCT 81
Orthoptera	0	0	0	0	0	0
Hemiptera-Heteroptera	0	0.02	0.21	0.22	0.05	0.71
Hemiptera-Homoptera	0	0.32	0.12	0.19	0.20	0.34
Total Hemiptera	0	0.28	0.18	0.20	0.10	0.48
Thysanoptera	0	0	0	0	0	0
Coleoptera	0.10	0.08	0.06	0.06	0.21	0.23
Total herbivores	0.04	0.20	0.14	0.12	0.09	0.39

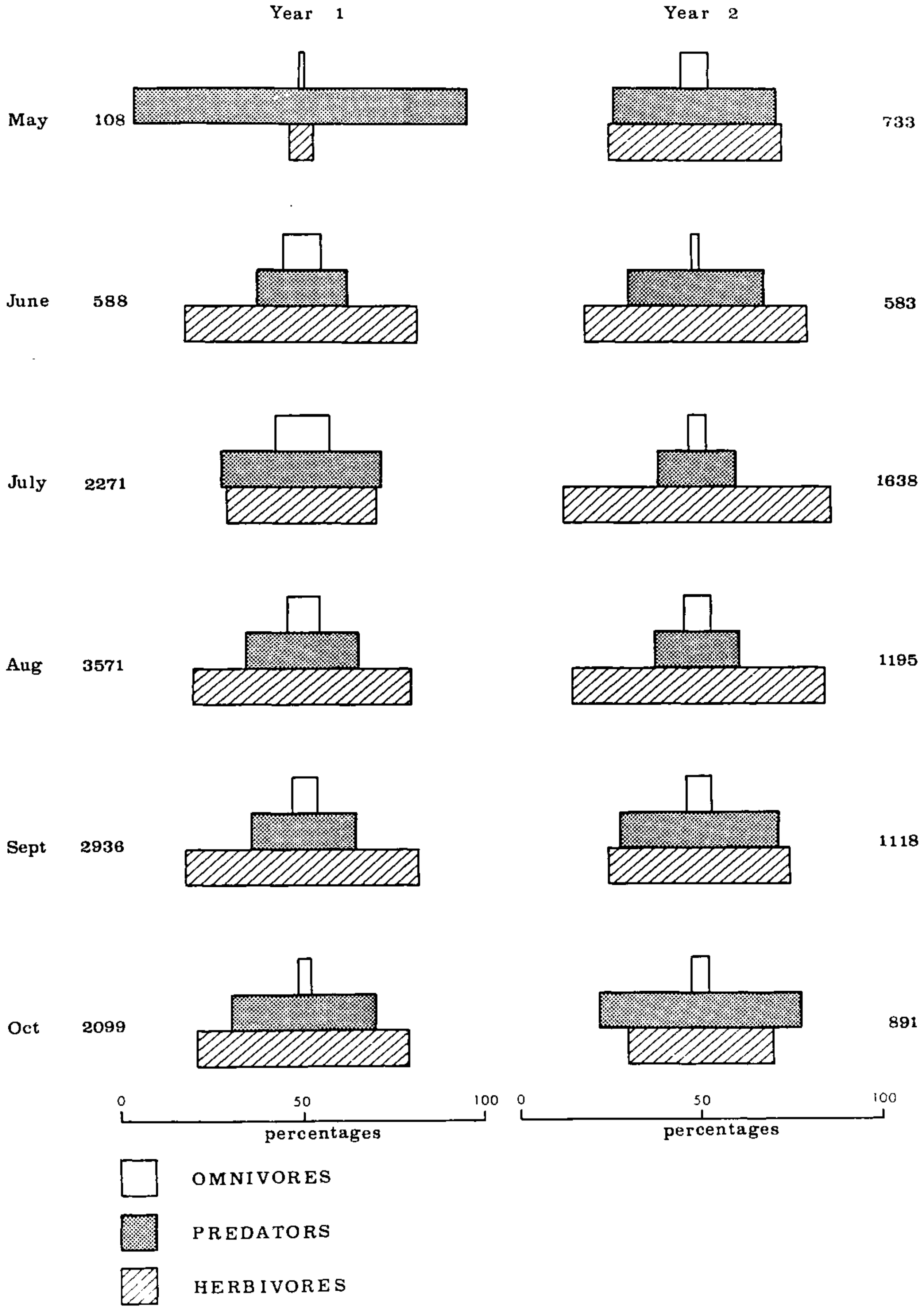
TABLE 4.8 : Diversity values for insect herbivores during the first two years of succession (Site A)

1 = excluding aphids; 2 = excluding Lepidoptera; $\infty^1 = n = 1, s = 1$; $\infty^2 = n = 2, s = 2$

* indicates high values of Williams α where relatively low numbers of n were found.

	YEAR 1						YEAR 2					
	MAY	JUNE	JULY	AUG	SEPT	OCT	MAY	JUNE	JULY	AUG	SEPT	OCT
Orthoptera	-	0.4	-	∞^1	-	-	-	-	∞^2	0.8	-	-
Hemiptera-Heteroptera	-	2.0	2.2	2.0	2.1	1.4	1.9	2.8	1.2	2.4	2.9	1.6
Hemiptera-Homoptera[1]	-	2.2	1.1	1.9	2.6	2.0	0.8	2.0	3.8	2.8	3.1	3.2
Total Hemiptera[1]	-	3.5	3.2	3.9	4.7	3.4	2.2	3.7	3.4	6.2	5.8	4.7
Thysanoptera	-	0.4	1.7	1.9	∞^1	∞^2	-	-	-	-	-	-
Coleoptera	5.7	9.2*	3.3	4.9	7.5	5.7	17.7*	6.5	3.8	5.0	6.1	6.9
Total herbivores[1,2]	5.7	12.1*	8.1	10.6	11.0	9.3	12.4	9.7	7.2	10.9	11.9	11.6

Fig. 4.6 Guild composition of the invertebrate community during the first two years of succession in terms of percentage contributions to abundance (Site A). Total insect + spider abundance is given for each month (excluding Diptera and Hymenoptera).


Year 1
Year 2
May
108
733
June
588
583
July
2271
1638
Aug
3571
1195
Sept
2936
1118
Oct
2099
891
0
50
100
percentages
0
50
100
percentages
OMNIVORES
PREDATORS
HERBIVORES

was quite different during the second year. In May there were similar and high contributions to total abundance by herbivores and predators (around 45% each) but this had progressed to a highly herbivore-biased community by July (73% herbivores, 21% predators). The contribution of predators rapidly increased after August and by the end of the growing season guild structure for abundance was predator-biased (39% herbivores, 56% predators); this was due to both a declining herbivore population and an increasing number of predators (mainly spiders) towards the end of the season (see later). The contribution to invertebrate abundance by the omnivore guild was very low and never more than 10% on any sampling occasion. The very low numbers of scavengers found could well be explained by the lack of a well defined litter layer in the early successional habitat.

Similarly constructed pyramids of biomass for the major guilds are presented in Fig. 4.7 and contain resemblances and differences to the pyramids of abundance. As for abundance, biomass was highly predator-biased (69% predators) in the first month following site establishment, although it was not until August that the invertebrate community biomass became orientated towards the herbivore guild (66%) and remained at this level through the rest of the growing season. The biomass dominance of the predator guild early on (from May to July) reflects the initial build up of populations of Carabidae, Coccinellidae and Staphylinidae (see later). The second year began with community biomass dominated by the predator guild in May and June (around 60%), but as for abundance, the herbivore guild reached its highest contribution of the year in July (72%) and by the end of the season had dropped to 51% herbivores: 48% predators. The biomass contribution of the omnivore guild during the first two years was even lower than that for abundance, averaging 4% and 5% in the first and second years respectively. This lower contribution to biomass is a reflection of the small size of these generally soil surface-dwelling forms, especially the Cryptophagidae, Lathridiidae and Nitidulidae.

The seasonal patterns in absolute levels of abundance and biomass of the insect herbivores and the predators (insects and spiders) can be clearly seen in Fig. 4.8. Changes in herbivore abundance and biomass were dramatic with both parameters rising extremely rapidly in the first season. A peak occurred either in August (164 individuals/m^2), followed by a plateau through to September (for abundance) or in September (for biomass). A rapid decline in herbivore abundance and biomass occurred at the end of the first season. Patterns of herbivore abundance and biomass during the second year followed a similar pattern to each other, both rising to relatively small peaks in July and then either rapidly (for abun-

Fig. 4.7 Guild composition of the invertebrate community during the first two years of succession in terms of percentage contributions to biomass (Site A). Total insect + spider biomass is given for each month (mgm dry weight) (excluding Diptera and Hymenoptera).

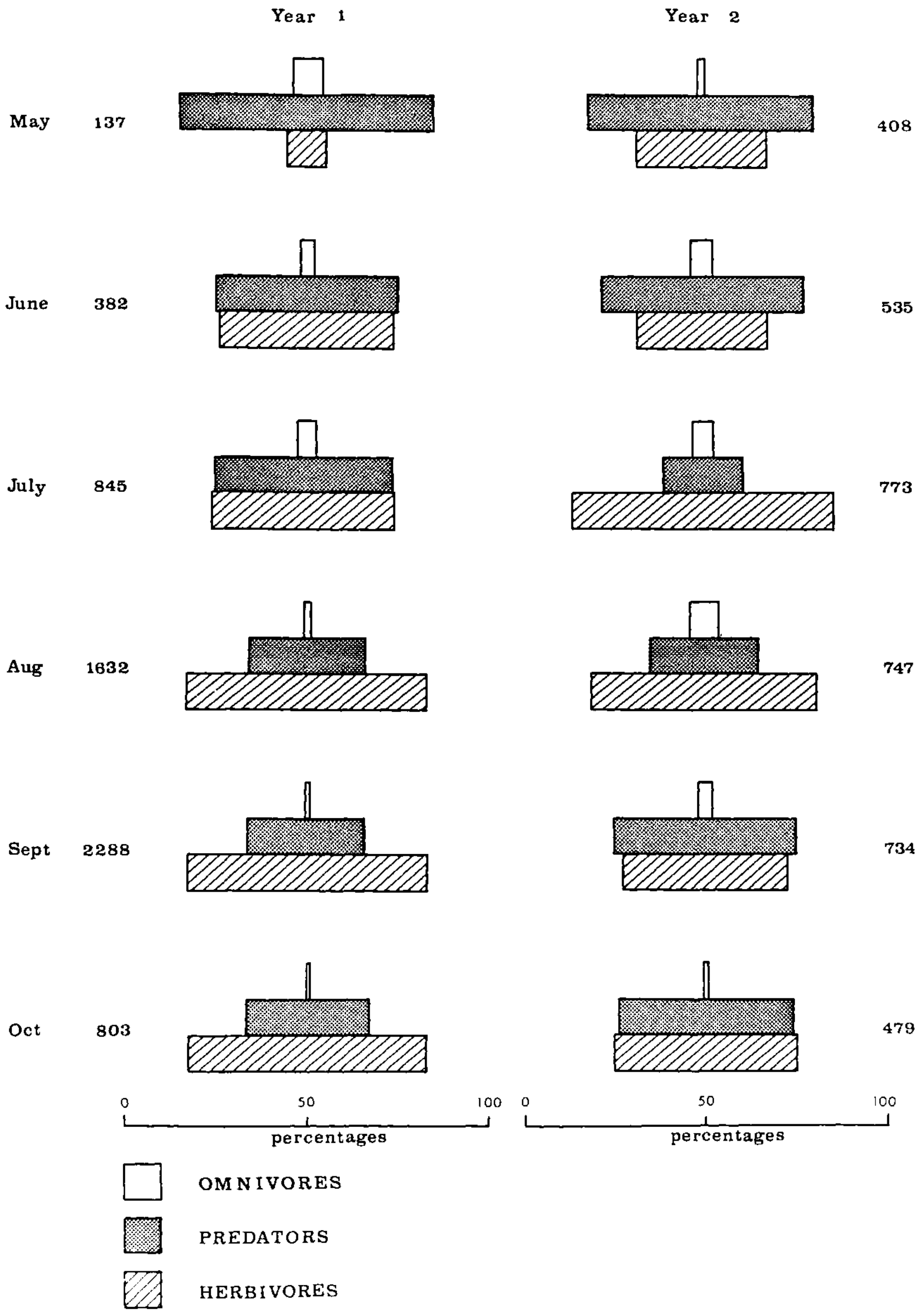
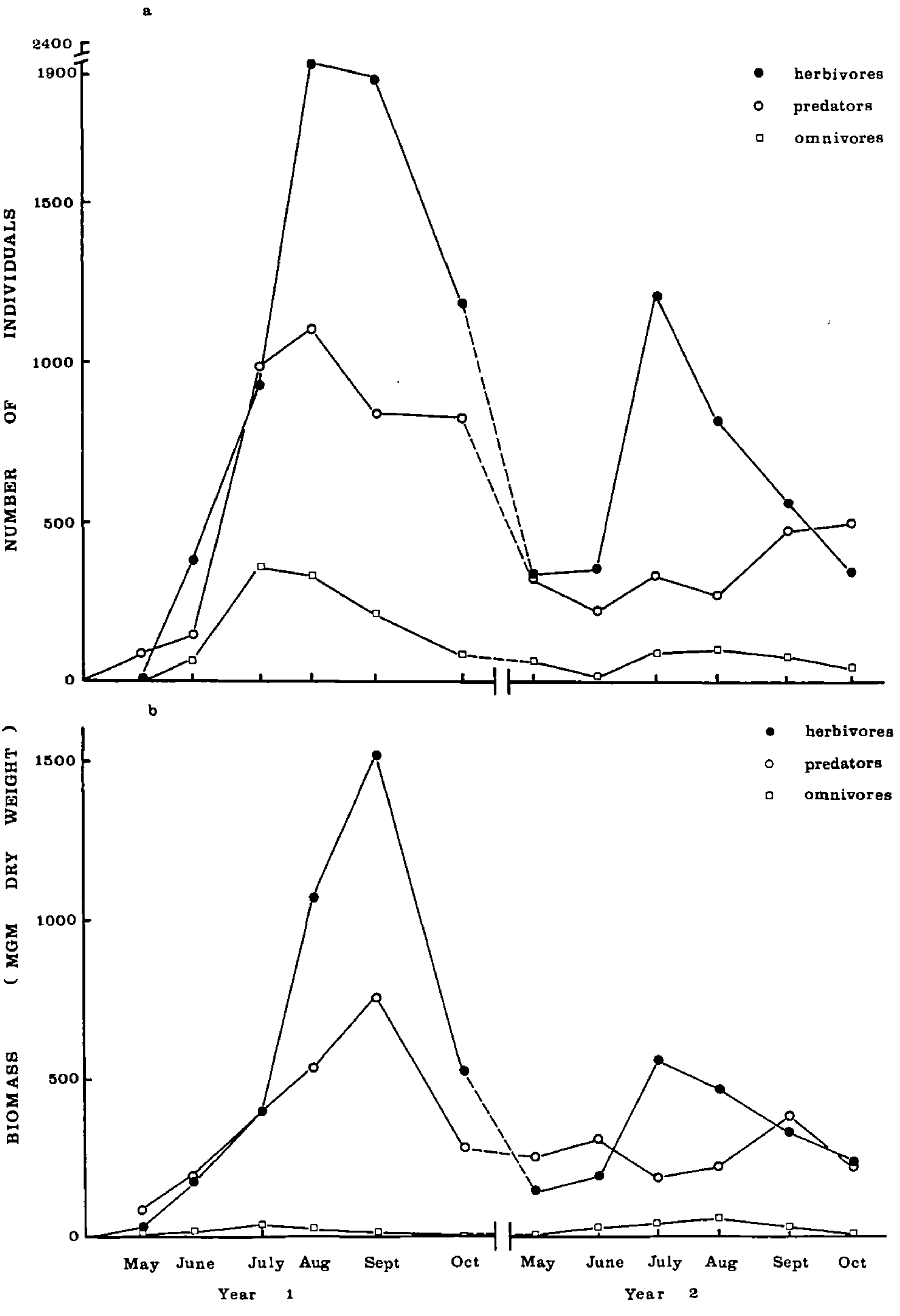

Year 1
Year 2
May
137
408
June
382
535
July
845
773
Aug
1632
747
Sept
2288
734
Oct
803
479
0
50
100
percentages
0
50
100
percentages
OMNIVORES
PREDATORS
HERBIVORES

Fig. 4.8 Abundance and biomass of the three major trophic guilds during the first two years of succession (Site A).

a. Abundance.
b. Biomass.


a
2400
1900
1500
1000
500
0
NUMBER OF INDIVIDUALS
● herbivores
○ predators
□ omnivores
b
1500
1000
500
0
BIOMASS (MGM DRY WEIGHT)
● herbivores
○ predators
□ omnivores
May
June
July
Aug
Sept
Oct
May
June
July
Aug
Sept
Oct
Year 1
Year 2

dance) or gradually (for biomass) falling off to the end of the season. Both second year peaks were considerably lower than those for the first year with abundance at 94 individuals/m^2 and biomass 63% lower. These differences in abundance and biomass between the two years were due to considerably lower numbers of Homoptera and phytophagous Heteroptera in the second year (see later for further details).

The abundance and biomass of the predator guild during the first year followed similar trends to those found for the insect herbivores. Predator abundance, however, rose rapidly to July (80 individuals/m^2) and remained relatively stable for the rest of the season. In the second year predator abundance remained at a lower level, undergoing relatively minor fluctuations but resulting in the highest level at the end of the season (but 55% lower than the first year maximum). Biomass was similarly maintained at comparatively low levels during the second year and the September peak was 50% less than the first year peak.

4.3.4 Abundance and biomass composition of the herbivore guild

The percentage contribution by the major herbivore taxa to total herbivore abundance and biomass during the first two years of succession is given in Table 4.9. The Hemiptera became numerically the most important group during the first year and remained so for the first half of the second season with the Homoptera especially important, although numbers of herbivorous Heteroptera were fairly high on several occasions. Contributions to total herbivore abundance and biomass by Coleoptera in the first year were kept at relatively low levels, except for June and August when contributions reached 30% and almost 50% for abundance and biomass respectively. In the second year levels were also low, until August, when there was a rather sudden switch from a mainly homopteran-dominated community to a predominantly beetle fauna (see later for details). Patterns of biomass contribution to the herbivore community followed similar trends as for abundance except that the drop in biomass contribution of Hemiptera in the mid-summer of the second year was not as marked as that for abundance. Consequently, the Hemiptera and Coleoptera had an almost equal share in herbivore biomass for the latter half of the second year.

Table 4.10 gives details of the structure of the insect herbivore guild in terms of the 18 families encountered during the first two years. The Miridae was by far the most important heteropteran family during both years, but especially in the first year where contributions to total abundance and biomass had risen to 31% and 56% respectively by September. *Lygus*

TABLE 4.9: Percentage contribution by the major herbivore taxa to total herbivore abundance and biomass during the first two years of succession (Site A). Abundance contribution = upper figure; Biomass contribution in italics.

	YEAR 1						YEAR 2					
	MAY	JUNE	JULY	AUG	SEPT	OCT	MAY	JUNE	JULY	AUG	SEPT	OCT
Orthoptera	0 *(0)*	1 *(10)*	0 *(0)*	<1 *(2)*	0 *(0)*	0 *(0)*	0 *(0)*	0 *(0)*	<1 *(<1)*	<1 *(6)*	0 *(0)*	0 *(0)*
Hemiptera-Heteroptera	0 *(0)*	4 *(5)*	14 *(16)*	22 *(19)*	35 *(60)*	9 *(21)*	7 *(15)*	6 *(11)*	62 *(61)*	8 *(7)*	11 *(19)*	20 *(30)*
Hemiptera-Homoptera	0 *(0)*	50 *(38)*	46 *(35)*	42 *(29)*	51 *(23)*	78 *(44)*	77 *(59)*	61 *(68)*	21 *(25)*	19 *(36)*	26 *(39)*	18 *(26)*
Total Hemiptera	0 *(0)*	53 *(43)*	60 *(51)*	64 *(48)*	86 *(83)*	87 *(65)*	84 *(74)*	67 *(79)*	83 *(86)*	27 *(43)*	37 *(58)*	38 *(56)*
Thysanoptera	0 *(0)*	14 *(1)*	12 *(<1)*	6 *(<1)*	<1 *(<1)*	<1 *(<1)*	0 *(0)*	0 *(0)*	0 *(0)*	0 *(0)*	0 *(0)*	0 *(0)*
Lepidoptera	0 *(0)*	<1 *(<1)*	3 *(19)*	<1 *(<1)*	0 *(0)*	<1 *(<1)*	0 *(0)*	<1 *(<1)*	<1 *(<1)*	<1 *(<1)*	0 *(0)*	0 *(0)*
Coleoptera	100 *(100)*	30 *(45)*	25 *(29)*	30 *(49)*	14 *(17)*	13 *(35)*	16 *(26)*	33 *(21)*	16 *(13)*	73 *(50)*	63 *(42)*	62 *(44)*
TOTAL HERBIVORE ABUNDANCE	8	379	923	2132	1889	1188	348	356	1217	823	563	350

TABLE 4.10: Percentage Contributions to Total Insect Herbivore Abundance and Biomass by Insect Families During the First Two Years of Succession (Site A).

	Year 1						Year 2					
	May	June	July	Aug	Sept	Oct	May	June	July	Aug	Sept	Oct
Orthoptera												
Acrididae	0	1	0	<1	0	0	0	0	<1	<1	0	0
	(0)	*(10)*	*(0)*	*(2)*	*(0)*	*(0)*	*(0)*	*(0)*	*(<1)*	*(6)*	*(0)*	*(0)*
Hemiptera-Heteroptera												
Miridae	0	3	13	21	31	3	1	5	61	7	4	5
	(0)	*(5)*	*(15)*	*(17)*	*(56)*	*(12)*	*(4)*	*(9)*	*(60)*	*(5)*	*(10)*	*(12)*
Tingidae	0	0	0	<1	<1	0	0	0	0	0	<1	0
	(0)	*(0)*	*(0)*	*(<1)*	*(<1)*	*(0)*	*(0)*	*(0)*	*(0)*	*(0)*	*(<1)*	*(0)*
Berytinidae	0	<1	0	0	0	0	0	0	0	0	0	0
	(0)	*(<1)*	*(0)*	*(0)*	*(0)*	*(0)*	*(0)*	*(0)*	*(0)*	*(0)*	*(0)*	*(0)*
Lygaeidae	0	0	<1	<1	2	5	5	<1	<1	1	7	15
	(0)	*(0)*	*(<1)*	*(1)*	*(2)*	*(8)*	*(10)*	*(1)*	*(1)*	*(<1)*	*(9)*	*(18)*
Rhopalidae	0	0	<1	<1	<1	<1	0	0	0	0	0	0
	(0)	*(0)*	*(<1)*	*(<1)*	*(<1)*	*(<1)*	*(0)*	*(0)*	*(0)*	*(0)*	*(0)*	*(0)*
Coreidae	0	0	0	0	<1	0	0	0	0	0	0	0
	(0)	*(0)*	*(0)*	*(0)*	*(2)*	*(0)*	*(0)*	*(0)*	*(0)*	*(0)*	*(0)*	*(0)*
Cydnidae	0	0	0	<1	<1	0	0	0	0	0	0	0
	(0)	*(0)*	*(0)*	*(<1)*	*(<1)*	*(0)*	*(0)*	*(0)*	*(0)*	*(0)*	*(0)*	*(0)*
Piesmidae	0	<1	<1	<1	<1	1	<1	<1	0	0	0	0
	(0)	*(<1)*	*(<1)*	*(<1)*	*(<1)*	*(<1)*	*(<1)*	*(<1)*	*(0)*	*(0)*	*(0)*	*(0)*

Continued.....

TABLE 4.10: (Cont...)

	Year 1						Year 2					
	May	June	July	Aug	Sept	Oct	May	June	July	Aug	Sept	Oct
Hemiptera-Homoptera												
Aphididae	0	16	22	11	22	63	48	11	10	1	0	0
	(0)	*(4)*	*(9)*	*(3)*	*(4)*	*(23)*	*(7)*	*(6)*	*(4)*	*(<1)*	*(0)*	*(0)*
Cercopidae	0	0	0	0	0	0	0	0	<1	0	<1	0
	(0)	*(0)*	*(0)*	*(0)*	*(0)*	*(0)*	*(0)*	*(0)*	*(1)*	*(0)*	*(1)*	*(0)*
Cicadellidae	0	32	24	29	29	9	10	48	7	16	25	17
	(0)	*(30)*	*(26)*	*(23)*	*(19)*	*(17)*	*(28)*	*(59)*	*(16)*	*(33)*	*(37)*	*(26)*
Delphacidae	0	2	0	2	0	6	19	2	4	2	<1	1
	(0)	*(4)*	*(0)*	*(3)*	*(0)*	*(4)*	*(24)*	*(3)*	*(4)*	*(2)*	*(1)*	*(<1)*
Thysanoptera												
Aeolothripidae	0	3	<1	<1	0	0	0	0	0	0	0	0
	(0)	*(<1)*	*(<1)*	*(<1)*	*(0)*	*(0)*	*(0)*	*(0)*	*(0)*	*(0)*	*(0)*	*(0)*
Thripidae	0	12	11	6	<1	<1	0	0	0	0	0	0
	(0)	*(1)*	*(<1)*	*(<1)*	*(<1)*	*(<1)*	*(0)*	*(0)*	*(0)*	*(0)*	*(0)*	*(0)*
Coleoptera												
Chrysomelidae	37	14	3	11	2	<1	<1	2	<1	1	4	9
	(20)	*(21)*	*(5)*	*(20)*	*(2)*	*(<1)*	*(<1)*	*(1)*	*(<1)*	*(<1)*	*(2)*	*(4)*
Curculionidae	50	16	22	19	11	12	15	31	16	72	59	53
	(30)	*(20)*	*(24)*	*(29)*	*(15)*	*(34)*	*(25)*	*(20)*	*(12)*	*(50)*	*(40)*	*(40)*

TABLE 4.10: (cont...)

	Year 1						Year 2					
	May	June	July	Aug	Sept	Oct	May	June	July	Aug	Sept	Oct
Elateridae	13	1	0	0	0	0	<1	0	0	0	0	0
	(50)	*(4)*	*(0)*	*(0)*	*(0)*	*(0)*	*(<1)*	*(0)*	*(0)*	*(0)*	*(0)*	*(0)*

Abundance = upper figure; biomass in italics.

rugulipennis was the dominant mirid in the first year and reached around 45 individuals/m^2 in September. Another mirid species, *Plagiognathus chrysanthemi*, was also important during the first year. The Miridae was less important in the second year although *P.chrysanthemi* was exceptionally common in July with 54 individuals/m^2. Of the Homoptera, the Aphididae and Cicadellidae were the most important families, with the Delphacidae relatively insignificant. Aphids contributed between 10-22% to total abundance for most of the growing season and by the end of the year this had risen to 63%. The following spring, aphid contribution was still high at 48% of total abundance, but their importance subsequently declined rapidly. However, the small size of the Aphididae made their percentage contribution to total biomass considerably lower and less than 10%, except in October of the first season when aphids contributed as much as 23% to total biomass. The cicadellids were important contributors to total herbivore abundance and biomass throughout much of the first two years. Their percentage contribution ranged between 24-32% and 17-30% for abundance and biomass respectively in the first year, although the abundance contribution did drop in October to 9%. *Macrosteles laevis* and *M.sexnotatus* were the most important cicadellids during the first season with *Euscelis lineolatus* also occurring in significant numbers. In the second year the percentage contributions of the Cicadellidae to total herbivore abundance and biomass fluctuated considerably, ranging from between 7-48% and 16-59% for abundance and biomass respectively. *E.lineolatus* and *E.incisus* were the most important species found during the second year with *M.laevis* and *Mocydiopsis parvicauda* fairly common on several occasions. The percentage contribution to total abundance and biomass by the Delphacidae was generally minor although in May of the second year their contributions were relatively high at 19% and 24% respectively.

The Curculionidae was the most important family of herbivorous beetles encountered during both years. Although the curculionids represented a major component of the herbivore guild in May (50% abundance, 30% biomass) of the first year it should be noted that total herbivore abundance was extremely low at this time (0.6 individuals/m^2). For the remainder of the first year and the first three months of the second growing season the percentage contribution of the weevils to total herbivore abundance and biomass ranged between 11-31% and 12-34% respectively. By the latter half of the second year these respective contributions had risen dramatically to 53-72% and 40-50%. The most important species of weevil found during the first year were *Ceutorhynchus floralis* and *Sitona lineatus*. The genus *Apion* was the most common type in the second year, especially *Apion apricans*, *A.hookeri*, *A.trifolii* and to a lesser extent, *A.dichroum* and *A.virens.*

4.3.5 Abundance and biomass composition of the predator guild

The percentage contributions by the major predator taxa to total predator abundance and biomass during the first two years of succession is given in Table 4.11. Spider abundance and biomass contributions rose rapidly during the first year, eventually representing 87% and 62% of total predator abundance and biomass respectively. Similar proportions were reached at the end of the second year following an early summer increase. Insect predator contributions show almost reverse trends to those of the Araneae with abundance and biomass contributions generally falling off after mid-summer. The Coleoptera was the most important insect predator taxum for most of the first year and the first two months of the second year. The Heteroptera were especially important for biomass contributions to the insect predator guild in October of the first year and from July onwards in the second year (see below).

Details of the structure of the guild are given in Table 4.12, where the relative importance is shown for the 9 families of insect predators and 11 spider families encountered during the two year period. Only information on spider abundance is available and then solely in the first year. The most important family of heteropteran predators was the Nabidae, with contributions to total biomass rising to 21% at the end of the first year and fluctuating for the most part of the second year between 17-36%. Nabid abundance was very low in the first year (<6% of the predator guild) and higher, but still relatively low, in the second year. *Nabis rugosus* was the dominant nabid in both years while in the second year *N.ferus* and *N.flavomarginatus* made small contributions. The Carabidae and Staphylinidae, and to a lesser extent the Coccinellidae, were the dominant Coleoptera predators although the smaller size of the staphylinids made them only relatively small contributors to biomass. For example, maximum values in the first year of 50-56% and 20-22% for abundance and biomass respectively for Staphylinidae and 7-9% and 25-35% respectively for Carabidae. In the second growing season the highest levels for these taxa were reached in May for Staphylinidae (36% abundance, 26% biomass) and in June for Carabids (13% abundance, 40% biomass). *Bembidion lampros* was the most abundant carabid during the first year. No information is available on individual carabid species for the second year. The limited information on the spider fauna for the first year shows that the Linyphiidae were the most important family with the Theridiidae gaining in importance towards the end of the season.

TABLE 4.11: Percentage contributions by major predator taxa to total predator abundance and biomass during the first two years of succession (Site A) Abundance contribution = upper value; biomass contributions in italics.

	YEAR 1						YEAR 2					
	MAY	JUNE	JULY	AUG	SEPT	OCT	MAY	JUNE	JULY	AUG	SEPT	OCT
Hemiptera-Heteroptera	0 *(0)*	0 *(0)*	1 *(2)*	9 *(13)*	10 *(16)*	5 *(24)*	4 *(10)*	12 *(17)*	18 *(36)*	14 *(37)*	9 *(26)*	4 *(21)*
Neuroptera	0 *(0)*	0 *(0)*	<1 *(<1)*	2 *(2)*	0 *(0)*	<1 *(<1)*	0 *(0)*	0 *(0)*	0 *(0)*	<1 *(<1)*	0 *(0)*	0 *(0)*
Coleoptera	100 *(100)*	75 *(96)*	69 *(75)*	59 *(56)*	23 *(14)*	8 *(14)*	48 *(59)*	39 *(62)*	13 *(18)*	12 *(9)*	17 *(15)*	11 *(16)*
Araneae	0 *(0)*	25 *(4)*	30 *(22)*	30 *(29)*	67 *(70)*	87 *(62)*	48 *(31)*	49 *(21)*	69 *(46)*	73 *(54)*	74 *(59)*	85 *(63)*
Total Predator abundance	99	146	994	1110	845	829	327	214	327	273	475	500

TABLE 4.12: Percentage Contributions to Total Predator Abundance and Biomass by Invertebrate Families During the First Two Years of Succession (Site A).

	Year 1						Year 2					
	May	June	July	Aug	Sept	Oct	May	June	July	Aug	Sept	Oct
Hemiptera-Heteroptera												
Anthocoridae	0	0	0	4	4	2	1	1	2	2	1	0
	(0)	*(0)*	*(0)*	*(3)*	*(1)*	*(3)*	*(1)*	*(<1)*	*(2)*	*(1)*	*(<1)*	*(0)*
Nabidae	0	0	1	5	5	3	3	11	16	12	8	4
	(0)	*(0)*	*(2)*	*(10)*	*(14)*	*(21)*	*(9)*	*(17)*	*(34)*	*(36)*	*(25)*	*(21)*
Saldidae	0	0	<1	<1	1	<1	0	<1	0	0	<1	0
	(0)	*(0)*	*(<1)*	*(<1)*	*(1)*	*(<1)*	*(0)*	*(<1)*	*(0)*	*(0)*	*(<1)*	*(0)*
Neuroptera												
Chrysopidae	0	0	<1	0	0	0	0	0	0	0	0	0
	(0)	*(0)*	*(<1)*	*(0)*	*(0)*	*(0)*	*(0)*	*(0)*	*(0)*	*(0)*	*(0)*	*(0)*
Hemerobiidae	0	0	0	2	0	<1	0	0	0	<1	0	0
	(0)	*(0)*	*(0)*	*(2)*	*(0)*	*(<1)*	*(0)*	*(0)*	*(0)*	*(<1)*	*(0)*	*(0)*
Coleoptera												
Cantharidae	0	0	<1	0	0	0	0	0	0	0	0	0
	(0)	*(0)*	*(2)*	*(0)*	*(0)*	*(0)*	*(0)*	*(0)*	*(0)*	*(0)*	*(0)*	*(0)*
Carabidae	100	45	9	7	7	2	10	13	2	2	3	4
	(100)	*(26)*	*(34)*	*(25)*	*(5)*	*(6)*	*(31)*	*(40)*	*(2)*	*(2)*	*(3)*	*(4)*
Coccinellidae	0	10	3	2	1	2	2	6	1	9	7	4
	(0)	*(58)*	*(17)*	*(11)*	*(1)*	*(3)*	*(2)*	*(14)*	*(2)*	*(6)*	*(6)*	*(6)*

Continued....

TABLE 4.12: (Cont..)

	Year 1						Year 2					
	May	June	July	Aug	Sept	Oct	May	June	July	Aug	Sept	Oct
Staphylinidae	0	20	56	50	15	4	36	20	10	1	7	3
	(0)	*(12)*	*(22)*	*(20)*	*(8)*	*(5)*	*(26)*	*(8)*	*(14)*	*(1)*	*(6)*	*(6)*
Araneae												
Aranidae	0	1	<1	<1	1	1						
Clubionidae	0	0	0	<1	2	1						
Gnaphosidae	0	0	0	0	<1	0						
Linyphiidae	0	12	22	15	33	52						
Lycosidae	0	0	<1	1	3	<1						
Mimetidae	0	0	<1	0	<1	0						
Pisauridae	0	0	0	2	2	2						
Salticidae	0	0	0	0	<1	0						
Tetragnathidae	0	0	1	7	11	3						
Theridiidae	0	4	1	1	12	24						
Thomisidae	0	0	1	4	3	3						
Unidentified immatures	0	8	4	0	0	0						

Abundance contribution, upper figure; biomass contribution in italics. Biomass data is not available for spider families or smaller taxa and abundance data for spider families is available for one year only.

Bathyphantes gracilis, Erigone atra and *Lepthyphantes ericaeus* were the most common linyphiids and the most important theridiid was *Theridion bimaculatum.*

4.3.6 Abundance and biomass composition of the omnivore guild

As has already been mentioned, the omnivore guild represented a relatively insignificant contribution to the insect and spider community in terms of abundance and biomass. Of this feeding type, the Miridae was the most important heteropteran group and was represented by *Phytocoris varipes, Plagiognathus arbustorum* and *Dicyphus errans* in both years. Of the beetle omnivores the Cryptophagidae, Lathridiidae and Nitidulidae were the most important (Table 4.13a,b).

4.4 LIFE-HISTORY STRATEGIES

4.4.1 Introduction

This section analyses the strategies of insect herbivores in terms of:-

(1) the herbivore load on each of the four major plant groupings;
(2) the degree of specialisation on host-plants;
(3) herbivore feeding strategies;
(4) overwintering strategies;
(5) voltinism.

Problems arose when attempting to provide accurate information for (1) and (2) because sources of host-plant records from the literature are not always complete or reliable. This shortcoming has also frustated a number of researchers such as Lawton & Schroeder (1978) and Hill (1982 and *pers.comm.*) where it was especially applicable to obtaining host-plant information in studies of biological control of weeds. Also, since this study was not concerned with insect stages living within plant structures, such as borers and miners, records for the Coleoptera whose immature stages are predominantly internal feeders may not be totally reliable. This especially concerns the Curculionidae whose adults may or may not feed and, in-

TABLE 4.13: Percentage contributions to total omnivore abundance and biomass during the first two years of succession (Site A).

a. *% contributions by major omnivore taxa*
b. *% contributions by insect families*
Abundance contribution = upper figure; biomass contribution in italics.

(a)	YEAR 1						YEAR 2					
	MAY	JUNE	JULY	AUG	SEPT	OCT	MAY	JUNE	JULY	AUG	SEPT	OCT
Hemiptera-Heteroptera	0 *(0)*	0 *(0)*	0 *(0)*	<1 *(8)*	<1 *(20)*	0 *(0)*	2 *(25)*	8 *(4)*	40 *(91)*	38 *(93)*	20 *(80)*	2 *(30)*
Coleoptera	100 *(100)*	100 *(100)*	100 *(100)*	99 *(92)*	99 *(80)*	100 *(100)*	98 *(75)*	92 *(96)*	60 *(9)*	62 *(7)*	80 *(20)*	98 *(70)*
Total Omnivore abundance	1	63	353	329	202	82	58	13	94	99	76	41

(b)	YEAR 1						YEAR 2					
	MAY	JUNE	JULY	AUG	SEPT	OCT	MAY	JUNE	JULY	AUG	SEPT	OCT
Hemiptera-Heteroptera												
Berytinidae	0 *(0)*	0 *(0)*	0 *(0)*	0 *(0)*	0 *(0)*	0 *(0)*	2 *(25)*	0 *(0)*	6 *(18)*	7 *(13)*	3 *(8)*	2 *(30)*
Miridae	0 *(0)*	0 *(0)*	0 *(0)*	*(<1)* *(8)*	*(<1)* *(20)*	0 *(0)*	0 *(0)*	8 *(4)*	34 *(73)*	31 *(80)*	17 *(72)*	0 *(0)*

Continued

TABLE 4.13: (Continued)

(b) continued	YEAR 1 MAY	 JUNE	 JULY	 AUG	 SEPT	 OCT	YEAR 2 MAY	 JUNE	 JULY	 AUG	 SEPT	 OCT
Coleoptera												
Cryptophagidae	0 *(0)*	2 *(<1)*	49 *(26)*	31 *(25)*	21 *(16)*	7 *(7)*	88 *(65)*	31 *(1)*	52 *(8)*	48 *(5)*	35 *(6)*	17 *(9)*
Lathridiidae	0 *(0)*	2 *(<1)*	26 *(13)*	63 *(51)*	72 *(56)*	89 *(88)*						
Histeridae	0 *(0)*	0 *(0)*	0 *(0)*	0 *(0)*	0 *(0)*	0 *(0)*	0 *(0)*	15 *(87)*	0 *(0)*	0 *(0)*	0 *(0)*	0 *(0)*
Nitidulidae	0 *(0)*	77 *(94)*	23 *(54)*	3 *(14)*	<1 *(2)*	0 *(0)*	0 *(0)*	46 *(8)*	1 *(<1)*	1 *(<1)*	4 *(<1)*	0 *(0)*
Oedemeridae	0 *(0)*	0 *(0)*	<1 *(6)*	0 *(0)*	0 *(0)*	0 *(0)*	0 *(0)*	0 *(0)*	0 *(0)*	0 *(0)*	0 *(0)*	0 *(0)*
Phalacridae	0 *(0)*	19 *(5)*	2 *(1)*	2 *(2)*	6 *(6)*	4 *(5)*	10 *(10)*	0 *(0)*	7 *(1)*	13 *(2)*	41 *(14)*	81 *(61)*
Silphidae	100 *(100)*	0 *(0)*	0 *(0)*	0 *(0)*	0 *(0)*	0 *(0)*	0 *(0)*	0 *(0)*	0 *(0)*	0 *(0)*	0 *(0)*	0 *(0)*

deed, in many cases (*e.g. Apion* spp.) the adults most likely cannot feed to any great extent (R.T.Thompson, *pers.comm.*).

Furthermore, when describing the abundance and biomass of herbivores on each of the plant groupings, some species are associated with more than one group and must have their numbers and biomass included in each. For example, if 10 individuals of species *X* attack both annual and perennial herb species then the abundance 'score' given to each group is 10 for that insect species. Biomass is similarly treated.

Where information was available for insect species it was used for a particular life strategy analysis. For example, information on aphids and the few species of Lepidoptera was not always available although abundance and biomass figures have been used in the description of herbivore feeding strategies, since these are known, and could thus be included to provide a more detailed breakdown of the herbivore community.

The question of defining precisely a specialist and a generalist was solved by devising 3 grades of specialists and 1 generalist category. They are defined as follows:-

Specialist Grade 1 : restricted to a single host-plant species.
Specialist Grade 2 : restricted to a single host-plant genus but to more than species.
Specialist Grade 3 : restricted to within a plant family but to more than one genus.
Generalist : any numbers of host-plant genera and species in more than one family.

Clearly, one drawback in using this classification is that the categories get wider from Grade 1 specialists to generalists. However, it will be shown later (Section 4.4.3) that this was an adequate framework within which to quantify and compare the relative proportions of specialist and generalist habits adopted by insect herbivores colonising the early successional habitat.

It was also hoped to present information on the preference of insect species for different plant structures (*i.e.* vegetative *vs* reproductive tissue). However, because of a paucity of reliable sources, it has not been possible to achieve this here, although in Chapter Five, where insect-plant relationships are investigated, various insect associations with plant structure types (or architecture) are presented.

Full details of life-history strategy information used here is given in Appendix 6.

4.4.2 The herbivore load on the four major plant groupings

Patterns of abundance and biomass during the first two years of succession are shown in Fig. 4.9 for insects attacking annuals, biennials, perennials and grasses (data from literature records and various personal communications). The abundances of all four feeding groups in the first year rose to maximum levels in August; with the exception of the perennials this gradually declined to October (Fig. 4.9a). Maximum abundances during the first year were equivalent to 86, 61, 51 and 28 individuals/m^2 for annuals, perennials, Gramineae and biennial feeders respectively. Levels of abundance in the second season show similar trends although certain differences are evident. The peak abundance occurred earlier in July for perennial, annual and biennial feeders with abundances of 72, 63 and 58 individuals/m^2 respectively. Populations of grass feeders remained extremely low throughout the second year and never exceeded an abundance equivalent to 14 individuals/m^2.

Biomass patterns were similar to those for abundance although differences between the two years were greater (Fig. 4.9b). Annual and perennial feeders were equally important in the first season where their biomass rose extremely rapidly to September. Insects feeding on biennials and grasses had a lower and more consistent biomass peaks during this ruderal period. The biomass of the four plant feeding groups during the second year was considerably lower than in the previous year.

The relative importance of the insect herbivore groups in terms of percentage contribution to abundance and biomass is given in Table 4.14 for major taxa. Heteroptera (Miridae) and Coleoptera (Curculionidae and, to a lesser extent, Chrysomelidae) were the most important groups attacking the three herb groups with the Homoptera (Cicadellidae and, to a lesser extent, Delphacidae) the dominant grass feeders.

The numbers of species attacking the major plant groupings over the two years is compared in Table 4.15. Apart from the May sample of the first year (where numbers of species were low) the proportions of species on each major plant group remained remarkably stable, ranging from 50-58% and 43-53% for annual feeders through the first and second years respectively and apparently declining by the end of the second season. The species contribution by perennial feeders shows a general rise during the first year, after May, reaching 52% at the end of the season and forming 56% of the community by the end of the second year.

Fig. 4.9 Abundance and biomass of insect herbivores attacking the four major plant groupings during the first two years of succession (Site A).

a. Abundance.
b. Biomass.

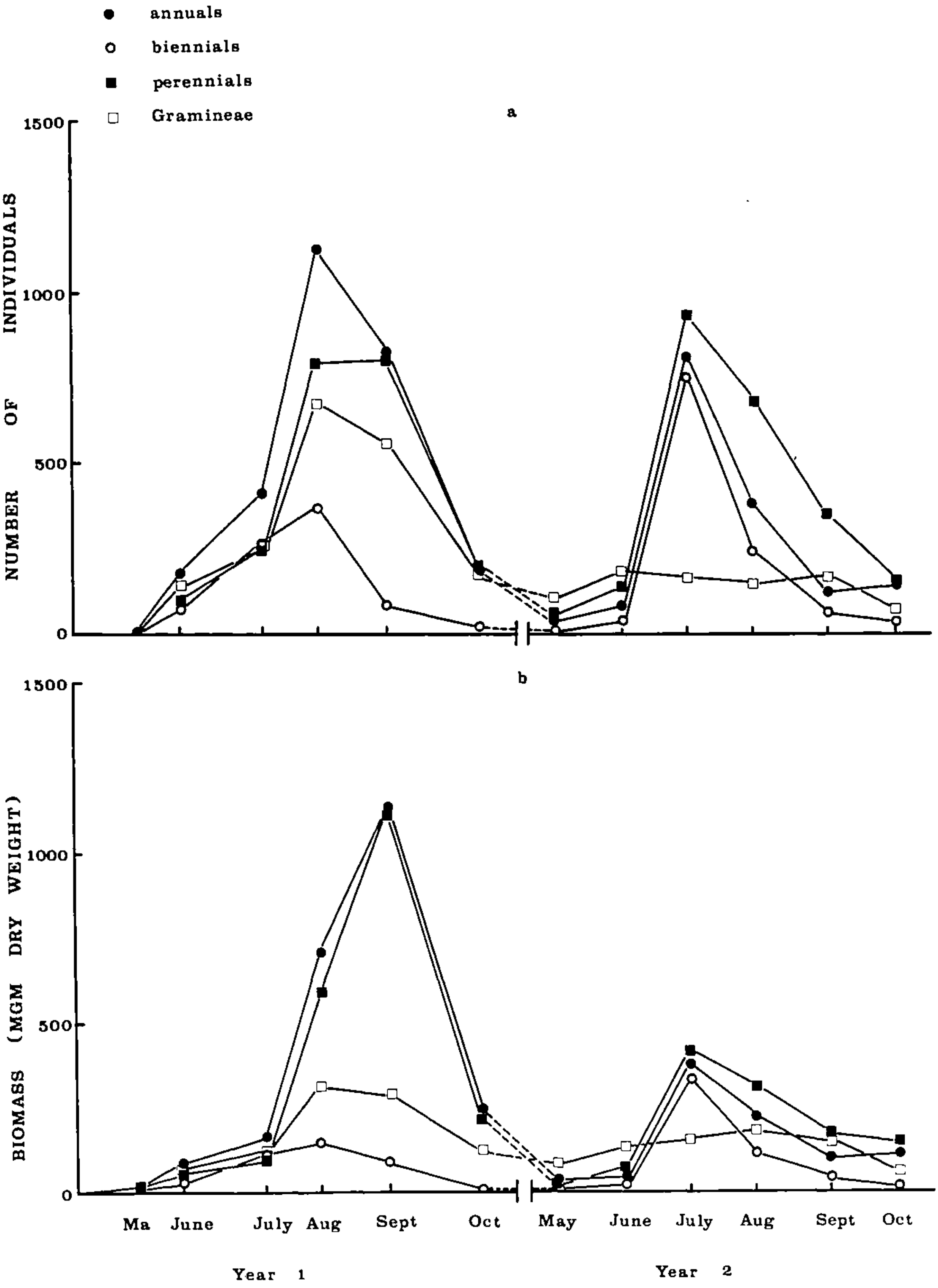

● annuals
○ biennials
■ perennials
□ Gramineae
a
NUMBER OF INDIVIDUALS
1500
1000
500
0
b
BIOMASS (MGM DRY WEIGHT)
1500
1000
500
0
Ma
June
July
Aug
Sept
Oct
May
June
July
Aug
Sept
Oct
Year 1
Year 2

TABLE 4.14: Percentage Contributions to Insect Herbivore Abundance and Biomass by Major Insect Taxa Attacking the Major Plant Groupings (Site A).

Abundance contribution, upper value; biomass contribution in parentheses.

	Year 1						Year 2					
	May	June	July	Aug	Sept	Oct	May	June	July	Aug	Sept	Oct
Annuals												
Hemiptera-Heteroptera	0	4	19	24	41	11	2	5	69	11	4	4
	(0)	*(5)*	*(21)*	*(19)*	*(60)*	*(17)*	*(3)*	*(11)*	*(65)*	*(17)*	*(13)*	*(12)*
Thysanoptera	0	17	12	7	1	1	0	0	0	0	0	0
	(0)	*(<1)*	*(1)*	*(<1)*	*(<1)*	*(<1)*	*(0)*	*(0)*	*(0)*	*(0)*	*(0)*	*(0)*
Coleoptera	87	33	28	28	16	31	23	20	6	36	19	37
	(100)	*(41)*	*(35)*	*(49)*	*(15)*	*(44)*	*(23)*	*(13)*	*(5)*	*(29)*	*(17)*	*(34)*
Total	87	54	59	59	57	43	25	25	75	47	23	41
	(100)	*(46)*	*(57)*	*(68)*	*(75)*	*(61)*	*(26)*	*(24)*	*(70)*	*(46)*	*(30)*	*(46)*
Biennials												
Hemiptera-Heteroptera	0	0	13	6	3	1	0	6	68	10	3	0
	(0)	*(0)*	*(12)*	*(4)*	*(1)*	*(<1)*	*(0)*	*(10)*	*(62)*	*(14)*	*(8)*	*(0)*
Thysanoptera	0	2	1	<1	0	0	0	0	0	0	0	0
	(0)	*(<1)*	*(<1)*	*(<1)*	*(0)*	*(0)*	*(0)*	*(0)*	*(0)*	*(0)*	*(0)*	*(0)*
Coleoptera	12	22	24	12	3	3	1	6	1	20	9	10
	(2)	*(15)*	*(22)*	*(9)*	*(5)*	*(1)*	*(<1)*	*(2)*	*(1)*	*(9)*	*(4)*	*(5)*
Total	12	24	38	19	6	4	1	12	69	30	12	10
	(2)	*(15)*	*(35)*	*(14)*	*(6)*	*(1)*	*(1)*	*(12)*	*(63)*	*(23)*	*(12)*	*(5)*

Continued....

TABLE 4.14:(cont..)

	Year 1						Year 2					
	May	June	July	Aug	Sept	Oct	May	June	July	Aug	Sept	Oct
Perennials												
Hemiptera-Heteroptera	0	3	18	23	40	9	1	6	69	11	4	4
	(0)	*(5)*	*(21)*	*(19)*	*(59)*	*(16)*	*(2)*	*(11)*	*(65)*	*(17)*	*(11)*	*(12)*
Thysanoptera	0	17	12	7	<1	<1	0	0	0	0	0	0
	(0)	*(<1)*	*(1)*	*(<1)*	*(<1)*	*(<1)*	*(0)*	*(0)*	*(0)*	*(0)*	*(0)*	*(0)*
Coleoptera	50	8	4	12	14	34	27	35	17	74	60	38
	(93)	*(18)*	*(11)*	*(38)*	*(15)*	*(44)*	*(26)*	*(21)*	*(13)*	*(50)*	*(39)*	*(41)*
Total	50	28	34	42	54	43	28	41	86	85	64	42
	(93)	*(23)*	*(33)*	*(57)*	*(74)*	*(61)*	*(28)*	*(32)*	*(78)*	*(67)*	*(50)*	*(53)*
Gramineae												
Orthoptera	0	1	0	<1	0	0	0	0	<1	<1	0	0
	(0)	*(11)*	*(0)*	*(2)*	*(0)*	*(0)*	*(0)*	*(0)*	*(<1)*	*(6)*	*(0)*	*(0)*
Hemiptera-Heteroptera	0	0	<1	0	0	0	2	0	3	<1	3	1
	(0)	*(0)*	*(<1)*	*(0)*	*(0)*	*(0)*	*(3)*	*(0)*	*(5)*	*(<1)*	*(5)*	*(1)*
Hemiptera-Homoptera	0	41	31	35	38	40	56	57	12	18	26	19
	(0)	*(35)*	*(36)*	*(26)*	*(19)*	*(27)*	*(56)*	*(66)*	*(22)*	*(36)*	*(39)*	*(26)*
Total Hemiptera	0	41	31	35	38	40	58	57	15	18	29	20
	(0)	*(35)*	*(36)*	*(26)*	*(19)*	*(27)*	*(59)*	*(66)*	*(27)*	*(36)*	*(44)*	*(27)*

TABLE 4.14 (cont..)

	Year 1						Year 2					
	May	June	July	Aug	Sept	Oct	May	June	July	Aug	Sept	Oct
Thysanoptera	0	0	3	<1	0	0	0	0	0	0	0	0
	(0)	*(0)*	*(<1)*	*(<1)*	*(0)*	*(0)*	*(0)*	*(0)*	*(0)*	*(0)*	*(0)*	*(0)*
Coleoptera	0	2	0	0	0	0	<1	0	0	0	<1	0
	(0)	*(1)*	*(0)*	*(0)*	*(0)*	*(0)*	*(<1)*	*(0)*	*(0)*	*(0)*	*(<1)*	*(0)*
Total	0	44	35	35	38	40	59	57	15	18	29	20
	(0)	*(47)*	*(36)*	*(29)*	*(19)*	*(27)*	*(59)*	*(66)*	*(27)*	*(42)*	*(44)*	*(27)*

Note that total contributions of each major group (on each sample occasion), when summed, will be greater than 100%.

TABLE 4.15 Comparison of the number of different herbivore species attacking the four major plant groups over the first two years of succession (Site A)

	YEAR 1						YEAR 2					
	MAY	JUNE	JULY	AUG	SEPT	OCT	MAY	JUNE	JULY	AUG	SEPT	OCT
Total species richness	5	40	36	55	54	36	34	34	36	47	46	40
% annuals	100	57	58	58	50	50	52	53	50	43	48	40
% biennials	20	28	31	36	22	22	6	21	28	15	22	10
% perennials	60	33	48	47	52	52	68	62	58	57	55	56
% Gramineae	0	28	26	27	26	25	18	27	42	36	35	27

TABLE 4.16. The diversity of insect herbivores attacking the four major plant groupings during the first two years of succession (Site A) (Williams α). Note, ∞ represents very low values of n and s:- $\infty^1 = (n = 1, s = 1)$; $\infty^2 = (n = 2, s = 2)$.

	YEAR 1						YEAR 2					
	MAY	JUNE	JULY	AUG	SEPT	OCT	MAY	JUNE	JULY	AUG	SEPT	OCT
Annuals	7.8	7.1	4.7	6.1	5.3	4.9	10.9	7.2	3.3	4.5	2.7	8.9
Biennials	∞^1	3.6	2.3	4.6	3.8	5.9	∞^2	2.6	1.6	1.3	1.3	1.2
Perennials	5.5	4.2	4.2	4.9	5.6	5.3	16.1	7.1	3.8	5.6	6.4	7.7
Gramineae	-	3.1	2.1	2.9	2.6	2.0	1.4	2.0	4.0	5.0	4.4	3.7
Total	5.7	11.7	8.1	11.1	11.2	9.3	12.9	10.0	7.1	11.4	12.4	12.0

Biennial and grass feeders contributed similar, but lower, numbers of species in the first year (22-36%). In the second season grass feeders rose to a 42% maximum contribution (in July) and then declined; the species contribution of biennial feeders was again low and fluctuated from 6-28%. Although data are not available for aphid species the overall trends are likely to be similar, since the majority of early successional aphid species (from similar sites) attack the three herb groupings with few feeding on Gramineae (M.Llewellyn, *pers.comm.* and from data of Southwood *et al*, *pers.comm.*).

Insect diversity over the two years was greatest for annual and perennial herb feeders although α-diversity of grass feeders had risen to significant levels by July of the second season (Table 4.16). The Coleoptera were the main contributors to insect diversity on all three herb feeding groups with the Homoptera contributing most to α of grass feeders. The high levels of α found for May of the first year for total herbivores is an artefact of extremely low numbers of individuals and species.

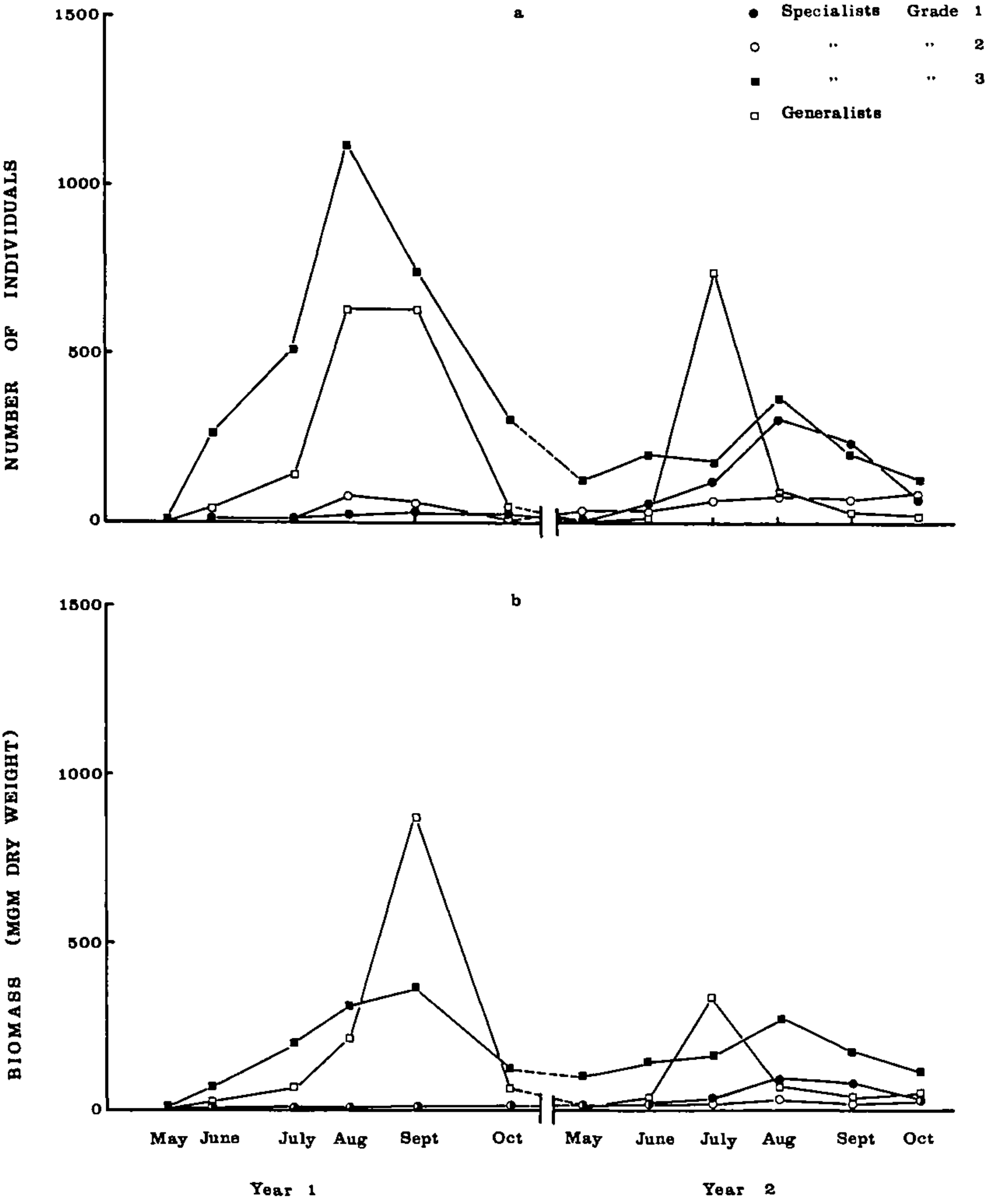
4.4.3 The degree of specialisation on host-plants

Host-plant affinities may be further analysed by considering the degree of specialisation of their associated phytophagous insects. Fig.4.10 shows the patterns of abundance and biomass of the generalists and three categories of specialist feeders over the two year period. In abundance Grade 3 specialists were most important during the first year (Fig. 4.10a) with a rapid rise to August (86 individuals/m^2) followed by an equally rapid decline to October. Generalists were also important during this period with abundance rising to an August-September plateau (48 individuals/m^2) and then falling off in numbers at the end of the season. Both Grade 1 and 2 specialists were very uncommon during the first year. Levels of Grade 3 specialists were considerably lower in the second year and showed only minor fluctuations. This category only attained a maximum abundance of 28 individuals/m^2 (in August) during the second season. Generalist herbivores in the second year had low abundance through May and June followed by a dramatic rise to a maximum in July (58 individuals/m^2) with a subsequent decline to low numbers the following month. Numbers of Grade 2 specialists were maintained at very low levels throughout the second year. Specialists Grade 1, on the other hand, followed similar levels of abundance to the Grade 3 specialists in the second year and reached an abundance of 24 individuals/m^2 in mid-summer.

Biomass patterns for the four feeding categories in the second year closely resembled

Fig. 4.10 Abundance and biomass of specialists and generalists during the first two years of succession (Site A).

a. Abundance.
b. Biomass.


a
● Specialists Grade 1
○ " " 2
■ " " 3
□ Generalists
NUMBER OF INDIVIDUALS
1500
1000
500
0
b
BIOMASS (MGM DRY WEIGHT)
1500
1000
500
0
May
June
July
Aug
Sept
Oct
May
June
July
Aug
Sept
Oct
Year 1
Year 2

those for abundance during the same period (Fig. 4.10b). In the first year, however, generalists dominated the biomass with maximum values in September, with specialists Grade 3 making a lower but more consistent contribution.

The relative importance of phytophagous insects in terms of percentage contributions to total herbivore abundance and biomass by specialists and generalists is given in Table 4.17 for the four feeding categories. The rather surprising high contribution of Grade 1 specialists in the second year was a result of large numbers of two monophagous curculionids, *Apion apricans* and *A.trifolii*, both attacking *Trifolium pratense*, and contributing 43% and 23% to herbivore abundance and biomass respectively in September of the second year. The relatively insignificant Grade 2 specialists were represented primarily by Curculionidae and, to a lesser extent, the Chrysomelidae. The most common Grade 2 specialists were associated with *Senecio* spp. (Chrysomelidae: *Longitarsus flavicornis*), *Trifolium* spp. (Curculionidae: *Apion assimile, A.dichroum, A.virens*) and *Polygonum* spp. (Curculionidae: *Rhinonchus bruchoides*). The grass-feeding Homoptera were the dominant Grade 3 specialists, contributing 33-45% and 24-62% to herbivore abundance and 12-63% and 21-66% to herbivore biomass in the first and second years respectively. Of the Homoptera the cicadellids were the most important (mainly *Euscelis incisus, E.lineolatus, Macrosteles laevis, M.sexnotatus* and *Mocydiopsis parvicauda*) although numbers of the delphacid *Javesella pellucida* were fairly high in May of the second year. The Curculionidae was also a significant group of Grade 3 specialists, with the major representatives feeding on Cruciferae (*Ceutorhynchus assimilis* and *C.floralis*), Leguminosae (*Sitona lineatus* and *S.sulcifrons*) and *Matricaria-Tripleurospermum* spp. (*Apion hookeri*).

The generalist herbivores were represented almost exclusively by heteropteran bugs and then again predominantly by one family, the Miridae. The dominant mirid species, with host-plants given in parentheses, were *Lygus rugulipennis* (Chenopodiaceae, *Urtica, Rumex* spp. and *Trifolium* spp.) and *Plagiognathus chrysanthemi* (*Achillea millefolium, Medicago lupulina, Tripleurospermum maritimum inodorum*). The large increase in generalists in July of the second year was due to the sudden appearance of *P.chrysanthemi* (mainly nymphal stages); adults of this univoltine species were present in large numbers in July and August of the first year at which time they were presumably ovipositing in host-plants (Southwood & Leston, 1959).

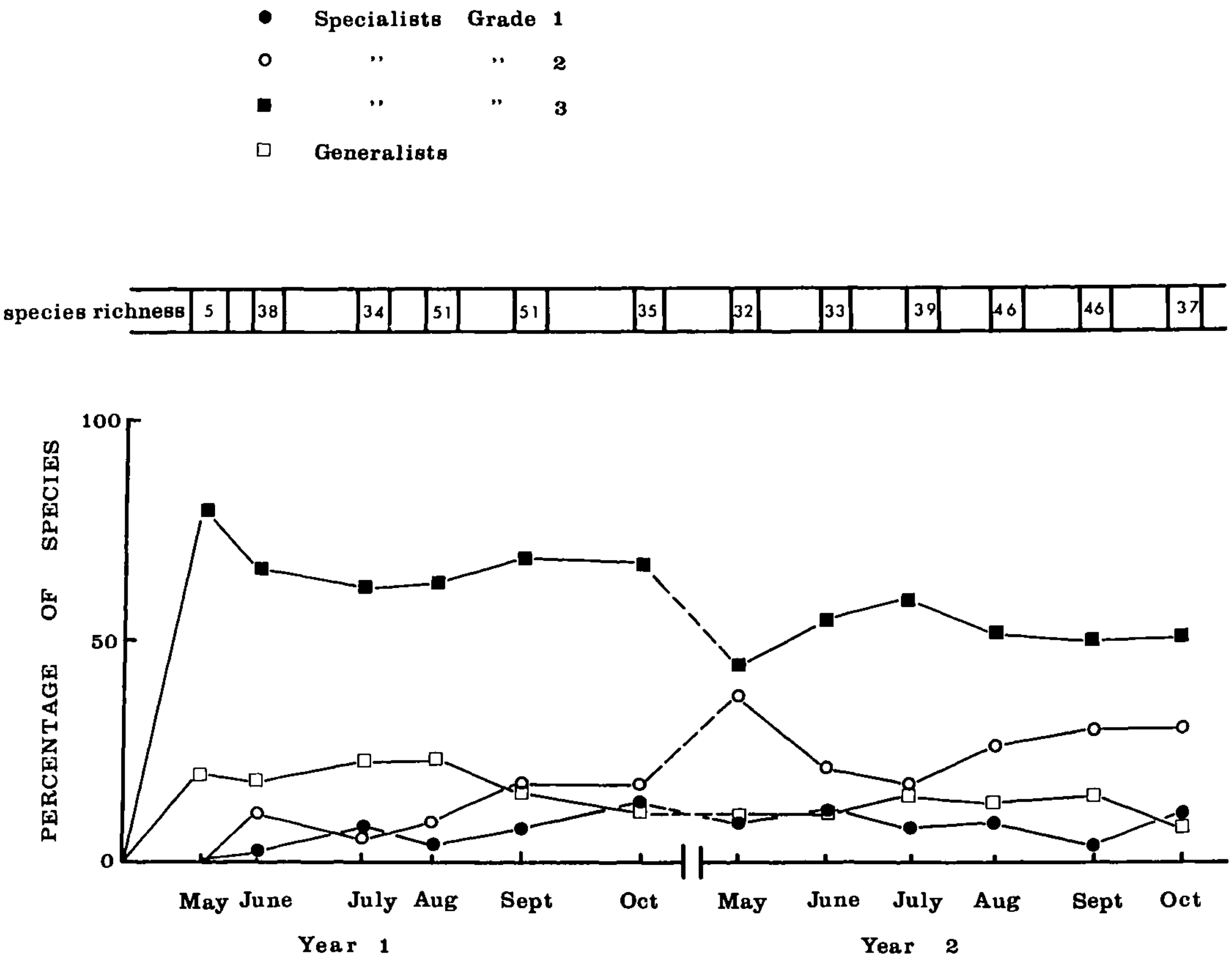
Information on species contributions by the four feeding categories is given in Fig. 4.11. The species composition of the various specialist types and generalists remained relatively uniform during each year. Grade 3 specialists were the main contributors during the first

TABLE 4.17: Percentage Contributions to Insect Herbivore Abundance and Biomass by Specialists and Generalists During the First Two Years of Succession (Site A).

	Year 1						Year 2					
	May	June	July	Aug	Sept	Oct	May	June	July	Aug	Sept	Oct
Specialists Grade 1	0	1	2	1	2	7	4	17	11	36	43	23
	(0)	(<1)	(<1)	(1)	(1)	(2)	(1)	(9)	(7)	(20)	(23)	(11)
Specialists Grade 2	0	2	1	4	3	3	18	12	6	10	12	28
	(0)	(<1)	(<1)	(1)	(<1)	(<1)	(13)	(5)	(5)	(6)	(7)	(14)
Specialists Grade 3	71	85	78	61	52	79	76	65	16	43	41	41
	(71)	(89)	(66)	(60)	(29)	(64)	(83)	(75)	(28)	(60)	(58)	(60)
Generalists	29	12	20	34	43	11	2	6	67	11	4	8
	(29)	(11)	(33)	(38)	(70)	(34)	(3)	(11)	(60)	(14)	(12)	(15)

Abundance contribution, upper figure; biomass contribution in parentheses

Fig. 4.11 Comparison of the number of species attacking the four major plant groupings during the first two years of succession (Site A). Species richness of insect herbivores is given along the figure top.


● Specialists Grade 1
○ ,, ,, 2
■ ,, ,, 3
□ Generalists
species richness
5
38
34
51
51
35
32
33
39
46
46
37
PERCENTAGE OF SPECIES
100
50
0
May
June
July
Aug
Sept
Oct
May
June
July
Aug
Sept
Oct
Year 1
Year 2

year (around 65%) with lower contributions from generalists (10-20%), Grade 2 specialists (2-14%) and Grade 1 specialists (3-13%). In the second season the Grade 3 specialists were again dominant although their contributions had declined slightly (around 50%) as a result of increased importance of the Grade 2 specialists (18-38%). The generalists and Grade 1 specialists remained at low levels throughout the second year with species contributions of 8-15% and 4-12% respectively.

It is unlikely that these trends would be affected by the inclusion of the Aphididae since the majority of species would fall into the specialist Grade 3 category with a considerably smaller number of generalists.

The Grade 3 specialists were the most diverse group during both years, although Grade 2 specialists increased in diversity during the second season. Generalists had a consistently low level of diversity throughout the two years and Grade 1 specialists remained insignificant (Table 4.18). The Coleoptera was the main contributor to α for specialists Grades 2 and 3, although the Grade 3 Homoptera also maintained a high level of diversity. The Coleoptera and Heteroptera were also major contributors to the diversity of generalists for the first year and to a lesser extent the second year.

4.4.4 Herbivore feeding strategies

To a certain extent these patterns can be obtained from the taxonomic composition of the fauna, although it is useful to see how the main feeding strategies, chewing and sap-feeding, develop during the early succession. Patterns of abundance and biomass of these two feeding types can be seen in Fig. 4.12. The sap-feeders are numerically dominant in the first year rising extremely rapidly in abundance and to a lesser extent biomass, with an August-September maximum for abundance (120 individuals/m^2) and a September maximum for biomass. Sap-feeder abundance and biomass were lower in the second year with an abundance maximum in July equivalent to 81 individuals/m^2. Chewers were less important in the first year with numbers only rising to 49 individuals/m^2 and remained similar in the second season. Biomass patterns for chewers in the second year were similar to those found in the first season although the maximum was almost 60% lower than in the first year.

The relative importance of chewers and sap-feeders is given in Table 4.19. Curculionid and chrysomelid beetles were the main chewing insects in the first season ranging, after May, from 11-22% and 14-34% (curculionids) and 1-14% and up to 20% (chrysomelids) for abun-

TABLE 4.13: The taxonomic diversity of insect specialists and generalists during the first two years of succession (Site A) (Williams α)

* High values of α due to low n and s values ($n = 5$, $s = 4$ for Grade 3 specialists and $n = 7$, $s = 5$ for total α)
Note that ∞ represents very low values of n and s:- $\infty^2 = (n = 2, s = 2)$, $\infty^3 = (n = 3, s = 3)$

	YEAR 1						YEAR 2					
	MAY	JUNE	JULY	AUG	SEPT	OCT	MAY	JUNE	JULY	AUG	SEPT	OCT
Specialists Grade 1	-	∞^2	1.3	0.6	1.2	1.8	2.4	1.0	0.6	0.6	0.3	0.9
Specialists Grade 2	-	3.9	∞^2	1.2	3.3	5.4	7.5	2.5	2.0	3.8	5.6	3.4
Specialists Grade 3	9.3*	6.7	4.4	6.1	6.3	4.8	4.1	4.7	7.1	5.8	6.5	6.3
Generalists	0.8	2.5	1.9	2.1	1.3	1.1	∞^3	1.6	0.9	1.5	3.1	1.3
Total herbivores	5.7*	11.7	8.1	11.1	11.2	9.3	12.9	10.0	7.1	11.4	12.4	12.0

Fig. 4.12 Abundance and biomass of chewers and sap-feeders during the first two years of succession (Site A). Contributions by phloem-, xylem- and mesophyll-feeders are given along the top of each figure.

a. Abundance.
b. Biomass.

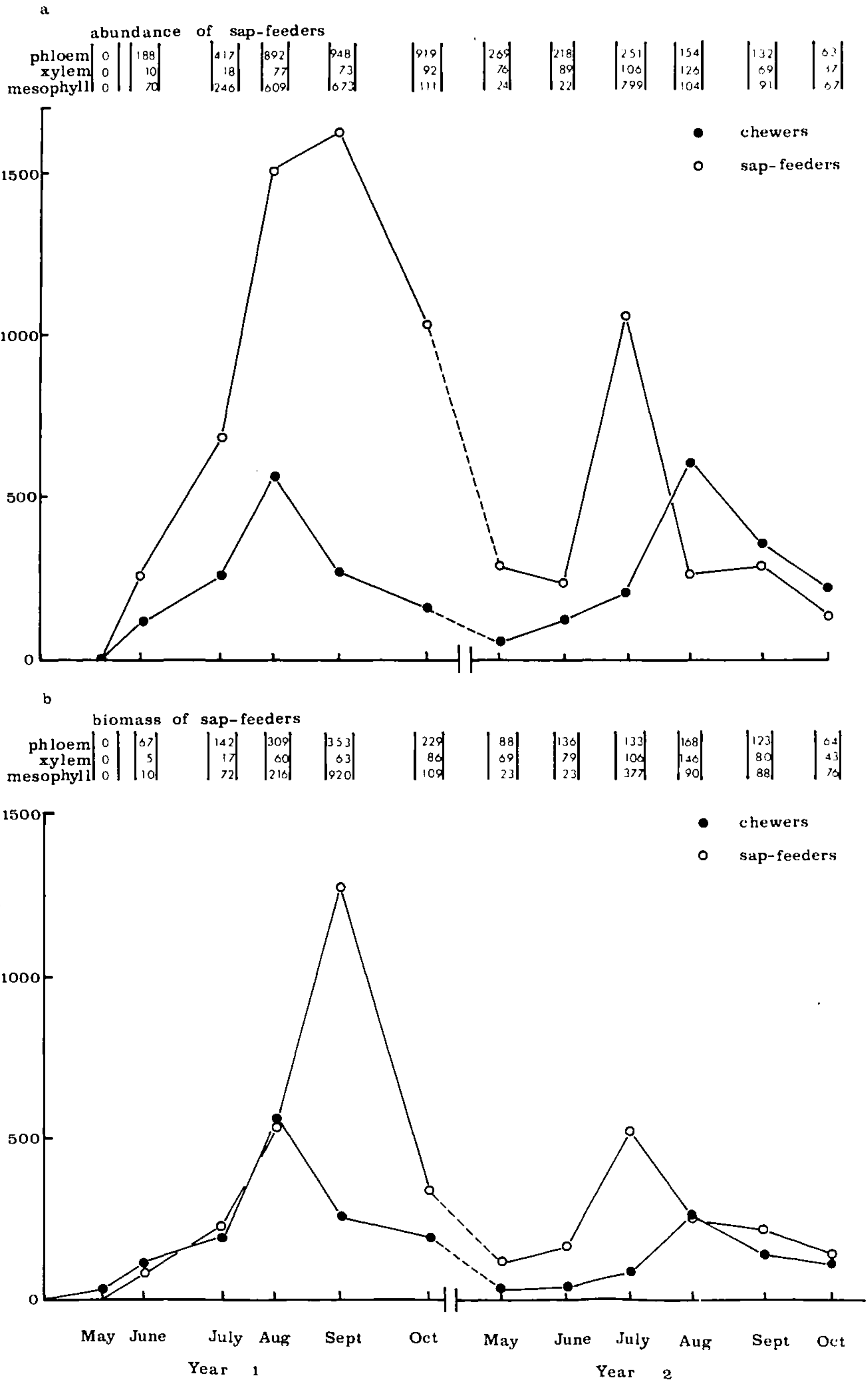

a
abundance of sap-feeders
phloem 0 188 417 892 948 919 269 218 251 154 132 63
xylem 0 10 18 77 73 92 76 89 106 126 69 37
mesophyll 0 70 246 609 673 111 24 22 799 104 91 67
NUMBERS OF INDIVIDUALS
1500
1000
500
0
● chewers
○ sap-feeders
b
biomass of sap-feeders
phloem 0 67 142 309 353 229 88 136 133 168 123 64
xylem 0 5 17 60 63 86 69 79 106 146 80 43
mesophyll 0 10 72 216 920 109 23 23 377 90 88 76
BIOMASS (MGM DRY WEIGHT)
1500
1000
500
0
● chewers
○ sap-feeders
May June July Aug Sept Oct
May June July Aug Sept Oct
Year 1
Year 2

TABLE 4.19 Percentage contributions to total insect herbivore abundance and biomass by chewers and sap-feeders during the first two years of succession (Site A). Abundance contribution, upper figure; biomass contribution in parentheses.

	YEAR 1						YEAR 2					
	MAY	JUNE	JULY	AUG	SEPT	OCT	MAY	JUNE	JULY	AUG	SEPT	OCT
CHEWERS												
Orthoptera Acrididae	0	1	0	<1	0	0	0	0	<1	<1	0	0
	(0)	*(10)*	*(0)*	*(2)*	*(0)*	*(0)*	*(0)*	*(0)*	*(<1)*	*(6)*	*(0)*	*(0)*
Lepidoptera	0	<1	3	<1	0	<1	0	<1	1	<1	0	0
	(0)	*(<1)*	*(19)*	*(<1)*	*(0)*	*(<1)*	*(0)*	*(<1)*	*(1)*	*(<1)*	*(0)*	*(0)*
Coleoptera Elateridae	12	<1	0	0	0	0	<1	0	0	0	0	0
	(51)	*(4)*	*(0)*	*(0)*	*(0)*	*(0)*	*(<1)*	*(0)*	*(0)*	*(0)*	*(0)*	*(0)*
Chrysomelidae	38	14	3	11	3	1	1	2	<1	1	4	9
	(20)	*(21)*	*(5)*	*(20)*	*(2)*	*(<1)*	*(<1)*	*(1)*	*(<1)*	*(<1)*	*(2)*	*(4)*
Curculionidae	50	16	22	19	11	12	15	31	15	68	57	52
	(29)	*(21)*	*(24)*	*(28)*	*(14)*	*(34)*	*(24)*	*(20)*	*(12)*	*(44)*	*(37)*	*(40)*
Total	100	30	25	30	14	13	16	33	15	69	61	61
	(100)	*(46)*	*(29)*	*(48)*	*(16)*	*(34)*	*(26)*	*(21)*	*(12)*	*(45)*	*(39)*	*(44)*
Total chewers	100	32	28	30	14	13	16	33	16	70	61	61
	(100)	*(57)*	*(48)*	*(51)*	*(16)*	*(35)*	*(26)*	*(21)*	*(13)*	*(51)*	*(39)*	*(44)*

Continued...

TABLE 4.19: (Continued)

	YEAR 1						YEAR 2					
	MAY	**JUNE**	**JULY**	**AUG**	**SEPT**	**OCT**	**MAY**	**JUNE**	**JULY**	**AUG**	**SEPT**	**OCT**
SAP FEEDERS												
Hemiptera-Heteroptera	0 *(0)*	3 *(5)*	14 *(16)*	22 *(20)*	35 *(60)*	9 *(21)*	7 *(15)*	6 *(11)*	64 *(63)*	12 *(17)*	14 *(24)*	19 *(31)*
Hemiptera-Homoptera	0 *(0)*	51 *(38)*	46 *(35)*	42 *(29)*	51 *(23)*	78 *(44)*	77 *(59)*	61 *(68)*	20 *(24)*	18 *(32)*	25 *(37)*	20 *(25)*
Total Hemiptera	0 *(0)*	54 *(43)*	60 *(51)*	64 *(49)*	86 *(83)*	87 *(65)*	84 *(74)*	67 *(79)*	84 *(87)*	30 *(49)*	39 *(61)*	39 *(56)*
Thysanoptera	0 *(0)*	14 *(<1)*	12 *(1)*	6 *(<1)*	<1 *(<1)*	<1 *(<1)*	0 *(0)*	0 *(0)*	0 *(0)*	0 *(0)*	0 *(0)*	0 *(0)*
Total sap-feeders	0 *(0)*	68 *(43)*	72 *(52)*	70 *(49)*	86 *(84)*	87 *(65)*	84 *(74)*	67 *(79)*	84 *(87)*	30 *(49)*	39 *(61)*	39 *(56)*

dance and biomass respectively. The curculionids remained the dominant chewers in the second year and contributed 15-68% and 12-44% respectively to herbivore abundance and biomass during the season. The Orthoptera were important chewers on only one occasion when a 19% contribution to biomass was made in July of the first year; otherwise, this group contributed insignificant levels of abundance and biomass throughout the two years. The sap-feeders were represented primarily by the Hemiptera in both years with the Homoptera especially important; the Homoptera contributed 42-78% (abundance) and 23-44% (biomass) in the first year and 18-77% (abundance) and 24-68% (biomass) in the second year. The Heteroptera were also important, especially in the first year, with contributions of 3-35% (abundance) and 5-60% (biomass).

The sap-feeding species have been further sub-divided into phloem-, xylem- and mesophyll-feeders. The abundance and biomass of the three sap-feeding types is given in Fig. 4.12. Phloem- and, to a lesser extent, mesophyll-feeders increased rapidly in numbers during the first year to August; the phloem-feeders maintained their numbers into October (around 73 individuals/m^2) whereas the mesophyll-feeders declined at the end of the season. Phloem-feeders, although still the major type, were considerably less abundant in the second year while mesophyll-feeders only reached a significant level of abundance in July when the population flush of *Plagiognathus chrysanthemi* occurred. Xylem-feeders remained at a very low level throughout although there was a tendency for them to increase in the second year. Patterns of biomass for the three sap-feeding types were dominated by a single peak in each year.

The relative contributions of phloem-, xylem- and mesophyll-feeders to total herbivore abundance and biomass are given in Table 4.20. In the first year phloem-feeders were represented mainly by aphids (11-64% of abundance and 3-23% of biomass) and cicadellids (9-31% of abundance and 17-30% of biomass). Cicadellids were the dominant phloem-feeders during the second year (6-48% of abundance and up to 59% of biomass) although aphids and delphacids were also significant in May. The most important phloem-feeding cicadellid species were *Euscelis incisus* and *E.lineolatus*, the *Macrosteles* complex and *Mocydiopsis parvicauda*. The Cicadellidae were also the main source of the very small numbers of xylem-feeders; the two *Euscelis* species were most important here, and to a lesser extent the phloem+xylem-feeder, the delphacid *Javesella pellucida*.

The Miridae was the main mesophyll-feeding group, although the Thysanoptera (mainly Thripidae) were quite numerous during the summer months of the first year.

TABLE 4.20 Percentage contributions to total insect herbivore abundance and biomass by phloem-, xylem- and mesophyll-feeders during the first two years of succession (Site A).

Abundance contribution, upper figure; biomass contribution in parentheses.

	YEAR 1						YEAR 2					
	MAY	JUNE	JULY	AUG	SEPT	OCT	MAY	JUNE	JULY	AUG	SEPT	OCT
PHLOEM-FEEDERS												
Hemiptera-Homoptera Aphididae	0 *(0)*	16 *(3)*	22 *(9)*	11 *(3)*	21 *(5)*	64 *(23)*	48 *(7)*	11 *(7)*	10 *(3)*	1 *(<1)*	0 *(0)*	0 *(0)*
Cicadellidae	0 *(0)*	31 *(30)*	22 *(25)*	29 *(23)*	29 *(18)*	9 *(17)*	10 *(28)*	48 *(59)*	6 *(15)*	15 *(30)*	20 *(<1)*	17 *(25)*
Delphacidae	0 *(0)*	3 *(4)*	0 *(0)*	2 *(3)*	0 *(0)*	5 *(4)*	19 *(24)*	2 *(1)*	4 *(4)*	2 *(2)*	1 *(35)*	1 *(1)*
Total	0 *(0)*	50 *(37)*	44 *(35)*	42 *(29)*	50 *(23)*	78 *(44)*	77 *(59)*	61 *(67)*	20 *(22)*	18 *(32)*	21 *(35)*	18 *(26)*
XYLEM-FEEDERS												
Hemiptera-Homoptera Cercopidae	0 *(0)*	0 *(0)*	0 *(0)*	0 *(0)*	0 *(0)*	0 *(0)*	0 *(0)*	0 *(0)*	<1 *(1)*	0 *(0)*	<1 *(1)*	0 *(0)*
Cicadellidae	0 *(0)*	2 *(2)*	2 *(4)*	2 *(3)*	4 *(4)*	8 *(16)*	9 *(26)*	23 *(37)*	6 *(14)*	14 *(27)*	10 *(22)*	11 *(17)*
Delphacidae	0 *(0)*	<1 *(<1)*	0 *(0)*	2 *(2)*	0 *(0)*	0 *(0)*	13 *(20)*	2 *(2)*	2 *(3)*	1 *(1)*	<1 *(<1)*	<1 *(<1)*
Total	0 *(0)*	3 *(3)*	2 *(4)*	4 *(5)*	4 *(4)*	8 *(16)*	22 *(46)*	25 *(39)*	8 *(18)*	15 *(28)*	11 *(23)*	11 *(17)*

Continued...

TABLE 4.20: (Continued)

	YEAR 1						YEAR 2					
	MAY	JUNE	JULY	AUG	SEPT	OCT	MAY	JUNE	JULY	AUG	SEPT	OCT
MESOPHYLL-FEEDERS												
Hemiptera-Heteroptera												
Miridae	0 *(0)*	3 *(5)*	13 *(15)*	21 *(18)*	31 *(57)*	3 *(12)*	1 *(4)*	5 *(10)*	62 *(61)*	10 *(14)*	6 *(15)*	4 *(12)*
Lygaeidae	0 *(0)*	0 *(0)*	<1 *(1)*	1 *(1)*	2 *(1)*	5 *(8)*	5 *(10)*	<1 *(1)*	1 *(1)*	1 *(2)*	6 *(8)*	14 *(18)*
Tingidae	0 *(0)*	0 *(0)*	0 *(0)*	<1 *(<1)*	<1 *(<1)*	0 *(0)*	0 *(0)*	0 *(0)*	0 *(0)*	0 *(0)*	<1 *(<1)*	0 *(0)*
Berytinidae	0 *(0)*	<1 *(<1)*	0 *(0)*	0 *(0)*	0 *(0)*	0 *(0)*	0 *(0)*	0 *(0)*	<1 *(<1)*	1 *(1)*	<1 *(1)*	<1 *(<1)*
Rhopalidae	0 *(0)*	0 *(0)*	<1 *(<1)*	<1 *(<1)*	<1 *(<1)*	<1 *(<1)*	0 *(0)*	0 *(0)*	0 *(0)*	0 *(0)*	0 *(0)*	0 *(0)*
Piesmidae	0 *(0)*	<1 *(<1)*	<1 *(<1)*	<1 *(<1)*	1 *(<1)*	1 *(<1)*	1 *(<1)*	1 *(<1)*	0 *(0)*	0 *(0)*	0 *(0)*	0 *(0)*
Coreidae	0 *(0)*	0 *(0)*	0 *(0)*	0 *(0)*	<1 *(2)*	0 *(0)*	0 *(0)*	0 *(0)*	0 *(0)*	0 *(0)*	0 *(0)*	0 *(0)*
Cydnidae	0 *(0)*	0 *(0)*	0 *(0)*	<1 *(<1)*	<1 *(<1)*	0 *(0)*	0 *(0)*	0 *(0)*	0 *(0)*	0 *(0)*	0 *(0)*	0 *(0)*
Hemiptera-Homoptera												
Cicadellidae	0 *(0)*	1 *(<1)*	<1 *(<1)*	<1 *(<1)*	1 *(<1)*	<1 *(<1)*	0 *(0)*	0 *(0)*	0 *(0)*	0 *(0)*	2 *(<1)*	1 *(<1)*
Thysanoptera												
Aeolothripidae	0 *(0)*	1 *(<1)*	<1 *(<1)*	<1 *(<1)*	0 *(0)*	0 *(0)*	0 *(0)*	0 *(0)*	0 *(0)*	0 *(0)*	0 *(0)*	0 *(0)*
Thripidae	0 *(0)*	13 *(<1)*	11 *(<1)*	6 *(<1)*	<1 *(<1)*	<1 *(<1)*	0 *(0)*	0 *(0)*	0 *(0)*	0 *(0)*	0 *(0)*	0 *(0)*
Total	0 *(0)*	18 *(6)*	26 *(17)*	29 *(20)*	36 *(60)*	9 *(21)*	7 *(15)*	6 *(11)*	64 *(63)*	12 *(17)*	14 *(25)*	19 *(31)*

Information on the species contributions of chewers and sap feeders is given in Fig. 4.13a. Species contributions of each feeding type show very similar trends from one year to the next (excluding May of the first year) where numbers of species were small. It appears that chewing insects predominate early in the season, decline in mid season (26% decline) and rise later in the season (>50%). Contributions of sap feeders obviously follow a mirror-image of this pattern. The mid season decline in the number of chewer species in each year may be due to the disappearance of spring-ovipositing Coleoptera and the eventual rise in mid-late summer due to the appearance of newly emerged adults and immigrant species.

Mesophyll-feeders were the main contributors to the species richness of the sap-feeders although if the aphids were included the phloem-feeders would probably have a similar overall contribution (Fig. 4.13b). Xylem-feeders had a low species richness throughout the two years.

Information on α-diversity of the main feeding types is also given in Fig. 4.13. The diversity of chewers and sap-feeders fluctuated throughout the period but was generally high (Fig. 4.13a). Mesophyll-feeders were the most diverse group of sap-feeders in the first year and this was maintained throughout the second growing season (Fig. 4.13b). α-diversity of phloem-feeders was relatively low in the first year but in the second season approached levels found for mesophyll-feeders. The main contributors to the diversity of the different feeding types over the two years were Coleoptera (chewers), Homoptera (phloem- and xylem-feeders) and Heteroptera (mesophyll-feeders).

4.4.5 Overwintering strategies

Overwintering strategies of the major insect herbivore taxa during the first two years of succession are given in Table 4.21. Based on available literature and various personal communications (see Appendix 6 for details) the insect orders are listed and the numbers of species adopting the strategy of overwintering as egg, immature (nymph/larva, pupa) or adult are given. Overwintering as an adult is clearly the dominant strategy for these early successional herbivores and enables these species to be available for immigration and oviposition in the following spring. This is quite clear from the May samples in the first year where all herbivore species invading the ruderal site at this time (all Coleoptera) were species that had overwintered as adults. This is also evident in May of the second year where 23 species (79% of total) overwintered as adults. Subsequently, as each season progressed species began to ap-

Fig. 4.13 Comparison of the number of herbivore species found during the first two years of succession (Site A). Species richness and Williams α are provided at the top of each figure.

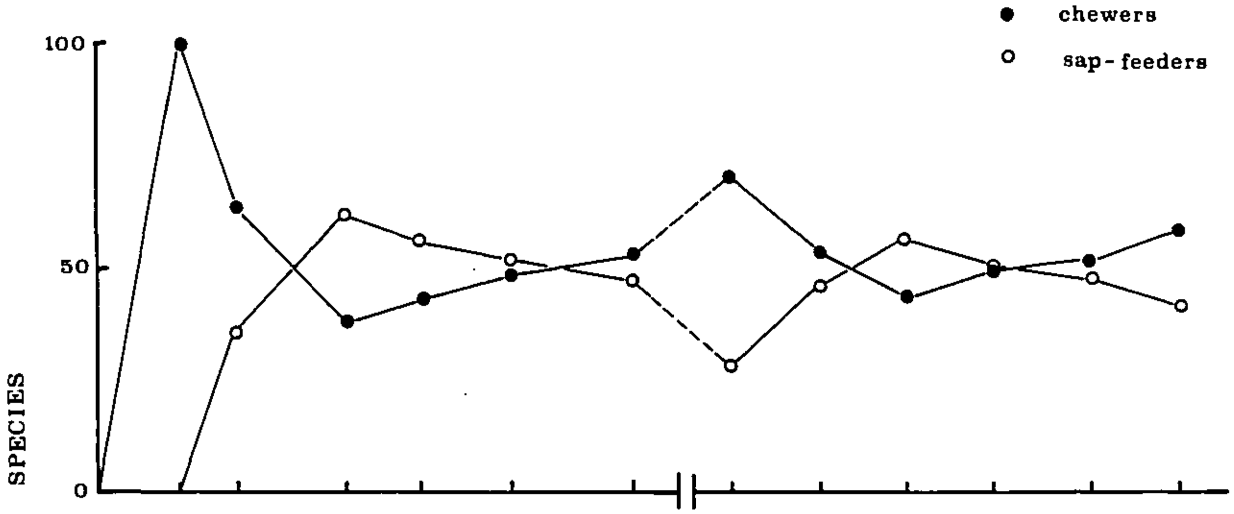
a. Chewers and sap-feeders.
b. The three sap-feeding types.

species richness

total	5	39	37	57	55	36	35	35	39	50	48	41
●	5	25	14	25	27	19	25	19	17	25	25	24
○	0	14	23	32	28	17	10	16	22	25	23	17

diversity (Williams α)

total	5·7	11·7	8·1	11·1	11·2	9·3	12·9	10·0	7·1	11·4	12·4	12·0
●	5·7	9·7	3·3	5·2	7·5	5·7	17·7	6·5	4·5	5·3	6·1	6·9
○	–	3·4	5·1	6·0	5·1	4·0	2·6	4·1	4·0	6·9	6·4	5·1



b

species richness

●	0	8	4	10	10	6	4	9	9	14	9	8
○	0	2	1	3	2	3	3	3	5	3	4	3
■	0	6	19	22	18	11	6	7	11	11	13	9

diversity (Williams α)

●	-	1·9	0·7	1·7	1·7	1·2	0·8	2·0	2·2	3·8	2·2	2·4
○	-	0·8	0·2	0·6	0·4	0·6	0·6	0·6	1·1	0·6	0·9	0·8
■	-	1·6	5·3	4·5	3·4	3·0	2·6	3·5	1·8	3·1	4·4	2·8

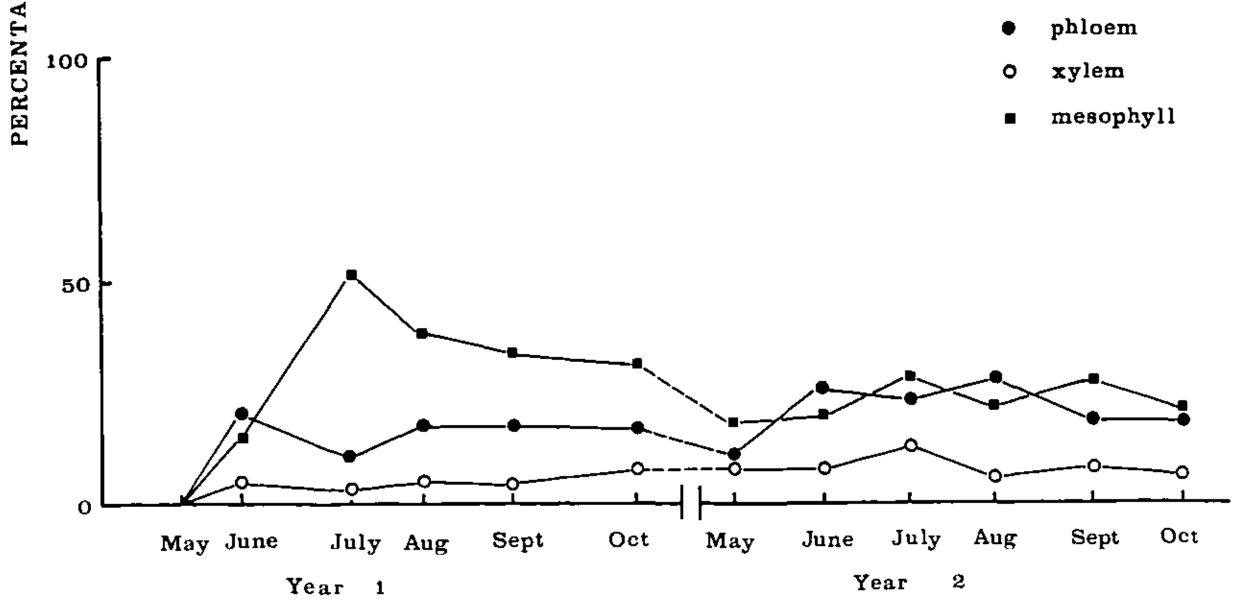


TABLE 4.21: Overwintering strategies of major insect herbivore taxa occurring in Site A during the first two years of succession. Values given are the number of species falling into the three overwintering stages (based on available literature and various personal communications). E = egg; I = immature; A = adult. I includes nymphs and larvae and also the single case of an overwintering pupa (*Sitona lepidus*). The few species that have more than one possible overwintering stage are included in each category.

	YEAR 1																		YEAR 2																	
	MAY			JUNE			JULY			AUG			SEPT			OCT			MAY			JUNE			JULY			AUG			SEPT			OCT		
OVERWINTERING STAGE	E	I	A	E	I	A	E	I	A	E	I	A	E	I	A	E	I	A	E	I	A	E	I	A	E	I	A	E	I	A	E	I	A	E	I	A
Orthoptera	-	-	-	1	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	2	-	-	1	-	-	-	-	-	-	-	-
Heteroptera	-	-	-	-	-	3	2	1	7	5	1	6	4	1	8	-	1	5	-	1	6	3	1	4	7	1	4	4	1	6	4	1	7	1	1	5
Homoptera	-	-	-	3	5	-	3	1	1	4	4	2	6	2	3	2	4	1	-	3	1	5	3	1	4	7	-	7	6	1	3	4	4	2	3	4
Thysanoptera	-	-	-	-	-	2	-	-	6	1	2	7	-	-	1	-	-	2	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Coleoptera	-	-	5	1	-	20	1	1	10	1	4	16	2	2	15	2	1	14	1	1	16	1	1	12	1	2	8	2	2	16	3	6	16	2	4	15
Total	-	-	5	5	5	25	6	3	24	12	11	31	12	5	27	4	6	22	1	5	23	9	5	17	14	10	12	14	9	23	10	11	27	5	8	24

pear (as invaders to the ruderal site and as either immature residents or immigrants in the second season) with developmental stages as overwintering strategies. These species were most common in August of the first year and over a more extensive period in the second year (July-September).

Different overwintering strategies are also employed by the different insect groups. The Heteroptera mainly overwinter as adults, although species overwintering in the egg stage frequently occurred. Cicadellids favour the strategy of overwintering as an egg whereas the Delphacidae usually pass the winter as nymphs. Both the Thysanoptera and Coleoptera overwinter predominantly as adults.

One final point that should be stressed is that the sparse numbers of egg-overwintering species at the beginning of each season may merely reflect a delay in the egg-hatching of these species.

4.4.6 Voltinism

Table 4.22 gives details of the number of generations per year for insect herbivore species colonising Site A during the first two years. The insect orders are listed and the number of species adopting a particular voltinism (uni-, bi- or polyvoltine) given. The majority of species (at this geographic situation) were univoltine although bivoltine species did occur. Coleoptera species occurring on the site were almost exclusively univoltine, the exception being the chrysomelid *Gastrophysa polygoni* with two generations a year. Heteroptera species were mainly univoltine although a few bivoltine species were also present (*e.g Lygus rugulipennis* and *Notostira elongata*). The Homoptera was a fairly mixed assemblage with both single and double brooded species commonly occurring. A small number of homopteran species were also polyvoltine (Cicadellidae: Typhlocybinae) but these were of low abundance. Information on the Thysanoptera indicates that they have one or two generations in the year but no certainty can be attached to the exact voltinism of any of these species (B.Pitkin, *pers.comm.*). Of course the number of polyvoltine species would be greatly increased if the Aphididae had been included.

TABLE 4.22 : Voltinism of major insect herbivore taxa occurring in Site A during the first two years of succession. Values given are the number of species falling into the three voltine categories (based on available literature and various personal communications). Thysanoptera have 1 or 2 generations/year and have been included as both uni- and bi- voltines.

	MAY			JUNE			JULY			AUG			SEPT			OCT			MAY			JUNE			JULY			AUG			SEPT			OCT		
No. generations/year	1	2	>2	1	2	>2	1	2	>2	1	2	>2	1	2	>2	1	2	>2	1	2	>2	1	2	>2	1	2	>2	1	2	>2	1	2	>2	1	2	>2
ORTHOPTERA	-	-	-	1	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	2	-	-	1	-	-	-	-	-	-	-	-
HETEROPTERA	-	-	-	2	1	-	7	4	-	10	3	-	10	5	-	3	3	-	3	4	-	6	3	-	8	2	-	7	3	-	7	3	-	3	3	-
HOMOPTERA	-	-	-	2	5	1	-	3	2	3	6	1	3	5	3	-	5	1	1	3	-	2	5	1	5	6	-	5	8	1	5	5	1	4	4	1
THYSANOPTERA	-	-		2	-		7	-		8	-		1	-		2	-		-	-		-	-		-	-		-	-		-	-		-	-	
COLEOPTERA	4	1	-	20	1	-	10	1	-	21	-	-	19	-	-	14	-	-	19	-	-	14	-	-	10	-	-	17	-	-	20	-	-	19	-	-
TOTAL	4	1	-	27	9	1	24	15	2	43	17	1	33	11	3	19	10	1	23	7	-	22	8	1	25	8	-	30	11	1	32	8	1	26	7	1

4.5 COMPARISON OF THE INVERTEBRATE FAUNA OF TWO YOUNG FIELDS WITH DIFFERENT HISTORIES OF LAND USE

4.5.1 Introduction

This Section looks briefly at the Site D invertebrate community in terms of taxonomic composition, abundance and biomass, trophic structure and life-history strategies; it also compares findings with the ruderal development in the first year of the Site A invertebrate community. Only the herbivore groups have been identified to species and although the Aphididae and larval Lepidoptera were not identified their abundance and biomass have been included in certain calculations. Predator and omnivore species have been identified as far as family.

4.5.2 Abundance and biomass of insects and spiders

Levels of abundance and biomass of insects and spiders in Site D during the first year are shown in Table 4.23. Unlike the situation in Site A, where insect abundance and biomass rose rapidly through the first season to maximal levels in August (abundance) or September (biomass) (see Figs. 4.3a and 4.4a), both insect abundance and biomass in Site D climbed gradually during the year and reached a maximum in September and then declined in October. Values of abundance and biomass in Site D, for the main part of the season, were always considerably lower than corresponding values found for Site A in the first year (*e.g.* peaks of abundance and biomass in Site D were lower by 64% and 65% respectively). Levels of spider abundance and biomass in Site D followed similar patterns to those found for Site A in the first year although both parameters were also usually well below values reached in Site A; final maximal levels of spider abundance and biomass at the end of the season in Site D were 63% and 71% respectively lower than those found in Site A during the first year.

The contributors to these general differences are also given in Table 4.23. Here, mean abundances/m^2 for major insect taxa and spiders have been calculated and levels of significance (from the t-test) are given where applicable. All major insect taxa and Araneae

TABLE 4.23 : Total abundance and biomass of insects and mean abundance/M^2 of insects and spiders in Site D and Site A during the first year of succession.

Biomass is in mgm dry weight. Insects exclude Diptera and Hymenoptera. Mean values (with ± standard deviation) are given only when density was $>1/M^2$. Significant differences in means between the two Young Fields on particular sampling occasions are denoted:- * = 0.05>p>0.01 ** = 0.01>p>0.001; *** = p<0.001; n = 23 on all occasions.

		YEAR 1					
		MAY	JUNE	JULY	AUG	SEPT	OCT
Total values							
Insect abundance	A	108	551	1970	3240	2340	1379
	D	61	256	409	785	1399	984
Insect biomass	A	137	375	757	1478	1763	632
	D	45	165	131	395	740	447
Mean abundance/M^2							
Collembola	A						
	D					2.1±4.7	
Orthoptera	A		<1		<1		
	D		<1			2.1±4.7	
Heteroptera	A		<1	11.0±8.0	43.7±30.6	57.8±28.0	11.3±6.2
	D	<1	<1	1.4±2.0***	3.5±3.5***	9.2±7.2***	4.2±4.0***
Homoptera	A		14.4±14.9	32.6±22.6	68.8±49.5	72.6±49.1	64.5±53.2
	D	1.1±5.1	12.9±7.8	15.4±13.4**	22.2±23.8***	54.6±37.0	26.1±18.0**
Thysanoptera	A		4.2±6.8	8.2±10.3	11.3±12.5	<1	<1
	D		<1**	1.6±5.3**	2.3±5.4**		<1
Neuroptera	A			<1	1.4±1.6		
	D				<1***	<1	<1
Lepidoptera	A		<1	2.3±2.3	<1		<1
	D		<1	<1***		<1	<1

(Continued)

TABLE 4.23 : (Continued)

		YEAR 1					
		MAY	JUNE	JULY	AUG	SEPT	OCT
Coleoptera	A	8.2±8.3 **	23.3±14.2 ***	97.4±39.1 ***	125.0±49.0 ***	52.0±18.4 ***	24.3±15.9
	D	3.2±2.5	3.1±3.9	8.0±10.1	26.0±23.0	20.2±14.0	23.7±15.6
Total insects	A	8.2±8.3	43.2±16.6 ***	151.5±58.4 ***	251.1±88.0 ***	182.8±61.1 ***	100.3±55.0 ***
	D	4.5±6.1	17.0±8.6	26.4±19.3	54.0±36.0	86.4±53.0	54.2±30.0
Araneae	A		2.8±3.3	23.0±15.1 ***	25.2±19.1 ***	45.52±20.1 ***	55.1±28.0 ***
	D	<1	1.6±1.6	6.4±5.2	8.7±5.8	17.9±5.5	20.6±7.3

were almost always very significantly less abundant in Site D than Site A. An exception to this was the Homoptera (in September) and Coleoptera (in October) which had similar levels in both sites. Of the three major insect groups encountered in Site A during the first year both the Homoptera and Coleoptera were also important in Site D; however, the Heteroptera were a relatively insignificant component of the insect community (see Table 4.23).

4.5.3 Basic trophic structure

Pyramids of numbers of individuals and biomass of the major trophic guilds (adults and immatures) for the first year in Site D are shown in Fig. 4.14. As for Site A (see Section 4.3.3, Figs. 4.6 and 4.7) the community began highly predator-biased in May, again due to the foraging carabid, *Bembidion lampros.* The most important predators during June and July were Carabidae and, to a lesser extent, Coccinellidae and Staphylinidae. Numbers and biomass of these three groups were declining during this period and as herbivore populations built up the pyramids become orientated towards the phytophage guild. The slower progression to a herbivore-dominated pyramid for biomass contributions, compared to the abundance pattern, again reflect (as for Site A) size differences between insect predators and herbivores during the first three months of sampling. As in Site A in the first year Araneae increased in importance in Site D as the season progressed; by August the spiders were contributing 69% and 65% to total predator abundance and biomass respectively and by the end of the season these contributions had risen to 87% and 75% respectively. The low importance of the omnivore guild in Site A was also evident in Site D. Omnivore contributions to the insect and spider community ranged from 0-15% for abundance but never exceeded 5% for biomass. As in Site A, the most important omnivore groups were Coleoptera (Cryptophagidae, Lathridiidae and Nitidulidae) and certain Heteroptera (Miridae).

The seasonal patterns in absolute levels of abundance and biomass of the insect herbivores and predators (insects and spiders) can be seen clearly in Fig. 4.15. Changes in herbivore abundance and biomass were not as dramatic as those found in Site A (*cf* Fig. 4.8). Abundance of herbivores rose throughout the season and reached a maximum in September, one month later than the maximal level in Site A; however, peak numbers (79 individuals/m^2) were 52% lower than in Site A (164 individuals/m^2). Herbivore biomass in Site D followed similar patterns to Site A although the September peak in Site D was 65% lower than the corresponding level in Site A. Predator abundance and biomass rose gradually

Fig. 4.14 Guild composition of the invertebrate community during the first year of succession in terms of percentage contributions to abundance and biomass (Site D). Total insect + spider abundance and biomass (mgm dry weight) is given for each month (excluding Diptera and Hymenoptera).

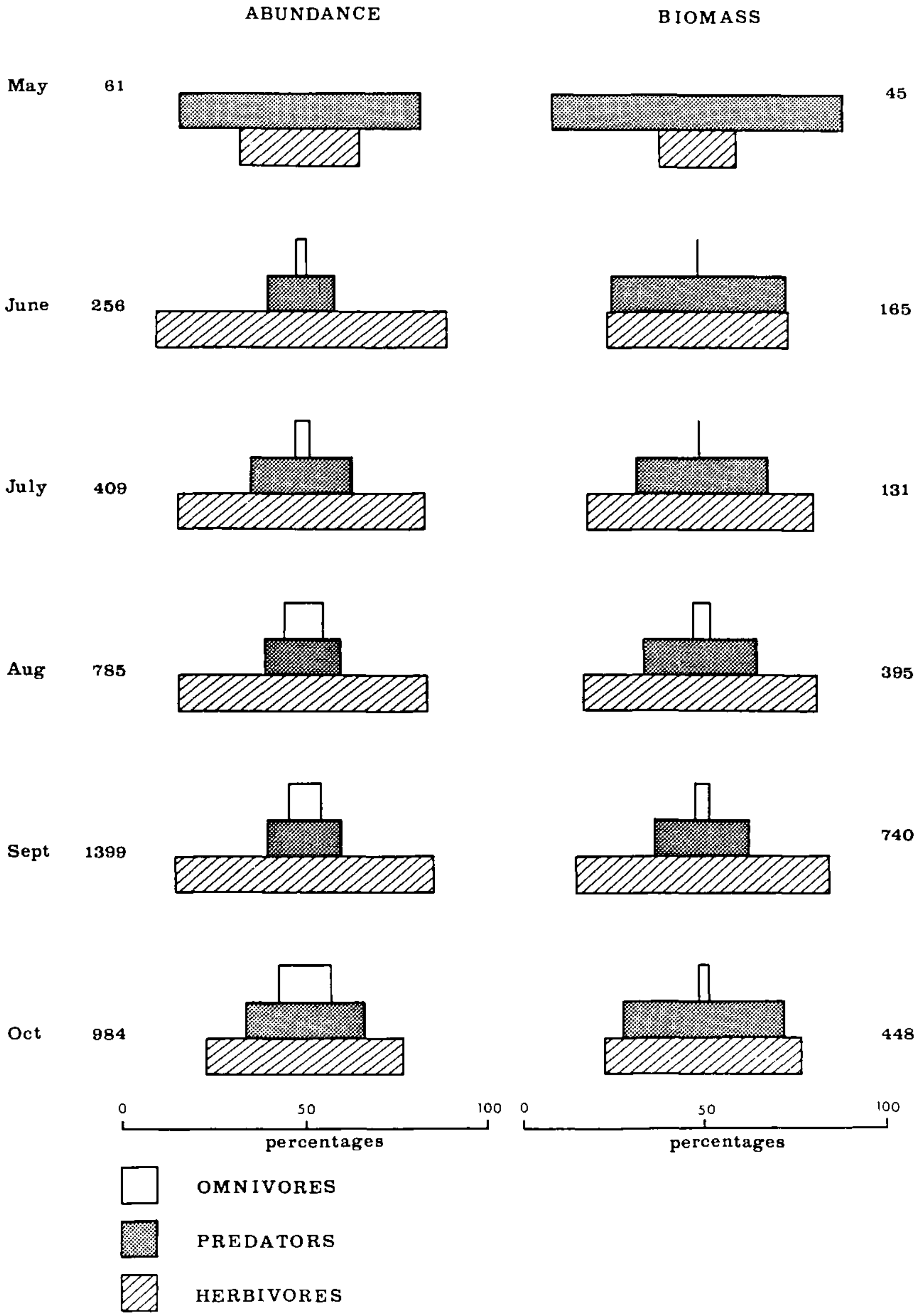
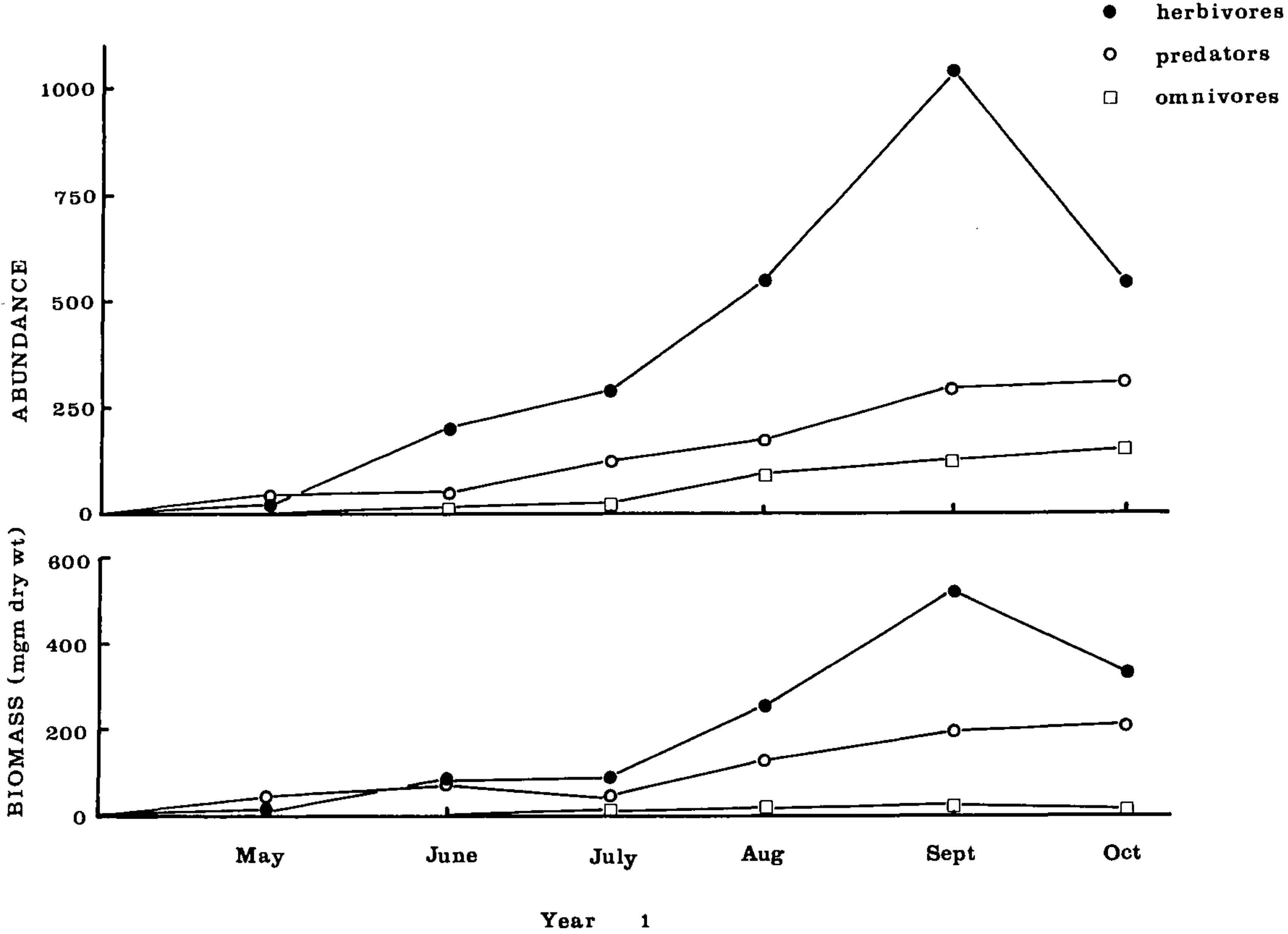

ABUNDANCE
BIOMASS
May
61
45
June
256
165
July
409
131
Aug
785
395
Sept
1399
740
Oct
984
448
0
50
100
percentages
0
50
100
percentages
OMNIVORES
PREDATORS
HERBIVORES

Fig. 4.15 Abundance and biomass of the three trophic guilds during the first year of succession (Site D).


● herbivores
○ predators
□ omnivores
ABUNDANCE
1000
750
500
250
0
BIOMASS (mgm dry wt)
600
400
200
0
May
June
July
Aug
Sept
Oct
Year 1

through the season, in great contrast to patterns found in Site A. Like the herbivores all insect predator groups and spiders occurred in considerably lower numbers in Site D.

4.5.4 The herbivore community

4.5.4(a) Species richness; composition and diversity

Herbivore species richness for Site D in 1981 increased gradually through the year and reached a maximum of 50 species in September. Although this seasonal pattern of species richness was similar to that found for Site A herbivore species numbers and colonisation rates were generally lower in Site D; the exception was in October where Site D had slightly more species (Table 4.24a). These differences were due mainly to a lower immigration rate of Coleoptera species (and Homoptera to a lesser extent) early in the season together with reduced species immigrations of Thysanoptera (in July-August) and Heteroptera and Coleoptera (in August-September). These reduced levels of species richness in Site D are reflected in the relatively low values of Sorensen's Index of Similarity (I_s) for the two sites shown in Table 4.24b. The Similarity was lowest for Heteroptera (48%) and highest for Homoptera (70%).

Details of taxonomic change within Site D are provided by I_s (for species composition) and I_w values (for abundance and biomass, separately) in Appendix 7. As found before, I_s tends to overestimate habitat similarity. Briefly, similarity (both numbers and biomass) changed fairly quickly during the season, rising from I_w (abundance) values of 1% (May-June) to 40% (September-October) and from I_w (biomass) values of 12% (May-June) to 38% (September-October). Comparison of the herbivore community of Site D with the first year in Site A shows differences in levels of abundance and biomass. The two herbivore communities had low similarities in terms of both numbers of individuals and biomass. Similarity in total herbivore numbers never exceeded 36% (Table 4.25a), although the Homoptera and Coleoptera did reach just over 50% similarity during the season. Similarity in total insect herbivore biomass between the two sites was generally very low (mainly around 15-20%) and, not surprisingly, the Homoptera and Coleoptera had the highest I_w values (Table 4.25b).

Values of Williams Index of α-diversity for the main groups of insect herbivores (excluding aphids and Lepidoptera) in Site D together with differences from the first year fauna in Site A are given in Table 4.26. As for Site A, herbivore diversity fluctuated throughout the year. The Coleoptera was again the most diverse group, a feature related to the high species

TABLE 4.24: Comparison of the Insect Herbivore Species Between Two Young Fields (Site A 1980 and Site D 1981) in the First Year of Succession.

(a). Differences in insect herbivore species richness and gain between Site A and Site D.

Species richness and colonisation is given for Site D with the corresponding difference to Site A in italics.

Colonisation refers to the accumulation of species through the season.

Year 1

	May	June	July	Aug	Sept	Oct
Species richness						
Total	5	18	21	45	50	41
	(0)	*(-22)*	*(-15)*	*(-10)*	*(-4)*	*(+5)*
Collembola					1	
					(+1)	
Orthoptera		2		0		
		(+1)		*(-1)*		
Heteroptera		3	4	5	12	6
		(-1)	*(-5)*	*(-6)*	*(0)*	*(0)*
Homoptera		3	4	12	13	12
		(-6)	*(-2)*	*(+1)*	*(-1)*	*(+3)*
Thysanoptera		2	2	4	1	1
		(0)	*(-5)*	*(-4)*	*(0)*	*(-1)*
Coleoptera	5	8	11	24	23	22
	(0)	*(-16)*	*(-3)*	*(0)*	*(-4)*	*(+3)*
Colonisation	5	21	32	59	78	85
	(0)	*(-19)*	*(-29)*	*(-34)*	*(-36)*	*(-37)*

TABLE 4.24 (b) Comparison of the Total Numbers of Insect Herbivore Species Encountered with Indices of Similarity (I_s) Between Site A and Site D.

	Total Species			
	Site A 1980	Site D 1981	Number of Species Shared	I_s
Collembola	0	1	0	0
Orthoptera	1	2	1	0.66
Hemiptera-Heteroptera	21	12	8	0.48
Hemiptera-Homoptera	20	17	13	0.70
Total Hemiptera	41	29	21	0.60
Thysanoptera	11	4	4	0.53
Coleoptera	48	37	27	0.64
Total Herbivores	101	73	53	0.61

TABLE 4.25: Indices of Similarity in Insect Herbivores Between Site A and Site D During the First Year of Succession

a. Insect Abundance: I_s value above; I_w value (for number of individuals) in italics

b. Insect Biomass: I_w value

a.	May	June	July	Aug	Sept	Oct
Collembola						
Orthoptera		0.66 *(0.50)*				
Hemiptera-Heteroptera		0.29 *(0.11)*	0.53 *(0.17)*	0.43 *(0.08)*	0.63 *(0.17)*	0.60 *(0.37)*
Hemiptera-Homoptera		0.33 *(0.17)*	0.60 *(0.22)*	0.61 *(0.31)*	0.74 *(0.55)*	0.48 *(0.29)*
Total Hemiptera		0.32 *(0.17)*	0.56 *(0.20)*	0.54 *(0.29)*	0.70 *(0.40)*	0.52 *(0.32)*
Thysanoptera		1.00 *(0.31)*	0.29 *(0.25)*	0.66 *(0.28)*	1.00 *(1.00)**	0.66 *(0.66)*
Coleoptera	0.20 *(0.15)*	0.25 *(0.10)*	0.32 *(0.30)*	0.50 *(0.53)*	0.56 *(0.22)*	0.54 *(0.14)*
Total Herbivores	0.20 *(0.15)*	0.34 *(0.17)*	0.44 *(0.24)*	0.49 *(0.30)*	0.67 *(0.36)*	0.53 *(0.24)*

b.	May	June	July	Aug	Sept	Oct
Collembola						
Orthoptera		0.19				
Hemiptera-Heteroptera		0.33	0.43	0.07	0.16	0.45
Hemiptera-Homoptera		0.18	0.22	0.28	0.57	0.41
Total Hemiptera		0.19	0.31	0.20	0.31	0.21

TABLE 4.25 cont......

	May	June	July	Aug	Sept	Oct
Thysanoptera		0.31	0.22	0.17	0.66*	0.44
Coleoptera	0.28	0.20	0.23	0.36	0.20	0.14
Total Herbivores	0.28	0.19	0.42	0.14	0.14	0.15

*Only 1 individual found in each site.

TABLE 4.26 : Comparison of William s α -diversity for insect herbivores over the first year of succession. Site D = top figure; difference to Site A in italics. Aphids, and the few species of Lepidoptera and the omnivore guild are not included here.

	YEAR 1					
	MAY	JUNE	JULY	AUG	SEPT	OCT
Collembola	-	-	-	-	0.2 *(+0.2)*	-
Orthoptera	-	1.6 *(+1.2)*	-	-	-	-
Hemiptera-Heteroptera	-	3.2 *(+1.2)*	2.0 *(-0.2)*	2.1 *(+0.1)*	3.7 *(+1.6)*	2.4 *(+1.0)*
Hemiptera-Homoptera	-	0.6 *(-1.6)*	1.3 *(+0.2)*	2.6 *(+0.7)*	2.3 *(-0.3)*	3.2 *(+1.2)*
Total Hemiptera	-	1.3 *(-2.2)*	4.2 *(+1.0)*	3.4 *(-0.5)*	3.8 *(-0.9)*	4.3 *(+0.9)*
Thysanoptera	-	0.8 *(+0.4)*	0.5 *(-1.2)*	1.2 *(-0.7)*	∞ *(0)*	∞ *(0)*
Coleoptera	∞^5 *(-5.7)*	13.2 *(+4.0)*	4.2 *(+0.9)*	6.8 *(+1.9)*	7.3 *(-0.2)*	7.1 *(+1.4)*
Total herbivores	∞^5 *(-5.7)*	5.2 *(-6.9)*	7.5 *(-0.6)*	11.8 *(+1.2)*	11.4 *(+0.4)*	12.5 *(+3.2)*

$\infty^1 = (n = 1;\ s = 1)$

$\infty^5 = (n = 5;\ s = 5)$

richness and colonisation rate compared to other major herbivore groups.

4.5.4(b) Abundance and biomass composition of the herbivore guild

The herbivore community in Site D differs further from the ruderal stage of Site A when the percentage contributions to herbivore abundance and biomass are considered (Table 4.27a). The main herbivore group, as found for Site A, was the Homoptera with lower contributions from the Coleoptera. The Heteroptera was poorly represented in Site D, unlike the situation in Site A where this group became fairly abundant on several occasions. Table 4.27b summarises the main differences in abundance and biomass contributions between the two sites for the three main herbivore groups. Homopteran contributions were nearly always higher in Site D than Site A; the reverse being true for the Heteroptera. Coleopteran contributions in Site D were lower during the first three months and greater (for abundance) in the latter part of the season.

As found for Site A the aphids and the cicadellids were the most important Homoptera and the Curculionidae were the main beetle phytophages. The most important individual herbivore species in Site D were *Macrosteles laevis* and *M.sexnotatus* (Cicadellidae) and *Ceut orhynchus floralis* (Curculionidae); these species were also common in Site A although other species occurred in high numbers there as well (see Section 4.3.4).

4.5.5 Life-history strategies

4.5.5(a) Introduction

This Section analyses life-history strategies of insect herbivores in Site D using the methodology and criteria (described in Section 4.4.1). Comparisons are also made with the herbivore fauna in Site A during the first year. Given the differences in basic taxonomic composition of the vegetation between the two sites it was not surprising to discover accompanying differences in the two first year herbivore faunas.

TABLE 4.27: Abundance and biomass composition of the insect herbivore community in Site D during the first year of succession

a. % contribution by major herbivore taxa to total herbivore abundance and biomass in Site D. Abundance contribution, upper value; biomass contribution in italics. Values of total abundance and biomass are given at the bottom of the table. Biomass is in mgm dry weight.

a

	YEAR 1					
	MAY	JUNE	JULY	AUG	SEPT	OCT
Collembola	0 *(0)*	0 *(0)*	0 *(0)*	0 *(0)*	3 *(<1)*	0 *(0)*
Orthoptera	0 *(0)*	2 *(4)*	0 *(0)*	0 *(0)*	0 *(0)*	0 *(0)*
Hemiptera-Heteroptera	0 *(0)*	2 *(3)*	5 *(31)*	4 *(2)*	9 *(16)*	7 *(14)*
Hemiptera-Homoptera	75 *(12)*	85 *(78)*	69 *(43)*	49 *(44)*	71 *(66)*	65 *(56)*
Total Hemiptera	75 *(12)*	87 *(81)*	74 *(74)*	53 *(46)*	80 *(82)*	72 *(70)*
Thysanoptera	0 *(0)*	5 *(<1)*	7 *(<1)*	6 *(<1)*	<1 *(<1)*	<1 *(<1)*
Lepidoptera	0 *(0)*	<1 *(<1)*	<1 *(<1)*	0 *(0)*	<1 *(<1)*	<1 *(<1)*
Coleoptera	25 *(88)*	5 *(14)*	19 *(24)*	41 *(53)*	16 *(16)*	28 *(29)*
Total herbivore abundance	20	202	285	543	1028	538
" " biomass	9.66	82.57	79.98	255.17	521.60	231.12

Continued...

TABLE 4.27 : (Continued)

b. Differences in percentage contributions of the three major herbivore taxa in Site D compared to Site A during the first year. Abundance difference, upper value; biomass difference in italics.

YEAR 1

b	MAY	JUNE	JULY	AUG	SEPT	OCT
Heteroptera	0 *(0)*	-2 *(-35)*	-9 *(+15)*	-18 *(-17)*	-26 *(-44)*	-2 *(-7)*
Homoptera	+75 *(+12)*	+35 *(+40)*	+23 *(+8)*	+7 *(+15)*	+20 *(+43)*	-13 *(+12)*
Coleoptera	-75 *(-12)*	-25 *(-31)*	-6 *(-5)*	+11 *(+4)*	+2 *(-1)*	+15 *(-6)*

4.5.5(b) The herbivore load on the four major plant groupings

Trends in abundance and biomass of herbivores attacking the four major plant groupings in Site D contrast strongly with the situation found in Site A (Fig. 4.16a and b). Instead of rapid rises in abundance and biomass to August for most groups, as found for Site A, all four herbivore categories show a general but gradual rise in these two parameters through the main part of the growing season. The herb-feeding groups though always had considerably lower values in Site D. For example, maximal levels of abundance and biomass in Site D were respectively lower by 79% and 87% (annual-feeders), 58% and 62% (biennial-feeders) and 69% and 86% (perennial-feeders) compared to corresponding maximas in Site A. Insects attacking annual and perennial herbs in the first year were considerably less important in Site D. Gramineae-feeders had become the most important herbivore group by September in Site D when peak numbers and biomass occurred; differences to Site A were minimum at this time with abundance only 7% lower and biomass 1% higher compared to the corresponding maximal levels in August of the first year in Site A.

The relative importance of the different herbivore feeding groups in Site D in terms of percentage contributions to abundance and biomass by the main herbivore taxa (Heteroptera, Homoptera and Coleoptera) is given in Table 4.28; differences to Site A (Year 1) are also included. It is clear, in terms of abundance and biomass, that the structure of the Site D insect community differed from Site A in the earlier establishment of grass-feeding Homoptera, a later establishment of herb-feeding Coleoptera and the relatively minor contribution of herb-feeding Heteroptera in Site D. As found for Site A the Coleoptera were represented primarily by Curculionidae and the most important homopteran group was the Cicadellidae.

Further differences to Site A are evident when the species richness of the herbivores associated with the four major plant groupings is considered (Table 4.29). As found for Site A more insect species were associated with annual and perennial herbs although all groups were impoverished to a certain extent when compared to species numbers in Site A. Annual-feeders had the lowest overall reduction in richness for most of the season in Site D, due mainly to reduced numbers of Coleoptera species. Gramineae-feeders were species deficient early in the season (June and July) in Site D compared to Site A but built up to a similar richness by the autumn. Fig. 4.16c shows the trends in percentage contributions of the four insect plant-feeding groups during the year in Site D (total species richness is given along the top of the figure). In addition, differences to Site A are given adjacent to the appropriate symbols. Unlike the ruderal stage in Site A, where herbivore species attacking perennial herbs gradually

Fig. 4.16 The insect herbivore load on the four major plant groupings during the first year of succession (Site D).

a. Abundance.
b. Biomass.
c. Comparison of the number of different species attacking each plant grouping. Difference to Site A (Year 1) for % contributions is given adjacent to each symbol. Total herbivore species richness is given along the figure top.

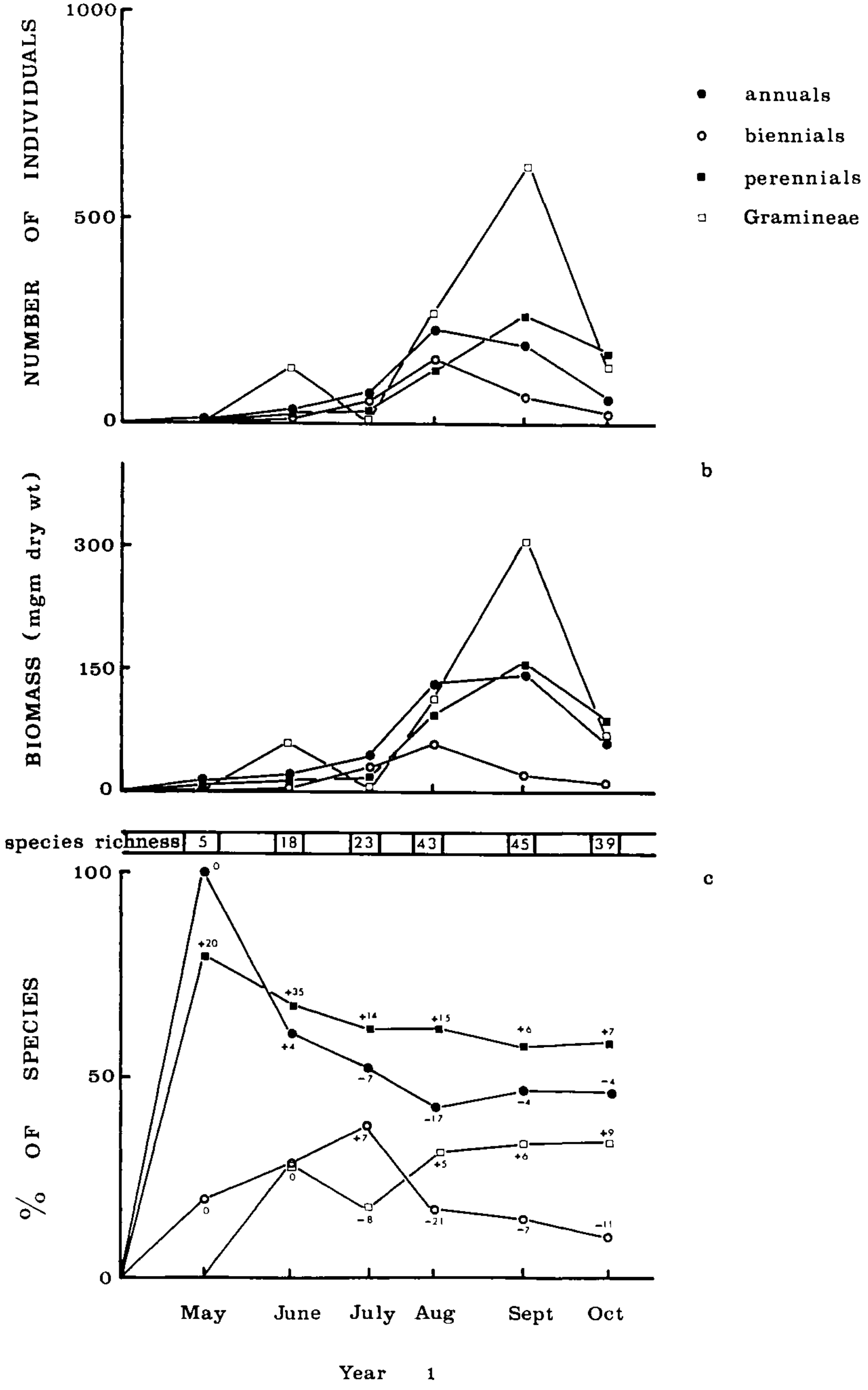

NUMBER OF INDIVIDUALS
1000
500
0
● annuals
○ biennials
■ perennials
□ Gramineae
b
BIOMASS (mgm dry wt)
300
150
0
species richness
5
18
23
43
45
39
c
% OF SPECIES
100
50
0
0
+20
+35
+4
+14
-7
+15
-17
+6
-4
+7
-4
0
0
+7
-8
+5
-21
+6
-7
+9
-11
May
June
July
Aug
Sept
Oct
Year 1

TABLE 4.28 : Comparison of the percentage contributions to total herbivore abundance and biomass by the main herbivore taxa attacking each of the four main plant groupings in Site D and Site A during the first year of succession. Percentage contributions to abundance (upper value) and biomass (in italics) are given for Site D with corresponding differences to Site A alongside. Totals represent total contributions (and differences) and include groups of minor importance (see Appendix 9 for full details).

YEAR 1

	MAY		JUNE		JULY		AUG		SEPT		OCT	
Site →	D	DIFF	D	DIFF	D	DIFF	D	DIFF	D	DIFF	D	DIFF
Annuals												
Hemiptera-Heteroptera	0 *(0)*	0 *(0)*	3 *(4)*	-1 *(-1)*	11 *(44)*	-8 *(+23)*	4 *(3)*	-20 *(-57)*	8 *(17)*	-33 *(-43)*	7 *(14)*	-4 *(-3)*
Coleoptera	100 *(100)*	+13 *(0)*	6 *(14)*	-27 *(-27)*	38 *(28)*	+10 *(-7)*	35 *(49)*	+7 *(0)*	10 *(14)*	-6 *(-1)*	13 *(20)*	-18 *(-24)*
Totals	100 *(100)*	+13 *(0)*	15 *(19)*	-39 *(-27)*	67 *(72)*	+8 *(+15)*	44 *(52)*	-15 *(-16)*	22 *(31)*	-35 *(-44)*	21 *(34)*	-20 *(-12)*
Biennials												
Hemiptera-Heteroptera	0 *(0)*	0 *(0)*	3 *(2)*	+3 *(+2)*	5 *(20)*	-8 *(+8)*	4 *(2)*	-2 *(+2)*	5 *(3)*	+2 *(+2)*	4 *(2)*	+3 *(+2)*
Coleoptera	20 *(20)*	+8 *(+18)*	3 *(2)*	-19 *(-13)*	36 *(27)*	+12 *(+5)*	25 *(19)*	+13 *(+10)*	2 *(1)*	-1 *(-4)*	4 *(3)*	+1 *(+2)*
Totals	20 *(20)*	+8 *(+18)*	7 *(4)*	-17 *(-11)*	51 *(48)*	+13 *(+13)*	29 *(21)*	+10 *(+7)*	7 *(4)*	+1 *(-2)*	8 *(5)*	+4 *(+4)*

Continued...

TABLE 4.28 (Continued)

	YEAR 1											
	MAY		JUNE		JULY		AUG		SEPT		OCT	
Site ⟶	D	DIFF	D	DIFF	D	DIFF	D	DIFF	D	DIFF	D	DIFF
Perennials Hemiptera-Heteroptera	0 *(0)*	0 *(0)*	3 *(4)*	0 *(-1)*	11 *(44)*	-7 *(-23)*	4 *(3)*	-19 *(-16)*	8 *(14)*	-32 *(-45)*	8 *(15)*	-1 *(-1)*
Coleoptera	80 *(80)*	+30 *(-13)*	4 *(13)*	-4 *(-5)*	10 *(6)*	+6 *(-5)*	18 *(35)*	+6 *(-3)*	16 *(18)*	+2 *(+3)*	42 *(36)*	+8 *(-8)*
Totals	80 *(80)*	+30 *(-13)*	13 *(17)*	-15 *(-6)*	39 *(51)*	+5 *(+22)*	27 *(39)*	-15 *(-18)*	28 *(32)*	-26 *(-42)*	50 *(51)*	+7 *(-10)*
Gramineae Hemiptera-Homoptera	0 *(0)*	0 *(0)*	81 *(77)*	+40 *(+42)*	24 *(22)*	-7 *(-14)*	47 *(44)*	*(+12)* *(+18)*	68 *(62)*	+30 *(+43)*	41 *(41)*	+1 *(+14)*
Totals	0 *(0)*	0 *(0)*	84 *(81)*	+40 *(+34)*	24 *(22)*	-11 *(-14)*	48 *(44)*	+13 *(+15)*	69 *(65)*	+31 *(+46)*	42 *(42)*	+2 *(+15)*

TABLE 4.29: Differences Between Site D and Site A in the Species Richness of Herbivores Associated with the Four Major Plant Groupings During the First Year of Succession.

For each month the number of species is given for Site D with the difference to Site A alongside.

Year 1

	May		June		July		Aug		Sept		Oct	
Site	D	Diff	D	Diff	D	Diff	D	Diff	D	Diff	D	Diff
Annuals												
Collembola	0	0	0	0	0	0	0	0	1	+1	0	0
Hemiptera-Heteroptera	0	0	3	0	4	-2	3	-4	5	-1	2	-2
Thysanoptera	0	0	2	0	2	-2	2	-2	1	0	1	0
Coleoptera	5	0	6	-12	5	-6	13	-8	15	-5	14	+1
Totals	5	0	11	-12	11	-10	18	-14	22	-5	17	-1
Biennials												
Hemiptera-Heteroptera	0	0	2	+2	3	-1	2	-4	3	-1	1	-1
Thysanoptera	0	0	1	0	1	-2	1	-2	0	0	0	0
Coleoptera	1	0	2	-8	4	0	4	-7	4	-4	3	-3
Totals	1	0	5	-6	8	-3	7	-13	7	-5	4	-4
Perennials												
Collembola	0	0	0	0	0	0	0	0	1	+1	0	0
Hemiptera-Heteroptera	0	0	4	+3	4	-1	3	-4	5	-2	3	0
Thysanoptera	0	0	2	0	2	-1	2	-2	1	0	1	-1
Coleoptera	4	+1	6	-4	7	-2	19	+5	20	0	18	+4
Totals	4	+1	12	-1	13	-4	24	-1	27	-1	22	+3
Gramineae												
Orthoptera	0	0	2	+1	0	0	0	-1	0	0	0	0
Hemiptera-Heteroptera	0	0	0	0	0	-1	0	0	3	+3	1	+1
Hemiptera-Homoptera	0	0	3	-6	4	-2	12	+1	13	-1	12	+3
Thysanoptera	0	0	0	0	0	-3	2	-1	0	0	0	0
Coleoptera	0	0	0	-2	0	0	0	0	0	0	0	0
Totals	0	0	5	-7	4	-10	14	-1	16	-2	13	+4

increased in importance during the first few months, this herbivore group in Site D was established shortly after site establishment. The contributions of perennial herb-feeding species after May (where total species numbers were very low) was higher than the other groups and averaged around 60%. Annual herb-feeders contributed less than perennial-feeders, with species contributions declining quickly to August where a fairly stable level (42-47%) was maintained for the rest of the year. The other important herbivore group, the grass-feeders, showed a greater species contribution from August onwards compared with Site A.

Insect diversity in Site D (as in Site A) was greatest for the annual and perennial herb-feeders (Table 4.30). Although differences in diversities between Site A and Site D in the first three months are not clearcut, trends during the latter half of the first year indicate higher diversities of grass-feeders and especially perennial herb-feeders (mainly due to an increase in the diversity of Coleoptera during this period).

4.5.5(c) The degree of specialisation on host plants

Fig. 4.17(a and b) shows the patterns of abundance and biomass of the generalists and three categories of specialist feeders in Site D. The domination by Grade 3 specialists through the main part of the growing season contrasts strongly with the first year situation in Site A where generalism was also an important feeding strategy. In Site D the generalists and specialists Grades 1 and 2 were relatively unimportant in terms of abundance and biomass; these latter two groups were similarly at relatively innocuous levels in Site A during the first year. Grade 3 specialists increased rapidly in abundance and biomass from July to September where maximal levels were reached. These peaks were lower, however, by 37% for abundance but higher by 5% for biomass when compared to the maximal levels of the Grade 3 specialists in Site A in the first year.

The relative importance of the specialist categories and generalists in terms of percentage contributions to abundance and biomass with the most important herbivore groups (Heteroptera, Homoptera and Coleoptera) are given in Table 4.31; differences to Site A are also included.

The two first year sites differed primarily in the abundance and biomass contributions of the Grade 3 specialists, Homoptera (mainly Cicadellidae) and Coleoptera (mainly Curculionidae). These two groups both showed pronounced fluctuations in importance throughout the year when compared to Site A. Also, the generally lower contributions of generalist herbivores in Site D were due to the reduced importance of the Heteroptera as compared to

TABLE 4.30 : **Differences in diversity (Williams α) of insect herbivores associated with four major plant groups between Site D and Site A during the first year of succession. Diversity value in Site D is given with corresponding difference to Site A alongside.**

YEAR 1

	MAY		JUNE		JULY		AUG		SEPT		OCT	
	D	DIFF	D	DIFF	D	DIFF	D	DIFF	D	DIFF	D	DIFF
Annuals	∞^5	-7.8	7.9	+0.8	3.5	-1.2	4.6	+1.5	6.3	+1.0	7.3	-2.4
Biennials	∞^1	0	3.5	-0.1	2.5	+0.2	1.5	-3.1	2.0	-1.8	1.3	-4.6
Perennials	∞^4	-5.5	11.6	+7.4	6.1	-1.9	8.4	+3.5	7.7	+2.1	6.9	+1.6
Gramineae	-	0	1.0	-2.1	1.3	-0.8	3.2	+0.3	3.0	+0.4	3.6	+1.6
Total	∞^5	-5.7	5.2	-6.5	7.5	-0.6	11.8	+0.7	11.4	+0.2	12.5	+3.2

∞ represents very low values of n and s: $\infty' = (n = 1, s = 1)$; $\infty^4 = (n = 4, s = 4)$ etc.

Fig. 4.17 Abundance, biomass and species contributions of specialists and generalists during the first year of succession (Site D).

a. Abundance.
b. Biomass.
c. Comparison of the number of specialist and generalist species. Difference to Site A (Year 1) for % contributions is given adjacent to each symbol. Total herbivore species richness is given along the figure top.

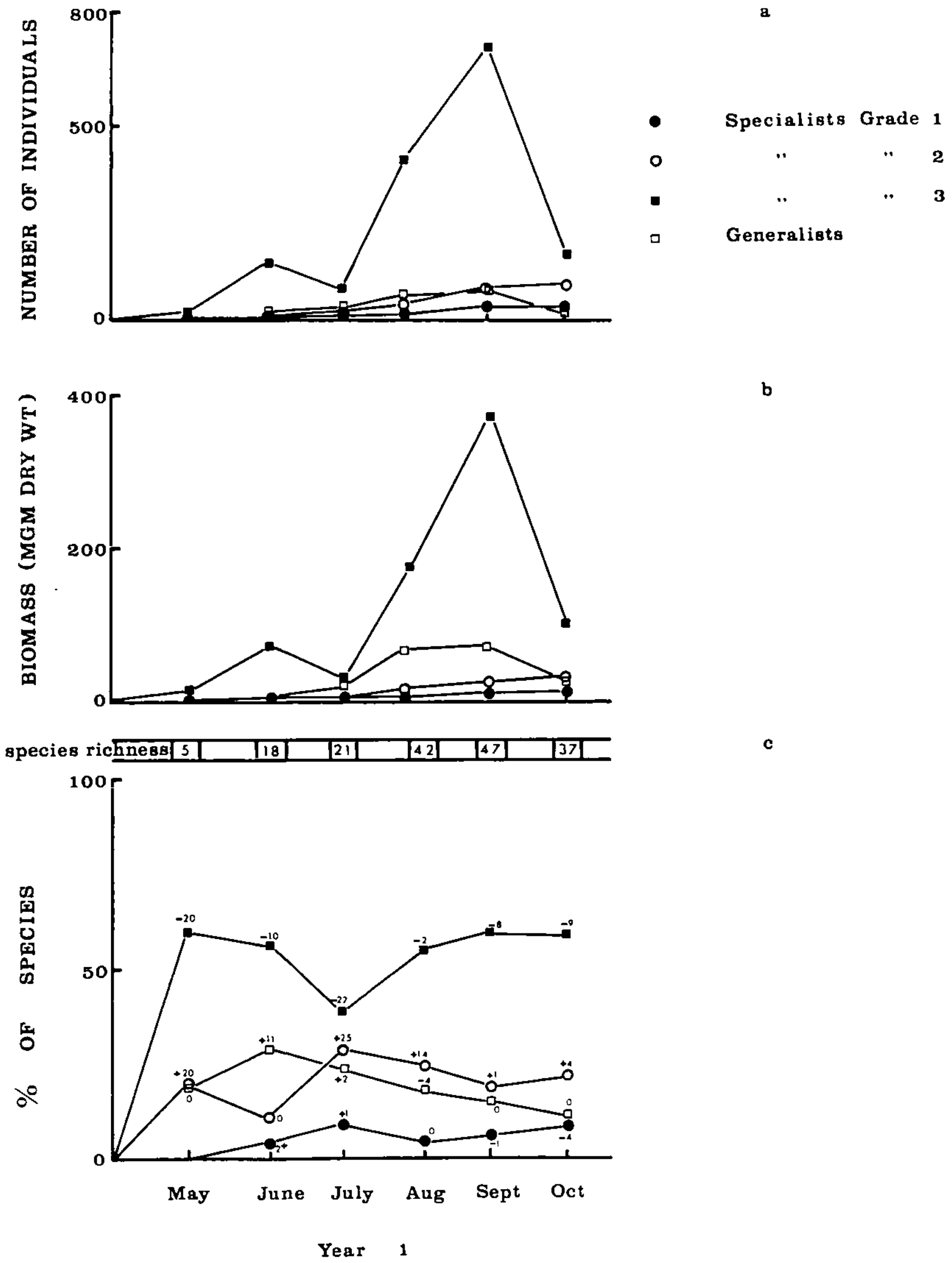

a
NUMBER OF INDIVIDUALS
800
500
0
● Specialists Grade 1
○ " " 2
■ " " 3
□ Generalists
b
BIOMASS (MGM DRY WT)
400
200
0
c
species richness
5
18
21
42
47
37
% OF SPECIES
100
50
0
-20
-10
-22
-2
-8
-9
+20
0
+11
0
+25
+2
+14
-4
+1
0
+4
0
+1
2+
0
-1
-4
May
June
July
Aug
Sept
Oct
Year 1

TABLE 4.31: Comparison of the percentage contributions to total herbivore abundance and biomass in the major specialist and generalist groups in Site D and Site A during the first year of succession.

Percentage contributions to abundance (upper value) and biomass (in italics) are given for Site D with corresponding differences to Site A alongside.

Totals represent total contributions (and differences) and include groups of minor importance.

YEAR 1

	MAY		JUNE		JULY		AUG		SEPT		OCT	
Site →	D	DIFF	D	DIFF	D	DIFF	D	DIFF	D	DIFF	D	DIFF
Specialists Grade 1												
Hemiptera-Heteroptera	0 *(0)*	0 *(0)*	0 *(0)*	-<1 *(-<1)*	0 *(0)*	-1 *(-<1)*	0 *(0)*	-<1 *(-<1)*	<1 *(<1)*	-<1 *(0)*	<1 *(<1)*	-3 *(-<1)*
Coleoptera	0 *(0)*	0 *(0)*	1 *(<1)*	+<1 *(0)*	3 *(2)*	+2 *(+2)*	1 *(1)*	+<1 *(+<1)*	3 *(2)*	+2 *(+1)*	9 *(5)*	+5 *(+4)*
Totals	0 *(0)*	0 *(0)*	1 *(<1)*	0 *(0)*	3 *(2)*	+1 *(+2)*	1 *(1)*	0 *(0)*	3 *(2)*	+1 *(+1)*	9 *(6)*	+2 *(+4)*
Specialists Grade 2												
Hemiptera-Heteroptera	0 *(0)*	0 *(0)*	0 *(0)*	0 *(0)*	0 *(0)*	0 *(0)*	0 *(0)*	-<1 *(-<1)*	0 *(0)*	0 *(0)*	0 *(0)*	0 *(0)*
Coleoptera	20 *(4)*	+20 *(+4)*	2 *(11)*	0 *(+<1)*	8 *(5)*	+8 *(+5)*	8 *(5)*	+4 *(+4)*	9 *(5)*	+6 *(+5)*	28 *(18)*	+25 *(+17)*
Totals	20 *(4)*	+20 *(+4)*	2 *(1)*	0 *(+<1)*	8 *(5)*	+7 *(+4)*	8 *(5)*	+4 *(+4)*	9 *(5)*	+6 *(+4)*	28 *(18)*	+25 *(+17)*

(Continued...)

TABLE 4.31: (Continued)

YEAR 1

	MAY		JUNE		JULY		AUG		SEPT		OCT	
Site →	D	DIFF	D	DIFF	D	DIFF	D	DIFF	D	DIFF	D	DIFF
Specialists Grade 3												
Hemiptera-Heteroptera	0 *(0)*	0 *(0)*	0 *(0)*	0 *(0)*	0 *(0)*	-<1 *(-<1)*	0 *(0)*	0 *(0)*	1 *(6)*	+<1 *(+4)*	<1 *(1)*	0 *(+<1)*
Hemiptera-Homoptera	0 *(0)*	0 *(0)*	80 *(76)*	+39 *(+14)*	24 *(22)*	-9 *(-34)*	47 *(43)*	+11 *(-6)*	68 *(61)*	+29 *(+37)*	43 *(43)*	-2 *(-15)*
Coleoptera	60 *(86)*	-11 *(15)*	4 *(11)*	-23 *(+4)*	36 *(27)*	+6 *(+19)*	28 *(26)*	+10 *(+20)*	6 *(11)*	-6 *(+10)*	10 *(16)*	-24 *(+10)*
Totals	60 *(86)*	-11 *(+15)*	92 *(92)*	+7 *(+3)*	69 *(49)*	-9 *(-17)*	80 *(69)*	*(+21)* *(+9)*	79 *(78)*	+27 *(+49)*	54 *(60)*	-25 *(-4)*
Generalists												
Hemiptera-Heteroptera	0 *(0)*	0 *(0)*	3 *(4)*	0 *(-5)*	11 *(44)*	-8 *(+11)*	4 *(3)*	-20 *(-32)*	9 *(14)*	-32 *(-56)*	8 *(15)*	-2 *(-18)*
Coleoptera	20 *(10)*	-9 *(-19)*	1 *(2)*	-6 *(0)*	0 *(0)*	-<1 *(-<1)*	6 *(22)*	-4 *(+19)*	<1 *(1)*	-1 *(+<1)*	1 *(1)*	0 *(+<1)*
Totals	20 *(10)*	-9 *(-19)*	5 *(7)*	-7 *(-4)*	20 *(44)*	0 *(+11)*	11 *(25)*	-23 *(-13)*	9 *(15)*	-34 *(-55)*	9 *(16)*	-2 *(-18)*

Site A where this group played a dominant role in the herbivore community. Both Grades 1 and 2 specialists in Site D showed little difference in their contributions to those in Site A.

When species richness of the different Grades of specialists and generalists is considered further differences between the two first year sites are detected (Table 4.32). As found for Site A, there were more species of Grade 3 specialists throughout the season although species richness was always lower in Site D; this was mainly due to lower numbers of Coleoptera species compared to Site A. There were also lower numbers of generalist species in Site D compared to Site A; this group had similar levels of species richness to the Grade 2 specialists. As for Site A, there were few species of Grade 1 specialists.

Trends in the percentage contributions of the specialists and generalists to herbivore species richness are shown in Fig. 4.17c; total species richness is given at the top of the figure. Also, differences to Site A are given adjacent to the relevant symbols as a measure of the disparity in species richness between the two sites. As found for Site A Grade 3 specialists were the most diverse group in Site D although values of α-diversity were often considerably lower in Site D (mainly due to reductions in the diversity of Homoptera and Coleoptera) (Table 4.33).

4.5.5(d) Herbivore feeding strategies

Similar patterns of abundance and biomass of the two major feeding types, the chewers and the sap-feeders, occurred in Site D as in Site A during the first year. Levels reached during the season, however, were always much lower in Site D; maximum levels (around September) for abundance and biomass were respectively lower by 59% and 79% for chewers and 48% and 66% for sap-feeders (Fig. 4.18a and b). Phloem-feeders were the most important sap-feeding type during the first season as in Site A (Fig. 4.18c and d).

The relative importance in terms of abundance and biomass of the chewers and sap-feeders is given in Table 4.34; differences to the first year herbivore community in the Site A Young Field are also provided for comparison. Unlike Site A it was the sap-feeders (mainly Homoptera) that dominated early in the season rather than chewers and this trend continued throughout the growing season. Respective contributions to herbivore abundance and biomass fluctuated from 8-41% and 18-88% (chewers) and 59-92% and 12-82% (sap-feeders) in Site D. As for Site A the phloem-feeders were the dominant sap-feeding group; of this group the aphids and cicadellids were also the most important.

The species contributions of the chewers and the sap-feeders in Site D are given in Fig.

TABLE 4.32 : Differences between Site D and Site A in the species richness of specialist and generalist insect herbivores during the first year of succession. For each month the number of species is given for Site D with the difference to Site A alongside

YEAR 1

	MAY		JUNE		JULY		AUG		SEPT		OCT	
Site	D	DIFF	D	DIFF	D	DIFF	D	DIFF	D	DIFF	D	DIFF
Specialists Grade 1												
Hemiptera-Heteroptera	0	0	0	-1	0	-1	0	-1	1	-1	1	0
Thysanoptera	0	0	0	0	0	0	0	0	0	0	0	1
Coleoptera	0	0	1	0	2	0	2	+1	2	0	2	1
Total	0	0	1	-1	2	-1	2	0	3	-1	3	-2
Specialists Grade 2												
Hemiptera-Heteroptera	0	0	0	0	0	0	0	0	0	-1	0	0
Coleoptera	1	+1	2	-2	5	+3	7	+2	7	-1	7	+1
Total	0	+1	2	-2	5	+3	7	+2	7	-2	7	+1
Specialists Grade 3												
Collembola	0	0	0	0	0	0	0	0	1	+1	0	0
Orthoptera	0	0	2	+1	0	0	0	-1	0	0	0	0
Hemiptera-Heteroptera	0	0	0	0	0	-1	0	0	4	+2	1	0
Hemiptera-Homoptera	0	0	3	-6	4	-2	12	+1	13	-1	12	+3
Thysanoptera	0	0	1	0	1	-4	3	-2	1	0	1	0
Coleoptera	3	-1	4	-10	3	-6	8	-7	9	-4	8	-1
Total	3	-1	10	-15	8	-13	23	-9	28	-2	22	+2
Generalists												
Hemiptera-Heteroptera	0	0	3	+1	4	-1	3	-4	4	0	2	0
Thysanoptera	0	0	1	0	1	-1	1	-1	0	0	0	0
Coleoptera	1	0	1	-3	0	-1	3	0	3	-1	2	0
Total	1	0	5	-2	5	-3	7	-5	7	-1	4	0

TABLE 4.33: Differences in diversity (Williams α) of the specialist and generalist herbivores between Site D and Site A during the first year of succession. Diversity value in Site D is given with the corresponding difference to Site A alongside.

YEAR 1

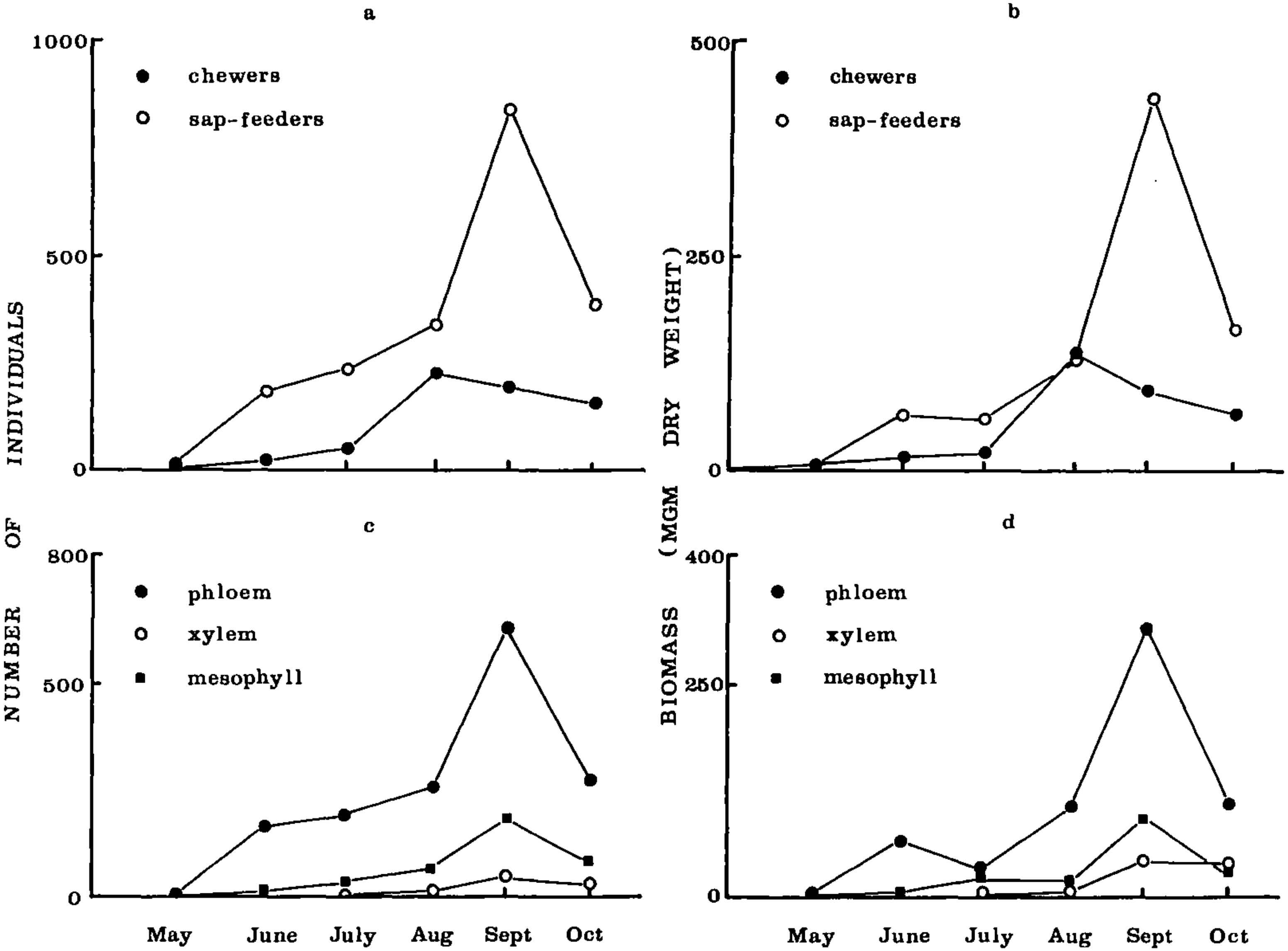
	MAY		JUNE		JULY		AUG		SEPT		OCT	
	D	DIFF	D	DIFF	D	DIFF	D	DIFF	D	DIFF	D	DIFF
Specialists Grade 1	-	0	∞^1	0	2.6	+1.3	0.9	+0.3	0.9	+0.3	0.8	+1.0
Specialists Grade 2	∞^1	0	2.6	-1.3	7.9*	+7.9	4.2	+3.0	2.6	+0.7	2.1	-3.3
Specialists Grade 3	∞^3	9.3*	2.4	-4.3	2.2	-2.2	5.3	-0.8	5.8	-0.5	6.8	-2.0
Generalists	∞^1	0.8	5.7*	+3.2	1.9	0	2.1	0	1.9	+0.6	1.3	+0.2
Total	∞^5	5.7*	5.2	-6.5	7.5	-0.6	11.8	+0.7	11.4	+0.2	12.5	+3.2

*Abnormally high value of α caused by low numbers of n:-

Specialists Grade 2 (n = 9; s = 6) Specialists Grade 3 (n = 11; s = 6).

Fig.4.18 Abundance and biomass of chewers, sap-feeders and the three sap-feeding types during the first year of succession (Site D).

a. Abundance of chewers and sap-feeders.
b. Biomass of chewers and sap-feeders.
c. Abundance of the three sap-feeding types.
d. Biomass of the three sap-feeding types.


a
b
c
d
NUMBER OF INDIVIDUALS
BIOMASS (MGM DRY WEIGHT)
1000
500
0
400
250
800
chewers
sap-feeders
phloem
xylem
mesophyll
May
June
July
Aug
Sept
Oct

Year 1

TABLE 4.34: Comparison of the percentage contributions to total herbivore abundance and biomass by the main herbivore feeding types occurring in Site D and Site A during the first year of succession.

Percentage contributions to abundance (upper value) and biomass (in italics) are given for Site D with corresponding differences to Site A alongside.

YEAR 1

		MAY		JUNE		JULY		AUG		SEPT		OCT	
	Site →	D	DIFF	D	DIFF	D	DIFF	D	DIFF	D	DIFF	D	DIFF
CHEWERS													
Collembola													
	Sminthuridae	0	0	0	0	0	0	0	0	3	+3	0	0
		(0)	*(0)*	*(0)*	*(0)*	*(0)*	*(0)*	*(0)*	*(0)*	*(<1)*	*(+<1)*	*(0)*	*(0)*
Orthoptera													
	Acrididae	0	0	2	+1	0	0	0	-<1	0	0	0	0
		(0)	*(0)*	*(4)*	*(-6)*	*(0)*	*(0)*	*(0)*	*(-2)*	*(0)*	*(0)*	*(0)*	*(0)*
Lepidoptera		0	0	<1	0	1	-2	0	-<1	1	+1	<1	0
		(0)	*(0)*	*(<1)*	*(0)*	*(2)*	*(-17)*	*(0)*	*(-<1)*	*(1)*	*(+1)*	*(<1)*	*(0)*
Coleoptera													
	Elateridae	0	-12	0	-<1	0	0	0	0	0	0	0	0
		(0)	*(-51)*	*(0)*	*(-4)*	*(0)*	*(0)*	*(0)*	*(0)*	*(0)*	*(0)*	*(0)*	*(0)*
	Chrysomelidae	0	-38	<1	-14	<1	-3	6	-5	1	-2	1	0
		(0)	*(-20)*	*(2)*	*(-19)*	*(<1)*	*(-5)*	*(22)*	*(+2)*	*(1)*	*(+1)*	*(2)*	*(-2)*
	Curculionidae	25	-25	5	-11	18	-4	35	+16	15	+4	26	+14
		(88)	*(+59)*	*(12)*	*(-9)*	*(23)*	*(-1)*	*(30)*	*(+2)*	*(16)*	*(+2)*	*(27)*	*(-7)*
	Total	25	-75	5	-25	18	-7	41	+11	16	+2	27	+14
		(88)	*(-12)*	*(14)*	*(-32)*	*(24)*	*(-5)*	*(52)*	*(+4)*	*(17)*	*(+1)*	*(29)*	*(+5)*
Total chewers		25	-75	8	-24	19	-9	41	+11	19	+5	28	+15
		(88)	*(-12)*	*(18)*	*(-39)*	*(26)*	*(-22)*	*(52)*	*(+1)*	*(18)*	*(+2)*	*(29)*	*(-6)*

Continued...

TABLE 4.34: (Continued)

YEAR 1

	MAY		JUNE		JULY		AUG		SEPT		OCT	
Site →	D	DIFF	D	DIFF	D	DIFF	D	DIFF	D	DIFF	D	DIFF
SAP- FEEDERS												
Hemiptera-Heteroptera	0	0	2	-1	5	-9	5	-17	10	-25	7	-2
	(0)	*(0)*	*(3)*	*(-2)*	*(31)*	*(+15)*	*(5)*	*(-15)*	*(17)*	*(-43)*	*(15)*	*(-6)*
Hemiptera-Homoptera	75	+75	85	+34	69	+23	48	+6	71	+20	64	-14
	(12)	*(+12)*	*(78)*	*(+40)*	*(43)*	*(+8)*	*(43)*	*(+14)*	*(65)*	*(+42)*	*(55)*	*(+11)*
Thysanoptera	0	0	5	-9	7	-5	6	0	<1	0	<1	+<1
	(0)	*(0)*	*(<1)*	*(<1)*	*(<1)*	*(-<1)*	*(<1)*	*(0)*	*(<1)*	*(-<1)*	*(<1)*	*(+<1)*
Total suckers	75	+75	92	+24	81	+9	59	-11	81	-5	72	-15
	(12)	*(+12)*	*(82)*	*(-39)*	*(74)*	*(+22)*	*(48)*	*(-1)*	*(82)*	*(-2)*	*(71)*	*(+6)*

4.19a (*cf* Fig. 4.13a) and show similar trends to Site A in the first year. The Site D community was, however, less species rich for both chewers and sap-feeders for the main part of the growing season (May-August) and especially so for Coleoptera (all chewers) and the three sap-feeding types (Heteroptera, Homoptera and Thysanoptera) (Table 4.35). Seasonal changes in species richness of the three sap-feeding types were similar to those found for Site A in the first year (Fig. 4.19b); again the phloem-feeders were the most important with the xylem-feeders least significant. The main difference was a reduction in species richness in Site D of homopteran phloem-feeders and heteropteran and thysanopteran mesophyll-feeders.

Information on α-diversity of the different feeding types in Site D is given in Appendix 8; corresponding differences to α-diversity in Site A are also provided for comparison. Both the chewers and the sap-feeders increased in diversity as the season progressed, with the former the most diverse. As for Site A the mesophyll-feeders were the most diverse sap-feeding type. The main differences between the two first year sites was a general increase in diversity in Site D for the chewers (mainly Coleoptera) and decrease in diversity of sap-feeders (especially homopteran mesophyll-feeders).

4.5.5(e) Overwintering strategies

Overwintering strategies of the insect herbivores occurring in Site D followed the general pattern set in Site A, with most colonising species passing the winter in the adult stage (Table 4.36). Also, as found for Site A, as the season progressed species began to appear with overwintering strategies as developmental stages.

4.5.5(f) Voltinism

Species colonising Site D, as shown for Site A, were primarily univoltine although a relatively small number of bivoltine species did occur (Table 4.36).

4.6 DISCUSSION

The descriptions of the insect and spider communities in Sites A and D provide the only detailed information on colonisation rates, taxonomic composition, abundance, biomass, trophic structure and herbivore life-history strategies in a developing early successional habitat. The majority of successional studies have focused on descriptions of vegetation (*e.g.*

Fig. 4.19 Comparison of the number of species of chewers, sap-feeders and the three sap-feeding types during the first year of succession (Site D).

a. Species contributions of chewers and sap-feeders. Sap-feeder species richness is given along the figure top. Differences to Site A (Year 1) for % contributions is given adjacent to each symbol.
b. Species contributions of the three sap-feeding types. Species richness is given along the figure top.

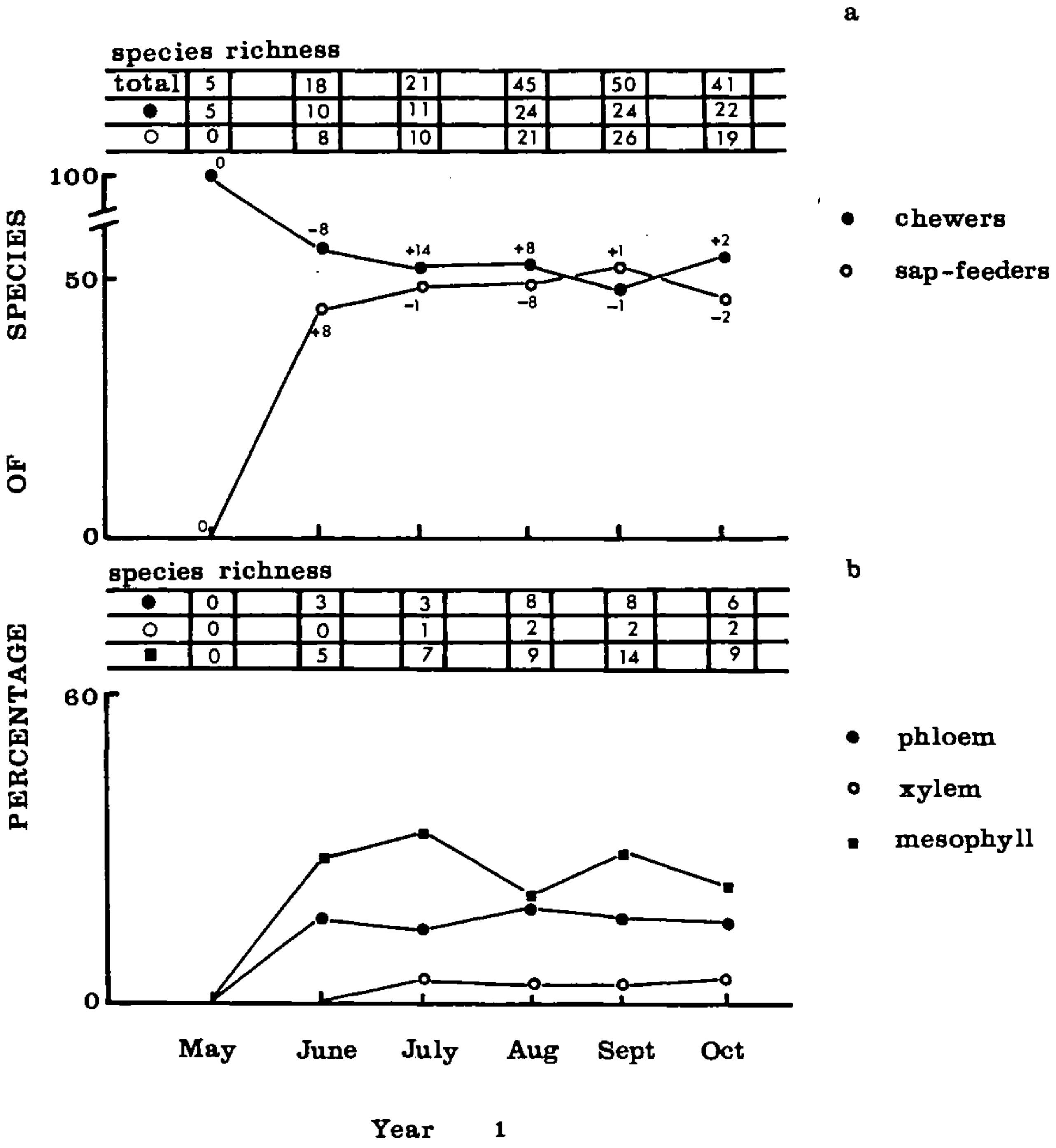

a
species richness
total 5 18 21 45 50 41
● 5 10 11 24 24 22
○ 0 8 10 21 26 19
100
50
0
0 -8 +14 +8 +1 +2
0 +8 -1 -8 -1 -2
chewers
sap-feeders
b
species richness
● 0 3 3 8 8 6
○ 0 0 1 2 2 2
■ 0 5 7 9 14 9
60
0
phloem
xylem
mesophyll
PERCENTAGE OF SPECIES
May
June
July
Aug
Sept
Oct
Year 1

TABLE 4.35 **Differences in species richness of chewing and sap-feeding insects in Site D and Site A during the first year of succession.** Species richness is given for Site D with the corresponding difference to Site A alongside.

a. Chewers and Sap-feeders; b. The different types of sap-feeders.

(a)

YEAR 1

	MAY		JUNE		JULY		AUG		SEPT		OCT	
Site →	D	DIFF	D	DIFF	D	DIFF	D	DIFF	D	DIFF	D	DIFF
CHEWERS												
Collembola	0	0	0	0	0	0	0	0	1	+1	0	0
Orthoptera	0	0	2	+1	0	0	0	-1	0	0	0	0
Coleoptera	5	0	8	-16	11	-3	24	0	23	-4	22	+3
Totals	5	0	10	-15	11	-3	24	-1	24	-3	22	+3
SAP-FEEDERS												
Hemiptera-Heteroptera	0	0	3	0	4	-6	5	-8	12	-1	6	0
Hemiptera-Homoptera	0	0	3	-6	4	-2	12	+1	13	-1	12	+3
Thysanoptera	0	0	2	0	2	-5	4	-4	1	0	1	-1
Totals	0	0	8	-6	10	-13	21	-11	26	-2	19	+2

Continued..

TABLE 4.35 : (Continued)

YEAR 1

(b)	MAY		JUNE		JULY		AUG		SEPT		OCT	
Site →	D	DIFF	D	DIFF	D	DIFF	D	DIFF	D	DIFF	D	DIFF
PHLOEM-FEEDERS												
Hemiptera-Homoptera	0	0	3	-5	3	-1	8	-2	8	-2	6	0
XYLEM-FEEDERS												
Hemiptera-Homoptera	0	0	0	-2	1	0	2	-1	2	0	2	-1
MESOPHYLL-FEEDERS												
Hemiptera-Heteroptera	0	0	3	0	4	-6	5	-8	12	-1	6	0
Hemiptera-Homoptera	0	0	0	-1	1	-1	0	-1	1	-3	2	-1
Thysanoptera	0	0	2	0	2	-5	4	-4	1	0	1	-1
Totals	0	0	5	-1	7	-12	9	13	14	-4	9	-2

TABLE 4.36': Overwintering strategies and voltinism of major insect herbivore taxa occurring in Site D during the first year of succession. Values given are the number of species falling into each category. E = egg , I = immature, A = adult ; I includes Nymphs and larvae and also the single case of an overwintering pupa (*Sitona lepidus*). The few species that have more than one possible overwintering stage are included in each category. 1, 2 and >2 refer to uni-, bi- and polyvoltine categories. Thysanoptera have 1 or 2 generations per year and are included as both uni- and bivoltines.

	OVERWINTERING STRATEGIES																		VOLTINISM																	
	MAY			JUNE			JULY			AUG			SEPT			OCT			MAY			JUNE			JULY			AUG			SEPT			OCT		
	E	I	A	E	I	A	E	I	A	E	I	A	E	I	A	E	I	A	1	2	>2	1	2	>2	1	2	>2	1	2	>2	1	2	>2	1	2	>2
Orthoptera	-	-	-	2	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	2	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Heteroptera	-	-	-	1	-	1	2	-	1	1	-	3	3	1	8	1	1	4	-	-	-	2	1	-	3	1	-	3	1	-	8	5	-	3	4	-
Homoptera	-	-	-	2	1	-	2	1	1	6	3	1	5	3	3	2	3	5	-	-	-	1	2	-	1	2	1	5	6	-	6	6	1	6	4	1
Thysanoptera	-	-	-	-	-	2	-	-	2	-	1	4	-	-	1	-	-	1	-	-	-	2		-	2		-	4		-	1		-	1		-
Coleoptera	-	1	3	-	-	5	-	1	6	2	3	13	2	3	13	1	2	14	4	-	-	5	-	-	7	-	-	15	-	-	16	-	-	16	-	-
Total	-	1	3	5	1	8	4	2	10	9	7	21	10	7	25	4	6	24	4	-	-	12	5	-	13	5	1	27	11	-	31	12	1	26	9	1

Odum 1969; Tramer 1975) and those few studies that have analysed the insect fauna are usually restricted to measures of taxonomic composition (*e.g.* species diversity and relative abundance) such as Cameron 1972, Witkowski 1973, Rogers & Woodley 1978 and Southwood *et al* 1979. Moreover, most successional studies have described only part of the gradient (*e.g.* Evans & Murdoch 1968; Murdoch, Evans & Peterson 1972; Witkowski 1973; Rogers & Woodley 1978; Nagel 1979). The only studies over a secondary successional gradient have been made by Southwood *et al* (1979) on colonisation rates and taxonomic composition of Heteroptera and Coleoptera and the more recent publication by Brown & Southwood (1983) on trophic diversity, niche breadth and generation times of exopterygote insects in the secondary succession.

In Section 4.2 it was shown how quickly species of insects and spiders colonised an early successional habitat. The rapid arrival of species was accompanied by a build up in numbers and biomass of the invertebrate fauna. As found by Simberloff & Wilson (1969), in their study of arthropod colonisation of defaunated islands, the early colonisers were highly mobile insects. In Site A these were species that showed the characteristic early successional *r*-type strategies of efficient dispersal and location of the newly disturbed area, a rapid establishment on arrival and for certain of these species to become temporarily highly abundant; this latter aspect will be considered in detail later when the insect herbivore community is discussed. Such pioneer species in Site A were found chiefly amongst Coleoptera, Heteroptera and Homoptera whilst in Site D (Section 4.5.2) the pioneers were mainly Coleoptera and Homoptera. These colonisation trends have also been found in similar early successional sites by Southwood *et al* (1979) for Coleoptera and Heteroptera. Other major insect taxa (Orthoptera, Thysanoptera, Lepidoptera, Neuroptera, Diptera, Hymenoptera *etc*) as well as other species of beetles and sap-feeders are more characteristic of later seral stages with more *K*-related life-histories (*e.g.* Brown & Southwood 1983 for exopterygotes). Other examples of a similar rapid colonisation of freshly exposed habitats by arthropods with typically *r* characteristics include acarine succession on ley pasture (Whelan 1978), the colonisation of industrial reclamation sites by microarthropods (Hutson & Luff 1978) and for the invertebrate fauna associated with pasture establishment on an arable site (Purvis & Curry 1980).

A detailed breakdown of the trophic structure of the insect and spider community in Site A was provided in Section 4.3. In the introductory comments the use of the term 'guild' in ecological studies was assessed and showed that depending on the aim of a particular research study a variable number of guilds may be recognised. So, for example, in a trophic study the possible set of guilds could range from a very basic description using just two categories (Cole 1980) to more informative sub-groupings (Evans & Murdoch 1968; Moran & Southwood 1982; Southwood, Moran & Kennedy 1982). In this present study it was realised that it would have been desirable to sub-divide the herbivore guild into leaf-, stem- and flower-feeders in a similar fashion to Murdoch & Evans (1968). However, because sources of host-plant records from the literature are not always complete or reliable (let alone the plant structures which are preferentially attacked), this subdivision was not possible and herbivores were placed in one guild. Despite these shortcomings the simple treatment of the insects and spiders, by recognising just three major trophic guilds of herbivores, predators and omnivores, has provided a valuable description of the trophic dynamics of the early successional invertebrate community.

The trends in abundance of the two main guilds in Site A, the herbivores and predators, followed certain interesting patterns (Section 4.3.3). Herbivore and predator numbers increased rapidly to July in the first year, mainly by immigration of highly mobile adults. Herbivore numbers continued to rise to a high asymptote in mid-summer and numbers then subsequently declined towards the end of the season. In contrast, population levels of predators remained around their July abundance for the remainder of the season. The predators that were arriving during the first year were relatively large in size (chiefly Coleoptera: Carabidae, Coccinellidae, Staphylinidae, Heteroptera: Nabidae and Araneae) in relation to their prey.

These events, found in the first year of the succession, tie in closely with both theory and observations in the field of predator-prey interactions along the *r*-*K* continuum, and it is possible to test some of the predictions that have been made about interactions at the the *r*-end of the continuum. Southwood (1975) developed a model incorporating population density, population growth and habitat stability. The model was elaborated by Southwood & Comins (1976) and Southwood (1977c) and can be used to predict how successful natural enemies would be in maintaining endemic prey populations in habitats ranging along the *r*-*K* continuum. The central theme of the model is the 'natural enemy ravine' where the effects of predators are most significant. The width of the ravine at any one point on the continuum is influenced by the different parameters of the functional and numerical responses of the natural enemies. At the *r*-end of the ravine the attack rate and handling time (*i.e.* the functional response) is of prime importance but because of a shortage of time (*i.e.* low durational stability of the habitat as in Sites A and D), and because the predators are often large, the numerical response of natural enemies to the high population growth of their prey is limited.

The model predicts that insect herbivores in this early successional environment will tend to escape from their enemies in time and space. Their predators will tend to have low population equilibration levels, to be polyphagous and of large size in relation to their prey. The early successional features were again demonstrated in the second year in Site A with a rapid rise and subsequent fall of the herbivore population and with relatively low predator levels throughout the season. Although the pattern of herbivore abundance in the second year in Site A was similar to that found in the first season the abundance was considerably lower (almost by 50% for maximum levels) in the second year. This initial high population density may be a common feature of the very early stages of the succession, especially the ruderal habitat. Indeed data from Southwood *et al* (*pers.comm.* for exopterygotes) and P.Hyman (*pers.comm.* for Coleoptera) support this; their information has accounted for seasonal fluctuations in herbivore abundance in sites of different successional age. This would also suggest that the ruderal habitat is a more extreme *r*-type system than the initial stages of the main phase of the early succession that develops after the decline of the short-lived annual herbs. Site A exemplifies this well with a main ruderal period in the first year followed by establishment and subsequent numerical dominance in the second year by perennial herbs and grasses.

The descriptions of the abundance (and biomass) in Site A were also illustrated with pyramids of abundance (and biomass) of the herbivores, predators and omnivores in Fig. 4.6 (abundance) and Fig. 4.7 (biomass). Note that the pyramids did not include tourists, parasitoids in the predator guild or internal and root-feeding herbivores; interpretation of the pyramids is therefore limited. It was shown that at certain times during the two years in Site A the insect and spider community became predator-biased. The occurrence of relatively high numbers of predators with low prey density may be related to the structure (*i.e.* biological and physical) of the plant community (Dempster 1976; Smith 1976 and see reviews by Price, Bouton, Gross, McPheron, Thompson & Weiss 1980 and Crawley 1983). For example, Smith 1976 and Dempster 1976 have observed that natural enemy numbers are greater in structurally complex weedy crops than in more simple-structured weed-free crops. Similar observations that more diverse habitats often have higher predator densities and lower prey numbers led Root (1973) to formulate his 'enemies hyphothesis'. More structurally diverse habitats may be important in the provision of food sources (*e.g.* nectar and pollen) for adult predators (Root 1973; Price *et al* 1980; Crawley 1983) and a more complex physical structure may allow for a greater diversity and abundance of predators (this is documented for spiders by

Duffey 1962,1963,1966 and Robinson 1981).

After the initial colonisation and establishment on host-plants, insect herbivores in Site A would be expected to remain fairly static since plant resources are usually available (see Price 1976). Predatory insects and spiders, on the other hand, have to actively search for their prey and in certain cases this difference in behaviour might lead to a greater catch of predators compared to herbivores in D-vac samples. Predators may also move in from adjacent habitats looking for or attracted to plant food sources, prey items, refuge (Price *et al* 1980, Root 1973) or simply as 'vagrants' or 'tourists' (Hill 1982 and *pers.comm.*; Moran & Southwood 1982).

The highly predator-biased catch in May of the first year in Site A was a result of large numbers of the immigrating carabid, *Bembidion lampros*. Plant cover was sparse at this early stage of the succession (around 10%) and this highly active ground beetle could be seen quickly searching for prey over the bare ground between seedlings and young plants. The build up of populations of Staphylinidae and Araneae in June and July suggest that structural attributes of the developing plant community were producing higher predator/prey ratios than might be expected. Pollen or nectar sources could have attracted an influx of predatory adult Staphylinidae (see Price *et al* 1980), whereas an increasingly complex physical structure of the system would aid the establishment of a spider fauna. This latter point is further suggested since the spider population increased gradually in numbers to the end of the season during which time the physical structure of the plant community was developing both vertically as well as horizontally, especially with the formation of a litter layer. Similar arguments may be applied to the pyramids of abundance (and biomass) for the second year. The only occasion where the pyramids become highly herbivore-biased would appear to be during the mid-season period when the classical population 'scramble' or 'boom and bust' phase occured; at this time r_{max} is approached as the herbivore population builds up to an asymptote followed by a subsequent crash (Southwood 1977a,b,c; see also Chapter One, Section 1.2.2). For the first year in Site D (Section 4.5.3), except for a similar high predator density (*Bembidion lampros*) in May, herbivore abundance was always greater (often considerably so) than predator abundance and this is reflected in the pyramids of abundance and biomass (Fig. 4.14) for this site. This lack of predator-bias may relate to the lower structural complexity in Site D compared to Site A and may be explained by the 'enemies hypothesis' as discussed above or else by an advance in succession in Site D.

Information on the species richness of predatory insects and spiders was available for the first year only in Site A (Section 4.3.2) and this showed that predator species (mainly Coleoptera and Araneae) entered the ruderal community very quickly. Many of these predator species, especially Carabidae, Staphylinidae and Araneae may have been caught for reasons other than predation as discussed above.

A third trophic category described in this study, the omnivore guild, was of relatively minor importance in Site A and Site D. These omnivores included species that are believed to feed on both animal and plant material as well as a small number of scavengers. This trophic group would be expected to have a more important role in later successional stages (see Brown & Southwood 1983) where the litter layer is more defined.

The remainder of this section of the discussion will be concerned with the early successional herbivores and considers their life-history strategies in relation to the habitat. Section 4.3.2 demonstrated how rapidly insect herbivore species colonised Site A during the first two years of the succession and Site D (but to a lesser extent) during the first year. These species had appropriate *r*-selected traits in being highly mobile and mainly adult (*i.e.* overwintering in the adult stage and and therefore available for immediate oviposition); these pioneers were chiefly Coleoptera, Homoptera and Heteroptera in Site A and Coleoptera and Homoptera in Site D. As a consequence of this rapid immigration, the diversity (as measured by both species richness and Williams α) of the herbivore community rose in each year in Site A and in the first year in Site D, but fluctuated because of the rapid changes in both species richness and the relative abundance of individual species. In addition to these patterns low values of Sorensen's Index (the quantitative I_w) for abundance and biomass demonstrated that the insect herbivore species were turning over rapidly during the two years in Site A; this was also found by Southwood *et al* (1979).

Sections 4.4 and 4.5.5 looked at the herbivore load on each of the four major plant groupings and the degree of specialisation (*i.e.* host-plant specificity and mode of feeding). Some descriptions and discussions of overwintering strategies and voltinism were also presented. During the first year in Site A the herbivore load (in terms of abundance and biomass) on each of the plant groupings showed a characteristic *r*-strategy of a rise to high levels followed by a decline or 'crash' phase. Herbivore species numbers also built up in association with each plant grouping. Analysis of this herbivore load showed that in the first year abundance was greatest on annual herbs. The fact that the load on perennial herbs was higher than expected may be a reflection of species which are able to feed on both plant groups; although it is likely that these insect species are probably feeding chiefly on the more abundant annual herbs. The abundance and biomass of grass-feeding insects was lower than that for insects on annual herbs although the herbivore load on the Gramineae was still considerable in the first year.

In the second year in Site A the strategy of rapid multiplication was again evident among herbivores associated with the three herb groupings, but not for the Gramineae. The numbers of grass-feeding insects remained fairly stable throughout the second year (a more *K*-strategy). Conversely, patterns of abundance and biomass in the second year in Site A showed that the perennial herbs had the greatest herbivore load. This time the annual herb-feeders (and biennial-feeders) had a higher load than expected and this again reflects species feeding on more than one plant category. It seems reasonable to suggest that, compared to perennial herbs, the annual and biennial herbs in the second year in Site A should have considerably lower herbivore loads since these latter two groups had relatively low abundances (especially the biennials) and were heading for extinction.

The plant community in Site D was more advanced (*i.e.* less of a ruderal system, more of a true early successional community) compared to Site A in the first year. Consequently, it is not surprising to find few traits characteristic of life in an ephemeral habitat in the Site D insect fauna compared to Site A. The more Gramineae-dominated vegetation in Site D had an associated insect herbivore community in which numbers of grass-feeding insects became increasingly dominant as the season progressed. A reduced colonisation rate of insect herbivore species in Site D further differentiated the two sites and emphasised the more permanent nature (*i.e.* advanced in terms of succession) of the vegetation in the Site D Young Field.

The degree of specialisation on host-plants in Site A was assessed in Section 4.4.3 for three grades of specialists and the single generalist category. It was shown that in the first year of the succession the Grade 3 specialists and generalists were the most important groups in terms of abundance and biomass; Grade 1 and 2 specialists were of little importance. There was also a predominance of Grade 3 specialist species (60-70% of total species) during this first year although generalists were also fairly species rich (around 20% of the total). This trend for a less specialised type of herbivore to dominate the very early stages of the succession follows current theory on the life-history strategies of insect herbivores along the *r*-*K* continuum as presented by Feeny (1975,1976) and Rhoades & Cates (1976). The essence of this theory is based on the anti-herbivore defense strategy employed by *r*- and *K*-selected plant species. Since early successional plants are characteristic of temporary habitats, to the insect herbivore they are 'unapparent' (Feeny 1975,1976) or 'unpredictable' (Rhoades & Cates 1976) and therefore hard to find. The selective pressures of grazing on these early successionals are somewhat reduced because they are *r*-strategists and can escape from their herbivores in time and space. As has been illustrated in the description of the vegetation in Sites A and D such plant species manage this by rapidly colonising newly-exposed areas, growing quickly, reproducing rapidly and producing large numbers of propagules.

It would be expected, therefore, that these early successional plants should utilise relatively low energy-costing chemical defenses, since most of their energy will be directed into growth and reproduction. Furthermore, because escape in time and space is more effective against specialist herbivores the type of anti-herbivore chemistry used by these early species should be directed against generalist herbivores. Such defenses are of a 'qualitative' nature (*i.e.* they are most effective in relatively low concentrations) and take the form of secondary compounds such as glucosinolates in crucifers, cyanogenic glycosides or alkaloids in legumes and coumarins and essential oils in umbellifers (see Feeny 1976 and Rhoades & Cates 1976) and nutrient immobilisation in grasses (McNeill & Southwood 1978; Lawton & McNeill 1979; Prestidge & McNeill 1981,1982). In contrast, at the other end of the spectrum the later successional plant species are characteristic of more permanent habitats. To the insect herbivores these species are 'apparent' (Feeny 1975,1976) or 'predictable' (Rhoades & Cates 1976) and therefore bound to be found. Since later successional plants cannot escape from herbivory in time and space (*i.e.* they are relatively slow-growing and long-lived) selection will favour the use of 'quantitative' barriers (Feeny 1975,1976) or digestibility reducing substances (Rhoades & Cates 1976), such as tannins, that act in a dosage-dependent way against specialist herbivores.

The predominance of Grade 3 specialists and generalists in the first year of succession in Site A supports the predictions of specialisation made by Feeny and Rhoades & Cates in that early successional plants will be attacked by a more generalist fauna. In great contrast are the patterns of abundance for the three specialist and generalist herbivores in the second year. Total herbivore abundance and biomass was much lower in the second year and with relatively minor fluctuations. Except for a single peak (due to the sudden appearance of the mirid *Plagiognathus chrysanthemi* mainly in nymphal stages) the generalists were relatively uncommon in the second year. A further notable change was the increase in abundance of Grade 1 specialists (*i.e. Apion apricans* and *A.trifolii* attacking the highly abundant *Trifolium pratense*); this category together with the Grade 3 specialists (mainly grass-feeding

Cicadellidae and Delphacidae) were the most abundant feeding types during the second season.

So, just as the plant community changed dramatically from a dominant ruderal system in the first year to a more 'apparent' early successional community in the second year, accompanying changes in the structure of the insect herbivore community were equally dramatic. The sudden transition from a distinct generalist fauna to a more specialist herbivore community in the second year is remarkable. On its own, this information concerning a switch in feeding specificity from one year to the next would indicate that a major change had occurred in the plant community. In terms of Feeny (1975,1976) and Rhoades & Cates (1976) this would have been seen in the light of a switch in the plant community from a mainly 'non-apparent' or 'unpredictable' vegetation in the first year to a more 'apparent' or 'predictable' plant community in the second year. The vegetation trends in Site A, as described by Chapter Three, support this. However, this rapid loss of a generalist fauna after the very early stages of the succession (*i.e.* after year 1) may be a characteristic of this particular successional gradient. A recent study by Hyman (in prep) certainly shows this for phytophagous Coleoptera along the experimental gradient at Silwood Park; as the succession proceeds Grade 2 specialists become increasingly important in terms of abundance and species contributions and with a rapid decline in more generalist groups. Comparable studies on other seres need to be carried out to test this suggestion.

The description of the degree of specialisation for the Site D herbivores in Section 4.5.5(c) illustrated a more advanced stage of succession in Site D with generalists in low abundance and low species richness. The Site D community was dominated (in terms of abundance, biomass and species richness) by Grade 3 specialists and the most numerically abundant species were the typical *r*-strategists that were also common in Site A in the first year; *e.g. Ceutorhynchus floralis* (on Cruciferae) and *Macrosteles laevis* and *M.sexnotatus* (on Gramineae).

Another important characteristic of the herbivore community is the seasonal trend in abundance of individual species. As described in Section 4.4.3 although most species existed at relatively low levels a few species were highly abundant. Those highly abundant species were found chiefly in the first year and represent extreme *r*-strategists with generalist or Grade 3 specialist feeding habits. These were species that are highly mobile, probably increase at a rate approaching r_{max} and have high dispersal tendencies to new habitats. In Site A these were represented by Miridae (*Lygus rugulipennis* and *Plagiognathus* chrysanthemi), Cicadellidae (*Macrosteles laevis, M.sexnotatus* and *Euscelis lineolatus*), Aphididae (*Aulacorthum solani*) and Curculionidae (*Ceutorhynchus floralis* and *Sitona lineatus*). This trend also occurred in Site D.

Although information on seasonality was not presented in the results it was evident that peak levels of abundance for taxa within particular feeding groups tended to occur at different times of the year. This trend was well exemplified by the main grass-feeding group of Grade 3 specialists, the Homoptera. In her excellent review of British grassland Auchenorrhyncha Waloff (1980) summarises this characteristic property of grassland leafhoppers as *"Alternate waves of abundance of delphacids and cicadellids* [the two largest families] *are an example of spacing in time of many species occupying the same habitat"*. Relatively low levels of peak abundance of individual herbivores (all groups) were found in the second year in Site A, demonstrating species as expected from a more specialist fauna.

Based on the concept of *r*- and *K*-selection and 'apparency', Lawton & McNeill have predicted that one might expect a greater abundance of herbivores on non-apparent (*i.e.* early successional) plants and with larger fluctuations compared to later successional plants. Indeed they go on to state that *"These predictions urgently need testing along a successional gradient over a comparatively small spatial scale"*. The successional sites at Silwood may be used to test this idea and from other works it seems that this is the case (Brown *et al*, unpublished data; P.Hyman *pers.comm.*). Certainly the abundances (and their differential fluctuations) that were found between the two years in Site A fully support Lawton & McNeill's prediction. This also raises the intriguing question as to the effect of insect grazing on early successional plant communities. From this current reasoning one would expect that an early successional habitat, typified by Site A, would be more affected early in the succession simply by nature of the greater herbivore load in the early stages. This subject will be explored in detail in Chapter Six.

It is now logical to discuss factors limiting population size during the second year in Site A. Of prime importance are the consequences, to the structure of the insect fauna, of the sudden switch from a ruderal based plant community to a largely more 'apparent' early successional system in the second year. Hitherto, it has been reasoned (from theory based on *r*- and *K*-selection and anti-herbivore chemistry) that a lower insect abundance would be expected in the second year of the succession.

Further characteristics of the ruderal and early successional herbivore community in Site A were described in Section 4.4. There it was shown that the herbivore guild may be subdivided into 'chewers' and 'sap-feeders'; the latter group, as Brown & Southwood (1983) point out, has quite often been incorrectly referred to as 'suckers'. The sap-feeders were subsequently divided according to the particular plant tissue attacked. It was shown how rapidly a sap-feeding insect population built up in the first year whereas, in comparison, the chewers were always considerably less abundant. Such a difference between the population levels of these two herbivore guilds may be explained by differential rates of reproduction rather than to differences in immigration rates. Immigration rates were probably similar for both groups since these pioneering chewers (chiefly Chrysomelidae and Curculionidae) and sap-feeders (mainly Aphididae, Cicadellidae, Delphacidae and Miridae) are both highly mobile. This idea/prediction remains to be tested.

The first year of a secondary succession marks a period of rapid rates of colonisation and growth of early successional plants. It is at this time when nutrients are readily available in the soil for immediate plant uptake. As a consequence, those pioneer species arriving during the first year will experience a nutrient flush which is more likely to be far greater than in any of the future years of the succession (S.McNeill *pers.comm.*). Those insects that will respond most to these relatively high nutrient levels will be species that have the most direct access to their food source; these will undoubtedly be sap-feeders, especially those tapping the phloem (chiefly Aphididae, Cicadellidae and Delphacidae) and mesophyll (mainly Heteroptera, especially Miridae and Thysanoptera: Thripidae). A sap-feeding *r*-strategist would therefore do best to exploit the phloem or mesophyll rather than a less nutritious xylem system. As indicated by the abundance levels this appears to be the trend for the first season colonisers. In addition, most of the sap-feeding species in the first year were phloem- and mesophyll-feeders, especially the latter and with very few xylem-feeders; this latter group appears to have low species richness and abundance throughout the succession (Brown & Southwood 1983). Maximum species richness levels reached (in August) were 10 for phloem-, 22 for mesophyll- and 3 for xylem-feeders. Supportive evidence comes from Hill (1976), McNeill & Southwood (1978), Lawton & McNeill (1979) and Prestidge (1980) who show that populations of phloem-feeders are closely linked to soluble nitrogen levels and mesophyll-feeders to levels of total leaf nitrogen whereas xylem-feeders do not appear to respond to changes in plant nitrogen levels. A greater abundance of sap-feeders (and then predominantly phloem- and mesophyll-feeders) in Site D would also support this view although the species richness of chewers and sap-feeders was similar. A change from a relatively open-nutrient cycle in the first year of succession in Site A to a more closed system in the second year undoubtedly occurs (S.McNeill *pers.comm.*). Indeed this trend towards a more internal cycling is one property of plant communities along a successional gradient (Odum 1969).

Section 4.4.5 presented information on the types of overwintering strategies favoured by the various insect herbivore taxa and in Section 4.4.6 voltinism was considered. It was shown that the adult stage is clearly the most popular overwintering strategy for these very early successional species and enables them to be ready for immigration and oviposition in the following spring. Of course, overwintering in the egg or immature stages was displayed by some taxa and may in part explain the occurrence of waves of abundance of different taxa in the field (from this study and see also Waloff 1980). For herbivores in Site D (Section 4.5.5(e)) it was shown that the pattern of overwintering strategies was similar to that for Site A. It is equally difficult to make general statements about the type of voltinism that one might expect in early successional insect herbivore species. This particular life-history strategy will be a function of various factors including the degree of host-plant specialisation, host-plant phenology, type of tissue attacked and the nutrient status of the plant as well as the overwintering strategy adopted and climatic factors (McNeill & Southwood 1978; Waloff 1980; S.McNeill *pers.comm.*). The majority of species found in Site A and Site D were univoltine although bivoltine species did occur. Exopterygote insects contained both single- and double-brooded species whereas the endopterygote Coleoptera were virtually all univoltine. Southwood, Brown & Reader (1983) show that, as plant generation time increases along the successional gradient at Silwood Park, habitat durational stability increases for the insect. As predicted by Southwood (1977a) and described for exopterygotes by Brown & Southwood (1983) the associated insect fauna will show a lengthening of their average generation time. Univoltinism will, therefore, tend to be favoured by insects in later successional habitats whereas early successional plant communities will have an insect herbivore fauna in which species have relatively short life-cycles and may have more than one generation per year.

CHAPTER FIVE

INSECT - PLANT RELATIONSHIPS IN THE EARLY SUCCESSIONAL HABITAT

5.1 INTRODUCTION

This Chapter brings together the separate descriptions of plants and insect herbivores made in Chapters Three and Four; comparisons of Site A with Site D are made throughout. The whole herbivore and plant community is first analysed in terms of colonisation or establishment rates. The structure of the insect community is then related to the various vegetational parameters measured in this study. Further analysis involves the breakdown of the herbivore community into herb-feeders and grass-feeders and an analysis of their host-plant relationships. It has not been possible to include any breakdown of the structure preferences of herbivores for particular plant structures due to either a total lack of information or a paucity of reliable information.

It should be borne in mind that any mention of insect species (colonisation, diversity *etc*) excludes information on unidentified taxa (mainly Aphididae); however, these groups are included in abundance and biomass measures.

5.2 COLONISATION RATES OF PLANTS AND INSECT HERBIVORES

In Chapter Four (Section 4.3.2) the seasonal and successional changes in the phytophagous insect fauna in Site A were described. The low values of the Sorensen's Index of Similarity indicated a rapid turnover of insect herbivore species. Certainly, from Table 5.1a and b where plant and insect herbivore total I_w values (for numbers of individuals) are reproduced, insect similarities either during or between seasons were lower (often considerably so) than corresponding plant I_w values. A similar difference has also been detected by Southwood *et al* (1979) and, as they suggest, probably reflects the greater mobility and species richness of insects. The same situation was also found for the first year of the Site D Young Field (Table 5.1c).

A difference in the rate of establishment of plants and insect herbivore species can be shown by plotting the successive accumulations of insect species against plant species (Fig. 5.1a). It is

TABLE 5.1: Values of Sorensen's Index of Similarity (I_w for numbers of Individuals) for plants and total herbivores in Site A

a. Within each year (Site A)

b. Between years (Site A)

c. Within the first year (Site D)

Year 1 Year 2

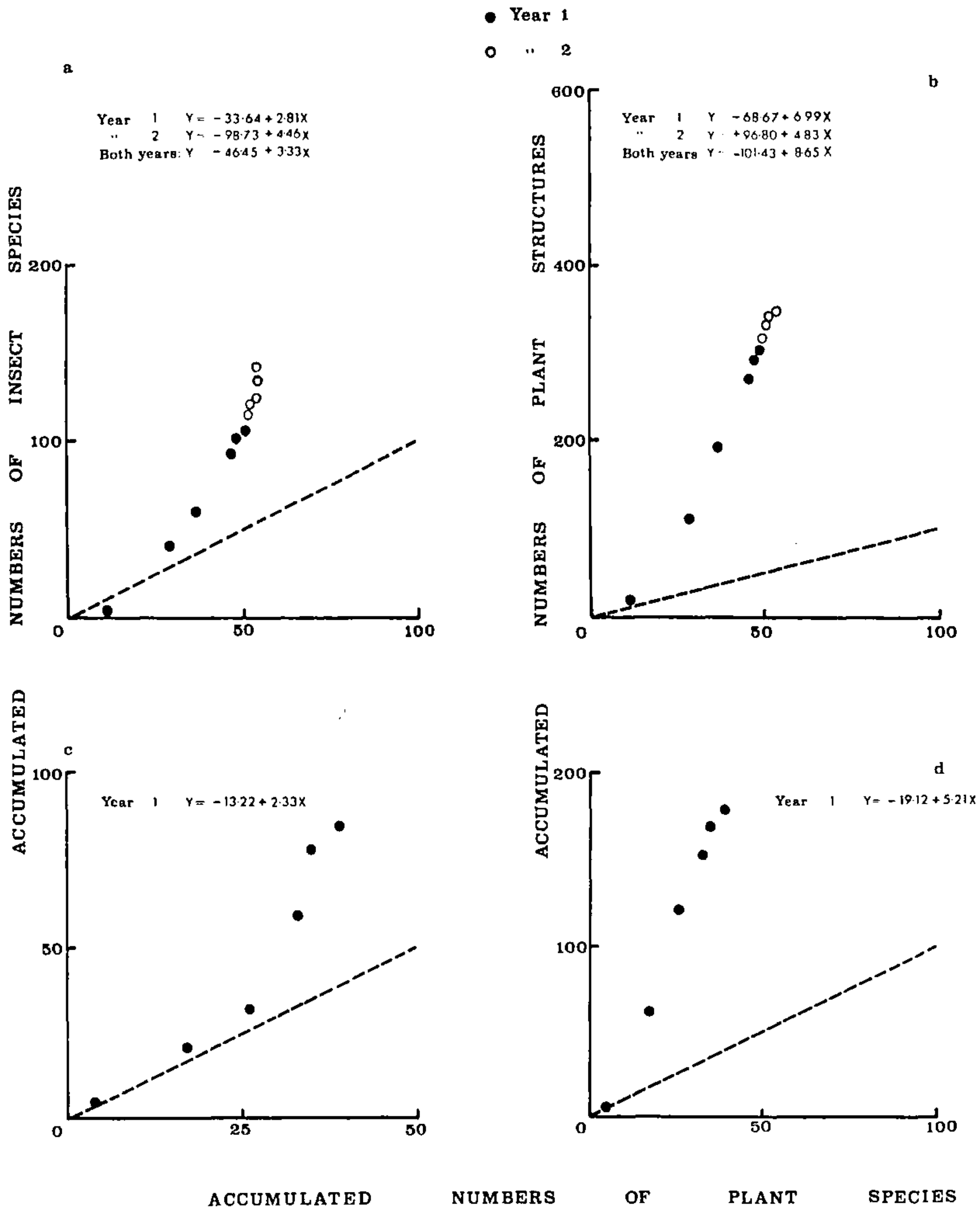
	May – June	June – July	July – Aug	Aug – Sept	Sept – Oct	Oct '80 – May '81	May – June	June – July	July – Aug	Aug – Sept	Sept – Oct
Plants	0.16	0.71	0.66	0.72	0.64	0.43	0.69	0.70	0.82	0.77	0.70
Insects	0.10	0.37	0.29	0.34	0.20	0.17	0.20	0.24	0.14	0.58	0.58

	May 80 – May 81	June 80 – June 81	July 80 – July 81	Aug 80 – Aug 81	Sept 80 – Sept 81	Oct 80 – Oct 81
Plants	0.11	0.06	0.26	0.30	0.28	0.23
Insects	0.02	0.21	0.12	0.10	0.14	0.18

	May – June	June – July	July – Aug	Aug – Sept	Sept – Oct
Plants	0.04	0.58	0.72	0.76	0.81
Insects	0.05	0.10	0.14	0.16	0.17

Fig. 5.1 Relationship between the accumulation of total insect herbivore species and total plant structures with total plant species during the first two years (Site A) or the first year (Site D) of succession.

a. Insect species *vs* plant species (Site A).
b. Plant structures *vs* plant species (Site A).
c. Insect species *vs* plant species (Site D).
d. Plant structures *vs* plant species Site (D).


● Year 1
○ " 2
a
Year 1 Y = −33·64 + 2·81X
" 2 Y = −98·73 + 4·46X
Both years: Y = −46·45 + 3·33X
NUMBERS OF INSECT SPECIES
200
100
0
50
100
b
600
Year 1 Y = −68·67 + 6·99X
" 2 Y = +96·80 + 4·83 X
Both years Y = −101·43 + 8·65 X
NUMBERS OF PLANT STRUCTURES
400
200
0
50
100
c
ACCUMULATED
100
Year 1 Y = −13·22 + 2·33X
50
0
25
50
d
ACCUMULATED
200
Year 1 Y = −19·12 + 5·21X
100
0
50
100
ACCUMULATED NUMBERS OF PLANT SPECIES

clear that the relationship between insect and plant species is virtually linear. In the Site A Young Field new insect herbivore species arrived at around three times the rate of plant species during the two years ($b=3{\cdot}33$). This difference again reflects the greater mobility and species richness of the insect fauna. In addition, it is important to consider how plant structures accumulate with plant species. The relationship is also linear with new structures being added at around eight times the rate of plant species during the two years (Fig. 5.1b, $b=8{\cdot}69$. Newly colonising ruderal plant species were continually adding structures and being replaced by other plant species (either the highly structured herbs or less complex Gramineae). Very similar insect-plant species and insect-plant structure relationships were found for Site D in the first year and the slopes between the two first year sites are similar, although the species richness is considerably less (see Fig. 5.1c and d).

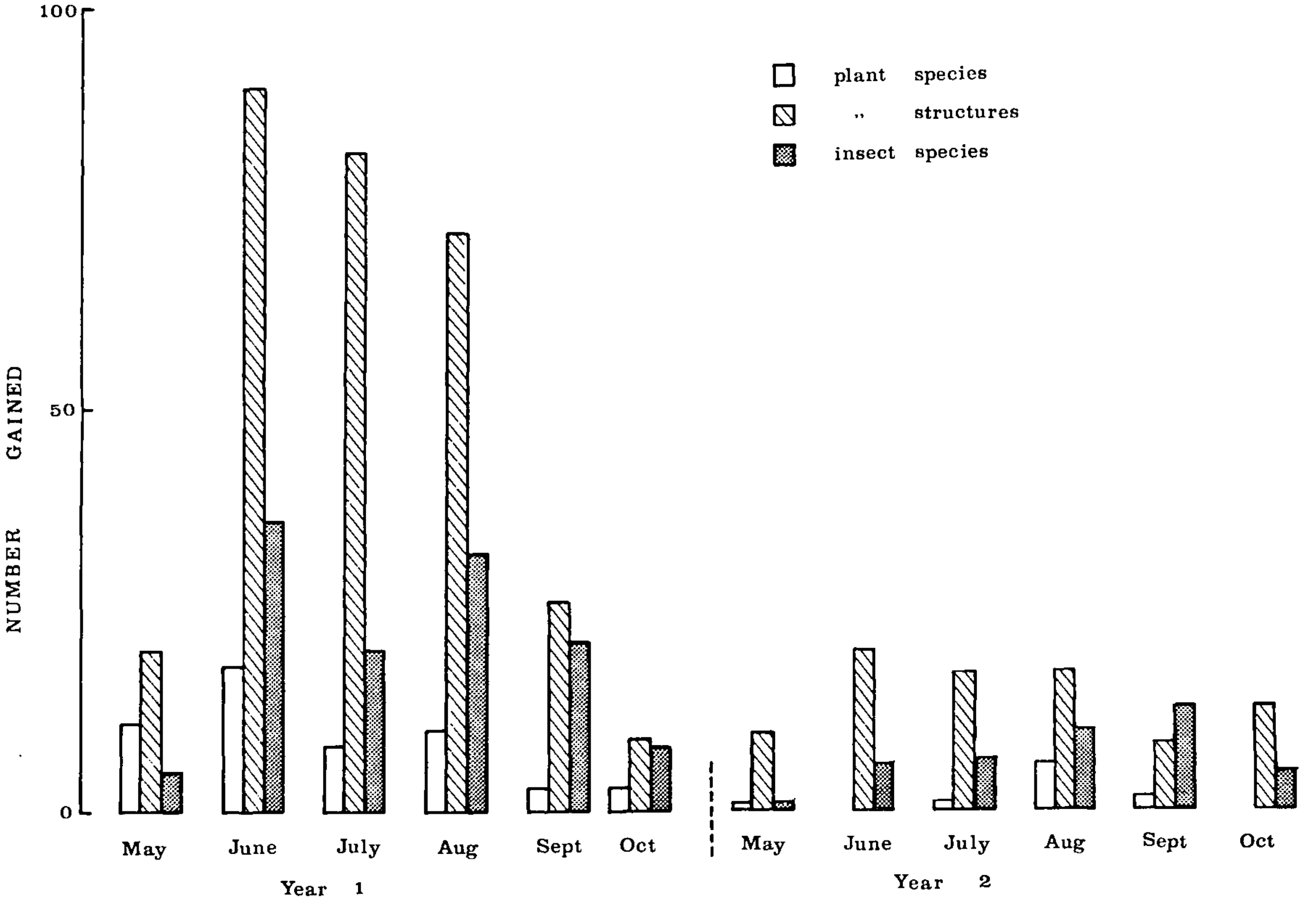
The relative importance of plant species and plant structures to insect species colonisation may be shown when actual numbers gained are taken into account. In Fig. 5.2 the gains in plant species, plant structures and insect herbivore species at each sampling occasion are shown for two years in Site A. In the first year newly colonising insect herbivores were more closely related to the appearance of new structures ($r=0.83$, $0.05>p>0.01$) than new plant species ($r=0.68$, $p>0.05$). There was no significant relationship between gains in either plant species or structures and insect species in the second year ($r=0.37$ and 0.64 respectively, $p>0.10$). It is also interesting to note that gains in plant species and corresponding structure gains were not significantly correlated in either year (Year 1, $r=0.68$, $p>0.10$; Year 2, $r=0.17$, $p>0.10$).

Site D resembled the second year vegetation in Site A with insect species gain not significantly correlated with either plant species or structures ($r=0.18$ and 0.30 respectively, $p>0.10$).

5.3 INSECT COMMUNITY STRUCTURE AND PLANT RELATIONS

The structure of the insect herbivore community in Site A is investigated here in terms of species composition (both species richness and α-diversity), abundance and biomass. Variation in these parameters through two years (Site A) and one year (Site D) is analysed with respect to seasonal patterns in a number of plant factors including cover (number of pins touched), abundance (mean number of touches per pin, regarded here as equivalent to biomass), two measures of plant species composition (richness and α-diversity), two measures of architectural complexity (the number of different structures and α-diversity) and two measures of spatial complexity (size, or

Fig. 5.2 Seasonal trends in colonisation by plant species, structures and insect herbivore species.


100
50
0
NUMBER GAINED
plant species
" structures
insect species
May
June
July
Aug
Sept
Oct
Year 1
May
June
July
Aug
Sept
Oct
Year 2

the number of height categories, and α-diversity).

In Table 5.2 correlations of insect and plant parameters (based on total values of each of the six monthly samples) are given. In the first year (Table 5.2a) insect herbivore species richness was highly correlated with five plant parameters:- species richness ($p<0.001$), cover ($0.01>p>0.001$), species α ($0.01>p>0.001$) and both measures of architecture ($0.01>p>0.001$ for number of structures and $0.05>p>0.01$ for α). Separation of these plant factors in terms of their relative importance to the insect community is difficult because of the high correlations between them (Appendix 9). Significant correlations include plant species richness with each of the four other significant plant parameters (see above) and plant architecture with cover and species richness.

The value of plant cover as a predictor of insect species richness in the first year is questionable, since the insect herbivores associated with the early successional habitat are relatively specialised in terms of their host-plants and fall into restricted feeding groups (*e.g.* Auchenorrhyncha on Gramineae; see Section 5.5). Thus, factors relating more to their host-plants specifically than mere total cover would be expected to be important for these insects.

Plant species richness alone explains 96% of the variation in insect species richness in the first year ($r=0.98$, $p<0.001$). The combined effects of plant species richness with all other plant factors, both singly and in combinations, were analysed using multiple regression (stepwise) techniques; insect species richness was used as the dependant variable and various non-correlated plant parameters were used as predictors. No other plant factors (in any order in the regression) were significant in explaining any further variance in insect species richness during the first year.

Plant architecture may also be an important predictor of insect species richness but this is impossible to test, since it is highly correlated with plant species richness ($r=0.93$, $0.01>p>0.001$ and $r=0.97$, $p<0.001$ for number of structures and architectural α respectively). If the architectural measurement, number of structures, is used on its own then 72% of the variance (or 83% if the α statistic is used) in insect species richness can be explained. Inclusion of either spatial parameter or plant abundance in multiple regression analysis does not significantly explain any further variation in insect species richness. Neither plant abundance nor spatial attributes were significantly correlated with insect species richness during the first year. The only significant predictor of insect taxonomic diversity was plant species richness; other plant factors did not explain any additional variation.

Similar problems were encountered when attempting to separate plant species and architectural effects on insect abundance in the first year. Plant species richness, plant species α and architectural α all show strong correlations with insect abundance (Table 5.2a). When all plant

TABLE 5.2: Correlation Coefficients (*r*) for Comparisons Between Insect Herbivore and Plant Parameters (Site A)

a. Year 1

b. Year 2

Plant Parameters

Insect Parameters	Cover	Abundance	Species Richness	Species α	Architecture (no. of structures)	Architectural α	Size (no. of height categories)	Spatial α
a. Year 1								
Species Richness	0.93**	0.57	0.98***	0.91**	0.85*	0.91**	0.73	0.66
Species α	0.79	0.31	0.81*	0.77	0.63	0.70	0.39	0.32
Abundance	0.73	0.47	0.85*	0.88*	0.77	0.86*	0.76	0.74
Biomass	0.63	0.33	0.75	0.75	0.65	0.72	0.62	0.57
b. Year 2								
Species Richness	0.23	0.36	0.57	0.63	0.44	0.55	0.71	0.75
Species α	-0.34	-0.59	-0.01	0.03	-0.45	-0.30	-0.26	-0.19
Abundance	0.13	0.81*	0.28	0.02	0.73	0.63	0.63	0.57
Biomass	0.23	0.83*	0.36	0.12	0.79	0.69	0.74	0.69

* $0.05 > p > 0.01$ ** $0.01 > p > 0.001$ *** $p < 0.001$

parameters were considered in a multiple regression plant species α was found to be the most important predictor of insect abundance; there was no additional explanation by other plant factors to the 77% variation accounted for by plant species α. Plant architectural α, on its own, is also a good predictor of insect abundance (74% of variation explained); inclusion of either spatial statistic and plant abundance in a multiple regression did not account for any of the unexplained variation in insect abundance. Insect abundance was not significantly correlated with either plant abundance or plant spatial attributes during the first year.

Biomass of insect herbivores during the first year was not significantly correlated with any of the plant parameters measured. As numbers of insects declined after August biomass rose and reached a maximum level one month later. Insect biomass in August was contributed mainly by exopterygote nymphs which had increased in size and therefore compensated for a drop in numbers.

Similar analysis of the Site D Young Field for the first year, however, shows that spatial attributes (as described either by size or spatial α) were highly correlated with taxonomic diversity of insect herbivores (Table 5.3); cover was the only other significant factor. Also, insect species richness, abundance and biomass were not significantly correlated with plant parameters.

Plant factors associated with insect herbivore parameters in the second year show generally lower values of r throughout (Table 5.2b); as in the first year some plant parameters were correlated amongst themselves (Appendix 9). There were no significant correlations of insect species richness with plant species diversity or architecture measurements. Both insect abundance and biomass were found to be highly correlated with plant abundance (66% and 69% variance explained respectively, $0.05>p>0.01$) but multiple regression further indicated that no other plant factors added to the variance explained.

5.4 HERB-FEEDING INSECTS AND HOST-PLANT ASSOCIATIONS

5.4.1 Colonisation of herbs and herb-feeding insects

The accumulation of herb species and their associated insect fauna follows a similar pattern to that found for the whole insect and plant communities (Fig. 5.3a). The relationship between herb-feeding insect species and herb species is again virtually linear. For the Site A Young Field new colonisers of herb-feeding insects were arriving at around 2 times the rate of host species

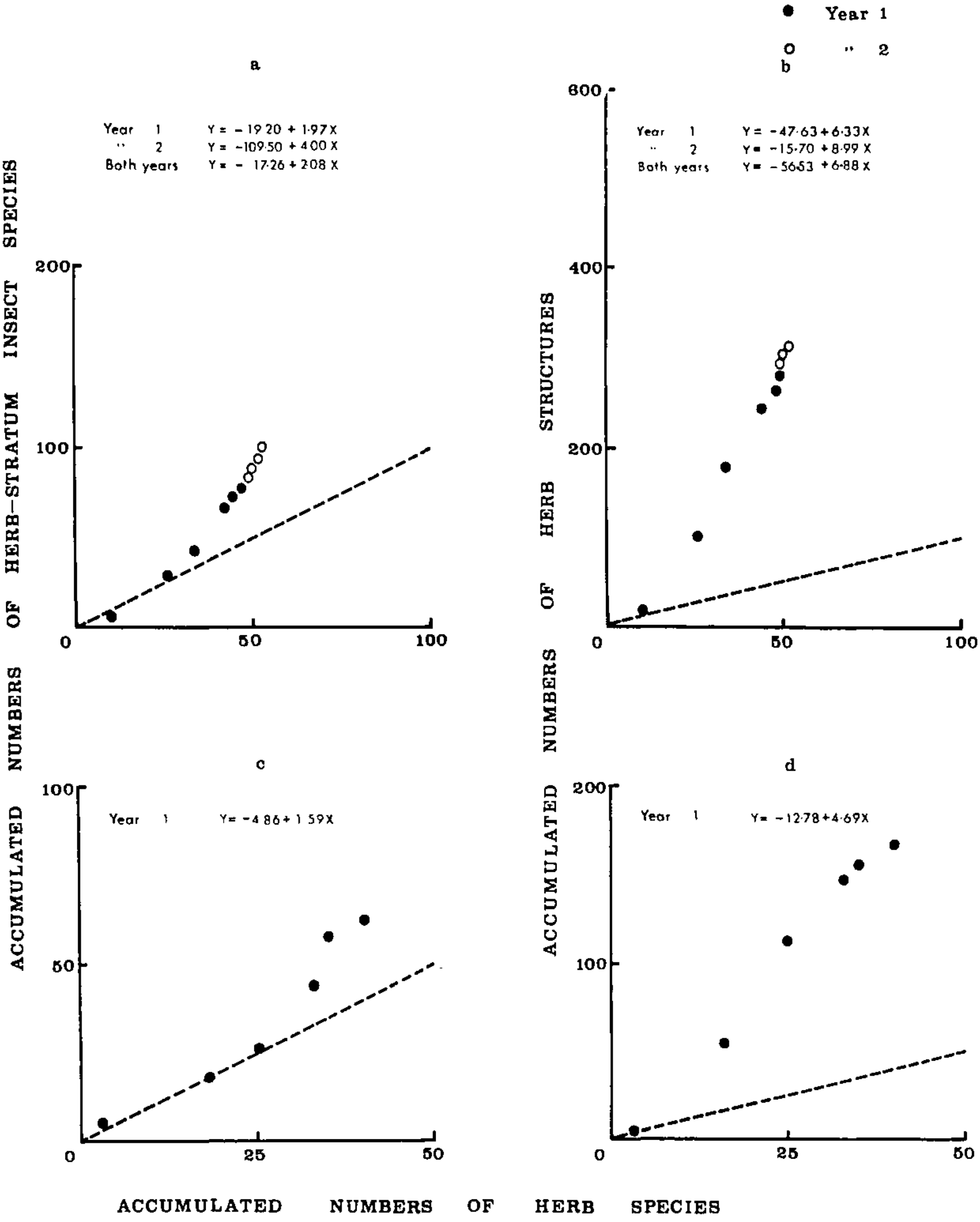
TABLE 5.3: Correlation Coefficients (r) for Comparisons Between Insect Herbivore and Plant Parameters (Site D)

	Plant Parameters							
Insect Parameters	Cover	Abundance	Species Richness	Species α	Architecture (no. of structures)	Architectural α	Size (no. of height categories)	Spatial α
Year 1								
Species Richness	0.81^{*}	0.64	0.51	-0.01	0.47	0.32	0.78	0.76
Species α	0.93^{**}	0.74	0.61	0.04	0.59	0.45	0.85^{*}	0.81^{*}
Abundance	0.70	0.49	0.37	-0.11	0.33	0.19	0.62	0.59
Biomass	0.61	0.40	0.29	-0.14	0.24	0.11	0.54	0.52

* $0.05 > p > 0.01$ ** $0.01 > p > 0.001$

Fig. 5.3 Relationship between the accumulation of herb-stratum insect species and herb structures with herb species during the first two years (Site A) or the first year (Site D) of succession.

a. Insect species *vs* plant species (Site A).
b. Plant structures *vs* plant species (Site A).
c. Insect species *vs* plant species (Site D).
d. Plant structures *vs* plant species (Site D).


● Year 1
○ " 2
a
Year 1 Y = − 19·20 + 1·97X
" 2 Y = −109·50 + 4·00 X
Both years Y = − 17·26 + 2·08 X
0
50
100
200
b
Year 1 Y = −47·63 + 6·33X
" 2 Y = −15·70 + 8·99 X
Both years Y = − 56·53 + 6·88 X
0
50
100
200
400
600
c
Year 1 Y= −4·86 + 1·59X
0
25
50
100
d
Year 1 Y = −12·78 + 4·69X
0
25
50
100
200
ACCUMULATED NUMBERS OF HERB-STRATUM INSECT SPECIES
ACCUMULATED NUMBERS OF HERB STRUCTURES
ACCUMULATED NUMBERS OF HERB SPECIES

during the two year period. The majority of new colonisers were Grade 3 specialists. The accumulation of herb structures with herb species is linear and shows that new herb structures were being added at around 7 times the rate of herb species during the two years (Fig. 5.3b, $b=6{\cdot}88$). This picture is similar for the first year in Site D (Fig. 5.3c and d).

The immigration of herb-stratum insects may be further assessed when actual numbers gained are considered. In the first year in Site A new colonisers of herb-feeding insects were more closely associated with the appearance of new structures ($r=0.81$, $0.05>p>0.01$) than with the appearance of new plant species ($r=0.53$, $p>0.10$); these new insect species arrivals were mainly generalists and Grade 3 specialists (Table 5.4). There was no significant relationship between gains in either herb species or structures with herb-stratum insect species for the second year ($r=0.45$ and -0.26 respectively, $p>0.10$); these new insect species were chiefly Grade 2 and 3 specialists (Table 5.4). In addition, gains in herb plant species and corresponding gains in herb structures were not significantly correlated with each other in either year (Year 1, $r=0.66$, $p>0.10$; Year2, $r=0.05$, $p>0.10$).

5.4.2 Community structure of herb-stratum insects

The structure of the herb-stratum insect community is analysed here in a similar fashion to the whole herbivore community in Section 5.3. A table of correlations of herb-feeding insects and plant parameters is given in Table 5.5 for Site A. For the first year insect species richness was closely associated with herb species richness, both measures of architecture and plant cover. Further separation of plant parameters is again hampered by plant-plant correlations (Appendix 10).

On its own, herb species richness explains some 96% of insect species variation ($r=0.98$, $p<0.001$). Application of multiple regression analysis, as before, indicated that the combination of other plant parameters with herb species richness does not significantly explain any further variation compared with herb species richness alone.

Plant architecture was again highly correlated with insect species richness and, as found for total herbivores and plants, was highly correlated with herb plant species richness (especially for architectural α; $r=0.96$, $0.01>p>0.001$). If architectural α is considered on its own then it may explain some 83% of herb insect species richness in the first year. Furthermore, addition of either the spatial factor or abundance does not explain any further variation in the insect species richness.

Herb-feeding insect abundance was highly correlated with herb species richness, species α and

TABLE 5.4: Monthly Gains in Herb-Feeding Insect Species During the First Two Years of Succession (Site A)

	Year 1						Year 2					
	May	June	July	Aug	Sept	Oct	May	June	July	Aug	Sept	Oct
Specialists Grade 1	0	2	2	0	2	1	0	1	0	1	0	2
Specialists Grade 2	0	4	1	5	5	1	10	1	3	5	6	3
Specialists Grade 3	4	22	8	19	10	3	4	7	12	10	8	5
Generalists	1	6	7	6	2	1	2	4	3	2	3	1

TABLE 5.5: Correlation Coefficients (*r*) for Comparisons Between Herb-Feeding Insect and Herb Parameters (Site A).

a. Year 1

b. Year 2

Plant parameters

Insect Parameters	Cover	Abundance	Species Richness	Species α	Architecture (no. of structures)	Architectural α	Size (no. of height categories)	Spatial α
a. Year 1								
Species Richness	0.87*	0.55	0.98***	0.74	0.81*	0.91**	0.74	0.66
Species α	0.50	0.10	0.43	0.03	0.43	0.38	-0.03	-0.25
Abundance	0.62	0.43	0.87*	0.82*	0.68	0.84*	0.77	0.79
Biomass	0.55	0.29	0.74	0.59	0.57	0.67	0.60	0.54
b. Year 2								
Species Richness	-0.44	-0.37	0.31	0.62	-0.11	0.14	0.21	0.30
Species α	-0.83*	-0.85*	-0.80*	0.52	-0.69	-0.44	-0.47	-0.34
Abundance	0.79	0.83*	0.10	-0.48	0.69	0.46	0.51	0.38
Biomass	0.73	0.77	0.02	-0.57	0.62	0.41	0.49	0.38

* $0.05 > p > 0.01$ ** $0.01 > p > 0.001$ *** $p < 0.001$

architectural α. Again, multiple regression analysis indicated that herb species richness was the most important factor with 76% of the variation in herb insect abundance explained by this parameter. However, when plant architecture is considered on its own it is almost as good a predictor of insect abundance with 74% of the variation in abundance accounted for. Also, combinations of the spatial factor and plant abundance in multiple regression does not increase the explained variation accounted for by herb architectural α.

In sharp contrast to Site A, similar analysis of herb-stratum insects and their host plants in Site D yielded no significant insect-plant relationships (Table 5.6).

For the second year the most important association was the high positive correlation between herb-feeding insect abundance and herb abundance and negative correlations of the insect taxonomic diversity and herb cover, abundance and species richness (Table 5.5b).

5.4.3 Specialist and generalist herb-feeders

This Section looks briefly at important plant factors that may affect the structure of the three specialist categories and the generalist herb-feeders; the specialist Grade 1 (monophage) category is not dealt with since there are few species (and low abundances) in this category. The herb community has been considered here in terms of the characteristics of the main groupings (annuals and perennials). Tables 5.7 and 5.8 give a summary of significant correlations for the generalists and two specialist groups in Site A and Site D.

The majority of Grade 2 specialists during both years were curculionids; their most important host plants found in Site A were *Trifolium* spp. (mostly perennial). During the first year positive correlations were found for species richness of these specialists and species richness of perennial (r=0.90, 0.01>p>0.001) and annual (r=0.82, 0.05>p>0.01) herbs. In the second year the species richness and α-diversity of these specialist herb feeders was highly correlated with species α of perennials (r=0.95, 0.01>p>0.001 and r=0.81, p=0.05 respectively). For the first year in Site D the Grade 2 specialists were also highly associated with the species richness of annuals (r=0.82, 0.05>p>0.01) as well as with the abundance of perennials (r=0.90, 0.05>p>0.01).

The Grade 3 specialists show a striking dichotomy of plant relations between the two years. Curculionidae were again the most important group, with host plants mainly in Leguminosae (both annuals and perennials). For the first year insect species richness was highly correlated with both species richness and the architecture of their host plants. During this period the architecture of both annuals and perennials provided good predictors of insect abundance; biomass was only sig-

TABLE 5.6: Correlation Coefficients (r) for Comparisons Between Herb-Feeding Insect and Herb Parameters (Site D).

Plant Parameters

Insect Parameters	Cover	Abundance	Species Richness	Species α	Architecture (no. of structures)	Architectural α	Size (no. of height categories)	Spatial α
Year 1								
Species Richness	0.75	0.42	0.47	0.24	0.38	0.26	0.74	0.78
Species α	0.80	0.48	0.46	0.21	0.42	0.31	0.76	0.78
Abundance	0.42	0.12	0.27	0.12	0.14	0.05	0.45	0.48
Biomass	0.42	0.10	0.25	0.09	0.13	0.03	0.44	0.47

TABLE 5.7 : Summary of correlation analysis for the specialist and generalist herb-feeders with the two important herb groupings (annuals and perennials) in Site A. A = annuals; P = perennials. No significant insect-plant correlations were found with biennial herbs.

Plant parameters

YEAR 1

	ABUNDANCE		SPECIES RICHNESS		ARCHITECTURE (NO. OF STRUCTURES)		ARCHITECTURAL α	
Insect parameters	A	P	A	P	A	P	A	P
Specialists Grade 2								
Species richness		0.90	0.82					
Species α								
Abundance								
Biomass								
Specialists Grade 3								
Species richness			0.94	0.85		0.83	0.91	
Species α								
Abundance					0.90	0.89	0.92	0.94
Biomass		0.86						
Generalists								
Species richness			0.91		0.97	0.89	0.99	0.88
Species α								
Abundance						0.85		
Biomass		0.87						
Specialists Grade 3 + Generalists combined								
Species richness			0.95		0.90		0.97	
Species α				-0.84				
Abundance					0.82	0.93	0.88	0.84
Biomass		0.87						

Significant levels with values of r in parentheses:-

5% = (0.81)
1% = (0.91)
0.10%= (0.97)

TABLE 5.7 :(Continued)

Plant parameters

YEAR 2

	ABUNDANCE		SPECIES RICHNESS		SPECIES α		ARCHITECTURE (NO. OF STRUCTURES)		ARCHITECTURAL α		SIZE (NO. OF HEIGHT CATEGORIES)		SPATIAL α	
	A	P	A	P	A	P	A	P	A	P	A	P	A	P
Specialists Grade 2														
Species richness						0.95								
Species α						0.81								
Abundance														
Biomass														
Specialists Grade 3														
Species richness				-0.89										
Species α														
Abundance				0.84										
Biomass				0.83										
Generalists														
Species richness								0.85		0.85	0.90	0.92	0.81	0.93
Species α													0.88	
Abundance	0.85													
Biomass	0.85													
Specialists Grade 3 + Generalists combined														
Species richness											0.84			
Species α														
Abundance	0.88													
Biomass	0.82													

Significant levels with values of r in parentheses:- 5% = (0.81)
1% = (0.91)
0.10% = (0.97)

TABLE 5.8 : Summary of correlation analysis for the specialist and generalist herb-feeders in Site D with the two important herb groupings. A = annuals; P = perennials. No significant insect-plant correlations were found with biennial herbs.

YEAR 1

	ABUNDANCE		SPECIES RICHNESS		SPECIES α		ARCHITECTURE (NO. OF STRUCTURES)		ARCHITECTURAL α		SIZE (NO. OF HEIGHT CATEGORIES)		SPATIAL α	
	A	P	A	P	A	P	A	P	A	P	A	P	A	P
Specialists Grade 2														
Species richness		0.99										0.87	0.92	
Species α	0.95		0.81				0.89	0.86		0.96	0.81			0.83
Abundance				0.81									0.93	
Biomass													0.93	
Specialists Grade 3														
Species richness		0.82											0.83	
Species α		0.83												
Abundance					0.86						0.81			
Biomass		0.85			0.85									
Generalists														
Species richness			0.81	0.90	0.90	0.86		0.81	0.96		0.81			
Species α														
Abundance				0.88										
Biomass				0.92							0.81			

(Continued)

TABLE 5.8 : (Continued)

	YEAR 1													
	ABUNDANCE		SPECIES RICHNESS		SPECIES α		ARCHITECTURE (NO. OF STRUCTURES)		ARCHITECTURAL α		SIZE (NO.OF HEIGHT CATEGORIES)		SPATIAL α	
	A	P	A	P	A	P	A	P	A	P	A	P	A	P
SpecialistsGrade 3 +														
Generalists combined														
Species richness				0.85									0.81	
Species α														
Abundance				0.86	0.91				0.83					
Biomass				0.89	0.88									

Significant levels with values of r in parentheses:- 5% (0.81)
1% (0.91)
0.1% (0.97)

nificantly correlated with the abundance of perennial herbs. In the second year in Site A the abundance and biomass of Grade 3 specialists was highly correlated with species richness of perennial herbs. A negative correlation was also found between perennial species and insect species richness, although this may be an artifact of significant negative correlations between perennial species richness and perennial abundance. In Site D the structure of this insect group was highly correlated with both annual and perennial herbs (species α and spatial attributes of the former and abundance of the latter).

Generalist herb-feeders in Site A were mainly mirid bugs; these species are known to attack several families of both annual and perennial herbs. In the first year the species richness of generalists was extremely highly correlated with the architecture of annual herbs, for both the number of different structures ($r=0.97$, $p<0.001$) and architectural α ($r=0.99$, $p<0.001$). Insect species richness in the first year was also highly correlated with annual herb species richness and the architecture of perennial herbs. The abundance and biomass of generalists were highly correlated with the architecture (number of structures) and abundance respectively of perennial herbs.

In the second year generalist species richness was highly correlated with spatial diversity (measured either by size or spatial α) of both annuals and perennials; perennial architecture, on the other hand, was also a good predictor of insect species richness. For abundance and biomass of insects the only significant predictor was annual herb abundance. For Site D the species richness of generalists was strongly associated with species richness (and α) and architecture (and α) of annuals and perennials and size (*i.e.* number of height categories) of annuals; insect abundance and biomass was highly correlated with species richness of annuals and perennials and size of annuals was also significant for insect biomass.

5.5 GRASS-FEEDING INSECTS AND HOST-PLANT ASSOCIATIONS

5.5.1 Colonisation of Gramineae and grass-feeding insects

All grass-feeding insects identified in this study fell into the Grade 3 specialist category, with their host plants exclusively graminaceous, but feeding widely within this family. The grass-feeders were represented primarily by cicadellid leafhoppers and with relatively minor roles (in terms of species richness and abundance) played by other insects (Orthoptera, Heteroptera, Thysanoptera and Coleoptera); a few aphid species may also have been specialists on Gramineae (*e.g. Holcaphis* holci).

The accumulation of grass-feeding insect species and Gramineae species and structures in Site A differs markedly to that found for herb-feeders and their host plants (Fig.5.4a). First, colonisation of insects continued rapidly even though very few Gramineae species were accumulating. Consequently, the relationship is non-linear with grass species rising quickly to an early asymptote. The relatively greater species richness of grass-feeding insects is shown by the continuous gain of insect species (note the increase in b for the second year). In fact, no further gain of Gramineae species occurred after July of the second year. Grass structures also follow a non-linear relationship with grass species because the number of different structures produced was limited by the few grass species present (Fig. 5.4b). Consequently, the 'curve' will show little change until new grass species become established. It is interesting to note that the second year in Site A was similar to that found for the first year in Site D (Fig. 5.4c and d).

As before, colonisation may be further assessed when actual species gain of grass-feeding insects is considered with gains in grass species and grass structures. In the first year, the gain in grass-feeding insects is closely correlated with the gain in grass structures but not with grass species ($r=0.88$, $0.05>p>0.01$ and $r=0.61$, $p>0.05$, respectively). The situation was quite different in the second season (as found for herb-stratum insects and their host plants) with neither grass species nor structures being significant predictors of the grass-feeding insect species gain ($r=0.15$ and -0.08 respectively, $p>0.10$). This also occurred in Site D ($r=-0.44$ and -0.15 respectively; $p>0.10$).

5.5.2 Community structure of grass-feeding insects

Various host-plant factors may be important in determining the structure of the grass-feeding insect community. Table 5.9 shows correlations of parameters of Gramineae and their insect herbivores in Site A. The species richness of grass-feeding insects was closely correlated with both species richness and architecture of Gramineae. Taxonomic α of grass-feeding insects was similarly related. Grass architecture, as measured by the number of grass structures, was the only significant predictor of abundance and biomass of grass-feeding insects in the first year (accounting for 90% and 92% of the variance respectively). Insect-plant relations in the second year also show the importance of grass architecture as a predictor of abundance and biomass of grass-feeding insects. Spatial factors were also significant, showing high correlations with insect abundance and biomass. Insect species diversity, as measured by either richness or α, did not correlate sig-

Fig. 5.4 Relationship between the accumulation of grass-feeding insect species and grass structures with grass species accumulation during the first two years (Site A) or the first year (Site D) of succession.

a. Insect species *vs* plant species (Site A).
b. Plant structures *vs* plant species (Site A).
c. Insect species *vs* plant species (Site D).
d. Plant structures *vs* plant species (Site D).
e. Colonisation of grass species, structures and leafhopper species during the first year of succession in Site A (see also Stinson & Brown 1983).

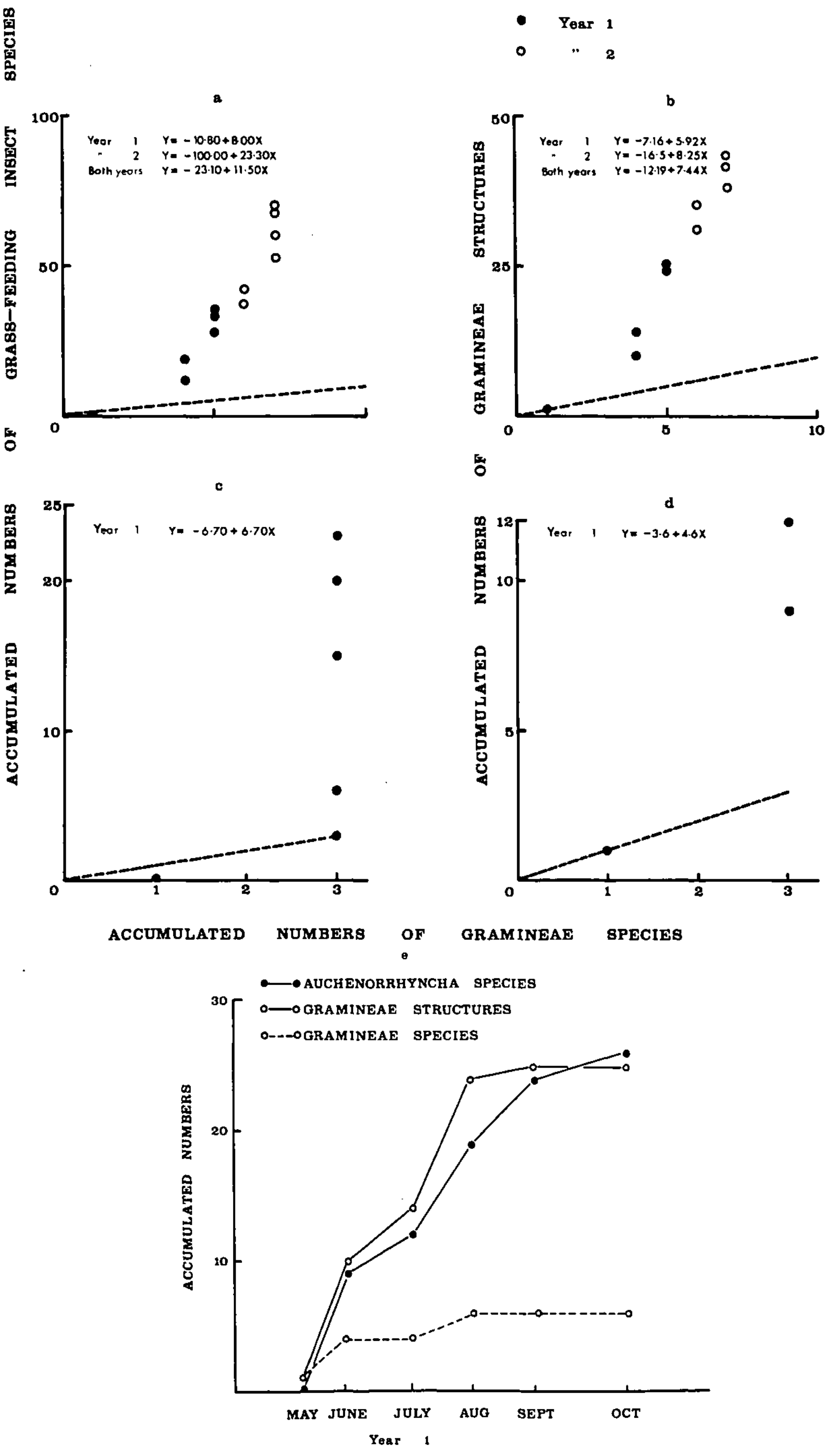

● Year 1
○ " 2
a
ACCUMULATED NUMBERS OF GRASS-FEEDING INSECT SPECIES
100
50
0
Year 1 Y= -10·80+8·00X
" 2 Y= -100·00+23·30X
Both years Y= -23·10+11·50X
b
ACCUMULATED NUMBERS OF GRAMINEAE STRUCTURES
50
25
0
5
10
Year 1 Y= -7·16+5·92X
" 2 Y= -16·5+8·25X
Both years Y= -12·19+7·44X
c
25
20
10
0
1
2
3
Year 1 Y= -6·70+6·70X
d
12
10
5
0
1
2
3
Year 1 Y= -3·6+4·6X
ACCUMULATED NUMBERS OF GRAMINEAE SPECIES
e
AUCHENORRHYNCHA SPECIES
GRAMINEAE STRUCTURES
GRAMINEAE SPECIES
ACCUMULATED NUMBERS
30
20
10
MAY
JUNE
JULY
AUG
SEPT
OCT
Year 1

TABLE 5.9: Correlation Coefficients (r) for Comparisons Between Grass-Feeding Insect and Host Plant (Gramineae) Parameters (Site A).

a. Year 1

b. Year 2

	Plant Parameters							
Insect Parameters	Cover	Abundance	Species Richness	Species α	Architecture (no. of structures)	Architectural α	Size (no. of height categories)	Spatial α
a. Year 1								
Species Richness	0.40	0.42	0.97***	0.77	0.96**	0.91**	0.60	0.70
Species α	0.29	0.30	0.94**	0.90*	0.83*	0.96**	0.62	0.64
Abundance	0.45	0.48	0.77	0.35	0.95**	0.60	0.32	0.73
Biomass	0.54	0.58	0.77	0.35	0.96**	0.60	0.36	0.70
b. Year 2								
Species Richness	-0.55	0.37	0.30	0.25	0.38	0.50	0.79	0.79
Species α	-0.67	0.20	0.20	0.24	0.13	0.27	0.68	0.69
Abundance	0.28	0.63	0.30	0.02	0.94**	0.93**	0.62	0.58
Biomass	-0.20	0.63	0.20	-0.01	0.81*	0.88*	0.96**	0.95**

* $0.05 > p > 0.01$ ** $0.01 > p > 0.001$ *** $p < 0.001$

nificantly with any grass parameter during this period.

In a recent paper certain insect-plant relationships of the Auchenorrhyncha were described using data from the ruderal-early successional habitat in Site A (Stinson & Brown 1983); a reprint of this paper is given inside the back cover of this thesis. Analysis of leafhopper and grass parameters in that paper showed that insect species richness and abundance were strongly correlated with the architecture of their host plants, as measured by the availability of different structures. The latter gave higher levels of correlation than measures of architectural α. The number of grass structures alone accounted for 79% and 86% of the variance in leafhopper species richness and abundance respectively and successional gain of leafhopper species closely followed that of grass structures (Fig. 5.4e; $r=0.98$, $p<0.001$). Other plant parameters were not significantly correlated with insect parameters. Further information revealed here shows that leafhopper biomass was also highly correlated with grass architecture (Table 5.10a).

Information on the second year shows a similar pattern, in that leafhopper abundance and biomass were strongly influenced by host plant architecture, while spatial attributes were also significant predictors of insect biomass (Table 5.10b).

The Site D Young Field had similar host-plant relations to the second year in Site A when Auchenorrhyncha and Gramineae are considered (Table 5.10c). In Site D leafhopper species richness and α were highly correlated with Gramineae abundance (*e.g.* $r=0.98$, $p<0.001$ for the latter). Spatial diversity as measured by size (number of height categories) was also a significant predictor of leafhopper species richness (both plant parameters were also highly correlated with one another); insect abundance and biomass were also strongly correlated with spatial diversity.

5.6 DISCUSSION

The observed patterns of insect taxonomic composition and abundance on host-plants has been attributed to a number of plant factors such as apparency, species-area effects, plant chemistry and defense mechanisms (as outlined in Chapter One, Section 1.1). This present chapter has looked at a number of plant parameters including species composition and structural complexity (with architectural and spatial components) that may be important in determining seasonal patterns in the abundance and species richness of phytophagous insects associated with early successional habitats.

The correlations tested do not allow for clearcut interpretations of insect-plant relationships because of high plant-plant parameter correlates (often to extreme levels). Indeed this type of

TABLE 5.10: Correlation Coefficients for Comparisons Between Auchenorrhyncha and Host Plant (Gramineae) Parameters

a. Year 1 (SITE A)
b. Year 2 (SITE A)
c. Year 1 (SITE D)

Plant parameters

Leafhopper parameters	Cover	Abundance	Species Richness	Species α	Architecture (no. of structures)	Architectural α	Size (no. of height categories)	Spatial α
a. Year 1								
Species Richness	0.64	0.62	0.77	0.59	0.89*	0.71	0.80	0.68
Species α	0.61	0.55	0.70	0.64	0.78	0.75	0.71	0.60
Abundance	0.46	0.50	0.80	0.44	0.93**	0.55	0.76	0.70
Biomass	0.58	0.62	0.73	0.29	0.93**	0.54	0.68	0.69
b. Year 2								
Species Richness	-0.57	0.27	0.14	0.14	0.33	0.45	0.79	0.80
Species α	-0.70	0.06	0.08	0.17	0.05	0.18	0.64	0.66
Abundance	0.39	0.65	0.06	-0.20	0.93**	0.89*	0.57	0.54
Biomass	-0.06	0.69	0.08	-0.14	0.86*	0.91**	0.92**	0.91**

* 0.05 > p > 0.01 ** 0.01 > p > 0.001 *** p < 0.001

(Continued.....)

TABLE 5.10: Correlation Coefficients for Comparison Between Auchenorrhyncha and Host Plant (Gramineae) Parameters.

(Cont..)

Plant parameters

Leafhopper Parameters	Cover	Abundance	Species Richness	Species α	Architecture (no. of structures)	Architectural α	Size (no. of height categories)	Spatial α
c. Year 1								
Species Richness	0.96**	0.98***	-0.02	-0.07	0.47	0.09	0.83*	0.68
Species α	0.96**	0.95**	0.05	-0.02	0.41	0.06	0.68	0.53
Abundance	0.65	0.72	-0.04	-0.06	0.55	0.23	0.86*	0.77
Biomass	0.66	0.73	-0.05	-0.06	0.55	0.22	0.85*	0.76

* 0.05 > p > 0.01 ** 0.01 > p > 0.001 *** p < 0.001

crisis has vexed several workers in other similar studies (*e.g.* Lawton & Price 1979; Fowler & Lawton 1982) and others who have simply found problems in explaining the biological significance of certain correlates. This latter point will receive further consideration later in this discussion.

Section 5.2 described the colonisation rates of plants and insect herbivores and looked at how the arrival of new insect herbivore species was related to the appearance of new plant species and new plant structures. The first point to be made was that the insect species were turning over more rapidly compared to the plant species, reflecting the greater mobility and species richness of the insect fauna. The second point concerned the relationship between the production of new plant structures and the appearance of new plant species. In neither site were significant correlations found between plant structures and plant species. This is not surprising if one considers that the production of structures takes place over time and is related to the phenology of individual plant species. For the first year in Site A a linear relationship indicated that new structures were being added at around 7 times the rate of new plant species ($b=6.99$). Although Sites A and D have similar slopes the greater slope for Site A reflects a more highly structured plant community (compare b and d of Fig. 5.1). As shown in Chapter Three the plant community in Site D had fewer annual herbs and was dominated by a high coverage of perennial herbs and Gramineae. These two plant groupings (especially the grasses), by nature of their growth habit, will produce fewer structures compared to the rapid production and turnover in annual herbs.

When the colonisation of insect herbivores with plant species and plant structure arrivals were considered two patterns were seen to emerge. In the first year new insect species arriving were more closely related to the appearance of new structures ($r=0.83$, $0.01>p>0.001$) than new plant species ($r=0.68$, $p>0.05$). In the second year no significant relationship was found for herbivore colonisation with either new plant species or structures. This would suggest that two types of colonisation processes are involved for the insects. In the first year colonisation was related to new plant structure additions and this may reflect the *r*-strategy nature of the insects colonising the ruderal community. Many (if not all) of these insects are probably attracted to specific structures (*e.g.* certain mirids to fruiting structures) and their arrival may be synchronised with the appearance of relevant host-plant structures. Thus the high correlation would be expected. For the second year the plant community had developed beyond the ruderal stage and become more permanent with the establishment of vegetatively spreading and relatively long-lived perennial herbs and grasses. The insect community had also become more specialised and new species arrivals appear to be linked to some other process of colonisation. Of course, this lack of significant correlation between new insect species and plant structures (or plant species) does not necessarily mean that these two plant parameters are unimportant. For example, there may be a time-lag in the insect's response to one or both of these factors. As in previous descriptions (Chapters Three & Four) events in Site D were similar to those in Site A during the second year, yet again illustrating the more mature vegetation in Site D.

A final point to consider about this initial colonisation process is the comparison of insect species accumulation between the two first year sites; more insect species colonised Site A during this period with a final end of season total of 122 species compared to 85 species in Site D. Such a difference is probably related to the more highly structured ruderal community in Site A and suggests that a greater structural diversity will attract a richer fauna as indicated by Lawton & Schroeder (1977,1978), Price (1977), Southwood (1977b) and Strong & Levin (1979).

The detailed descriptions of insect community structure and plant relations in Section 5.3 produced interesting results as well as illustrating just how difficult it can be to interpret such analyses. This is particularly so if there is an absence or uncertainty in important background information (*e.g.* life-history strategies of herbivores). Another major problem is the difficulty in interpretating the correlation matrices. This is not only because several plant parameters may be strongly associated with one another but also because, as Lawton (1978) states, *"Correlation, of course, does not imply causation"*. In addition, one could argue that, because of the nature of the sampling methods used, significant but spurious insect-plant correlations could arise.

The idea that plant architecture might be important in explaining differences in the species richness and abundance of insect herbivores on plants is very recent. It initially arose consequent to considerations of species-area effects and the taxonomic isolation of host-plants. The species-area effect shows that, within a geographic region, common (*i.e.* widespread) plant species have more insect species associated with them than do rare plants (Southwood 1960; Opler 1974; Strong 1974; Lawton & Schroeder 1977,1978; Cornell & Washburn 1979). In addition, the species richness on major plant groupings, with a similar geographical range, declines from large, structurally complex species of plants to small simple structured species, in the series trees > woody shrubs > perennial herbs > weeds and other annuals > monocotyledons (excluding grasses) (Lawton & Schroeder 1977,1978; Price 1977; Southwood 1977b; Strong & Levin 1979). These differences are significant even when taxonomic isolation is accounted for and led Lawton (1978) to suggest that differences in plant architecture or 'living space' are responsible. Lawton defined architecture in such a way that it covers gross differences between plants (*i.e.* physical size and the quantity and variety of plant structures) as well as differences in their seasonal phenology.

Plant architecture (as measured by architectural α) was an excellent predictor of insect species richness and abundance in the first year ((r=0.91, 0.01>p>0.001 and r=0.86, 0.05>p>0.01 respectively) and seems a more likely explanation for the observed variance in the two insect parameters. Seasonal changes in plant architecture have been shown to be dramatic in single species studies (*e.g.* Addicott 1978 on fireweed, *Epilobium angustifolium*; Thompson 1978 and Berenbaum 1981 on wild parsnip, *Pastinaca sativa*; Lawton 1978 on bracken, *Pteridium aquilinum*). In this study the first detailed study of seasonal changes in the architecture of a natural plant communities has been made (*i.e.* Sites A and D as described in Chapter Three and see Stinson & Brown 1983). However, very few studies have attempted to relate plant architecture to the associated species richness or abundance of insects. A few single plant species studies that have related the seasonal phenology of the plant (architecture or 'living space' (Lawton 1978) or 'habitat space' (Price 1976)) include work on salt-marsh grasses *Spartina* and *Salicornia* (Cameron 1972; Denno 1977), collards *Brassica oleracea* (Root 1973), stinging nettle *Urtica dioica* (Davis 1973; Lawton 1978), bracken *P.aquilinum* (Lawton 1978,1982) and soybean (Price 1976; Lawton 1978).

Even fewer studies have described the relationship between plant community architecture and insect faunal diversity. Murdoch *et al* (1972) suggest that Foliage Height Diversity (*FHD*, a measure of structural diversity similar to the spatial component in this study and in Southwood *et al* 1979) was important in determining the diversity of Homoptera in their study of three Old Fields in Michigan. However, they were not able to resolve how important plant structural diversity was because the *FHD* measurement was strongly correlated with plant species diversity. They suggest that *"both plant species diversity and plant structural diversity are important in determining the insect species diversity in this case"*. In another study (Allan, Alexander & Greenberg 1975) found a correlation between insect diversity and *FHD* but again could not resolve the influence of structural complexity because of a high correlation between plant species richness and *FHD*.

In the work by Southwood *et al* (1979) it was suggested that in the early stages of a secondary succession insect diversity is associated with plant taxonomic diversity whereas in the later seral stages plant structural attributes (with both architectural and spatial components) become increasingly important. Their work did not account for seasonal changes in community architecture and their measurement of architecture was in fact rather simple. In this study similar structures (*e.g.* mature leaf; see also Harper's 1981 'modules') of different species were considered as architecturally distinct and were recorded as such. This leads to a more detailed description of architectural diversity of the early successional habitat than in that original work over the successional gradient by Southwood *et al* (1979).

In the second year insect abundance and biomass were highly correlated with plant abundance (r=0.81 and 0.83 respectively, 0.05>p>0.01). It would appear then that the colonisation process in the first year (for insect species and their abundance) is strongly related to the architecture of the plant community, whereas in the second year it is plant abundance that determines the abundance and indeed biomass of insects. Insect species richness (and taxonomic α) was not significantly correlated with any plant parameter in the second season and this would suggest that some other process is involved. Brown & Southwood (1983) also found a high correlation (r=0.82, 0.05>p>0.01) between insect abundance and plant abundance in the second year of succession. However, they found in the first year that insect species colonisation was dependent on the species composition of the vegetation although they did not consider architectural effects in this context. But the definition of architecture in this study actually incorporates a measure of plant species richness because it distinguishes between similar structures of different species. Thus, the conclusion that architecture is important for first year insect colonisation does not undermine the possibility that plant species composition, as found by Brown & Southwood (1983), is involved in this initial colonisation. It is not possible to compare the relative merits of plant species richness and community architecture for insect colonisation, since they are both so intimately related.

A final point to consider about the herbivore community structure in the second year concerns the significant correlation of plant abundance with insect abundance and biomass. In Section 5.3 it was stated that plant abundance could be used to forecast plant biomass and this certainly seems a reasonable suggestion. At the same time, because abundance was measured by the sum of multiple touches on point quadrats this particular parameter also provides a measure of plant complexity or indeed architecture. Thus, the second year insect-plant relation involving plant abundance in Site A, as well as in the study of Brown & Southwood (1983), may be an architectural relationship rather than one based on plant abundance or biomass.

Analysis of the herb-feeding insects and their host-plant associations in Section 5.4 showed very similar patterns to those for the whole herbivore community and two colonisation processes appear to be involved.

Further analysis of the herb-feeding insects looked at the importance of the various plant factors as predictors of insect species richness, diversity, abundance and biomass. Yet again interpretations of the correlations were hampered by plant-plant associations. As for the whole plant community seasonal change in plant architecture (as measured by architectural α) was probably the best explanation for the observed variation in the species richness and abundance of herb-feeding insects during the first year (Table 5.5a). Second year events in Site A also showed that plant abundance was the best predictor of herb-feeding insect abundance (Table 5.5b). The significant negative correlations of insect taxonomic α with herb abundance and herb species richness is strange and I cannot offer any satisfactory explanation for this.

The summary of the correlation analysis in Table 5.7 between specialist and generalist herb-feeding insects in Site A and the major plant groupings, the annual and perennial herbs, yet again points out the difficulties one faces when dealing with closely associated plant parameters as well as having a limited knowledge of the ecology of the insect species themselves. An overall comparison of the two years in Site A shows an interesting trend in insect associations with herb abundance, species richness and architecture in the first year and with spatial attributes becoming significant in the second year in addition to the other four plant factors; both annual and perennial herb parameters were involved.

The main herb-feeding group (in terms of taxonomic composition, abundance and biomass) in the first year in Site A were Grade 3 specialists (chiefly Curculionidae, with leguminous hosts) and generalists (chiefly Miridae); both groups have annual and perennial hosts. Although correlates were found for particular parameters of these two insect categories with the species richness and architecture of the host-plant groupings, plant architecture as argued earlier is probably of greater importance to this insect fauna. Indeed these herbivores are probably fairly structure specific as regards their food preferences although they may attack several closely related species of plant; the mirids are a good example of this. The correlations also show that host-plant abundance (*i.e.* either as a criterion for biomass or as another measure of architecture) may also be important to these generalist herb-feeders as they colonise and rapidly build up in species richness and in numbers of individuals.

In the second year the important herb-feeding groups were Grade 2 and 3 specialists (mainly Curculionidae). The significant correlation of species richness (and α) of Grade 2 specialists with species α of perennial herbs suggests that host-plant taxonomic composition is an important factor in the community structure of these insects. The herb-feeding Grade 3 specialists, on the other hand, exhibit a significant negative correlation for insect species richness with the species richness of perennial herbs, whilst their abundance is strongly and positively correlated with perennial herb species richness. Such relationships contrast with the correlates found with species richness, abundance and architecture of perennial herbs in the first year and further suggest a different type of population structuring for the second year of succession. Although the generalists were rare in the second year it is interesting to note that spatial attributes may have been important for the insect abundance and biomass.

The separate analysis of herb-feeding and grass-feeding insects enables a direct comparison to be made of the structuring of these two main trophic groups. Certainly one might expect different processes to operate since the grass community in the two sites had an extremely low species richness throughout and, consequently, a relatively simple structure (in terms of the limited number of different structures). Site D was again seen to further resemble the second year in Site A with the appearance of the few new grass structures early in the season and thereafter new structures ceasing to appear.

When the herb-feeders are compared to the grass-feeding insects similar trends in colonisation were found to emerge. As for the herb-feeding insects the arrival of new species of grass-feeders in the first year was strongly correlated with the production of new plant structures (Site A, $r=0.88$, $0.05>p>0.01$) rather than the appearance of new grass species. Similarly the second year showed no relation of grass-feeding insects with their host plants. Yet again Site D reflected the second year trend in Site A.

The separation of leafhoppers from other grass-feeding groups was a logical step to take because the Auchenorrhyncha and their host plants, the Gramineae, form an ideal tool to assess the importance of plant structural diversity to insect herbivores (see Stinson & Brown 1983). First, all developmental stages (of the species encountered in this study) are associated with the Gramineae and can be sampled by the same methods. In this way data for a single taxonomic group of plant species are provided and yet some of the difficulties of the much needed single species studies are minimised. Second, monocotyledons (and weeds and other annuals) are assumed to have a lower insect species diversity than other green plants (Lawton & Schroeder 1977,1978; Strong & Levin 1979) and are therefore appropriate to such a study. Third, the seasonal change in the structural characters of monocotyledons and annuals is considerable and enhances such a study. Finally, by using only the grasses the species richness may be retained at a low and more or less constant level and the relative effects of spatial and architectural properties fully assessed. In Site A seasonal changes in grass architecture (as measured by the number of different structures) during the first year gave the best explanation for observed changes in leafhopper species richness, abundance and biomass (see also Stinson & Brown 1983). The effect of architecture for these grass-feeding Auchenorrhyncha appeared to be greater than the spatial or size attributes in the first year (see Table 5.10a). Spatial attributes (for insect biomass) in addition to architecture (for insect abundance and biomass) are the important correlates in the second year (see Table 5.10b) and may indicate the properties of a more mature or firmly established grass system.

This information on insect-plant relationships from Site A seems to reflect an underlying difference in insect community structure between herb-feeding insects and the main grass-feeding taxon, the Auchenorrhyncha. During the first year herb-feeders (as a whole) and leafhoppers appeared to colonise and build up in numbers in relation to the rapidly developing architecture of the plants. In the second season herb-feeders appeared to be responding to changes in plant abundance (although from an earlier argument this could be an architectural or biomass effect, or both) whereas the Auchenorrhyncha seemed to be responding to the grass structural complexity (with both spatial and architectural criteria being important).

The vertical stratification of grass-feeding Auchenorrhyncha has been reported or implied by several researchers (*e.g.* Andrzejewska 1965; Whittaker 1969; Murdoch *et al* 1972; McClure & Price 1975,1976; Denno 1977; Tallamy & Denno 1979; Morris 1971,1973,1974,1978,1981; Prestidge 1980; Prestidge & McNeill 1981). Indeed stratification of leafhopper assemblages in the vertical plane may allow for resource partitioning (or niche separation) and therefore stratification of herbivore species. Such may be a characteristic feature of insect communities living in habitats of low species richness and a consequent low architectural diversity (as defined in this study).

To conclude then, one cannot emphasise enough that the correlates found here do not necessarily imply causation. Factors other than those parameters measured in this study would also be expected to be important in structuring the early successional insect community (*e.g.* secondary chemistry, nutrient mobilisation or plant patchiness). It is hardly surprising that such a dichotomy of events occurred between the two years in Site A. As described in Chapter Three the first year of succession represented a period of rapid canopy development which might act like a blotter by 'soaking up' insects as they pass into the expanding habitat space (see Price 1976). Observed differences in plant architecture have provided, or at least helped to provide, satisfactory explanations for observed differences in species richness and abundance of insect herbivores on different species of plants (Lawton & Schroeder 1977,1978; Price 1977; Southwood 1977b), on the same species of plant (*e.g.* Davis 1973; Lawton 1978) and in natural plant communities (*e.g.* Denno 1977; Southwood *et al* 1979; Prestidge 1980; Morris 1981). The results presented here provide additional evidence of the possible influence of habitat structural diversity on insect community structure. These studies also backup the contention that habitat structure is important in diversification in other animal communities such as marine gastropods (Kohn 1967,1971; Kohn & Nybakken 1975; Kohn & Leviten 1976; Salvat 1970; Richard & Salvat 1971), fish (Talbot 1965; Risk 1972), lizards (Pianka 1966,1973), rodents (Rosenzweig & Winaku 1969) and birds (MacArthur, MacArthur & Preer 1962; Cody 1968; Karr 1968; Recher 1969; Karr & Roth 1971; Rotenberry &

Weins 1980).

Seasonal changes in plant structural diversity reflect an increase in size (analagous to increasing 'apparency' as defined by Feeny 1975,1976) and complexity of form. The latter also provides a measure of resource availability in terms of feeding sites, resting and oviposition sites in addition to protection from physical conditions and natural enemies (see Lawton 1978 and Price *et al* 1980). The analyses in this study suggest that plant structural diversity is important in providing a templet for insect colonisation. Furthermore, during the first year of the succession the effect of the plant architecture component (for both herb-feeding and grass-feeding insects) is probably greater than the spatial or size attributes. The influence of spatial diversity probably becomes more important after the first year by which time the ruderal community has declined and the early successional community proper has established itself. Other studies have suggested that spatial attributes are important in Old Fields characteristic of mid-succession (*e.g.* Murdoch *et al* 1972) or increase in importance along the successional gradient (Southwood *et al* 1979).

CHAPTER SIX

THE EFFECTS OF INSECT HERBIVORES ON EARLY SUCCESSIONAL HABITATS

6.1 MATERIALS AND METHODS

6.1.1 Description of study areas

Two study areas (each of 384m^2), each containing two experimental sites, were established in March, one in 1980 (Sites B and C) and another in 1981 (Sites E and F). These two areas lay adjacent to Sites A and D (see Chapter Two for full descriptions). Sites B and C were in an area of long-standing arable land (Hill Bottom) and formed a parallel study with Site A. Sites E and F originated from the meadow area described for Site D. Preparation and establishment of these sites followed similar methods used for sites A and D (see Chapter Two).

6.1.2 Experimental exclusion of insects

Each study area was enclosed by an agricultural fruit cage (suppliers: Agriframes Ltd., East Grinstead, Sussex) to prevent bird grazing; the cage measured 24m x 16m and with a 3/4inch mesh size. The whole area was already part of a rabbit exclusion zone. Mollusc grazing was not controlled though regular samples indicated extremely low populations on the light sandy soil.

The two experimental sites within each netted area were subdivided into 12 subplots arranged in a 3 x 4 pattern. Insects were chemically excluded from Site B over a two year period (Site C acting as a control) and Site E for one year (Site F acting as a control). Malathion-60 (60% w/v; Cyanamid), an organophosphate insecticide with short persistence, was used as an emulsifiable concentrate (suppliers: Berks., Bucks. and Oxon. Farmers Ltd., Twyford, Oxfordshire). The amount of chemical used at any one time conformed with the standard UK agricultural rate of 1.26 kg a.i./ha (Martin and Worthing 1976). Insecticide was applied with a hand-held ULV (ultra-low-volume) sprayer (the Micron Herbi 77; Micron Sprayers Ltd., Bromyard, Herefordshire). Malathion in emulsion (21ml of concentrate in

479ml H_2O) was sprayed in Sites B and E using a flow rate of 2ml/sec and walking at 0.5m/sec with a 1.2m swathe width to give the required coverage of active ingredient. Spraying was carried out early in the morning or late evening, thereby avoiding times of hot convective weather conditions. After each treatment control sites were sprayed with water at the same rate and volume.

A 3m buffer zone separated the control and sprayed sites within each netted area. Unfortunately it was not possible to replicate this treatment in any way because further cages were not available. The frequency of spraying depended on insect activity (*i.e.* time of year) and was determined by observations at intervals of two days. Sites were sprayed as follows:-

Site C 1980 11 applications.
Site C 1981 7 applications.

Site E 1981 8 applications.

Experiments were carried out to establish whether there were any secondary effects of the insecticide on the vegetation.

6.1.3 Sampling procedure

This was essentially the same as decsribed in Chapter Two. Each site was 5-6 weeks old at the time of the first sample. Samples were taken from within each subplot. Sites B and C were sampled for the first two years (1980 + 1981) and Sites E and F for the first year (1981); observations were continued into early 1982. Control sites (*i.e.* insect grazing not restricted) were sampled for green plants and insects six times during the growing season at the same times as those described in Chapter Two. Insecticide treated sites (*i.e.* controlled grazing) were sampled only for plants although insect activity was monitored by observation and D-vac sampling to test the efficacy of insect control (D-vac catches showed that insect activity was generally low in control sites with abundances of herbivores never exceeding 10 individuals/m^2).

6.1.3(a) Vegetation sampling

For Sites B and C in 1980, 30 pins were placed at random within each subplot (a total of 360 point quadrats on each sampling occasion in each site). A reduced sample was taken in October (10 pins per subplot: a total of 120 pins). For the second year in 1981, 10 pins per subplot were used throughout.

For Sites E and F in 1981 the same sampling intensity was used as in Sites B and C in the first year.

6.1.3(b) Seed bank

A seed bank assessment test was run for each site using similar methodology as described in Chapter Two.

6.1.3(c) Testing for phytotoxicity or phytostimulation as a result of insecticide application

The test was started when Sites E and F were established; plant biomass was used as an indicator. Four 3m x 3m subplots lying adjacent to Sites D, E and F in 1981 were used to determine whether there were any toxic or stimulatory effects due to the insecticide. Malathion was sprayed on two subplots and water on the other two at times corresponding to treatments in Sites E and F; all four subplots were D-vacced regularly to remove any insects. Biomass samples were taken on two occasions; in mid-August and mid-October. Five 25 x 25cm quadrats were placed at random within each subplot and the vegetation in each clipped to ground level. Biomass measurements were made as described in Chapter Two.

6.1.3(d) Insect sampling

The same D-vac method and sorting routines were used as described in Chapter Two. On each sampling occasion 36 sucks (*i.e.* 3 sucks per subplot) were made in the control sites.

6.1.4 Data recording and analysis of plants

This was essentially the same as that for Sites A and D (see Chapter Two). All point quadrat data were analysed using SIR retrieval programmes as outlined in Chapter Two and Appendix 2.

6.1.5 Data recording and analysis of insects

Methods of sorting, identification and analysis of insects were the same as described in Chapter Two. Only insect herbivore groups were identified.

6.2 SEED BANK ASSESSMENT

The seed bank test for Sites B and C, as found for Site A, revealed a rich reservoir of potential colonisers. In contrast, but similar to Site D, Sites E and F were relatively impoverished. Full details of the seed bank are given in Table 6.1. Sites B and C had the same plant species in their seed banks and individual species were generally present in similar numbers (I_s=1.00, I_w=0.89). Exceptions to this were *Raphanus* with more seedlings in Site B (later, insect-free: 37 seedlings compared to 20 seedlings, greater by a factor of 1.85) and *Polygonum persicaria* with more seedlings appearing in Site C (later, insect-grazed: 21 seedlings compared to 10 seedlings, greater by a factor of 2.10). For Sites E and F the same species were also present in the two sites and again comparisons of individual species show general similarity in seedling numbers (I_s=1.00, I_w=0.90). One exception to this was the considerably greater number of *Rumex acetosella* seedlings in Site F (later, insect-grazed: 17 seedlings compared to 5 seedlings, greater by a factor of 3.40).

6.3 RESULTS OF THE INSECTICIDE TEST

The results of this test are given in Table 6.2. Total vegetation biomass and the biomass of the major plant groupings were very similar between the two treatments on each sampling occasion. Mean biomass/quadrat comparisons between control and test areas on each sampling occasion did not show any significant differences (t-test: $p>0.05$).

TABLE 6.1: Seed bank results for insect-free and insect-grazed areas.

Volume of soil sampled from each site = 785 cm^3.

Insect-free areas = Sites B and E;
Insect-grazed areas = Sites C and F

	Total number of seedlings			
Species	Site B	Site C	Site E	Site F
Spercula arvensis	172	186	86	77
Raphanus raphanistrum	37	20	7	9
Polygonum persicaria	10	21		
Trifolium pratense	43	37	62	69
T. repens	11	6	4	7
Sonchus asper	7	4	3	3
Cirsium arvense	5	2	4	2
Crepis capillaris	7	4	15	17
Stellaria media	4	1	2	1
Vicia sativa	2	1		
Fallopia convolvulus	5	3		
Plantago lanceolata	1	1	24	19
Rumex acetosella	1	1	5	17
Agrostis capillaris	3	4	2	3
Holcus lanatus	41	39	26	20
Poa annua	12	15	1	1

	Site B		Site C		Site E		Site F	
Plant groupings	no. species	no. seedlings	no. species	no. seedlings	no. species	no. seedlings	no. species	no. seedling
Annuals	7	237	7	236	4	98		90
Perennials	6	68	6	51	6	114		131
Gramineae	3	56	3	58	3	29		24
Total	16	361	16	345	13	241		245

TABLE 6.2: Biomass (gm dry weight) of the major plant groupings in areas sprayed with water (= control) and insecticide (= Test).

Values represent the combination of 5 25x25 cm quadrats. Comparisons of mean biomass/quadrat between control and test areas on each sample occasion did not show any significant differences (t-test: $p > 0.05$).

	MID-AUGUST		MID-OCTOBER	
	CONTROL	TEST	CONTROL	TEST
Annuals	19.97	23.22	0.21	0.10
Perennials	34.16	37.99	81.66	88.51
Gramineae	11.72	10.14	73.43	68.05
Total	65.85	71.35	155.30	156.66

6.4 THE INSECT HERBIVORE COMMUNITY

Total monthly abundance values for major insect herbivore taxa are given in Table 6.3 for the insect-grazed areas (Site C during the first two years and Site F during the first year). The two sets of data for the first year of succession show the rapid build up of herbivore numbers. In Site C the grass-feeding Homoptera (Grade 3 specialists) were the dominant group. These were mainly Cicadellidae and the abundances of this family from July to October were equivalent to 30, 62, 148 and 32 individuals/m^2; *Macrosteles laevis* and *M.sexnotatus* were the most numerically important cicadellids with *Euscelis lineolatus* also occurring in significant numbers. Aphid abundance in Site C from July-October was equivalent to 15, 26, 17 and 35 individuals/m^2 respectively. The most common aphid species was *Aulacorthum solani*, a generalist attacking a wide variety of plants (Blackman 1974). Heteroptera in the first year in Site C were almost all Miridae with the generalist herb-feeders *Lygus rugulipennis* and *Dicyphus errans* the most numerically important. Mirids were most abundant in August and September with values equivalent to 15 and 18 individuals/m^2. Coleoptera were fairly common throughout the first season (around 12 individuals/m^2) and had reached their peak in August (around 34 individuals/m^2). These herbivores were chiefly Chrysomelidae and the most numerically important species were two generalists, *Cassida vitata* (mainly on *Spergula*) and *Chaetocnema concinna* (on *Chenopodium album*, *Polygonum* spp. and *Rumex* spp.). Thysanoptera were common in July in Site C and especially August with abundances equivalent to 14 and 59 individuals/m^2 respectively. These were chiefly Thripidae; the most common species was the generalist herb-feeder *Thrips atratus*. Lepidopterous larvae were only common on one occasion, in July, at around 10 individuals/m^2.

In Site F the dominant herbivores in the first year were again Cicadellidae with abundances from July to October equivalent to 43, 112, 194 and 96 individuals/m^2; again these were represented mainly by *M.laevis* and *M.sexnotatus*. Aphididae were extremely common on one occasion (July) where they reached 111 individuals/m^2; *Myzus persicae*, a generalist, was the main aphid species present. Heteroptera were common also on just one occasion (September) with an abundance of 18 individuals/m^2; again these were mainly Miridae, with *Lygus rugulipennis* and *Dicyphus errans* the common species. The Coleoptera was the only other taxum of numerical importance , the Curculionidae being the most important group. The abundance of Coleoptera from August to October was equivalent to 20, 20 and 15 individuals/m^2. The most common curculionids were *Ceutorhinchus floralis* (in August), a

TABLE 6.3: Abundance of the major insect herbivore taxa in insect-grass areas (Sites C and F). Each value represents an area of 3.46 M^2 sampled each month.

	SITE C												SITE F					
	YEAR 1						YEAR 2						YEAR 1					
	MAY	JUNE	JULY	AUG	SEPT	OCT	MAY	JUNE	JULY	AUG	SEPT	OCT	MAY	JUNE	JULY	AUG	SEPT	OCT
Collembola	0	0	3	4	0	0	0	0	0	0	0	0	0	0	24	0	0	0
Homoptera	0	20	156	308	573	248	153	132	92	30	39	40	0	48	518	413	709	298
Heteroptera	0	0	8	58	65	19	9	4	50	12	14	24	0	0	6	14	61	15
Thysanoptera	0	0	50	204	3	8	0	0	0	0	0	0	0	0	5	0	2	0
Lepidoptera	0	0	35	3	6	3	0	0	0	0	0	0	0	0	0	0	0	2
Coleoptera	1	20	27	116	53	18	16	53	56	246	93	104	1	2	22	69	68	52
Total	1	40	279	693	700	296	178	189	198	288	146	168	1	50	575	496	840	367

Grade 3 specialist on Cruciferae and two species of Grade 2 specialists on *Rumex* spp., *Apion marchicum* and *A.rubens.*

As found for Site A in the second year insect herbivore abundance was considerably lower in Site C. The Homoptera were again the most numerous group for the first half of the season with the Coleoptera dominating from August to the end of the season. The most numerous Homoptera were Aphididae in May and July, with abundances equivalent to 35 and 20 individuals/m^2 (*Uroleucon* sp., probably a Grade 3 specialist on Compositae, was the most common species), and Cicadellidae in June with 35 individuald/m^2 (*M.laevis, M.sexnotatus* and *M.cristatus* were the common species). Phytophagous Heteroptera were common on one occasion, in July, with the herb-feeding generalist *Plagiognathus chrysanthemi* (Miridae) present at a density of 11 individuals/m^2. The phytophagous Coleoptera were virtually all Curculionidae with abundances of 71, 27 and 30 individuals/m^2 from August to October. The most common species were in the genus *Apion* with *A.apricans* from August to October (Grade 1 specialist on *Trifolium pratense*), *A.dichroum* in August (Grade 2 specialist on *Trifolium* spp.), *A.hookeri* in August (Grade 3 specialist on Compositae), *A.trifolii* in August (Grade 1 specialist on *T.pratense*) and *A.virens* in October (Grade 2 specialist on *Trifolium* spp.).

6.5 EFFECTS OF INSECT GRAZING

6.5.1 Introduction

This major Section looks at the effects of insect grazing on the development and structure of early successional habitats by comparing various vegetation parameters between insect-free and insect-grazed areas either over the first two years (Site B with Site C, 1980 + 1981) or over the first year (Site E with Site F, 1981) of succession. The plant parameters which were considered include cover, the grass/forb ratio, taxonomic composition, plant structure production, abundance and the spatial distribution of plant material.

Since sites were not replicated statistical analysis, where appropriate, has been restricted to the use of combined point quadrat information. For example, when comparing plant abundance between insect-grazed and insect-free sites on a particular sampling occasion the abundance in each site is obtained by combining all multiple touch information. Comparisons are then made using the Chi-square test (if expected values ≥ 5) or the Fisher Exact test (if expected values <5). Both monthly comparisons (paired comparison, $df=1$) and comparisons over one season (2 x 6 contingency table with $n\text{-}1=11df$) have been made. Where a statistical significance is mentioned in the text, Tables or Figures, this refers only to the outcome of either the Chi-square or Fisher Exact tests.

6.5.2 General trends

General vegetation trends in Sites B and C over the first two years were similar to those for Site A (see Chapter Three, Section 3.1.1), although the dominant species *Medicago lupulina* in Site A was not present. Differences between Sites B and C were visibly quite dramatic during the first season (and even after two months colonisation) with a more rapid cover, attainment of structural complexity and appearance of reproductive structures in the insect-free area (Site B). In the grazed area (Site C) the vegetation was much sparser and more patchy. Later in the season the insect-free site displayed a much more rapid establishment and spread of Gramineae, especially the dominant *Holcus lanatus*. Differences during the second year were not apparent after May by which time the vegetation in each site was developing into a community dominated almost entirely by *Holcus*.

Vegetation trends in Sites E and F over the first year were similar to those for Site D (see Chapter Three, Section 3.2.1). However, differences between Sites E and F were less dramatic than those seen in Sites B and C in the first year. The main trend was again for the earlier establishment and more rapid spread of *Holcus* in the insect-free area (Site E).

6.5.3 Plant cover

A comparison of plant cover between the insect-free and insect-grazed areas (Sites B and C) during the first two years of succession is given in Table 6.4a. Total cover rose rapidly in both sites during the first year and then declined slightly. Cover was approximately 10% greater in the insect-free zone during the first year although the first sample (in May) was the only time when the difference was statistically significant (19.17% cover compared to 10.00%, $0.01>p>0.001$). At the end of the first season plant cover was 92.50% in the insect-free area and 83.70% in the grazed site. Making an overall seasonal comparison between the two areas in a 2 x 6 contingency table showed no significant difference in total cover be-

TABLE 6.4: Comparison of Total Percentage Plant Cover and Seedling Cover Between Insect-Free and Insect-Grazed Areas

a. Total % cover in Sites B and C during the first two years of succession.
b. Total % cover in Sites E and F during the first year of succession.
c. % cover of seedlings in Sites B and C at the time of the first sample in May (1980).
d. % cover of seedlings in Sites E and F at the time of the first sample in May (1981).

		Year 1						Year 2					
a.		May	June	July	Aug	Sept	Oct	May	June	July	Aug	Sept	Oct
Insect-free	(B)	19.17	77.22	98.89	90.55	91.39	92.50	96.66	93.33	93.33	100	60	98.33
Insect-grazed	(C)	10.00 **	64.72	89.44	85.00	79.20	83.70	90.00	96.66	98.33	98.33	100	100

** 0.01 > p > 0.001 (Chi-square)

b.		May	June	July	Aug	Sept	Oct
Insect-free	(E)	1.11	39.72	95.27	99.17	99.72	95.00
Insect-grazed	(F)	0.22	28.33	73.77 *	96.11	97.22	86.66

* 0.05 > p > 0.01 (Chi-square)

Continued.....

TABLE 6.4: (Cont..)

c.		Annuals	Biennials	Perennials	Gramineae	Total
Insect-free	(B)	6.66	0	0	0.27	6.66
Insect-grazed	(C)	1.66	0	0.27	0.83	1.66

d.		Annuals	Biennials	Perennials	Gramineae	Total
Insect-free	(E)	0.55	0	0	0.11	0.55
Insect-grazed	(F)	0.22	0	0	0	0.22

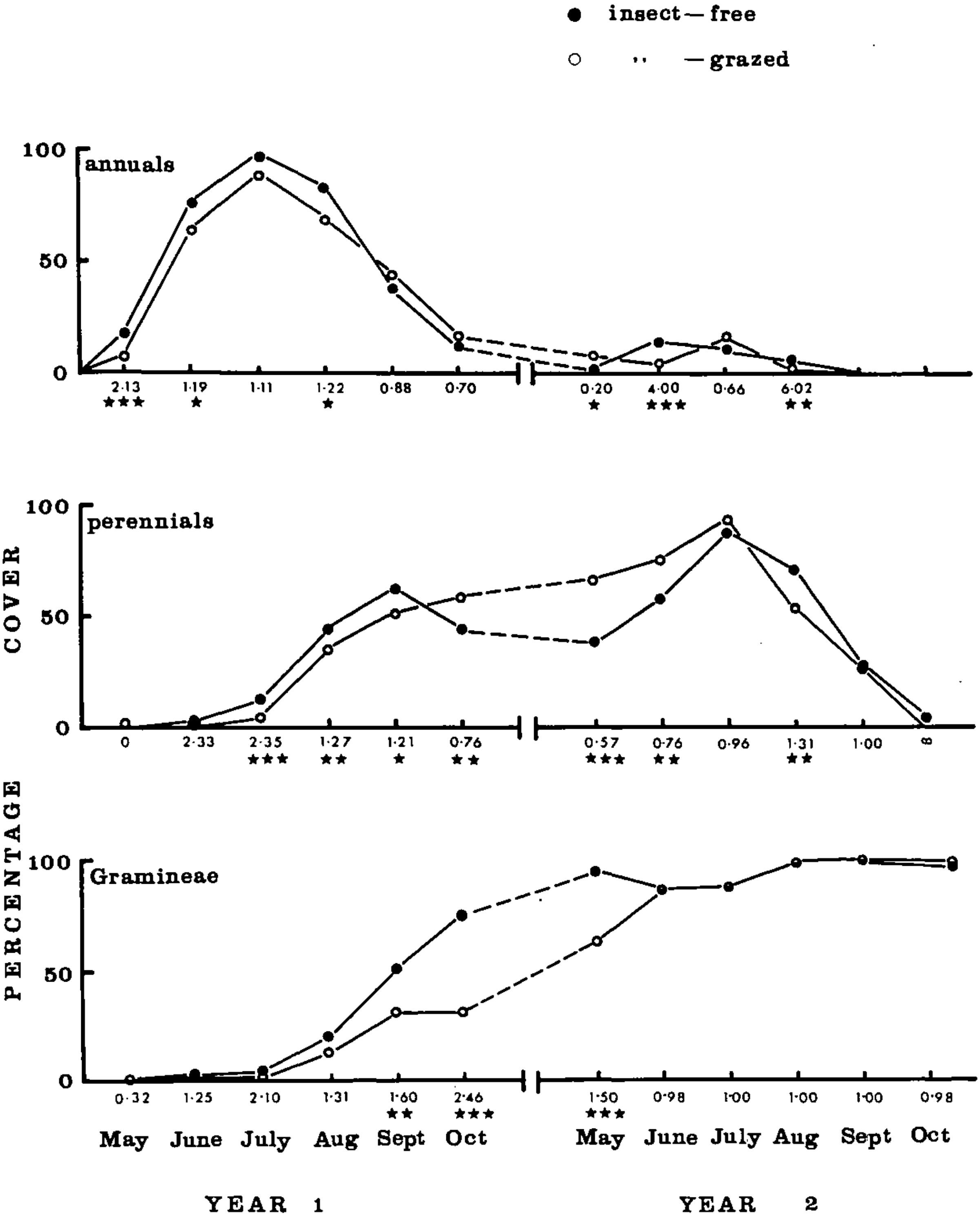
tween the two sites ($p > 0.05$). In the second year cover in each site was virtually complete and no significant differences were found either for monthly comparisons or for the entire season ($p > 0.05$).

Cover comparisons have been further broken down into differences in the cover contributed by the three major plant groupings, annual and perennial herbs and Gramineae (Fig. 6.1); the monthly cover ratio (insect-free/insect-grazed) is given below the abscissae together with any significant differences (see figure legend for explanation). Annual herb cover rose rapidly in both sites during the first three months and then declined. Cover of annuals was considerably greater for the main part of the first season (May-August) in the insect-free zone with values of 18.88, 76.39, 98.01 and 83.05% compared with 8.88, 64.17, 88.88 and 68.05% respectively in the grazed area. Differences during this period were statistically significant for the samples in May (x 2.13, $p < 0.001$), June (x 1.19, $0.05 > p > 0.01$) and August (x 1.22, $0.05 > p > 0.01$). The greatest annual herb cover differential (in May) was accompanied by a significantly greater seedling cover of annual herbs (seedlings had 6.66% cover in the insect-free area compared to 1.66% cover in the grazed zone; $0.05 > p > 0.01$)(Table 6.4c). Overall seasonal differences in annual herb cover were significant for the first year (2 x 6 contingency table, $0.05 > p > 0.01$). Cover of annuals declined rapidly after August of the first year and by September of the second year the annuals had become extinct from each site (as far as the sampling data are concerned). Although differences in annual herb cover were significant on several occasions during the second year annual herbs always contributed very low and declining levels of cover (<15%) to the plant community during this period. Overall seasonal differences in the second year were not significant (2 x 6 contingency table, $p > 0.05$).

Perennial herbs showed a gradual increase in cover to September in both sites during the first year. Cover was significantly greater in the insect-free site during July-September (11.11, 44.72 and 62.71% cover compared to 4.72, 35.27 and 51.67% in the grazed area with significance levels of $p < 0.001$, $0.01 > p > 0.001$ and $0.05 > p > 0.01$ respectively). Perennial cover declined sharply from September to October in the insect-free area (from 62.71% to 44.17%) but showed a slight rise in October in the grazed site (51.67% to 58.33%); the greater cover of perennials in the grazed area is significant at $0.01 > p > 0.001$. Overall seasonal differences were significant at $0.01 > p > 0.001$ (2 x 6 contingency table); this accounts for the reversal in direction in October. For May and June of the second year perennial cover rose gradually in both sites and the difference in favour of the grazed zone was still significant at $p < 0.001$ and $0.01 > p > 0.001$ respectively. After July the cover of perennial herbs declined rapidly in both

Fig. 6.1 Comparison of percentage cover of annual and perennial herbs and Gramineae between insect-free and insect-grazed areas during the first two years of succession.

Site B=insect-free; Site C=insect-grazed. Values lying below the abscissae indicate the cover ratio (insect-free/insect-grazed). Significant differences (from Chi-square or Fisher Exact tests) are marked by asterisks (1=5% level, 2=1% level, 3=0.1% level).


● insect — free
○ ,, — grazed
annuals
100
50
0
2·13 ★★★
1·19 ★
1·11
1·22 ★
0·88
0·70
0·20 ★
4·00 ★★★
0·66
6·02 ★★
perennials
COVER
100
50
0
0
2·33
2·35 ★★★
1·27 ★★
1·21 ★
0·76 ★★
0·57 ★★★
0·76 ★★
0·96
1·31 ★★
1·00
∞
PERCENTAGE
Gramineae
100
50
0
0·32
1·25
2·10
1·31
1·60 ★★
2·46 ★★★
1·50 ★★★
0·98
1·00
1·00
1·00
0·98
May
June
July
Aug
Sept
Oct
May
June
July
Aug
Sept
Oct
YEAR 1
YEAR 2

sites and by the end of the season these herbs had become extinct in the grazed area and negligible in the insect-free area (3.33% cover). Seasonal differences were highly significant for the second year (2 x 6 contingency, $p<0.001$).

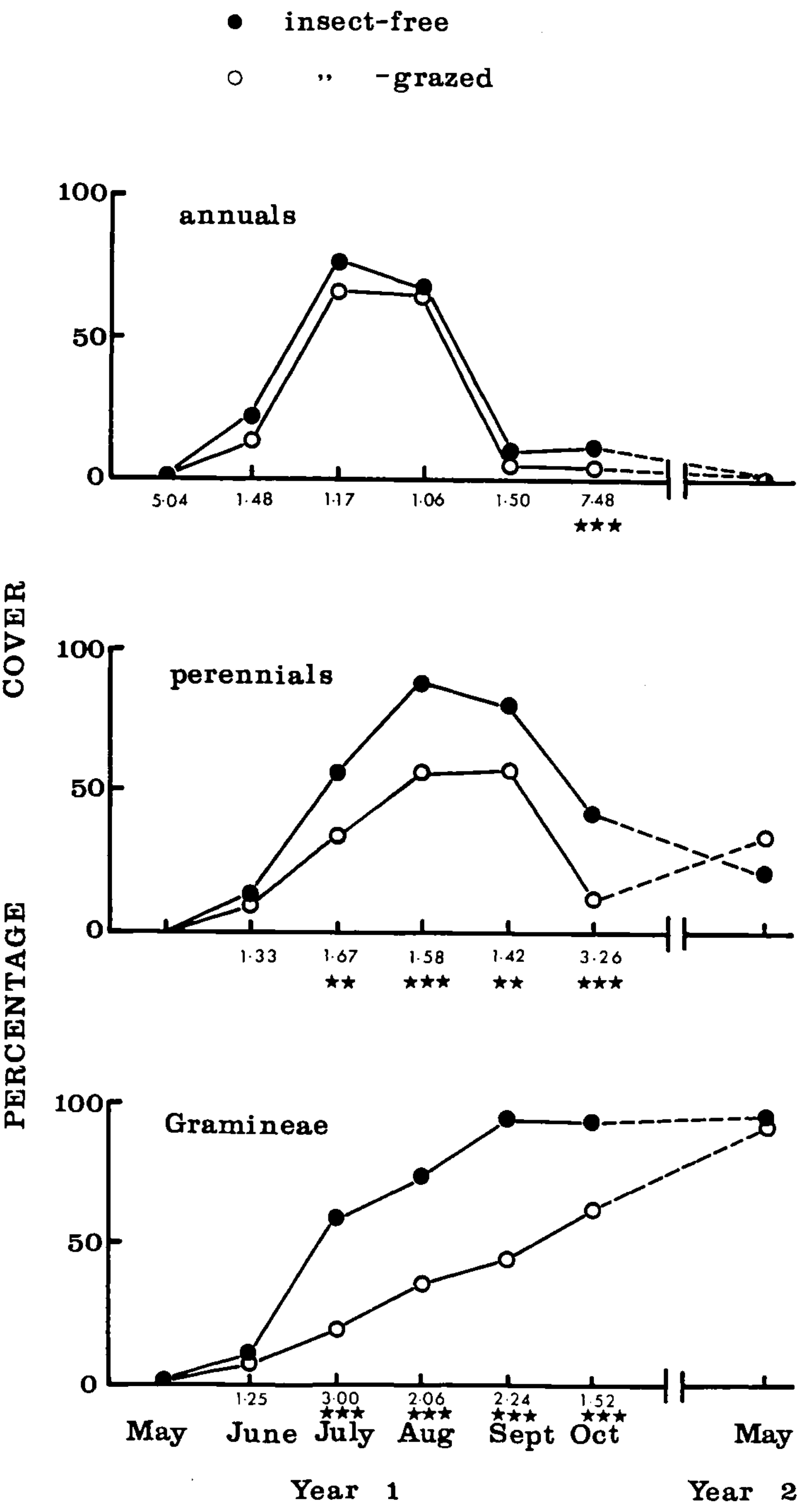
The most dramatic difference was the higher rate of grass establishment in the insect-free site during the first year (Fig. 6.1). The grass cover ratio (given below the abscissa for Gramineae in Fig. 6.1) in Site B showed a general rise to the largest differences towards the end of the first season (September, 50.28% compared to 31.39% cover, $0.01>p>0.001$; October, 75.83% compared to 30.83% cover, $p<0.001$). The difference in May of the second season was also highly significant (95.00% compared to 63.33% cover, $p<0.001$). Overall comparisons of the two sites in the first year showed no significant differences in grass cover (2 x 6 contingency, $p>0.05$) although the period September (Year 1) to May (Year 2) is highly significant at $p<0.001$. By June of the second year grass cover in the grazed site had reached very high levels (approaching 100% cover) comparable to the insect-free site and for the rest of the second season the two sites experienced the eventual decline of annual and perennial herbs and the maintenance of virtually sole grass coverage in each site.

Unlike Sites B and C the total plant cover in Sites E and F in the first year did not decline at the end of the season. Cover showed a general rise through the season in these two latter sites (Table 6.4b) with the only significantly greater coverage in the insect-free site (Site E) in July (95.27% compared to 73.77% in the insect-grazed area). The overall seasonal comparison between the two sites (2 x 6 contingency) was not significant ($p>0.05$).

In contrast to Sites B and C the annual herbs were less numerically important in Sites E and F in the first year and did not show any significant trends (Fig. 6.2); cover of annual herb seedlings was extremely low and similar at the time of the first sample in May (Table 6.4d; *cf* Table 6.4c). Additional sampling indicated that these herbs were rapidly heading for extinction by May of the second year. On the other hand, comparisons of the vegetation trends in the other two major plant groupings, the perennial herbs and Gramineae, show very similar results to those found for Sites B and C. Fig. 6.2 clearly shows the more rapid spread of perennial herbs and grasses in the insect-free site (Site E); seasonal differences for these two plant groupings were significant at $0.01>p>0.001$. A brief comparison of Fig. 6.2 with Fig. 6.1 shows the obvious earlier and more acute differences in the cover of perennial herbs and grasses between Sites E and F. The differences in grass cover in Sites E and F were considerable with cover values from July-October of 59.44, 72.50, 94.17 and 93.33% (insect-free) compared to 20.00, 35.50, 42.00 and 61.50% (grazed). By May of the second

Fig. 6.2 Comparison of percentage cover of annual and perennial herbs and Gramineae between insect-free and insect-grazed areas during the first two years of succession.

Site E=insect-free; Site F=insect-grazed. Values lying below the abscissae indicate the cover ratio (insect-free/insect-grazed). Significant differences (from Chi-square or Fisher Exact tests) are marked by asterisks (1=5% level, 2=1% level, 3=0.1% level).


● insect-free
○ " -grazed
PERCENTAGE COVER
annuals
100
50
0
5·04
1·48
1·17
1·06
1·50
7·48
★★★
perennials
100
50
0
1·33
1·67
★★
1·58
★★★
1·42
★★
3·26
★★★
Gramineae
100
50
0
1·25
3·00
★★★
2·06
★★★
2·24
★★★
1·52
★★★
May
June
July
Aug
Sept
Oct
May
Year 1
Year 2

year these two sites did not show any detectable differences in their cover and (as found for the end of the second season in Sites B and C) *Holcus lanatus* was again showing strong domination over the perennial herbs.

6.5.4 The grass/forb ratio

In Chapter Three the grass/forb ratio was used to reflect overall successional changes occurring in the Young Field plant community. It was shown that as grasses became established in the early successional community their cover and abundance rose and the ratio of grasses to forbs increased (for cover and abundance).

The grass/forb ratio is used here to compare the rate of succession to a grass-dominated community in the insect-free and insect-grazed areas. It is clear from Table 6.5a that succession was accelerated in the insect-free zone (Site B) during the first year (1980). This is especially noticable at the end of the season where cover and abundance ratios were extremely high (1.52 and 1.60 respectively) compared to very low ratios in the grazed area (0.45 and 0.22 respectively). After May of the second year the grass/forb ratios for cover and abundance increased to levels similar to those found in the insect-free zone; grazing did not appear to further reduce the rate of succession.

For Sites E and F this succession to a grass-dominated community was even more rapid in comparison to Sites B and C (Table 6.5b). Yet again the insect-free area (Site E) showed a greater increase in the grass-forb ratio through the first season, with these main differences starting earlier, in July (Table 6.5b and *cf* Table 6.5a).

6.5.5 Taxonomic composition

6.5.5(a) Colonisation, extinction, species richness and diversity

For Site B (insect-free) and Site C (insect-grazed) no significant differences were found in the number of plant species gained or lost in each monthly sample during the two years ($p>0.05$). Also, overall seasonal comparisons between the two areas for each year showed no significant differences in species gain or loss (2 x 6 contingency table, $p>0.05$). However, there are trends in the accumulation rates of plant species (Fig. 6.3a). During the early part of the first season (June-July) new plant species appeared more rapidly in the insect-free site. This difference was mainly due to the earlier appearance of annual and perennial herbs,

TABLE 6.5: Comparison of the grass/forb ratio for cover and abundance between insect-free and insect-grazed areas

a. During the first two years of succession (1980 + 1981); Site B = insect-free, Site C = insect-grazed.

b. During the first year of succession (1981); Site E = insect-free, Site F = insect-grazed.

a.

		YEAR 1						YEAR 2					
	Site ↓	MAY	JUNE	JULY	AUG	SEPT	OCT	MAY	JUNE	JULY	AUG	SEPT	OCT
Grass/forb index (cover)	B	0.01	0.02	0.06	0.22	0.65	1.52	2.28	1.19	0.98	1.31	3.53	19.66
	C	0.09	0.02	0.02	0.18	0.41	0.45	0.90	1.13	0.93	1.68	3.75	∞*
Grass/forb index (abundance)	B	<0.01	<0.01	0.01	0.07	0.34	1.60	4.25	1.61	1.13	3.08	14.22	67.50
	C	0.07	<0.01	<0.01	0.07	0.20	0.22	0.64	1.05	0.87	4.45	14.88	∞*

*herbs extinct by end of second year in Site C.

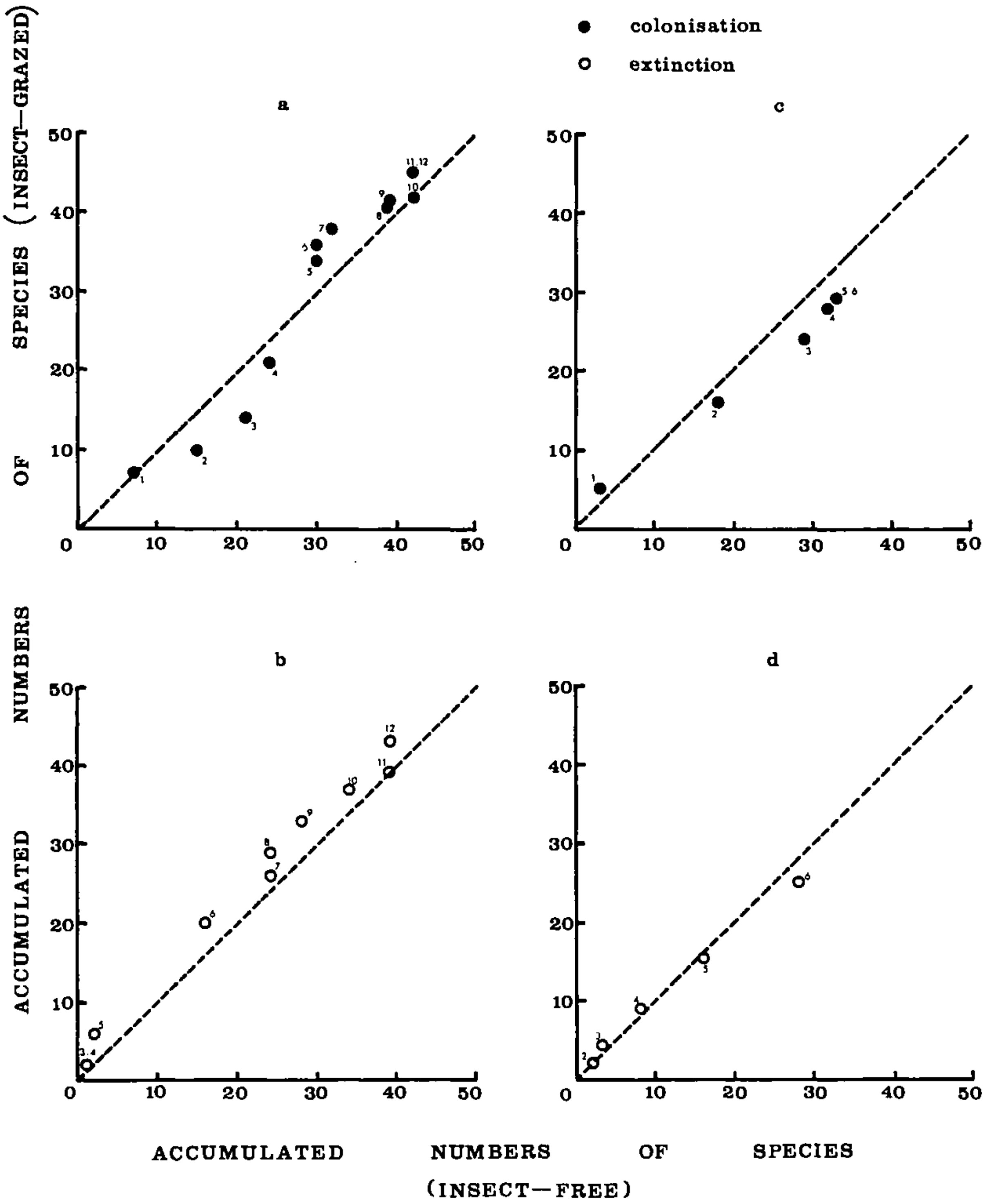
b.

		YEAR 1					
	Site ↓	MAY	JUNE	JULY	AUG	SEPT	OCT
Grass/forb ratio (cover)	E	0.99	0.31	0.65	0.75	1.13	5.89
	F	0	0.29	0.22	0.41	0.72	4.60
Grass/forb ratio (abundance)	E	1.00	0.22	0.23	0.32	1.69	3.39
	F	0	0.20	0.12	0.26	1.03	2.26

Fig. 6.3 Comparison of colonisation and extinction rates of plant species in insect-free and insect-grazed areas.

Sites B and E=insect-free; Sites C and F=insect-grazed. The number (1-12) adjacent to each data point indicates the sampling date from May-October in each year:- 1-6=Year 1; 7-12=Year 2.

a. Colonisation during the first two years of succession (Sites B and C).
b. Extinction “ “ “ “ “ “ “ (“ “ “ “).
c. Colonisation during the first year of succession (Sites E and F).
d. Extinction “ “ “ “ “ “ “ (“ “ “ “).


● colonisation
○ extinction
a
b
c
d
ACCUMULATED NUMBERS OF SPECIES (INSECT—GRAZED)
ACCUMULATED NUMBERS OF SPECIES (INSECT—FREE)
0
10
20
30
40
50

especially the latter. The first perennials in the insect-free area were mainly species that appeared either one month earlier (*Trifolium pratense* in June, *Crepis capillaris* and *Ranunculus repens* in July) or two months earlier (*Cirsium arvense* in June and *Hypochaeris radicata* in July) compared to the grazed site. The rate of extinction of plant species, on the other hand, was exremely low and similar in both sites during these early months (Fig. 6.3b). This together with the different species accumulation resulted in a higher plant species richness in the insect-free site from June-August (Table 6.6a). These differences in plant species accumulation are highlighted in Table 6.7 where ratios of species accumulation in the insect-free and insect-grazed sites are given. The biennial herbs and Gramineae have not been separated from the total values because these two groups had a low species richness throughout the two years. Clearly the main differences in the rate of accumulation in the first year were due to annual herbs from May-June and perennial herbs during June and July. After August annual and perennial herbs were gained more rapidly in the insect-free area and with similar extinction rates the two sites ended the first season with a similar plant species richness (insect-free, 14 spp.: insect-grazed, 16 spp.; Table 6.6a). Relatively few new species were added to either site during the second year and as extinction progressed (Fig. 6.3b) plant species richness declined rapidly. Annual herbs were extinct in both sites by September and the second season ended with just three species in the insect-free area (*Holcus lanatus*, *Agrostis capillaris* and *Trifolium pratense*) and only two species in the grazed area (mainly *Holcus lanatus* but with small amounts of *A.tenuis*) (Table 6.6a). These trends are also reflected in values of the Williams Index of α-diversity (Appendix 11a). These show a greater plant taxonomic diversity in June, July and August of the first year in the insect-free area and with similar values at other times during the two years. The higher values of α in the insect-free zone were due to a greater diversity of annual and perennial herbs.

Sites E (insect-free) and F (insect-grazed) were comparable to Sites B and C in the first year in that no significant differences were found in the number of plant species gained or lost in each monthly sample ($p>0.05$) or in an overall seasonal comparison (2 x 6 contingency table, $p>0.05$). However, unlike Sites B and C, Sites E and F did not show any differences in species accumulation (Fig. 6.3c); species gain and loss were similar through the season. As extinction progressed towards the end of the season (Fig. 6.3d) plant species richness declined rapidly in the two sites (Table 6.6b). At the end of the first year the taxonomic composition of Sites E and F resembled the mid-season in the second year in B and C, with a relatively

TABLE 6.6 Comparison of plant species richness between insect-free and insect-grazed areas.

a. During the first two years of succession (1980 + 1981); Site B = insect-free, Site C = insect-grazed

b. During the first year of succession (1981); Site E = insect-free, Site C = insect-grazed.

a.

		YEAR 1						YEAR 2					
		MAY	JUNE	JULY	AUG	SEPT	OCT	MAY	JUNE	JULY	AUG	SEPT	OCT
Annuals	B	6	8	11	11	14	5	2	5	2	2	0	0
	C	5	6	8	10	17	7	4	4	3	1	0	0
Biennials	B	0	0	0	0	1	0	1	3	3	1	0	0
	C	0	0	1	1	3	1	2	2	3	1	0	0
Perennials	B	0	4	6	8	11	6	3	6	5	4	1	1
	C	1	1	3	6	6	6	5	5	3	2	4	0
Gramineae	B	1	3	3	4	3	3	3	3	3	2	2	2
	C	1	3	1	3	3	3	3	3	3	2	2	2
Total	B	7	15	20	23	28	14	8	15	11	8	3	3
	C	7	10	12	19	28	16	12	12	9	5	6	2

TABLE 6.6: (Continued)

b.

		YEAR 1					
		MAY	JUNE	JULY	AUG	SEPT	OCT
Annuals	E	2	9	14	14	7	1
	F	5	7	10	8	5	1
Biennials	E	0	2	3	3	3	1
	F	0	1	3	2	2	0
Perennials	E	0	5	7	8	7	3
	F	0	4	7	6	6	2
Gramineae	E	1	1	3	2	2	1
	F	0	3	3	3	2	1
Total	E	3	16	26	24	17	5
	F	5	14	20	19	14	4

TABLE 6.7: Ratio of plant species accumulations (insect-free/insect-grazed).

During the first two years of succession (1980 + 1981) Site B (insect-free) and Site C (grazed)

	YEAR 1						YEAR 2					
	MAY	JUNE	JULY	AUG	SEPT	OCT	MAY	JUNE	JULY	AUG	SEPT	OCT
Annuals	1.2	1.33	1.37	1.1	0.82	0.82	1.06	1.11	1.05	1.05	1.05	1.05
Perennials	0	4.00	2.66	1.66	1.30	1.08	1.08	1.23	1.23	1.46	1.18	1.18
Total	1.00	1.50	1.50	1.14	0.88	0.83	0.84	0.95	0.93	1.00	0.93	0.93

low species richness and a high cover of perennial herbs and grasses. At the end of the first season there were just five species remaining in Site E (insect-free) and four species in Site F (grazed); again the dominant species in each site were *Holcus lanatus* and *Trifolium pratense*. Comparisons of Williams α between Sites E and F resemble events in the major two-year study with a greater diversity in the insect-free area for the main part of the first year (Appendix 11b). These differences were contributed mainly by a greater diversity of annual herbs in Site E.

6.5.5(b) Similarity Coefficients

Seasonal and successional changes in basic taxonomic composition, or species turnover, of early successional plants and insects were described in Chapter Three using Sorensen's Index of Similarity. Here the index is used to compare the vegetation in insect-free and insect-grazed areas. The two areas are compared in four different ways. First a comparison is made of the number of different plant species that were found in the two sites in each year using the qualitative *Is* statistic. Second the *Is* statistic is again used on a seasonal basis but only species that attained at least 5% cover during one season are included. The outcome of these two exercises is to give an indication of habitat similarity for all species and for the numerically important ones. Table 6.8a shows that Sites B and C had a high similarity in the number of species appearing during each year (Is=0.77 and 0.73 for the first and second years respectively). Furthermore when the relatively important species (*i.e.* with at least 5% cover) are assessed the similarity is even higher (Is=0.88 and 0.90). These two descriptions show that the sites were comparable in the plant species present and in those species that were important in terms of cover during the two years.

The third measure is used to describe the species turnover rate (or β-diversity) within the grazed and insect-free areas. This is achieved by computing the *Iw* statistic (*i.e.* accounting for the number of individuals of common species) between years for the same month in each site. The results are given in Table 6.9 for Sites B and C and show that the rate of successional change expressed in terms of species turnover is different in the two sites. Succession to a grass-dominated community occurred at a much greater rate in the insect-free area as displayed by the earlier occurrence of high similarity. Appreciable differences occurred in September of the first year when a large rise in β-diversity in the insect-free site (27% to 58% for Gramineae; 30-72% overall) was not matched in the insect-grazed area (22-38% for Gramineae; 29-35% overall). This difference in successional advance was even greater

TABLE 6.8: Comparison of the total number of plant species and plant species with > 5% cover on insect-free and insect-grazed areas.

a. During the first two years of succession (1980 + 1981)
Site B = insect-free; Site C = insect-grazed.

b. During the first year of succession (1981)
Site E = insect-free; Site F = insect-grazed.

a.

	YEAR 1	YEAR 2
Total species		
Total species Site B	29	16
Total species Site C	33	17
Number species shared	24	12
I_s	0.77	0.73
Species with > 5% cover		
Total species Site B	11	10
Total species Site C	14	10
Number species shared	11	9
I_s	0.88	0.90

b.

	YEAR 1
Total species	
Total species Site E	29
Total species Site F	27
Number shared	25
I_s	0.89
Species with > 5% cover	
Total species Site E	9
Total species Site F	8
Number shared	8
I_s	0.94

TABLE 6.9: Sorensen's Index of Similarity (I_w) to Compare the Rate of Successional Change within Insect-Free and Insect-Grazed Areas During the First Two Years of Succession (1980 & 1981).

Site B = insect-free

Site C = insect-grazed

		May '80 May '81	June '80 June '81	July '80 July '81	Aug '80 Aug '81	Sept '80 Sept '81	Oct '80 Oct '81
Annuals	B	0	0.06	0.01	0.07	0	0
	C	0	0	0.01	0.02	0	0
Biennials	B	0	0.10	0.12	0.76	0	0
	C	0	0	0.14	0.28	0	0
Perennials	B	0	0.04	0.16	0.58	0.45	0.12
	C	0.05	0.02	0.07	0.68	0.51	0
Gramineae	B	0.005	0.03	0.09	0.27	0.58	0.83
	C	0.02	0.01	0.04	0.22	0.38	0.39
Total	B	0.003	0.04	0.07	0.30	0.72	0.63
	C	0.01	0.01	0.05	0.29	0.35	0.22

by the following month with similarities of 83% (Gramineae) and 63% (overall) in the insect-free site and just 39% (Gramineae)and 22% (overall) in the insect-grazed area.

The fourth assessment makes direct comparisons between Sites B and C on each monthly sampling occasion, again using the *Iw* quantitative index. The results are shown in Table 6.10a and show an overall similarity around 70% during the first year to over 90% similarity after June of the second year. This analysis detects the successional differences between the two sites, indicating large differences in the first year whereas by the end of the second season the two sites had an extremely high similarity.

These values also reflect the patterns of plant cover described for Sites B and C in Fig. 6.1.

For the first year vegetation patterns in Sites E (insect-free) and F (insect-grazed) similar trends are found when the various *Is* and *Iw* comparisons are made. Sites E and F are comparable in the different types of plant species that were present (*Is*=0.89) and in those species that were numerically important (*Is*=0.94); full details are given in Table 6.8b. Although a comparison of β-diversity in Sites E and F cannot be directly made, since only one complete season's sample was made, the increase in the rate of successional change in the insect-free site for both perennial herbs and Gramineae (as reflected by the patterns of plant cover shown in Fig. 6.2) may be quantified in the *Iw* index (Table 6.10b).

6.5.5(c) Comparisons of individual plant species

Major differences in individual plant species cover in Sites B and C, with a greater cover in Site B (insect-free), occurred for examples from the three major plant groupings (annual and perennial herbs and Gramineae) in the first year. For the annuals the main differences were in *Spergula arvensis* (July and August, 95.00% and 64.17% compared to 76.11% and 41.94%, *Polygonum persicaria* (July and August, 36.67% and 28.61% compared to 16.11% and 18.06%) and *Raphanus raphanistrum* (June and July, 41.11% and 51.94% compared to 8.06% and 19.44%). For perennial herbs major differences were displayed by *Trifolium pratense* (August and September, 29.44% and 48.61% compared to 13.33% and 29.17%) and *Crepis capillaris* (August and September, 8.89% and 15.56% compared to 4.17% and 7.22%). For the Gramineae, *Agrostis capillaris* (September and October, 12.22% and 13.33% compared with 2.22% and 5.00%) and *Holcus lanatus* (September and October, 35.28% and 62.50% compared with 23.61% and 21.70%) showed substantial differences in cover. The only case in the first year where a particular species had a consistent larger

TABLE 6.10: Indices of Similarity (I_w for Number of Individuals) Between Insect-Free and Insect-Grazed Areas

a. During the first two years of succession (1980 & 1981) Site B = insect-free: Site C = insect-grazed

b. During the first year of succession (1981) Site E = insect-free: Site F = insect-grazed.

a	Year 1						Year 2					
	May	June	July	Aug	Sept	Oct	May	June	July	Aug	Sept	Oct
Annuals	0.63	0.72	0.74	0.80	0.73	0.65	0.40	0.36	0.66	0.86		
Biennials			0.88	0.76	0.92	0.33	0.40	0.53	0.66	1.00		
Perennials		1.00	0.59	0.60	0.68	0.73	0.70	0.80	0.92	0.84	0.82	
Gramineae	0.50	0.80	0.64	0.88	0.73	0.64	0.77	0.98	0.97	0.96	0.98	0.95
Total	0.62	0.73	0.74	0.76	0.71	0.68	0.71	0.82	0.91	0.91	0.94	0.92

Continued...

TABLE 6.10:(cont...)

b Year 1

	May	June	July	Aug	Sept	Oct
Annuals	0.25	0.63	0.87	0.75	0.42	0
Biennials	0	0.88	0.67	0.34	0.61	0
Perennials	0	0.48	0.46	0.56	0.65	0.70
Gramineae	0	0.70	0.51	0.66	0.61	0.79
Total	0.20	0.66	0.68	0.65	0.63	0.75

coverage in the grazed area was *Trifolium repens* from August to October with cover values of 18.06, 34.72, and 20.80% compared with 8.06, 17.50 and 5.80% in the insect-free area.

Fewer differences (again in favour of the insect-free site) were found with individual species in the second season and these mostly occurred early on in the season (*e.g. Agrostis capillaris* (May, 23.33% compared with 10.00%) and *Holcus lanatus* (May, 73.33% compared with 46.67%)).

Main differences in individual species cover in Site E and F, with a greater cover in Site E (insect-free), occurred for perennials and Gramineae. For the perennial herbs these differences happened chiefly from July to September for *Trifolium pratense* (38.06, 75.83 and 63.06% compared with 10.56, 42.78 and 46.11%), *Plantago lanceolata* (10.83, 30.28 and 26.39% compared with 3.61, 7.50 and 4.72%) and *Crepis capillaris* (12.50, 32.78 and 13.33% compared to 5.00, 2.50 and 3.89%). Grass differences were again chiefly due to *Holcus* with main differences from July to October (58.61, 71.67, 94.17 and 93.33% compared with 20.00, 35.50, 42.00 and 61.50%). Only one species, *Rumex acetosella*, had a greater coverage in the insect-grazed area (from June to September, with cover values of 4.17, 15.00, 10.00 and 16.38% compared to 0.56, 2.50, 5.56 and 3.89%).

6.5.6 Plant structure production

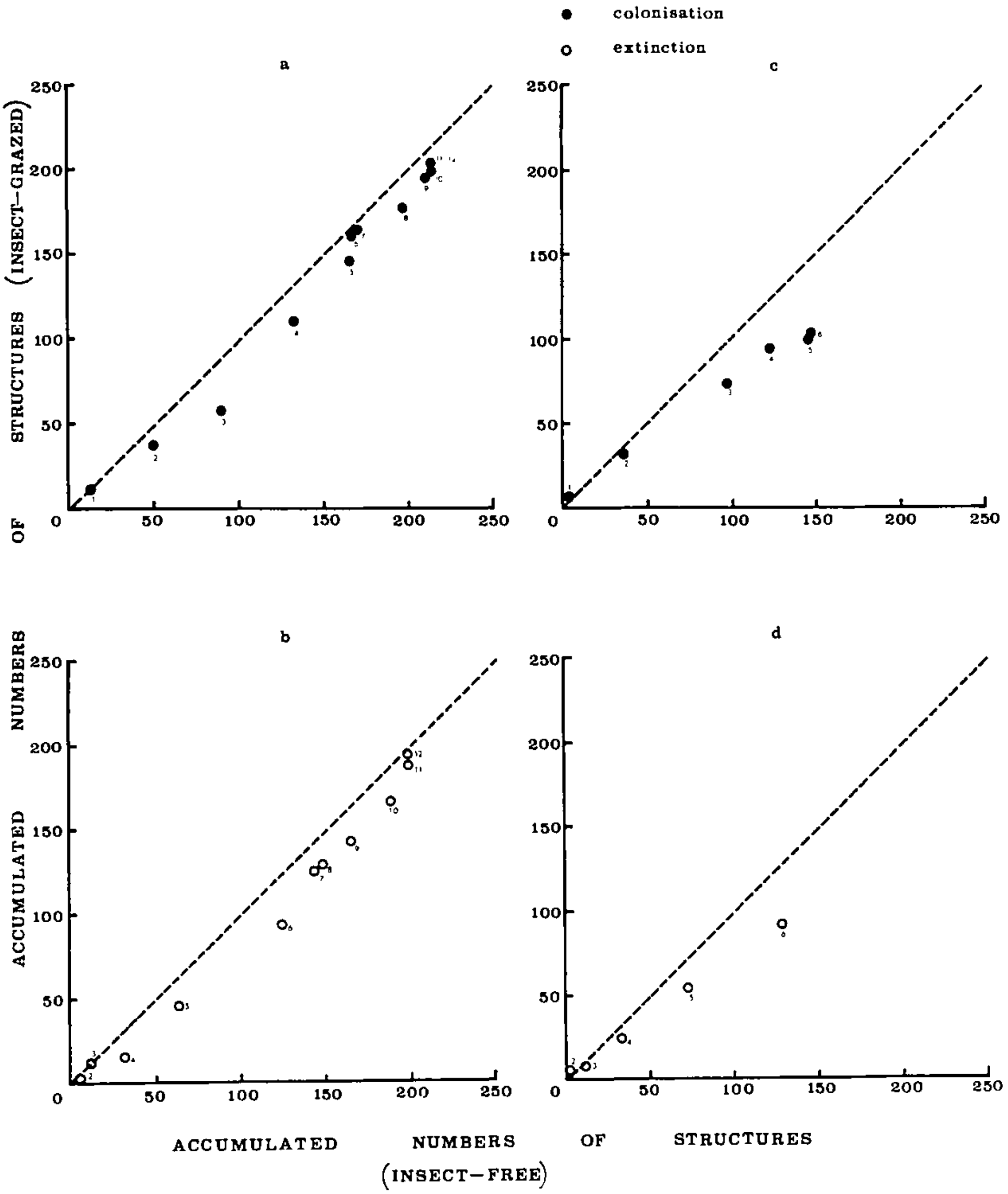
6.5.6(a) Structure colonisation, extinction and richness

For Site B (insect-free) and Site C (insect-grazed) no significant differences were found in the number of different plant structures gained or lost over each season (2 x 6 contingency table, p>0.05). In Fig. 6.4a trends in the accumulation of structures are compared between the two areas. Not surprisingly, a greater colonisation rate of plant species in the insect-free area during the early part of the first season (June -July) was accompanied by a greater production of new plant structures during this period, although this is not significant (p>0.05). This difference was mainly due to the earlier appearance of annual herb structures and to a lesser extent structures from perennials. This is the reverse situation to the early plant species arrivals and is because annual herbs were relatively species rich and produced more structures (both vegetative and reproductive) whereas the perennial herbs in this ruderal period had low species richness, were slowly establishing themselves vegetatively and were thus less structured. The particular species and structure types involved will be related in the next section (6.5.6(b)).

Fig. 6.4 Comparison of colonisation and extinction rates of plant structures in insect-free and insect-grazed areas.

Sites B and E=insect-free; Sites C and F=insect-grazed. The number (1-12) adjacent to each data point indicates the sampling date from May-October in each year:- 1-6=Year 1; 7-12=Year 2.

a. Colonisation during the first two years of succession (Sites B and C).
b. extinction " " " " " " " (" " " ").
c. Colonisation during the first year of succession (Sites E and F).
d. Extinction " " " " " " " (" " " ").


● colonisation
○ extinction
a
b
c
d
ACCUMULATED NUMBERS OF STRUCTURES (INSECT-GRAZED)
ACCUMULATED NUMBERS OF STRUCTURES (INSECT-FREE)
0
50
100
150
200
250

The extinction rate of plant structures was very low and similar in the two sites during this ruderal period (Fig. 6.4b) and together with the different structures acquired resulted in a higher structure richness in the insect-free site from June to July (Table 6.11a); structure extinction is really another reflection of plant species richness. By July 90 different structures (64 annuals, 15 perennials, 11 grasses) had appeared in the insect-free zone compared to 58 structures (39 annuals, 7 perennials, 10 grasses, 2 biennials) in the grazed area. Greater structure gains in August (mainly annuals, $p>0.05$) and October (mainly perennials, $p>0.05$) occurred in the insect-grazed site; greater structure losses occured in August (mainly annual herbs, $0.05>p>0.01$) and October (mainly perennials, $p>0.05$) in the insect-free site. By the end of the first season the two sites had accumulated similar numbers of structures (Site B, 164 structures; Site C 160 structures) but more structures had been lost in the insect-free site (Site B, 124 structures; Site C, 93 structures). Consequently, the season ended with a greater structural richness in the grazed area (67 structures compared to 40 structures; Table 6.11a).

As expected from the few new species arrivals, as well as a lower and declining species richness in the second year, relatively few structures were added to either site during this period. A similar decline in the two sites of structure richness of annuals and the eventual decline in perennial herb structure numbers left both sites with a similar low number of structures (mainly associated with the Gramineae) at the end of the second year (Fig. 6.4a,b and Table 6.11a).

Sites E (insect-free) and F (insect-grazed) were similar to Sites B and C in that no significant differences were found in the number of different plant structures gained and lost in the first year (2 x 6 contingency, $p>0.05$). The trends in structure appearances and extinctions for Sites E and F are shown in Fig. 6.4c and d. These show a greater production of new structures in the insect-free area for the main part of the growing season (July-September; Fig. 6.4c). With fairly low extinctions of structures during this ruderal period (Fig. 6.4d) the number of structure types was generally considerably greater in Site E at any one time, although Sites E and F were generally less diverse in structure types when compared to Sites B and C in the first season (Table 6.11b *cf* Table 6.11a). By July 97 different structures (50 annuals, 38 perennials, 7 Gramineae, 2 biennials) had accumulated in the insect-free area (Site E) compared to 73 structures (38 annuals, 24 perennials, 8 Gramineae, 3 biennials) in the grazed area (Site F). By the end of the season considerably fewer structures had appeared in the grazed site with 146 structures (70 annuals, 65 perennials, 9 Gramineae, 2 biennials) in Site E and 103 structures (47 annuals, 44 perennials, 8 Gramineae, 4 biennials)

TABLE 6.11: Comparison of the number of different plant structures present in insect-free and insect-grazed areas.

a. During the first two years of succession (1980 + 1981). Site B = insect-free; Site C = insect grazed.

b. During the first year of succession (1981). Site E = insect-free; Site F = insect-grazed.

a.

		YEAR 1						YEAR 2					
		MAY	JUNE	JULY	AUG	SEPT	OCT	MAY	JUNE	JULY	AUG	SEPT	OCT
Annuals	B	12	33	57	63	53	12	6	16	10	9	0	0
	C	8	25	32	59	56	32	13	14	17	11	0	0
Biennials	B	0	0	0	0	3	0	2	5	3	1	0	0
	C	0	0	2	4	4	1	1	2	2	0	0	0
Perennials	B	0	7	12	26	33	18	12	22	26	15	7	1
	C	1	3	6	19	24	23	15	19	21	18	11	0
Gramineae	B	1	6	9	12	13	10	9	8	8	6	4	4
	C	2	6	6	13	16	11	8	10	11	9	5	4
Total	B	13	46	78	101	102	40	29	51	47	31	11	5
	C	11	34	46	95	100	67	37	45	51	38	16	4

Continued..

TABLE 6.11: (Continued)

b.

YEAR 1

		MAY	JUNE	JULY	AUG	SEPT	OCT
Annuals	E	2	19	44	48	22	1
	F	5	14	31	24	15	1
Biennials	E	0	4	8	9	6	3
	F	0	4	5	2	3	0
Perennials	E	0	12	33	32	41	12
	F	0	8	24	37	25	6
Gramineae	E	1	3	6	7	7	3
	F	0	6	8	7	4	3
Total	E	3	34	85	89	72	17
	F	5	28	66	70	46	10

in Site F. The only occasion where the greater structure gain in the insect-free area was significant was in September (0.05>p>0.01) and this was chiefly due to a large gain in perennial herb structures in Site E. Since there were few plant species remaining at the end of the first season in Site E and F the number of structures was also obviously very low and the situation thus resembled latter stages of the second season in Sites B and C (*cf* Tables 6.11a and b). Section 6.5.6(b) considers the chief plant species and structures contributing to the differences between Sites E and F.

6.5.6(b) Production of vegetative and reproductive structures

Trends in structure colonisation and extinction will now be described in terms of the type of structure (vegetative *vs* reproductive). For Site B (insect-free) and Site C (insect-grazed) these trends are shown in Fig. 6.5. Clearly, the greater colonisation of plant structures in the insect-free site during the early ruderal period (June-July) was due to a greater production of vegetative structures (Fig. 6.5a,c) and these were predominantly annual and perennial herbs; however, these monthly trends are not significant (p>0.05). These early appearances of vegetative structures in the insect-free site were due to particular species either arriving early and producing structures or else simply developing new types of structures more rapidly. Annual herb species that were present at the same time in the two sites but produced more vegetative structures were, for example, *Spergula arvensis* in May (seedling, mature leaf) and June (immature leaf) and *Fallopia convolvulus* in May (seedling). The appearance of the annual *Polygonum aviculare* one month earlier in Site B (in June) produced three new vegetative structures. Similarly, the early appearance of a few perennial herb species added to the early production of annual herb structures in the insect-free site (*e.g. Cirsium arvense, Hypochaeris radicata* and *Ranunculus repens*). Similar low extinction rates (p>0.05) of vegetative structures in the two sites during the early period (Fig. 6.5b) resulted in a higher structure richness to July in Site B (Table 6.12a). By July 64 vegetative structures had accumulated in the insect-free site (40 annuals, 15 perennials, 9 Gramineae) compared to 45 vegetative structures in the grazed area (29 annuals, 7 perennials, 9 Gramineae). In August a greater gain of vegetative structures in the grazed area compared to the insect-free site resulted in a similar number of vegetative structures in the two sites and for the rest of the first season similar gains occurred in the two sites (Fig. 6.5a). Extinction of vegetative structures, on the other hand, was greater in the insect-free area in August and October (annual herbs, p>0.05). By the end of the first season the two sites had accumulated

Fig. 6.5 Comparison of colonisation and extinction rates of vegetative and reproductive structures in insect-free and insect-grazed areas during the first two years of succession.

Site B=insect-free; Site C=insect-grazed. The number (1-12) adjacent to each data point indicates the sampling date from May-October in each year:- 1-6=Year 1; 7-12=Year 2.

a. Vegetative structures: colonisation.
b. “ “ : extinction.
c. Reproductive “ : colonisation.
d. “ “ : extinction.

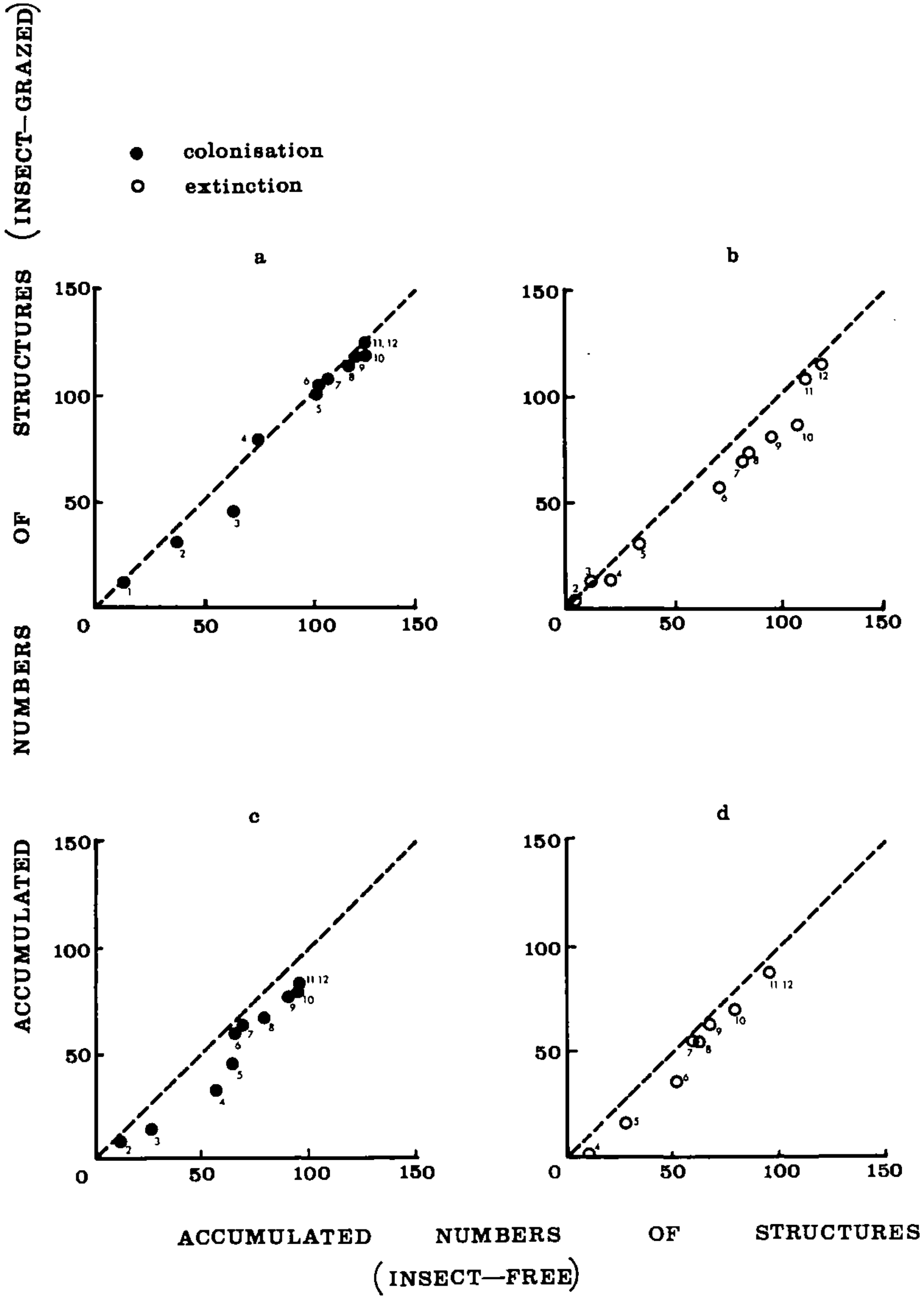

● colonisation
○ extinction
a
b
c
d
0
50
100
150
ACCUMULATED NUMBERS OF STRUCTURES (INSECT—GRAZED)
ACCUMULATED NUMBERS OF STRUCTURES (INSECT—FREE)

TABLE 6.12: Comparison of the number of different vegetative and reproductive structures present in insect-free and insect-grazed areas during the first two years of succession (1980 + 1981).

a. Vegetative structures; b. Reproductive structure. Site B = insect-free; Site C = insect-grazed.

a.

		YEAR 1						YEAR 2					
		MAY	JUNE	JULY	AUG	SEPT	OCT	MAY	JUNE	JULY	AUG	SEPT	OCT
Annuals	B	12	23	33	27	27	3	1	8	1	0	0	0
	C	8	18	20	35	35	20	11	12	11	9	0	0
Biennials	B	0	0	0	0	3	0	2	3	2	0	0	0
	C	0	0	2	4	4	1	1	2	1	0	0	0
Perennials	B	0	7	12	19	29	17	12	14	14	11	7	1
	C	1	3	6	15	20	16	15	13	12	10	11	0
Gramineae	B	1	5	7	9	9	8	9	7	6	4	4	4
	C	2	6	5	11	11	9	6	7	6	4	5	4
Total	B	13	35	52	55	68	28	24	32	23	15	11	5
	C	11	27	33	65	70	46	33	34	30	23	16	4

Continued..

TABLE 6.12: (Continued)

b.

		YEAR 1						YEAR 2					
		MAY	JUNE	JULY	AUG	SEPT	OCT	MAY	JUNE	JULY	AUG	SEPT	OCT
Annuals	B	0	10	24	36	26	9	5	8	9	9	0	0
	C	0	7	12	24	21	12	2	2	6	2	0	0
Biennials	B	0	0	0	0	0	0	0	2	1	1	0	0
	C	0	0	0	0	0	0	0	0	1	0	0	0
Perennials	B	0	0	0	7	4	1	0	8	12	4	0	0
	C	0	0	0	4	4	7	0	6	9	8	0	0
Gramineae	B	0	1	2	3	4	2	0	1	2	2	0	0
	C	0	0	1	2	5	2	2	3	5	5	0	0
Total	B	0	11	26	46	34	12	5	19	24	16	0	0
	C	0	7	13	30	30	21	4	11	21	15	0	0

the same number of vegetative structures (103 structures) but more of these structures had been lost in the insect-free site (72 structures compared to 54 structures) and this difference was mainly due to the annual herbs (48 structures compared to 36 structures). As a consequence the season ended with a greater vegetative structural richness in the insect-grazed area (46 structures compared to 28 structures; Table 6.12a).

Further accumulations and extinctions of vegetative structures were similar in Sites B and C during the second year ($p>0.05$). The eventual seasonal decline in vegetative structure types resulted with just four vegetative structures remaining in October in the insect-grazed area (all Gramineae) and just five vegetative structures in the insect-free area (one perennial and four Gramineae) (Table 6.12a).

Reproductive structures (predominantly annual herbs) appeared chiefly from June-September in Sites B and C during the first season. Their rate of production was greater in the insect-free zone from July-August (Fig. 6.5c). By August 56 reproductive structures had been recorded in the insect-free area compared to 32 reproductive structures in the grazed site. This earlier rate of reproductive structure production was due to certain plant species maturing more rapidly in the insect-free site and this gave a greater reproductive structure richness in that site during this early period (Table 6.12b). One example of this early maturation was *Polygonum persicaria.* This annual herb was present in both sites from May of the first year. In the insect-free site the pre-anthesis stage had been reached in June and both pre- and post- reproductive structures were present the following month (July), whereas reproductive structures did not appear until August in the grazed area.

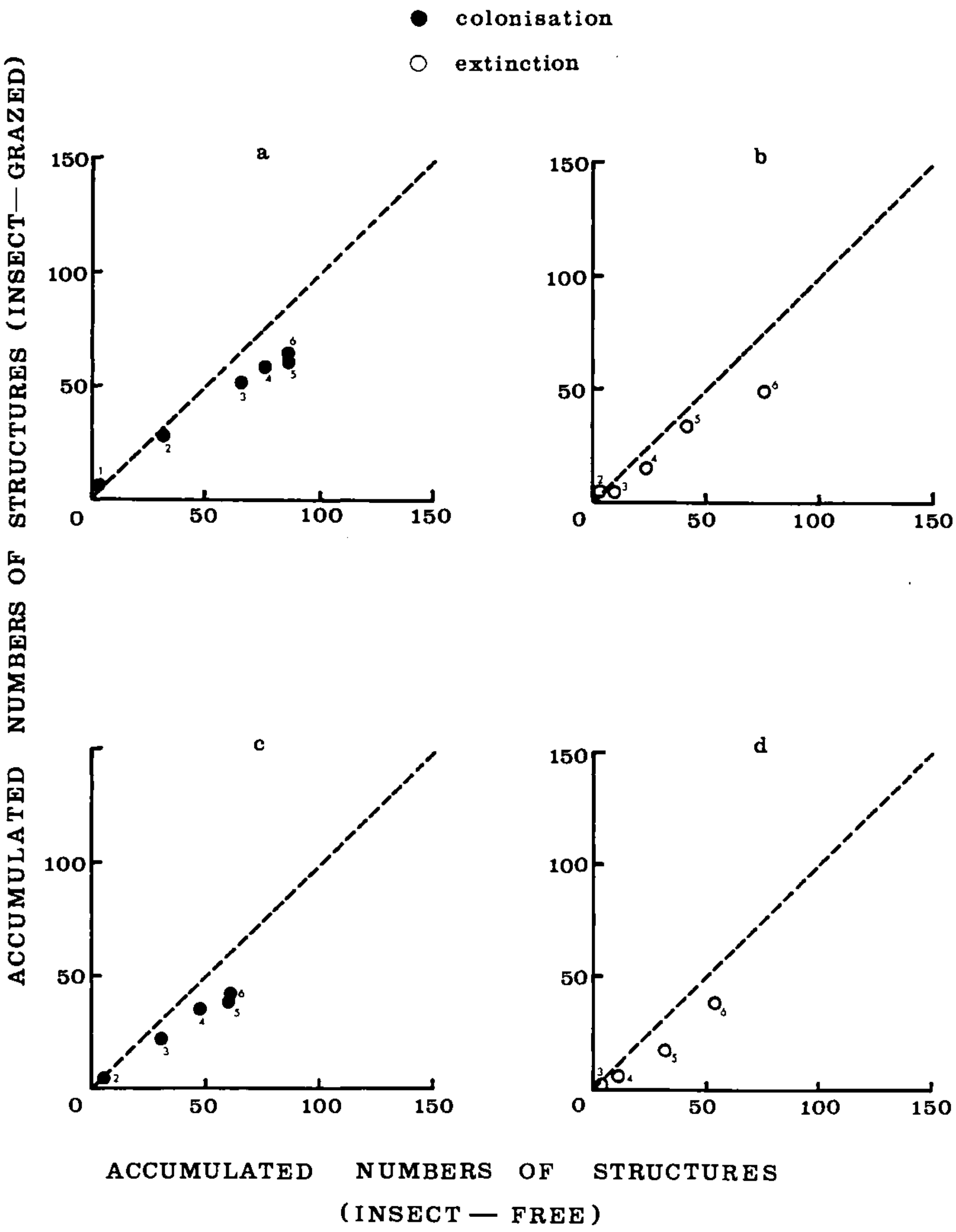
The later appearance of reproductive structures in the insect-grazed area after August together with a reduced production in the insect-free area resulted, at the end of the season, with similar accumulations in the two sites (Fig. 6.5c). Reproductive structures in Site B, on the other hand, disappeared at a faster rate (Fig. 6.5d) and consequently reproductive structure richness at the end of the season was slightly greater in the grazed area (Table 6.12b). As for vegetative structures the accumulations and extinctions of reproductive structures were similar in Sites B and C in the second year ($p>0.05$; Fig. 6.5c,d) and the number of different structures found at any one time (*i.e.* to August) were generally low.

Fig. 6.6 shows the trends in colonisation and extinction of vegetative and reproductive structures in Sites E (insect-free) and F (insect-grazed). Overall seasonal comparisons of the gain or loss of these two structure categories were not significantly different between Sites E and F (2 x 6 contingency, $p>0.05$). The trend for a greater structure appearance in the insect-

Fig. 6.6 Comparison of colonisation and extinction rates of vegetative and reproductive structures in insect-free and insect-grazed areas during the first year of succession.

Site E=insect-free; Site F=insect-grazed. The number (1-6) adjacent to each data point indicates the sampling date from May-October in the first year.

a. Vegetative structures: colonisation.
b. " " : extinction.
c. Reproductive " : colonisation.
d. " " : extinction.


● colonisation
○ extinction
a
b
c
d
0
50
100
150
ACCUMULATED NUMBERS OF STRUCTURES (INSECT — GRAZED)
ACCUMULATED NUMBERS OF STRUCTURES
(INSECT — FREE)

free site for the main part of the growing season (July-September) was due to both vegetative and reproductive material. This was mainly due to particular species (mainly perennial herbs but also a few annuals) producing structures earlier in the insect-free area. Species contributing most to vegetative structures were the annual herb species *Sonchus oleraceus* (June-July), *F allopia convolvulus* (July) and *Stellaria media* (July) and the perennials *Trifolium pratense* and *T.repens* (June) and *Crepis capillaris* (July). The main species contributing to reproductive structures were the annual herb species *Chenopodium album* (July-August), *Polygonum aviculare* (July-August) and *Conyza canadensis* (August) and the perennial species *T.pratense* (July) and *Crepis capillaris* (July). By August 76 vegetative structures had appeared in the insect-free site (38 annuals, 29 perennials, 7 Gramineae, 2 biennials) compared to 59 vegetative structures in the grazed area (24 annuals, 25 perennials, 8 Gramineae, 2 biennials). At this time 47 reproductive structures had accumulated in Site E (27 annuals, 19 perennials, 1 Gramineae) compared to 35 reproductive structures in Site F (18 annuals, 16 perennials, 1 biennial). Unlike Site C the Site F grazed area did not show a late season increase in structure production of either vegetative or reproductive material. With a more rapid late season structure loss in Site E (Fig. 6.6b,d) the two sites finished the season with similar and low numbers of structures (Table 6.13a,b). Over the whole season 86 vegetative structures had appeared in Site E (39 annuals, 38 perennials, 7 Gramineae, 2 biennials) compared to 63 vegetative structures in Site F (26 annuals, 26 perennials, 8 Gramineae, 3 biennials) and with 60 reproductive structures in Site E (31 annuals, 27 perennials, 2 Gramineae) compared to 40 reproductive structures in Site F (21 annuals, 18 perennials, 1 biennial).

6.5.7 Plant abundance

6.5.7(a) Total vegetation trends

Fig. 6.7 compares the total abundance of green plant material between the insect-free (Site B) and insect-grazed (Site C) areas during the first two years of succession. Trends in the three major plant groupings are shown with total vegetation differences given at the top of the figure. Making an overall season comparison between the two areas in a 2 x 6 contingency table indicates highly significant differences in total abundance between the two areas for the first year ($p<0.001$) but not for the second season ($p>0.05$); this contrasts with the cover comparisons described in Section 6.5.3 where no overall seasonal differences were found (although differences were found in some monthly samples). Total plant abundance rose

TABLE 6.13: Comparisons of the number of different vegetative and reproductive structures present in insect-free and insect-grazed areas during the first year of succession (1981).

a. Vegetative structure; b. Reproductive structure.

Site E = insect-free; Site F = insect-grazed.

a.

YEAR 1

		MAY	JUNE	JULY	AUG	SEPT	OCT
Annuals	E	2	15	28	27	14	0
	F	5	11	15	12	4	1
Biennials	E	0	3	5	5	3	1
	F	0	3	3	0	2	0
Perennials	E	0	11	21	18	24	6
	F	0	8	19	22	14	5
Gramineae	E	1	3	6	6	5	3
	F	0	6	8	7	4	3
Total	E	3	29	57	53	45	10
	F	5	25	44	41	24	9

b.

YEAR 1

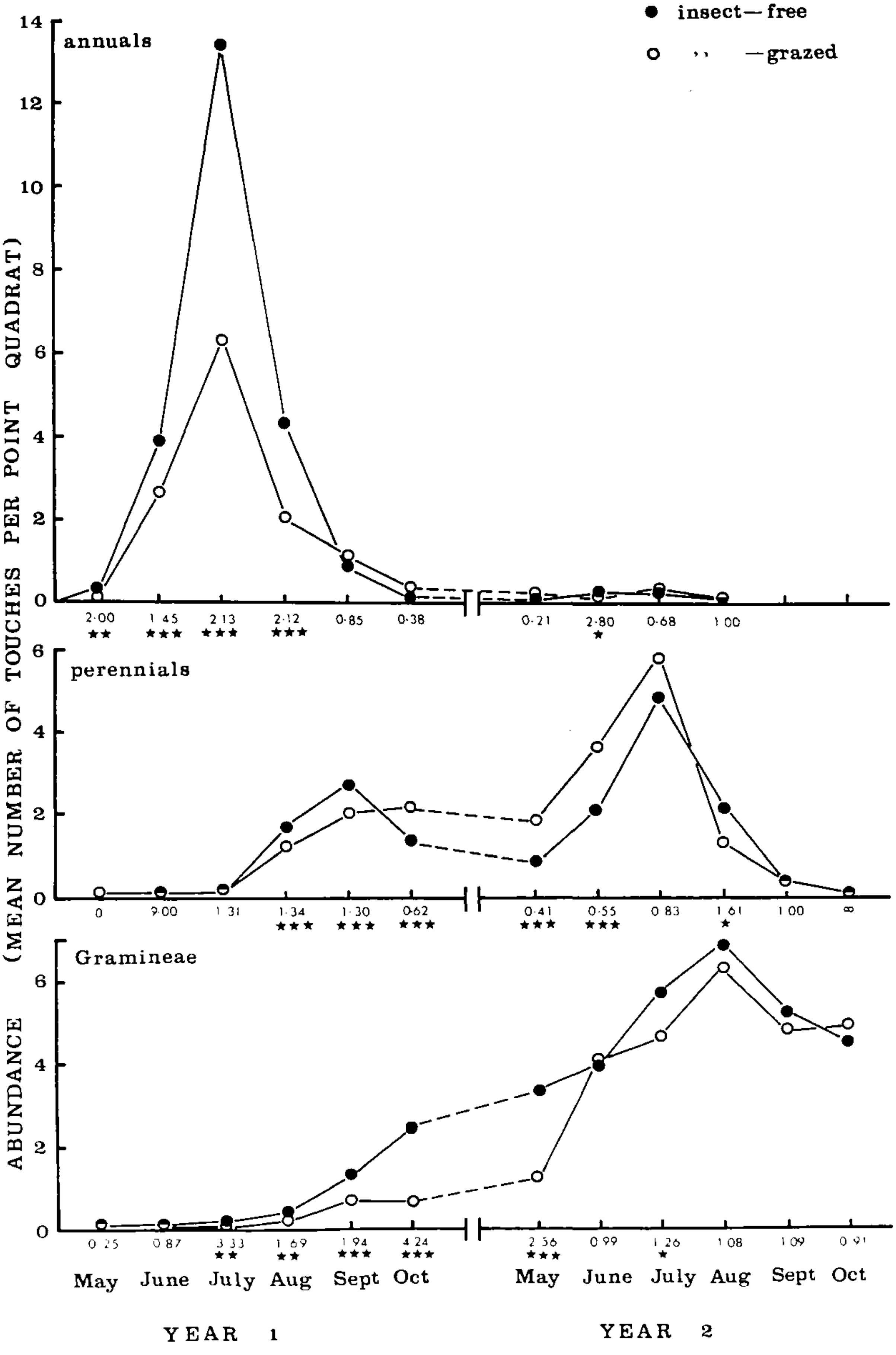
		MAY	JUNE	JULY	AUG	SEPT	OCT
Annuals	E	0	4	16	21	8	1
	F	0	3	16	14	11	0
Biennials	E	0	1	3	4	3	2
	F	0	1	2	2	2	0
Perennials	E	0	1	12	14	17	6
	F	0	0	5	15	11	1
Gramineae	E	0	0	0	1	2	0
	F	0	0	0	0	0	0
Total	E	0	5	28	36	27	7
	F	0	3	22	29	22	1

Fig. 6.7 Comparison of abundance of annual and perennial herbs and Gramineae between insect-free and insect-grazed areas during the first two years of succession.

Site B=insect-free; C=insect-grazed. Total vegetation abundance (expressed as the mean number of touches per point quadrat) is given along the figure top. Values given below the total abundance information and below the abscissae indicate the abundance ratio (insect-free/insect-grazed). Significant differences (from Chi-square or Fisher Exact tests) in monthly samples between grazed and ungrazed areas are marked by asterisks (1=5% level, 2=1% level, 3=0.1% level).

Total plant abundance

●	0·3	3·9	13·7	6·4	4·9	3·8	4·1	6·7	10·8	9·9	5·6	4·5
○	0·2	2·7	7·8	3·6	3·8	3·1	3·4	7·9	10·7	7·9	5·1	4·9
	★★	★★★	★★★	★★★	★★★	★				★★		



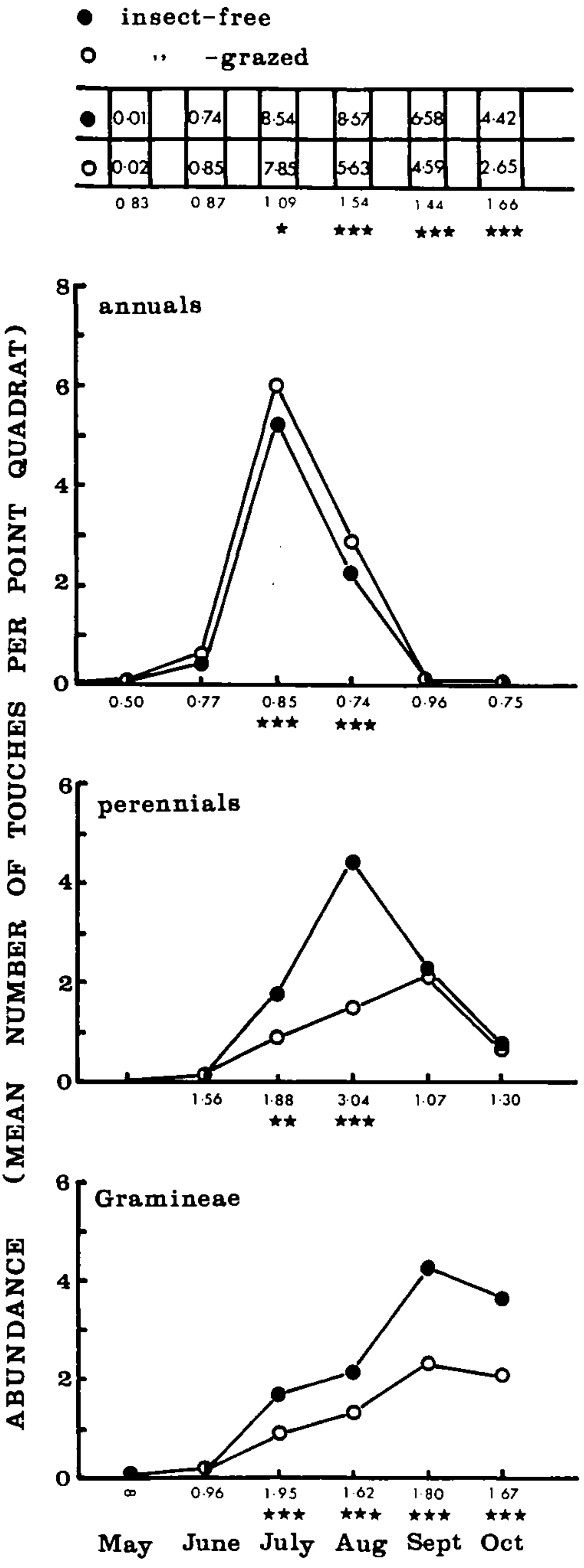
rapidly in the two sites to July in each year and then declined quickly (Year 1) or more gradually (Year 2). The main difference in total abundance between the two sites was during the first year where plant material was always more abundant in the insect-free site. The greatest difference occurred in July during the ruderal phase where abundance values (expressed as the mean number of touches per point quadrat) of 13.7 in the insect-free zone compared to 7.8 in the grazed site (greater by a factor of 1.76, $p<0.001$). Differences in monthly samples were generally non-significant during the second year ($p>0.05$); the exception was in August where there was a greater abundance in the insect-free site (9.9 touches compared to 7.9 touches, $p<0.001$).

These trends in total plant abundance can be explained by the patterns of abundance of the three main vegetation components, the annual and perennial herbs and Gramineae. Fig. 6.7 shows that the greater abundances in Site B in June to August of the first year were contributed chiefly by annual herbs ($p<0.001$ for each month, greater by factors of 1.45, 2.13 and 2.12 respectively) and by perennial herbs in August and September ($p<0.001$ for each month, greater by factors of 1.34 and 1.30 respectively) and by Gramineae in September and especially in October ($p<0.001$ for each month, greater by factors of 1.94 and 4.24). For the second season the two major groups, the perennial herbs and the Gramineae reflect the differences already described for plant cover in Fig. 6.1 (Section 6.5.3). This shows a greater abundance of perennial herbs, from October of the first year to June of the second season, in the insect-grazed site ($p<0.001$ for each monthly comparison) and a continuing greater grass abundance from October of the first year to May of the second year in the insect-free area ($p<0.001$). Apart from a some minor differences, the perennials and grasses had similar abundances for the remainder of the second year.

For Sites E (insect-free) and F (insect-grazed) the first year trends in total plant abundance are shown in Fig. 6.8. These trends show both similar and contrasting features to those found for Sites B and C in the first year. Like these latter areas overall seasonal comparisons of total plant abundance between Sites E and F is highly significant at $p<0.001$ (2 x 6 contingency) with a generally greater abundance in the insect-free site. The greatest difference between Site E and Site F in this ruderal period occurred in August where total abundance (expressed as the mean number of touches per point quadrat) values of 8.67 in the insect-free zone compared to 5.63 in the grazed area (greater by a factor of 1.54, $p<0.001$). The greater abundances in Site E occurred chiefly from July to October with contributions from perennial herbs in July and August ($p<0.001$ for each monthly comparison)

Fig. 6.8 Comparison of abundance of annual and perennial herbs and Gramineae between insect-free and insect-grazed areas during the first year of succession.

Site E=insect-free; Site F=insect-grazed. Total vegetation abundance (expressed as the mean number of touches per point quadrat) is given along the figure top. Values given below the total abundance information and below the abscissae indicate the abundance ratio (insect-free/insect-grazed). Significant differences (from Chi-square or Fisher Exact tests) in monthly samples between grazed and ungrazed areas are marked by asterisks (1=5% level, 2=1% level, 3=0.1% level).



●	0·01	0·74	8·54	8·67	6·58	4·42
○	0·02	0·85	7·85	5·63	4·59	2·65
	0 83	0 87	1 09	1 54	1 44	1 66
			★	★★★	★★★	★★★

Year 1

and Gramineae from July to October ($p<0.001$ for each monthly comparison). Unlike Sites B and C the annual herbs in Sites E and F were less important in terms of their contribution to total plant abundance. These herbs generally showed much lower levels of abundance in Sites E and F (*cf* Fig. 6.8 with Fig. 6.7). In Sites E and F in July and August the abundance of annual herbs was greater in the insect-grazed site ($p<0.001$ for each monthly comparison).

6.5.7(b) Abundance of vegetative and reproductive material

Comparisons of the abundance of vegetative and reproductive material in Sites B and C are given in Figs. 6.9 and 6.10 respectively. Patterns of vegetative abundance in the two sites (Fig. 6.9) closely reflect those for total plant material (Fig. 6.7). As for total plant abundance, the overall seasonal comparison of vegetative abundance between Sites B and C showed significant differences for the first year (2 x 6 contingency table, $p<0.001$) but not for the second year (2 x 6 contingency table, $p>0.05$). Comparisons of individual monthly samples also showed a significantly greater abundance of vegetative material in the insect-free site throughout the first year ($p<0.001$, see table at top of Fig. 6.9) and with fewer differences in the second season. Again the greatest difference occurred in July in the ruderal phase where vegetative abundance (mean number of touches per point quadrat) was 8.0 compared to 4.5 in the grazed area ($p<0.001$, greater by a factor of 1.79).

Contributions to vegetative abundance differences by the major plant groupings in the first year also closely follow the total abundance pattern described in Section 6.5.7(a). In summary, the greater abundance in the insect-free site was due to annual herbs (June-August), perennial herbs (August) and Gramineae (September and October). Similar differences occurred in the early part of the second season with a greater vegetative abundance of perennial herbs from October of the first year to June of the second year in the grazed area and a continuing greater vegetative abundance of Gramineae in May of the second year.

Seasonal comparisons of the abundance of reproductive material in Sites B and C for each year indicate no significant differences ($p>0.05$). Plant reproduction in Sites B and C occurred chiefly from June to August in each year, but particularly in July. The abundance of reproductive material was generally greatest in the insect-free site for the first year and the differences in June and July were significant at $p<0.001$ (see table at top of Fig. 6.10). This was mainly the result of annual herbs although perennial herbs and grasses flowered predominantly in the second year; no significant differences were found for the latter al-

Fig. 6.9 Comparison of abundance of vegetative structures of annual and perennial herbs and Gramineae between insect-free and insect-grazed areas during the first two years of succession.

Site B=insect-free; Site C=insect-grazed. Total abundance of vegetative structures (expressed as the mean number of touches per point quadrat) is given along the figure top. Values given below the total vegetative abundance information and below the abscissae indicate the vegetative abundance ratio (insect-free/insect-grazed). Significant differences (from Chi-square or Fisher Exact tests) in monthly samples between grazed and ungrazed areas are marked by asterisks (1=5% level, 2=1% level, 3=0.1% level).

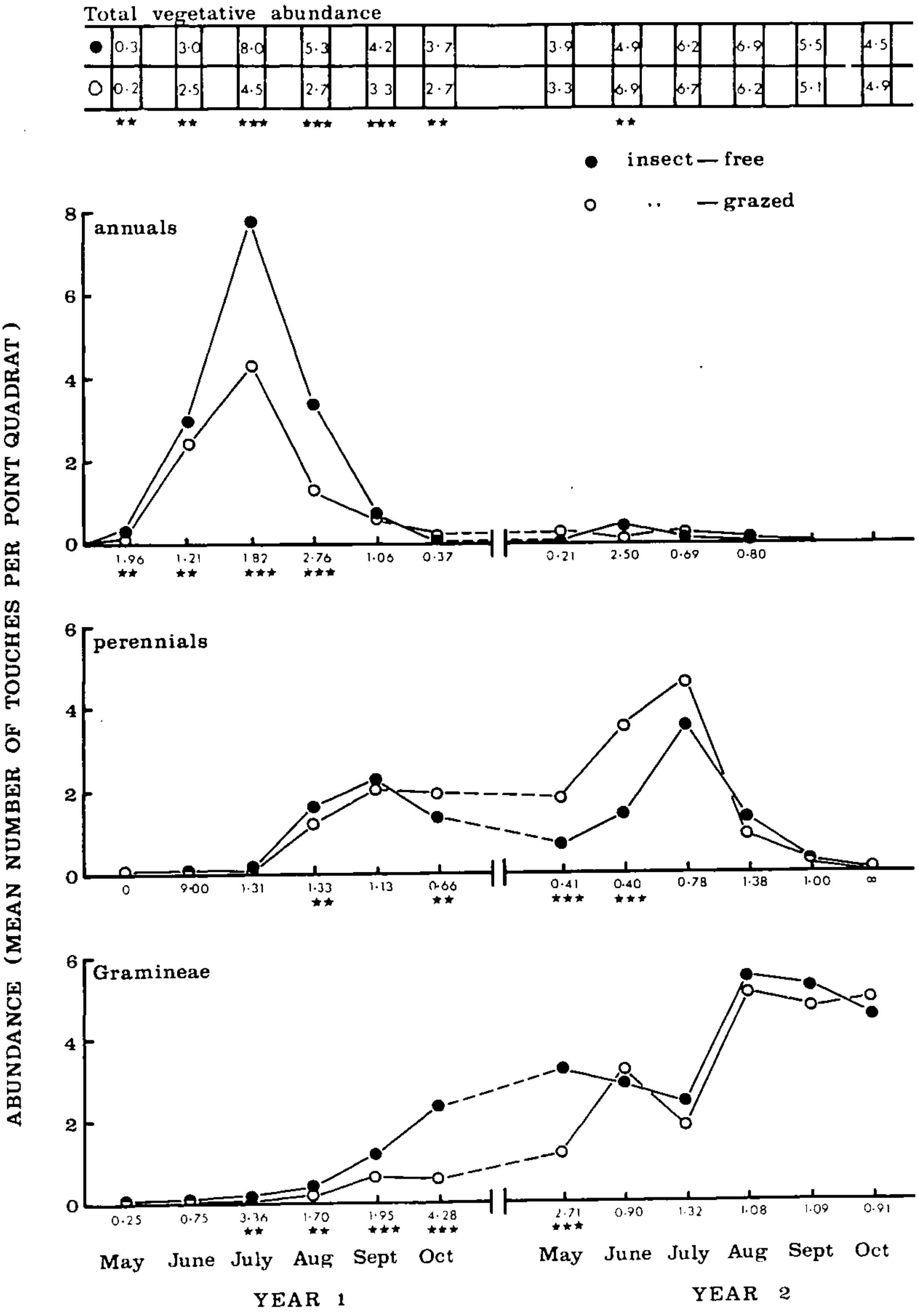
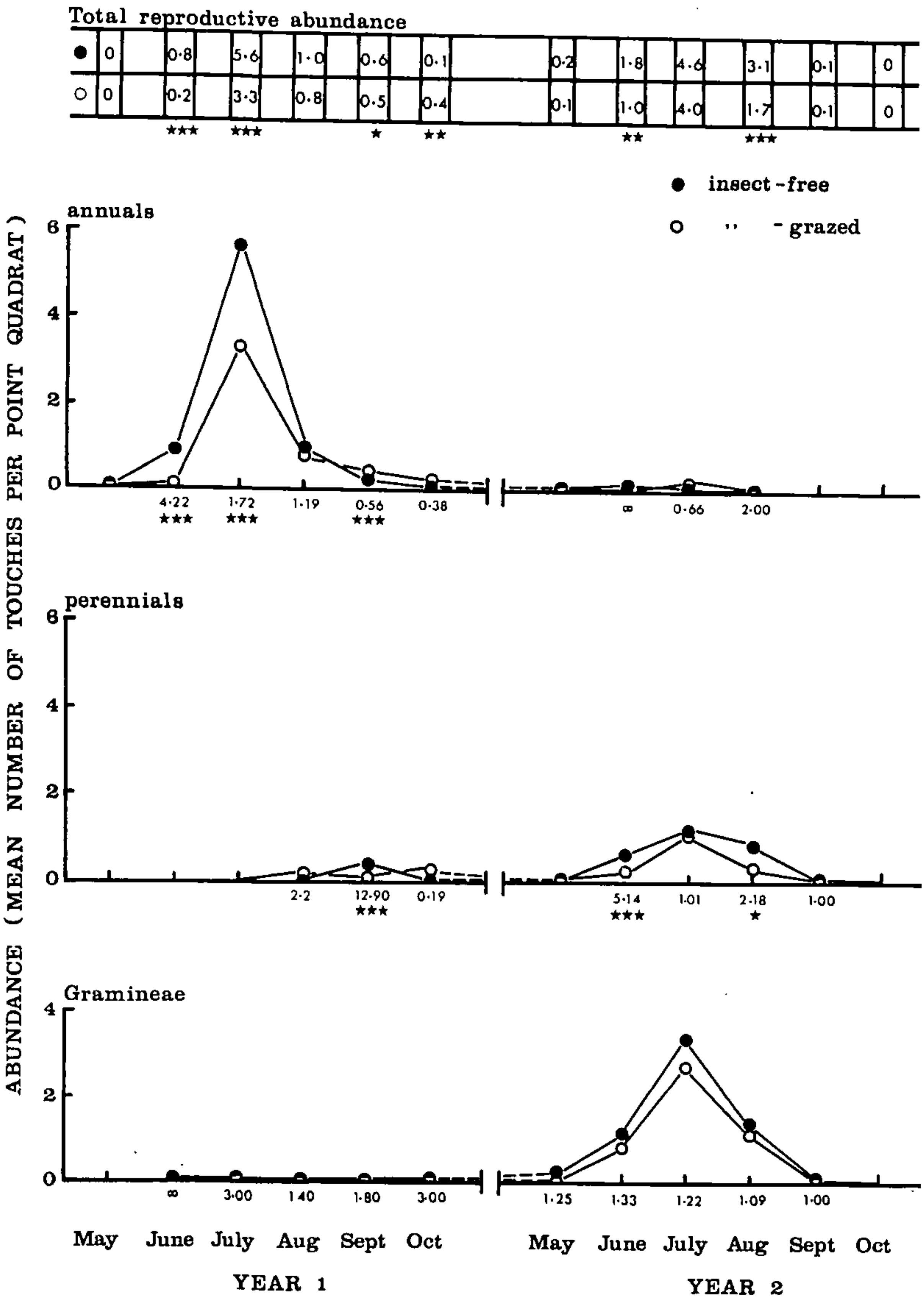

Total vegetative abundance
● 0·3 3·0 8·0 5·3 4·2 3·7 3·9 4·9 6·2 6·9 5·5 4·5
○ 0·2 2·5 4·5 2·7 3 3 2·7 3·3 6·9 6·7 6·2 5·1 4·9
** ** *** *** *** ** **
● insect — free
○ .. — grazed
ABUNDANCE (MEAN NUMBER OF TOUCHES PER POINT QUADRAT)
annuals
8
6
4
2
0
1·96 1·21 1·82 2·76 1·06 0·37 0·21 2·50 0·69 0·80
** ** *** ***
perennials
6
4
2
0
0 9·00 1·31 1·33 1·13 0·66 0·41 0·40 0·78 1·38 1·00 ∞
** ** *** ***
Gramineae
6
4
2
0
0·25 0·75 3·36 1·70 1·95 4·28 2·71 0·90 1·32 1·08 1·09 0·91
** ** *** *** ***
May June July Aug Sept Oct May June July Aug Sept Oct
YEAR 1
YEAR 2

Fig. 6.10 Comparison of abundance of reproductive structures of annual and perennial herbs and Gramineae between insect-free and insect-grazed areas during the first two years of succession.

Site B=insect-free; Site C=insect-grazed. Total abundance of reproductive structures (expressed as the mean number of touches per point quadrat) is given along the figure top. Values given below the total abundance information and below the abscissae indicate the abundance ratio (insect-free/insect-grazed). Significant differences (from Chi-square or Fisher Exact tests) in monthly samples between grazed and ungrazed areas are marked by asterisks (1=5% level, 2=1% level, 3=0.1% level).


Total reproductive abundance
● 0 0·8 5·6 1·0 0·6 0·1 0·2 1·8 4·6 3·1 0·1 0
○ 0 0·2 3·3 0·8 0·5 0·4 0·1 1·0 4·0 1·7 0·1 0
*** *** * ** ** ***
● insect-free
○ " -grazed
ABUNDANCE (MEAN NUMBER OF TOUCHES PER POINT QUADRAT)
annuals
6
4
2
0
4·22 1·72 1·19 0·56 0·38
*** *** ***
∞ 0·66 2·00
perennials
6
4
2
0
2·2 12·90 0·19
***
5·14 1·01 2·18 1·00
*** *
Gramineae
4
2
0
∞ 3·00 1·40 1·80 3·00
1·25 1·33 1·22 1·09 1·00
May June July Aug Sept Oct
YEAR 1
May June July Aug Sept Oct
YEAR 2

though the relatively low levels of perennial herb reproductive abundance in June and August of the second year were significantly greater in the insect-free site (Fig. 6.10).

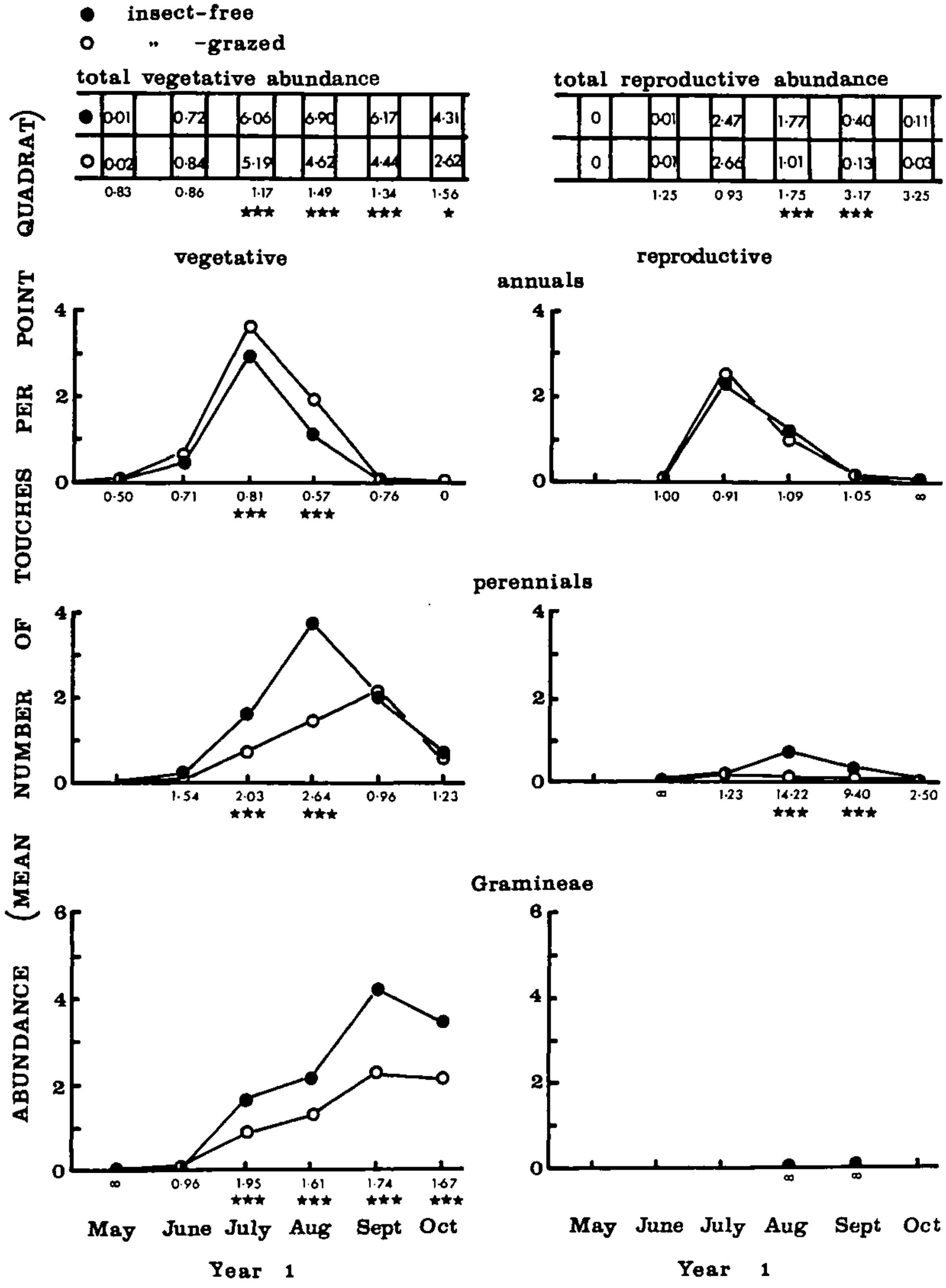
By contrast, in Sites E and F the differences in total plant abundance were mainly of a vegetative nature (Fig. 6.11) and as such reflect the trends for total abundance (Fig. 6.8). Comparisons of vegetative abundance between the insect-free and insect-grazed areas of these Sites indicate an overall greater abundance in the insect-free area ($p<0.001$, 2 x 6 contingency). As for total plant abundance, these differences were for perennial herbs in July and August ($p<0.001$ for each monthly comparison) and for Gramineae from July to October ($p<0.001$ for each monthly comparison). The greater abundance of annual herbs in the grazed area in July and August was significant at $p<0.001$ for each monthly comparison. Abundance of reproductive material in Sites E and F was considerably lower than vegetative abundance. Overall seasonal differences were not significant ($p>0.05$, 2 x 6 contingency). Monthly comparisons of the abundance of reproductive material for each of the main plant groupings was generally not significant; perennial herb reproductive abundance, although at low levels in each site, was significantly greater in Site E in July and August ($p<0.001$ for each monthly comparison).

6.5.7(c) Differences in abundance of dominant plant species

Three species of annual herbs, one perennial herb species and one species of Gramineae were the main contributors to the overall abundance differences in Sites B and C described in Section 6.5.7(a) and (b) and Figs. 6.7, 6.9 and 6.10. These species were *Spergula arvensis*, *Polygonum persicaria* and *Raphanus raphanistrum* (annuals), *Trifolium pratense* (perennial) and *Holcus lanatus* (Gramineae). For the vegetative material the main periods where abundance was greater in the insect-free area (Site B) were, for the first year, June-August (annuals), August (perennials) and September and October and May of the second year (Gramineae) (see Fig. 6.9). In Table 6.14 a comparison is given of the abundance of vegetative structures of these dominant species in Sites B and C. For annual herbs the greatest ratios of vegetative abundance (insect-free/insect-grazed) was for *Spergula* in July (green stem, x 1.50; mature leaf, x 1.88) and August (green stem, x 3.46; mature leaf, x 4.36), for *Polygonum* in July (green stem, x 5.00; mature leaf, x 1.85) and August (green stem, x 2.75; mature leaf, x 1.69) and *Raphanus* in June (mature leaf, x 4.73) and July (green stem, x 3.57; mature leaf, x 8.00). For perennial herbs the greatest ratios were for *Trifolium* in September (petiole, x 1.76; mature leaf, x 2.38). The greatest ratio for *Holcus* was for the first

Fig. 6.11 Comparison of abundance of vegetative and reproductive structures of annual and perennial herbs and Gramineae between insect-free and insect-grazed areas during the first year of succession.

Site E=insect-free; Site F=insect-grazed. Total abundance of vegetative and reproductive structures (expressed as the mean number of touches per point quadrat) is given along the figure top. Values given below the total abundance information and below the abscissae indicate the abundance ratio (insect-free/insect-grazed). Significant differences (from Chi-square or Fisher Exact tests) in monthly samples between grazed and ungrazed areas are marked by asterisks (1=5% level, 2=1% level, 3=0.1% level).



total vegetative abundance

●	0·01	0·72	6·06	6·90	6·17	4·31
○	0·02	0·84	5·19	4·62	4·44	2·62
	0·83	0·86	1·17 ★★★	1·49 ★★★	1·34 ★★★	1·56 ★

total reproductive abundance

●	0	0·01	2·47	1·77	0·40	0·11
○	0	0·01	2·66	1·01	0·13	0·03
		1·25	0 93	1·75 ★★★	3·17 ★★★	3·25

TABLE 6.14: Comparison of the Abundance of Vegetative Structures of Dominant Species in Insect-Free and Insect-Grazed Areas During the First Two Years of Succession

Site B = Insect-free, Site C = Insect-grazed

Values given are for major vegetative structures of dominant species of annual and perennial herbs and Gramineae. Abundance is expressed as the mean number of touches per point quadrat.

The period covered by each plant grouping represents the time where plant abundance was significantly greater in the insect-free site for that group. (see Fig. 6.9).

		Year 1					Year 2
Vegetative Structures		June	July	Aug	Sept	Oct	May
Annual Herbs							
Spergula arvensis							
Green stem	B	0.19	1.47	0.83			
	C	0.28	0.98	0.24			
Mature leaf	B	1.61	4.76	1.57			
	C	1.54	2.52	0.36			
Polygonum persicaria							
Green stem	B	0.02	0.30	0.11			
	C	0.02	0.06	0.04			
Mature leaf	B	0.25	0.37	0.39			
	C	0.14	0.20	0.23			
Raphanus raphanistrum							
Green stem	B	0.04	0.25	0.03			
	C	0.01	0.07	0.02			
Mature leaf	B	0.52	0.32	0.02			
	C	0.11	0.04	0.01			
Perennial Herbs							
Trifolium pratense							
Petiole	B			0.37			
	C			0.21			
Immature leaf	B			0.13			
	C			0.10			
Mature leaf	B			0.62			
	C			0.26			

Continued...

TABLE 6.14: (cont...)

		Year 1					Year 2
		June	July	Aug	Sept	Oct	May
Gramineae							
Holcus lanatus							
Sheath	B				0.10	0.31	0.75
	C				0.09	0.15	0.13
Immature blade	B				0.06	0.13	0.08
	C				0.01	0.06	0.02
Mature blade	B				0.64	1.25	1.52
	C				0.39	0.24	0.78

year in September (mature blade, x 1.64) and October (sheath, x 2.07; immature blade, x 2.17; mature blade, x 5.21) and for the second season in May (sheath, x 5.77; mature blade, x 1.95).

The greater abundance of reproductive material in the first year in Site B and C (see Fig. 6.10) was due predominantly to a higher production of reproductive structures by the three annuals, especially *Spergula* and *Raphanus* (Table 6.15). For *Spergula* the highest ratios (insect-free/insect-grazed) occurred in June (pre-anthesis, x 1.82) and July (mature flowering stem, x 7.66; pre-anthesis, x 4.00; anthesis, x 2.12), for *Polygonum* in July (anthesis, 0.25/0) and for *Raphanus* in June (pre-anthesis, x 15.00; anthesis, x 32.00) and July (mature flowering stem, x 10.00; anthesis, x 4.66; post-anthesis, x 2.5; ripening or ripe fruit, x 7.25).

For Sites E (insect-free) and F (insect-grazed) the greater abundance of plant material in the insect-free site (as described in Sections 6.5.7 (a) and (b) and Figs. 6.8 and 6.11) was due chiefly to differences in abundance of vegetative material of three species of perennial herbs (*Trifolium pratense, Plantago lanceolata* and *Crepis capillaris*) and one species of Gramineae (*Holcus lanatus*). In Table 6.16 a comparison is given of the abundance of main vegetative structures of these dominant species in Site E and F. For perennial herbs the greatest ratios of vegetative abundance (insect-free/insect-grazed) were for *Trifolium pratense* (July-September), *Plantago* (July-September) and *Crepis* (July-August) and *Holcus* (July-October). The greater abundance of annual herbs in the insect-grazed area in July and August was due mainly to two vegetative structures (green stem and mature leaf) of one species, *Spergula arvensis*.

6.5.8 Spatial distribution of plant material

Spatial (or height) profiles were used in Chapter Three to reflect both seasonal and successional changes in the distribution of plant material in the vertical plane in Sites A and D. For the two year study in Site A it was shown that the canopy had a rapid vertical development in the first year but towards the end of the second season there was a trend towards maximal density at ground level. The one year study in Site D resembled a condensed version of the two-year profiles for Site A and indicated a predominance of low growing perennial herbs and grasses.

These trends were also exhibited by Sites B and C (similar to Site A) and Sites E and

TABLE 6.15: Comparison of the Abundance of Reproductive Structures of Dominant Species of Annual Herbs During the Main Reproductive Period in the First Year of Succession

Site B = insect-free; Site C = insect-grazed.

Abundance is expressed as the mean number of touches per point quadrat.

Reproductive Structures Annual Herbs		Year 1	
		June	July
Spergula arvensis			
Immature flowering stem	B	0.07	0.02
	C	0.06	0.01
Mature flowering stem	B	0.01	0.69
	C	0.01	0.09
Pre-anthesis	B	0.20	1.36
	C	0.11	0.34
Anthesis	B	0.01	0.17
	C	0	0.08
Post-anthesis	B	0	0.22
	C	0.01	0.23
Ripening/ripe fruit	B	0	1.05
	C	0	0.83
Polygonum persicaria			
Mature	B	0	0.03
	C	0	0
Pre-anthesis	B	0.01	0.02
	C	0	0
Anthesis	B	0	0.25
	C	0	0
Post-anthesis	B	0	0
	C	0	0
Ripening/ripe fruit	B	0	0.01
	C	0	0

Continued...

TABLE 6.15: (cont...)

		Year 1	
		June	July
Raphanus raphanistrum			
Immature flowering stem	B	0.02	0.01
	C	0	0
Mature flowering stem	B	0.07	0.40
	C	0.01	0.04
Pre-anthesis	B	0.15	0.04
	C	0.01	0.01
Anthesis	B	0.32	0.28
	C	0.01	0.06
Post-anthesis	B	0.03	0.15
	C	0	0.06
Ripening/ripe fruit	B	0	0.87
	C	0	0.12

TABLE 6.16: Comparison of the Abundance of Vegetative Structures of Dominant Species in Insect-Free and Insect-Grazed Areas During the First Year of Succession.

Site E = insect-free: Site F = insect-grazed

Values given are for major vegetative structures of dominant species of perennial herbs and Gramineae. Abundance is expressed as the mean number of touches per point quadrat.

The period covered by each plant grouping represents the time where plant abundance was significantly greater in the insect-free site for that group (see Fig. 6.8).

		Year 1			
Vegetative Structures Perennial Herbs		July	Aug	Sept	Oct
Trifolium pratense					
Green stem	E	0.09	0.12	0.25	
	F	0.01	0.10	0.14	
Petiole	E	0.38	1.02	0.45	
	F	0.06	0.24	0.69	
Immature Leaf	E	0.07	0.13	0.10	
	F	0.04	0.04	0.05	
Mature Leaf	E	0.55	1.71	0.62	
	F	0.08	0.55	0.53	
Plantago lanceolata					
Mature Leaf	E	0.09	0.29	0.30	
	F	0.04	0.07	0.02	
Crepis capillaris					
Mature Leaf	E	0.14	0.24		
	F	0.04	0.01		
Gramineae					
Holcus lanatus					
Sheath	E	0.46	0.28	0.98	
	F	0.09	0.18	0.71	
Mature blade	E	1.11	1.79	3.12	2.68
	F	0.65	1.06	1.59	1.26

F (similar to Site D) and are shown in Figs. 6.12 and 6.13. The spatial profiles between insect-free and insect-grazed areas over the first two years (Sites B and C) or the first year (Sites E and F) do not appear to show any striking differences. Although differences at particular times have been detected between insect-free and insect-grazed areas in cover, the grass/forb ratio, taxonomic composition, plant structure production and plant abundance the relative distribution of plant material in the vertical plane does not appear to have been affected by insect grazing. Numerically important species also had similar spatial profiles in the grazed and ungrazed zones; for Sites B and C these were *Spergula, Polygonum persicaria, Raphanus, Trifolium pratense* and *Holcus* and for Sites E and F these were *T.pratense, Plantago lanceolata, Crepis* and *Holcus*. Of course, the actual amount of material in the vertical plane will be affected by grazing as detected for total abundance in the previous Section (6.5.7).

6.6 DISCUSSION

The impact of herbivores on plant communities may be assessed experimentally using one of three types of manipulation: *(a)* exclusion of herbivores, *(b)* addition of herbivores and *(c)* control of the intensity or periodicity of herbivore activity (see Harper 1969,1977). All three methods have been used in studies of vertebrate grazing. In the few studies of insect grazing the first approach has commonly been employed, using insecticide to remove insects from the vegetation.

A change in vegetation following insecticide application has been observed in several studies. Fox (1958) looked at the effectiveness of organochlorine insecticides (aldrin, chlordane and lindane) in controlling root-feeding insects (four species of wireworm, *Agriotes* spp.). The study was started as a result of deterioration in yield and quality of pasture and haylands, and the effects of pesticide were observed for several years. Treatments by the various insecticides resulted in effective wireworm control, increased the yield and quality of hay and reduced the incidence of weeds. More recently, Henderson & Clements (1977) and Clements (1978) also showed that control of insects from grassland with insecticide improves herbage yield and greatly retards the rate of weed invasion. Cantlon (1969)investigated the effect of excluding insects from the semi-parasitic annual herb *Melampyrum lineare* (cow-wheat), normally attacking roots of jack pine, using aldrin application. The result was to increase cow-wheat seedling density in treated plots (and also to decrease jack pine dry weight). Malone

Fig. 6.12 Spatial profiles for vegetation in insect-free and insect-grazed areas during the first two years of succession.

Site B=insect-free; Site C=insect-grazed.

a. Year 1.
b. Year 2.

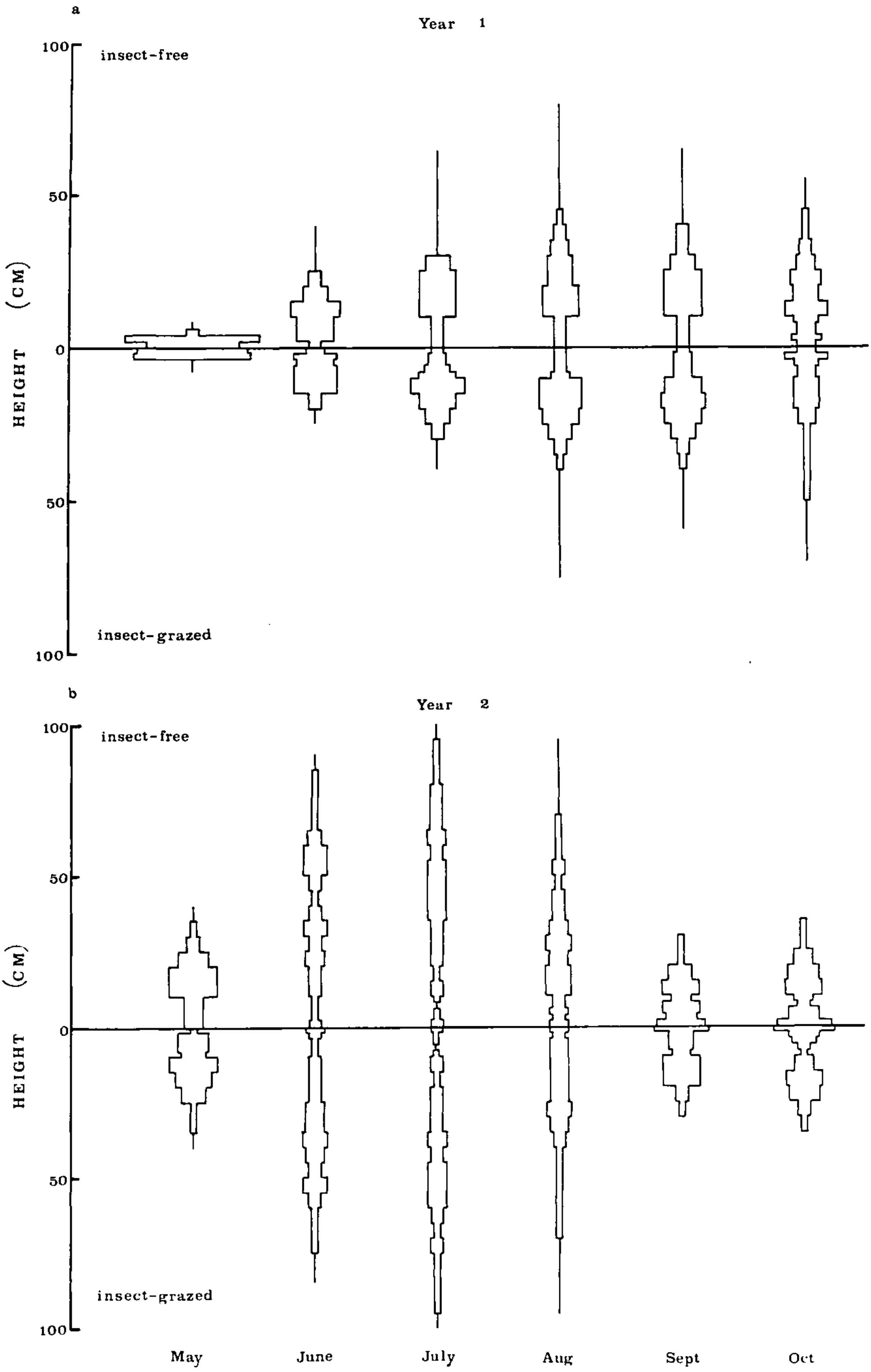
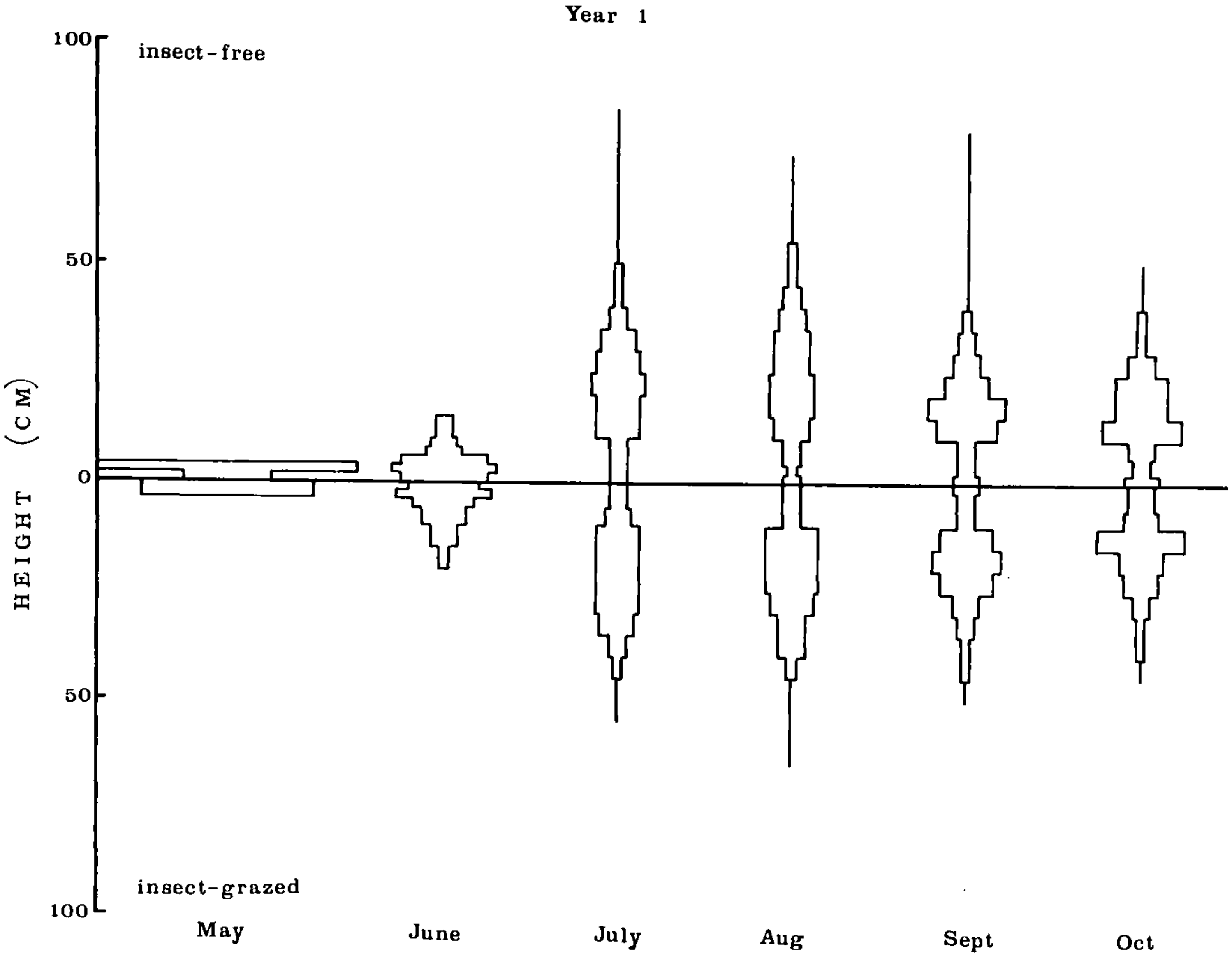

a
Year 1
100
insect-free
50
0
50
insect-grazed
100
HEIGHT (CM)
b
Year 2
100
insect-free
50
0
50
insect-grazed
100
HEIGHT (CM)
May
June
July
Aug
Sept
Oct

Fig. 6.13 Spatial profiles for vegetation in insect-free and insect-grazed areas during the first year of succession.

Site E=insect-free; Site F=insect-grazed.


Year 1
insect-free
insect-grazed
HEIGHT (CM)
100
50
0
50
100
May
June
July
Aug
Sept
Oct

(1969) studied the effects of diazinon contamination in an Old Field and found that in the first year following insecticide treatment the plant species diversity, total plant density and nett primary production was greater in the treated area than in the control. Shure (1971) also found an increase in plant species diversity and plant density after diazinon application in an Old Field system similar to that used by Malone (1969). Later Waloff & Richards (1977) attempted to assess the impact of insect grazing on growth, mortality and natality of broom, *Sarothamnus scoparius*. An area containing broom plants was sprayed with a dimethoate-malathion mixture 1-3 times per year for 11 years. Unsprayed bushes did not attain full growth, their mortality rate was higher and the natality rate was lower compared with sprayed bushes. The seed yield of unsprayed broom over the average 10 year life-span of a bush was also reduced by 75%. Morrow & LaMarche (1978), investigating insect herbivory on *Eucalyptus* trees with the use of insecticidal exclusion, suggest that long-term continuous feeding by insects severely depressed tree growth and productivity over a 25 year period.

As in this present work a major problem in the use of a pesticide in the above studies is the unknown effect(s) of the chemical on the vegetation (*i.e.* as a possible fertilising or phytotoxic effect). Examples of phytostimulation by insecticides on crop plants have been reported in several studies (*e.g.* Allen & Casida 1951; Bourne 1948; Boswell, Clare, Pepper, Taylor, Gilmer & Carter 1955; Brown, Cathey & Lincoln 1962; Long, Anderson, Isa & Kyle 1967). Other studies have suggested that nutrient cycling may be enhanced following application of insecticide. In Malone's (1969) study it was recognised that application of diazinon could have induced the observed changes in the Old Field vegetation by increasing the rate of nutrient cycling. This might occur via pesticide stimulation of the activities of detritivores (Bollen 1961; Heath & Arnold 1962). In addition to these difficulties in making accurate interpretations about the impact of insect grazing the study of an Old Field in New Jersey by Shure (1971) highlighted the problem of phytotoxicity. Although removal of insects resulted in a change in the vegetation (*i.e.* an increase in plant species diversity and plant density) the insecticide used turned out to be differentially toxic to *Convolvulus sepium*. This species was significantly reduced in treated areas and other plant species normally inhibited by *C.sepium* subsequently flourished.

The chemical exclusion method is thus confounded with several problems in its application but, at present, it is the only practical technique available for such studies of insect grazing in plant communities. Indeed the few studies on insect herbivores and plant communities demands such methods (see also Whittaker 1979 and Crawley 1983). It is encouraging that the tests undertaken in the present work showed that the insecticide was having no marked effect on plant biomass.

The detailed description of the ecological characteristics of the early sucessional insect herbivore fauna in Chapter Four showed how rapidly the insects colonised the habitat and subsequently increased in numbers and biomass. The major study of Sites B and C showed that the majority of these herbivores in the first year of succession had essentially *r*-strategy life-histories (the dominant species were extreme *r*-types) and were chiefly generalists and Grade 3 specialists. Also, because the herbivore load is probably greater in the first, compared to subsequent years of the succession, and because of the high turnover rate of plant species during this period, it was predicted that the very early stages of succession might be more affected (Odum's (1969) ideas on the effect of a stress, such as grazing, on immature or early successional habitats fit in here). Events described in this present chapter support this viewpoint. Results from the two year study in Sites B and C, and from the single year study in Sites E and F, indicate that insect herbivores may have a profound effect on the early successional plant community. The overall outcome of these exclusion experiments was to apparently accelerate the rate of succession from a chiefly ruderal and annual herb vegetation to a predominantly *Holcus lanatus* grassland habitat; or, conversely, the impact of insect grazing was to slow down the rate of succession.

Consideration of plant cover in Sites B and C showed the early domination and subsequent decline of annual herbs in the first year and gradual establishment of perennial herbs and grasses with the perennial herbs declining mid-way through the second year. The cover comparisons in Section 6.5.3 between Sites B and C suggest that insect grazing was influencing the development of the plant community at the very early stages of the succession. This was indicated by the considerably greater coverage of annual herbs in the insect-free site for the main part of the first year, but especially at the time of the first sample in May (successional age = 5.6 weeks) where cover was 18.88% compared to 8.88% in the grazed area. These very early differences were at a time when annual herb seedlings were more numerous in the insect-free area (6.66% cover compared to 1.66% cover). Perennial herbs also showed a more rapid establishment in the insect-free site where the cover was significantly greater during the main establishment phase from July to September of the first year. Finally, the insect-free site was remarkable with regard to the higher rate of grass establishment during the first year and this difference was carried over into May of the second season. From all appearances then, the vegetation development was more advanced (in terms of succession) in the absence of herbivore grazing pressure.

The other few studies, or observations, on insect grazing relationships with plant community dynamics indicate that herbivory may affect secondary succession. The study of Bews (1920) suggests that seed destruction of dominant trees by insects in the coastal forest of Natal might alter succession by the ecological release of previously suppressed tree species (see also Leonard 1974). In the study of root-feeding *Agriotes* spp., in pasture in Nova Scotia, Fox (1958) concluded *"...that since certain soil inhabiting insects are apparently capable of causing considerable floristic changes, they should not be neglected as ecological factors in grassland succession."* More recently, Janzen (1970) and Whelan & Main (1979) have suggested that insect attack on seeds and seedlings, the most vulnerable stages in the life-history of a plant (see Harper 1977), may influence succession. Other studies have described secondary effects of insect herbivores. These are shown by a 'telescoped succession' around termitaria (Glover, Trump & Wateridge 1964). More significantly, Jonkman (1978) reports that dead nests of the leaf-cutting ant *Atta vollenweideri* in Paraguayan pastures gives rise to so-called 'wood-nuclei' and suggests that the nests may play an important role as accelerators of the succession into woodland of the pastures in which they occur.

At the time of the first sample in May the difference in seedling cover of annual herbs may have been attributed, at least in part, to grazing by the chrysomelid *Cassida vitata* on *Spergula arvensis* seedlings in Site C (most of the seedlings at this time were *Spergula*), even though herbivore density was low at this time (<1 individual/m^2). Without the constraint of grazing the annual herb community in Site B was able to develop and flourish. The later establishment of perennial herbs in Site C may have been due to grazing pressure by aphids and Coleoptera. Differences in grass establishment between grazed and ungrazed areas coincided with the build up in numbers of grass-feeding Homoptera, mainly cicadellid leafhoppers. The drop in perennial herb cover in the insect-free site in October of the first year may reflect the superior competitive ability of the increasingly dominant grasses in the absence of insect-grazing. In the grazed area perennial herb cover did not decline until mid-summer of the second season by which time *Holcus* had attained a high level of cover similar to the insect-free site.

Removal of insects from vegetation in Site E provided similar consequences to those found for Site B with an earlier establishment of perennial herbs and Gramineae. Yet again the greatest differences in grass cover between the grazed and insect-free areas occurred at the same time as the rapid build up in leafhopper numbers.

Colonisation and extinction rates of plant species in the insect-free (Site B) and insect-grazed (Site C) areas (Section 6.5.5) showed that there was a trend for new plant species to appear more rapidly in the insect-free area during the main ruderal period (up to July). This earlier colonisation resulted in a greater plant species richness and taxonomic diversity (as measured by α). From this, the apparent effect of insect grazing at this very early stage in the succession may also be to retard the rate of recruitment of new plant species into the community. Mechanisms that might operate to produce this result could be the direct mortality of seedlings by the new species or altered competition due to preferential grazing of seedlings by the new colonisers, or both. Further work needs to be carried out here, since point quadrat data alone are not adequate. Seedling mortality resulting from insect herbivores is believed to play an important role in the structuring of plant communities, although the majority of evidence comes from forest habitats (*e.g.* Janzen 1970; Whelan & Main 1979). Evidence from observations in the biological control of weeds indicates that even modest levels of insect grazing in conjunction with an additional stress, especially competition, may seriously affect a plant's ability to successfully compete with other species. Holloway & Huffaker (1952) and Huffaker (1962) suggest that grazing by the chrysomelid beetle *Chrysolina quadrigemina* on the weed *Hypericum perforatum* (St. John's Wort), at the same time as interspecific competition with range plants, successfully reduced the weed population and prevented its establishment into rangeland. Weldon, Blackburn & Durdan (1973) also observed that insect control of a weed is enhanced by plant competition; the effect of the chrysomelid *Agasicles hygrophila* for the control of alligatorweed (*Alternanthera philoxeroides* is increased when the weed is in interspecific competition with smartweed (*Polygonum* sp.) and water primrose (*Jussiaea* sp.). Chater (1931) found that seedling damage to gorse (*Ulex europaeus*) by insects often results in death to the plant when in competition with grasses. More recent and elaborate studies by Whittaker and his co-workers have shown that grazing by the chrysomelid *Gastrophysa viridula* on *Rumex crispus* affects the plant more severely when it is growing under conditions of interspecific competition with *R.obtusifolius* (Bentley & Whittaker 1979; Whittaker 1982; and see also Bentley, Whittaker & Malloch 1980). Altered plant competition is also implicit in a few other studies of insect grazing (Fox 1958; Burdon & Chilvers 1974; Clements 1978; Springett 1978). Burdon & Chilvers (1974) believe that it is inevitable that insect grazing in conjunction with intense intra- and interspecific plant competition in Australian *Eucalyptus* forest will alter the competitive balance within the plant community.

Plant species appeared more gradually in the grazed area (Site C) during the first year and by the end of the season similar numbers of species had appeared in the two sites (insect-free, 30spp.: insect-grazed, 36 spp.). One important consequence of the earlier establishment of the Gramineae in the insect-free site was that it seriously restricted the availability of competition-free germination microsites (see Harper 1977 and Crawley 1983) and may partly explain the lower total species accumulation in the insect-free site.

Consideration of plant structure production in insect-free and insect-grazed areas (Section 6.5.6) suggests that insect herbivores may greatly alter the architecture (*i.e.* as measured by the number of different structure types present) of the early successional habitat during the first year of succession. Exclusion of insects from Sites B and E resulted in a more architecturally diverse/complex vegetation for the main part of the growing season. In Site B this increase in architecture was due to plant species either appearing early and producing structures or else species appearing at the same time as in the grazed area but actually producing structures (and especially reproductive structures) earlier.

Removal of insect herbivore pressure also increased plant abundance (regarded in this context as equivalent to biomass) in the first year in Sites B and E. Trends were essentially similar to those described for plant cover differences between the insect-free and insect-grazed areas. These results suggest that removal or reduction of insect grazing pressure from plant communities may increase standing crop biomass and provides additional evidence to support findings by Fox (1958), Henderson & Clements (1977), Clements (1978) and Waloff & Richards (1977). The lower abundance of reproductive material in the Site C insect-grazed area would suggest that insect herbivores may affect the future composition of the seed bank, and therefore potential seedling success, by their impact on parent plants. Bentley *et al* (1980) have suggested that the production of smaller seedlings by *Rumex crispus* and *R.obtusifolius* due to grazing by *Gastrophysa viridula* on parent plants could lead to reduced competitive abilities of seedlings arising from such small seeds. Insect herbivores may thus affect the future taxonomic composition and relative abundances of constituent species within the community.

Evidence provided in previous chapters, as well as in other works (Southwood *et al* 1979; Brown & Southwood 1983), have shown that the ruderal-early stages of this particular secondary succession represent a period of rapid species turnover of plants and phytophagous insects and where herbivore pressure is high. In Chapter One, Section 1.2.1, the various theories of plant succession were described and it was mentioned that this study allowed for the opportunity to test the three models of succession proposed by Connell & Slatyer (1977). There I suggested that if insect herbivores preferentially attacked early successional species rather than later ones then there could be three possible outcomes from the three models - decelerated succession ('facilitation' model), no effect ('tolerance' model) or accelerated succession ('inhibition' model). In the developing early successional habitat, as described in Chapters Three and Four, the potential herbivore load was highest on both annual and perennial herbs, although it was suggested that the annuals were probably fed on preferentially since they were more abundant for the main part of the growing season. From this one might expect that insect grazing would accelerate plant succession (as predicted by the 'inhibition' model) as damage and mortality to ruderals would open up gaps in the vegetation for later species (*i.e.* perennial herbs and grasses) to invade and become established. However, Chapters Four and Five showed that these later species are likely to be colonised by insect herbivores as soon as they appear on the site (just like the ruderals). Thus, the consequences appear to be a retardation in the establishment of each of the major plant groupings, the predominantly ruderal annual herbs, the perennial herbs and the Gramineae, and the overall impact is to decelerate the succession. However, there is no direct evidence from this study that insect herbivores might slow down the rate of succession by lowering the 'reaction' rate as would be the expected outcome from the 'facilitation' model of Connell & Slatyer (1977); the results, in fact, do not lend support to any of the models.

To conclude then, results from this study indicate that insect herbivores may have a considerable impact on the development and structure of early successional plant communities, and especially in the very early stages. This work provides additional evidence to support the view from other studies that insect herbivores may play a major role in the structure and diversity of plant communities (Fox 1958; Gillett 1962; Ehrlich & Breedlove 1964; Bullock 1967; Breedlove & Ehrlich 1968; Ehrlich 1970; Janzen 1970; Ehrlich, Breedlove, Brussard & Sharp 1972; Breedlove & Ehrlich 1972; Brown 1982; and see reviews by Harper 1977, Whittaker 1979 and Crawley 1983).

This study has demonstrated that insect grazing may lower seedling density at the beginning of the succession, reduce the establishment rate of plant species (and thus lower the taxonomic diversity), extend the period of herb domination over Gramineae (as expressed by the grass/forb ratio and Sorenson's Index of Similarity) and cause a reduction in plant cover. Additionally, in the absence of herbivory there may be an overall increase in the number of reproductive structures and their production may be advanced. The biomass (as measured by abundance) and architecture of the vegetation was much greater in insect-free areas during the first year of succession. By causing a reduction in the rate of succession insect herbivores in the early successional habitat show a remarkably similar impact to vertebrate herbivores on later successional plant communities (see reviews by Ellison 1960 and Harper 1977). As Brown (1982) states *"The effects of insects on these later stages must be the next question to pose"*.

SUMMARY

CHAPTER ONE

1. This Chapter contains an introduction to the thesis and includes reviews of plant succession and herbivory.

CHAPTER TWO

2. This Chapter describes the general materials and methods used in the study. Of special interest is the use of the SIR database system for the management and analysis of bulky data files.

CHAPTER THREE

3. This Chapter describes the ecological characteristics of the early successional plant community. Descriptions are made of vegetational trends during the first two years of succession in the Site A Young Field.

4. Plant cover increased rapidly after abandonment in May of the first year. There was also a rapid colonisation of plant species during this time. Annual (chiefly ruderal) herbs were the dominant cover and species contributors during the first year. By the end of the first season perennial herbs and Gramineae had become established and represented the early successional community proper. By the end of the second year the plant community had become grass-dominated and had a characteristic low species richness. Successional change during the two years was demonstrated by the use of Sorensen's Index of Similarity and the grass/forb ratio. Seasonal changes in structural attributes were described in terms of spatial profiles (and spatial α) and community architecture. Plant architecture showed dramatic changes with a rapid rise to August followed by a similarly rapid decline to the end of the season in each year.

5. A one-year study was also made of a Young Field (Site D) that had been created on an area that had previously been a long-standing meadow. The Site D plant community showed a more rapid succession compared to Site A. This was evidently due to a reduced seed bank in Site D where there were lower numbers of annual herb species and reflected its previous

history of land use. The frequent exposure of the Site A arable area, through annual cultivation, produced a richer seed bank and, consequently, a more distinct ruderal community.

6. The characteristics of the early successional plant community are discussed in relation to other studies and current ecological theory.

CHAPTER FOUR

7. This Chapter describes the ecological characteristics of the early successional insect and spider fauna in Site A. Descriptions are made of predator, herbivore and omnivore guilds in terms of taxonomic composition, abundance and biomass.

8. Insect herbivores colonised extremely rapidly during the first year; species richness reached a maximum of 55 species in August and then declined. In the second season richness ranged from 34 to 47 species. Hemiptera and Coleoptera were the main contributors to species richness. Seasonal and successional changes in species composition, abundance and biomass of the herbivore guild occurred over the two years. Changes in β-diversity were much lower than for accompanying vegetational changes.

9. Life-history strategies of the herbivore community were described in terms of (1) the herbivore load on the four major plant groupings, (2) the degree of specialisation on host plants, (3) feeding strategies, (4) overwintering strategies and (5) voltinism. In the first year herbivore load (*i.e.* abundance and biomass) was greatest on annual herbs followed by perennial herbs and then Gramineae. In the second year load was greatest on perennial herbs followed by annuals; populations of grass-feeders were low at this time. The most important herbivores in terms of abundance and biomass were Heteroptera (Miridae), Homoptera (Aphididae, Cicadellidae and Delphacidae) and Coleoptera (Chrysomelidae and Curculionidae). Grade 3 specialists were the most important of the three grades of specialists and the generalists during the first year; generalists were also important. These two categories were less significant in the second year, whereas Grade 1 and 2 specialists had increased in importance during this time. Overwintering as an adult was clearly the dominant overwintering strategy for early successional herbivores and enables these species to be available for immigration and oviposition in the following spring. Different overwintering strategies were employed by dif-

ferent insect groups though the Heteroptera, Thysanoptera and Coleoptera mainly overwinter as adults, Delphacidae as nymphs and Cicadellidae in the egg stage. The majority of species were univoltine.

10. The herbivore fauna in Site D showed similar trends to those found for Site A. In Site D, however, the dominant insects (in terms of abundance and biomass) were grass-feeders and these were Grade 3 specialists; generalism was not a significant strategy in Site D. Overwintering and voltinism followed the general pattern set in Site A.

11. The various trends exhibited by the early successional insect fauna are discussed in relation to current theory. The trend for a less specialised type of herbivore (and with *r*-type characteristics) to dominate the very early stages of the succession follows current theory on the life-history strategies of insect herbivores along the *r*-*K* continuum. It is also argued that an early successional habitat, typified by Site A, would be more affected early on in the succession simply by nature of the greater herbivore load in the early stages.

CHAPTER FIVE

12. This Chapter provides an analysis and discussion of insect-plant relationships in the early successional habitat. The whole herbivore and plant community is first analysed in terms of colonisation or establishment rates. The structure of the insect community is then related to the various vegetational parameters measured. Further analysis involves the breakdown of the herbivore community into herb-feeders and grass-feeders and an analysis of their host-plant relationships.

13. Correlations tested did not allow for clearcut interpretations of insect-plant relationships because of high plant-plant parameter correlates. However, it appeared that the colonisation process (for insect herbivores) in the first year was strongly related to plant community achitecture, whereas in the second season it was plant abundance (*i.e.* biomass) that was important (plant abundance, however, could be interpretated either as a biomass or architecture effect, or both). It was concluded that it is not possible to test the relative merits of plant species richness and plant architecture, for insect colonisation, since they are both so intimately related. However, the analyses in this study suggest that plant structural diversity is

important in providing a templet for insect colonisation. During the first year of succession the effect of the architectural component is probably greater than the spatial or size attributes. The influence of spatial diversity most likely becomes more important after the first year.

CHAPTER SIX

14. This Chapter described a parallel study that looked at the effects of insect herbivores on early successional plant communities. Two study sites were established, one in 1980 (containing Sites B and C) and one in 1981 (containing Sites E and F). Insects were chemically excluded from Site B (over 2 years) and Site E (over 1 year) and the effects on the vegetation observed by comparison with unrestricted grazing in Sites C and F.

15. The overall outcome of the exclusion experiments appeared to be an acceleration of the rate of succession from a chiefly ruderal and annual herb vegetation to a predominantly *Holcus lanatus* grassland habitat; or, conversely, the impact of insect grazing was to slow down the rate of succession. The various mechanisms that might be operating to produce this result are described. The results do not lend support to any of the models proposed by Connell & Slatyer (1977).

16. It was concluded that insect herbivores may have a considerable impact on the development and structure of early successional plant communities, especially in the very early stages. The study demonstrated that insect grazing may lower seedling density at the beginning of the succession, reduce the establishment rate of plant species (and thus lower the taxonomic diversity), extend the period of herb domination over Gramineae and cause a reduction in plant cover. In addition, in the absence of herbivory there may be an increase in the number of reproductive structures and their production may be advanced. The biomass and architecture of the vegetation was much greater in the insect-free area during the first year of succession. The work in this study provides additional evidence to support the view from other studies that insect herbivores may play a major role in the structure and diversity of plant communities.

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APPENDICES

APPENDIX 1: INITIAL SCHEMA DEFINITION COMMAND SET.

```
RUN NAME        INITIAL SCHEMA DEFINITION
TASK NAME       CASE DEFINITION COMMANDS
CASE ID       SITE
RECTYPE COL     3
N OF CASES     10
RECS PER CASE  20000
MAX REC TYPES   4
MAX REC COUNT   150000
DOCUMENT        THE SCHEMA DEFINITION COMMANDS COMPLETELY DESCRIBE
               THIS SIR DATA FILE. THE COMMANDS ARE SEPARATED INTO
               3 GROUPS:-
               (1) CASE DEFINITION COMMANDS SUPPLY INFO RE- THE
               NATURE OF THE DATA FILE AS WELL AS GENERAL INFO THAT
               APPLIES TO EACH CASE IN THE FILE. IN THIS STUDY THERE
               ARE 6 CASES (=SITES).
               (2) RECORD DEFINITION COMMANDS DESCRIBE THE VARIOUS
               RECORD TYPES IN THE FILE, ONE SET OF COMMANDS FOR
               EACH RECORD TYPE. IN THIS STUDY THERE IS ONLY 1 RECORD
               TYPE.
               (3) SCHEMA LISTING COMMANDS PRODUCE LISTINGS OF THE
              SCHEMA DEFINITION TO PROVIDE THE USER WITH A PERMAN-
              ENT RECORD OF THE COMPOSITION OF THE DATA FILE.

              CASE DEFINITION COMMANDS WILL NOW BE DESCRIBED:-
              FILE NAME      ALWAYS USED WHEN CREATING A NEW SIR
                           FILE AND ALWAYS HAS SCHEMA DEFINITION
                           COMMANDS.
              CASE ID        IDENTIFIES THE VARIABLE THAT IS USED
                           AS THE CASE IDENTIFIER AND MUST APPEAR
                          IN THE VARIABLE LIST (=SITE). THE CASE ID IS
                          REFERRED TO AS A,B,C,D,E, OR F DEPENDING
                          ON THE SITE UNDER INVESTIGATION.
              RECTYPE COL     COLUMN LOCATION (FOR SIR) OF RECORD
                            TYPE NUMBER ON DATA INPUT RECORD (=3)
              N OF CASES      UPPER LIMIT (FOR SIR) ON NO. OF CASES
                           THAT WILL RESIDE IN A DATA FILE (=10
                             ,MORE THAN THE SIX CASES USED, TO
                            ALLOW FOR THE ESTABLISHMENT OF
                           ADDITIONAL STUDY SITES).
              RECS PER CASE   TELLS SIR THE AVERAGE NO. OF RECORDS
                            THAT ARE EXPECTED FOR EACH CASE.
              MAX REC TYPES   THIS SPECIFIES THE MAX. NO. OF DIFF-
                            ERENT RECORD TYPES THAT MAY BE USED
                            IN THIS STUDY (=4).
              MAX REC COUNT   AN ABSOLUTE UPPER LIMIT ON THE NO. OF
                            DATA RECORDS (OF THE GIVEN TYPE) THAT
                            WILL APPEAR IN ANY CASE.
              COMMON LIST   THESE ARE THE VARIABLES THAT FORM THE
              (OR C.I.R.    COMMON INFORMATION RECORD(C.I.R.).
              VARIABLES)     THE C.I.R. IS A SINGLE DATA RECORD THAT
                           IS ASSOCIATED WITH AN ENTIRE CASE.
                           THESE COMMON LIST VARIABLES MAY BE REFER-
                           ENCED AND USED IN COMPUTATIONS DURING
                           DATA INPUT, AS WELL AS DATA RETTRIEVAL.
                           THE VARIABLES ARE ALWAYS AVAILABLE RE-
                           GARDLESS OF THE RECORD TYPE BEING INPUT
                          OR RETRIEVED. IN THIS STUDY THE COMMON LIST
                          HAS ONLY 1 VARIABLE, WHICH IS ALSO THE
                          CASE ID (=SITE).      NOTE THAT THE
                          COMMON LIST COMMAND HAS NOT BEEN INCLUDED
                          IN THE CASE DEFINITION COMMAND SET; THIS IS
                          BECAUSE THE CASE ID COMMAND REGOGNISES THAT
                          SITE IS THE ONLY COMMON VARIABLE.
```

```
TASK NAME       RECORD 1 ( BOTANY ) SCHEMA DEFINITION.
RECORD SCHEMA   1 BOTANY
MAX REC COUNT   150000
SORT RECORDS    SPECIES,STRUCTUR,HEIGHT,SUBPLOT,PIN,TOUCHES,DDATE
DOCUMENT          THIS IS A DESCRIPTION OF THE RECORD TYPE USED IN THIS
                STUDY. FOR THE PARTICULAR CASE IN QUESTION(A,B,OR C)
                AT A PARTICULAR SAMPLING DATE, 30 PINS ARE PLACED AT
                RANDOM IN EACH SUB-PLOT AND A RECORD MADE OF THE VEGET-
                ATION TOUCHING EACH PIN WHERE 1 OR MORE TOUCHES OCCURRED
                . FOR EACH SUB-PLOT A RECORD IS MADE OF THE PIN NUMBER
                (1-30) INVOLVED IN A TOUCH, WHAT PLANT SPECIES TOUCHED
                THE PIN, THE PARTICULAR PLANT STRUCTURE INVOLVED, THE
                HEIGHT DIVISION ON THE PIN WHERE THE TOUCH OCCURRED,
                AND THE NUMBER OF TOUCHES.

                THE DATA INPUT ONLY CONTAINS INFO ON PINS WHERE TOUCHES
                OCCURRED. WHERE A PIN LOCATED BARE GROUND THERE IS NO
                DATA INPUT.

               EACH RECORD IN THE DATA BASE IS UNIQUELY IDENTIFIED BY A
              RECORD KEY. THIS KEY IS COMPOSED OF THE CASE ID (A,B OR C),
              THE RECORD TYPE NUMBER AND 1 OR MORE ADDITIONAL IDENTIFIERS
            CALLED SORT ID VALUES. THE SORT RECORDS COMMAND DEFINES THE
            VARIABLES THAT ARE USED AS RECORD IDENTIFIERS WITHIN A GIVEN
            RECORD TYPE. SORT ID VALUES ALSO ENABLE HIERARCHICAL
            RELATIONSHIPS TO BECOME ESTABLISHED AMONG THE RECORD TYPES.
            THE SORT ID VARIABLES MUST BE USED FOR RECORD TYPES HAVING
            MORE THAN 1 RECORD PER CASE(AS IN THIS STUDY) AND MUST APPEAR
            IN THE VARIABLE LIST OF THE GIVEN RECORD TYPE (I.E. THEY ARE RECORD
            VARIABLES); THEY CANNOT BE 'COMMON VARIABLES'
            THE HIERARCHY ESTABLISHED FOR THE NO. OF TOUCHES RECORDS IS THUS:-
                -THE SITE                (CASE ID)
                -THE RECORD TYPE NO.     (1)
                -THE SAMPLING DATE       (THE FIRST SORT ID)
                -THE PLANT SPECIES NO.   (THE SECOND SORT ID)
                -THE PLANT STRUCTURE NO  (THE THIRD SORT ID)
                -THE HEIGHT DIVISION     (THE FOURTH SORT ID)
                -THE SUBPLOT NO.         (THE FIFTH SORT ID)
                -THE PIN NO.             (THE SIXTH SORT ID)
                -THE NO. OF TOUCHES      (THE SEVENTH SORT ID)

                THERE ARE THEREFORE 8 VARIABLES IN THE VARIABLE LIST
               :- SITE,DDATE,SPECIES,STRUCTUR,HEIGHT,SUBPLOT,PIN,TOUCHES

                THE VARIABLE LIST BELOW TOGETHER WITH THE INPUT
                FORMAT SPECIFICATION COMPLETELY DESCRIBES THE DATA
                RECORD FOR THIS RECORD TYPE.
                THE INPUT FORMAT DESCRIBES THE DATA FIELDS ON THE INPUT
                LINES FOR THIS RECORD TYPE.
VARIABLE LIST   SITE,DDATE,SUBPLOT,PIN,SPECIES,STRUCTUR,HEIGHT,TOUCHES
INPUT FORMAT     (A1, 3X, A8, 6I3)
DATE VAR LIST    DDATE(DDIMMIYY)
VAR RANGES        DDATE('01/05/80','10/11/80')/SUBPLOT(1,45)/PIN(1,30)/
                SPECIES(1,75)/STRUCTUR(1,30)/HEIGHT(1,35)/TOUCHES(1,10)
VAR LABELS        SITE,SITE/
                DDATE,SAMPLING DATE/
                SUBPLOT,SUBPLOT NO./
                PIN,PIN NO./
                SPECIES,SPECIES NO./
                STRUCTUR,STRUCTURE NO./
                HEIGHT,HEIGHT LEVEL/
                TOUCHES,NO. OF TOUCHES/
FINISH
```

APPENDIX 2: LISTING OF MAJOR PROGRAMS.

PROG1

```
RUN NAME        PROG1: TOTAL VEG.COVER(HERBS+GRASSES): PINS/SUBPLOT/DATE.
RETRIEVAL
COMMENT            THIS PROGRAM IS DESIGNED TO PROVIDE A COUNT OF THE NO. OF
                PINS TOUCHED IN EACH SUBPLOT AND THEN PRODUCE A TOTAL FOR
                SITE.
                A BARE GROUND COUNT IS COMPUTED FROM BG=TOTAL PINS USED
                -TOTAL PINS TOUCHED.
                THE PERCENTAGE COVER FOR THE SITE IS CALCULATED FROM
               TOTC=(TOTS/NO. OF PINS USED)*100.

                'FOR EACH CASE' SPECIFIES THE SITE.
                'FOR EACH REC' SPECIFIES THE RECORD TYPE.
                'SELECT REC IF' SELECTS SPECIFIED RECORDS.
                'MOVE VAR LIST' MOVES THE SPECIFIED RECORD VARIABLES INTO
                THE 'SUMMARY FILE'.
                THIS IS THE RETRIEVAL PROCEDURE.

                THE REPORT PROCEDURE FOLLOWS:———
                THE SUMMARY RECORDS ARE SORTED IN ORDER OF APPEARANCE
                IN THE 'SORT COMMAND'. FOR EACH SUBPLOT A TOTAL PIN
                COUNT IS PRODUCED.
                AT THE END OF THE REPORT SECTION THE TOTAL NO. OF
                PINS TOUCHED FOR THE SITE IS GIVEN.
                TOTS=0 ACCUMULATES THE TOTAL PIN COUNT FOR THE  SITE
                AS RECORDS ARE READ.
                TS=0 ACCUMULATES INDIVIDUAL SUBPLOT PIN COUNTS
                AS RECORDS ARE READ.
                BG=0 ACCUMULATES THE BARE GROUND COUNT FOR THE SITE.
                TOTC=0 ACCUMULATES THE  COVER FOR THE SITE.
                THE OUTPUT FOR THE REPORT PROCEDURE IS SENT TO A LOCAL
                SIR FILE.

FOR EACH CASE      LIST='A'
FOR EACH REC       BOTANY
SELECT REC IF   ((DDATE LT CDATE('01/01/81','DDIMMIYY'))
  AND NOT(STRUCTUR=4 OR 6 OR 9 OR 12 OR 17 OR 19 OR 21 OR 24 OR 26
  OR 28))
MOVE VAR LIST       SITE,DDATE,SUBPLOT,PIN
REPORT      FILENAME=DVAC2/
                PAGESIZE=80,132/
      SORT=DDATE,SUBPLOT,PIN/
LEVEL         1,DDATE
WRITE             52X,'****************************'
WRITE             52X,'*',26X,'*'
WRITE             52X,'*',1X,'O U T P U T    P R O G 1 *'
WRITE             52X,'*',26X,'*'
WRITE             52X,'****************************'
BLANK LINES        20
WRITE             38X,'S I T E    T O U C H E S    A N D    ',
                'A B U N D A N C E S '
BLANK LINES        8
COMPUTE             DATE=JULC(DDATE)
WRITE             52X,'S I T E  =  ',SITE,4X,DATE
SPACE             10
BLANK LINES        16
WRITE             54X,'C. S. A.  S T I N S O N'
HEADING             /////50X,'SUBPLOT',8X,'TOTAL  PINS',20X,'PROG1',
                 15X,'PAGE',PAGE(I3)/
COMPUTE             TOTS=0;BG=0;TOTC=0
AT END
BLANK LINES        2
WRITE             /53X,'————————'
```

```
WRITE             ///37X,'TOTAL PINS TOUCHED FOR SITE =  ',TOTS(I4)
WRITE             //37X,'BARE GROUND COUNT FOR SITE  =  ',BG(I4)
WRITE             //37X,'PERCENTAGE COVER FOR SITE   =  ',TOTC(F7.3)
PAGE EJECT
LEVEL             2,SUBPLOT
COMPUTE             TS=0;SPLOT=SUBPLOT
AT END
WRITE             53X,SPLOT('ZZ'),15X,TS(I2)
LEVEL             3,PIN
COMPUTE          TS=TS+1;TOTS=TOTS+1
 ;BG=(1350-TOTS);TOTC=(TOTS/1350)*100
FINISH
```

PROG5

```
RUN NAME              PROG.5: TOTAL TOUCHES (TOTTS).
COMMENT               THIS PROGRAM IS DESIGNED TO SUM THE TOUCHES
                  FOR THE SITE. IT ALSO GIVES A COUNT OF THE TOTAL
                  NO. OF DATA RECORDS READ.
                  'FOR EACH CASE' DEFINES THE SITE.
                  'FOR EACH REC' DEFINES THE REC TYPE.
                  'SELECT REC IF' DEFINES THE 'DDATE' PARAMETER
                  TO BE SELECTED.
                  'MOVE VAR LIST' MOVES THE 'TOUCHES' PARAMETER
                  VALUES FROM THE SELECTED DATA RECORDS INTO
                  THE SUMMARY FILE.
                  SUMMARY VARIABLE 'COUNT' IS A MEASURE OF THE NO. OF
                  INDIVIDUAL DATA RECORDS USED IN THE COMPUTATION.
                  'COMPUTE' CREATES THE SUMMARY VARIABLE 'COUNT' WITH
                  VALUE=CNTR(TOUCHES).
                  'COMPUTE' CREATES THE SUMMARY VARIABLE 'TOTTS' WITH
                  VALUE=SUMR(TOUCHES).
                  AS THE COMPUTATIONS IN EACH 'COMPUTE' COMMAND PROCEED
                  THE SUMMARY RECORDS ARE CUMULATED. THE FINAL CUMULATED
                  VALUE PROVIDES THE CORRECT RESULT. THE AFTER RETRIEVAL
                  COMMAND SELECTS THE LAST SUMMARY RECORD AND PREVENTS
                  THE OUTPUT OF THE WHOLE CUMULATIVE PROCESS.
RETRIEVAL
FOR EACH CASE         LIST='A'
FOR EACH REC          BOTANY
SELECT REC IF    (DDATE=CDATE('13/05/80','DDIMMIYY'))
MOVE VAR LIST         SITE,DDATE,TOUCHES
COMPUTE              COUNT=CNTR(TOUCHES)
COMPUTE              TOTTS=SUMR(TOUCHES)
END
AFTER RETRIEVAL
BLANK LINES          10
WRITE             /////52X,'****************************'
WRITE             52X,'*',26X,'*'
WRITE             52X,'* O U T P U T    P R O G 5 *'
WRITE             52X,'*',26X,'*'
WRITE             52X,'****************************'
BLANK LINES         5
COMPUTE             DATE=JULC(DDATE)
WRITE             52X,'S I T E  =  ',SITE,4X,DATE
BLANK LINES         5
WRITE               21T,'COUNT(=TOTAL DATA RECORDS READ)            =',
                  COUNT(I7)//
WRITE               21T,'TOTTS(=TOTAL TOUCHES FOR SITE)            =',
                  TOTTS(I7)
BLANK LINES          15
WRITE                54X,'C. S. A.  S T I N S O N'
FINISH
```

PROG6A

```
RUN NAME          PROG6A : INDIVIDUAL SPECIES PIN STATISTICS.
RETRIEVAL
COMMENT             THIS PROGRAM IS DESIGNED TO PROVIDE,FOR EACH PLANT SPECIES,
                THE TOTAL NO. OF PINS TOUCHED,A BARE GROUND COUNT
                AND PERCENTAGE COVER.

                'FOR EACH CASE' SPECIFIES THE SITE.
                'FOR EACH REC' SPECIFIES THE RECORD TYPE.
                'SELECT REC IF' SELECTS SPECIFIED RECORDS.
                'MOVE VAR LIST' MOVES THE SPECIFIED RECORD VARIABLES INTO
                THE 'SUMMARY FILE'.
                THIS IS THE RETRIEVAL PROCEDURE.

                THE REPORT PROCEDURE FOLLOWS:———
                THE SUMMARY RECORDS ARE SORTED IN ORDER OF APPEARANCE
                IN THE 'SORT' COMMAND.
                TOTS=0 ACCUMULATES THE TOTAL PIN COUNT FOR EACH SPECIES
                AS RECORDS ARE READ.
                BG=0 ACCUMULATES THE BARE GROUND COUNT FOR EACH SPECIES.
                TOTC=0 ACCUMULATES THE PERCENTAGE COVER FOR EACH SPECIES.

                THE OUTPUT FOR THE REPORT PROCEDURE IS SENT TO A LOCAL
                SIR FILE.

FOR EACH CASE     LIST='A'
FOR EACH REC      BOTANY
SELECT REC IF    (DDATE=CDATE('13/05/80','DDIMMIYY'))
MOVE VAR LIST     SITE,DDATE,SPECIES,SUBPLOT,PIN
REPORT             FILENAME=SPPINS/
                SORT=SITE,SPECIES,SUBPLOT,PIN/
                PAGESIZE=85,132/
BEFORE REPORT
WRITE            52X,'******************************'
WRITE            52X,'*',28X,'*'
WRITE            52X,'* O U T P U T   P R O G 6 A *'
WRITE            52X,'*',28X,'*'
WRITE            52X,'******************************'
BLANK LINES        20
WRITE            30X,'P L A N T   S P E C I E S   P I N - C O V E R',
                '   S T A T I S T I C S'
BLANK LINES        8
COMPUTE            DATE=JULC(DDATE)
WRITE            52X,'S I T E  =  ',SITE,4X,DATE
BLANK LINES        16
WRITE            54X,'C. S. A.  S T I N S O N'
END
LEVEL            1,SITE
HEADING            /51X,'SPECIES',2X,'PINS',3X,'BARE-GRND',5X,'COVER'
                ,15X,'PROG6A',10X,'PAGE',PAGE(I4)//
LEVEL              2,SPECIES
COMPUTE            SPP=SPECIES
COMPUTE            TOTS=0;BG=0;TOTC=0
AT END
WRITE              54X,SPP('ZZ'),TOTS(I8),BG(I9),TOTC(F13.3)/
LEVEL            3,SUBPLOT
LEVEL            4,PIN
COMPUTE            TOTS=TOTS+1;BG=(1350-TOTS);
               TOTC=(TOTS/1350)*100
END REPORT
```

PROG6B

```
RUN NAME          PROG6B : INDIVIDUAL SPECIES HEIGHT-PIN STATISTICS.
RETRIEVAL
COMMENT           THIS PROGRAM IS DESIGNED TO PROVIDE, FOR EACH SPECIES,
```

```
                  THE TOTAL NO. OF PINS TOUCHED, A BARE-GROUND COUNT AND
                 PERCENTAGE COVER FOR EACH HEIGHT LEVEL.

                   'FOR EACH CASE' SPECIFIES THE SITE.
                   'FOR EACH REC' SPECIFIES THE RECORD TYPE.
                   'SELECT REC IF' SELECTS SPECIFIED RECORDS.
                   'MOVE VAR LIST' MOVES THE SPECIFIED RECORD VARIABLES INTO
                   THE 'SUMMARY FILE'.
                   THIS IS THE RETRIEVAL PROCEDURE.

                   THE REPORT PROCEDURE FOLLOWS:--------
                   THE SUMMARY RECORDS ARE SORTED IN ORDER OF APPEARANCE
                   IN THE 'SORT' COMMAND.
                   HTPINS=0 ACCUMULATES THE PIN COUNT OF EACH HEIGHT LEVEL
                   FOR INDIVIDUAL SPECIES.
                   HTBG=0 ACCUMULATES THE BARE GROUND COUNT OF EACH HEIGHT
                   LEVEL FOR INDIVIDUAL SPECIES.
                   HTCOVER=0 ACCUMULATES THE PERCENTAGE COVER OF EACH HEIGHT
                   LEVEL FOR INDIVIDUAL SPECIES.

                   THE OUTPUT FOR THE REPORT PROCEDURE IS SENT TO A LOCAL
                   SIR FILE.

FOR EACH CASE       LIST='A'
FOR EACH REC        BOTANY
SELECT REC IF      (DDATE=CDATE('13/05/80','DDIMMIYY'))
MOVE VAR LIST       SITE,DDATE,SPECIES,HEIGHT,SUBPLOT,PIN
REPORT               FILENAME=SPPINS/
                   SORT=SITE,SPECIES,HEIGHT,SUBPLOT,PIN/
                   PAGESIZE=85,132/
BEFORE REPORT
WRITE              52X,'******************************'
WRITE              52X,'*',28X,'*'
WRITE              52X,'* O U T P U T    P R O G 6 B *'
WRITE              52X,'*',28X,'*'
WRITE              52X,'******************************'
BLANK LINES          20
WRITE                30X,'P L A N T    S P E C I E S    P I N - C O V E R',
                   '    S T A T I S T I C S'
BLANK LINES          8
COMPUTE               DATE=JULC(DDATE)
WRITE                52X,'S I T E  =  ',SITE,4X,DATE
BLANK LINES          16
WRITE                54X,'C. S. A.  S T I N S O N'
END
LEVEL                1,SITE
HEADING             42T,'SPECIES',6X,
                 'HEIGHT',4X,'PINS',3X,'BARE-GRND',5X,'COVER',15X,'PROG6B',
                 10X,'PAGE',PAGE(14)//
LEVEL                2,SPECIES
COMPUTE                SPP=SPECIES
AT END
BLANK LINE
WRITE              45T,SPP('ZZ')
WRITE                42T,'................................................'/
LEVEL               3,HEIGHT
COMPUTE               HITE=HEIGHT
COMPUTE               HTPINS=0;HTBG=0;HTCOVER=0
AT END
WRITE                56X,HITE('ZZ'),HTPINS(I10),HTBG(I9),HTCOVER(F13.3)
LEVEL               4,SUBPLOT
LEVEL               5,PIN
COMPUTE             HTPINS=HTPINS+1;
                   HTBG=(1350-HTPINS);HTCOVER=(HTPINS/1350)*100
END REPORT
```

```
PROG7

RUN NAME          PROG7 : INDIVIDUAL SPECIES TOUCHES-ABUNDANCES STATS.
RETRIEVAL
COMMENT              THIS PROGRAM IS DESIGNED TO PROVIDE,FOR EACH PLANT
                  SPECIES,TOTAL TOUCHES,ABUNDANCE AND LOG. ABUNDANCE.
                  IN ADDITION, EACH SPECIES HEIGHT LEVEL IS TAKEN AND
                  THE TOTAL TOUCHES,ABUNDANCE AND LOG. ABUNDANCE VALUES
                  ARE COMPUTED.

                  INDIVIDUAL SPECIES ABUNDANCE AT EACH HEIGHT LEVEL IS
                  COMPUTED FROM HTAB=(HTTOTS/173),WHERE HTTOTS=NO. TOUCHES
                  AT PARTICULAR HEIGHT LEVEL/TOTAL TOUCHES FOR THE SITE;
                  CORRESPONDING LOG. ABUNDANCE VALUES ARE COMPUTED FROM
                  HTLAB=ALOG10(HTAB). TOTAL INDIVIDUAL SP. ABUNDANCE IS
                  COMPUTED FROM SPAB=(SPTOTTS/173), WHERE SPTOTS=SPECIES
                  TOTAL TOUCHES /TOTAL TOUCHES FOR THE SITE ;
                  THE CORRESPONDING LOG. ABUNDANCE VALUES ARE COMPUTED
                  FROM SPLAB=ALOG10(SPAB).
                  'FOR EACH CASE' SPECIFIES THE SITE.
                  'FOR EACH REC' SPECIFIES THE RECORD TYPE.
                  'MOVE VAR LIST' MOVES THE SPECIFIED 'RECORD VARIABLES'
                  INTO THE 'SUMMARY FILE'. THIS IS THE RETRIEVAL PROCEDURE

                  THE REPORT PROCEDURE FOLLOWS:----------
                  THE 'SUMMARY RECORDS' ARE SORTED IN ORDER OF APPEARANCE
                  IN THE 'SORT' COMMAND. FOR EACH PLANT SPECIES, THE TOTAL
                  TOUCHES ARE COMPUTED FOR EACH HEIGHT LEVEL TOGETHER WITH
                  HEIGHT LEVEL ABUNDANCE AND LOG.ABUNDANCE AND FOLLOWED BY
                  SPECIES TOTAL TOUCHES,SPECIES TOTAL ABUNDANCE AND
                  SPECIES TOTAL LOG. ABUNDANCE.
                  SPTOTS=0 ACCUMULATES INDIVIDUAL SPECIES TOTAL TOUCHES.
                  SPAB=0 ACCUMULATES INDIVIDUAL SPECIES ABUNDANCE VALUES.
                  SPLAB=0 ACCUMULATES INDIVIDUAL SPECIES LOG. ABUNDANCE
                  VALUES.
                  HTOTTS=0 ACCUMULATES INDIVIDUAL SPECIES TOTAL TOUCHES,
                  FOR EACH HEIGHT LEVEL.
                  HTAB=0 AND HTLAB=0 ACCUMULATE INDIVIDUAL SPECIES
                  ABUNDANCE AND LOG. ABUNDANCE, FOR EACH HEIGHT LEVEL.

                   ******************* N O T E *************************
                   BEFORE THIS PROGRAM IS RUN THE TOTAL TOUCHES
                   FOR THE SITE MUST BE COMPUTED FROM PROG5.
                   THE VALUE OBTAINED IS THEN USED AS THE DENOMINATOR IN
                   THE ABUNDANCE EQUATIONS.
                   **************************************************

                  THE OUTPUT FOR THE REPORT PROCEDURE IS SENT TO A LOCAL
                  S I R FILE.

FOR EACH CASE       LIST='A'
FOR EACH REC        BOTANY
SELECT REC IF      (DDATE=CDATE('13/05/80','DDIMMIYY'))
MOVE VAR LIST       SITE,DDATE,SPECIES,HEIGHT,SUBPLOT,PIN,STRUCTUR,TOUCHES
REPORT               FILENAME=SPABUND/
                  SORT=SITE,SPECIES,HEIGHT,SUBPLOT,PIN,STRUCTUR,TOUCHES/
                  PAGESIZE=85,132/
BEFORE REPORT
WRITE               52X,'****************************'
WRITE               52X,'*',26X,'*'
WRITE               52X,'*',1X,'O U T P U T   P R O G 7 *'
WRITE               52X,'*',26X,'*'
WRITE               52X,'****************************'
BLANK LINES          20
WRITE               28X,'P L A N T   S P E C I E S   T O U C H E S',
                  '   A N D   A B U N D A N C E S'
BLANK LINES          8
```

```
COMPUTE             DATE=JULC(DDATE)
WRITE             52X,'S I T E  =  ',SITE,4X,DATE
BLANK LINES         16
WRITE             54X,'C. S. A.  S T I N S O N'
END
LEVEL              1,SITE
HEADING             /11X,'SPECIES   TOUCHES    ABUNDANCE  LOG.ABUND',
                 6X,'HEIGHT   TOUCHES    ABUNDANCE  LOG.ABUND',
                 8X,'PROG7',5X,'PAGE',PAGE(I4)//
LEVEL              2,SPECIES
COMPUTE             SPP=SPECIES
COMPUTE             SPTOTS=0;SPAB=0;SPLAB=0
AT END
BLANK LINE
WRITE              14X,SPP('ZZ'),SPTOTS(I12),SPAB(F10.3),SPLAB(F13.3)/
WRITE              11X,'..................................................'
                 ,'...................................'//
LEVEL              3,HEIGHT
COMPUTE             HITE=HEIGHT
COMPUTE             HTTOTS=0;HTAB=0;HTLAB=0
AT END
WRITE              60X,HITE('ZZ'),HTTOTS(I12),HTAB(F10.3),HTLAB(F13.3)
LEVEL              4,SUBPLOT
LEVEL              5,PIN
LEVEL              6,STRUCTUR
LEVEL              7,TOUCHES
COMPUTE             SPTOTS=SPTOTS+TOUCHES;
                 SPAB=(SPTOTS/173);SPLAB=ALOG10(SPAB);
                 HTTOTS=HTTOTS+TOUCHES;HTAB=(HTTOTS/173);
                 HTLAB=ALOG10(HTAB)
END REPORT
```

PROG10

```
RUN NAME            PROG10 : GENERAL HEIGHT PROFILE ANALYSIS.
RETRIEVAL
COMMENT             THIS PROGRAM IS DESIGNED TO PROVIDE,FOR EACH HEIGHT LEVEL,
                 THE TOTAL NO. OF PINS TOUCHED, A BARE GROUND COUNT AND
                 PERCENTAGE COVER.
                 A BARE GROUND COUNT FOR EACH HEIGHT LEVEL IS COMPUTED
                 FROM BG=TOTAL PINS USED-TOTAL PINS TOUCHED.
                 THE PERCENTAGE COVER FOR EACH HEIGHT DIVISION IS COMPUTED
                 FROM TOTC=(TOTS/1350)*100

                 'FOR EACH CASE' SPECIFIES THE SITE.
                 'FOR EACH REC' SPECIFIES THE RECORD TYPE.
                 'SELECT REC IF' SELECTS SPECIFIED RECORDS.
                 'MOVE VAR LIST' MOVES THE SPECIFIED RECORD VARIABLES INTO
                 THE 'SUMMARY FILE'.
                 THIS IS THE RETRIEVAL PROCEDURE.

                 THE REPORT PROCEDURE FOLLOWS:---------
                 THE SUMMARY RECORDS ARE SORTED IN ORDER OF APPEARANCE
                 IN THE 'SORT' COMMAND.
                 TOTS=0 ACCUMULATES THE TOTAL PIN COUNT FOR THE  SITE
                 AS RECORDS ARE READ.
                 BG=0 ACCUMULATES THE BARE GROUND COUNT FOR EACH HEIGHT
                 LEVEL AS RECORDS ARE READ.
                 TOTC=0 ACCUMULATES THE COVER VALUE FOR EACH HEIGHT LEVEL
                 AS RECORDS ARE READ.
                 THE OUTPUT FOR THE REPORT PROCEDURE IS SENT TO A LOCAL
                 SIR FILE.

FOR EACH CASE     LIST='A'
FOR EACH REC      BOTANY
SELECT REC IF    (DDATE=CDATE('13/05/80','DDIMMIYY'))
MOVE VAR LIST     SITE,DDATE,HEIGHT,SUBPLOT,PIN
```

```
REPORT            FILENAME=HITEPIN/
                SORT=SITE,HEIGHT,SUBPLOT,PIN/
                PAGESIZE=85,132/
BEFORE REPORT
WRITE            52X,'****************************'
WRITE            52X,'*',26X,'*'
WRITE            52X,'*',1X,'O U T P U T    P R O G10 *'
WRITE            52X,'*',26X,'*'
WRITE            52X,'****************************'
BLANK LINES       20
WRITE            32X,'G E N E R A L    H E I G H T    P R O F I L E'
                ,'   A N A L Y S I S'
BLANK LINES       5
WRITE            48X,'-P I N S    A N D    C O V E R-'
BLANK LINES       10
COMPUTE            DATE=JULC(DDATE)
WRITE            52X,'S I T E  =  ',SITE,4X,DATE
BLANK LINES       16
WRITE            54X,'C. S. A.  S T I N S O N'
END
LEVEL            1,SITE
HEADING           /50T,'HEIGHT   PINS   BARE-GRND      COVER',20X,
                'PROG10',10X,'PAGE',PAGE(I4)//
LEVEL            2,HEIGHT
COMPUTE            HITE=HEIGHT
COMPUTE            TOTS=0;BG=0;TOTC=0
AT END
BLANK LINE
WRITE            52T,HITE('ZZ'),TOTS(I9),BG(I9),TOTC(F13.3)
LEVEL            3,SUBPLOT
LEVEL            4,PIN
COMPUTE            TOTS=TOTS+1;BG=(1350-TOTS);
                TOTC=(TOTS/1350)*100
END REPORT
```

PROG11

```
RUN NAME            PROG11 : GENERAL HEIGHT PROFILE ANALYSIS.
RETRIEVAL
COMMENT             THIS PROGRAM IS DESIGNED TO PROVIDE,FOR EACH HEIGHT LEVEL,
                A LIST OF THE SPECIES PRESENT FOLLOWED BY A SPECIES TOTAL.

                'FOR EACH CASE' SPECIFIES THE SITE.
                'FOR EACH REC' SPECIFIES THE RECORD TYPE.
                'SELECT REC IF' SELECTS SPECIFIED RECORDS.
                'MOVE VAR LIST' MOVES THE SPECIFIED RECORD VARIABLES INTO
                THE 'SUMMARY FILE'.
                THIS IS THE RETRIEVAL PROCEDURE.

                THE REPORT PROCEDURE FOLLOWS:————
                THE SUMMARY RECORDS ARE SORTED IN ORDER OF APPEARANCE
                IN THE 'SORT' COMMAND. FOR EACH HEIGHT LEVEL THE SPECIES
                FOUND ARE LISTED IN DESCENDING ORDER AND A TOTAL COUNT IS
                PRODUCED.
                TS=O ACCUMULATES INDIVIDUAL HEIGHT LEVEL SPECIES COUNTS
                AS RECORDS ARE READ.
                THE OUTPUT FOR THE REPORT PROCEDURE IS SENT TO A LOCAL
                SIR FILE.

FOR EACH CASE      LIST='A'
FOR EACH REC       BOTANY
SELECT REC IF     (DDATE=CDATE('13/05/80','DDIMMIYY'))
MOVE VAR LIST      SITE,DDATE,HEIGHT,SPECIES
REPORT            FILENAME=HITESPP/
                SORT=SITE,HEIGHT,SPECIES(D)/
                PAGESIZE=85,132/
BEFORE REPORT
```

```
WRITE           52X,'******************************'
WRITE           52X,'*',28X,'*'
WRITE           52X,'*',1X,'O U T P U T    P R O G 1 1 *'
WRITE           52X,'*',28X,'*'
WRITE           52X,'******************************'
BLANK LINES       20
WRITE           32X,'G E N E R A L    H E I G H T    P R O F I L E',
              '   A N A L Y S I S '
BLANK LINES       5
WRITE           40X,'-S P E C I E S    L I S T    A N D    C O U N T-'
BLANK LINES       10
COMPUTE           DATE=JULC(DDATE)
WRITE           52X,'S I T E  =  ',SITE,4X,DATE
BLANK LINES       16
WRITE           54X,'C. S. A.  S T I N S O N '
END
LEVEL           1,SITE
HEADING           'INDIVIDUAL HEIGHT LEVEL SPECIES LIST AND COUNT',
               5X,'SITE = ',SITE,30X,'PROG11',15X,'PAGE',PAGE(I4),
               //59T,'HEIGHT',8X,'SPECIES'
AT END
BLANK LINES       2
LEVEL           2,HEIGHT
BLANK LINE
WRITE           61T,HEIGHT('ZZ')
COMPUTE           TS=0
AT END
WRITE           /68T,'TOTAL  =',TS(I3)
BLANK LINE
WRITE           59T,'....................'
LEVEL           3,SPECIES
WRITE           76T,SPECIES('ZZ')
COMPUTE           TS=TS+1
END REPORT
```

PROG13

```
RUN NAME            PROG13 : GENERAL HEIGHT PROFILE ANALYSIS.
RETRIEVAL
COMMENT             THIS PROGRAM IS DESIGNED TO PROVIDE,FOR EACH HEIGHT
                LEVEL,TOTAL TOUCHES,ABUNDANCE AND LOG. ABUNDANCE.

                INDIVIDUAL HEIGHT LEVEL TOTAL TOUCHES IS COMPUTED FROM
                HTTOTS=HTTOTS+TOUCHES.
                PLANT ABUNDANCE AT EACH HEIGHT LEVEL IS COMPUTED FROM
                HTAB=(HTTOTS/173), WHERE 173 = TOTAL TOUCHES FOR SITE.
                        THE CORRESPONDING LOG. ABUNDANCE VALUES ARE
                COMPUTED FROM HTLAB=ALOG10(HTAB).

                'FOR EACH CASE' SPECIFIES THE SITE.
                'FOR EACH REC' SPECIFIES THE RECORD TYPE.
                'MOVE VAR LIST' MOVES THE SPECIFIED 'RECORD VARIABLES'
                INTO THE 'SUMMARY FILE'. THIS IS THE RETRIEVAL PROCEDURE

                THE REPORT PROCEDURE FOLLOWS:-----------
                THE 'SUMMARY RECORDS' ARE SORTED IN ORDER OF APPEARANCE
                IN THE 'SORT' COMMAND. FOR EACH HEIGHT LEVEL,THE TOTAL
               TOUCHES ARE COMPUTED TOGETHER WITH HEIGHT LEVEL ABUNDANC
                AND LOG. ABUNDANCE.
                HTOTTS=0 ACCUMULATES INDIVIDUAL HEIGHT LEVEL TOTAL TOUCH
                HTAB=0 ACCUMULATES INDIVIDUAL HEIGHT LEVEL ABUNDANCE.
                HTLAB=0 ACCUMULATES INDIVIDUAL HEIGHT LEVEL LOG.
                ABUNDANCE.

                 ****************** N O T E ************************
                 BEFORE THIS PROGRAM IS RUN THE TOTAL TOUCHES
                 FOR THE SITE MUST BE COMPUTED FROM PROG5.
```

```
                 THE VALUE OBTAINED IS THEN USED AS THE DENOMINATOR IN
                 THE ABUNDANCE EQUATIONS.
                 ***************************************************

                THE OUTPUT FOR THE REPORT PROCEDURE IS SENT TO A LOCAL
                S I R FILE.

FOR EACH CASE      LIST='A'
FOR EACH REC       BOTANY
SELECT REC IF     (DDATE=CDATE('13/05/80','DDIMMIYY'))
MOVE VAR LIST      SITE,DDATE,HEIGHT,SUBPLOT,PIN,SPECIES,STRUCTUR,TOUCHES
REPORT            FILENAME=HITEAB/
                SORT=SITE,HEIGHT,SUBPLOT,PIN,SPECIES,STRUCTUR,TOUCHES/
                PAGESIZE=85,132/
BEFORE REPORT
WRITE             52X,'******************************'
WRITE             52X,'*',28X,'*'
WRITE             52X,'*',28X,'*'
WRITE             52X,'*',1X,'O U T P U T    P R O G 1 3 *'
WRITE             52X,'*',28X,'*'
WRITE             52X,'******************************'
BLANK LINES         20
WRITE             32X,'G E N E R A L    H E I G H T    P R O F I L E'
                ,'    A N A L Y S I S'
BLANK LINES         5
WRITE             40X,'-T O U C H E S    A N D    A B U N D A N C E S-'
BLANK LINES         10
COMPUTE             DATE=JULC(DDATE)
WRITE             52X,'S I T E  =  ',SITE,4X,DATE
BLANK LINES         16
WRITE             54X,'C. S. A.  S T I N S O N'
LEVEL             1,SITE
HEADING            /46T,'HEIGHT',3X,'TOUCHES',4X,'ABUNDANCE',2X,'LOG.ABUND'
                ,20X,'PROG13',10X,'PAGE',PAGE(I4)//
LEVEL              2,HEIGHT
COMPUTE             HITE=HEIGHT
COMPUTE             HTTOTS=0;HTAB=0;HTLAB=0
AT END
BLANK LINE
WRITE             48T,HITE('ZZ'),HTTOTS(I12),HTAB(F10.3),HTLAB(F13.3)
LEVEL             3,SUBPLOT
LEVEL             4,PIN
LEVEL             5,SPECIES
LEVEL             6,STRUCTUR
LEVEL             7,TOUCHES
COMPUTE             HTTOTS=HTTOTS+TOUCHES;
                HTAB=(HTTOTS/173);HTLAB=ALOG10(HTAB)
END REPORT

PROG21

RUN NAME           PROG21 : INDIVIDUAL SPECIES STRUCTURE TOUCHES-ABUND STATS.
RETRIEVAL
COMMENT            THIS PROGRAM COMPLIMENTS PROG7.
               FOR EACH PLANT SPECIES,TOTAL TOUCHES,ABUNDANCE AND
               LOG. ABUNDANCE ARE COMPUTED FOR EACH STRUCTURE AT EACH
               HEIGHT LEVEL. THESE 3 PARAMETERS ARE THEN COMPUTED OVERALL
               FOR EACH SPECIES' STRUCTURE AND OVERALL FOR EACH SPECIES.

               INDIVIDUAL SPECIES' STRUCTURE ABUNDANCE AT EACH HEIGHT
               LEVEL IS COMPUTED FROM HTAB=(HTTOTS/X), WHERE HTTOTS
               = NO. OF TOUCHES AT PARTICULAR HEIGHT LEVEL/TOTAL TOUCHES
               FOR THE SITE; CORRESPONDING LOG. ABUNDANCES ARE COMPUTED
               FROM HTLAB=ALOG10(HTAB). TOTAL INDIVIDUAL SPECIES'
               STRUCTURE ABUNDANCE IS COMPUTED FROM STRAB=(STRTOTS/X),
               WHERE STRTOTS=SPECIES' STRUCTURE TOTAL TOUCHES/SITE TOTAL
               TOUCHES; CORRESPONDING LOG. ABUNDANCES ARE COMPUTED FROM
```

```
                  STRLAB=ALOG10(STRAB).
                  INDIVIDUAL SPECIES OVERALL ABUNDANCE IS COMPUTED FROM
                  SPAB=(SPTOTS/X),WHERE SPTOTS=TOTAL TOUCHES FOR SPECIES;
                  SPECIES LOG. ABUNDANCE COMPUTES FROM SPLAB=ALOG10(SPAB).

                  'FOR EACH CASE' SPECIFIES THE SITE.
                  'FOR EACH REC' SPECIFIES THE RECORD TYPE.
                  'MOVE VAR LIST' MOVES THE SPECIFIED 'RECORD VARIABLES'
                  INTO THE 'SUMMARY FILE'. THIS IS THE RETRIEVAL
                  PROCEDURE.

                  THE REPORT PROCEDURE FOLLOWS:------
                  THE 'SUMMARY RECORDS' ARE SORTED IN ORDER OF APPEARANCE
                  IN THE 'SORT' COMMAND. FOR EACH SPECIES,THE TOTAL
                  TOUCHES ARE COMPUTED FOR EACH STRUCTURE AT EACH HEIGHT
                  LEVEL TOGETHER WITH ABUNDANCE AND LOG. ABUNDANCE. THIS
                  IS FOLLOWED BY THE COMPUTATION OF THESE 3 PARAMETERS
                  FOR EACH SPECIES' STRUCTURE OVERALL AND THEN,FINALLY,
                  FOR EACH SPECIES OVERALL.
                  SPTOTS=0 ACCUMULATES INDIVIDUAL SPECIES TOTAL TOUCHES.
                  SPAB=0 ACCUMULATES INDIVIDUAL SPECIES ABUNDANCE VALUES.
                  SPLAB=0 ACCUMULATES INDIVIDUAL SPECIES LOG.
                  ABUNDANCE VALUES.
                  HTOTTS=0 ACCUMULATES INDIVIDUAL SPECIES TOTAL TOUCHES,
                  FOR EACH STRUCTURE, AT EACH HEIGHT LEVEL.
                  HTAB=0 AND HTLAB=0 ACCUMULATE INDIVIDUAL SPECIES
                  ABUNDANCE AND LOG. ABUNDANCE, FOR EACH STRUCTURE AT EACH
                  HEIGHT LEVEL.
                  STRTOTS=0 ACCUMULATES INDIVIDUAL SPECIES TOTAL TOUCHES FOR
                  EACH STRUCTURE.  .
                  STRAB=0 ACCUMULATES INDIVIDUAL SPECIES ABUNDANCE, FOR EACH
                  STRUCTURE.
                  STRLAB=0 ACCUMULATES INDIVIDUAL SPECIES LOG. ABUNDANCE
                  FOR EACH STRUCTURE.

                    ****************** N O T E ************************
                    BEFORE THIS PROGRAM IS RUN THE TOTAL TOUCHES
                    FOR THE SITE MUST BE COMPUTED FROM PROG5.
                    THE VALUE OBTAINED IS THEN USED AS THE DENOMINATOR IN
                    THE ABUNDANCE EQUATIONS.
                    ***************************************************

                  THE OUTPUT FOR THE REPORT PROCEDURE IS SENT TO A LOCAL
                  S I R FILE.

FOR EACH CASE      LIST='A'
FOR EACH REC       BOTANY
SELECT REC IF     (DDATE=CDATE('13/05/80','DDIMMIYY'))
MOVE VAR LIST      SITE,DDATE,SPECIES,HEIGHT,SUBPLOT,PIN,STRUCTUR,TOUCHES
REPORT            FILENAME=SPSTRAB/
                  SORT=SITE,SPECIES,STRUCTUR,HEIGHT,SUBPLOT,PIN,TOUCHES/
                  PAGESIZE=85,132/
BEFORE REPORT
WRITE              52X,'******************************'
WRITE              52X,'*',28X,'*'
WRITE              52X,'* O U T P U T    P R O G 2 1 *'
WRITE              52X,'*',28X,'*'
WRITE              52X,'******************************'
BLANK LINES          20
WRITE              12X,'I N D I V I D U A L   S P E C I E S',
                  '   S T R U C T U R E - H E I G H T',
                  '   T O U C H E S   S T A T S'
BLANK LINES          8
COMPUTE             DATE=JULC(DDATE)
WRITE              52X,'S I T E  =  ',SITE,4X,DATE
BLANK LINES          16
WRITE              52X,'C. S. A.  S T I N S O N'
```

```
END
LEVEL            1,SITE
HEADING            100T,'PROG21',15X,'PAGE',PAGE(I3)/
               2T,'SPECIES',2X,'TOUCHES',3X,'ABUNDANCE',1X,'LOG.ABUND',
               5X,'STRUCTURE',2X,'TOUCHES',3X,'ABUNDANCE',1X,'LOG.ABUND'
               ,5X,'HEIGHT',2X,'TOUCHES',3X,'ABUNDANCE',1X,
               'LOG.ABUND'/
LEVEL            2,SPECIES
COMPUTE            SPP=SPECIES
COMPUTE            SPTOTS=0;SPAB=0;SPLAB=0
AT END
BLANK LINE
WRITE            4T,SPP('ZZ'),SPTOTS(I12),SPAB(F9.3),SPLAB(F12.3)/
WRITE            2T,'————————————'/
LEVEL            3,STRUCTUR
COMPUTE            STRUCT=STRUCTUR
COMPUTE            STRTOTS=0;STRAB=0;STRLAB=0
AT END
WRITE            48T,STRUCT('ZZ'),STRTOTS(I13),STRAB(F9.3),STRLAB(F12.3)/
WRITE            45T,'..................................................',
               '................................'/
LEVEL            4,HEIGHT
COMPUTE            HITE=HEIGHT
COMPUTE            HTTOTS=0;HTAB=0;HTLAB=0
AT END
WRITE            92T,HITE('ZZ'),HTTOTS(I11),HTAB(F9.3),HTLAB(F12.3)
LEVEL            5,SUBPLOT
LEVEL            6,PIN
LEVEL            7,TOUCHES
COMPUTE            SPTOTS=SPTOTS+TOUCHES;SPAB=(SPTOTS/173);
               SPLAB=ALOG10(SPAB);
               STRTOTS=STRTOTS+TOUCHES;STRAB=(STRTOTS/173);
               STRLAB=ALOG10(STRAB);
               HTTOTS=HTTOTS+TOUCHES;HTAB=(HTTOTS/173);
               HTLAB=ALOG10(HTAB)
END REPORT
```

PROG22

```
RUN NAME            PROG22 : INDIVIDUAL STRUCTURE SPECIES-HEIGHT-PIN STATS.
RETRIEVAL
COMMENT             THIS PROGRAM COMPLIMENTS PROG14.
               FOR EACH PLANT STRUCTURE, THE TOTAL PINS TOUCHED PLUS
               BARE GROUND COUNT AND PERCENTAGE COVER ARE COMPUTED
               FOR EACH SPECIES AT EACH HEIGHT LEVEL.

               'FOR EACH CASE' SPECIFIES THE SITE.
               'FOR EACH REC' SPECIFIES THE RECORD TYPE.
               'SELECT REC IF' SELECTS SPECIFIED RECORDS.
               'MOVE VAR LIST' MOVES THE SPECIFIED RECORD VARIABLES INTO
               THE 'SUMMARY FILE'.
               THIS IS THE RETRIEVAL PROCEDURE.

               THE REPORT PROCEDURE FOLLOWS:————
               THE SUMMARY RECORDS ARE SORTED IN ORDER OF APPEARANCE
               IN THE 'SORT' COMMAND.
               FOR INDIVIDUAL STRUCTURE'S SPECIES.
               HTBG=0 ACCUMULATES THE BARE GROUND COUNT OF EACH HEIGHT
               LEVEL FOR INDIVIDUAL STRUCTURE'S SPECIES.
               HTCOV=0 ACCUMULATES THE PERCENTAGE COVER OF EACH HEIGHT
               LEVEL FOR INDIVIDUAL STRUCTURE'S SPECIES.
               THE OUTPUT FOR THE REPORT PROCEDURE IS SENT TO A LOCAL
               S I R FILE.

FOR EACH CASE     LIST='A'
FOR EACH REC      BOTANY
SELECT REC IF     (DDATE=CDATE('13/05/80','DDIMMIYY'))
```

```
MOVE VAR LIST      SITE,DDATE,SPECIES,STRUCTUR,HEIGHT,SUBPLOT,PIN
REPORT              FILENAME=STRSPHT/
                SORT=SITE,STRUCTUR,SPECIES,HEIGHT,SUBPLOT,PIN/
                PAGESIZE=85,132/
BEFORE REPORT
WRITE             52X,'******************************'
WRITE             52X,'*',28X,'*'
WRITE             52X,'* O U T P U T    P R O G 2 2 *'
WRITE             52X,'*',28X,'*'
WRITE             52X,'******************************'
BLANK LINES         20
WRITE             16X,'I N D I V I D U A L    S T R U C T U R E    ',
                'S P E C I E S - H E I G H T - P I N    S T A T S.'
BLANK LINES         8
COMPUTE             DATE=JULC(DDATE)
WRITE             52X,'S I T E  =  ',SITE,4X,DATE
BLANK LINES         16
WRITE             52X,'C. S. A.  S T I N S O N'
END
LEVEL             1,SITE
HEADING             /24T,'STRUCTUR',5X,'SPECIES',3X,'HEIGHT',3X,'PINS',
                3X,'BARE-GRND',5X,'COVER',15X,'PROG22',10X,'PAGE',PAGE(I3)
                ,//
LEVEL             2,STRUCTUR
COMPUTE             STRUCT=STRUCTUR
COMPUTE             TOTS=0;BG=0;TOTC=0
AT END
BLANK LINE
WRITE            27T,STRUCT('ZZ')
BLANK LINE
WRITE            24T,'——————————————————————',
                '————'//
LEVEL            3,SPECIES
WRITE            39T,SPECIES('ZZ')
AT END
BLANK LINE
WRITE            39T,'........................................'
BLANK LINE
LEVEL            4,HEIGHT
COMPUTE            HITE=HEIGHT
COMPUTE             HTPINS=0;HTBG=0;HTCOV=0
AT END
WRITE            49T,HITE('ZZ'),HTPINS(I9),HTBG(I10),HTCOV(F12.3)
LEVEL            5,SUBPLOT
LEVEL            6,PIN
COMPUTE            HTPINS=HTPINS+1;
                HTBG=(1350-HTPINS);HTCOV=(HTPINS/1350)*100
END REPORT
```

PROG24

```
RUN NAME           PROG24 : INDIVIDUAL SPECIES PIN STATISTICS.
RETRIEVAL
COMMENT            THIS PROGRAM IS DESIGNED TO PROVIDE,FOR EACH PLANT SPECIES,
                THE TOTAL NO. OF PINS TOUCHED,A BARE GROUND COUNT
                AND PERCENTAGE COVER.

                'FOR EACH CASE' SPECIFIES THE SITE.
                'FOR EACH REC' SPECIFIES THE RECORD TYPE.
                'SELECT REC IF' SELECTS SPECIFIED RECORDS.
                'MOVE VAR LIST' MOVES THE SPECIFIED RECORD VARIABLES INTO
                THE 'SUMMARY FILE'.
                THIS IS THE RETRIEVAL PROCEDURE.

                THE REPORT PROCEDURE FOLLOWS:————
                THE SUMMARY RECORDS ARE SORTED IN ORDER OF APPEARANCE
                IN THE 'SORT' COMMAND.
```

```
                TOTS=0 ACCUMULATES THE TOTAL PIN COUNT FOR EACH SPECIES
                AS RECORDS ARE READ.
                BG=0 ACCUMULATES THE BARE GROUND COUNT FOR EACH SPECIES.
                TOTC=0 ACCUMULATES THE PERCENTAGE COVER FOR EACH SPECIES.

                THE OUTPUT FOR THE REPORT PROCEDURE IS SENT TO A LOCAL
                SIR FILE.

FOR EACH CASE     LIST='A'
FOR EACH REC      BOTANY
REJECT REC IF     (STRUCTUR = 4 OR 6 OR 9 OR 12 OR 17 OR 19 OR 21
        OR 24 OR 26 OR 28)
MOVE VAR LIST  SITE,DDATE,SPECIES,STRUCTUR,SUBPLOT,PIN
REPORT            FILENAME=SPPINS/
     SORT=DDATE.SPECIES.STRUCTUR,SUBPLOT,PIN/
                PAGESIZE=85,132/
LEVEL      1,DDATE
WRITE             52X,'******************************'
WRITE             52X,'*',28X,'*'
WRITE             52X,'* O U T P U T    P R O G 2 4 *'
WRITE             52X,'*',28X,'*'
WRITE             52X,'******************************'
BLANK LINES        20
WRITE             30X,'P L A N T    S P E C I E S    P I N - C O V E R',
                '    S T A T I S T I C S'
BLANK LINES        8
COMPUTE            DATE=JULC(DDATE)
WRITE             52X,'S I T E   =   ',SITE,4X,DATE
BLANK LINES        16
WRITE             54X,'C. S. A.  S T I N S O N'
HEADING       /40T,'SPECIES',3X,'STRUCTURE',2X,'PINS',5X,'COVER'
             ,15X'SPECIES',3X,'STRUCTURE',2X,'PINS',5X,'COVER'
COMPUTE         TP=0
AT END
BLANK LINES    2
WRITE      47T,'TOTAL PINS =',TP(16)
LEVEL             2,SPECIES
COMPUTE             SPP=SPECIES
AT END
WRITE       43T,SPP('ZZ')
WRITE      40T,'....................................'/
LEVEL       3,STRUCTUR
COMPUTE    STRUCT=STRUCTUR
COMPUTE     TOTS=0;TOTC=0
AT END
WRITE     53T,STRUCT('ZZ'),TOTS(I10),TOTC(F10.3)
LEVEL      4,SUBPLOT
LEVEL       5,PIN
COMPUTE     TOTS=TOTS+1;TOTC=(TOTS/1350)*100;
          TP=TP+1
END REPORT
```

APPENDIX 3: SIR DATABASE STATUS.

```
FILE BASE3 STATISTICAL REPORT                                    83/03/23. 16.53.53.

SIR FILE STATISTICS.

   SIR FILE NAME                                                               BASE3
   DATE OF CREATION                                               20.46.40 81/03/05.
   DATE OF LAST UPDATE                                            21.51.29 82/03/27.
   DATE OF LAST ACCESS                                            16.53.53 83/03/23.
   NUMBER OF UPDATES                                                             136
   NUMBER OF ACCESSES                                                            749
   MAXIMUM/CURRENT NUMBER OF CASES                                              10/6
   MAXIMUM/CURRENT NUMBER OF RECORDS                                    200010/92726
   CURRENT LOADING FACTOR                                                        .50
   NUMBER OF DATA FILE INDEX LEVELS                                                4
   MAXIMUM ENTRIES PER INDEX LEVEL                                                84
   INDEX/DATA BLOCK SIZE IN WORDS                                            253/511
   ACTIVE/INACTIVE INDEX BLOCKS                                                 28/0
   ACTIVE/INACTIVE DATA BLOCKS                                                1371/0
   KEY SIZE IN BITS                                                               94
   MAXIMUM/MINIMUM RECORD SIZE IN WORDS                                          3/2
   NUMBER OF COMMON VARIABLES                                                      1
   COMMON INFORMATION RECORD SIZE IN WORDS                                         3
   MAXIMUM INPUT COLUMNS                                                          80

  RECORD TYPE CONTENTS.

   RECORD TYPE    NUMBER OF  MAXIMUM   TOTAL IN  LENGTH
   NO.  NAME      VARIABLES PER CASE   DATA BASE (WORDS)

    1. (BOTANY )      7       150000      92720      2
```

APPENDIX 4 Contributions to Architectural Diversity (Williams α) by Vegetative and Reproductive Structures of Major Plant Groupings (Site A).

	1980						1981					
	MAY	JUNE	JULY	AUG	SEPT	OCT	MAY	JUNE	JULY	AUG	SEPT	OCT
Vegetative α												
Annuals	4.6	11.8	10.4	11.9	11.1	14.5	8.8	8.5	4.8	4.2	11.4	9.1
Biennials	-	1.2	0.9	8.3	0.9	2.3	3.2	3.4	1.5	1.7	2.4	0.3
Perennials	1.6	4.3	6.0	7.3	5.5	5.6	10.8	7.4	6.9	8.3	11.0	8.2
Gramineae	∞*	3.0	2.4	3.2	2.3	1.6	2.5	2.3	1.7	2.4	1.9	1.7
Reproductive α												
Annuals	-	5.1	10.7	14.2	9.1	2.5	5.2	10.2	4.7	5.2	1.7	0.8
Biennials	-	5.7	0.9	2.4	-	-	-	4.6	5.5	0.8	-	-
Perennials	-	-	4.2	5.9	2.7	2.6	-	-	8.6	11.3	4.9	-
Gramineae	-	1.1	1.2	3.2	1.2	0.3	0.6	1.6	2.2	1.7	2.3	0.9

* $n = 1$, $s = 1$

APPENDIX 5 A List of the Insect Families in Each Trophic Guild

Herbivores

Collembola	Sminthuridae
Orthoptera	Acrididae
Heteroptera	Miridae
	Lygaeidae
	Coreidae
	Pentatomidae
	Cydnidae
	Tingidae
	Berytinidae
	Rhopalidae
	Piesmidae
Homoptera	Aphididae
	Cercopidae
	Cicadellidae
	Delphacidae
Thysanoptera	Aeolothripidae
	Thripidae
Coleoptera	Chrysomelidae
	Curculionidae
	Elateridae

Predators

Heteroptera	Anthocoridae
	Nabidae
	Saldidae
Neuroptera	Chrysopidae
	Hemerobiidae
Coleoptera	Cantharidae
	Carabidae
	Coccinellidae
	Staphylinidae
Araneae	Aranidae
	Clubionidae
	Gnaphosidae
	Linyphiidae
Araneae	Lycosidae
(cont)	Mimetidae
	Pisauridae
	Salticidae
	Tetragnathidae
	Theridiidae
	Thomisidae

Omnivores

Heteroptera	Berytinidae
	Miridae
Coleoptera	Cryptophagidae
	Lathridiidae
	Histeridae
	Nitidulidae
	Oedemeridae
	Phalacridae
	Silphidae

APPENDIX 6: Life-history strategy information for individual insect herbivore species found in the study areas. Host-plant group is denoted by A, B, P and G for annual, biennial and perennial herbs and Gramineae respectively. Specialisation is given for the three specialist types and the generalists. Mode of feeding is referred to by C (chewers) and S (sap-feeders); this latter group is further specified as feeding on mesophyll (M), phloem (P) or xylem (X). Voltinism refers to the number of generations/year.

? = unknown; ? after information = suspected.

Superscripts for Chrysomelidae and Curculionidae denote whether larvae feed on roots (R), above-ground vegetative tissue (V) or reproductive structures. Note that combinations of host structures attacked may occur.

Source references to particular species are included. A General Reference list is provided at the end of this appendix.

	HOST PLANT GROUP	SPECIAL -ISATION	MODE OF FEEDING	VOLT -INISM	OVER-WINTERING STAGE	SOURCE
Orthoptera (Acrididae)						
Chorthippus brunneus (Thunb.)	G	S3	C	1	EGG	See General
C. parallelus (Zett.)	G	S3	C	1	EGG	Reference list
Hemiptera Heteroptera						"
Miridae						
Adelphocoris lineolatus Goeze	A,B,P	G	S(M)	1	EGG	
Calocoris norvegicus Gmel.	A,B,P	G	S(M)	1	EGG	
Capsus ater L.	G	S3	S(M)	1	EGG	
Dicyphus epilobii Reut.	P	S1	S(M)	1-2	EGG	
D. errans (Wolff)	A,B,P	G	S(M)	1-2?	ADULT	
Leptopterna dolobrata (L.)	G	S3	S(M)	1	EGG	
Lygus rugulipennis Popp.	A,P	G	S(M)	2	ADULT	
Notostira elongata (Geoff).	G	S3	S(M)	2	ADULT	
Orthocephalus saltator (Hahn)	A,B,P	S3	S(M)	1	EGG	
Pachytomella parallela (Meyer-Dür)	A	S2	S(M)	1?	EGG?	
Phytocoris varipes Bohem.	A,B,P	G	S(M)	1	EGG	
Plagiognathus arbustorum (F).	A,B,P	G	S(M)	1	EGG	
P. chysanthemi (Wolff)	A,B,P	G	S(M)	1	EGG	
Stenodema calcaratum (Fall).	G	S3	S(M)	1	ADULT	
S. laevigatum (L.)	G	S3	S(M)	1	ADULT	
Lygaeidae						
Kleidocerys trunculatus (Wlk.)	?	?	S(M)	?	?	
Scolopostethus affinis (Schill).	?	?	S(M)	?	?	
Stygnocoris fuligineus (Geoff).	?	?	S(M)	2	ADULT, NYMPH	
S. pedestris (Fall.)	?	?	S(M)	1	EGG	
Taphropeltus contractus (Herr.-Schaeff).	?	?	S(M)	1 or 2	ADULT	
Tingidae						
Tingis ampliata Herr.-Schaeff.	?	?	S(M)	1	ADULT	
Tingid sp.	?	?	S(M)	?	?	
Berytinidae						
Cymus claviculus (Fall.)	A	G	S(M)	1	ADULT	
Berytinus minor (Herr.-Schaeff.)	A,P	S2	S(M)	?	ADULT	
Rhopalidae						
Rhopalus parumpunctatus Schill.	A,B,P	G	S(M)	1	ADULT	
Strictopleurus punctato-nervosus (Goeze)	A,B,P	S3	S(M)	1	ADULT	
Piesmidae						
Piesma maculatum (Costa)	A	S1	S(M)	2	ADULT	
Coreidae						
Coreus marginatus (L.)	A,P	S3	S(M)	1	ADULT	
Cydnidae						
Cydnid sp.	?	?	S(M)	?	?	
Hemiptera-Homoptera						
Aphididae	?	?	S(P)	?	?	See also General Reference list
Cercopidae						
Philaenus spumarius (L.)	G	S3	S(X)	1	EGG	Wiegert (1964)
Neophilaenus lineatus (Puton)	G	S3	S(X)	1	EGG	Prestidge (19

Continued....

APPENDIX 6 : (Cont)

	HOST PLANT GROUP	SPECIAL-ISATION	MODE OF FEEDING	VOLTINISM	OVER-WINTERING STAGE	SOURCE
Cicadellidae						Hill (1976);
Adarrus ocellaris Rib.	G	S3	S(P)	2	EGG	Port (1978)
Agallia ribauti Oss.	G	S3	S(P?)	1	ADULT	Payne (pers comm).
Aphrodes albifrons (L.)	G	S3	S(P?)	1	EGG	"
A. bicinctus (Schrank)	G	S3	S(P?)	1	EGG	"
A. histrionicus (F.)	G	S3	S(P?)	1	EGG	" (80)
Arthaldeus pascuellus (Fall.)	G	S3	S(P)	2	EGG	Prestidge(80)Waloff
Balclutha punctata	G	S3	S(P)	1	ADULT	Waloff (1980)
Diplocolenus abdominalis	G	S3	S(P)	1	EGG	Hill(76)Port(78)Wal- off 80)
Elymana sulphurella (Zett.)	G	S3	S(P)	1	EGG	Hill (1976)
Euscelis incisus (Kirs.)	G	S3	S(P,X)	2	NYMPH	Port(78)Prestidge
E. lineolatus Brullé	G	S3	S(P,X)	2	NYMPH	Prestidge (1980)
Macrosteles cristatus (Rib).	G	S3	S(P)	>2?	EGG	Payne (pers.comm.)
M. laevis (Rib.)	G	S3	S(P)	2	EGG	Port(78)Waloff(80)
M. quadripunctatus (Kirs).	G	S3	S(P?)	>2?	EGG	Payne (pers.comm.)
M. sexnotatus (Fall).	G	S3	S(P)	2	EGG	Waloff (1980)
Mocydiopsis parvicauda Rib.	G	S3	S(P?)	1	ADULT	" ; Payne (pers c.
Typhlocybinae spp.	G	S3	S(M)	?	?	Brown (pers.comm.)
Zyginidia scutellaris (Herr-Schaeff.)	G	S3	S(M)	numerous	ADULT	Port (1978)
Delphacidae						
Criomorphus albomarginatus (Curt.)	G	S3	S(P?)	1	NYMPH	Payne (pers. comm).
Muellerianella brevipennis/fairmairei Wag.	G	S3	S(P?)	2	NYMPH	"
Javesella dubia (Kirs).	G	S3	S(P?)	2	NYMPH	" ; Waloff (1980)
J. pellucida (F).	G	S3	S(P,X)	2	NYMPH	Nuorteva (62) Pres- tige(80)Waloff(80)
Dicranotropis hamata (Bohem).	G	S3	S(P)	1	NYMPH	Hill(76)Prestidge(80
Stenocranus minutus (F.)	G	S3	S(P?)	1	ADULT	Port(78)Waloff(80)
Thysanoptera						See General reference list.
Aeolothripidae						
Aeolothrips intermedius Bagn.	A,B,P	G	S(M)	1 or 2	ADULT?	
Thripidae						
Anaphothrips obscurus Müll.	G	S3	S(M)	1 or 2	LARVA,ADULT	
Chirothrips manicatus Hal.	G	S3	S(M)	1 or 2	ADULT	
Frankliniella intonsa Try.	A,B,P	G	S(M)	1 or 2	ADULT?	
F. tenuicornis Uzel	G	S3	S(M)	1 or 2	ADULT?	
Limothrips cerealium Hal.	G	S3	S(M)	1 or 2	ADULT	
Sericothrips abnormis (Karny)	P	S1	S(M)	1 or 2	ADULT?	
Thrips atratus Hal.	A,P	S3	S(M)	1 or 2	ADULT?	
T. angusticeps Uzel	A,B	S3	S(M)	1 or 2	ADULT	
T. tabaci Lind.	A,B,P	S3	S(M)	1 or 2	EGG?LARVA, ADULT	
Coleoptera						
Chrysomelidae						See General Referen list
Altica palustris Weise.	P	S1	C	1	ADULT	
Cassida vitata^{v} Vill.	A,P	G	C	1	ADULT	
Chaetocnema concinna^{r} (Marsh.)	A	G	C	1	ADULT	
Crepidodera ferruginea^{v,r} (Scop.)	A,B,P,G	G	C	1	LARVA	
Galleruca tanaceti^{v} (L.)	P	G	C	1	EGG	
Gastrophysa polygoni^{v} (L.)	A,P	S3	C	2	ADULT	
Longitarsus flavicornis (Steph.)	A,B	S2	C	1	LARVA	
L. gracilis Kuts.	A,B	S2	C	1	LARVA	
L. kutscherae (Rye.)	P	S2	C	1	?	
L. luridus^{r} (Scop.)	A,B,P	G	C	1	EGG/LARVA/ADULT	
L. melanocephalus^{r} (De.G.)	P	S2	C	1	ADULT	
L. pratensis^{r} (Pz.)	P	S2	C	1	EGG/LARVA/ADULT	
L. suturellus^{r} (Duft.)	A,B	S2	C	1	ADULT	
L. succineus (Foud.)	A,B,P	S3	C	1	LARVA?	
Phyllotreta atra (F.)	A,B	S3	C	1	ADULT	
P. diademata (Foud.)	A,B	S3	C	1	ADULT	
P. nemorum^{v} (L.)	A,B	S3	C	1	ADULT	
P. nigripes^{r} (F.)	A,B	S3	C	1	ADULT	
P. undulata^{r} Kuts.	A,B	S3	C	1	ADULT	

Continued.....

APPENDIX 6 : (Cont)

	HOST PLANT GROUP	SPECIAL-ISATION	MODE OF FEEDING	VOLT-INISM	OVER-WINTERING STAGE	SOURCE
Curculionidae						
Amalus scortillum (Hbst.)	A,P	S3	C	?	?	
Apion apricans^{fv} Hbst.	P	S1	C	1	ADULT	
A. assimile ^{f} Kirb.	A,P	S2	C	1	ADULT	
A. carduorum ^{vr} Kirb.	P	S2	C	1	ADULT	
A. craccae ^{f} (L.)	A,P	S2	C	1	ADULT	
A. curtirostre^{v} Germ.	P	S2	C	1	ADULT	
A. dichroum Bed.	A,P	S2	C	?	?	
A. frumentarium^{v} (Pk.)	P	S2	C	1	ADULT	
A. hookeri ^{f} Kirb.	A,B,P	S3	C	1	ADULT	
A. loti^{r} Kirb.	P	S1	C	1	ADULT	
A. marchicum^{r} Hbst.	P	S2	C	1	ADULT	
A. miniatum ^{r} Germ.	P	S2	C	1	ADULT	
A. nigritarse Kirb.	A,P	S2	C	?	?	
A. pisi ^{v} (F.)	A,P	S3	C	1	ADULT	
A. reflexum Gyll.	P	S1	C	?	?	
A. rubens Steph.	P	S2	C	?	?	
A. tenue Kirb.	A,P	S3	C	?	?	
A. trifolii (L.)	P	S1	C	?	?	
A. virens ^{r} Hbst.	A,P	S2	C	1	ADULT	
Ceutorhynchus assimilis^{f} (Pk.)	A,B	S3	C	1	ADULT	
C. erysimi ^{v} (F.)	A,B	S3	C	1	ADULT	
C. floralis ^{v} (Pk.)	A,B	S3	C	?	?	
C. pleurostigma^{r} (Marsh.)	A,B	S3	C	1	ADULT	
C. punctiger ^{f} Gyll.	P	S1	C	1	ADULT	
C. quadridens ^{v} (Panz.)	A,B	S3	C	1	ADULT	
C. rugulosus ^{f} (Hbst.)	A,B,P	S3	C	1	ADULT	
Gronops lunatus (F.)	A,B,P	G	C	?	?	
Gymnetron pascuorum^{f} (Gyll.)	P	S2	C	?	?	
Hypera arator^{vf} (L.)	A,P	S3	C	1	ADULT	
H. nigrirostris ^{vf} (F.)	A,P	S2	C	1	ADULT	
H. postica ^{vf} (Gyll.)	A,P	S3	C	1	ADULT	
Mecinus pyraster ^{vr} (Hbst.)	P	S2	C	1	ADULT	
Miccotrogus picirostris (F.)	P	S2	C	?	?	
Phyllobius maculicornis^{r} (Germ.)	G	S3	C	1	ADULT	
P. pyri ^{r} (L.)	G	G	C	1	ADULT	
Phytobius quadrituberculatus^{v}(F.)	A	S2	C	1	ADULT	
Rhinoncus bruchoides^{v}(Hbst.)	A	S2	C	1	ADULT	
R. castor (F.)	A,P	S3	C	1	ADULT	
R. perpendicularis (Reich)	A	S2	C	1	ADULT	
Sitona lepidus ^{r}(Gyll.)	A,P	S3	C	1	PUPA	
S. hispidulus ^{r} (F.)	A,P	S3	C	1	ADULT	
S. humeralis ^{r} Steph.	A,P	S3	C	1	ADULT	
S. lineatus ^{r} (L.)	A,P	S3	C	1	ADULT	
S. sulcifrons ^{r} (Thunb.)	A,P	S3	C	1	EGG,ADULT	
Tychius pusillus^{f}(Germ.)	A,P	S3	C	1	ADULT	

General references on life-histories

Orthoptera	Raage (1965); V. Brown (pers. comm.)
Heteroptera	Southwood and Leston (1959); Cobben (1978, 1979); V. Brown, G. McGavin (pers comms.)
Homoptera	le Quesne (1960, 1965, 1969).
Thysanoptera	Lewis (1961, 1979); Pitkin (1976) and pers. comm.
Coleoptera	Chysomelidae: Cox (1976) and pers. comm. Curculionidae: Hoffman (1950, 1954, 1958); Sherf (1964); R.T. Thompson and P. Hyman (pers. comms.).

APPENDIX 7 Indices of Similarity Between Insect Herbivores During the First Year of Succession (Site D).

a. Species Composition and Abundance. I_s value above; I_w value (for number of individuals) in italics.

b. Biomass. I_w value

a.

	Year 1				
	May -June	June -July	July -Aug	Aug -Sept	Sept -Oct
Collembola	-	-	-	-	-
Orthoptera	-	-	-	-	-
Hemiptera-Heteroptera		0.66 *(0.56)*	0.66 *(0.29)*	0.60 *(0.29)*	0.91 *(0.47)*
Hemiptera-Homoptera		0.29 *(0.22)*	0.38 *(0.20)*	0.64 *(0.43)*	0.72 *(0.27)*
Total Hemiptera		0.50 *(0.25)*	0.48 *(0.21)*	0.63 *(0.41)*	0.78 *(0.30)*
Thysanoptera	0 *0*	1.00 *(0.65)*	0.66 *(0.53)*	0.40 *(0.06)*	1.00 *(1.00)*
Coleoptera	0.15 *(0.13)*	0.42 *(0.22)*	0.51 *(0.14)*	0.77 *(0.36)*	0.80 *(0.73)*
Total herbivores	0.09 *(0.01)*	0.49 *(0.29)*	0.52 *(0.21)*	0.68 *(0.38)*	0.79 *(0.40)*

b.

	Year 1				
	May -June	June -July	July -Aug	Aug -Sept	Sept -Oct
Collembola	-	-	-	-	-
Orthoptera	-	-	-	-	-
Hemiptera-Heteroptera	-	0.23	0.22	0.14	0.52
Hemiptera-Homoptera	-	0.16	0.11	0.42	0.25
Total Hemiptera	-	0.17	0.13	0.38	0.30
Thysanoptera	-	0.60	0.53	0.06	1.00
Coleoptera	0.54	0.16	0.09	0.33	0.65
Total herbivores	0.12	0.17	0.11	0.36	0.38

APPENDIX 8 : Differences Between Site D and Site A (Year 1) in Williams α - Diversity of Chewing and Sap-Feeding Insects

Year 1

	MAY		JUNE		JULY		AUG		SEPT		OCT	
	D	DIFF	D	DIFF	D	DIFF	D	DIFF	D	DIFF	D	DIFF
Chewers	∞^5	-5.7	13.1*	+3.4	4.2	+0.9	6.8	+1.6	7.3	-0.2	7.1	+1.4
Phloem-feeders	-	0	0.6	-1.3	0.9	-0.2	1.6	-0.1	1.3	-0.4	1.6	+0.4
Xylem-feeders	-	0	-	-0.8	∞^1	-0.2	0.9	+0.3	0.4	0	0.5	-0.1
Mesophyll-feeders	-	0	2.6	+1.0	2.6	-2.7	2.9	-1.6	3.5	+0.1	2.5	-0.5
Total sap-feeders	-	0	1.8	-1.6	3.4	-1.7	5.1	-0.9	5.3	+0.2	5.4	+1.4
Total herbivores	∞^5	-5.7	5.2	-6.5	7.5	-0.6	11.7	+0.6	11.4	+0.2	12.4	+3.1

*abnormally high value of α due to small values of n of Coleoptera ($n = 15$, $s = 10$). Note also that ∞ represents low values: $\infty^1 = (n = 1, s = 1)$ and $\infty^5 = (n = 5, s = 5)$.

APPENDIX 9 Correlation Coefficients (r) for Comparisons Between Plant Parameters (Site A)

a. Year 1; b. Year 2.

a. YEAR 1	Cover	Abundance	Species richness	Species α	Architecture (No. of structures)	Architectural α	Size (No. of height categories)
Cover							
Abundance	0.77						
Species richness	0.97	0.73					
Species α	0.85	0.42	0.88				
Architecture (no. of structures)	0.88	0.87	0.93	0.67			
Architectural α	0.90	0.79	0.97	0.79	0.98		
Size (no. of height categories)	0.85	0.86	0.84	0.74	0.84	0.84	
Spatial α	0.77	0.70	0.75	0.79	0.67	0.71	0.95
b. YEAR 2							
Cover							
Abundance	0.53						
Species richness	0.66	0.74					
Species α	0.55	0.52	0.95				
Architecture (no. of structures)	0.57	0.98	0.85	0.67			
Architectural α	0.56	0.93	0.92	0.77	0.98		
Size (no. of height categories)	0.61	0.86	0.86	0.74	0.92	0.95	
Spatial α	0.60	0.81	0.86	0.75	0.88	0.92	0.99

Significance levels with values of r in parentheses:- 5% (0.81); 1% (0.91); 0.1% (0.97).

APPENDIX 10 : Correlation Coefficients (r) for Comparisons Between Herb Parameters (Site A)

a. Year 1. b. Year 2.

a. Year 1	Cover	Abundance	Species richness	Species α	Architecture (no. of structures)	Architectural α	Size (no. of height categories)
Cover							
Abundance	0.85						
Species richness	0.91	0.68					
Species α	0.46	0.18	0.74				
Architecture (no. of structures)	0.93	0.89	0.87	0.36			
Architectural α	0.91	0.79	0.96	0.60	0.96		
Size (no. of height categories)	0.81	0.86	0.85	0.60	0.84	0.87	
Spatial α	0.60	0.61	0.76	0.81	0.58	0.72	0.91
b. Year 2							
Cover							
Abundance	0.98						
Species richness	0.52	0.47					
Species α	-0.18	-0.21	0.72				
Architecture (no. of structures)	0.91	0.90	0.77	0.18			
Architectural α	0.75	0.71	0.92	0.43	0.94		
Size (no. of height categories)	0.72	0.69	0.86	0.35	0.91	0.98	
Spatial α	0.55	0.50	0.83	0.44	0.79	0.93	0.96

Significance levels with values of r in parentheses:- 5% (0.81); 1% (0.91); 0.1% (0.97).

APPENDIX 11 Comparison of the Williams Index of α-diversity Between Insect-Grazed and Insect-Free Sites.

a. During the first two years of succession. Site B = insect-free; Site C = insect-grazed.

b. During the first year of succession. Site E = insect-free; Site F = insect-grazed.

∞^1 = (n = 1, s = 1) ∞^2 = (n = 2, s = 2) etc.

a.

		Year 1						Year 2					
		May	June	July	Aug	Sept	Oct	May	June	July	Aug	Sept	Oct
Annuals	B	1.55	1.21	1.85	2.02	3.61	1.43	0.57	2.25	0.41	0.52	-	-
	C	1.59	1.09	1.07	1.69	3.81	∞^7	0.96	1.57	0.52	0.41	-	-
Perennials	B	-	0.51	1.92	1.68	2.19	1.17	0.54	0.86	0.81	1.10	0.15	0.21
	C	∞^1	0.52	0.99	1.28	1.08	1.06	0.83	0.82	0.43	0.31	0.56	-
Gramineae	B	∞^1	1.58	0.99	1.20	0.47	0.46	0.44	0.45	0.44	0.28	0.27	0.27
	C	∞^1	1.46	0.28	0.78	0.56	0.56	0.47	0.45	0.43	0.28	0.27	0.27
Total	B	1.60	3.61	3.75	4.52	5.49	2.61	1.30	2.72	1.15	0.60	0.42	0.43
	C	1.52	2.06	2.21	3.41	5.59	2.76	1.51	2.44	1.04	0.56	0.38	0.40

b.

		Year 1					
		May	June	July	Aug	Sept	Oct
Annuals	E	∞^2	2.39	2.92	2.46	3.14	0.52
	F	∞^3	1.72	1.92	1.52	2.50	0.43
Perennials	E	-	1.41	1.57	0.43	1.21	0.51
	F	-	1.17	1.55	0.51	1.60	0.49
Gramineae	E	∞^1	0.19	0.49	0.29	0.28	0.12
	F	-	0.11	0.60	0.36	0.50	0.13
Total	E	∞^3	4.90	5.01	4.27	3.07	0.95
	F	∞^3	3.60	3.98	3.63	2.74	0.63

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Seasonal Changes in the Architecture of Natural Plant Communities and its Relevance to Insect Herbivores

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Summary. The seasonal changes in plant community architecture and its importance to insect herbivores during the ruderal-early stages of an experimental secondary successional gradient are described. The dominant group of insect herbivores, the Auchenorrhyncha (Hemiptera: Homoptera) are considered together with their host plants, the Gramineae. Here plant structure is analysed in terms of the height profile of the vegetation and its complexity of form. Correlations between insect and plant parameters indicate that the number of different types of grass structure (a measure of architecture) account for 79% and 86% of the variance in leafhopper species richness and total abundance respectively. It is suggested that plant architecture may influence insect herbivore diversity by providing a templet, principally in terms of resource availability, for insect colonisation.

Introduction

Major factors believed to influence insect herbivore diversity on plants include plant chemistry and defence mechanisms (e.g. Southwood 1973; Lawton 1976; Levin 1976; Prestidge and McNeill 1982), plant 'apparency' (Feeny 1975, 1976), species-area relationships (e.g. Southwood 1960; Strong 1974, 1979) and plant architecture (e.g. Lawton 1978; Southwood et al. 1979). Correlations between insect herbivore diversity and plant architecture, or 'living space' (Lawton 1978), have been found in a number of studies. Differences in architectural complexity between major plant groupings, or within particular taxa, may in part explain corresponding differences in the diversities of their insect fauna (e.g. Lawton & Schröder 1977; Strong and Levin 1979; Neuvonen and Niemelä 1981). In several studies of single plant species good correlations of phytophagous insect diversity with seasonal changes in architecture have been found (e.g. Cameron 1972; Davis 1973; Root 1973; Lawton 1978), although plant architecture has been measured in a number of different ways.

There have been relatively few studies in which the plant architecture (cf. structure) of natural communities has been studied. The seasonal changes in plant architecture of a habitat are likely to be of considerable importance to herbivorous insects, especially when the plants are annuals (or biennials) when all (or most) of their growth occurs in a single season.

The present study analyses plant structure in terms of the above-ground height profile of the vegetation and its complexity of form (measured as the number of plant structures available to insects). The former is referred to as a spatial (or size) attribute and the latter as architecture. The work traces the change in plant structure through the season and considers this as a templet for herbivorous insects. It employs part of an experimental successional gradient created at Silwood Park, Berkshire and focuses on the first year of succession when the turnover of plant species is known to be at a high level (Southwood et al. 1979). Here we describe the dominant group of herbivorous insects, the Auchenorrhyncha, and the plants on which they feed, the Gramineae. Such a study enables the relative importance of the plant's spatial and architectural attributes to be assessed, since the species richness of the grasses is relatively low. The remainder of the herbivorous insect fauna and its relation to the dicotyledonous vegetation is part of an intensive study currently being undertaken by C. Stinson.

Materials and Methods

The experimental site was an area of arable land, harrowed in March and left to recolonise. Such a site is referred to as a Young Field with both ruderal and early successional plant species (see Southwood et al. 1979). Green plants and invertebrates were sampled six times during the growing season (at monthly intervals from early May to late October). Details of the sampling methods are given in Southwood et al. (1979) although here the sample size was increased considerably (plants: a total of 1,350 point quadrats, insects: a total of 135 D Vac samples). The samples were divided equally between 45 subplots each 3 m × 3 m. Measures of plant species or taxonomic, spatial and architectural diversity were based on plant species, height categories and plant structures respectively. Williams α is used as the measure of diversity. In this study similar structures (e.g. mature leaf) of different species were considered as architecturally distinct and were recorded as such. This leads to a more detailed description of architectural diversity than in earlier work. The results described here are taken from 1980, replication in 1981 showed a remarkable similarity in all parameters.

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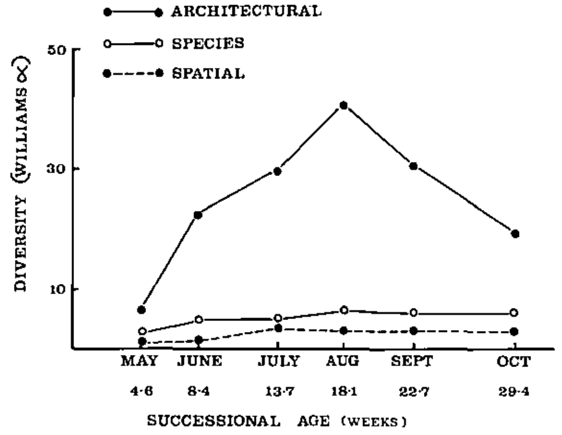

Fig. 1. Seasonal development in taxonomic, architectural and spatial diversity

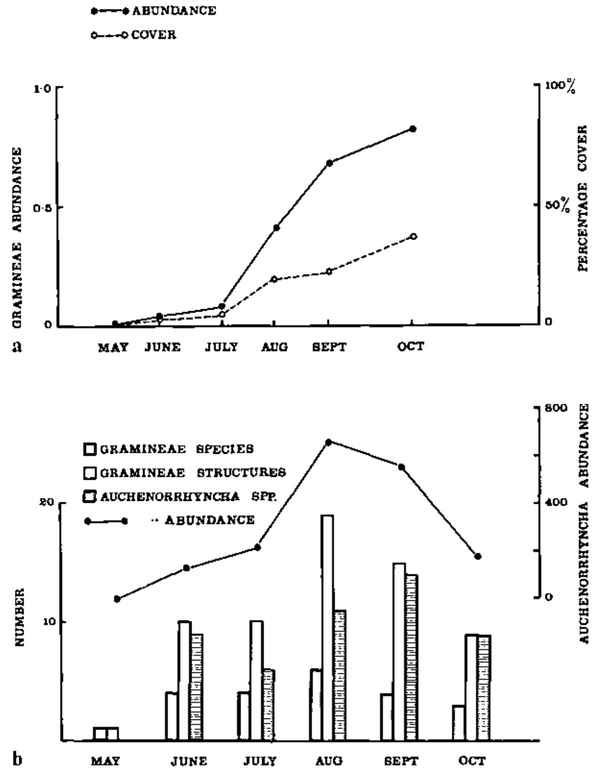

Fig. 2a, b. Seasonal trends in: **a** Percentage cover and abundance (mean number of touches per point quadrat) of Gramineae **b** The number of grass species, structures and the associated leafhopper fauna, (for the successional age at each sample date see Fig. 1)

Results and Discussion

Figure 1 shows the seasonal development of taxonomic, spatial and architectural diversity in the ruderal-early successional site during 1980. Although plant taxonomic and spatial diversity remained relatively low but fairly stable throughout the season architecture rose rapidly to a peak in August and then declined.

Six species of grasses colonised the site during the first season and both the cover and abundance gradually rose (Fig. 2a; also Brown 1982). 20 species of leafhoppers (15 species of Cicadellidae: 5 species of Delphacidae) were found during the year and the seasonal progression in leafhopper species richness and abundance in relation to the number of grass species and structures is shown in Fig. 2b. The total leafhopper abundance very closely mimics the number of grass structures, or indeed the architectural diversity (Fig. 1).

In Table 1 correlations of plant and insect parameters are given. Both leafhopper species richness and abundance are strongly correlated with the architecture of their host plants as measured by the availability of different structures. The latter gives higher levels of correlation than measures of architectural diversity. The number of grass structures alone accounts for 79% and 86% of the variance in leafhopper species richness and total abundance respectively, and successional gain of leafhopper species closely follows that of grass structures (Fig. 3: $r = 0.98$, $P < 0.001$).

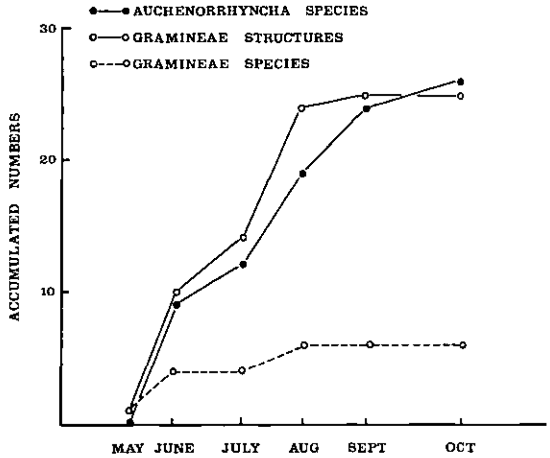

Fig. 3. Relationship between the seasonal gain in grass species and structures and the number of leafhopper species, (for the successional age at each sample date see Fig. 1)

Table 1. Correlation coefficients (r) for comparisons between insect and plant parameters

Leafhopper Parameters	Plant parameters						
	Species richness	Abundance	Species α	Architecture (No. of structures)	Architectural α	Size (No. of height categories)	Spatial α
Species richness	0.77	0.62	0.59	0.89[a]	0.71	0.81	0.68
Abundance	0.80	0.50	0.44	0.93[b]	0.55	0.76	0.70
α	0.70	0.55	0.64	0.78	0.75	0.71	0.60

[a] $0.05 > P > 0.01$ [b] $0.01 > P > 0.001$

The plant's spatial attributes, in terms of height categories or diversity (equivalent to foliage height diversity of some workers), were not significantly correlated with leafhopper parameters, although in other studies these were found to be important factors in the structure of homopteran and other insect communities (e.g. Murdoch et al. 1972; Allan et al. 1975).

The Auchenorrhyncha and their host plants, the Gramineae, form an ideal tool to assess the importance of plant structure to insect herbivores. First, all developmental stages (of the species encountered in this study) are associated with Gramineae and can be sampled by the same methods. In this way data for a single taxonomic group of plant species are provided and yet some of the difficulties of the much needed single species studies are minimised. Second, monocotyledons (and weeds and other annuals) are assumed to have a lower insect species diversity than other green plants (Lawton and Schröder 1977; Strong and Levin 1979) and are therefore appropriate to preliminary studies of this type. Third, the seasonal change in the structural characters of monocotyledons and annuals is considerable and also enhances such a study. Finally, by using only the grasses the species richness of the plants may be retained at a low and more or less constant level and the relative effects of spatial and architectural properties fully assessed.

Seasonal changes in plant architecture reflect an increase in size and complexity of form. The latter also provides a measure of resource availability in terms of feeding sites, resting and oviposition sites in addition to protection from physical conditions and natural enemies. This study has shown conclusively that for the Auchenorrhyncha, associated with early successional plant communities, it is the increase in resources (as expressed by the number of different structure types) that is important. The effect of plant species architecture is greater than the spatial or size attributes in providing a templet for insect colonisation.

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'Stability' of the Fouling Communities on the Pilings of Two Piers in South Australia

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Summary. The subtidal communities of sessile organisms on the pilings of two piers were observed by photography of fixed quadrats over a period of two years. Data are presented on species-composition, relative abundance of species, and maximum longevities of individuals and colonies. The fluctuations in various properties of the communities (e.g. measures of species diversity, and percentage covers of species and phyletic groups) are tested by *a priori* defined criteria for "narrow stochastic boundedness" and most are found to be narrowly bounded, despite considerable turnover of space. We conclude that most properties of the community vary less through time – that is, the community is in a sense more "stable" – than fouling communities previously studied using small plates immersed for relatively short periods. Long-lived species are relatively more abundant on the pilings than in plate-studies. These differences are attributed to the large size and long period of submersion of the pilings. Our results appear similar to those of other studies on large, old substrata.

Introduction

In the field of community ecology stability has many definitions (e.g. see Elton 1958; MacArthur 1955; Margalef 1969; May 1975; Holling 1973; Orians 1975; Whittaker 1975; Goodman 1975; Sutherland 1981). One of the most easily employed meanings is the idea of constancy, that is, of little or no variability over time in some variable which describes the community. Others, such as that preferred by Sutherland (1981) which concerns the effect of perturbations, cannot be employed until one knows much about interactions within the system in question.

In this paper we shall use the word stability in the sense that the amplitude of fluctuation of the community variable is small. (See Whittaker (1975) for other meanings of "constancy".) The meaning of "small" is defined using Keough and Butler's (in prep.) concept of "narrow stochastic boundedness" (see *Data Processing and Analysis*).

Many fouling communities are characterized by continuous, large and unpredictable changes in the abundances of species over time (Sutherland 1976; Sutherland and Karlson 1977). Sutherland and Karlson (1977) propose that this lack of constancy is due to three aspects of the life-histories of the species in these communities, namely short life span, variable recruitment and the unequal ability of species to invade occupied substratum and resist larval recruitment. In these communities free space is vacated frequently and often a cleared patch is invaded by a species different from the previous occupant.

However, the investigations giving rise to these generalizations were conducted on artificial plates, often no larger than 232 cm^2, which had been submerged at the longest for 4 years (Sutherland 1974, 1975, 1976; Sutherland and Karlson 1973, 1977), and the identity and abundance of sessile organisms established on a piece of substratum are often a function of its age (Jackson 1977; Osman 1977; Karlson 1978; Harris 1978; Anger 1978; Russ 1980) and its size (Jackson 1977; Keough 1981).

This paper describes the structure of the fouling communities on the subtidal sections of pilings supporting two piers in the Gulf of St. Vincent, South Australia (Fig. 1). In both cases the communities under investigation have had access to the pilings for 15 years.

We conclude that the communities we have observed are more "stable" than those studied on plates and comprise a greater proportion of long-lived species, with the ability for rapid vegetative extension, and argue that this can be explained by the large size and long period of submersion of the pilings.

Materials and Methods

Study Areas

A description of the first study site, Edithburgh pier (Fig. 1 A) is given in Kay and Keough (1981).

The second study site, Rapid Bay pier (138° 11′ E, 35° 31′ S) extends 395 metres into a northerly facing bay on the eastern side of the gulf (Fig. 1 A, B). Field work was restricted to the steel "tee head" section (Fig. 1 B) which consists of six "dolphins", three each side of a central platform, connected by walkways. The pilings are H-shaped, 42 cm × 25 cm, in cross section (Fig. 1 C). All pilings were originally coated with bituminous tar and were at least 15 years old when the survey began. The "tee head" section stands in nine metres of water at M.L.L.W. and is sur-

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