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Syed Shahid Shaukat

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APPROACHES TO THE ANALYSIS OF RUDERAL WEED VEGETATION

by

Syed Shahid Shaukat

Department of Plant Sciences

Submitted in partial fulfillment
of the requirements for the degree of
Doctor of Philosophy

Faculty of Graduate Studies
The University of Western Ontario
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ABSTRACT

The investigation which I described in this thesis focused on methodological problems in community ecology as well as the actual properties of structure and composition in ruderal weed communities. The study sites were located within the city limits of London, Ontario. Concerning the methdodology, the problem of the choice of an optimal plot size for phytosociological sampling was addressed on an experimental basis. As an outcome, an effective and efficient procedure was developed. In addition, various conventional vegetation data types used in phytosociology were evaluated for their suitability to depict underlying group structure and trends in vegetation. The untransformed ordinal data sets yielded comparable pattern information to that of percentage cover data. However, as further analyses have shown, presence/absence data gave different results from those obtained with the ordinal data.

The problem of data reduction and minimization of misclassification was also investigated. A ranking procedure based on within species sum of squares was developed and described. Studies on this method revealed that its principal advantage lies in its compatibility with important numerical techniques. Using different ranking techniques to identify species of low importance at various cut-off points, it was found that relatively few species in a data set carry the bulk of pattern information. An iterative rank-clustering technique using the within species sum of squares (ranking) and within clusters sums of squares (clustering) was found to reduce 'noise' and thereby increase the clarity of the definition of inherent group structure.

The present investigation focuses on three ruderal habitats (i.e., man-made habitats created by or subject to severe human disturbance), namely, old fields, vacant lots, and topsoil mounds for quantitative examination of the vegetation and its relationships to environment. Vegetation was sampled using a stratified multistage random sampling design. An optimal plot size (7.5*7.5 m^2) was determined in a pilot study and quantitative vegetation data were gathered (251 plots). Soil samples from each plot were analysed physically and chemically. Data sets from each habitat were submitted to analysis by clustering techniques and ordinations.

The vegetation types resulting from cluster analyses for each data set were found to be interpretable with respect to a temporal (successional) sequence of the sites. Besides suggesting potential continuity in vegetation, ordinations disclosed successional trends and environmental gradients. Variation in environmental factors such as moisture availability and nutrient supply were found closely associated with the successional trends.

The successional patterns of each of the three habitats, though unique in many respects, had a general likeness with respect to invasion and dominance of life-span categories. Annuals were most prominent in the earliest stage. Biennials generally attained dominance in the second year but often remained conspicuous until the fourth year of succession. Perennials though present in the first two years did not attain predominance until the third or fourth year of succession and remained so afterwards. Succession-diversity trends were interpreted in terms of an r-K selection continuum. General diversity (H') was found to vary as a function of equitability.

Secondary succession appeared to be an orderly, directional and somewhat predictable process. The successional patterns have supported the initial floristic composition hypothesis of Egler. An attempt was also made to fit generalized models of secondary succession to the oberved successional pattern. This was achieved with partial success.

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CHAPTER 1

INTRODUCTION

1.1 Weeds and their categories

Weed communities prevailing in crops, along roadsides, in waste places, fallow fields and other rural or urban situations constitute an important part of the semi-natural vegetation of a region. Such communities are ecologically as well as economically of great significance. Since 'weed' is not a scientific term but a word in general usage, we must have a precise definition of 'weed' before we can comprehend the nature and scope of weed communities. A wide variety of definitions have been proposed (cf. Harlan and deWet, 1965; Wells, 1978; Holzner, 1982) involving relationships of weeds to the activities and interests of mankind (Harper, 1960; Salisbury, 1961; King, 1966; Wells, 1978) or those based on the ecological characteristics of weeds (Bunting, 1960; Pritchard, 1960, Holzner, 1978). The most convenient definition within the scope of the present study seems to be a slightly modified definition of Holzner (1978) who defined weeds as "plants adapted to man-made habitats that often [though not always] interfere with human activities or welfare". It is noteworthy, however, that in spite of the availability of numerous definitions none is completely satisfactory, including the one given above, and it may still be difficult to label a plant species as a weed (Holzner, 1982), since some species are weeds in some situations but not in others.

Weeds may be classified (1) on the basis of their life span, (2) with respect to their usual habitat, and (3) in accordance with the degree of unwantedness (Harlan and de Wet, 1965). The second proposal is obviously appealing to ecologists. Holzner (1978) broadly classified weeds into three categories according to the habitat in which they occur: (1) agrestal (or segetal) which grows on cultivated land; (2) ruderal, which may be found on a wide variety of man-made habitats such as old-fields, roadsides, railway tracks, city dumps, vacant urban lots, etc.; (3) plants that are a part of natural vegetation in which they originate or into which they invade and naturalize (e.g. many aquatic weeds).

Agrestals include weeds that occur in cereal, vegetable and fiber crops, orchards and various kinds of plantations such as that of coffee, tea and rubber. The life-form of agrestal weeds depends to a great extent upon the mode of cultivation, particularly the frequency and season of soil cultivation (Holzner, 1982).

Ruderals constitute a diverse weed group that includes annuals to woody perennials. Ruderals prevail on sites created by or subject to severel human disturbance. Curtis (1959: 413), while classifying the degree and type of artificial disturbance, defined the 'ruderal' habitat as one where "the original community is destroyed and the destructive agent is repeatedly applied". However, once a 'ruderal' site has been invaded by ruderal plants the degree and frequency of subsequent perturbance may be low or negligible. As an example, following invasion of ruderals on abandoned fields succession of communities may proceed uninterrupted for considerably long periods with little or no artificial disturbance.

One reason for the great heterogeneity of ruderal plants is the fact that the community changes with time on ruderal sites are often quite rapid with a variety of life forms dominating various stages of successional development. A characteristic succession on a ruderal site involves a usually short phase of colonization by annuals, with biennials invading shortly. These in turn are dominated by herbaceous perennials which may continue to dominate for many years but are gradually replaced by woody, often heliophilous species. Given enough time and suitable substratum, the latter may eventually be replaced by local natural vegetation. Thus, a temporal gradient exists from ruderal to natural communities (Weber, 1961; Holzner, 1982).

The ruderal communities, particularly those in the early stages of succession are composed of a substantial proportion of agrestals. Such agrestals are typical pioneer species that are endowed with the characteristics of colonizers (Baker, 1965; Harper, 1965). On the other hand, most elements of ruderal vegetation are unable to invade cultivated fields, even if they possess characteristics that enable them to colonize ruderal sites (Holzner, 1982).

1.2 Significance of weed communities

The importance of weed communities lies in the fact that they play a significant ecological role such as:

(1) Establishing as pioneer communities on unvegetated artifically disturbed sites, thereby covering bare soil and reducing erosion, preventing leaching of nutrients and building up organic matter and soil structure.

(2) Competing with the crop or natural vegetation for space, light, nutrients and moisture (Hull, 1973, cf. Glauninger and Holzner, 1982).

(3) Providing a source for new floral element as well as genetic variation (Baker, 1972; Barrett, 1982; Oka and Morishima, 1982).

(4) Weed species or communities can often serve as indicators of habitat conditions (Dale et al., 1965; Kutschera, 1966; Ellenberg, 1979).

The economic importance of weed communities is associated with the following:

(1) Their control and management.

(2) Indirect expenses and losses that are incurred because many weeds harbour insects or fungi which can attack and damage crops.

(3) As source of hazard to man, domesticated animals and equipment.

1.3 The weed communities under study

The present study focuses attention on selected ruderal weed communities within the city limits of London, Ontario. These occur within certain types of unused land, are almost unmanaged, except for sporadic mowing at a few sites, and are not a part of the climatic or edaphic climax of the area. THe weed communities under investigation are associated with three kinds of situation, as follows:

(1) Abandoned agricultural fields.

(2) Sites cleared for construction purposes, where the topsoil has been removed. These will be referred to as 'vacant lots'.

(3) Topsoil mounds, generally located at construction sites or developed subdivisions and are presumably constituted from the topsoil excavated from the respective sites.

The choice of such site (habitat) types was made for the following reasons:

(a) In each of these habitat types, communities in various stages of secondary succession are abundant and a fairly large population of each habitat type is available.

(b) Origin, age, and freedom from artifical disturbance can be verified.

(c) Whereas a vast number of studies on old-fields have been conducted in United States and other countries, no such study has been conducted in Canada. Studies on topsoil mounds and vacant lots are few, mostly in Europe, but none in Canada.

1.4 Objectives of the study

The objectives of the present research are multifold, as follows:

1. To develop an effective and efficient methodology for sampling weed communities. This methodology should be applicable under a wide variety of conditions. Of particular importance here are sampling design, and the size of sampling unit.

2. To examine the group structure in vegetation (i.e., vegetation types) on an objective basis. Here, the interest centres on the notions and methods of cluster analysis and their suitability. A clustering technique is considered suitable if it is capable of producing a meaningful classification when a structure is known to exist. An attempt is made to develop a method capable of producing a stable classification by minimizing the effects of random events.

3. To relate vegetation types to present environmental conditions as well as the past disturbances.

4. To disclose coenoclines (environmental gradients) and to reveal relationships between vegetation and environmental gradients. Of principal concern here are concepts regarding linearity/non-linearity and continunity/discontinunity of variation in samples.

5. To trace community dynamics by data analytical means with the help of a static model. This problem is approached by the use of ordination and analysis of concentration.

6. To study the effect of data type on the results obtained by classification and ordination.

7. To study the effect of data reduction on classification and ordination. Here, the effect of reduced number of species (by eliminating unimportant ones from data set) on the resulting classification and ordination was examined.

1.5 Literature review

1.5.1 General

The literature review presented in this section pertains only to phytosociological and ecological aspects of weed communities. Literature relevant to methodological developments is reviewed in the appropriate sections of Chapter 2.

Before reviewing the literature on weed communities it would be pertinent to briefly mention the work that has been done on weed floras, specially the local weed flora and the ecology and biology of individual weed species. The agrestals or the weeds of arable land, which constitute the most important group from an economic standpoint, have been the object of greater concern to the weed ecologists and biologists than other weed groups such as ruderals, aquatic weeds, grassland weeds, etc.

Substantial effort has been made in the compilation of local or regional weed flora (e.g. Montgomery, 1964 for northern United States and Canada; Alex and Switzer, 1976 for Ontario) and determining the geographic distribution of weed species across various regions (King, 1966; Holm et al., 1977; Alex, 1982). A weed flora not only provides the lists and taxonomic features of weeds of a region but almost invariably provides useful information regarding their origin, distribution, the usual habitats of their occurrence, and control measures (e.g. Frankton, 1955).

A great deal of attention has been paid to the biology of individual weed species (e.g. Williams, 1963; Palmer and Sagar, 1963; Sagar and Harper, 1964; Sukopp, 1971; Baskin and Baskin, 1979; Burdon, 1983). In Canada, such intensive studies on the biology of individual weed species began with a proposal by Cavers and Mulligan (1972). Since then substantial contributions have been made in this area of research (e.g. Turkington et al. 1978; Bassett and Crompton, 1978, 1982; Gross and Werner, 1978; Best et al., 1978, 1980; Cavers et al., 1979, 1980; Turkington and Cavers, 1979; Miyanishi and Cavers, 1980). The importance of such studies, from an ecological viewpoint, is that they identify and often quantify factors that determine the distribution of single populations.

1.5.2 Agrestal vegetation and communities

Although the present study is concerned with ruderal communities (including those on abandoned fields), a brief literature survey of agrestal vegetation and communities is relevant since it has been suggested that the initial floristic composition, i.e., the vegetative propagules and the soil seed bank at the time of last cultivation, (Egler, 1954), and the last crop on the field (which often has some particular weeds associated with it) (Drew, 1942) are important factors in the composition of early developmental stages of old-field vegetation. Besides, weed communities on arable land are important sources of diaspore for the colonization of many kinds of ruderal sites and for these reasons the vegetation on ruderal sites often resembles the nearby agrestal vegetation. However, only broad areas of research on arable weed vegetation will be mentioned omitting details except where they are pertinent to the present study or are of related ecological or methodological interest.

Numerous weed surveys have been conducted in various parts of the world. For example, Groh (1942) conducted an extensive survey of weeds which encompassed nearly all of the agricultural regions of Canada. A detailed survey by Alex (1966) covered the prairie provinces of Canada. Kankainen (1975) and Raatikainen et al. (1978) carried out weed surveys in cereal growing regions of Finland. Fiveland (1975) recorded the density of annual weeds on arable lands in Norway. Chancellor (1977) carried out a survey of arable weeds in Britain with a view to assessing changes in the weed flora after a period of several years in response to the accelerated use of herbicides. Vorobey (1980) compiled the records of weed surveys carried out in parts of the Ukraine and the Crimea. Chaudhary et al. (1979) conducted an extensive weed survey of central, southern and eastern Arabian Peninsula.

Weed surveys have been conducted for most provinces of Canada, including Alberta (Manson, 1932; Alex, 1966; Dew, 1978), Saskatchewan (Thomas, 1978a, 1979a), Manitoba (Thomas, 1978b, 1979b; Donaghy, 1979), Ontario (Basset, 1955; Richards, 1979), Quebec (Rousseau, 1968) and New Brunswick (Basset, 1954). A review by Alex (1982) condenses the results of various weed surveys in Canada and provides information on the mode of introduction, spread and the distribution of important weeds in Canada.

Often extensive weed surveys use weak sampling designs and may rely on information from secondary sources (e.g. Chancellor, 1977). However, such surveys are useful in that they provide information on the distribution of various weed species in a region. Once the distribution of weed species in a region is known, an explanation for different patterns of occurrence may be sought. For example, the distribution of weed species in the three Prairie Provinces of Canada (Manson, 1932; Alex, 1966) corresponds well with the Great Soil Groups recognized by Clayton et al. (1977) (Alex, 1982). In large scale surveys, the distribution of weeds has also been reported to be correlated with the variation in climatic conditions (Shlyakova, 1980; Walter, 1981).

The widespread distribution of certain weeds over large territories is often attributed to their efficient dispersal mechanism and their colonizing ability over a wide range of habitats. As an example, the ubiquitous distribution of the European weed Taraxacum officinale L.

in Canada is explained on the basis of its excellent fruit dispersal mechanism and the ability to colonize and establish in a wide variety of man-made habitats, apparently without regard to edaphic and climatic conditions (Alex, 1982). The distribution of a weed species, in a region is often correlated with certain crop types (Neogi and Rao, 1980; Ambasht, 1982; Alex, 1982; Wells and Striton, 1982). The intimate relationship between a crop and a weed has been attributed to two important factors: (1) genetic relationships and (2) cultural relationships (Harlan, 1965, 1975).

Weed surveys have often been conducted for a regional or local crop, e.g. maize (Pandeya and Sood, 1974; Doyon and Bouchard, 1981), wheat (Bir and Sidhu, 1979), paddy (Pandeya and Shaha, 1966; Singh and Singh, 1979), sorghum (Pandeya and Purohit, 1976), barley (Nath and Gupta, 1982), coffee (Reddy and Reddy, 1980), tea (Ohsawa, 1982) and jute (Kundu, 1980), etc.

Most of the regional or local weed surveys report only the frequency or density of weeds and do not attempt to recognize communities. However, some studies do provide useful ecological information, such as seasonal variation in species composition (e.g., Pandeya and Shaha, 1966; Anwar-ul-Haq et al., 1981), biomass and productivity of weeds (Pandeya and Sood, 1974; Pandeya and Purohit, 1976) and species diversity (Anwar-ul-Haq et al., 1981).

The influence of management and cultural practices on the agrestal vegetation has been the objective of several investigations. The effect of crop rotation on weed vegetation has been studied by Vrkoi (1977) and Pekanovic (1978). Crop rotation reduced the number of weeds species as well as the weed density. Froud-Williams et al. (1983) studied the influence of cultivation practices and regimes and found a marked effect on weed composition and this was related to the effect of seasonal germination patterns. The effect of fertilizers on weed density and composition has been evaluated in a number of studies (Malicki and Reszl, 1979; Pawlowski and Wesolowski, 1979; Callauch, 1981; Pysek, 1983). Weed density and species diversity were found to be greater on herbicide-free farms than on conventionally managed fields and higher rates of PK application increased the proportion of perennial weeds. Hume (1982) used principal component analysis to study the interaction between fertilizer application and crop rotation on weed composition in wheat. It was found that fertilizer applications tended to reduce community differences between continuous cropping and short-term wheat-fallow rotations.

Change in weed species composition in response to herbicide application have often been studied (Rola, 1979; Anwar-ul-Haq, et al., 1981; Heinzle, 1981). Long-term application of certain herbicides resulted in the more or less complete disappearance of certain weeds (Heinzle, 1981). Anwar-ul-Haq et al. (1981) found that a pre-emergence application of herbicides reduced weed density as well as weed diversity over the controls in a cotton field.

Weed surveys and other investigations concerning the effect of cultural practices on weed composition invariably have not attempted typification nor did they use numerical methods to expose underlying patterns in weed vegetation. However, a number of investigations of arable weed vegetation have been conducted that aimed at the recognition of communities (Kuwabara, 1957; Miyawaki, 1969; Passarge and Juko, 1975; Sharp, 1975; DiMartion and Raimando, 1976; Volf et al., 1977; Kubjatko and Pagac, 1978; Oesan, 1979; Schubert, 1979; Kim and Moody, 1980; Galinato and Sajise, 1981; Nakama et al., 1981; Warcholinsk, 1981; Ishimine et al., 1982; Kuhn, 1982; Konstantinov and Nikolova, 1983). Most of these studies based their categorization on the Braun-Blanquet system (cf. Becking, 1957; van der Maarel, 1975; Westhoff and van der Maarel, 1978) and recognized associations and other vegetational units (e.g., DiMartino and Raimando, 1976; Kubjatco and Pagac, 1978; Schubert, 1979; Nakama et al., 1981; Ishimine et al., 1982). A few studies relied upon numerical methods (Sharp, 1976; Feoli and Raimando, 1979; Kuhn, 1982). Sharp (1976) utilized a program developed by Lieth and Moore (1971) for clustering of species with character and indicator value, in phytosociological tables. Feoli and Raimando (1979) used cluster analysis to analyse weed vegetation of wheat fields in western Sicily. Furthermore, they used various objective methods to test the interrelationships of species groups and environmental characteristics in an attempt to assess the relative merits of such methods (cf. Feoli, 1976). Kuhn (1983) classified 5000 releves into 31 associations with the aid of numerical methods. Streibig (1979) subjected the data on weed communities to cluster and factor analyses to seek relationships between crop types and the weed flora.

In studies where weed communities of arable fields are recognized, they have often been found to be correlated with edaphic conditions (Passarge and Jurko, 1975; Schubert, 1979; Nakama et al., 1981), age of the field (Ishimine et al., 1982) or crop type (Streibig, 1979; Galinato and Sajise, 1981). Thus the knowledge of weed commmunities and their associated environmental characteristics is of great practical significance as the ecological characteristics of weed communities not only reflect the current state of the ecological- productive potential of the agroecosystems but can also aid in formulating control strategies.

1.5.3 Ruderal vegetation and communities

Most investigations on ruderal weed communities have been conducted in urban areas or human settlements, i.e., on ruderal and semi-ruderal sites, in Europe (Sissingh, 1950; St. Grigore, 1968; Falinski, 1971; Gutte, 1972; Sukopp, 1960; Sukopp et al., 1974, 1979; Bornkamm, 1973, 1984; Kopecky and Hejney, 1973; Spiridon, 1973; Wittig, 1973; Gutte and Hilbig, 1975; Passarge, 1976; Elias, 1978, 1979; Hadac, 1978; Matvejeva, 1978; Olsson, 1978; Jarolimek and Mucina, 1979; Mucina and Jaralimek, 1979; Regula-Bevilacqua, 1979; Grull, 1980; Brandes and Brandes, 1981; Mucina, 1981a,b,c; Swies and Pleban, 1983; Parr and Way, 1984). Comparatively less attention has been paid in North America to the analysis of ruderal weed communities with the exception of old-fields (Frenkel, 1970; Bornkamm, 1975; Sharp, 1976). A few such studies have been conducted in other countries, e.g. Australia (Lane, 1976), Japan (Miyawaki, 1969), Peru (Gutte, 1978), Somalia (Raimando and Warfa, 1979). The ruderal sites in the above studies include waste places, vacant lots, roadsides, backyards, parking lots, city dumps, topsoil mounds, dung hills, railway yards, etc., whereas semi-ruderal sites include pastures, pathways, field margins and other peripheral areas where change from arable fields to urban land is in progress. Abandoned fields or old-fields also support ruderal vegetation but because of the huge amount of work that has accumulated in this area, they will be treated separately.

An overwhelming majority of European studies on ruderal or semi-ruderal sites were based on the Zurich-Montpellier (Z-M) methodology (Braun-Blanquet system) as the framework for vegetational analysis and synthesis (e.g. Zajac, 1974; Elias, 1979; Kopecky, 1980, 1984; Passarge, 1976; Olsson, 1978; Grull, 1980; Mucina, 1981a,b,c). The vegetational units recognized by the authors were almost invariably interpreted within the syntaxonomical system of Braun-Blanquet (e.g. Braun-Blanquet, 1932; Tuxen, 1937, 1950; Oberdorfer, 1957, 1979; Gors, 1969) and the vegetational units (association, alliances, orders, etc.) identified in one European country, most often corresponded with those described from other European countries, though not necessarily from similar site types. However, Kopecky and Hejney (1973) appreciated that a number of communities, at a lower level of hierarchy, could not be classed within the syntaxonomic framework of Z-M school. To overcome difficulties associated with the traditional Braun- Blanquet approach, Kopecky and Hejney (1974) developed a new approach to classify lower syntaxonomic units. Three different categories were made to place the ambiguous units: (1) basal communities (Basalgesellschaften), (2) derivative communities (Derivatgesellschaften), and (3) coenologically saturated communities (Sozilogischgesattigte Gesellschaften). They suggested that these lower units should only be dynamically fitted into the main system in accordance with their spatial and temporal changes in species composition.

The vegetational units recognized in the studies on ruderal vegetation (often associations) were generally correlated well with substratum characteristics (Gutte, 1972, Zajac, 1974; Olsson, 1978; Jarolimek and Mucina, 1979; Mucina and Jarolimek, 1979; Mucina, 1981a,b,c; Lejoly and Nyakabwa, 1982), microclimatic factors (Jarolimek and Mucina, 1979) and climatic conditions (Brandes and Brandes, 1981). Variation in species composition and the distribution of communities in relation to changing economic and social factors was described by Kopecky (1981). Mucina (1981a) presented preliminary results of parallalization of ruderal plant communities and the mapping units of potential natural vegetation by making use of the indicator properties of ruderal communities. Successional relations in ruderal communities have also been frequently treated (Gutte, 1972; Zajac, 1974; Elias, 1978; Bornkamm, 1975; Jarolimek and Mucina, 1979). Bornkamm and Hennig (1982) and Bornkamm (1984) experimentally investigated the succession of ruderal communities in the city of Berlin (west). Early successional stages were examined on experimental fields that varied in soil texture and nutrient content. The soil types were found to influence the composition of vegetation and the duration of successional phases. Harvesting first year fields in spring resulted in low species diversity and a higher proportion of grasses. With the vegetational progression from annual stage to stable forb community dominated by *Solidago canadensis* L. the shoot-root ratio declined from 6 to unity. Studies on ruderal vegetation often looked at the community structure, particularly with respect to physiognomy or life-form spectrum (Elias, 1978; Matvejeva, 1978; Jarolimek and Mucina, 1979; Mucina and Jarolimek, 1979;

Regula-Bevilacqua, 1979; Grull, 1980). Most workers found a predominance of therophytes and hemicryptophytes in the ruderal or semi-ruderal communities. Mucina (1981a) also determined the species diversity and equitability for the various associations that he recognized. However, no attempt was made to relate diversity with succession. Kopecky (1980) found the structure and composition of pioneer ruderal communities to depend upon the initial presence of diaspores in soil and/or their immigration from the surroundings. Functional characteristics of communities were almost invariably neglected, though Lejoly and Nyakabwa (1982) dealt with productivity and mineral nutrient immobilization.

The above mentioned studies on ruderal communities were either based on the traditional system of Braun-Blanquet or made no attempt at the recognition of communities or gradients; the objective methods were not utilized. Because of the lack of use of appropriate methods of trend seeking and cluster recognition it is possible that in thse studies some important environmental or temporal gradients would have been overlooked and the subjectively recognized communities may not necessarily represent the inherent group structure in vegetation.

1.5.3.1 Old-field communities

The phytosociological and ecological aspects of old-fields have received a great deal of attention, particularly from the standpoint of secondary succession. Particularly in North America studies dealing with old-field vegetation are numerous. In the United States ecological studies on old-field vegetation have been conducted in the Northeastern Appalachian Plateau (Swan, 1970; Hurd *et al.*, 1971; Dayton, 1975; Mellinger and McNaughton, 1975), the southeastern and mid-Atlantic coastal plain (McCormick and Buell, 1957; Odum, 1960; Woodwell and Oosting, 1965; Golley, 1965; Golley and Gentry, 1966, Levin, 1966), Piedmont region (Crafton and Wells, 1934; Oosting, 1942; Keever, 1950; Bard, 1952; Daniel and Platt, 1968; Buell *et al.*, 1971; Hanks, 1971; Nicholson and Monk, 1974; Pickett, 1982), in the midwest (Booth, 1941; Thomson, 1943; Evans and Cain, 1952; Beckwith, 1954; Evans and Dahl, 1955; Wiegert and Evans, 1964; Bazzaz, 1968, 1975; Perino and Risser, 1972, Hopkins and Wilson, 1974; Tramer, 1975; Kapustka and Moleski, 1976; Reed, 1977; Bailey and Chaney, 1980), and in the southwest (Karpiscak, 1981). Substantial contributions to the phytosociology and ecology of old-fields also have been made in Japan (Numata and Yamai, 1955; Numata, 1956; Kuwabara, 1957; Numata and Suzuki, 1958; Kawakami and Noda, 1963, 1964; Sawada and Sawada, 1963, 1964; Hayashi, 1970, 1977; Hayashi and Numata, 1967, 1968). However, European studies on this topic are few (Barry, 1960; Escarre *et al.*, 1983).

Though most of the preceding articles deal principally with the description and causes of secondary succession (e.g., Crafton and Wells, 1934; Keever, 1950, 1979; Bard, 1952; Beckwith, 1954; Quarterman, 1957; Levin, 1966; Perino and Risser, 1972; Nicholson and Monk, 1974; cf. a review article by Keever, 1983), some studies on old-fields emphasize the distribution of assemblages in relation to environmental parameters (e.g. Evans and Dahl, 1955; Bailey and Chaney, 1980), whilst others concentrate on community structure and function (Getz, 1960; Wiegert and Evans, 1964; Golley, 1965; Reed, 1977; Pinder, 1978; Pratt, 1980).

Most of the studies on old-field succession documented the species composition of fields that had been abandoned for known time periods (e.g. Thomson, 1943; Bard, 1952; Beckwith, 1954; Quarterman, 1957; Bazzaz, 1968; Perino and Risser, 1972) whilst others recorded the sequence of species invasion in the revegetation of a selected field at various time intervals (McCormick and Buell, 1957; Daniel and Platt, 1968; Dayton, 1975; Keever, 1979). A variety of temporal patterns of compositional changes in vegetation have been recorded. Some typical examples of successional sequence following abandonment of cultivated fields are described in the succeeding paragraphs.

Oosting (1942) gave an account of old-field succession in the Piedmont of North Carolina. Digitaria sanguinalis (L.) Scop. was found to occupy fields in the late summer and autumn following the last cultivation. One year after abandonment Erigeron canadensis L. dominated the community composed of 33 species, mostly annuals, that sprang from the seed bank at the time of abandonment. In the second and third year dominance was shifted to Aster pilosus Willd. and Andropogon viriginicus (L.) Scop. Several species of pine (Pinus spp.) were found to invade the fields in the fourth year of abandonment, and in 11 to 15 year-old fields pines represented the climax vegetation.

Thompson (1943) described succession on abandoned fields in the central Wisconsin sand plain area. The vegetation in one-year-old fields was remarkably similar to that during cultivation and was dominated by Ambrosia artemisiifolia L., Cenchrus pauciflorus Benth.

and Erigeron canadensis L. with some European weeds and prairie species in low proportions. Little change was noticed in the second year after abandonment, except for a slight increase in the abundance of prairie plants such as Euphorbia corollata L., Andropogon furcatus B.&B. and A. scoparius Michx. Three to five year old-fields exhibited the prominence of prairie species like Lespedza capitata Michx. and Euphorbia corallata coupled with the invasion of more prairie species but the disappearance of Cenchrus pauciflorus. Prairie plants attained dominance at about 15th year after abandonment. In 37 year-old-fields, it was found that the forest had encroached on the prairie flora and Jack pine (Pinus banksianan Lamb.) and oaks (Quercus spp.) represented the climax vegetation.

Bard (1952) analysed the successional sequence in old-fields on the Piedmont of New Jersey and found it somewhat comparable to that on the North Carolina Piedmont (Crafton and Wells, 1934; Oosting, 1942; Keever, 1950). Ambrosia artemisiifolia L. and Oenothera parviflora L. were dominant in first year fields, followed by Solidago nemoralis Ait., Daucus carota L. and Potentilla simplex Michx. in the second year. By the fifth year, the community was dominated by S. nemoralis and Aster ericoides L. Andropogon scoparius Michx. with some A. virginicus L. attained dominance by the 15th year after abandonment and remained so far more than 45 years. Though Juniperus virginiana L. was found to invade young fields, it did not attain dominance before 60 years of abandonment.

Quarterman (1957) found varied combinations of dominants in the first-year fields in the central Basin of Tennessee. One or more of the major dominants - *Erigeron strigosus* Muhl., *E. canadensis* L., and *Ambrosia artemisiifolia* var. *elatior* (L.) B.&B. were found in association with one or more of the codominants - *Aster pilosus* Willd., *Gnaphalium obtusifolium* L., and *Ambrosia trifida* L. In second year fields, the dominants remained the same but *Ambrosia artemisifolia* var. *elatior* attained the position of leading dominant. Dominance was shifted to *Aster pilosus* Willd. and *Solidago altissima* L. in third year fields. By the eighth year, *Andropogon virginicus* was one of the dominant species. In 25 year old-fields dominant herbaceous species were being replaced by hardwood trees like *Ulmus* spp. and *Celtis* spp.

Bazzaz (1968) studied the plant succession of old-fields in the Shawnee Hills of southern Illinois where corn fields had been abandoned because of low productivity. *Ambrosia artemisifolia* L., *Digitaria sanguinalis* (L.) Scop., *Erigeron canadensis* and *E. annuus* (L.) Pers. were dominant in 1st year fields followed by *Aster pilosus* Willd., *Solidago nemoralis* and *E. annus* in the second year with *S. nemuralis* becoming the dominant in the third year. *Andropogon virginicus* and *Solidago nemoralis* shared the dominance for over ten years but declined gradually afterwards. Deciduous trees and shrubs, such as *Diospyros virginiana* L., *Sassafras albidum* (Nutt.) Nees., *Ulmus alata* Michx., *Juniperus virginiana* L. and *Carya* spp. were found to be the major constituents of vegetation in fields abandoned for 40 years or more.

Hanks (1971) found *Conyza canadensis* (L.) Cronq. [*Erigeron canadensis* L.] and *Anthemis arvensis* L. to be the dominants in 1st and second year abandoned fields on the inner coastal plain of New Jersey. The herbaceous vegetation of 10 to 15-year old-fields was dominated by *Solidago junce*[illegible]t. and *Andropogon virginicus* L., with *Rubus* spp. being important in the shrub stratum. Young forests, dominated by *Liquidamber styraciflua* L. and *Acer rubrum* L., prevailed on 25 to 40 year old-fields.

Hopkins and Wilson (1974) found that the first year abandoned field or in bottomlands of southeastern Indiana was dominated by *Erigeron canadensis*, *E. anuus* and *Setaria glauca* (L.) Beauv., with *Aster ericoides* L. and *Solidago canadensis* L. becoming important in the second year and attaining dominance by third year. By the tenth year most perennial forbs had declined in abundance and were being replaced by *Acer negundo* L., *Populus deltoides* Marsh., *Ulmus rubra* Muhl. and *Prunus serotina* Ehrh.

Karpiscak (1981) studied the secondary succession of abandoned fields in southern Arizona. Exotic species such as *Salsola kali* L. quickly bcame dominant, with *Sisymbrium irio* L., *Descurainia sophia* (L.) Webb., and in some instances *D. pinnata* (Walt.) Britt. dominating in second and third year fields. The introduced grasses of the genus *Schismus* spp. and to a lesser extent, *Erodium cicutarium* (L.) L'Her. and composite *Lactuca serriola* L. together with some native ruderal shrubs followed.

The old-field successional sequences outlined above were studied on different fields that were abandoned for known time periods. The studies that are described in the succeeding paragraphs document successional changes in the same field following abandonment or plowed experimental plowing.

The vegetation of a formerly cultivated field in the New Jersey Pine Barrens was analysed by McCormick and Buell (1957) 5 and 13 months after abandonment. At both the sampling times Panicum virgatum L., P. capillare and Cyperus filiculmis var. macilentus Fern. were the dominant species. However, in the second-year survey 53 additional species were recorded, including 14 species of grasses, sedges and rushes, 33 species of forbs, and 6 woody species.

Daniel and Platt (1968) studied the successional chronosequence in the revegetation of two sites on sandy flood plain of the upper Piedmont Province of Georgia. Erigeron pusillus, Haplopappus divaricatus (Nutt.) Gray were dominant for the first two years, with Monarda punctata L. and Smilax bona-nox L. taking over the dominance in the third year. Pines and hardwoods invaded the fields in 2nd year but did not achieve dominance until the 7th or 8th year of secondary succession.

Bayton (1975) recorded the compositional changes in the early stages of secondary succession in a small field in central New York State and found the species composition to be markedly different from that described for old-fields from southerly locations in United States but similar to that of southeastern Michigan old-fields. In the first year of abandoment, the biennial legume Melilotus alba Desr. was dominant, with Phleum pratense L. and Agrostis stolonifera L. as co-dominants, along with Solidago candensis L., S. graminifolia (L.) Salisb., Erigeron annuus, Trifolium hybridum L. and Chrysanthemum leucanthemum L. as other important species. Two years after abandonment, Phleum pratense L. became dominant, along with Agrostis stolonifera L., Agropyron repens (L.) Beauv., Poa compressa L., Solidago canadensis and Solidago graminifolia as co-dominants. Two important phenomena were noticed in this example of old-field succession: (a) The perennial forb stage that occurred in the 2-year old-fields in other studies was by-passed and instead a perennial grass stage was established in the second year of abandonment. (b) Among the species recorded in the first year field 74% were found to be introduced in contrast to 1 year fields in other studies (Bard, 1952; McCormick and Buell, 1957; Levin, 1966; Bazzaz, 1968; Daniel and Platt, 1968) where at the most 39% of the species were introduced.

Keever (1979) found Barbarea vulgaris R.Br., Setaria spp. and Ambrosia artemisiifolia important in 1st year abandoned fields in southeastern Pennsylvania, with Aster pilosus becoming dominant in 2nd year and remaining so for 3 or 4 years, until replaced by the native shrubs.

The above examples of old-field succession clearly demonstrate that the dominants of various stages of secondary succession differ in different regions to a varied extent. Even where dominants are similar the duration of the stages vary. However, some similarity in the dominant species in old-field seres, irrespective of successional stage seems to prevail in neighbouring regions. Though the observed dissimilarity in dominants can be accounted for, to a certain extent, by geographic differences, it has been found that even closely situated fields that do not differ in soil type, vary with respect to successional dominants (McCormick, 1968; Keever, 1983). However, despite compositional dissimilarity, similarities among the different examples of old-field seres do often exist with respect to life-form dominance in various stages of secondary succession. The succession begins almost invariably with the colonization by annuals and biennials (frequently non-native), followed by herbaceous perennials that often are succeeded by native grasses, and eventually culminates in native (or naturalized) shrubs and trees.

The preceding paragraphs described only the changes in species composition during secondary succession on old-fields. Attempts have also been made to analyse successional changes in community structure and function of old-field seres (Odum, 1960; Golley and Gentry, 1966; Perrino and Risser, 1972; Nicholson and Monk, 1974; Mellinger and McNaughton, 1975; Tramer, 1975; Kapustka and Moleski, 1976). In Aiken, South Carolina the net primary productivity was high in one-year old-fields. The net primary productivity declined in the 2-year fields and remained almost steady up to 7-12 years (Odum, 1960; Golley and Gentry, 1966). Peri[illegible]o and Risser (1972) obtained the above trend in net primary productivity (reported by Odum) in Oklahoma old-fields succession up to stage 2 (9 to 13 year fields). However, a shift to grass dominance in 40 year old-fields was found to result in increased net primary production. Whereas aerial cover, species richness, and dominance more or less increased, species diversity tended to decline with the advancement of the secondary sere.

Mellinger and McNaughton (1975) analysed structure and function of old-field seral communities in central New York State. Species richness [S/Log N] (where S = number of species, and N = total number of individuals) increased, whilst average net primary productivity decreased with successional development. The functional role of species diversity in dictating the relative roles of species in community function was studied by examining the dominance relations in two fields after fertilizer application. Although there was change in the dominant species, the relative dominance pattern remained unchanged. This led Mellinger and McNaughton to suggest that "the relative ability of the dominants to draw resources from the ecosystem is primarily a function of species packing and consequent community diversity, rather than available resources".

The preceding paragraphs dealt only with sequential changes in the composition, structure and function of seral communities in old-field succession. Many articles deal with the causes of these changes. A variety of mechanisms have been suggested to account for successional changes in composition, including competition (Keever, 1950, 1979; Shontz and Oosting, 1970; Werner, 1976), allelopathy (Abdul-Wahab and Rice, 1967; Wilson and Rice, 1968; Parenti and Rice, 1969; Neill and Rice, 1971; Rice, 1974; Jackson and Willemsen, 1976), complex interaction of physical and biotic factors (Rice et al., 1960, Bazzaz, 1968; Gross and Werner, 1982) and soil mineral status and mineralization (Rice, 1976; Haines, 1977; Foster et al., 1980).

Many workers have attempted to make generalizations and to apply or develop models to explain the causes of succession. Bazzaz (1979) regarded the contrasting ecophysiological characteristics of early to late successional species in a sere as the principal cause of community changes in a successional sequence. Among the ecophysiological characteristics emphasized were: seed germination, emergence, and growth and development (including photosynthesis, respiration, transpiration, plant resistance, water use, and growth rate) and competition including allelopathy. The data presented by Bazzaz (1979) suggests the applicability of his model to old-field succession.

The three models suggested by Connell and Slatyer (1977), namely facilitation, tolerance and inhibition, have received considerable attention (Keever, 1979; Pickett, 1982; Escarre et al., 1983). Keever (1979, 1983) supported the tolerance model as the most relevant model to explain the mechanism of old-field succession. However, she pointed out that none of the Connell-Slatyer models can fully explain the causes of early old-field succession. Escarre et al. (1983) found that the three models fit rather well, in turn, at successive stages of old-field succession in a field near Montpellier, France. Hils and Vankat (1982) attempted to test Conell-Slatyer models experimentally. The facilitation model (i.e., Clements' reaction hypothesis) was not supported by the results but the tolerance model and the inhibition model did explain the mechanism of species replacement in old-field succession. Noble and Slatyer (1981) and van der Valk (1980) proposed a scheme for prediction of succession and based upon "vital attributes" or the life history characteristics (similar to those of Bazzaz (1979)). These concepts were found useful in predicting old-field succession in Japan (Hayashi, 1984).

1.6 The study area

The three ruderal habitat types chosen for study, namely old fields, vacant lots and topsoil, were located within the city limits of London, Ontario (Fig. 1.1). The city of London is situated in the centre of southwestern Ontario between 42°55'-43°2' N and 81°8'-31°21'W. The London area is topographically classified as level to predominantly rolling consisting of various types of loams. The area was originally covered by a glacial lake. Silts, clays and gravels received from glacial spillways accumulated on the lake bottom during the Wisconsin recession (10000, 12000 years B.P.). With the advancement of the recession the lake gradually drained to the southwest spreading a gravelly alluvium over the lower parts of the basin (Chapman and Putman, 1973: 236). The mixture of sand, silt and clay resulted in the present loamy soils. The soil of the area, in general, is characterized as Fox fine sandy loam (Webber and Hoffman, 1967). The soil has very good to excessive drainage.

According to Koppen's (1936) system the climate of the area belongs to the type Dfa. The mean annual precipitation is 94 cm out of which 44.6% occurs between May to September (Fig. 1.2). The coldest month is January with a mean temperature of -6°C while the warmest month is July with a mean temperature of 20.5°C. The growing season which on average begins on 11th April lasts for 215 days (Webber and Hoffman, 1967).

The history of each study site differs with its land use. The age of each study site from the time of its last major disturbance was obtained from local residents, landlords, or construction companies. The nature of disturbance was also obtained from these sources and the public utilities commission.

Fig. 1.1 A map of the city of London showing study sites. Only the important roads and streets are shown. Study sites indicated by numbers 1-34 (enclosed within circles) are as follows: 1, Highbury Ave./Trafalgar St.; 2, Clark Sideroad/Trafalgar St.; 3, Stoneybrook St./Bobybrook St. I; 4, Stoneybrook St./Bobybrook St. II; 5, W. Southdale Rd./Wharncliffe Rd.; 6, Springbank/Kernohan Rd.; 7, Oxford West (end); 8, Trossac Ave.; 9, Hyde Park Rd. near Oxford crossing; 10, Clark Sideroad/Pension St.; 11, Boler Rd./Wayne St.; 12, Boler Rd./Baseline Rd.; 13, Trafalgar St./Falcon St.; 14, Airport Rd./Ajax St.; 15, Airport Rd./Dundas Rd.; 16, Clarke Sideroad/Dundas Rd.; 17, Blue Forest; 18, Bradley Ave./Jalna Blvd.; 19, Brunswick Ave./Blanchard Cr.; 20, Southdale Rd./Ernest Ave.; 21, Norwood Ave./Wedgewood Dr.; 22, Deveron Cr./ Sundridge Ct.; 23; Speight Cr./Carlyle Dr.; 24, Sloane Cr./ Bexhill Dr.; 25, Oxford Rd./Industrial Rd.; 26, Aldersbrook Cr./ Ardley Rd.; 27, Dundee Cr./Dundee Pl.; 28, Commissioners Rd./ Wharncliffe Rd.; 29; Grandview Ave.; 30, Bradley Ave./Newbold St.; 31, Aldersbrook Cr./Acron Pl.; 32, Upper Queen's St./ Wilkins St.; 33, Clark Sideroad/near Hamilton Rd.; 34, Huron St./ Vesta Rd.

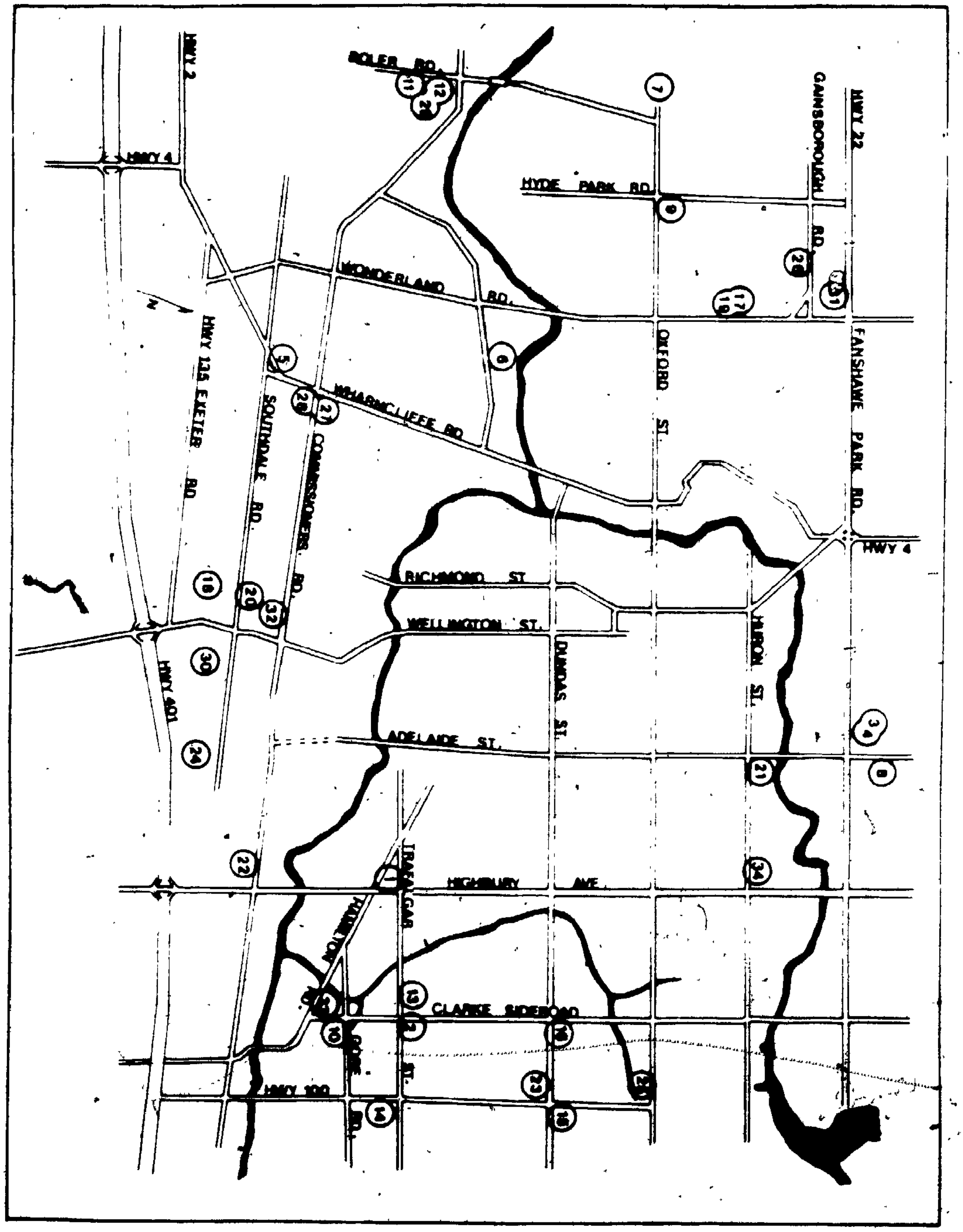
HWY 2
BOLER RD.
HWY 4
HYDE PARK RD.
GAINSBOROUGH RD.
HWY 22
WONDERLAND RD.
N
HWY 135 EXETER RD.
SOUTHDALE RD.
COMMISSIONERS RD.
WHARNCLIFFE RD.
OXFORD ST.
FANSHAWE PARK RD.
HWY 4
RICHMOND ST.
WELLINGTON ST.
DUNDAS ST.
HURON ST.
HWY 401
ADELAIDE ST.
HIGHBURY AVE.
TRAFALGAR
HAMILTON
CLARKE SIDEROAD
GORE RD.
ST.
HWY 100
1
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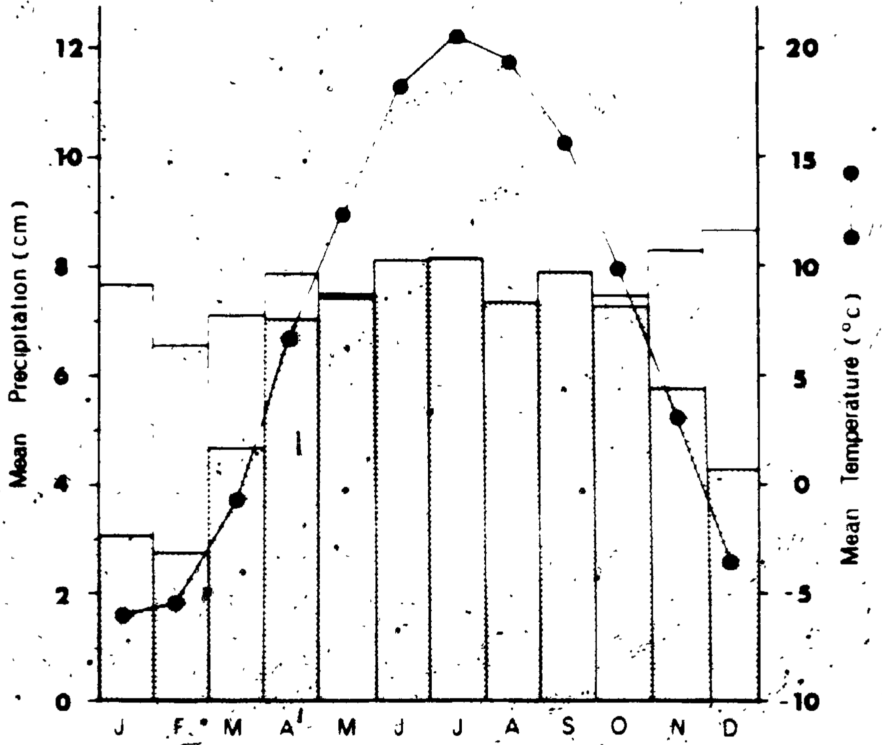
Fig. 1.2 Climatic data for London, Ontario (1941-1970). Shaded area shows the proportion of precipitation received as rainfall while the non-shaded area shows the proportion falling as snow.


Mean Precipitation (cm)
12
10
8
6
4
2
0
Mean Temperature (°C)
20
15
10
5
0
-5
-10
J
F
M
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M
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CHAPTER 2

THE METHODOLOGY

2.1 Sampling

2.1.1 Introduction

An appropriate sampling strategy is of crucial importance in terms of the value of ecological data, the kinds of analytical procedures to which the data can be subjected and the extent to which valid conclusions can be drawn (Mueller-Dombois and Ellenberg, 1974; Green, 1979; Greig-Smith, 1983). It must be pointed out that although the statistical theory of sampling (Sampford, 1962; Cochran, 1963) is the basis of the development of many vegetational (or ecological) sampling procedures, the implementation of statistical sampling methods in field surveys is not as straightforward as ecologists would like it to be. A number of practical and logistic problems create difficulty in strictly fulfilling the theoretical requirements in choosing a statistically efficient design.

Sampling of vegetation generally involves four steps (Mueller-Dombois and Ellenberg, 1974): 1) recognition of the vegetation segments that the worker considers to be within the scope of the study, (2) selection of sampling units within the vegetation segments, (3) decisions regarding the size and shape of sampling units, and (4) the decisions as to what variables should be recorded. These decisions must be based on the objectives of the study.

The purposes of the sampling design in the present study were (1) to capture as closely as possible the total range of vegetational (and environmental) variation within the study areas, (2) to supply suitable data for detection of the underlying group structure in vegetation (i.e., typification), and (3) to provide a basis for recognition of coenoclines and other gradients.

2.1.2 Problems associated with sampling

The first step, in the sampling process is invariably subjective. The vegetation segments of interest are subjectively chosen by the investigator, irrespective of whether the investigator chooses subjective or objective methods for the subsequent selection of sampling units within the segments (Mueller-Dombois and Ellenberg, 1974).

The choice of an effective and also efficient sampling design should take into consideration the objectives, the available sampling models, intended data analysis, choice of variables, economic constraints and practical difficulties (Orlóci, 1978; Green, 1979). The major sampling problems pertaining to phytosociological surveys are dealt with in the following sections.

2.1.2.1 Sampling variance

Vegetation data generally exhibit a fair degree of sampling variance. Owing to this fact, vegetation measurement with extreme care using highly precise methods is unrewarding as the sampling error masks the accuracy gained by the extra recording effort (Goodall, 1970). However, as Orlóci (1978) points out, every effort must be made to eliminate bias. Thus, a vegetation sample should be taken in such a way as to ensure that it is representative.

2.1.2.2 Consequences of multivariate sample

Sampling theory has been developed mostly in relation to univariate samples. However, phytosociological sampling involves mixtures of variables, viz. vegetational and environmental, simultaneously. It is important to see clearly the practical consequences. It is true that if one of the variables is sampled randomly then the other variables associated with the sample will automatically be sampled randomly. Undoubtedly, such a sample would be unbiased with respect to the variables of interest in the sample. However, the choice of a sampling strategy that maximizes the precision of the sample for all the variables is difficult for several reasons (Kenkel, 1981). (1) The difference in the variability of different variables in the sample limits the determination of an optimal sample size that would provide uniform sampling error for all the variables. (2) Since variables in a multivariate sample are likely to have different distributions in the population, a sampling strategy (such as random, systematic, stratified-random, etc.) suitable for one variable is unlikely to be optimal for all the others. (3) The differences in the scales of ground pattern and patch size (Kershaw, 1973; Pielou, 1977: 193-199; Greig-Smith, 1983) of individuals create difficulty in the choice of an optimal size of the sampling unit.

2.1.2.3 Typification as the sampling objective

Statistical sampling theory assumes that estimation is the ultimate objective (Sampford, 1962; Cochran, 1963). Most investigations of vegetational sampling directed their efforts to estimation for which the problem was defined as one of determining the number and size of sampling units (plots) that would allow increased precision by minimizing the sampling error (Bormann, 1953; Wiegert, 1962; van Dyne et al., 1963; McNeill et al., 1977; Taaffe, 1979; Zeide, 1980). These investigations assumed known population limits.

In phytosociological studies, however, the major primary objective is usually typification, i.e. partition of the entire vegetation sample into vegetation types. To this extent partition of the sample is sought that minimize the within and maximizes the between partitions variation as well as covariation. While pursuing typification, the sample obtained must be adequate to supply reasonably accurate description of types. When the objective is estimation large plots, usually rectangular in shape, provide increased precision (Greig-Smith, 1983). However, when typification is the principal aim, large, rectangular plots are detrimental and so are the excessively small ones (Orloci, 1978).

2.1.2.3.1 Determination of an effective plot size

An effective plot size, in the context of typification, may be defined as one which maximizes the average value (expectation) of some suitable dissimilarity function between plots (see Section 2.4). Theoretically, a plot of expected dissimilarity against plot size is unimodal (Fig. 2.1) in which the peak indicates the most effective plot size (Podani, 1982). Alternatively, if expected similarity is used instead of dissimilarity, the minimum value corresponds to the most effective plot size. The following are the relevant notions.

(1) Vegetational heterogeneity. Most types of vegetation are considerably heterogeneous with regard to mingling of species and their ground pattern. Often an analysis of areas of vegetation that appear to be fairly homogeneous, even to a careful observer, may reveal a variety of patterns (Kershaw, 1973). Goodall (1954a) states "... no area of vegetation has ever been shown to be fully homogeneous. It is even doubted whether areas with greater or a smaller variance between replicate samples may be distinguished in natural vegetation." Dahl and Hadac (1949) also hold similar views regarding vegetation. It has also been noted that vegetational heterogeneity increases with an increase in the number of species (Romell, 1926; cf. Goodall, 1952). The compositional heterogeneity in weed communities can be expected to be particularly high, since these communities are usually rich in species.

(2) Objectivity. The sampling method must make provision for the fact that the communities can not be recognized a priori. This is unlike traditional releveing (e.g. Braun-Blanquet) in which one subjectively chooses seemingly homogeneous areas of vegetation by employing preconceived notions about the vegetation and conscious selection of sites.

(3) Maximum dissimilarity. To unravel the underlying group structure of vegetation, plot size should be chosen to maximize dissimilarity between plots. A plot size to achieve this would presumably correspond to the most distinguishable scale of pattern inherent in the vegetation.

2.1.2.4 Logistic considerations

The choice of a sampling design is often based on a compromise between theoretical and logistic considerations. Usually, sampling efficiency and accuracy in a survey have to be sacrificed to economy. Sampling designs other than random, low sampling intensity, reduced number of variables, and less time-consuming methods of data recording are the sectors where savings may be made (Orlóci, 1978). Specifically in the present case, the survey area consisted of a large number of sites scattered throughout the city of London, Ontario. Because of this, simple random sampling was certainly unsuitable. To obtain a representative sample of total range of vegetational (as well as environmental and temporal) variation economically, a more flexible design, namely a stratified multistage random sampling method was employed. Logistic constraints also dictated a certain degree of parsimony in the sectors of sampling intensity and in size of sampling units used in the main survey. Details regarding these will be discussed below.

2.1.3 The sampling strategy of the present study

The sampling strategy used was such as to ensure the elucidation of the vegetational pattern on an objective basis without preconceived ideas regarding types or the environmental factors responsible for the underlying pattern, though the importance of temporal factor was recognized in the decision regarding stratification and sampling intensity. The strategy involved a reconnaissance of the area, a pilot study, and a main survey.

2.1.3.1 Reconnaissance

A reconnaissance survey of the study area was conducted during June, 1981 with three objectives in mind (1) to become familiar with the ruderal weed vegetation in the area, (2) to collect plant specimens, and (3) to record the potential sampling sites and their general characteristics. The area within the city limits of London was traversed and the salient features of the ruderal weed vegetation were noted. Plant specimens were collected, pressed, mounted on sheets and identified. Attempt was also made to attain the ability to recognize plants in their vegetative and seedling stages. A directory of potential sampling sites was prepared comprising a total of 104 sites including 63 abandoned fields, 25 vacant lots, and 16 topsoil mound sites. Three strata were recognized on the basis of site types mentioned, taking into account the kind of disturbance. No attempt was made at subjective recognition of vegetation entities.

2.1.3.2 Pilot survey

A stratified multistage random sampling design was employed for the pilot survey in July, 1981. The principal aim of this survey was to determine an effective and efficient plot size for the main survey. Sampling sites were randomly chosen from each stratum size. Sampling units (plots) were laid randomly at the sampling sites using random coordinates. Since a small sample size was used, no more than 5 plots were scored at each site. At each sampling point square plots of side 2.5, 5, 7.5, and 10 m were laid in a nested system with a common corner. Relative abundance of all species were estimated by a modified

Braun-Blanquet cover abundance scale because it is relatively easy to use (van der Maarel, 1979).

The pilot survey produced 30 releves, each with four different plot sizes. The smallest plot size (2.5 m side) included on average about 25% of the species in the site as determined by species area curves.

2.1.3.3. The main survey

The main survey was carried out from 25th June to 20th August, 1982. It was important to complete the sampling in July and August to avoid a time gradient in the data owing to rapidly changing aspect in weed vegetation. As in the pilot survey, a stratified, multistage random sampling design was used but with higher sampling intensity. This design proved to be flexible and also economic under the circumstances.

Three strata were recognized based on the initial perturbance of the site, namely: (1) abandoned fields, (2) vacant lots, and (3) topsoil mounds. The advantage of stratification is the obvious increase of sampling precision in terms of yielding relatively homogeneous sub-samples. Also, separate analyses can be performed in the different strata, and thus the underlying vegetation-environmental pattern within each stratum (kind of disturbed site) can be examined.

2.1.3.3.1 Sampling sites

Sampling sites were randomly chosen from the three strata, with variable sampling intensities. Proportionally greater numbers of sites were chosen from 'vacant lots' and 'topsoil mounds'. These two strata were comparatively smaller in size than the stratum 'abandoned fields'.

The sampling intensity for these two strata was increased in order to capture the variation in site age.

2.1.3.3.2 Distribution of sampling units

Once the sites had been selected in each stratum, sampling units (plots) were laid down randomly within each site. Randomization was achieved by using random numbers on coordinates that defined sampling points. A scale of half a metre was chosen for the coordinate axes. The number of sampling units used at a site was roughly proportional to the area of the site. However, because of limited time, the maximum number of sampling units at any site was fixed at ten units.

2.1.3.3.3 Size and shape of sampling units

It is generally agreed among ecologists that the choice of an appropriate plot size is an important decision in a vegetation survey as it may determine, to a large extent, the outcome of the study (Evans, 1952; Goodall, 1961; Noy-Meir et al., 1970; Fekete and Szocks, 1974; Goff and Mitchell, 1975; Matthews, 1978a). Suitable plot sizes for various kinds of vegetation have been suggested on the basis of experience with various kinds of vegetation and communities (Cain and Castro, 1959; Mueller-Dombois and Ellenberg, 1974; Westhoff and van der Maarel, 1978). Some investigators resort to the suggested plot size for the kind of vegetation under study. Most studies, however, select a plot size by some empirical approach. The most popular in this connection has been the 'minimal area' approach (Cain, 1938; Vestal, 1949; Hopkins, 1955; van der Maarel, 1970; cf. Tuxen, 1970). The minimal area has been variously defined. However, all definitions seem to converge on the idea that the 'true' characteristics of a community emerge at the scale of the 'minimal area' (Greig-Smith, 1983). The determination of minimal area has been approached in a variety of manners, differing in the selection criteria - namely, (1) species composition, (2) species frequency (constancy), (3) homogeneity of composition, and (4) floristic similarity. The species composition approach involves the determination of a sample area that contains an adequate number of species, i.e., the minimal area is derived on the basis of a species - area curve (Cain, 1938; Vestal, 1949; Hopkins, 1955; Rice and Kelting, 1955; Mueller-Dombis and Ellenberg, 1974). Scandinavian ecologists used to determine the minimal area on the basis of frequency-area (constancy-area) curves (e.g., DuRietz, 1930). Homogeneity of values of quantitative measures of species importance in replicate samples at increasing distance has been used by Goodall (1954b, 1961) in attempts to determine minimal area on a quantitative basis. The floristic similarity approach (Gounot and Calleja, 1962; Moravec, 1973) utilizes the functional relationship between mean floristic similarity (of equal-sized plots) and plot size as the basis for minimal area determination.

The minimal area methods, in particular, the species-area and frequency-area approaches suffer from serious drawbacks and limitations (Pearsall, 1924; Ashby, 1948; Goodall, 1952; Hopkins, 1955, 1957; Poore, 1955; Becking, 1957; Podani, 1984). Poore (1955) noted that the definitions of minimal area, in general, are vague and arbitrary. The procedures used in the determination of minimal area invariably involve subjective decisions, such as the choice of 'uniform' (homogeneous) area in a community. The latter itself is recognized visually. Visual asssessment of homogeneity is, however, unreliable. Furthermore, the minimal area may be prohibitively large or absolutely non-existent in reality (Becking, 1957; Goodall, 1961).

True homogeneity in vegetation is rare. Characteristically vegetation generally exhibits patterns at various scales which are manifestations of scale and the intensity of pattern of the individual species constituting the vegetation. Only Goodall's approach to minimal area takes into account the scale of patterning of individual species. One major problem with this approach is the selection of a single optimal sampling unit for a multispecific assemblage as a whole. Even with respect to individual species, Goodall was unsuccessful in determining the minimal area in a variety of situations because of the fact that the variance of species cover over the sampling units increased continuously with increasing ground distance. Another problem associated with the minimal area approach, in general, is the extrapolation of minimal area from the concrete to abstract community (Podani, 1984).

In the present study, the optimal size of the sampling unit was determined in a pilot study, based on the approach described in Section 2.1.2.3.1. A plot size 10*10 m maximized the expected dissimilarity between plots. The group structure and gradients resulting from the data set pertaining to 10*10 m plot size were found to be highly consistent with those resulting from pilot data sets obtained with 5*5 and 7.5*7.5 m plots and to a lesser extent with that of 2.5*2.5 m plots (Section 3.3.1.4). Thus, to increase sampling efficiency, i.e. to reduce the sampling effort, a plot size of 5*5 m was chosen for the main study.

Square-shaped sampling units were used for several reasons. Firstly, they can be marked out in the field with relative ease. Secondly, they have the advantage of reduced edge-effect compared to rectangular plots of the same area (Greig-Smith, 1983). Thirdly, the square sampling units are less likely to include overlapping community-type boundaries or other discontinuities compared to rectangular plots. Thus, they permit minimization of the within-plot heterogeneity and maximization of between plot variance (Podani, 1984).

2.1.3.3.4 Choice of variables

The choice of vegetation variables depends upon several factors, including the overall precision of the sample required, ease of measurement, and cost. More time-consuming methods may be more precise, but visual estimation of cover is often preferred as it is much more rapid. The higher sampling intensity that can be achieved with rapid visual estimation far outweigh the extra information generated by more precise methods of data recording (cf. Goodall, 1970). Consequently, visual estimation of percentage cover of vascular species (relative to the area of the sampling unit) was used in the present study, without breaking the range of cover values into cover categories.

Duplicate soil samples were randomly collected from 0-20 cm depth using random coordinates (in centimeters) from each plot for physical and chemical labqratory analyses (Appendix A). The following soil properties were determined: pH, organic matter %, water retaining capacity, soil texture (% sand, silt + clay), available phosphorus, nitrate, and exchangeable Ca^{++}, Mg^{++} and K^{+}.

2.2. Ordination

2.2.1 General

Orlóci (1978) defined ordination as the "ordering of points (e.g., releves) on axes to achieve different objectives such as summarizing variation, multidimensional scaling, trend seeking, cluster recognition, prediction, or reciprocal ordering". In principle, satisfactory ordination results are obtained when an appropriate ordination procedure is applied to achieve limited objectives (Orlóci, 1978). A host of formal and informal ordination techniques have been developed in the last three decades and these have been extensively reviewed (Cottam et al., 1978; Whittaker and Gauch, 1978; Noy-Meir and Whittaker, 1978, Orlóci, 1978; Gauch, 1982; Greig-Smith, 1983).

The ordination techniques differ in the degree of robustness and most of the techniques are adversely affected by non-linearity and non-normality of the data structure. In fact the literature abounds in examples of the uncritical use of some popular ordination models. Thus, in order to select an ordination method, it is necessary to examine the limitations and advantages of the available methods in relation to the objectives and the kind of data structure at hand.

2.2.2 Mathematical techniques

The basic mathematical technique by which most ordinations are produced involves two successive transformations of original data. The first transformation is performed to obtain a resemblance matrix. The second, which is generally more complex, derives ordination coordinates from the resemblance matrix. The following ordination techniques were used in the present study:

1. Principal component analysis
2. Reciprocal ordering
3. Non-metric multidimensional scaling

These are briefly treated in the following sections.

2.2.2.1 Principal component analysis

This method (PCA) was developed by Hotelling (1933) and first introduced to ecology by Goodall (1954c). The object of PCA is to transform the original variables, viz. species, of a sample into new variables, the principal components. The latter are linear combinations of original variables. The computations involve the extraction of eigenvalues and eigenvectors of the variance-covariance matrix (centred PCA) or correlation matrix (centred and standardized PCA) of the original variables. The centred PCA algorithm proceeds as follows.

(1) The original pxn data matrix X is first centred by rows (variables)

$$A_{hj} = (X_{nj}-\bar{X}_n)/(n-1)^{1/2} \quad n = 1, \ldots, p; \; j = 1, \ldots, n$$

where X_{nj} is the original value of the variable (species) n in individual (releve) j.

(2) Obtain a matrix of cross products between variables

$$\underset{\sim}{S} = \underset{\sim}{A}\underset{\sim}{A}'$$

where $\underset{\sim}{S}$ is a pxp variance-covariance matrix.

(3) Extract all $t < p$ non-zero eigenvalues $\lambda_1 \geq \lambda_2 \geq \ldots \geq \lambda_t$ and the corresponding eigenvectors $\underset{\sim}{b}_1, \underset{\sim}{b}_2, \ldots, \underset{\sim}{b}_t$. These are obtained by solving characteristic equation

$$|\underset{\sim}{S} - \underset{\sim}{\lambda}\underset{\sim}{I}| = 0$$

where $\underset{\sim}{I}$ is an identity matrix and $\underset{\sim}{\lambda}$ is a diagonal matrix of eigenvalues of $\underset{\sim}{S}$.

(4) The eigenvectors are normalized to obtain vectors of unit length

$$\underset{\sim}{b}_i \underset{\sim}{b}_i' = 1 \qquad i = 1, \ldots, t$$

(5) Finally, compute component scores for individuals (releves)

$$\underset{\sim}{Y} = \underset{\sim}{b}'\underset{\sim}{A}$$

In the algorithm just described the dispersion matrix was obtained between variables (species). This is called the R-technique of PCA. Conversely, if a dispersion matrix between individuals is computed based on the same centred $\underset{\sim}{A}$, then the analysis is the Q-technique of PCA. The D-algorithm, on the other hand, uses a distance matrix $\underset{\sim}{D}$.

Orloci (1978) states that "component analysis is an efficient summarizer, since the components extracted, unlike the species, are uncorrelated (orthogonal) and thus free from the redundancy attributable to linear correlations. Since the components are not redundant, fewer are needed to completely redescribe a set of quadrats [individuals] than the number of species on which the original descriptions are based". PCA to have this property requires that the data sets comply with certain basic assumptions. The major ones are linearity of the covariation and in a broader sense multivariate normality of variables. Biological data sets can only rarely satisfy these assumptions fully. However, the assumptions need only be met rigidly when PCA is used as a hypothesis testing model. Because PCA is a fairly robust technique, when used as a descriptive model, i.e., for the purpose of assessment and interpretation of resemblance structure, it can tolerate a certain degree of violation of assumptions (Orloci, 1978; Green, 1979; Greig-Smith, 1980; Gauch, 1982). In the present study PCA was used only as a descriptive model. The PCA of environmental data sets were performed after normalizing the variables (cf. Austin, 1968: 743). Geary's test of normality was then performed (D'Augustino, 1970). The hypothesis of normality was accepted, in general.

2.2.2.2 Reciprocal ordering

Reciprocal ordering (RO), also known as correspondence analysis (Benzecri, 1969), is also from the family of eigen-analysis procedures. It was developed by Hirschfeld (1935) and introduced to ecology by Hill (1973a, 1974). This technique, sometimes presented as a generalization of Whittaker's (1967) gradient analysis, is an equivalent to Fisher's contingency analysis and Hotellings canonical correlation anaysis (Hill, 1974). The principal advantage of RO is that both individuals (releves) and variables (species) are ordered simultaneously in the course of the analysis. RO is best suited for categorical data given in a pxn contingency table $\underset{\sim}{A}$. Such a table contains frequencies or counts of p variables in n individuals. RO solutions can be obtained by various algorithms. The one that was used in the present study employs eigenanalysis and is reproduced here in accordance with Orloci (1978). The linear assumption regarding the data structure is required. The following is the algorithm.

(1) Obtain a pxn matrix U from the pxn contingency table $\underset{\sim}{A}$ such that the elements of U represent deviations from expectation,

$$U_{hj} = A_{hj}/[A_{h.}A_{.j}]^{1/2} - [A_{h.}-A_{.j}]^{1/2}/A_{..}$$

h = 1, ..., p; i = 1, ..., n

(2) Compute the pxp cross product matrix

$$S = \underset{\sim}{U}\underset{\sim}{U}'$$

a characteristic element of $\underset{\sim}{S}$ is

$$S_{hi} = \sum_{i} U_{hj}U_{ij} \text{ , } j = 1, \dots, s$$

(3) Extract the t non-zero eigenvalues $\underset{\sim}{\lambda}_1 \geq \underset{\sim}{\lambda}_2 \geq \dots \underset{\sim}{\lambda}_t$ and the associated eigenvectors $\underset{\sim}{u}_1, \underset{\sim}{u}_2, \dots, \underset{\sim}{u}_t$ by solving the characteristic equation

$$|\underset{\sim}{S} - \lambda \underset{\sim}{I}| = 0$$

The eigenvalues represent the squared canonical correlations

$$\lambda_1 \geq \lambda_2 \geq \dots \geq \lambda_t = R_1^2 \geq R_2^2 \geq \dots \geq R_t^2$$

The ith eigenvector has the elements

$$\underset{\sim}{u}_i = [u_{1i}\ u_{2i}\ \dots\ u_{pi}] \qquad i = 1, \dots, t$$

such that

$$\underset{\sim}{u}_i' \underset{\sim}{u}_i = 1 \text{ and } \sum_h u_{hi}[A_{..}]^{1/2} = 0 \qquad h = 1, \dots, p$$

(4) Obtain the standardized canonical scores (species scores

$$X_{hm} = u_{hm}[A_{..}/A_{h.}]^{1/2} \qquad m = 1, \dots, t\ ;\ h = 1, \dots, p$$

(5) Obtain the releve scores

$$Y_{jm} = \sum_{h=1}^{n} A_{hj} X_{hm}/[A_{.j} R_m]$$

$$j = 1, \dots, t;\ m = 1, \dots, n$$

The results of RO, in terms of interpretability, have been believed to be generally superior to those of PCA (Bouxin, 1976; Gauch et al., 1977; Robertson, 1978; Clymo, 1980; Gauch, 1982) but in fact they are not much of an improvement over PCA when the species turn-over rate is excessive (Orlóci et al., 1985).

2.2.2.3 Non-metric multidimensional scaling

The ordination methods described above are metric scaling methods that attempt to relate output distances linearly to input (original) dissimilarities. Non-metric methods, on the other hand, substitute the linearity constraint with a less restrictive monotonic relation between output distances and input dissimilarities,

$$d_{hj} < d_{uv} \Rightarrow d^{*}_{hj} \leq d^{*}_{uv}$$

where d_{hj} denotes the original dissimilarity between individuals h and j and d^{*}_{hj} the corresponding distance in the ordination space. Since the method uses only the rank order of original dissimilarities rather than their actual values, it is called 'non-metric'. The resulting ordination coordinates are, of course, cartesian.

Non-metric multidimensional scaling (MDSCAL) was developed by Shepard (1962) and Kruskal (1964a,b) and was apparently first used in ecology as an ordination method by Anderson (1971). The MDSCAL algorithm used in this study is due to Brambilla-Fewster-Kenkel (Kenkel, 1984).

(1) Compute the dissimilarity matrix $\underset{\sim}{D}_{nxm}$ based on the original data $\underset{\sim}{X}_{pxn}$ and order the off-diagonal elements,

$$d_{hi} \leq \ldots\ldots \leq d_{uv}$$

(2) Based on a matrix X^*_{txn} ($t \leq p$), which represents an initial configuration of random numbers, compute a dissimilarity matrix D^*_{nxn} and monotonically relate the numbers d^*_{jk} to d_{jk}

$$d_{hi} < d_{uv} \Rightarrow d^*_{hi} < d^*_{uv} \text{ for all } h < i,\ u < v$$

In the highly improbable situation where the initial configuration of X^* is such that the order of d_{jk} perfectly corresponds to that of d^*_{jk}, a scatter plot of these (called a Shepard diagram) will show a monotonically increasing curve. But when this ideal monotonicity does not exist the estimated values $\hat{d}_{jk}$ are obtained on a best-fitted monotonically rising curve to the scatter of points (d^*_{jk}, d_{jk}). Calculations are performed using non-parametric regression.

(3) Compute the departure from monotonicity using the stress function (S),

$$S = \left[\frac{\sum_{j<k}^{n} (d^*_{jk} - \hat{d}_{jk})^2}{\sum_{j<k}^{n} d^{*2}_{jk}} \right]^{1/2}$$

(4) The configuration X^* is iteratively moved so that the stress function (S) is minimized. This is achieved by the method of steepest descent (Kruskal, 1964b).

Because of less restrictive assumptions and a non-parametric approach to computation, MDSCAL is a more robust technique than either PCA or RO. MDSCAL is less vulnerable to high β-diversities than metric scaling techniques (Fasham, 1977; Prentice, 1977) and is not affected by sample clusters and outliers (Fasham, loc. cit.). Fasham also demonstrated that MDSCAL is "less susceptible to distortion of the ordination by single gradients of high beta-diversity and two gradient situation when each gradient is of a different beta diversity". Prentice (1977) suggested that MDSCAL can be applied to data sets incorporating broad ranges of variation. The success of the method will largely depend on the resemblance function (Orlóci, 1978; Fewster and Orloci, 1983; Orloci et al., 1985).

MDSCAL can use a variety of resemblance functions for the computation of input dissimilarity/similarity matrix. Among the various resemblance measures evaluated, Fasham (1977) found cos-theta function to be the most effective. Orlóci (1979) derived a distance function based on Gaussian response model and suggested its use for constructing an input dissimilarity matrix in MDSCAL. Kenkel (1984) has shown the superiority of the chord distance (Orlóci, 1967). Distributions other than Gaussian can also be used as response models to derive resemblance functions on which the input matrix can be based (Prentice, 1977; Fewster and Orlóci, 1983).

2.2.3 Ordination graphics

Graphical representation permits description and facilitates interpretation of ordination results. Futhermore, it allows the examination of existing relationships between vegetation and environmental characteristics (Orlóci, 1978). Ordination graphics were used in this work for the following purposes.

1. To display the ordination results and examine the hidden properties of the data structure as trends or group structure.
2. To examine the environmental gradients in relation to vegetational variation.
3. To disclose succesional changes in structure and composition.

Ordination results were displayed by plotting the joint distribution of ordination scores on the first few components or axes or by developing stereograms (Fewster and Orlóci, 1978).

2.2.4 Comparisons

The results of two different kinds of ordination, or those based on data sets pertaining to different plot sizes, were objectively compared. This was accomplished by first computing the distances between points (releves or species) in the ordination space for a fixed number of dimensions (or components) using the Euclidean distance

$$D_{jk} = [(X_{1j} - X_{1k})^2 + (X_{2j} - X_{2k})^2 + \ldots + (X_{nj} - X_{nk})^2]^{1/2}$$

where D_{jk} is the distance between two points having ordination coordinates X_{1j}, X_{2j}, ... X_{nj} and X_{1k}, X_{2k}, ..., X_{nk} respectively. In some cases up to six dimensions (n=6) were used. The distances derived from two ordination spaces D_1 and D_2 were compared using product-moment correlation coefficient (r). Since the distances in the ordinations were not independent, the correlation coefficient was applied as an index of similarity but rather than as a test statistic.

2.3 Classification

2.3.1 General

Classification involves the grouping of objects (such as relevés) into classes, the members of which share some common attributes in which they differ from members of the other classes. In vegetation studies the attributes are customarily some measures of species importance. Though the idea of vegetation classification is as old as vegetation science, until recently it was based on subjective approaches (see Becking, 1957; Whittaker, 1962; Shimwell, 1971). The objective methods of classification or 'cluster analysis techniques', on the other hand, have gained popularity within the last two or three decades.

2.3.2 Clustering techniques

Cluster analysis aims at organizing data in such a way as to expose the underlying group structure or to impose a group structure according to some a priori specifications. A variety of clustering techniques is available and these have been reviewed (Cormack, 1971; Williams, 1971; Anderberg, 1973, Sneath and Sokal, 1973; Everitt, 1974; Goodall, 1973; Orlóci, 1978). Clustering algorithms are basically of two kinds - non-hierarchical and hierarchical. A non-hierarchical algorithm organizes the n individuals into g clusters by labelling each individual in some way (e.g., Jancey, 1966). A hierarchical algorithm involves a sequence of clusterings. Generally, hierarchical clustering allows greater computational efficiency and relative ease in the interpretation of results (Greig-Smith, 1983). Depending upon the algorithmic approach chosen, a hierarchical clustering begins with n clusters, one individual (or pattern) per cluster, and through a sequence of clusterings in n-1 steps forms one cluster containing n individuals, or begins with one cluster containing all individuals (or patterns) and successively divides until n clusters, each with one individual is obtained. The former procedure is called 'agglomerative' and the latter 'divisive'.

A choice of a clustering strategy is also available with respect to the descriptors used in cluster formation. In a monothetic strategy, membership in a cluster is based solely on the presence or absence of a single attribute (species). In contrast, in a polythetic strategy fusions or subdivisions are based on overall similarity or difference with respect to a number of attributes. Because a monothetic agglomerative procedure cannot exist (Williams et al., 1966), the choice of a hierarchical classification is limited to the remaining three possible strategies, namely divisive monothetic (Goodall, 1952; Williams and Lambert, 1959), divisive polythetic (Macnaughton-Smith et al., 1964; Edwards and Cavalli-Sforza, 1965; Hill et al., 1975), and agglomerative polythetic (Sneath, 1957; Sokal and Michner, 1958; Lance and Williams, 1966, 1967; Orloci, 1967, 1971, 1976; Jancey, 1974).

In order to choose between divisive and agglomerative strategies one should rationally weigh the relative merits and demerits of the two approaches. The greatest merit attributed to divisive methods is that they use the information contained in the entire data at the outset. Consequently, unlike agglomerative clustering the higher level clusters are not affected by the information contained in the lower level clusters. However, in case of monothetic divisive methods e.g., Williams and Lambert's (1959) association analysis, much useful information remains unused after the process of subdivision.

The polythetic divisive method of Edward and Cavalli-Sforza (1965) is theoretically sound (Pielou, 1977) but examines all possible $2^{n-1}-1$ partitions of the n individuals to arrive at a division which would maximize the between set sum of squares. This process is repeated at each division. As a consequence, the computational time is prohibitive even at very moderate sample size (e.g., n=16). The analysis of variance used for testing the significance of groups is inappropriate because the groups are not obtained in a random manner but are obtained by maximizing the between-group variation. The dissimilarity analysis proposed by Macnaughton-Smith et al. (1964) is similar to the method of Edwards and Cavalli-Sforza (1965). However, unlike the latter it does not require the examination of all possible partitions of the sample and subsamples. The only drawback of this latter method is that no test of significance is incorporated. The indicator species analysis (Hill et al., 1975) approach to polythetic divisive clustering uses ordination to accomplish classification. At each division the first axis of reciprocal ordering (RO) is artifically bisected at the centroid. The division point is then adjusted using indicator scores of individuals situated to the left and right of the centroid, based on a given number of indicator species.

The agglomerative strategies, by contrast, are generally free from computational problems. At any particular stage in the clustering, process, when there are g clusters (or individuals) the two individuals or two clusters which possess the least of the 1/2 g(g-1) inter-cluster or inter-individual dissimilarity (or highest similarity) are fused together. The variety of manners in which dissimilarity (or similarity) between an individual and a cluster or between two clusters can be defined has given rise to various agglomerative strategies. Such strategies are said to be 'combinatorial'. Since these strategies utilize solely the information contained in the resemblance matrix without recourse to the original data, they are computationally efficient. The dissimilarity matrix is updated according to the following general relationships adduced by Lance and Williams (1966):

$$d_{k.ij} = \alpha_i d_{ik} + \alpha_j d_{jk} + \beta d_{ij} + \gamma |d_{ik} - d_{jk}|$$

where the symbol $d_{k.ij}$ indicates the dissimilarity of cluster k with the union of cluster i and j; α, β and γ are coefficients whose value changes with the kind of strategy. The following agglomerative techniques were used in the present study.

(a) Single linkage clustering. This method defines the intercluster dissimilarity as the least dissimilarity between the members of the two clusters. The values for the parameters are:

$$\alpha_i = \alpha_j = 0.5, \quad \gamma = -0.5, \ \beta = 0$$

therefore $d_{k.ij} = 0.5 \, (d_{ik} + d_{jk} - |d_{ik} - d_{jk}|)$. Single linkage strategy is space contracting and often results in chaining.

(b) Simple average clustering. This method defines intercluster dissimilarity as the mean dissimilarity between clusters irrespective of cluster sizes, i.e., clusters are weighed equally. Clustering parameters are

$$\alpha_i = \alpha_j = 0.5, \beta = \gamma = 0$$

$$d_{k.ij} = 0.5 (d_{ik} + d_{jk})$$

Simple average clustering is more or less space-conserving.

(c) Group average clustering. In defining the mean dissimilarity, this method takes into account the sizes of the clusters being fused, i.e., clusters are weighed in accordance with their sizes. Clustering parameters are

$$\alpha_i = n_i/(n_i+n_j), \quad \alpha_j = n_j/(n_i+n_j), \quad \beta = \gamma = 0$$

Thus,

$$d_{k.ij} = [n_i \, d_{ik}/(n_i+n_j)] + [n_j \, d_{jk}/(n_i+n_j)]$$

This strategy is space conserving or space contracting.

(d) Sum of squares clustering. In this method, at any stage of clustering those clusters are fused that would minimize the within-cluster sum of squares (Orlóci, 1967). The constants of this strategy are:

$$\alpha_i = \frac{n_i}{n_i+n_j} \qquad \alpha_j = \frac{n_j}{n_i+n_j} \qquad \beta = \frac{n_i n_j}{n_i+n_j}, \qquad \gamma = 0$$

so that

$$d^2_{k.ij} = \frac{n_i}{n_i+n_j} d^2_{ik} + \frac{n_j}{n_i n_j} d^2_{jk} - \frac{n_i n_j}{n_i+n_j} d^2_{ij}$$

where d^2 is the squared Euclidean distance (Orloci, 1978) and n_i and n_j are numbers of individuals in the groups i and j respectively. This clustering strategy, which has gained popularity in recent years, is space conserving.

2.3.3 Clustering graphics

The results of hierarchical clustering were presented as dendrograms. A dendrogram is a tree-like figure representing the hierarchical relationships in terms of dissimilarities or similarities among the individuals (or species). The results of cluster analysis were also presented by superimposing the group structure at a specific level of hierarchy, on the scatter plots of ordinations.

2.3.4 Comparisons

The results of hierarchical clusterings were compared based on (a) topology matrices Tm, and (b) cophenetic matrices Cm. A topology matrix is a triangular matrix, an element of which is defined as the number of nodes separating two individuals i and j in the dendrogram (Phipps, 1971). A cophenetic matrix is also a triangular matrix in which a given element represents the dissimilarity (or similarity) between individuals i and j as implied in the dendrogram (Sneath and Sokal, 1973; Rohlf, 1974). Pairs of topology or cophenetic matrices, describing classifications, were compared using the following coefficients:

(a)

$$ {}^{*}u(\underset{\sim}{D}_1,\underset{\sim}{D}_2) = [\Sigma\,|\overset{*}{D}_1-\overset{*}{D}_2|^{1/u}]^{1/2} $$

$$ \overset{*}{D} = \tilde{D}/[\Sigma\,|D|^{1/u}]^{1/2} \quad , \quad u = 1/2 . $$

where $\underset{\sim}{D}_1$ and $\underset{\sim}{D}_2$ represent two topology or cophenetic matrices and D represents an element of the topology matrix (T_{ij}) or that of the cophenetic matrix (C_{ij}). ${}^{*}u$ was proposed by Jardine and Sibson (1968).

(b) Cophenetic correlation $r(\underset{\sim}{D}_1,\underset{\sim}{D}_2)$ proposed by Sokal and Rohlf (1962).

$$ r(\underset{\sim}{D}_1,\underset{\sim}{D}_2) = \Sigma(D_1-\bar{D}_1)(D_2-\bar{D}_2)/[\Sigma(D_1-D_1)^2\,\Sigma(D_2-\bar{D}_2)^2]^{1/2} $$

Summation is over n*n-1/2 elements. The cophenetic correlation coefficient is scale-free and measures the degree of linear relationship between D_1 and D_2 (Rohlf, 1974). Since elements of Cm or Tm are not independent, the cophenetic correlation coefficient is used as a descriptive measure only.

(c) Information statistic suggested by Orloci (1978)

$$I(\underset{\sim}{T}_1,\underset{\sim}{T}_2) = \sum_i \sum_j \left[t_{1ij} \ln \frac{2t_{1ij}}{t_{1ij}+t_{2ij}} + t_{2ij} \ln \frac{2t_{2ij}}{t_{2ij}+t_{2ij}} \right]$$

where T_1 and T_2 are two topology matrices with elements t_{1ij} and t_{2ij}.

2.4 Expected resemblance

Expected resemblance provides information regarding spatial variability in vegetation in the context of the size of the sampling unit used. The utility of expected resemblance in the determination of an effective size of sampling unit (plot) has already been mentioned in Section 2.1.2.3.1. Expected resemblance is simply computed as the average of non-diagonal elements in a resemblance matrix (Podani, 1982).

$$E(\overline{d}) = 2 \sum_{j=1}^{n-1} \sum_{k=j+1}^{n} d_{jk}/(n^2-n)$$

where d_{jk} is dissimilarity (or similarity) between plots j and k and n is the sample size. When qualitative (0,1) data is used the following resemblance functions can be used

$$d(1)_{jk} = \sqrt{b+c} \quad \text{(Euclidean distance)}$$

$d_{(2)jk} = (a+d)/(a+b+c+d)$ (simple matching coefficient of Sokal and Michner (1958)) $d_{(3)jk} = a/(a+b+c+d)$ (index proposed by Russell and Rao 1940); $d_{(r)jk} = 2a/(2a+b+c)$ (Sorensen's (1948) coefficient).

2.5 Characteristic functions

The choice of a plot size (sampling unit) can also be made with respect to characteristic functions (viz. florula diversity, local distinctiveness, associatum and number of realized species combinations) that are dependent upon plot size (Juhasz-Nagy, 1967, 1982; Juhasz-Nagy and Podani, 1983). The characteristic functions which represent some important community property are based on well-known information theory functions (Kullback, 1959; Renyi, 1961; Feoli <u>et</u> <u>al</u>., 1982). These are applicable to binary (0,1) data but their extension to other data types is possible.

The concept of characteristic functions is an extension of the concept of species/individual diversity to the entire sample. Here the basic unit is not an individual but a set of individuals (i.e., those represented in a plot) in the sample as a whole. For this reason, it is termed as supraindividual diversity, or in the context of plant community, as florula diversity. Conceptual details appear at length elsewhere (Juhasz-Nagy, 1976; Juhasz-Nagy and Podani, 1983). The florula diversity which gives the uncertainty regarding species composition of n sampling units of size j is estimated as

$$n \hat{H}j(A,B,\ldots,S) = n \log_2 n - \sum_{k=1}^{w} f_k \log_2 f_k$$

where A,B,...,S are species, n is the sample size, f_k is the frequency of kth species combination out of a total possible combinations of $w = 2^s$ (i.e. different potential florulas), where s is the number of species in the sample. Since florula diversity is a function of the number of species for comparative purposes florula evenness is more appropriate. It is a scaled value obtained as florula diversity expresses as a proportion of maximum florula diversity.

$$n\,\hat{V}(A,B,\ldots,S) = n\,\hat{H}(A,B,\ldots,S)/\max\{n\,\hat{H}(A,B,\ldots,S)\}$$

$$= (1.0 - \sum_{k=1}^{w} f_k \log_2 f_k)/(n \log_2 n)$$

Local distinctiveness is calculated as the pooled entropy of all species in the sample.

$$n\,\hat{H}[L] = \sum_{i=1}^{s} [n\,\hat{H}i]$$

$$= s\,n \log_2 n - \Sigma(n_{i.} \log_2 n_{i.} + (n-n_{i.})\log_2$$

$(n-n_{i.}))$, where $n\hat{H}_i$ is entropy of species I, and n_i is the number of sampling units containing species I.

The associatum or mutual information among species is estimated as

$$n\,I(A,B,\ldots,S) = n\,H[L] - n\,H(A,B,\ldots,S)$$

$$= (s-1)\,n\,\log_2 n + f_k \log_2 f_k -$$

$$n_{i.} + (n-n_{i.}) \log_2 (n-n_{i.})$$

2.6 Identification and assignment

The objective of identification is to find the group that is the most likely parental group for a given individual (relevé). Through the process of identification we can either increase the class membership or reallocate individuals among classes. In this study, identification was used for the latter purpose.

Identification was accomplished using generalized distance (Mahalanobis, 1936; Rao, 1952), defined, as follows:

$$d(\underset{\sim}{X}_j,\underset{\sim}{\bar{X}}_m) = [(\underset{\sim}{X}-\underset{\sim}{\bar{X}}_m)'\ \underset{\sim}{S}_m^{-1}(\underset{\sim}{X}_j-\underset{\sim}{\bar{X}}_m)]^{1/2}$$

where $\underset{\sim}{X}_j$ is the vector of an external individual, $\underset{\sim}{\bar{X}}_m$ is the mean vector of group m and $\underset{\sim}{S}_m^{-1}$ is the inverse of the group variance-covariance matrix.

Difficulty in computation was encountered because of singularity of $\underset{\sim}{S}_m$ due to correlations among species in the raw data. To overcome this problem a set of orthogonal component axes, extracted by performing component analysis on the raw data of each group, were used to compute S_m^{-1} (Bradfield and Orlóci, 1975). Assignments were made deterministically, i.e. an individual was assigned to a class m if its generalized distance to this class was minimal.

2.7 Vegetation dynamics

2.7.1 Introduction

One important characteristic of vegetation is its dynamic nature. Small changes in vegetation, that do not alter the general appearance of vegetation are classed as 'fluctuations', whereas changes that appreciably alter the species composition and physiognomy of vegetation are included under the term 'succession' (Kershaw, 1973; Miles, 1979). Succession has been variously conceptualized. Margalef (1968: 27), for instance, views succession as "the occupation of an area by organisms involved in an incessant process of action and reaction which in time results in change in both the environment and the community, both undergoing continuous reciprocal influence and adjustment". Succession is often regarded as orderly, directional and a more or less predictable process.

Since the pioneering works of Warming (1896), Cowles (1901) and Clements (1916) the classical succession theory has been considerably modified and widened through more intensive examination by a variety of new approaches (Margalef, 1968; Langford and Buell, 1969; Odum, 1969; Drury and Nisbet, 1973; Horn, 1974; Connell and Slatyer, 1977; van Hulst, 1978; Noble and Slatyer, 1981). While most successional theory is controversial (reviews by McCormick, 1968; Drury and Nisbet, 1973; van Hulst, 1978; Miles, 1979), the opinion of ecologists is undivided regarding the kinds of succession with respect to the nature and timing of perturbation. Two kinds of succession are distinguished - primary and secondary. A successional process taking place on a virgin substrate is termed primary succession. By contrast, secondary succession refers to vegetation changes that occur in a grossly disturbed ecosystem. The present study is concerned with secondary succession.

Detailed examination of the vegetation changes involved in a particular succession and predictions regarding its development can only be made effectively by the use of analytical techniques. Successional trends can be analysed by the application of a variety of numerical methods (see reviews by Austin, 1977; van der Maarel and Werger, 1977). Predictions about succession involve the use of models including their development and testing (Horn, 1975; van Hulst, 1979; Usher, 1979, 1981; Austin and Belbin, 1981).

Successional changes in vegetation can be examined through two main approaches - static and dynamic (Austin, 1977). The static analysis involves reconstruction of successional sequence from data obtained on stands of various ages at one point in time. The dynamic analysis, by contrast, involves data on different successional stages collected at various time intervals in a selected concrete community. The present study employed the static approach to examine successional changes in vegetation.

2.7.2 The static analysis

In static analysis data on spatial pattern (e.g. zonations) within phytocoenoses of known age are serialized to produce an analogue pattern of temporal sequence. Because the time span of most seres is often much longer than the human life span, successional changes in vegetation are most often interpreted by means of analogue patterns. While using static approach, it is important to remember that changes in vegetation are not always unidirectional (van der Maarel and Werger, 1977). Varied sequential changes may often lead to the same successional stage of a sere (Quarterman, 1953; Londo, 1974; Keever, 1983). Furthermore, it must also be borne in mind that the temporal sequence inferred from spatial sequence represents only a generalized sequence that may not exactly match with that on a particular site (Austin, 1977).

A variety of multivariate techniques have been used to unravel the successional trends in vegetational composition. Williams and Lambert (1960) used divisive clustering technique to interpret the post-disturbance vegetational changes. However, ordination methods have been used more often in seeking successional trends or temporal gradients (Itow, 1963; Habeck, 1968; Goff and Zedler, 1968, 1972; Zedler and Goff, 1973). Matthews (1979), Birks (1980) and Gittins (1981) employed canonical analysis as an approach to static analysis. Orlóci (1981) provided an example of the successful application of analysis of concentration (AOC) (Feoli and Orlóci, 1979) in elucidating successional trends. Since AOC is particularly useful in decomposing complex trends (Orlóci, 1981), it was used here to gain insight into the compositional changes during the secondary succession.

2.7.2.1 Analysis of concentration

Analysis of concentration (AOC), developed by Feoli and Orlóci (1979) is a technique suitable for analyzing structured tables based on the statistical theory of contingency tables (Lancaster, 1949). AOC involves testing for the sharpness of 'block structure' and the 'decomposition' of underlying trends in the data structure into independent components (Orlóci, 1981). The following outline is based on the exposition of Orlóci (1981).

(a) Test for sharpness

Before performing the analysis the elements of structured table are adjusted for uneven sample sizes, as follows:

$$A_{hj} = \frac{\left[\frac{F_{hj}}{N_{hj}}\right] F_{..}}{\sum_k \sum_l \left[\frac{F_{kl}}{N_{kl}}\right]_{..}}$$

$$k = 1,\ldots,q \;;\; l = 1,\ldots t.$$

where A_{hj} is an adjusted value, corresponding to the observed value F_{hj} in the unadjusted matrix (structured table) $\underset{\sim}{F}$, $F_{..}$ is the grand total of $\underset{\sim}{F}$ and N_{hj} are sample sizes, i.e. number of rows x number of columns within a block.

The sharpness of the block structure is then tested [illegible]g chi-squared statistic, as follows:

$$\chi^2 = \sum_h \sum_j (A_{hj} - \hat{A}_{hj})^2 / A_{hj}$$

$$h = 1,\ldots,q \; ; \quad j = 1,\ldots,t$$

with $\nu = (q-1)(t-1)$ degrees of freedom.

(b) Extraction of canonical correlations and scores

When a significant block structure exists, the analysis proceeds to the next step in which independent components are isolated. The total chi-square is partitioned into $m \leqslant \mathrm{INF}\,(q,t)$ additive components

$$\chi^2 = \chi_1^2 + \ldots + \chi_m^2 = R_1^2 A_{..} + \ldots + R_m^2 A_{..}$$

Where R_i^2 are squared canonical correlation coefficients (or eigenvalues, λ_i)

$$R_i = \sqrt{\lambda_i} \quad ; \quad 0 \leqslant R_i \leqslant 1$$

These are extracted in an eigenanalysis of a cross products matrix S

$$S = \underset{\sim}{U}\underset{\sim}{U}'$$

A characteristic element of $\underset{\sim}{U}$ is

$$U_{hj} = \frac{A_{hj}}{(A_{h.}\, A_{.j})^{1/2}} - \frac{(A_{h.}\, A_{.j})^{1/2}}{A_{..}}$$

With each R_i^2 is associated an eigenvector $_1, _2, \ldots, _m$. The canonical scores for species (row) groups and releve (column) groups are then derived as follows:

$$X_{ji} = \frac{(\ _{ji} - \ _{i})}{[_e(\ _{ei} - \bar{\ }_{i})^2]^{1/2}} \left[\frac{A_{..}}{A_{.j}}\right] ; \quad e = 1, \ldots, q$$

where X_{ji} is a canonical score for releve group j on the ith canonical variate, and

$$Y_{hi} = A_{hj} X_{ji} / R_i A_{h.}$$

where Y_{hi} is a canonical score for species group h (Orloci, 1981).

2.8 Species ranking

2.8.1 Introduction

Ranking methods provide a means of assigning weights to species in accordance with their importance. The importance of species in a given vegetation vary since species differ in their sensitivity of response to environmental factors and factor complexes, and thereby in their ability to contribute to the vegetation pattern. Furthermore, the environmental response of many species is inherently similar, thus giving rise to redundancy of pattern information. Several ranking methods have been proposed that define weights using different formulations. Once the species are weighted, highly ranked species from among the total set can be used (1) to economize the subsequent data analysis without undue loss in the resulting information (Orlóci and Mukkatu, 1973; Orlóci, 1978b; Jancey, 1979), (2) to eliminate lowly ranked species, i.e., species with larger random component at various levels in a hierarchical clustering so as to minimize misclassification (Wishart, 1967; Jancey, 1980), and (3) to reduce the number of species (variables) to increase the power of some statistical techniques and tests (Dempster, 1971; Gittins, 1979).

2.8.2 Techniques

A wide variety of ranking techniques have been proposed and these differ in the criteria of species importance as well as in the underlying ranking philosophy. Some involve computationally simple weighting criteria such as the arithmetic mean and standard deviation (Grigal and Goldstein, 1971; Grigal and Ohman, 1975) or mean square contingency (Williams et al., 1964; Macnaughton-Smith et al., 1964), whilst others are based on maximal unique variance or information and related quantities (Orloci, 1978b). The details of the ranking techniques used in the present study are described in the sequel.

2.8.2.1 Sum of squares

In this method, once the rank of a species has been determined, it does not play any further part in the analysis. The technique uses a pxp matrix of sums of squares and cross products S and its residuals to determine, for each species, its independent share of the total sum of squares (Orloci, 1973). The method proceeds as follows:

(a) Define an initial weight Q_i for any variable as

$$Q_i = \sum_{h=1}^{p} Y_{hi}^2$$

where $Y_{hi} = S_{hi}/\sqrt{S_{ii}}$

This is the sum of squared projections of p vectors (each representing a species) on the line of the ith vector

(b) Find the maximum

$$Q_m = \max\,(Q_1,\ Q_2,\ \ldots,\ Q_p)$$

and declare weight $W_m = Q_m$ or species m

(c) Compute the first residual $\underset{\sim}{S}^{(1)}$ of $\underset{\sim}{S}$

$$S_{hi}^{(1)} = S_{hi} - Y_{hm}Y_{im}$$

This implication of this step is that the mth row and mth column of $\underset{\sim}{S}^{(1)}$ are zeroed.

(d) Compute a new weight

$$Q_i^{(1)} = \Sigma\, S_{hi}^{(1)2}/S_{ii}^{(1)}$$

(e) Find the maximum and declare rank 2 for the corresponding species.

(f) Go to step (c) and continue until weights are assigned to all the species and the cross-products matrix have been reduced to zeros. The weights W_1 are such that

$$\sum_{i=1}^{p} W_1 = \sum_{i=1}^{p} S_{11}$$

This method, which involves co-variation of species, is of fundamental importance when the eventual aim of the user is a formal ordination such as PCA.

2.8.2.2 Equivocation information

Any information based ranking method is capable of handling nominal (multi-state), ordinal or even mixed data. Such methods ~~are~~, therefore, more flexible. Equivocation information weighting gives higher weight to variables that carry greater amounts of unshared information. Equivocation information is simply the main effect information in the distribution $\underset{\sim}{F}_i$. The equivocation information of variable X_i is given by

$$\Delta_i = I(\underset{\sim}{F}_i;\underset{\sim}{F}_i) = \sum_{j=1}^{S_i} f_{j.} \ln (F_{j.} S_i/N)$$

The method has been treated in detail elsewhere (Orloci and Bowles (1982).

2.8.2.3 Within descriptor sum of squares

If the final objective is typification or identification then a ranking algorithm based on independent pattern information of species is appropriate as it permits increased discrimination. Within descriptor sum of squares method ranks species solely with respect to their unique component of pattern information.

Let X_{ij} be an element in a pxn raw data matrix $\underset{\sim}{X}$. The total sum of squares in the data matrix is partitioned into two independent components - a within species sum of squares and a between species sum of squares:

$$\sum_{i=1}^{p} \sum_{j=1}^{n} (\bar{X}_{ij} - X_{..})^2 = \sum_{i=1}^{p} \sum_{j=1}^{n} (X_{ij} - X_i)^2 + \Sigma^n (\bar{X}_j - \bar{X}_{..})^2$$

where $\bar{X}_{..}$ is the grand mean and $\bar{X}_i$ equals the mean of ith species. The ~~first~~ term to the right is the total within-species sum of squares. Species are ranked in accordance with their contribution to the total within-species sum of squares, Q_i; for the ith species this would be:

$$Q_i = \sum_{i=1}^{m} (X_{ij} - \bar{X}_i)^2 / \sum_{i=1}^{p} \sum_{j=1}^{n} (X_{ij} - \bar{X}_i)^2$$

Next, the values of Q_i are ranked (Q_j) and a cut-off level C is specified to obtain the reduced species list consisting of m species that stand above the cut-off point.

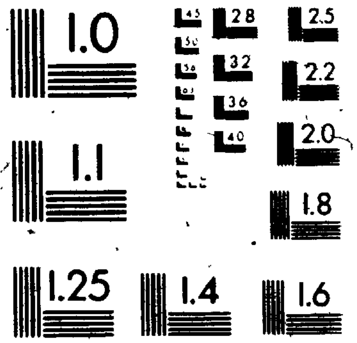
$$\sum_{j=1}^{m} Q_j / \sum_{i=1}^{p} Q_i \geq C$$

The greatest advantage of using the above ranking approach is that it is directly compatible with some important numerical techniques of data analysis, such as minimum variance (sum of square) hierarchical clustering (Ward, 1963; Orlóci, 1967) and Jancey's k-mean method of non-hierarchical clustering (Jancy, 1966) which are based on total within-group sum of squares. In addition, this ranking method also appears to be compatible with distance-based non-metric ordination methods such as Kruskal's non-metric multidimensional scaling.

2.8.3 An iterative ranking-clustering method

As pointed out by Jancey (1980), in order to minimize misclassification in a hierarchical clustering, species displaying a locally greater random component should be excluded from clustering procedure at the corresponding clustering level. The reduced species set comprising of highly ranked species, represents the non-random component of pattern information in a group of releves. Thus, at each clustering pass, the total species set should be subjected to the ranking procedure since species that are unimportant in the complete releve set may attain significance in a subset of releves being used for subclustering.

2



The iterative ranking and agglomerative clustering developed by Jancey (1980) was modified in order to reduce the risk of misclassification. The technique originally used sum of squares ranking which minimizes redundancy of pattern information in a reduced data set. However, increased classification efficiency can be attained by maximizing discrimination. The within descriptor sum of squares ranking described above is suitable in this regard. Thus, the iterative clustering used here incorporated the sum of squares clustering (Orloci, 1967) and the within descriptor sum of squares ranking method. This combination of ranking and clustering techniques permitted me to achieve compatibility between the two algorithms.

2.9 Data type

In vegetation studies, one may collect only presence-absence (0,1) data or gather some additional quantitative information regarding species performance, such as abundance, cover, frequency, density, biomass, etc. The quantative data may be based on an ordinal scale, e.g., cover or abundance classes, or on a continuous scale, e.g. density, percentage cover or biomass.

The studies dealing with the relative roles of presence-absence and quantitative information in unfolding the underlying pattern in vegetation by means of numerical methods have yielded controversial results (Webb et al., 1967; Austin and Greig-Smith, 1968; Noy-Meir, 1971; Orloci and Mukkattu, 1973; Smart et al., 1974). In some studies, the importance of the qualitative component has been emphasized (Lambert and Dale, 1964; Norris and Barkham, 1970; Noy-Meir, 1971; Orloci and

Mukkattu, 1973). It seems that the relative importance of qualitative and quantitative components vary, depending upon the vegetation characteristics, such as species richness (Austin and Greig-Smith, 1968).

Presence-absence data, though relatively easy to collect, can only provide limited phytosociological information. On the other hand, accurate quantitative data such as density or coverage per unit area, collected by precise methods, are extremely useful but its collection is highly time consuming. Because visual estimation of coverage and abundance is more rapid, it has become increasingly popular. Besides being quicker, it has the advantage of causing least disturbance in the vegetation. Visual estimation of coverage (or abundance) is usually done using arbitrary scales. A number of such scales have been developed and practiced. The two most widely used scales are those of Braun-Blanquet (1932) and Domin (1923), and these have been variously modified and refined (Krajina, 1933; Daubenmire, 1959; Bailey and Poulton, 1968; Londo, 1971). The original Braun-Blanquet and Domin scales combine cover with abundance in defining the scale value. The modified scales, however, are based solely on percentage cover. Other independently developed scales of cover estimation, which are in less common use, are those referred to by Cain and Castro (1959) as Hult-Sernander (used in Scandinavian countries) and Lagerberg-Raunkiaer scales. The definition of most scales is based on uneven ranges of percentage cover, often at either end of the scale (Sernander, 1921; Daubenmire, 1959) or only at the lower end of the scale (Domin, 1923; Braun-Blanquet, 1932; Bailey and Poulton, 1968). Most of these scales have been developed to assess the spatial variation in vegetational composition and are generally too broad to reflect short-term successional changes. Londo (1976) proposed a more refined scale which is a modification of the 'decimal scale' suggested earlier by Doing Kraft (1954). The points of this scale are related to actual cover values, since each scale point is one-tenth of the average cover value of the interval.

It is believed that the use of the raw quantitative data as such, in a numerical analysis, may involve a risk of overemphasizing dominant species. For this reason various kinds of transformations or standardizations have been proposed. The often recommended transformations include square root (Greig-Smith, 1983) and logarithmic transformations (Williams et al., 1973; Poole, 1974; Noy-Meir and Whittaker, 1977; Green, 1979; Jensen, 1978). Jensen (1978) used the logarithmic transformation in the forms: $Y = 100\ (\mathrm{Log}_{10}(\%\ \mathrm{cover} + 1))$ and $Y = 100\ (n + \mathrm{Log}_{10}\ \%\ \mathrm{cover})$.

The influence of various ordinal scales and variously transformed quantitative vegetation data on the resulting numerical classification and ordination were examined and compared with the results based on qualitative data and untransformed percentage cover data.

2.10 Species diversity and dominance

Species diversity is an important parameter of an organized community. It has intrigued ecologists for over half a century (reviews by McIntosh, 1967a; Eberhardt, 1969; Whittaker, 1972; Hill, 1973b; Pielou, 1975). Measurement (or representation) of diversity has been variously approached (reviews by Hurlbert, 1971; Peet, 1974; May, 1975; Pielou, 1975, Shaukat et al., 1981). It is generally agreed that species diversity has two essential components-species richness and equitability or evenness (Lloyd and Glelardi, 1964; Whittaker, 1972; Peet, 1974; Pielou, 1975: 14). Diversity and its components were measured in this study as follows:

(1) Species richness was simply measured as number of species S.

(2) General diversity, which incorporates both richness and evenness components of diversity, was measured by the popular Shannon-Weiner information function, H' (Margalef, 1957):

$$H' = \sum_{i=1}^{S} p_i \ln p_i$$

where p_i is the proportion of ith species.

(3) Equitability, E' or evenness abundance (coverage) was measured using an index proposed by Alatalo (1981):

$$E' = (N_2-1)/(N_1-1), \quad \text{where}$$

$$N_2 = 1/\sum_{i=1}^{S} p_i, \quad \text{and}$$

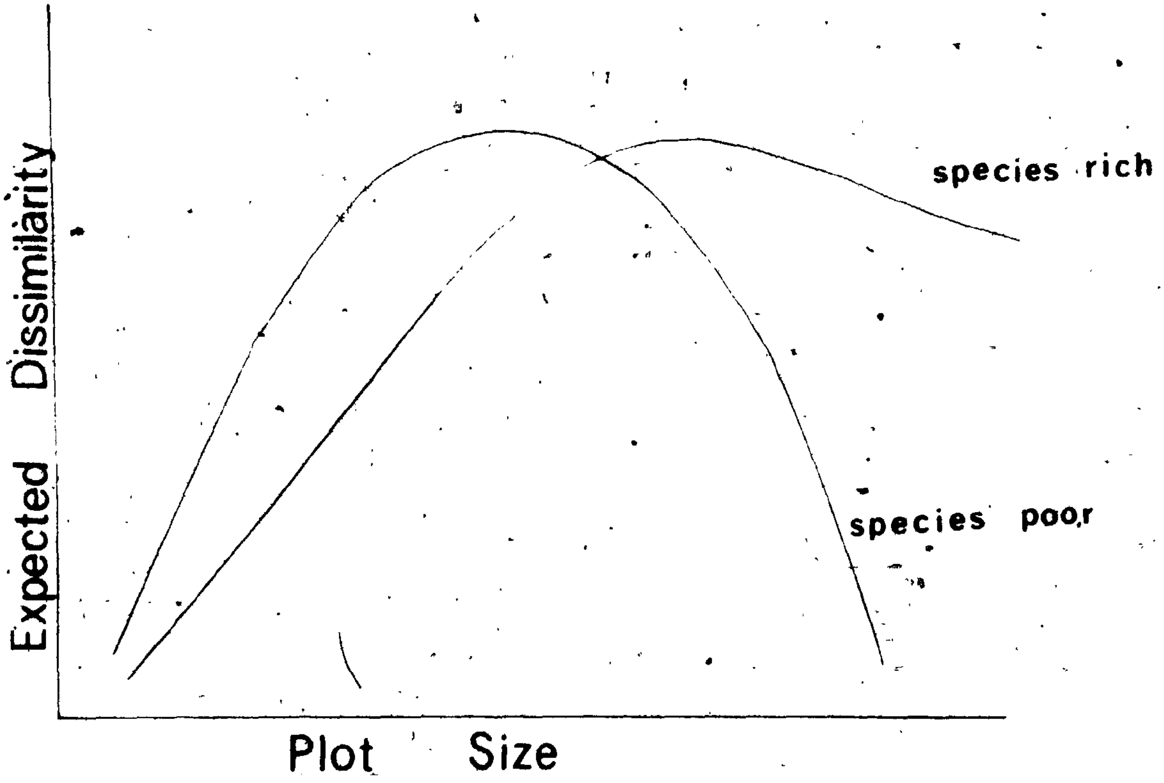
$$N_1 = \exp(H') \qquad \text{(Hill, 1973b)}$$

Finally, the degree of 'dominance' was expressed by Simpson's (1949) index (D'):

$$D = \sum_{i=1}^{S} p_i^2$$

Fig. 2.1 Theoretical curve for expected resemblance against plot size in species rich and species poor situations.

THEORETICAL CURVES



CHAPTER 3

RESULTS AND DISCUSSION OF PILOT SURVEY AND SPECIFIC FIELD EXPERIMENTS

3.1 Introduction

This chapter is devoted to some fundamental methodological problems in phytosociology, particularly those associated with vegetational sampling and pattern recognition. The following problems were addressed: (1) Choice of an optimal plot size; (2) Influence of data type on the resulting pattern information; and (3) The effect of data reduction on ordination and minimization of misclassification. These problems have been introduced in the appropriate sections of Chapter 2. It needs to be emphasized that the point of focus in this Chapter is methodological development. Thus, specific ecological remarks involving individual species or details of community characteristics are not essential and are kept to minimum in order to avoid divergence from the main theme. The methodological developments made are expected to be applicable to a wide variety of vegetation types including the weed communities under study.

3.2 Sources of data

Besides the pilot survey data, various field data sets were employed in the methodological studies. The following vegetation data sets were used.

3.2.1 The pilot survey data

This data set consisted of thirty releves of ruderal vegetation, each sampled with four different plot sizes. The total number of species in various plot size data sets were: 2.5*2.5 m, 74; 5*5, 85; 7.5*7.5 m, 93; and 10*10 m, 106. The vegetation data comprised of cover estimates based on van der Maarel (1979) scale.

3.2.2 Stoneybrook site data

These data were collected in an area, adjacent to Fanshawe Road at Stoneybrook, London. Three topographic formations were recognized: (1) a flat-topped mound, (2) an adjacent depression, somewhat filled with topsoil, followed by a (3) plain abandoned field (>10 years old). The site was sampled during July 6 to July 11, 1984. A stratified random sampling design was employed with the three topographic formation constituting the strata. In each stratum ten random sampling points were located and at each point rectangular plots of eight different sizes were laid down in a nested system with a common side. The plot sizes used were 0.35*0.71, 0.50*1.0, 071*1.42, 1.0*2.0, 1.41*2.83, 2.0*4.0, 2.83*5.66, and 4.0*8.0 m and the corresponding data sets included 36, 37, 56, 56, 56, 56, 56 and 57 species respectively. A length to breadth ratio of 2:1 was maintained for the plots and the series of plot sizes were obtained by successively doubling the area. Percentage cover of vascular species was visually estimated in each plot.

3.2.3 Wilkins site data

This set comprises data from random sampling of a map of ruderal vegetation in an early stage of secondary succession. The vegetation mapping was performed during August 6 to 8, 1984, at Wilkins St. site, London, where topsoil was removed only 2 years prior to mapping. A rectangular plot of 8*16 m was laid down randomly and divided into 512 continguous units of size 0.5*0.5 m. The position of each individual plant was recorded in the entire grid. Fortunately, sod and mat-forming species were rare at this site; thus the recording of individual plants was relatively easy. A total of 33 species were encountered.

3.2.4 Maple forest data

This data set came from random sampling of J. T. Curtis's vegetation map (250*185' or 76.2*56.38 m) for a section of maple forest in southern Wisconsin (cf., Curtis and Cottam, 1962). The map provides location along with basal area of each individual of the 11 tree species in an area of 1.06 acres (0.429 hectare). Of the 11 species, three rare species were excluded from the analyses.

3.3 Results and discussion

3.3.1 Choice of plot and consequences

This section presents results pertaining to the pilot study conducted in an attempt to determine an effective and an efficient plot size for the main survey under similar conditions. The procedure for the selection of an optimal plot size was described in Section 2.1.2. 3.1. Besides the pilot survey data, the procedure has been applied and tested for a variety of other data sets including such diverse vegetation types as forest and ruderal vegetation.

3.3.1.1 Species area curves

The species area curves were constructed for three randomly chosen sites from the directory of potential sampling sites for ruderal vegetation in London area. The aim was to obtain an estimate of the proportion of total number of species in a site being represented in plots of given sizes that could be used for the pilot survey. It should be noticed that the species area curves were not used in the usual context of minimal area determination or homogeneity assessment. The starting point for building up a set of nested plots was randomly chosen in a site, irrespective of visual uniformity of vegetation.

Fig. 3.1 shows the species area curves for three different sites and a composite (average) curve for all the three sites. Whereas, species-area curves for two sites (Fig. 3.1a,c) tend to level off that of southcrest site (Fig. 3.1b) appears to be rising with the enlargement of plot area indicating greater species richness at this site compared to the other two. The composite curve indicates that the smallest plot size chosen for the pilot study, i.e., 2.5*2.5 m included 25% of the total species within a site; whereas a plot size of 5*5 m that was also used in the main survey included 50% of the total number of species within a site. It is apparent, therefore, that a fairly high proportion of species were sampled in the pilot as well as in the main survey.

3.3.1.2 Expected resemblance and plot size

The relationship between expected resemblance and plot size was examined for the pilot survey data and a variety of other field data sets. These will be treated separately in the following subsections.

3.3.1.2.1 Pilot survey data

Changes in the expected resemblance for four different resemblance functions, based on 0/1 data are depicted in Fig. 3.2. With the exception of Sokal and Michner's simple matching coefficient, the expected resemblance increased more or less linearly with the increase in plot size from 2.5*2.5 to 10*10 m. The expected resemblance as measured with the simple matching coefficient declined initially with the plot size increment but then remained more or less at a constant level.

3.3.1.2.2 Other field data

Fig. 3.3 shows the relationship between expected resemblance and plot size for the Stoneybrook data. The expected similarity based on Russell-Rao and Sorensen's coefficients depicted more or less continuously rising monotonic curves. On the other hand, the expectation derived from Euclidean distance showed a monotonic curve that tended to level off between plot sizes 16 and 32 m^2. By contrast, the expectation of similarity based on simple matching coefficient exhibited essentially a unimodal curve with mode at a plot size of 1 m^2.

Fig. 3.4 displays the changes in expected dissimilarity based on Euclidean distance (0/1 data) with increasing plot size for the maple forest data. The expectation for this data set showed a unimodal curve with the peak at a plot size of 30*30' (9.14*9.14 m). Expectations using other resemblance functions were not evaluated for this data set.

3.3.1.2.3 Computerized sampling

The weed vegetation map constructed for Wilkins site was sampled using the computer program EXPRES developed by Podani (1982). Circular plots of various sizes were used for computerized sampling. The program takes random pairs of non-overlapping sample plots within the sample space (vegetation map) and computes resemblance between them. Thus, the standard deviation of expected resemblance has statistical meaning in this case. The plot size expected similarity curves based on Russell-Rao and Sorensen's coefficients exhibited monotonic trends (Fig. 3.5a,b). The rate of increase in the expectations with the increasing plot size was slightly higher for Russell-Rao's function compared to that of Sorensen. The expected dissimilarity curve for Euclidean distance levelled off at a plot size of 6 sq. m. and slightly dropped at a plot size of 16 sq. m. (Fig. 3.5c). The expectation derived from matching coefficient showed a rapid decline initially and then remained more or less at a constant level (Fig. 3.5d).

3.3.1.3 Characteristic functions

Characteristic functions for plot size relationships were evaluated for pilot survey data and Stoneybrook data sets.

3.3.1.3.1 Pilot survey data

The values of various characteristic functions for different plot sizes of the pilot study are presented in Table 3.1. The florula diversity and the florula evenness (Juhasz-Nagy and Podani, 1983), and the number of realized combinations (NRC) remained unchanged over the range of plot sizes. However, local distinctness, relative local distinctness and associatum slightly increased with the increasing plot size.

3.3.1.3.2 Stoneybrook site data

For this data set characteristic functions were evaluated using complete data sets of eight different plot sizes and also for reduced data sets. Data reductions were based on the total within species sum of squares ranking. Ranking was performed on the data set pertaining to the smallest plot size (0.35*0.71 m) and species standing above the cut-off level of either 0.85 or 0.7 were retained; these were 11 and 6 species respectively. The same species sets were retained in the reduced data sets of other plot sizes.

The florula diversity, the florula evenness and the number of realized combinations did not change over the range of sampling units when complete data sets were used (Table 3.2). Other characteristic functions exhibited consistent and gradual decrease with the increase in plot size when reduced data sets were used (Table 3.2).

3.3.1.4 Plot size and vegetational pattern

This section examines the degree of similarity in the pattern information, i.e., underlying trends or group structure in vegetation, resulting from data sets obtained with a range of plot sizes. The main purpose of such comparisons was to find a plot size smaller than the most effective plot size that would still disclose similar group structure and/or trends as those revealed by the most effective plot size.

In this set of analyses, the pilot survey data and two other field data sets were used.

3.3.1.4.1 Effect on ordination

3.3.1.4.1.1 Pilot survey data

Figs. 3.6 and 3.7 show the results of PCA and RO releve ordinations respectively in the form of stereograms based on the data sets obtained with various plot sizes. PCA and RO ordinations of different data sets showed general similarity over the range of plot sizes. Continuity of vegetation was apparent in each case (Figs. 3.6 and 3.7). Comparison of the releve positions on the first two components of PCA and RO are presented in Figs. 3.8 and 3.9 respectively. A great deal of similarity in the rank order of ordination co-ordinates of the first two PCA components for data pertaining to the four plot sizes is readily apparent in Fig. 3.8. However, the releve positions on the first component showed greater similarity among the four data sets (Kendall's coefficient of concordance, $w = 0.9714$, $p < 0.001$) than that among those of the second component ($w = 0.8621$ $p < 0.01$). On the second component, rank order of some releves was changed markedly with the increasing plot size. In general, greater similarity was observed in the rank order of releves on a component for the data set of a given plot size and that of the next higher plot size. Rank order of releves on the first two axes of RO (Fig. 3.9a,b) exhibited close similarity. Coefficient of concordance for the order on the first axis pertaining to ordinations of four data sets was found to be 0.9648 ($p < 0.001$) and that for the second axis 0.8394 ($p < 0.01$).

First four eigenvalues, percentage of total variance accounted for by the components or axes and cumulative variance accounted for by the components of PCA and RO for data sets pertaining to different plot sizes are presented in Table 3.3 and Table 3.4. The corresponding values of these statistics for PCA ordinations based on various plot sizes are remarkably similar, though there is a slight tendency in the cumulative variance accounted for by the first four components to decrease very slightly but consistently with the increasing plot size (53.117% for plot size 2.5*2.5 m and 51.235% for plot size 10*10 m) (Table 3.3). Eigenvalues and the associated statistic of RO ordinations for data sets of the four plot sizes were also found markedly similar (Table 3.4). Percentage of variance and the cumulative variance accounted for by the first four components of RO were found to be comparable with those of the corresponding PCA ordinations.

PCA ordinations pertaining to data sets coming from varied plot sizes were objectively compared by computing Euclidean distances between releve pairs, considering 2, 3, 4, 5 or 6-dimensions (components). Product moment correlations were then computed between Euclidean distances for the pairs of ordinations compared (Table 3.5). RO releve ordinations were similarly compared (Table 3.6). In general, ordinations dervied from different plot sizes were found to be highly similar with one another as indicated by the high values of correlation coefficient. The significance of correlation coefficients was not tested since the usual test of significance is not valid in this situation because of the non-independent nature of distances between releves in pairs of ordinations. A heuristic test was developed that uses local constraints (Appendix 3.1). However, the program was too expensive to run and was used on only some values of r in Table 3.5. The degree of relationship was generally of higher order for ordinations of a given plot size and that derived from the data of next higher plot size.

The effect of plot size on species ordinations was also examined based on the pilot survey data. The total number of species encountered in the 30 sample plots of the four different sizes varied, therefore, for the purpose of comparison of species ordinations, data sets were reducd to those 74 species that occurred in the smallest plot size (2.5*2.5 m). Comparison of species positions (of eleven important species) on the first two components of PCA and RO are presented in Figs. 3.10 and 3.11 respectively. The rank order of selected species on the first axis of either PCA or RO was highly similar for the data sets coming from different plot sizes (Figs. 3.10a, 3.11a). The rank order on the second axis of PCA and RO was slightly changed with the increasing plot size (Figs. 3.10b, 3.11b). Based on all 74 species, the coefficient of concordance between rank order of species for the four data sets were 0.9518 and 0.8080 for the first and the second PCA components respectively; the corresponding values for RO being 0.8080 and 0.8001 respectively.

First four eigenvalues, percentage of total variance accounted for by the components and the cumulative variance accounted for by the PCA and RO components for the four data sets (each containing 74 species), is presented in Table 3.7. Eigenvalues resulting from PCA of various data sets were similar in magnitude. However, there was some tendency for the percentage variance and cumulative variance accounted for by the first four components to decrease slightly with the increasing plot size. The eigenvalues and the associated statistics for RO were also found to decrease slightly but consistently with the increasing plot size.

PCA and RO ordinations of species were objectively compared in the same manner as was done for releve ordinations. Species ordinations derived from data sets based on various plot sizes were found to be highly similar as indicated by high levels of correlation coefficient (Table 3.8). Included number of dimensions (axes) in the comparisons had very little effect on the degree of similarity although there was a slight tendency for the correlation coefficiencts to increase with the greater number of included dimensions up to 5 but inclusion of sixth dimension slightly lowered the levels of correlations in most comparisons. In both, PCA and RO species ordinations, the highest level of similarity was found between those based on plot sizes 5*5 and 7.5*7.5 m when 4 or 5 dimensions were included in the comparisons.

3.3.1.4.1.2 Stoneybrook data

The results of releve ordinations performed by MDSCAL for the data of eight different plot sizes are presented in the form of stereograms (Fig. 3.12). MDSCAL ordination was used here since it is regarded as a more powerful technique in various respects than eigenanalysis procedures such as PCA and RO (Fasham, 1977; Prentice, 1977). Changes in the releve positions on the first axis of MDSCAL ordinations with increasing plot size are depicted in Fig. 3.13. Stereograms ordinations based on different plot sizes were found to be closely similar, with the exception of the ordination pertaining to the smallest plot size (0.35*0.71 m) (Fig. 3.12). However, releve positions on the first ordination axis changed remarkably up to a plot size of 0.71*1.42 m. Objective comparisons of the ordinations based on correlation coefficient between inter-releve distances, in the three-dimensional space, between pairs of ordinations are outlined in Table 3.9. Very high levels of correlation coefficient were found between ordination pairs based on the data sets obtained with different plot sizes with the exception of the two smallest plot size. Fig. 3.14 shows the dendrograms resulting from simple average and group average clustering performed on the correlation matrix between ordination pairs. Again, close similarity between ordinations derived from plot sizes 0.71*1.42 to 4*8 m was found. The ordination based on the two smallest plot sizes were found to be the least similar to the rest of the six ordinations.

3.3.1.4.1.3 Maple forest data

The maple forest map was randomly sampled using plots of various sizes. Smaller plot sizes were sampled with higher sampling intensity compared to the larger ones. Since the sampling points differed for various plot sizes, the comparison of releve ordinations was out of question. For this reason, only species ordinations were performed and compared for different plot sizes.

Figs. 3.15 shows the three-dimensional species ordinations for the data of 7 different plot sizes in the form of stereograms. The general similarity of species ordinations was indicated in Fig. 3.15 particularly among plot sizes 20*k20, 30*30, 40*40 and 50*50'. Fig. 3.16 shows the changes in the species position on the first ordination axis in response to increase in the plot size. Changes in species position on the first ordination axis were more dramatic with the increase in plot size from 5*10 to 20*20'. Thereafter, the changes were less marked, until the plot size increased to 50*50' whose ordination axis again showed substantial changes in the rank order of species positions. Interestingly, the position of two species - Celtis occidentalis and Ostrya virginiana on the first ordination axis changed only slightly across the range of sampling units, compared to the rest of the six species. Fig. 3.17 is a trellis diagram showing the levels of correlation coefficients, based on species distances in the 3-dimensional ordination space, between pairs of ordinations. High levels of correlations were found between ordinations based on plot sizes 20*20 to 50*50'. The ordinations, based on the plot sizes 5*10 and 10*10 showed lowest similarity (correlation) with the other ordinations. The dendrogram in Fig. 3.18 resulting from simple average clustering performed on the correlation matrix used in Fig. 3.17 essentially depicted the results verbally stated above.

3.3.1.4.2 Effect on cluster recognition

3.3.1.4.2.1 Pilot survey data

Fig. 3.19 shows dendrograms resulting from sum of squares (SSA) clustering performed on the data sets obtained with four different plot sizes in the pilot survey. A general similarity in the hierarchical structure was indicated between dendrograms based on the different data sets and the dendrogram dervied from plot size 2.5*2.5 m appeared to be least similar to the rest of the dendrograms. Comparisons of the cophenetic and the topological matrices derived from SSA clustering on the data sets pertaining to the four plot sizes is outlined in Table 3.8. Pairs of matrices were compared using three different functions, viz. the complement of Jardine and Sibson's $\overset{*}{\Delta}_u(\overset{*}{\delta}_u = \overset{*}{\Delta}_u \max - \overset{*}{\Delta}_u)$, information function (2I) and product-moment correlation coefficient $(r(D_1,D_2))$. The cophenetic and the topological matrices corresponding to different plot sizes were found to be highly similar, as indicated by high levels of r and $\overset{*}{\delta}_u$ or low values of 2I. The topology and the cophenetic matrices corresponding to a plot size and the next higher one were generally found to be more similar.

3.3.1.4.2.2 Stoneybrook data

The dendrograms resulting from SSA clustering of releves performed on the data sets obtained by sampling with eight different plot sizes are presented in Fig. 3.20. With the exception of the dendrogram pertaining to the smallest plot size (0.35*0.71 m) all others showed close similarity in the hierarchical structure of each indicating the existence of two main groups. Of the two groups, the smaller one consisted of 10 releves (21 to 30) that belonged to the abandoned field, whilst the larger one comprising 20 releves (1 to 20) was associated with the topsoil at the Stoneybrook site. Table 3.11 presents the level of correlation coefficients and $\overset{*}{\delta}_u$ between the cophenetic matrices of the different classification hierarchies. These values bespeak of the high levels of similarity between the dendrograms, with the exception of that derived from the smallest plot size. The dendrograms resulting from simple average and group average clustering (Fig. 3.21) performed on the correlation matrix between cophenetic matrices of Table 3.11 show the above results graphically.

3.3.1.4.2.3. Maple forest data

Fig. 3.22 shows the dendrograms of species hierarchies resulting from SSA clustering performed on the data sets obtained with varied plot sizes. Though the structure of species groupings differed to some extent in the classification hierarchies pertaining to different plot sizes, the change in the association pattern of species over the range of sampling units was gradual and interestingly certain species groups emerged consistently in the dendrograms, e.g. the group of four species, including Ostrya virginiana, Carya cordifolia, Juglans cinerea and Celtis occidentalis. Fig. 3.23 shows a trellis diagram of the correlation matrix computed between cophenetic matrices resulting from SSA clustering (lower half) and between dissimilarity matrices (upper half) based on data sets collected by sampling with varied plot sizes. In general, the levels of correlation coefficient were high. High levels of similarities, as indicated by high values of r, were found particularly among the plot sizes 5*10' to 20*20' and between 30*30 and 50*50' plot sizes. The dendrogram in Fig. 3.24 resulting from simple average clustering of the dendrograms shown, in Fig. 3.22 based on the levels of correlation coefficients between the cophenetic matrices graphically portrays the relationships outlined above.

3.3.1.5 Discussion

Selection of an effective as well as an efficient plot size for phytosociological sampling is of crucial importance in seeking trends and identifying group structure in vegetation. However, the major concern of ecologists with regard to sampling has been to obtain an adequate sample of vegetation with a minimum of effort. One widely used classical approach for determining plot size and sampling adequacy is the use of species-area curves (Cain, 1938; Ashby, 1948; Vestal, 1949, Rice and Kelting, 1955), though in some surveys the size of sampling plot is chosen arbitrarily. Apart from serious limitations and drawbacks of species area curves (Poore, 1955; Hopkins, 1957; Moore, 1962; Goodall, 1970; Podani, 1984) the minimal area of sample plot, chosen for the purpose of sampling, by the species area curve or other empirical methods (e.g., Hopkins, 1957; Goodall, 1961; Moravec, 1973; Dietvorst _et al_., 1982) may not necessarily provide an effective plot size for disclosing inherent trends or group structure in vegetation. As an alternative to the empirical approach to attain a certain level of sampling adequacy, interest may centre around the determination of an effective plot size capable of disclosing trends and/or group structure in vegetation. In the latter context, the most effective plot size is defined as one that gives the highest average value (expectation) of a suitable dissimilarity function (Podani, 1982) for a given tract of vegetation, conditional upon random sampling. A relatively small plot size capable of disclosing similar trends and/or group structure as the most effective plot size is regarded as the most efficient plot size. An efficient plot size may be derived in the pilot studies, by comparing the objective classifications and ordinations resulting from other plot sizes and those based on the most effective plot size. Such a plot size would fulfill the sampling objectives while minimizing the sampling effort.

The expected resemblance/plot size curve for the maple forest data, where Euclidean distance was used as the resemblance function, was found to be unimodal, yielding a point on the curve corresponding to the most effective plot size. The expected resemblance based on Euclidean distance for other data sets, with the exception of pilot survey data, showed monotonic curves that after rising initially levelled off. Thus, expected resemblance/plot size curves based on Euclidean distance, generally yielded a point or an interval on the curve corresponding to a specific plot size or an interval of plot size respectively that would maximize dissimilarity between sampling units. When simple matching coefficient was used, the expected resemblance for different data sets tended to decline initially and then remained more or less at a constant level. By contrast, the expectation based on Russell and Rao's or Sorensen's coefficient, in general, showed continuously rising monotonic curves with the increasing plot size with the result that the point or an interval of plot size corresponding to maximal dissimilarity (minimal similarity) remained unknown. Similar results with the different resemblance functions have been reported by Podani (1982) for a variety of vegetation types.

Based on the results of the present study, the Euclidean distance seems to be the most suitable resemblance (dissimilarity) function in the determination of a plot size or a range of plot size that would maximize the dissimilarity. Both Sorensen's and Russell and Rao's coefficients (similarity functions) which disregard joint absences are unsuitable in this respect. The simple matching coefficient, on the other hand, provides erratic results due to fluctuations in the number of matches as well as mismatches that are likely to increase with the increase in the number of species. Similar conclusions were drawn by Podani (1982).

The results of the present study as well as that of Podani (1982) suggest the suitability of Euclidean distance whilst unsuitability of Sorensen and Russell and Rao's coefficients as similarity functions in the determination of most effective plot size. Sorensen's coefficient does not take joint absences into account and emphasizes the joint occurrences whereas the denominator in Russell and Rao's coefficient masks the mutual mismatches (Podani, 1982). Some other disadvantages of Russell and Rao's coefficient have been noted by Hubalek (1982).

The possible use of characteristic functions of other types in the determination of most effective plot size was also investigated. In case of pilot survey data, the number of realized species combinations and consequently the florula diversity and florula evenness remained unchanged, whereas local distinctness, relative local distinctness and associatum increased continuously over the range of sampling units. Similar results were obtained for the Stoneybrook site data. Thus, maxima of these functions could not be located over the plot size ranges. Two possible explanations can be given for these results: (1) the data sets used represented species rich heterogeneous vegetation, whereas maxima at a certain plot size or within an interval of size are yielded by characteristic functions only when the vegetation is homogeneous (Podani, 1982; Juhasz-Nagy and Podani, 1983); (2) the number of plots used were relatively low compared to the number of species in the data sets, hence each florula was unique.

To achieve a higher ratio between sample size and the number of species so as to increase the homogeneity of the entire sample artifically, the Stoneybrook data sets corresponding to 8 different plot sizes were reduced to the same 6 or 11 species that could explain about 70 to 85 percent of total variation in the data sets. All the characteristic functions showed continuous decrease with the increasing plot size when reduced data sets were employed making it difficult to locate the maxima. Thus, it appears that characteristic functions have no practical utility in the determination of an optimum plot size, at least in the situation where vegetation is heterogeneous and rich in species composition.

The general pattern of releve or species ordinations performed by PCA, RO or MDSCAL was found to be consistent across the range of sampling units for a variety of data sets. Similarities in ordinations were generally of higher order for those derived from one plot size and the next higher one in a set of ordinations. Similarly, Goff and Mitchell (1975) found high degree of similarity in the general pattern of species ordinations derived from stand data and from various sizes of sampling units. The practical implication of this finding is that a small plot size capable of disclosing similar trends or gradients to that of the most effective, possibly larger plot size, in a pilot survey can be used in the main study to reduce the data recording effort without losing the information related to trends or gradients. Furthermore, the consistency of trends over a range of plot sizes not only confirms the existence of such trends in vegetation but also

Within different sets of data, the group structure of releves (or species) pertaining to different plot sizes were also found to be closely similar as shown by the high order of similarities in the classification hierarchies which were more highly similar, particularly at the higher levels. In the only study of this nature, Noy-Meir et al. (1970) found that the variation of plot size over the range 2-16 m^2 hardly affected the first 3-4 divisions of the normal association analysis, but did affect lower divisions. However, their study was based solely on qualitative data.

It is well known that small scale pattern variations are affected by plot (block) size (Greig-Smith, 1961, 1983; Kershaw, 1961, 1973; Westman and Anderson, 1970). However, in this study large scale pattern in vegetation was examined and it was found that plot size had minimal effect on the emerging pattern information. Where a large number of species are contributing patterns at a number of scales, the use of multiple pattern analysis may be appropriate (Noy-Meir and Anderson, 1971; Walker et al., 1972). Therefore, in pilot surveys the determination of an optimal plot size to maximize the underlying pattern information is dictated by the level of pattern variation being sought.

3.3.2 Effect of data type

The subject of data type has been introduced in section 2.9. Two experiments were performed to study the effect of data type on ordination and cluster recognition. The object of the first experiment was to examine the influence of binary, ordinal and percentage cover data on the resulting ordinations and numerical classifications and to what extent they were influenced by changes in plot size. This data on the resulting ordinations and numerical classifications and to what extent they were influenced by changes in plot size. This experiment was based on the pilot survey data which consisted of cover estimates on van der Maarel's ordinal scale. The data sets pertaining to the four plot sizes were transformed to presence-absence and cover percentage using an power transformation of the form (van der Maarel, 1979).

$$Y = X^w$$

where X and Y are original and transformed values respectively and w = 2 for transformation to percentage cover. The 3 types of data sets for each of the 4 plot sizes were subjected to PCA ordinations and SSA clustering.

The object of the second experiment was to study the relative influence of various commonly and infrequently used ordinal scales and some simple transformation on the resulting information from ordinations and cluster analysis when compared with the untransformed percentage cover values. The Stoneybrook data of plot size 2.83*5.66 m was used. Percentage cover values were converted into various ordinal scales and were variously transformed (Greig-Smith, 1964; Jensen, 1978).

3.3.2.1 Results

3.3.2.1.1 Effect of data type and plot size on ordination

The results of PCA ordinations in the form of stereograms for the different data types and plot sizes are given in Fig. 3.25. The ordinations based on ~~ordinal~~ data and those based on % cover data showed considerable similarity whilst binary ordinations appear somewhat dissimilar from the rest. Fig. 3.26 presents a PCAD ordination of the twelve ordinations. A close similarity in the ordinations based on ordinal scale and the corresponding ones based on percentage cover data was readily apparent while those derived from binary data were placed apart indicating dissimilarity. The series of ordinations derived from the three data types showed continuous trends within the series with respect to increasing plot size. The simple average and SSA clustering of the 12 ordinations also give similar results as above (Fig. 3.27a,b).

3.3.2.1.2 Effect of data type and plot size on group structure

The dendrograms resulting from SSA clustering of the different data types are presented in Fig. 3.28. A general similarity in the classification hierarchies derived from binary data was readily apparent. The dendrograms based on ordinal or percentage cover data appeared to be similar but somewhat dissimilar to the ones derived from binary data. Fig. 3.29 shows a 2-dimensional PCAD ordination of the dendrograms. The ordination broadly separated out two groups of dendrograms - one group of those based on 0/1 data and the other group of those based on ordinal and % cover data. Binary dendrograms showed a continuous trend with respect to increasing plot size in the ordination plane.

3.3.2.1.3 Effect of data type and transformations on ordination

Fig. 3.30 presents the stereograms of MSDCAL ordinations based on various data types and transformations. Generally, two groups of releves could be recognized, a small group of ten at the top and a larger group of 20 releves at the bottom of the ordination which corresponded to the two main habitat types. However, ordinations based on Lagerberg-Raunkiaer's and Daubenmire's scales did not separate out the two groups as neatly as did other data types. The ordinations, in general, seemed to be closely similar to one another; in particular, those based on Braun-Blanquet, Domin-Krajina, Hult-Sernandes and Londo's scales were remarkably similar. Table 3.12 shows the levels of correlation coefficient between the inter-releve distances in pairs of ordinations and Fig. 3.31 shows simple average and group average dendrograms based on the correlation matrix. Some interesting results were shown by these dendrograms for the hierarchy of the ordinations. The ordination based on percentage cover was found closely similar to that based on Londo's decimal scale. The ordination based on van der Maarel's scale was closely related to that derived from Jensen's log (% cover + 1) transformation. The ordinations derived from arcsine and square root transformations were highly similar. On the other hand, the ordination based on Jensen's 100+% cover transformation was found to be relatively dissimilar to the rest of the ordinations.

3.3.2.1.4 Effect of data type and transformations on group structure

Fig. 3.32 shows the dendrograms resulting from SSA clustering of releves performed on different data types and transformed data sets. The classification hierarchies, in general, showed marked similarity, with each of the dendrogram showing two major groups corresponding to the two main habitat types. Table 3.13 shows the levels of correlation coefficient and $_u$ between cophenetic matrices derived from the classification hierarchies. High order of similarity between dendrograms was clearly demonstrated. Fig. 3.33 shows the dendrograms resulting from simple average and group average clustering of the cophenetic matrices. The results of classification of ordinations were more or less duplicated in the classification of classifications with a few notable exceptions. It was disclosed that the dendrogram based on Lagerberg-Raunkiaer scale was least similar to others. The dendrograms derived from van der Maarel's scale and Hult-Sernander scale showed high levels of similarity.

3.3.2.2 Discussion

The ordinations based on three data types in the first experiment depicted a continuum with respect to increasing plot size, indicating that the plot size enlargement does bring about continuous and gradual changes in the resulting ordinations presumably owing to changes in inter-species correlations. The ordination results obtained with qualitative data were markedly different from those obtained with quantitative (ordinal or % cover) data. This finding accords well with the results of Orloci (1966) and Bouxin (1975) who found considerable discrepencies in the ordination results based on qualitative and quantitative data sets. Orloci (1966) observed that in the presence/absence ordination both gradients and clusters were less obvious. The present 0/1 ordinations also showed lesser degree of clustering compared to quantitative ordinations. The qualitative ordination is unrevealing in situation where species richness is low to moderate and the dominance is shared by a few species which was the case in the present study. By contrast, under species rich low predominance conditions qualitative data are likely to be more satisfactory for ordination than quantitative data (Austin and Greig-Smith, 1968).

The dendrograms derived from binary data sets showed considerable dissimilarity with those based either on ordinal or percentage cover data. Numerical classification approaches have often favoured the use of presence/absence data (Williams and Lambert, 1959; Ivemey-Cook and Proctor, 1966; Flenley, 1969) and under high diversity, agglomerative techniques may also yield satisfactory results (Austin and Greig-Smith, 1968). Presumably, because of the low-moderate diversity situation the binary data in the present study gave deviating results from the dendrograms derived from quantitatives data sets. The binary dendrograms showed a continuum corresponding to increasing plot size. This latter result contrasts well with the findings of Podani (1982) who in a similar experiment found the binary dendrograms derived from different plots sizes to form a cluster in the ordination space. He concluded that classifications using binary data are less dependent on the size of sampling unit and are consequently more stable. Contrary to this conclusion, greater stability of classifications based on ordinal or % cover data was indicated as the dendrograms resulting from ordinal and percentage cover data formed separate groups in the ordination of dendrograms.

A number of interesting results were found in the second experiment. It was disclosed that most of the ordinal scales of cover estimation in the situation of low to moderate diversity can provide almost the same ordination as well as classification results as those based on the percentage cover data. Closest results to those of percentage cover data were those obtained with the use of Domin-Krajina and Londo's decimal scale. The obvious reason is that these scales are much more elaborated (10 and 13 classes respectively) compared to those of Braun-Blanquet and Daubenmire's scales that have only 7 and 6 categories respectively. Due to higher number of categories the percentage cover data is well represented by such scales. Relatively most dissimilar numerical results to the percentage cover data were obtained when Lagerberg-Raunkiaer scale was used which is only a four part scale.

Interestingly, it was found that simple transformations such as arcsine, square root and various log transformation do not make noticeable change in the classification or ordination results. All these results, though, dependent on the data structure viz. heterogenity and species richness are presumably applicable to similar situations of data structure which may not be uncommon.

3.3.3 Effect of data reduction

The subject of data reduction has been introduced in section 2.8. Reduction of species in data sets was achieved by three different weighting procedures - namely, sums of squares method (Orloci, 1973), within descriptor sum of squares weighting developed in the present study and equivocation information (Orloci, 1978b). These differ in the underlying philosophies as well as their effectiveness and compatibility in the subsequent data analysis. The object of the following experiments was to examine as to what extent the data can be reduced without loosing the pattern information. Species ranking on a sums of squares criterion is compatible with the eigenvector ordinations based on covariance matrix. Thus, the effect of data reduction on PCA ordinations was studied using the sums of squares ranking criterion. The within descriptor sum of squares weighting appeared to be compatible to SSA clustering and MDSCAL ordination and was used for data reduction in both cases. Similarly, equivocation information weighting was also employed for data reduction prior to SSA clustering and MDSCAL ordinations on the grounds that the data set used comprised of categorical data and also to test its comparative success with the within descriptor sum of squares weighting.

3.3.2.1 Results

3.3.2.1.1 Effect on ordination

3.3.2.1.1.1 Effect on PCA ordination

The data set used was the pilot survey data of plot size 5*5 m which had a total of 85 species. Various levels of data reduction were achieved by setting the minimum of cumulative explained variance by the ranked species at 0.7, 0.8, 0.9 and 0.98 (a proportion of a total of 1). Fig. 3.34 shows the number of species retained at various cut-off levels. The PCA releve ordinations in the form of stereograms are presented in Fig. 3.35 and the eigenvalues and related statistic for these results appear in Table 3.14. The first 4 eigenvalues and the cumulative variance accounted for by these increased with the data reduction level.

The correlation coefficients computed between distances in ordination space (2 to 6 dimensions included) of reduced set and that of complete data set (Fig. 3.36) were found to be of high order. [Note that correlation coefficient is used here as an index of similarity, not as a test statistic, hence no significance level is attached.] Highest levels of correlation coefficients were associated with comparisons between reduced data set at 0.98 level and complete data set. Levels of correlation coefficients were generally high when six dimensions were included and decline slightly with the lesser number of included dimensions. In general, the level of correlation coefficients between ordinations of reduced data sets with that of complete data set declined with the decrease in the cut-off level.

For the comparison of PCA species ordinations at various levels of data reduction with that of complete data reduction with that of complete data, only the coordinate scores of those species were retained that occurred in the most reduced data set (viz. 0.7 cumulative variance). Thus, nine species were included in the analysis. Changes in species positions, with data reduction, on the first principal component depicted in Fig. 3.37 were small and the rank order was not changed until a data reduction level of 0.7 was reached. Correlation coefficients between inter-species distances in the ordination based on complete data and those based on reduced data sets considering 2 to 6 dimensions are given in Fig. 3.38. The levels of correlation coefficient were, in general, high and were higher when 6 dimensions were included. The levels of correlations between species ordination based on complete data and those derived from reduced data sets declined with the lowering of the cut-off point.

3.3.3.1.1.2 Effect on MDSCAL ordination

Reduced data sets were obtained at cut-off levels of 0.98, 0.9, 0.8, 0.7 and 0.6 using the within species sum of squares and equivocation information rankings. Fig. 3.39a/b shows the number of species retained at different cut-off levels by the two ranking techniques. Fig. 3.40 shows the 3-D MDSCAL releve ordinations of complete data and those of data sets reduced by within species sum of squares ranking. In general, the distribution of releves in the stereogram for complete data set matches remarkably well with the configurations derived from reduced data sets. Table 3.15 gives the product-moment correlation coefficients (r) between the inter-releve distances in the ordination of complete and reduced data sets in 1, 2 and 3-dimensional ordination spaces. The values of r were generally high indicating a high level of similarity between the ordination based on complete data and those based on reduced data sets. The levels of r were generally higher when 3 dimensions were considered rather than one or two dimensions. The levels of correlation coefficient decreased as more and more species were excluded from the analyses.

Fig. 3.41 shows the MDSCAL ordinations derived from data sets reduced by equivocation information ranking. Close similarity was apparent only between the ordination based on complete data and that based on reduced data at a level of 0.98. The levels of correlation coefficient betwen pairwise releve distances of complete and reduced data sets are given in Table 3.16. High level of correlation was found only between the ordination of complete data set and that of reduced data set at 0.98 cut-off level. Other comparisons yielded lower levels of correlations, particularly when only one or two-dimensions were included in the comparisons.

3.3.3.1.2 Effect on group structure

The dendrograms resulting from SSA releve clustering of complete data set and those from data sets reduced by within species sum of squares ranking are presented in Fig. 3.42. A marked degree of correspondence in the hierarchies based on complete and reduced data sets was readily apparent. Fig. 3.43a shows the comparison of the cophenetic matrices of complete data set with those derived from reduced data set. High levels of correlation coefficient indicate great degree of similarity between the dendrograms derived from clustering performed on reduced data sets with that developed from complete data set. Though the level of r declined slightly and gradually with the decrease in the ranking cut-off point, even at the species reduction level of 0.6 the value of r was a high as 0.9775. The disagreement function ($_u$) showed a declining trend with the increasing cut-off point. The consistent low values of disagreement function indicate a great degree of correspondence between the cophenetic matrices derived from reduced data sets with that corresponding to complete data set. Fig. 3.43b shows a gradual decline in the values of r between the topology matrices derived from clustering of reduced data sets and that derived from complete data set but even the lower values were high enough to indicate high order of similarity between the dendrograms. The $_u$ showed a mirror image trend of that shown by the correlation coefficient.

Fig. 3.44 shows the dendrograms resulting from SSA clustering of data sets reduced by equivocation information ranking. Marked similarity in the dendrograms was found only between the one derived from reduced data at 0.98 cut-off point and that based on complete data set. Dendrograms derived from reduced data sets obtained at cut-off levels of 0.9 to 0.7 were considerably dissimilar from that corresponding to unreduced data set. Objective comparisons of the cophenetic matrices are made in Fig. 3.45. The levels of correlation coefficient between cophenetic matrics derived from SSA clustering of reduced and complete data sets were low upto the cut-off point of 0.9 but at 0.98 the value of r was high. Disagreement function showed, not unexpectedly a mirror image of correlation coefficient. Very similar results were obtained when the dendrogram of complete data set was compared with those obtained from reduced data sets using topology matrices (Fig. 3.45b).

3.3.3.2 Discussion

A wide variety of ranking techniques have been proposed (e.g. Feoli, 1972; Orloci, 1973, 1975, 1978b). Most ranking techniques are based on shared sums of squares or information (e.g., Orloci, 1973; Rohlf, 1977), whereas the 'within' species sum of squares ranking is exclusively based on the independent pattern information contained in the species and disregards the shared information. In a recent review, Jancey (1979) concluded: "The decision whether to rank on maximal shared variance as opposed to specific variance has not been resolved". He pointed out that: "Perhaps more important than the question of which is fundamentally correct is the need to match the ranking philosophy to that of subsequent data analysis." In this regard, the ranking method based on the partition of total within species sum of squares is exactly compatible with the sum of squares clustering (Orloci, 1967; Ward, 1963) that minimizes the total within group sum of squares. For the purpose of comparison also because categorical data was used the equivocation information technique was also employed for data reduction.

The PCA ordinations based on subsets of species obtained at successively lower cut-off levels of sums of squares ranking showed close correspondence with that resulting from full species compliment. Similarly, species reduction by means of within species sum of squares also did not distort the MDSCAL ordination results. The fact that MDSCAL works on proximities (or distances) between objects and that the sum of squares divergence between two objects is a function of their distances provides the basis for compatibility between within species sum of squares ranking and the MDSCAL ordination. In the case of eigenanalytical ordination (viz. PCA, RO), however, co-variation of species is of paramount importance, therefore, in that situation species ranking on the basis of covariance or shared information is obviously the appropriate approach.

An examination of the effect of species reduction, by within species sum of square ranking, on the disclosure of group structure strongly indicated that relatively a small proportion of the total species present in a study area account for the information on the underlying group structure in vegetation. There was little change in the classification hierarchies derived from successively reduced subsets of species obtained at various ranking cut-off points. This corroborates and extends the findings of Orloci and Mukkatu (1973) who found little distortion in the resemblance structure of the releve sample even when the number of species were drastically reduced, though their species subsets were derived from covariance ranking.

Equivocation information ranking was not as successful as the within species sum of squares ranking in yielding subsets that could retain bulk of pattern information contained in the full species compliment.

3.3.4 Iterative clustering

This section describes and evaluates an iterative clustering technique that automatically discards at each clustering cycle those species which do not carry pattern information in the releve subset.

Regardless of weighting criterion, as Jancey (1980) points out, species ranking is a matter of local relevance and the reduced species set comprising of highly ranked species, represents the non-random component of pattern information in a specific tract of vegetation. Extension of this concept can be utilized for minimizing random events in order to achieve a more refined definition of the underlying group structure (Jancey, 1980). In a hierarchic agglomerative clustering, at each successive level of clustering, only highly ranked species in the subset of releves are included in the analysis to reduce the risk of misclassification. Inclusion of lowly ranked species, i.e., species with larger random component, at any level of clustering would only blur the underlying non-random pattern. Details of the clustering algorithm based on the locality of species importance approach appear in Jancey (1980). The utility of within species sum of squares ranking in the minimization of noise while unfolding group structure is examined uisng Jancey's iterative ranking-clustering algorithm which originally used Orloci's sums of square ranking. Pilot survey data obtained with a plot size of 2.5*2.5 m was used and the ranking cut-off point was set at 0.7 (proportion of the total within species sum of squares).

3.3.4.1 Results

Fig. 3.46 shows a dendrogram derived from iterative agglomerative clustering. Comparison of this dendrogram with that based on complete data set (Fig. 3.42a) reveals that the group structure in the former is much more compact with lower total within group sum of squares than in the latter. Furthermore, two releves, 2 and 13 which were members of group 2 in the SSA clustering based on full species compliment fall in group 1 in the iterative clustering. Examination of various ordinations and environmental data corresponding to releves all indicated that releves 2 and 13 were misclassified in the agglomerative classification based on all species. In order to test the affiliation of releves 2 and 13 with either group 1 or 2, Mahalanobis' generalized distance (D^2) was computed between the two releves and group 1 and 2. The D^2 values between group 1 and releves 2 and 13 were 2.98 and 4.12 respectively as opposed to 63.05 and 36.65 between group 2 and releves 2 and 13 respectively, indicating that the two releves were better placed in group 1 in the iterative clustering procedure.

3.3.4.2 Discussion

When minimization of misclassification is the objective, Jancey's (1980) iterative clustering using SSA and the within species sum of squares ranking criterion, evidently, not only minimizes 'noise' in unfolding group structure, but also provides internal consistency and compatibility in the iterative clustering. The principal advantage of such a consistency in the algorithm is that at each clustering cycle the ratio of the total within species sum of squares of the reduced species set to that of complete species set is a constant ratio equal to the ranking cut-off level. Thus, despite the changing role of species in the pattern formation in the differentsubsets of the total sample space, together the ranked species represent a correspondent non-random component, of pattern information as a constant proportion of the total information in the sample subset. Such a consistency and compatibility is unique to the within species sum of squares ranking algorithm when used in conjunction with the SSA algorithm for iterative clustering.

Table 3.1 The values of characteristic functions for different plot sizes used in the pilot survey.

PLOT SIZE (sq.m.)	FLORULA DIVERSITY	FLORULA EVENNESS	LOCAL DISTINCTNESS	RELATIVE LOCAL DISTINCTNESS	ASSOCIATUM	# OF REALIZED COMBINATIONS
2.5 * 2.5	147.207	1	1165.71	0.5250	1018.5	30
5 * 5	147.207	1	1401.74	0.5497	1254.5	30
7.5 * 7.5	147.207	1	1534.70	0.5500	1387.3	30
10 * 10	147.207	1	1728.84	0.5436	1581.6	30

Table 3.2 The values of characteristic functions for different plot sizes of Stoneybrook site data.

The values were computed for complete and reduced data sets. (C.D. = complete data sets, R.D. = reduced data sets)

PLOT SIZE (sq.m.)	FLORULA DIVERSITY	FLORULA EVENNESS	LOCAL DISTINCTNESS	RELATIVE LOCAL DISTINCTNESS	ASSOCIATUM	# OF REALIZED COMBINATIONS
C.D.						
0.35*0.71	147.20	1	606.79	0.5618	459.58	30
0.5 *1.0	147.20	1	677.28	0.6101	530.07	30
0.71*1.42	147.20	1	729.22	0.4340	582.01	30
1.0 *2.0	147.20	1	776.97	0.4624	629.77	30
1.41*2.83	147.20	1	854.78	0.5080	707.58	30
2.0 *4.0	147.20	1	896.52	0.5336	749.32	30
2.83*5.66	147.20	1	962.70	0.5730	815.49	30
4.0 *8.0	147.20	1	958.88	0.5607	811.68	30
R.D.(11 spp)						
0.35*0.71	143.20	0.972	288.33	0.8737	145.12	28
0.5 *1.0	138.45	0.940	274.12	0.8306	135.67	26
0.71*1.42	141.20	0.939	260.82	0.7903	119.61	27
1.0 *2.0	127.20	0.864	235.55	0.7138	108.35	21
1.41*2.83	122.84	0.834	223.22	0.6764	100.38	20
2.0 *4.0	122.94	0.835	195.55	0.5925	72.61	21
2.83*5.66	120.18	0.816	191.54	0.5804	71.35	20
4.0*8.0	117.59	0.798	182.95	0.5544	65.35	19
R.D. (6 spp)						
0.35*0.71	119.69	0.813	160.42	0.8912	40.73	18
0.5 *1.0	107.69	0.731	146.69	0.8149	38.99	15
0.71*1.42	97.33	0.661	133.53	0.7418	36.204	12
1.0 *2.0	87.98	0.597	122.69	0.6816	34.707	10
1.41*2.83	88.31	0.599	113.70	0.6316	25.39	10
2.0 *4.0	80.67	0.5480	100.37	0.5576	19.69	9
2.83*5.66	80.34	0.5458	96.35	0.5353	16.01	10
4.0 *8.0	79.90	0.5428	97.08	0.5393	17.18	11

Table 3.3 Eigenvalues, % variance and cumulative variance accounted for by the first four components of PCA ordinations for the four data sets of pilot survey.

DATA SET (plot size)	FIRST FOUR EIGENVALUES	% VARIANCE	CUMULATIVE VARIANCE
2.5 m	19.1	20.804	20.804
	11.9	12.945	33.749
	9.66	10.501	44.250
	8.16	8.867	53.117
5.0 m	20.2	21.755	21.755
	11.8	12.640	34.395
	8.95	9.620	44.015
	7.56	8.128	52.143
7.5 m	20.1	21.36	21.36
	11.6	12.54	33.90
	8.8	9.55	43.45
	8.1	8.26	51.31
10 m	20.6	19.923	19.923
	12.6	12.198	32.121
	10.4	10.002	42.123
	8.02	7.740	49.863

Table 3.4 Eigenvalues, % variance and cumulative variance accounted for by the first four components of RO ordinations for the four data sets of pilot survey.

DATA SET (plot size)	FIRST FOUR EIGENVALUES	% VARIANCE	CUMULATIVE VARIANCE
2.5 m	0.000462	22.248	22.248
	0.000264	12.696	34.944
	0.000220	10.604	45.548
	0.000186	8.938	54.486
5.0 m	0.000382	22.866	22.866
	0.000205	12.279	35.145
	0.000161	9.650	44.795
	0.000137	8.230	53.025
7.5 m	0.000317	21.785	21.785
	0.000176	12.052	33.837
	0.000150	10.306	44.143
	0.000115	7.932	52.075
10 m	0.000226	20.399	20.399
	0.000130	11.795	32.194
	0.000118	10.700	42.894
	0.000085	7.729	50.623

Table 3.5 Comparison of ordinations of data of various plot sizes using different number of principal components.

PLOT SIZES COMPARED	NUMBER OF DIMENSIONS USED				
	2	3	4	5	6
2.5m^2 & 5m^2	0.88922	0.91064	0.89814	0.92119	0.91261**
2.5m^2 & 7.5m^2	0.85888	0.79113	0.86485	0.88018	0.80619**
2.5m^2 & 10m^2	0.70842	0.61923	0.741756	0.6557	0.64941**
5m^2 & 7.5m	0.94702	0.92020	0.93625	0.95106	0.91905
5m^2 & 10m^2	0.75494	0.73600	0.84661	0.72297	0.72380
7.5m^2 & 10m^2	0.83711	0.86017	0.85310	0.76110	0.79626

** $P < 0.01$ as indicated by a simulated distribution of r (heuristic test).

Table 3.6 Correlation of distances between releve ordinations (RO) axes for various plot sizes (pilot survey data).

DATA SETS (plot sizes)	NUMBER OF DIMENSIONS USED				
	2	3	4	5	6
$2.5m^2$ & $5.0m^2$	0.89768	0.92088	0.92695	0.91553	0.92051
$2.5m^2$ & $7.5m^2$	0.84671	0.79778	0.88420	0.87091	0.80276
$2.5m^2$ & $10m^2$	0.62985	0.60131	0.70530	0.65008	0.66059
$5.0m^2$ & $7.5m^2$	0.94162	0.91370	0.94259	0.94783	0.89513
$5.0m^2$ & $10m^2$	0.67140	0.71229	0.81330	0.73827	0.75744
$7.5m^2$ & $10m^2$	0.75514	0.85398	0.83219	0.79213	0.83243

Table 3.7 First four eigenvalues, percentage and cumulative variance accounted for by the PCA and RO components of the four plot sizes used in the pilot survey. (Each data set contains 74 species).

	PCA ORDINATION OF SPECIES		
DATA SET (plot size)	FIRST FOUR EIGENVALUES	% VARIANCE	CUMULATIVE VARIANCE
2.5 m	19.1	20.804	20.804
	11.9	12.945	33.749
	9.66	10.501	44.250
	8.16	8.867	53.117
5 m	20.2	22.005	22.005
	11.7	12.803	34.808
	8.92	9.731	44.539
	7.52	8.201	52.740
7.5 m	19.7	21.461	21.461
	11.3	12.324	33.785
	9.8	10.695	44.480
	7.38	8.022	52.502
10 m	20.5	20.579	20.579
	12.5	12.526	33.105
	10.2	10.238	43.343
	7.86	7.892	51.235
	RO ORDINATION OF SPECIES		
2.5 m	0.000462	22.248	22.248
	0.000264	12.696	34.944
	0.000220	10.604	45.548
	0.000186	8.938	54.486
5 m	0.000394	23.199	23.199
	0.000211	12.421	35.620
	0.00016	9.758	45.378
	0.00014	8.318	53.696
7.5 m	0.000335	22.362	22.362
	0.000185	12.371	34.733
	0.000157	10.464	45.197
	0.000121	8.100	53.297
10 m	0.000244	21.150	21.150
	0.000139	12.079	33.229
	0.000124	10.794	44.023
	0.000091	7.930	51.953

Table 3.8 Correlation of distances between species in PCA and RO species ordinations of various plot sizes used in the pilot survey. (All data sets were reduced to 74 species).

ORDINATIONS AND PLOT SIZES COMPARED	NUMBER OF DIMENSIONS USED				
	2	3	4	5	6
1. <u>PCA</u>					
2.5m² & 5m²	0.980491	0.986464	0.986784	0.983794	0.989938
2.5m² & 7.5m²	0.980206	0.973308	0.985725	0.983558	0.957318
2.5m² & 10m²	0.969521	0.949761	0.954597	0.927122	0.917193
5m² & 7.5m²	0.978737	0.985795	0.991351	0.992584	0.969124
5m² & 10m²	0.948514	0.956146	0.962893	0.957806	0.932123
7.5m² & 10m²	0.969519	0.972435	0.96537	0.953592	0.972262
2. <u>RO</u>					
2.5m² & 5m²	0.98239	0.985954	0.989707	0.989796	0.986515
2.5m² & 7.5m²	0.972454	0.962528	0.985489	0.987166	0.953489
2.5m² & 10m²	0.967458	0.957359	0.954626	0.945694	0.939252
5m² & 7.5m²	0.978261	0.984374	0.991436	0.990658	0.977684
5m² & 10m²	0.952011	9.964395	0.961018	0.958585	0.960417
7.5m² & 10m²	0.961768	0.96691	0.955962	0.95118	0.971355

Table 3.9 Correlation of distances between releves ordinations (MDSCAL) pertaining to 8 plot sizes used at Stoneybrook site.

Plot sizes								
1. 0.35*0.71 m								
2. 0.5 *1.0 m	0.880							
3. 0.71*1.42 m	0.844	0.932						
4. 1.0 *2.0 m	0.816	0.907	0.968					
5. 1.41*2.83 m	0.799	0.904	0.957	0.978				
6. 2.0 *4.0 m	0.803	0.899	0.952	0.970	0.986			
7. 2.83*5.66 m	0.788	0.899	0.955	0.962	0.982	0.986		
8. 4 *8 m	0.784	0.885	0.940	0.961	0.975	0.975	0.973	
Plot sizes (Numbers refer to sizes shown on left side)	1	2	3	4	5	6	7	8

Table 3.10 Comparison of cophenetic matrices and topology matrices derived from SSA clustering of releves based on 4 different plot sizes ued in the pilot survey.

PLOT SIZES COMPARED (side m)	Cophenetic matrix			Topology matrix		
	$\overset{*}{\delta}_u$	2I	r	$\overset{*}{\delta}_u$	2I	r
2.5 and 5.0	1.02321	6274	0.57326	1.12290	89.58	0.59749
2.5 and 7.5	0.16371	4012	0.83938	1.11744	97.58	0.64411
2.5 and 10	1.0834	6026	0.69437	1.10424	101.27	0.56629
5.0 and 7.5	0.99720	8453	0.54465	1.10093	99.61	0.58290
5.0 and 10	0.92599	10931	0.32157	1.08391	115.97	0.44768
7.5 and 10	1.02501	8333	0.60345	1.07709	127.00	0.50877

$\overset{*}{\delta}_u = \overset{*}{\delta}_u \max - \overset{*}{\delta}_u$

Table 3.11 Comparison of cophenetic metrics derived from SSA of various plot sizes used at Stoneybrook site. Entries in the lower half are the correlation coefficients while in the upper half $\overset{*}{\delta}_u(D_1,D_2)$.

$\overset{*}{\delta}_u(D_1,D_2)$

Plot sizes								
1. 0.35*0.71 m		0.8429	0.79682	0.79994	0.79106	0.73112	0.77551	0.76211
2. 0.5 *1.0 m	0.53923		1.28107	1.28282	1.2736	1.25782	1.25822	1.24061
3. 0.71*1.42 m	0.50884	0.98204		1.37131	1.35931	1.33522	1.33635	1.32996
4. 1.0 *2.0 m	0.51760	0.98344	0.99705		1.36954	1.33335	1.32812	1.32020
5. 1.41*2.83 m	0.51673	0.98360	0.99705	0.99803		1.34154	1.33885	1.33150
6. 2.0 *4.0 m	0.51024	0.98049	0.99413	0.99350	0.99430		1.37013	1.36230
7. 2.83*5.66 m	0.50244	0.98190	0.99445	0.99263	0.99391	0.99738		1.36878
8. 4.0 *8.0 m	0.49991	0.98005	0.99555	0.99320	0.99394	0.99772	0.99832	
Plot sizes (Numbers corespond to the sizes shown on left side)	1	2	3	4	5	6	7	8

$r(D_1,D_2)$

Table 3.12 Comparison of MDSCAL ordinations based on various data types and transformations. Each element of the triangular matrix is a correlation coefficient between releve distances between a pair of ordination.

Data types and transformations	1	2	3	4	5	6	7	8	9	10	11	12	13	14
	(Numbers represent ordinations of data types as shown on left)													
1. % cover														
2. van der Maarel scale	0.98596													
3. Brau-Blanquet scale	0.98661	0.99221												
4. Domin Krajina scale	0.97819	0.98874	0.99149											
5. Daubenmire scale	0.97057	0.97795	0.98693	0.98939										
6. Hult-Sernander scale	0.98904	0.99141	0.99237	0.99045	0.98731									
7. Lagerberg-Raunkiaer scale	0.96558	0.96506	0.97115	0.98437	0.98224	0.97737								
8. Londo's decimal scale	0.99107	0.97314	0.97943	0.97136	0.96667	0.98324	0.96142							
9. Bailey and Poulton scale	0.97314	0.98519	0.98768	0.99039	0.99130	0.98465	0.97922	0.96475						
10. Jensen's log 100 (2 + log % cover)	0.94841	0.96841	0.96332	0.98037	0.97927	0.96802	0.97290	0.93772	0.98454					
11. Jensen's log (% cover + 1)	0.98931	0.99727	0.99256	0.98929	0.97793	0.99238	0.96659	0.97851	0.98436	0.96660				
12. Jensen's 100 + % cover	0.95898	0.93587	0.95078	0.95022	0.95398	0.95622	0.95744	0.96311	0.94475	0.92487	0.94027			
13. Arcsine	0.99354	0.99162	0.99260	0.99014	0.98062	0.99323	0.97374	0.98661	0.98415	0.96341	0.99663	0.95763		
14. Square root	0.99339	0.99331	0.99313	0.98975	0.98022	0.99310	0.97238	0.98473	0.98509	0.96420	0.99737	0.95384	0.99908	0.00000

Table 3.13 Comparison of cophenetic matrices derived from SSA of untransformed (% cover) and various data types and transformations. Entries in lower half are correlation coefficients while in the upper half are $\overset{*}{\lambda}(D_1,D_2)$.

(Numbers correspond to data types as shown on left side.)

Data types and transformations	1	2	3	4	5	6	7	8	9	10	11	12	13	14
1. % cover		0.0576	0.05151	0.0582	0.0651	0.0557	0.0848	0.0518	0.0578	0.0676	0.0617	0.0453	0.6002	0.0620
2. van der Maarel scale	0.99643		0.0358	0.0409	0.0506	0.[illegible]301	0.0812	0.0688	0.0358	0.0458	0.0358	0.0680	0.0394	0.0344
3. Bran-Blanquet scale	0.99716	0.99861		0.0411	0.0466	0.0364	0.0807	0.0619	0.0438	0.0530	0.0427	0.0590	0.0338	0.0376
4. Domin Krajina scale	0.99661	0.99889	0.99889		0.0434	0.0398	0.0619	0.0701	0.0511	0.0430	0.0563	0.0688	0.0560	0.0519
5. Daubenmire scale	0.99575	0.99803	0.99849	0.99783		0.0420	0.0607	0.0683	0.0317	0.0469	0.0567	0.0735	0.0640	0.0632
6. Hault-Sernander scale	0.99659	0.99910	0.99866	0.99852	0.99840		0.0602	0.0552	0.0341	0.0470	0.0452	0.0620	0.0483	0.0445
7. Lagerberg-Raunkiaer scale	0.99505	0.99670	0.99684	0.99690	0.99688	0.99887		0.0889	0.0691	0.0640	0.0974	0.0858	0.0991	0.0965
8. Londo's decimal scale	0.99705	0.99494	0.99594	0.99472	0.99506	0.99529	0.99368		0.0682	0.0762	0.0724	0.0576	0.0688	0.0710
9. Bailey and Poulton scale	0.99639	0.99889	0.99820	0.99791	0.99900	0.99876	0.99669	0.99484		0.0415	0.0431	0.0715	0.0533	0.0521
10. Jensen's log 100 (2 + log % cover)	0.99577	0.99907	0.99830	0.99796	0.99751	0.99826	0.99584	0.99407	0.99843		0.0632	0.0790	0.0659	0.0650
11. Jensen's log (% cover + 1)	0.99632	0.99880	0.99822	0.99818	0.99832	0.99833	0.99543	0.99495	0.99893	0.99819		0.0745	0.0304	0.0277
12. Jensen's 100 + % cover	0.99777	0.99499	0.99623	0.99534	0.99472	0.99584	0.99549	0.99643	0.99458	0.99421	0.99431		0.0678	0.0677
13. Arcsine	0.99670	0.99499	0.99904	0.99851	0.99765	0.99810	0.99561	0.99569	0.99809	0.99817	0.99904	0.95763		0.0170
14. Square root	0.99638	0.99862	0.99872	0.99890	0.99767	0.99852	0.99601	0.99529	0.99815	0.99806	0.99919	0.95384	0.99969	

Table 3.14 Eigenvalues and associated statistics for complete and reduced data sets. Data sets reduced by sum of squares ranking. C.D. = complete data set; R.D. = reduced data sets at the ranking cut-off shown.

LEVEL OF DATA REDUCTION	FIRST FOUR EIGENVALUES	PERCENTAGE VARIANCE ACCOUNTED	CUMULATIVE PERCENTAGE VARIANCE
C.D.	20.2	21.75	21.75
	11.8	12.64	34.39
	8.9	9.62	44.01
	7.6	8.13	52.14
R.D. 0.98	19.5	23.97	23.97
	11.2	13.74	37.71
	7.9	9.72	47.43
	7.0	8.71	56.14
R.D. 0.9	16.6	25.11	25.11
	10.1	15.17	40.28
	7.3	10.95	51.23
	6.2	9.40	60.63
R.D. 0.8	13.0	24.43	24.43
	9.8	18.43	42.86
	6.9	12.99	55.85
	5.6	10.47	66.32
R.D. 0.7	12.2	27.59	27.59
	7.8	17.67	45.26
	6.1	13.93	59.19
	4.9	11.14	70.33

Table 3.15 Degree of similarity (r) between MDSCAL ordination of complete data set and that of reduced data sets. Data reduction was performed by total within species sum of squares ranking.

DATE SETS COMPARED	NUMBER OF DIMENSIONS USED		
	1	2	3
CD and 11 spp. [0.6]	0.88645	0.870805	0.939265
CD and 14 spp. [0.7]	0.94616	0.934553	0.964844
CD and 18 spp. [0.8]	0.978202	0.960259	0.974728
CD and 24 spp. [0.9]	0.985994	0.974302	0.985698
CD and 44 spp. [0.98]	0.991923	0.982578	0.991579

CD = complete data set with 74 species.

Numbers in brackets indicate the ranking cut-off points (proportion of the sum of within species sum of square for the species above cut-off point to the total within species sum of squares of all species).

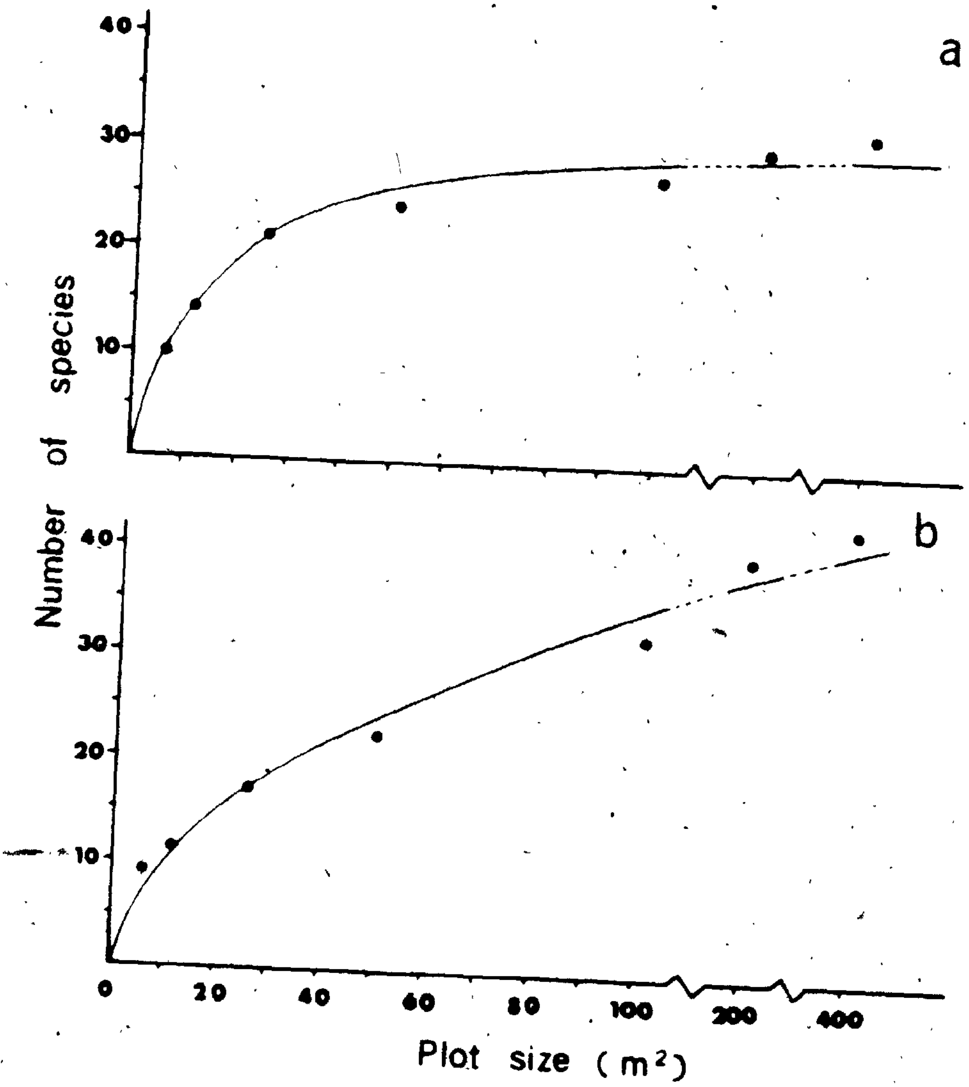
Table 3.16 Degree of similarity (r) between MDSCAL ordination of complete data set and those of reduced data sets. Data reduction was performed by Equivocation information ranking.

DATE SETS COMPARED	NUMBER OF DIMENSIONS USED		
	1	2	3
CD and 33 spp. [0.6]	0.07866	0.37913	0.55929
CD and 42 spp. [0.7)	0.08586	0.38401	0.56019
CD and 52 spp. [0.8]	0.34076	0.50640	0.62180
CD and 60 spp. [0.9]	0.44139	0.43400	0.61882
CD and 71 spp. [0.98]	0.79529	0.57882	0.99635

CD = complete data

Numbers in brackets indicate the ranking cut-off points.

Fig. 3.1 Species area curves for three sites and the composite curve. Curves fitted by eye. (a) Hyde Park, (b) Southcrest, (c) Clarkside/Pension, (d) Composite (average) curve for all sites.


a
b
Number of species
40
30
20
10
40
30
20
10
0
20
40
60
80
100
200
400
Plot size (m²)

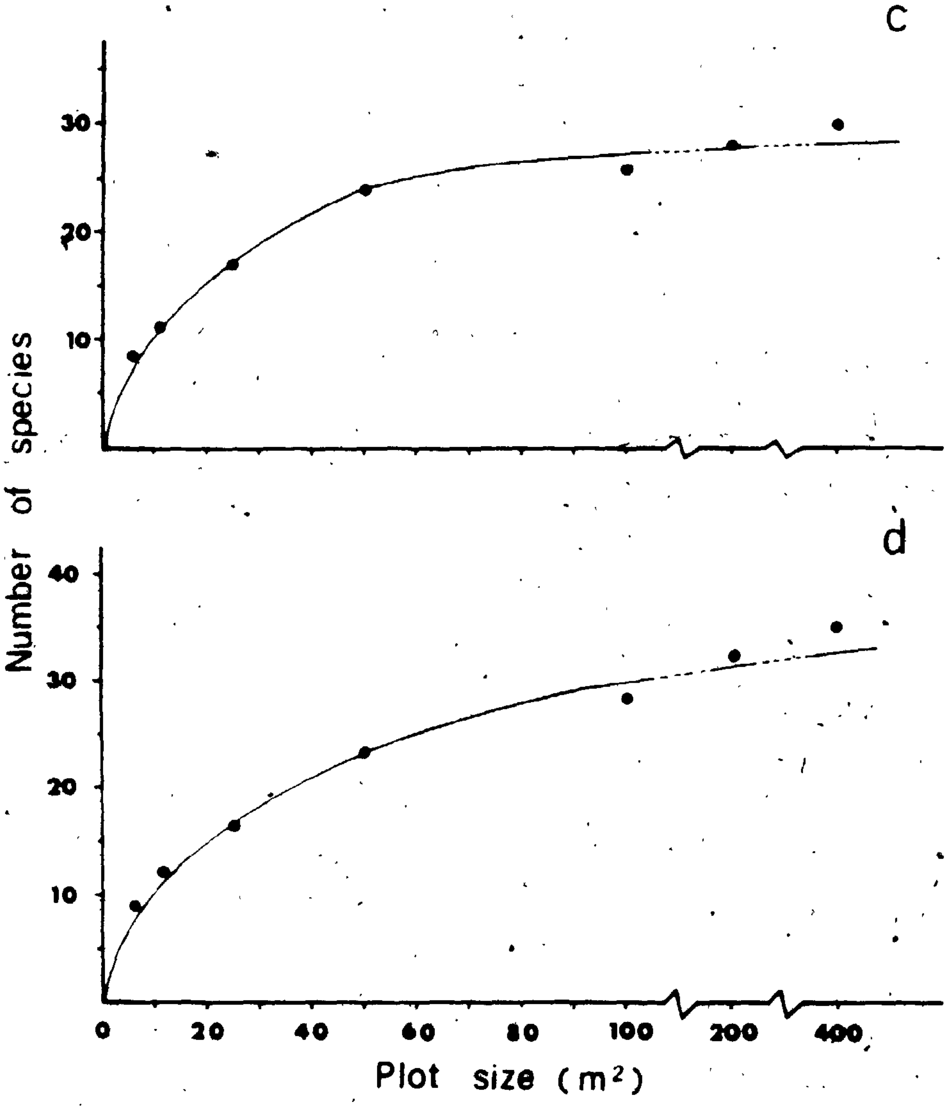

c
30
20
10
d
40
30
20
10
0
20
40
60
80
100
200
400
Number of species
Plot size (m²)

Fig. 3.2 Relationship between expected resemblance and plot size for the pilot survey data. (a) Euclidean distance, (b) Sorensen's coefficient, (c) Russell and Rao's coefficient, (d) Sokal and Mitchner's simple matching coefficient.

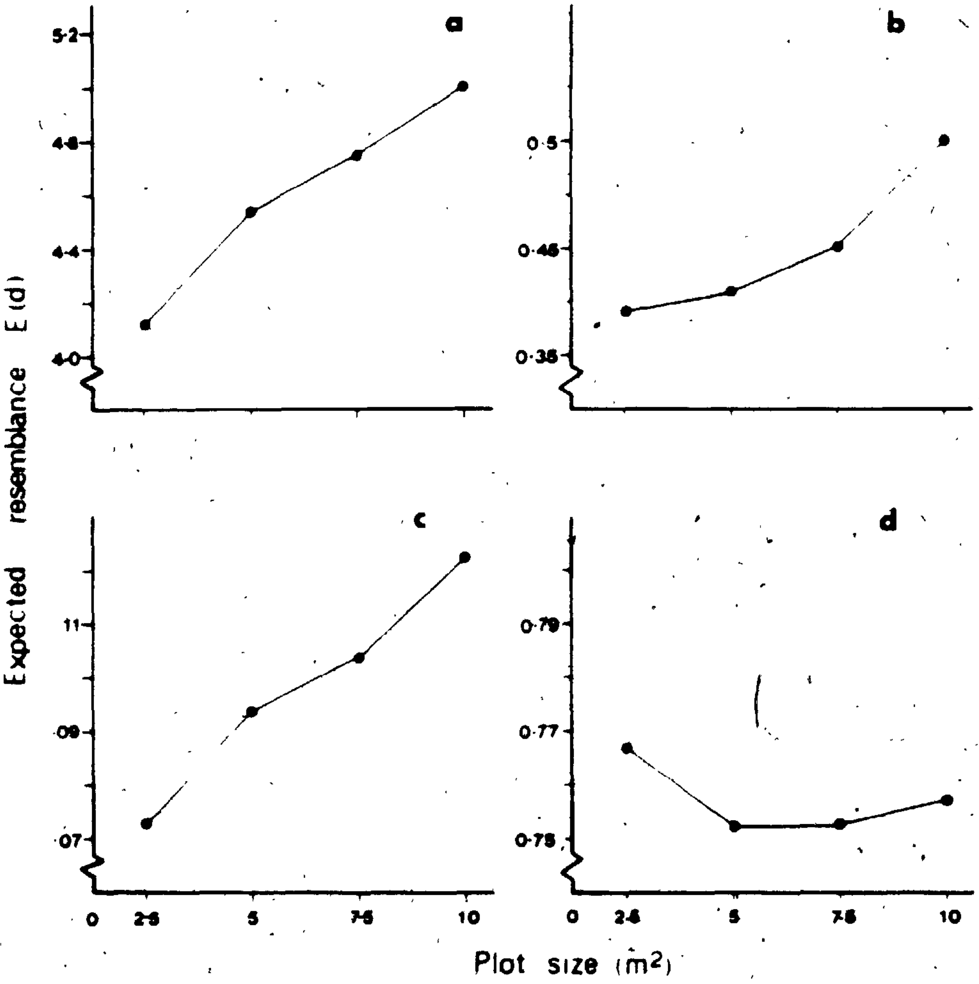
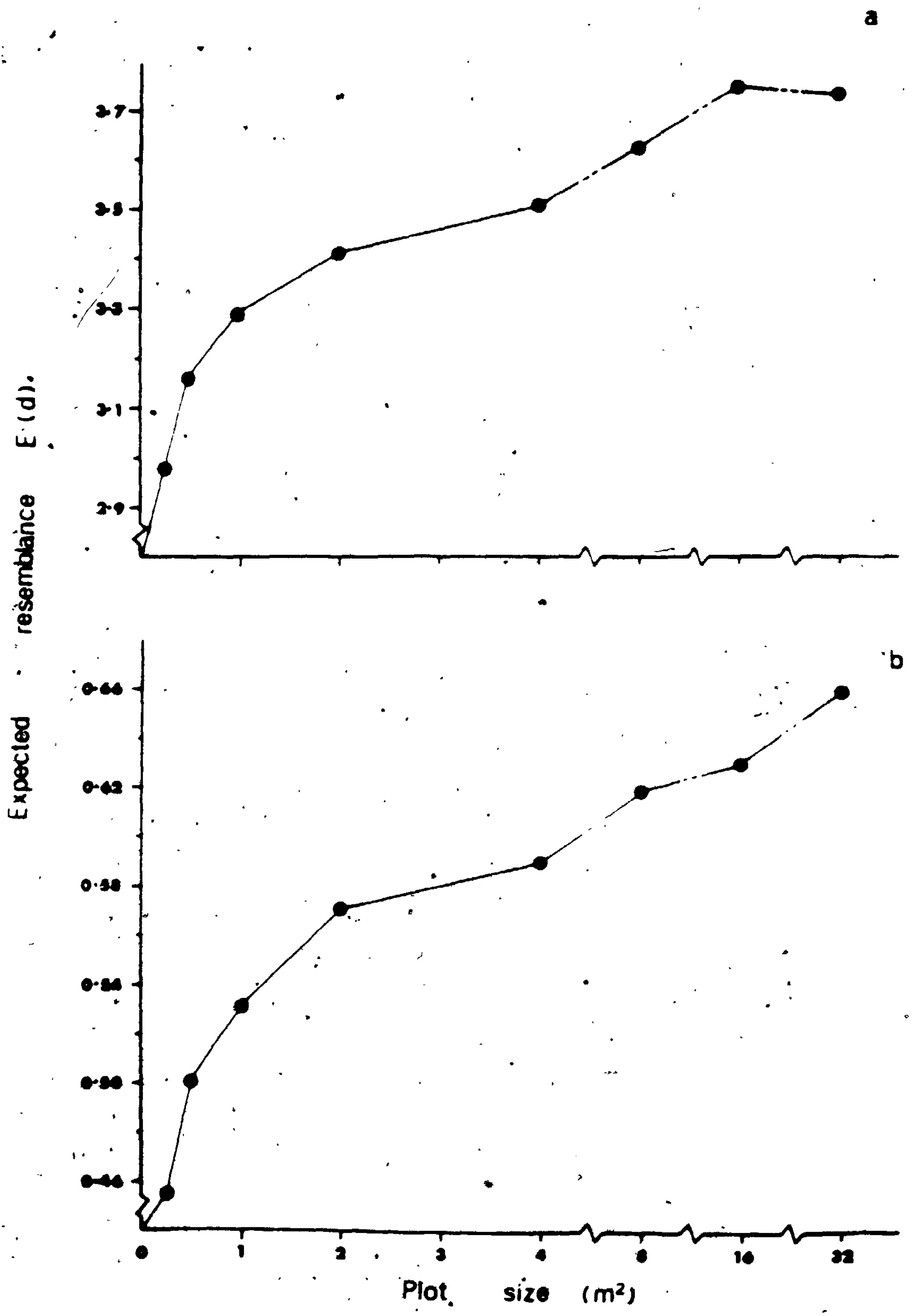

a
b
c
d
Expected resemblance E(d)
5·2
4·8
4·4
4·0
0·5
0·45
0·35
11
09
07
0·79
0·77
0·75
0
2·5
5
7·5
10
Plot size (m2)

Fig. 3.3 Relationship between expected resemblance and plot size for Stoneybrook site. (a) Euclidean distance, (b) Sorensen's coefficient, (c) Russell and Rao's coefficient, (d) Sokal and Mitchner's coefficient.


a
3·7
3·5
3·3
3·1
2·9
Expected resemblance E(d).
b
0·66
0·62
0·58
0·54
0·50
0·46
0
1
2
3
4
8
16
32
Plot size (m²)

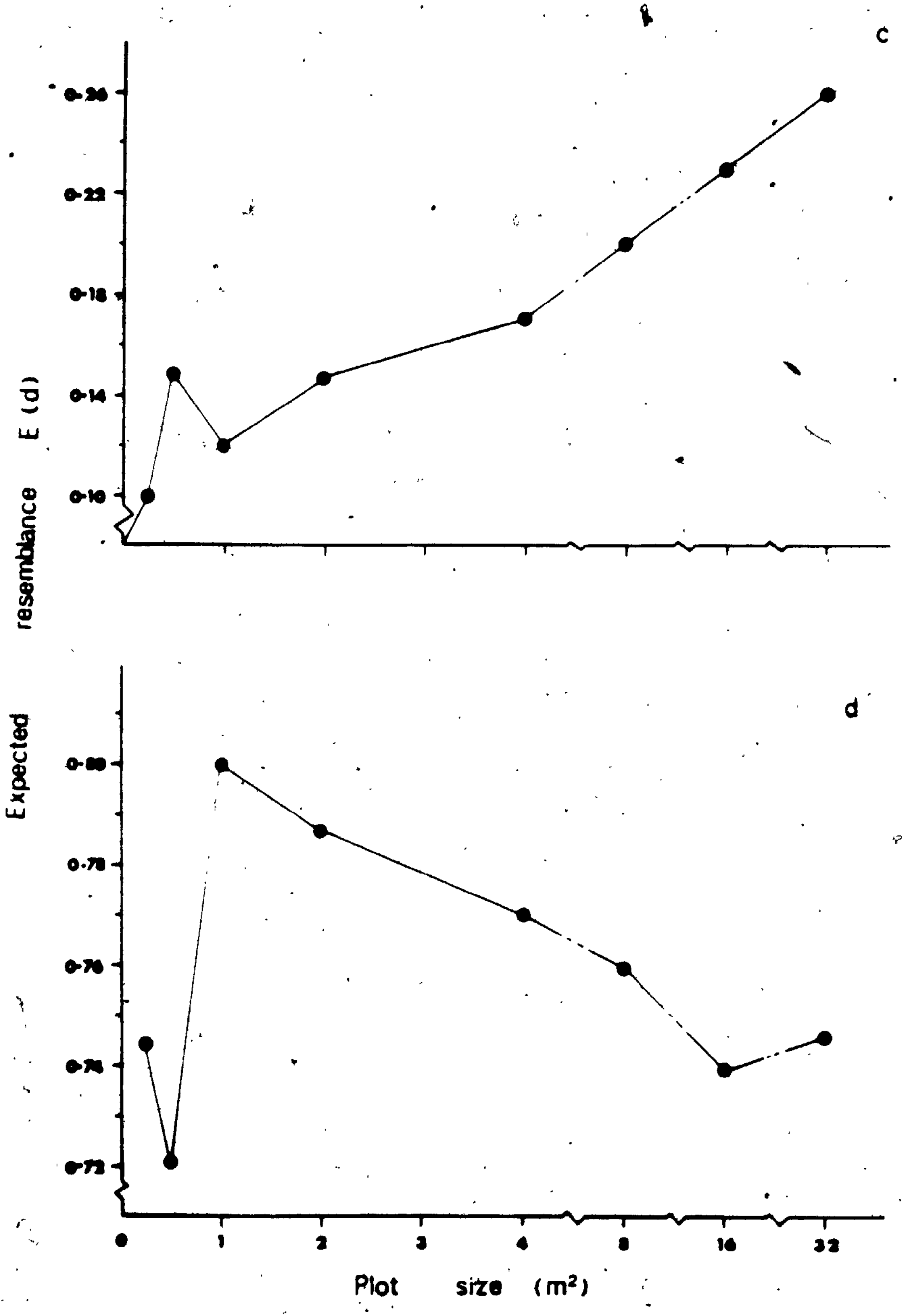

c
0·26
0·22
0·18
0·14
0·10
Expected resemblance E (d)
d
0·80
0·78
0·76
0·74
0·72
0
1
2
3
4
8
16
32
Plot size (m²)

Fig. 3.4 Relationship between expected resemblance and plot size for the maple forest data. Euclidean distance was used, based on 0/1 data. Plot sizes numbered 1 to 7 are as follows: 1, 5*10 ft (1.52*3.04m); 2, 10*10(3.04*3.04 m); 3, 10*20(3.04*6.08 m); 4, 20*20 ft (6.08*6.08 m); 5, 30*30 ft (9.14*9.14 m); 6, 40*40 (12.19*12.19 m); 7, 50*50(15.23*15.23 m).

EUCLIDEAN DISTANCE (0,1) DATA

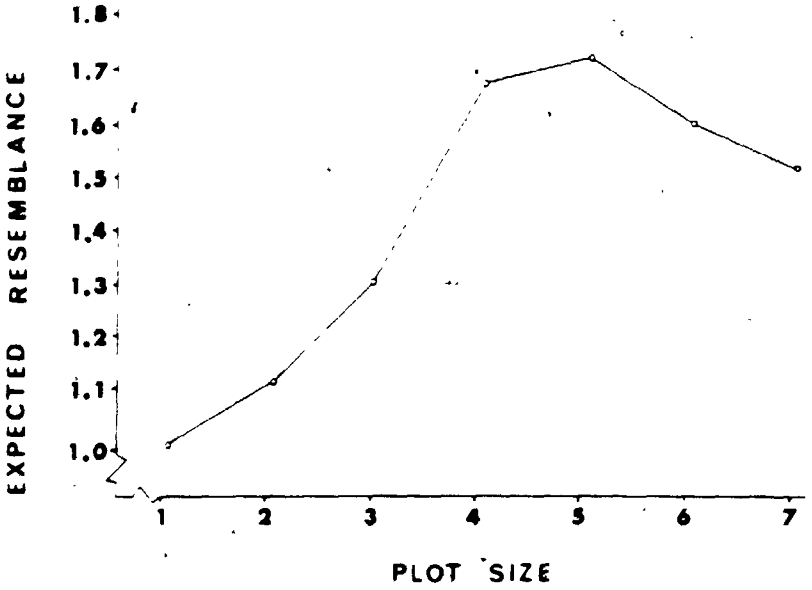
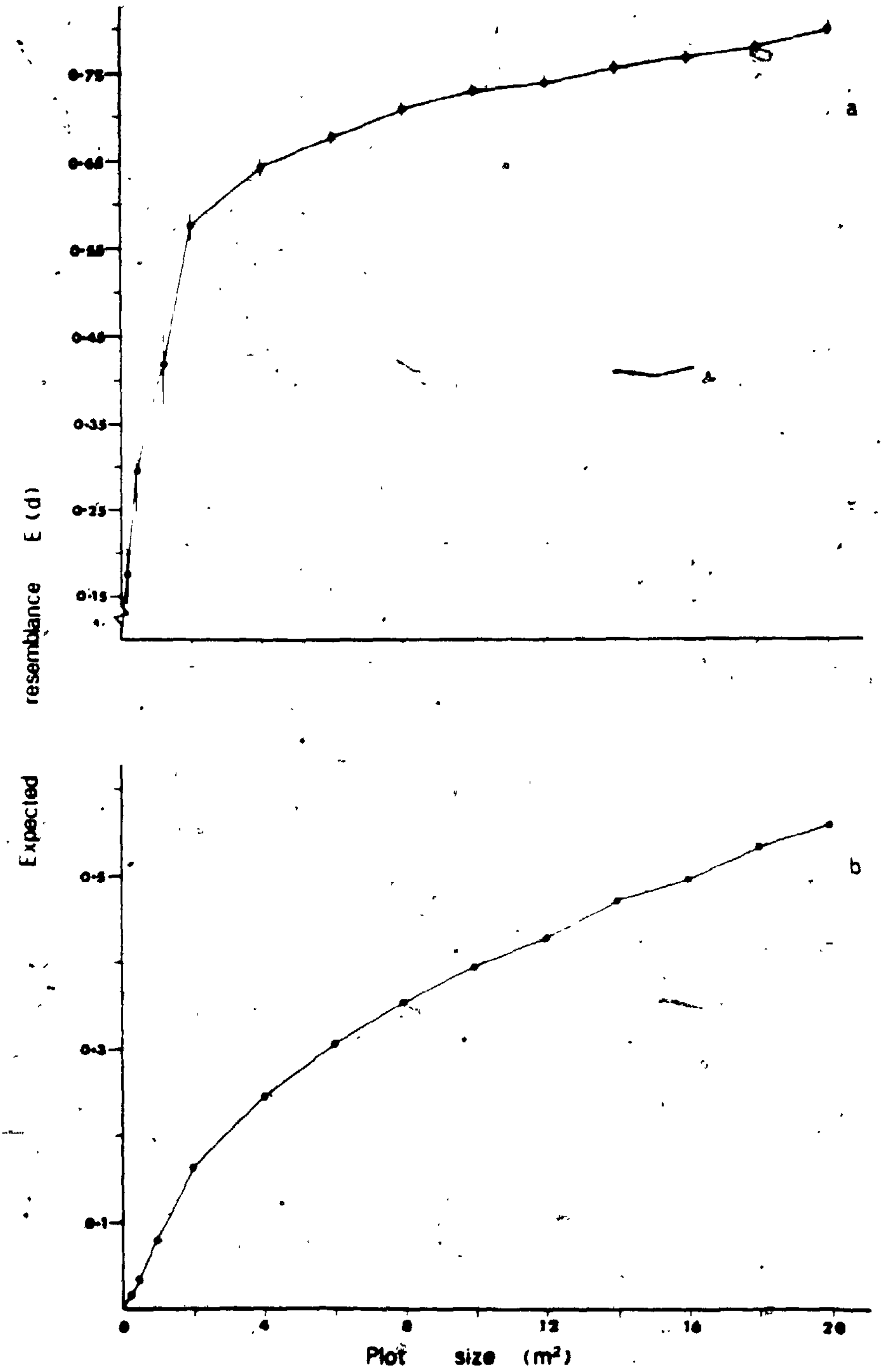


Fig. 3.5 Relationship between expected resemblance and plot size for Wilkins site (a) Euclidean distance, (b) Sorensen's coefficient, (c) Russell and Rao's coefficient, (d) Sokal and Mitchner's coefficient. Vertical bars indicate standard deviation.


0·75
0·65
0·55
0·45
0·35
0·25
0·15
0.
a
Expected resemblance E (d)
0·5
0·3
0·1
b
0
4
8
12
16
20
Plot size (m²)

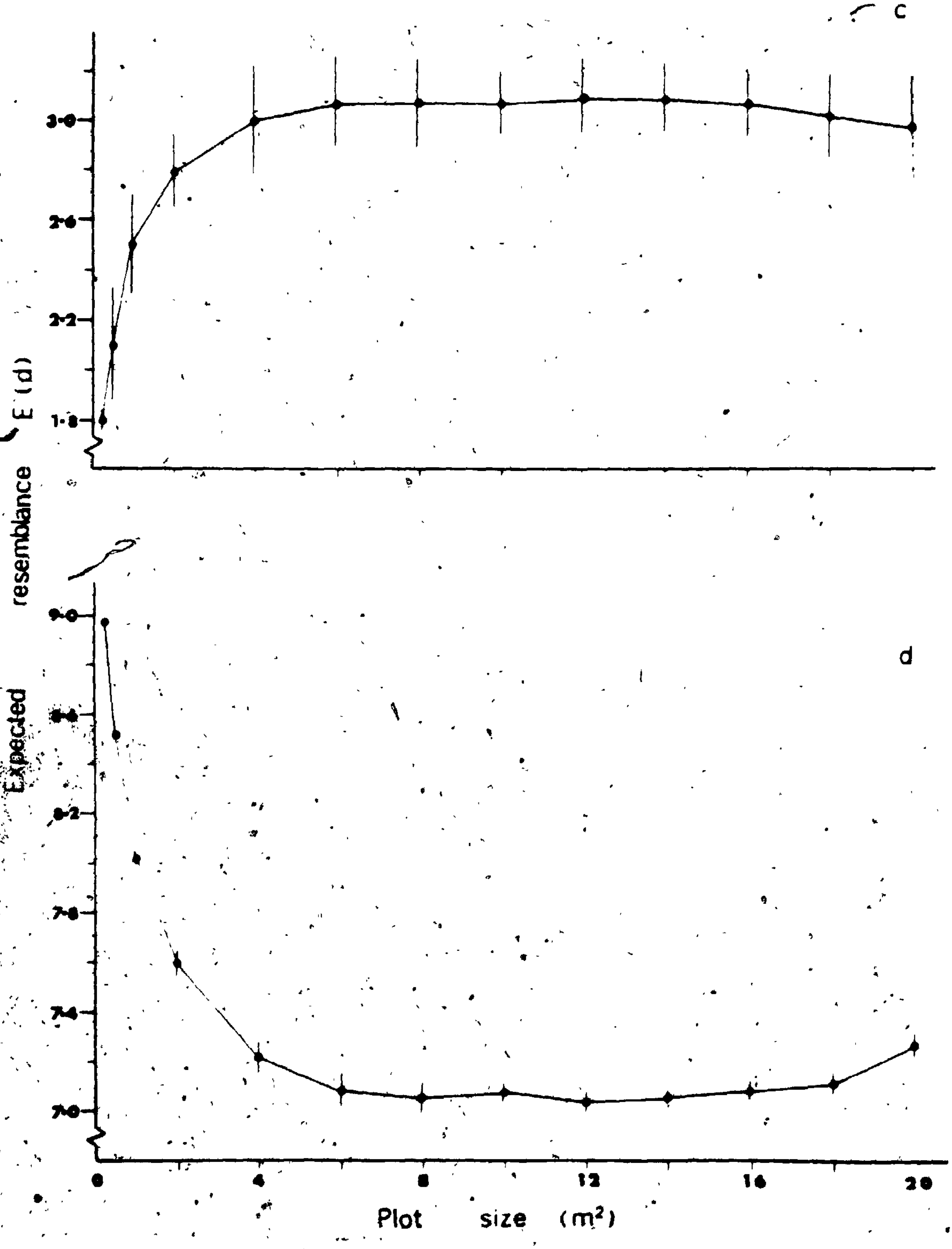
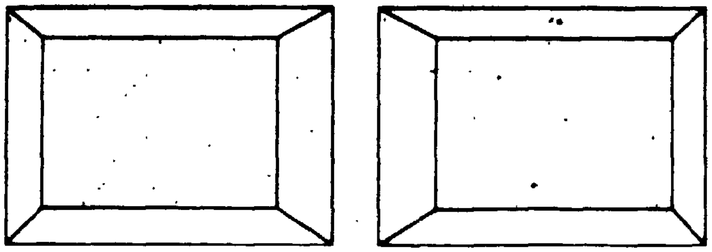
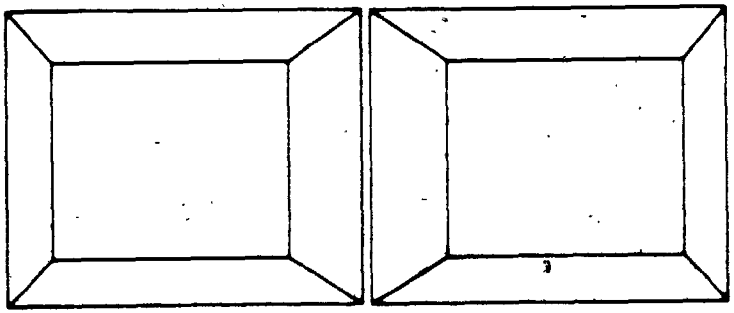

c
3·0
2·6
2·2
1·8
Expected resemblance E (d)
d
9·0
8·6
8·2
7·8
7·4
7·0
0
4
8
12
16
20
Plot size (m²)

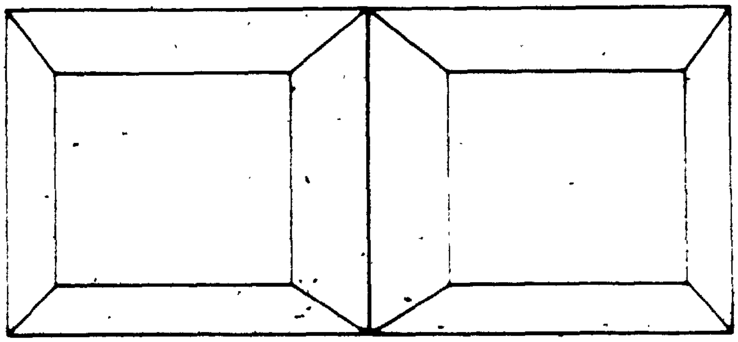
Fig. 3.6 Effect of plot size on PCA ordination of releves using pilot survey data. Stereograms show first three components. Stereograms a-d correspond to the ordinations resulting from the data obtained with 4 different plot sizes: (a) 2.5*2.5 m, (b) 5*5 m, (c) 7.5*7.5 m, and (d) 10*10 m. (Reference plots of these stereograms as well as of others presented in the dissertation exist but are not presented because of space limitations).



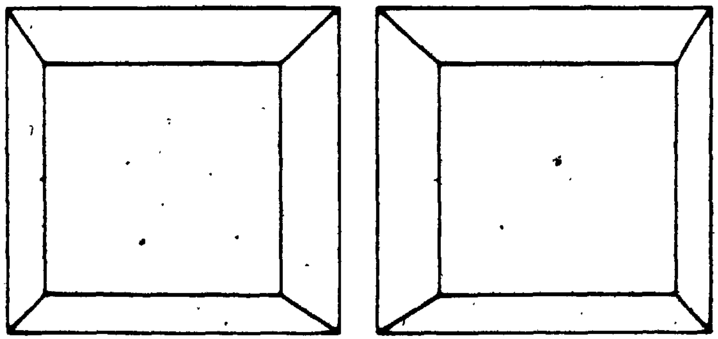
a



b

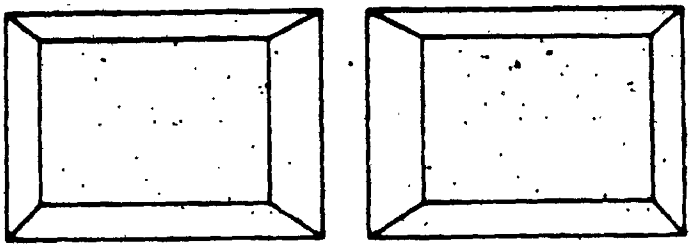


c

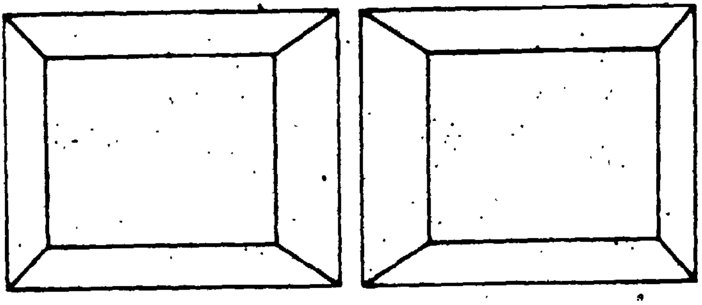


d

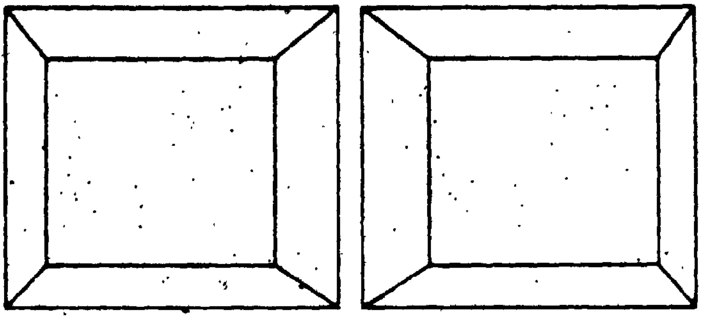
Fig. [illegible] Effect of plot size on R ordination of relevés using pilot survey data. First three axes are shown. Stereograms a-d correspond to the ordinations resulting from the data obtained with 4 different plot sizes: (a) 2.5*2.5 m, (b) 5*[illegible] m; (c) 1.5*1.5 m, and (d) 1.*1. m.



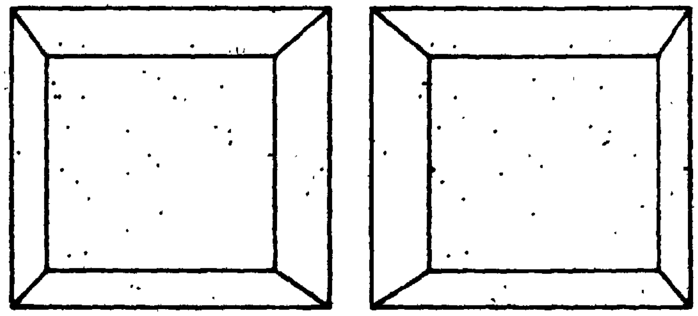
a



b

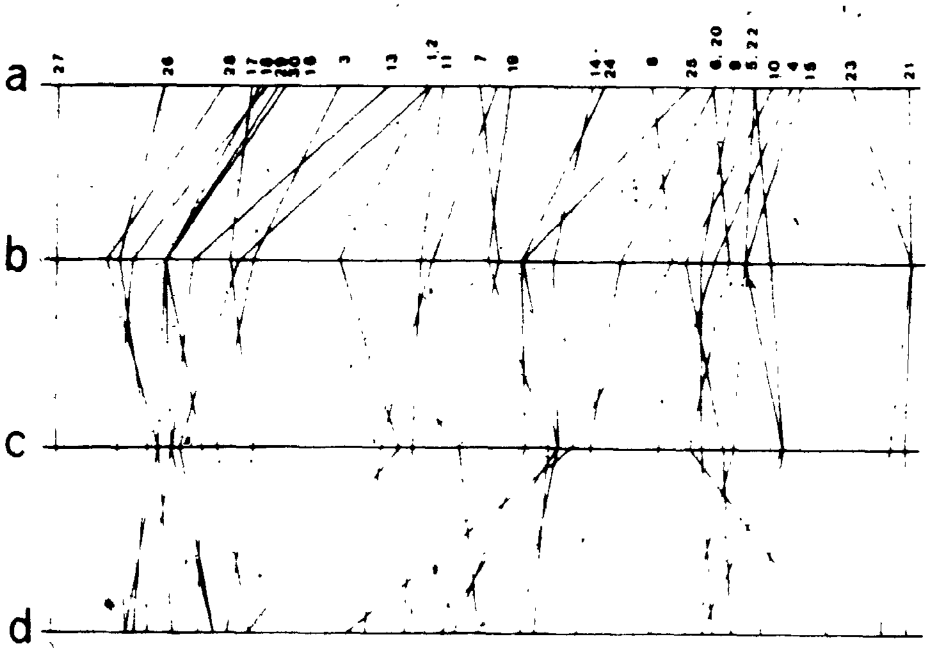


c



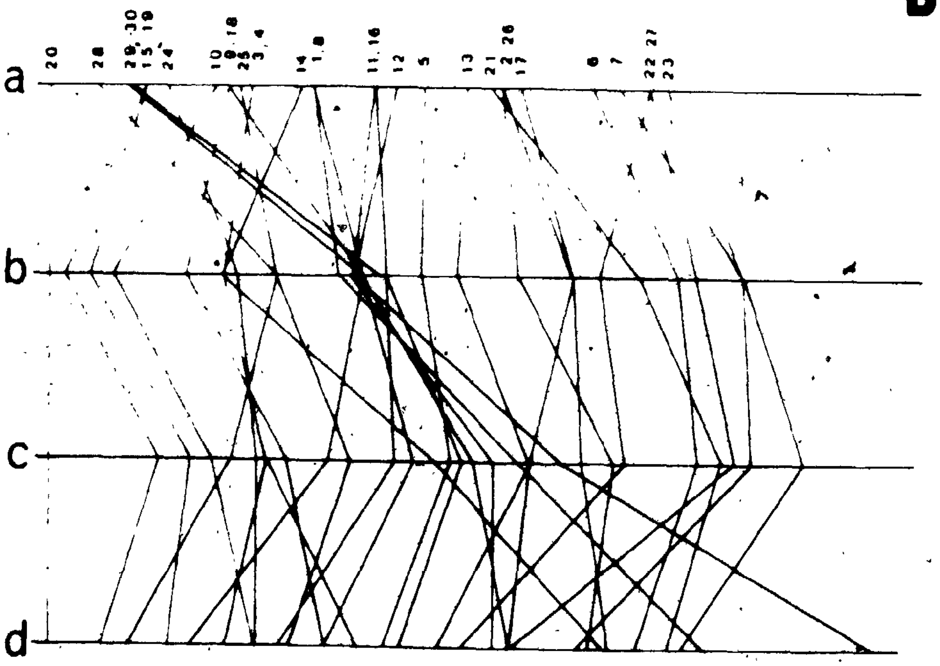
d

Fig. 3.8 Comparison of releve positions on the first two components of PCA ordinations resulting from the four different plot sizes used in the pilot survey. Fig. 3.8a, component 1; Fig. 3.8b, component 2. Letters against axes represent plot sizes - a, 2.5*2.5 m; b, 5*5 m, c, 7.5*7.5 m; d, 10*10 m. Numbers at the top identify releves.



a

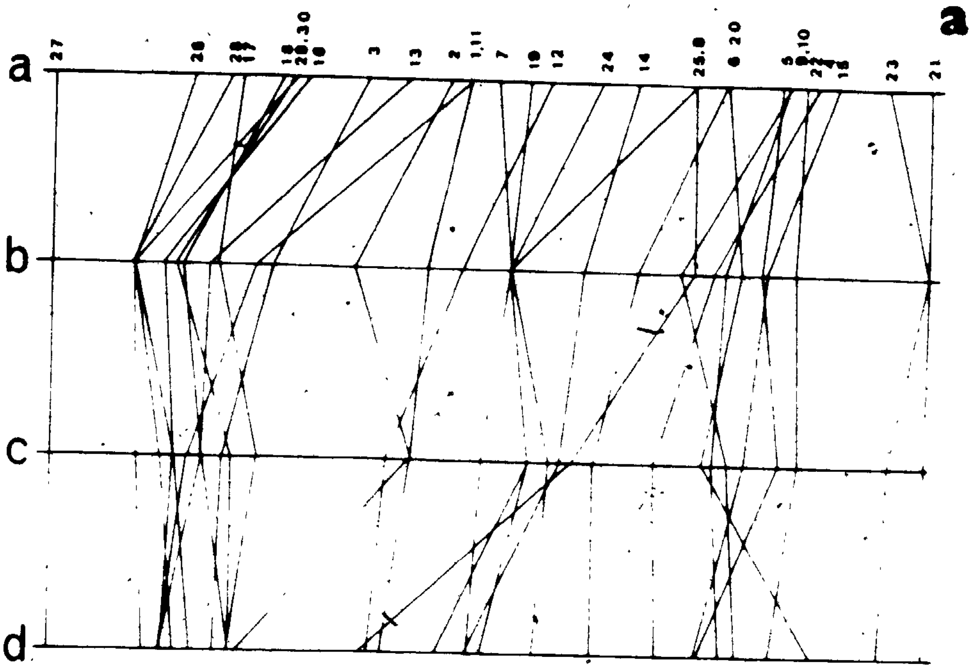
27
26
28
17
19
29
30
16
3
13
1,2
11
7
18
14, 24
9
25
6, 20
8
5, 22
10
4
15
23
21
a
b
c
d



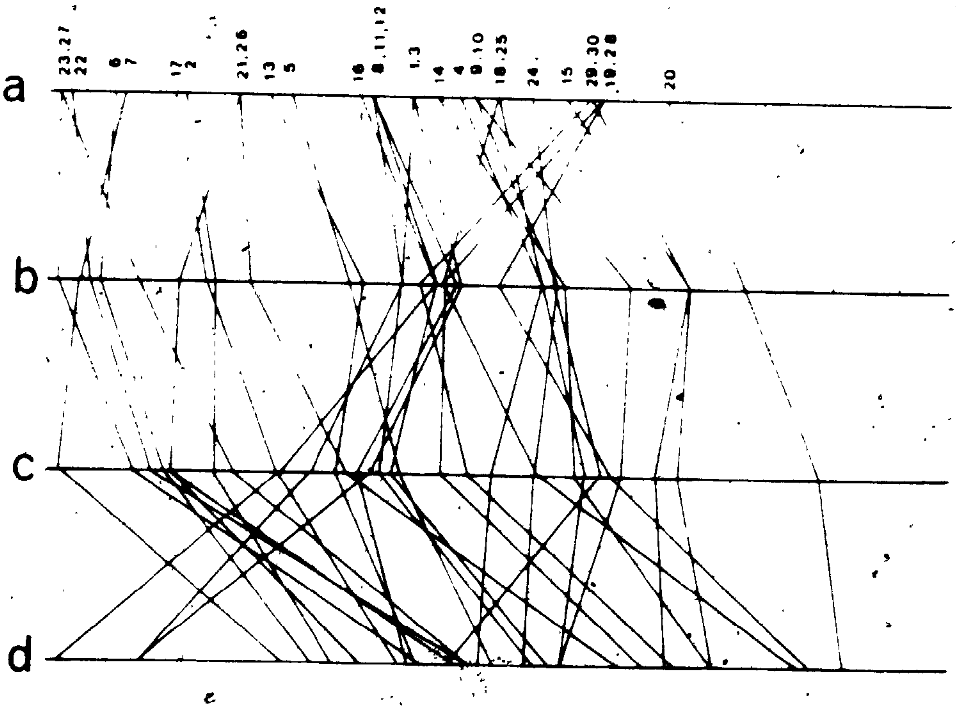
b

20
28
29, 30
15 19
24
10
9, 18
25
3, 4
14
1, 8
11, 16
12
5
13
21
2 26
17
6
7
22 27
23
a
b
c
d

Fig. 3.9 Comparison of releve positions on the first two axes of RO ordinations resulting from the four different plot sizes used in the pilot survey. Fig. 3.8 a, axis 1; Fig. 3.8b, axis 2. Letters against axes represent plot sizes - a, 2.5*2.5 m; b, 5*5 m; c, 7.5*7.5 m; d, 10*10 m. Numbers at the top identify releves.


a
b
c
d
27
26
28
17
18
26,30
16
3
13
2
1,11
7
19
12
24
14
25,8
6 20
5
9,10
22
4
15
23
21

a


a
b
c
d
23,27
22
6
7
17
2
21,26
13
5
16
8,11,12
1,3
14
4
9,10
18,25
24
15
29,30
19,28
20

b

Fig. 3.10 Comparison of species positions on the first two components of PCA species ordinations of the 4 different plot sizes used in the pilot survey. Only the positions of 11 important species are shown. Fig. 3.10a, component 1; Fig. 3.10b, component 2. Key to species codes:

Ar, *Agropyron repens*; Ast, *Agrostis stolonifera*; Dc, *Daucus carota*; Es, *Erigeron strigosus*; Ma, *Melilotus alba*; Ml, *Medicago lupulina*; Pc, *Poa compressan;* P_p, *Phleum pratense*; Sca, *Solidago canadensis*; Tp, *Trifolium pratense*; Tr, *Trifolium repens*.

Numerals against the axes indicate plot size: 1, 2.5*2.5 m; 2.5*5 m; 3, 7.5*7.5 m; 4, 10*10 m.

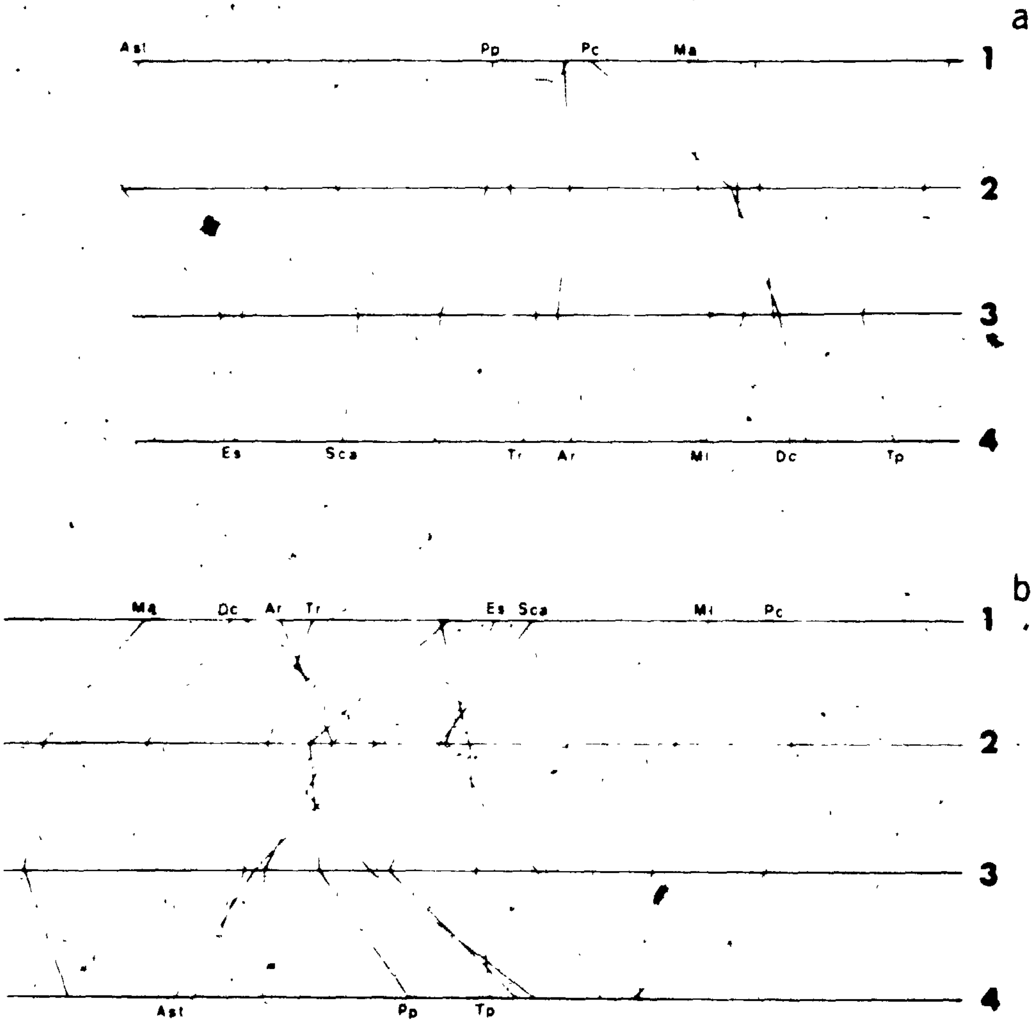
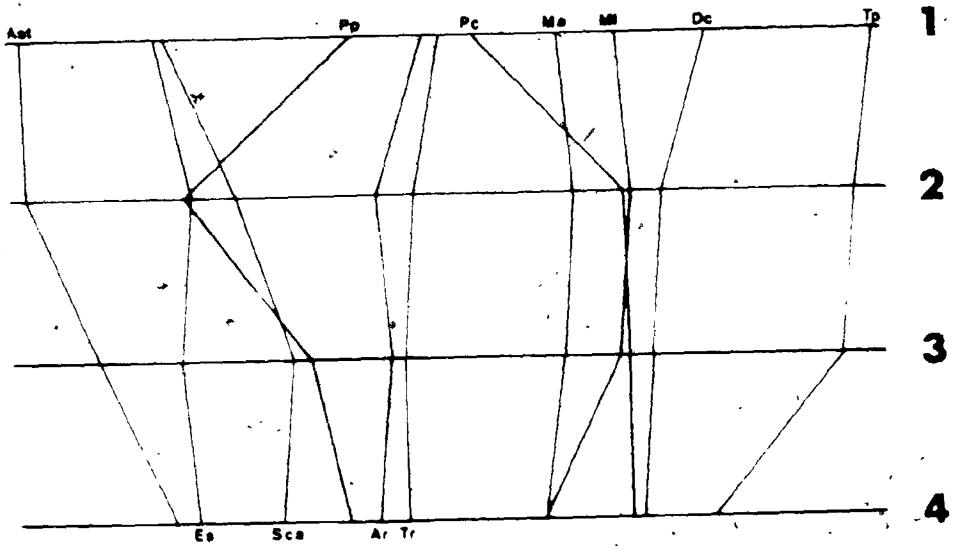

a
Ast
Pp
Pc
Ma
1
2
3
4
Es
Sca
Tr
Ar
Mi
Dc
Tp
b
Ma
Dc
Ar
Tr
Es
Sca
Mi
Pc
1
2
3
4
Ast
Pp
Tp

Fig. 3.11 Comparison of species positions on the first two axes of RQ species ordinations of the 4 different plot sizes used in the pilot survey. Only 11 important species are shown. a) axis 1, b) axis 2. Numerals against the axes indicate plot size as in the legend of Fig. 10. Species codes are the same as given in the legend of Fig. 10a.

a


Ast
Pp
Pc
Ma
Ml
Dc
Tp
1
2
3
4
Es
Sca
Ar
Tr

b

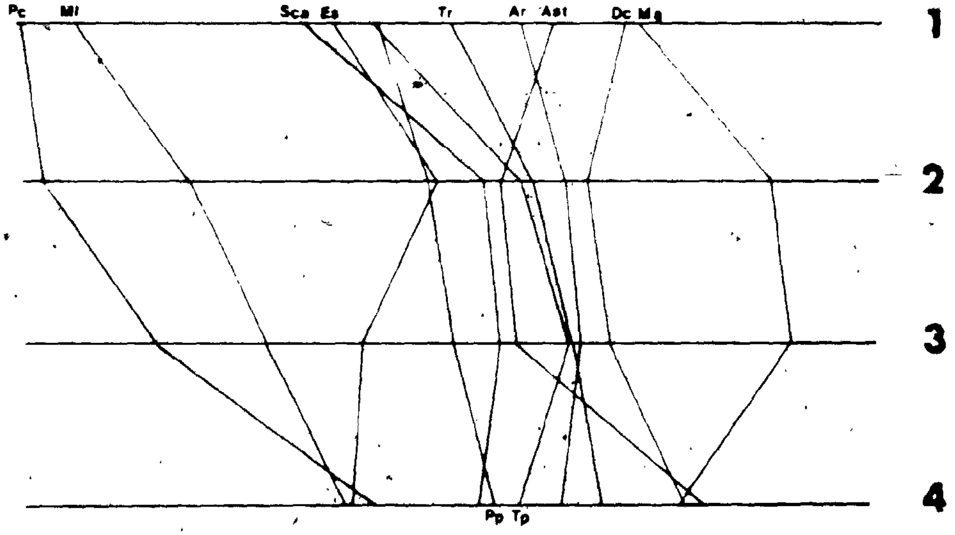
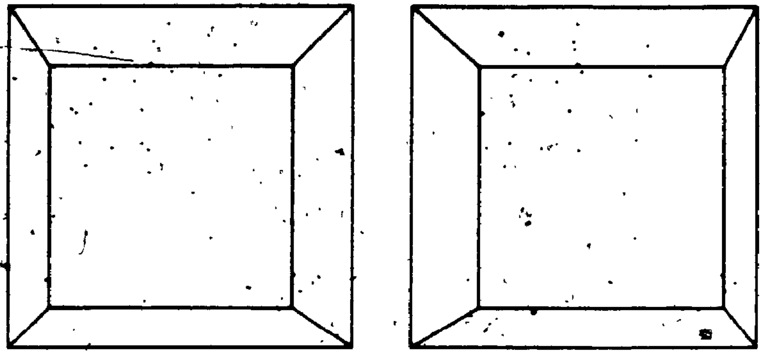
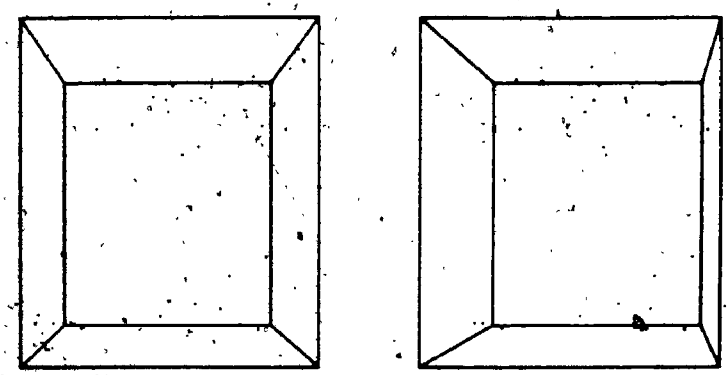

Pc
Ml
Sca
Es
Tr
Ar
Ast
Dc
Ma
1
2
3
4
Pp
Tp

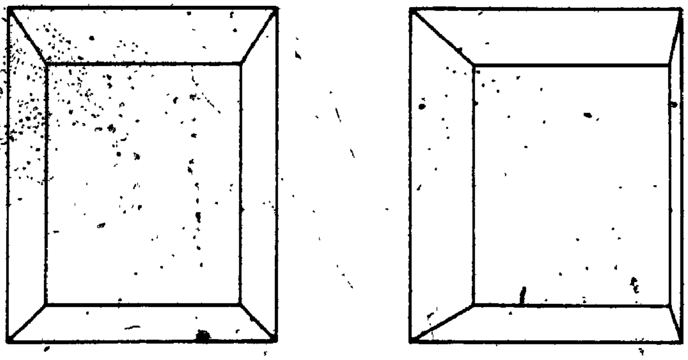
Fig. 3.12 Effect of plot size on releve MDSCAL ordination for Stoneybrook data of 8 different plot sizes. Stereograms show the first 3 axes. Three dimensional solutions were sought using chord distance. The stress values were invariably low, < 6.5%. Ordinations a to h correspond to data sets obtained by different plot sizes: a, 0.35*0.71 m; b, 0.5*1.0 m; c, 0.71*1.42 m; d, 1.0*2.0 m; e, 1.41*2.83 m; f, 2.0*4.0 m; g, 2.83*5.66 m; h, 4.0*8.0 m.



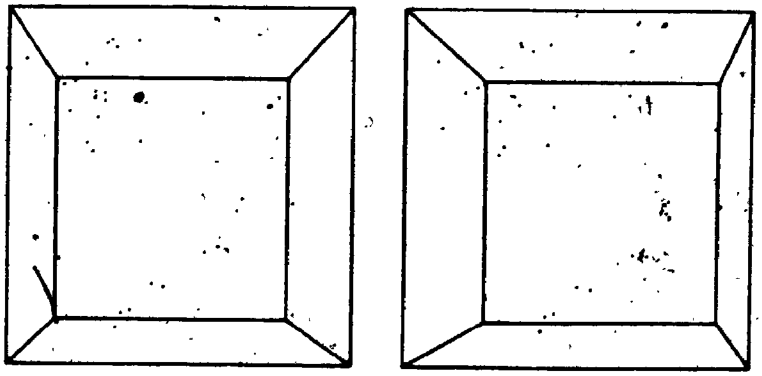
a



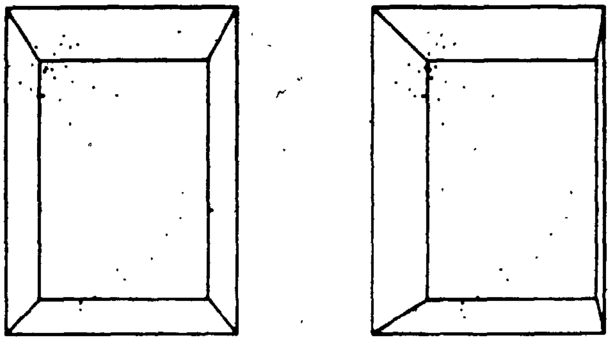
b



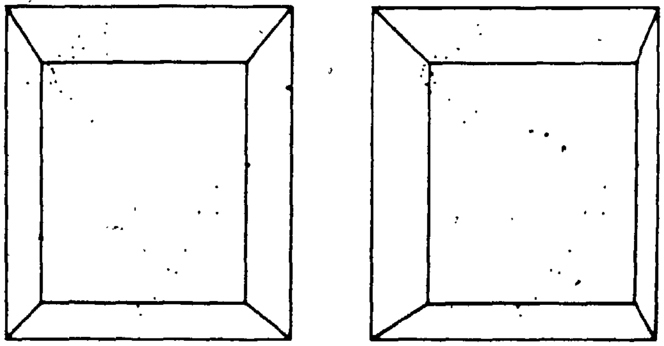
c



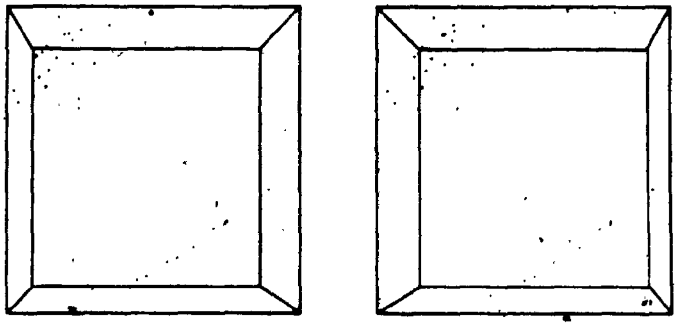
d



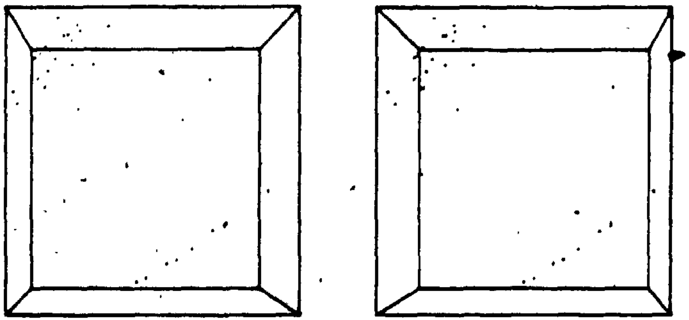
e



f



g



h

Fig. 3.13 Changes in the releve position on the first axis of MDSCAL releve ordination of the 8 different plot sizes used at Stoneybrook site. Letters against the axes a-h correspond to different plot sizes as given in the legend of Fig. 3.12. Numbers at the top identify releves.

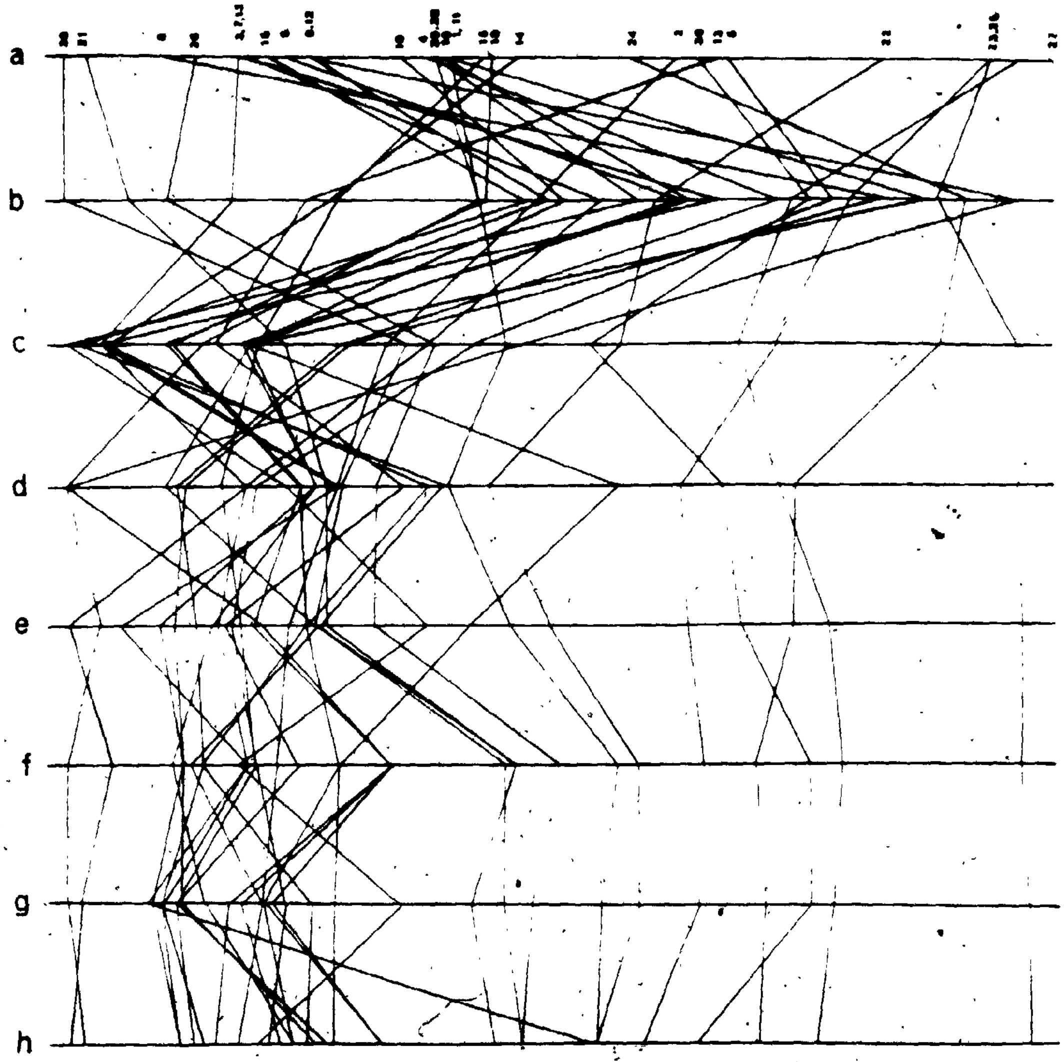
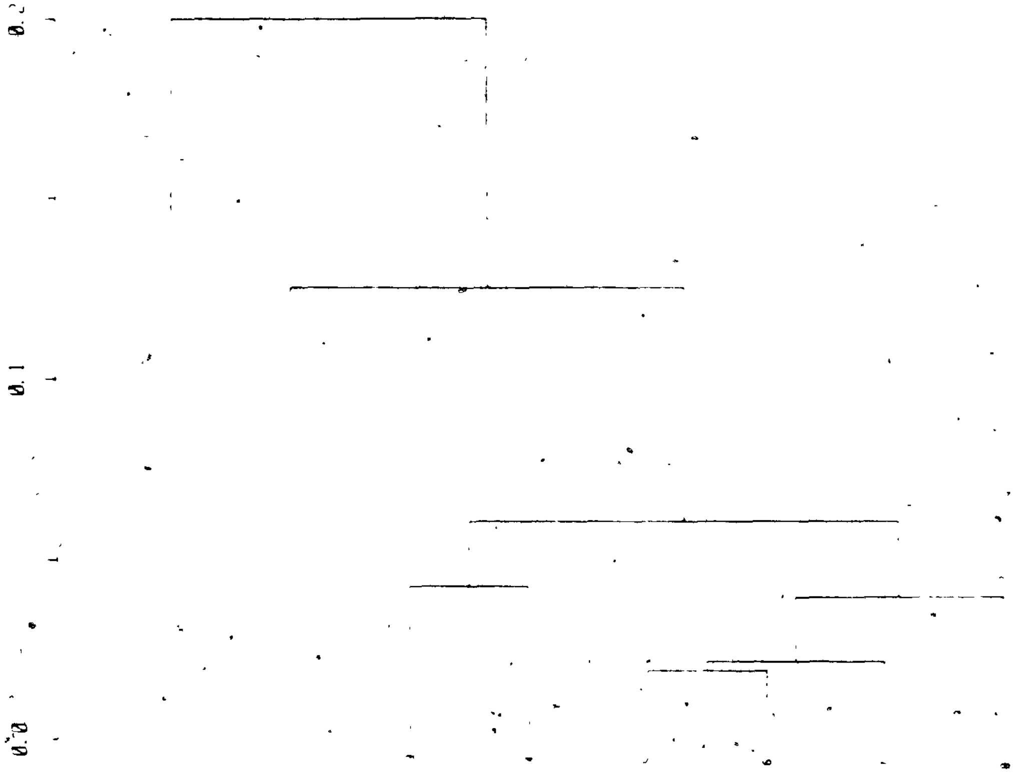

a
b
c
d
e
f
g
h

Fig. 3.14 Dendrograms resulting from simple average (a) and group average (b) clustering of the 8 MDSCAL ordinations based on the 8 plots sizes used at Stoneybrook site. The vertical axis represents sum of squares at group fusion levels. Numbers at the bottom represent plot sizes: 1, 0.35*0.71 m; 2, 0.5*1.0 m; 3, 0.71*1.42 m; 4, 1.0*2.0 m; 5, 1.41*2.83 m; 6, 2.0*4.0 m; 7, 2.83*5.66 m; 8, 4.0*8.0 m.

a



b

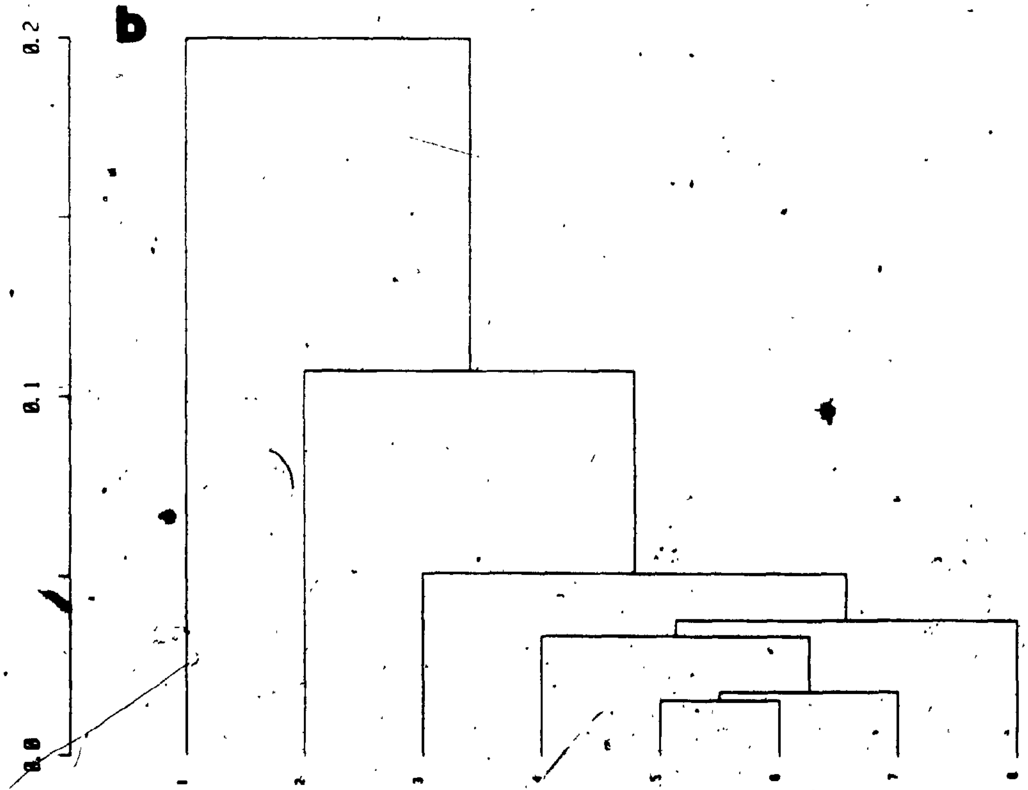
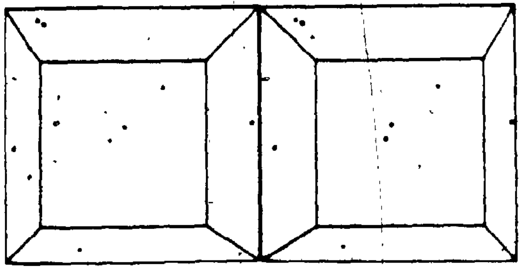
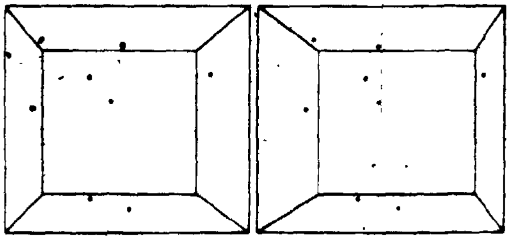
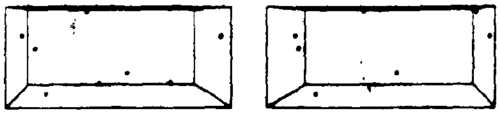
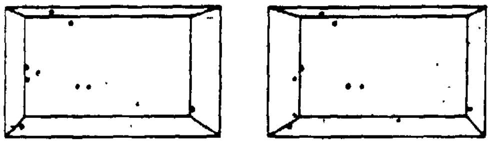


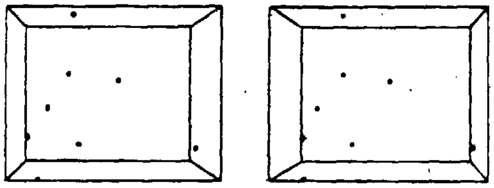
Fig. 3.15 Stereograms resulting from MDSCAL ordination of species based on the data sets obtained by sampling the maple forest map with seven different plot sizes. Three dimensional solutions were obtained using chord distance. All the stress values were less than 7%. The 8 species used in the ordination were: 1, *Acer saccharum*; 2, *Telia americana*; 3, *Ulmus rubra*; 4, *Ostrya virginiana*; 5, *Quercus rubra*; 6, *Carya cordiformis*; 7, *Juglans cinerea*; 8, *Celtis occidentalis* (Refer to Fig. 3.16 for species positions on the first axis). Ordinations a-g correspond to different plot sizes: a, 5*10 ft; b, 10*10; c, 10*20; d, 20*20 ft; e, 30*30 ft; f, 40*40 ft; g, 50*50 ft. (The original grid was in imperial units. The corresponding values in metric system appear in the legend of Fig. 3.4).

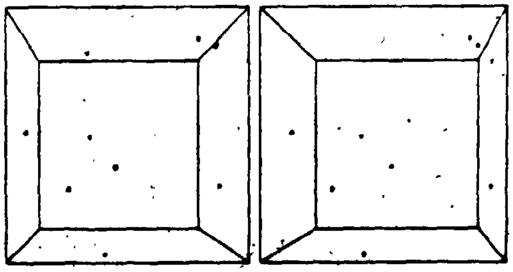

a


b


c


d


e


f

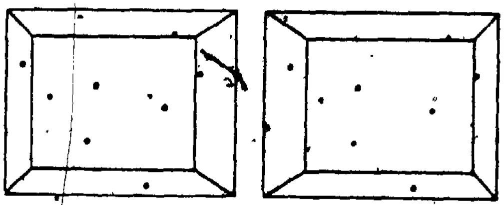

g

Fig. 3.16 Sequence of changes in species position on the first axis of MDSCAL species ordinations corresponding to data sets derived from 7 different plot sizes used in sampling maple forest vegetation map. Refer to Fig. 3.15 for species codes.

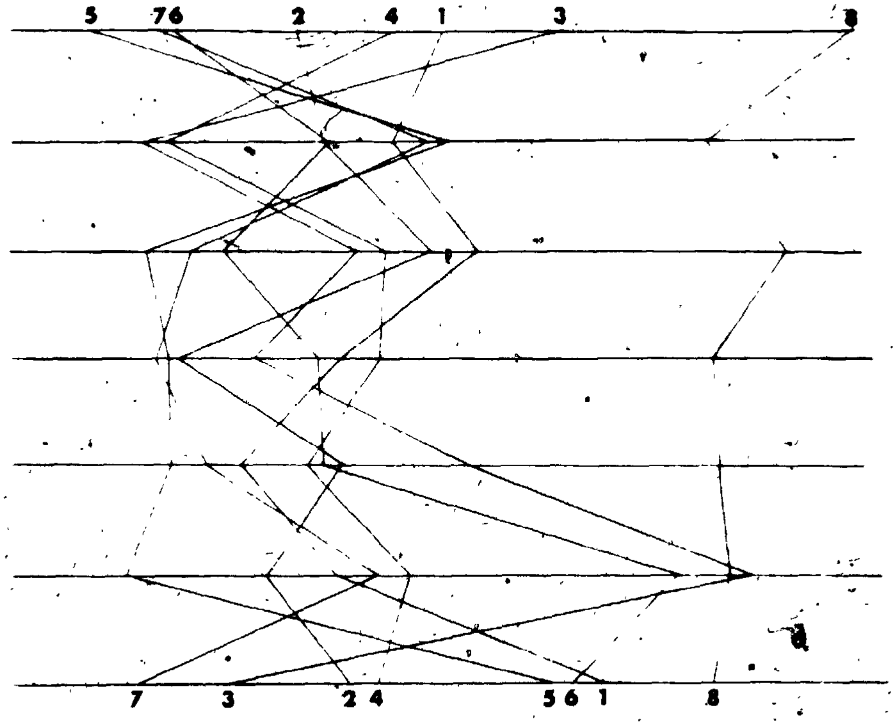

5
7 6
2
4
1
3
8
7
3
2 4
5 6 1
8

Fig. 3.17 Trellis diagram showing similarity (correlation coefficient) between 3-dimensional species ordinations corresponding to the data sets pertaining to 7 different plot sizes used in sampling the maple forest vegetation map.

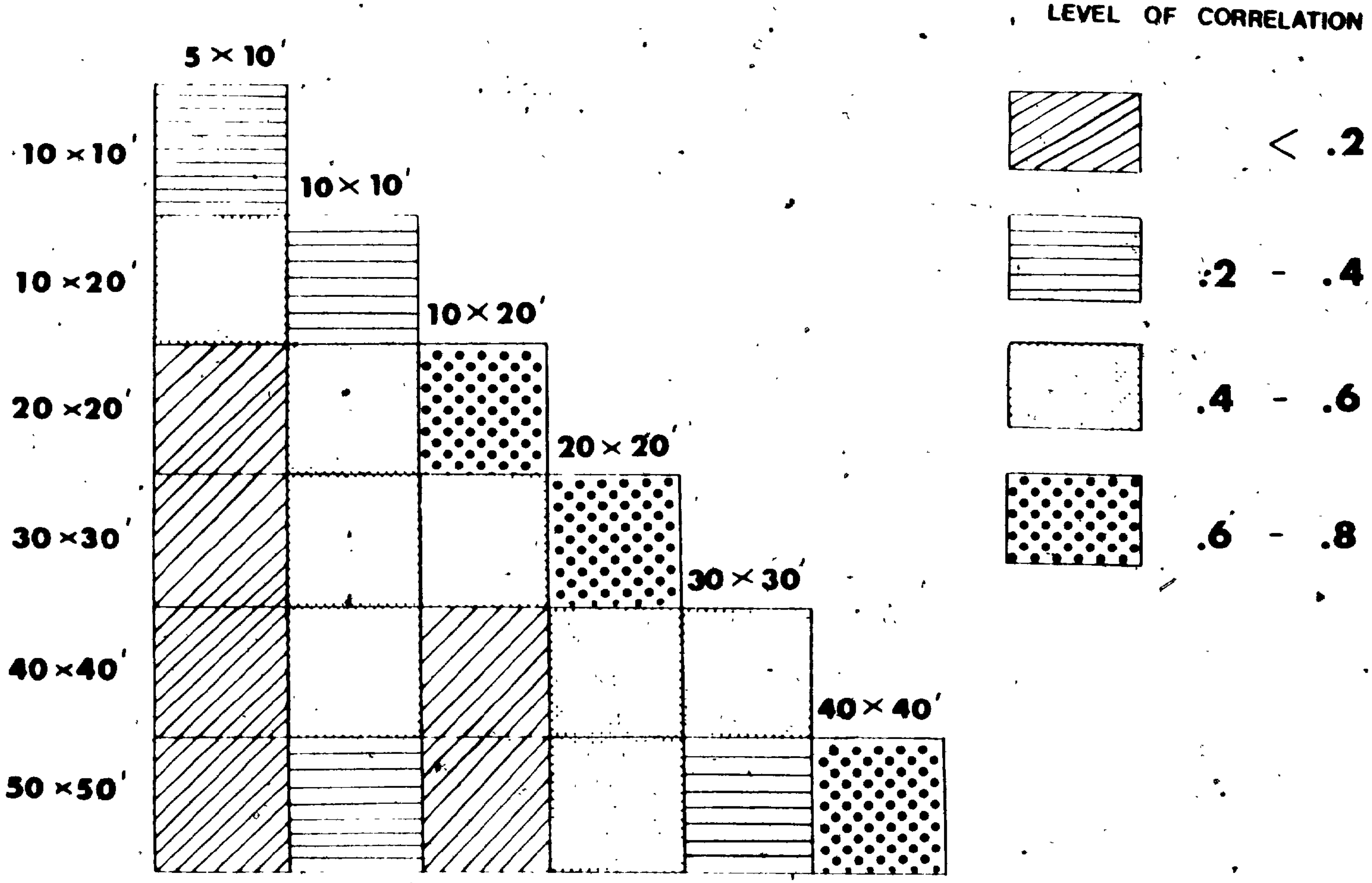
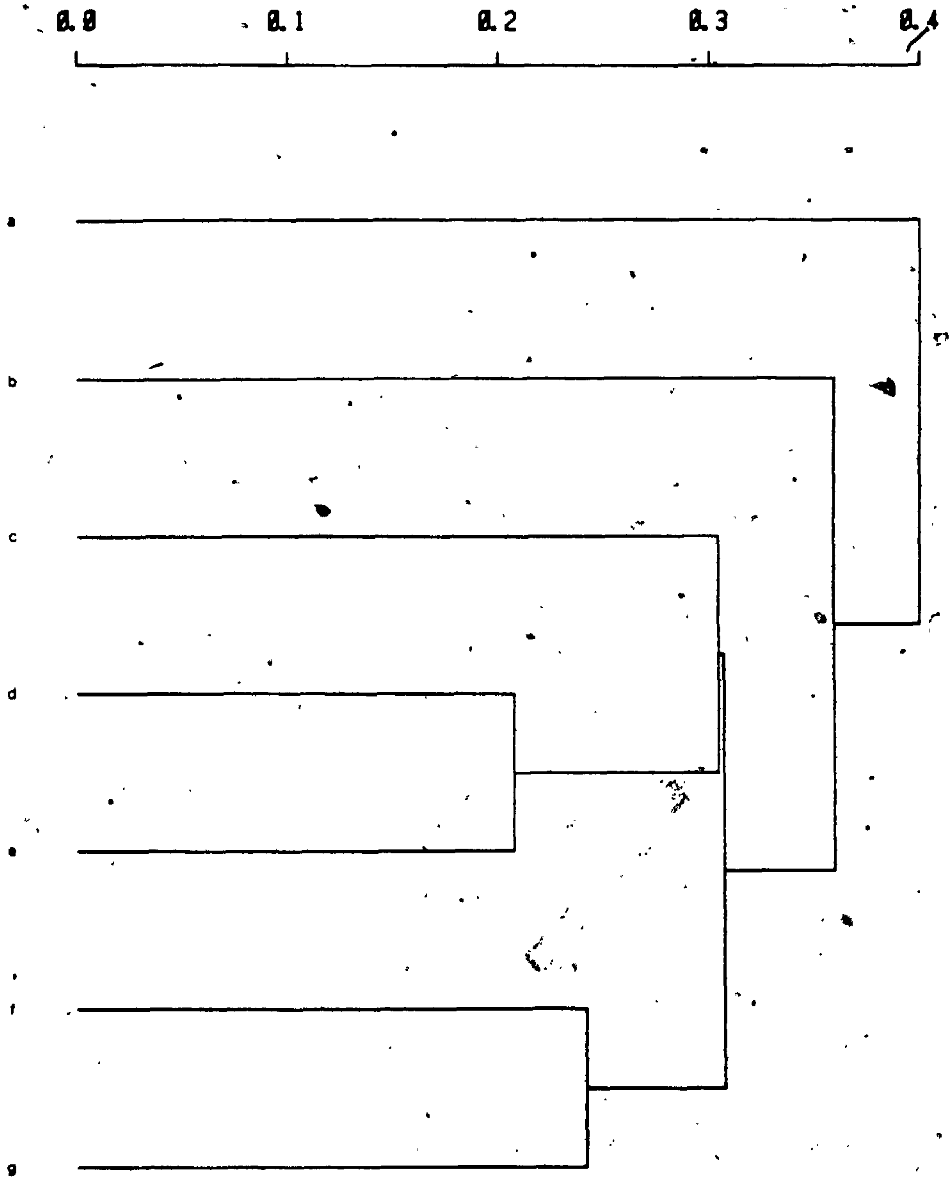

LEVEL OF CORRELATION
< .2
.2 - .4
.4 - .6
.6 - .8
5 × 10'
10 × 10'
10 × 20'
20 × 20'
30 × 30'
40 × 40'
10 × 10'
10 × 20'
20 × 20'
30 × 30'
40 × 40'
50 × 50'

Fig. 3.18 The dendrogram resulting from clustering of 7 MDSCAL species ordinations corresponding to the seven different plot sizes used in sampling the maple forest. Simple average clustering was performed using correlation coefficients between ordinations. Vertical axis shows 1-compliment of correlation coefficient. Numbers at the bottom correspond to plot sizes a to g as in Fig. 3.15.



0.0
0.1
0.2
0.3
0.4
a
b
c
d
e
f
g

3

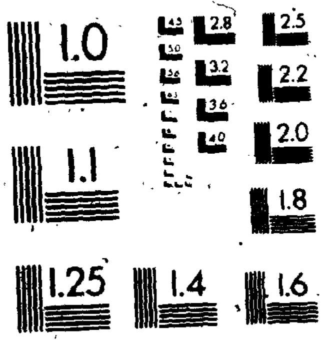
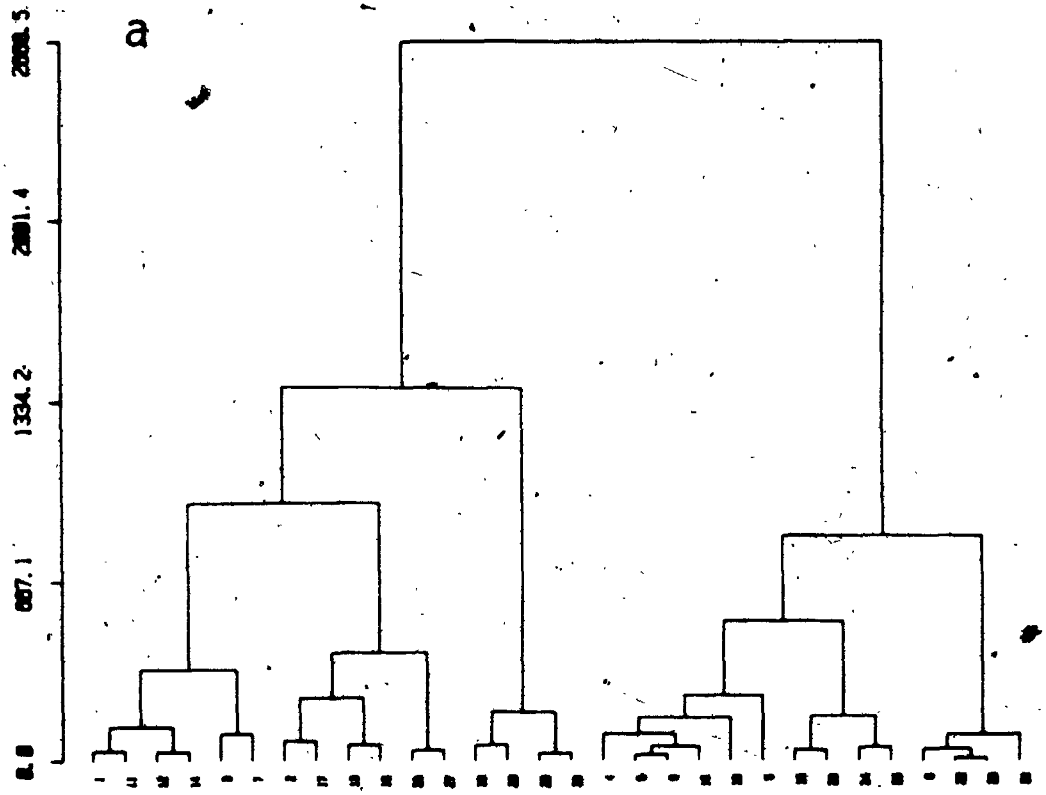
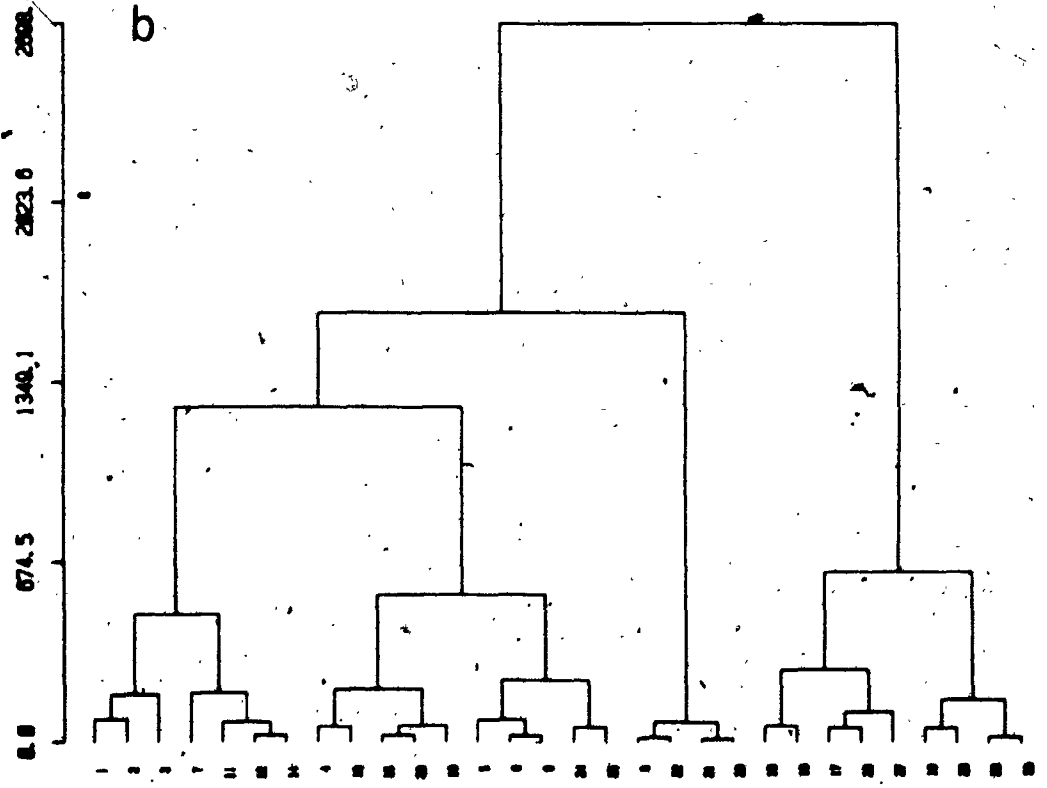
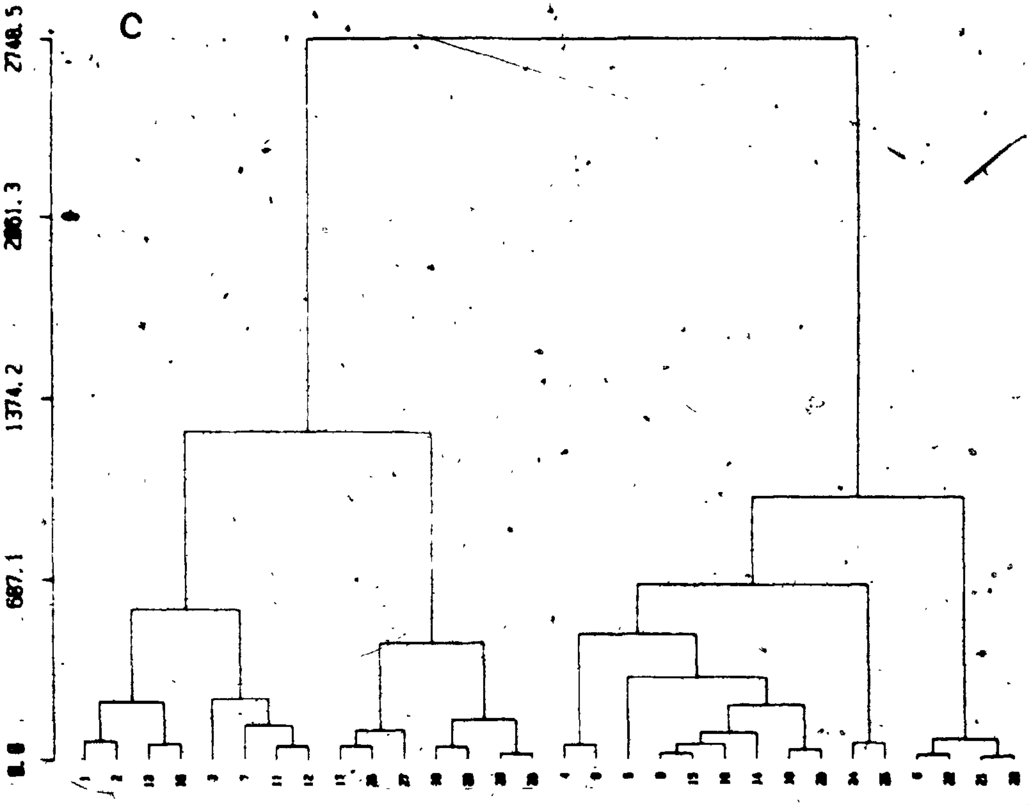


Fig. 3.19 Effect of plot size on group structure. SSA dendrograms resulting from the data sets obtained with 4 different plot sizes used in the pilot survey; dendrograms a to d correspond to different plot sizes: a, 2.5*2.5 m; b, 5*5 m; c, 7.5*7.5 m; d, 10*10 m. Vertical axis represents sum of squares while numbers at the bottom identify relevés.


a
2668.5
2001.4
1334.2
667.1
0.0


b
2698.1
2023.6
1349.1
674.5
0.0


c
2748.5
2061.3
1374.2
687.1
0.0

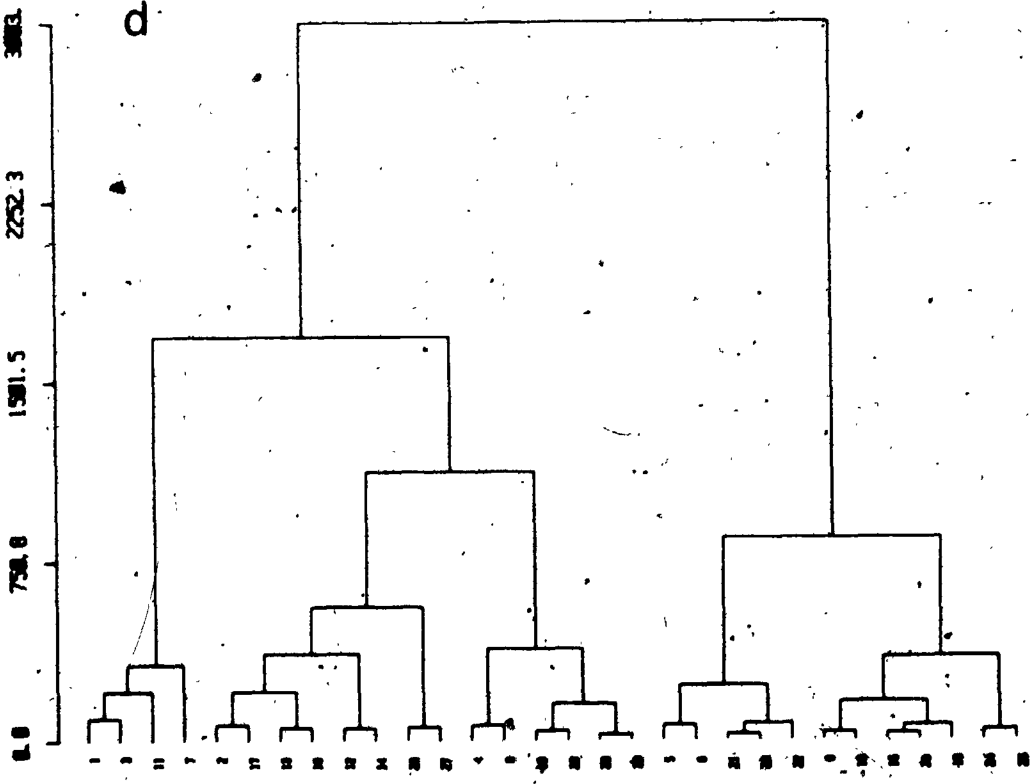
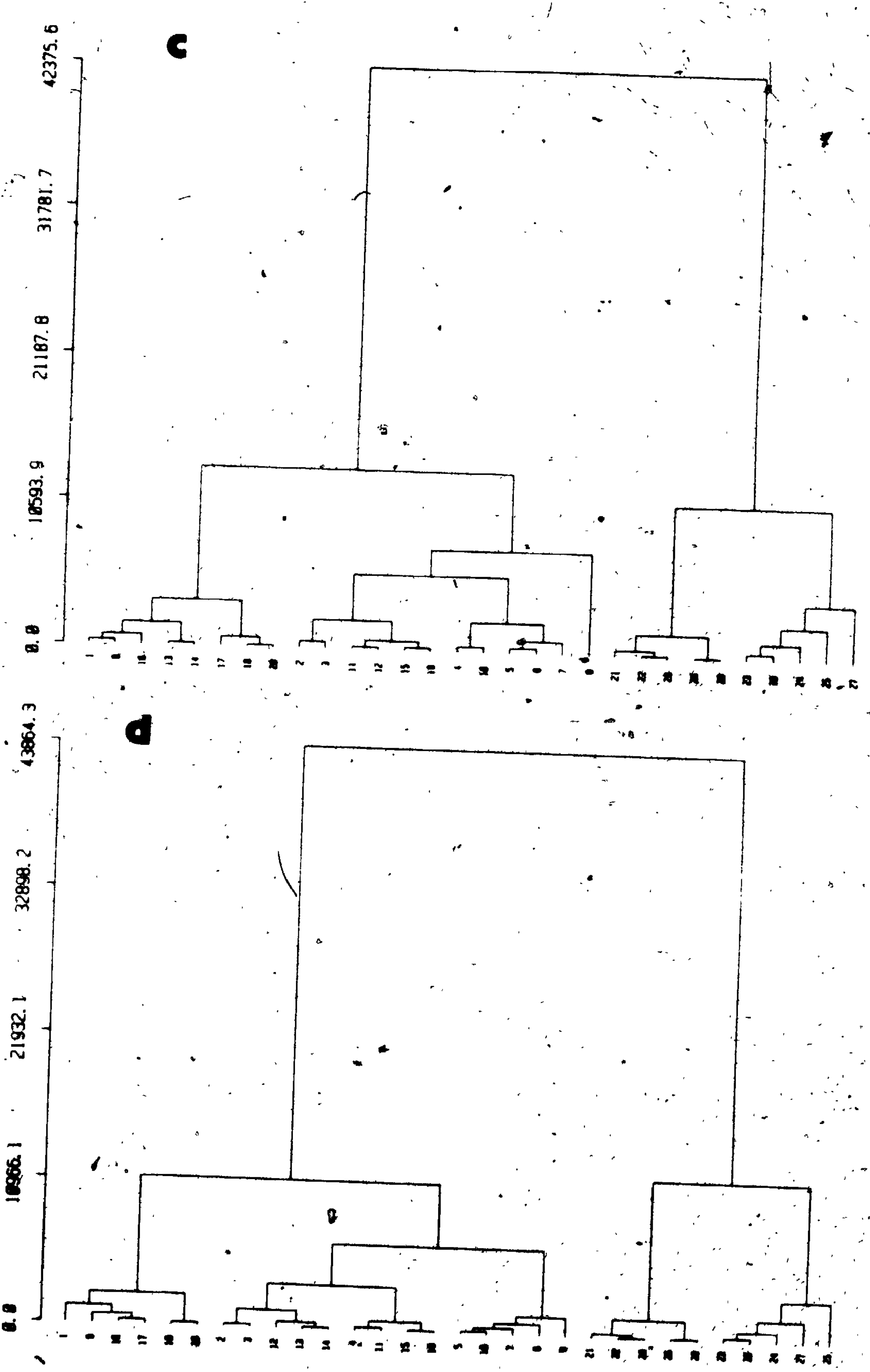
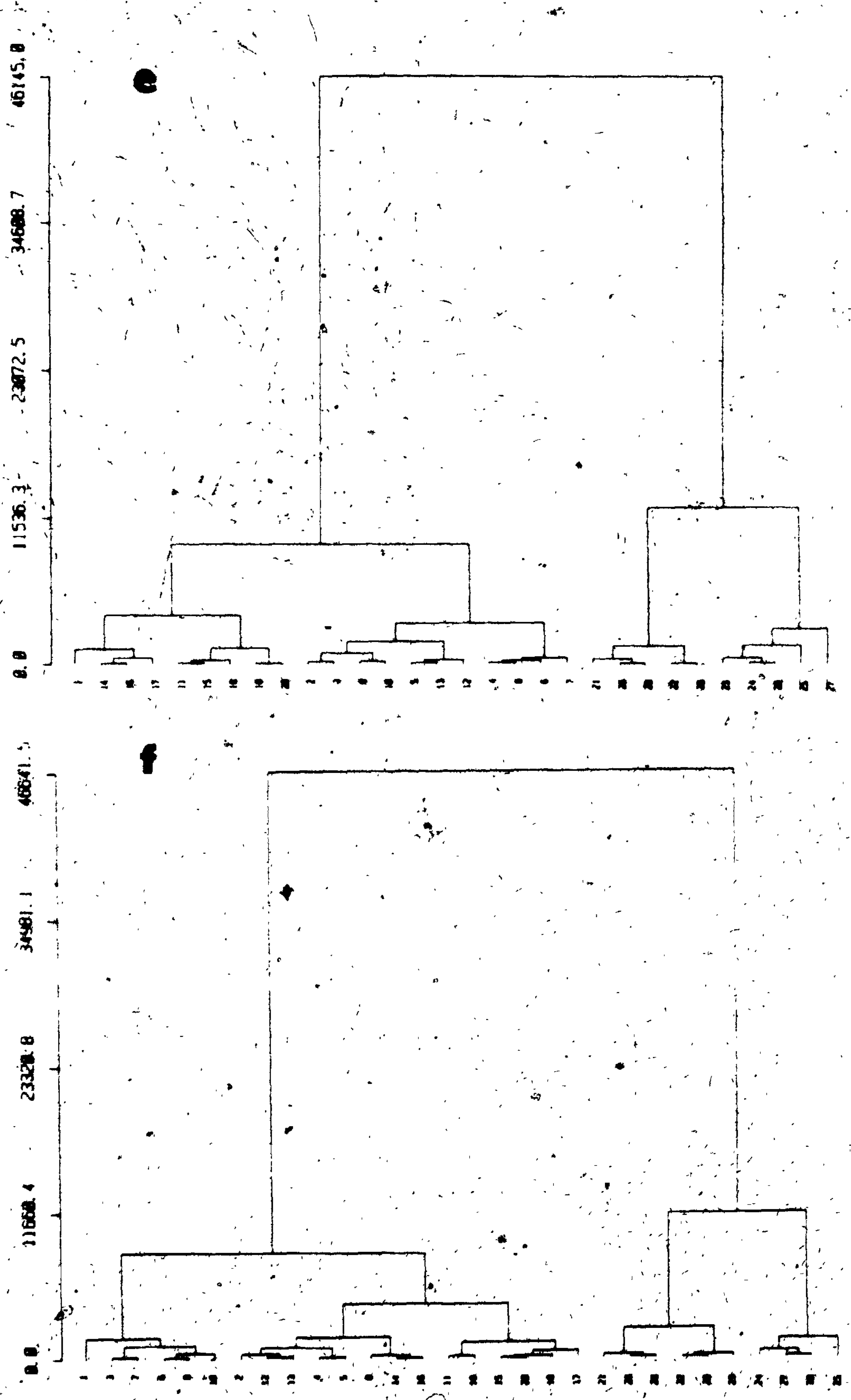

d
3003.1
2252.3
1501.5
750.8
0.0

Fig. 3.20 Effect of plot size on group structure. Dendrograms resulting from SSA clustering of data sets obtained with 8 different plot sizes at Stoneybrook site; a to h correspond to different plot sizes: a, 5*0.71 m; b, 0.5*1.0 m; c, 0.71*1.42 m; d, 1.0*2.0 m; e, 1.41*2.83 m, f, 2.0*4.0 m; g, 2.83*5.66 m; h, 4.0*8.0 m. Vertical axis in each dendrogram represents sum of squares while numbers at the bottom correspond to releves.


a
42938.3
32203.7
21469.1
10734.6
0.0
b
45604.5
34203.4
22802.3
11401.1
0.0


c
42375.6
31781.7
21187.8
10593.9
0.0
d
43864.3
32898.2
21932.1
10966.1
0.0


e
46145.0
34608.7
23072.5
11536.3
0.0
f
46641.5
34981.1
23320.8
11660.4
0.0

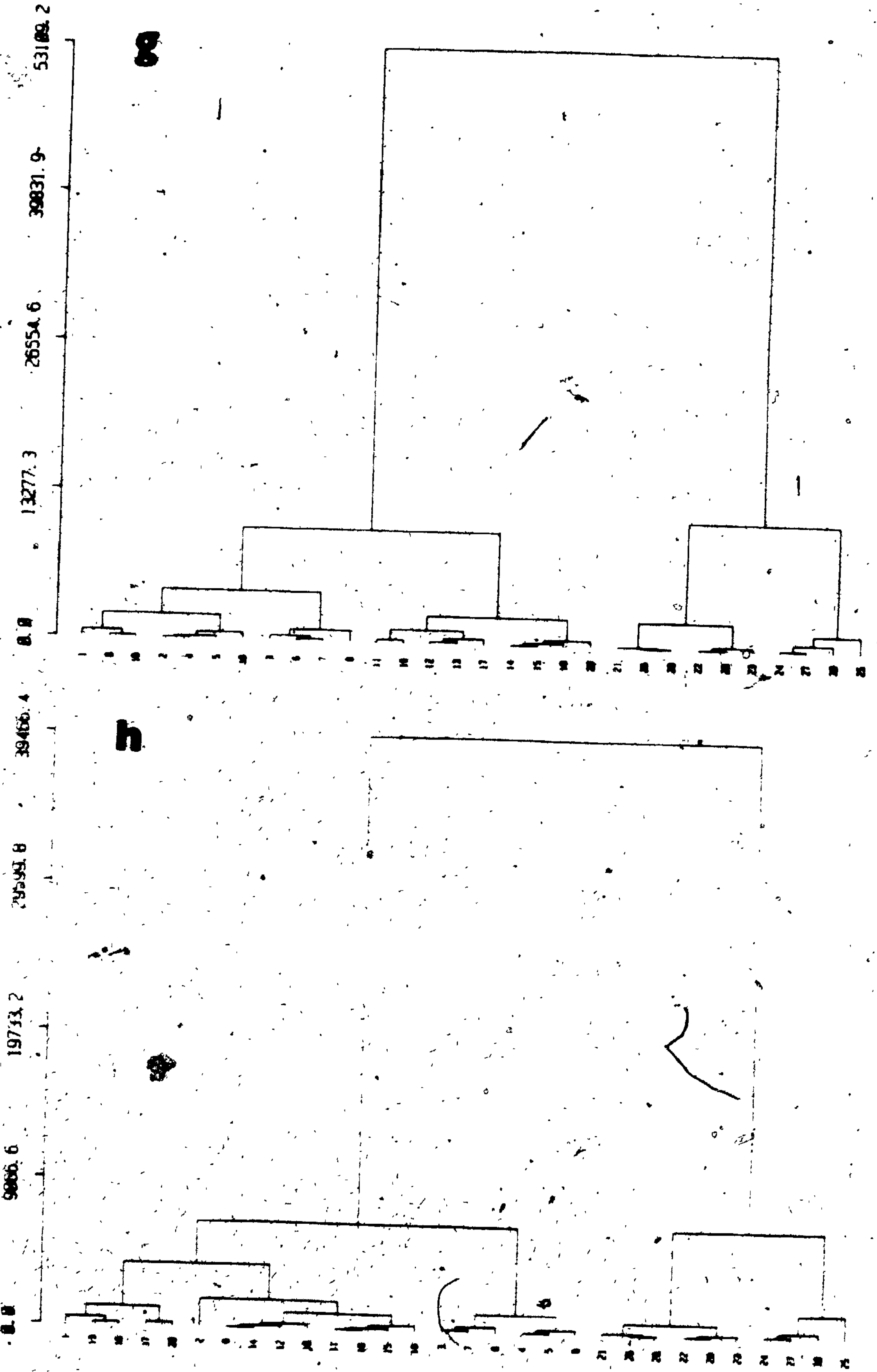

g
53108.2
39831.9
26554.6
13277.3
0.0
h
39466.4
29599.8
19733.2
9866.6
0.0

Fig. 3.21 Dendrograms resulting from simple average (a), and group average clustering (b) performed on the matrix of correlation coefficients between cophenetic matrices of the dendrograms given in Fig. 3.20. Vertical axis represents 1-compliment of correlation coefficient while letters a to h at the bottom correspond to the 8 plot sizes as given in the legend of Fig. 3.20.

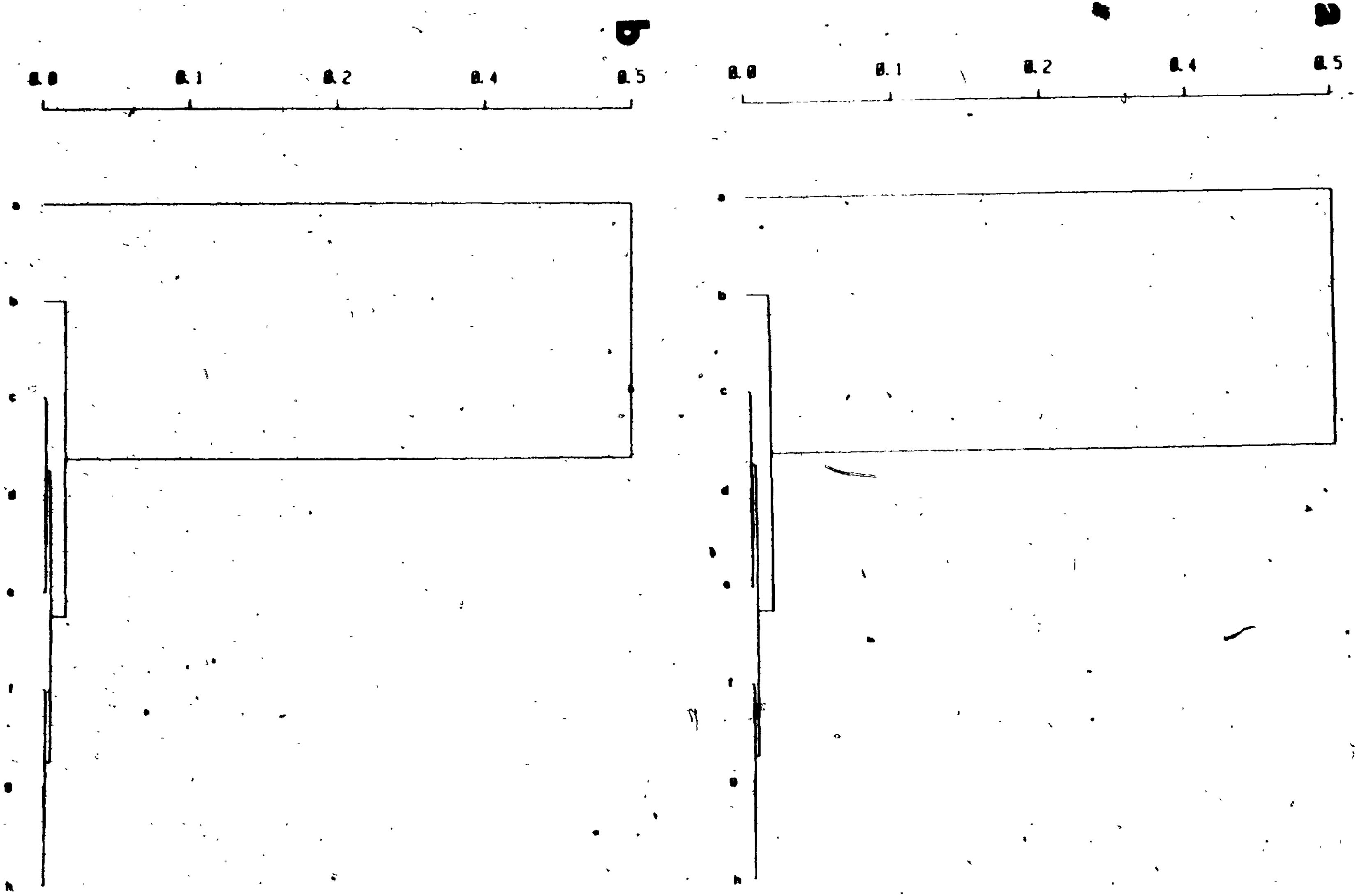
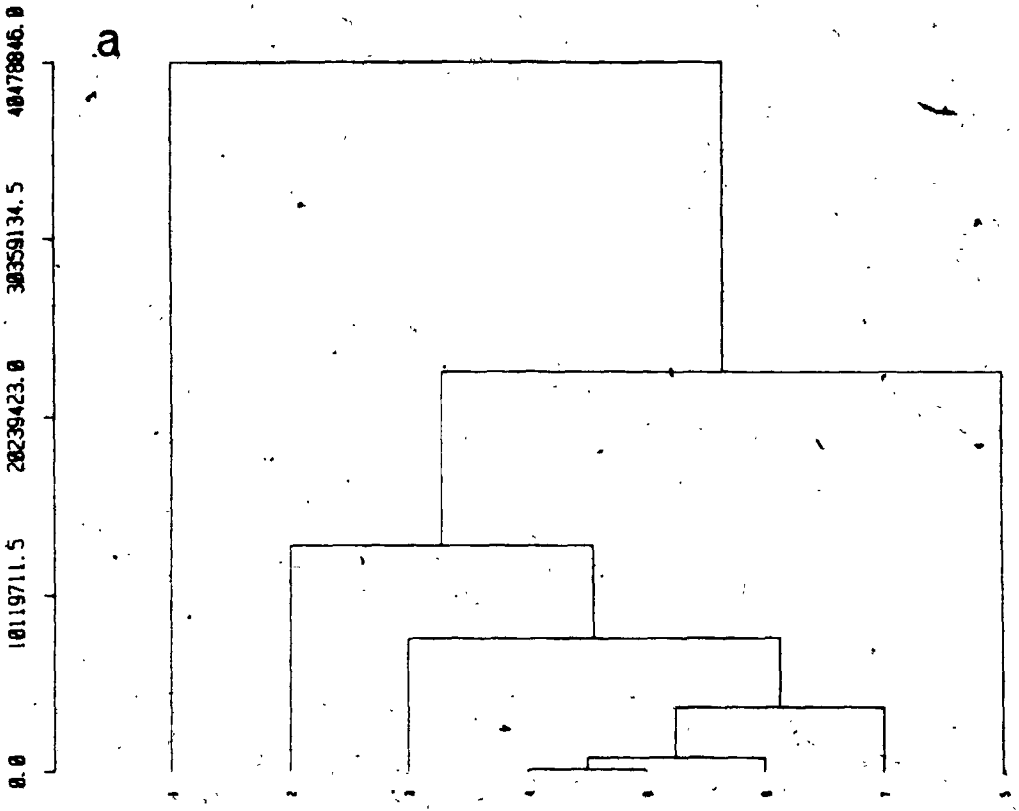
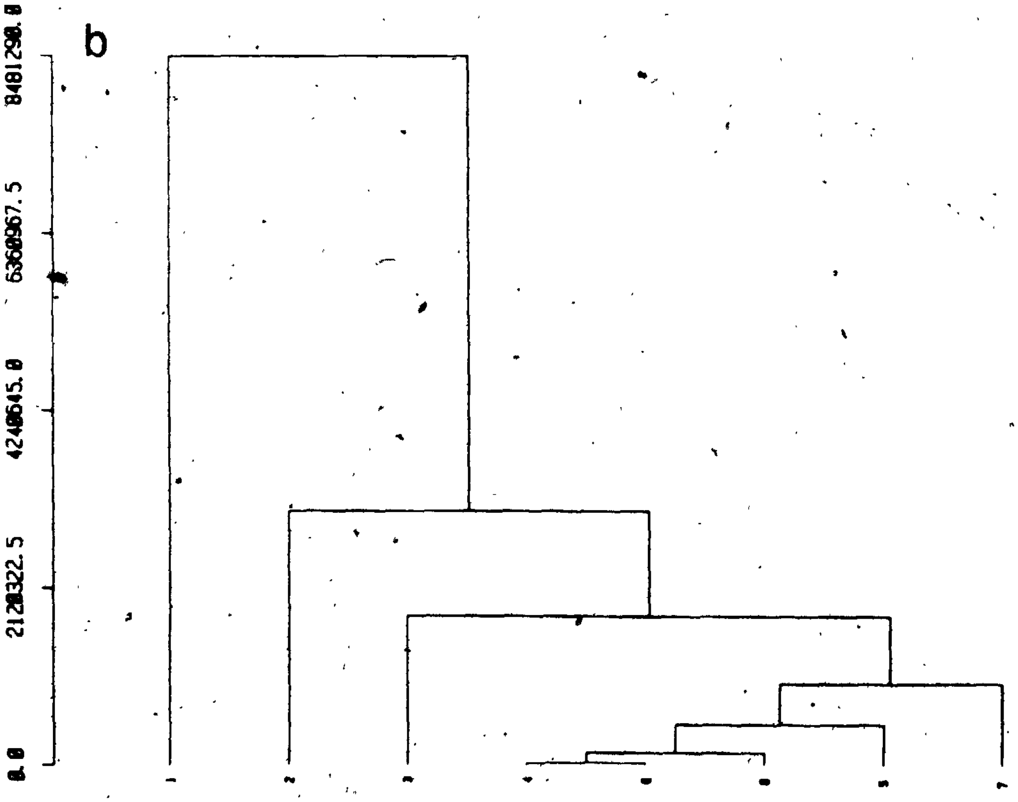
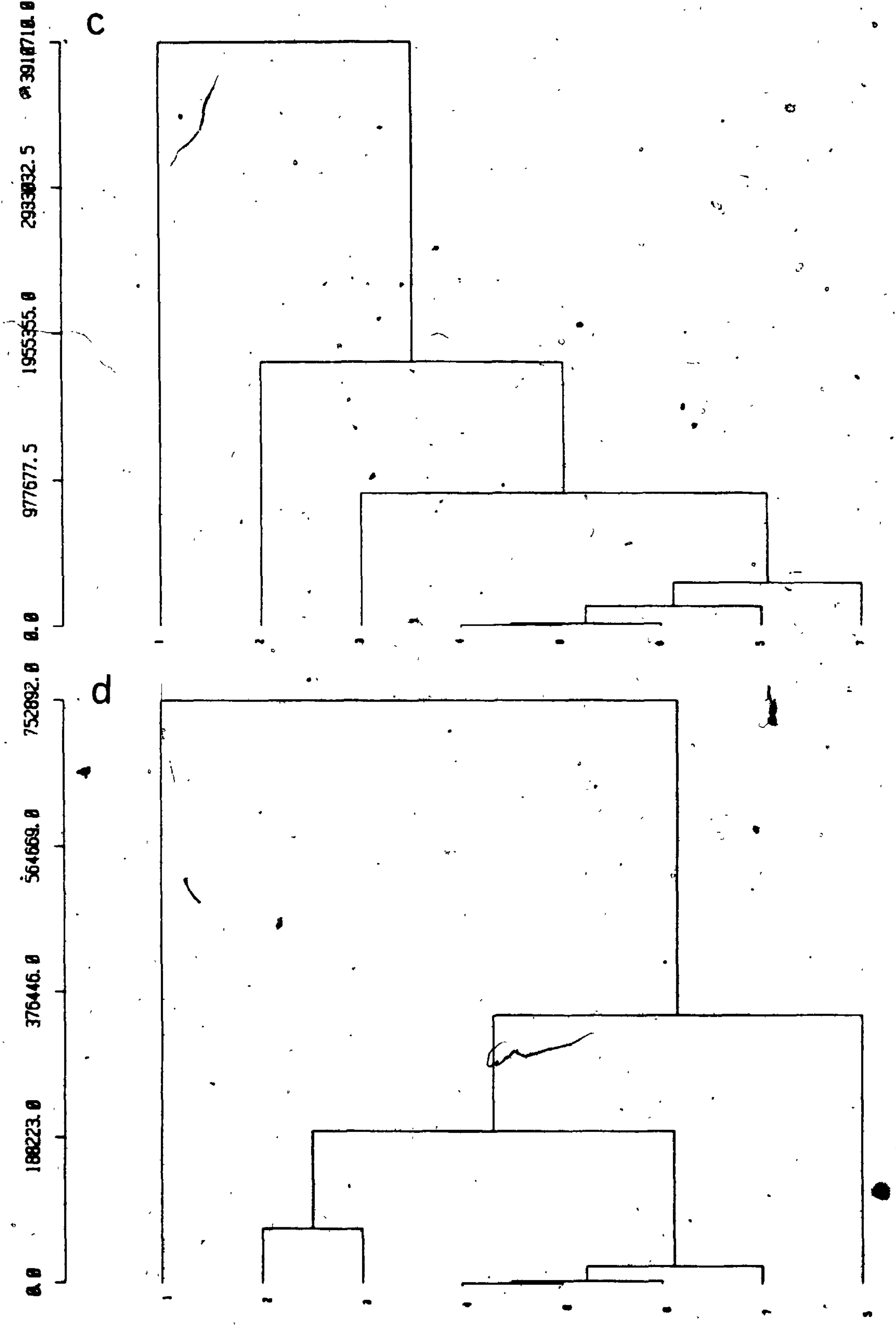
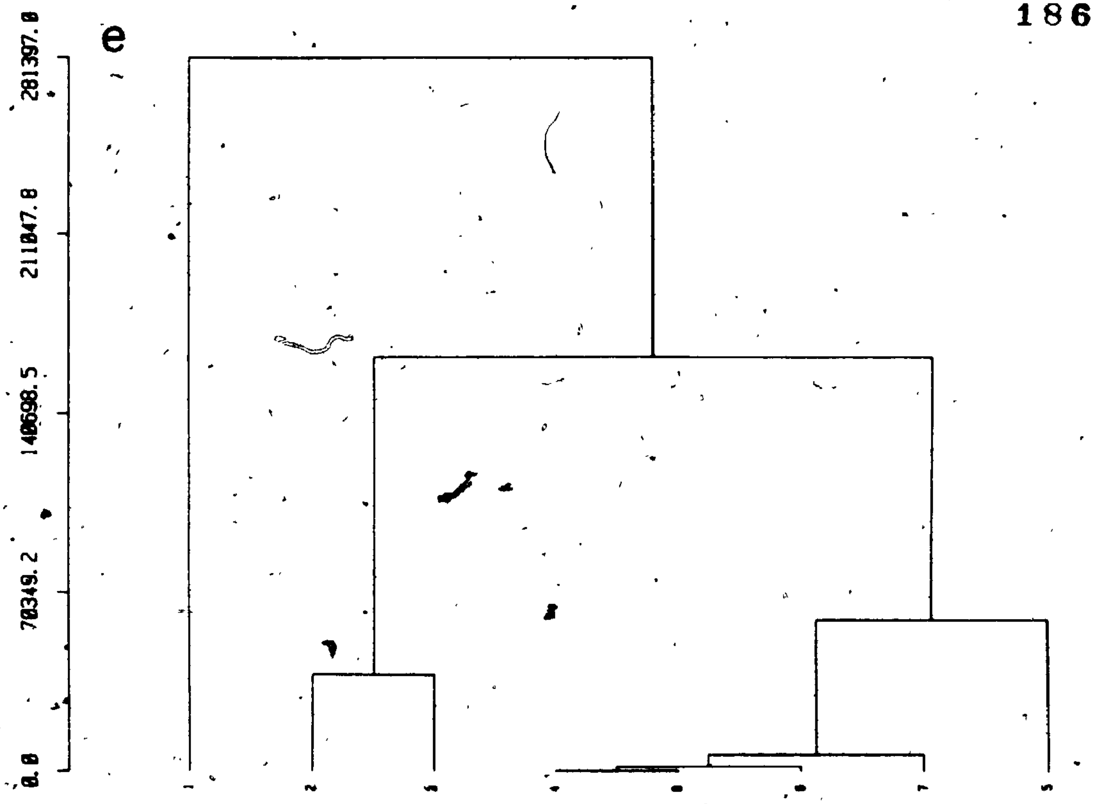

b
0.0
0.1
0.2
0.4
0.5
a
b
c
d
e
f
g
h
a
0.0
0.1
0.2
0.4
0.5
a
b
c
d
e
f
g
h

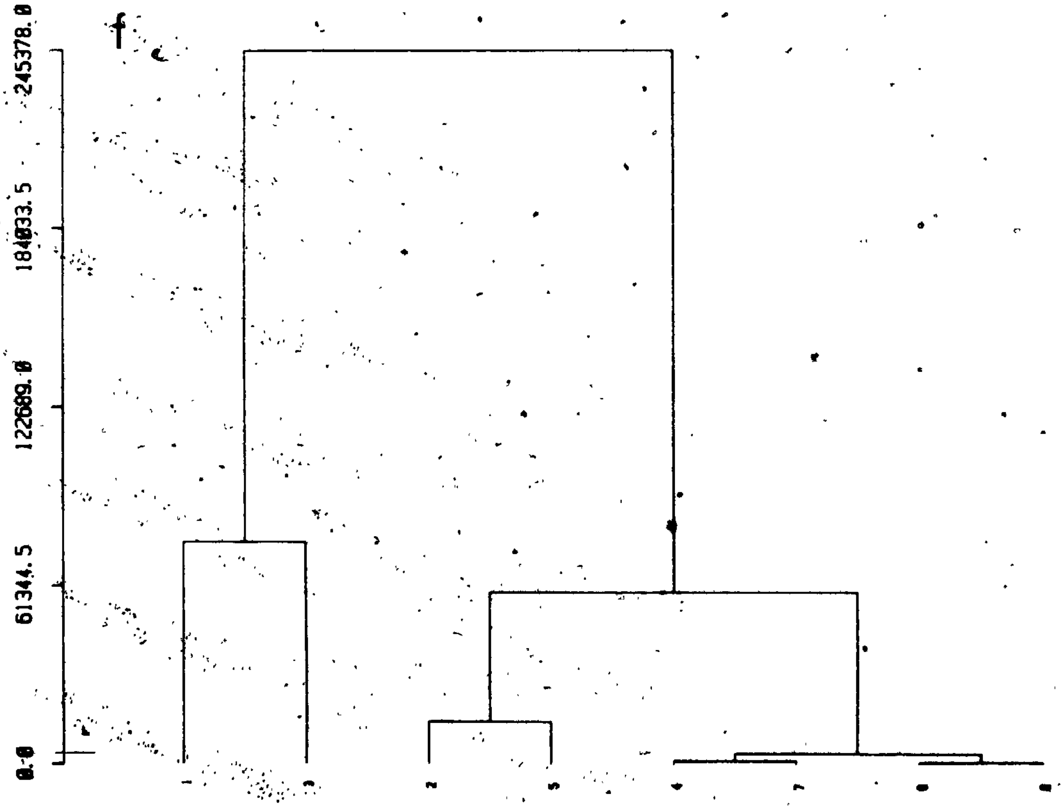
Fig. 3.22 Effect of plot size on group structure of species. Dendrograms resulting from SSA clusterings based on seven different plot sizes used in the sampling of maple forest vegetation map. Dendrograms a to g correspond to the different plot sizes as given in the legend of Fig. 3.15. Vertical axis in each represents the sum of squares. Numbers at the bottom of each dendrogram correspond to species as given in Fig. 3.15.


a
40478846.0
30359134.5
20239423.0
10119711.5
0.0


b
8481290.0
6360967.5
4240645.0
2120322.5
0.0


c
3910710.0
2933032.5
1955355.0
977677.5
0.0
d
752892.0
564669.0
376446.0
188223.0
0.0


e
281397.0
211047.8
140698.5
70349.2
0.0


f
245378.0
184033.5
122689.0
61344.5
0.0

g

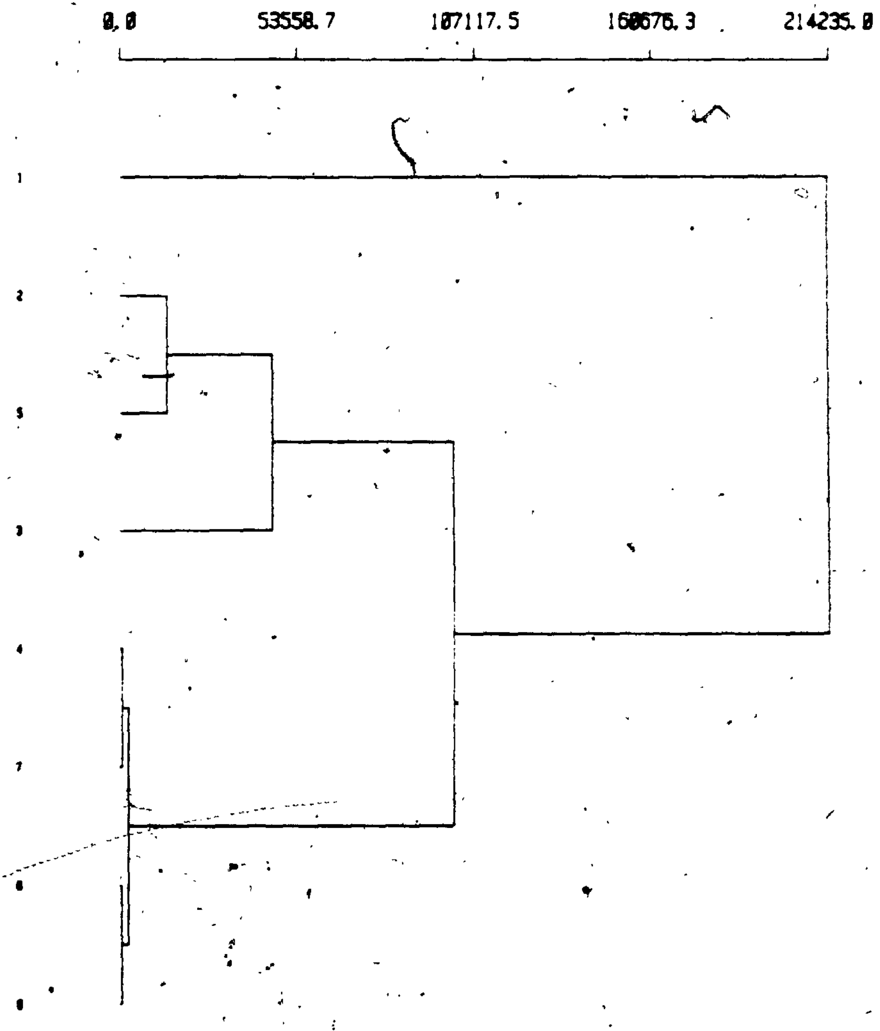


Fig. 3.23 Trellis diagram showing levels of correlation coefficient between cophenetic matrices (lower half) and dissimilarity matrices (upper half) based on data sets pertaining to 7 plot sizes used in sampling maple forest vegetation map.

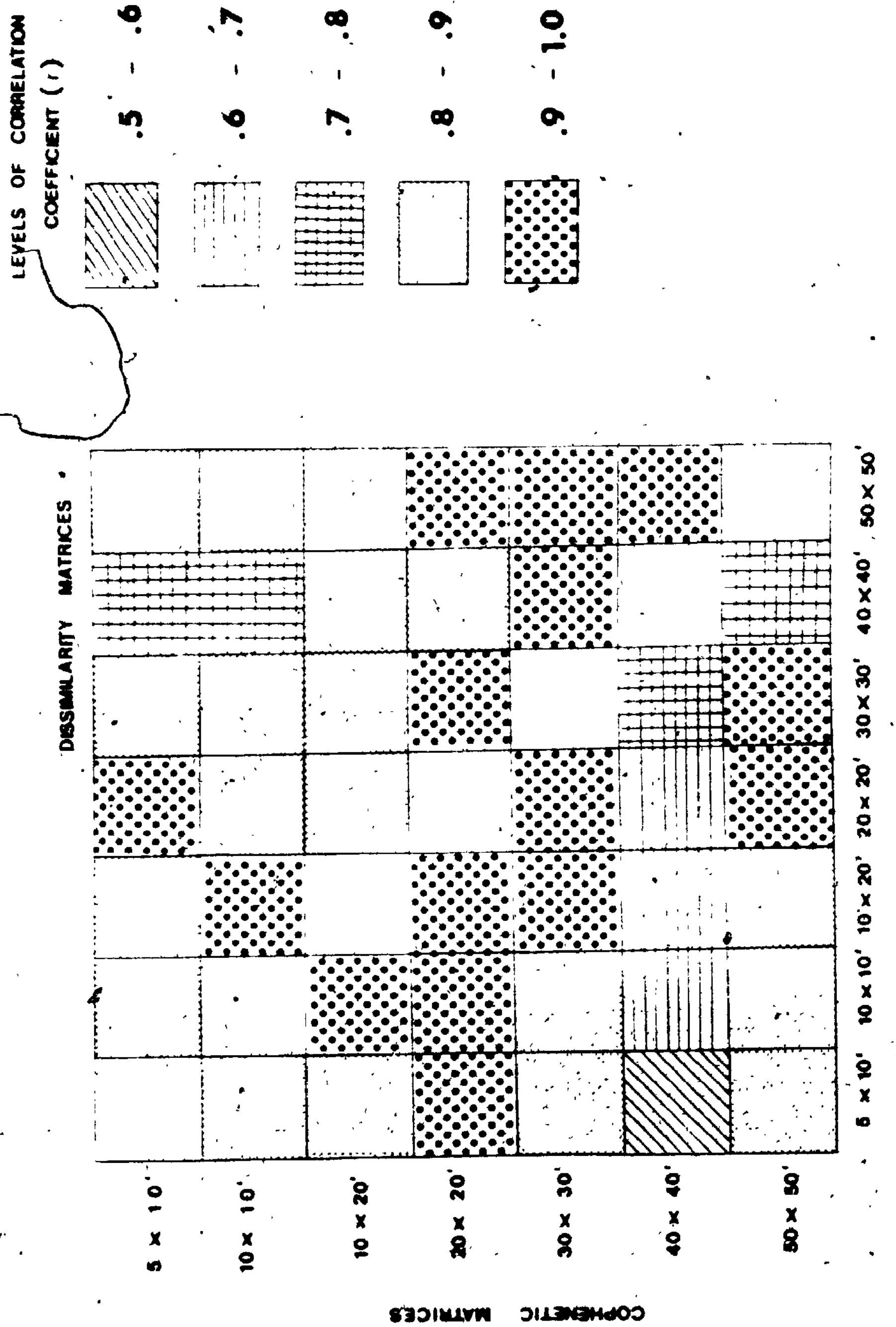
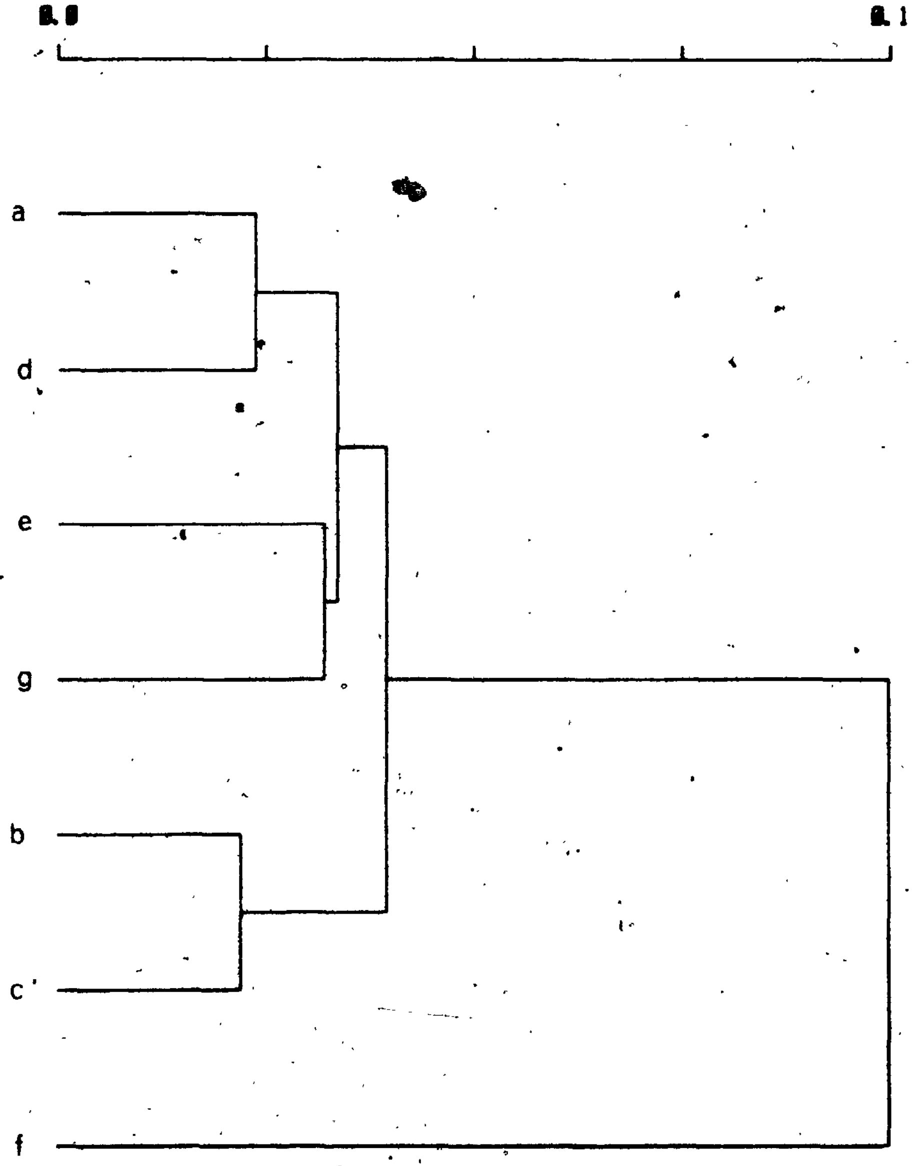
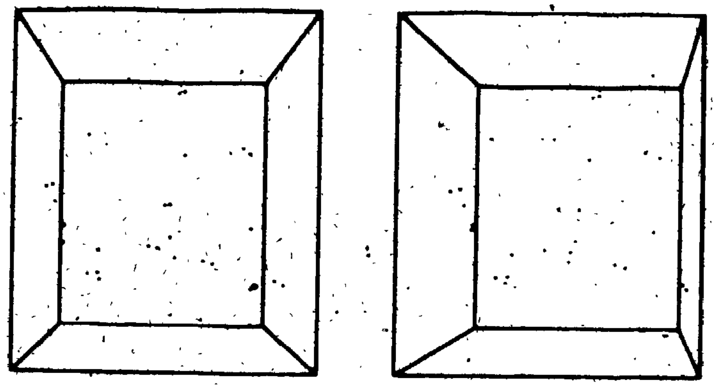

LEVELS OF CORRELATION COEFFICIENT (r)
.5 - .6
.6 - .7
.7 - .8
.8 - .9
.9 - 1.0
DISSIMILARITY MATRICES
5 x 10'
10 x 10'
10 x 20'
20 x 20'
30 x 30'
40 x 40'
50 x 50'
COPHENETIC MATRICES
5 x 10'
10 x 10'
10 x 20'
20 x 20'
30 x 30'
40 x 40'
50 x 50'

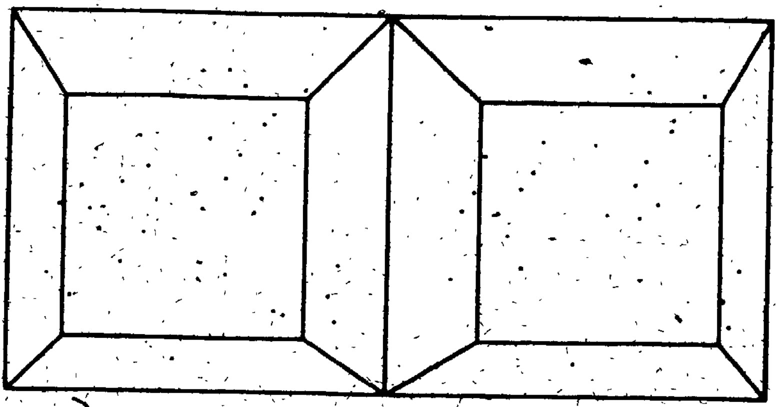
Fig. 3.24 Dendrogram showing the relationships between the classifications (dendrograms shown in Fig. 3.22) pertaining to 7 data sets based on different plot sizes used in the sampling of maple forest vegetation map. Simple average clustering was used based on correlation coefficient. The vertical axis represents 1-compliment of correlation coefficient. The letters at the bottom, a-g correspond to plot sizes as in the legend of Fig. 3.15.

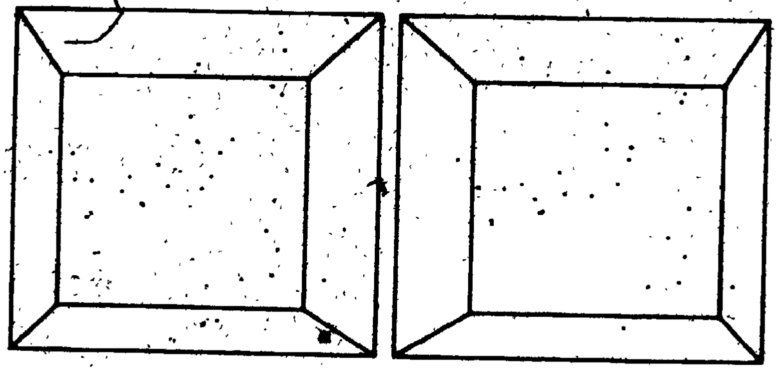


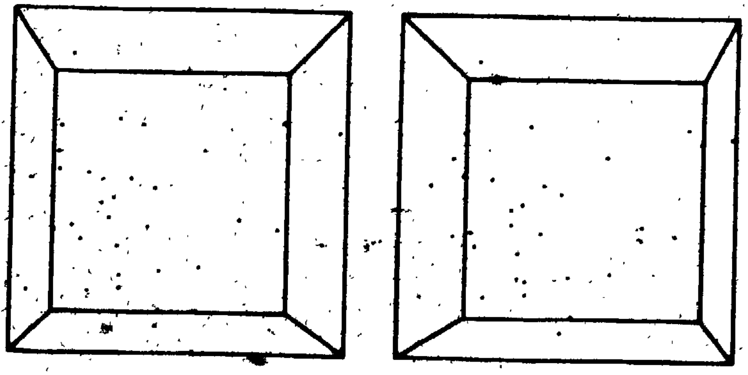
0.0
0.1
a
d
e
g
b
c'
f

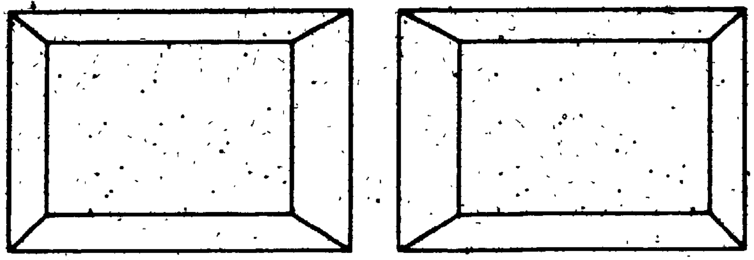
Fig. 3.25 PCA ordinations resulting from 4 different plots sizes and 3 different data types (ordinal, cover and binary) based on pilot survey data. Originally the data sets were obtained on van der Maarel's ordinal scale and then transformed to % cover and binary data sets. Stereograms a-d are based on binary data of the 4 plot sizes: a, 2.5*2.5 m; b, 5*5 m; c, 7.5*7.5 m; d, 10*10 m; stereograms e to h are based on ordinal data: e, 2.5*2.5 m; f, 5*5 m; g, 7.5*7.5 m; k, 10*10 m; stereograms i to l are based on % cover data: i, 2.5*2.5 m; j, 5*5 m; k, 7.5*7.5 m; l, 10*10 m.


a

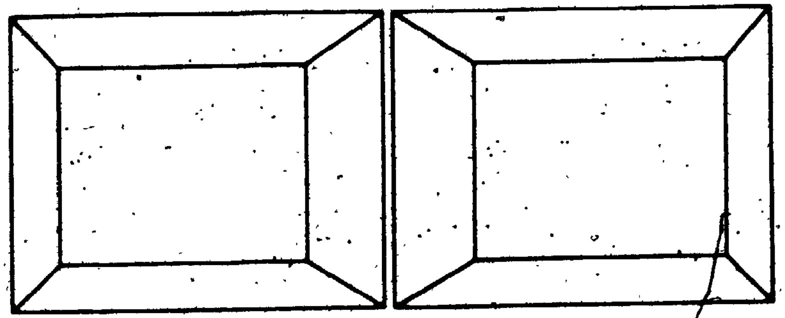

b


c

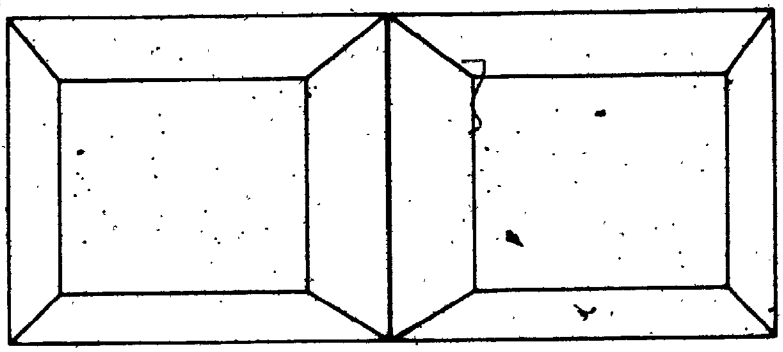

d



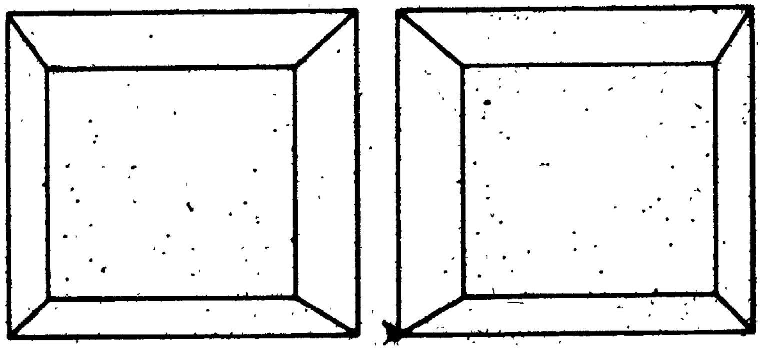
e



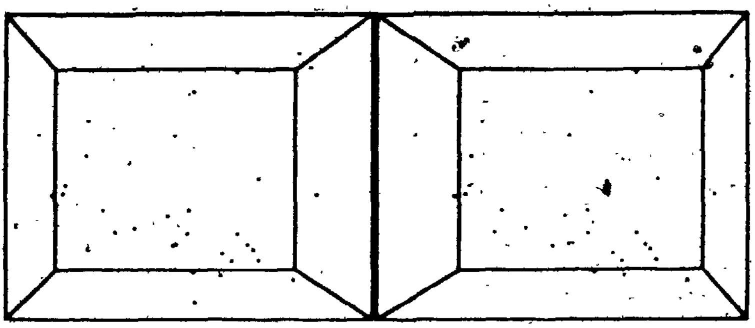
f



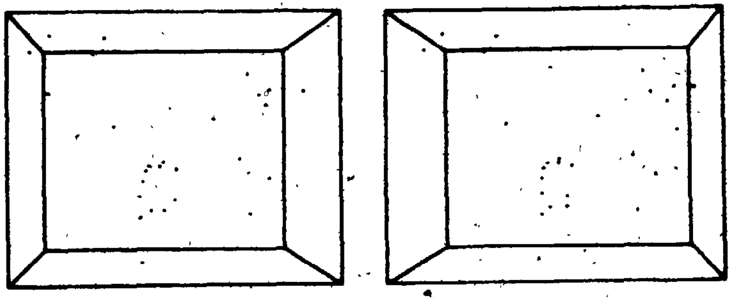
g



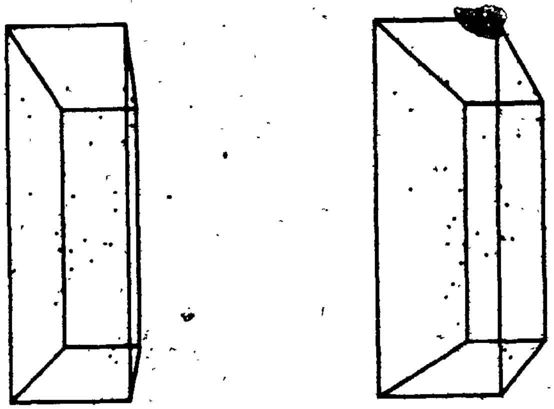
h



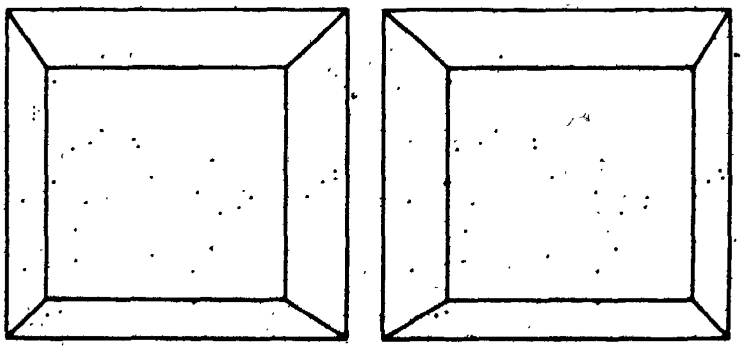
i



j

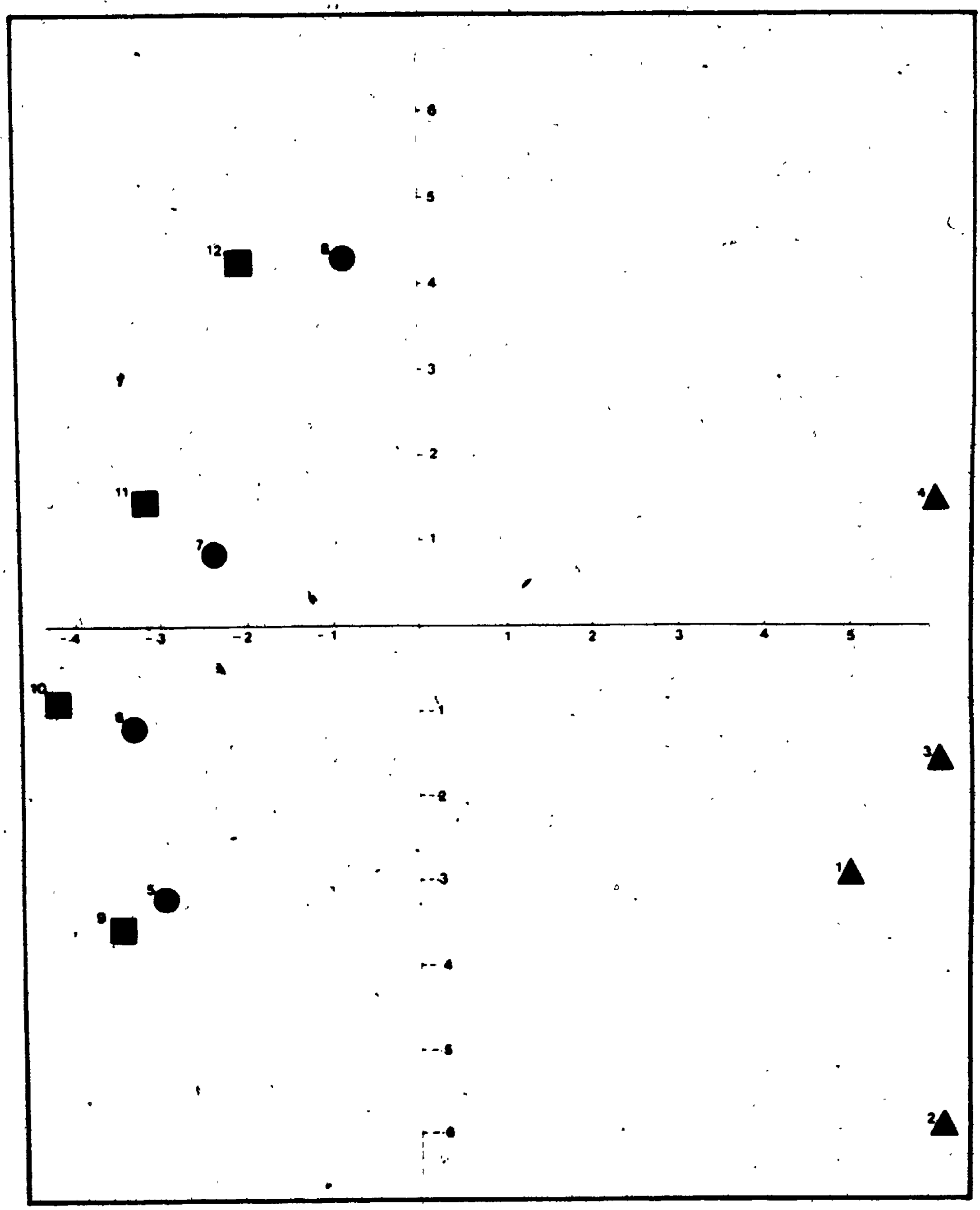


k



l

Fig. 3.26 An ordination of PCA ordinations based on 3 different data types and 4 different plot sizes obtained in the pilot survey. Points 1-4 binary data of the four plot sizes: 1, 2.5*2.5 m; 2, 5*5 m; 3, 7.5*7.5 m; 4, 10*10 m; 5-8 ordinal data: 5, 2.5*2.5 m; 6, 5*5 m; 7, 7.5*7.5 m; 8, 10*10 m; 9-12 % cover data: 9, 2.5*2.5 m; 10, 5*5 m; 11, 7.5*7.5 m; 12, 10*10 m.



6
5
4
3
2
1
-1
-2
-3
-4
-5
-6
-4
-3
-2
-1
1
2
3
4
5
1
2
3
4
5
6
7
8
9
10
11
12

Fig. 3.27 Dendrograms resulting from simple average (a) and SSA clustering (b) of the ordinations derived from 3 different data types and 4 different plot sizes. Vertical axis in (a) represents 1-compliment of correlation coefficient while in (b) it represents sum of squares. Numbers at the bottom of each correspond to data type and plot size as in the legend of Fig. 3.26.

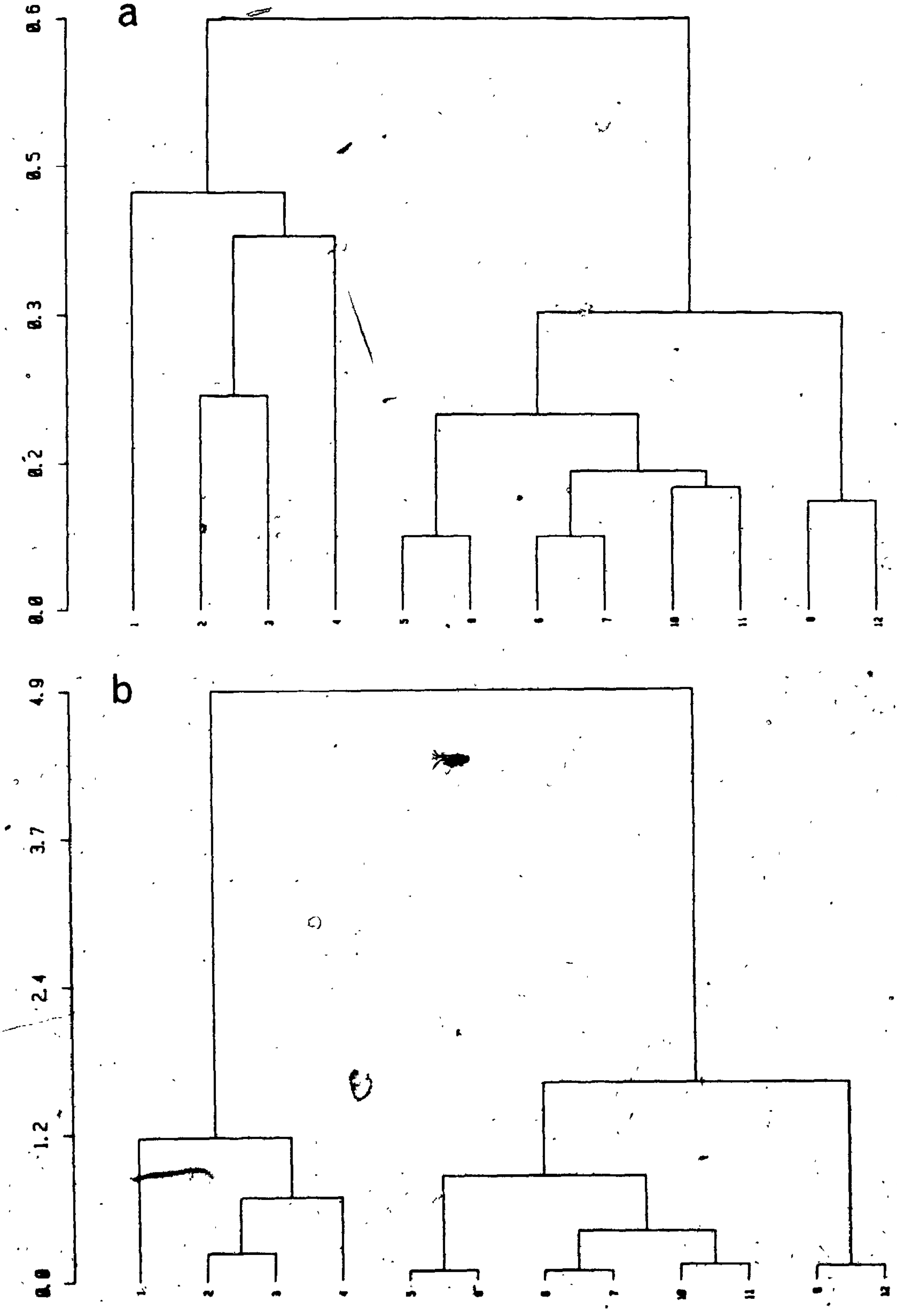
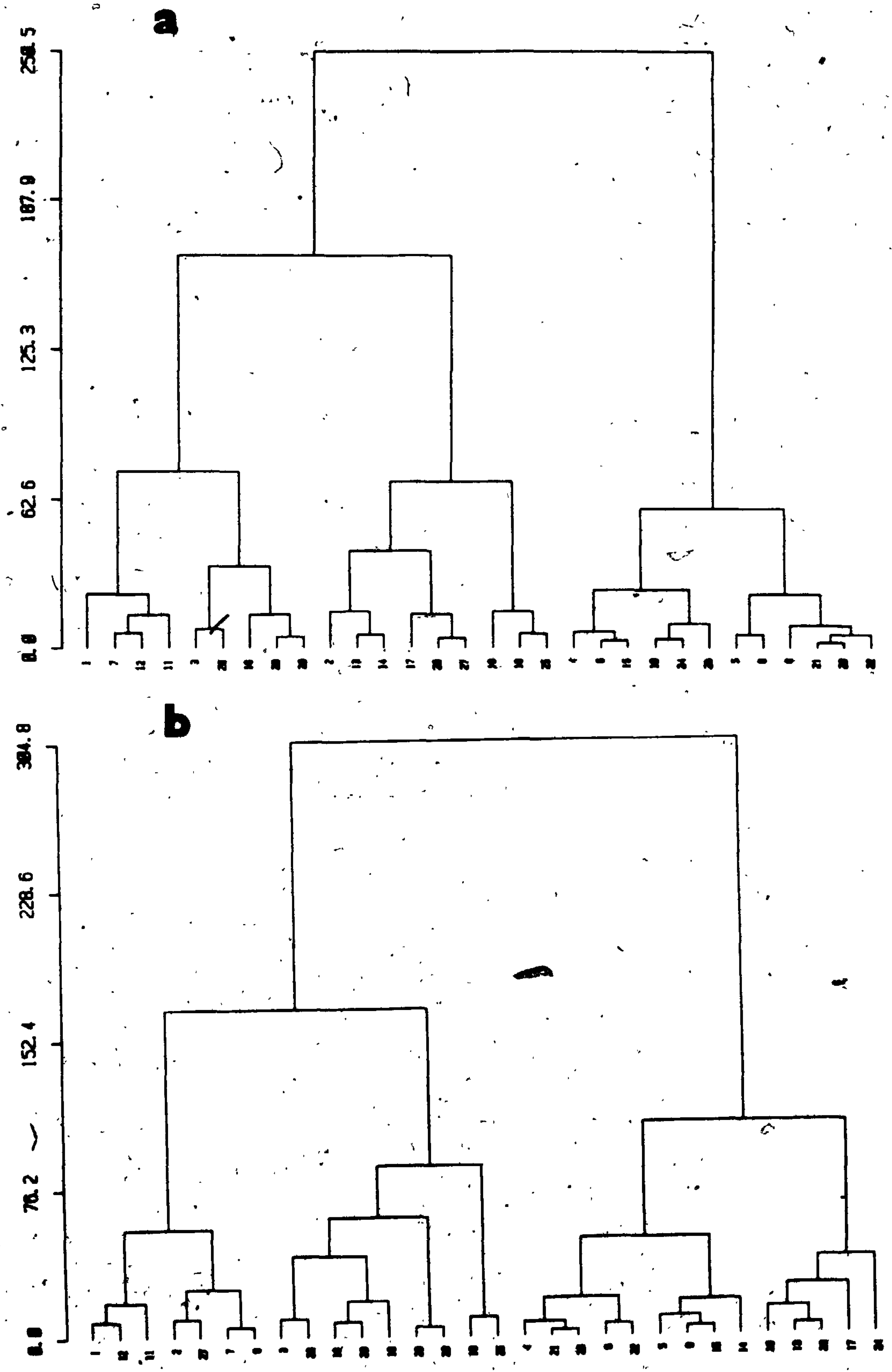
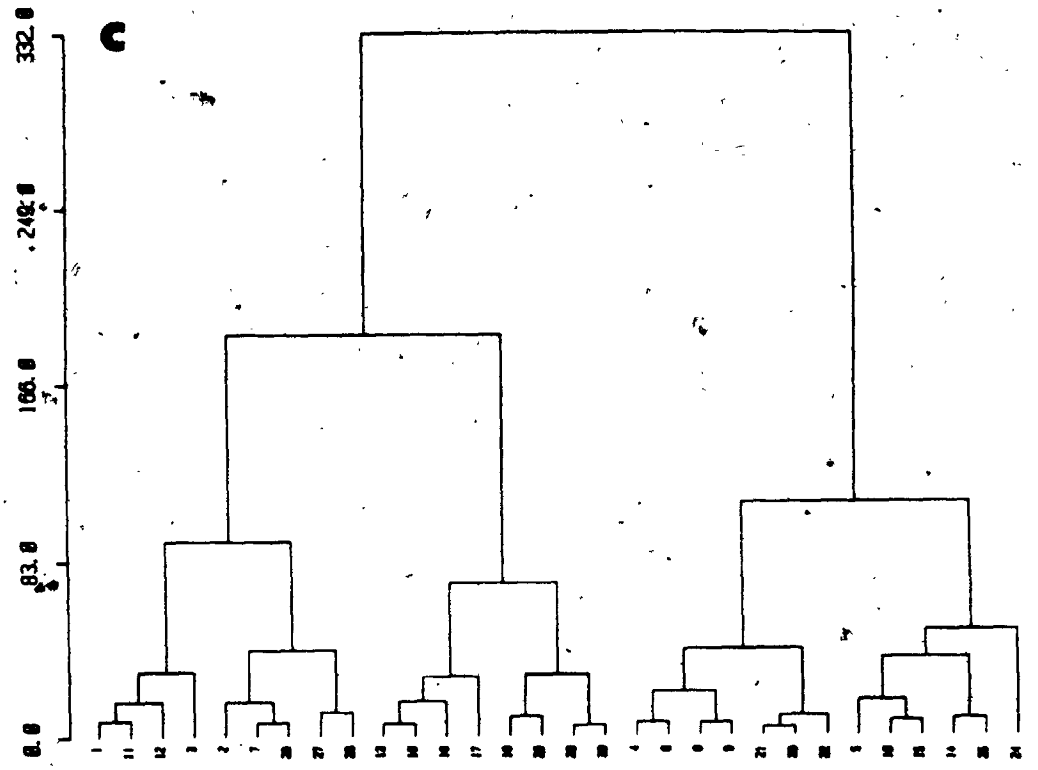
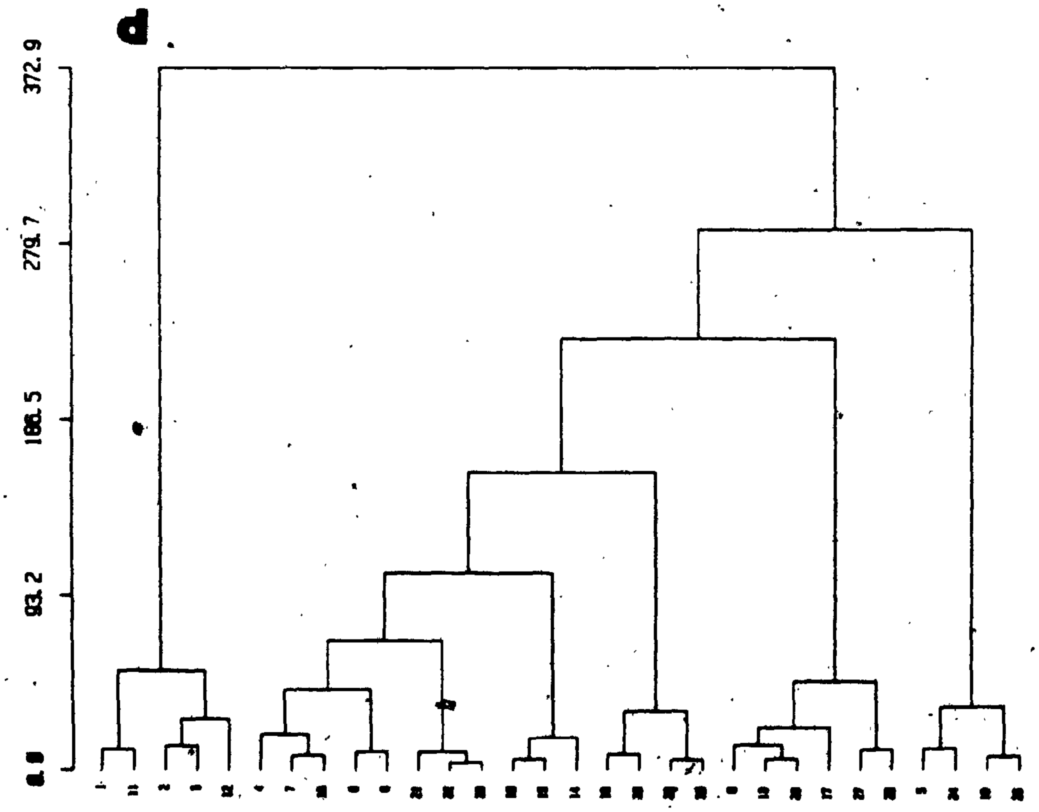
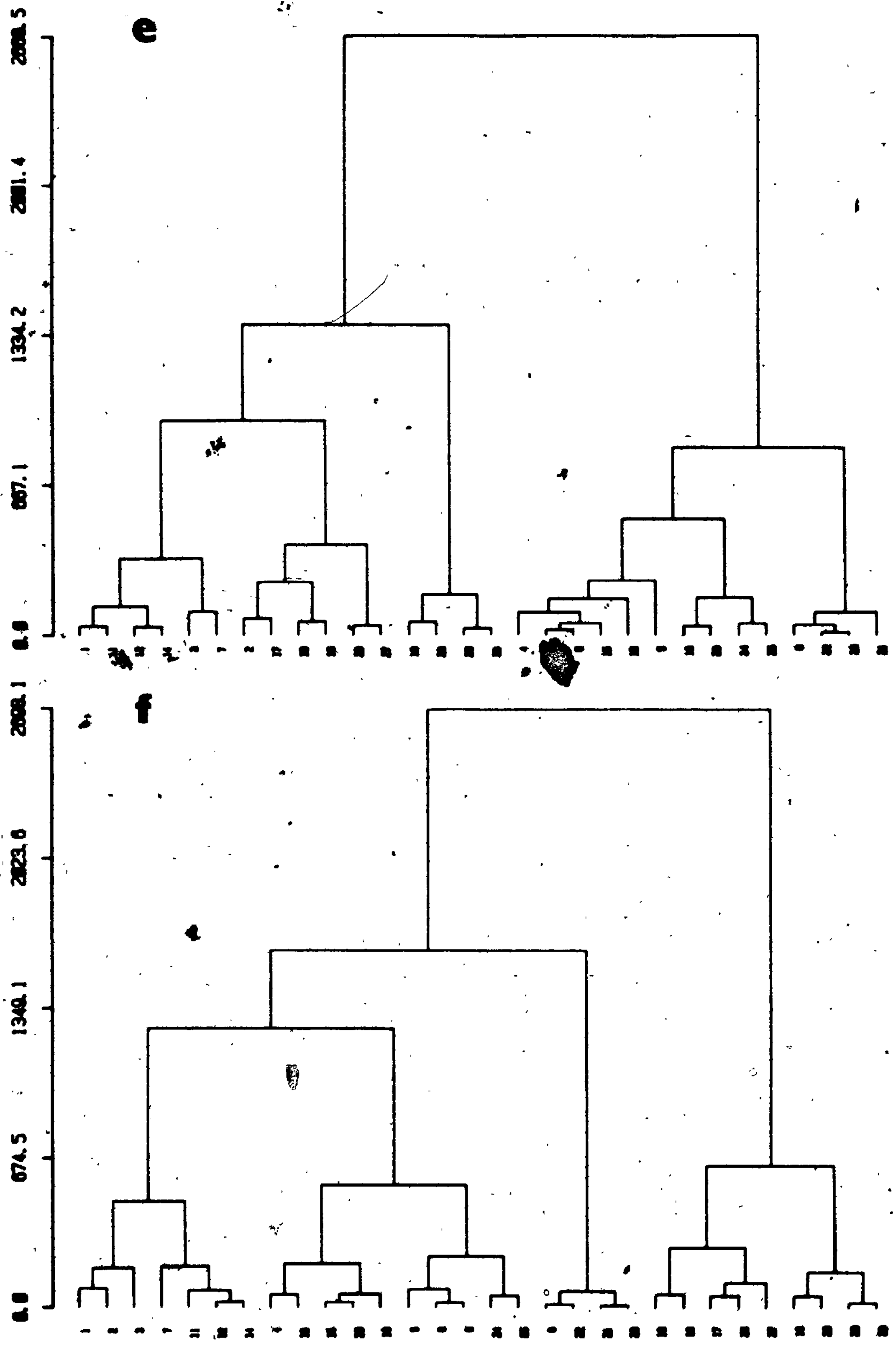

a
0.6
0.5
0.3
0.2
0.0
1
2
3
4
5
6
8
7
10
11
9
12
b
4.9
3.7
2.4
1.2
0.0
1
2
3
4
5
6
8
7
10
11
9
12

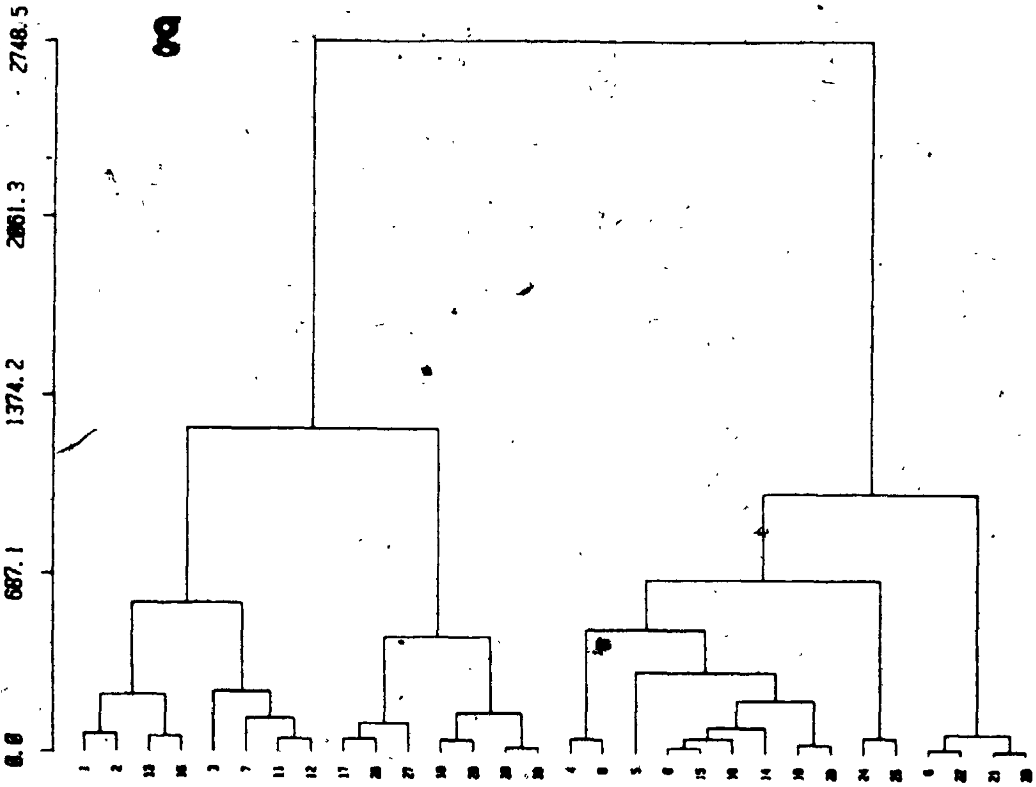
Fig. 3.28 Dendrograms resulting from SSA clustering performed on the data sets based on 3 different data types and 4 plot sizes obtained in the pilot survey. Vertical axis in each represents sum of squares. Numbers at the bottom identify releves. Dendrograms a to l correspond to data types and plot sizes as outlined in the legend of Fig. 3.25.

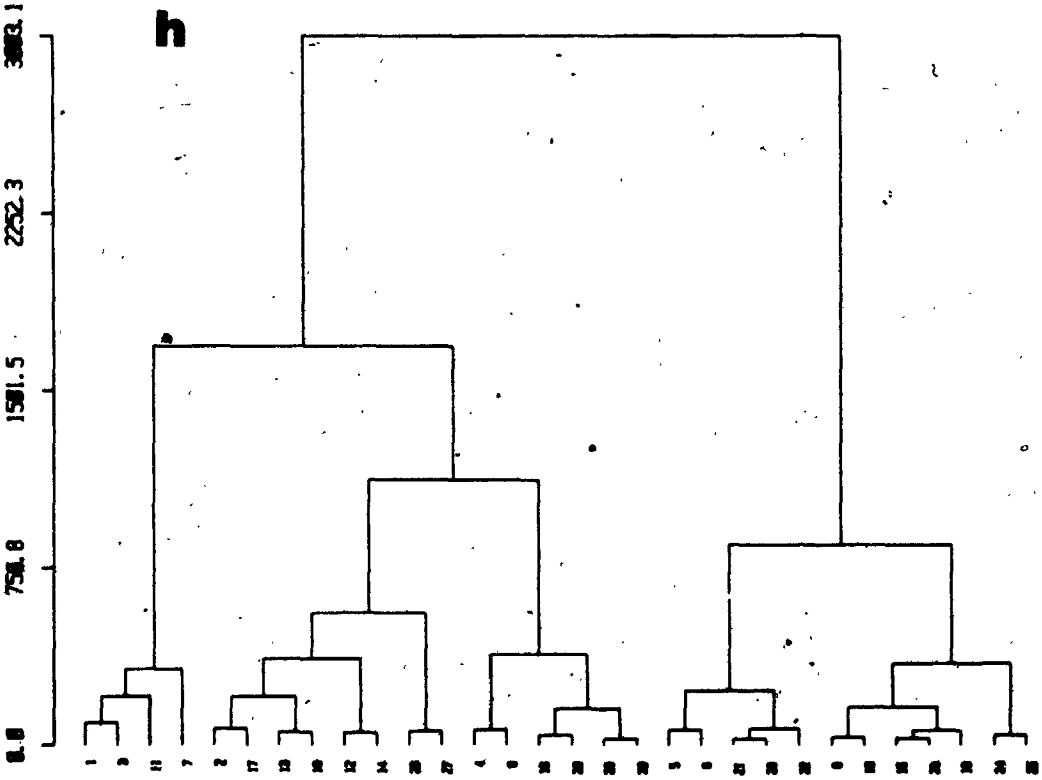

a
250.5
187.9
125.3
62.6
0.0
b
304.8
228.6
152.4
76.2
0.0

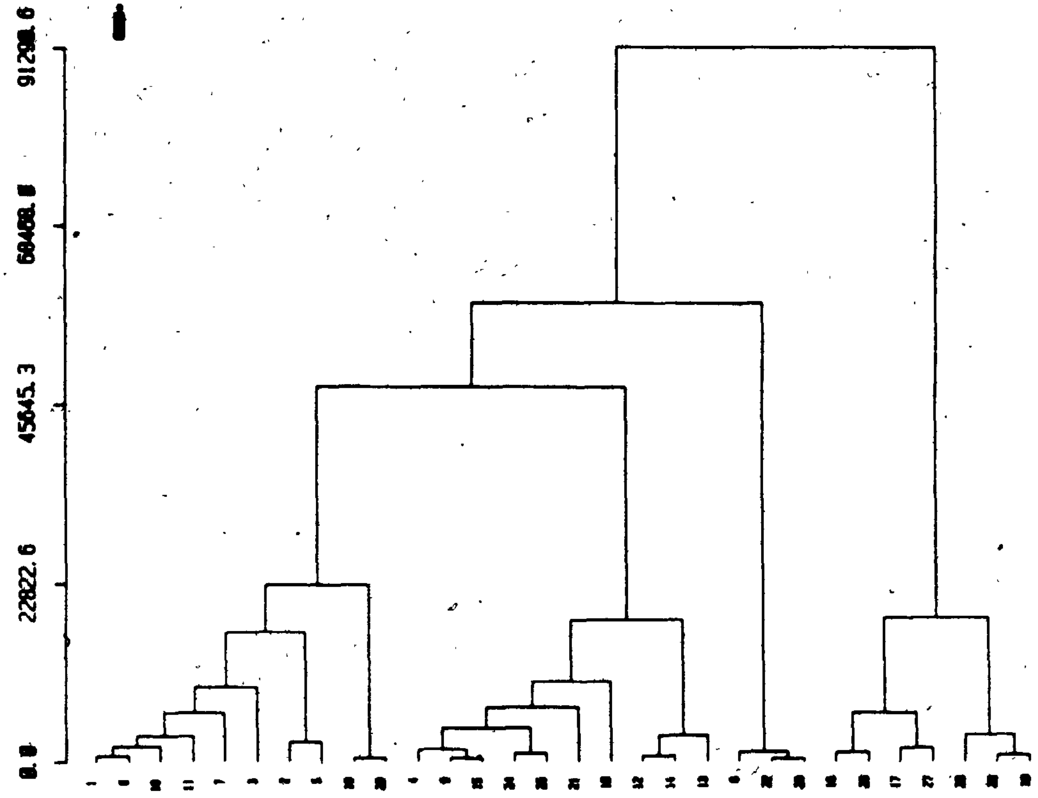

c
332.0
249.0
166.0
83.0
0.0

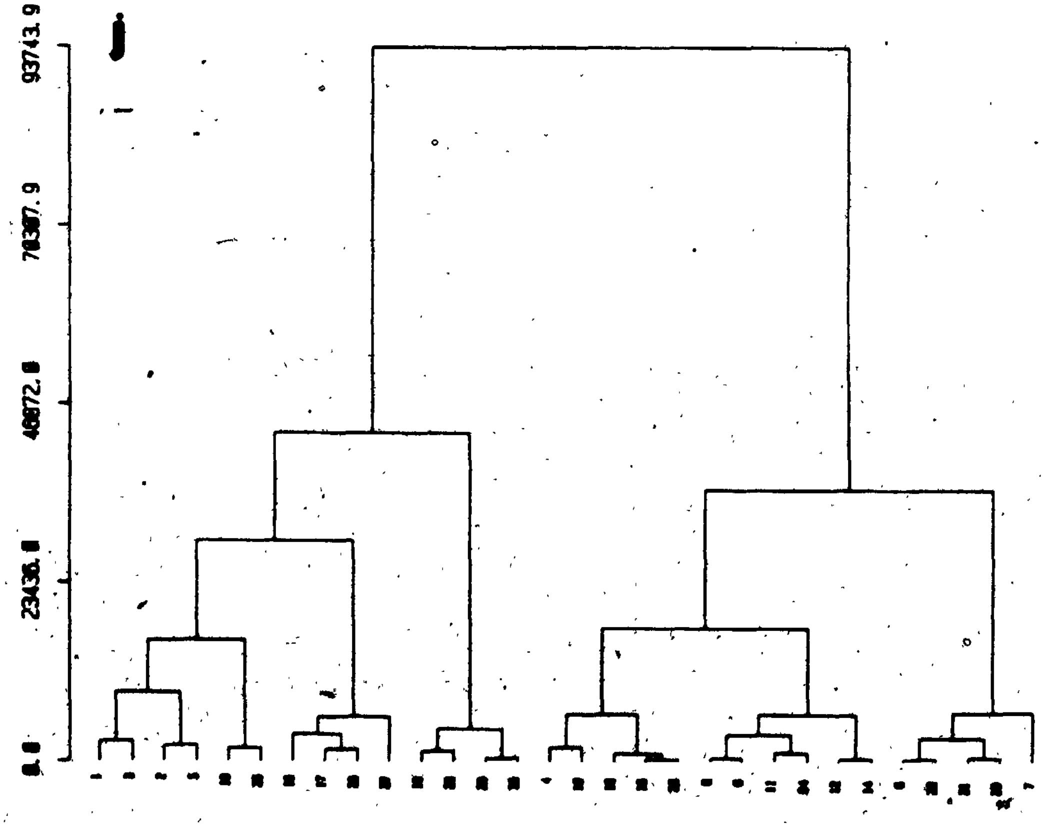

d
372.9
279.7
186.5
93.2
0.0

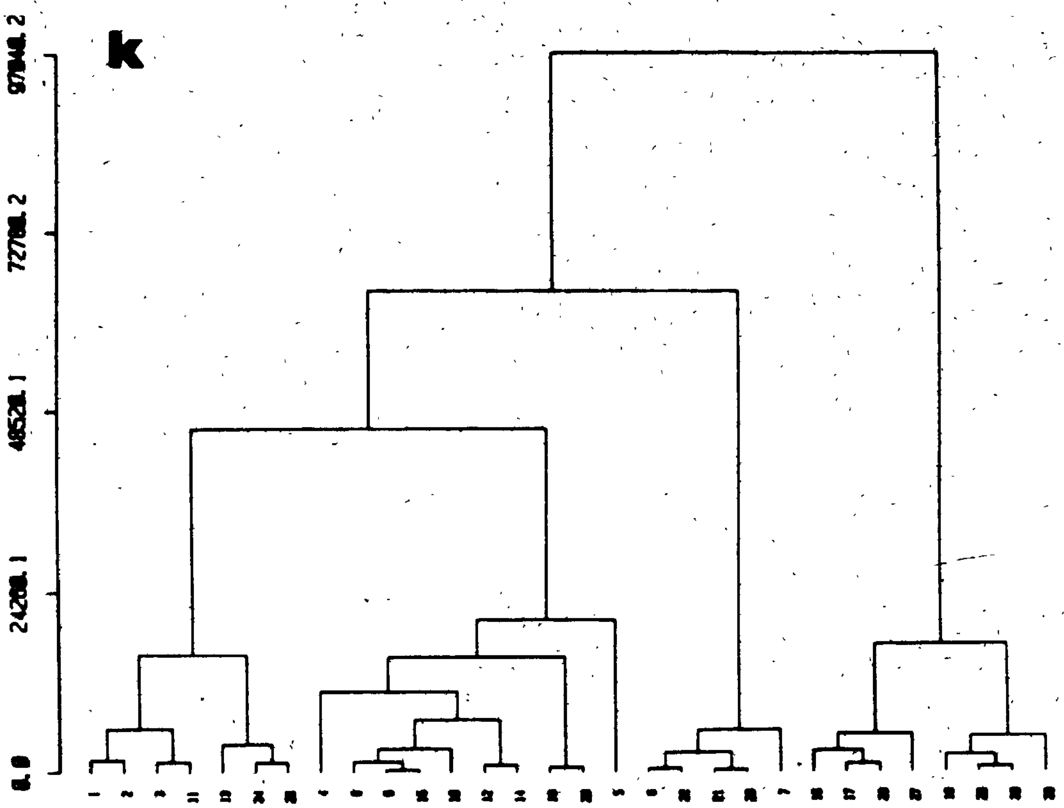

e
2668.5
2001.4
1334.2
667.1
0.0
f
2698.1
2023.6
1349.1
674.5
0.0


g
2748.5
2061.3
1374.2
687.1
0.0


h
3003.1
2252.3
1501.5
750.8
0.0


i
91298.6
68408.8
45645.3
22822.6
0.0


j
93743.9
70307.9
46872.0
23436.0
0.0


k
97040.2
72780.2
48520.1
24260.1
0.0

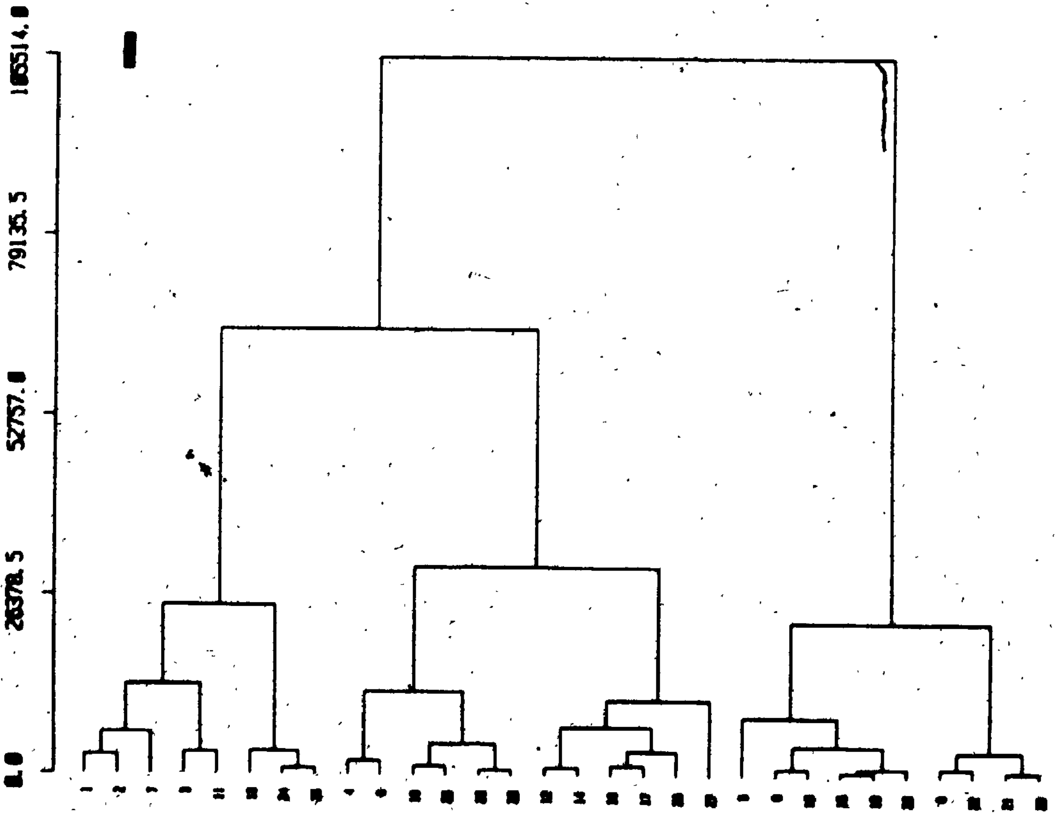

l
105514.0
79135.5
52757.0
26378.5
0.0

Fig. 3.29 An ordination of classifications based on 3 data types and 4 plot sizes pertaining to the pilot survey (dendrograms shown in Fig. 3.28). Points 1 to 12 in the ordination correspond to the 3 data types and 4 plot sizes as outlined in the legend in Fig. 3.26.

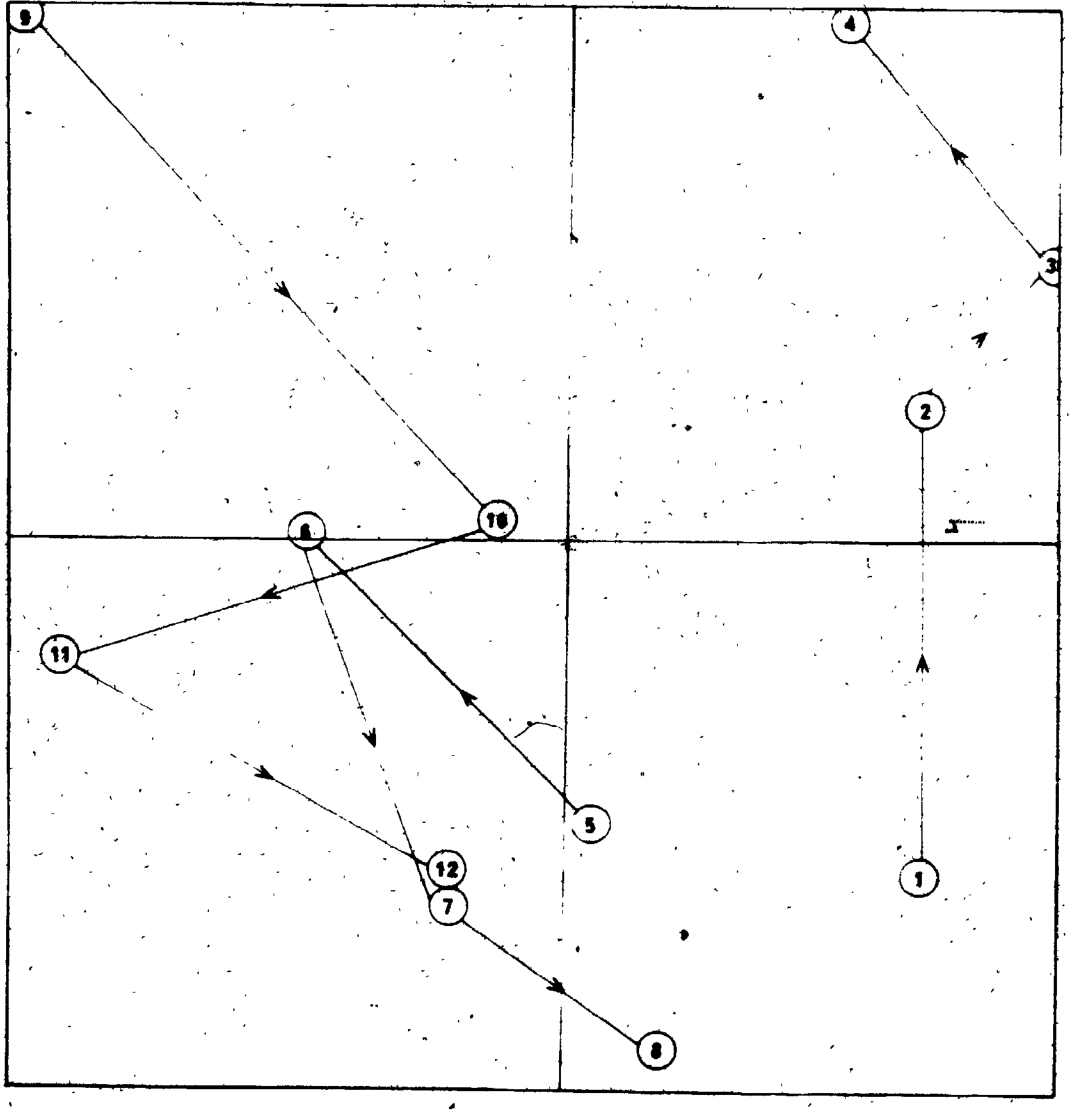
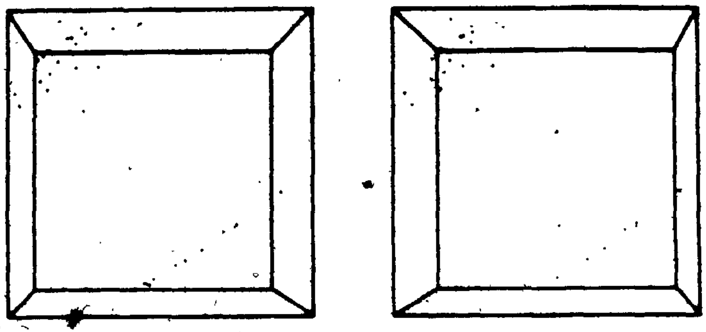
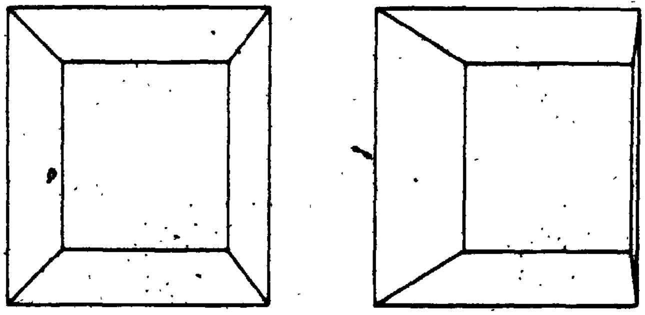

9
4
3
2
10
6
11
5
12
7
1
8

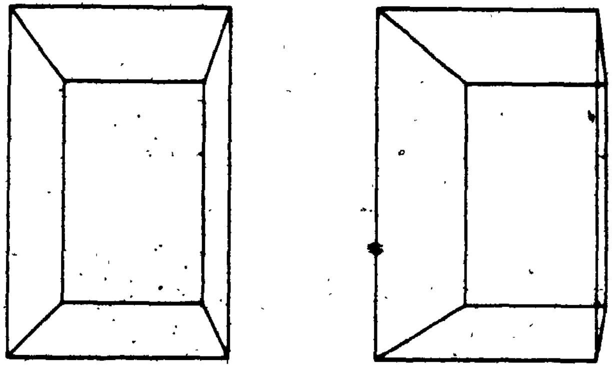
Fig. 3.30 Stereograms of MDSCAL ordinations based on various data types and tansformations. The percentage cover data obtained with 2.83*5.66 m plots at Stoneybrook site was converted to various ordinal scales and was transformed by simple transformations (see text for details). Three dimensional solutions were sought using chord distance. a) % cover data, b) van der Maarel's scale, c) Braun-Blanquet scale, d) Domin-Krajina scale, e) Daubenmire scale, f) Hult-Sernander scale, g) Lagerberg-Raunkiaer scale, h) Londo's decimal scale, i) Bailey and Poulton scale, j) Jensen's log 100 (Q+Log % cover), k) Jensen's log (% cover+1), l) Jensen's 100+% cover, m) arcsine, n) square root.



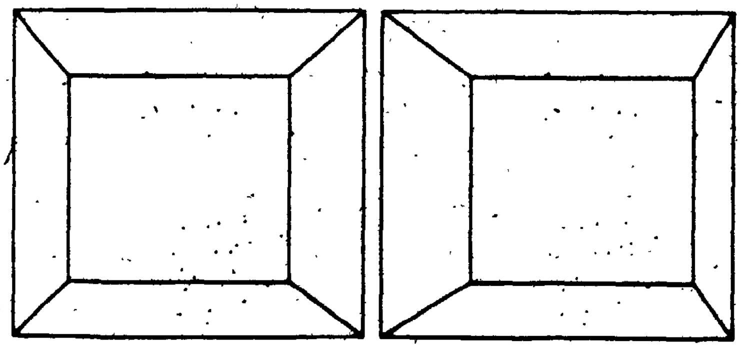
a



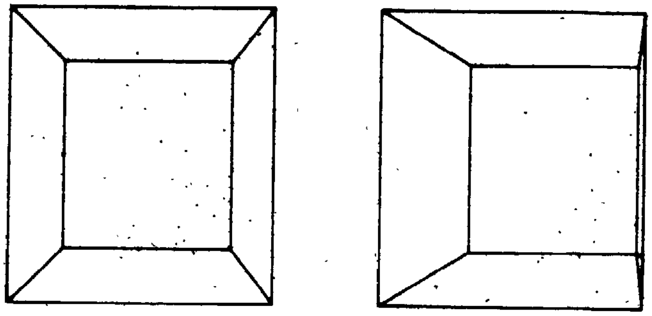
b



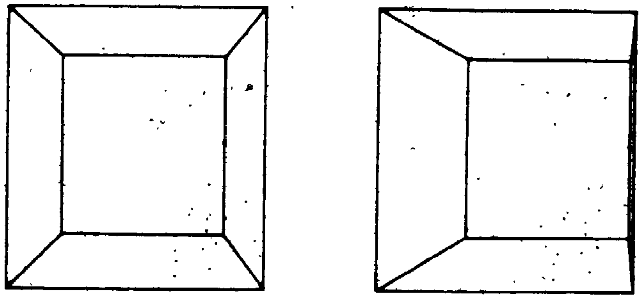
c



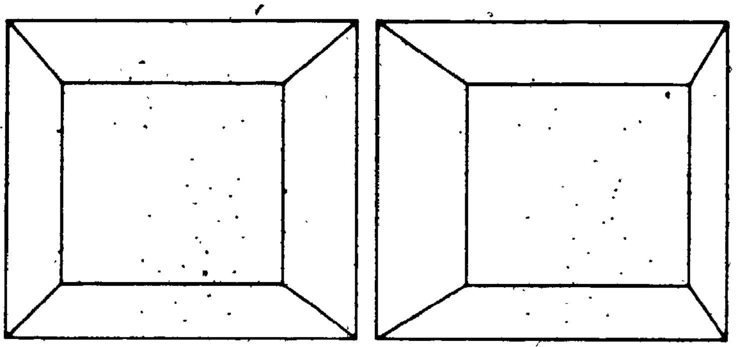
d



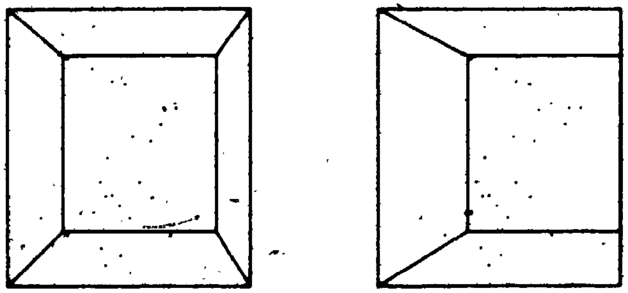
e



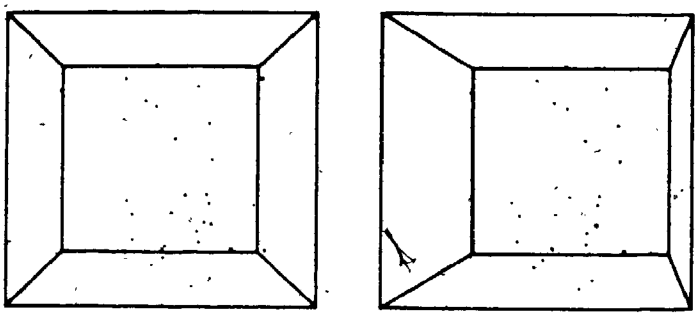
f



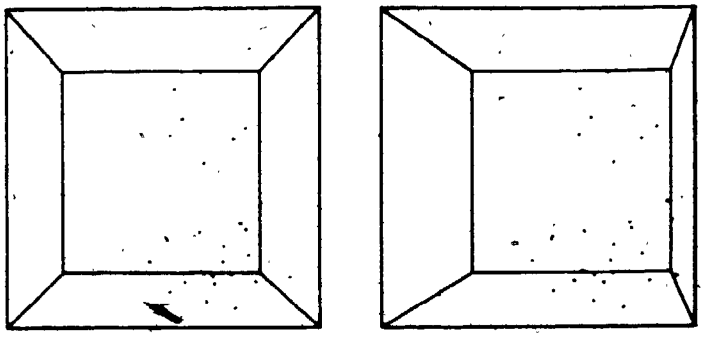
g



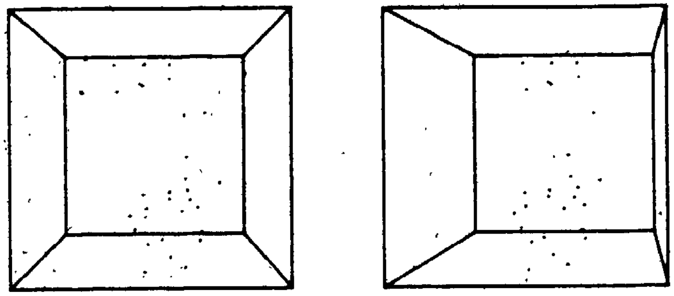
h



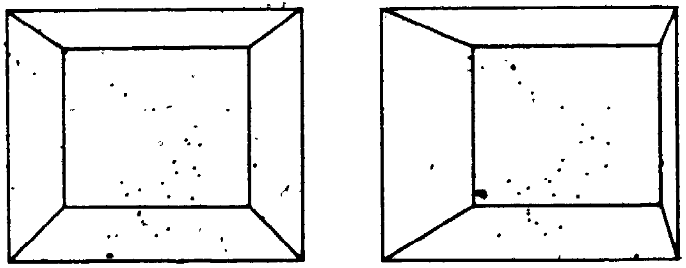
i



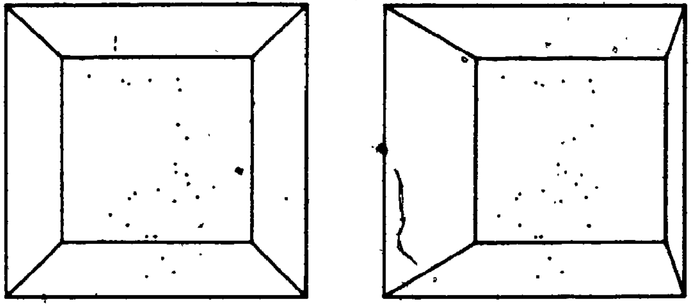
j



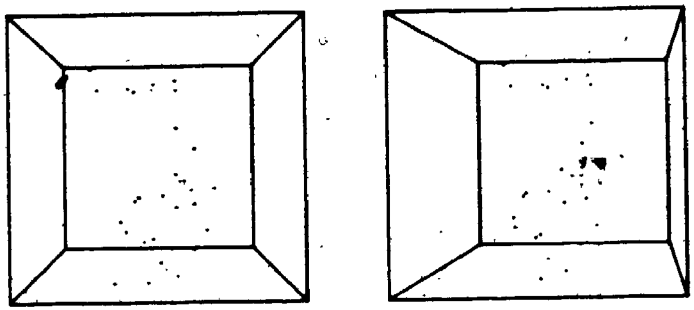
k



l

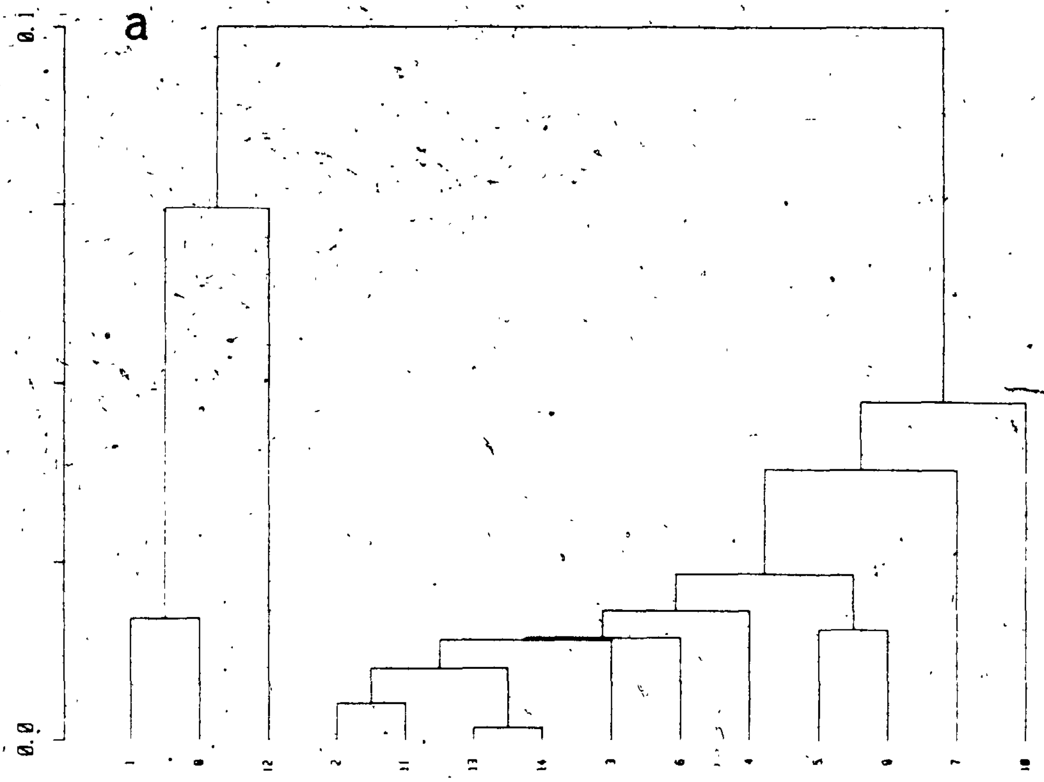


m



n

Fig. 3.31 Dendrograms resulting from simple average (a) and group average clustering (b) of the MDSCAL ordinations based on different data types and simple transformations (presented in Fig. 4.30). Vertical axis in each represents 1-compliment of correlation coefficient. Numbers at the bottom of each dendrogram correspond to different data types and transformations: 1, % cover data; 2, van der Maarel's scale; 3, Braun-Blanquet scale; 4, Domin-Krajina scale; 5, Daubenmire scales, 6, Hult-Sernander scale; 7, Lagerberg-Raunkiaer scale; 8, Londo's decimal scale; 9, Bailey and Poulton scale; 10, Jensen's log 100 (Q + Log % cover); 11, Jensen's log (% cover + 1); 12, Jensen's 100 + % cover; 13, arcsine; 14, square root.


a
0.1
0.0
1
8
12
2
11
13
14
3
6
4
5
9
7
10

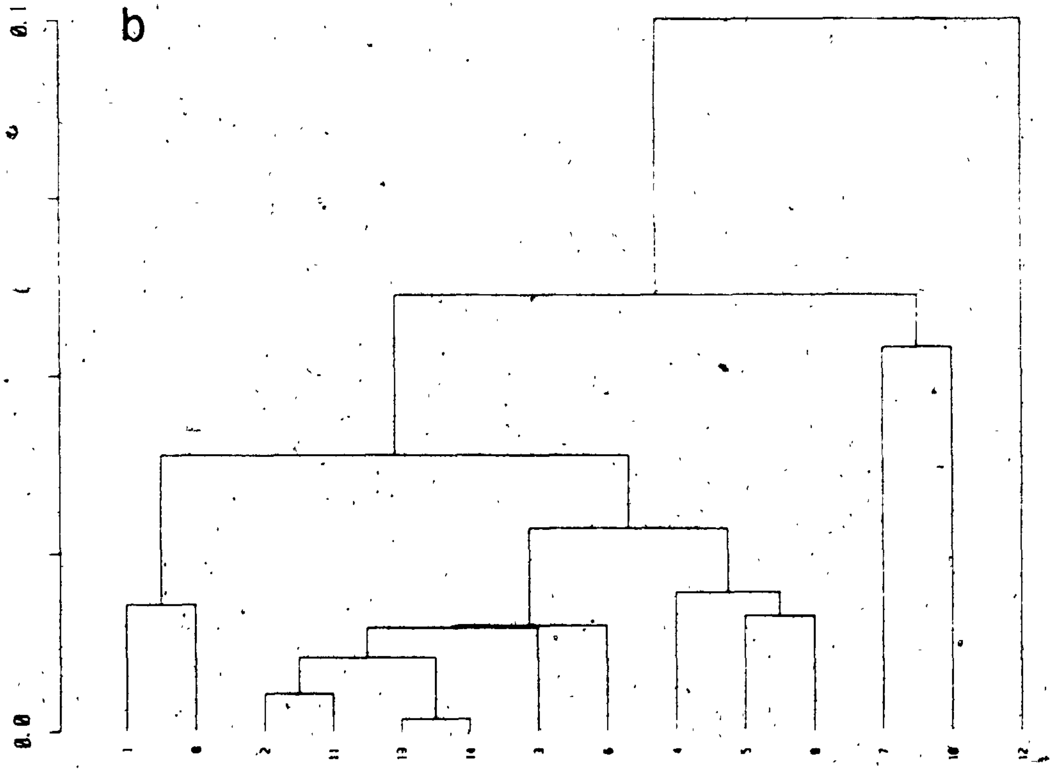
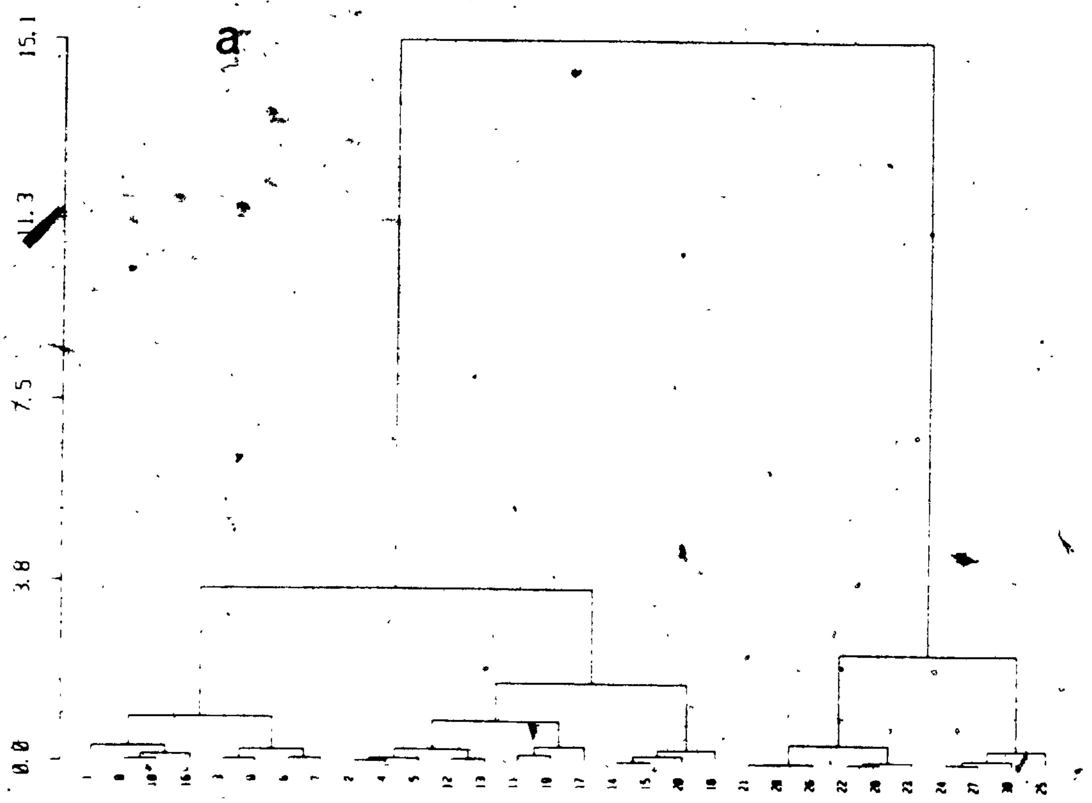
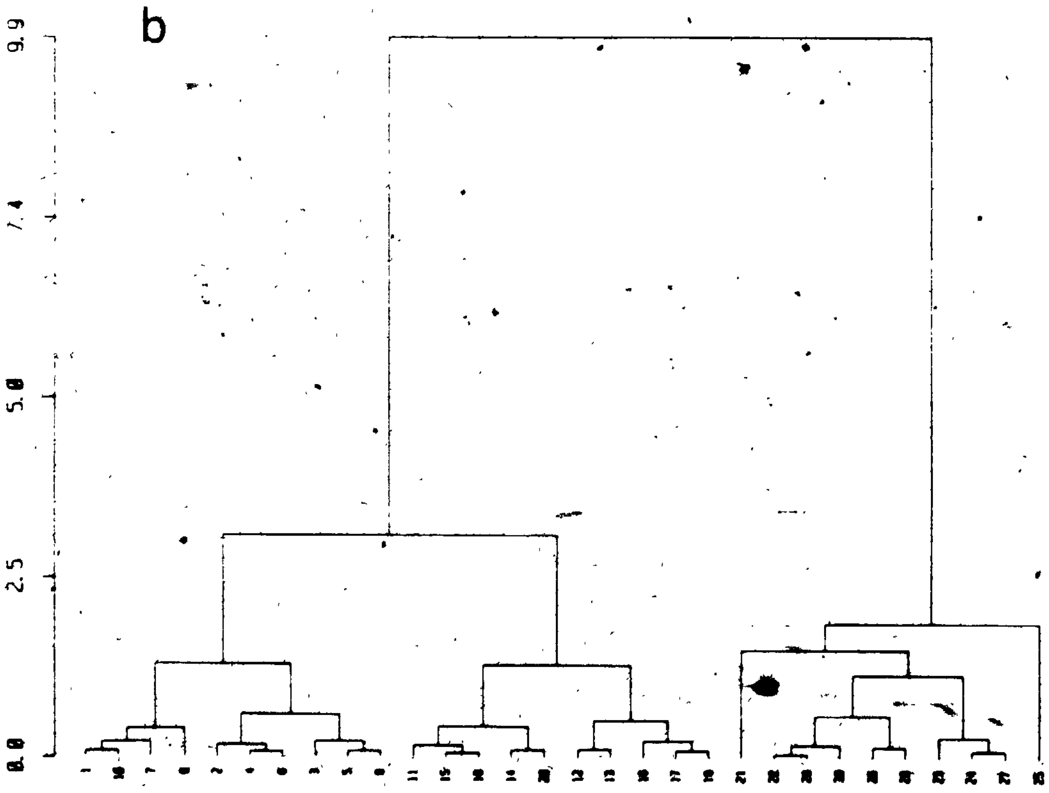
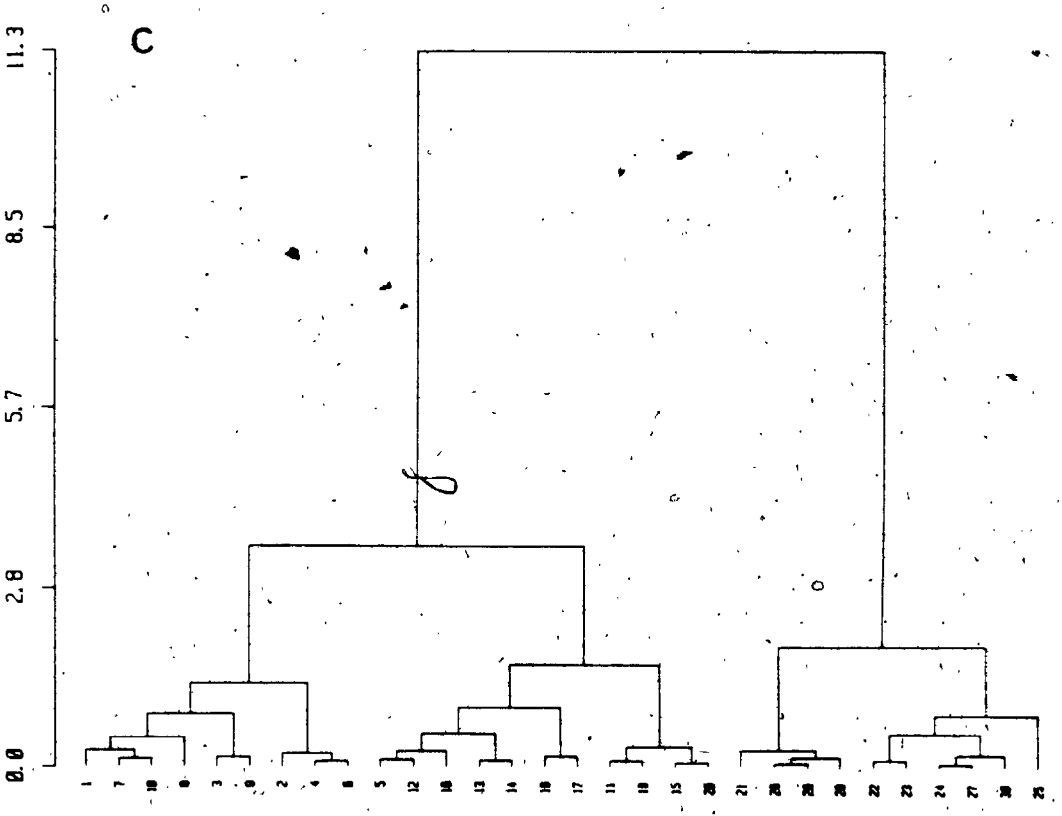
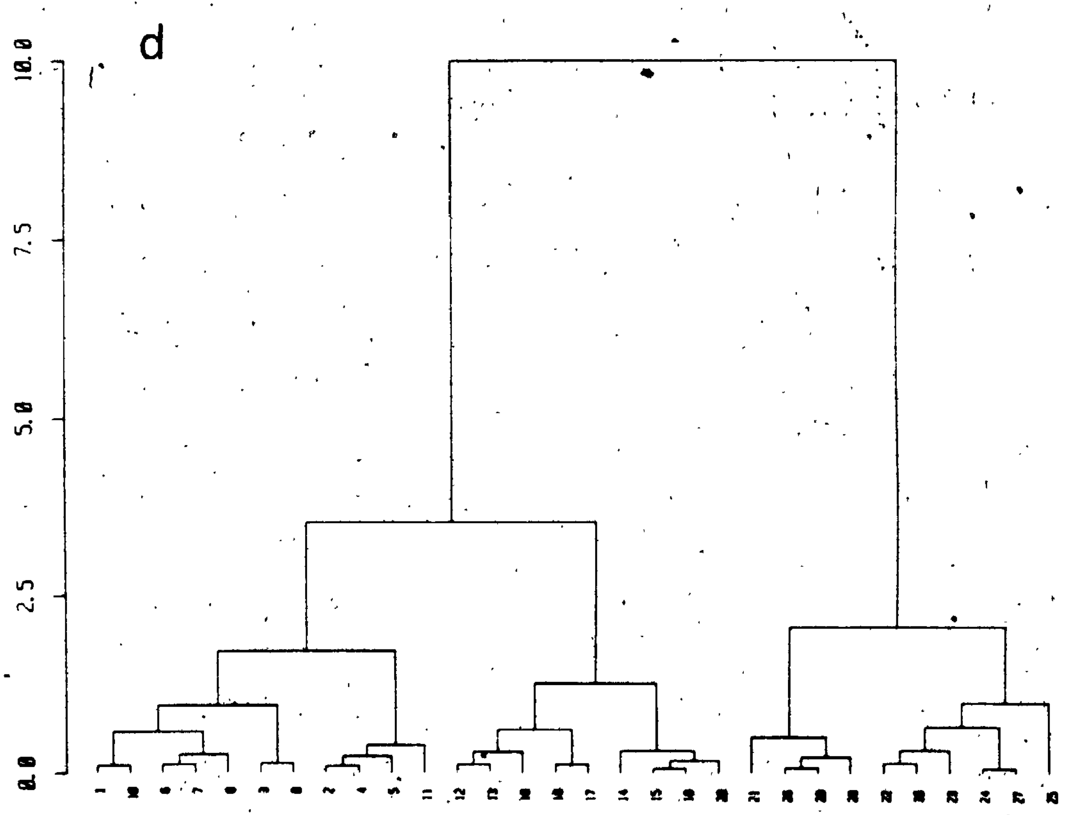

b
0.1
0.0
1
8
2
11
13
14
3
6
4
5
9
7
10
12

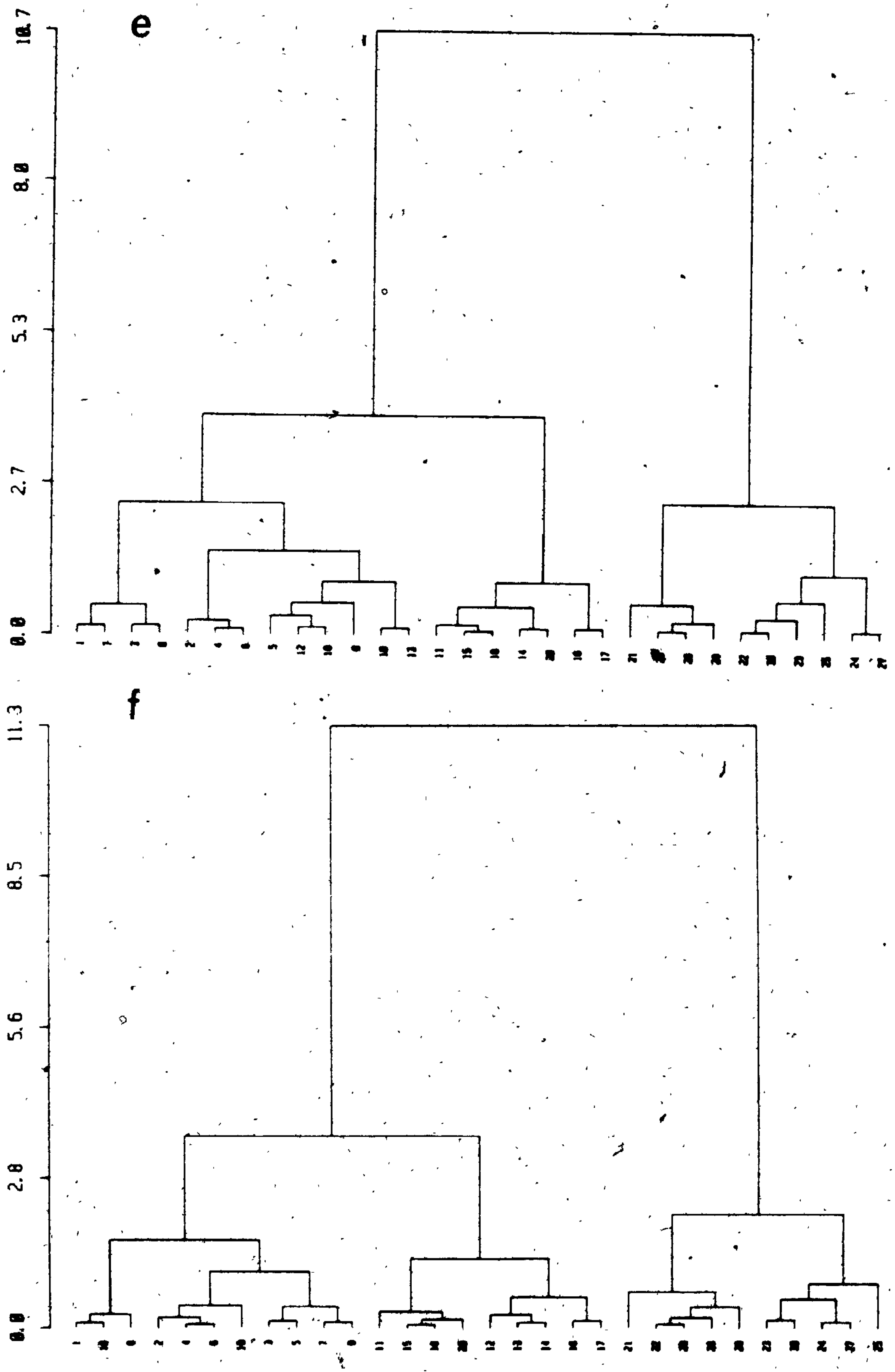
Fig. 3.32 Dendrograms resulting from SSA clustering performed on various data types and variously transformed data sets. Dendrogram a to n correspond to various data types and transformations as outlined in the legend of Fig. 4.30. Vertical axis in each represent sum of squares while numbers at the bottom identify relevés.


a
15.1
11.3
7.5
3.8
0.0

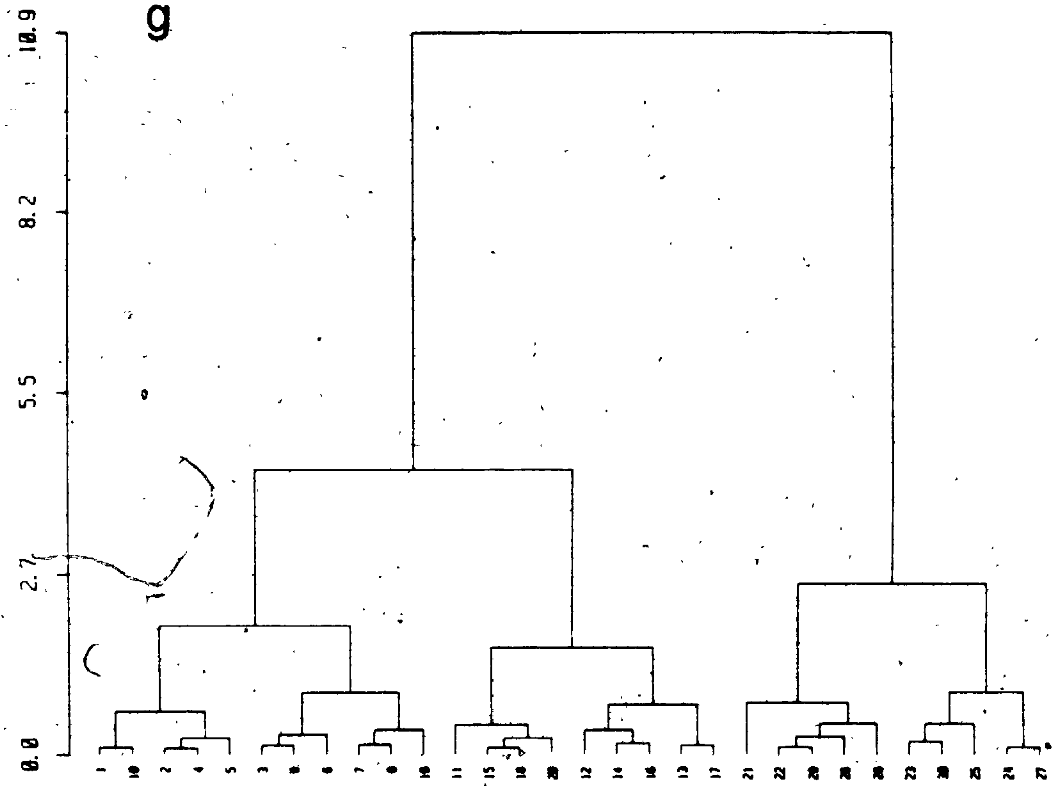

b
9.9
7.4
5.0
2.5
0.0


c
11.3
8.5
5.7
2.8
0.0

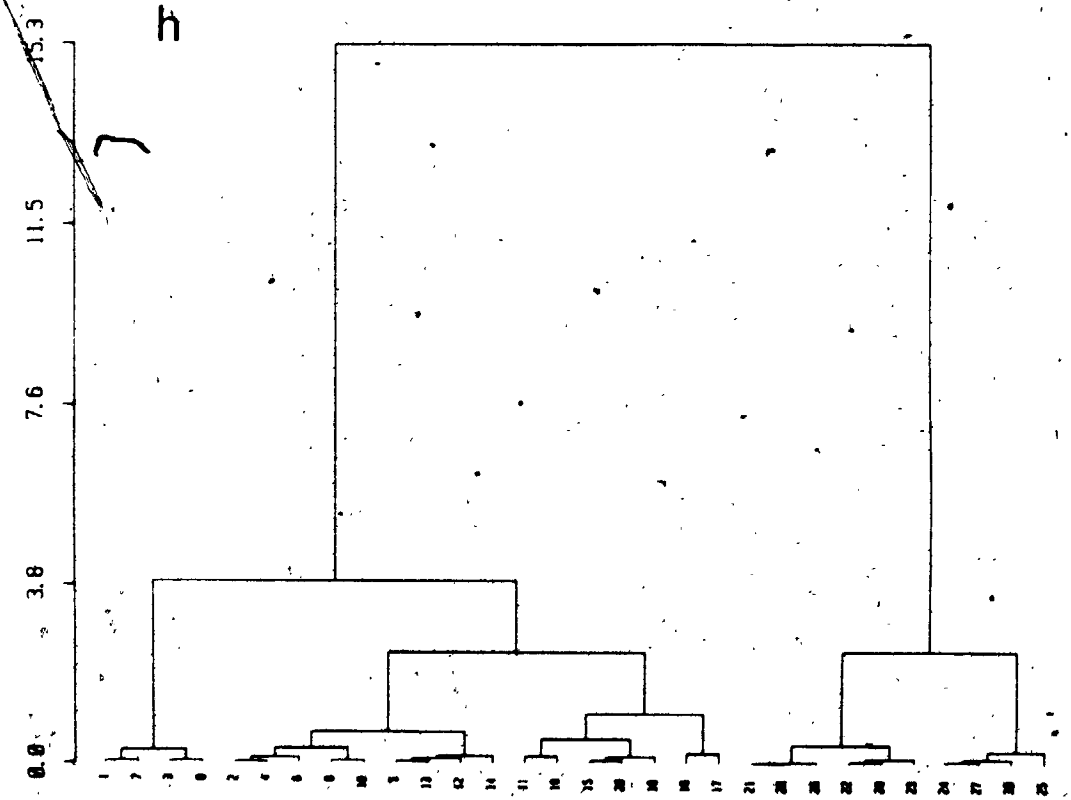

d
10.0
7.5
5.0
2.5
0.0

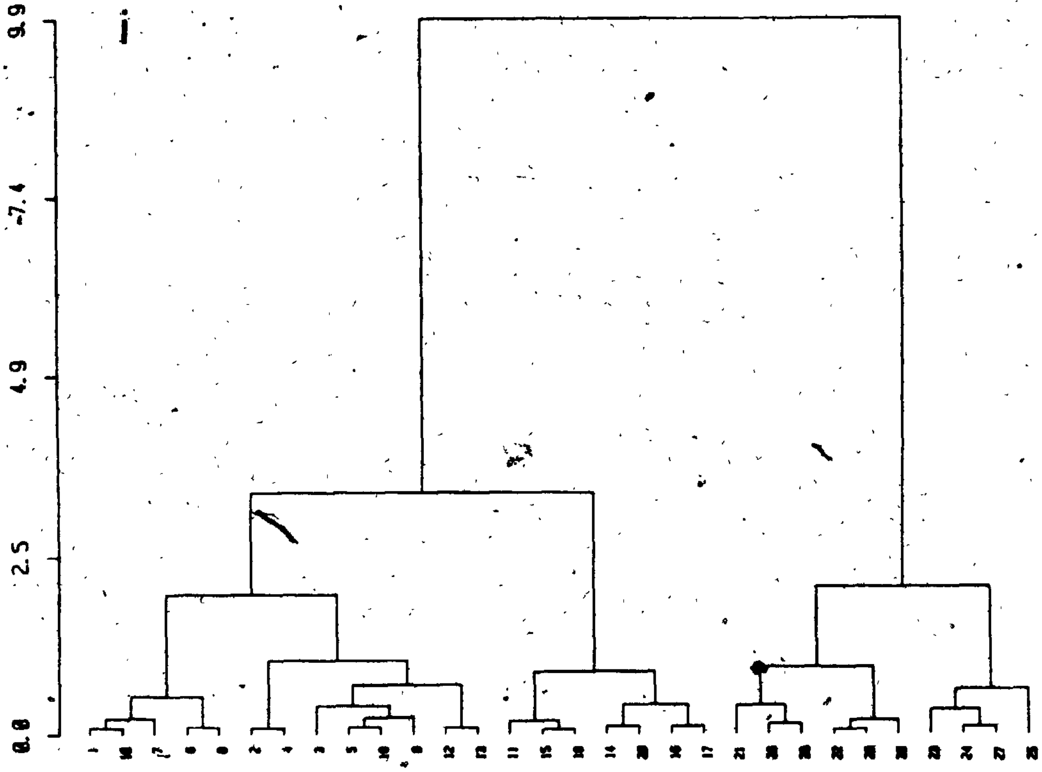

e
10.7
8.0
5.3
2.7
0.0
f
11.3
8.5
5.6
2.8
0.0

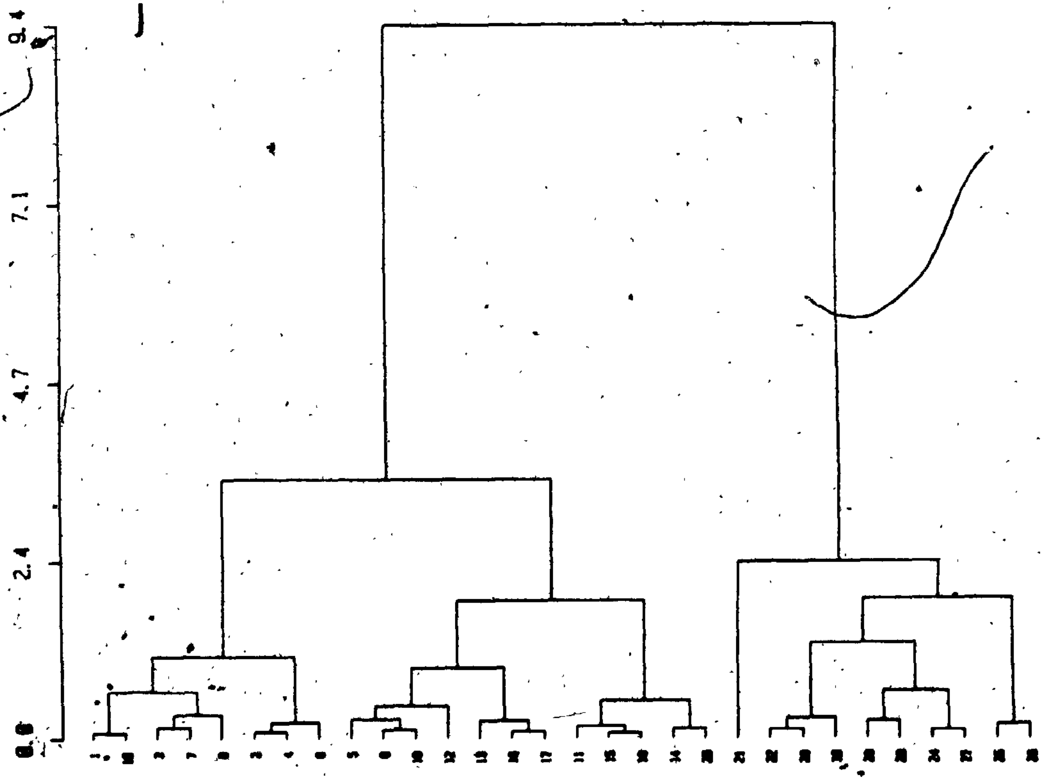
g

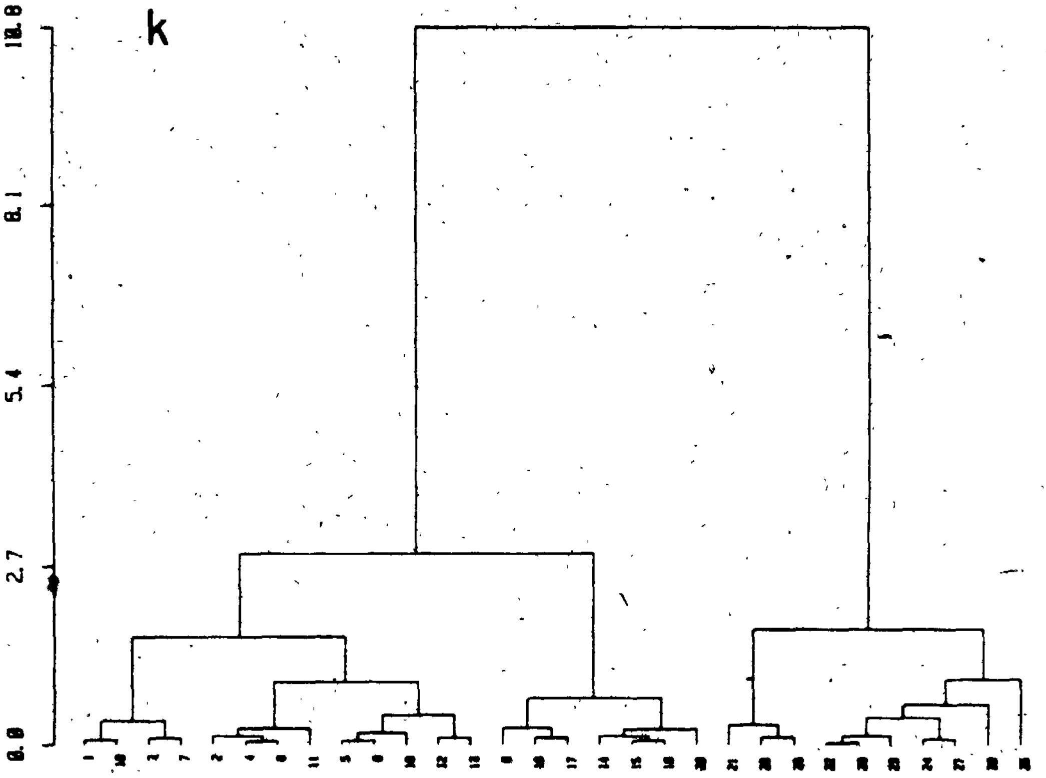


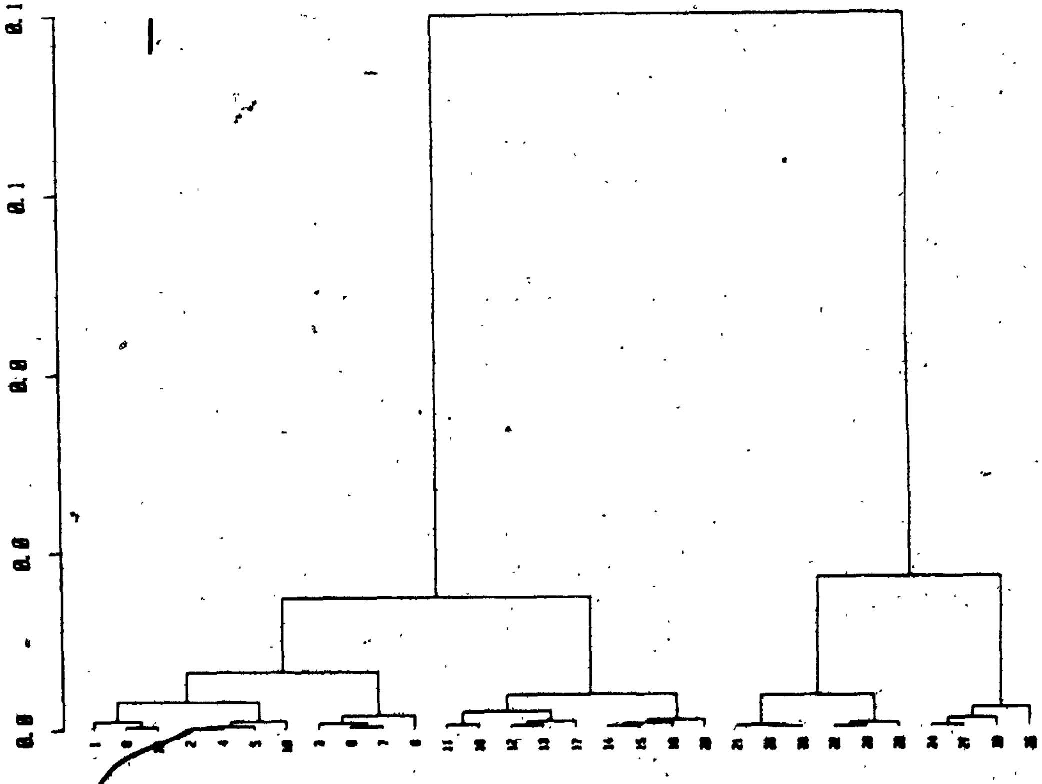
h

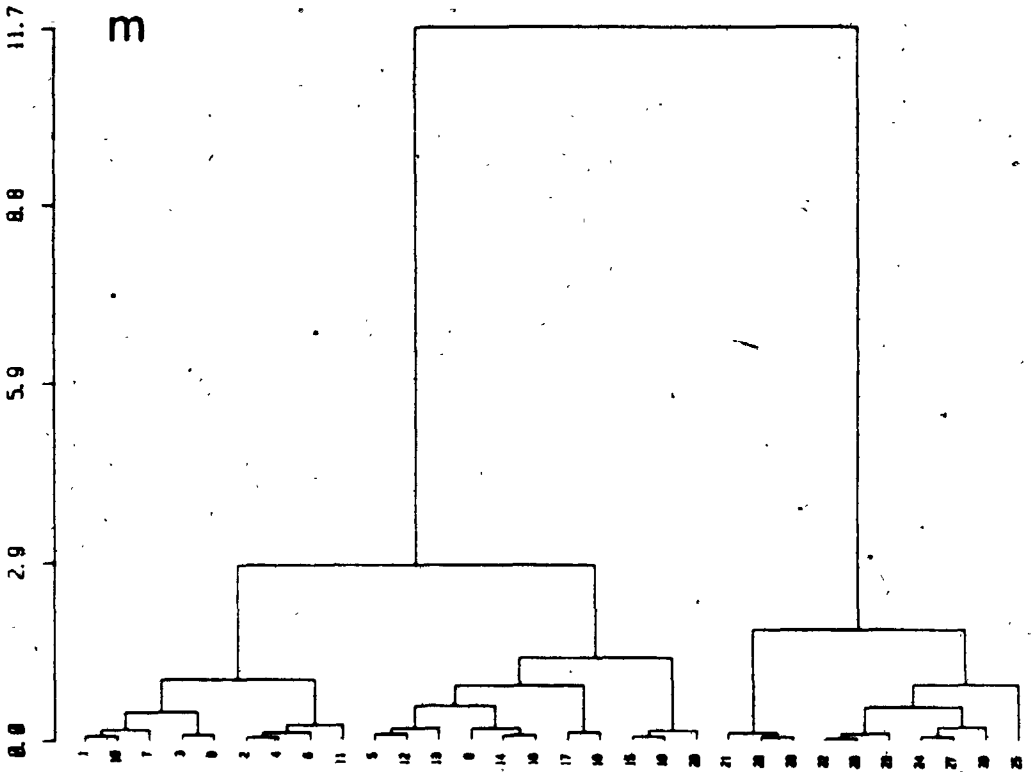



i
9.9
7.4
4.9
2.5
0.0


j
9.4
7.1
4.7
2.4
0.0


k
10.8
8.1
5.4
2.7
0.0


l
0.0


m
11.7
8.8
5.9
2.9
0.0

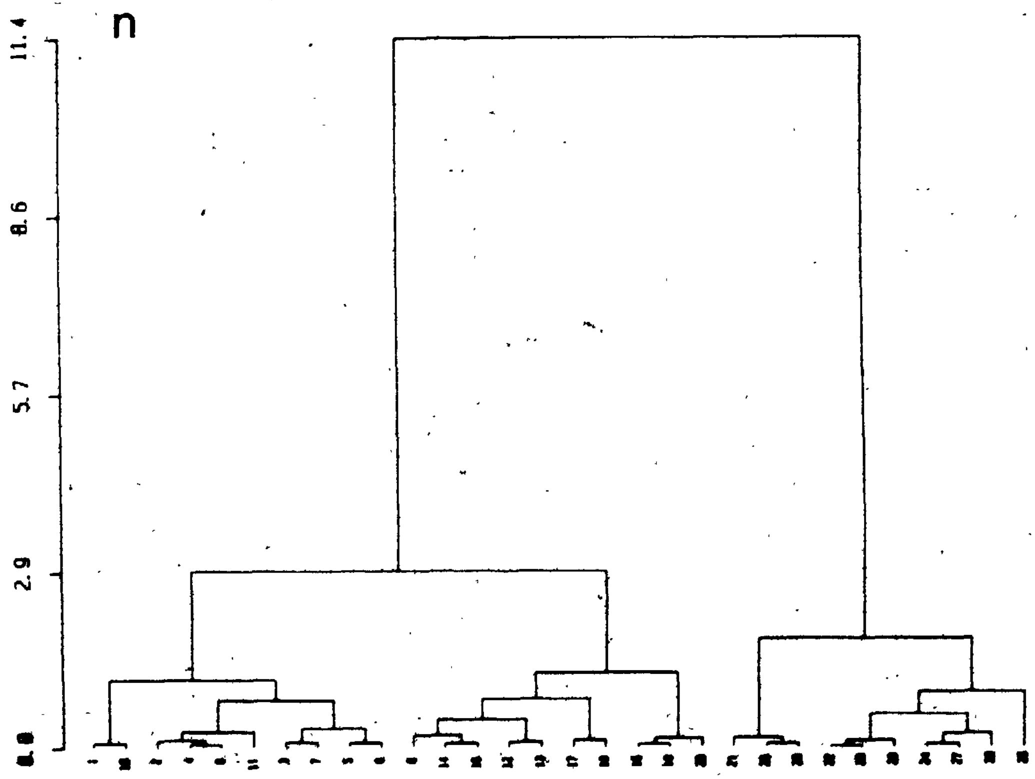
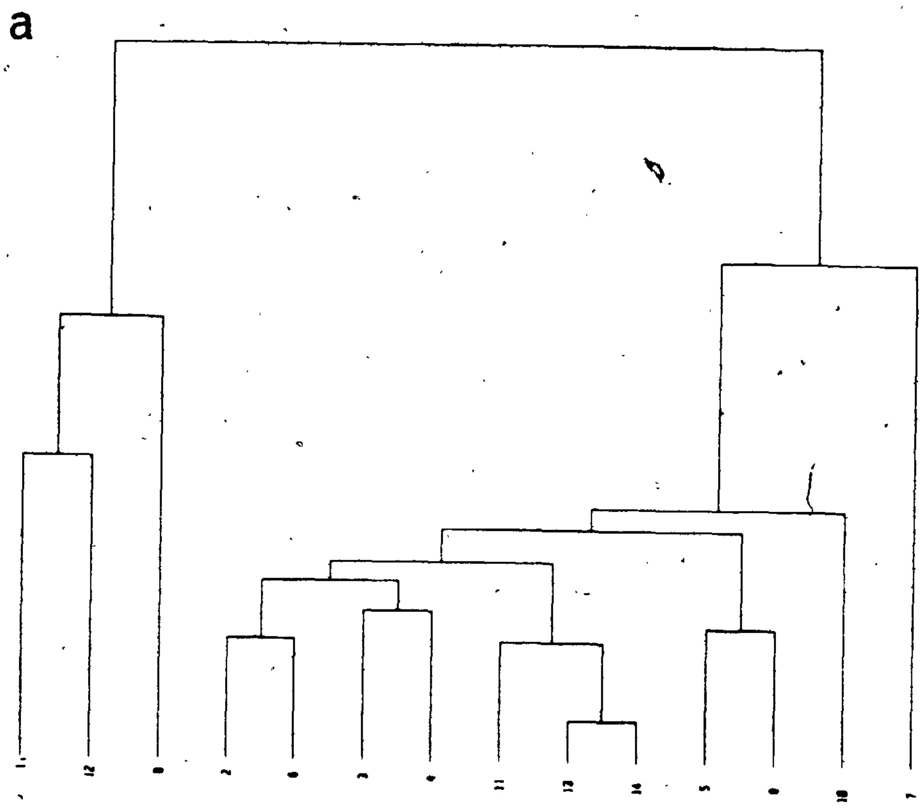

n
11.4
8.6
5.7
2.9
0.0

Fig. 3.33 Dendrograms resulting from simple average (a) and group average clustering (b) of the classifications resulting from various data types and transformations. Correlation coefficients between cophenetic matrices constituted the resemblance matrix. Vertical axis in each represents 1-compliment of correlation coefficient. Numbers at the bottom identify data types and transformations as outlined in the legend of Fig. 3.31.


a
1
12
8
2
9
3
4
11
13
14
5
6
10
7

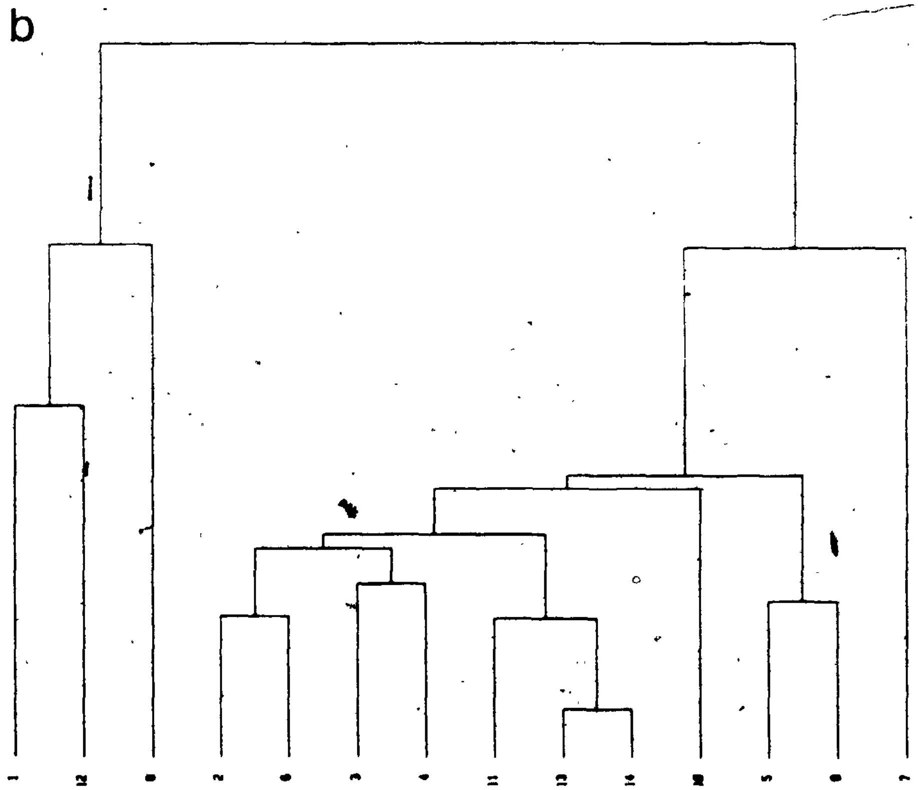

b
1
12
8
2
9
3
4
11
13
14
10
5
6
7

Fig. 3.34 The number of species retained at various ranking cut-off points (0.7 to 0.98) that represent the proporation of the total variance accounted for by the reduced subsets to the total variance in the complete data set. Sum of squares ranking of Orlóci (1973) was used.

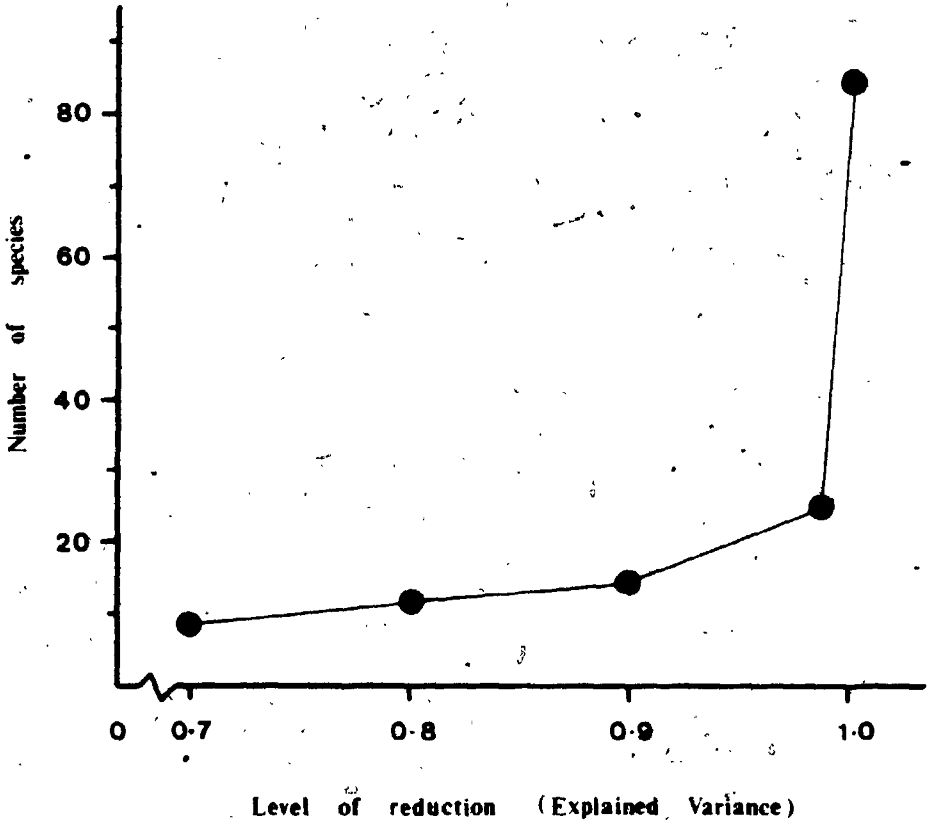
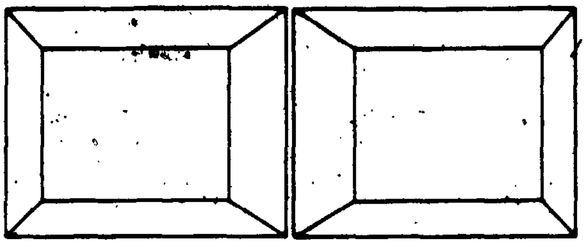
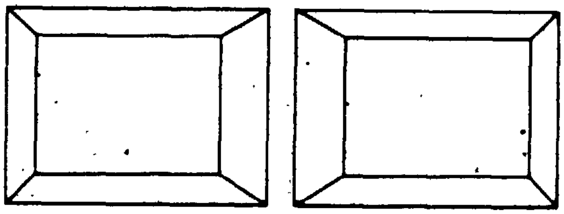
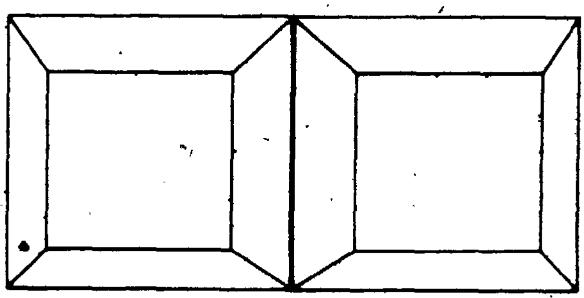
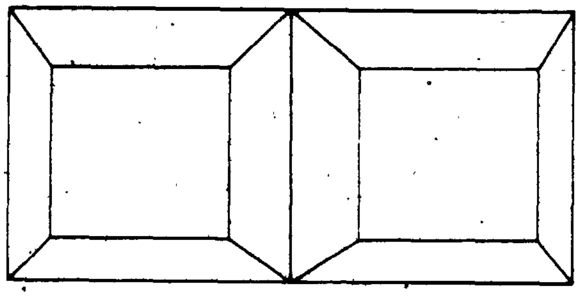

Number of species
80
60
40
20
0
0·7
0·8
0·9
1·0
Level of reduction (Explained Variance)

Fig. 3.35 Stereograms of PCA ordinations resulting from complete and reduced data sets (complete data set used was that obtained with 5*5 m plots in the pilot survey). Data reductions were achieved using Orlóci's sum of squares ranking. (a) Complete data, (b) reduced data at 0.98 E.V., (c) reduced data at 0.9 E.V., d) reduced data at 0.8 E.V., (e) reduced data at 0.7 E.V. (explained variance).


a


b


c


d

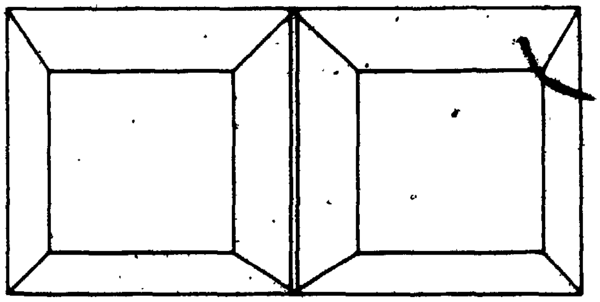

e

Fig. 3.36 Effect of data reduction (species) reduction on releve ordination. The levels of correlation coefficient between distances in releve ordination space of complete data set and those of reduced data sets. Data reduction was based on Orlóci's sum of squares ranking. Correlation coefficients were computed using releve distances in 2, 3, 4, 5 and 6 dimensions (components of PCA).

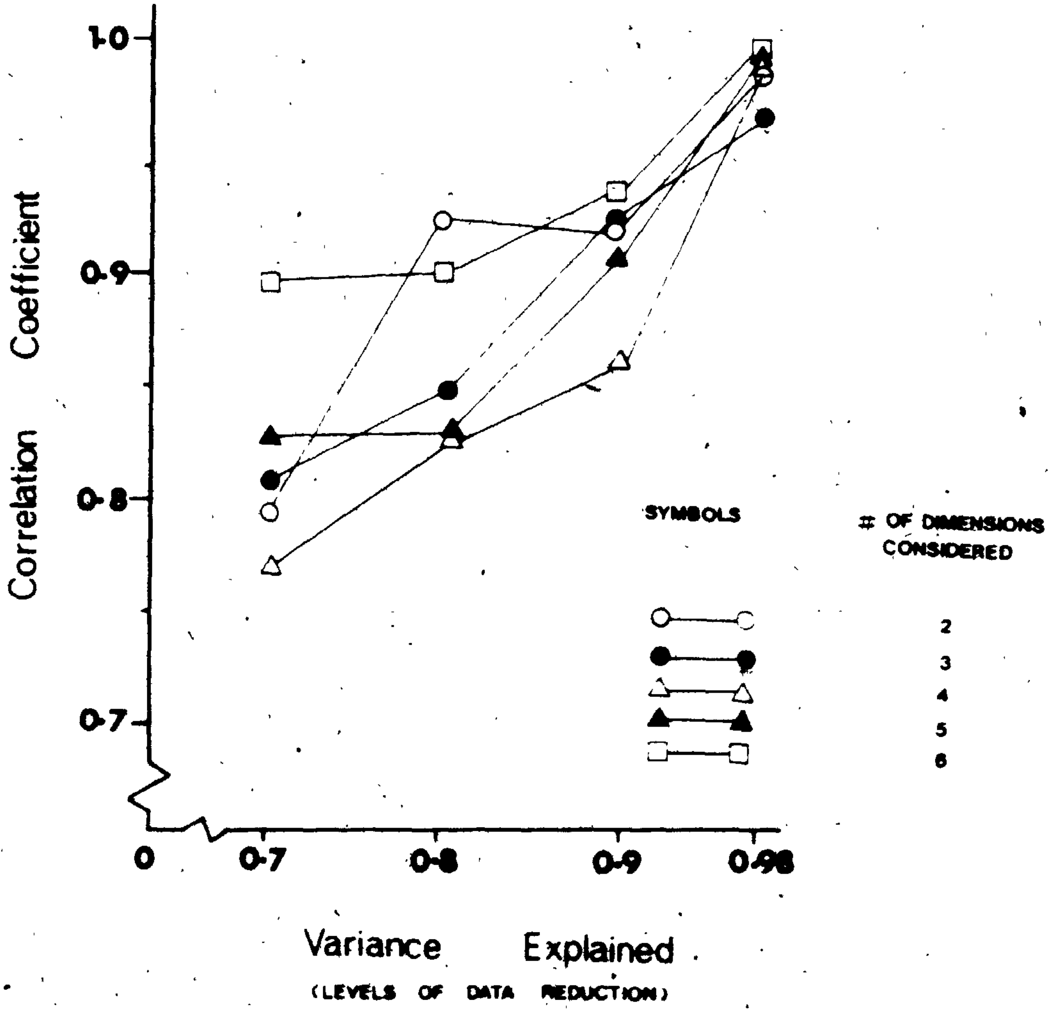

1·0
0·9
0·8
0·7
Correlation Coefficient
0
0·7
0·8
0·9
0·98
Variance Explained
(LEVELS OF DATA REDUCTION)
SYMBOLS
OF DIMENSIONS CONSIDERED
○—○ 2
●—● 3
△—△ 4
▲—▲ 5
□—□ 6

Fig. 3.37 Changes in species position on the first principal component of PCA species ordination with data reduction. Data reduction was accomplished by Orloci's sum of squares ranking. Numerals against the axes indicate the level of data reduction: 1, complete data; 2, reduced data at 0.98 E.V.; 3, reduced data at 0.9 E.V.; 4, reduced data at 0.8 E.V.; 5, reduced dat at 0.7 E.V. (explained variance). Key to species codes: As, Agrostis stolonifera; Dc, Daucus carota; Es, Erigeron strigosus; Ma, Melilotus alba; Pc, Poa compressa; Pp, Phleum pratense; Sc, Solidago canadensis; Tp, Trifolium pratense; Tr, Trifolium repens.

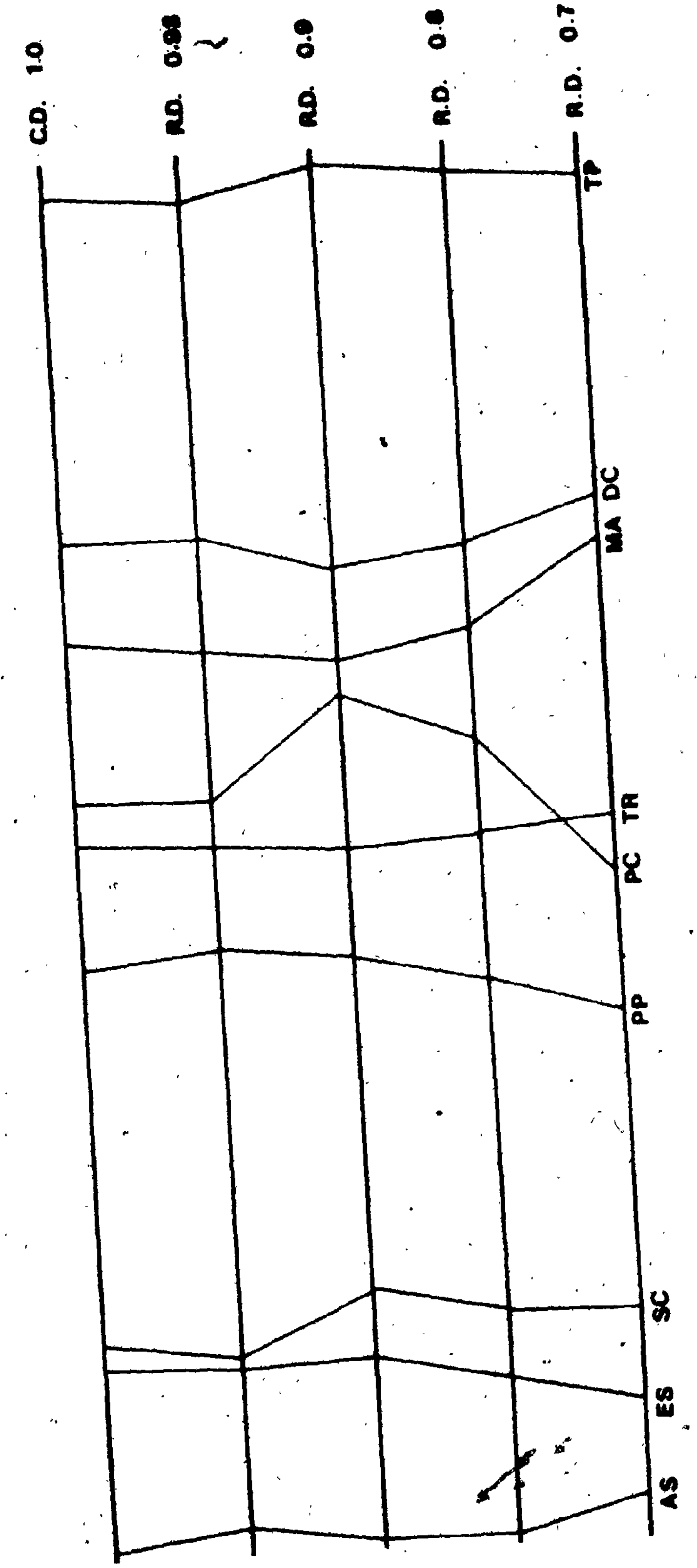

C.D. 1.0
R.D. 0.98
R.D. 0.9
R.D. 0.8
R.D. 0.7
TP
DC
MA
TR
PC
PP
SC
ES
AS

Fig. 3.38 Effect of data reduction (species reduction) on species ordination. The levels of correlation coefficient between distances in species ordination space of complete data set and those of reduced data sets. Data reduction was based on Orlóci's sum of squares ranking. Correlation coefficients were computed using species distances in 2, 3, 4, 5 and 6 dimensions (PCA components).

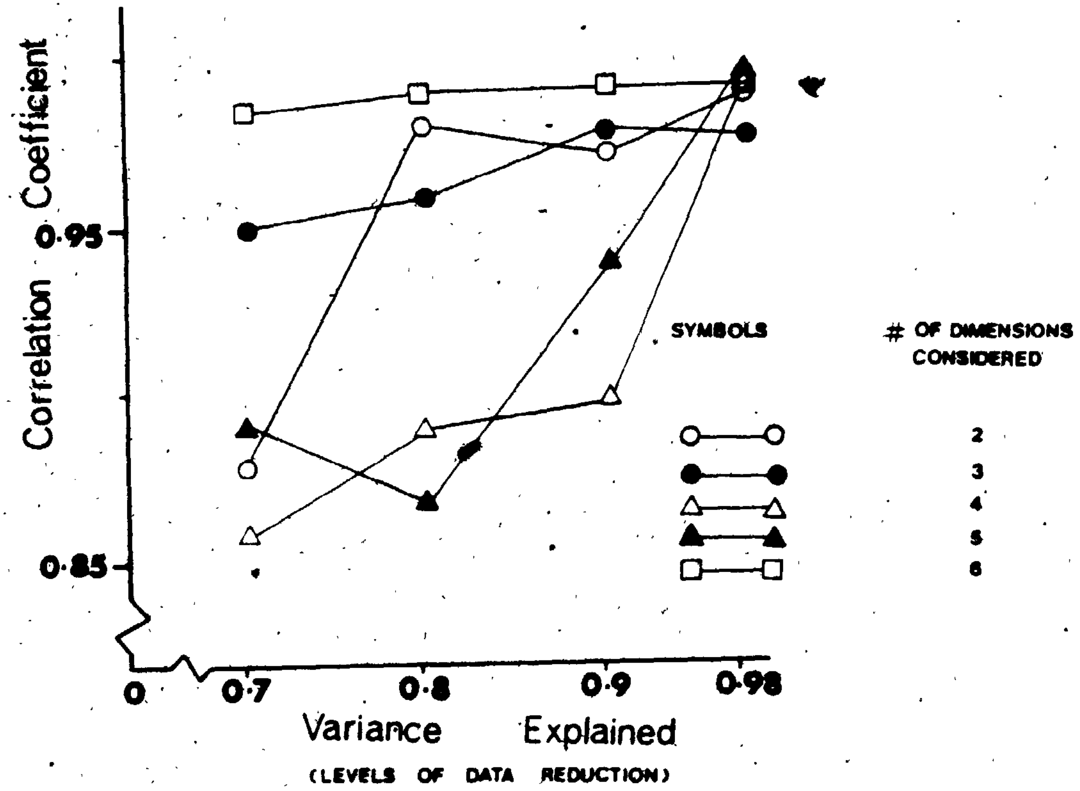

Correlation Coefficient
0·95
0·85
0
0·7
0·8
0·9
0·98
Variance Explained
(LEVELS OF DATA REDUCTION)
SYMBOLS
OF DIMENSIONS CONSIDERED
○—○ 2
●—● 3
△—△ 4
▲—▲ 5
□—□ 6

Fig. 3.39 The number of species retained at various ranking cut-off points; (a) based on within species sum of squares ranking, and (b) based on equivocation information ranking. The data set used for species reduction was that obtained with 2.5*2.5 m plots in the pilot survey. Cut-off points for the ranking in (a) represent the within species sum of squares of the species standing above the ranking cut-off point to the total within species sum of squares. In (b) the cut-off points represent the proporation of equivocation information of the species standing above the cut-off point to the total equivocation information in all the species.

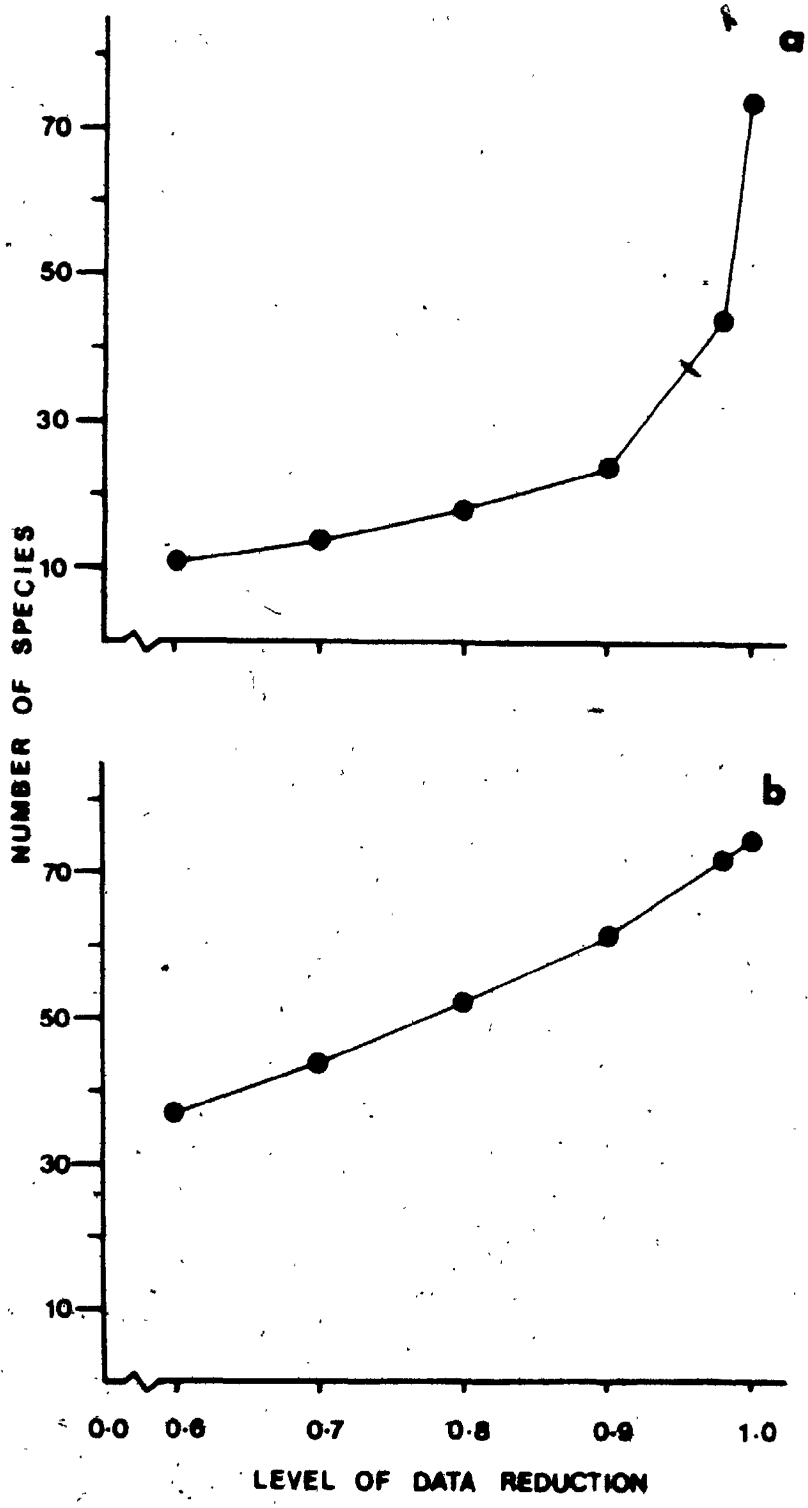
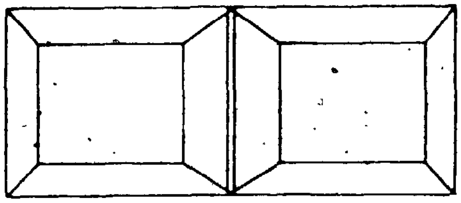
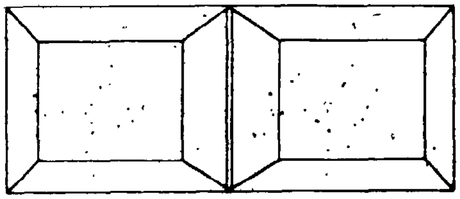

a
b
NUMBER OF SPECIES
10
30
50
70
0·0
0·6
0·7
0·8
0·9
1·0
LEVEL OF DATA REDUCTION

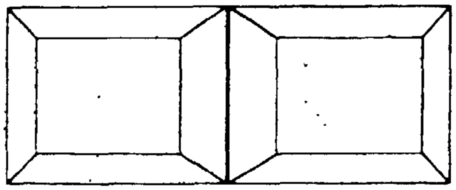
Fig. 3.40 Stereograms representing 3-dimensional MDSCAL ordinations based on complete and reduced data sets obtained at various ranking cut-off points using within species sum of squares ranking. The data set used for species reduction was that obtained with 2.5*2.5 m plots in the pilot survey. a, complete data; b-f reduced data sets at various cut-off levels; b, 0.98 E.V.; c, 0.9 E.V., d, 0.8 E.V.; e, 0.7 E.V.; f, 0.6 E.V. (explained within species variation, i.e., within species sum of squares of the species standing above the cut-off point to the total within species sum of squares.)



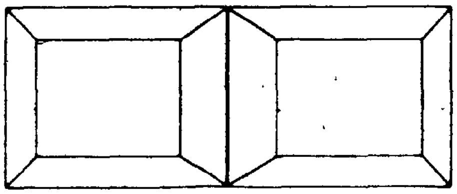
a



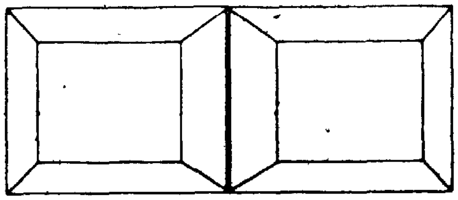
b



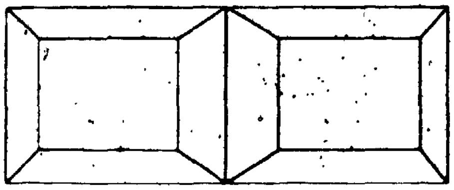
c



d



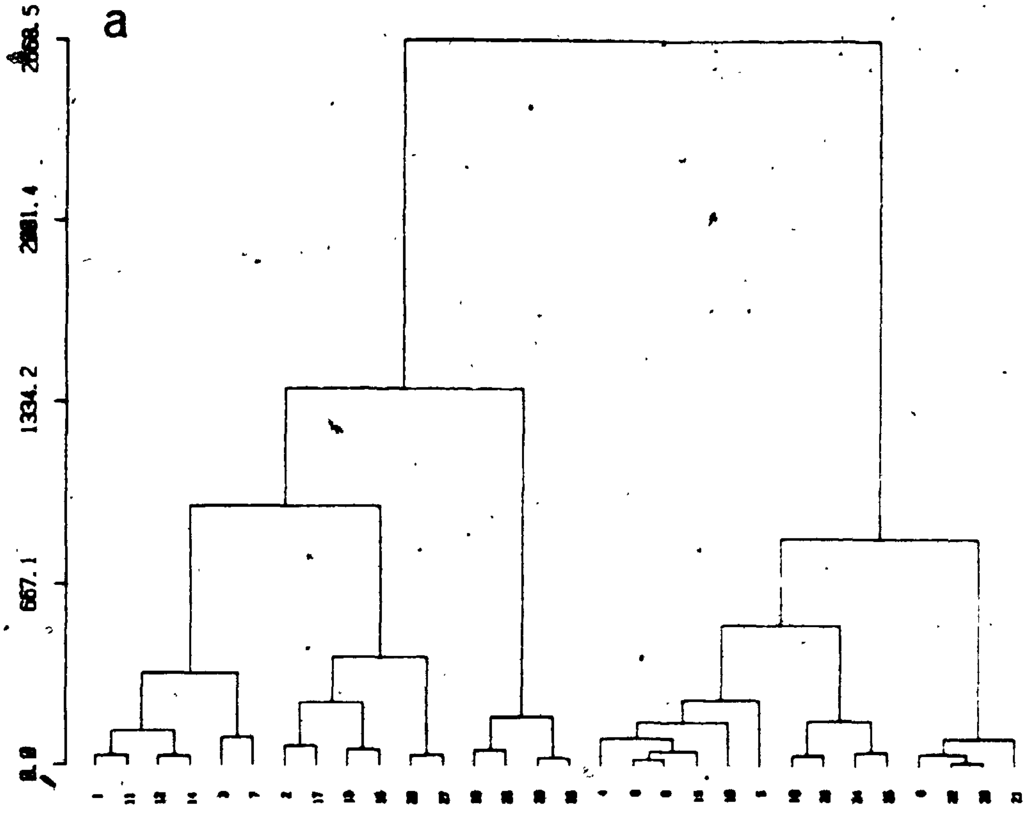
e

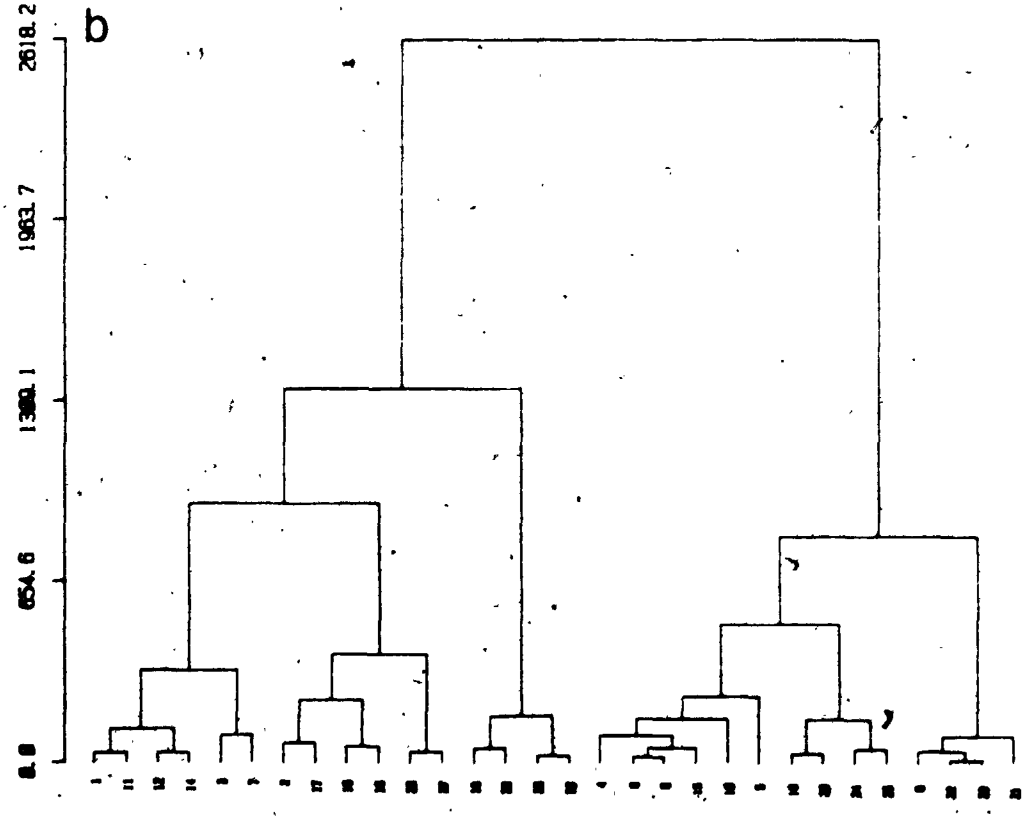


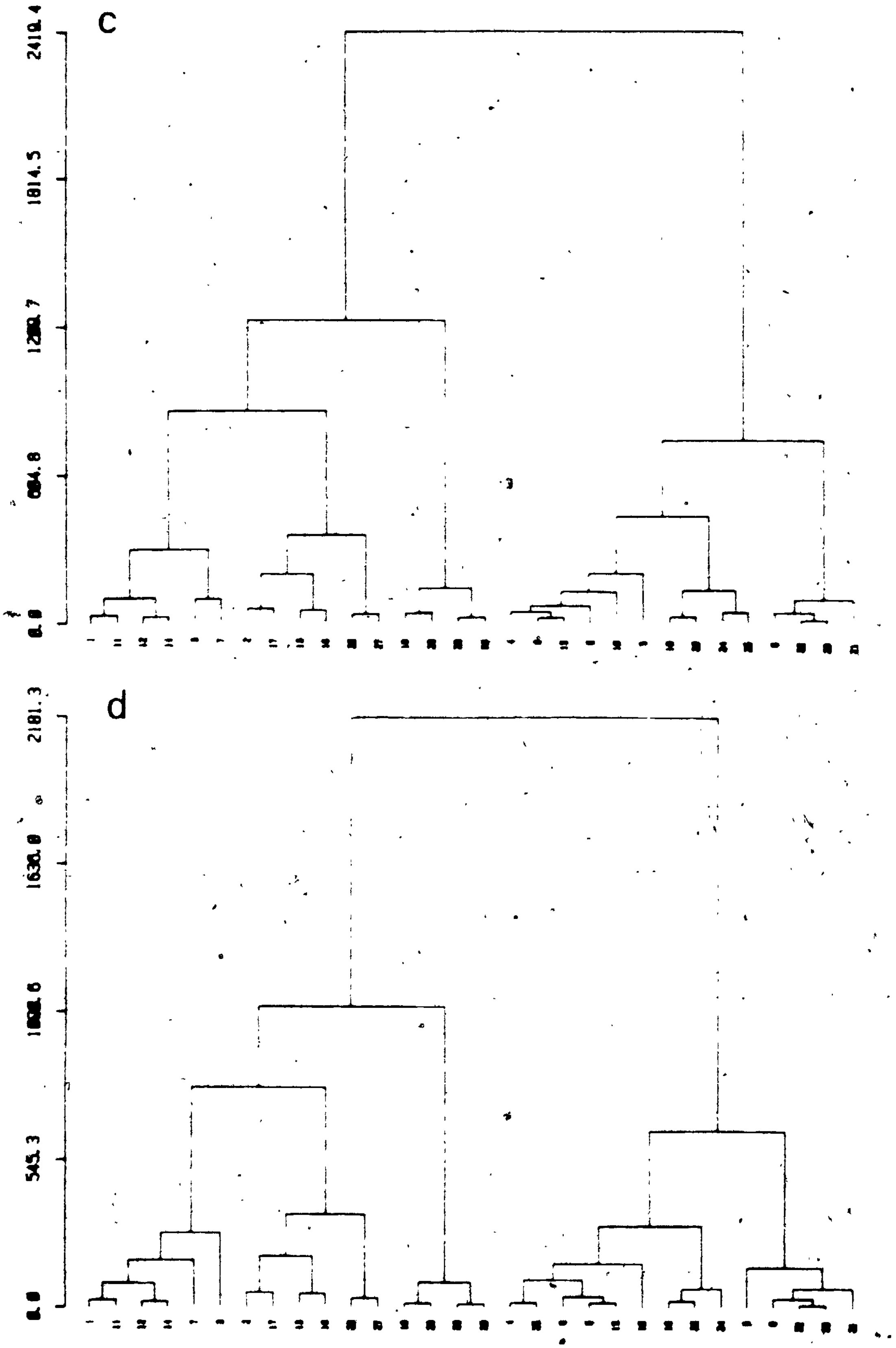
f

Fig. 3.41 Stereograms representing 3-dimensional MDSCAL ordinations based on complete and reduced data sets obtained at various ranking cut-off points usng equivocation information ranking. a, complete data set; b-f data sets with reduced number of species obtained at successive cut-off points: b, 0.98; c, 0.9; d, 0.8; e, 0.7; f, 0.6. Cut-off points represent the proportion of equivocation information in the reduced subset to that in the complete set.

Fig. 3.42 Dendrograms resulting from SSA clustering of complete and reduced data sets at various ranking cut-off points. Data reduction was accomplished by within species sum of squares ranking. a, dendrogram based on complete data set; b-f, dendrograms based on reduced data sets; b, 0.98; c, 0.9, d, 0.8, e, 0.7; f, 0.6 E.V. Refer to the legend of Fig. 3.40 for the explanation of cut-off points. Vertical axis in each dendrogram represents sum of squares while numbers at the bottom identify relevés.


a
2668.5
2001.4
1334.2
667.1
0.0


b
2618.2
1963.7
1309.1
654.6
0.0


c
2419.4
1814.5
1209.7
604.8
0.0
d
2181.3
1636.0
1090.6
545.3
0.0


e
1928.3
1446.2
964.1
482.1
0.0
f
1681.2
1260.9
840.6
420.3
0.0

Fig. 3.43 Degree of similarity (correlation coefficient) and disagreement ($\overset{*}{\Delta}_u(D_1,D_2)$) between the cophenetic matrices (a) and the topology matrices (b) of complete data set with those of reduced data sets obtained at various ranking cut-off points based on within species sum of squares ranking.

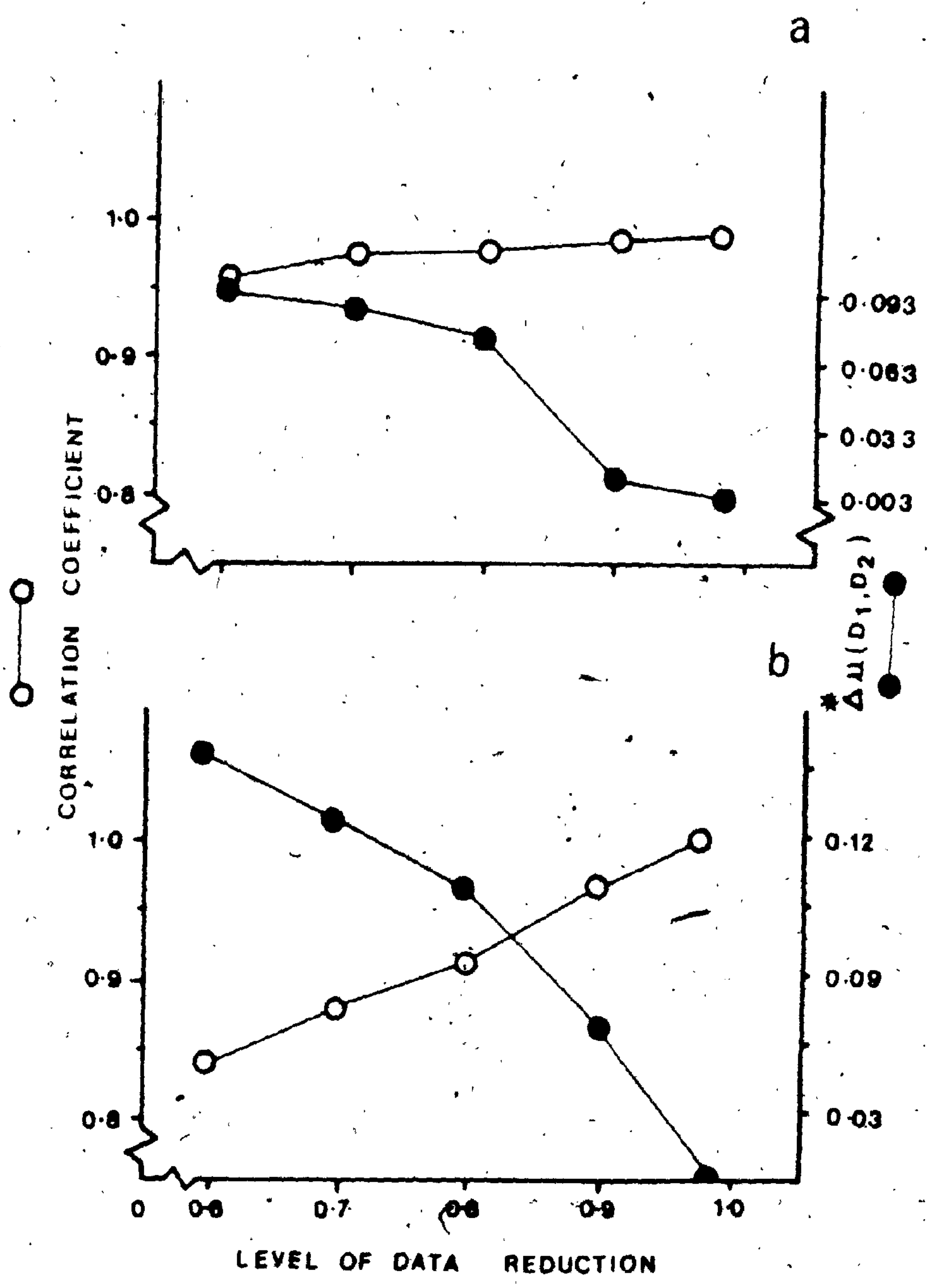
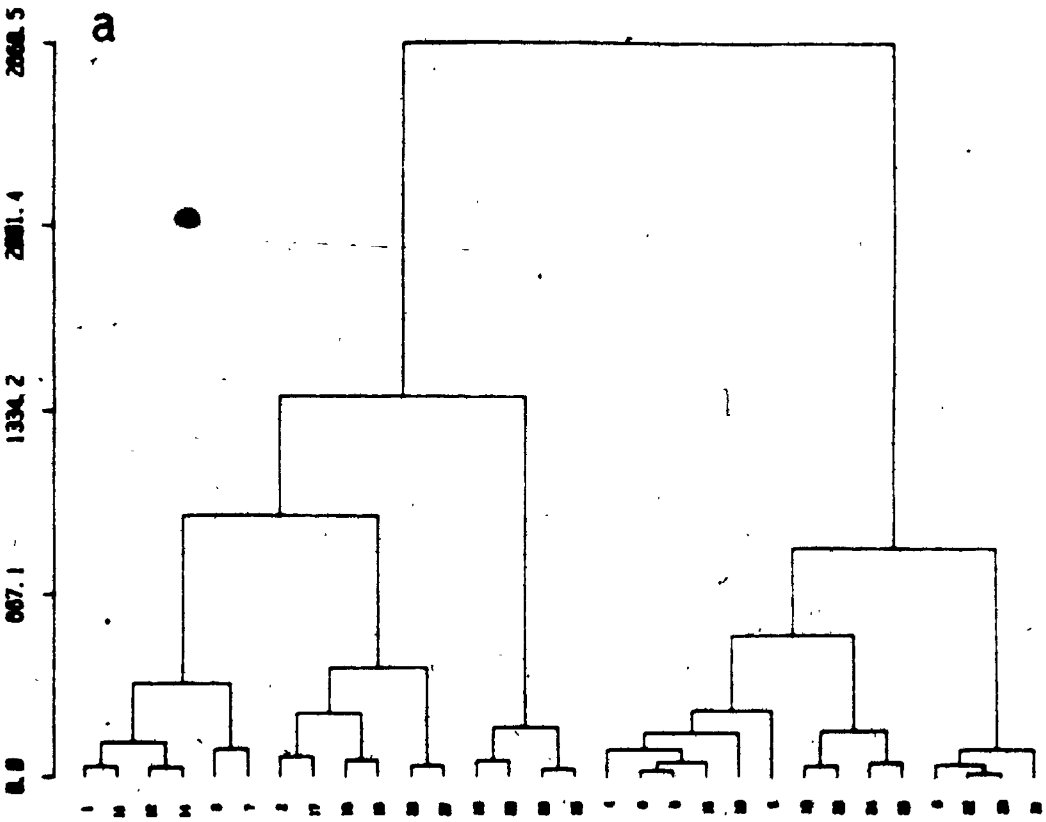
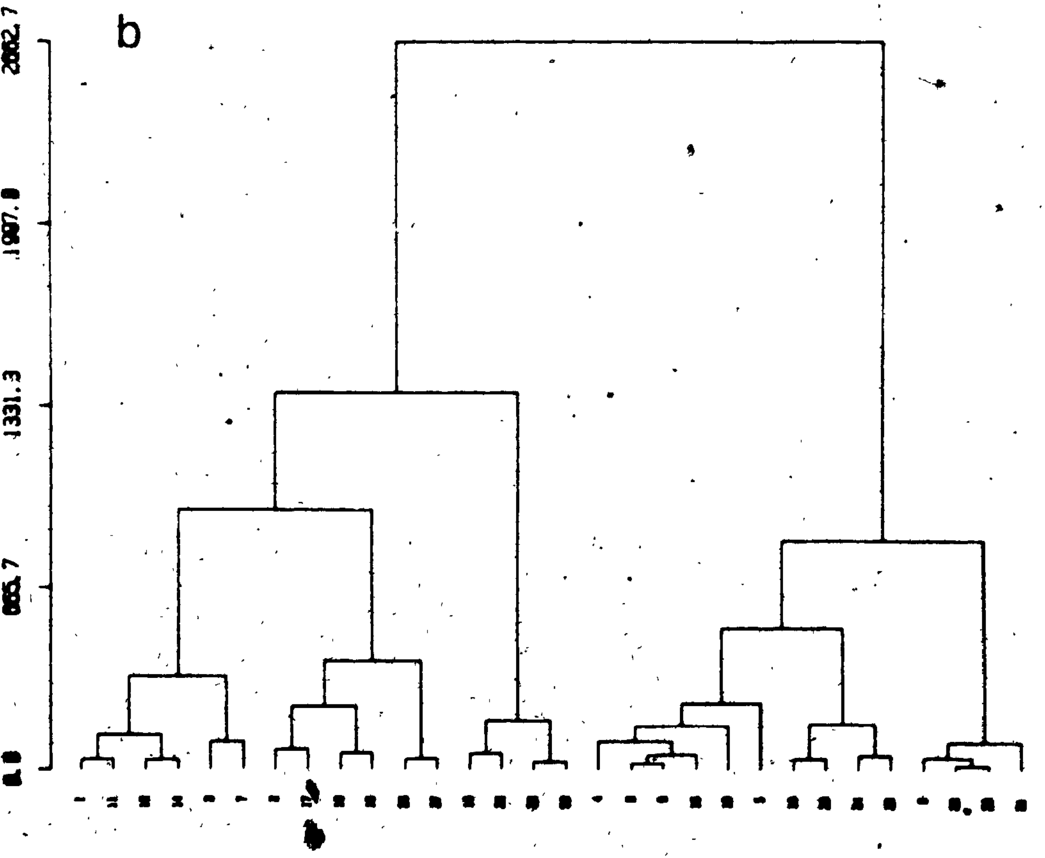
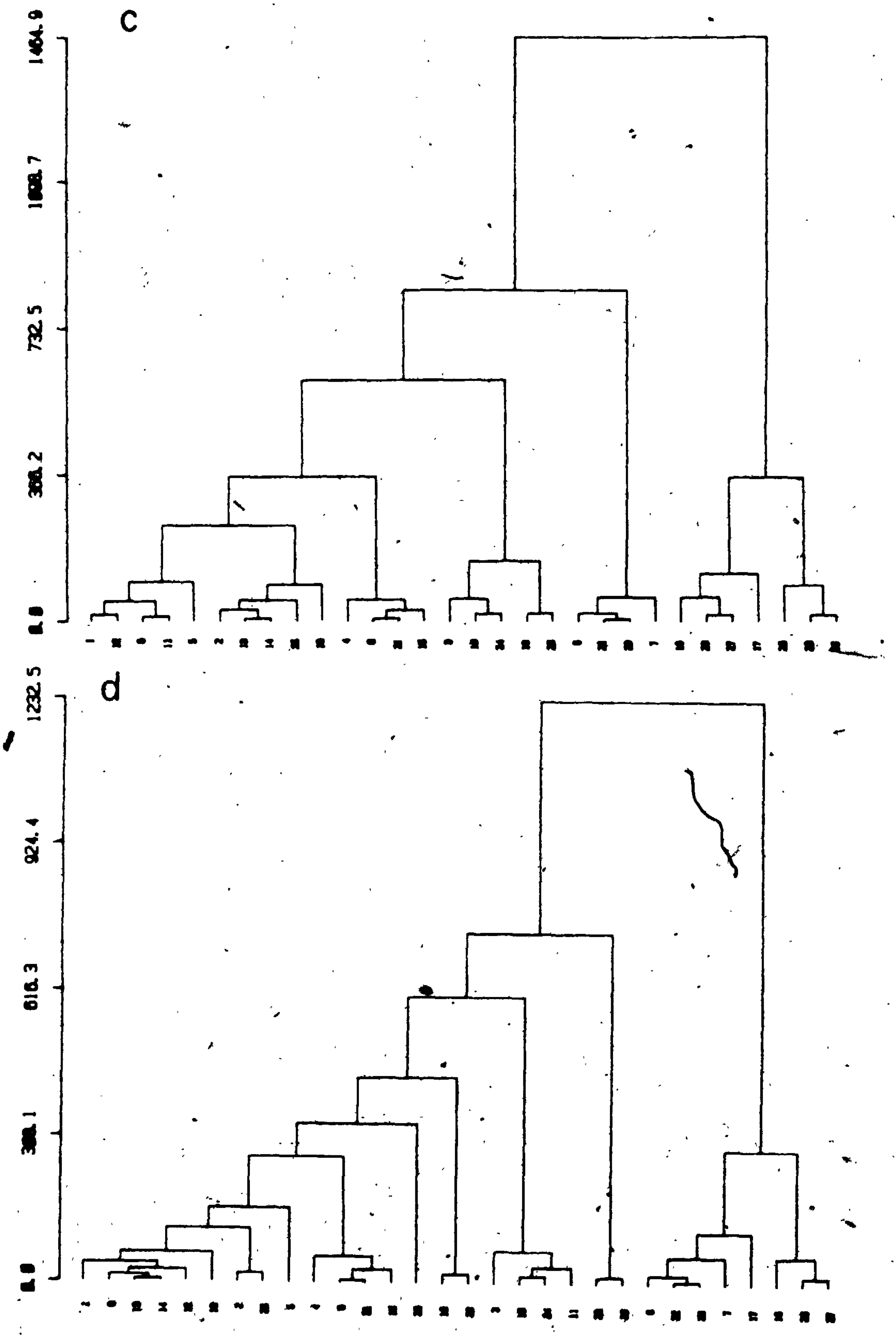
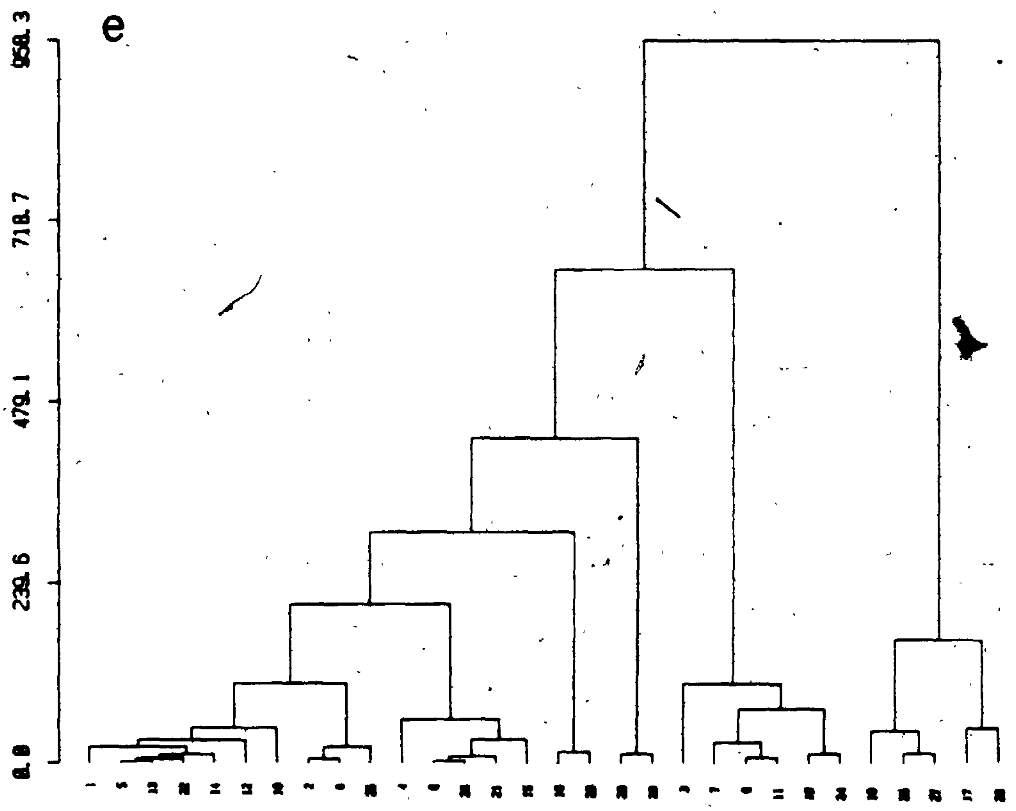

a
1·0
0·9
0·8
0·093
0·063
0·033
0·003
CORRELATION COEFFICIENT
$\Delta\mu(D_1, D_2)^*$
b
1·0
0·9
0·8
0·12
0·09
0·03
0
0·6
0·7
0·8
0·9
1·0
LEVEL OF DATA REDUCTION

Fig. 3.44 Dendrograms resulting from SSA clustering of complete and reduced data sets at various ranking cut-off points. Data reduction was accomplished by the equivocation information ranking. a, dendrogram based on complete data set; b-f, dendrograms based on reduced number of species at various cut-off points: b, 0.98; c, 0.9; d, 0.8, e, 0.7, f, 0.6. Refer to the legend of Fig. 3.41 for the explanation of cut-off points. Vertical axis in each dendrogram represents sum of squares while numbers at the bottom identify relevés.


a
2668.5
2001.4
1334.2
667.1
0.0


b
2662.7
1997.0
1331.3
665.7
0.0


c
1464.9
1098.7
732.5
366.2
0.0
d
1232.5
924.4
616.3
308.1
0.0


e
958.3
718.7
479.1
239.6
0.0

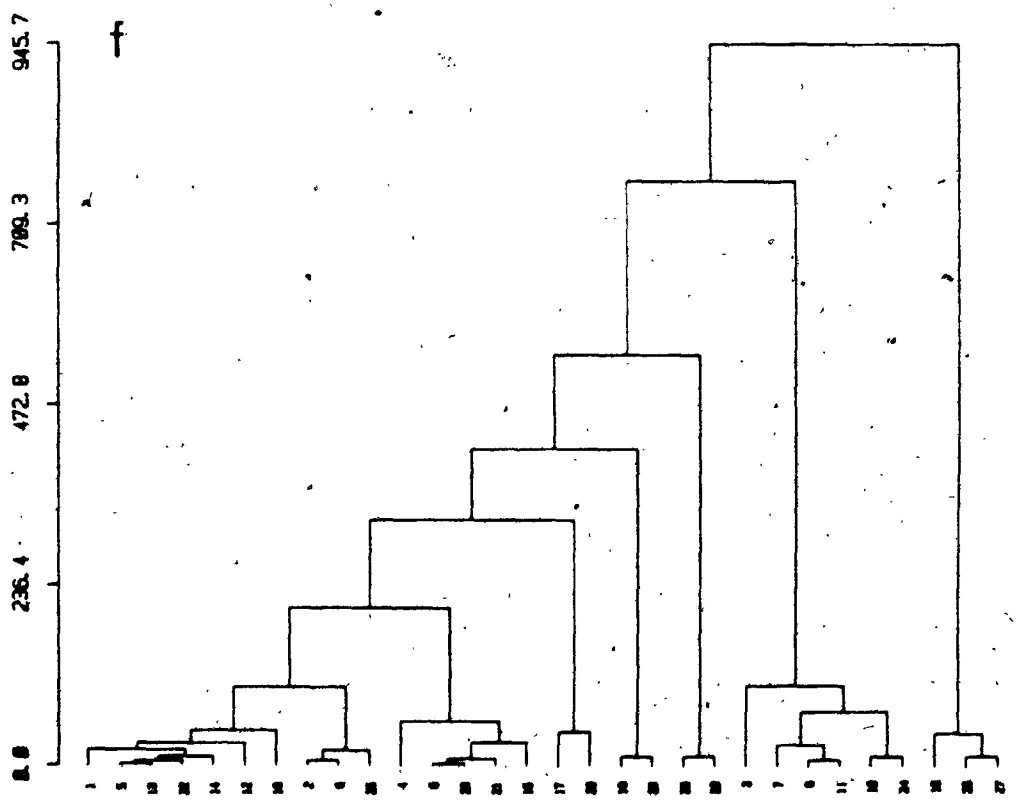

f
945.7
709.3
472.8
236.4
0.0

Fig. 3.45 Degrees of similarity (correlation coefficient and disagreement (${}^{*}_{u}(D_1, D_2)$)) between the cophenetic matrices (a) and the topology matrices (b) of complete data set with those of reduced data sets obtained at various ranking cut-off points based on equivocation information ranking.

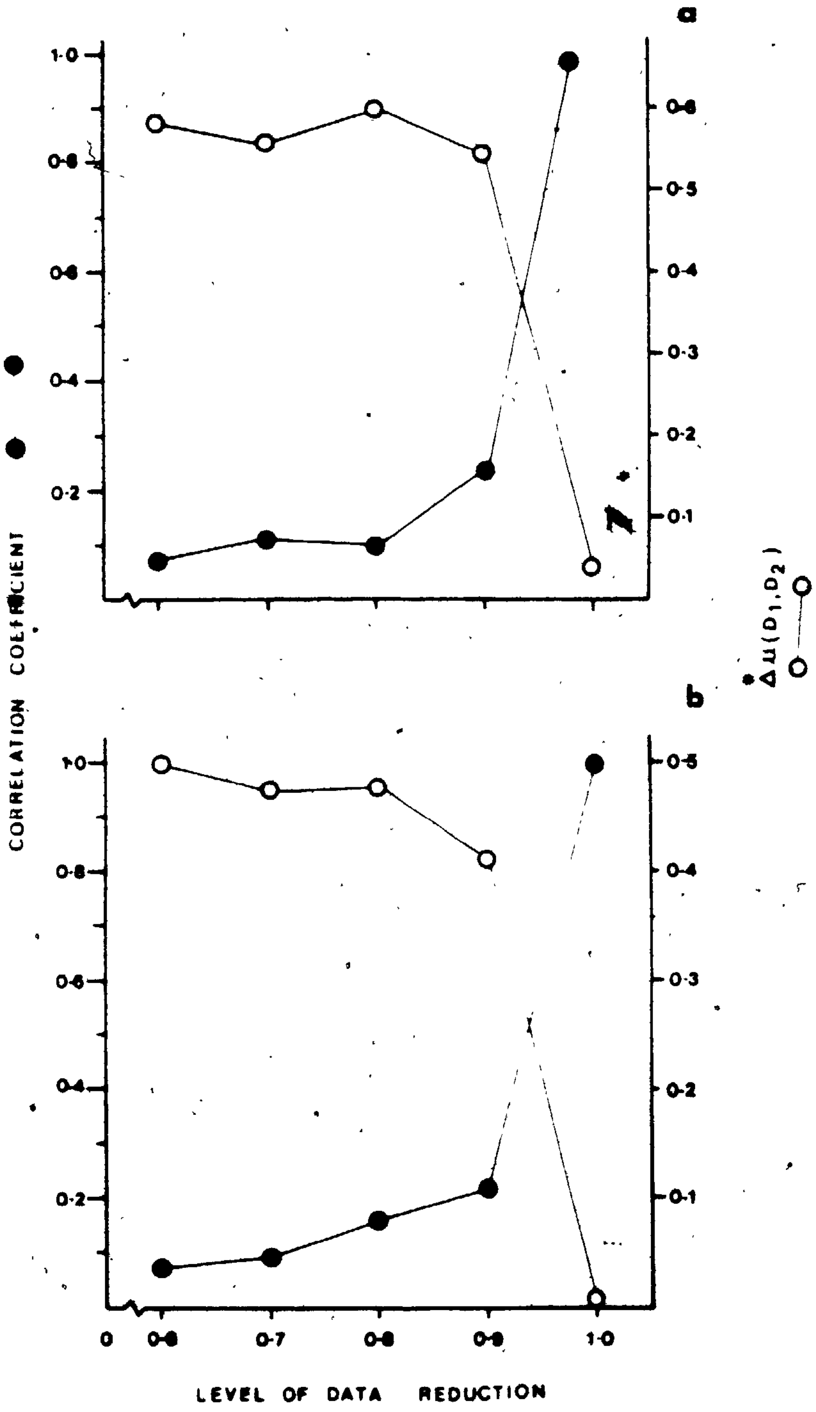
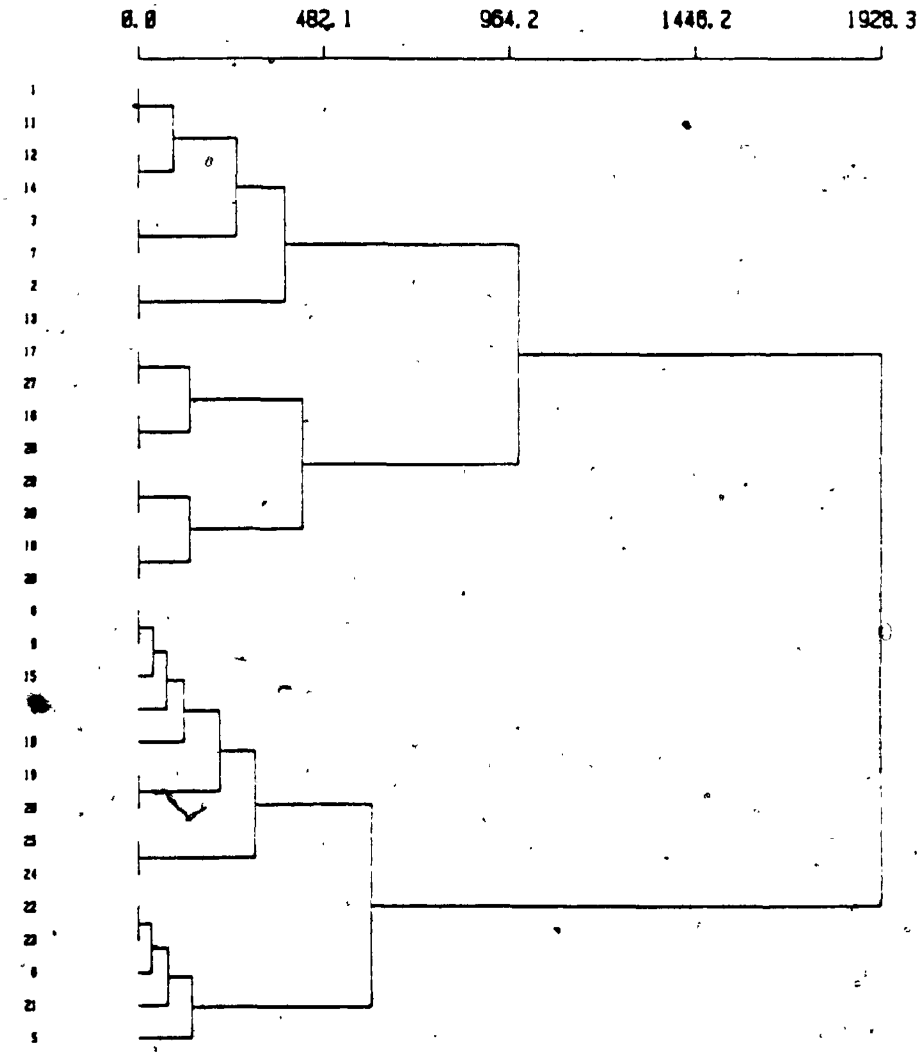

a
b
CORRELATION COEFFICIENT ●
Δμ(D1,D2) ○—○
1·0
0·8
0·6
0·4
0·2
0·6
0·5
0·4
0·3
0·2
0·1
1·0
0·8
0·6
0·4
0·2
0·5
0·4
0·3
0·2
0·1
0
0·6
0·7
0·8
0·9
1·0
LEVEL OF DATA REDUCTION

Fig. 3.46 Dendrograms derived from the iterative clustering. The iterative clustering algorithm uses SSA and within species sum of squares ranking (details in Section 3.3.4.1). Data set obtained with 2.5*2.5 m plot size in the pilot survey was used. Vertical axis represents sum of squares. Numbers at the bottom identify relevés.


0.0
482.1
964.2
1446.2
1928.3
1
11
12
14
3
7
2
13
17
27
16
10
6
9
15
10
19
25
24
22
8
21
5

APPROACHES TO THE ANALYSIS OF RUDERAL WEED VEGETATION

by

Syed Shahid Shaukat

Department of Plant Sciences

Submitted in partial fulfillment
of the requirements for the degree of
Doctor of Philosophy

Faculty of Graduate Studies
The University of Western Ontario
London, Ontario
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VOLUME TWO

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(Volume 2)

CHAPTER 4

RESULTS AND DISCUSSION OF MAIN STUDY

4.1 General

This chapter presents a comprehensive analysis of the vegetation and environment of the three main strata or habitats (with respect to nature of perturbance) viz., old fields, vacant lots and topsoil mounds. In order to maintain the continuity of description and to facilitate interpretation, the three strata are treated separately in the succeeding sections. The quantitative description of the vegetation of each habitat (stratum) begins with an account of species composition of vegetational cover, followed by delineation of vegetational groups (types) and enumeration of their ecological characteristics. Gradients and trends are then examined through ordination approach. The ecological relationships among the constituent species are evaluated through species classification and species ordination. The successional trends in the vegetation are assessed next, with particular regard to life-form and life-span characteristics of species constituting the vegetation. Finally, diversity patterns in relation to succession are described.

Data analysis employed the use of both classification and ordination strategies as the two approaches are often complementary to one another. Objective classification was used with a view to (a) delimit the major vegetation 'types', and (b) to disclose the underlying relationships between vegetation and environmental and temporal factors. Conversely, ordinations were performed to (a) unravel the environmental and temporal gradients (coenoclines) and (b) to examine the relative continuity/discontinuity of vegetation.

Numerical classification of the data sets was performed by the following agglomerative strategies: simple average, group average, sum of squares and iterative clustering. However, the results derived from simple average and group average clustering were comparatively less interpretable than those obtained with sum of squares and iterative clustering strategies and are not presented. Iterative clustering was used only for releve classification; it is not meaningful in the context of species classification. The "standardized Euclidean distance", called chord distance was used as a resemblance function for sum of squares and iterative clustering. Chord distance has a number of virtues. It has a fixed upper bound, it minimizes differences due to site productivity and emphasizes qualitative differences (Orloci, 1967; Noy-Meir et al., 1975).

The ordination method employed was Kruskal's non-metric multidimensional scaling (MDSCAL). Again chord distance was used for releve as well as species ordinations. Chord distance has been advocated as a good summarizer for inherent nonlinearity in data structure (Orloci, 1980; Orloci et al., 1984). For one data set (viz. topsoil mounds), PCA and RO were also performed but their results being inferior to those of MDSCAL with regard to interpretability are not presented. However, PCA of the environmental data sets were performed after normalizing the variables. The component scores derived from PCA of environmental data sets were used in the interpretation of MDSCAL vegetational ordinations.

The vegetational groups based on the time since the occurrence of major perturbance were related to life-forms or life-span characteristics of the groups with the aid of analysis of concentration (AOC). This technique has been shown to be an effective trend seeking method in structured tables (Feoli and Orloci, 1979; Gerdol and Piccoli, 1982; Lausi and Nimis, 1985).

Data analysis was accomplished through a variety of programs and program packages on the Decsystem-10 at UWO (Appendix C).

4.2 Analysis of old field vegetation

4.2.1 Vegetation

The vegetational cover in old fields, in general, was high (95%). The average percentage cover was slightly higher in the older fields, 101.6% in > 10 year old fields compared to 94.75% in 2 year old field.

A total number of 139 vascular species were recorded (Appendix D). Table 4.1 presents eighty-six species that occurred in at least three releves along with their average percentage cover, its variance, and the origin (native or introduced). The vegetation was mostly dominated by perennial grasses, including *Poa pratensis*, *Phleum pratense*, *Agrostis stolonifera*, *Agropyron repens* and *Poa compressa*. *Arrhenatherum elatius* was one of the dominant species at one site and *Phalaris arundinacea* was abundant at two sites. Besides grasses, the other dominant species were dicots, including *Solidago canadensis*, *Daucus carota*, *Trifolium pratense*, *Medicago lupulina*, *Hypericum perforatum*, *Erigeron strigosus* and *Aster simplex*. *Fragaria virginiana*, *Festuca rubra*, *Lactuca serriiola*, *Nepeta cataria* and *Leonorus cardiaca* were prominent to a greater or lesser extent in some releves.

Of the total number of 139 species recorded from old fields, 86 (=61.87%) were introducted 52 (=37.41%) were native, and one native or introduced (=0.71%).

4.2.2 Classification of releves

The dendrograms resulting from sum of squares agglomeration (SSA) and iterative clustering are depicted in Fig. 4.1a,b. Three main ecologically meaningful groups or 'types' could be recognized in the dendrogram resulting from iterative clustering, giving a classification efficiency of 30.1% (Fig. 4.1b). The resulting dendrogram from sum of squares clustering was essentially similar to that of iterative clustering but a few releves were better placed in iterative clustering. Since the latter is more effective than the former in the elucidation of 'types' the groups derived from it (iterative clustering) will be treated in detail. The vegetational characteristics of the groups (types) and the subgroups (subtypes) are summarized in Table 4.2 which gives the dominant or major species along with their average percentage cover and its variance. The term "dominant" as used here implies those species that contribute a high proportion of the total vegetational cover. The environmental characteristics associated with the types are outlined in Table 4.3. The description of the types follows:

Type 1: This type comprised 25 releves which mostly came from 4 year old fields. The type is characteristically dominated by _Solidago canadensis_, _Nepeta cataria_ and _Leonorus cardiaca_ which are herbaceous perennial forbs. _Lactuca serriola_ an annual-perennial and _Erigeron strigosus_ an annual are also abundant in this type, indicating early (though not pioneer) vegetation of old fields. Distinctive environmental features of this group are relatively high level of soil nitrate contents and relatively low exchangeable K^+, and low water retaining capacity of the soil.

Type 2: This large group comprising 71 releves represents an advanced stage over that of type 1. The releves included in this type come from 6 to 15 year old abandoned fields. This type is dominated by perennial grasses - Phleum pratense, Poa pratensis and Agrostis stolonifera. Daucus carota, a biennial is abundant. Some grasses like Arrhenatherum elatius, Dactylis glomerata, Poa compressa and Phalaris arundinacea share dominance in some releves. Annuals like Medicago lupulina and Erigeron strigosus are often conspicuous.. The soil supporting this type is characterized by lower levels of organic matter and nitrate but higher levels of exchangeable K^+, Ca^{++} and Mg^{++}. Soil texture (indicated by the percentage of silt + clay) and the water retaining capacity of the soil in this group are generally intermediate to that of group 1 and 3. Three meaningful subgroups (sub-types) can be recognized as follows:

Sub-type 2a: Of the three [illegible]ypes of type 2 this subtype represents a relatively earlier successional stage than the other two subtypes as indicated by a substantial average cover of Daucus carota. However, the community type is dominated by the grasses Phleum pratense and Poa pratensis. Three other grass species, namely Dactylis glomerata, Agrostis stolonifera and Agropyron repens are also important in this sub-type along with the short-lived perennial forb Trifolium pratense. Erigeron strigosus a pioneer annual species is also fairly well represented. The soil associated with this community is characterized by relatively low levels of NO_3^-, available phosphorus, and exchangeable K^+, Ca^{++}, and Mg^{++}.

Sub-type 2b: This sub-type consists of 6 relevés from an eight year old site. The community is dominated by the grass *Arrhenatherum elatius*. *Poa pratensis* and *P. compressa* occur as co-dominants. The bulk of the vegetation cover is composed of perennials but biennials such as *Echium vulgare* and *Daucus carota* also contribute a small portion of the total cover. The soil supporting this sub-type is rich in available phosphorus and exchangeable cations while pH is close to neutral.

Sub-type 2c: This is a large sub-group of 40 releves from 4 to 8 year old fields. *Agrostis stolonifera* is the leading dominant along with *Poa pratensis*, *Trifolium pratense*, *Phleum pratense*, *Phalaris arundiancea* and *Poa compressa* as co-dominants. Annuals like *Erigeron strigosus* and *Medicago lupulina* contribute a significant proportion to plant cover. *Daucus carota*, a biennial is also important in this sub-type. The soils are relatively low in organic matter content, available P, exchangeable cations and nitrate.

Type 3: The 22 releves belonging to this type come from generally 10 to 20 year old fields. The phytocoenose is predominated by *Poa pratensis*. Other major components of this type are *Festuca rubra*, *Agropyron repens* and *Agrostis stolonifera*, all perennial grasses. Composites such as *Aster sagittifolius*, *A. novae-angliae*, *A. simplex*, *Cirsium arvense* and *Solidago canadensis* are also somewhat important. The soil supporting this community type has neutral pH, high organic matter content, silt and clay percentage (fine textured), water retaining capacity, and exchangeable K^+ content.

4.2.3 Ordination of releves

Two dimensional MDSCAL solution provided interpretable results. Fig. 4.2 shows the MDSCAL releve ordination with the principal vegetation groups derived from the iterative clustering superimposed on the ordination configuration. The stress value was high (23.7%). A high stress value is expected when the number of dimensions and the number of data points (releves) is large and when the ratio between the two is high (Young, 1970). Furthermore, as pointed out by Shepard (1974), the numerical value of stress is of lesser consequence than the 'stability and accessibility to interpretation'. Shepard advocated the use of two-dimensional solutions on the grounds that such configurations can be visually examined and can be interpreted more easily. When the configuration is interpretale, the obtained solution is considered as a valid summarization of the data structure.

Besides disclosing the coenoclines and trends, the MDSCAL ordination, to a certain extent, validated the major groups derived from iterative clustering. Type 1, dominated by Solidago canadensis, Nepeta cataria and Leonorus cardiaca, formed a more or less loose but distinctive group in the lower right of the ordination configuration. Type 3, pre-dominated by Poa pratensis formed a tight group in the upper left. The three sub-types of type 2 occurred more or less in between groups 1 and 3. Type 2a dominated by Phleum pratense and Poa pratensis and co-dominated by Daucus carota formed a somewhat diffused but recognizable group at middle left side of the ordination. This sub-type showed intergradation with sub-type 2c which was dominated by Agrostis stolonifera, Poa pratensis, Trifolium pratense and Phleum pratense.

Sub-type 2c showed some affinity with type 1. Sub-type 2b formed a tight group (with the exception of 1 releve) in the upper right of the ordination. Sub-type 2b exhibited some affinity for type 3 and sub-type 2c. In general, the vegetation groupings superimposed on the ordination scattergram depicted some degree of integradation which suggests, at least in the ordination space, continuity of vegetational composition. This implies that the groups derived from iterative clustering though useful for descriptive purposes are not separated by sharp boundries. Besides the compositional gradient, a temporal gradient could be recognized with releves mostly from 4 year old fields at the lower right to releves from 15 + year old fields at the upper left of the ordination configuration. In order to disclose the underlying environmental trends in relation to compositional variation, component scores derived from PCA of the environmental data set were superimposed on the MDSCAL vegetational (releve) ordination (Fig. 4.3). The correlation coefficients among the 9 soil variables used in PCA are given in Table 4.4 which showed some expected results. Soil pH was found to be negatively correlated with organic matter content and water retaining capacity (WRC). Organic matter content was positively correlated with WRC. The first principal component which accounted for 30.26% of total variability in the environmental data set was primarily a function of soil pH, water retaining capacity, exchangeable K^+ and % organic matter as indicated by eigenvector coefficients (Table 4.5). The numerical value and sign of the eigenvector coefficients indicate the relative importance and direction of the effect of particular variables (Gittins, 1979). The first principal component scores are superposed on the

MDSCAL scattergram in Fig. 4.3a. The larger circles correspond to higher importance of a variable if the sign of the corresponding eigenvector coefficient is positive, but if this sign is negative then smaller circle sizes correspond to higher importance of the variable. Each set of component scores was divided into 5 equal classes, represented by circle sizes that increased with the magnitude of the scores. A complex gradient of soil pH, nutrients and moisture availability seems to exist in the ordination plane, running from lower right to upper left, i.e. along the temporal (successional) gradient. With the successional progression (lower right to upper left in the ordination configuration) pH slightly increases initially but then it declines to around neutral in the relatively mature *Poa pratensis* dominated communities. WRC of soil, by contrast, declines slightly at first but then gradually increases with the build up of organic matter with the advancement of the sere. Exchangeable K^+, however, increases continuously with the successional march. The second PCA component that explains 18.66% of the total variation is largely governed by exchangeable Mg^{++} and Ca^{++} , WRC and organic matter, i.e., this component essentially represents nutrient availability. The scores of the second component are superimposed on the MDSCAL configuration in Fig. 4.3b. There appears to be a trend in nutrient availability from lower right to upper left of the figure, along the temporal (successional) gradient. The third PCA component that accounts for 15.72% of the variation is chiefly a function of available P, NO_3 and exchangeable K^+ concentration ~~in the~~ soil. The scores are superposed on the vegetational ordination in Fig. 4.3c. The third component also represents soil nutrient regime. There seems to be a general trend of increasing nutrient availability along the direction of successional development. However, this trend is not as clear-cut as shown by the first-two components.

4.2.4 Classification of species

Classification of species was accomplished by the sum of squares method using chord distance as the resemblance function. Two clusterings were performed based on two types of reduced data sets. The data set used in the first species clustering contained only those 68 species that occurred in at least 5 releves. The second species clustering was performed on those 14 species that accounted for 90% of the total variation in the complete data set. The resulting dendrograms are presented in Fig. 4.4a,b. In the 68 species clustering (Fig. 4.4a) five groups could be recognized at a classification efficiency of 17.31%. The description of these groups follows:

Group A: This is a large group of 27 species. The important species (in terms of overall coverage) of this group are Melilotus alba, Dactylis glomerata, Festuca pratensis, Phleum pratense, Hypericum perforatum, Trifolium pratense, Phalaris arundinacea, Chrysanthemum leucanthemum, Daucus carota and Medicago lupulina. Most of these species are characteristic of 6 to 8 year old fields. This group shows affinity to sub-type 2a of releve clustering.

Group B: This group is constituted by 15 species of which the important ones are: Agropyron repens, Vicia cracca, Agrostis stolonifera, Arrhenatherum elatius, Geum allepicum, fragaria virginiana, Cirsium arvense and Festuca rubra. This group shows affinity for types 3 and 2b.

Group C: Of the 10 species comprising this group, the important ones are: Poa compressa, Aster simplex, Solidago canadensis, and Taraxacum officinale. Most species belonging to this group are characteristic of 2 to 4 year old fields. This group shows propinquity for type 1 of the releve grouping.

Group D: This group includes Achillea millefolium, Dipsacus sylvestris, Rhamnus catharticus, Bromus inermis, Echium vulgare and Erigeron strigosus. All these species are relatively less common. This species group did not show affinity to any of the releve groups.

Group E: This group comprises 10 species of which the important ones are Cirsium arvense, Nepeta cataria, Lactuca serriola and Leonorus cardiaca. The species included in this group are largely associated with type 1. Characteristically these are found in 2 to 4 year old fields.

The dendrogram resulting from the clustering of 14 important species is shown in Fig. 4.4b. The species associations revealed here differ somewhat from those obtained using 68 species data set. Five species groups can be recognized at a classification efficiency of 41.44%.

Group A': This group comprises two perennial grasses Agrostis solonifera and Phleum pratense. These are characteristic of 4 to 6 year old fields.

Group B': In this group, Dactylis glomerata is associated with Poa compressa. This association is seen in 8 to 10 or more year old fields.

Group C': This group comprises 3 species. Daucus carota a biennial-perennial is associated with the perennials Phalaris arundinacea and Solidago canadensis. This kind of association prevails in 4 to 6 year old fields.

Group D': The four species included in this group are Arrhenatherum elatius, Fragaria virginiana, Poa pratensis and Festuca rubra. These species generally flourish in 8 to 20 year old fields.

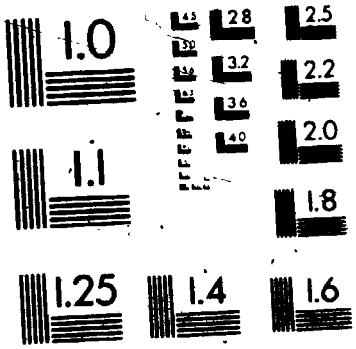
Group E': The three species forming this group - Medicago lupulina, Trifolium pratense and Nepeta cataria are characteristically conspicuous in 2 to 4 year old fields.

4.2.5 Ordination of species

Species ordinations were developed using 68 species (with >5 occurrences) and 14 species (explaining 90% of the total variation in the complete data set) using MDSCAL.

The MDSCAL ordination of 68 species yielded high stress values in repeated runs of the program, with varied starting configurations, for two or three dimensional solutions. Higher dimensional solutions could possibly reduce the stress value though at the expense of interpretability. The two-dimensional ordination of 68 species with a stress value of 32% is given in Appendix E. The distribution of species in the ordination plane was continuous and the major species groups derived from species clustering, with the exception of one group, did not clearly separate out. Species groups A and B more or less overlapped in the central part of the configuration. Group C overlapped with group B. Species belonging to Group D scattered widely and did not show tendency towards grouping. However, group E neatly separated out in the lower right of the scattergram.

4



The two-dimensional ordination of 14 species is presented in Fig. 4.5. The stress value was low, 16.4%. The ordination by and large reproduced the results of the corresponding species clustering, though here the distribution tended to be continuous. There seems to be a successional gradient running from the top edge to the bottom edge of the species ordination with species characteristic of early stages of old field succession, viz. Medicago lupulina, Daucus carota, Nepeta cataria and Solidago canadensis at the top middle part to Festuca rubra, a species of advanced stage, in the lower middle of the scattergram. However, the trend is not well defined because the temporal (successional) trend, to some extent, is modified by within and between site environmental variation as well as management practices.

4.2.6 Life-form and life-span characteristics during the sere

A plant life-form is regarded as a growth form reflecting adjustments to the environmental complex. The most widely used system for the classification of life-form is that of Raunkiaer (1934). Raunkiaer's system is ecologically oriented and is widely applicable (Mueller-Dombois and Ellenberg, 1974). Species occurring in at least 3 releves were categorized into their appropriate life form classes in accordance with Clapham et al. (1962) and Ellenberg (1979).

Releves were classified into four groups based on the age after abandonment of their respective site. The contribution to the total ground cover by each life-form category in each of the age group was subjected to the analysis of concentration (AOC) so as to assess the relationship between life-form and releve groups, i.e., to examine as to what extent the life-form composition (spectrum) undergoes changes during the course of successional development.

The high value of chi-square (7790.1) indicates a marked degree of association between life-form categories and releve groupings. The total chi-square is partitioned into the canonical variates in Table 4.6. The first canonical variate that accounted for 48.46% of the total chi-square represents the temporal gradient. The joint scattergram of the life-form and the releve groupings (Fig. 4.6) reflects the major trends in the life-form characteristics along the vegetational progression. The first canonical variate separates therophytes chamaephytes-hemicryptophytes and hemicryptophytes from the rest of the life-form categories. Releve group 1 that represents the youngest stage (2 yrs.) shows affinity for therophytes, chamaephytes-hemicryptophytes and to a lesser extent for hemicryptophytes. Therophytes-hemicryptophytes, therophytes-geophytes, hemicryptophytes-geophytes, geophytes and chamaephytes are most highly associated with releve group 2 and 3 and to a lesser extent with group 4. Fig. 4.7 shows deviation from random expectation with respect to pooled life-form composition for the first lattice which isolates the successional (temporal) trend in life-form composition from other causes including chance factor. Fig. 4.7 indicates that the proportion of therophytes, hemicryptophytes-geophytes and chamaephytes-hemicryptophytes declines sharply in the second stage (4 yrs.) and subsequently rises very slightly. An exactly reverse trend is shown by therophytes- hemicryptophytes that increase in proportion at first (in stage 2) but thereafter decline at a slow rate.

The relationship between the kind of life-cycle strategy in response to time after abandonment of fields was also investigated. The contribution to the total ground cover by each of the life-span category in each of the releve groups, established on the basis of the age after abandonment, was computed. The two-way table showed a high value of chi-square (6500.37) indicating a high level of association between life-cycle strategy and the successional stages. The total chi-square is partitioned into canonical variates in Table 4.7. The first canonical variate that accounts for 53.94% of the total chi-square represents the temporal gradient. The joint scattergram of releve and life-span groups is given in Fig. 4.8. Group 1 representing stage 1 (2 yrs.) shows affinity for annuals and biennials. Group 2 or stage 2 (4 yrs.) is associated with annuals-biennials and annuals-perennials. Group 3 or stage 3 (6-8 yrs.) and stage 4 (>10 yrs.) are associated with biennials-perennials and perennials. Fig. 4.9 shows deviation from random expectation with respect to pooled life-span composition, for the first lattice. Annuals and biennials being prominent in age group 1 sharply declined in group 2 and then very slightly increased in group 3 and 4. On the other hand, perennials, biennials-perennials, and perennials increased rapidly from group 1 to 2 but afterwards declined slightly.

4.2.7 Diversity trends during the sere

Species diversity and dominance concentration were examined using the following measures: a) number of species (S) or species richness, b) general diversity or Shannon's information statistic (H'), c) equitability (E) and d) dominance (D'). These statistics were averaged for the four groups established on the basis of their age after abandonment.

In the earliest stage (2 yrs.) the species richness and the general diversity were found to be relatively high (Fig. 4.10). However, both richness and general diversity more or less declines gradually with the advancement of succession. Not unexpectedly, the reverse trend was shown by the dominance concentration. The level of equitability increased slightly at first but subsequently declined to the level found in the youngest community.

4.2.8 Discussion and conclusions

The major goals of the study of old fields have been attained as the major relationships between vegetation and environment as well as the principal dynamic trends in the vegetation have been revealed.

The releve and species ordinations, performed using non-metric multidimensional scaling, yielded ecologically meaningful results. Ordinations of both kinds revealed not only the major trends in the compositional variation but also disclosed the pattern in environmental factors and factor complexes associated with these changes. The successional (temporal) trend in the vegetation was more clearly unfolded by the releve ordination in comparison to species ordination.

The ordinations, in general, depicted continuity in vegetation. Abrupt discontinuities were not observed. Continuous nature of vegetation, i.e. the existence of vegetational continuum (Whittaker, 1967; McIntosh, 1967b) is clearly implied. Obviously, the vegetation groups (types) extracted from cluster analysis overlap to some extent and do not represent discrete entities. Nonetheless, such types serve the useful purpose of vegetation description (Gleason, 1926; Krajina, 1961; Orloci, 1978a; Kenkel, 1984).

Previous studies on old fields, mostly conducted in the United States, have established successional schemes for different geographical regions (e.g., Oosting, 1942; Keever, 1950, 1979; Daniel and Platt, 1968; Swan, 1970; Hurd et al., 1971; Dayton, 1975; Mellinger and McNaughton, 1975). The dominance sequence differs to some extent with the geographical setting. The general pattern has been summarized by McCormick (1968) and Haug and Van Dyne (1968). Abandoned field is first colonized by annuals, though side by side some biennials and perennials also appear. Because of their colonizing ability and tolerance to perturbance, these pioneers may persist in the field for several years. In the second year, dominance is generally taken over by biennials but annuals may still remain conspicuous. In due course of time, these give way to perennials (often grasses). This general scheme was more or less verified in the present study with the aid of the analysis of concentration (AOC). The pattern of life-cycle strategy during the course of secondary succession involved a sharp decline in sexually reproducing annuals and biennials with a concomitant rise in mostly vegetatively reproducing perennials. The pattern of life-form composition during the sere was also analyzed with the aid of AOC. With the successional advancement, the proportion of therophytes and hemicryptophytes declined while that of geophytes, chamaephytes and phanerophytes increased. Similar changes in life-form composition have been reported by Escaree et al. (1983) for old fields in Montpellier, France. The proposed scheme of secondary succession on old fields for London area is given in Fig. 4.11.

Despite numerous studies on old-field succession, very few have attempted to correlate vegetational progression with edaphic factors. In the present study, several trends were noted with respect to edaphic characteristics. The water retaining capacity of soil, exchangeable K^+, Ca^{++} and Mg^{++} increased while pH decreased from early to advanced stage. The observed pattern of increasing mineral nutrient availability through time is in general agreement with that described by Rice (1971) but contradicts the result of Hanks (1971) who found available K^+, Ca^{++} and Mg^{++} to decrease with the vegetational progression on old fields in the coastal plain of New Jersey.

The study suggests that succession is an orderly process of vegetation change, though some characteristics change in a manner somewhat different from that predicted by the traditional succession theory. Many species exhibited certain degree of multimodal dominance (i.e., dominance at two or more time periods) when individual plots (relevés) are considered (e.g., Agropyron repens, Agrostis stolonifera, Medicago lupulina and Plantago spp.). This phenomenon has been previously noticed (McCormick, 1968; Pickett, 1982; Keever, 1983). Keever observed that closely situated fields or even parts of the same field vary to a considerable extent in the dominant vegetation. The reasons for such fluctuations are not usually clear, though the hypothesis that different parts of the field may vary in successional stage (Watt, 1947) seems reasonable.

With respect to population turnover and persistence it was observed that many species involved in the secondary sere did not enter sequentially ("relay floristics") but largely occurred throughout the time period. However, the population dominance shifted in an orderly fashion through the time period. These results corroborate the findings of Bard (1952), Beckwith (1954) and Pickett (1982) and tend to support Egler's (1954) concept of "initial floristic composition". However, Egler's hypothesis cannot be fully accepted in the original form. As Keever (1983) points out, it is hard to accept that diaspore of all future species to occur in a field already exist at the time of it's abandonment. It is likely that seeds and vegetative propagules of most future dominants are initially present. Invasion of other species takes place by means of propagules that arrive from nearby sources year after year. The rate of arrival of such dissiminules depends upon the distance from the propagule source and the mode of dispersal of the source species (McQuilkin, 1940; Rice et al., 1960; Werner and Harbeck, 1982; Keever, 1983). The species that vanish from the sere usually persist for a length of time, some even to centuries in the form of buried viable seeds (Oosting and Humphreys, 1940; Livingston and Allessio, 1968; Takahashi and Hyashi, 1978).

Examination of changes in diversity patterns along successional development not only allow documentation of the diversity patterns for the study area but also permit evaluation of generalized models of successional diversity. Both species richness and general diversity were highest in the earliest stage (2 yrs. old community) and with the successional advancement, richness as well as general diversity declined gradually. The observed diversity pattern is somewhat contradictory to the often accepted model of Margalef (1968) and Odum (1969) which hypothesizes that following initial increase along succession, diversity levels off in later stages, and eventually decreases somewhat in more stable 'climax' communities. The high diversity observed in the first stage was presumably because of the availability of diaspore from the species rich seed bank at the time of abandonment (Oosting and Humphreys, 1940) and also because the incoming propagules from adjacent sources find plenty of available empty niches. The decrease in diversity in the later stages of succession presumably resulted owing to competitive exclusion (Whittaker, 1965). The present diversity pattern can best be explained using the model of r-K selection continuum (MacArthur, 1962; MacArthur and Wilson, 1967; Pianka, 1972) as suggested by Tramer (1975). Tramer advocated that if the diversity pattern conforms to r-K selection continuum, the colonization pattern should be similar to that observed by Simberloff and Wilson (1970) on mangrove islands near Florida following complete extermination of their faunas. The initial phase is characterized by rapid colonization. The second phase is brief and involves over-packing of species in the system. The final phase attains equilibrium with the decline in species diversity.

The operation of r-K selection continuum with respect to diversity changes is supported by several observations. The population of annuals and biennials declined sharply with the concomitment increase in the proportion of perennials. This presumably resulted in increased competitive pressure and consequently reduced diversity. As noted by Tramer (1975) decreased levels of between-releve variance of species were observed in the advanced stages of succession, presumably reflecting the stabilization of the system. Furthermore, the diversity pattern observed shows some similarity to colonization curves of island faunas with the exception of that the part of the curve which represents colonization phase (equivalent to first year of abandonment) was not observed as the random sample chosen for study did not include one-year old fields.

Although no formal attempt was made to evaluate the mechanisms that determine the sequential replacement of groups of species during the secondary sere, field observations and the available ecological information of individual species permit some general comments to be made. The three models proposed by Connell and Slatyer (1977), namely facilitation, inhibition and tolerance have been widely discussed, in relation to secondary sere, in recent years (Pickett, 1982; Werner and Habeck, 1982; Escarre et al., 1983; Keever, 1983).

The 'facilitation' model considers that transitory species can establish and flourish only when the earlier colonists have "prepared the way" for later colonists by changing the environment in favour of the latter (Clements "reaction" model or Egler's "relay floristics"). The occurrence of the dominant species of different stages throughout the sere which conforms to "initial floristic composition" clearly suggests that the facilitation model does not operate in case of the old field succession. The 'inhibition' model holds that the earlier colonists inhibit the invasion of later arrivals by securing the space and/or other resources. The early occupants disappear when they are damaged or killed either by herbivores or parasites or simply by senescence. They are then succeeded by species with longer life-span and less susceptible to perturbations. Substantial evidence exist to support this model for the old fields under study. A number of species of early stages are known to produce allelopathic substances, e.g., Ambrosia artemisifolia (Raynal and Bazzaz, 1975; Jackson and Willemsen, 1976), Erigeron spp. (Kobayaski et al., 1980), Solidago spp. (Tsuji et al., 1975; Kobayaski et al., 1980), Agropyron repens (Ohman and Kommeduhl, 1960, 1964; Toai and Linscott, 1979), Cirsium arvense (Wilson, 1981). It has been experimentally demonstrated that certain early colonizing species of old fields reduce the rates of germination and growth of the later arriving species (Keever, 1950; McCormick, 1968; Parenti and Rice, 1969: Fleet, 1970). The 'tolerance' model assumes that the later arriving species can settle irrespective of the environmental changes, caused by the earlier colonists. In this model, species sequence is governed entirely by life-history characteristics. The late appearing species are slow growing, more tolerant of limiting resources and are able to survive and out-compete the early succesional species. Evidence in favour of the tolerance model has been provided by Keever (1979) who concluded that "the early occupants ... make the habitat less suitable for other individuals of [the] same shade intolerant species ... The presence of [the] early dominants has little or no effect on the entrance of species important in later stages of [secondary] succession". Species removal expeirments by Hills and Vankat (1982) also provided support to the 'tolerance model'. I agree with Keever (1983) that none of these models is entirely adquate to explain causes of early old-field succession and that more than one model (possibly 'inhibition' and 'tolerance' models) may operate simultaneously in the same field as a consequence of the great spatial heterogeneity that is so characteristic of old-field communities.

4.3 Vegetation analysis of the vacant lots

4.3.1 Vegetation

The vegetational cover in the vacant lots was not as high as in the old field. The average percentage cover was 70% and varied with age. One year old lots had an average cover of 36.5% as opposed to 94.6% in the 4^+ year old vacant lots.

A total number of 116 species were recorded from 10 different sites (vacant lots) (Appendix F). Table 4.8 presents the 73 species that occurred in at least 3 releves along with their average cover, its variance and the origin (native or introduced). The vegetation, in general, was dominated by forbs including *Trifolium pratense*, *Daucus carota*, *Medicago lupulina* and *Melilotus alba*. Perennial grasses, including *Agrotis stolonifera* and *Agropyron repens* were also important. *Ambrosia artemisifolia* was dominant in one-year-old vacant lots. *Poa compressa* and *Phleum pratense* frequently occurred with large cover. *Trifolium hybridum*, a perennial legume occurred in scattered populations. Perennial composites such as *Solidago canadensis*, *Taraxacum officinale*, and *Chrysanthemum leucanthemum* and annual-biennial composite *Lactuca serriola* were also fairly well-represented. Of the 116 species recorded from the vacant lots, eighty (=68.96%) were introduced, thirty-five (=30.17%) were native and one (0.86%) was native/introduced.

4.3.2 Classification of releves

The dendrograms based on SSA and iterative clustering are given in Fig. 4.12a,b. Seven ecologically meaningful groups (types) could be recognized based on the iterative clustering, giving a classification efficiency of 62.27%l (Fig. 4.12b). Results of SSA were somewhat similar and are given for the purpose of comparison (Fig. 4.12a). Only the seven types derived from iterative clustering are treated in detail. The vegetational characteristics of the types are summarized in Table 4.9 and the environmental characteristics are summarized in Table 4.10. The description of the types follows:

Type 1: This type includes 13 releves that generally come from one-year-old vacant lots. The community was pre-dominated by the native annual Ambrosia artemisifolia. Other important annuals were Brassica kaber, Polygonum persicaria, P. lapathifolium, Medicago lupulina, Erigeron canadense and Chenopodium album. Besides annuals, a number of biennials including Melilotus officinalis and M. alba and annual-biennial Lactuca serriola were also conspicuous. Perennial grass Agropyron repens occurred as a co-dominat. The soil associated with this type had relatively high NO_3^- content and relatively higher proportion of silt and clay (i.e. relatively finer soil texture) but relatively lower changeable Mg^{++} levels.

Type 2: The thirteen releves belonging to this type come from 2 to 3 year old vacant lots. The community was dominated by the grasses Agropyron repens and Poa compressa. Daucus carota a biennial occurred as co-dominant. Important associates were the perennial forbs Trifolium hybridum, Chrysanthemum leucanthemum, Taraxacum officinale, Solidago canadensis and Rumex crispus. Melilotus officinalis and Cichorium intybrus were frequently present. The soil supporting this type was found to below in nitrate, exchangeable K^+ and silt and clay content.

Type 3: The releves constituting this type came from a 2 year old vacant lot. The type was dominated by Agrostis stolonifera and co-dominated by a biennial Melilotus alba and a biennial-perennial Daucus carota. Perennials like Trifolium pratense, Phleum pratense, Solidago canadensis, Taraxacum officinale and Aster simplex were also important. Ambrosia artemisifolia a native annual and Brassica kaber an introduced annual also occurred with substantial cover. The soil associated with this type had a relatively high proportion of silt and clay (fine textured) and consequently high WRC. Organic matter percentage and exchangeable K^+ levels were also high.

Type 4: The releves comprising this type came from a 2 year old vacant lot. Community dominants were Melilotus alba, a biennial and Daucus carota a biennial-perennial. Two perennial grasses, Agrostis stolonifera and Agropyron repens were co-dominants. The legumes Trifolium hybridum and T. pratense were the important associates. The soil in this type had relatively low levels of organic matter and NO_3 but high level of available phosphorus.

Type 5: The releves in this type mostly belonged to a two year old vacant lot. An annual legume, Medicago lupulina, was predominant. Trifolium pratense and Daucus carota were the co-dominants. Lactuca serriola, an annual-biennial, Taraxacum officinale and Poa compressa were the important associates. The soil associated with this type was characteristically low in NO_3 content.

Type 6: This type was based on releves from 1 to 2 year old vacant lots. Community dominants were Daucus carota, Chrysanthemum leucanthemum, Solidago canadensis, Medicago lupulina and Poa compressa. Beside these, Trifolium pratense, T. hybridium and Lactuca serriola were also important. The soil supporting this type was high in NO_3, available P, and exchangeable Mg^{++}, but relatively low in organic matter percentage.

Type 7: This type comprising of 25 releves represented 3 to 4 year old vacant lots. The community was predominated by Trifolium pratense. Daucus carota a biennial-perennial was co-dominant. Perennial grasses Poa compressa and Phleum pratense were also well represented. The soil supporting this type was found to be rich in available P and had somewhat higher percentage of silt and clay (relatively finer texture).

4.3.3 Ordination of releves

Fig. 4.13 shows the two-dimensional MDSCAL releve ordination with the seven groups derived from iterative clustering superimposed on the scatter of points. The stress value was 23.61%, but replicate runs of the program with varied random starting configurations gave virtually the same solution thereby suggesting the stability and consequently the validity of the obtained configuration.

The MDSCAL releve ordination, to a remarkable extent, duplicated the group structure derived from iterative clustering. However, not all the types neatly separated out in the ordination plane but intergradation of types occurred which implies compositional continuity as well as multidimensional relationships between the releves. This finding based on ordination, however, does not contradict the result of cluster analyses, as the latter technique imposes a group structure on the data, on an objective basis, irrespective of continuity or discontinuity.

Ambrosia artemisiifolia dominated type 1 formed a somewhat loose cluster in the lower right of the ordination. Just above this group, towards left was located the Daucus carota dominated type 6. In the middle right of the configuration, type 2 dominated by Agropyron repens formed a loose group which overlapped with type 6 in the left. Trifolium pratense dominated type 7 separated out as a tight cluster in the upper left of the configuration. In the upper middle part of the ordination, Agrostis stolonifera dominated type 3 formed a somewhat loose cluster. Melilotus alba dominated type 4 occurred between type 2 and 3.

Besides revealing trends in compositional variation, the ordination also disclosed the underlying temporal (successional) and environmental gradients. A temporal gradient can be seen in the configuration running across lower right to upper left with one year old Ambrosia artemisiifolia dominated type through 1 to 2 year old Daucus carota dominated type to 3-4 year old Trifolium pratense dominated vegetation. Another gradient seem to occur in the ordination configuration in a circular manner in clockwise direction. This gradient appears to be an amalgum of temporal and environmental gradients and is also presumably influenced by frequency of mowing. However, this trend is not well-defined.

The environmental gradients or coenoclines were sought by superimposing the component scores yielded by the PCA of the corresponding environmental data set on the MDSCAL vegetational ordination (Fig. 4.14). Table 4.11 presents product moment correlation coefficients between environmental (edaphic) variables while Table 4.12 summarizes the information on the first three components of PCA performed on the environmental data set. As expected pH and organic matter were negatively correlated while organic matter content and water retaining capacity (WRC) were highly positively correlated. The first PCA component which accounted for 40.36% of the total variation in the environmental data set was largely a function of soil organic matter content, WRC and pH (Table 4.12). The larger circle sizes in Fig. 4.14a should be interpreted as lower levels of organic matter and WRC and higher values of soil pH. There seems to be an environmental gradient along the direction of the major temporal gradient, characterized by increasing organic matter and WRC, but decreasing soil pH. The second PCA axis which accounted for 20.03% of the total variation was primarily correlated with available P, silt and clay and WRC. The component scores of the second PCA component are superimposed on MDSCAL vegetational (releve) ordination in Fig. 4.14b. The larger circle sizes represent higher levels of available P and silt and clay and lower levels of WRC. Along the major temporal gradient, there appears to be an increasing trend in available phosphorus from young *Ambrosia* dominated type in the lower right through *Daucus carota* dominated type to relatively advanced *Trifolium pratense* dominated type in the upper left of the configuration. It must be pointed out that the coenoclines observed here were relatively less clear cut compared to those observed for old fields, perhaps because these sites (vacant lots) are more recently (and perhaps more severely) disturbed and are therefore by their nature more variable.

4.3.4 Classification of species

Classification of species was performed by the sum of squares (SSA) technique using chord distance as the resemblance function. The hierarchical agglomerative clustering was either performed on 53 species data set (species with at least 5 occurrences) or 9 species data set (species explaining 90% of the total variation in the complete data set). The resulting dendrograms are presented in Fig. 4.15a,b.

The hierarchical clustering of 53 species (Fig. 4.15a) suggested the six groups giving a classification efficiency of 30%. Characteristics of the groups are as follows:

Group A: This small group of six species includes two annuals, *Barbarea vulgaris* and *Chenopodium album*, a biennial, *Tragopogon dubius* and 3 perennials, *Agropyron repens*, *Rumex crispus* and *Taraxacum officinale*. With the exception of *T. officinale* which exhibits wide distribution, the rest are generally characteristic of 1 to 3 year old vacant lots. This species group shows affinity to type 1 of releve clustering.

Group B: This is a large group of 19 species. Among the species included in this group the important ones are: Trifolium pratense, Daucus carota, Medicago lupulina, Poa compressa, Solidago canadensis, Lactuca serriola, Chrysanthemum leucanthemum, Melilotus officinalis and Poa pratensis. Of the 19 species comprising this group, 2 were annual-biennial, four biennial and 13 perennial. Most species of this group are characteristic of 2 to 3 year old vacant lots. This species group shows affinity for type 6 and to a lesser extent for type 2 of releve clustering.

Group C: This group comprising of 9 species includes one annual, Erigeron strigosus a biennial-perennial, Cichorium intybus and seven perennials of which the important ones are Agrostis stolonifera, Phleum pratense, Aster simplex and Solidago graminifolia. Most species belonging to this group are prominent in 2 to 4 year old vegetation. This species group shows some affinity for types 3 and 7.

Group D: The 6 species comprising this group include two annuals, Digitaria sanguinalis, a biennial Echium vulgare and 3 perennials, Silene cucubalus, Plantago lanceolata and Populus tremuloides (seedlings). With the exception of Populus, the rest of the species generally occur in 2 year old vacant lots. Slight affinity is indicated for type 6.

Group E: Of the eight species constituting this group, one is a biennial, Melilotus alba, one a biennial-perennial, Oenothera parviflora while the rest are perennials, including Centurea repens, Dipsacus sylvestris, Vicia cracca, Cirsium arvense, Trifolium hybridum and Lolium perenne. Melilotus alba and Oenothera parviflora characteristically occur in two year old vacant lots. This species group exhibits some affinity for type 4.

Group F: This is a small group of 5 short-lived species. It includes 4 annuals, Ambrosia artemisiifolia, Brassica kaber, Plygonum lapathifolium and P. persicaria, and one annual-biennial, Lepidium compestre. These are characteristically pioneer species of the secondary sere on the vacant lots. The group of species show high order of affinity for type 1 of releve classification.

Species clustering based on the 9 species data set (Fig. 4.15b) revealed three meaningful groups. The species associations somewhat differed from those found in 53 species data set. Characteristics of the three groups are as follows:

Group A': This group comprises of a biennial, Melilotus alba and 3 perennials, Agropyron repens, Poa compressa and Agrostis stolonifera. These species characteristically dominate 2 to 3 year old vacant lots.

Group B': This group comprise of two annuals, Ambrosia artemisiifolia and Medicago lupulina and a short-lived perennial, Trifolium pratense.

Whereas Ambrosia artemisiifolia is characteristically a dominant species of one year old vacant lot, Medicago lupulina may occur as a dominant in one as well as two year old lots. Trifolium pratense, on the other hand, generally dominates 2 to 4 year old vegetation.

Group C': This group includes Daucus carota and Phleum pratense which characteristically dominate 2 to 3 year old vegetation.

4.3.5 Ordination of species

Two dimensional MDSCAL ordinations of 53 species (with > 5 occurrences) and 9 species (that explained 90% of total variation in complete data set) are depicted in Fig. 4.16a and 4.16b respectively.

The ordination of 53 species yielded a stress value of 20.6%. Repeated runs of the program gave similar species constellation (and similar stress values) indicating the stability of the ordination structure. Despite the high stress value, the species ordination was interpretable. The ordination more or less separated out the species groups derived from species clustering. However, overlapping of species groups and somewhat even distribution of species in the ordination plane strongly suggests continuity. Members of species group E occurred at the upper edge of the ordination plane. Underneath group E, group A extended from upper middle to the centre of the configuration as a somewhat loose group. Group B occurred as a diffused group beneath group A. The latter two were partially overlapped. Group C formed an almost neatly separated cluster to the middle left of the configuration whilst in the middle right of the scatter-plot group F formed a compact cluster that slightly overlapped group B. Group D formed a well-separated cluster at the lower edge of the configuration. A few species were misplaced with respect to species groupings. Such species presumably required higher number of dimensions for their inclusion in the appropriate species group.

A temporal (successional) gradient can be seen to extend from middle right to the left of the ordination plane, with pioneer species like Ambrosia artemisiifolia, Chenopodium album, Polygonum lapathifolium and P. persicaria in the middle right, through Lactuca serriola, Medicago lupulina, and Agropyron repens characteristic of 1 to 2 year old vegetation and Melilotus alba, Daucus carota and Solidago canadensis characteristic of second to third year of vegetational development to Trifolium pratense, Phleum pratense, Aster simplex and A. novae-angliae that characteristically form the dominant vegetation of 3 to 4^+ year old vacant lots. A number of species did not occur along the successional trend in the ordination configuration but occurred elsewhere in the ordination plane. It appears that the distribution of these species is predominately governed by edaphic factors such as soil moisture and nutrient regimes. The group of species at the upper edge and in the middle of the configuration generally occur in 2 to 3 year old vacant lots where soil is poor in NO_3 and organic matter content but rich in available phosphorus. By contrast, the group of species at the bottom of the configuration which are also representative of 2 to 3 year old vegetation seem to be associated with soils that are rich in NO_3 but poor in organic matter content. It is possible that Melilotus officinalis and Trifolium repens, both legumes, enrich the soil with nitrate through the process of nitrification.

The MDSCAL ordination of 9 species (Fig. 4.15b) had a relatively low stress value, 17.3%. This species ordination more or less reproduced the result of the corresponding species clustering. Species belonging to group A', with one exception, occurred in the upper left of the ordination. Members of group B' with the exception of Tifolium pratense in the lower right of the configuration. The two species of group C', Daucus carota and Phleum pratense were located in the upper left corner of the ordination. A successional gradient seem to exists which runs in a circular manner in clockwise direction, starting with the early colonizers, Ambrosia artemisiifolia and Medicago lupulina in the lower right of the scattergram through biennial Melilotus alba and short-lived perennial Trifolium pratense in the middle right and Poa compressa and Agropyron repens in the upper right to Phleum pratense in the upper left of the ordination. Daucus carota and Agrostis stolonifera being inappropriately placed in two-dimensions do not fit into this scheme.

4.3.6 Life-form and life-span characteristics during the sere

Releves were classified into four groups based on the time following the removal of topsoil from the respective sites. The releve groups represented successional stages. The contribution to the total ground cover by each life-form category or life-span category was computed by each releve group. The structured tables were submitted to AOC to disclose the successional trends in life-form and life-span characteristics.

The total chi-square of the life-form against releve group structured table is partitioned into the canonical variates in Table 4.13. The high value of chi-square indicates a high order of dependence of life-form on the successional stages. The first canonical variate that accounted for 71.73% of the total variation represents the temporal (successional) gradient. The joint ordination of life-form and relevé groups (Fig. 4.17) reflects the principal trends in the life-form characteristics during the successional development. The first canonical variate separates therophytes, geophytes and phanerophytes from the other life-form categories, whilst the second canonical variate primarily separates the relevé groups. Relevé group 1 (1 yr. old vacant lots) appears to be associated with therophytes, geophytes and phanerophytes. Relevé group 2 (2 yrs. old lots) and 4 (4 yrs. old lots) show affinity for therophytes-hemicryoptophytes, hemicryptophytes and hemicryptophytes-geophytes while releve group 3 (3 yrs. old lots) exhibits affinity for chamaephytes-hemicryptophytes. Fig. 4.18 shows deviation from random expectation with respect to pooled life-form composition, for the first lattice. Therophytes, geophytes and phanerophytes decline sharply from group 1 to group 2, i.e., from first to second year of successional development, but subsequently decline very slightly. By contrast, hemicryptophytes, therophytes-hemicryptophytes, hemicryptophytes-geophytes and chamaephytes-hemicryptophytes increase markedly in the second year (group 2) and tend to increase at a slow rate afterwards.

The total chi-square of life-span against releve group structured table is partitioned into canonical variates in Table 4.14. A strong association between life-span categories and releve groups is shown by a high chi-square value. The first canonical variate that accounted for 94.39% of the total chi-square represents the temporal (successional) gradient. The simultaneous ordination of releve groups and life-span categories with respect to the two canonical variates resulting from AOC is given in Fig. 4.19. Releve group one, representing first year of vegetational development is strongly associated with annuals and annuals-biennials. On the other hand, releve groups 2, 3 and 4, represent 2, 3 and 4+ year old vegetation respectively are markedly association with biennials, biennials-perennials and perennials. Fig. 4.20 shows deviation from random expectation for each of the life-span category. Annuals and annuals-biennials sharply decline from first to second year of successional development and thereafter decline gradually upto fourth year. Contrarywise, biennials, biennials-perennials and perennials rapidly increase from first to second year of succession but afterwards tend to increase gradually.

4.3.7 Diversity trends during the sere

Species richness and diversity slightly increased from first to second year of vegetational development but thereafter both measures declined (Fig. 4.21). The most advanced stage in the successional sequence had the least richness and general diversity. Dominance concentration, not surprisingly, showed a reverse trend to that of diversity. Equitability did not change upto third year but declined later.

4.3.8 Discussion and conclusions

The results presented in this section have summarized the pattern of vegetational composition, its relationships with the environmental characteristics and the major dynamic trends in community structure and composition.

The seven vegetation types extracted from iterative clustering were found associated with characteristic edaphic conditions related to moisture availability and nutrient supply. Among the factors regulating moisture availability, water retaining capacity (WRC) was strongly correlated with the vegetatation types. Organic matter content and levels of nitrate and available phosphorus were the important components of nutrient regime that showed greatest association with the vegetation types.

Most of the types, recognized for descriptive purposes, somewhat overlapped with one another in the releve ordination, suggesting continuity in the vegetation. The ordination disclosed the major successional trend and the relationships of this trend with a set of environmental characteristics. Vegetational progression was accompanied by a progressive increase in soil organic matter, WRC and available phosphorous and a gradual decrease in soil pH.

Succession on vacant lots was found to be an orderly and a directional process of vegetation change, though not all successional characteristics changed in accordance with the classical succession theory. The proposed scheme of the secondary sere is outlined in Fig. 4.22. This successional scheme shows some similarity with that developed for old fields, though some important differences can readily be noticed. Solidago canadensis which attained dominance in the 4-6 year old abandoned fields remained at a lower level of importance in the 4^+ year old vacant lots; instead, Trifolium pratense a short-lived perennial attained the position of leading dominant in the fourth year of succession on vacant lots. The possible explanation is that the rhizomes of Solidago canadensis with which it reproduces after first year of seedling growth (Werner et al., 1980) were removed at the time of excavation and removal of topsoil from the vacant lots. Furthermore, annual mowing at the vacant lot sites was also, presumably, responsible for restricted growth and abundance of S. canadensis since flowering in this species is confined to individual shoots that attain a minimum height of between 40 to 50 cm (Werner et al., 1980). Thus, mowing must have precluded flowering and sexual reproduction. Some biennial species such as Daucus carota and Melilotus alba exhibited a 2-year-cycle of dominance. A similar dominance pattern in biennials has been noted by Tramer (1975) in Ohio old fields. This phenomenon has a theoretical basis of reproductive strategy and the selection of optimal life history characteristics in biennials (Schaffer and Gadgil, 1975). In general, however, the successional pattern with respect to life-history strategy was similar to that observed for old fields. Annuals dominated the system in the first year of topsoil removal. These are predominantly r-selected species which because of their specific characteristics (see Pianka, 1972; Gadgil and Solbrig, 1972; Putman and Wratten, 1984: 272) are able to colonize impermanent and relatively harsh environment created as a result of destruction of the previous ecosystem. Perennials become progressively more important as the succession proceeds and eventually dominate the system. The increase in such K-strategist species suggests greater environmental stability in the advanced stages of succession (Sousa, 1980; Leps et al., 1982). No attempt was made to test stability of the communities. However, experimental studies conducted by Mellinger and McNaughton (1975) and Leps et al. (1982) in old fields (an environment similar to vacant lots) have demonstrated greater stability (as assessed by the resistance to external perturbations) in the advanced stages of succession.

Both, species richness and general diversity increased initially and then declined with the further successional advancement. The diversity-succession trend closely followed the colonization pattern on defaunated mangrove islands documented by Simberloff and Wilson (1969, 1970), strongly suggesting the operation of r-K selection continuum with respect to species diversity as explained earlier (section 4.2.8). The low diversity observed in the advanced stage of succession (4 yrs. old vacant lots) indicates monopolization of resources by the dominants in the relatively old communities. Seral changes in equitability, as indicated by Alatalo's index, were more closely related to general diversity (H') than to species richness (S'). This result is in agreement with Tramer (1969, 1975) who suggested that H' in early successional communities should be correlated with equitability, whereas in mature community H' should reflect changes in species richness. The decreased diversity level in the advanced stage was apparently associated with relatively greater ecosystem stability. Thus, the often quoted hypothesis that increased diversity leads to increased stability (Elton, 1958; Margalef, 1968; Odum, 1971) is not supported by the results. However, recent theoretical studies by May (1973, 1976) have suggested the converse to be true.

4.4 Vegetation analysis of topsoil mounds

4.4.1 Vegetation

The average percentage cover on the topsoil mounds was 93%. The percentage cover was comparatively lower on the younger mounds (88.6%) than on the older mounds 93.6%. A total of 108 species were recorded from seven different sites. Table 4.15 presents the list of 71 species that occurred in at least 3 releves along with their average cover, its variance and the origin (native or introduced). One or more of the following constituted the dominant vegetation in the specific sites: *Agropyron repens*, *Afmbrosia artemisifolia*, *Chenopodium album*, *Solidago canadensis*, *Lactuca serriola* and *Daucus carota*. Other important species were: *Phleum pratense*, *Trifolium pratense*, *Poa compressa*, *Erigeron strigosus*, *Melilotus alba*, *Agrostis stolonifera*. The younger mounds (1 yr. old) were found to be dominated by annuals, particularly *Ambrosia artemisifolia* and *Chenopodium album*. Other important annuals were *Panicum capillare* and *Chenopodium hybridium*. *Melilotus alba*, a biennial, *Daucus carota*, a biennial-perennial and *Lactuca serriola*, an annual-biennial generally formed the dominant vegetation on 2 to 3 year old topsoil mounds. Perennials like *Solidago canadensis*, *Agropyron repens* and *Phleum pratense* represented the dominant vegetation of 4$^+$ years old topsoil mounds.

Of the 108 species (Appendix G) 75 (=69.4%) were introduced and 33 (=30.6%) were native to North America.

4.4.2 Classification of releves

Classification of releves was performed by 4 different agglomerative techniques, namely, single linkage, simple average, SSA, and iterative clustering. Single linkage resulted in chaining, which basically indicates continuity in the vegetation. Results of simple average clustering were similar to those of SSA except that the groups were not as compact as obtained in SSA. For these reasons only the results of SSA and iterative clustering are presented (Fig. 4.22a,b). The dendrogram resulting from SSA (Fig. 4.23a) is shown only for the purpose of comparison with that of iterative clustering (Fig. 4.23b). The results of these two clustering were similar but because of greater reliability of iterative clustering owing to minimization of random events, only the results of the latter are dealt with in details. Three major ecologically interpretable types (groups) could be recognized in iterative clustering, at a classification efficiency of 41.09%. The vegetation and the environmental characteristics of these types are summarized in Tables 4.16 and 4.17 respectively. The type characteristics are described below:

Type 1: The 16 releves included in this type came from the slopes of 1 year old topsoil mounds. The releves were associated with the slopes of the topsoil mounds dominated by the annuals Ambrosia artemiisifolia and Chenopodium album individually or jointly. Lactuca serriola, an annual-biennial, Panicum capillare and Chenopodium hybridum both annuals, were also important. Agropyron repens, Brassica kaber, Daucus carota and Oenothera parviflora were of lesser importance.

The soil supporting this vegetation type had relatively high levels of NO_3^-, organic matter, and exchangeable K^+ but had relatively low levels of available phosphorus and exchangeable Mg^{++}. Two subtypes could be recognized.

Sub-type 1a. This sub-type was characterized by Ambrosia artemisiifolia, Panicum capillare and Lactuca serriola as co-dominants. Agropyron repens, Brassica kaber, Daucus carota and Oenothera parviflora were the other important species. The soil was found to be rich in NO_3 and exchangeable K^+ content but was poor in available phosphorus and exchangeable Mg^{++} concentrations.

Sub-type 1b: This sub-type was characterized by Chenopodium album, Lactuca serriola and Chenopodium hybridum as co-dominants. Ambrosia artemisiifolia and Agropyron repens were also important. The soil supporting this sub-type was relatively rich in available phosphorus and exchangeable K^+ content but was poor in exchangeable Mg^{++} content.

Type 2: This type comprised 8 releves that belonged to 2 to 3 year old topsoil mounds. The community dominance was shared between a biennial-perennial, Daucus carota and a short-lived perennial Trifolium pratense. The co-dominants were Phleum pratense, Agropyron repens, Melilotus alba and Poa pratensis. Annuals like Medicago lupulina and Erigeron strigosus were also important.

This type prevailed on relatively fine-textured soil (higher proportion of silt and clay) that was relatively low in NO_3 and exchangeable K^+ content but had relatively high levels of available phosphorus and exchangeable Mg^{++}. The average percentage slope of the mounds supporting this type was 22%.

Type 3: The 24 releves comprising this type came from 4+ year old mounds. Out of 24 releves, 19 were associated with slopes while 5 were associated with flat tops. The community type was dominated by the perennial grass Agropyron repens and the perennial composite Solidago canadensis, with Lactuca serriola and Daucus carota as co-dominants. Phleum pratense and Erigeron strigosus were also represented with substantial cover. Aster simplex and Melilotus alba were also common.

This type was associated with soil that had relatively low levels of NO_3 and exchangeable K^+ but relatively high levels of available P and exchangeable Mg^{++}. Two sub-types could be recognized in this type.

Sub-type 3a. This sub-type was dominated by Agropyron repens and Solidago canadensis with Lactuca serriola and Poa compressa as co-dominants. Phleum pratense and Daucus carota were also important. This sub-type typically prevailed on relatively fine textured soil compared to sub-type 3b. The soil had relatively high level of exchangeable K^+ but relatively low level of exchangeable Mg^{++}, compared to sub-type 3b. The releves were often associated with the flat top of the mounds.

Sub-type 3b. This sub-type is characterized by Daucus carota and Solidago canadensis as co-dominants. Other important species include Lactuca serriola, Aster simplex and Cirsium arvense. This sub-type typically occurred on coarse-textured soil with high levels of available phosphorus and exchangeable Mg^{++}. The slope was steep (average 42%) compared to sub-type 3a (average 50.16%).

4.4.3 Ordination of releves

Two ordination techniques, PCA and MDSCAL, were employed to examine vegetation trends. In comparison to MDSCAL, the results of PCA were less interpretable and less complementary to either SSA or iterative clustering. On the other hand, MDSCAL provided a meaningful summary of the compositional variation in two-dimensions, though the disclosure of the temporal gradient required the use of a third dimension. Only the results of MDSCAL are given.

Fig. 4.24a shows the two-dimensional MDSCAL releve ordination of topsoil mounds with the three major types (groups) superimposed on the scattergram. The stress value was 12.19% which is "fair" by Kruskal's (1964a) criterion. However, considering the ratio of the number of points (releves) to the number of dimensions (species) such a value is relatively low (Young, 1970; Kruskal and Wish, 1978).

The ordination separated out the three preincipal types though some overlap of types occurred suggesting continuity. Type 1 dominated by Ambrosia artemisiifolia and Chenopodium album formed a diffused group in the upper part of the configuration with Ambrosia artemisiifolia dominated sub-type 1a in the right and Chenopodium album dominated sub-type 1b in the left. Type 2 dominated by Daucus carota and Trifolium pratense formed a diffuse group in the lower right of the configuration. Type 3 dominated by Solidago canadensis and Agropyron repens occurred as a somewhat loose group in the middle right of the ordination plane, slightly overlapping with type 2.

Fig. 4.24b shows the MDSCAL ordination using the first and third dimensions. A successional gradient can readily be recognized. This gradient runs from the upper to the lower edge of the configuration with the youngest type 1 at the top and the relatively advanced type 3 at the bottom.

Vegetational composition was related to environmental characteristics by superimposing the scores of the first three components of PCA performed on the environmental data set (Fig. 4.25). The matrix of correlation coefficients between the six environmental variables used in the PCA are given in Table 4.18. Water retaining capacity of soil (WRC) was positively correlated with organic matter content while organic matter content was positively correlated with the percentage of silt and clay. The first PCA component that accounted for 37.35% of the total variation in the environmental data set was primarily a function of soil organic matter, silt and clay and WRC (Table 4.19). The first component appears to represent a complex gradient involving moisture status and nutrient supply. The scores of the first PCA component are superimposed upon the MDSCAL vegetational (releve) ordination in Fig. 4.25a. The large circle sizes should be interpreted as the lower levels of organic matter, silt and clay and WRC. Higher levels of organic matter and silt and clay occur at the top of the configuration which decline in the middle part and then again increase in the lower part. The trend with respect to WRC was not clear. The second component which explains 26.97% of the total variation in the environmental data set is chiefly a function of available phosphorus, pH and NO_3 content of soil and can be labelled as a soil chemistry gradient. The corresponding component scores are superposed on the MDSCAL vegetational ordination in Fig.

4.25b. Smaller circle sizes represent higher levels of available phosphorus but lower levels of pH and NO_3^-. There appears to be a gradual decline in soil pH and NO_3 content from the upper to the lower middle of the ordination plane. Along the same direction, the concentration of available phosphorus gradually rises to the middle part of the configuration and then declines towards the lower edge of the scattergram. The third component that accounts for 15.56% of the total variation in the environmental data set is largely related to silt and clay, WRC and available phosphorus. This component primarily represents the availability of soil moisture and secondarily the supply of nutrients, particularly the available phosphorus. The scores of the third component are superposed on the MDSCAL ordination in Fig. 2.25c. The larger circles correspond to higher proportion of silt and clay but to lower levels of WRC and available phosphorus. The third PCA component largely repeats the trend indicated by the first two components. The level of silt and clay declines from the upper to the middle of the configuration but gradually rises from middle to the lower part of the ordination. By contrast, the levels of available phosphorus and WRC of soil gradually rise from the upper to the middle part of the configuration and decline from the middle to the bottom part of the configuration.

4.4.4 Classification of species

Species with at least 5 occurrences were classified using the sum of squares technique with chord distance as the resemblance function. The resulting dendrogram of 47 species is shown in fig. 4.26. Four species groups could be recognized at a classification efficiency of

20.25%. The group characteristics are as follows:

Group A: This group of 10 species includes 8 perennials and two annuals. *Ambrosia artemisiifolia*, a characteristic of one year old vegetation grouped together with some important elements of 2 to 3 year old vegetation. This is not surprising as the species richness was fairly high in the pioneer stage of succession presumably due to species rich seed bank in the topsoil. The important perennials in this group were *Phleum pratense*, *Chrysanthemum leucanthemum* and *Solidago graminifolia*. This group shows affinity for type 1 of releve clustering.

Group B: This group of 14 species includes five annuals, four biennials and five perennials. Important species in this group include two annuals, *Erigeron strigosus* and *Setaria viridis*, two biennials, *Oenothera parviflora* and *Cirsium vulgare* and the perennials, *Aster simplex*, and *Cirsium arvense*. Species belonging to this group tended to prevail on one to two year old topsoil mounds.

Group C: This group includes 9 species of which the important ones are: *Agropyron repens*, *Solidago canadensis*, *Daucus carota* and *Chenopodium album*. The last mentioned is a characteristic species of one year old vegetation whilst the others are generally dominant in second to fourth year of succession. With a few exceptions, the members of this group show affinity for type 3.

Group D: This group includes 14 species of which two are annuals, *Panicum capillare* and *Medicago lupulina*, two annual-biennial, *Lepidium compestre* and *Lactuca serriola*, two biennials, *Melilotus alba* and *Tragopogon dubius* and 8 perennials of which the important ones are *Agrostis stolonifera*, *Trifolium pratense*, and *Plantago major*. This group shows affinity for type 2.

4.4.5 Ordination of species

A two-dimensional MDSCAL species ordination of topsoil mounds having a stress value of 23.36% was more or less uninterpretable. However, a 3-dimensional solution having a stress value of 19.49% was fairly interpretable and is presented in Fig. 4.27. The 3-D MDSCAL species ordination more or less duplicated the species groupings obtained from species clustering. Members of group A including *Ambrosia artemisiifolia, Sonchus arvensis, Plantago lanceolata, Setaria glauca, Acer pseudoplatanus* (seedlings), *Chrysanthemum leucanthemum* and *Hypericum perforatum*, etc. formed a diffused cluster in the lower part of the configuration. Group B elements including *Oenothera biennis, Cirsium vulgare, Verbascum thapsus* and *Setaria viridis*, etc. formed a loose cluster in the middle left of the ordination. Species belonging to group C, such as *Agropyron repens, Solidago canadensis, Erigeron strigosus, Chenopodium album* and *Daucus carota* etc. occurred together in the middle right part of the configuration. Members of species group D, such as *Agrostis stolonifera, Dactylis glomerata, Plantago major, Melilotus alba, Medicago lupulina, Tragopogan dubius*, etc. formed a diffused cluster, extending from middle left to upper right of the configuration. Beside reproducing the species groupings, the ordination also showed some trends. A successional (temporal) gradient appears, starting from the lower edge of the figure with an early colonizer, *Ambrosia artemisiifolia* and running in an anticlockwise direction through intermediate stage species such as *Cirsium vulgare, Oenothera biennis, Melilotus alba* and *Verbascum thapsus* in the middle left to the species of perennial-dominated stage, including *Agropyron repens, Agrostis stolonifera, Trifolium pratense*, and *Solidago canadensis* in the upper middle portion of the configuration. This trend is somewhat blurred by the occurrence of some elements irrespective of the temporal sequence along the path of the successional trend in the figure. However a flawless reproduction of the successional gradient cannot be expected under the conditions where habitats are created by and subject to severe perturbance.

4.4.6 Life-form and life-span characteristics during the sere

The three vegetation types based on releve clustering were used to represent the age groups. For the topsoil mound data set, classification of releves could not be based directly on the age because the slopes of some mounds had been deposited with freshly excavated topsoil from the adjacent construction sites. Owing to this flat tops often represented older vegetation than the corresponding slopes. While the ages of the mounds, as a whole, were known, the exact ages of some slopes were not available. The vegetation types 1, 2 and 3 represented the successional stages 1, 2 and 3 respectively. Total coverage of each of the life-form or life-span categories in each of the successional stage or type were computed to develop the 'structured tables'.

The total chi-square of structured table of life-forms against successional stages is partitioned into the canonical variates in Table 4.20. The life-form categories were highly correlated with the successional stages as shown by the high chi-square value (2267.81). The first canonical variate that accounted for 76.81% of the total chi-square primarily represents the successional (temporal) gradient. The joint scatter-plot of the successional stages (releve groups) and the life-form categories on the first two canonical variates is presented in Fig. 4.28. Therophytes, therophytes-geophytes, chamaephytes-hemicryptophytes, chamaephytes and to a lesser extent therophytes-hemicrypotophytes and phanerophytes show affinity for successional stage 1. The unexpected association of phanerophytes with stage 1 was mostly because of the presence of a number of seedlings of <u>Acer pseudoplatanus</u> from a nearby tree at a one year old topsoil mound site. Stage 2 (representing 2 to 3 year vegetation) shows affinity for hemicryptophytes whilst stage 3 (representing 4+ year old vegetation) is associated with hemicryptophytes-geophytes and geophytes. Deviations from random expectations for the first lattice, corresponding to the first canonical variate, are plotted in Fig. 4.29. Therophytes that have a high level in stage 1 decline sharply in stage 2 but rise again in stage 3. On the other hand, therophytes-geophytes, hemicryptophytes and phanerophytes exhibit continuous linear decrease from stage 1 to stage 3. By contrast, hemicrytophytes-geophytes and geophytes tend to increase with the vegetational progression.

Table 4.30 decomposes the total chi-square of the life-span against successional stages (releve groups) structured table into independent components. Life-span categories were highly correlated with the successional stage as evidenced by the high chi-square value (χ^2 = 1904.28, df = 10). The first canonical variate accounted for 79.63% of the total chi-square indicating that this component represents the major trend in the structured table. Since the releve groups represent stage of succession, correlated with the age of the vegetation, the first canonical variate isolates the successional (temporal) trend in the vegetation. The simultaneous plot of releve groups coresponding to successional stages and life-span groups on the (first) two canonical variates is given in Fig. 4.30. Stage 1 representing the youngest and pioneer vegetation tends to be associated with annuals, annuals-biennials, annuals-perennials and to a lesser extent with biennials-perennials. Biennials are associated with the successional stage 2 whilst perennials with stage 3. Fig. 4.30 presents the deviation from random expectation for the first lattice. Annuals, annuals-biennials, annuals-perennials and biennials-perennials show a closely similar temporal trend; they decline sharply from stage 1 to stage 2 and subsequently rise somewhat. By contrast, biennials and perennials increase markedly from stage 1 to stage 2 but slightly decline thereafter.

4.4.7 Diversity trends during the sere

Species richness remained unaltered with time in the different seral stages (Fig. 4.32a). However, general diversity (H') slightly increased in stage 2 (2 to 3 yr. old vegetation) but subsequently declined in stage 3 (4+ yr. old vegetation). Equitability showed a pattern similar to that of general diversity (Fig. 4.32b). Dominance concentration was highest in the youngest stage but declined thereafter (Fig. 4.32c).

4.4.8 Discussion and conclusions

This section has described the vegetational pattern on topsoil mounds, the vegetational-environmental relationships and successional trends in community structure and composition. Such phytosociological information is particularly valuable as the topsoil mound ecosystem has not received much attention in the past. However, local construction practices have given rise to a number of topsoil mounds at construction sites and at newly developed subdivisions of the city in recent years on which many of the weed species have found refuge.

The three major vegetation types derived from iterative clustering represented the successional stages. Type 1 or stage 1, representing the one year old community was dominated by short-lived annual species Ambrosia artemisiifolia and Chenopodium album. Type 2 or stage 2, representing the 2 to 3 year old community was dominated by biennials and perennials such as Daucus carota, Melilotus alba and Trifolium pratense. Perennial species, Agropyron repens and Solidago canadensis were dominant in type 3 or stage 3, representing 4+ year old vegetation.

Among the soil properties associated with the vegetation types, organic matter content, available phosphorus and water retaining capacity of soil and exchangeable K^+ and Mg^{++} were most important.

The successional stages recognized were not discrete, instead there was a more or less gradual and a continuous change in species composition, as observed in releve and species ordinations. The releve ordination and to a lesser extent the species ordination also disclosed the successional trends in species composition and the associated trends in environmental factors and factor complexes. Vegetational succession was accompanied by increase in water retaining capacity and the levels of available phosphorus and exchangeable Mg^{++} and a decrease in exchangeable K^+. Soil NO_3^- level which was relative high initially, declined at first but subsequently increased somewhat.

The relationships between life-span and life-form characteristics and the successional stages were successfully examined through the analysis of concentration (AOC). Annuals, annuals-biennials, and annuals-perennials dominated the system in stage 1. Dominance rapidly shifted to biennials and perennials in stage 2. Perennials increased in proportion progressively and dominated the system in stage 3. Such a change in dominance with respect to life history strategy obviously involves a gradual shift from r-strategy to K-strategy. The sequence of life-form invasion during the sere essentially involved dominance of therophytes in stage 1, hemicryptophytes in stage 2, and geophytes and hemicryptophytes-geophytes in stage 3. This succession pattern of life-form dominance differs from that of vacant lots where 4+ year old vegetation was dominated by hemicryptophytes. One apparent explanation for this disparity is the difference in the way the vacant lots and topsoil mounds are managed. Whereas the vacant lots are mowed annually, the vegetation of topsoil mounds is almost never mowed. In vacant lots mowing prevents the dominance of Solidago canadensis but in the absence of mowing on topsoil mounds S. canadensis is able to attain dominance (see section 4.3.8 for detailed explanation).

Succession-diversity patterns documented for topsoil mounds somewhat differed from those of old fields and vacant lots. Species richness did not change appreciably with the successional development. However, both general diversity and equitability increased from stage 1 to stage 2 and declined subsequently in stage 3. The trend in species richness did not reflect the colonization pattern of defaunated mangrove islands (Simberloff and Wilson, 1969, 1970). Nonetheless, the observed changes in the life-history strategy of the successional dominants and greater stability in the advanced stages of succession as evidenced by the dominance of K-strategists and the lesser degree of between releve variability suggest the operation of an r-K selection continuum (cf. Tramer, 1975) in the topsoil mound ecosystem similar to that observed for the other two habitat types. The correlated changes in general diversity (H') and equitability (E') observed here, once again corroborate Tramer's (1969) hypothesis that "H' varies as a function of E'" in early successional communities.

Dominance concentration exhibited a contrasting trend to general diversity along the successional progression. Dominance was highest in stage 1, declined sharply in stage 2 and increased slightly in stage 3. The highest levels of dominance concentration in stage 1 and 3 corresponds well with the allelopathic nature of the dominants of these stages. The dominants of stage 1 have been shown to exert non-competitive allelopathic influence (*Ambrosia artemisiifolia*: Raynal and Bazzaz, 1975; Jackson and Willemsen, 1976; *Chenopodium album*: Caussanel, 1979). Similarly, the allelopathic properties of the dominants of stage 3 are also known (*Solidago canadensis*: Smith, 1969; *Ag[illegible]ron repens*: Welbank, 1960; Toai and Linscott, 1979).

Based on the results of this section a few generalized statements regarding the secondary sere can be made. (1) A more or less constant species richness throughout the successional stages examined clearly suggests that the diaspore of most of the species to occur during the sere was already present in the topsoil seed bank which can be taken as partially supporting evidence for Egler's (1954) "initial floristic composition" hypothesis. (2) The presence and abundance of many allelopathic species throughout the sere seems to favour the "inhibition" model (Connell and Slatyer, 1977) as the most important mechanism of succession on topsoil mounds.

Table 4.1 Average cover, its variance and origin of the 86 species (with greater than 3 occurrences) in the old field habitat.

I = introduced, N = native. Nomenclature follows Gleason (1963)

	SPECIES	LIFE-FORM	ORIGIN	AVERAGE COVER	VARIANCE
1	Acer negundo	Ph	N	0.0677	0.0765
2	Achillea millefolium	Ch	I	0.1949	0,9104
3	Agropyron repens	G	I	3.7563	35.346
4	Agrostis stolinifera	H	I	6.3050	108.675
5	Ambrosia artemisiifolia	Th	N	0.1080	0.2729
6	Anagallis arvensis	Th	I	0.0127	0.0051
7	Arctium minus	H	I	0.3432	1.5756
8	Arrhenatherum elatius	H	I	4.5550	360.503
9	Asclepias syriaca	G	N	0.2457	0.4967
10	Aster ericoides	H	N	0.0169	0.0125
11	Aster novae-angliae	H	N	0.4131	0.975
12	Aster sagittifolius	H	N	0.6440	6.107
13	Aster simplex	H	N	1.5360	18.967
14	Brassica kaber	Th	I	0.1864	0.3110
15	Bromus inermis	H,G	I	0.3050	1.0856
16	Capsella bursa-pastoris	Th	I	0.0105	0.0036
17	Carex sparganioides	H,G	N	0.0720	0.2533
18	Carex vulpinoidea	H,G	N	0.0233	0.0363

Table 4.1 (cont'd)

	SPECIES	LIFE-FORM	ORIGIN	AVERAGE COVER	VARIANCE
19	Cerastium vulgatum	Ch	I	0.0233	0.0106
20	Chrysanthemum leucanthemum	H	I	0.9449	5.819
21	Cichorium intybus	H	I	0.0805	0.1067
22	Cirsium arvense	G	I	0.3474	1.027
23	Cirsium vulgare	H	I	0.0945	0.1634
24	Cornus stolonifera	Ph	N	0.0932	0.4955
25	Crataegus punctata	Ph	N	0.1271	0.5221
26	Dactylis glomerata	H	I	3.6991	149.394
27	Daucus carota	H	I	4.01695	78.8235
28	Dianthus armeria	Th,H	I	0.0190	0.0129
29	Dipsacus sylvestris	H	I	0.1016	0.3143
30	Echium vulgare	H	I	0.2245	1.2846
31	Equisetum arvense	G	I	0.4343	5.267
32	Erigeron annuus	Th	N	0.0381	0.03485
33	Erigeron strigosus	Th	N	2.2245	17.660
34	Fragaria virginiana	H	N	2.1779	91.369
35	Festuca pratensis	H	I	0.2500	1.229
36	Festuca rubra	H	I	2.0932	83.008
37	Gallium mollugo	H	I	0.0847	0.3175
38	Geum aleppicum	H	N	0.2627	2.2113
39	Glecoma hedracea	H	I	0.0550	0.0845
40	Hypericum perforatum	H	I	2.2817	34.005

Table 4.1 (cont'd)

	SPECIES	LIFE-FORM	ORIGIN	AVERAGE COVER	VARIANCE
41	<u>Juncus dudleyi</u>	H	N	0.0572	0.0837
42	<u>Lactuca serriola</u>	H,Th	I	1.3644	20.190
43	<u>Leonorus cardiaca</u>	H	I	1.3135	20.695
44	<u>Lepidium compestre</u>	H,Th	I	0.0572	0.0624
45	<u>Linaria vulgaris</u>	G,H	I	0.1525	0.3558
46	<u>Lychnis alba</u>	H	I	0.5635	3.344
47	<u>Medicago lupulina</u>	Th	I	2.4915	53.914
48	<u>Medicago sativa</u>	H	I	0.0932	0.3785
49	<u>Melilotus alba</u>	H	I	0.4661	2.622
50	<u>Melilotus officinalis</u>	H	I	0.1440	0.4106
51	<u>Nepeta cataria</u>	H	I	2.0847	60.791
52	<u>Oenothera biennis</u>	H	N	0.0148	0.0109
53	<u>Oenothera parviflora</u>	H	N	0.0169	0.0125
54	<u>Oxalis stricta</u>	Th,G	N	0.2669	0.9131
55	<u>Phalaris arundinacea</u>	G,H	I	2.6016	108.413
56	<u>Phleum pratense</u>	H	I	12.6144	388.933
57	<u>Plantago lanceolata</u>	H	I	0.4766	1.091
58	<u>Plantago major</u>	H	I	0.25423	0.6559
59	<u>Poa compressa</u>	H	I	3.1440	53.406
60	<u>Poa pratensis</u>	H	I	17.4915	578.248
61	<u>Populus deltoides</u>	Ph	N	0.0169	0.0125
62	<u>Potentilla argentea</u>	H	I	0.0127	0.0062
63	<u>Potentilla norvegica</u>	H,Th	I,N	0.0423	0.02810

Table 4.1 (cont'd)

	SPECIES	LIFE-FORM	ORIGIN	AVERAGE COVER	VARIANCE
64	Potentilla recta	H	I	0.3389	0.532
65	Prunella vulgaris	H	I	0.1122	0.1106
66	Rhamnus cathartica	Ph	I	0.1949	0.9104
67	Rhamnus frangula	Ph	I	0.0211	0.0187
68	Rudbeckia serotina	H	N	0.1525	0.4209
69	Rumex crispus	H	I	0.449	1.4210
70	Silene cucubalus	H	I	0.6059	2.781
71	Sisymbrium altissimum	Th	I	0.3262	1.911
72	Sisyrinchium montanum	H	N	0.0296	0.0183
73	Solidago canadensis	H,G	N	5.76059	181.958
74	Solidago graminifolia	H,G	N	0.1991	0.4450
75	Taraxacum officinale	H	I	0.4851	0.882
76	Thlaspi arvense	Th	I	0.1694	0.6206
77	Tragopogon dubius	H	I	0.0911	0.0669
78	Tragopogon prantense	H	I	0.0466	0.0597
79	Trifolium hybridium	H	I	0.6610	4.020
80	Trifolium pratense	H	I	4.0000	48.4915
81	Trifolium repens	Ch,H	I	0.2161	0.7152
82	Tussilago farfara	H,G	I	0.0423	0.0922
83	Verbascum thapsus	H	I	0.1525	0.2457
84	Vicia cracca	H	I	0.4957	2.160
85	Viola arvensis	Th	I	0.0847	0.0313
86	Vitis ripparia	Ph	N	0.0190	0.0129

Table 4.2. Average cover and variance of major species in types and sub-type for old field data set.

	MEAN	VARIANCE
TYPE 1		
Solidago canadensis	22.16	509.307
Nepeta cataria	9.8	217.667
Leonurus cardiaca	6.2	69.3333
Lactuca serriola	5.92	69.7225
Erigeron strigosus	4.86	58.5108
Aster simplex	4.72	52.46
Poa compressa	2.92	23.9933
Lychnis alba	2.4	11.6667
Daucus carota	2.18	8.72333
Medicago lupilina	2.14	7.69833
Chrysanthemum leucanthemum	2.1	19.9167
Agrostis stolonifera	1.8	11.5833
Equisetum arvense	1.7	22.1667
Phleum pratense	1.64	19.5525
Sisymbrium altissimum	1.54	7.37332
TYPE 3		
Poa pratensis	61.1364	349.838
Festuca rubra	11.1364	356.981
Agropyron repens	7.54545	38.5455
Agrostis stolonifera	6.09091	106.182
Vicia cacca	1.59091	7.30087
Dactylis glomerata	1.56818	19.1499
Fragaria virginiana	1.47727	6.58279
Aster sagittifolius	1.38636	10.8555
Cirsium arvense	1.36364	3.45671
Geum aleppicum	1.27273	10.9221
Solidago canadense	1.11364	1.76028
Aster novae-angliae	1.11364	1.76028
Aster simplex	1	10.1429

Table 4.2 (cont'd.)

	MEAN	VARIANCE
TYPE 2		
Phleum pratense	20.1268	498.855
Poa pratensis	9.74648	103.935
Agrostis stolonifera	7.95775	135.785
Arrhenatherum elatius	7.28169	581.605
Daucus carota	5.76761	63.6774
Dactylis glomerata	5.47887	234.732
Poa compressa	4.09859	77.433
Phalaris arundinaceae	3.92958	167.952
Agropyron repens	3.84155	38.3504
Hypericum perforatum	3.61268	52.0943
Medicago lupulina	3.34507	84.8899
Fragaria virginiana	3.14085	148.037
Erigeron strigosus	1.88028	5.65332
Solidago canadensis	1.40493	6.03815
Trifolium hybridum	1.01408	6.30694
Sub-type 2a		
Phleum pratense	45.8	278.5
Poa pratensis	14.24	131.523
Daucus carota	8.36	84.8233
Dactylis glomerata	6.74	122.607
Trifolium pratense	5.9	46.4583
Agrostis stolonifera	3.96	32.3733
Agropyron repens	3.81	41.0067
Erigeron strigosus	1.96	6.62333
Silene cucubalus	1.96	9.04
Hypericum perforatum	1.12	4.36
Festuca pratensis	1.02	4.96833
Sub-type 2b		
Arrhenatherum elatius	85.8333	54.1667
Poa pratensis	4	6.3
Poa compressa	2	3.2
Hypericum perforatum	1.91667	3.44167
Silene cucubalus	1.75	3.175
Echium vulgare	1.58333	7.64167
Bromus inermis	1.00	4.00
Agropyron repens	0.916667	1.64167
Potentilla recta	0.833333	0.566667
Daucus carota	0.583333	0.641667

Sub-type 2c

	MEAN	VARIANCE
Agrostis stolonifera	11.6	190.913
Poa pratensis	7.8	82.8821
Trifolium pratense	7.6	80.3487
Phleum pratense	7.1	65.1179
Phalaris arundinaceae	6.925	280.276
Poa compressa	6.775	121.102
Dactylis glomerata	5.5125	340.224
Hypericum perforatum	5.425	82.584
Medicago lupulina	5.425	141.263
Fragaria virginiana	5.2	254.882
Daucus carota	4.925	52.8404
Agropyron repens	4.3	41.8564
Erigeron strigosus	2.1125	5.4679
Solidago canadenis	1.85	9.09231
Trifolium hybridum	1.7375	10.0383

Table 4.3 Averages of a environmental variables for the types and sub-types of old field habitat.

Variable	Main Types 1	 2	 3	Sub-types 2a	 2b	 2c
1. pH	7.44 ± 0.094	7.54 ± 0.043	7.03 ± 0.086	7.46 ± 0.057	7.35 ± 0.914	7.62 ± 0.051
2. Organic Matter %	9.50 ± 0.952	8.86 ± 0.138	9.99 ± 0.115	9.18 ± 0.238	9.06 ± 0.158	8.63 ± 0.189
3. No_3^- (ppm)	7.89 ± 0.550	7.24 ± 0.389	6.690 ± 0.690	7.95 ± 0.487	8.21 ± 0.894	6.66 ± 0.596
4. Silt + Clay %	13.16 ± 1.255	16.54 ± 0.856	22.07 ± 1.404	19.39 ± 1.965	15.34 ± 2.096	14.94 ± 0.751
5. WRC %	43.960 ± 2.166	46.85 ± 1.213	60.93 ± 1.871	48.82 + 2.116	44.29 ± 1.630	37.3100 ± 1.641
6. P (ppm)	11.89 ± 0.726	12.43 ± 0.477	12.82 ± 0.906	11.6700 ± 0.459	17.33 ± 1.187	12.175 ± 0.718
7. K^+ (ppm)	182 ± 33.748	191.90 ± 16.80	215.90 ± 22.712	194.44 ± 23.742	320.83 ± 10.034	170.97 ± 24.606
8. Ca^{++} (ppm)	1594 ± 91.119	1680.28 ± 59.65	1629.55 ± 91.088	1494 ± 115.734	2000 ± 0.0	1748.75 ± 71.532
9. Mg^{++} (ppm)	248.4 ± 32.234	275 ± 17.973	203.18 ± 18.193	232 ± 29.426	408.33 ± 32.804	281.87 ± 24.005

Table 4.4 Correlation coefficients between 9 environmental variables for old field data set.

	1 pH	2 organic matter	3 NO_3	4 silt + clay	5 WRC	6 P	7 K^+	8 Ca^{++}
2. Organic matter	-0.4058							
3. NO_3^-	0.4058	0.1663						
4. Silt + Clay	0.3920	0.1820	-0.1161					
5. WRC	-0.5595	0.6159	0.0627	0.3034				
6. P	-0.1722	0.1318	-0.2718	-0.0331	0.2858			
7. K^+	-0.3441	0.1899	-0.2159	-0.0010	0.4006	-0.0996		
8. Ca^{++}	0.3249	-0.0575	0.0857	0.0024	0.0057	0.0756	-0.0996	
9. Mg^{++}	0.3217	-0.0037	0.1778	-0.1285	-0.0080	-0.0258	-0.1989	0.5904

Table 4.5 PCA of environmental data of the old field habitat. Nine variables were used.

Component	Eigenvalue	% of total variance accounted for	Cumulative variance %	Ranked Eigenvector Elements	Associated variable
1	2.7242	30.269	30.269	0.49846	pH
				-0.46381	WRC %
				-0.37725	Exchangeable K^+
				-0.36470	Organic matter %
2	1.6802	18.669	48.939	0.57517	Exchangeable K^+
				0.55958	Exchangeable Ca^{++}
				0.35463	WRC %
				0.34215	Organic matter %
3	1.4152	15.724	64.664	0.58922	Available P
				-0.46032	NO_3
				0.41134	Exchangeable K^+
				-0.29005	Silt + Clay %

Table 4.6 Partition of chi-square in the AOC of life-form categories and releve groups for the old field data set.

Canonical variate (i)	Canonical correlation (R_i)	Chi-square	Percentage	Cumulative Percentage
1	0.5691	3775.511	48.465	48.465
2	0.5143	3084.057	39.589	88.054
3	0.2825	930.5567	11.9453	99.999
TOTAL		χ^2 = 7790.126 df = 24	100	

Table 4.7 Partition of chi-square in the AOC of life-span categories and releve groups for the old field data set.

Canonical variate (i)	Canonical correlation (R_i)	Chi-square	Percentage	Cumulative Percentage
1	0.5484	3506.855	53.948	53.948
2	0.4817	2705.089	41.614	95.562
3	0.1572	288.434	4.437	100.00
TOTAL		χ^2 = 6500.379 df = 15	100	

Table 4.8 Average cover, its variance and origin of 73 species (with greater than 3 occurrences) in the vacant lot habitat. N, native, I, introduced. Nomenclature follows Gleason (1963).

	SPECIES	ORIGIN	AVERAGE COVER	VARIANCE
1	*Acer negundo*	N	0.205882	2.68627
2	*Achillea millefolium*	I	0.0617647	0.199265
3	*Agropyron repens*	I	4.54118	57.7215
4	*Agrostis stolonifera*	I	5.14118	109.069
5	*Ambrosia artemisiifolia*	N	3.87647	106.279
6	*Arctium minus*	I	0.352941	1.70728
7	*Asclepias syriaca*	N	0.211765	0.222479
8	*Aster ericoides*	N	0.223529	0.354202
9	*Aster laevis*	N	0.0470588	0.0691877
10	*Aster novae-angliae*	N	0.0458824	0.745308
11	*Aster sagittifolius*	N	0.0323529	0.0264706
12	*Aster simplex*	N	0.752941	1.78347
13	*Barbarea vulgaris*	I	0.105882	0.137465
14	*Brassica kaber*	I	0.835294	7.3163
15	*Bromus inermis*	I	0.0470588	0.0632353
16	*Centaurea nigra*	I	0.0329412	1.19972
17	*Chenopodium album*	I,N	0.0326471	1.07444
18	*Chrysanthemum leucantuemum*	I	1.21176	3.87724

TABLE 4.8 (cont'd)

	SPECIES	ORIGIN	AVERAGE COVER	VARIANCE
19	*Cichorium intybus*	I	0.847059	2.94062
20	*Cirsium arvense*	I	0.235294	0.688025
21	*Cirsium vulgare*	I	0.352941	0.862045
22	*Convolvulus arvensis*	I	0.0470588	0.0453782
23	*Dactylis glomerata*	I	0.0588235	0.127451
24	*Daucus carota*	I	9.41176	82.8641
25	*Digitaria sanguinalis*	I	0.138235	0.40105
26	*Dipsacus sylvestris*	I	0.141176	0.336975
27	*Echium vulgare*	I	0.1	0.207143
28	*Equisetum arvense*	I	0.144118	1.19401
29	*Erigeron canadensis*	N	0.423529	2.02682
30	*Erigeron strigosus*	N	0.485294	1.29219
31	*Festuca pratensis*	I	0.270588	1.00924
32	*Fragaria virginiana*	N	0.0941176	0.229132
33	*Hieracium floribundum*	I	0.1	0.135714
34	*Hypericum perforatum*	I	0.132353	0.143732
35	*Juncus dudleyi*	N	0.0705882	0.29859
36	*Lactuca serriola*	I	1.28529	7.04933
37	*Lepidium compestre*	I	0.0647059	0.0582633
38	*Lolium perenne*	I	0.1500	0.457143
39	*Medicago lupulina*	I	6.15294	155.863
40	*Medicago sativa*	I	0.0588235	0.103041
41	*Melilotus alba*	I	5.77647	98.2233

TABLE 4.8 (cont'd)

	SPECIES	ORIGIN	AVERAGE COVER	VARIANCE
42	*Melilotus officinalis*	I	0.841176	11.7751
43	*Oenothera biennis*	N	0.185294	0.480882
44	*Onopordum acanthium*	I	0.0647059	0.153501
45	*Oxalis stricta*	N	0.0176471	0.00861345
46	*Phalaris arundinacea*	I	0.100	0.35
47	*Phleum pratense*	I	2.20588	13.091
48	*Plantago lanceolata*	I	0.267647	0.544328
49	*Plantago major*	I	0.335294	0.274632
50	*Poa annua*	I	0.0823529	0.147399
51	*Poa compressa*	I	2.85294	22.3382
52	*Poa pratensis*	I	0.664706	1.50825
53	*Polygonum convolvulus*	I	0.0705882	0.114006
54	*Polygonum lapathifolium*	I	0.411765	5.31653
55	*Polygonum persicaria*	I	0.541176	11.037
56	*Populus tremuloides*	N	0.0705882	0.0842437
57	*Potentilla norvegica*	N, I	0.0764706	0.128011
58	*Prunella vulgaris*	I	0.0735294	0.0830707
59	*Salsola pestifer*	I	0.0941176	0.205322
60	*Setaria viridis*	I	0.0294118	0.0259104
61	*Silene cucubalus*	I	0.0852941	0.124335
62	*Sisymbrium altissimum*	I	0.0235294	0.0172969
63	*Solidago canadensis*	N	1.82941	8.34853
64	*Solidago graminifolia*	N	0.494118	3.17556

TABLE 4.8 (cont'd)

	SPECIES	ORIGIN	AVERAGE COVER	VARIANCE
65	*Sonchus arvensis*	I	0.129412	0.631863
66	*Taraxacum officinale*	I	1.45294	2.74776
67	*Tragopogon dubius*	I	0.147059	0.165616
68	*Trifolium hybridum*	I	1.67059	10.2711
69	*Trifolium pratense*	I	12.4765	285.511
70	*Trifolium repens*	I	0.152941	0.464426
71	*Verbena hastata*	N	0.0264706	0.023844
72	*Viburnum acerifolium*	N	0.0294118	0.0482318
73	*Vicia cracca*	I	0.0823529	0.12409

Table 4.9 Average cover and variance of species for the types recognized in the vacant lot habitat.

		MEAN	VARIANCE
	TYPE 1:		
1.	*Ambrosia artemisiifolia*	18.4615	456.103
2.	*Agropyron repens*	7.3846	1.935
3.	*Brassica kaber*	3.9230	36.5769
4.	*Polygonum persicaria*	3.4615	66.2692
5.	*Medicago lupulina*	2.8461	7.8076
6.	*Polygonum lapathifolium*	2.6923	30.5641
7.	*Melilotus officinalis*	2.6153	68.2564
8.	*Melilotus alba*	2.0769	47.5769
9.	*Trifolium pratense*	1.8461	8.3076
10.	*Erigeron canadense*	1.7692	8.8589
11.	*Poa compressa*	1.6153	8.5897
12.	*Solidago canadensis*	1.4230	8.6185
13.	*Chenopodium album*	1.3846	3.5897
14.	*Lactuca serriola*	1.3653	1.2564
15.	*Taraxacum officinale*	0.9230	1.9102
	GROUP 2:		
1.	*Agropyron repens*	12.2727	122.618
2.	*Poa compressa*	6.5000	132.45
3.	*Daucus carota*	3.7272	18.6182
4.	*Phleum pratense*	3.4090	23.9409
5.	*Trifolium hybridum*	2.7272	18.8182
6.	*Medicago lupulina*	2.6363	9.2045
7.	*Chrysanthemum leucanthemum*	2.4545	10.0727
8.	*Taraxacum officinale*	2.0909	7.8909
9.	*Solidago canadensis*	1.5909	3.94091
10.	*Melilotus officinalis*	1.4545	3.2727
11.	*Rumex crispus*	1.4090	3.7409
12.	*Cichorium intybus*	1.3636	6.2545
13.	*Trifolium pratense*	1.0454	1.5227
14.	*Poa pratensis*	1.0909	3.0909
15.	*Arctium minus*	1.0000	9.0000

Table 4.9 (cont'd)

		MEAN	VARIANCE
TYPE 3:			
1.	*Agrostis stolonifera*	35.000	91.6667
2.	*Melilotus alba*	10.1429	63.4762
3.	*Daucus carota*	8.8571	62.4762
4.	*Trifolium pratense*	7.8571	57.1429
5.	*Phleum pratense*	6.000	28.6667
6.	*Ambrosia artemisiifolia*	3.000	7.3333
7.	*Solidago canadensis*	2.8571	12.8095
8.	*Taraxacum officinale*	2.8571	5.1428
9.	*Aster simplex*	2.5714	7.6190
10.	*Brassica kaber*	2.2857	5.9047
11.	*Agropyron repens*	1.0000	2.0000
12.	*Erigeron strigosus*	0.8571	3.4761
13.	*Poa compressa*	0.8571	1.1428
14.	*Prunella vulgaris*	0.7142	0.5714
15.	*Hieraceum floribundum*	0.5000	0.2500
TYPE 4:			
1.	*Melilotus alba*	27.50	79.1667
2.	*Daucus carota*	13.50	28.0556
3.	*Agrostis stolonifera*	8.40	24.7111
4.	*Agropyron repens*	7.50	16.7222
5.	*Trifolium hybridum*	3.80	35.9556
6.	*Trifolium pratense*	3.00	7.3333
7.	*Ambrosia artemisiifolia*	2.80	1.9555
8.	*Centaurea repens*	2.80	3.5111
9.	*Medicago lupulina*	2.30	4.2333
10.	*Solidago canadensis*	2.30	2.6777
11.	*Lactuca serriola*	1.50	1.3888
12.	*Oenothera parviflora*	1.50	2.2777
13.	*Poa compressa*	1.50	2.0555
14.	*Cichorium intybus*	1.15	4.6694
15.	*Poa pratensis*	1.1	1.6555

Table 4.9 (cont'd)

	MEAN	VARIANCE
TYPE 5:		
1. *Medicago lupulina*	34.50	358.056
2. *Trifolium pratense*	10.70	28.2333
3. *Daucus carota*	10.50	56.0556
4. *Lactuca serriola*	3.90	22.9889
5. *Taraxacium officinale*	2.70	2.0111
6. *Poa compressa*	2.20	2.6222
7. *Agrostis stolonifera*	1.90	9.2111
8. *Aster simplex*	1.50	2.7222
9. *Poa pratensis*	1.50	2.7222
10. *Trifolium hybridum*	1.50	4.500
11. *Festuca pratensis*	1.40	6.4888
12. *Phleum pratense*	1.40	2.4888
13. *Rumex crispus*	0.80	0.8444
14. *Solidago canadensis*	0.80	0.8444
15. *Ambrosia artemisiifolia*	0.7	0.6777
TYPE 6:		
1. *Daucus carota*	7.1111	10.1111
2. *Chrysanthemum leucanthemum*	3.000	10.250
3. *Solidago canadensis*	2.6666	21.7500
4. *Medicago lupulina*	2.1111	3.6111
5. *Poa compressa*	2.000	3.750
6. *Trifolium pratense*	1.2222	3.1944
7. *Trifolium hybridum*	1.111	5.3611
8. *Lactuca serriala*	1.000	2.750
9. *Digitaria sanguinalis*	0.8888	2.8611
10. *Melilotus alba*	0.8888	2.8611
11. *Taraxacum officinale*	0.7777	0.8819
12. *Ambrosia artemisiifolia*	0.7222	0.4444
13. *Silene cucubalus*	0.6944	0.7152
14. *Phleum pratense*	0.6666	2.750
15. *Plantago lanceolata*	0.6666	1.1875

Table 4.9 (cont'd)

TYPE 7:	MEAN	VARIANCE
1. *Trifolium pratense*	32.880	318.610
2. *Daucus carota*	15.240	132.107
3. *Melilotus alba*	3.880	26.276
4. *Poa compressa*	3.560	5.590
5. *Phleum pratense*	3.160	16.140
6. *Aster ericoides*	2.920	40.243
7. *Agropyron repens*	2.760	9.5858
8. *Medicago lupulina*	2.680	19.560
9. *Solidago canadensis*	1.780	10.2725
10. *Trifolium hybridum*	1.440	6.4233
11. *Cichorium intybus*	1.360	3.3233
12. *Ambrosia artemisifolia*	1.080	2.0558
13. *Taraxacum officinale*	1.060	0.8400
14. *Lactuca serriola*	1.020	9.885
15. *Chrysanthemum leucanthemum*	0.98	2.0933

Table 4.10 Type averages of environmental variables for vacant lot data set. Mean values ± standard error. Numbers in parenthesis indicate sample size when it is smaller than the number of releves in the type.

	Type 1	Type 2	Type 3	Type 4	Type 5	Type 6	Type 7
pH	7.9300 ±0.0520	8.0355 ±0.0573	7.3814 ±0.1004	7.8510 ±0.0346	7.9060 ±0.0368	7.9867 ±0.0576	7.7940 ±0.0520
Organic Matter %	6.8046 ±0.7059	7.1773 ±0.3777	8.8429 ±0.2809	6.8550 ±0.3693	6.9350 ±0.2473	6.6833 ±0.3175	7.1720 ±0.2167
NO_3^- ppm	8.4107 ±0.0639	6.8955 ±0.7617	6.6714 ±0.8655	5.6500 ±0.3628	6.9100 ±0.3628	11.5856 ±1.8691	7.8564 ±0.7954
Silt + Clay %	14.6654 ±1.6803	6.6600 ±1.7787	23.3671 ±2.3596	10.3610 ±1.2818	7.0230 ±1.4592	6.0811 ±0.8949	9.2279 ±1.3916
WRC %	37.9415 ±3.1479	42.8900 ±1.7955	53.0543 ±1.2744	34.4340 +1.3011	38.7460 ±1.7447	37.3100 ±1.8479	42.7884 ±1.1398
Phosphorus ppm	10.7885 ±1.1474	8.2727 ±0.7417	9.8929 ±0.7152	11.2500 ±0.6347	10.2000 ±0.8513	11.1667 ±0.5221	11.2800 ±0.9519
Ca^{++} (ppm)	2000 ±0	1963.3 ±63.3	2000 ±0	-	2000 [1]	2000 ±0	2000 ±0 [14]
Mg^{++} (ppm)	358.84 ±56.55	559.90 ±17.08	600 ±2.0	-	4.10 [1]	553.3 ±42.49	542.13 ±97.11 [14]
K^+ (ppm)	69.61 ±5.47	58.18 ±8.42	75.0 ±1.58	-	20 [1]	65.0 ±2.50	62.67 ±3.5 [14]

Concentrations above 2000 ppm were regarded as 2000 ppm.

Table 4.11 PCA of Environmental data.

	1. pH	2. organic matter	3. NO_3^-	4. silt + clay	5. WHC
2. Organic Matter	-0.4304				
3. NO_3^-	0.2113	-0.1980			
4. Silt + Clay	-0.4337	0.2889	-0.2167		
5. WRC	-0.4368	0.7151	-0.2362	0.2238	
6. Phosphorus	-0.1285	-0.1467	-0.0510	0.0498	-0.1671

Table 4.12 PCA of environmental data of the vacant lots. Six variables listed in Table 4.11 were used.

Component	Eigenvalue	% of total variance accounted for	Cumulative variance %	Ranked Eigenvector Elements	Associated variable
1	2.4219	40.365	40.365	-0.52725	Org. matter
				-0.52281	WRC %
				-0.47273	pH
2	1.2023	20.038	60.403	0.76286	Available P
				0.34578	Silt + Clay
				-0.29571	WRC %
3	0.8548	14.247	74.6511	0.91911	NO_3^-
				0.29051	pH
				0.19328	Available P

Table 4.13 Partition of chi-square in the AOC of life-form categories and releve groups for the vacant lot data set.

Canonical variate (i)	Canonical correlation (R_i)	Chi-square	Percentage	Cumulative Percentage
1	0.5072	1572.478	71.732	71.732
2	0.2684	440.342	20.087	91.820
3	0.1712	179.313	8.179	100.00
TOTAL		χ^2 = 2192.134 df = 18	100	

Table 4.14 Partition of chi-square in the AOC of life-span categories and releve groups for the vacant lot data set.

Canonical variate (i)	Canonical correlation (R_i)	Chi-square	Percentage	Cumulative Percentage
1	0.5838	1018.842	94.399	94.399
2	0.1337	105.937	4.953	99.35
TOTAL		χ^2 = 2124.779 df = 12	100	

Table 4.15 Average cover, its variance and origin of 71 species (with greater than 3 occurrences) in the topsoil mound habitat. N, native; I, introduced. Nomenclature follows Gleason (1963).

	SPECIES	ORIGIN	AVERAGE COVER	VARIANCE
1	*Acer negundo*	N	0.07812	0.1067
2	*Acer pseudoplatanus*	I	0.3333	2.2269
3	*Achillea millefolium*	I	0.1770	0.6966
4	*Agropyron repens*	I	15.2813	316.52
5	*Agrostis stolonifera*	I	2.0416	20.338
6	*Ambrosia artemisiifolia*	N	12.2604	483.319
7	*Arctium minus*	I	0.2500	0.4042
8	*Asclepias syriaca*	N	0.0416	0.3014
9	*Aster novae-angliae*	N	0.1145	0.1834
10	*Aster simplex*	N	1.7500	7.2446
11	*Barbarea vulgaris*	I	0.3333	1.5035
12	*Bidens cernua*	I	0.0833	0.0673
13	*Brassica kaber*	I	0.9166	4.5886
14	*Capsella bursa-pastoris*	I	0.0312	0.0293
15	*Carex vulpinoidea*	N	0.0468	0.04163
16	*Chenopodium album*	I	6.6250	319.346
17	*Chenopodium hybridium*	I	1.2708	28.1591
18	*Chrysanthemum leucanthmum*	I	1.0520	3.5557
19	*Cichorium intybus*	I	0.3541	0.8187
20	*Cirsium arvense*	I	1.1093	6.6274
21	*Cirsium vulgare*	I	0.9583	3.7429

Table 4.15 (continued)

	SPECIES	ORIGIN	AVERAGE COVER	VARIANCE
22	*Dactylis glomerata*	I	0.3125	0.8151
23	*Daucus carota*	I	6.2916	61.3599
24	*Dipsacus sylvestris*	I	0.1458	0.4250
25	*Echium vulgare*	I	0.1250	0.2819
26	*Equisetum arvense*	I	0.1041	0.2229
27	*Erigeron canadensis*	N	0.2083	0.7216
28	*Erigeron strigosus*	N	2.8750	35.3452
29	*Hypericum perforatum*	I	0.3333	0.9078
30	*Lactuca serriola*	I	6.3958	103.861
31	*Lepidium campestre*	I	0.6458	1.5421
32	*Lychnis alba*	I	0.1041	0.1378
33	*Medicago lupulina*	I	1.8958	26.4357
34	*Melilotus alba*	I	2.5208	25.446-
35	*Melilotus officinalis*	I	0.2083	0.6790
36	*Monarda fistulosa*	N	0.0312	0.0293
37	*Nepeta cataria*	I	0.1979	0.7099
38	*Oenothera biennis*	N	0.0677	0.0498
39	*Oenothera parviflora*	N	0.8333	6.5673
40	*Oxalis stricta*	N	0.0937	0.0814
41	*Panicum lanuginosum*	N	0.6250	5.9840
42	*Panicum capillare*	N	1.7395	44.8908
43	*Phleum pratense*	I	3.7812	23.8501
44	*Plantago lanceolata*	I	0.1875	0.1875

Table 4.15 (continued)

	SPECIES	ORIGIN	AVERAGE COVER	VARIANCE
45	*Plantago major*	I	0.1770	0.1727
46	*Poa compressa*	I	3.1354	3.7525
47	*Poa pratensis*	I	2.0415	31.2323
48	*Polygonum convolvulus*	I	0.3333	0.5248
49	*Polygonum persicaria*	I	0.2552	0.2752
50	*Potentilla norvegica*	I	0.0729	0.1067
51	*Potentilla recta*	I	0.0729	0.0504
52	*Rubus* sp.	-	0.1458	0.2123
53	*Rumex crispus*	I	0.3802	0.3536
54	*Setaria glauca*	I	0.1354	0.1568
55	*Setaria viridis*	I	0.3125	0.7726
56	*Silene cucubalus*	I	0.0525	0.0492
57	*Sisymbrium altissimum*	I	0.0364	0.0265
58	*Solidago canadensis*	N	6.4687	73.7703
59	*Solidago graminifolia*	N	0.8125	8.5811
60	*Solidago juncea*	N	0.1927	1.0378
61	*Sonchus arvensis*	I	0.2708	0.4038
62	*Taraxacum officinale*	I	0.2343	0.1367
63	*Trifolium hybridum*	I	0.2291	0.3825
64	*Trifolium pratense*	I	3.5052	59.7087
65	*Trifolium repens*	I	0.1250	0.2319
66	*Tragopogon dubius*	I	0.1145	0.1302

Table 4.15 (continued)

	SPECIES	ORIGIN	AVERAGE COVER	VARIANCE
67	*Tussilago farfara*	I	0.2083	0.7641
68	*Verbascum thapsus*	I	0.1666	0.2583
69	*Verbena urticifolia*	N	0.0572	0.0884
70	*Vicia cracca*	I	0.0520	0.0344
71	*Vitis riparia*	N	0.1250	0.1968

Table 4.15 Average cover and variance of major species in the types and sub-types recognized in the topsoil mounds habitat.

	TYPE 1: species	MEAN	VARIANCE
1	*Ambrosia artemisiifolia*	35.0625	575.390
2	*Chenopodium album*	19.750	724.867
3	*Lactuca serriola*	8.375	164.55
4	*Panicum capillare*	5.2187	121.241
5	*Chenopodium hybridum*	3.4125	17.3958
6	*Agropyron repens*	3.3437	4.325
7	*Brassica kaber*	2.3125	10.6292
8	*Daucus carota*	1.8125	3.3625
9	*Oenothera parviflora*	1.5625	5.1958
10	*Acer pseduoplatanus*	1.000	5.2666
11	*Barbarea vulgaris*	1.000	4.900
12	*Solidago graminifolia*	1.000	14.000
13	*Polygonum convolvulus*	0.4375	0.9958
14	*Solidago canadensis*	0.90625	3.1406
15	*Setaria viridis*	0.750	1.9333
	TYPE 2: species		
1	*Daucus carota*	18.125	135.268
2	*Trifolium pratense*	15.000	219.000
3	*Phleum pratense*	8.375	55.3821
4	*Agropyron repens*	7.625	25.5536
5	*Melilotus alba*	7.500	71.4286
6	*Poa pratensis*	7.500	117.714
7	*Medicago lupulina*	6.875	100.554
8	*Agrostis stolonifera*	5.000	44.571
9	*Erigeron strigosus*	3.625	58.2679
10	*Poa compressa*	3.3125	25.2813
11	*Panicum lanuginosum*	2.500	21.4286
12	*Chrysanthemum leucanthemum*	2.125	10.6964
13	*Solidago candensis*	2.125	11.3393
14	*Oenothera parviflora*	1.875	25.125
15	*Cirsium vulgare*	1.250	12.500

Table 4.16 (cont'd.)

Type 3:	Species	MEAN	VARIANCE
1	Agropyron repens	25.7917	398.172
2	Solidago canadensis	11.625	89.7228
3	Lactuca serriola	6.250	84.8913
4	Daucus carota	5.333	18.4058
5	Poa compressa	4.666	45.0145
6	Phleum pratense	4.2916	23.6938
7	Erigeron strigosus	3.5833	46.6014
8	Aster simplex	2.9166	10.6014
9	Melilotus alba	2.5416	17.2156
10	Trifolium pratense	1.9687	4.4364
11	Agrostis stolonifera	1.9166	19.9928
12	Cirsium arvense	1.9166	11.101
13	Poa pratensis	1.5833	17.558
14	Medicago lupulina	1.3333	13.4493
15	Chrysanthemum leucanthemum	1.1875	2.9741
Sub-type 1a:			
1	Ambrosia artemisiifolia	51.500	316.944
2	Panicum capillare	8.000	178.889
3	Lactuca serriola	7.000	154.000
4	Agropyron repens	3.500	11.611
5	Brassica kaber	3.200	14.844
6	Daucus carota	2.100	3.211
7	Oenothera parviflora	2.000	5.777
8	Acer pseudoplatanus	1.600	9.377
9	Solidago graminifolia	1.600	22.266
10	Barbarea vulgaris	1.500	5.833
11	Polygonum convolvulus	1.200	1.066
12	Cirsium vulgare	1.000	2.666
13	Dactylis glomerata	0.800	2.622
15	Phleum pratense	0.700	1.122
Sub-type 1b:			
1	Chenopodium album	51.666	216.667
2	Lactuca serriola	12.000	198.000
3	Chenopodium hybridum	10.1667	156.167
4	Ambrosia artemisiifolia	7.6666	14.666
5	Agropyron repens	3.083	5.441
6	Solidago canadensis	1.416	4.441
7	Daucus carota	1.333	3.866
8	Erigeron canadensis	1.000	4.000
9	Poa compressa	1.000	0.800

Table 4.16 (cont'd.)

Sub-type 1b: (continued)		MEAN	VARIANCE
10	*Rumex crispus*	1.000	0.800
11	*Phleum pratense*	0.750	0.575
12	*Arctum minus*	0.500	0.700
13	*Erigeron strigosus*	0.500	1.500
14	*Polygonum convolvulus*	0.500	0.700
15	*Verbascum thapsus*	0.500	1.500
Sub-type 3a:			
1	*Agropyron repens*	16.600	113.543
2	*Solidago canadensis*	15.133	97.409
3	*Lactuca serriola*	7.266	110.210
4	*Poa compressa*	6.366	59.266
5	*Phleum pratense*	5.400	31.257
6	*Daucus carota*	4.733	17.209
7	*Melilotus alba*	2.733	20.638
8	*Aster simplex*	2.600	3.542
9	*Poa pratensis*	2.400	26.828
10	*Medicago lupulina*	2.133	20.256
11	*Trifolium pratense*	1.816	5.968
12	*Agrostis stolonifera*	1.800	27.028
13	*Chrysanthemum leucanthemum*	1.366	39.159
14	*Solidago graminifolia*	1.333	12.381
15	*Lepidium compestre*	1.100	2.007
Sub-type 3b:			
1	*Agropyron repens*	41.111	523.611
2	*Daucus carota*	6.333	21.000
3	*Solidago canadensis*	5.777	25.944
4	*Lactuca serriola*	4.555	46.027
5	*Aster simplex*	3.444	15.027
6	*Cirsium arvense*	3.388	22.861
7	*Phleum pratense*	2.444	7.277
8	*Melilotus alba*	2.222	13.194
9	*Trifolium pratense*	2.222	2.194
10	*Agrostis stolonifera*	2.111	10.111
11	*Cirsium vulgare*	1.333	3.000
12	*Erigeron strigosus*	1.333	11.000
13	*Cichorium intybus*	1.000	1.000
14	*Poa compressa*	1.000	1.500
15	*Chrysanthemum leucanthemum*	0.888	2.8611

Table 4.17 Averages of environmental variables of the main types and sub-types of topsoil mounds habitat. Numbers in parenthesis indicate sample size when it is smaller than the complete sample of the type. Mean values ± standard error.

Environmental Factors	Main types			Sub-types			
	1	2	3	1a	1b	3a	3b
Soil pH	7.65 ± 0.057	7.41 ± 0.155	7.61 ± 0.077	7.72 ± 0.070	7.53 ± 0.087	7.53 ± 0.109	7.75 ± 0.088
NO_3 (ppm)	6.32 ±	4.9 ± 0.516	5.97 ± 0.383	6.73 ± 0.773	5.65 ± 0.438	5.81 ± 0.455	6.25 ± 0.714
Available P (ppm)	10.98 ± 0.867	11.406 ± 1.596	12.25 ± 0.649	8.9 ± 0.430	14.45 ± 1.208	12.03 ± 0.815	12.61 ± 1.127
WRC %	41.58 ± 1.015	46.56 ± 2.112	48.20 ± 1.366	43.40 ± 0.839	38.40 ± 1.736	47.66 ± 1.776	49.11 ± 2.226
Silt + Clay %	12.20 ± 0.914	18.03 ± 2.942	10.98 ± 2.067	11.80 ± 1.007	12.87 ± 1.871	14.45 ± 2.935	5.18 ± 0.962
Organic Matter %	8.61 ± 0.191	8.53 ± 0.247	8.13 ± 0.194	8.99 ± 0.120	7.97 ± 0.346	8.17 ± 0.230	8.08 ± 0.365
Exchangeable K^+ (ppm)	97.5[8] ± 25.088	63.12 ± 3.669	58.12 ± 4.057	78.33[6] ± 12.08	155.0[2] ± 104.99	70.66 ± 6.24	63.88 ± 2.97
Exchangeable Ca^{++} (ppm)	1850.0[8] ± 123.7	1975 ± 24.78	1962.5 ± 29.98	1833.3[6] ± 166.6	1900.0[2] ± 104.99	1940.0 ± 47.60	2000.0 ± 0
Exchangeable Mg^{++} (ppm)	240.0[8] ± 37.8	393.12 ± 62.57	484.37 ± 86.89	245.83[6] ± 50.56	222.50[2] ± 37.49	423.0 ± 34.11	586.66 ± 218.0
% Slope	47.31 ± 3.62	22[6] ± 3.33	47.26[19] ± 2.42	52.10 ± 2.46	39.33 ± 3.16	50.16[12] ± 3.16	42.28[7] ± 3.09

Table 4.18 Correlations of six environmental variables for topsoil mounds habitat.

	pH	NO_3^-	phosphorus	WRC	silt + clay
NO_3^-	0.5055				
Phosphorus	-0.2947	-0.2485			
WRC	-0.0342	-0.2346	-0.1002		
Silt + Clay	-0.4194	-0.2169	-0.1638	0.2003	
Organic Matter %	-0.1338	-0.1984	-0.2149	0.6303	0.4581

Table 4.19 PCA of the environmental data of six variables listed in Table 4.18 for the topsoil mound habitat.

Component	Eigenvalue	% of total variance accounted for	Cumulative variance %	Ranked Eigenvector Elements	Associated variable
1	2.2414	37.357	37.357	-0.50339	Org. matter
				-0.47366	Silt + Clay
				-0.42409	WRC
2	1.5968	26.6138	63.971	-0.60397	Available P
				0.48526	pH
				0.38528	NO_3^-
3	0.9339	15.565	79.537	0.58262	Silt + Clay
				-0.56828	WRC
				-0.46142	Available P

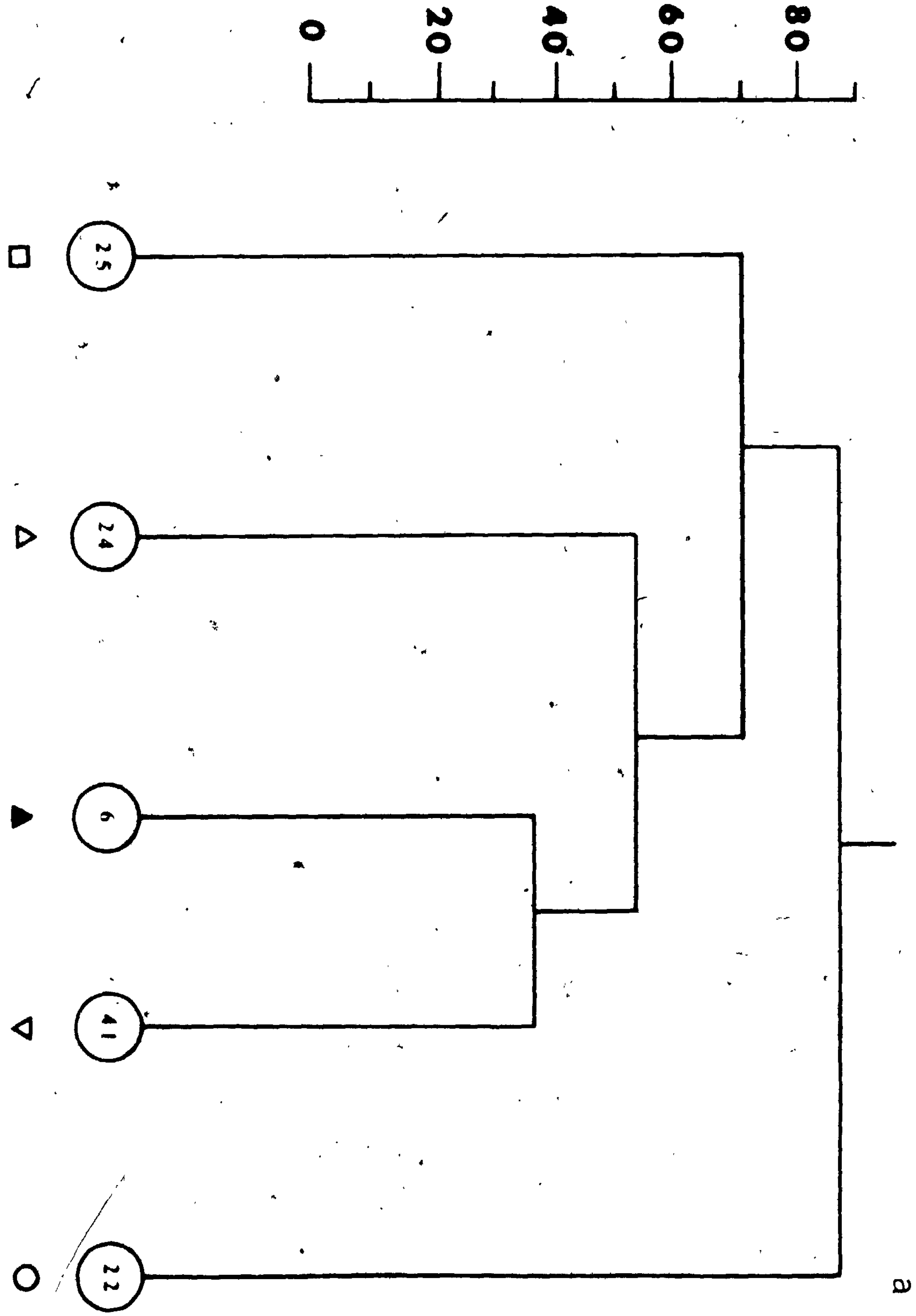
Table 4.20 Partition of chi-square in the AOC of life-form categories and releve groups for the topsoil mounds data set.

Canonical variate (i)	Canonical correlation (R_i)	Chi-square	Percentage	Cumulative Percentage
1	0.6195	1742.058	76.816	76.816
2	0.3403	525.756	23.184	100.00
TOTAL		$\chi^2 = 2267.814$ df = 16	100	

Table 4.21 Partition of chi-square in the AOC of life-span categories and releve groups for the topsoil mounds data set.

Canonical variate (i)	Canonical correlation (R_i)	Chi-square	Percentage	Cumulative Percentage
1	0.5780	1516.490	79.635	79.635
2	0.2922	387.746	20.365	100.00
TOTAL		χ^2 = 1904.236 df = 10	100	

Fig. 4.1 Dendrograms resulting from clusterings of 118 relevés of old field habitat. (a) Dendrogram based on sum of squares clustering. (b) Dendrogram based on iterative clustering. Vegetation types are indicated by Roman numerals. The numbers at the bottom represent the number of releves included in each type. The vertical axis represents the sum of squares. Symbols corresponding to types are used in relevé ordination.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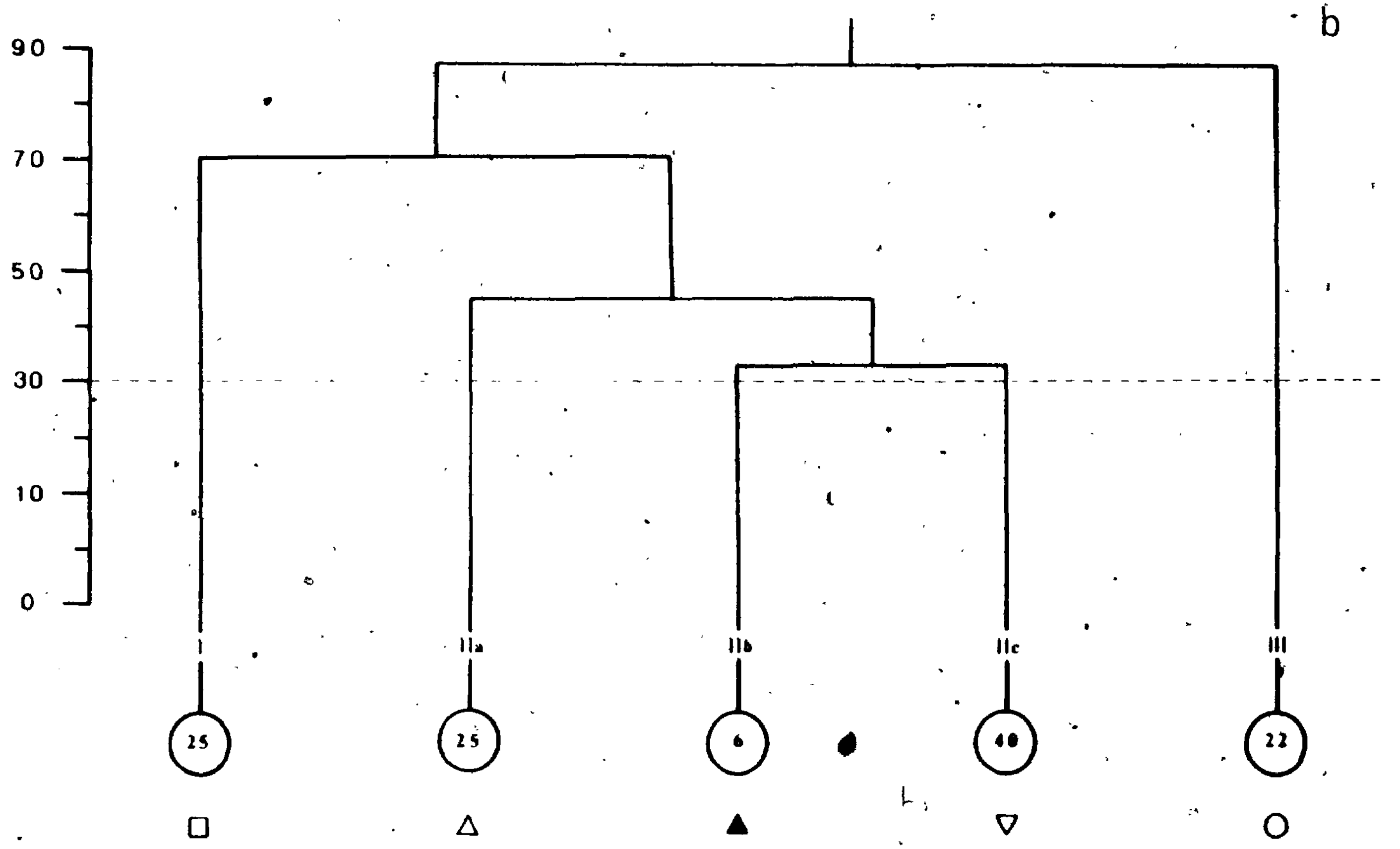
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▽
○

Fig. 4.2 Nonmetric multidimensional scaling ordination of 118 releves of old field habitat. A two-dimensional solution was sought. The symbols correspond to the types and sub-types: □ type 1; △ 2a; ▲ type 2b; ▽ type 2c; ○ type 3. Dots indicate overlapping points.

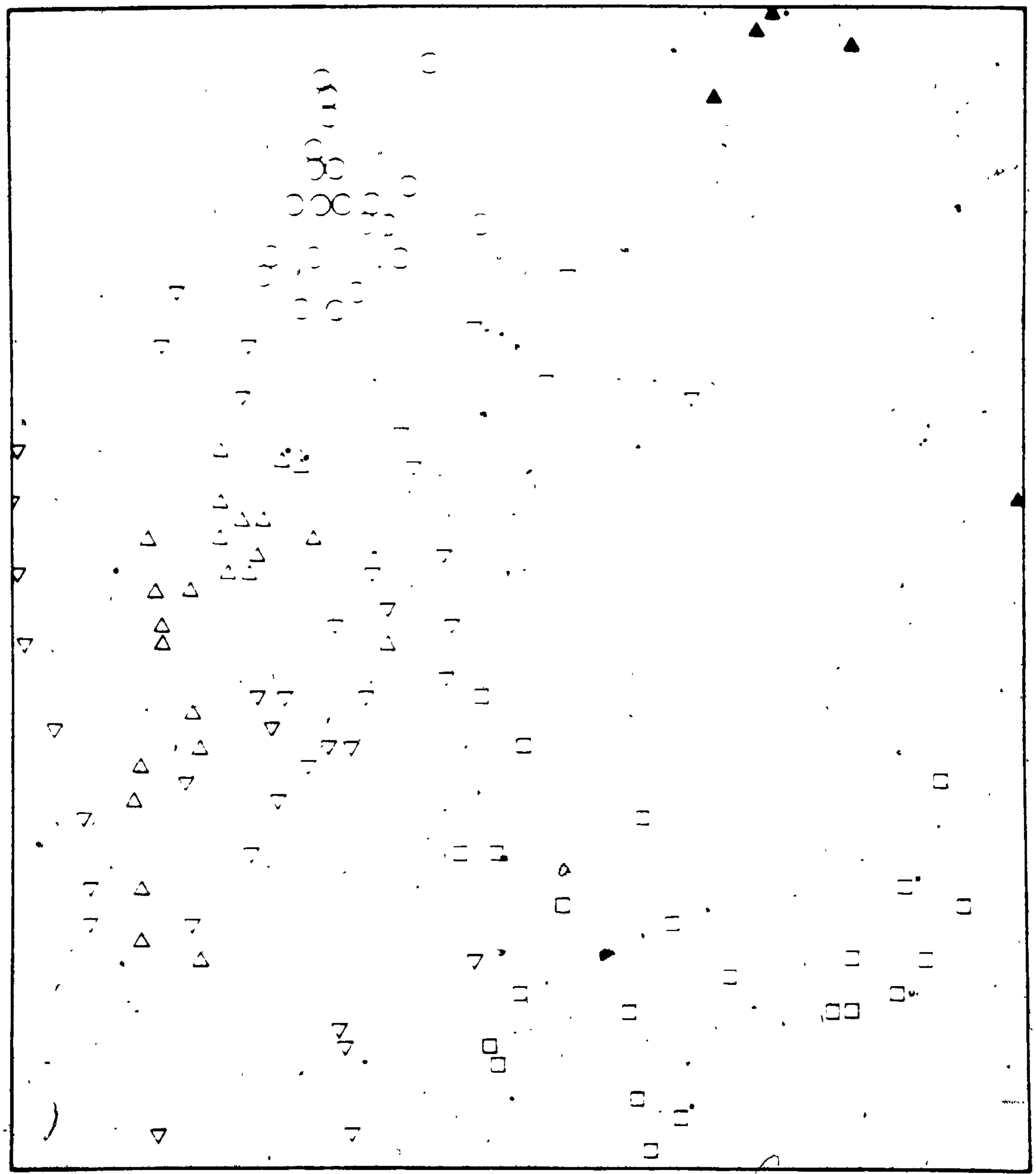
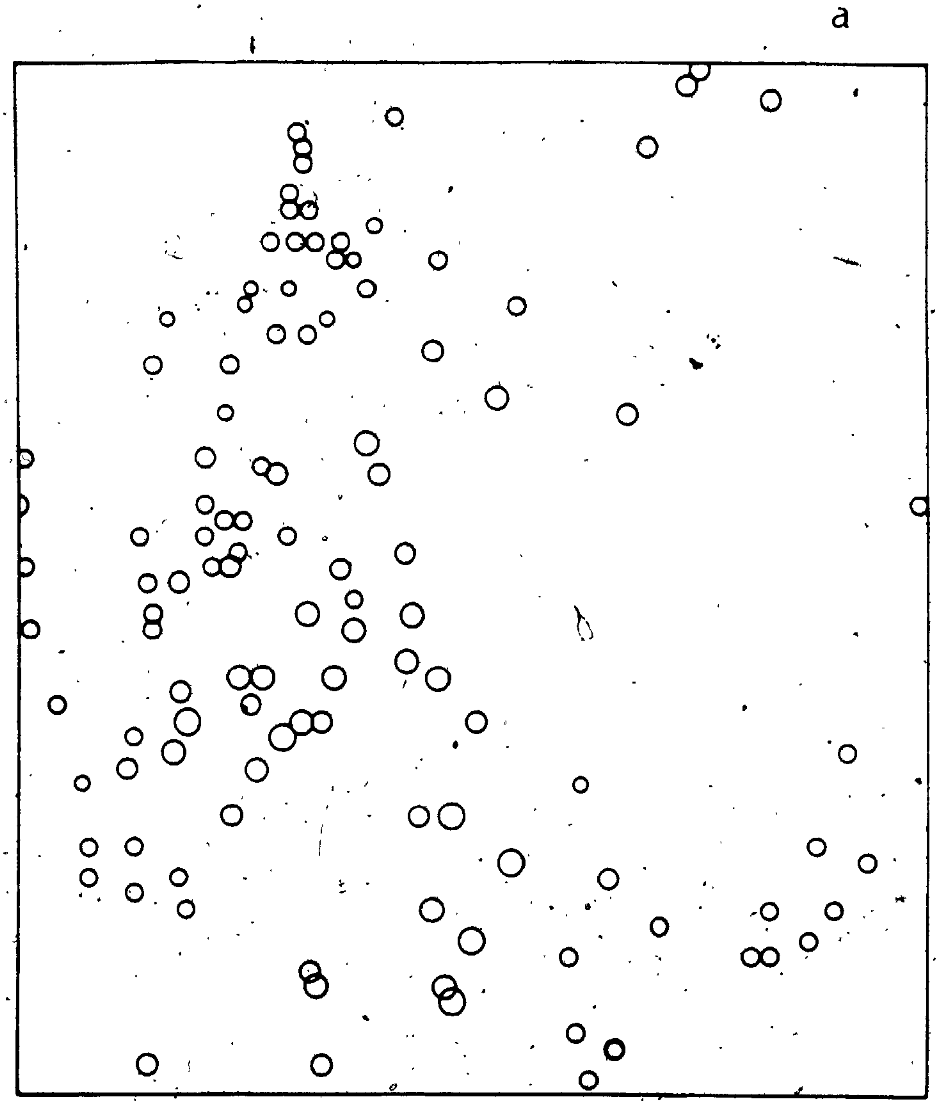
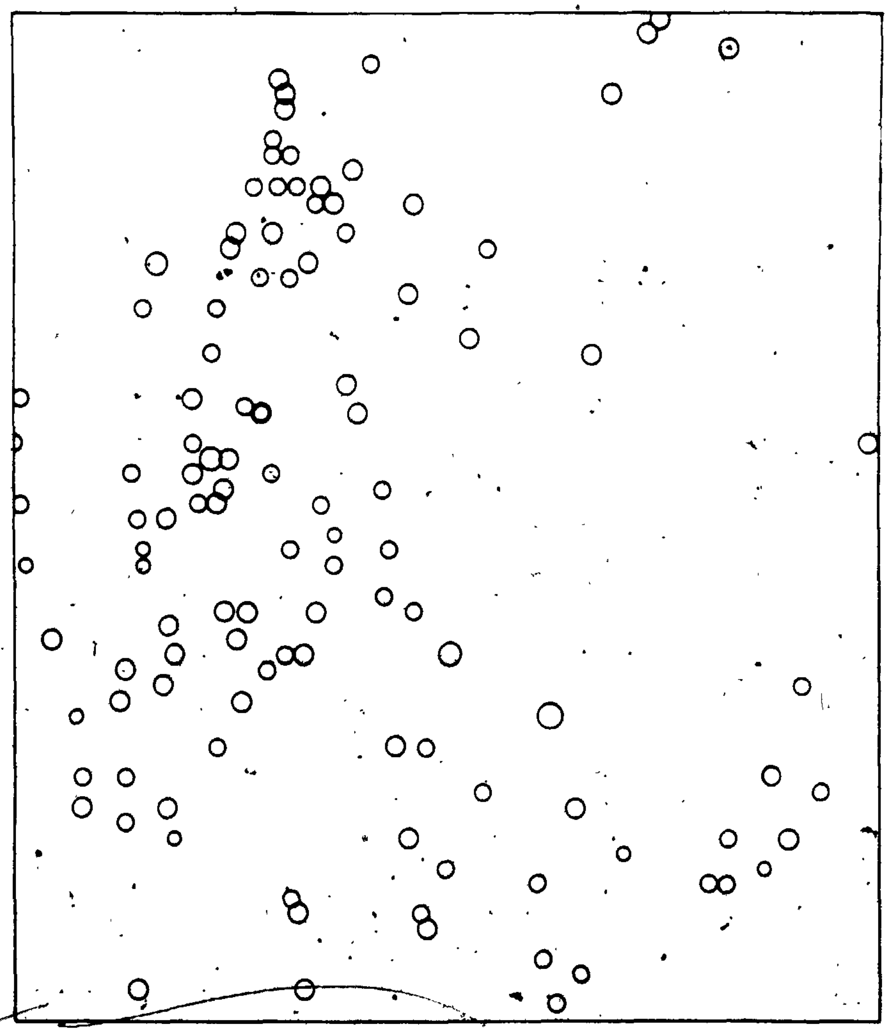


Fig. 4.3 Component scores corresponding to the first three components of PCA of environmental data superimposed on the MDSCAL relevé ordination. (a) first component scores, (b) second component scores, (c) third component scores. The scores of each component were divided into 5 classes indicated by various circle sizes. Larger circle sizes represent higher component scores.


a

b



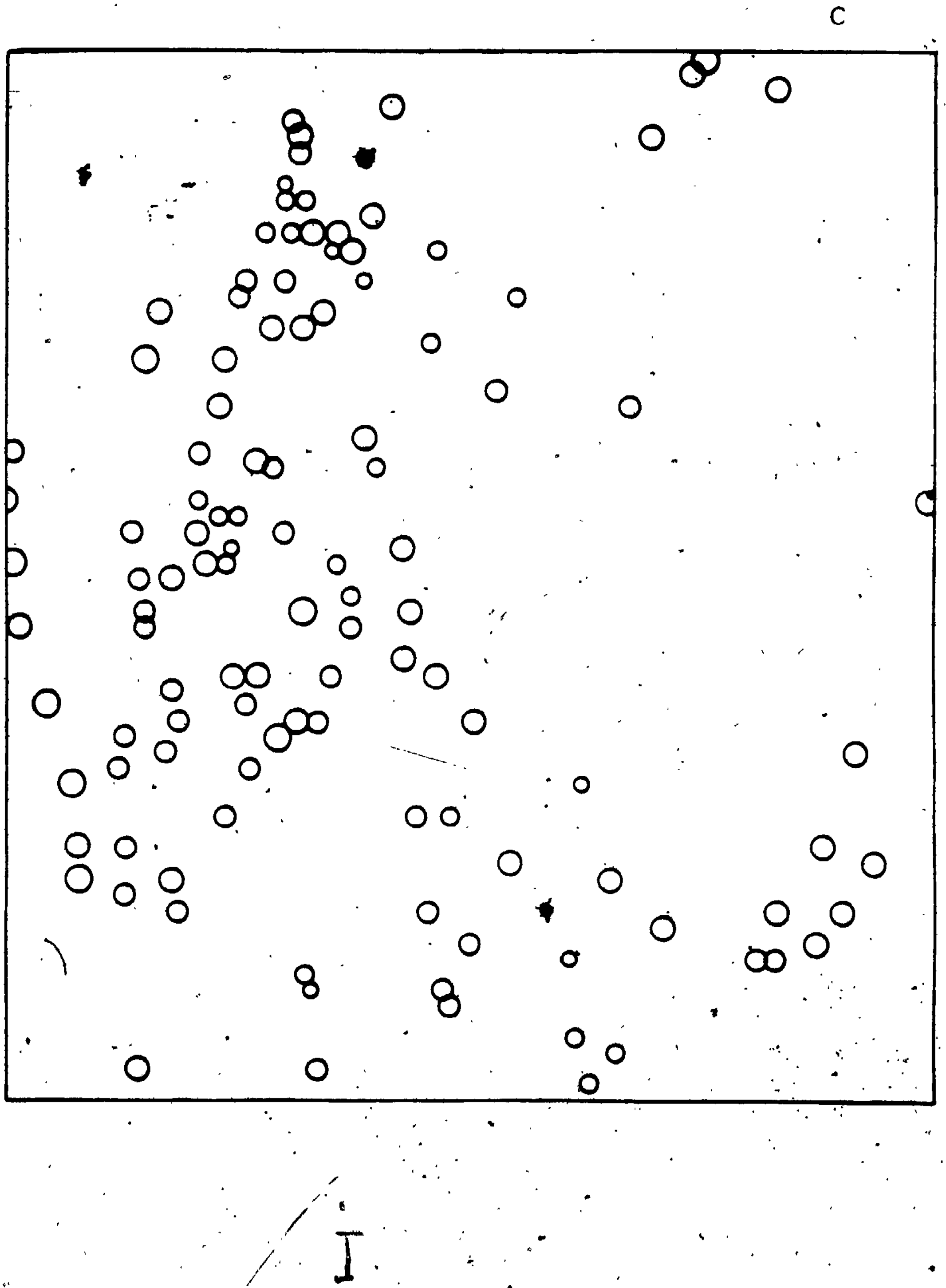
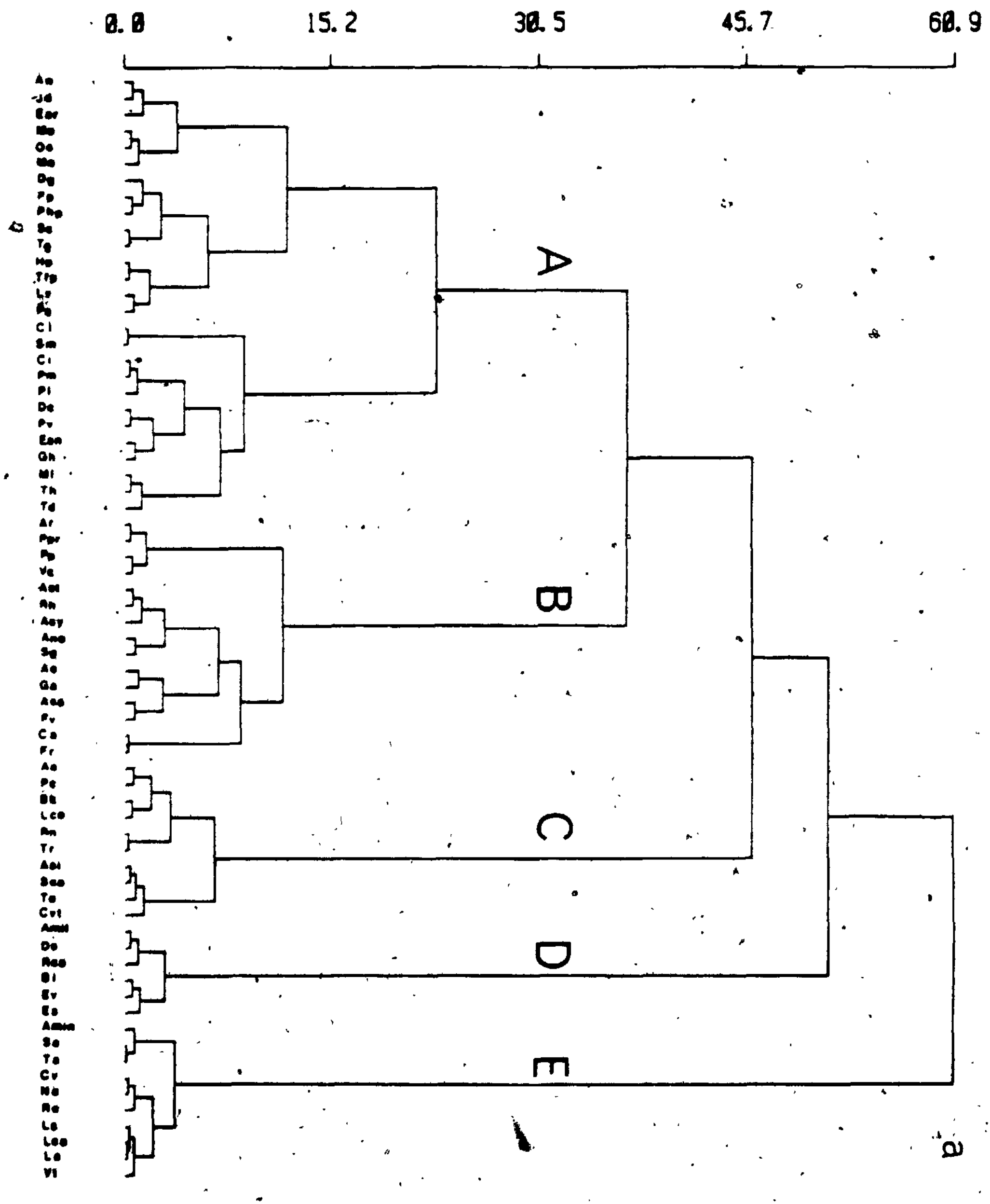

c

Fig. 4.4 Dendrograms resulting from sum of squares agglomeration of species. (a) dendrogram based on 68 species, (b) dendrogram based on 14 species. See text for full explanation.

Key to symbols:

An, *Acer negundo*; Amil, *Achillea millefolium*; Ar, *Agropyron repens*; Ast, *Agrostis stolonifera*; Aa, *Ambrosia artemisiifolia*, Amin, *Arctium minus*; Ae, *Arrhenatherum elatius*; Asy, *Asclepias syriaca*; Ano, *Aster novae-angliae*, Asa, *Aster sagittifolius*; Asi, *Aster simplex*; Bk, *Brassica kaber*; Bi, *Bromus inermis*; Cvt, *Cerastium vulgatum*; Cl, *Chrysanthemum leucanthemum*; Ci, *Cichorium intybus*, Ca, *Cirsium arvense*; Cv, *Cirsium vulgare*; Dg, *Dactylis glomerata*; Cc, *Daucus carota*; Ds, *Dipsacus sylvestris*; Ev, *Echium vulgare*; Ear, *Equisetum arvense*; Ean, *Erigeron annuus*; Es, *Erigeron strigosus*; Fp, *Festuca pratensis*; Fr, *Festuca rubra*; Ga, *Geum aleppicum*; Fv, *Fragariavirginiana*; Gh, *Glecoma hederacea*; Hp, *Hypericum perforatum*; Jd, *Juncus dudleyi*; Ls, *Lactuca serriola*; Lco, *Lepidum campestre*; Lca, *Leonurus cardiaca*; Lv, *Linaria vulgaris*; La, *Lychnis alba*; Ml, *Medicago lupulina*; Ma, *Melilotus alba*; Mo, *Melilotus officinalis*; Nc, *Nepeta cataria*, Os, *Oxalis stricta*; Pa, *Phalaris arundinacea*; Php, *Phleum pratense*, Pl. *Plantago lanceolata*; Pm, *Plantago major*; Pc, *Poa compressa*; Ppr, *Poapratensis*; Pn, *Potentilla norvegica*; Pr, *Potentilla recta*; Pv, *Prunella vulgaris*; Rca, *Rhamnus cathartica*; Rh, *Rudbeckia hirta*; Rcr, *Rumex crispus*; Sc, *Silene cucubalus*; Sa, *Sisymbrium altissimum*, Sca, *Solidago canadensis*; Sg, *Solidago graminifolia*; Sm, *Sisyrinchium montanum*; To, *Taraxacum officinale*; Ta, *Thlaspi arvensis*; Td, *Tragopogon dubius*; Tgp, *Tragopogon pratense*; Tr, *Trifolium repens*; Vc, *Vicia cracca*; Vt, *Verbascum thapsus*.


0.0
15.2
30.5
45.7
60.9
As
Jd
Esr
Ms
Os
Ms
Dg
Fp
Php
Ss
Tg
Hp
Tfp
Lv
Pg
Cl
Sm
Ci
Pm
Pl
Ds
Pv
Esn
Gh
Ml
Th
Td
Ar
Ppr
Pp
Vs
Asl
Rh
Asy
Ane
Sg
As
Ga
Aes
Pv
Ca
Fr
As
Pe
Bk
Lco
Rn
Tr
Asi
Sco
Ts
Cvt
Amil
Ds
Reo
Bl
Ev
Es
Amin
Ss
Ts
Cv
Ns
Rs
Ls
Lss
Ls
Vl
A
B
C
D
E
a

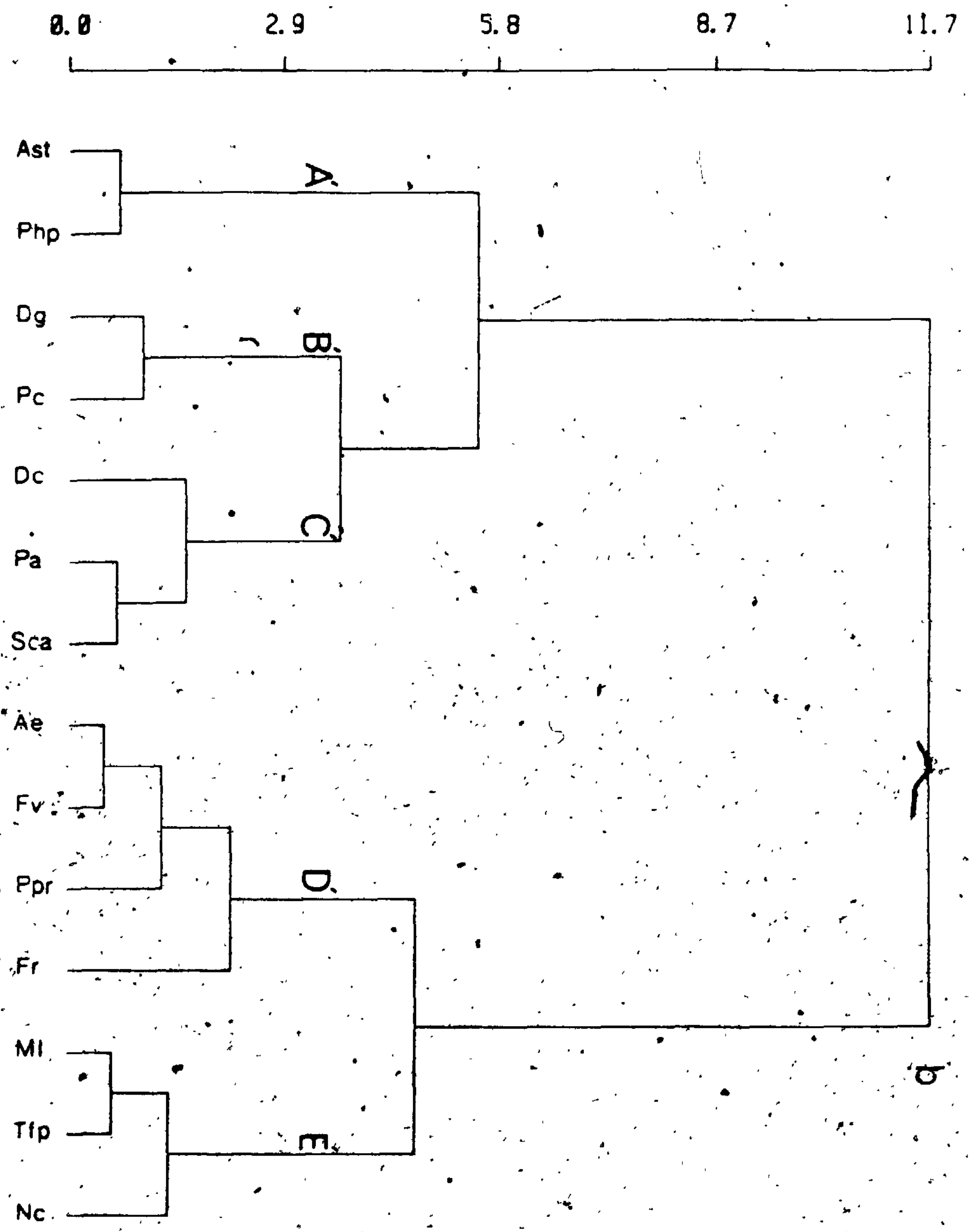

0.0
2.9
5.8
8.7
11.7
Ast
Php
Dg
Pc
Dc
Pa
Sca
Ae
Fv
Ppr
Fr
Ml
Tfp
Nc
A
B
C
D
E
b

Fig. 4.5 Nonmetric multidimensional scaling ordination of 14 important species. A two-dimensional solution was sought.

Key to symbols:

Ae, *Arrhenatherum elatius*; Ast, *Agrostis stolonifera*; Dc, *Daucus carota*; Dg, *Dactylis glomerata*; Fr, *Festuca rubra*; Fv, *Fragaria virginiana*; Ml, *Medicago lupulina*; Nc, *Nepeta cataria*; Pa, *Phalaris arundinacea*; Pc, *Poa compressa*; Php, *Phleum pratense*, Ppr, *Poa pratensis*; Sca, *Solidago canadensis*; Tfp, *Trifolium pratense*.

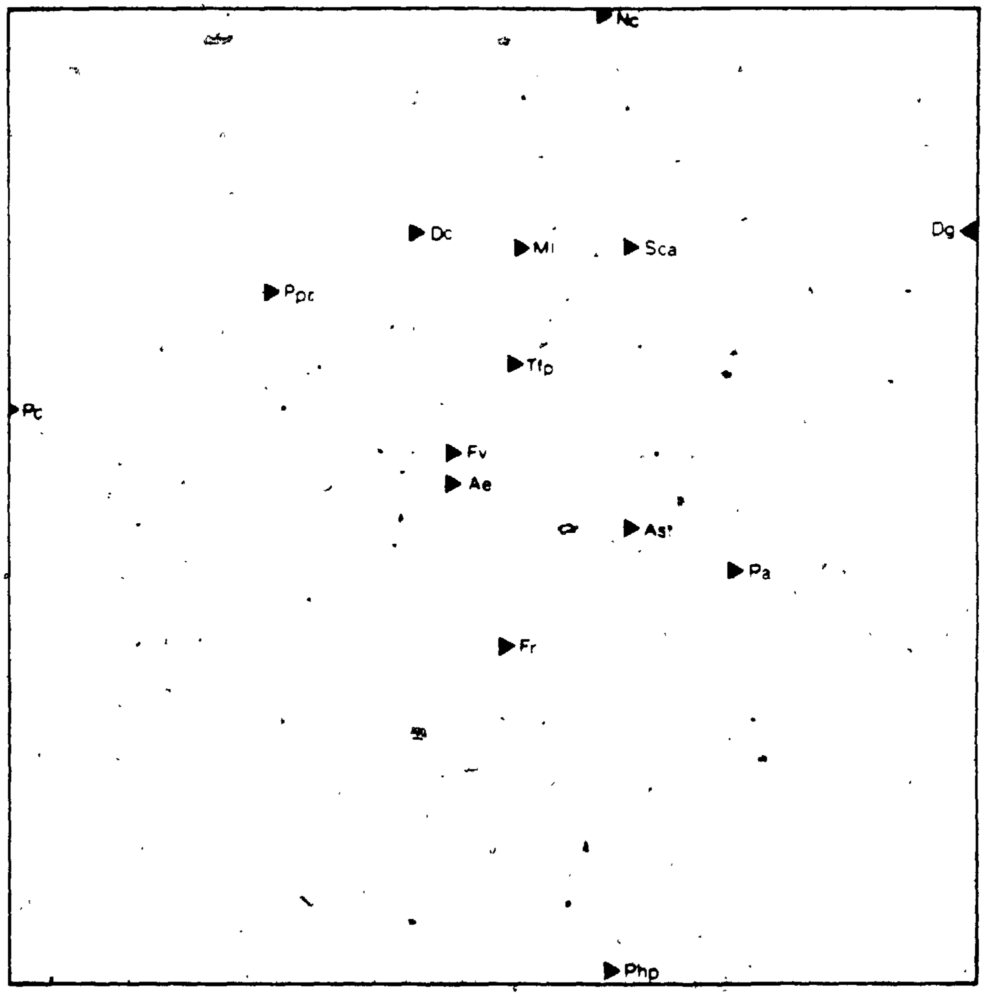

Nc
Dc
Mi
Sca
Dg
Ppc
Tfp
Pc
Fv
Ae
Ast
Pa
Fr
Php

Fig. 4.6 The joint scattergram of relevé groups (based on age since abandonment) and life-form categories for an oldfield data set. Relevé groups (shown by numerals) corresponded to th following age classes -

Group 1, 2 yrs.

Group 2, 4 yrs.

Group 3, 6-8 yrs.

Group 4, > 10 yrs.

Key to symbols of life-form categories:

A, theophytes; B, therophytes-hemicryptophytes; C, theophytes-geophytes; D, hemicryptophytes; E, hemicryptophytes-geophytes; F, geophytes; G, chamaephytes-hemicryptophytes; H, chamaephytes; I, phanerophytes.

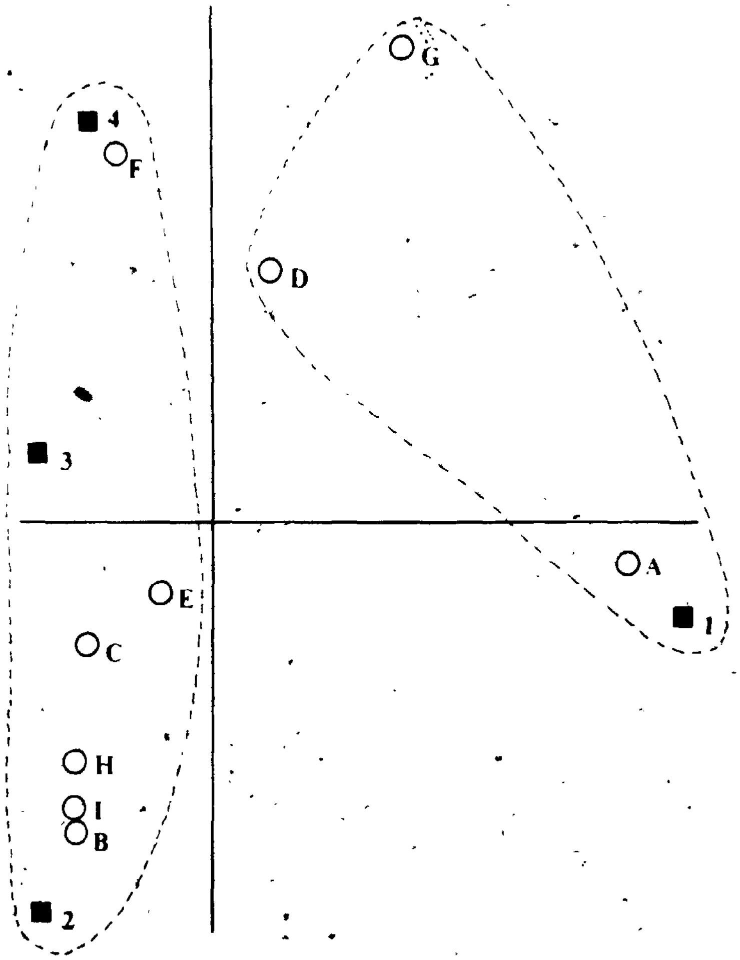
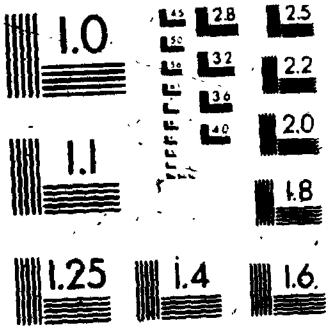

G
4
F
D
3
A
1
E
C
H
I
B
2

Fig. 4.7 Deviations from random expectation with respect to pooled life-form composition for the first lattice. The abscissa represents releve groups while the ordinate represents deviation from expectation. A, B, C, D, E, F, G, H and I corespond to the life-form cateogries as in the legend of Fig. 4.6.

5



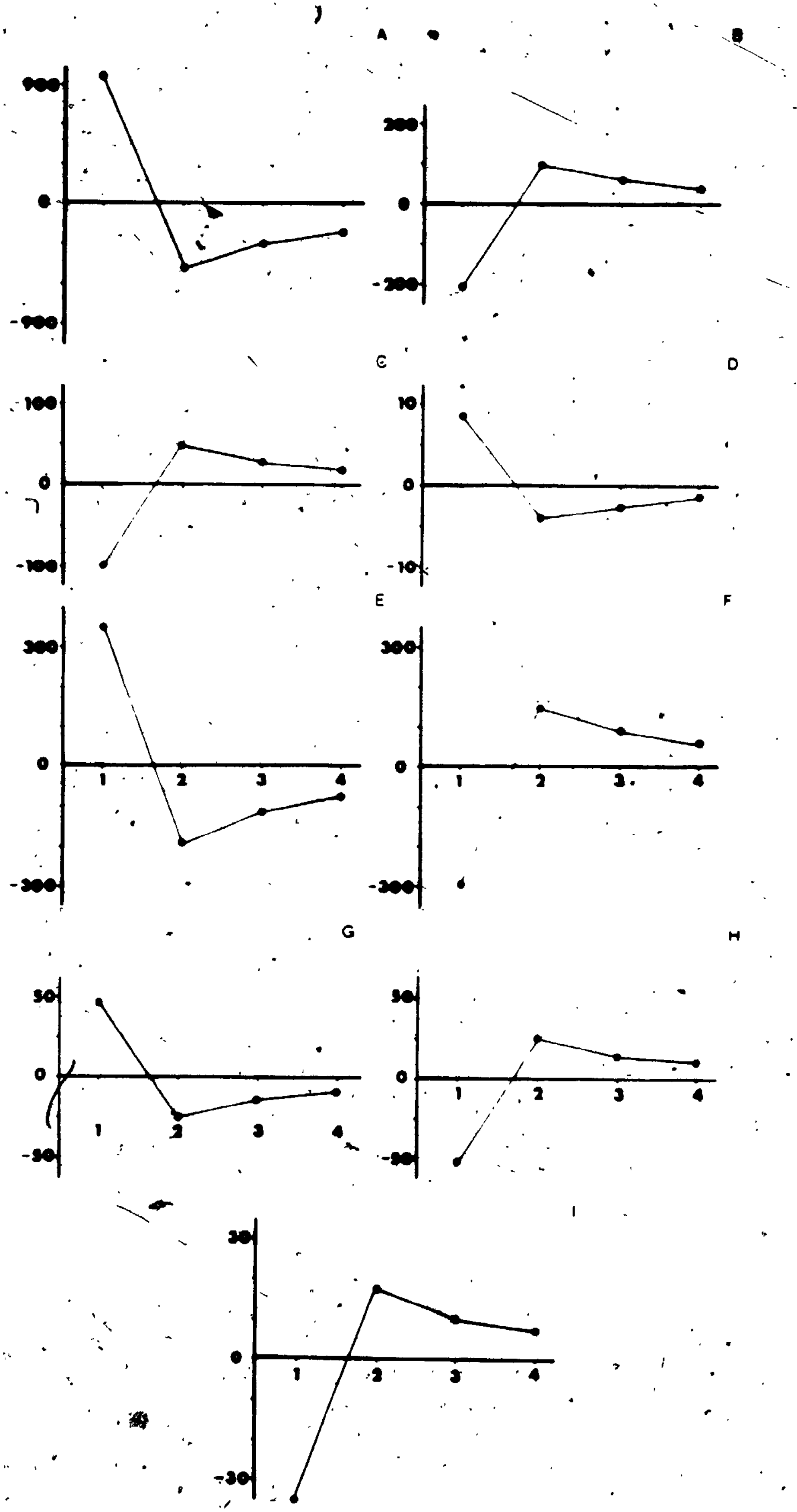

A
B
900
0
-900
200
0
-200
C
D
100
0
-100
10
0
-10
E
F
300
0
-300
1
2
3
4
G
H
50
0
-50
I
30
0
-30

Fig. 4.8 The joint scattergram of relevé groups (based on age since abandonment) and life-span groups for the old field data set. Refer to symbols of Fig. 4.6 for the age classes. Key to symbols of life-span categories: A, annual; B, annuals-biennials; C, annuals-perennials; D, Biennials; E, biennials-perennials; F, perennials.

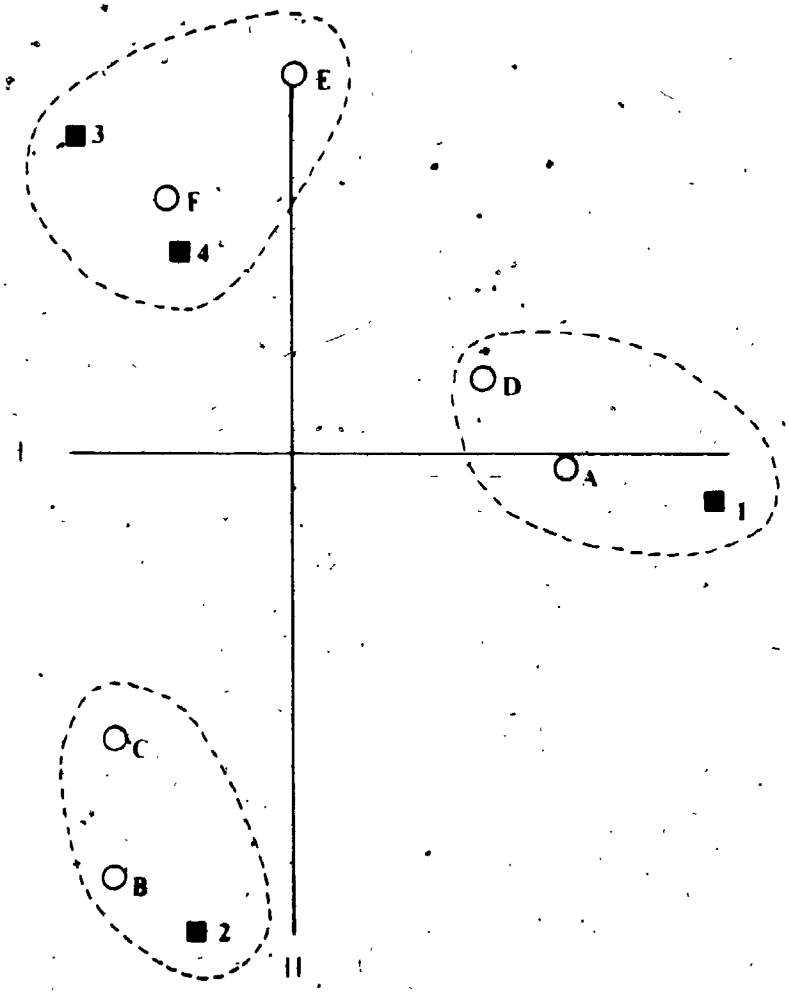

E
3
F
4
D
I
A
1
C
B
2
II

Fig. 4.9 Deviations from random expectation with respect to pooled life-span type composition for the first lattice. The abscissa represents releve groups 1 to 4 (as in Fig. 4.6) and the ordinate represents deviation from expectation. A, B, C, D, E and F correspond to life-span categories as in the legend of Fig. 4.8.

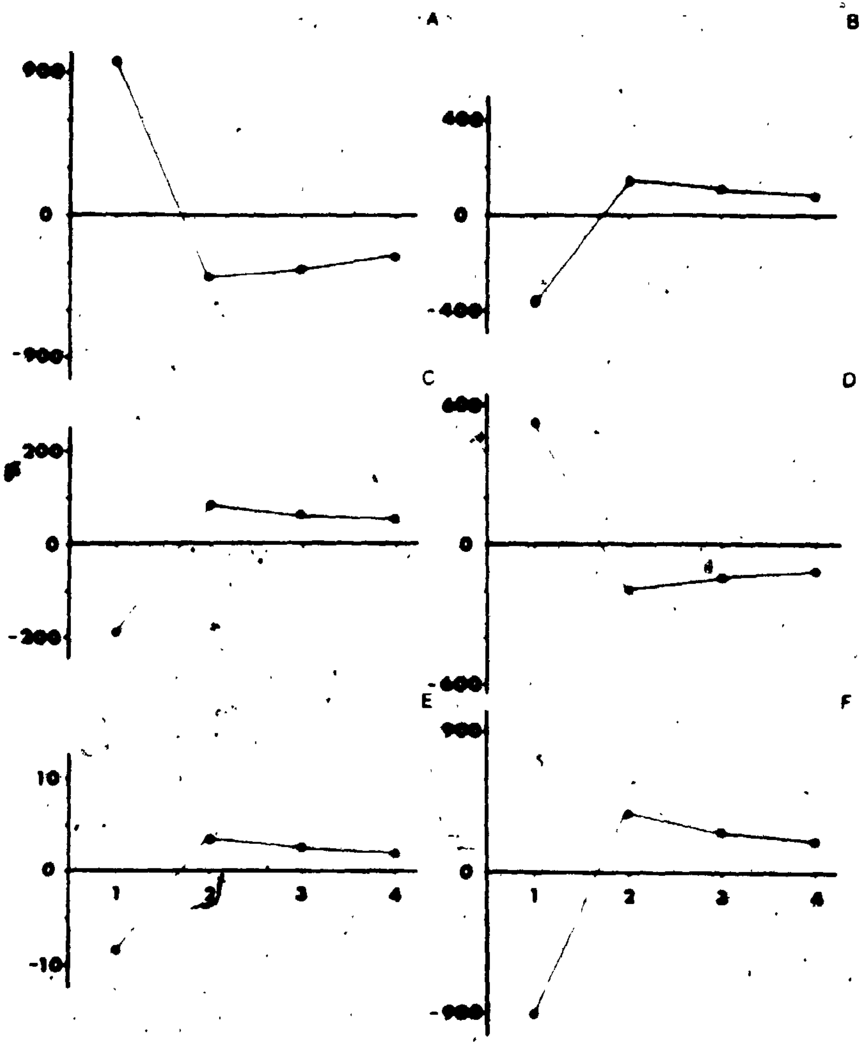

A
900
0
-900
B
400
0
-400
C
200
0
-200
D
600
0
-600
E
10
0
-10
1
2
3
4
F
900
0
-900
1
2
3
4

Fig. 4.10 Diversity and dominance patterns with respect to successional progression on old fields. The four successional stages correspond to the four relevé groups based on the site age as defined in the legend of Fig. 4.6. A, species richness and general diversity, B, equitability, and C, dominance.

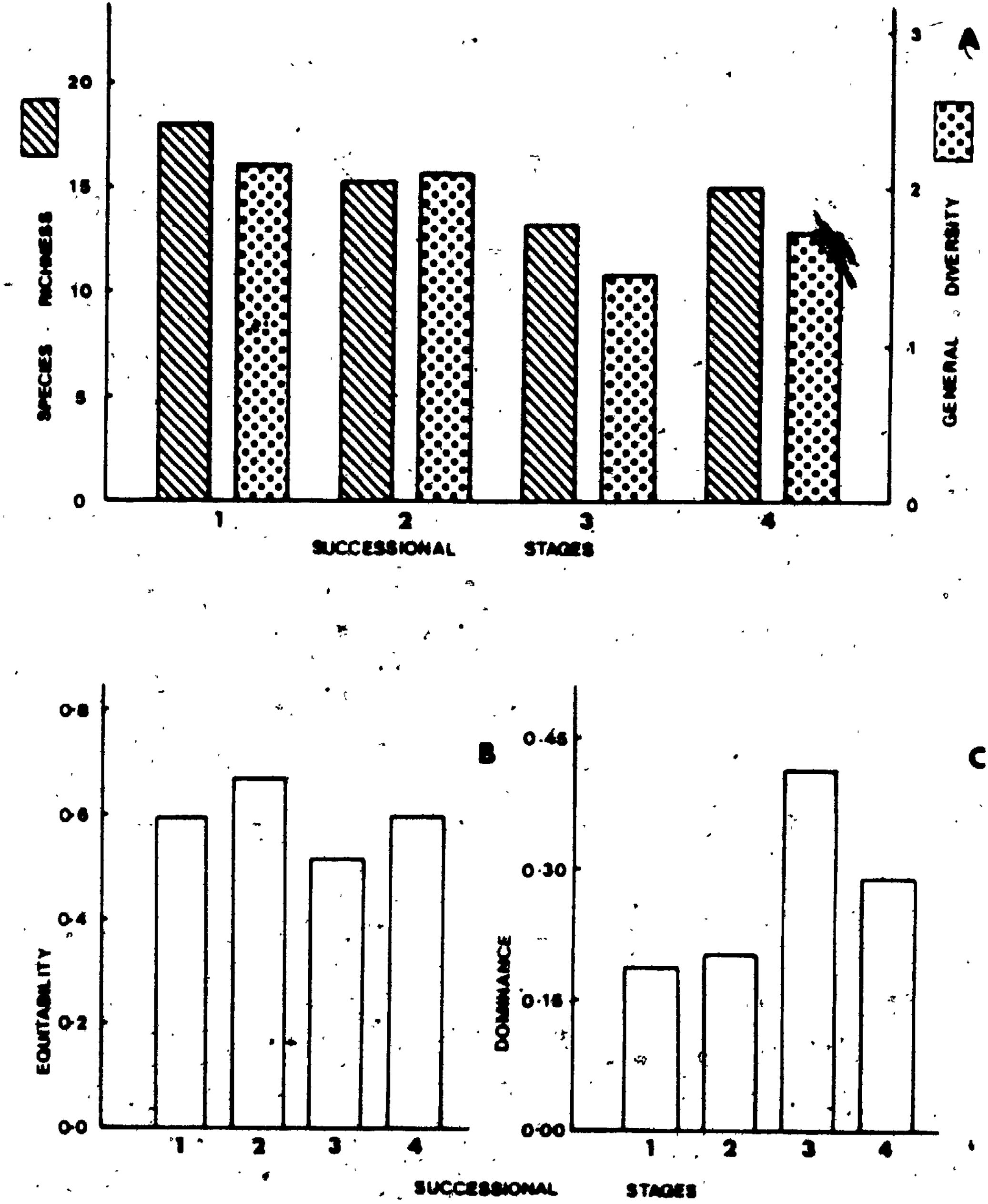

A
SPECIES RICHNESS
GENERAL DIVERSITY
0
5
10
15
20
0
1
2
3
1
2
3
4
SUCCESSIONAL STAGES
B
EQUITABILITY
0·0
0·2
0·4
0·6
0·8
1
2
3
4
C
DOMINANCE
0·00
0·15
0·30
0·45
1
2
3
4
SUCCESSIONAL STAGES

Fig. 4.11 Proposed scheme of secondary succession on old fields in London area. The climax stage was not examined. Only the successional dominants are shown.

* Climax stage and shrub stage were not studied.

Fig. 4.11

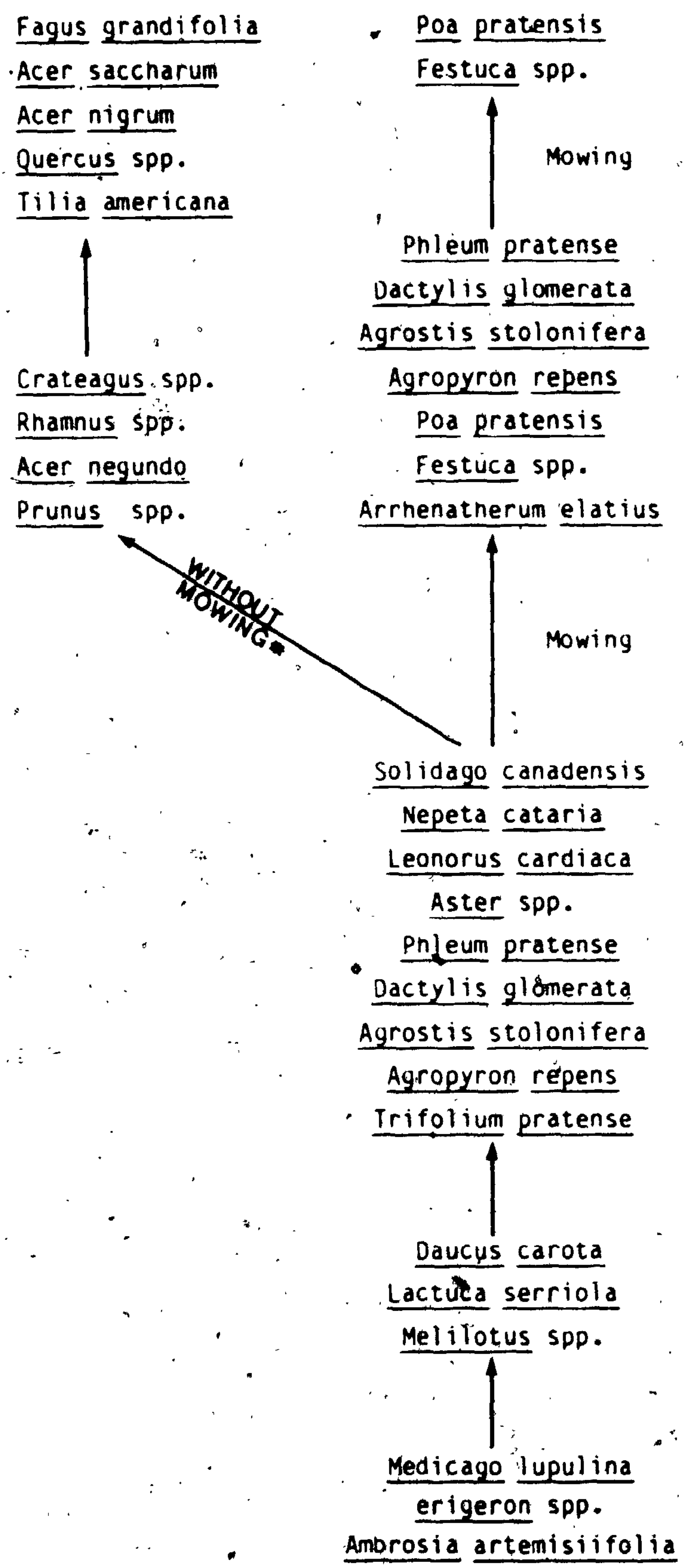
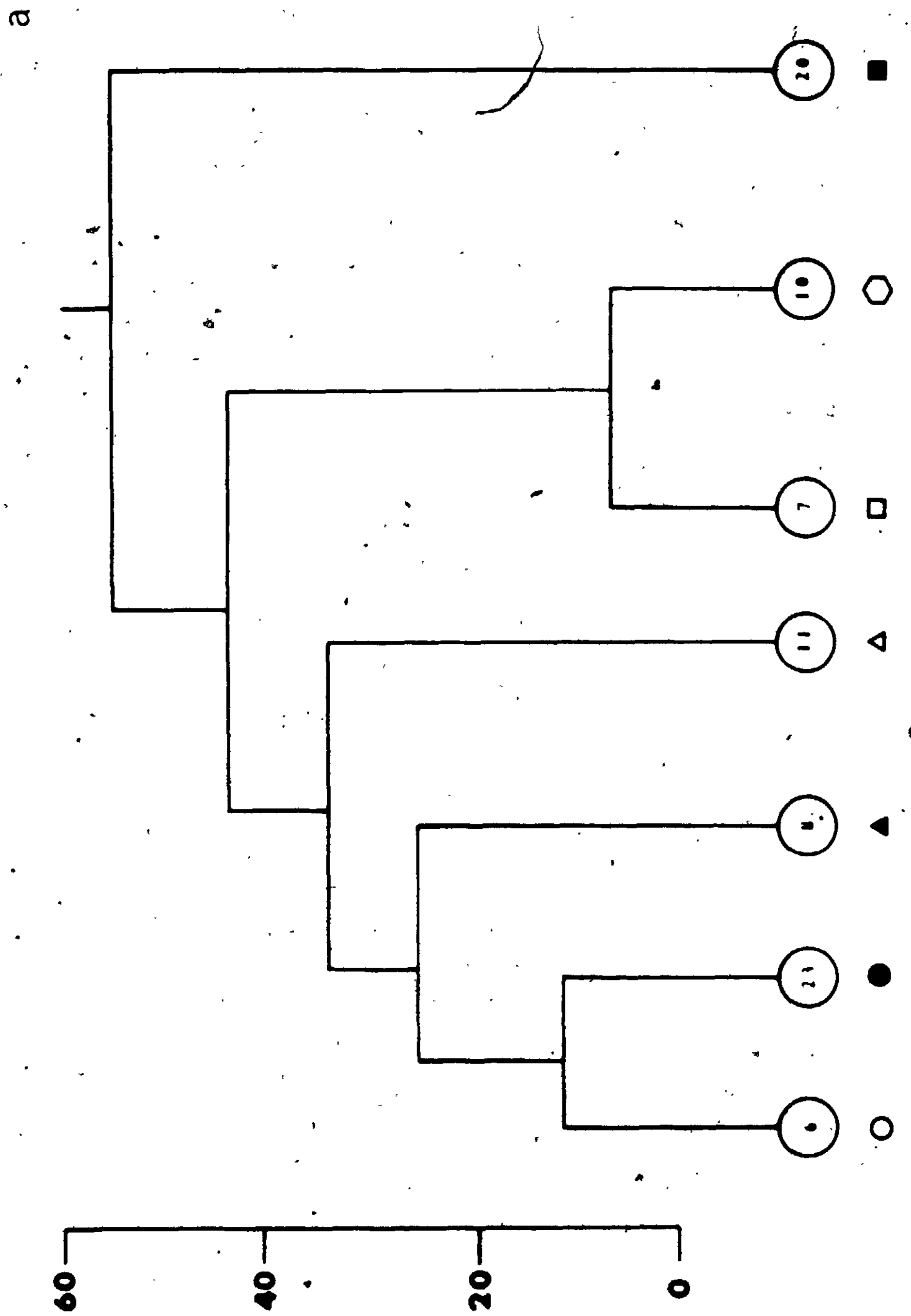

Fagus grandifolia
Acer saccharum
Acer nigrum
Quercus spp.
Tilia americana
Poa pratensis
Festuca spp.
Mowing
Crateagus spp.
Rhamnus spp.
Acer negundo
Prunus spp.
Phleum pratense
Dactylis glomerata
Agrostis stolonifera
Agropyron repens
Poa pratensis
Festuca spp.
Arrhenatherum elatius
WITHOUT MOWING
Mowing
Solidago canadensis
Nepeta cataria
Leonorus cardiaca
Aster spp.
Phleum pratense
Dactylis glomerata
Agrostis stolonifera
Agropyron repens
Trifolium pratense
Daucus carota
Lactuca serriola
Melilotus spp.
Medicago lupulina
erigeron spp.
Ambrosia artemisiifolia

Fig. 4.12 Dendrograms resulting from clusterings of 85 relevés of vacant lot habitat. (a) Dendrogram based on sum of squares clustering. (b) Dendrogram based on iterative clustering. Vegetation types are indicated by Roman numerals. The numbers at the bottom represent the number of releves included in each type. The vertical axis represent the sum of squares.


a
20
10
7
11
8
21
6
60
40
20
0

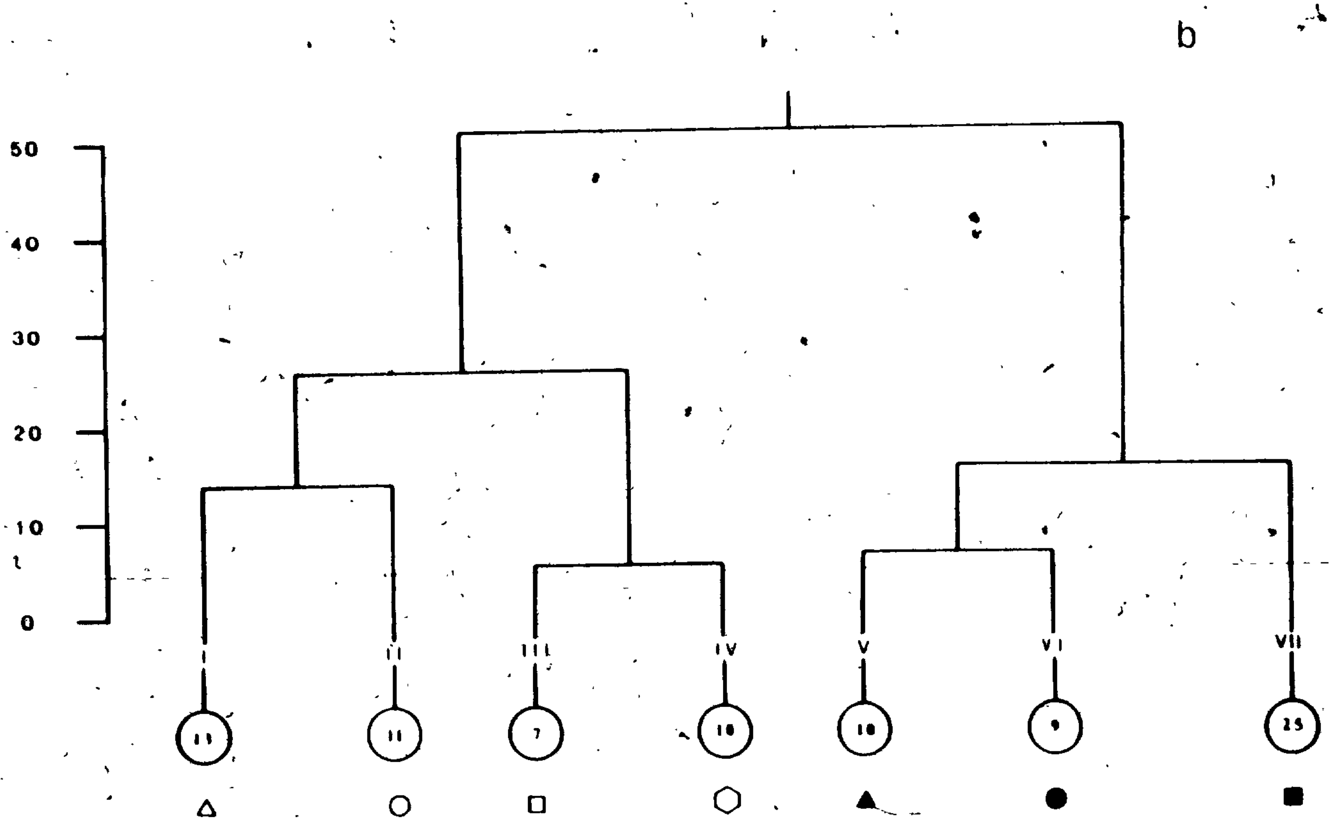

b
50
40
30
20
10
0
I
II
III
IV
V
VI
VII
11
11
7
10
10
9
25
△
○
□
⬡
▲
●
■

Fig. 4.13 Nonmetric multidimensional scaling ordination of 85 relevés of vacant lot habitat. Two dimensional solution was sought. The symbols correspond to the types as follows: △, type 1; ○ type 2; □ , type 3; ⬡, type 4; ▲ , type 5; ● , type 6; ■ , type 7. Dots indicate overlapping points.

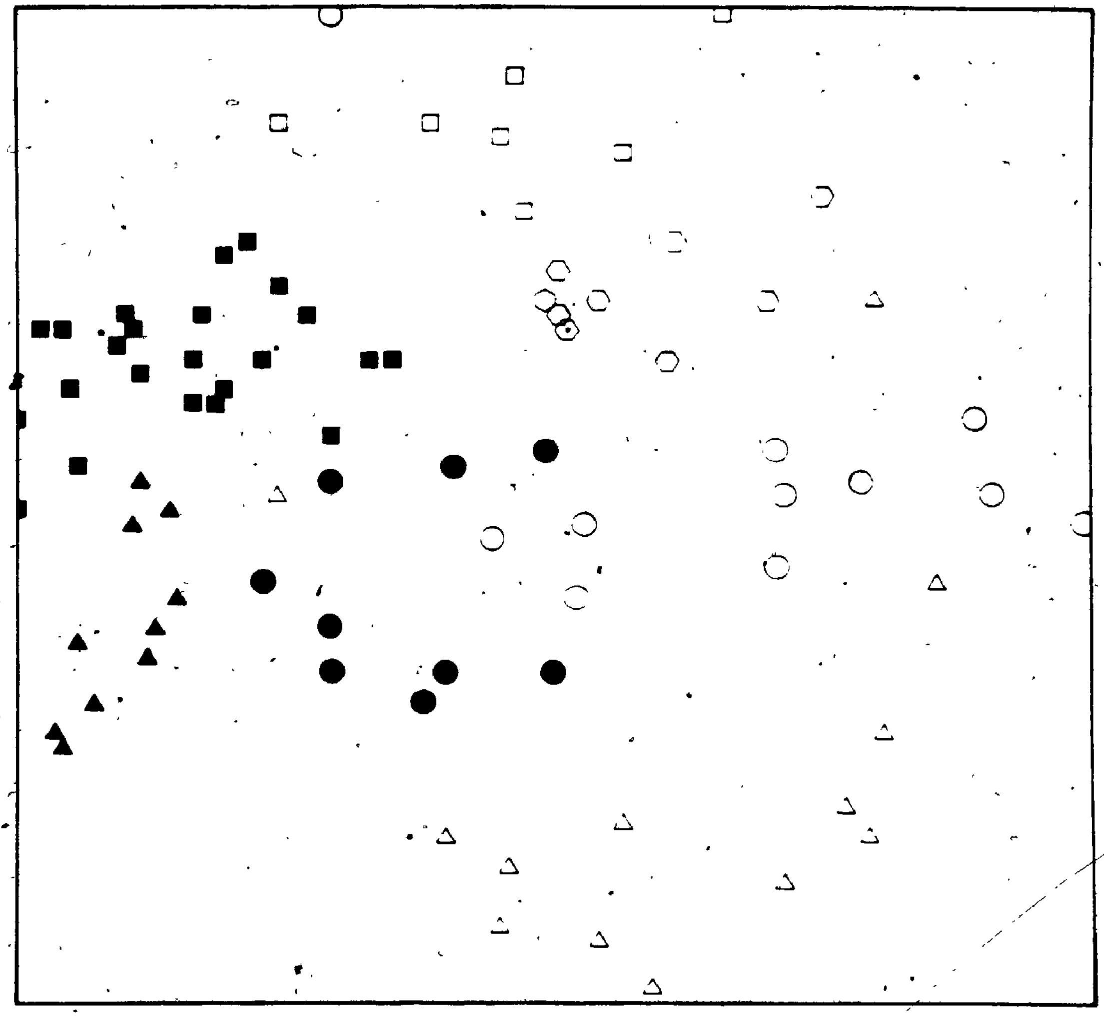
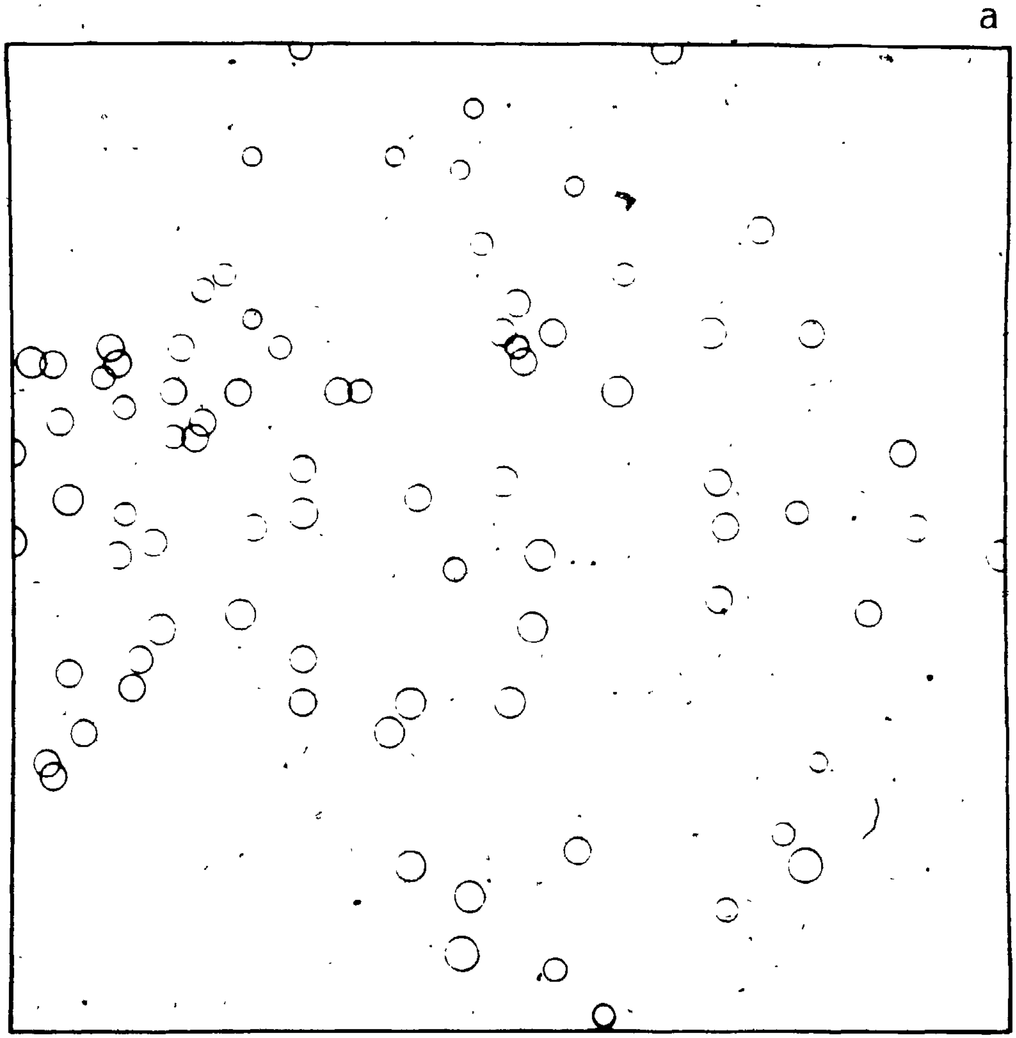


Fig. 4.14 Component scores corresponding to the first two components of PCA of environmental data superimposed on the MDSCAL relevé ordination. (a) First component scores, (b) Second component scores. The scores of each component were divided into 5 classes indicated by various circle sizes. Larger circle sizes represent higher component scores.


a

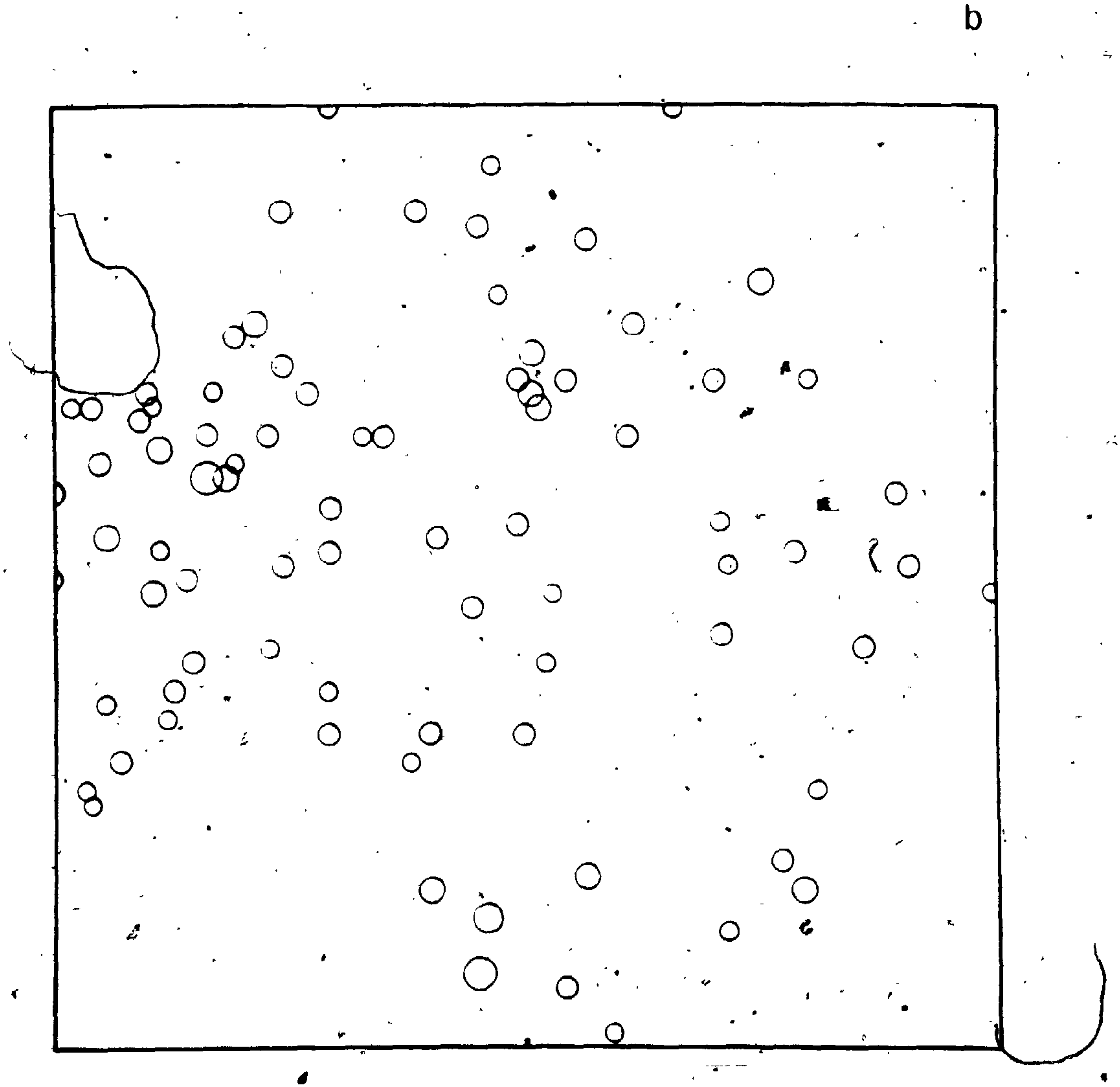
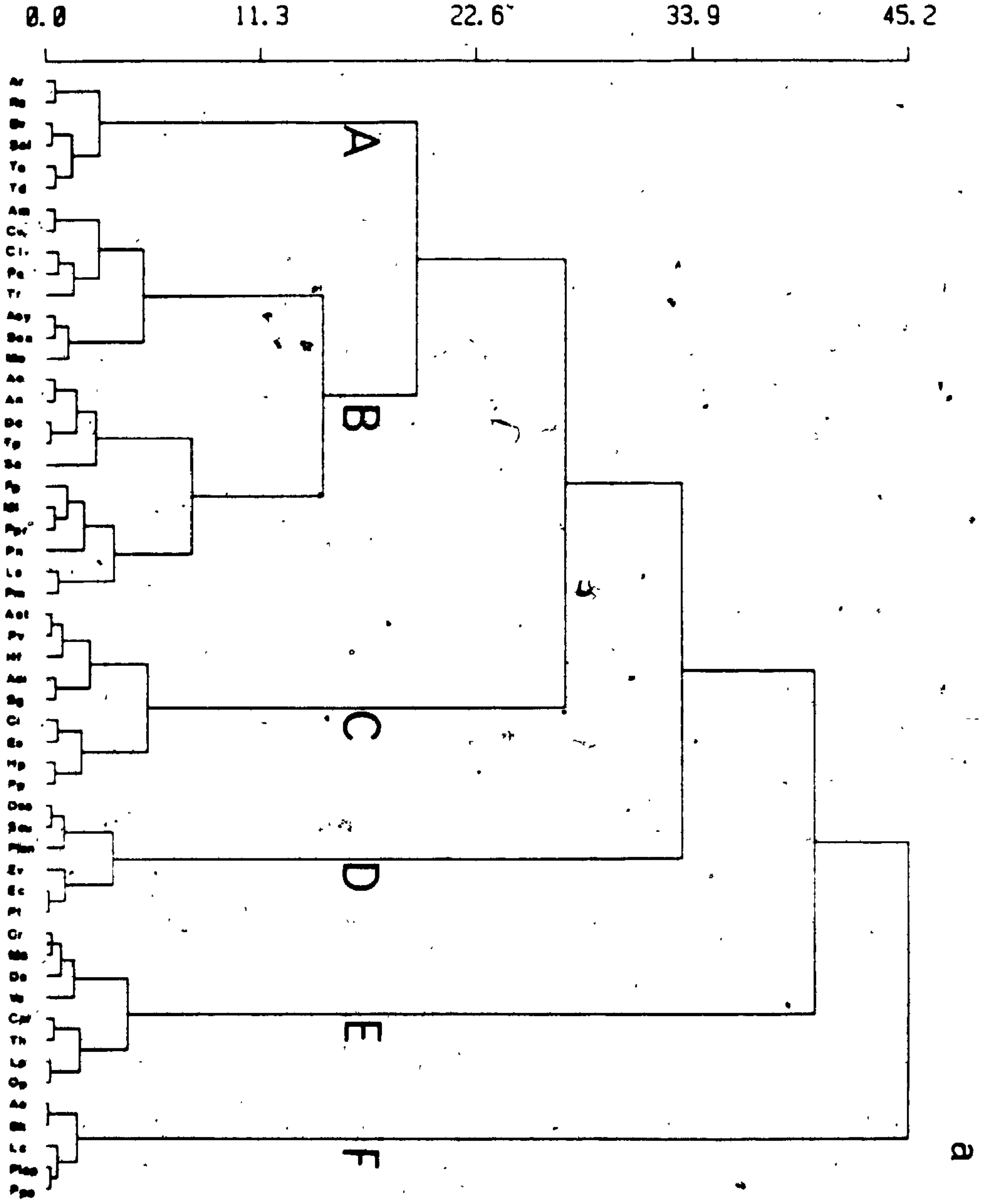

b

Fig. 4.15 Dendrograms rseulting from sum of squares agglomeration of species. (a) Dendrogram based on 53 species, (b) Dendrogram based on 9 species. See text for explanation.

Key of symbols:

Aa, Ambrosia artemisiifolia; Ae, Aster ericoides; Am, Arctium minus; An, Aster novae-angliae; Ar, Agropyron repens; Asi, Aster simplex; Ast, Agrostis stolonifera; Asy, Asclepia syriaca; Bk, Brassica kaber; Br, Barbarea vulgaris; Cal, Cheopodium album; Car, Cirsium arvense; Ci, Cichorium intybus; Cl, Chrysanthemum leucanthemum; Cr, Centaurea repens; Cv, Cirsium vulgare; Dc, Daucus carota; Dsa, Cigitaria sanguinalis; Ds, Dipsacus sylvestris; Ec, Erigeron canadensis; Es, Erigeron strigosus; Ev, Echium vulgare; Fp, Festuca pratensis; Hf, Hieracium floribundum; Hp, Hypericum perforatum; Lc, Lepidium compestre; Lp, Lolium perenne; Ls, Lactuca serriola; Ma, Melilotus alba; Ml, Medicago lupulina; Mo, Melilotus officinalis; Op, Oenothera parviflora; Pc, Poa compressa.


0.0
11.3
22.6
33.9
45.2
Te
Td
Am
Tr
Ae
An
Aot
Ci
Ev
Ec
Cr
Th
Lc
A
B
C
D
E
F
a

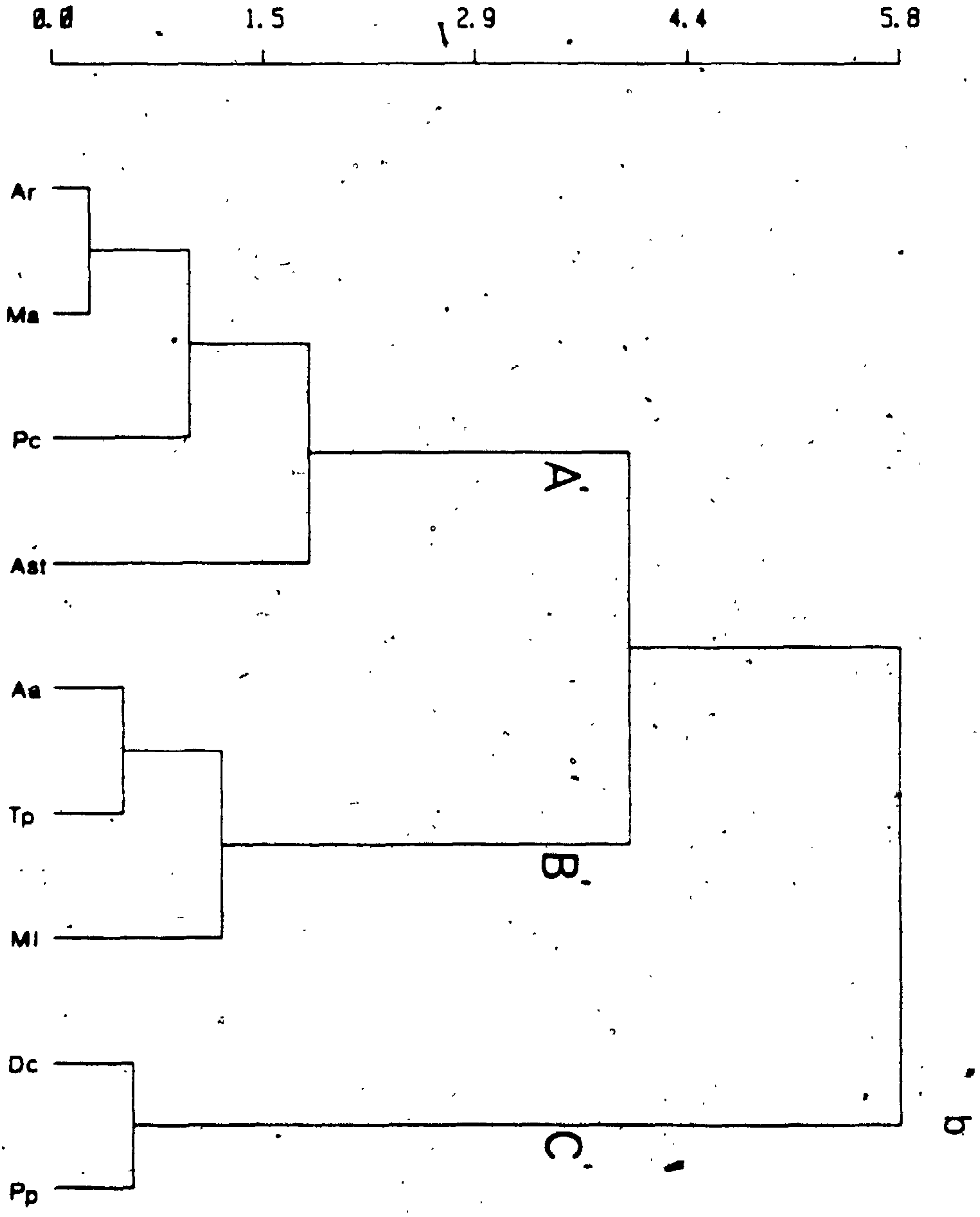
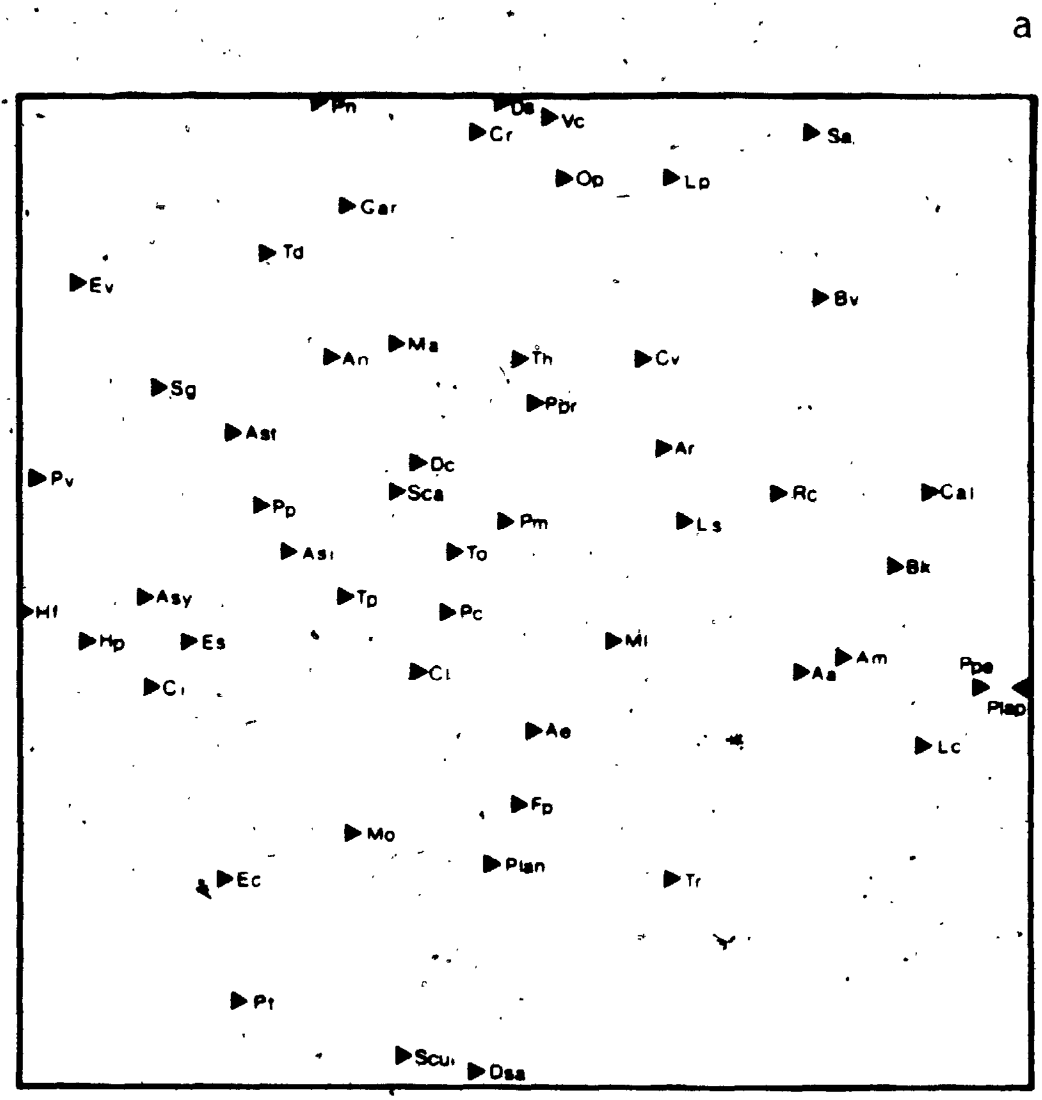

0.0
1.5
2.9
4.4
5.8
Ar
Ma
Pc
Ast
Aa
Tp
Ml
Dc
Pp
A
B
C
a

Fig. 4.16 Nonmetric multidimensional scaling ordination of species. (a) Ordination of 53 species, (b) Ordination of 9 species. See text for explanation. Two-dimensional solutions were sought for each. Refer to the caption of Fig. 4.15 for key to the symbols.


a
Pn
Ds
Vc
Cr
Sa
Op
Lp
Gar
Td
Ev
Bv
Ma
An
Th
Cv
Sg
Ppr
Ast
Ar
Dc
Pv
Sca
Rc
Cal
Pp
Pm
Ls
Asi
To
Bk
Asy
Tp
Hf
Pc
Hp
Es
Mi
Am
Ppe
Ci
Ct
Aa
Plap
Ae
Lc
Fp
Mo
Plan
Ec
Tr
Pt
Scu
Dsa

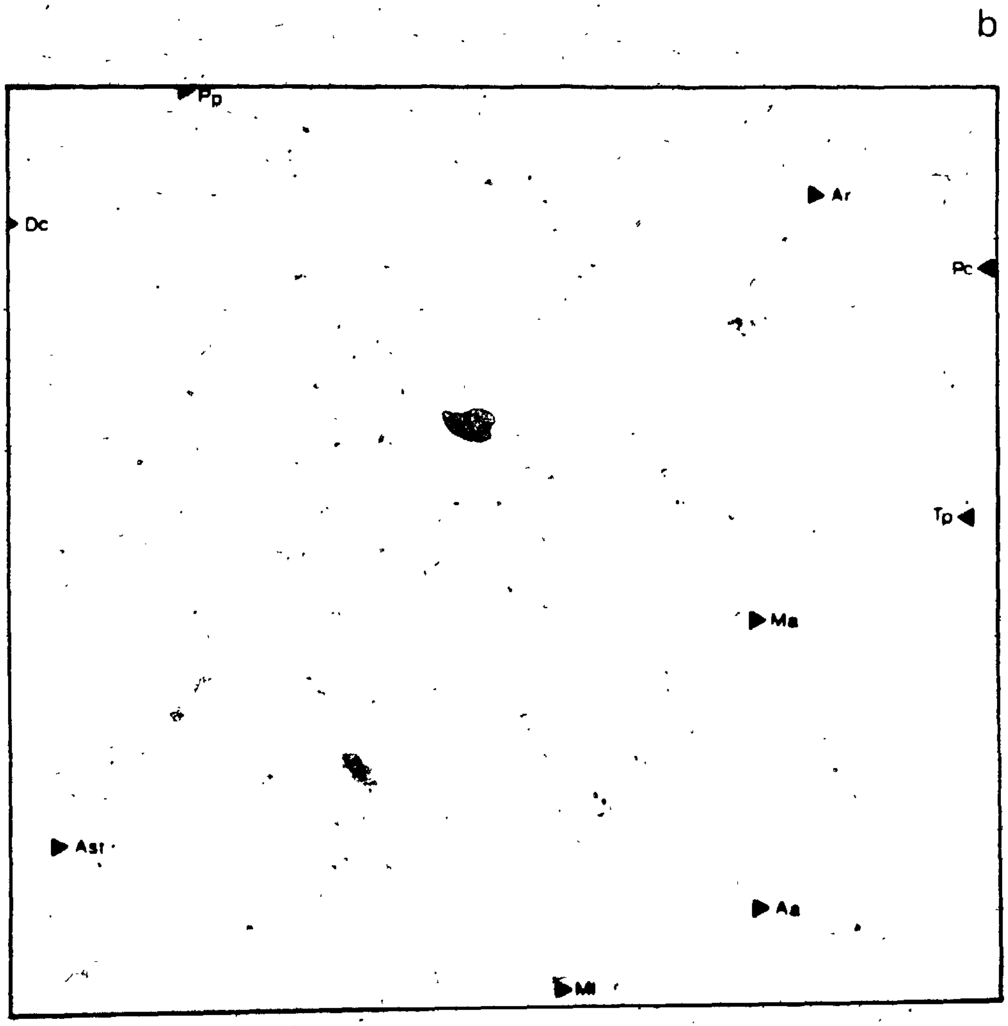

b
Pp
Dc
Ar
Pc
Tp
Ma
Ast
Aa
Ml

Fig. 4.17 The joint scattergram (ordination) of relevé groups (based on age since topsoil removal and clearance) and life-form categories for vacant lot data set. Relevé groups (numerals) corespond to the following age classes -

Group 1, 1 yr.

Group 2, 2 yrs.

Group 3, 3 yrs.

Group 4, 4 + yrs. (usually 4 yr.)

Key to symbols (letters) used for life-form categories, A, theophytes; B, hemicryptophytes-theorphytes; C, hemicryptophytes; D, hemicryptophytes-geophytes; E, geophytes; F, chamaephytes; G, phanerophytes.

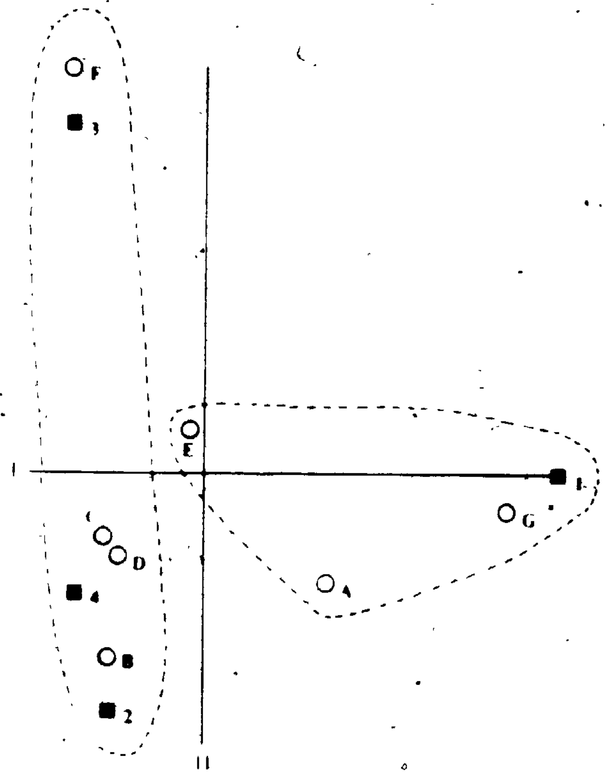

F
3
E
I
1
G
C
D
A
4
B
2
II

Fig. 4.18 Deviations from random expectation with respect to pooled life-form composition for the first lattice. The abscissa represents relevés groups while the ordinate represents deviation from random expectation. A, B, C, D, E, F and G correspond to the life-forms as in the legend of Fig. 4.17.

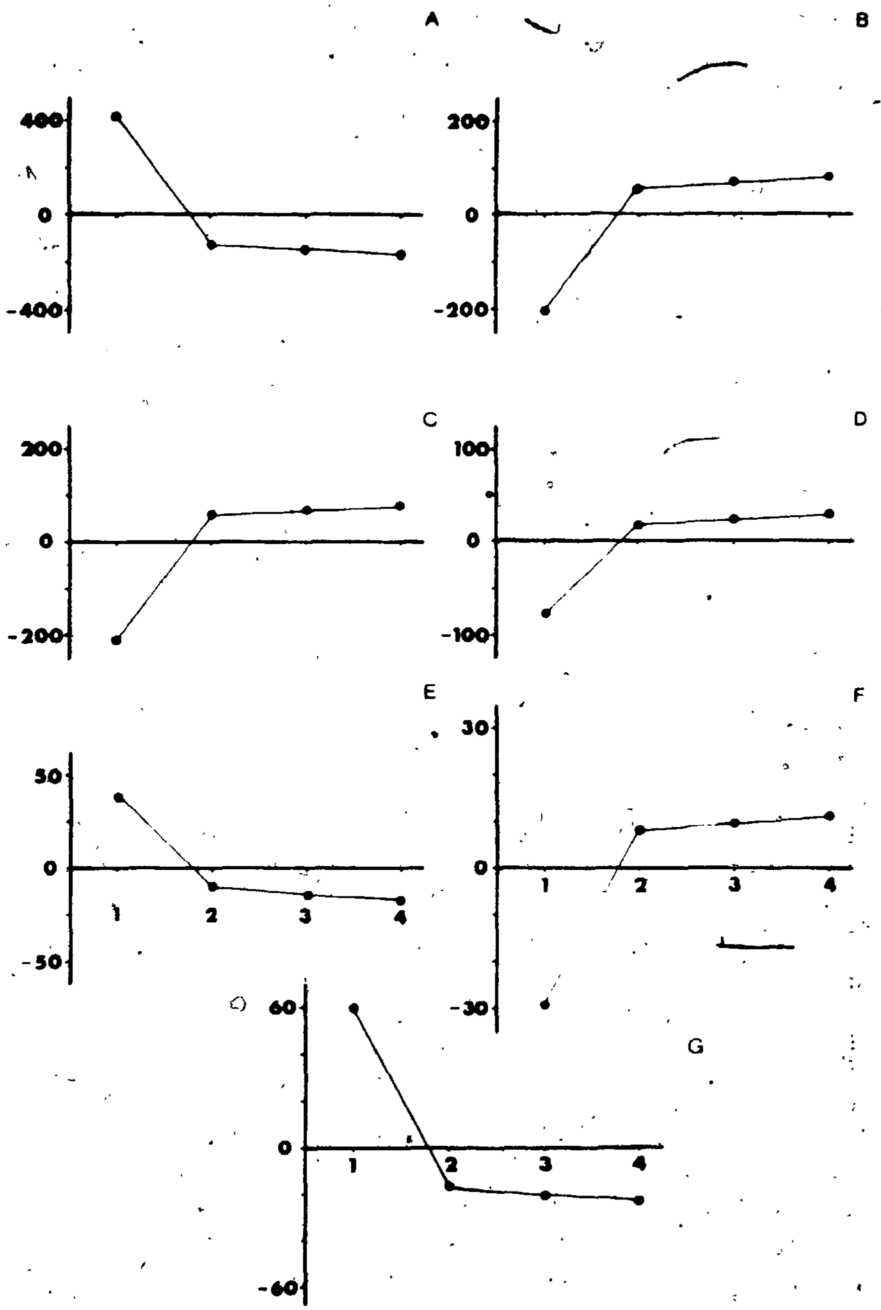

A
400
0
-400
B
200
0
-200
C
200
0
-200
D
100
0
-100
E
50
0
-50
1
2
3
4
F
30
0
-30
1
2
3
4
G
60
0
-60
1
2
3
4

Fig. 4.19 The joint ordination of releve groups (indicated by numerals) and life-span categories (indicated by letters). Releve groups are the same as in Fig. 4.17. Life-span categories are as follows:

A, annuals; B, annuals-biennials; C, biennials; D, biennials-perennials; E, perennials.

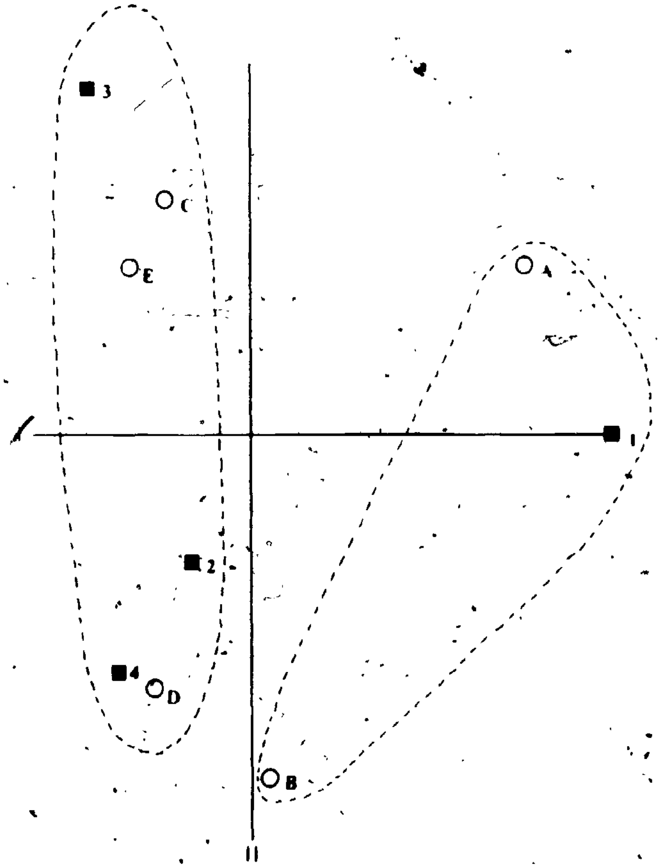

3
C
E
A
1
2
4
D
B
II

Fig. 4.20 Deviations from random expectation with respect to pooled life-span type composition for the first lattice. The abscissa represents relevé groups 1 to 4 (as defined in the legend of Fig. 4.17) and the ordinale represents deviation from expectation. A-E correspond to life-span categories as mentioned in the legend of Fig. 4.19.

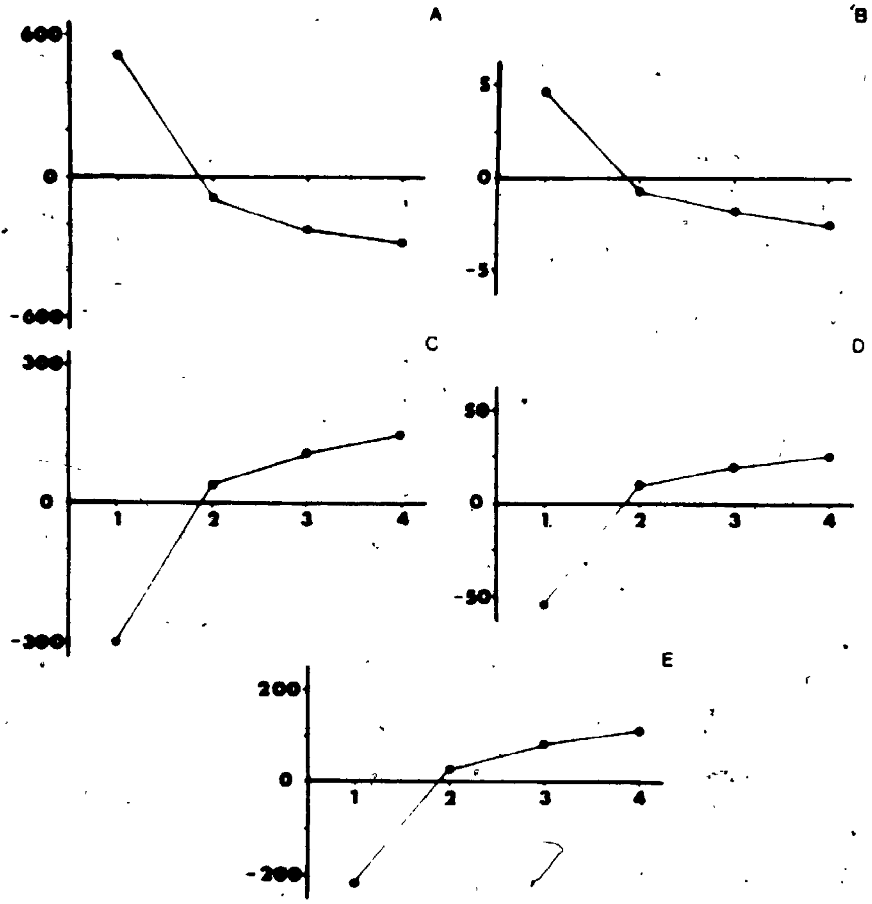

A
600
0
-600
B
5
0
-5
C
300
0
-300
1
2
3
4
D
50
0
-50
1
2
3
4
E
200
0
-200
1
2
3
4

Fig. 4.21 Diversity and dominance patterns with respect to successional progression on vacant lots. The four successional stages correspond to the four age groups of relevés as defined in the length of Fig. 4.17. A, species richness and general diversity; B, equitability; C, dominance concentration.

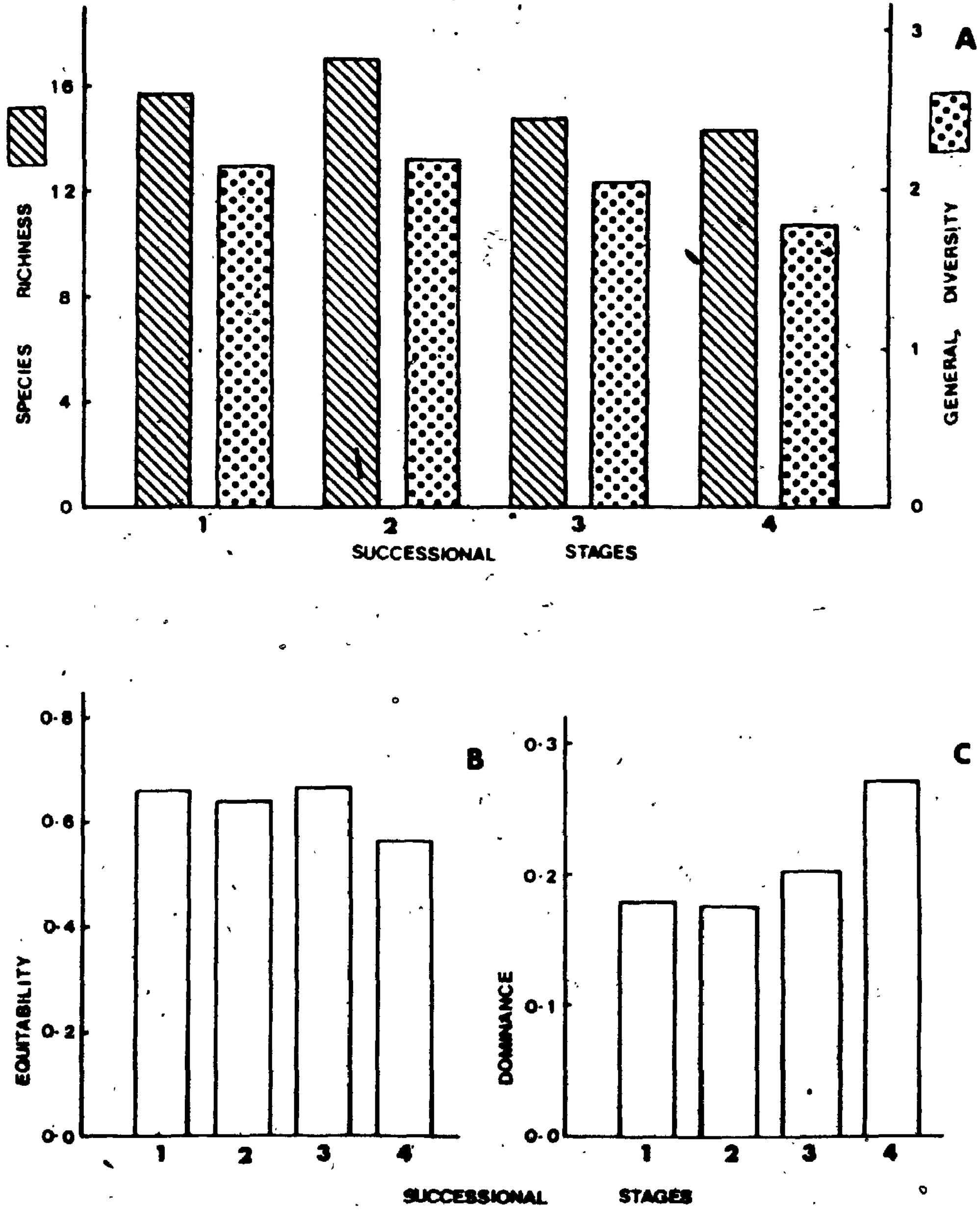

A
SPECIES RICHNESS
0
4
8
12
16
GENERAL DIVERSITY
0
1
2
3
1
2
3
4
SUCCESSIONAL STAGES
B
EQUITABILITY
0·0
0·2
0·4
0·6
0·8
C
DOMINANCE
0·0
0·1
0·2
0·3
1
2
3
4
1
2
3
4
SUCCESSIONAL STAGES

Fig. 4.22 Proposed scheme of secondary succession on the vacant lots. Only the successional dominants are shown.

Trifolium pratense
Daucus carota
Melilotus alba
Agropyron repens
Poa compressa
Phleum pratense

↑

Trifolium pratense
Agropyron repens
Daucus carota
Melilotus alba
Poa compressa
Phleum pratense
Solidago canadensis

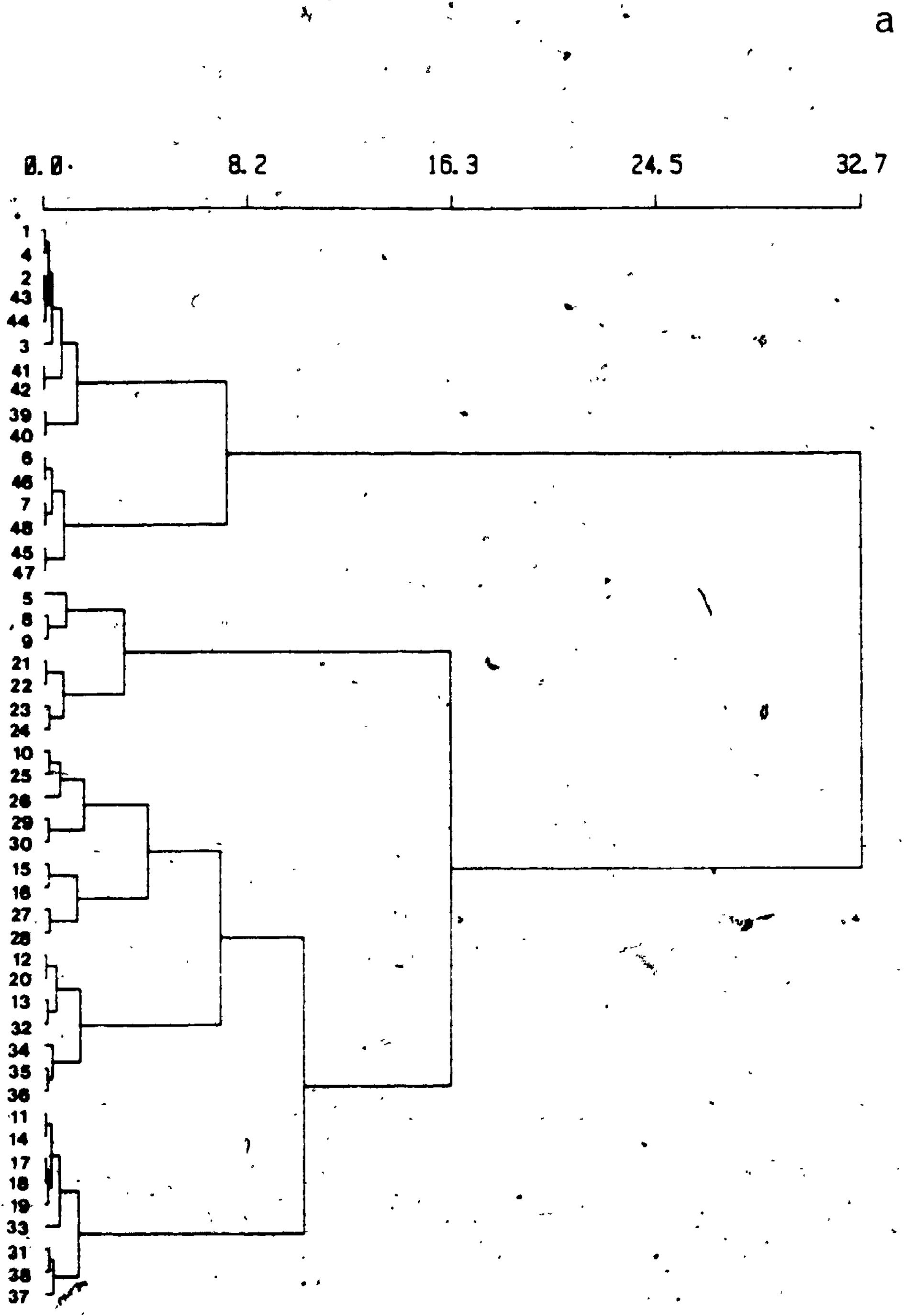
↑

Daucus carota
Agrostis stolonifera
Melilotus alba
Medicago lupulina
Trifolium pratense
Phleum pratense
Solidago canadensis

↑

Ambrosia artemisiifolia
Brassica kaker
Medicago lupulina
Polygonum lapathifolium
Polygonum persicaria
Erigeron spp.

Fig. 4.23 Dendrograms resulting from clustering of 48 relevés of topsoil mound habitat. (a) Dendrogram based on sum of squares clustering; (b) Dendrogram based on iterative clustering. Vegetation types are indicated by Roman numerals. The numbers at the bottom represent the number of releves included in each type. The vertical axis represents the sum of squares. Symbols corresponding to types are used in relevé ordination.


a
0.0
8.2
16.3
24.5
32.7
1
4
2
43
44
3
41
42
39
40
6
46
7
48
45
47
5
8
9
21
22
23
24
10
25
26
29
30
15
16
27
28
12
20
13
32
34
35
36
11
14
17
18
19
33
31
38
37

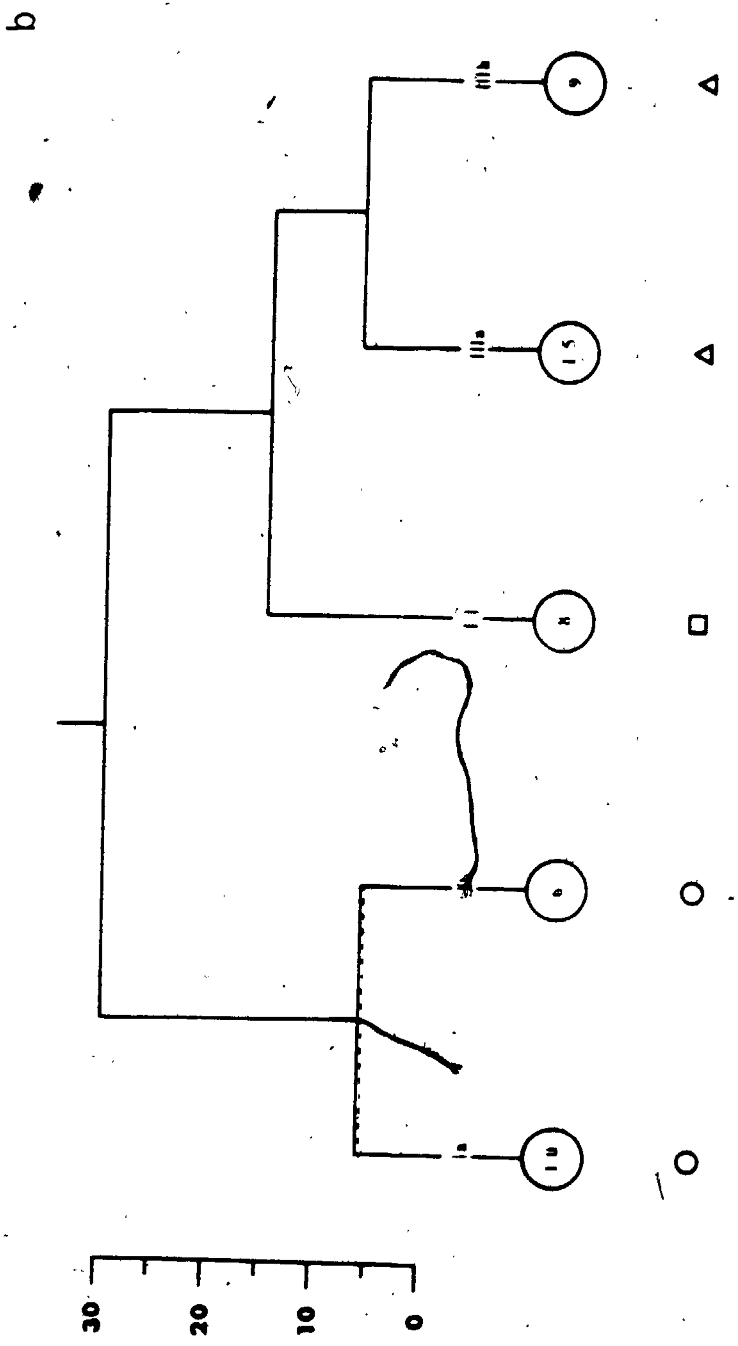
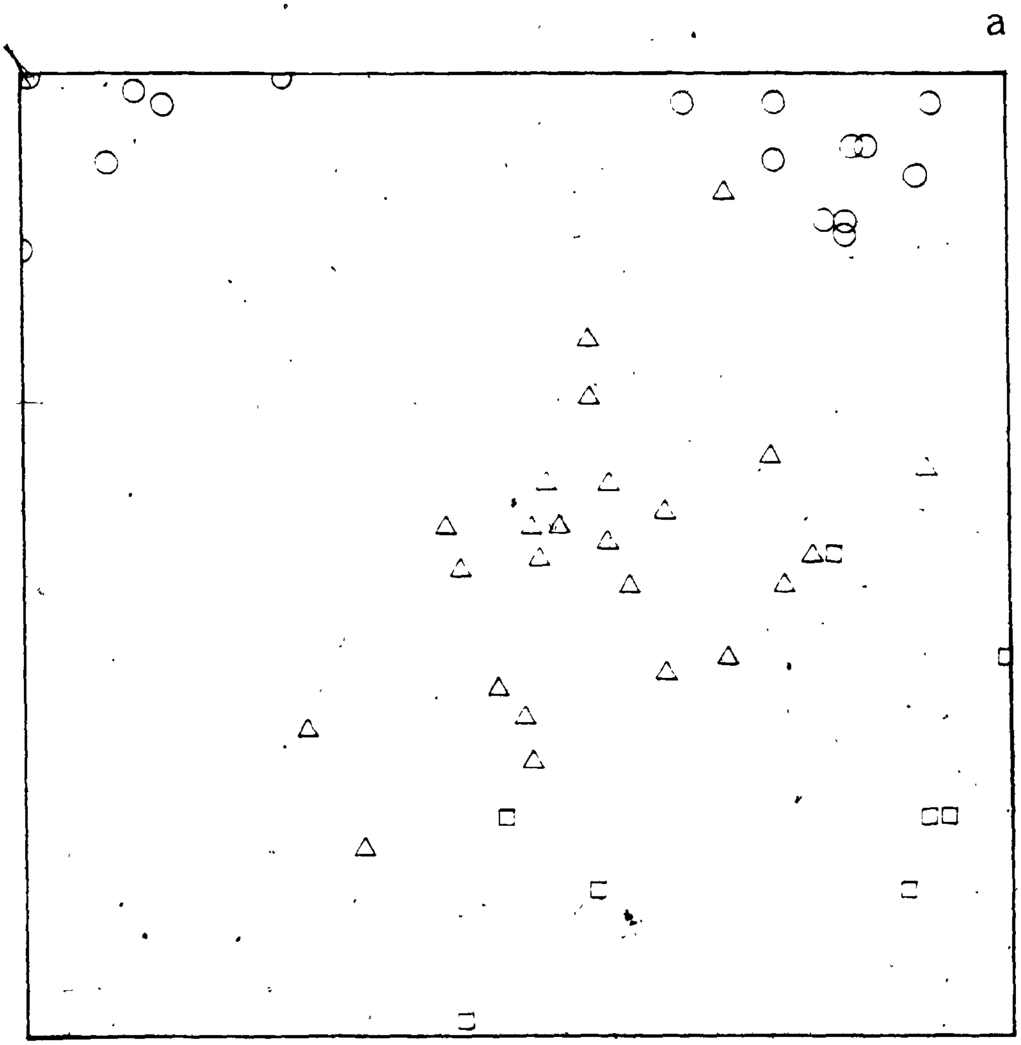

b
IIIa
9
IIIa
15
30
20
10
0

Fig. 4.24 Nonmetric multidimensional scaling ordination of 48 relevés of topsoil mounds. The three main types are superimposed. ○ type 1; □ type 2; △ type 3. Three dimensional solution was sought. (a) Ordination based on axes 1 and 2; (b) ordination based on axes 1 and 3.


a

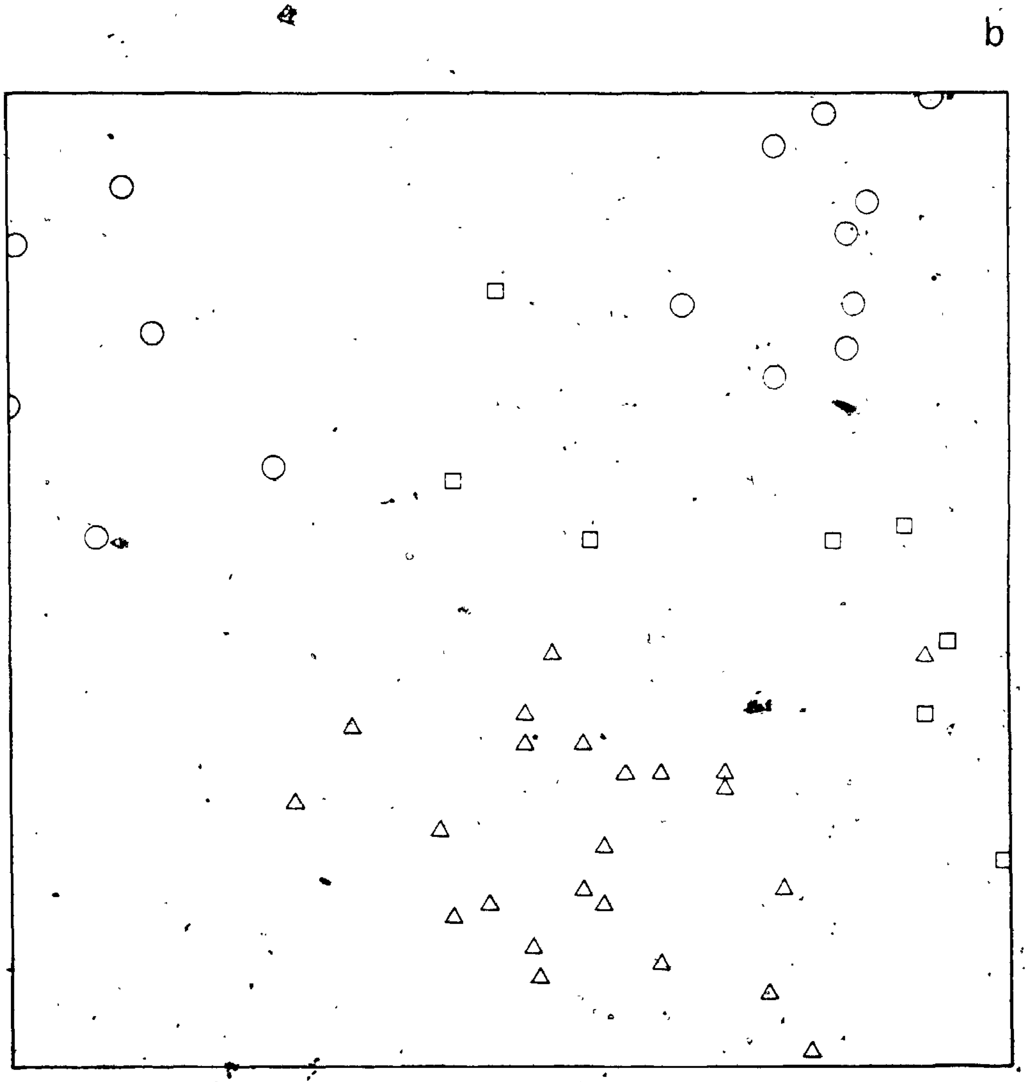
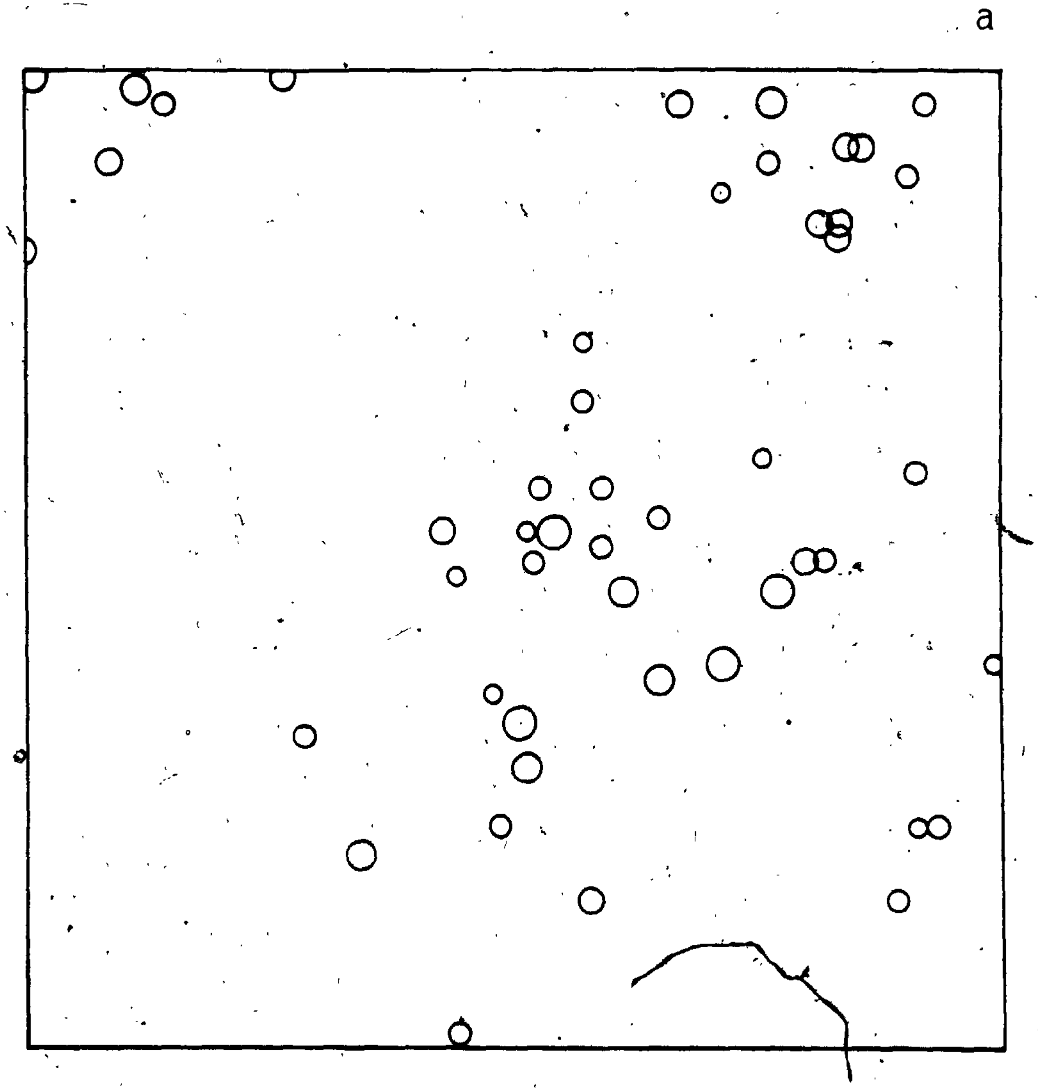
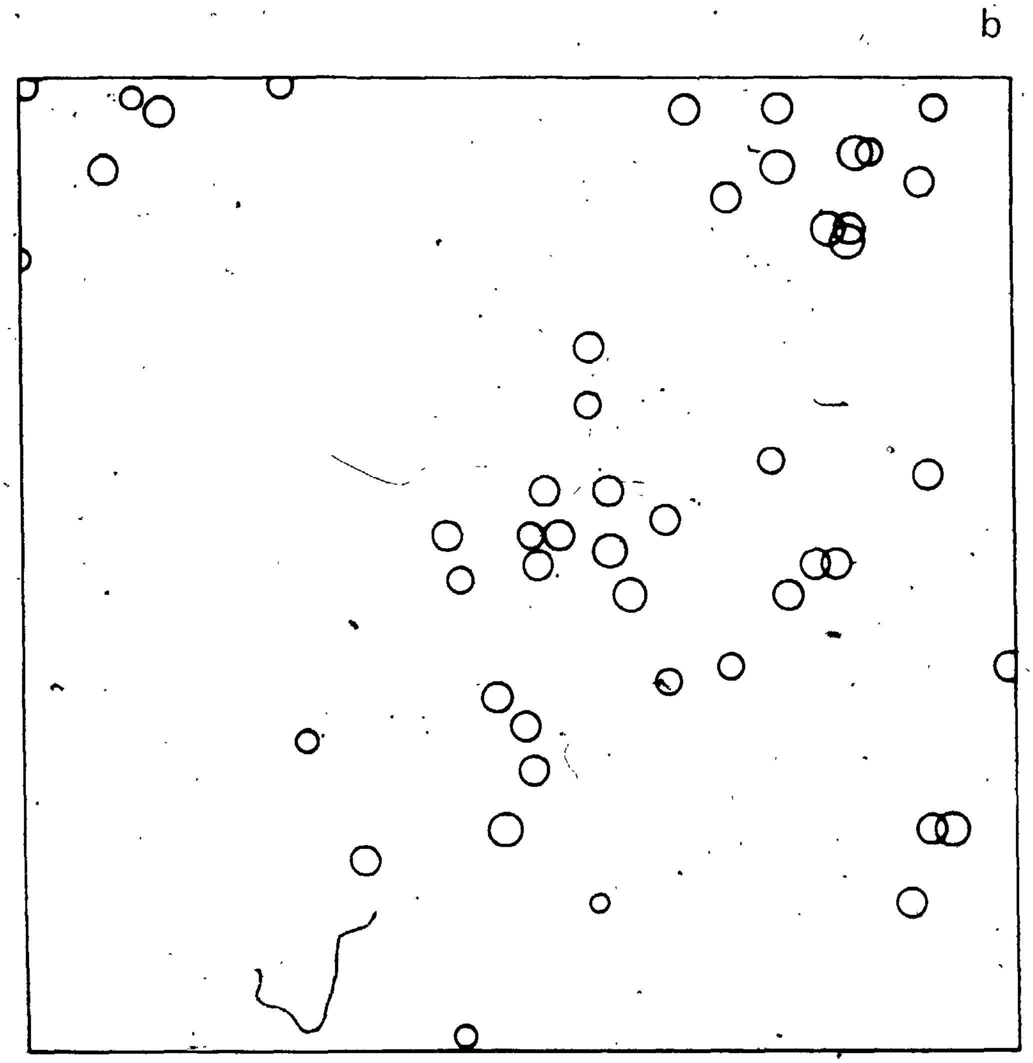

b

Fig. 4.25 Component scores corresponding to the first three components of PCA of environmental data superimposed on the MDSCAL relevé ordination. (a) First component scores, (b) Second component scores; (c) Third component scores. The scores of each component were divided into 5 classes indicated by various circle sizes. Progressively larger circle sizes represent higher component scores.


a


b

C

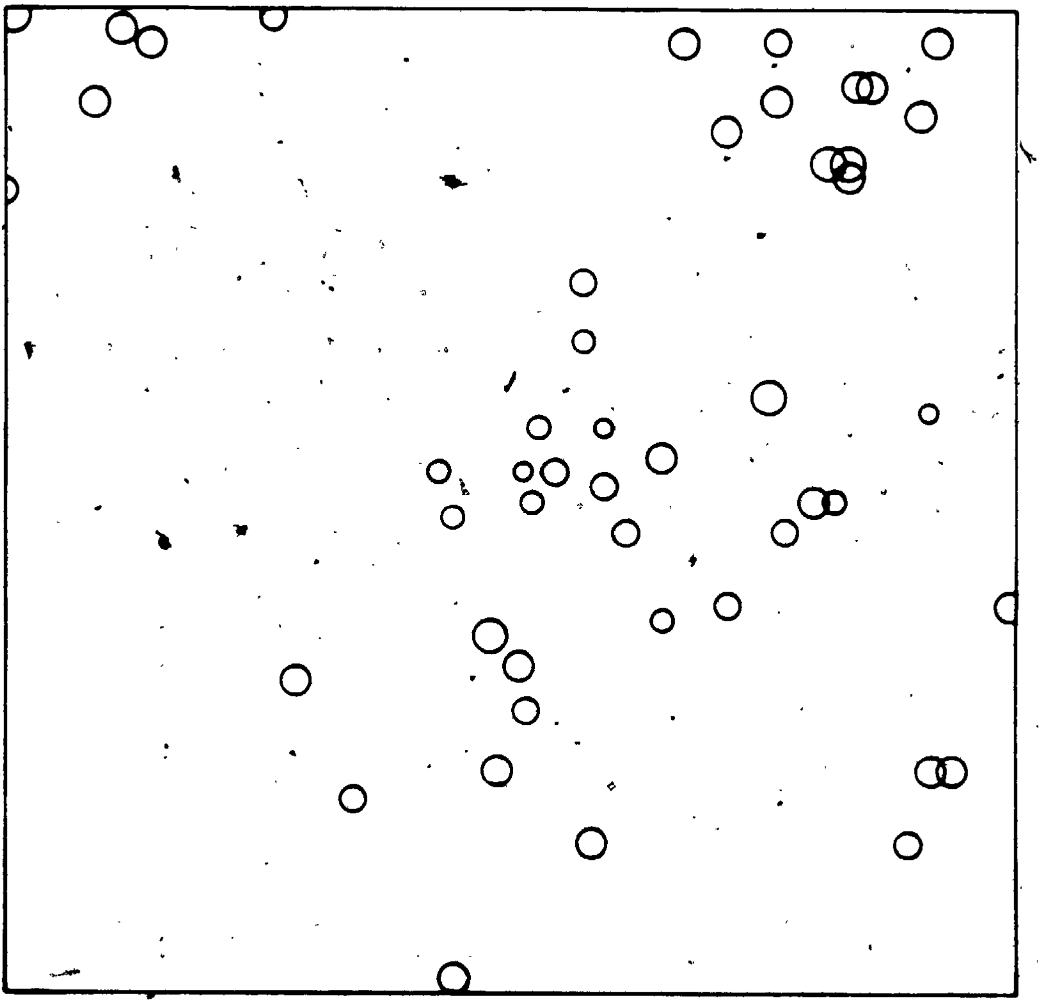


Fig. 4.26 Dendrogram resulting from sum of squares agglomeration of 47 species with > 5 occurrences.

Key to symbols:

Aa, *Ambrosia artemisiifolia*, Am, *Arctium minus*; An, *Aster novae-angliae*; Ap, *Acer pseudoplatanus*; Ar; *Agropyron repens*; As, *Aster simplex*; Ast, *Agrostis stolonifera*; Bc, *Bidens cernna*; Bk, *Brassica kaber*; Ca, *Chenopodium album*; Car, *Cirsium arvense*; Ci, *Chiorium intybus*; Cl, *chrysanthemum leucanthemum*; Cv, *Cirsium vulgare*; Da, *Daucus carota*; Dg, *Dactylis glomerata*; Es, *Erigeron strigosus*; Hp, *Hypericum perforatum*, Lc, *Lepidum compestre*; Ls, *Lactuca serriola*; Ma, *Melilotus alba*; Mf, *Monarda fistulosa*; Ml, *Medicago lupulina*; Ob, *Oenothera biennis*; Op, *Oenothera parviflora*, Os, *Oxalis stricta*; Pc, *Polygonum convolvulus*; Pca, *Panicum capillare*; Pco, *Poa compressa*; Pl, *Plantago lanceolata*; Pm, *Plantago major*; Pp, *Poa pratensis*; Ppe, *Polygonum pesicaria*; Ppr; *Phleum pratense*; Pr, *Potentilla recta*; Rc, *Rumex crispus*; Sc, *Sonchus arvensis*; Sc, *Solidago canadensis*; Sg, *Setaria glauca*; Sgr, *Setaria virdis*; Td, *Tragopogon dubius*; Th, *Trifolium hybridum*; To, *Taraxacum officinale*; Tp, *Trifolium pratense*; Vt, *Verbascum thapsus*.

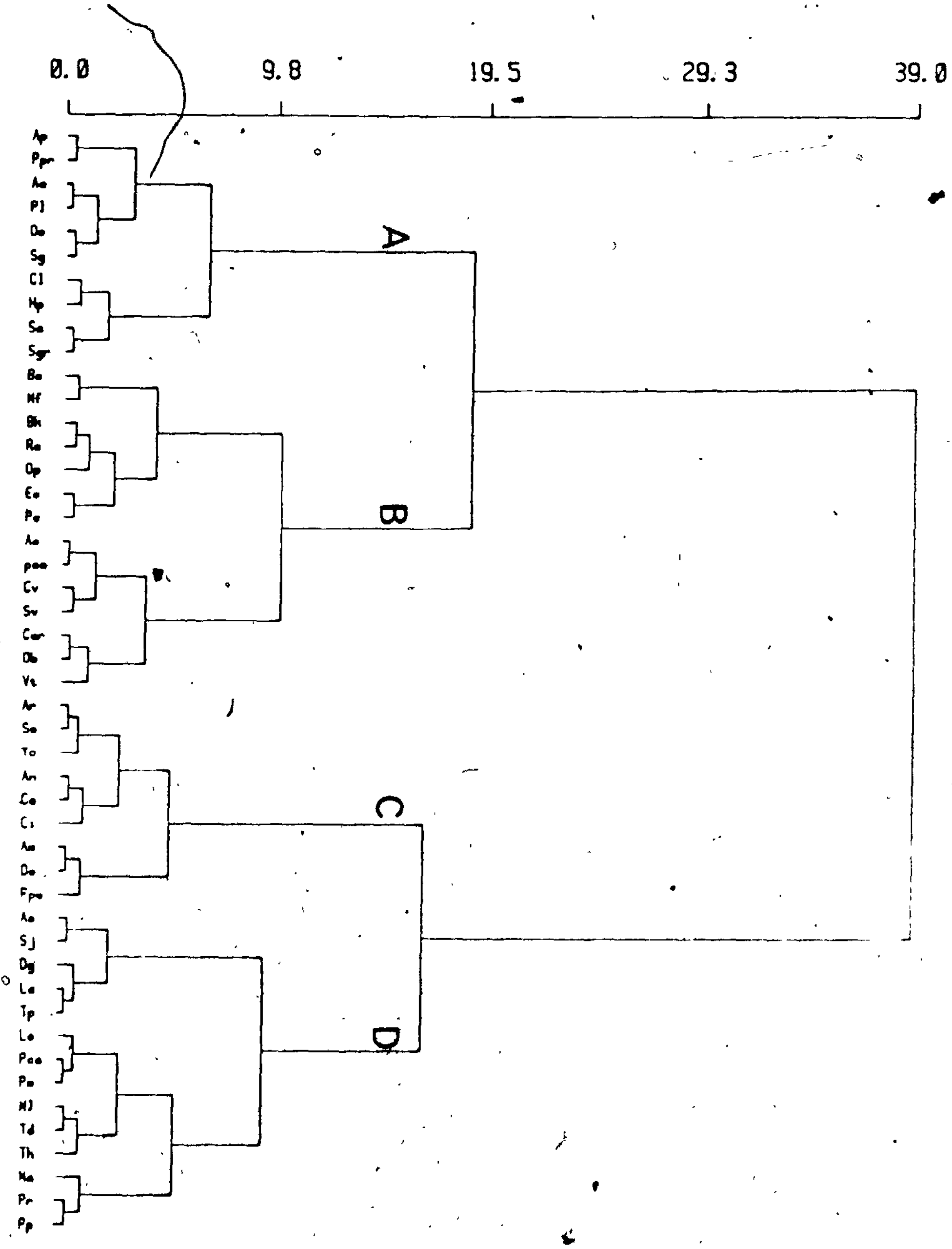

0.0
9.8
19.5
29.3
39.0
A
B
C
D
Ap
Ppr
Ae
Pl
Oe
Sg
Cl
Np
Se
Sgr
Be
Nf
Bk
Re
Op
Ee
Pe
Ae
pae
Cv
Sv
Car
Db
Vt
Ar
Se
To
An
Ce
Cs
Ae
De
Fpe
Ae
Sj
Dg
Le
Tp
Le
Pae
Pm
Nl
Td
Th
Ne
Pr
Pp

Fig. 4.27 Nonmetric multidimensional scaling ordination (3-dimensional solution) of 47 important species of topsoil mounds. For key to symbols, refer to caption of Fig. 4.26.

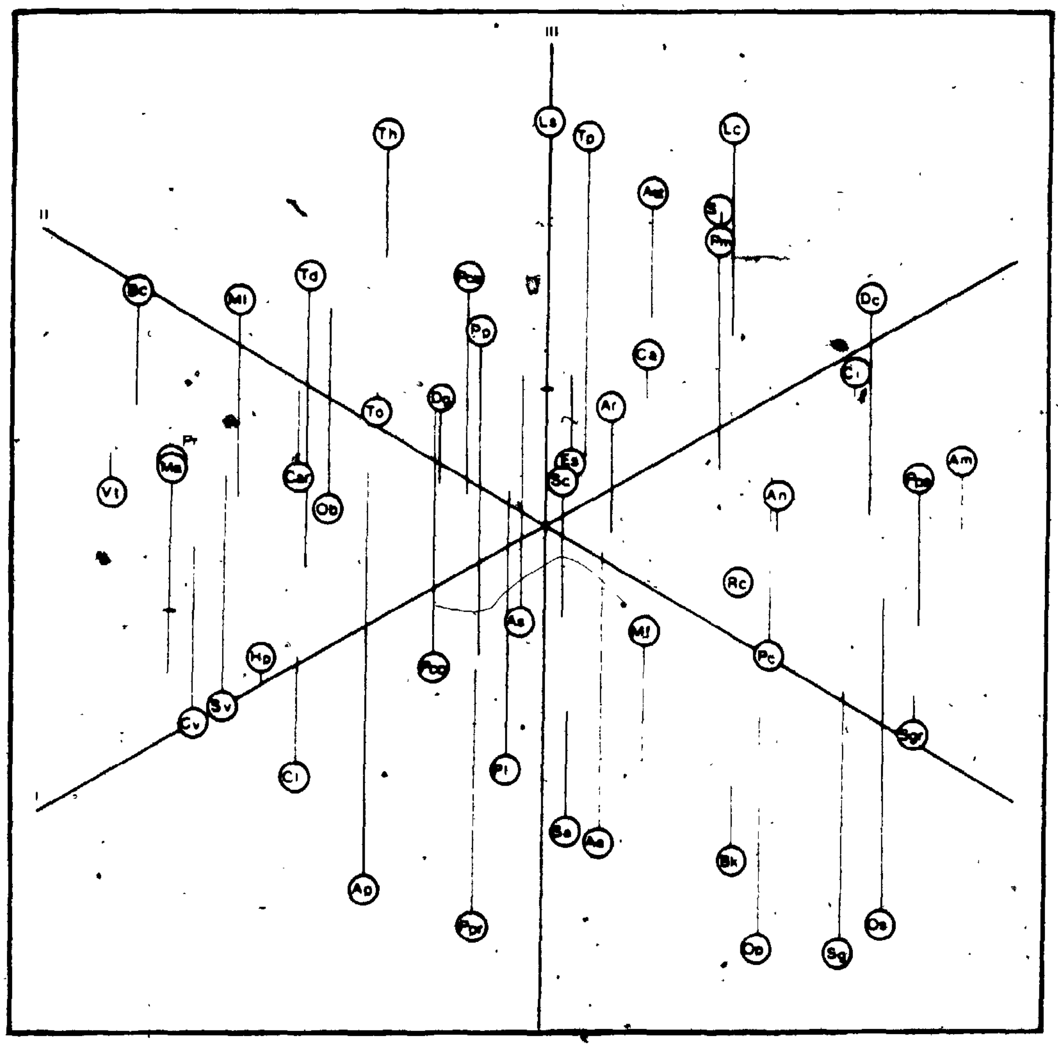

III
Ls
Tp
Th
Lc
Ag
Sj
Pw
II
Bc
Ml
Td
Pca
Dc
Pp
Ca
Ci
Dg
To
Ar
Pr
Ma
Es
Am
Vt
Car
Sc
Pba
An
Ob
Rc
As
Mf
Hp
Pc
Pcg
Sv
Sgr
Cv
Cl
Pl
I
Sa
Aa
Bk
Ap
Ppr
Os
Op
Sg

Fig. 4.28 The joint scattergram of successional stages (relevés groups) and life-form categories for the topsoil mound data set. Successional stages or relevé groups, indicated by numerals 1-3, belonged to the following age classes:

Stage 1 or group 1, 1 yr.

Stage 2 or group 2, 2 to 3 yrs.

Stage 3 or group 3, 4 + yrs old.

Key to life-forms, shown by letters, is a follows: A, theophytes; B, hemicyptophytes; C, theophytes-geophytes; D, hemicryptophytes; E, hemicryptophytes-geophytes; F, geophytes, G, chamaephytes-hemicryptophytes; H, chamaephytes; I, phanerophytes.

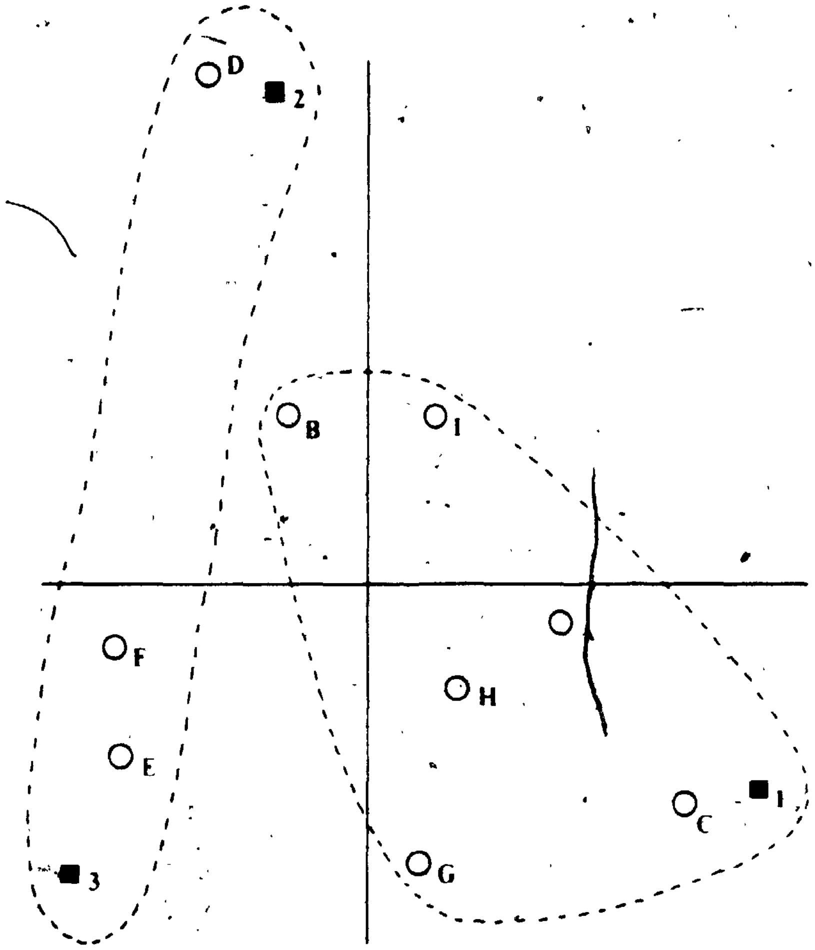
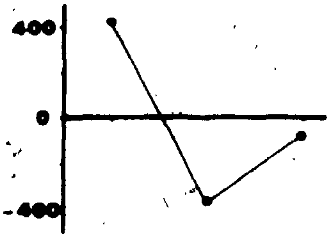
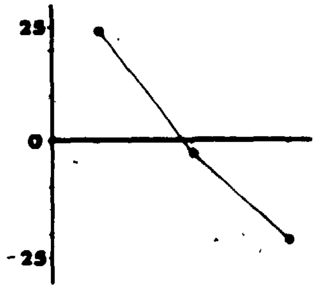

D
2
B
I
F
H
E
C
1
G
3

Fig. 4.29 Deviations from random expectation with respect to pooled life-form composition for the first lattice (topsoil mound data set). The abscissa represents successional stages (i.e., relevé groups) and the ordinate represents deviation from expectation. A-I correspond to the life-form categories as in Fig. 4.28.

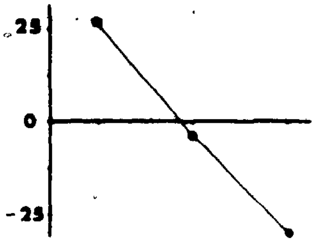

400
0
-400

A

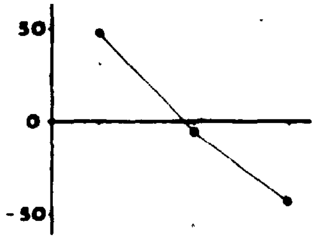

25
0
-25

B

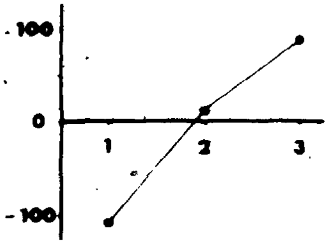
C


25
0
-25

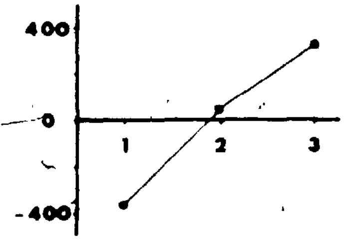
D


50
0
-50

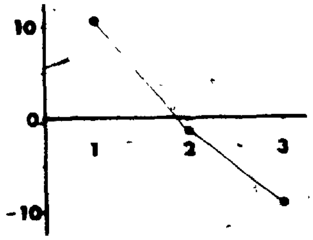
E


100
0
-100
1
2
3

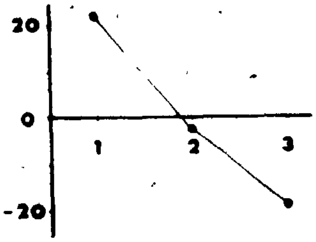
F


400
0
-400
1
2
3

G


10
0
-10
1
2
3

H


20
0
-20
1
2
3

I

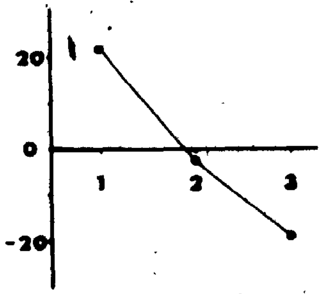

20
0
-20
1
2
3

Fig. 4.30 The joint scattergram of successional stage (relevé groups) and life-span categories for the topsoil mound data set. Successional stages or relevé groups indicated by numerals are the same as in Fig. 4.28. Life-span categories, indicated by letters, are as follows:

A, annuals, B, annuals-biennials; C, annuals-perennials; D, biennials; E; biennials-perennials; F, perennials.

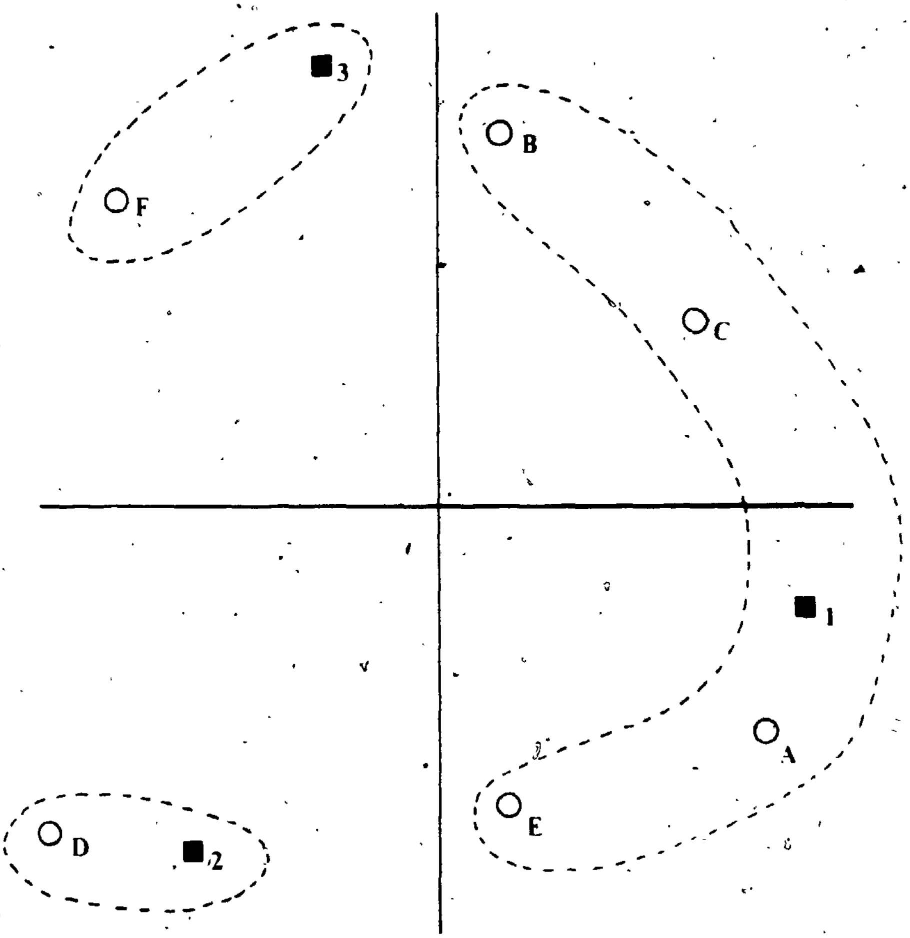

3
F
B
C
1
A
E
D
2

Fig. 4.31 Deviations from random expectation with respect to pooled life-span type composition for the first lattice (topsoil mound data set). The abscissa represents successional stages 1-3 (or relevé groups) and the ordinate represents deviation from expectation. A-F correspond to the life-span categories as in Fig. 4.30.

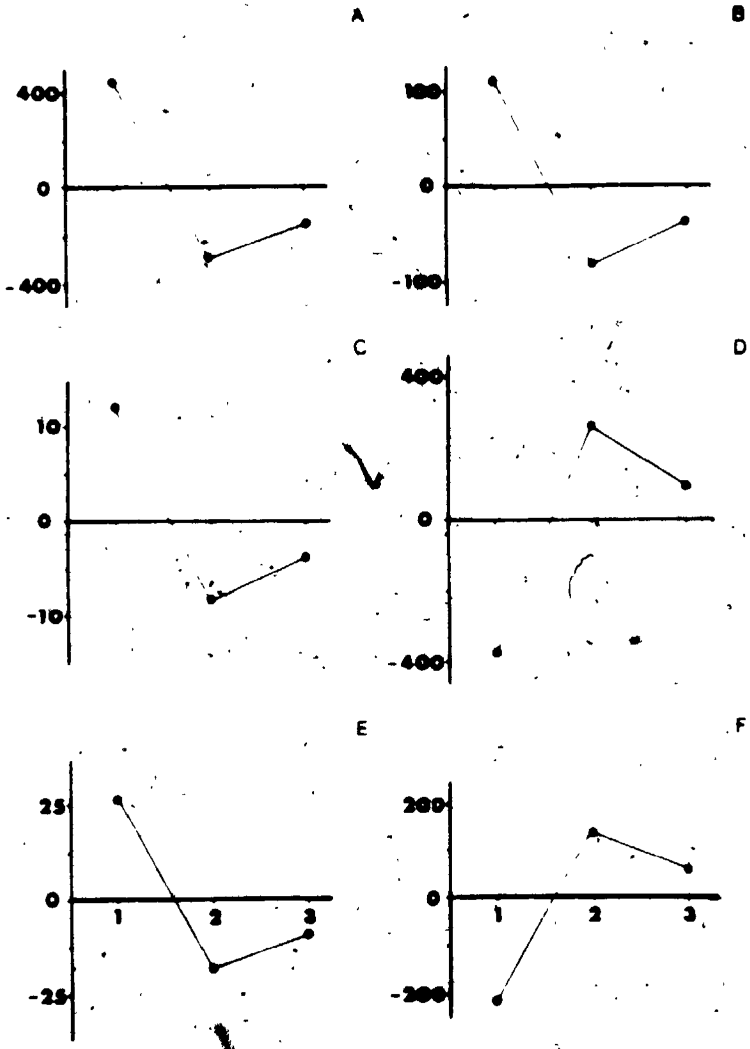

A
B
400
0
-400
100
0
-100
C
D
10
0
-10
400
0
-400
E
F
25
0
-25
1
2
3
200
0
-200
1
2
3

Fig. 4.32 Diversity and dominance patterns with respect to successional progression on topsoil mounds. The three successional stages correspond to the three relevés groups extracted from iterative clustering. Refer to the legend of Fig. 4.28 for the ages of the successional stages. A, species richness and general diversity; B, equitability; E, dominance concentration.

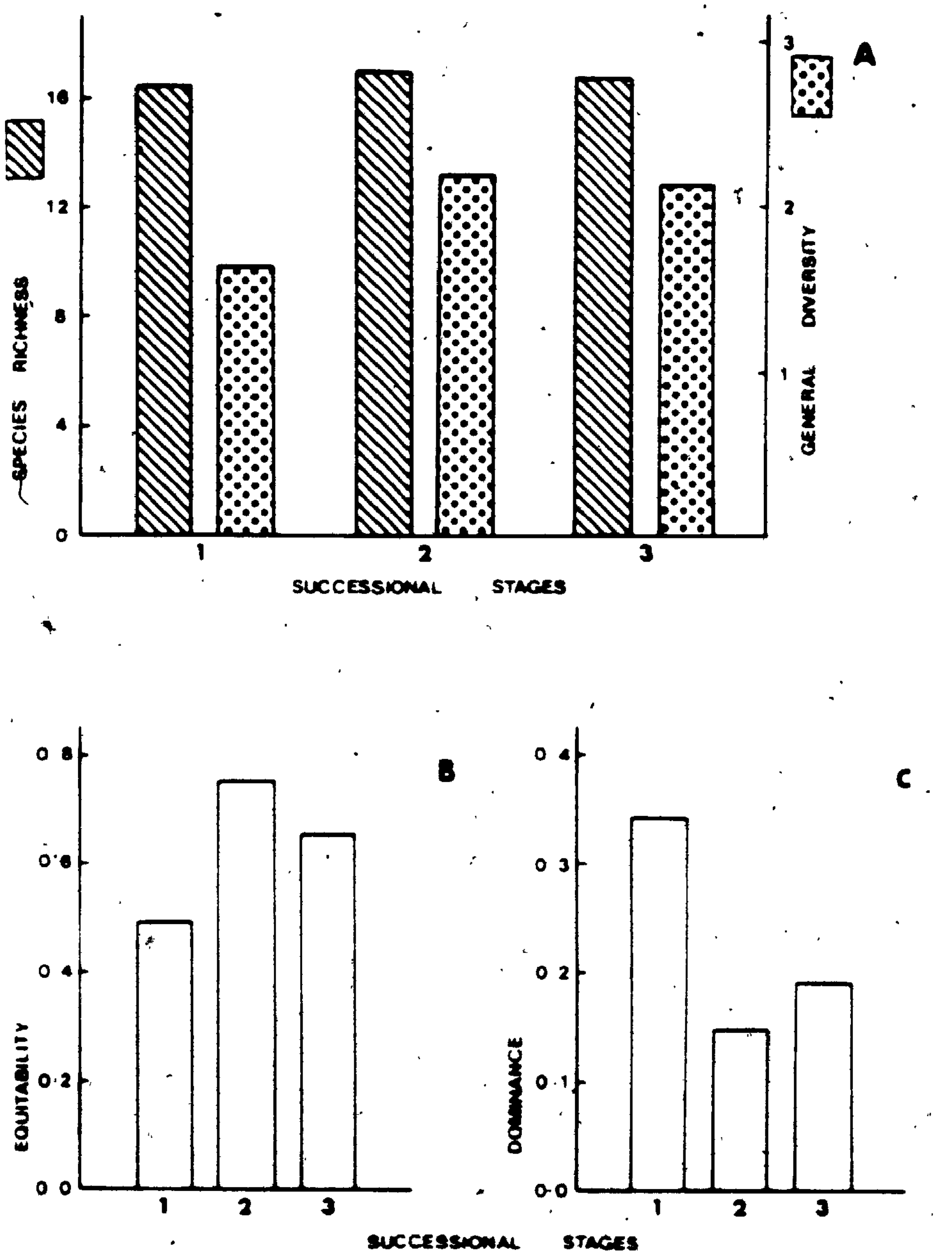
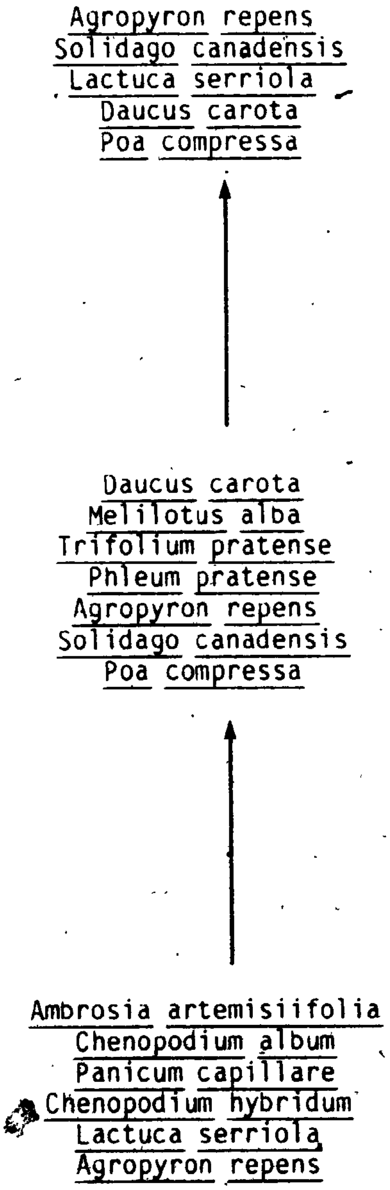

A
SPECIES RICHNESS
0
4
8
12
16
GENERAL DIVERSITY
1
2
3
1
2
3
SUCCESSIONAL STAGES
B
EQUITABILITY
0 0
0·2
0 4
0·6
0 8
C
DOMINANCE
0·0
0·1
0 2
0 3
0 4
1
2
3
1
2
3
SUCCESSIONAL STAGES

Fig. 4.33 Proposed scheme of secondary succession on the vacant lots. Only the successional dominants are shown.


Agropyron repens
Solidago canadensis
Lactuca serriola
Daucus carota
Poa compressa
Daucus carota
Melilotus alba
Trifolium pratense
Phleum pratense
Agropyron repens
Solidago canadensis
Poa compressa
Ambrosia artemisiifolia
Chenopodium album
Panicum capillare
Chenopodium hybridum
Lactuca serriola
Agropyron repens

CHAPTER 5

OVERVIEW AND CONCLUSIONS

In this dissertation an attempt has been made to develop methodologies which may assist community ecology in the sampling stage as well as in the analysis phase to reveal information about the structure and composition of ruderal weed communities. The study sites were located in the city of London. Three methodological problems were addressed. The first problem was the choice of an optimal plot size for community description. In contrast to many previous subjective and empirical attempts, I approached this problem purely on an experimental basis. My method involved repeated random sampling with a range of plot sizes in a pilot study and subsequent data analysis. The plot size which maximized the average value of a dissimilarity function among plots was regarded as the most effective plot size. The resulting pattern information (clusters, trends, etc.) from the data obtained with the most effective plot size and that of the smaller plot sizes were compared and the smallest plot size which disclosed a group structure and/or gradient without significant distortion was chosen as the most efficient plot size for the main survey.

The second problem involved the evaluation of various data types which phytosociologists use in community studies with regard to the resulting pattern information. Contrary to many earlier works, it was shown that various types of untransformed ordinal data sets can provide comparable pattern information to that resulting from percentage cover data, though ordinal scales with fewer cover categories were found to yield somewhat inferior results. The presence/absence data sets yielded the least precise results and consequently it was concluded to have limited utility. It was also concluded from the study of data types that simple tranformations, such as arcsin, square root and logarithmic represented no improvement as they yielded the same pattern information as the percentage data.

The third problem was that of data reduction and minimization of misclassification. Large number of variables are not only difficult to handle in data analysis but may contain a sizeable random component that can potentially obscure the clarity of ordinations and classifications. The problem of data reduction can be approached by determining weights of species based on a suitable 'ranking' cirterion and eliminating lowly ranked species from the data set. One important requirement of a ranking procedure is that it should be compatible with the method of subsequent data analysis. An algorithm for species ranking based on the within species sum of squares has been proposed. This ranking procedure is compatible with some important clustering strategies such as sum of squares agglomeration and the k-mean method. Non-metric multidimensional scaling ordination method is also compatible when a distance based measure is used as a resemblance function. Using ranking technique to identify unimportant species in the data sample, it was demonstrated that relatively a few species contain the bulk of pattern information. The best result to minimize 'noise' and consequently alleviating the misclassification problem at successive stages of a hierarchical classification was achieved by a modification of the iterative ranking-clustering technique of Jancey (1980) which originally ranked speices on a sum of squares criterion (Orloci, 1973). The within species sum of squares method of ranking, developed during the study, was used in conjunction with sum of square agglomeration to accomplish iterative rank- clustering. This algorithm not only increased the clarity of the underlying group structure by way of eliminating 'noise' but also permitted increased programming efficiency.

The vegetation of each of the three ruderal habitats, viz., old fields, vacant lots and topsoil mounds was effectively analyzed using a variety of quantitative approaches, including sum of squares and iterative clustering, non-metric multidimensional scaling and analysis of concentration. The underlying relationships between community pattern and environment were successfully exposed by superimposing the component scores resulting from PCA of the environmental data set on the MDSCAL vegetational ordination. Such an approach to the examination of vegetational-environmental relationships has several advantages. The MDSCAL vegetational ordination, compared to a PCA of the vegetation data, suffers little from non-linearity, discontinuous species distributions and high beta diversity (Fasham, 1977; Gauch et al., 1981). The non-linearity problem was circumvented by using monotonic environmental variables for PCA which yielded an effective summarization of environmental data into meaningful environmental gradients (Austin, 1976; Orloci, 1978). Such environmental gradients when examined in the framework of MDSCAL vegetational ordination permitted adequate exposition of the relationships (linear as well as non-linear) between vegetational composition and environmental factors and factor complexes.

The vegetation of each of the three habitats was found to contain greater proportions of introduced than native species. The percentage of introduced species was closely similar for the vacant lots and the topsoil mounds, 68.9 and 69.4% respectively. Old fields had a relatively lesser proportion of introduced floral element (61.8%). Releve clustering within each of the habitat produced vegetation 'types' that were readily interpretable in terms of the vegetational dynamics of the habitat with the types corresponding to the successional stages. The species groupings derived from species clustering corresponded with the respective vegetation types of plots only to a limited extent suggesting weak group structure in the vegetation. The releve ordinations within habitats, generally, depicted overlapping of the vegetation types obtained from releve clustering, once again suggesting that the 'types' recognized do not represent discrete entities and that the vegetation was continuous. The most noticeable trend in the releve ordination of each of the ruderal habitat was the temporal or successional trend. Environmental gradients or coenoclines representing moisture availability and nutrient supply were examined in relation to MDSCAL releve ordinations based solely on vegetation data and were found to be related to the corresponding successional trends.

Despite obvious differences, the successional patterns exhibited by the three habitats were characterized by a common trend. Annuals were the earliest colonizers. Biennials generally dominated the systems in second year but often remained prominent upto fourth year of succession. Perennials, though present in substantial proportion in the first two years did not attain pre-dominance until the third or fourth year of succession. Small deviations from this general scheme of succession regarding time of invasion and degree of dominance of the different longevity-forms existed and were presumably due mainly to the nature of initial perturbance and small variation in soil properties, particularly, the water retaining capacity of soil. Each of the habitat showed a characteristic pattern of life-form invasion and dominance. Therophytes were most conspicuous in the initial phase of succession in all the three habitats. Hemicrytophytes and geophytes attained dominance in second year of succession on vacant lots and topsoil mounds. In the fourth year of succession, vegetation of topsoil mounds was dominated by hemicryptophytes, geophytes and hemicryptophytes-geophytes whereas that of old fields was dominated by hemicryptophytes and hemicryptophytes- geophytes. The fourth year vegetation of vacant lots was dominated exclusively by hemicryptophytes. The oldest old field system (15+ yrs.) was dominated by hemicryptophytes. The pattern of life-form invasion and dominance appears to be influenced largely by (1) the nature of initial perturbance which, in the case of the habitats under study, determines the composition of the seed bank, and (2) the management practices, viz. mowing or the lack of it.

In the light of the present analysis, secondary succession was seen as an orderly, directional and a more or less predictable process, though some characteristics did not change in a manner expected based on classical succession theory. The majority of species involved in each of the three seres did not enter sequentially but prevailed more or less throughout the successional time span examined. These observations partially support Egler's (1954) model of "initial floristic composition". However, the model cannot be accepted in its entirety as many species entered at various points during the course of successional progressions.

Succession-diversity trends for the seres generally involved a rapid initial increase in general diversity and a gradual decline afterwards with the further successional advancement. Such a pattern is suggestive of an r-K-selection continuum. The initial and early colonizers that were predominately r-strategists were responsible for increase in diversity in the early successional stage. The later occupants that were predominately K-strategists caused decrease in diversity by way of competitive exclusion. Owing to dominance by long-lived (K-selected) species, community stability increased in the advanced stages of succession.

The three models of mechanisms that determine successional changes, proposed by Connell and Slatyer (1977) were evaluated in the light of the present findings as well as available ecological information on the successional dominants. An attempt was made to deduce from the observations some general rules regarding the secondary seres. Dominants of the seral communities upto 4th to 8th year of succession are generally by nature allelopathic and presumably suppress the establishment and growth of the later arrivals. Such allelopathic interference in the early successional communities is suggestive of the "inhibition" model as the principal mechanism underlying secondary succession. However, it is likely that more than one mechanisms are involved in the successive replacement of species or groups of species.

The ruderal ecosystems such as old fields, vacant lots and topsoil mounds are natural laboratories that potentially offer opportunities for a wide range of ecological studies. For instance, two important areas of research that can contribute substantially towards the understanding of the reasons for unique species assemblages are: a) Studies on seed dispersal characteristics including seed influx, germination and establishment of the successional dominants. b) Examination of viable soil seed bank. Another important aspect that needs attention is the understanding of the mechanism(s) of secondary succession, in particular, testing of the three models of succession described by Connell-Slatyer (opt. cit.) with the help of suitably designed field experiments such as those involving examination of the effect of removal of selected species from seral communities. Comparative studies on different phases of the life-history of successional dominants are also expected to be rewarding in this respect. Finally, information is also required regarding community structure, particularly, species interactions, competition and co-existence in order to understand mechanisms regulating assembly and organization in communities.

APPENDIX A

SOIL ANALYSIS

Preparation of soil:

Soon after collection, stones were removed from the soil samples and they were dried at 30°C. After drying the soil samples were crushed with a rubber mallet to break the aggregates without grinding the primary particles. The samples were then passed through a 2 mm mesh and the proportion finer than 2 mm was retained for analyses.

pH deletermination:

Soil pH was measured electronmetrically on a 1:2.5 fresh soil:distilled water suspension.

Organic matter percentage:

The wet combustion method described by Grewling and Peech (1960) was used. To develop the standard curve, seven different samples were analyzed and organic matter percentage calculated in accordance with Cox (1976). These were used to plot the standard curve. The percentage transmittance obtained by Grewling and Peech's method was then used to obtain the corresponding organic matter percentage.

Soil texture:

The soil texture was determined by passing the sample through a set of standard soil sieves to separate various particle sizes. The set of sieves with successively smaller mesh size from top to bottom were shaken for twenty minutes using a mechanical shaker. The separated soil fractions were weighed and the percentage of each was calculated (U.S.D.A., 1951).

Water retaining capacity of soil:

This was determined in accordance with Cox (1976) with minor modifications. 100 g air dried soil was placed in a tin can with a small hole and two Whatman No. 1 filter paper discs at the bottom. The can was tapped on two layers of cardboard to settle the soil and subsequently placed in a tray of water (4 cm depth) for 3 h to allow saturation of soil. Can was then placed on paper towels and allowed to drain for 3 h. The can was weighed to obtained weight of saturated soil and then dried at 105°C for 24 h to obtain the weight of oven dry soil. Water retaining capacity (WRC) was then calculated as follows:

$$\text{WRC}(\%) = \frac{\text{Saturated weight-Oven dry weight}}{\text{Oven dry weight}} \times 100$$

The optimal duration for saturation (3 h) and for draining excess water (3 h) were found by the author in a pilot experiment.

Soil nitrate:

This chemical analysis as well as those described below were carried out on sodium acetate-acetic acid extracts with the aid of standard procedures used at the Cornell Soil Testing Laboratory (Grewling and Peech, 1960). Nitrate was determined spectrophotometrically using brucine reagent. The final result partially includes nitrite along with nitrate nitrogren. This method is virtually free from interferences of various kinds.

Available phosphorus:

This was determined spectrophotometrically by the chlorostannous-molybdophosphoric blue colour method.

Exchangeable Ca^{++}, Mg^{++} and K^{+}:

Levels of major cations were determined on a Varian Techtron type AA-5 atomic absorption spectrophotometer.

APPENDIX B

Monte Carlo Simulation

Monte Carlo simulation generated empirical distributions of the correlation coefficients between inter-releve distances in ordination pairs, and a test of significance.

The method involves the following steps:

1. Define x_{ij} and y_{ij} as the elements in the two sets of comparable ordination co-ordinates, each with p axes and n points (releves), i.e., the matrices $\underset{\sim}{X}_{n \times p}$, $\underset{\sim}{Y}_{n \times p}$.

2. Compute Euclidean distances between releve pairs for each set of ordination.

$$d_{xih} = [\sum_j (x_{ij} - x_{hj})^2]^{1/2}, \quad j = 1, \ldots, p;$$
$$i = 1, \ldots, n-1; \; h = i+1, \ldots, n$$

$$d_{yih} = [\sum_j (y_{ij} - y_{hj})^2]^{1/2}, \quad j = 1, \ldots, p;$$
$$i = 1, \ldots, n-1; \; h = i+1, \ldots, n$$

Thus, obtain triangular distance matrices $\underset{\sim}{D}_x$ and $\underset{\sim}{D}_y$.

3. Compute the correlation coefficient $r(\underset{\sim}{D}_x, \underset{\sim}{D}_y)$ between $n(n-1)/2$ corresponding pairs of distances.

4. Define minima and the maxima of the axes in the set of ordination co-ordinates

$$\min X_j \; , \; \max X_j \qquad j = 1, \ldots, p$$

$$\min Y_j \; , \; \max Y_j \qquad j = 1, \ldots, p$$

5. Generate n random values between minima and maxima on each of the axes.

6. Compute n(n-1)/2 distances between points based on the random values to obtain simulated triangular distance matrices $\underset{\sim}{D}^*_x$ and $\underset{\sim}{D}^*_y$ with elements d^*_{in} and d^*_{in}.

7. Compute correlation coefficient between n(n-1)/2 pairs of distances $r(\underset{\sim}{D}^*_x, \underset{\sim}{D}^*_y)$ and take the absolute values $|r(D^*_x, D^*_y)|$.

8. Iterate through steps 4, 5, 6 and 7 to generate a large number of correlation values.

9. Arrange the generated correlation coefficients $r(D^*_x, D^*_y)$ in a monotonic decreasing order to form an empirical distribution.

10. Compare the observed correlation coefficient $r(D_x, D_y)$ against the empirical distribution to test significance.

APPENDIX C

Programs and Program Packages

1. Classification and comparisons:

Cluster analyses by sum of squares method and simple and group average methods were performed by the programs SSAS and ALCS which are the modified versions of the original programs SSA and ALC respectively, originally developed by Orlóci (1978). The present versions also create cophenetic and topology matrices. Single linkage clustering was performed using the program package of Wildi and Orlóci (1983). Iterative clustering was performed using the program SRUN (Jancey and Wells, manuscript) which is a modified version of a program originally developed by Jancey (1980). The current version incorporates the within species sum of squares ranking program RANK05 developed by the author. Dendrograms were plotted by a program DENDOS supplied by P. H. Fewster. Classifications were compared on the basis of their cophenetic and topology matrices by a program DISCOM, developed by the author.

2. Ordinations and comparisons:

Eigenvector ordinations were performed using the program package of Wildi and Orlóci (1983). Nonmetric multidimensional scaling ordinations were performed by a modified version of the program MDSCAL, originally developed by Kruskal (cf. Kenkel, 1984). Stereograms of ordinations were plotted using the program HPSTPL supplied by P. H. Fewster. To compute the similarity (correlation) between ordination pairs a program DISCOR was developed which can also generate an empirical distribution of correlation coefficients using local constraints and permits a test of significance.

3. Ranking of species:

Sum of squares ranking of species was performed using the package developed by Wildi and Orlóci (1983). Equivocation information ranking was performed using the program RANI03 (Orlóci, 1978). The program RANK05 was developed to rank species based on within species sum of squares.

4. Analysis of concentration:

This was accomplished using the program CONCENTRATION (Orlóci and Bowles, 1982).

5. Species diversity and dominance:

The program DIVER was developed to compute diversity, equitability and dominance based on a variety of functions.

APPENDIX D

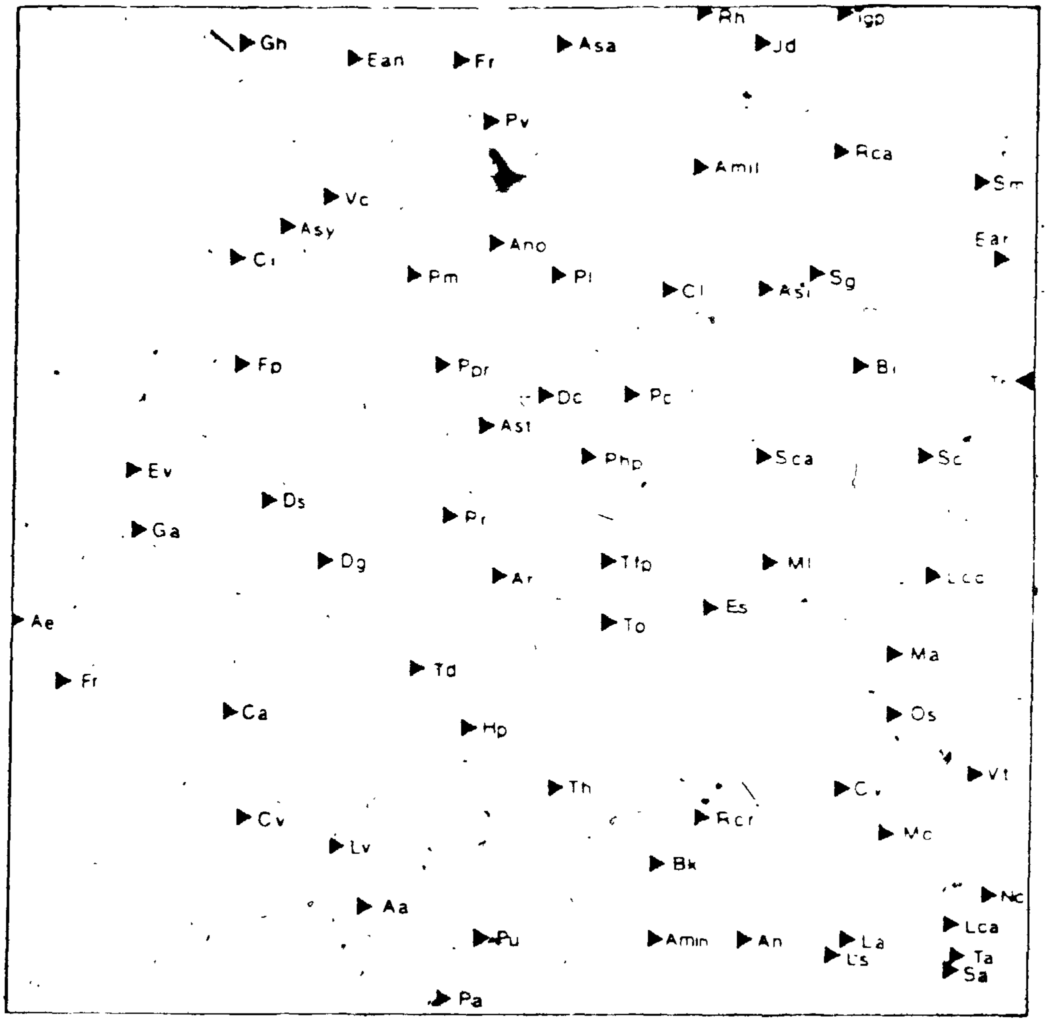
List of Species Recorded from Old Fields

1. *Acer negundo* L.
2. *Acer pseudoplatanus* L.
3. *Achillea millefolium* L.
4. *Agropyron repens* (L.) Beauv.
5. *Agrostis stolonifera* L.
6. *Ambrosia artemisiifolia* L.
7. *Anagallis arvensis* L.
8. *Anemone cylindrica* Gray
9. *Arctium minus* Schk.
10. *Arrhenatherum elatius* (L.) Mert. & Koch.
11. *Asclepias incarnata* L.
12. *Asclepias syriaca* L.
13. *Aster ericoides* L.
14. *Aster novae-angliae* L.
15. *Aster pilosus* Willd.
16. *Aster sagittifolius* Willd.
17. *Aster simplex* Willd.
18. *Berberis vulgaris* L.
19. *Brassica kaber* (DC.) L.
20. *Bromus inermis* Leuss.
21. *Bromus tectorum* L.
22. *Camelina microcarpa* Andrz.
23. *Capsella bursa-pastoris* (L.) Medic.
24. *Carex lupulina* Muhl.
25. *Carex* sp.
26. *Carex sparaginoides* Muhl.
27. *Carex vulpinoidea* Michx.
28. *Cerastium vulgatum* L.
29. *Chrysanthemum leucanthemum* L.
30. *Cichorium intybus* L.
31. *Cirsium arvense* (L.) Scop.
32. *Cirsium vulgare* (Savi) Tenore.
33. *Convolvulus arvensis* L.
34. *Cornus racemosa* Lam.
35. *Cornus stolonifera* Michx.
36. *Crataegus crus-galli* L.
37. *Crataegus holmesiana* Ashe
38. *Crataegus punctata* Jacq.
39. *Crepis tectorum* L.
40. *Dactylis glomerata* L.
41. *Daucus carota* L.
42. *Dianthus armeria* L.
43. *Dipsacus sylvestris* Huds.
44. *Echium vulgare* L.
45. *Equisetum arvense* L.
46. *Erigeron annuus* (L.) Pers.
47. *Erigeron canadensis* L.
48. *Erigeron philadelphicus* L.
49. *Erigeron strigosus* Muhl.
50. *Festuca arundinacea* Schreber

51 *Festuca pratensis* Hudson
52 *Festuca rubra* L.
53 *Fragaria virginiana* Duchesne.
54 *Galium mollugo* L.
55 *Galium verum* L.
56 *Geum aleppicum* Jacq.
57 *Glecoma hederacea* L.
58 *Hieraceum florentinum* All.
59 *Hieraceum floribundum* Wimmer and Grab.
60 *Hypericum perforatum* L.
61 *Hypericum punctatum* Lam.
62 *Inula helenium* L.
63 *Juncus dudleyi* Wieg.
64 *Juncus torreyi* Cov.
65 *Lactuca serriola* L.
66 *Lamium aplexicaule* L.
67 *Lepidium compestre* (L.) R.Br.
68 *Lepidum densiflorum* Schrader
69 *Leonurus cardiaca* L.
70 *Linaria vuglaris* Hill.
71 *Lolium perenne* L.
72 *Lotus corniculatus* L.
73 *Lychnis alba* Mill.
74 *Lythrum salicaria* L.
75 *Medicago lupulina* L.
76 *Medicago sativa* L.
77 *Melilotus alba* Desr.
78 *Melilotus officinalis* (L.) Desr.
79 *Myosotis scorpioides* L.
80 *Nepeta cataria* L.
81 *Oenothera biennis* L.
82 *Oenothera parviflora* L.
83 *Oxalis stricta* L.
84 *Panicum capillare* L.
85 *Panicum lanuginosum* Ell.
86 *Parthenocissus quinquefolia* (L.) Planch.
87 *Phalaris arundinacea* L.
88 *Phleum pratense* L.
89 *Plantago lanceolata* L.
90 *Plantago major* L.
91 *Plantago rugelii* Decne.
92 *Poa compressa* L.
93 *Poa pratensis* L.
94 *Polygonum aviculare* L.
95 *Polygonum convolvulus* L.
97 *Populus deltoides* Marsh.
98 *Populus tremuloides* Michx.
99 *Potentilla anserina* L.
100 *Potentilla argentea* L.
101 *Potentilla norvegica* L.
102 *Potentilla recta* L.
103 *Prunella vulgaris* L.
104 *Prunus virginiana* L.
105 *Ranunculus acris* L.
106 *Rhamnus catharticus* L.

107 *Rhamnus frangula* L.
108 *Rhus typhina* L.
109 *Rosa acicularis* Lindl.
110 *Rudbeckia hirta* L.
111 *Rumex crispus* L.
112 *Rumex obtusifolius* L.
113 *Salix rigida* Muhl.
114 *Sambucus canadensis* L.
115 *Satureja vulgaris* (L.) Fritsch.
116 *Setaria viridis* (L.) Beauv.
117 *Silene cucubalus* Wibel.
118 *Sisymbrium altissimum* L.
119 *Sisyrinchium montanum* Greene.
120 *Solidago canadensis* L.
121 *Solidago graminifolia* (L.) Salisb.
122 *Solidago juncea* Ait.
123 *Symphoricarpos albus* (L.) Blake.
124 *Tanacetum vulgare* L.
125 *Taraxacum officinale* Weber.
126 *Thlaspi arvense* L.
127 *Tragopogon dubius* Scop.
128 *Tragopogon pratensis* L.
129 *Trifolium hybridum* L.
130 *Trifolium pratense* L.
131 *Trifolium repens* L.
132 *Tussilago farfara* L.
133 *Verbascum thapsus* L.
134 *Verbena urticifolia* L.
135 *Veronica officinalis* L.
136 *Vicia cracca* L.
137 *Viola arvensis* Murr.
138 *Vitis riparia* Michx.
139 *Xanthium strumarium* L.

APPENDIX E. Species ordination of 68 species of of fields. Symbols as in Fig. 4.4.



APPENDIX F

List of Species Recorded from Vacant Lots

1 *Acer negundo* L.
2 *Acer saccharum* Marsh
3 *Achillea millefolium* L.
4 *Agropyron repens* (L.) Beauv.
5 *Agrostis stolonifera* L.
6 *Ambrosia artemisiifolia* L.
7 *Anagallis arvensis* L.
8 *Anthemis cotula* L.
9 *Arctium minus* Schk.
10 *Asclepias incarnata* L.
11 *Asclepias syriaca* L.
12 *Aster ericoides* L.
13 *Aster laevis* L.
14 *Aster novae-angliae* L.
15 *Aster sagittifoliusm* Willd.
16 *Aster simplex* Willd.
17 *Berberis vulgaris* L.
18 *Bidens cernua* L.
19 *Brassica kaber* (DC.) L.
20 *Bromus inermis* Leyss.
21 *Capsella bursa-pastoris* (L.) Medic.
22 *Carex vulpinoidea* Michx.
23 *Centaurea nigra* L.
24 *Cerastium vulgatum* L.
25 *Chenopodium album* L.
26 *Chenopodium glaucum* L.
27 *Chrysanthemum leucanthemum* L.
28 *Cichorium intybus* L.
29 *Cirsium arvense* (L.) Scop.
30 *Cirsium vulgare* (Savi) Tenore.
31 *Convolvulus arvensis* L.
32 *Cornus stolonifera* Michx.
33 *Crepis* sp.
34 *Crepis tectorum* L.
35 *Dactylis glomerata* L.
36 *Daucus carota* L.
37 *Digitaria sanguinalis* (L.) Scop.
38 *Dipsacus sylvestris* Huds.
39 *Echinochloa crusgalli* (L.) Beauv.
40 *Echium vulgare* L.
41 *Equisetum arvense* L.
42 *Eragrostis pectinaceae* (Michx.) Nees.
43 *Erigeron annuus* (L.) Pers.
44 *Erigeron canadensis* L.
45 *Erigeron strigosus* Muhl.
46 *Festuca pratensis* Hudson
47 *Fragaria virginiana* Duchesne.
48 *Galium verum* L.
49 *Geum aleppicum* Jacq.
50 *Hieraceum floribundum* Wimmer and Grab.
51 *Hypericum perforatum* L.

52 Juncus dudleyi Wieg.
53 Lactuca serriola L.
54 Lepidium compestre (L.) R.Br.
55 Linaria vuglaris Hill.
56 Lolium perenne L.
57 Lotus corniculatus L.
58 Lychnis alba Mill.
59 Lythrum salicaria L.
60 [illegible]lva moschata L.
6[illegible] [illegible]dicago lupulina L.
62 Medicago sativa L.
63 Melilotus alba Desr.
64 Melilotus officinalis (L.) Desr.
65 Nepeta cataria L.
66 Oenothera biennis L.
67 Oenothera parviflora L.
68 Onopordum acanthium L.
69 Oxalis stricta L.
70 Panicum capillare L.
71 Phalaris arundinacea L.
72 Phleum pratense L.
73 Picris hieracioides L.
74 Plantago lanceolata L.
75 Plantago major L.
76 Plantago rugelii Decne.
77 Poa annua L.
78 Poa compressa L.
79 Poa pratensis L.
80 Polygonum aviculare L.
81 Polygonum convolvulus L.
82 Polygonum lapathifolium L.
83 Polygonum persicaria L.
84 Populus tremuloides Michx.
85 Potentilla argentea L.
86 Potentilla norvegica L.
87 Potentilla recta L.
88 Prunella vulgaris L.
89 Ranunculus acris L.
90 Rhus typhina L.
91 Rubus strigosus Michx.
92 Rudbeckia hirta L.
93 Rumex crispus L.
94 Salix interior Rowlee.
95 Salsola pestifer A. Nels.
96 Satureja vulgaris (L.) Fritsch.
97 Setaria glauca (L.) Beauv.
98 Setaria viridis (L.) Beauv.
99 Setaria verticillata (L.) Beauv.
100 Silene cucubalus Wibel
101 Sisymbrium altissimum L.
102 Sisyrichium montanum Greene.
103 Solidago canadensis L.
104 Solidago graminifolia (L.) Salisb.
105 Sonchus arvensis L.
106 Tanacetum vulgare L.

107 Taraxacum officinale Weber.
108 Thlaspi arvense L.
109 Tragopogon dubius Scop.
110 Trifolium hybridum L.
111 Trifolium pratense L.
112 Trifolium repens L.
113 Verbena hastata L.
114 Viburnum opulus L.
115 Vicia cracca L.
116 Vitis riparia Michx.

APPENDIX G

List of Species Recorded from Topsoil Mounds

1 *Acer negundo* L.
2 *Acer pseudoplatanus* L.
3 *Achillea millefolium* L.
4 *Agropyron repens* (L.) Beauv.
5 *Agrostis stolonifera* L.
6 *Ambrosia artemisiifolia* L.
7 *Arctium minus* Schk.
8 *Asclepias syriaca* L.
9 *Aster laevis* L.
10 *Aster novae-angliae* L.
11 *Aster simplex* Willd.
12 *Barbarea vulgaris* R.Br.
13 *Bidens ceruna* L.
14 *Brassica kaber* (DC.) L.
15 *Bromus inermis* Leyss.
16 *Capsella bursa-pastoris* (L.) Medic.
17 *Carex sparaginoides* Muhl.
18 *Carex vulpinoidea* Michx.
19 *Chenopodium album* L.
20 *Chenopodium hybridum* L.
21 *Chrysanthemum leucanthemum* L.
22 *Cichorium intybus* L.
23 *Cirsium arvense* (L.) Scop.
24 *Cirsium vulgare* (Savi) Tenore.
25 *Convolvulus arvensis* L.
26 *Cyperus esculentus* L.
27 *Dactylis glomerata* L.
28 *Daucus carota* L.
29 *Desmodium rigidum* (Ell.) DC.
30 *Digitaria sanguinalis* (L.) Scop.
31 *Dipsacus sylvestris* Huds.
32 *Echinochloa crusgalli* (L.) Beauv.
33 *Echinosystis lobata* (Michx.) T. & G.
34 *Echium vulgare* L.
35 *Equisetum arvense* L.
36 *Erigeron annuus* (L.) Pers.
37 *Erigeron canadensis* L.
38 *Erigeron strigosus* Muhl.
39 *Euphorbia maculata* L.
40 *Festuca pratensis* Hudson
41 *Festuca rubra* L.
42 *Fragaria virginiana* Duchesne.
43 *Galinsoga ciliata* (Raf.) Blake.
44 *Glecoma hederacea* L.
45 *Hieraceum floribundum* Wimmer and Grab.
46 *Hypericum perforatum* L.
47 *Juncus dudleyi* Wieg.
48 *Lactuca serriola* L.
49 *Lepidium compestre* (L.) R.Br.
50 *Linaria vuglaris* Hill.
51 *Lychnis alba* Mill.

52 *Malva moschata* L.
53 *Malva neglecta* Wallr.
54 *Medicago lupulina* L.
55 *Melilotus alba* Desr.
56 *Melilotus officinalis* (L.) Desr.
57 *Monarda fistulosa* L.
58 *Nepeta cataria* L.
59 *Oenothera biennis* L.
60 *Oenothera parviflora* L.
61 *Onopordum acanthium* L.
62 *Oxalis stricta* L.
63 *Panicum capillare* L.
64 *Panicum lanuginosum* Ell.
65 *Penstemon digitalis* Nutt.
66 *Phleum pratense* L.
67 *Phalaris arundinacea* L.
68 *Plantago lanceolata* L.
69 *Plantago major* L.
70 *Poa compressa* L.
71 *Poa pratensis* L.
72 *Polygonum aviculare* L.
73 *Polygonum convolvulus* L.
74 *Polygonum lapathifolium* L.
75 *Polygonum persicaria* L.
76 *Potentilla norvegica* L.
77 *Potentilla recta* L.
78 *Prunella vulgaris* L.
79 *Rhus typhina* L.
80 *Ribes hirtellum* Michx.
81 *Rubus* sp.
82 *Rudbeckia hirta* L.
83 *Rumex acetosella* L.
84 *Rumex crispus* L.
85 *Setaria glauca* (L.) Beauv.
86 *Setaria viridis* (L.) Beauv.
87 *Silene cucubalus* Wibel.
88 *Sisymbrium altissimum* L.
89 *Solanum americanum* Mill.
90 *Solanum dulcamara* L.
91 *Solidago candensis* L.
92 *Solidago graminifolia* (L.) Salisb.
93 *Solidago juncea* Ait.
94 *Sonchusi arvenis* L.
95 *Sonchus asper* (L.) Hill.
96 *Tanacetum vulgare* L.
97 *Taraxacum officinale* Weber.
98 *Thlaspi arvense* L.
99 *Tragopogon dubius* Scop.
100 *Trifolium hybridum* L.
101 *Trifolium pratense* L.
102 *Trifolium repens* L.
103 *Tussilago farfara* L.
104 *Verbascum blattaria* L.
105 *Verbascum thapsus* L.
106 *Verbena urticifolia* L.
107 *Vicia cracca* L.
108 *Vitis riparia* Michx.

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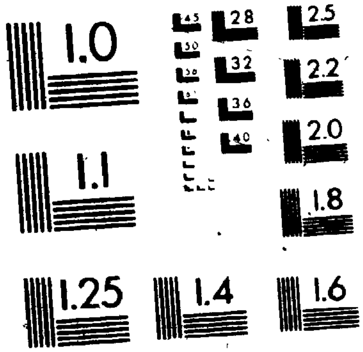

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