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Canada

The Ecology of Alvar Vegetation in Canada:
Description, Patterns, Competition

by

Joyce W. Belcher

Thesis submitted to
the School of Graduate Studies and Research
in partial fulfilment of the requirements for the degree of
Master of Science, Biology

University of Ottawa
Ottawa, Ontario
Canada

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Abstract

Alvars are areas with thin soil and dry grassland vegetation and they occur only in Scandinavia, the southeastern United States and central Canada. My research focused on (1) describing the vegetation of Canadian alvars, (2) examining ecological patterns in this system and (3) measuring the intensity of plant competition which occurs there.

In chapter 1, ordination and classification techniques were used to describe alvar vegetation at two scales: local (within one alvar) and regional (among 4 alvar sites). At the local scale, changes in species composition corresponded to changes in soil depth and biomass. There were two main vegetation types: (i) alvar meadows with complete vegetation cover and (ii) rock flats with incomplete vegetation cover over limestone rock. At the regional scale species composition was related primarily to geographic location - the southern site was distinct from the eastern and northern sites. Relationships between species distributions and soil depth and biomass could also be detected at this scale. At both local and regional scales, tall perennial graminoids dominated sites with deep soil while small annuals and stress-tolerant perennials dominated shallow soil sites. Average biomass levels were strongly, positively correlated with soil depth across vegetation types. Average species richness was curvilinearly related to biomass.

In chapter 2, I examined the empirical relationships among important alvar state variables (soil depth, biomass and species richness) in order to test the predictions of the species richness model (forwarded by Grime and others) in a low biomass terrestrial system, and compare the pattern among 4 alvar sites. At all sites biomass was positively correlated with soil depth, suggesting that the soil depth gradient represents a gradient of increasing below-ground resources and decreasing above-ground resources. At each alvar, species richness varied curvilinearly with both biomass and soil depth; maximum species richness occurred at intermediate levels of these factors, as predicted by species richness models. However, the predicted decline in species richness at higher levels of biomass or soil depth was evident at only one site. The specific pattern of species richness varied among sites; equations describing the relationships between species richness, biomass and soil depth were unique to each site. The observed within-habitat variability indicates that the species richness model requires further refinement to allow more accurate general predictions.

In chapter 3, I present the results of a field experiment which measured the intensity of total, root and shoot competition along the gradient of soil depth at one alvar. Phytometers (plant indicators) were grown without neighbours, with neighbours and with neighbour roots only and the final biomass of each (after one growing season) was compared in order to determine competition intensity. Over all sites, the intensities of total and root competition were greater than zero; that of shoot competition was not. This suggests that competition in this system was primarily below ground. Competition intensity did not vary along the soil depth gradient. Results of this and other field studies of competition have produced apparently contradictory results. I suggest a model which relates the various effects of competition and of mutualism to the biomass range of interest.

Résumé

Les alvars sont des zones formées d'une mince couche de sol et d'une végétation de prairie qui existent seulement en Scandinavie, dans le sud-est des États-Unis et dans le centre du Canada. Notre recherche a porté principalement sur (1) la description de la végétation des alvars canadiens, (2) l'étude des patterns écologiques présents dans ce système et (3) la mesure de l'intensité de la compétition végétale que l'on y retrouve.

Dans le premier chapitre, des techniques d'ordination et de classification ont été utilisées pour décrire la végétation des alvars à deux échelles différentes : locale (à l'intérieur d'un même alvar) et régionale (dans 4 alvars différents). À l'échelle locale, les changements dans la composition des espèces correspondaient à des modifications de l'épaisseur du sol et de la biomasse. On a observé deux principaux types de végétation : (i) prés d'alvars comportant un couvert végétal complet et (ii) bancs de roche calcaire comportant un couvert végétal incomplet. À l'échelle régionale, la composition des espèces était principalement liée à la situation géographique : le site situé au sud était différent des sites situés à l'est et au nord. On pouvait également observer, à l'échelle régionale, des relations entre la distribution des espèces, d'une part, et la profondeur du sol et la biomasse, d'autre part. Autant à l'échelle régionale que locale, les graminoïdes vivaces hautes dominaient sur les sites où le sol était épais, tandis que les petites plantes annuelles et les vivaces tolérantes au stress dominaient sur les sites où la couche de sol était mince. Les niveaux moyens de biomasse et l'épaisseur du sol présentaient une forte corrélation positive pour tous les types de végétation. La relation qui existe entre la diversité moyenne des espèces et la biomasse s'illustre par une

courbe polynômiale.

Dans le deuxième chapitre, nous avons examiné les relations empiriques qui existent entre des variables importantes mesurées (épaisseur du sol, biomasse et diversité des espèces) afin de vérifier les prévisions établies à partir du modèle de diversité des espèces (de Grime *et al.*) en ce qui concerne la végétation des alvars et de comparer les patterns de 4 sites différents. À tous les sites, la biomasse et l'épaisseur du sol présentaient une corrélation positive, ce qui donne à penser que le gradient d'épaisseur du sol correspond à un gradient de ressources souterraines croissantes et de ressources de surface décroissantes. À chaque alvar, la relation qui existe entre la diversité des espèces, d'une part, et la biomasse et l'épaisseur du sol, d'autre part, s'illustre par une courbe polynômiale. La diversité maximale des espèces a été observée aux valeurs intermédiaires de ces facteurs, tel que prédit par les modèles de diversité des espèces. Cependant, le déclin de la diversité des espèces prédit pour des valeurs élevées de biomasse ou d'épaisseur du sol n'était évident qu'à un seul site. Le pattern de diversité des espèces variait d'un site à l'autre, et les équations décrivant les relations qui existent entre la diversité des espèces, d'une part, et la biomasse et l'épaisseur du sol, d'autre part, étaient particulières à chaque site. La variabilité observée au sein d'un habitat indique que le modèle de diversité des espèces devra être perfectionné si l'on veut en tirer des prévisions générales plus précises.

Dans le troisième chapitre, nous présentons les résultats d'une expérience réalisée sur le terrain, qui mesurait l'intensité de la compétition totale, de la compétition des racines et de la compétition des pousses en fonction du gradient d'épaisseur du sol à un alvar donné. Des phytomètres (indicateurs végétaux) ont été cultivés en l'absence de voisins, en présence de

voisins et en présence de racines seulement, et la biomasse finale de chacun (après une saison de croissance) a été comparée afin de déterminer l'intensité de la compétition. Dans tous les sites, l'intensité de la compétition totale et de la compétition des racines était supérieure à zéro, tandis que la compétition des pousses ne l'était pas. Ces résultats donnent à penser que la compétition était essentiellement souterraine dans ce système. L'intensité de la compétition ne variait pas en fonction du gradient d'épaisseur du sol. Les résultats de la présente étude et ceux d'autres études sur la compétition effectuées sur le terrain sont apparemment contradictoires. Nous proposons un modèle qui lie les divers effets de la compétition et du mutualisme à la biomasse.

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General Introduction

Compared to other scientific disciplines, ecology is still in a relatively early stage of development. Early ecologists concerned themselves with identifying species and producing species lists. Eventually, the importance of quantifying ecological research, and of examining cause and effect relationships, was stressed (e.g., Clements and Goldsmith 1924). A decade later Clements discussed the importance of ecological information to other fields (Clements 1935). Today, with increasing anthropogenic pressures on natural systems, there is a great demand for ecological information and a need for ecology to furnish predictions about the responses of these systems to a plethora of perturbations. A necessary step towards forming general principles, and ultimately, predictive models in ecology, is the search for pattern in nature (Rigler 1982). The next step is to be able to explain the processes that are involved in producing the observed patterns.

Environmental gradients facilitate comparative studies and are useful tools for studying both patterns and processes (Austin 1990; Keddy 1990). One important pattern in ecology is the variation in species richness along environmental gradients. A number of theoretical models have been proposed which relate species richness levels to biomass, fertility and disturbance, and predict maximum species richness at intermediate levels of these factors (Grime 1973; Connell 1978; Huston 1979; Tilman 1982). However, there are differences in opinion regarding the processes which shape the species richness pattern. Competition is thought to be an important process shaping this and other vegetation patterns, but there is much controversy regarding how and why it varies along environmental gradients. It has been pointed out that much of the disagreement is due to differences in definitions and emphasis of the various theories (e.g., see Weldon and Slauson 1986; Grace 1990; Grace 1991; Keddy 1989). One remaining point of contention deals with the variation in competition along environmental gradients, especially in low fertility situations. Grime (1973; 1979) predicts that competition is relatively unimportant in low fertility situations and states that species richness will be limited by environmental stress, instead. Tilman (1982) predicts a trade-off in competition for above and belowground resources and therefore predicts that belowground competition intensity will be most intense in low fertility situations.

My main research objectives were to investigate species richness patterns and competition intensity along an environmental gradient, in low productivity conditions. I therefore chose a study system which would provide a good model: alvars represent a low productivity grassland system with strong gradients of soil depth. Alvar vegetation experiences extremes of moisture availability (Catling *et al.* 1975; Baskin and Baskin 1985a); in the spring and fall temporary pools of water cover the shallowest soil areas but during mid to late summer, moisture is limited and drought stress becomes a problem for the plants in these same locations (pers. obs.).

Although the alvar is a good model for my purposes, a solid descriptive base was lacking. The floristics and phytogeographic patterns among Canadian alvars have been described (Catling *et al.* 1975), but the ecology of this uncommon system is poorly understood. In the first chapter, I use multivariate analysis to describe the vegetation of alvars. My objective was to describe vegetation patterns within alvars by examining species associations and relating these to particular state variables (soil depth, biomass and species richness). I also attempted to produce a more general description by classifying habitat types within and among different alvar sites.

The second chapter looks at the empirical relationships between the state variables mentioned above and sets out to investigate the species richness pattern. The third chapter examines the process of competition. Few studies have tested for competition in a low biomass system, so I used a field experiment to test for the presence of competition in alvar vegetation. Also, since controversy surrounds the topic of variation in the intensity of root and shoot competition along environmental gradients (e.g., Keddy 1989; Grace 1990), I attempted to separate these components and examine their intensity along the alvar soil depth gradient.

Chapter 1

Alvar Vegetation in Canada:
a multivariate description at two scales

Introduction

Alvars are naturally treeless areas of herbaceous and shrubby vegetation in thin soil over flat limestone rock, and (e.g. Petterson 1965; Catling *et al.* 1975). The global distribution of alvars is apparently limited to the Baltic Sea region of Europe and to east-central North America. In the Baltic region alvars occur on the islands of Gotland and Oland in southern Sweden, and in Estonia (Petterson 1965, Sjogren 1988). In North America they occur in the eastern United States, (e.g. Freeman 1933; Baskin and Baskin 1985a) and in central Canada within the province of Ontario, in the eastern Great Lakes area (Catling *et al.* 1975). (A few limestone barrens also occur in Newfoundland, and arctic and western Canada; Catling pers. comm.). In parts of the United States the system is generally known as 'cedar glades' due to the abundance of red cedar (*Juniperus virginiana*). Canadian sites are referred to by the Estonian name 'alvar' (although *Juniperus* is also found here).

In alvars (and cedar glades), islands of essentially bare limestone outcrop are generally surrounded by concentric circles of successively denser vegetation, often grading into large grassland meadows. Mixed forest may also occur where soil is deep enough to support it (e.g. Erickson *et al.* 1942; Catling *et al.* 1975; Stephenson and Herendeen 1986). Temporary pools of water cover the shallowest soil areas during the spring and fall, but during mid to late summer, moisture is limited and drought stress becomes a problem for the plants in these same locations (pers. obs.). Natural disturbances include light grazing by native herbivores (deer, rabbits and insects), occasional fire (now mostly suppressed) (Catling *et al.* 1975) and some frost heaving where autumnal pools cover shallow soil areas (Krahulec *et al.* 1986, Erickson *et al.* 1942).

Most studies of alvar vegetation have been done in Sweden. Sjogren (1988) reviewed research that was conducted over the past century on the island of Oland. Recent studies have focused on assigning plant associations to taxonomic units (Krahulec *et al.* 1986; Bengtsson *et al.* 1988). Van der Maarel (1988) attempted to develop a guild classification for alvar vegetation, based on life form, growth form and strategy type, but the large number of (87) guilds produced did little to simplify the classification of alvars. Many U.S. cedar glades have also been described (e.g. Harper 1926; Freeman 1933; Erickson *et al.* 1942; Baskin and Baskin 1978, 1985a, 1985b). Baskin and Baskin (1985a) examined the life cycle ecology of cedar glade plants, and Stephenson and Herendeen (1986) studied the effects of drought at a Michigan alvar.

The flora of Canadian alvars was described by Catling *et al.* (1975), and they produced a list of significant alvar species. Brunton (1986) surveyed the vegetation of one site (Burnt Lands). However, the ecology of alvars in Canada, as elsewhere, has received little attention. Canadian alvars fall into three main phytogeographic groups: (1) The Bruce Peninsula - Manitoulin Island region (north of the Great lakes in Ontario), (2) the Western Lake Erie region and (3) the Precambrian Contact line (Catling, pers. comm.). These alvars include some large and relatively undisturbed sites and their conservation value is high as habitat for a number of rare species and as examples of the rare alvar system itself (Belcher and Keddy in press). My intention was to provide a basic description of alvar vegetation to serve as a baseline for future work on environmental gradients and conservation biology.

I studied 4 alvar sites which represent examples from each of the phytogeographic groups. My general objective was to describe Canadian alvar vegetation in detail at the within alvar scale and more generally at the among alvar scale. My specific objectives were to (1) describe species composition, (2) examine species relationships, and (3) examine the ecological relationships between species composition and measured variables, at both the within and among alvar scales. By relating species composition to easily measured variables like soil depth, biomass and species richness, I aimed to increase the generality of my description and develop some predictive relationships (Rigler 1982; Keddy 1990).

Methods

Study Sites

Four alvars in Ontario were sampled (Fig. 1.1). The Burnt Lands alvar in Eastern Ontario (45°15'N, 76°05'E) is a large and relatively undisturbed alvar with extensive areas of open rock flats and grassy meadows (Fig. 1.2a). Stone Road alvar is a small alvar on Pelee island in Lake Erie (41°45'N, 82°39'E). Here the herbaceous alvar vegetation occurs in openings within a mainly wooded area. La Cloche alvar is on Grand La Cloche island, at the Northwest tip of Manitoulin island (45°49'N, 81°44'E). Vegetation on the island is predominantly alvar and has been grazed by cattle to varying degrees. The soil depth gradient occurs over a longer distance than at the other sites. For this reason, sampling was carried out at 6 sub-sites in order to sample the entire soil depth range. Misery Bay alvar on the south shore of Manitoulin island (45°49'N, 82°44'E) is a large alvar with large areas of open rock flats. It differs from the other sites in that the limestone is dolomite (Morton and Venn 1984), a much harder rock that does not erode into a shaly surface, and therefore forms parent material for soil less readily. Thus, vegetation here is more rigidly restricted to surface cracks (Fig. 1.2b). (Specific locations of sample sites are given in Appendix 1.1).

Field Sampling

Sampling was carried out in the fall of 1988 (Burnt Lands) and the fall of 1989 (Stone Road, La Cloche and Misery Bay); specific locations and dates are given in Appendices 1.1 and 1.3, respectively. In order to ensure even sampling across the gradient, I identified 5 vegetation classes based on a subjective estimate of biomass, ranging from the scant vegetation cover where limestone rock is at the surface to the dense cover of the grassy meadows. Appendix 1.2 shows that biomass did increase across vegetation types. In each class, an approximately equal number of 0.25 m^2 (0.5 X 0.5 m) quadrats were randomly located for a total sample size of n = 99 at Burnt Lands, and n = 50 at Stone Road, La Cloche and Misery Bay.

Species composition of vascular plants was determined at each location by recording the presence of each species in each of 9 sub-quadrats, thereby obtaining a frequency, out of 9, for each species encountered. (The raw data for species composition is in Appendix 1.3). Species richness was the total number of species observed within the quadrat. Rare species richness was the total number of species classified as rare within Ontario (Argus *et al.* 1987) or in Canada (Argus and Pryor 1990). Vascular plant material within the quadrat was collected and dried to constant mass (at 70° C) for biomass determination. Soil depth the mean of 5 measurements (4 corners and the centre of the quadrat) taken with a 4mm diameter pin. (Measured variables for each quadrat are in Appendix 1.4).

Voucher specimens were collected and verified, and will be deposited in the herbarium of the Biosystematics Research Centre of Agriculture Canada (DAO). Nomenclature follows Morton and Venn (1990).

Analysis

In order to describe the variation in alvar vegetation, multivariate analysis was employed at two levels: (i) within a single site for a more detailed description, and (ii) among all four sites in order to describe broad-scale (across alvar) patterns. Within-site analysis was conducted on the entire Burnt Lands data set (n = 99). For the among site analysis, data from all four sites were combined; half of the Burnt Lands data was used (10 sites samples were randomly picked from each of the 5 vegetation classes) so that sample sizes would be equivalent (n = 50 for all sites).

Two multivariate methods were used: ordination and classification. Ordination summarizes the variation in community composition by calculating the mathematical relationships between samples and between species and by plotting samples and species along orthogonal axes. The first axis is extracted through an iterative algorithm such that it accounts for the maximum variation in the data set. The second and subsequent axes account for maximum residual variation (Orloci and Kenkel 1985). Classification is also based on mathematical relationships among samples and species, but whereas ordination illustrates trended variation in vegetation, classification produces 'distinct' groups of vegetation samples which have similar species composition (and groups of species which are closely associated with one another). Variation in natural communities is generally continuous and classification is thus somewhat artificial (e.g., Goldsmith 1973). However, by producing a small number of vegetation types, classification can be used to summarize the variation illustrated within an ordination diagram (e.g., Day *et al.* 1988). Classification is also useful where the study objective is to produce a taxonomic description (e.g., Krahulec *et al.* 1986; Bengtsson *et al.* 1988).

Data was ordinated using detrended correspondence analysis (DCA). DCA is commonly used in ecological studies (Ter Braak and Prentice 1988) and was introduced (Hill and Gauch 1980) as an ordination technique that improved on previous reciprocal averaging methods by eliminating their two inherent problems: the edge effect and the arch effect (Hill and Gauch 1980; Ter Braak and Prentice 1988). Hill and Gauch (1980) compared the efficiency of a number of ordination techniques and found that DCA consistently produced results that were easily interpreted. Swedish alvars have also been described using DCA (Bengtsson *et al.* 1988). DCA was conducted using CANOCO (Ter Braak 1988). Detrending by segment (26 segments) was employed.

DCA produces both sample and species scores along the ordination axes. A sample score is based on the species composition of that sample; a species score is simply the sample score at the position of that species' mode (Hill and Gauch 1980). Thus, a species ordination merely indicates the location of samples where each species was most frequent. Stand ordinations generally provide more reliable results (Hill and Gauch 1980). An alternate, and more informative method of illustrating the variation in species along the ordination axes is to produce a series of species overlays: plots of species frequency in each sample quadrat, within the ordination space. Bengtsson *et al.* (1988) used species overlays to illustrate the 'ecological amplitude' of Swedish alvar species. In this chapter, I present species overlays for a number of alvar species. These include 5 species which are taxonomically rare (Argus and Pryor 1990), as well as 8 species which I refer to as 'characteristic' alvar species because their distributions are largely limited to alvar habitats (Catling *et al.* 1975), and because they had high overall frequencies, or were dominants of particular habitat types, in my study.

Overlays can also be used to illustrate the variation in levels of environmental variables, along the ordination axes. Overlays are presented for the three measured variables: soil depth, biomass and species richness.

Data was classified using two way indicator species analysis (TWINSPAN). TWINSPAN is a divisive classification technique which is based on the first ordination axis of the Reciprocal averaging technique (Hill *et al.* 1975) and is therefore equivalent to the first axis of DCA (Hill and Gauch 1980). TWINSPAN's iterative algorithm involves splitting stands along this axis based on 5 indicators species (species which are highly associated with one end or the other); subsequent groups are divided in the same way (Hill *et al.* 1975). TWINSPAN uses only presence / absence data. However, it is possible to differentiate between frequent and infrequent occurrences of the same species by splitting it into pseudospecies. In my analysis, I defined 2 pseudospecies. Thus, for example, occurrences of

Sprobolus heterolepis with a frequency of 0 to 4 were called SPO HET 1, and occurrences of *S. heterolepis* with a frequency of 5 to 9 were defined as SPO HET 2. TWINSPAN was conducted on samples and species using ECOSURVEY (Carleton 1985). The minimum group size was set at 10 (thus final groups included from 1 to 9 samples or species); the maximum number of divisions was 3.

Species composition within TWINSPAN sample groups was summarized by calculating the mean frequency for each included species. Similarly, mean values for the measured variables (soil depth, biomass and species richness) were determined.

An important limitation of both DCA and TWINSPAN methods is their sensitivity to outliers and discontinuities in the data, and it was therefore recommended that rare (infrequent) species be removed (Hill and Gauch 1980; Hill *et al.* 1975). Thus, species which occurred in less than 5% of the quadrats were omitted from my analysis (The per cent of quadrats in which each species occurred is listed in Appendix 1.5 for the (a) within Burnt Lands and (b) among sites, data sets). This has the disadvantage of omitting species which are both taxonomically rare (and therefore interesting from a conservation point of view) and infrequent. However, the distributions of these species is illustrated in the species overlays.

Results

Within Burnt Lands

Ordination

A total of 43 species were sampled at the Burnt Lands alvar and 26 of these occurred in at least 5 % of the quadrats (Table 1.1). The first 4 axes extracted by DCA had eigenvalues of 0.72, 0.30, 0.25 and 0.15. Appendix 1.6a gives quadrat and species scores along these axes. Figure 1.3 shows the quadrat ordination results for axes 1 and 2. There was little separation along the third axis and, since the associated eigenvalue was relatively low, it was not examined further.

Biomass, soil depth and species richness generally declined from left to right along the first ordination axis, although species richness values were also low at the extreme left (Fig. 1.4). There were no evident trends along the second axis.

Species Overlays

The distribution of eight alvar species within the Burnt Lands alvar was illustrated by comparing their frequencies in the ordination space (Fig. 1.5) to the measured variable diagrams (Fig. 1.4). *Sporobolus heterolepis* and *Carex crawei* (Fig. 1.5a-b) were restricted to deep soil, high biomass locations. *Senecio pauperculus* and *Solidago ptarmicoides* (Fig. 1.5c-d) also occurred most frequently in these deep soil sites but were more widely distributed, with low frequencies in sites with intermediate soil depth and biomass levels. *Trichostema brachiatum* and *Panicum philadelphicum* (Fig. 1.5e-f) were widely distributed in intermediate to shallow soil sites while *Minuartia michauxii* and *Saxifraga virginiensis* (Fig. 1.5g-h) occurred only in extreme shallow soil, low biomass locations.

Classification

The variation in species composition was generally continuous within the ordination space (Fig. 1.3), but this variation can be summarized by examining average species composition (Table 1.1) and measured variable levels (Table 1.2) within quadrat groups. At three levels of division, classification analysis produced 7 quadrat groups (Fig. 1.6), as shown on the ordination diagram (Fig. 1.3); Appendix 1.7a lists quadrats included in each group. The first division separated the 'meadows' from the 'rock flats'. The 'meadows' had dense, continuous vegetation cover while 'rock flats' sites occurred on limestone outcrop or gravelly surfaces and had sparse or discontinuous vegetation cover (pers. obs.). The 'meadows' and 'rock flats' were further divided into 'tall meadows' and 'low meadows', and 'rocky grasslands' and 'bare rock flats', respectively (Fig. 1.6). Soil depth and biomass levels decreased across these groups (Table 1.2). The 7, 3rd-level groups (Fig. 1.6) differed in species composition and variable levels. Let us consider the two main groups, 'meadows' and 'rock flats', in more detail.

The meadows occurred in deep soil and had high biomass and species richness (Table 1.2). They included species like *Carex crawei, Danthonia spicata, Senecio pauperculus, Solidago ptarmicoides* and *Sporobolus heterolepis*, which were not present in the 'rock flat' habitats.

'Tall meadows' had deep soil and biomass levels. These variables were highest in the 'tall grassy meadows' which were dominated by *Sporobolus heterolepis*, a tall, perennial bunchgrass and by the sedge, *Carex crawei* (Table 1.1). Also important was *Senecio pauperculus*, a rosette, evergreen perennial which germinates and sends up new shoots in the fall and flowers in spring before *Sporobolus heterolepis* reaches its maximum biomass. The 'tall forb-rich meadows' occurred in slightly shallower soil (Table 1.2). *Carex crawei* was the dominant species. This group had higher species richness than the previous group (Table 1.2) and included more perennial rosette species in the Asteraceae like *Solidago nemoralis*, *Solidago ptarmicoides* and *Hieracium piloselloides*, as well as some smaller perennial grasses like *Poa pratensis* and *Danthonia spicata*.

The 'low meadows' occurred at intermediate soil depth, and had intermediate biomass and species richness (Table 1.2). Smaller annual grasses were most abundant here. The 'low grassy meadows' included more species than the other groups (25 out of the 26 species that occurred with a frequency of ≥ 5%). The most abundant species were the grasses, *Panicum philadelphicum* and *Sporobolus vaginiflorus*, as well as the rosette, *Senecio pauperculus* (Table 1.1). The 'low forb-rich meadows' represented a small group with maximum species richness (Table 1.2), and most of the included quadrats occurred high on the second ordination axis (Fig. 1.3). This group was dominated by *Panicum flexile* and *Hypericum perforatum*; both species were not present, or present infrequently, in the other groups. The presence of *Danthonia spicata* and *Scutellaria parvula* links this group to the 'tall forb-rich meadows' and the 'low grassy meadows', respectively (Table 1.1).

In contrast with meadows, 'rock flats' had low biomass, low species richness and shallow soil (mean depth < 2 cm; Table 1.2). The 'dry grassland' had a sparse but continuous vegetation cover and occurred in relatively large areas which had thin soil over a gravelly surface (pers. obs.). This group was dominated by the small annual grasses, *Panicum philadelphicum*, and to a lesser extent, *Sporobolus vaginiflorus*. The 'rock margin grassland' occurred in narrow bands around the periphery of limestone outcrops and were transitional to the 'low meadows' groups. This group was dominated by *Panicum* *philadelphicum*. Small evergreen perennials, *Saxifraga virginiensis* and *Minuartia michauxii*, were important component species and each reached its maximum in this group.

The 'bare rock flats' was a small group at the extreme low end of the soil depth gradient. Here, soil and plant cover occurred only in small pockets and cracks in the limestone rock. The dominant vascular plant of this group was *Saxifraga virginiensis*. *Minuartia michauxii* and the annual *Chaenorrhinum minus* were the only other species.

Ordination and Classification of Species

Ordination and classification of species was more difficult to interpret than the above quadrat analyses, and information provided was somewhat redundant. Results are therefore not presented here (but see Appendix 1.8).

Among Sites

Ordination

In the 4 alvars sampled, 67 species were encountered in total but only 36 of these occurred in at least 5 % of the quadrats (Table 1.3; per cent frequency for all 67 species is in Appendix 1.5b). The first four axes extracted by DCA had eigenvalues of 0.79, 0.51, 0.35 and 0.28. Quadrat and species scores along the first 4 axes are given in Appendix 1.6b. Figure 1.7 shows the results of the quadrat ordination for axes 1 and 2, and axes 1 and 3. The first axis separated Stone Road, the most southern alvar, from the other sites. Variation within Stone Road was also primarily along this axis. The other sites were roughly separated through the second and third dimensions of the ordination; Misery Bay from Burnt Lands along axis 2, and Misery Bay from La Cloche along axis 3.

Neither soil depth nor biomass showed any continuous trends along the ordination axes (Fig. 1.8); both were maximum at low levels on axis 1, where Stone Road sites were concentrated, and minimum at intermediate levels on this axis, corresponding to quadrats from each of the other 3 alvar sites (cf. Fig. 1.7). Species richness did not appear to be related to the ordination axes either (Fig. 1.8), although there were more rare species along the lower one-third of axis 1 where Stone Road sites occurred and one or less rare species occurred in quadrats at the other sites (cf. Figs. 1.7 and 1.8).

Species Overlays

The distribution of species among alvars was illustrated by comparing their frequencies within the ordination space (Fig. 1.9) to diagrams showing sites (Fig. 1.7) and measured variables (Fig. 1.8). *Sporobolus heterolepis*, *Carex crawei*, *Senecio pauperculus* and *Solidago ptarmicoides* (Fig. 1.9a-d) had similar distributions but did not occur at Stone Road (cf. Fig. 1.7). *Minuartia michauxii* and *Saxifraga virginiensis* (Fig. 1.9e-f) were distributed in the centre of the ordination, corresponding with shallow soil, low biomass sites (cf. Fig. 1.8), mainly at Burnt Lands and Misery Bay. *Trichostema brachiatum* and *Panicum philadelphicum* (Fig. 1.9g-h) were widely distributed. Rare species were more site specific: *Hymenoxys acaulis* (Fig. 1.9l) occurred infrequently, and only at Misery Bay in shallow soil locations; *Allium cernuum*, *Ratibida pinnata* and *Leucospora multifida* (Fig. 1.9i-k) occurred only at Stone Road; *Allium cernuum* was most abundant and *Leucospora multifida* occurred infrequently and was restricted to shallow soils.

Classification

As in the within Burnt Lands analysis, the generally continuous variation in species composition within the ordination space was summarized by examining species composition (Table 1.3) and average variable levels (Table 1.4) in TWINSPAN groups. At three levels of division, classification analysis produced 8 quadrat groups (Fig. 1.10), as shown on the ordination diagram (Fig. 1.11). The number of quadrats from each site that are included in each quadrat group are shown at the bottom of Table 1.3 (these are listed in Appendix 1.7b). The first division separated the Northern and Eastern sites (Misery Bay, La Cloche and Burnt Lands) from the Southern and Eastern sites (Stone Road and Burnt Lands). Burnt Lands quadrats occurred on both sides of the main division. The second division resulted in 'La Cloche-Burnt Lands', 'Misery - La Cloche', 'Burnt Lands mix', and 'Stone Road' Groups. Let us consider the main vegetation types in turn, moving from 'northern and eastern' sites to 'southern and eastern' sites.

Biomass and soil depth levels at the 'Northern and Eastern' sites were intermediate compared to the groups discussed above (Table 1.4). Stone Road quadrats were absent in this group but 80% of the quadrats from the other 3 sites were present (Table 1.3). The presence of *Sporobolus heterolepis* in this set is the main floristic difference from the 'Southern and Eastern' sites (Table 1.3).

The 'Burnt Lands - La Cloche' Groups had intermediate soil depth and biomass levels (Table 1.4). Important species included *Carex crawei* and *Danthonia spicata*. The 'La

Cloche mix' Group (67% of the included quadrats were from La Cloche; Table 1.3) had high biomass and deep soil (the highest levels of these variables outside of Stone Road). Dominant species were *Sporobolus heterolepis* and *Carex crawei* (Table 1.3). This group corresponded to the 'tall grassy meadows' within Burnt Lands, but included *Schizachyrium scoparium*, a prairie species not found at Burnt Lands or Stone Road. In the 'Burnt Lands low meadows', *Sporobolus vaginiflorus* and *Senecio pauperculus* were important component species (Table 1.3) and species richness was highest (Table 1.4). This group was similar to the 'tall forb-rich meadows' within the Burnt Lands site.

The 'Misery Bay - La Cloche' groups occurred at low-intermediate levels of biomass and soil depth (Table 1.4). *Calamintha arkansana* (a perennial found only at the Manitoulin sites) and *Sporobolus heterolepis* were abundant. The 'Misery Bay - La Cloche low meadows' were dominated by *Sporobolus vaginiflorus*; *Ambrosia artemesiifolia* was also abundant (Table 1.3). The 'Misery Bay pavement' occurred in shallow soil and *Minuartia michauxii* was the most abundant species (Table 1.3).

Based on biomass and soil depth (Table 1.4), the southern and eastern alvar groups represent extreme habitats.

The 'Burnt Lands mix' groups occurred where biomass, soil depth and species richness were lowest (Table 1.4). These sites included the stress-tolerant perennials *Saxifraga virginiensis* and *Minuartia michauxii* (Table 1.3). The small, 'mixed-site rock flats' included quadrats at Burnt Lands, Misery Bay and La Cloche (Table 1.3). Soil depth, biomass and species richness levels were lowest in this group (Table 1.4). The dominant species were *Saxifraga virginiensis* and *Poa compressa* (Table 1.3). The 'Burnt Lands Rock Flats', which included mainly sites from the Burnt Lands (Table 1.3) was dominated by *Panicum philadelphicum*.

The 'Stone Road' groups occurred where biomass and soil depth were high; they also had the most rare species (Table 1.4). A dominant species of these sites, *Allium cernuum*, is a provincially rare species not present at the other alvars studied. *Poa compressa* and *Eleocharis compressa* were also important here and found infrequently at other sites (Table 1.3). The 'Stone Road dry grassland' (which also included a few quadrats from other sites; Table 1.3) had slightly lower biomass and occurred in shallower soil (Table 1.4). It was dominated by *Panicum philadelphicum*. The 'Stone Road prairie' had the highest overall biomass and soil depth (Table 1.4). This group was dominated by *Poa compressa*, which had an average frequency of 100% (Table 1.3) and *Andropogon gerardii*, a tall-grass prairie bunchgrass which occurred only in this group.

Ordination and Classification of Species

Information provided by the ordination and classification of species is similar to the above quadrat analyses and results are therefore not presented here (but see Appendix 1.9).

Discussion

Within Burnt Lands

Within one alvar, species composition changed dramatically along the first ordination axis, corresponding to changes in soil depth and biomass (Fig. 1.4). Although the second axis was not related to measured variables, there was evidence that it was related to a gradient of increasing disturbance and/or decreasing moisture availability. Quadrats in the 'low forb-rich meadows' group, which occurred high on the second axis (Fig. 1.3) were situated where elevation was higher (pers. obs.) and drainage may have been greater. Also, there was evidence of past disturbance (possibly an old building site, pers. obs.) at the same location. The dominant species of this group (Table 1.1) were *Panicum flexile*, a species often found in disturbed sites in cedar glades (Baskin and Baskin 1985a) and *Hypericum perforatum*, a wide-ranging alien species of fields or disturbed sites (Gleason and Cronquist 1963). Two quadrats of the 'bare rock flats' also occurred high on the second axis; the only quadrats of the group without *Saxifraga virginiensis*. Both disturbance and low moisture are factors which could limit this species. Similar studies within Swedish alvars showed that dominant vegetation trends are related to edaphic factors, mainly soil depth; secondary trends are related to soil moisture (Bengtsson *et al.* 1988).

Classification of quadrats produced two main vegetation communities: 'rock flats' with incomplete vegetation cover and exposed limestone rock, and 'meadows' with complete vegetation cover in deeper soil, corresponding to 'open' and 'closed' vegetation types within Swedish alvars (Krahulec *et al.* 1986, Bengtsson *et al.* 1988). I described four 'meadows' groups and three 'rock flats' groups.

Several distinctive plant types could be recognized: in general, there was a trend along the gradient of decreasing soil depth, from (1) tall, perennial graminoids (e.g. *Sporobolus heterolepis, Carex crawei*), through (2) perennial forbs (mainly family Asteraceae, e.g. *Senecio pauperculus, Solidago ptarmicoides*), (3) small annual grasses (e.g. *Panicum flexile, Sporobolus vaginiflorus*), and (4) small annual forbs (e.g. *Trichostema brachiatum, Chaenorrhinum minus*) to (5) small, evergreen perennials (e.g. *Minuartia michauxii, Saxifraga virginiensis*).

The perennial graminoids and forbs which occurred in the deepest soils may be competitive dominants (Grime 1977) which exclude smaller species by competition. Wilson and Keddy (1986a) have shown that small, stress-tolerators are competitively excluded from fertile habitats. In the Burnt Lands alvar, competition did occur and was primarily for below-ground resources (chapter 1).

Summer annuals (e.g. *Panicum philadelphicum*) occurred in shallower soils, likely because they could germinate and flower in early summer when moisture is available. Some perennials act like winter annuals in that they germinate or sprout in the fall (e.g. *Campanula rotundifolia, Scutellaria parvula, Senecio pauperculus, Hieracium piloselloides*) and apparently cannot tolerate severe drought conditions (Baskin and Baskin 1985a); they therefore were restricted to somewhat deeper soils.

Small, evergreen perennials found in extreme shallow soil locations probably represent a stress-tolerant plant strategy (*sensu* Grime 1977). Shallow soil habitats experience extremes in moisture availability, from total inundation during the spring and fall to drought conditions during the summer (Catling *et al.* 1975; Baskin and Baskin 1978; Stephenson and Herendeen 1986; Krahulec *et al.* 1986; Bengtsson *et al.* 1988). Similar sites on rock outcrop have a high 'stress index' due to the low availability of moisture and nutrients and to high temperatures (Lugo and McCormick 1981). The stress-tolerant strategy is found in many other communities and habitats, including evergreen shrubs in deserts (Fonteyn and Mahall 1981), succulents in rock outcrop and arid habitats (e.g. Sharitz and McCormick 1973; Levitt 1980), isoetids in infertile wetlands (e.g. Boston and Adams 1987; Wisheu and Keddy 1989), narrow-leaved and tussock grasses and creeping or rosette dicotyledons in chalk grasslands (Grime 1979) and slow-growing evergreens in arctic alpine and subalpine communities (e.g. Del Moral 1983). Lichens, which also fall into the stress-tolerant category, often occur on exposed rock in cliff and rock outcrop communities (Larson 1980) and in alvars (Froberg 1988). Since this study concentrated on vascular plants, the extreme stress-tolerators (ie. the bryophytes and lichens) were not included. These should be examined in future studies.

Additionally, I looked at eight candidate species which could serve as indicators of healthy (*sensu* Rapport 1989) alvar vegetation (Fig. 1.5). These included *Sporobolus heterolepis*, a provincially rare species (Argus *et al.* 1987) and 7 significant alvar species (listed in Catling *et al.* 1975). All eight were dominant in at least one vegetation type (Table 1.1). Moreover, the limited distribution of, for example, *Sporobolus heterolepis* and *Saxifraga virginiensis* make them good indicators for healthy 'tall grassy meadows' and 'bare rock flats', respectively.

Among sites

Among alvars, species composition varied along geographic axes (Fig. 1.7) which did not correspond to simple variables (Fig. 1.8). I found that Stone Road, Burnt Lands and the two northern sites were separated along the first ordination axes and the northern sites, La Cloche and Misery Bay, were separated along the third axis. Thus, differentiation was due mainly to simple floristic differences among alvars. Similarly, classification produced quadrat groups which were based mainly on geographic location, but which also revealed some ecological relationships, specific habitat types, and interactions between geographic and ecological scales.

One vegetation type was restricted to Misery Bay. The 'Misery Bay pavement' group was dominated by *Minuartia michauxii*, a rock flat species. However, the high biomass and the presence of taller grasses (*Sporobolus heterolepis* and *Schizachyrium scoparium*) in this pavement vegetation show that species from both ends of the soil depth gradient were closely associated here. This vegetation was confined to cracks and small depressions in the rock. Species characteristic of deeper soil habitats grow in these cracks while small, stress-tolerant species can thrive on the virtually bare, adjacent rock.

Two other vegetation types were confined to Stone Road alvar. The 'Stone Road prairie' had deeper soil and higher biomass than any other vegetation type (Table 1.4) and was the only type with the tall-grass prairie species, *Andropogon gerardii*. The 'Stone Road dry grassland' included the remainder of the Stone Road quadrats, occurring in shallower soil (Table 1.4). This vegetation apparently included a range of alvar types, from meadows down to rock flats. *Poa compressa*, a Eurasian species, had invaded large portions of this gradient and contributed to the high biomass. Also abundant were *Panicum philadelphicum*, *Trichostema brachiatum* and *Scutellaria parvula* (Table 1.3), species found at low to intermediate soil depths within the Burnt Lands.

Other vegetation types were more subtle. For example, meadow habitats at Burnt Lands and La Cloche were similar where soil was deeper ('La Cloche-Burnt Lands' groups; Tables 1.3 - 1.4). Meadow habitats at Misery Bay and La Cloche were similar in slightly shallower soil ('Misery Bay - La Cloche' groups; Tables 1.3 - 1.4).

I examined the among-site distribution of the same eight indicator species examined within Burnt Lands (Fig. 1.9). Their distributions were closely related to the classification patterns. Tall meadow species (Fig. 1.9a-d) (e.g. *Sprobolus heterolepis*) were present at Burnt Lands, La Cloche and Misery Bay but not at Stone Road where meadow habitats were dominated by different species. Shallow soil species (Fig. 1.9e-f) (e.g. *Saxifraga virginiensis*) were also absent from Stone Road. Here, the rare species, *Leucospora multifida* (fig. 1.9k), occupied the rock flat habitat instead (pers. obs.). Shallow soil species were also infrequent at La Cloche where shallow soil habitats may have been damaged by grazing.

Synthesis

Species composition at both scales was related to soil depth, biomass and species richness. Let us examine relationships among these variables. Biomass was positively correlated with soil depth, both within Burnt Lands and among alvars ($r^2 = 0.96$ and 0.86, $P<0.001$; Fig. 1.12a), suggesting that the soil depth gradient does represent a resource gradient. Species richness was significantly curvilinearly related to biomass within Burnt

Lands ($r^2 = 0.88$, $P<0.001$, Fig. 1.12b). This agrees with the model proposed by Grime (1973) which predicts that species richness will be limited by stress or disturbance where biomass is low, and by competition where biomass is high. This relationship was not significant among alvars, although species richness appeared to decrease at maximum biomass. These relationships among biomass, soil depth and species richness will be examined in detail in chapter 2.

This chapter has implications for future research in alvars and for conservation planning. The within Burnt Lands analysis describes important species - environment relationships for this site and emphasizes the importance of soil depth and biomass gradients in this vegetation type. The among site analysis shows that while alvar floristics vary regionally, ecological patterns found at Burnt Lands also exist at a broader scale. Thus alvars provide a useful tool for the study of soil depth gradients, particularly as the species richness patterns are similar to those found in a range of other vegetation types from chalk grasslands (Grime 1973) to wetlands (Wisheu and Keddy 1989). From the perspective of conservation planning, these results show that the flora varies among Canadian alvars and comparison with other studies shows that flora also varies globally as there is apparently little species overlap between alvars in Canada and elsewhere (e.g. Baskin and Baskin 1985b; Bengtsson *et al.* 1988). The variation among and within alvars shows that a series of protected sites are needed to protect the full range of natural vegetation (Belcher and Keddy in press) and that management (if any) is likely to involve maintaining soil depth gradients.

Table 1.1.

Frequency of occurrence of alvar species; within Burnt Lands. Shown is the overall frequency (% of quadrats in which each species occurred) and the average species frequencies (average number of sub-quadrats, out of 9, in which each species occurred) in each TWINSPAN group. For each group: the frequency of the dominant species is indicated in bold text and the total number of species and quadrats included is shown at the bottom of the table (included quadrats are listed in Appendix 1.7a). 17 species which had an overall frequency of less than 5% were omitted from the analysis (see Appendix 1.5a).

Species	Overall Frequency (%)	Average Frequency (# of sub-quadrats) in: TWINSPAN Group: Tall Grassy Meadows	Tall Forb-Rich Meadows	Low Grassy Meadows	Low Forb-Rich Meadows	Dry Grassland	Rock Margin Grassland	Bare Rock Flats
Ambrosia artemesiifolia	20.4	0	0.3	1.6	1.3	0.7	0.3	0
Campanula rotundifolia	17.3	0.2	2.2	0.5	0.8	0	0	0
Carex bebbii	6.1	0.4	0.3	0.1	0.7	0	0	0
Carex crawei	44.9	7.4	8.1	1.5	0.3	0	0	0
Carex richardsonii	6.1	0.1	0.9	0.3	0	0	0	0
Carex umbellata	6.1	0.1	0.8	0.4	0.4	0	0	0
Chaenorrhinum minus	8.2	0	0	0.3	1.0	0	0.6	0.1
Danthonia spicata	43.9	2.4	3.7	1.9	3.1	0	0	0
Elmyus trachycaulus	6.1	0.1	0	0.8	0	0	0	0
Fragaria virginiana	12.2	0.8	1.1	0.2	0.7	0	0.4	0
Hedeoma hispida	5.1	0.1	0	1.1	0	0	0	0
Hieracium piloselloides	39.8	0.4	4.6	1.5	0.9	0	0.2	0
Hypericum perforatum	20.4	0.1	0.3	0.4	4.1	0	0.1	0
Minuartia michauxii	17.3	0	0	0.1	0	0.7	1.2	0.6
Panicum flexile	6.1	0	0	0	5.1	0	0	0
Panicum philadelphicum	6.0	0.3	0.1	5.1	0.1	7.8	6.9	0
Poa pratensis	21.4	0.2	3.3	1.6	0.6	0.2	0	0
Potentilla recta	8.2	0	0.5	0.2	0.8	0	0	0
Saxifraga virginiensis	21.4	0	0	0.1	0	1.2	5.6	2.5
Scutellaria parvula	23.5	0.1	0	2.6	2.8	0	0.7	0
Senecio pauperculus	58.2	5.3	1.8	4.1	1.4	0	0.3	0
Solidago nemoralis	18.4	0.1	2.4	0.3	1.2	0	0	0
Solidago ptarmicoides	33.7	0.7	3.9	0.4	1.2	0	0.3	0
Sporobolus heterolepis	23.5	8.4	0.1	0.1	0	0	0	0
Sporobolus vaginiflorus	35.7	0.3	2.4	4.5	1.8	4.0	0	0
Trichostema brachiatum	25.5	0.2	0.3	1.9	1.2	1.9	0.3	0
Total Number of Species	26	20	19	25	20	7	12	3
Total Number of Quadrats	98	22	17	21	9	9	12	8

Table 1.2.

Mean value for 3 measured variables (soil depth, biomass and species richness) in each TWINSPAN group; within Burnt Lands.

	TWINSPAN Group						
Variable	Tall Grassy Meadows	Tall Forb-Rich Meadows	Low Grassy Meadows	Low Forb-Rich Meadows	Dry Grassland	Rock Margin Grassland	Bare Rock Flats
Soil Depth (cm)	10.5	7.3	5.1	5.4	1.8	1.9	0.6
Biomass (g · 0.25m^{-2})	29.8	25.9	16.6	14.3	6.1	4.5	0.5
Richness (Number · 0.25m^{-2})	5.5	8.2	7.4	10.1	3.8	4.0	1.1

Table 1.3.

Frequency of occurrence of alvar species; among sites. Shown is the overall frequency (% of quadrats in which each species occurred) and the average species frequencies in each TWINSPAN group (mean number of sub-quadrats, out of 9, in which each species occurred). For each group: the frequency of the dominant species is indicated in bold text; total number of species and quadrats, and the number of quadrats from each site, are shown at the bottom of the table (included quadrats are listed in Appendix 1.7b). 49 species which had an overall frequency of less than 5% were omitted from the analysis (see Appendix 1.5b). 1 quadrat was omitted from the analysis due to insufficient vegetation data.

		Average Frequency (# of Sub-quadrats) in:							
		TWINSPAN Group							
Species	Overall Frequency (%)	La Cloche Tall Meadows	Burnt Lands Low Meadows	Misery Bay-La Cloche Low Meadows	Misery Bay Pavement	Mixed-Site Rock Flats	Burnt Lands Rock Margins	Stone Road Dry Grass-lands	Stone Road Dry Prairie
Allium cernuum	22.0	0	0	0	0	0	0	4.5	5.4
Ambrosia artemisiifolia	23.5	0	0.8	2.7	1.0	0	0.4	0.6	0.0
Andropogon gerardii	5.5	0	0	0	0	0	0	0	5.5
Antennaria neglecta	5.5	0.4	0	0	0	0	0	0	0
Artemisia campestris	6.5	0	0	0	1.4	1.3	0.5	0	0
Calamintha arkansana	14.0	0	0	2.5	2.6	0	1.1	0.1	0
Campanula rotundifolia	7.0	0.2	1.4	0.1	0.2	0	0.1	0	0
Carex crawei	27.0	5.2	4.3	0.5	0	0	0	0	0
Carex umbellata	5.5	0.5	0.4	0.1	0.5	0	0	0	0
Danthonia spicata	24.5	2.3	2.5	0	0.1	0	0	0	0
Deschampsia cespitosa	8.5	0	0	1.5	0.8	0	0.1	0.8	0
Eleocharis compressa	17.5	0.4	0.1	0.8	0.1	0.2	0	2.2	2.5
Elymus trachycaulus	7.5	0.2	0.5	0.1	0.7	0	0	0	0
Fragaria virginiana	8.0	0.3	0.5	0	0	0	0.3	0.1	1.1
Geranium bicknellii	7.0	0.1	0.1	0.1	0.2	0.8	0.7	0.1	0
Hieracium piloselloides	10.5	0	2.5	0.1	0	0.2	0.1	0	0
Hypericum perforatum	13.0	0	0.5	0.5	0.1	0	0.1	1.1	0.1
Juncus dudleyi	5.0	0.1	0	0	0	0	0.1	0.7	0
Melilotus spp.	5.0	0	0	0	0	0	0	0	2.6
Minuartia michauxii	17.0	0	0	0.3	2.8	1.2	1.4	0	0
Panicum philadelphicum	29.5	0	1.7	0.5	0.8	0	6.9	4.9	0
Poa compressa	26.5	0.1	0.3	0.4	0.3	2.0	0	3.9	9.0
Poa pratensis	5.5	0	1.9	0	0	0	0.1	0	0
Ranunculus fascicularis	6.0	0.5	0.2	0.1	0	1.5	0	0.1	0
Ratibida pinnata	8.0	0	0	0	0	0	0	0.8	0.4
Rumex crispus	6.5	0	0	0	0	0	0.2	0.6	0
Saxifraga virginiensis	11.0	0	0	0	0.4	2.3	3.5	0	0
Schizachyrium scoparium	19.5	3.5	0	0.5	1.8	0	0	0	0
Scirpus atrovirens	5.5	0	0	0	0	0	0	0.1	3.1
Scutellaria parvula	29.0	0	1.9	0.4	0.5	0.3	0.7	2.8	0.2
Senecio pauperculus	21.0	1.0	2.8	0.7	0.2	0	0.2	0	0
Solidago nemoralis	5.0	0	1.1	0	0	0	0	0.2	0

Solidago ptarmicoides	13.5	0.5	1.8	0	0.4	0	0.2	0.1	0
Sporobolus heterolepis	31.5	6.4	0.9	2.3	1.3	0	0	0	0
Sporobolus vaginiflorus	23.0	1.4	3.7	3.8	0	0	1.2	0.2	0
Trichostema brachiatum	23.5	0.1	1.2	0	0.4	0	1.0	3.4	0.1
Total Number of Species	36	24	25	21	21	9	20	21	11
Number of Quadrats from:									
Burnt Lands	49	8	21	2	1	2	13	2	0
Stone Road	50	0	0	0	0	0	1	32	17
La Cloche	50	31	5	11	1	1	0	1	0
Misery Bay	50	0	0	0	0	0	1	32	17
Total Number of Quadrats	199	45	26	30	18	6	17	40	17

Table 1.4.

Mean value for 4 measured variables (soil depth, biomass, species richness and rare species richness) in each TWINSPAN group; among sites.

	TWINSPAN Group							
Variable	La Cloche Tall Meadows	Burnt Lands Low Meadows	Misery Bay-La Cloche Low Meadows	Misery Bay Pavement	Mixed-Site Rock Flats	Burnt Lands Rock Margins	Stone Road Dry Grass-land	Stone Road Dry Prairie
Soil Depth (cm)	7.0	5.8	3.9	1.8	1.0	1.2	4.1	13.0
Biomass (g · $0.25m^{-2}$)	27.2	19.3	10.9	8.2	3.4	5.6	35.8	96.7
Richness (Number · $0.25m^{-2}$)	5.6	8.1	5.4	5.8	3.7	5.1	6.6	6.1
Rare Species Richness (Number · $0.25m^{-2}$)	0.9	0.2	0.4	0.5	0.2	0.1	1.1	1.2

Figure 1.1.

Locations of study sites in Ontario. Study sites are Burnt Lands alvar (B), Stone Road alvar (S), La Cloche alvar (L) and Misery Bay alvar (M).

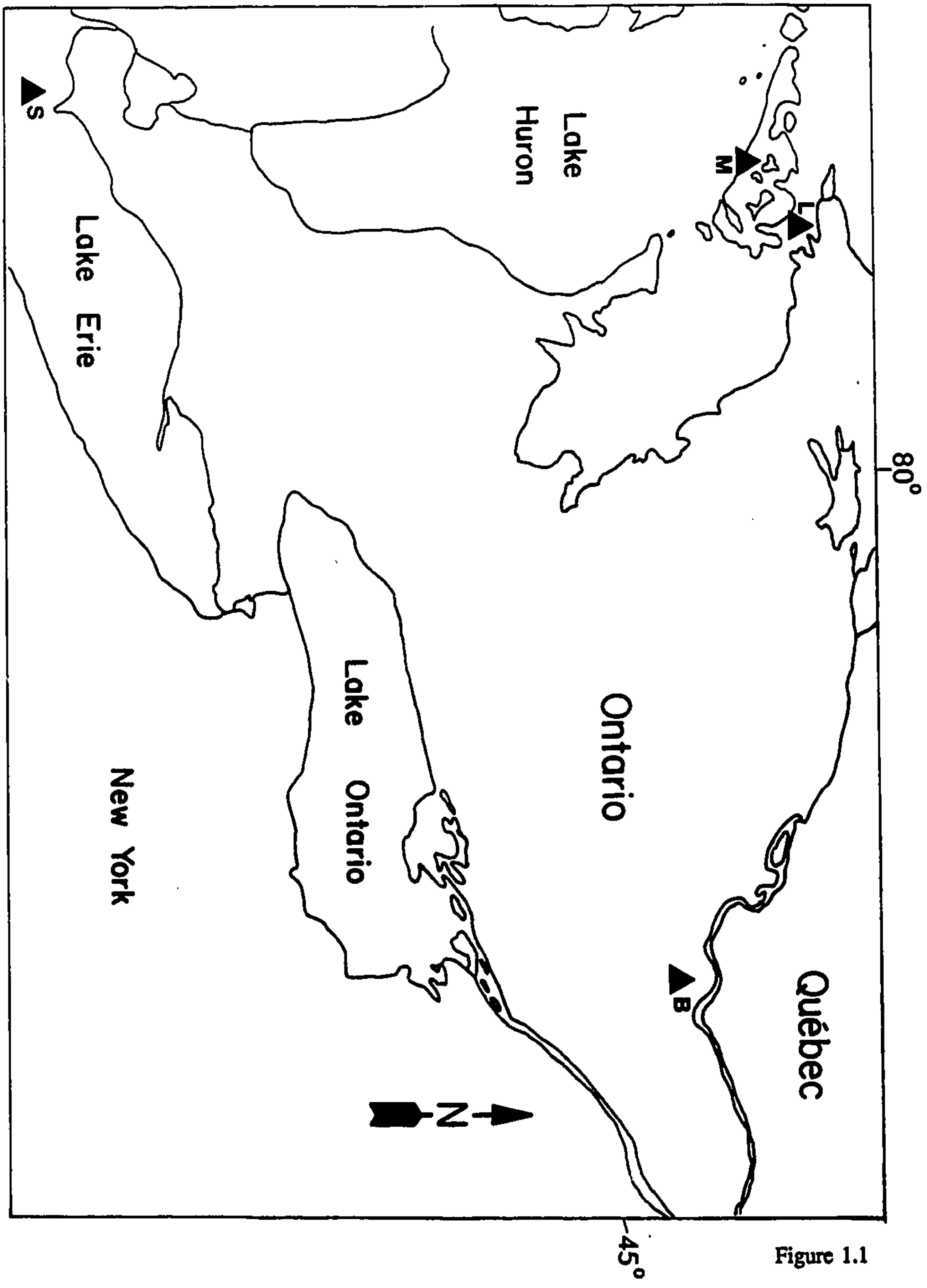
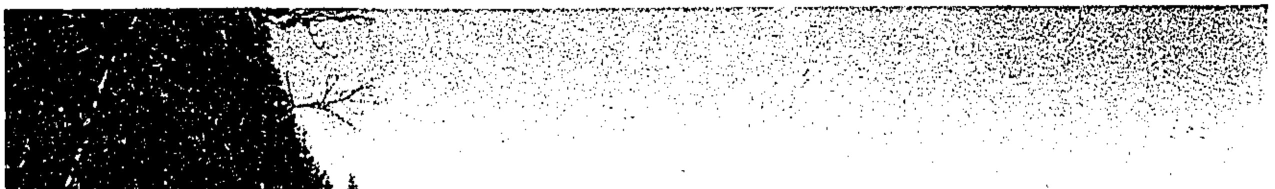

Lake Huron
Lake Erie
Lake Ontario
Ontario
Québec
New York
N
80°
45°
S
M
L
B

Figure 1.1

Figure 1.2.

Photographs of two alvar sites. (a) Burnt Lands alvar: vegetation occupies shallow soil over limestone. (b) Misery Bay alvar: soil and vegetation are largely restricted to cracks in the harder dolomite limestone.

A



B

Figure 1.3.

Within Burnt Lands quadrat ordinations. Quadrat scores, as determined by DCA, are plotted on axes 1 vs. 2 and 1 vs. 3. Symbols refer to seven TWINSPAN vegetation types (see Tables 1.1 - 1.2; Figure 1.6): Tall grassy meadows (filled triangle up), Tall forb-rich meadows (filled triangle down), Low grassy meadows (filled square), Low forb-rich meadows (filled circle), Dry grasslands (open triangle down), Rock margin grasslands (open square) and Bare rock flats (open circle).

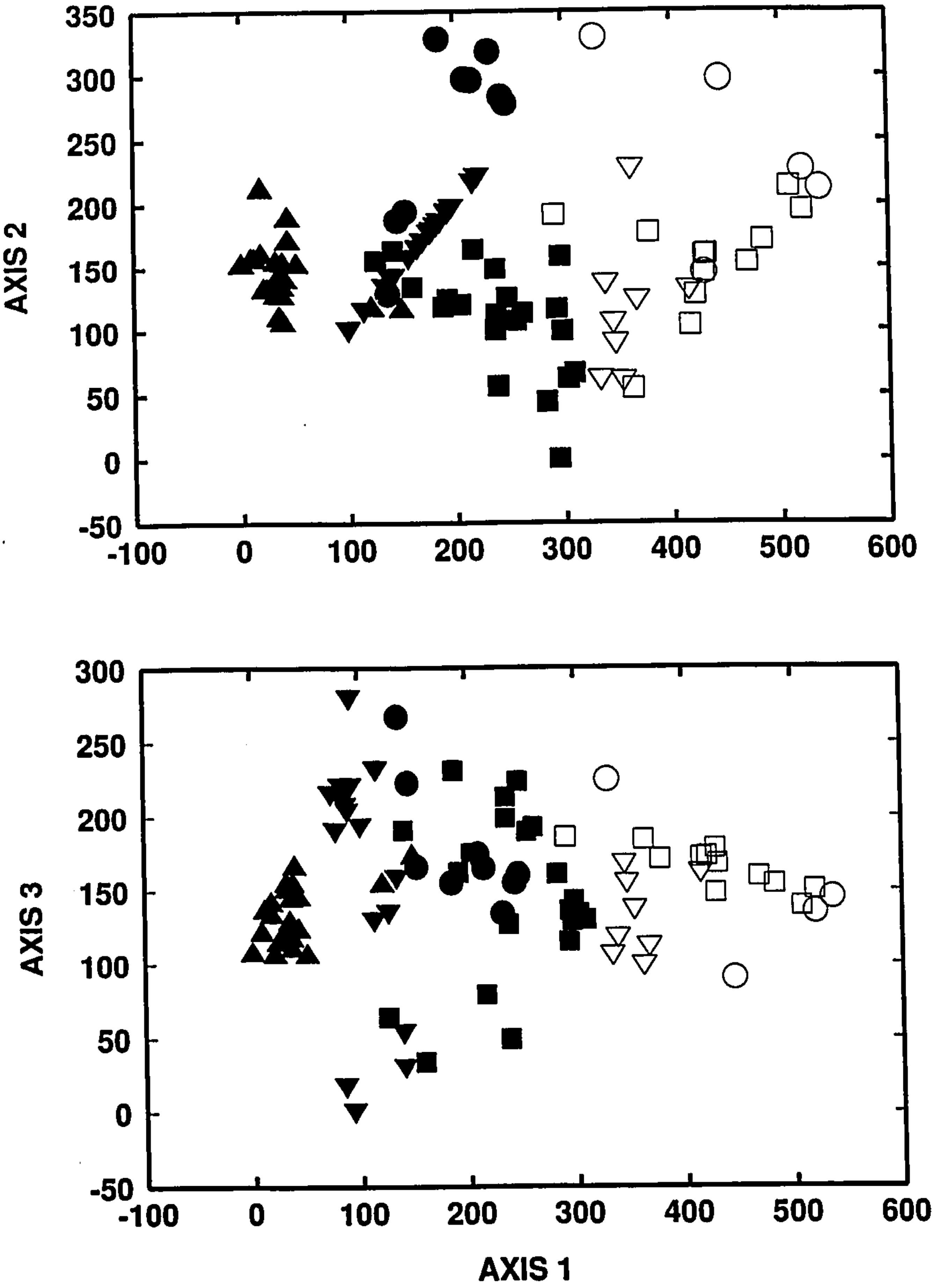
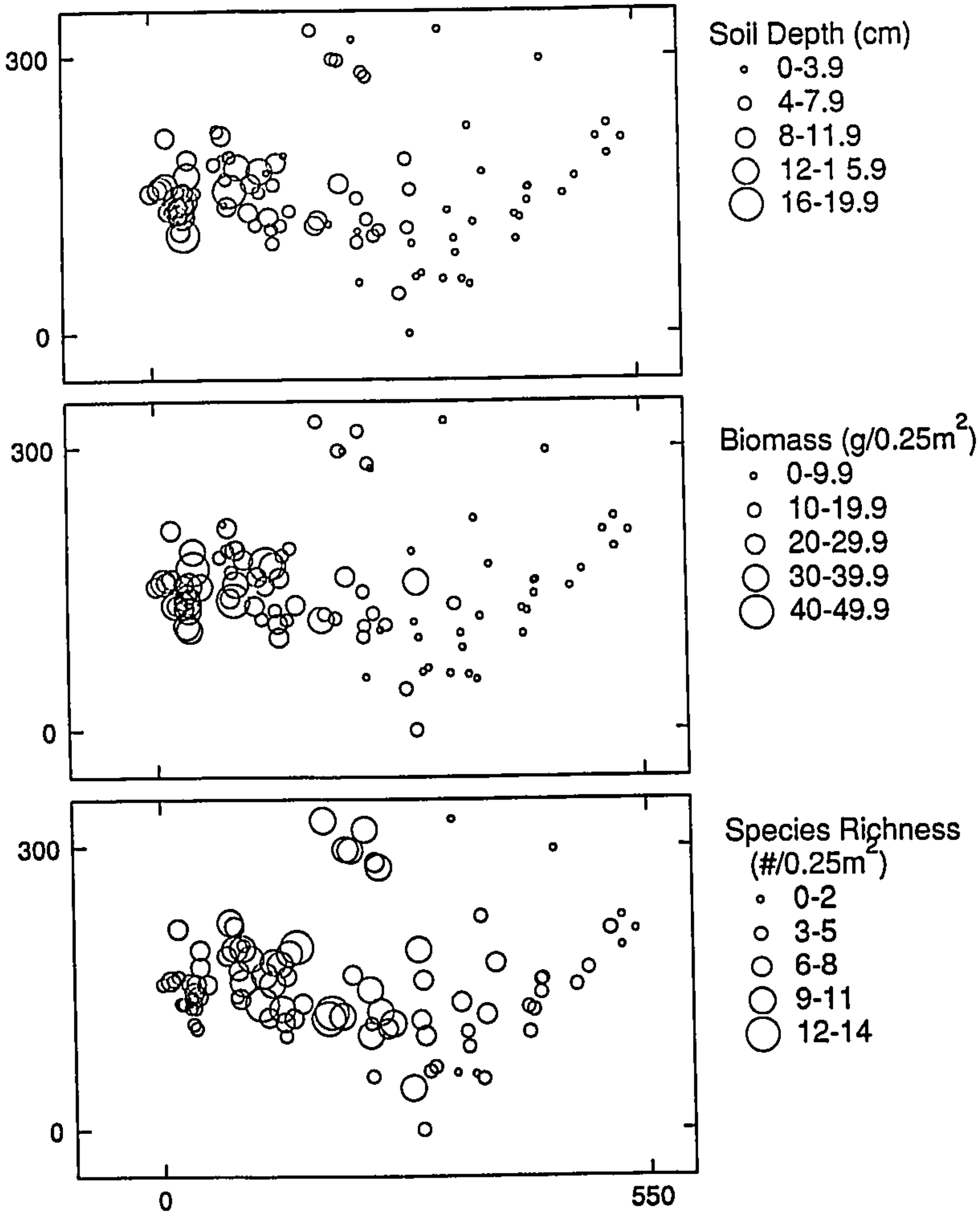

AXIS 2
350
300
250
200
150
100
50
0
-50
-100
0
100
200
300
400
500
600
AXIS 3
300
250
200
150
100
50
0
-50
-100
0
100
200
300
400
500
600
AXIS 1

Figure 1.3

Figure 1.4.

Within Burnt Lands measured variable overlays. For each quadrat on the ordination diagram (axes 1 vs. 2), the level of three variables (soil depth, biomass and species richness) is indicated by circle size (see legend).

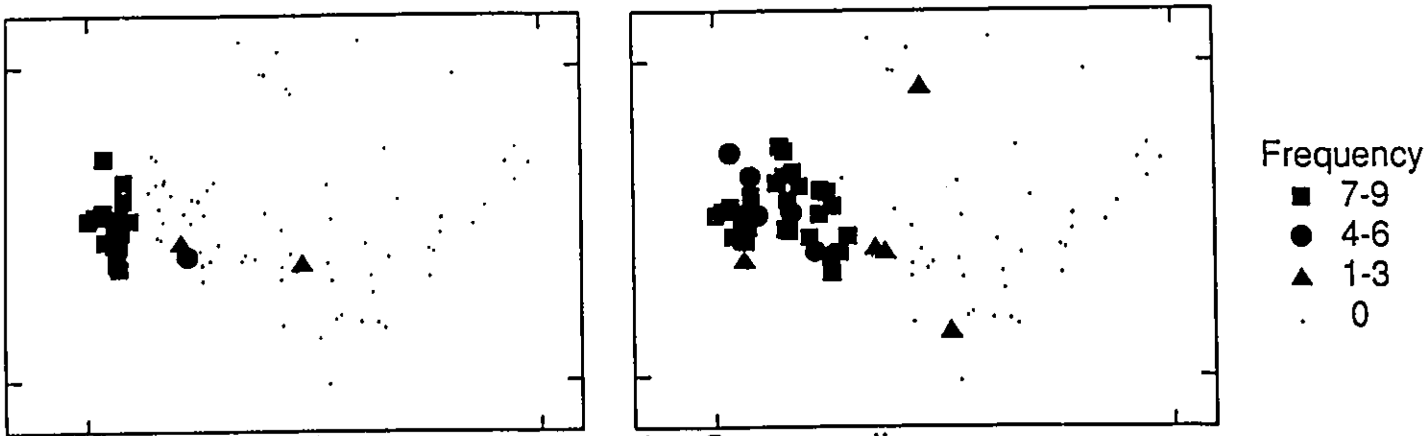


300
0
Soil Depth (cm)
0-3.9
4-7.9
8-11.9
12-1 5.9
16-19.9
300
0
Biomass (g/0.25m^2)
0-9.9
10-19.9
20-29.9
30-39.9
40-49.9
300
0
Species Richness (#/0.25m^2)
0-2
3-5
6-8
9-11
12-14
0
550

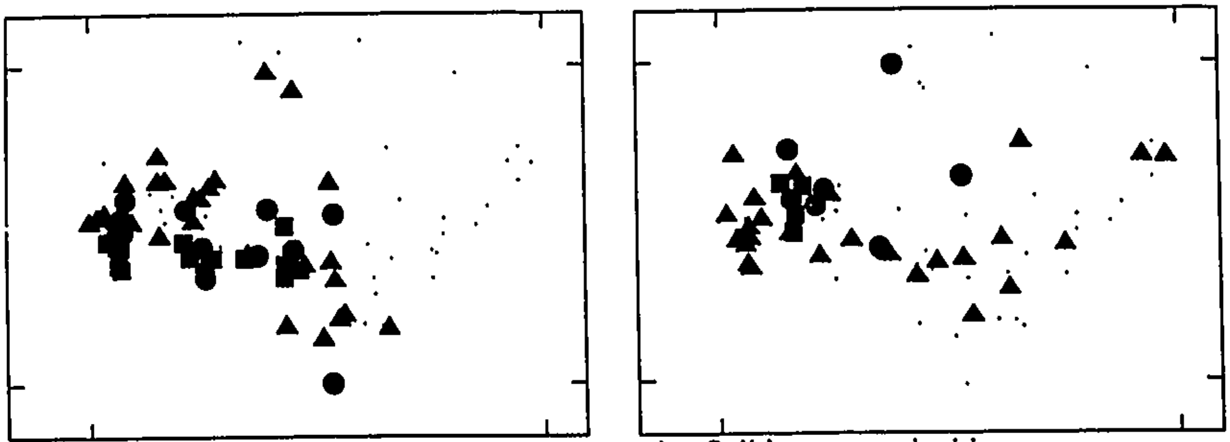
Figure 1.4

Figure 1.5.

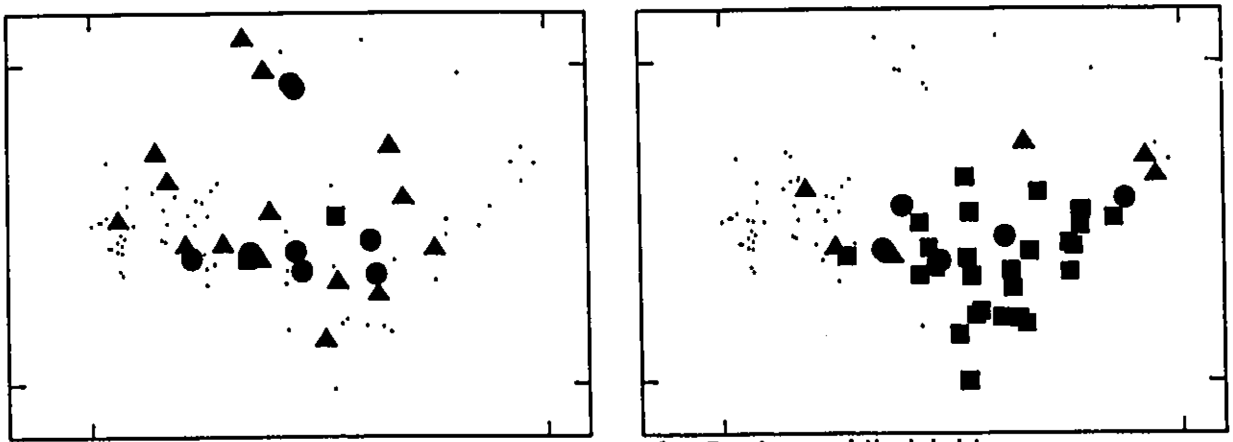
Within Burnt Lands species overlays. For each quadrat on the ordination diagram (axes 1 vs. 2), the frequency of occurrence of eight species is indicated by circle size (see legend). Species names are indicated below axis 1 on each plot.



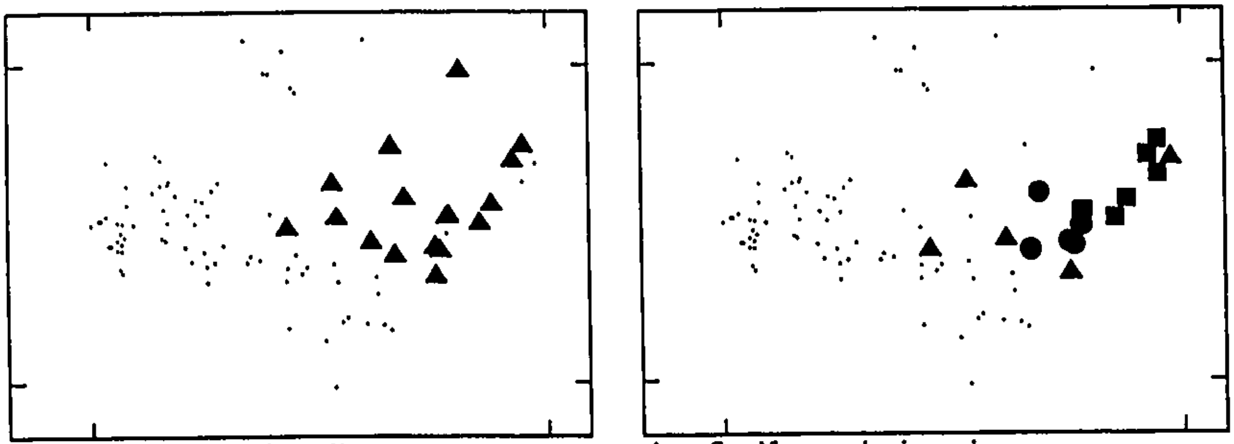
a *Sporobolus heterolepis* *b* *Carex craweii*



c *Senecio pauperculus* *d* *Solidago ptarmicoides*



e *Trichostema brachiatum* *f* *Panicum philadelphicum*



g *Minuartia michauxii* *h* *Saxifraga virginensis*

Figure 1.5

Figure 1.6.

Within Burnt Lands dendrogram for quadrat classification, as determined by TWINSPAN. The number of quadrats in each group is shown in brackets; symbols correspond to fig. 1.3.

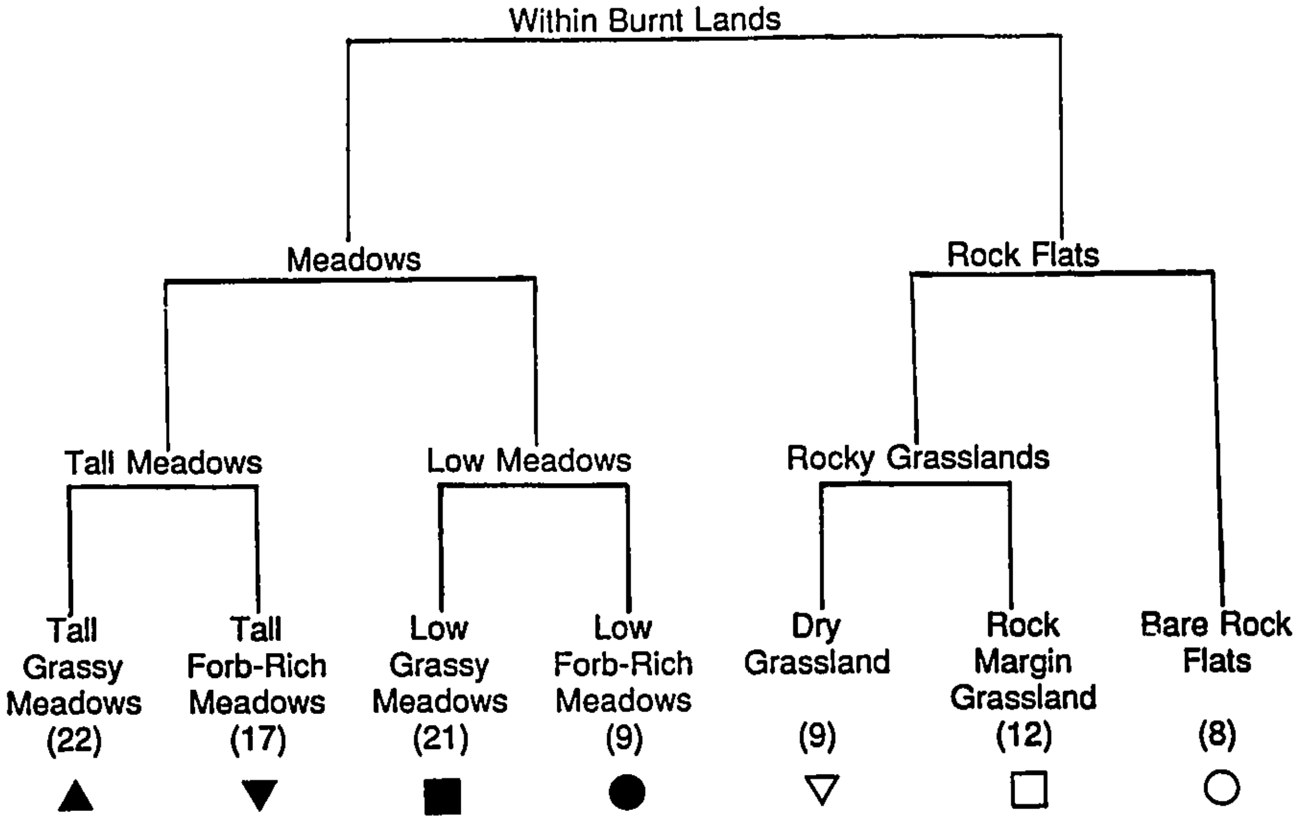

Within Burnt Lands
Meadows
Rock Flats
Tall Meadows
Low Meadows
Rocky Grasslands
Tall Grassy Meadows (22) ▲
Tall Forb-Rich Meadows (17) ▼
Low Grassy Meadows (21) ■
Low Forb-Rich Meadows (9) ●
Dry Grassland (9) ▽
Rock Margin Grassland (12) □
Bare Rock Flats (8) ○

Figure 1.6

Figure 1.7.

Among sites quadrat ordinations showing study sites. Quadrat scores, as determined by DCA, are plotted on axes 1 vs. 2 and 1 vs. 3. Letters represent the four study sites: Burnt Lands (B), Stone Road (S), La Cloche (L) and Misery Bay (M).

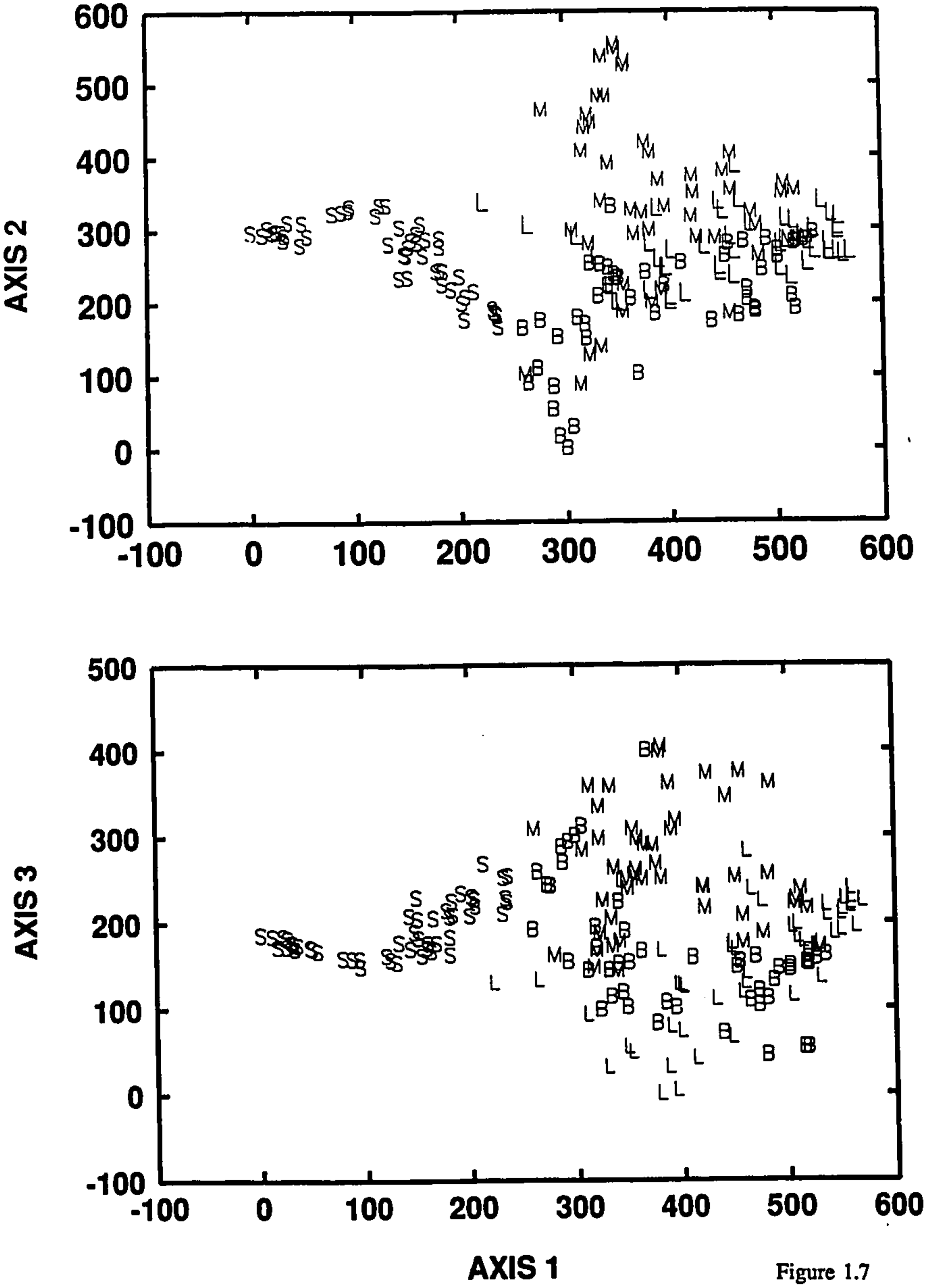

AXIS 2
600
500
400
300
200
100
0
-100
-100
0
100
200
300
400
500
600
AXIS 3
500
400
300
200
100
0
-100
-100
0
100
200
300
400
500
600
AXIS 1

Figure 1.7

Figure 1.8.

Among sites measured variable overlays. The level of four variables (soil depth, biomass, species richness and rare species richness) is indicated by circle size or number (see legend), for each quadrat on the ordination diagram; (a) axes 1 vs 2 and (b) axes 1 vs 3.

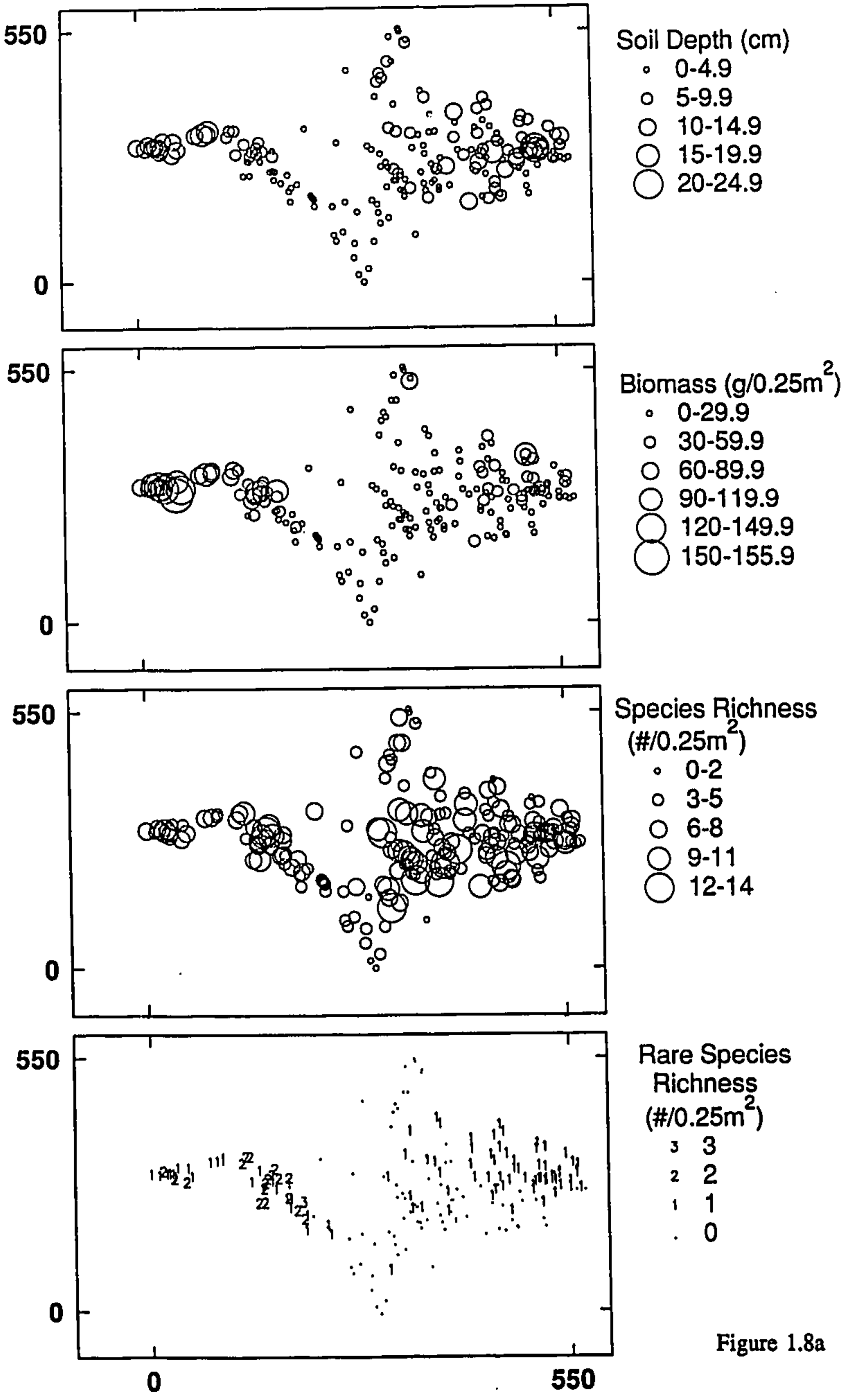

550
0
Soil Depth (cm)
0-4.9
5-9.9
10-14.9
15-19.9
20-24.9
550
0
Biomass (g/0.25m²)
0-29.9
30-59.9
60-89.9
90-119.9
120-149.9
150-155.9
550
0
Species Richness (#/0.25m²)
0-2
3-5
6-8
9-11
12-14
550
0
Rare Species Richness (#/0.25m²)
3 3
2 2
1 1
. 0
0
550

Figure 1.8a

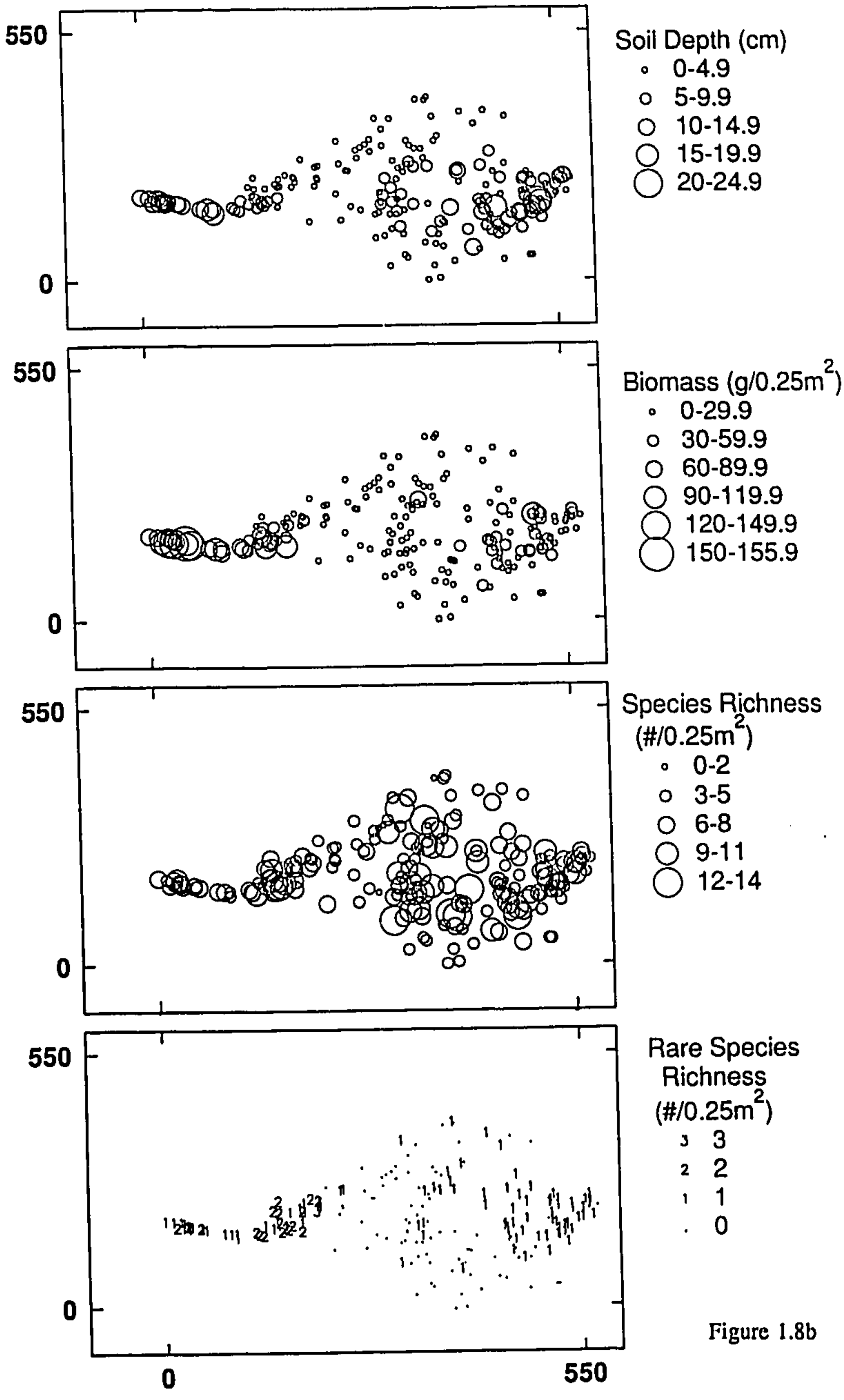
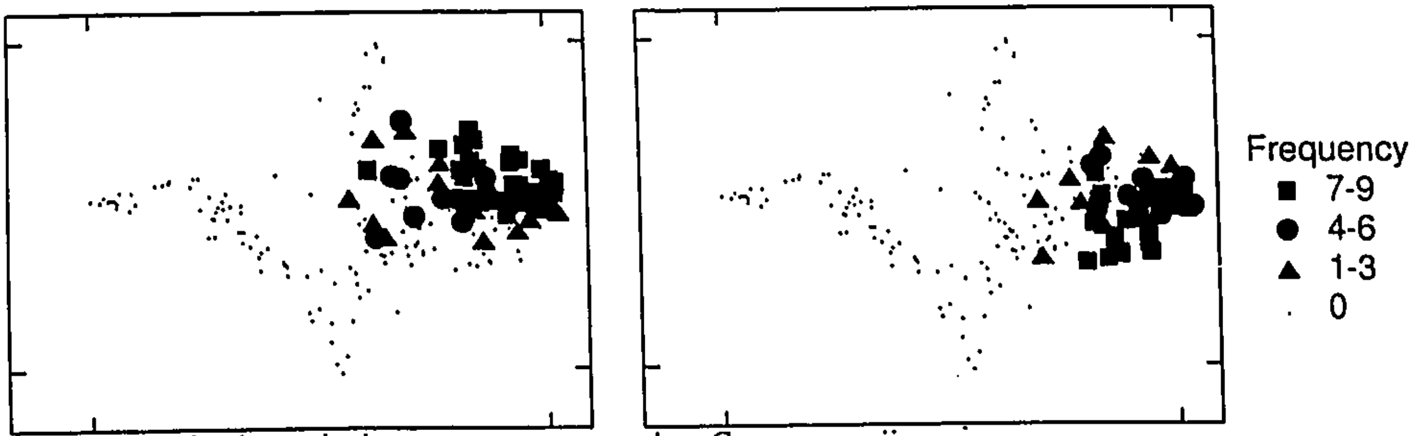

550
0
Soil Depth (cm)
0-4.9
5-9.9
10-14.9
15-19.9
20-24.9
550
0
Biomass (g/0.25m^2)
0-29.9
30-59.9
60-89.9
90-119.9
120-149.9
150-155.9
550
0
Species Richness
(#/0.25m^2)
0-2
3-5
6-8
9-11
12-14
550
0
Rare Species
Richness
(#/0.25m^2)
3
2
1
0
0
550

Figure 1.8b

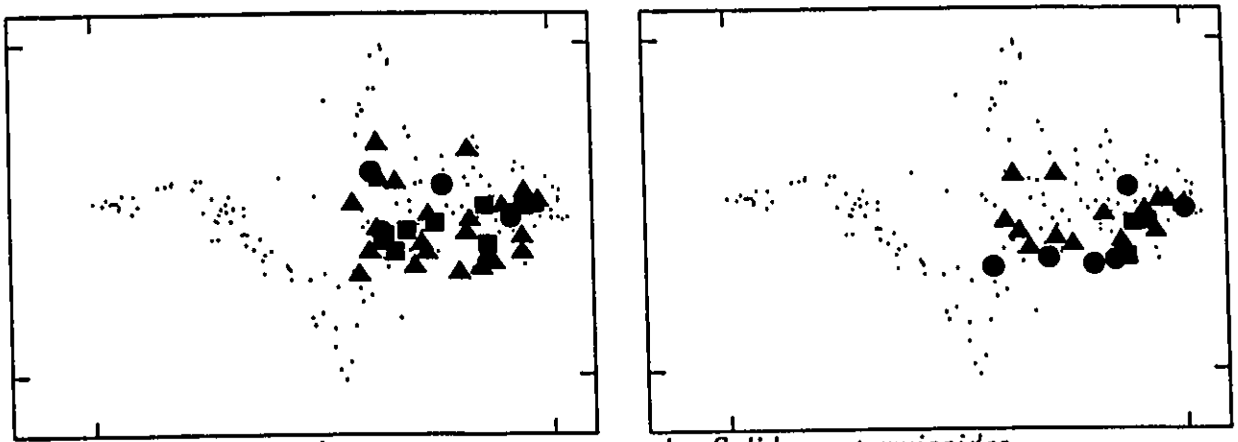
Figure 1.9.

Among sites species overlays. The frequency of occurrence 12 species is indicated by circle size (see legend), for each quadrat on the ordination diagram; (a) axes 1 vs 2 and (b) axes 1 vs. 3). Species names are indicated below axis 1 on each plot. Included are 5 rare species: rare in Ontario (a, i; Argus *et al.* 1987) and rare in Canada (j-l; Argus and Pryor 1990).



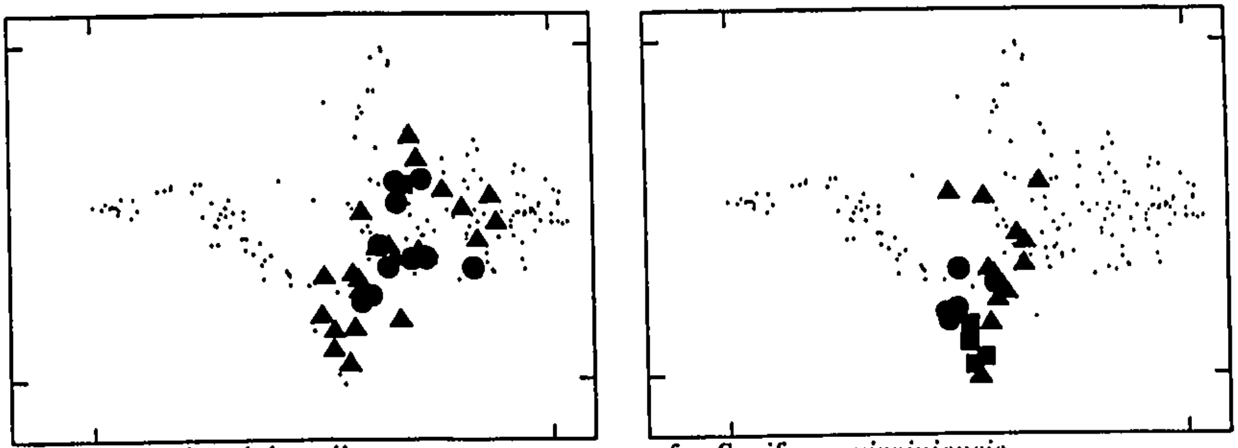
a *Sporobolus heterolepis*

b *Carex craweii*



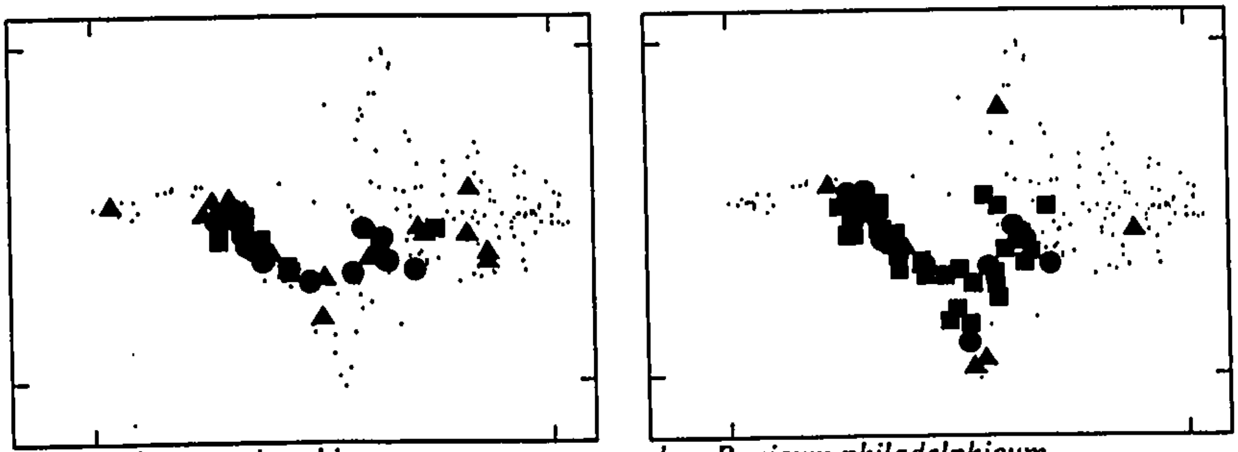
c *Senecio pauperculus*

d *Solidago ptarmicoides*



e *Minuartia michauxii*

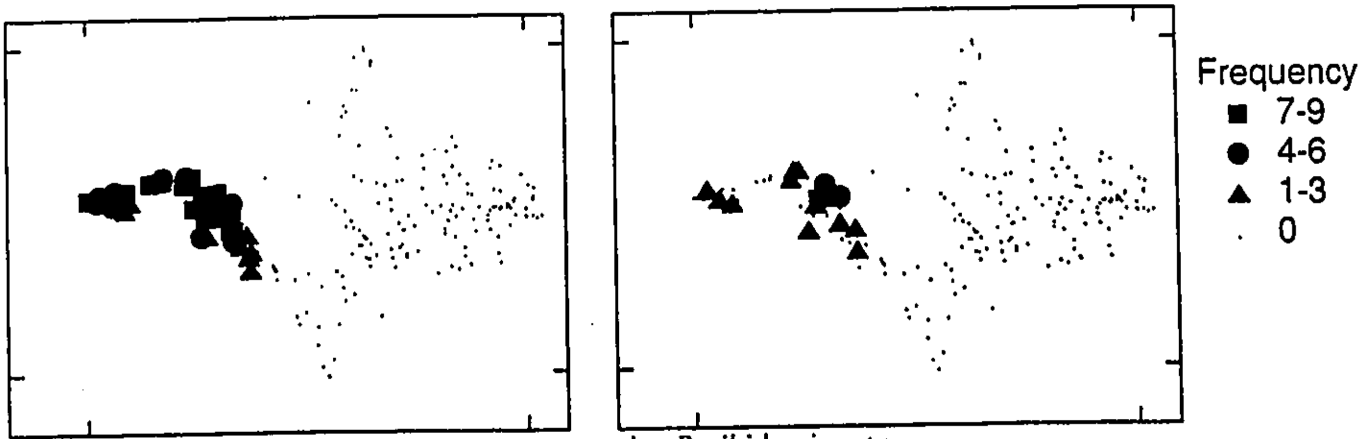
f *Saxifraga virginiensis*



g *Trichostema brachiatum*

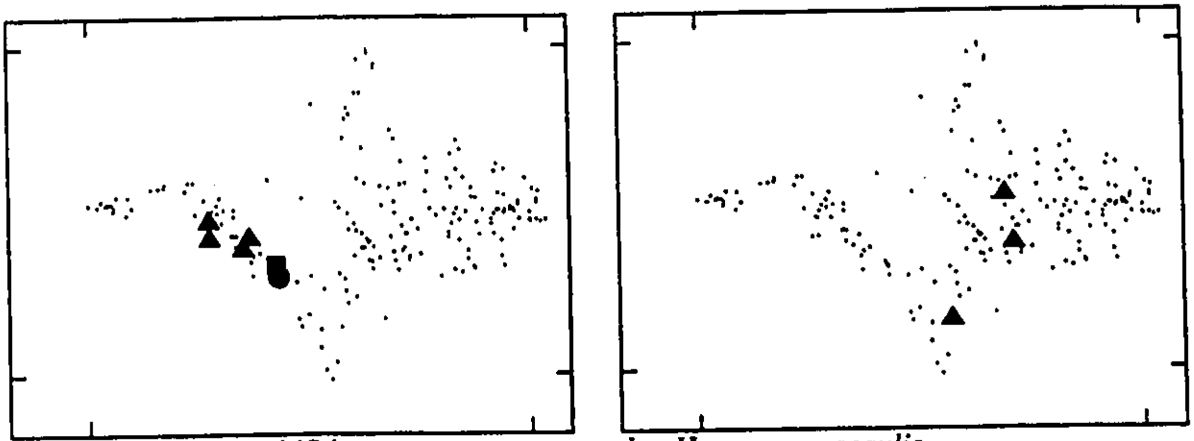
h *Panicum philadelphicum*

Figure 1.9



i *Allium cernuum*

j *Ratibida pinnata*



k *Leucospora multifida*

l *Hymenoxys acaulis*

Figure 1.9

Figure 1.10.

Among sites dendrogram for quadrat classification, as determined by TWINSPAN. The number of quadrats in each group is shown in brackets; symbols correspond to fig. 1.11.

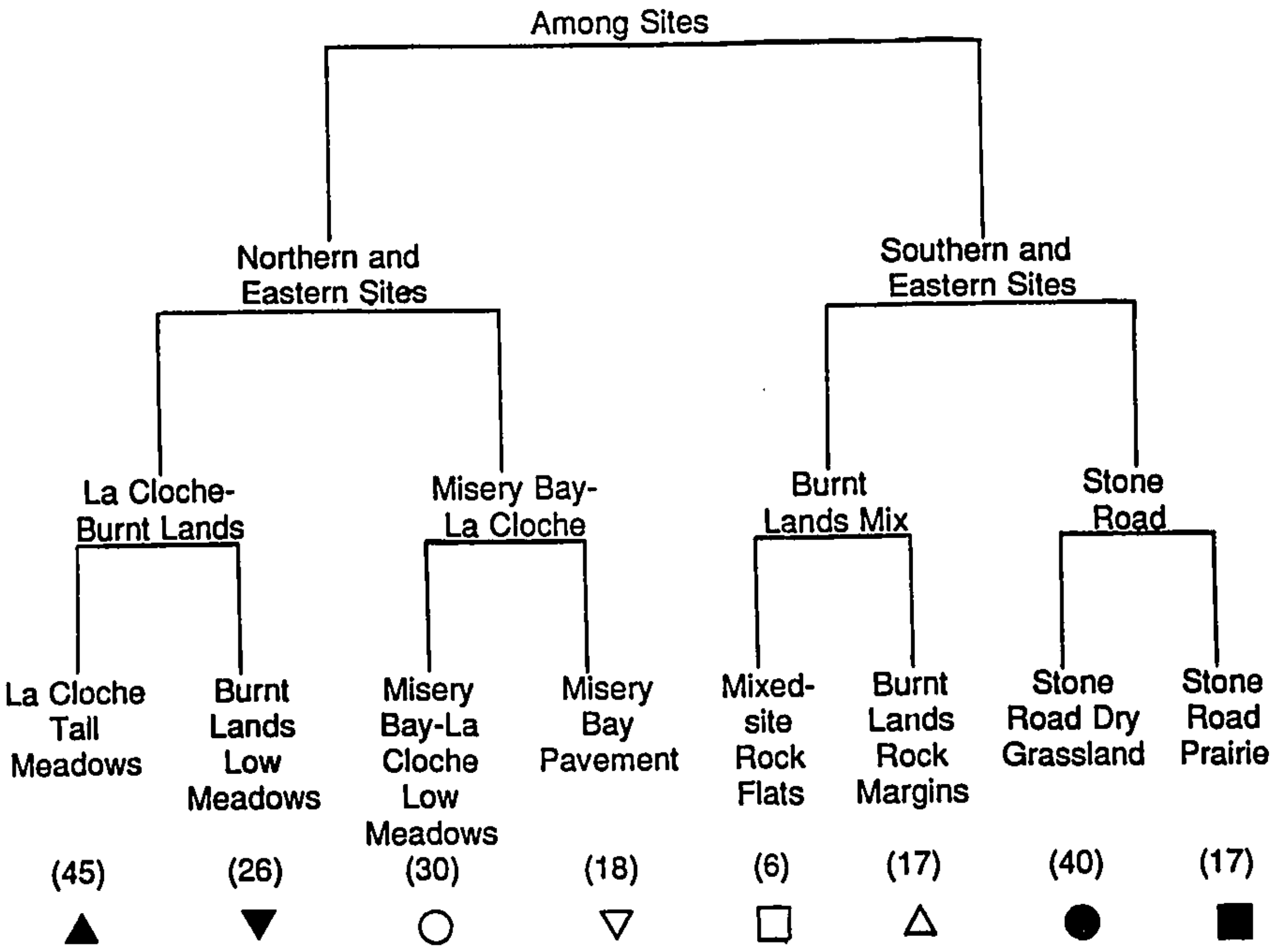

Among Sites
Northern and Eastern Sites
Southern and Eastern Sites
La Cloche-Burnt Lands
Misery Bay-La Cloche
Burnt Lands Mix
Stone Road
La Cloche Tall Meadows (45) ▲
Burnt Lands Low Meadows (26) ▼
Misery Bay-La Cloche Low Meadows (30) ○
Misery Bay Pavement (18) ▽
Mixed-site Rock Flats (6) □
Burnt Lands Rock Margins (17) △
Stone Road Dry Grassland (40) ●
Stone Road Prairie (17) ■

Figure 1.10

Figure 1.11.

Among sites quadrat ordinations, showing vegetation types. Quadrat scores, as determined by DCA, are plotted on axes 1 vs. 2 and axis 1 vs. 3. Symbols refer to eight TWINSPAN vegetation types (see Tables 1.3 - 1.4; Fig. 1.10): La Cloche tall meadows (filled triangle up), Burnt Lands low meadows (filled triangle down), Misery Bay - La Cloche low meadows (open circle), Misery Bay pavement (open triangle down), Mixed-site rock flats (open square), Burnt Lands rock margins (open triangle up), Stone Road dry grassland (filled circle) and Stone Road prairie (filled square).

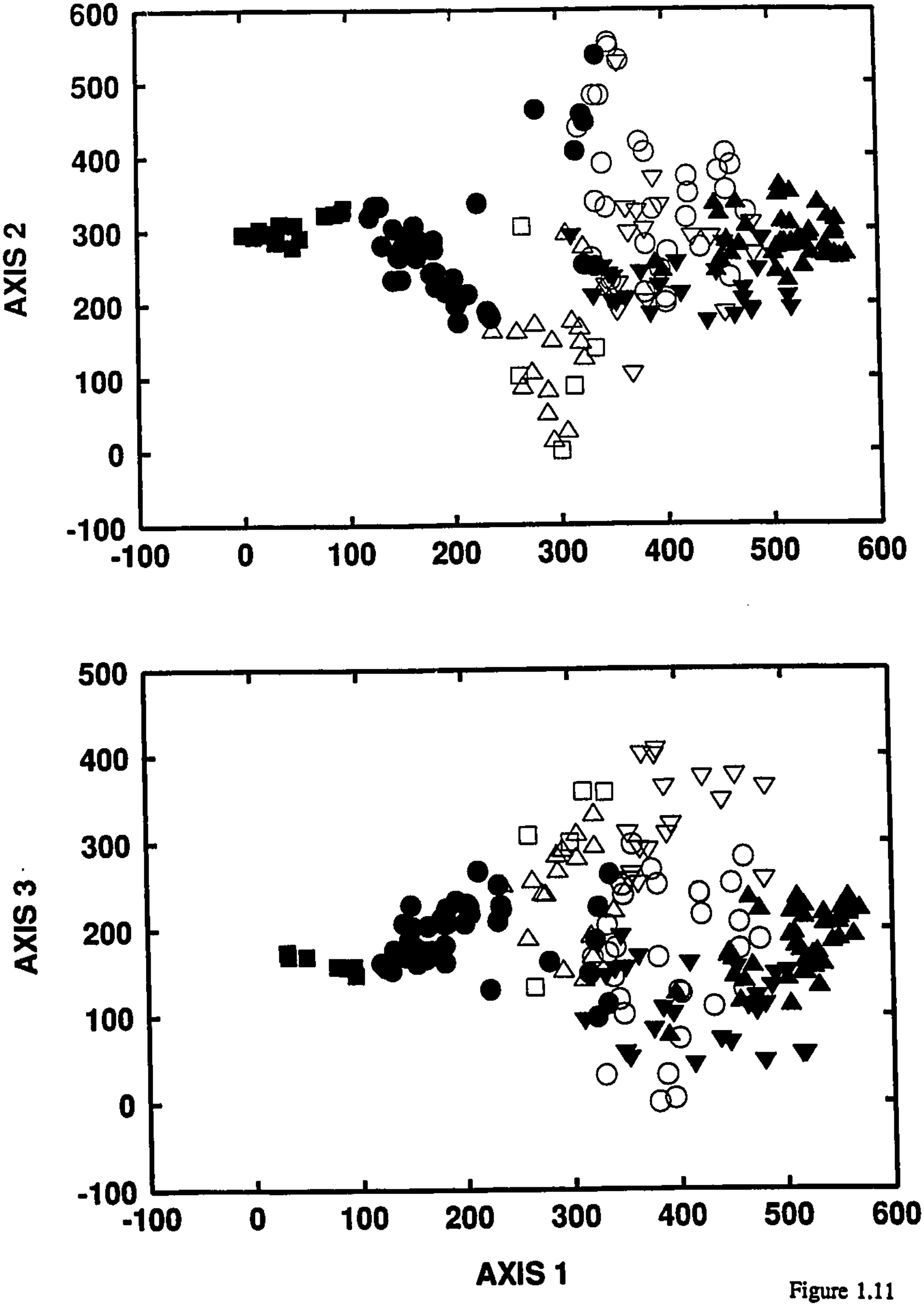

AXIS 2
600
500
400
300
200
100
0
-100
-100
0
100
200
300
400
500
600
AXIS 3
500
400
300
200
100
0
-100
-100
0
100
200
300
400
500
600
AXIS 1

Figure 1.11

Figure 1.12.

The relationships among measured variables. Plotted points are mean values for these variables in each vegetation type within Burnt Lands (Table 1.2) and among alvars (Table 1.4). (a) Biomass increased linearly with soil depth at both within and among alvar scales (within Burnt Lands: $r^2 = 0.96$, $P<0.001$, $y = -0.4 + 3.1x$; among alvar sites: $r^2 = 0.86$; $P<0.001$, $y = -8.0 + 7.2x$). (b) Species richness was curvilinearly related to biomass within Burnt Lands ($r^2=0.88$, $P<0.05$, $y = 0.2 + 0.9x - 0.02x^2$) but the relationship was not significant among sites ($r^2 = 0.40$, $P>0.05$).

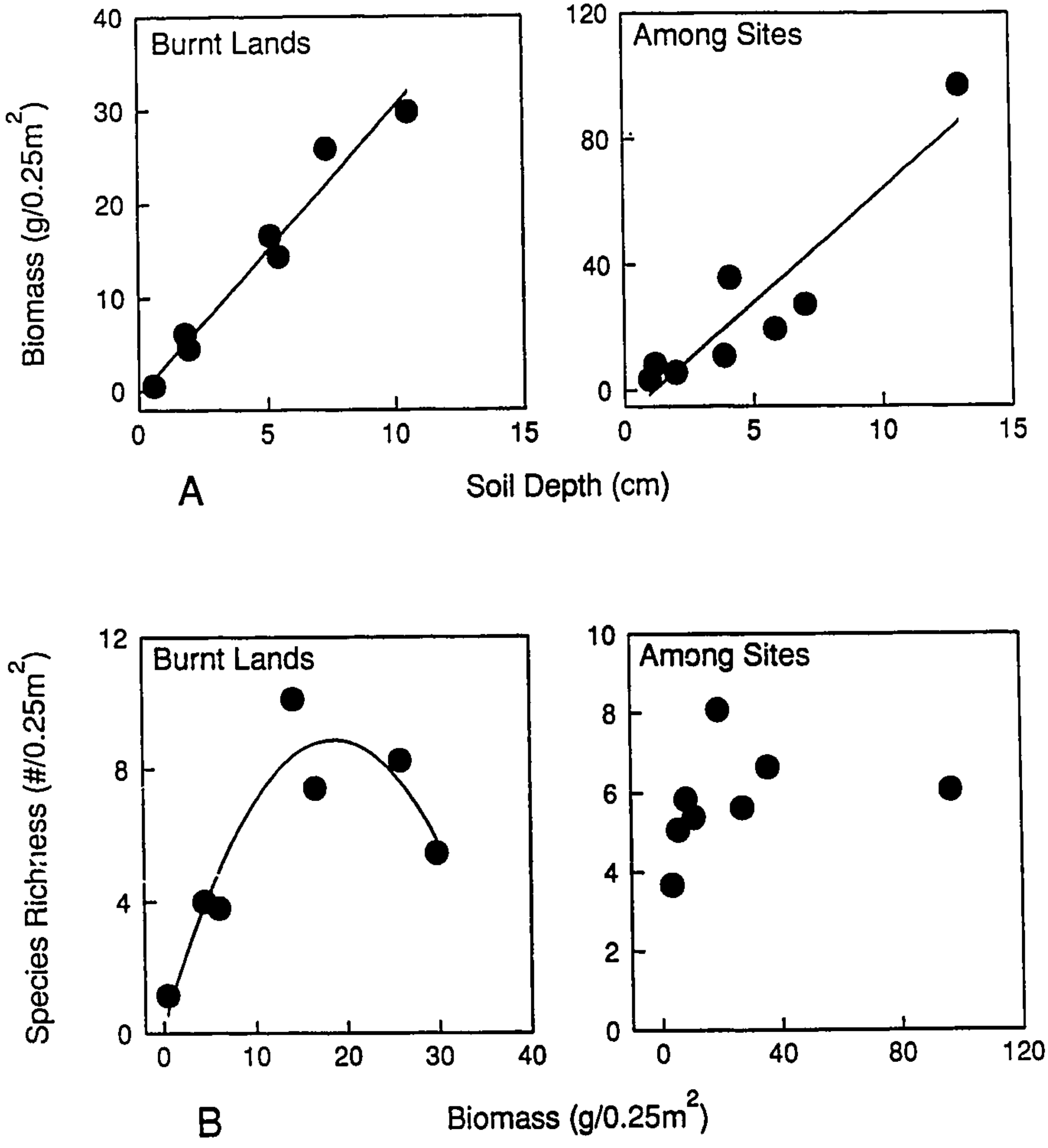

Burnt Lands
Among Sites
Biomass (g/0.25m^2)
40
30
20
10
0
120
80
40
0
0
5
10
15
Soil Depth (cm)
A
Burnt Lands
Among Sites
Species Richness (#/0.25m^2)
12
8
4
0
10
8
6
4
2
0
0
10
20
30
40
0
40
80
120
Biomass (g/0.25m^2)
B

Figure 1.12

Chapter 2

Species Richness Patterns in Alvar Vegetation

Introduction

An important goal of plant ecology is the ability to make predictions about natural systems. This involves moving from specific to more general variables of study and examining the empirical relationships between these state variables (Rigler 1982; Keddy 1987). The description of alvar vegetation presented in chapter 1 focused on species composition; the species was the unit of interest. However, results also showed that species richness is related to more general state variables such as biomass, soil depth and species richness. There was also evidence for functional relationships between these variables at the among-habitat scale (see Fig. 1.12).

One important generalization in plant ecology relates species richness to biomass, stress and disturbance and predicts an increase and subsequent decrease in species richness along gradients of these variables (Grime 1973, 1979; Connell 1978; Huston 1979; Tilman 1982). Empirical evidence for this pattern abounds. Species richness peaks at intermediate biomass levels in mesic and dry grasslands (Grime 1973, Al-Mufti *et al.* 1977; Willems 1980; Puerto *et al.* 1990), in wet grasslands and fens (Vermeer and Berendse 1983; Wheeler and Giller 1983), and in wetlands (Day *et al.* 1988; Wilson and Keddy 1988; Moore *et al.* 1989; Wisheu and Keddy 1989). These studies verify the model over a variety of biomass levels and biomass ranges, although there are differences in the biomass range where richness is greatest (Wisheu and Keddy 1989). Moore and Keddy (1989) also demonstrate limits to the scale at which this model applies; the predicted pattern occurred at the among-habitat scale but not within wetland habitats. The pattern has not been demonstrated in a vary low biomass, terrestrial system such as the alvar (although chapter one does provide evidence for this pattern, at least within the Burnt Lands site (Fig. 1.12b).

Biomass is the state variable generally used to examine and predict species richness patterns. However biomass gradients are in themselves a product of other gradients such as resource availability. In areas with shallow soil, soil depth should be strongly, positively correlated with all below ground resources (water, nutrients and support) and in addition is an easily measured factor. The strong gradients of biomass and soil depth characteristic of alvars make this is a useful system for exploring the relationships among richness, biomass and soil depth.

The main objective of my study was to explore and compare the relationships among soil depth, biomass and species richness. The second objective was to look for empirical evidence of the predicted species richness pattern in another habitat (this low biomass, terrestrial system), and across a number of sites. I therefore examine the relationship between species richness and biomass, and test the hypothesis that species richness increases and then decreases along a gradient of increasing biomass.

Methods

Study Sites

Four alvars in Ontario were sampled, as in chapter 1 (see Fig. 1.1). Burnt Lands alvar in Eastern Ontario (45°15'N, 76°05'E) is a large and relatively undisturbed alvar with extensive ares of open rock flats and grassy meadows. Stone Road alvar is on Pelee island in Lake Erie (41°45'N, 82°39'E). Here herbaceous alvar vegetation occurred in small openings within the mainly wooded area. La Cloche alvar is a large alvar on Grand La Cloche island in Lake Huron (45°49'N, 81°44'E). This site had been grazed by cattle to varying degrees. Misery Bay alvar on Manitoulin island (45°49'N, 82°44'E) has expansive areas of open rock flats. This site differs from the others in that the limestone is dolomite (Morton 1984), a harder limestone which does not erode into the shale-covered surface of the other sites. Here the vegetation is more rigidly restricted to cracks in the surface. The vegetation of these sites was described in detail in Chapter 1.

Field Sampling

Sampling of the herbaceous alvar vegetation occurred in the fall of 1988 (Burnt Lands) and the fall of 1989 (Stone Road, La Cloche and Misery Bay). (Refer to Appendix 1.1 for specific sampling dates and locations.) In order to ensure even sampling across the biomass gradient, vegetation was subjectively classified into 5 classes ranging from the scant vegetation cover where limestone rock is at the surface to the dense cover of the grassy meadows. In each of the 5 biomass classes, an approximately equal number of quadrats were randomly located for total sample sizes of 99 quadrats at Burnt Lands, 51 at Stone Road 50 at La Cloche and 50 at Misery Bay.

Species richness was determined as the number of species occurring in a 0.25 m^2 (0.5 X 0.5 m) quadrat. Vegetation and litter within the 0.25 m^2 quadrat were collected, dried at

70° C, and weighed. Mean soil depth was measured by inserting a 4 mm diameter pin at the 4 corners and the centre of the quadrat.

Raw data for each of the three measured variables is in Appendix 1.4.

Analysis

I compared the four alvar sites based on mean levels of the three measured variables (biomass, soil depth and species richness). For each variable, the null hypothesis of equal mean levels was tested using Scheffe's multiple comparison test.

I examined the relationship between biomass and soil depth among alvars (data from all four sites combined) and at each site. Linear regression (least squares technique; Sokal and Rohlf 1981) was used to test the null hypothesis of no functional relationship between these variables. The biomass - soil depth relationship was compared among sites using Dummy Variables (Kleinbaum *et al.* 1988). For each pairwise comparison of sites (6 comparisons in all), I tested the null hypotheses of equal intercepts and equal slopes, using analysis of variance.

The relationships between species richness and biomass, and between species richness, at each site, were explored using two methods. First the data were fitted using a scatterplot smoothing technique in order to determine the general form of the functional relationship (du Toit *et al.* 1986). Scatterplot smoothing was conducted using LOWESS, a robust, locally-weighted regression technique (Wilkinson 1990). LOWESS shows the overall trends in data sets without *a priori* specification of a mathematical model (Cleveland 1979). The 'smoothness' of the final LOWESS curve is determined by the tension value (f) (Cleveland 1979). I used f = 0.5 (ie. successive iterations included 50% of the data); the overall shape was little affected by increasing or decreasing f. Second, the mathematical function that best describes the data was identified in order to determine the predictive relationship between variables, using TableCurve (Brown 1990). The TableCurve program automatically tests the fit of up to 3320 mathematical functions to the data using regression (least squares) techniques (ie. tests the null hypothesis of no relationship between variables based on each function). Equations having the highest r^2 were selected, except where there were simpler models with only slightly lower r^2. When, for a given data set, the LOWESS curve was similar in shape to the regression curve, I assumed that the regression equation adequately described the true relationship.

I compared the relationship between species richness and biomass, or between species richness and soil depth at the different sites. When the relationship was described by the same functional form at more than one site, I compared the specific shapes of these curves using dummy variables (Kleinbaum *et al.* 1988). That is, the null hypotheses of equal intercepts and equal slopes were tested using analysis of variance.

Results

State Variables

The four alvar sites had similar biomass, soil depth and species richness (Table 2.1;

comparisons of means using Scheffe's multiple comparison test). Mean biomass was highest at Stone Road ($P<0.05$). At Misery Bay the biomass included a range much greater than at Burnt Lands or La Cloche, but the average biomass was similar at these three sites (Table 2.1). Based on mean soil depth, sites ranked from shallowest to deepest were as follows: Misery Bay, La Cloche, Burnt Lands and Stones Road (see Table 2.1 for significant differences). Mean species richness was similar at all sites ($P<0.05$).

The Biomass - Soil Depth Relationship

Biomass increased with soil depth at all four sites as shown by linear regression (Figs. 2.1 and 2.2). There was a weak positive relationship between these variables among sites ($r^2 = 0.66$, $P<<0.001$; Fig. 2.1). Within sites, the biomass - soil depth correlations appeared to be stronger at Burnt Lands and Stone Road alvars ($r^2 = 0.75$ and 0.81) than at La Cloche and Misery Bay ($r^2 = 0.48$ and 0.60, all $P<<0.001$; Fig. 2.2). The relationship between biomass and soil depth was described by the same linear equation at La Cloche and Misery Bay alvars (ie. there was no significant difference between equation parameters a and b; ANOVA; Table 2.2). However, equations were significantly different at the other sites (equation parameters a and/or b were significantly different; $P< 0.05$; ANOVA; Table 2.2). Biomass increased more sharply with increasing soil depth at Stone Road than at La Cloche or Misery Bay; the slope of the relationship at Burnt Lands was intermediate (Table 2.2).

Species Richness, Biomass and Soil Depth

Species richness varied with biomass in a non-monotonic fashion (Fig. 2.3). In three of the sites (Burnt Lands, Stone Road and La Cloche), the relationship was best described by a quadratic equation (regression; $P<0.05$; Table 2.3), although the exact shape of this relationship varied between sites as indicated by the intercepts and slopes (parameters a and b) of the equations (Table 2.3). The intercept was lower at Burnt Lands; slopes were different at each site (ANOVA; $P<0.05$). At the fourth site, Misery Bay, species richness and biomass were related by a more complex, log-normal relationship, (best-fitting curve; $r^2 = 0.44$, $P<0.001$). This indicates a species richness pattern very different from the other sites. (Note that this relationship remained even if the 5 high-biomass samples were removed.)

Species richness also varied non-monotonically with soil depth (Fig. 2.4). At Burnt Lands and Stone Road, the relationship between species richness and soil depth was best described by a quadratic relationship ($r^2 \leq 0.31$, $P<0.001$; Table 2.4); equation parameters a and b were not significantly different between sites (ANOVA; $P<0.05$). At both La Cloche and Misery Bay, more complex equations provided the best fit. The relationships were explained by a log-normal equation at La Cloche ($r^2 = 0.18$, $P<0.001$) and a Gaussian equation at Misery Bay ($r^2 = 0.27$, $P<0.001$). At Burnt Lands, Stone Road and La Cloche these relationships between species richness and soil depth were slightly stronger than between species richness and biomass, but at Misery Bay the opposite was true (cf. r^2, Tables 2.3 and 2.4).

Tables 2.3 and 2.4 also include the results of the data-smoothing procedure

(LOWESS). In all cases, LOWESS produced curves similar in shape and fit to the regression curves (Figs. 2.3 and 2.4) suggesting that each regression equation did indeed describe the relationship between species richness and biomass or soil depth. However, at high biomass or deep soil locations, the LOWESS curves indicated only a slight decline in species richness, contrary to the sharp decline indicated by the more symmetric quadratic equations (Figs. 2.3 and 2.4).

Discussion

State Variables

The three state variables (biomass, soil depth and species richness; Table 2.1) demonstrated important similarities among the four sites. All sites had the same average species richness suggesting similar plant diversity in the herbaceous vegetation of each alvar. Based on soil depth and biomass levels, Misery Bay and La Cloche (the northern sites) were similar. Stone Road (the southern site) was distinct, having deeper soil and higher biomass than the northern sites. Burnt Lands (the eastern site) had affinities with both northern and southern sites. This agrees with geographic affinities, among alvars, based on species composition (as shown in chapter 1).

I next examine the relationship between these variables to allow comparisons of sites based on ecological patterns.

Biomass and Soil Depth

The linear relationship between biomass and soil depth, within sites and when all sites were combined (Figs. 2.1 and 2.2) suggests that this soil depth / biomass gradient is characteristic of alvars in general. The ecological importance of this gradient was shown in chapter 1; species composition varied along the soil depth / biomass gradient. Soil depth may be a measure of resource availability; the amount of nutrients, moisture, and physical space available should be proportional to the cube of the soil depth (Ross and Harper 1972; McConnaughay and Bazzaz 1991). In rock outcrop, soil moisture increases with soil depth (Sharitz and McCormick 1973) and shallow soil sites have a high stress index (Lugo and McCormick 1981). In the alvars, biomass was probably limited by environmental stress in shallow soil sites.

The biomass - soil depth relationship was stronger at Burnt Lands and Stone Road than at the other two sites (Table 2.2). Since vegetation at La Cloche was grazed, the variation in biomass may have been partly attributable to variation in grazing intensity or in the time since grazing. The slightly weak relationship at Misery Bay may be due to limitations in the sampling method. At this site vegetation was restricted to cracks in the hard limestone. For the sake of consistent sampling, soil depth was measured in the corners of quadrats that extended beyond the crack and beyond where the vegetation was rooted. Therefore the true mean soil depth in the crevice was underestimated.

At Stone Road biomass increased more rapidly with increasing soil depth than at the other sites (Table 2.2). Perhaps the soil at this site is more fertile or has better water-holding capacity so that it can support more biomass per unit soil depth. This site also has the longest growing season of the four sites, since it occurs at the lowest latitude. *Andropogon gerardii*, a grass of the fertile tall-grass prairie system, grows at this alvar only.

The general correlation between biomass and soil depth suggests that the easily measured variable of soil depth may be used to predict biomass levels in alvar vegetation.

Species Richness

At each of the four alvar sites species richness showed a curvilinear relationship to biomass; species richness increased with biomass to a maximum of 12 to 14 species per unit area and then levelled off or decreased at higher biomass levels (Fig. 2.3). This conforms to Grime's (1973, 1979) 'hump-backed' model which predicts minimum species richness, due to environmental stress, at low biomass sites and maximum species richness at intermediate biomass levels. The model also predicts a decline in species richness at high biomass levels. Comparison of this upper end of each alvar biomass gradient reveals the main difference between sites.

At three of the sites (Burnt Lands, Stone Road and La Cloche) species richness changed gradually with biomass, and decreased only slightly at higher biomass levels (as indicated by LOWESS) (Fig. 2.3). The sharp decline in species richness predicted by species richness models (e.g., Grime 1973; 1979) apparently did not occur within the biomass range examined. Similarly, along a biomass gradient in a low productivity lakeshore community, species richness did not decline at maximum biomass levels (Wisheu and Keddy 1989).

Theory (e.g., Grime 1973; 1979) predicts that species richness should be limited by light competition at high biomass levels. In alvars, light competition may not be intense enough to limit species richness, even at maximum biomass levels. Indeed, as chapter 3 shows, plant competition at the Burnt Lands alvar was primarily for below-ground resources. Root competition could also act to limit species richness where biomass is greatest. However, the deeper soil corresponding to high biomass locations should have more available soil resources and therefore be capable of supporting more species, not fewer.

At Misery Bay, in contrast to the above 3 sites, species richness increased sharply to maximum levels within a 10 g/0.25 m^2 range at the lowest end of the biomass gradient, and then sharply decreased (Fig. 2.3). This shape more closely resembles Grime's model (1973, 1979). At this site vegetation is restricted to cracks in the limestone pavement. This crowding of vegetation into a narrow band may increase competition intensity (*sensu* Keddy 1989) relative to sites where vegetation is sparsely distributed over the limestone surface. It is possible that competition is producing the sharp decline in species richness, as theory predicts.

Less dramatic differences between the alvars were also apparent. Even among the three more similar sites (Burnt Lands, Stone Road and La Cloche), equations describing the species richness - biomass relationship were unique to each site (based on slopes and parameters; Table 2.3). As a result, predictions regarding minimum species richness and the biomass level associated with maximum richness vary from site to site. Table 2.5 shows that species richness peaks at biomass levels ranging from 10 g/0.25 m^2 (Misery Bay) to approximately 80 g/0.25 m^2 (Stone Road).

Soil Depth as the Predictor Variable

The similarities between the species richness - soil depth and species richness - biomass relationships indicate that soil depth may be a useful predictor variable for species richness pattern. As a predictor variable, soil depth was slightly better than biomass at Burnt Lands and Stone Road while at Misery Bay, the converse was true (*cf.* r^2, Tables 2.3 and 2.4). At La Cloche, the patterns of species richness were explained by different types of equations with soil depth and biomass as predictor variables. Although soil depth was a slightly better predictor, neither it nor biomass explained more than 18% or the variation in species richness (Tables 2.3 and 2.4). At this site (La Cloche), species richness may be controlled by non-resource levels factors, such as grazing. Soil depth was a better predictor of species richness where biomass and soil depth were most closely correlated (ie. Burnt Lands and Stone Road; Table 2.2).

Relationship to Other Work

The mechanism producing the species richness pattern common to natural systems (see reviews: Connell 1978; Huston 1979, 1985) is so far unknown. However, my results support the idea that species richness is limited by both environmental stress and competition (Grime 1973, 1979). Bare rock sets an obvious lower limit to richness, and species richness increased with resource availability (soil depth). At Misery Bay, as discussed earlier, light competition may have limited species richness where biomass levels were higher. But at the other 3 sites, where light competition is likely unimportant (Chapter 3), the decline in species richness was not evident. Future work could explore this apparent variation in the importance of competition (ie. relative to other factors; see Weldon and Slauson 1986) at the various sites.

The biomass level corresponding to maximum species richness varied between my sites from 40 g/m^2 at Misery Bay to 320 g/m^2 at Stone Road (or 10 - 80 g/ 0.25 m^2; Table 2.5). The model originally predicted species richness to be greatest within a biomass range of 350 - 750 g/m^2 (Al-Mufti *et al.* 1977; Grime 1979). Wisheu and Keddy (1989) show that the biomass corresponding to maximum species richness varies greatly between studies and systems (from 60 - 1500 g/m^2 in previously published studies).

The r^2 values corresponding to the alvar species richness - biomass relationships (Table 2.3) are relatively low indicating that biomass accounts for only part (less than 45%) of the variation in species richness. Exploration of the residuals may reveal other important patterns. Wisheu and Keddy (1989) suggest the inclusion of plant traits to improve the species richness model. Species richness in marsh vegetation can be better predicted by including an added term for the 'proportion of perennials' along with biomass (Shipley *et al.* 1991). In the alvar, phenology may play an important role in determining species richness. Al-Mufti *et al.* (1977) found that shoot phenology accounts for seasonal variation in biomass of chalk grasslands. My sampling may have missed certain sets (phenologies) of alvar species and could therefore detect only the species richness - biomass pattern of late summer. Future work in alvar vegetation could incorporate seasonal variation in species richness (phenology), plant traits (Wisheu and Keddy 1989; Shipley *et al.* 1991), and should further explore pattern at the upper end of the biomass gradient.

My findings increase the generality of the species richness model by extending it to a low biomass terrestrial grassland system in Canada. Few studies have compared, quantitatively, species richness patterns in this manner. Wisheu and Keddy (1989) found that richness pattern along lakeshores varies within a single lake. My results showed drastic variation in pattern among alvars. This variation among alvar sites suggests that the model needs more refining before it will be able to achieve more than coarse scale predictions.

Table 2.1.

Biomass, soil depth and species richness at each of the 4 study sites. Data are mean ± St. Dev. (range in parentheses). Means sharing the same letter are not statistically different (Scheffe's multiple comparison test, $P \leq 0.05$).

		State Variable		
Site	n	Biomass ($g/0.25m^2$)	Soil Depth (cm)	Species Richness ($\#/0.25m^2$)
Burnt Lands	99	16.8^{a} ± 12.7 (0-49.9)	5.6^{bc} ± 4.3 (0.1-17.9	6.3^{a} ± 3.2 (0-14)
Stone Road	51	58.3^{b} ± 40.0 (0.1-154.2)	7.2^{c} ± 4.8 (0.2-16.2)	6.3^{a} ± 2.2 (1-12)
La Cloche	50	17.3^{a} ± 12.2 (1.5-43.7)	4.6^{ab} ± 3.7 (0.5-24.4)	5.8^{a} ± 2.1 (3-12)
Misery Bay	50	14.6^{a} ± 17.3 (0.5-92.5)	3.5^{a} ± 3.3 (0.1-15.1)	5.6^{a} ± 2.8 (1-12)

Table 2.2.

Biomass is linearly related to soil depth both among and within the 4 alvar sites ($P<<0.001$). Shown are the r^2 values and the parameters for the relationship: $\ln(y+1) = a + b\ln(x+1)$ (y = biomass, x = soil depth, a = intercept and b = slope; slopes and intercepts sharing the same letter are not significantly different (ANOVA; $P<0.05$)).

Site	a	b	n	r^2	F
Burnt Lands	0.59^{a}	1.17^{ab}	99	0.75	291.05
Stone Road	1.22^{c}	1.34^{b}	50	0.81	209.96
La Cloche	1.08^{b}	1.00^{a}	49	0.48	43.41
Misery Bay	1.15^{b}	0.94^{a}	50	0.60	71.05
All Sites Combined	0.84	1.20	248	0.66	470.13

Table 2.3.

Species richness - biomass relationship: equations, parameters (a to e) and statistics describing the relationship at the 4 study sites (regression; * $P<0.05$, *** $P<0.001$). For equations of the same form, intercept (parameter a) and slope (parameter b) sharing the same letter are not significantly different (ANOVA; $P<0.05$). Also shown is the r^2 of LOWESS fits to the same data.

	Regression									LOWESS
Site	Equation	a	b	c	d	e	n	r^2	F	r^2
Burnt Lands	$y=a+bx+cx^2$	3.11^a	0.39^a	-0.01	-	-	99	0.253	16.3^{***}	0.428
Stone Road	$y=a+bx+cx^2$	4.12^b	0.08^b	-0.001	-	-	51	0.267	8.74^{***}	0.314
La Cloche	$y=a+bx+cx^2$	4.09^b	0.23^a	-0.01	-	-	50	0.125	3.35^{*}	0.133
Misery Bay	$y=(a+bf_1(x))^2$	1.76	1.14	-	9.40	0.59	50	0.438	37.34^{***}	0.433

$f_1(x) = \mathrm{Exp}(-1*\ln(x/d)^2/2e^2)$

Table 2.4.

Species richness - soil depth relationship: equations, parameters (a to e) and statistics describing the relationship at the 4 study sites (regression; *** $P<0.001$). For equations of the same form, intercept (parameter a) and slope (parameter b) sharing the same letter are not significantly different (ANOVA; $P<0.05$). Also shown is the r^2 of LOWESS fits to the same data.

	Regression									LOWESS
Site	Equation	a	b	c	d	e	n	r^2	F	r^2
Burnt Lands	$y=a+bx+cx^2$	2.68^a	1.31^a	-0.07			99	0.311	21.67^{***}	0.399
Stone Road	$y=a+bx+cx^2$	3.70^a	0.97^a	-0.06			50	0.295	9.83^{***}	0.304
La Cloche	$y=a+bf_1(x)$	5.04	2.36	-	3.90	0.24	49	0.182	10.43^{***}	0.281
Misery Bay	$y=a+bf_2(x)$	4.51	4.48	-	-3.40	1.08	50	0.274	18.12^{***}	0.206

$f_1(x) = Exp(-1*\ln(x/d)^2/2c^2)$
$f_2(x) = Exp(-1(x-d)^2/2c^2)$

Table 2.5.

Levels of biomass and soil depth predicted to occur at maximum species richness.

	Predicted level at maximum species richness	
Site	Biomass (g/0.25m^2)	Soil Depth (cm)
Burnt Lands	35	3
Stone Road	80	9
La Cloche	25	4
Misery Bay	10	4

Figure 2.1.

The relationship between above-ground biomass and soil depth in alvar vegetation, at the 4 sites combined, was described by the equation $\ln(y+1) = a + b\ln(x+1)$ ($r^2=0.66$, $P<0.001$; Table 2.2). (Plot of relationship on transformed scale is given in Appendix 2.1a.)

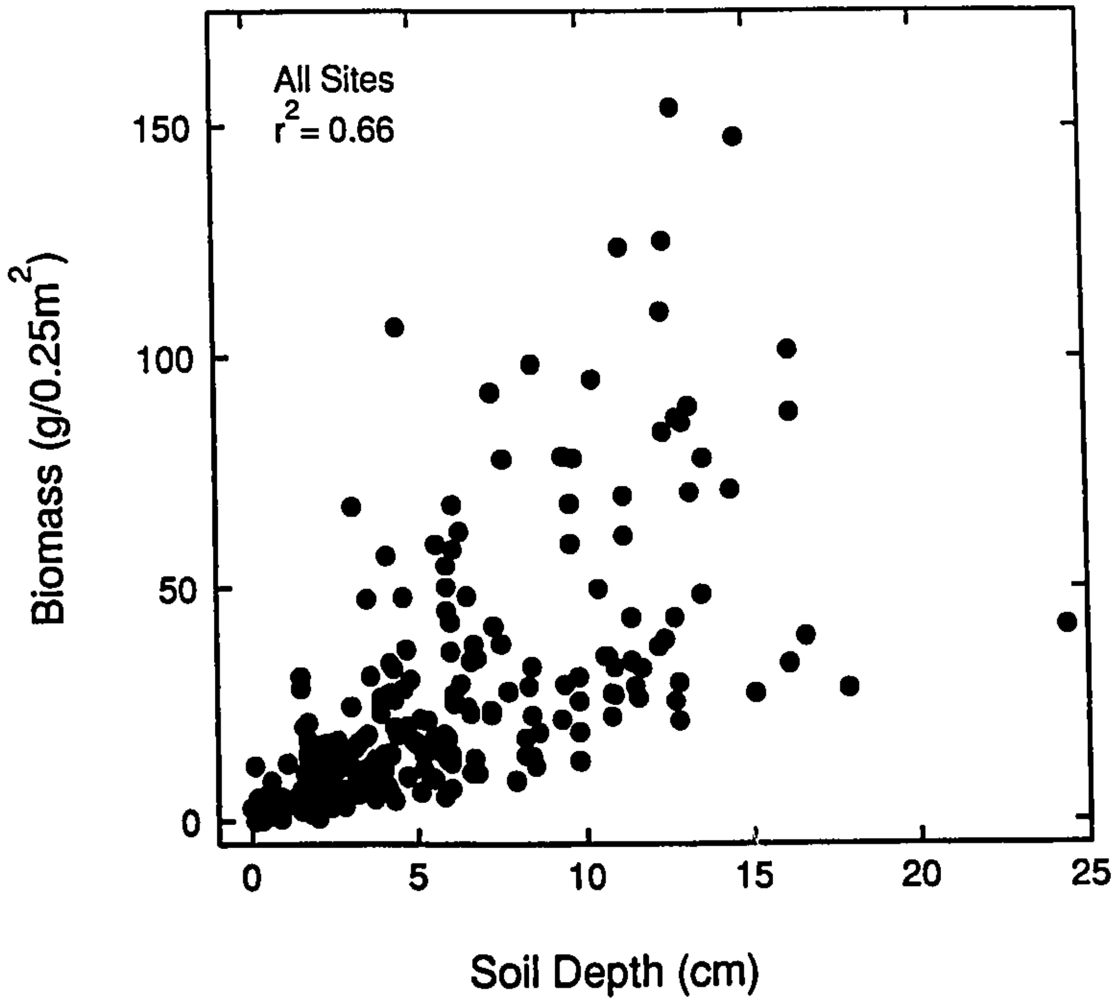
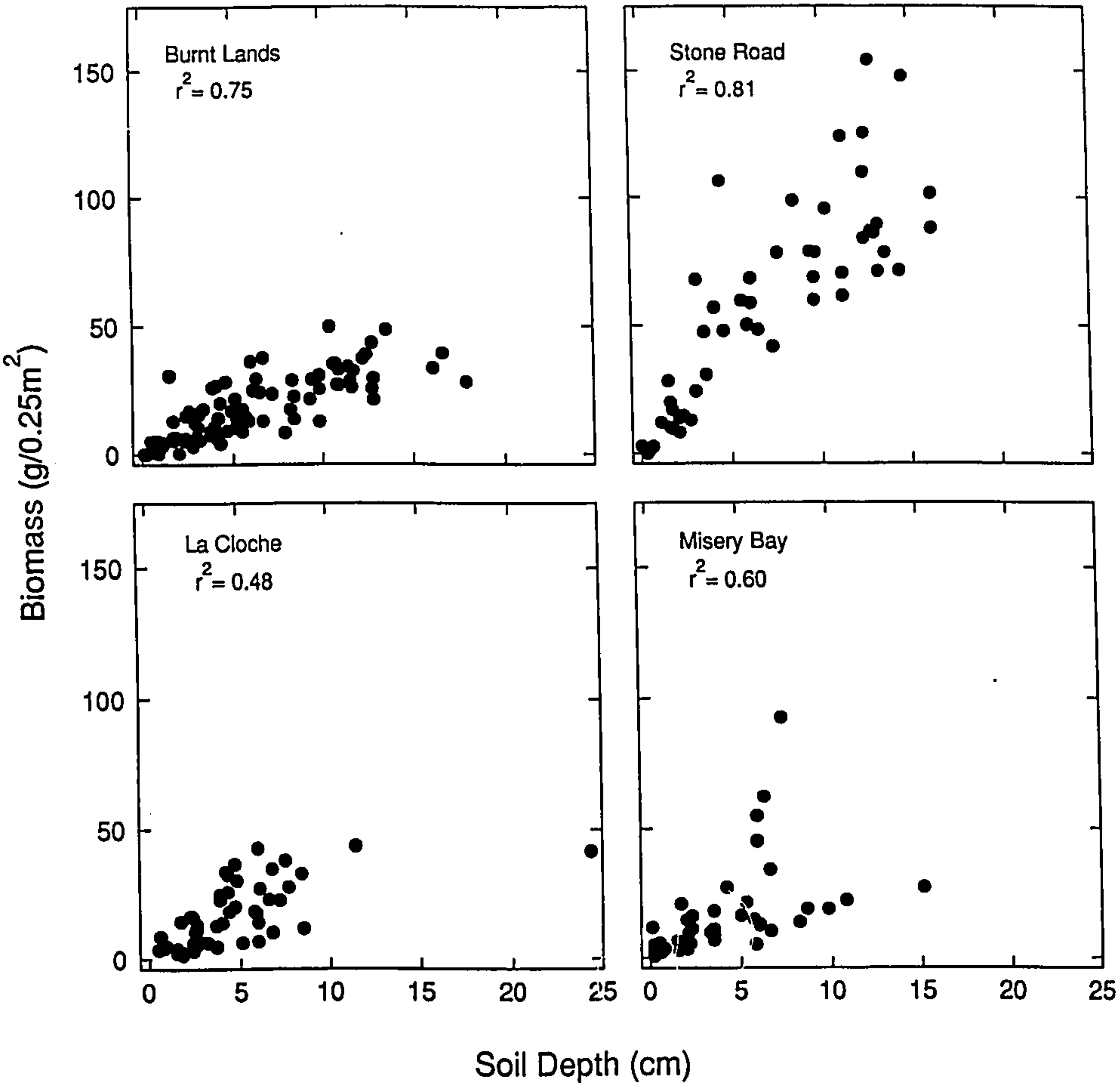

All Sites
$r^2 = 0.66$
Biomass (g/0.25m^2)
0
50
100
150
0
5
10
15
20
25
Soil Depth (cm)

Figure 2.1

Figure 2.2.

The relationship between above-ground biomass and soil depth at each of the four sampled sites was described by the equation $\ln(y+1) = a + b\ln(x+1)$; r^2 values are shown on each plot ($P<0.001$). The equation parameters are given in Table 2.2. (Plot of relationship on transformed scale is given in Appendix 2.1b.)



Burnt Lands
$r^2 = 0.75$
Stone Road
$r^2 = 0.81$
La Cloche
$r^2 = 0.48$
Misery Bay
$r^2 = 0.60$
Biomass (g/0.25m²)
0
50
100
150
0
5
10
15
20
25
Soil Depth (cm)

Figure 2.2

Figure 2.3.

The relationship between species richness and biomass at each of the four sampled alvars. Solid lines represent regression functions; r^2 values are shown on each plot ($P<0.001$; Table 2.3). The equations are second-order polynomials except at Misery Bay, where a log-normal relationship is drawn (equations are in Table 2.3). Dotted lines represent lines fit by LOWESS (the scatterplot smoothing procedure); r^2 are shown in Table 2.3. Note that the x-axis range differs between the left and right sides of the figure.

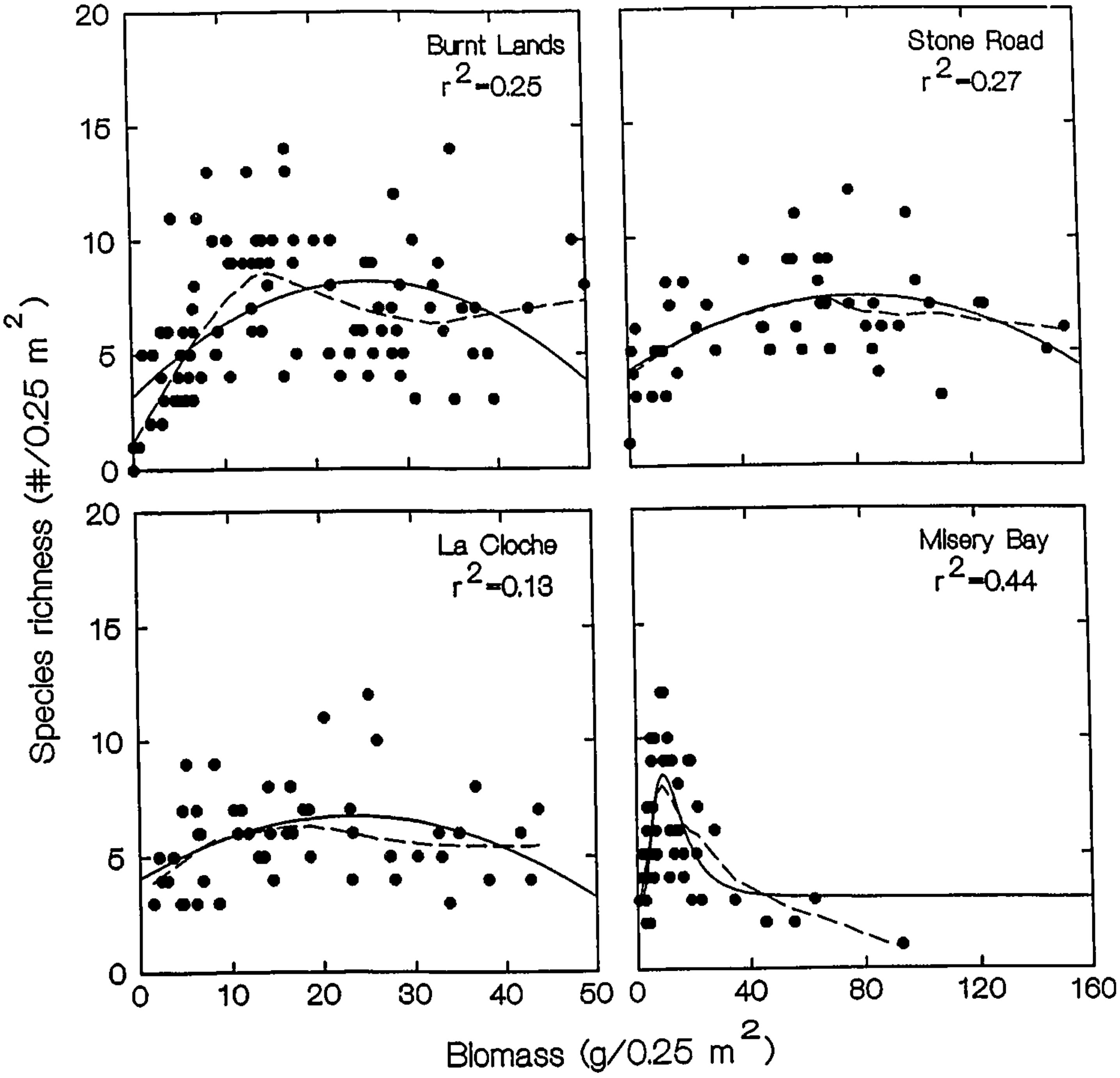
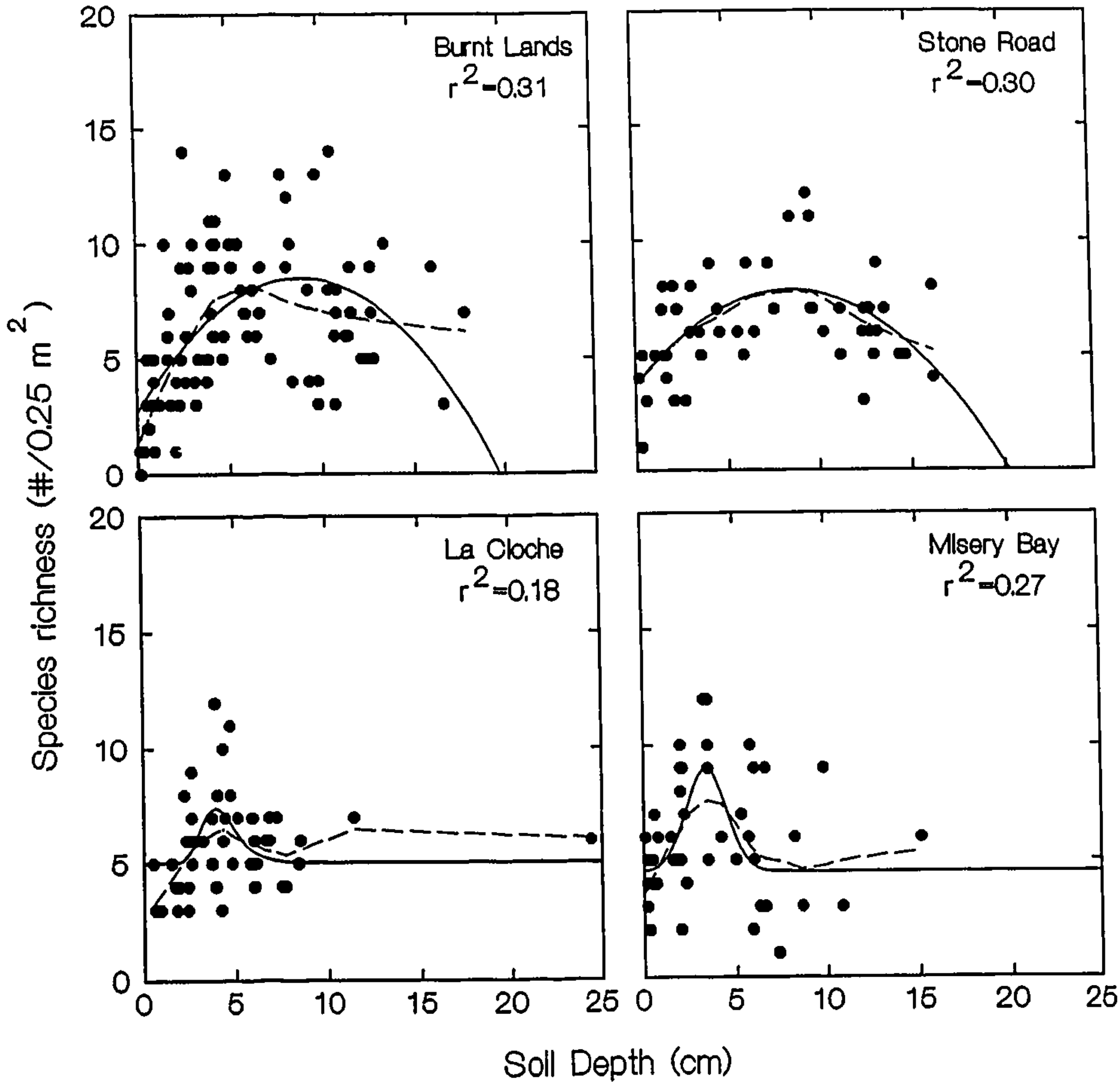

Burnt Lands
r^2=0.25
Stone Road
r^2=0.27
La Cloche
r^2=0.13
Misery Bay
r^2=0.44
Species richness (#/0.25 m^2)
Biomass (g/0.25 m^2)
0
5
10
15
20
0
10
20
30
40
50
0
40
80
120
160

Figure 2.3

Figure 2.4

The relationship between species richness and soil depth at each of the four sampled alvars. Solid lines represent regression functions; r^2 values are shown on each plot ($P<0.001$; Table 2.4). The lines are second-order polynomials at Burnt Lands and Stone Road, a log-normal relationship at La Cloche and a Gaussian relationship at Misery Bay (equations are in Table 2.4). Dotted lines represent lines fit by LOWESS (the scatterplot smoothing procedure); r^2 are shown in Table 2.4. Note that the x-axis range differs between the left and right sides of the figure.



Burnt Lands
$r^2=0.31$
Stone Road
$r^2=0.30$
La Cloche
$r^2=0.18$
Misery Bay
$r^2=0.27$
Species richness (#/0.25 m^2)
Soil Depth (cm)
0
5
10
15
20
25

Figure 2.4

Chapter 3

The Intensity of Root and Shoot Competition Along a Soil Depth Gradient

Introduction

The process of competition is one which has received much attention in the plant ecology literature (e.g., Tilman 1982; Keddy 1989; Grace and Tilman 1989). Competition is one of the processes involved in shaping the species richness pattern studied in chapter 2 (e.g., Grime 1973; 1979; Tilman 1982). Most studies of competition in plant communities have focused on pairwise interactions among a few species (e.g., Sharitz and McCormick 1973; Fowler 1982; Wilson and Keddy 1986a). Environmental gradients are a powerful tool for studying the relationship between competition and environmental factors (Keddy 1989). However, the variation in competition intensity (ie. competition involving all interacting species) has been examined in only a few systems and then with apparently contradictory results. For example, in wetlands, competition intensity increases along a gradient of increasing plant biomass and nutrient availability (Wilson and Keddy 1986a). Similarly, Reader and Best (1989) found that competition intensity increases with soil fertility and plant biomass in an abandoned pasture. However, the importance of competition does not vary predictably with biomass and nutrients in mixed-grass prairie (Wilson and Shay 1990). One difference among these systems is the amount of aboveground biomass. There have been few studies of plant competition at sites with very low biomass. In fact, competition is expected to be less important on nutrient poor soils (Grime 1979).

Competition intensity has two major components: aboveground and belowground (Donald 1958; Wilson 1988). The variation in root and shoot competition along environmental gradients is a topic of much dispute and has produced two main schools of thought. One theory predicts an increase in both root and shoot competition along a gradient of increasing soil resources and the corresponding gradient of increasing plant biomass (Grime 1973, 1979). The opposing theory (Tilman 1985) predicts a trade-off for above- and belowground resources, an inverse relationship between root and shoot competition. Tilman's model therefore predicts that root competition should be most important where soil resources are limiting. Surprisingly, there have been few studies published which address this question by separating out the effects of root and shoot competition along an environmental gradient. One study which did, however, found that competition occurs belowground in low productivity sites and occurs both below- and aboveground in more productive sites in old-field vegetation (Wilson and Tilman 1991) .

In this chapter I adopt Keddy's (1989) definition of competition: " the negative effects which one organism has upon another by consuming, or controlling access to, a reseource that is limited in availability." I use a phytometer (*sensu* Clements and Goldsmith 1924), or plant indicator, to measure the intensity of competition exerted by neighbouring plants. I make the assumption that if competition intensity is high, neighbouring plants will reduce the phytometer's performance. Other studies have similarly used the performance of a test species to measure competition (e.g., Wilson and Keddy 1986b; Shipley 1987; Wilson and Shay 1990; Wilson and Tilman 1991).

Alvars were chosen as the experimental system because of the strong environmental gradients of soil depth and the corresponding resource gradients. The strong, positive relationship between biomass and soil depth shown in chapter 2 suggests that the gradient of increasing soil depth represents a gradient of increasing belowground resource availability.

Furthermore, as biomass increases, aboveground resource availability (ie. light) is expected to decrease.

The objectives of my study were (1) to test for the presence of competition in a low biomass (low productivity) system where competition is predicted to be relatively unimportant (Grime 1973, 1979), (2) to separate the effects of above- and belowground competition (on the phytometer) and (3) to examine the variation in competition intensity along an environmental gradient.

Methods

Study Site

This study was carried out in herbaceous vegetation at the Burnt Lands Alvar near Almonte, Ontario (45°15'N, 76°05'E). This site has large areas of open alvar outcrop and meadow; the species composition was described in chapter 1.

The Field Experiment

Competition intensity was measured by comparing the final biomass of transplant phytometers (*sensu* Clements and Goldsmith 1924) grown with neighbour roots and shoots, with neighbour roots only, and without neighbours. The annual *Trichostema brachiatum* (family Labiatae) was chosen as the phytometer species. It is a common alvar species which occurs naturally over the entire soil depth gradient included in the study. In the spring, numerous seedlings can be found where the turf has been disturbed. Phytometer seedlings at the four-leaf stage were transplanted from filed populations into the experimental plots.

Competition intensity was measured along the soil depth gradient; to ensure equivalent sampling intensity along the gradient, vegetation was subjectively classified (as in chapter 1) into 5 biomass levels ranging between the sparse vegetation cover on limestone outcrops through to grassy meadows dominated by *Sporobolus heterolepis*. Ten to 13 plots (56 plots in total) were established in each vegetation type. Fifty-six plots, 25 by 130 cm, were established in May 1989. (See Appendix 3.1 for more details on plot location.) Plots were divided into 4 subplots 25 by 25 cm square, separated by 10 cm buffer strips. One of the two end-plots was left to be harvested in the fall to measure biomass. The other three subplots were randomly assigned one of the three competition treatments (Appendix 3.2) and a single seedling was transplanted into the centre of each. The three treatments were:

(1) Neighbour roots and shoots present (NRS): the seedling was planted into intact vegetation.

(2) No neighbours (NN): vegetation in the subplot was removed with a contact herbicide, and the seedling was grown without neighbours. Round-up (1.5% solution, 1.5 l of solution per m^2) was sprayed in the 25 x 25 cm subplot on May 23, 1989. As recommended by the herbicide manufacturer, I allowed 10 days for the herbicide to decay in the soil before seedlings were transplanted into treatment plots.

(3) Neighbour roots (NR): a chicken-wire cone (2.5 cm mesh; cone hole diameters 2 cm (bottom) and 25 cm (top) by 13 cm tall) was placed, narrow end down, in the centre of

the subplot; above-ground vegetation was guided to the outside of the cone. The seedling was planted into the centre of the cone and therefore grown in the presence of neighbour roots and in the absence of neighbour shoots. Wire cones were also placed in the NN and NRS treatments to allow for artifact 'cone' effects. In the NN treatment the vegetation was allowed to grow up and through the chicken wire. Wire cones were held in place by securing the top rim to a wire frame (25 x 95 x 13 cm tall) which surrounded the three treatment subplots. Throughout the summer, cones were checked weekly and new plant shoots were guided to the appropriate side of the cone.

Trichostema brachiatum seedlings were transplanted from field populations into the centre of each subplot on June 1-2, 1989. To reduce post-transplant seedling mortality, a 50 x 120 cm piece of shade cloth (65% shade) surrounded each plot for the first 2 weeks. During the first two weeks seedlings were watered and replaced as needed (Appendix 3.3). The experiment was harvested on August 27 - 28, 1989. Transplants were cut off at ground level using scissors and placed in individual envelopes. Above-ground biomass was harvested from the subplot reserved for this. Soil depth was measured using a 4 mm diameter pin (at the 4 corners and the centre) in each biomass subplot. Plant material was dried to constant mass in a 60° C drying oven and weighed.

Competition Intensity Calculations

Final transplant biomass was used to calculate three components of competition intensity, total, root and shoot, at each site.

Total Competition Intensity

Total competition intensity (CI_T) = (P_{NN} - P_{NRS})/P_{NN}

where CI_T is a measure of total competition, P_{NN} is the dry weight of the phytometer in the no neighbours treatment and P_{NRS} is the dry weight of the phytometer in the neighbour roots and shoots treatment. The difference between the weights of the phytometers grown without neighbours and with neighbour roots and shoots is divided by the weight of the phytometer grown without neighbours to account for variation in environmental conditions (Wilson and Keddy 1986b).

Competition Intensity of Roots

Root competition intensity (CI_R) = (P_{NN} - P_{NR})/P_{NN}

where CI_R is a measure of root competition, P_{NN} and P_{NR} are the dry weights of the phytometers in the no neighbours and neighbour roots treatments, respectively. As above, the difference between the weight of phytometers grown without and with neighbour roots is divided by the weight of the phytometer grown without neighbours.

Competition Intensity of Shoots

Shoot competition intensity (CI_S) = (P_{NR} - P_{NRS})/P_{NN} = CI_T - CI_R

where CI_S is a measure of shoot competition.

CI values greater than 0 occur where neighbours have a negative effect on transplant performance, and CI values less than 0 occur where neighbours have a positive effect on phytometer performance, ie. the phytometer measures the effect of commensalism.

Analysis

Plant community biomass measured at each experimental location was plotted against soil depth in order to illustrate the range of these variables included in the experiment. (Biomass measured in 0.0625 m^2 sub-quadrats was expressed as g/m^2 to allow comparisons of biomass levels among similar studies.) I tested for a linear relationship between these variables, as demonstrated at the different alvar sites in chapter 2. As in chapter 2, linear regression was used to test the null hypothesis of no functional relationship between biomass and soil depth.

Parametric statistics are more powerful, and in the case of linear regression, provide an estimate of the variance accounted for. However, non-parametric statistics were used for the remainder of the tests since sample sizes were small and since the parametric assumption of homoscedasticity could not be satisfied. Since non-parametric statistics are conservative (ie. have a low probability of rejecting a true null hypothesis) significant results are important.

I compared phytometer survivorship in each treatment. The null hypothesis of equal survivorship was tested with Chi^2. I also asked whether, on average, survivorship differed between the two ends of the soil depth gradient. I ordered the sites based on soil depth and divided the samples in half. I then tested the null hypothesis that the mean number of phytometers surviving (in total and in each treatment) was equal in the lower and the upper sections of the soil depth gradient, using Wilcoxon 2-sample test.

To test for treatment effects on phytometer biomass, I tested the null hypothesis that mean, final biomass was equal among treatments. Wilcoxon 2-sample test was used for each pairwise comparison.

To test for the overall occurrence of total, root, and shoot competition, I tested the null hypothesis that mean competition intensity (CI_T, CI_R and CI_S) was equal to zero using Wilcoxon signed rank test. The intensities of the different competition components (ie. total, root and shoot) were compared by testing the null hypothesis of equal mean competition intensity (ie. $CI_T = CI_S$; $CI_T = CI_R$; $CI_R = CI_S$) using Wilcoxon 2-sample test. Finally, I tested for a relationship between competition intensity (total, root and shoot) and both soil depth and biomass. Spearman rank correlation coefficients were used to test the null hypothesis of no correlation.

Results

Habitat Description

Plant community biomass was positively correlated with soil depth ($r^2 = 0.65$, $P<<0.001$; Fig. 3.1). Experimental plots occurred in a soil depth range of 0 to 17 cm and a biomass range of 0 to 560 g/m^2 (see Appendix 3.4 for raw data).

Transplant Performance

Figure 3.2 shows that less than 60% of the transplants survived in each of the competition treatments; survivorship was not significantly different among treatments (Chi^2; $x^2 = 1.5$; $P > 0.05$). In all treatments, fewer transplants survived in sites located on the lower half of the soil depth/biomass gradient ($P < 0.001$; Wilcoxon 2-sample test). No transplants survived in sites with less than 1.3 cm deep soil or 21.8 g/m^2 biomass (Appendix 3.5).

Comparisons among treatments of final mean biomass of phytometers (using Wilcoxon 2-sample test) showed that biomass was significantly higher in the no neighbours treatment ($P < 0.001$), but was not significantly different in the neighbour roots and the neighbour roots and shoots treatments (Fig. 3.3). Thus, overall, phytometer performance was better when grown in the complete absence of neighbours, suggesting that competition may have limited growth in the other treatments.

Competition Intensity

Due to mortality, all three components of competition could not be calculated in all experimental sites and the sample size was reduced (CI_T: n=20; CI_R: n=17; CI_S: n=15). Some sites had negative CI values: CI_T ranged between -0.35 and -2.15 at 5/20 sites; CI_R ranged between -0.01 and -1.08 at 5/17 sites; CI_S ranged between -0.10 and -2.83 at 7/15 sites

(Appendix 3.5).

However, mean values for total competition intensity and root competition intensity were significantly greater than zero ($P<0.05$; Wilcoxon signed rank test) but mean shoot competition intensity was not (Fig. 3.4). That is, there was a measurable effects of both total and root competition on the phytometer, but there was no measurable effect of shoot competition. Comparisons between total, root and shoot competition (using Wilcoxon 2-sample test) showed that the intensity of total competition and of root competition was greater than that of shoot competition ($P<0.05$) and that the intensities of total and root competition were not significantly different.

For all CI's the range of possible values has a lower limit of negative infinity. Note, however, that the upper limit is +1 for CI_T and CI_R, but extends to positive infinity for CI_S. This discrepancy between theoretical CI ranges could complicate results if, for example, ratios of CI values were calculated. Also, CI_S values significantly greater than CI_R or CI_T values may simply be an artifact of the higher maximum CI_S limit. However, this was not the case in this study; mean CI_S values were significantly lower than mean CI_R and CI_T values (Appendix 3.5 shows that only one CI_S value was greater than 1).

There were no significant relationships between competition intensity (total, root or shoot) and soil depth or biomass (Spearman's rank correlation coefficients; $r_S \leq 0.47$; $P>0.06$).

Discussion

Total Competition Intensity in Alvar Vegetation

The high mortality in this experiment (Fig. 3.2), suggests that environmental stress was high. Lugo and McCormick (1981) assign a high stress index to shallow soil communities. In spite of the stressful conditions, competition was still detectable in the alvar vegetation (Fig. 3.4). This is consistent with experimental studies of shallow soils (Sharitz and McCormick 1973). Fowler (1986) has also argued that competition is not uncommon in arid systems.

The negative competition intensity value for shoots (Fig. 3.4) is evidence for commensalism (ie. phytometers benefitted by having neighbours). (Note that the present methods could not measure mutual benefits (ie. mutualism) although it is possible that the phytometer had a positive influence on one or more of its neighbours.) Wilson and Keddy (1986b) found similar evidence for commensalism in low biomass sites along a shoreline gradient. At the alvar, limestone is often exposed and the temperature at ground level can be very high (Stephenson and Herendeen 1986). Neighbour shoots reduce heat stress and evaporation of the already limited water by providing some shade (Bradshaw and Goldberg 1989) and could therefore have a positive influence on phytometer performance. Neighbour roots may also be beneficial by providing mycorrhizae (Grime *et al.* 1987). Eissenstat and Newman (1990) tested the interaction of mycorrhizae and competition and found that mycorrhizae do not alter the competitive balance. In all the discussion over competition, such possibilities for mutualism are generally overlooked (Keddy 1989) and future studies might specifically include tests for its presence.

Root and Shoot Competition

The method used in this experiment allowed me to examine the importance of root and shoot competition separately, and I found that only root competition was significant. This is consistent with Tilman's theory which predicts that competition will be greatest where resources are most limiting (Tilman 1982). That is, competition for light should be intense where light is limited. In my low biomass site there was minimal shade and thus shoot competition should be unimportant. Instead, I found that competition for soil resources predominated in the alvar (Fig. 3.4). Similarly, in a fertilized grassland, Wilson and Tilman (1991) found that root competition is most important in lower biomass sites but shifts to both above- and below-ground where fertility and biomass are higher. Both sets of results support Tilman's idea that in sites where soil resources are limited competition should be below-ground (Tilman 1982). Tilman's model also predicts an inverse relationship between root and shoot competition but my results did not demonstrate this simple trade-off.

Resource Gradients

The alvar soil depth gradient likely represents a gradient of soil resources - nutrients and especially moisture. Soil resource availability should be proportional to the cube of the soil depth. Soil moisture increases with soil depth in similar rock outcrop communities (Sharitz and McCormick 1973; Lugo and McCormick 1981). Evidence for the resource gradient is provided by the close relationship between plant biomass and soil depth (Fig. 3.1).

I found no evidence for a gradient of competition intensity: there was no correlation between competition intensity and biomass or soil depth, although my final sample size may have been too small to detect significant correlations. Other study systems where this relationship is not evident, include marsh (Shipley 1987), fire-disturbed prairie (Wilson and Shay 1990) and fertilized prairie (Wilson and Tilman 1991). However, competition intensity does vary along a resource/biomass gradient in rock outcrop (Sharitz and McCormick 1973), shoreline (Wilson and Keddy 1986b), arid grassland (Gurevitch 1986), old-field (Goldberg 1987), and abandoned pasture (Reader and Best 1989) vegetation types.

Important differences between these studies and systems may account for their contradictory results. First is the type of gradient over which competition is being tested. These gradients include natural and experimental variations in resources and/or disturbance (see Fig. 3.5). Second is the choice of phytometer and response variable. While some studies use biomass or growth of an indicator plant to measure competition intensity (this study; Wilson and Keddy 1986b; Shipley 1987; Wilson and Shay 1990; and Wilson and Tilman 1991) others use population attributes such as recruitment, survival and population growth (Gurevitch 1986; Goldberg 1987; Reader and Best 1989). Different plant traits will be affected over different time scales and, perhaps, biomass levels. Further, various species react differently to stress and competition (Shipley 1987). Third, and probably most important, is the variation in the level and length of the biomass range considered in these studies (Fig. 3.5). Competition intensity has been studied over a variety of biomass ranges in a number of communities. Herbaceous communities studied include wetlands (Wilson and Keddy 1986b; Shipley 1987; Wilson and Keddy 1991), rock outcrop (Sharitz and McCormick 1973) and grasslands (Gurevitch 1986; Goldberg 1987; Reader and Best 1989; Wilson and Shay 1990; Wilson and Tilman 1991). The 'herbaceous vegetation' (tall herb, woodland floor and grassland communities) described in Al-Mufti *et al.* (1977) are also included in Fig. 3.5 since one of the theories predicting variation in competition intensity with biomass (Grime 1979), was developed in this system. My experiment included a biomass range of 0 to 560 g/m2 (Fig. 3.1). Compared to other studies I was working in the low to mid-range of the overall biomass gradient illustrated. To make direct comparisons of results it is necessary to consider such differences between studies.

Figure 3.6 presents one way which might reconcile some conflicting results. In this model, total competition intensity increases along a gradient of biomass and reaches a plateau at some level, the maximum competition intensity for the system. At extremely low biomass levels competition may be unimportant and in such situations the effect of mutualism (ie. shading and mycorrhizal associations) is probably more significant. Moving up the biomass gradient, the effect of mutualism decreases while the effect of competition increases. Initially, while biomass levels are still too low for shading to occur, shoot competition is not important and it is root competition that has the major effect. Continuing up the gradient, the intensity of root competition increases but its effect becomes relatively unimportant as light becomes the main limiting factor and the effect of shoot competition is increasingly evident.

My experiment involved biomass levels in the 0 to 560 g/m^2 range (Fig. 3.1). There was some evidence for commensalism, especially at the low end of the soil depth/ biomass gradient (although explicit tests are needed to confirm this). The effect of competition was measurable and primarily due to root competition. In a higher biomass grassland (450 to 1150 g/m^2: Fig. 3.5; Wilson and Tilman 1991) competition at the lowest end of the gradient is below-ground and at the upper end is both below- and above-ground.

Thus, root and shoot competition may each contribute to the overall competition effect within certain zones along the gradient, and depending on the section of the gradient examined, a range of conclusions could be drawn about relationships between root and shoot competition and competition intensity. Further tests will be necessary to determine whether this model is indeed correct.

Figure 3.1.

The relationship between aboveground biomass of natural vegetation and soil depth at experimental plot locations at the end of the growing season. This relationship is described by the linear equation: biomass = -9.85 + 25.59(soil depth) (r^2=0.65; $P<<0.001$).

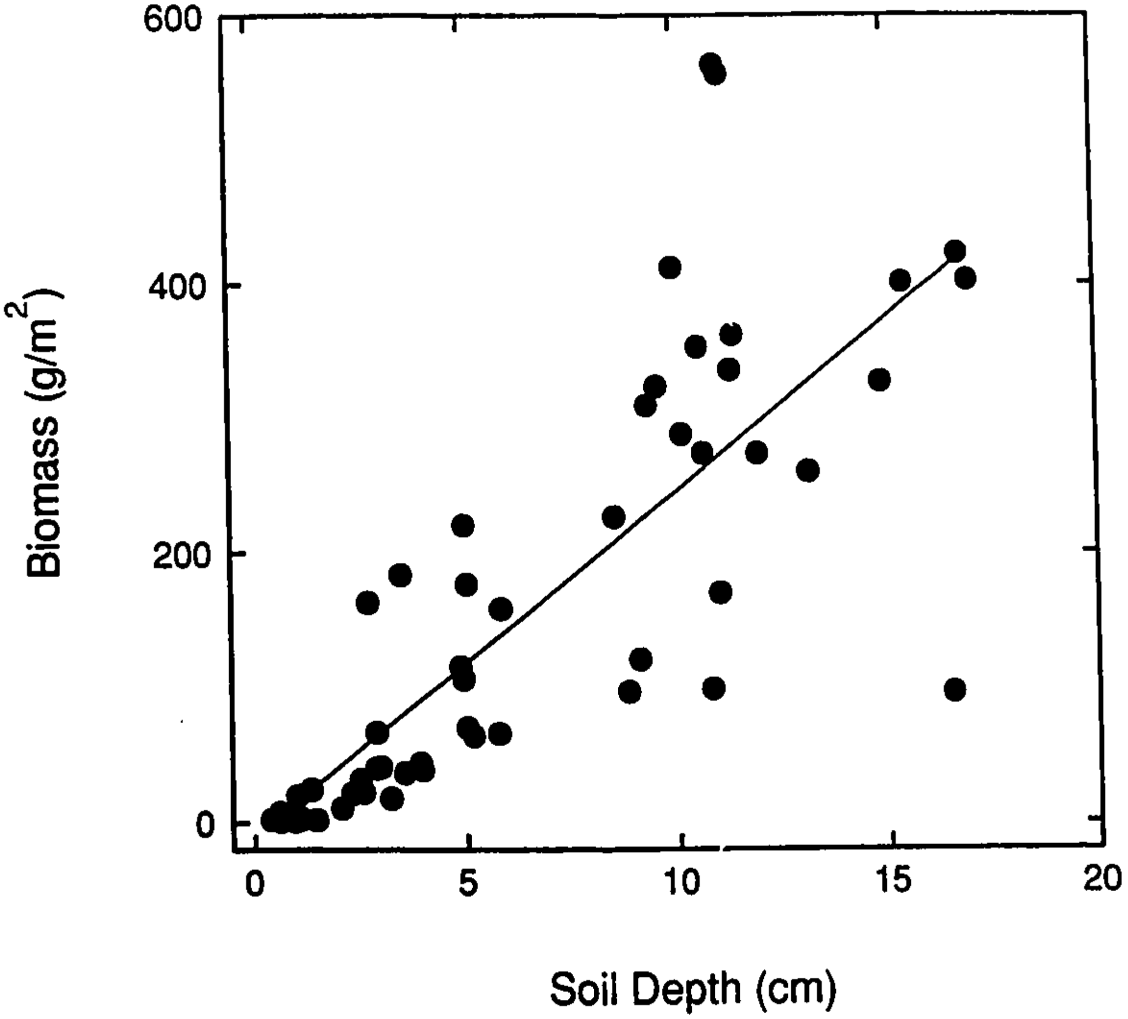


Figure 3.1

Figure 3.2.

Survivorship of transplant phytometers (% alive at the time of harvest) in each competition treatment (NN: no neighbours; NR: neighbour roots; NRS: neighbour roots and shoots). Survivorship was not significantly different among treatments (x^2 =1.5; P>0.05).

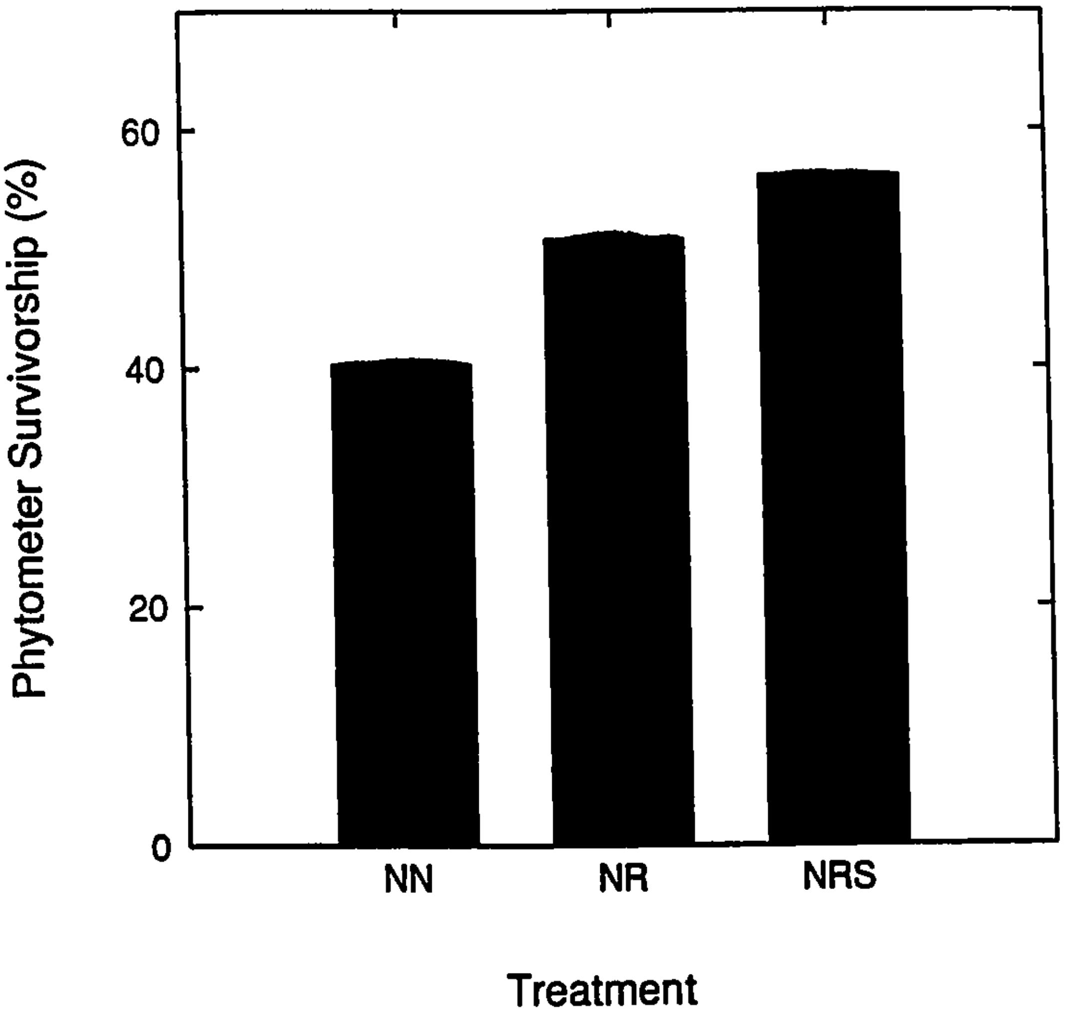
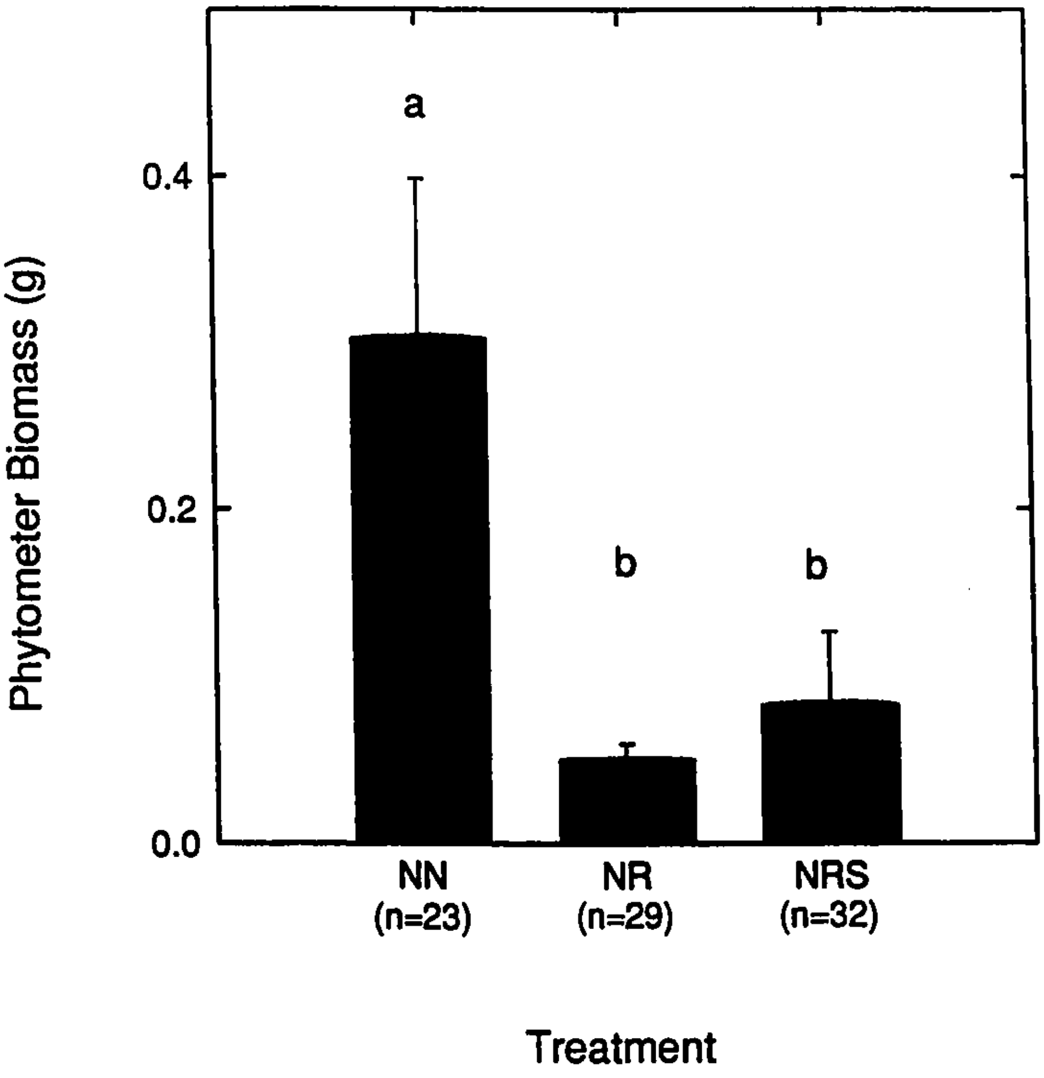


Figure 3.2

Figure 3.3.

Mean final biomass of transplant phytometers in each competition treatment (NN: no neighbours; NR: neighbour roots; NRS: neighbour roots and shoots).

Bars indicate +1 SE (sample sizes are shown in brackets below). Means sharing the same letter are not significantly different (Wilcoxon 2-sample test; P>0.05).



a
b
b
0.0
0.2
0.4
Phytometer Biomass (g)
NN
(n=23)
NR
(n=29)
NRS
(n=32)
Treatment

Figure 3.3

Figure 3.4.

Mean competition intensity for total, root and shoot competition. Bars indicate +1 SE (sample sizes are shown in brackets below). Asterisk (*) indicates that competition intensity was greater than 0 (Wilcoxon signed rank test; $P<0.05$). Means sharing the same letter are not significantly different (Wilcoxon 2-sample test; $P>0.05$).

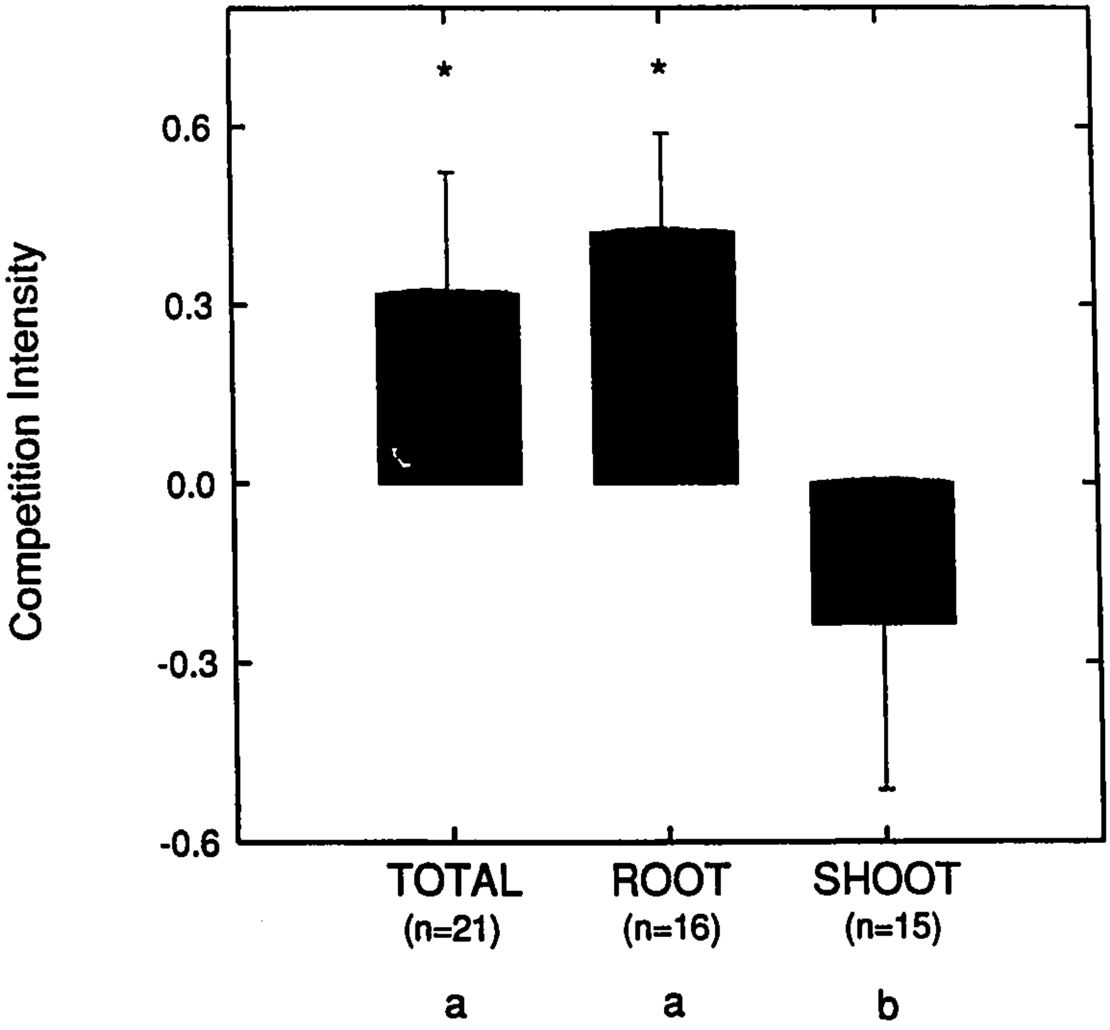

Competition Intensity
0.6
0.3
0.0
-0.3
-0.6
*
*
TOTAL
(n=21)
ROOT
(n=16)
SHOOT
(n=15)
a
a
b

Figure 3.4

Figure 3.5.

The range of aboveground biomass over which competition was examined in a number of community types. This range of biomass included in my experiment at the alvar is indicated by b (solid bar). Competition was not measured in c (stippled bar), but this study is included since it illustrates the biomass range relevant to Grime's theory (1979) predicting variation in competition along biomass gradients.

1 = competition measured in simulated rock outcrop conditions.

2 = experimentally created as opposed to naturally occurring gradients.

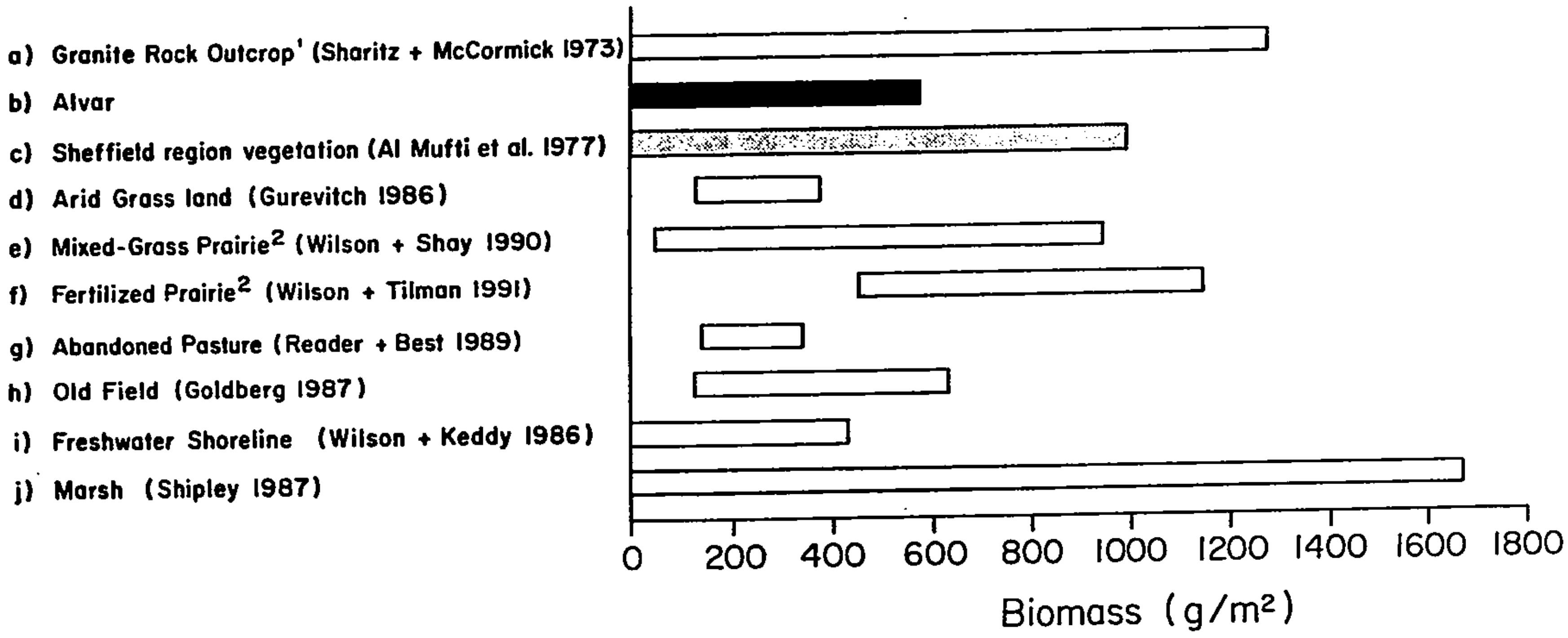

a) Granite Rock Outcrop¹ (Sharitz + McCormick 1973)
b) Alvar
c) Sheffield region vegetation (Al Mufti et al. 1977)
d) Arid Grass land (Gurevitch 1986)
e) Mixed-Grass Prairie² (Wilson + Shay 1990)
f) Fertilized Prairie² (Wilson + Tilman 1991)
g) Abandoned Pasture (Reader + Best 1989)
h) Old Field (Goldberg 1987)
i) Freshwater Shoreline (Wilson + Keddy 1986)
j) Marsh (Shipley 1987)
0
200
400
600
800
1000
1200
1400
1600
1800
Biomass (g/m²)

Figure 3.5

Figure 3.6.

Hypothesized changes in the intensity of mutualism and competition along a gradient of decreasing stress (see text for explanation).

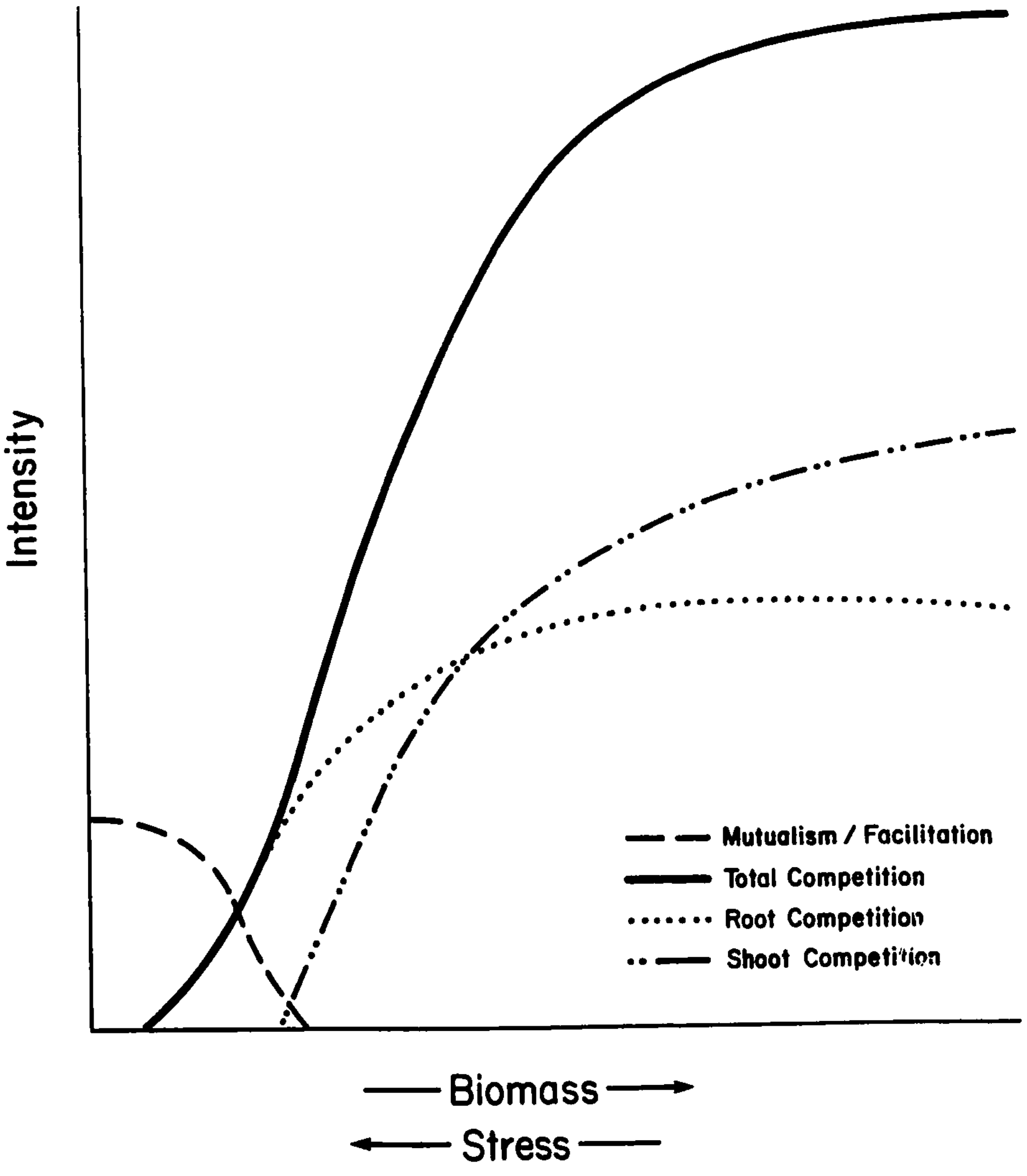

Intensity
Mutualism / Facilitation
Total Competition
Root Competition
Shoot Competition
Biomass →
← Stress

Figure 3.6

Summary and Applications

I chose the alvar as my study system for two reasons. First, the strong gradient of soil depth found in an alvar makes it a good system for examining general ecological patterns and testing for variation in processes along environmental gradients. The latter two research approaches were discussed in the second and third chapters of this thesis and represent the more theoretical aspect of this work. Second, the alvar system is uncommon, threatened and poorly understood. Ecological information about alvars is desperately needed. Chapter one provides a fairly comprehensive description of alvar vegetation in Canada and general ecological information which is applicable to the conservation and management of alvars is included in each of the chapters. Therefore, I would like to conclude this thesis by briefly summarizing the applications of my research.

My research sites include some of the best examples of alvar vegetation in Canada, and probably some of the most pristine sites in the world. Unfortunately, few of these alvars are protected (Belcher and Keddy in press). This study demonstrated important differences among alvar sites based on floristics, plant associations (chapter 1) and ecological patterns (chapter 2). This suggests that a reserve system will have to include a number of sites in order to be representative of alvars in Canada.

In order to protect alvars, we need to be able to identify priority sites. This research also demonstrated some important generalities among alvars which may be applicable to identifying healthy and representative alvars. Many aspects of alvar ecology were related to soil depth: species associations, plant morphologies (chapter 1), species richness (chapter 2), and survivorship (chapter 3). The utility of using soil depth as an easily measured predictor variable was demonstrated. I suggest that basic site inventories be related to soil depth.

I described a number of vegetation types which occur in Canadian alvar vegetation. These include meadow and rock flat habitats and other important vegetation types within. These habitats can be identified by indicator species or average soil depth (chapter 1). Habitat-type richness may be a useful measure of alvar 'quality'.

Species richness is another measure by which an alvar can be assessed. Within-site maximum species richness occurred at intermediate positions along the soil depth/biomass gradient chapter 2). Table 2.5 provides rough predictions of the biomass, or more simply the soil depth, associated with maximum species richness.

In order to conserve an alvar we must conserve the processes that maintain it. Stress, disturbance and competition all appear to be important. Shallow-soil sites in alvars apparently experience severe environmental stress (nutrient and especially moisture stresses). There was evidence for higher mortality in shallow-soil sites (chapter 3). These sites were occupied by small, evergreen perennial species, representative of the stress-tolerant plant strategy (Grime 1979). But the same areas that experience severe drought conditions during mid-summer, are flooded during the spring and fall and are subject to frost-heaving during the winter. Water regime appears to be a crucial aspect of alvar ecology. Disturbances which could alter the water regime (e.g., vehicle traffic and particularly quarrying, even on adjacent lands) should be prevented.

In closing, I note Peters' argument (1980) that ecology must divorce itself from natural history in order to become a rigorous science. This implies that an ecologist must also separate herself from the emotions associated with nature - a task I feel is impossible given the state of the world today. Indeed, pressures that we as a species place on the biosphere and its inhabitants, demand that we as ecologists provide some information immediately. Rigorous, scientific predictions are needed, but more specific information is also required. This thesis examines some important ecological generalizations but, I hope, has also succeeded at producing some specific and directly applicable results.

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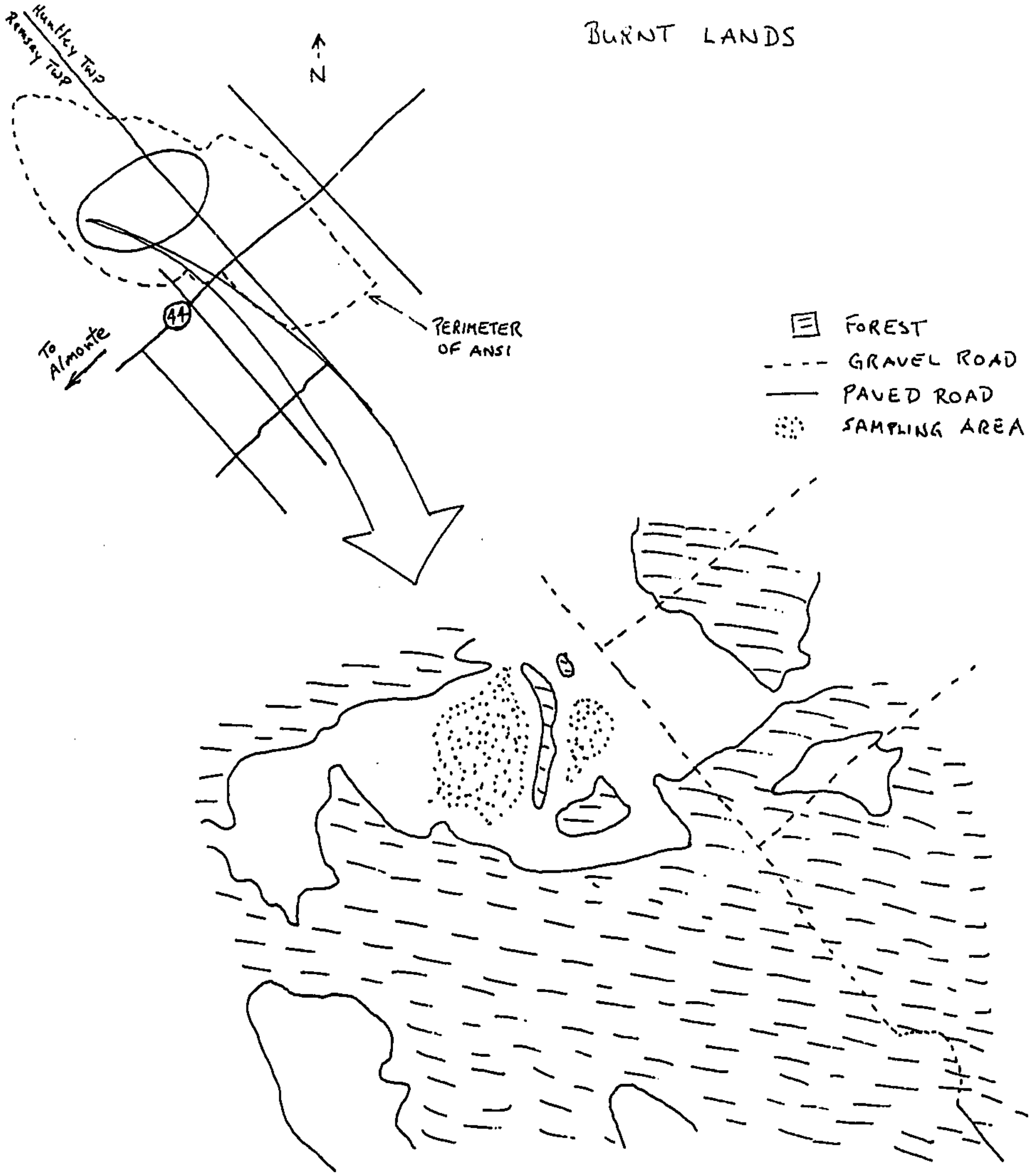
Appendix 1.1.

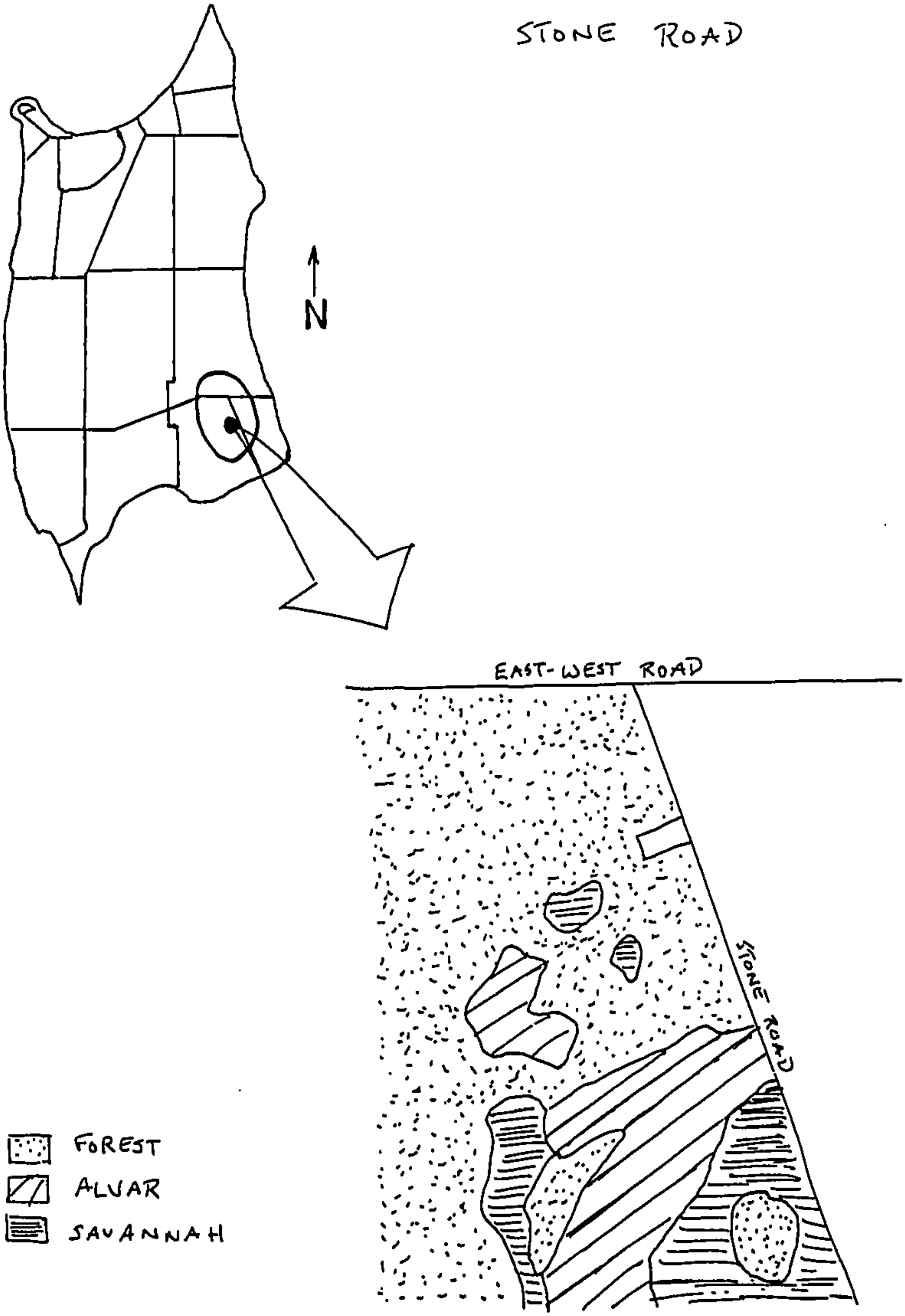
Maps showing the locations of the 4 alvar study sites: (a) Burnt Lands in eastern Ontario near Almonte, (b) Stone Road on Pelee Island in Lake Erie, (c) La Cloche on Great La Cloche Island, North of Manitoulin Island and (d) Misery Bay on the south shore of Manitoulin Island in Lake Huron. Approximate areas of descriptive sampling are indicated with stippling except at Stone Road (b) where samples were randomly located throughout the region indicated as 'ALVAR'.

BURNT LANDS



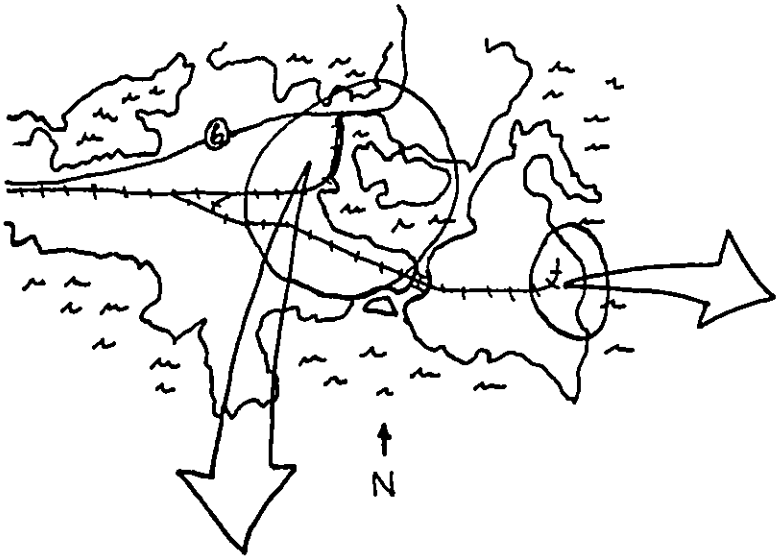
Appendix 1.1a

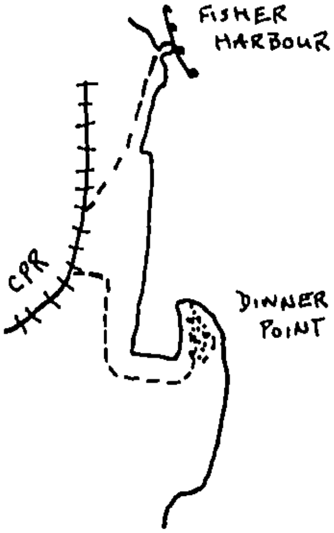
STONE ROAD

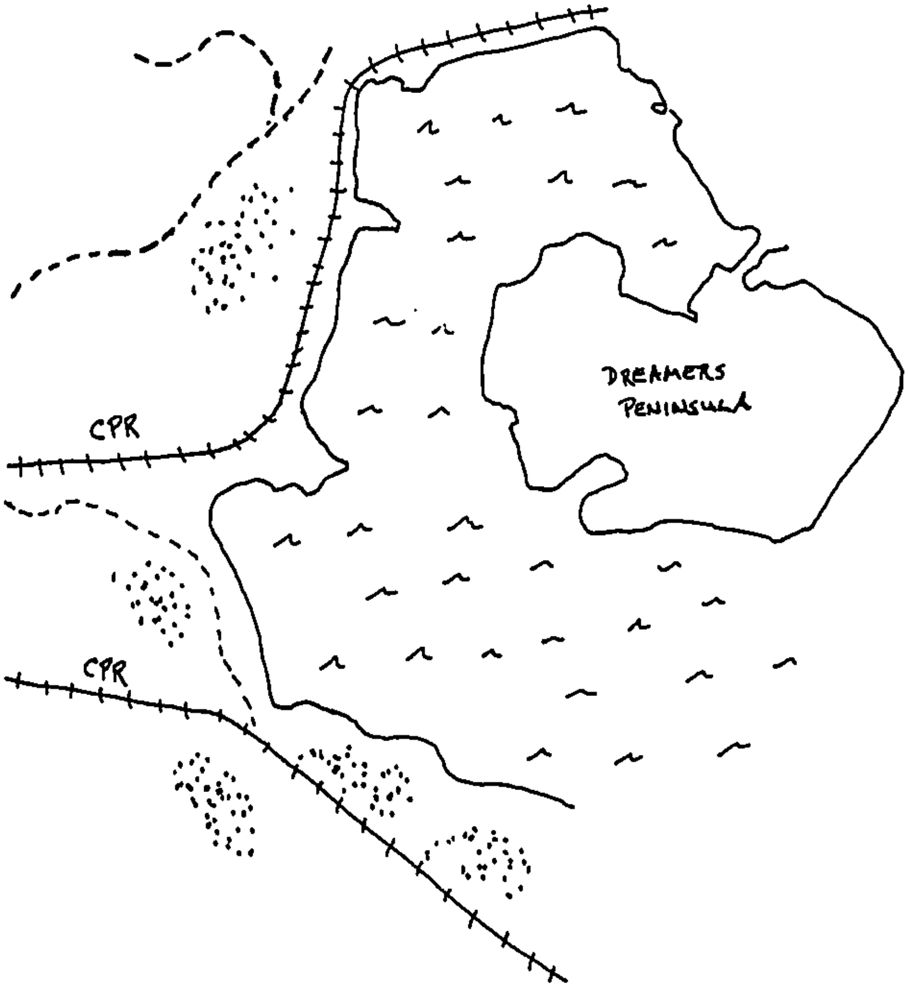


Appendix 1.1b

LA CLOCHE

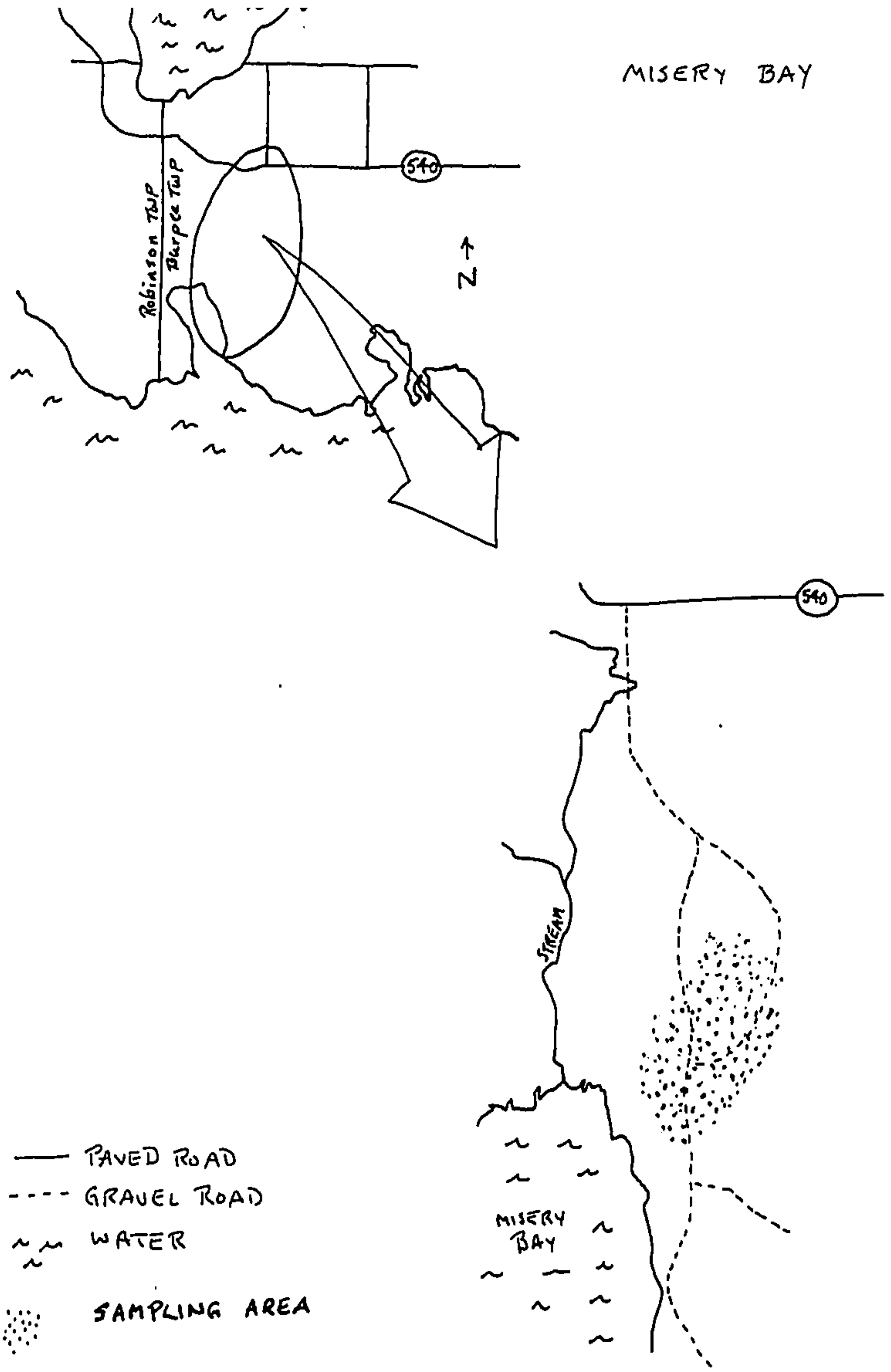






———	PAVED ROAD
- - - -	GRAVEL ROAD
~ ~ ~	WATER
⁘	SAMPLING AREA

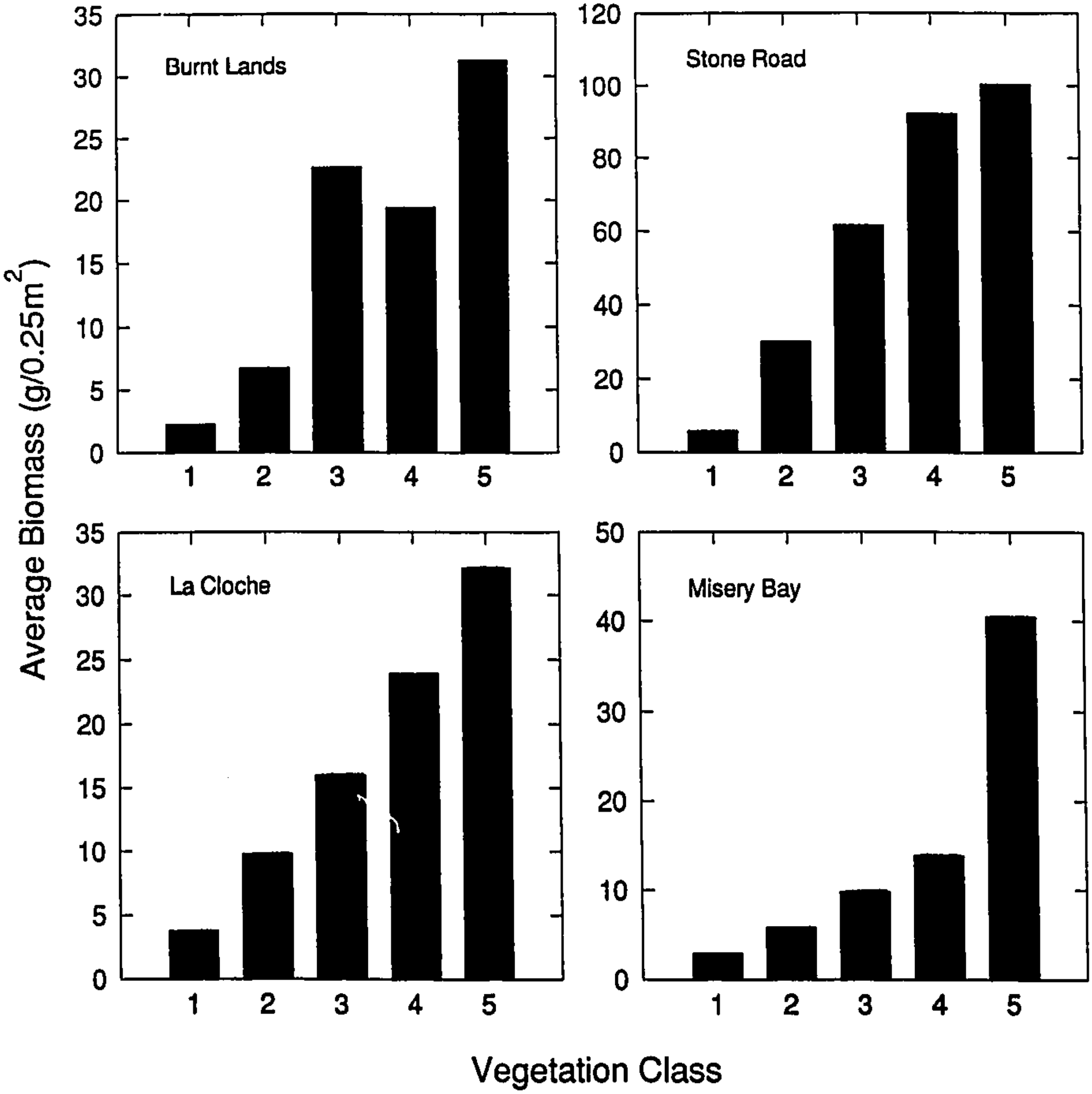
Appendix 1.1c



Appendix 1.1d

Appendix 1.2.

Average biomass generally increases across the 5 vegetation classes, at each study site. Vegetation classes were assigned at the time of sampling and were based on a visual approximation of above-ground biomass (see text).


Burnt Lands
Stone Road
La Cloche
Misery Bay
Average Biomass (g/0.25m^2)
Vegetation Class
0
5
10
15
20
25
30
35
0
20
40
60
80
100
120
0
10
20
30
40
50
1
2
3
4
5

Appendix 1.2

Appendix 1.3a.

Species frequencies (out of 9) in 99* quadrats sampled at the Burnt Lands, October 6-15, 1988. Data is shown in condensed format: each line begins with the quadrat number followed by data couplets of species (names given below) and frequency (1-9). For example, in quadrat 5, *Panicum philadelphicum* (species no. 27) has a frequency of 1 and *Saxifraga virginiensis* (species no. 33) has a frequency of 8.

```
BURNT LANDS VEGETATION 1988
(I4,10(I3,F4.0))                                  10
   1 27  9. 39  4.
   2  2  4.  7  2. 13  1. 16  2. 18  2. 20  2. 21  6. 26  5. 34  2. 35  2.
   2 37  1.
   3  2  1.  8  9. 10  4. 12  6. 15  4. 20  6. 29  6. 37  9.
   4 33  1.
   5 27  1. 33  8.
   7  1  3.  2  5.  6  1. 12  9. 15  6. 20  4. 21  1. 25  2. 34  1. 35  8.
   7 36  3. 39  4. 41  8.
   8  8  9. 15  1. 35  3. 38  9.
   9  8  9. 15  3. 35  3. 37  3. 38  9.
  10  4  2.  8  6. 10  3. 15  1. 17  9. 35  2. 37  2. 38  9.
  11  8  9. 15  7. 35  5. 38  9.
  12  8  7. 15  2. 35  3. 37  2. 38  9.
  13 20  1. 27  7. 35  2. 39  5.
  14  2  1.  9  4. 12  4. 15  9. 17  2. 20  2. 21  1. 27  1. 35  4. 37  3.
  15  2  3.  8  9.  9  1. 12  2. 15  3. 20  3. 27  1. 29  1. 37  9.
  16  6  9.  8  9. 15  2. 17  2. 20  9. 35  1. 36  6. 37  6.
  17  6  7.  8  8. 10  1. 15  6. 20  8. 24  5. 35  1. 36  4. 37  3.
  18  6  2.  8  9. 15  8. 20  6. 21  1. 28  1. 35  2. 36  7. 37  2. 41  1.
  19  8  9. 14  6. 20  1. 29  9. 30  1. 34  2. 39  9. 41  2.
  20  8  9. 20  3. 29  9. 30  8.
  21 33  2.
  22  8  5. 12  6. 14  2. 15  8. 20  9. 24  4. 36  3. 37  8. 40  2.
  23 13  3. 15  1. 19  5. 20  3. 27  5. 34  9. 35  3. 38  1. 39  2.
  24  8  9.  9  2. 15  3. 20  1. 24  2. 29  2. 35  7. 36  2. 37  1. 38  2.
  24 39  4. 41  2.
  25 19  7. 27  8. 35  5. 39  9.
  26  1  3.  8  2. 19  5. 20  1. 21  2. 27  9. 35  1. 39  7. 41  1.
  27 13  4. 17  5. 23  2. 27  9. 28  1. 33  3. 34  3. 35  3. 37  4.
  28 27  9. 39  9.
```

```
29 33  3.
30 13  1.
31 23  2. 27  1. 33  9.
32  2  6. 20  2. 27  9. 34  1. 35  3. 39  9.
33  1  2.  2  2.  6  2. 27  9. 34  1. 35  1. 39  7. 41  2.
34  8  9. 15  2. 35  8. 38  9.
35  8  8. 15  3. 20  1. 35  6. 36  2. 37  2. 38  9.
36  6  1.  8  6. 15  7. 19  1. 35  7. 38  5. 39  4. 41  4.
37 15  1. 34  8. 35  7. 39  9.
38  8  1. 15  5. 16  3. 20  2. 27  1. 34  4. 35  6. 39  5. 41  3.
39  8  9. 15  6. 20  2. 35  2. 38  9. 41  1.
40 15  3. 19  5. 20  4. 21  1. 27  7. 30  1. 34  9. 35  8. 37  1.
41  6  1. 27  9. 35  2. 39  6.
42 33  2.
43  5  1.  6  2.  8  9. 15  9. 17  8. 20  4. 21  3. 35  1. 37  1. 39  9.
44  6  6.  7  4. 15  7. 20  2. 21  5. 22  1. 25  1. 29  4. 30  1. 34  4.
44 35  3. 37  1. 39  4. 43  1.
45  8  9. 29  9. 35  5. 39  8. 43  1.
46  8  9. 21  1. 29  9. 35  1. 43  4.
47  6  6.  7  2.  8  9. 20  2. 22  1. 29  9. 30  2. 34  1. 35  3. 39  7.
48  8  9. 15  1. 20  1. 29  9. 35  3. 37  2. 39  9.
49 21  1. 23  3. 27  9. 33  4. 34  5. 41  3.
50
51 33  3.
52 27  9. 39  3. 41  3.
53  2  2. 23  1. 27  6. 33  2. 39  8. 41  6.
55  2  7. 17  5. 21  1. 27  4. 29  9. 35  5. 41  1.
56  2  2. 23  3. 27  1. 39  1. 41  1.
57 29  1. 35  3. 39  8.
58  8  5. 15  2. 29  2. 34  2. 35  1. 38  9. 39  2.
50  6  9.  8  8. 15  1. 17  8. 20  7. 29  9. 35  3. 36  4. 37  5. 39  9.
60  2  9. 23  2. 27  9. 29  2. 35  6. 41  7.
61 23  3.
62  2  1.  6  1.  8  1. 10  6. 15  3. 20  2. 27  5. 29  4. 35  2. 37  5.
62 39  7. 41  5.
63 24  1. 27  9. 35  1.
64  7  1.  8  9. 15  7. 18  1. 21  1. 27  7. 35  9. 37  2.
65 13  3. 15  5. 21  1. 23  1. 27  9. 34  4. 35  8. 36  3. 37  2.
66 23  2. 33  9.
67  2  1.  9  1. 10  4. 15  4. 20  3. 29  2. 35  6. 36  7. 37  5.
68  2  2. 23  1. 27  9. 29  2. 33  4. 39  4.
69 23  1. 27  7. 33  9.
70  1  1.  7  7.  8  4. 17  2. 20  2. 38  9.
71 23  1. 27  9. 33  5. 39  1. 41  2.
```

```
72  8  9. 15  1. 20  1. 35  3. 37  1. 38  9.
73  8  8. 15  8. 20  1. 35  5. 37  1. 38  9.
74  8  9. 15  1. 35  7. 38  9.
75  6  3.  8  9. 12  1. 15  2. 35  6. 37  1. 38  8.
76 29  1. 35  7. 38  9.
77  8  9. 29  1. 35  9. 37  1. 38  9.
78  8  9. 35  7. 38  9.
79  8  2. 35  8. 38  9.
80  8  9. 17  1. 35  9. 37  1. 38  9.
81  8  9. 17  6. 20  1. 31  1. 35  6. 36  1. 38  9.
82 23  1. 27  4. 33  8.
83 27  9. 39  4.
84 27  9. 39  2. 41  5.
85  2  1. 15  4. 27  9. 34  4. 35  9. 41  4.
86  1  5.  2  1. 15  7. 20  4. 21  3. 27  8. 33  1. 34  4. 35  5. 41  6.
87  2  3. 23  1. 27  9. 33  7.
88 13  1. 20  1. 23  2. 27  8. 33  7.
89 23  1. 27  9. 33  2.
90 20  1. 23  1. 27  9. 33  5.
91 13  2. 27  8. 33  5.
92  3  1. 15  9. 17  1. 20  2. 21  5. 29  1. 30  1. 35  3. 36  1.
93 11  7. 17  3. 21  4. 26  6. 30  3. 31  2. 34  2. 36  3. 37  2. 41  1.
93 42  6.
94  2  6. 11  1. 15  3. 21  4. 26  8. 30  2. 31  1. 32  2. 34  3. 42  4.
95 21  5. 26  9. 34  4. 36  3. 39  5. 41  4.
96 11  2. 21  2. 26  9. 34  2. 36  3. 37  4. 39  3. 41  2. 42  2.
97  1  3.  2  2.  8  9. 15  5. 20  6. 34  6.
98  2  1.  6  1.  8  3. 13  8. 21  5. 26  9. 34  8. 35  1. 36  1. 39  4.
98 41  4.
99  6  6.  8  9. 10  6. 11  2. 15  1. 20  9. 36  2. 37  7.
100 6  1.  8  9. 15  9. 20  5. 31  5. 37  6. 39  2.
101  3  2.  4  3.  6  1.  7  5.  8  9. 15  4. 20  4. 36  5. 37  2. 41  2.
00
```

Elymus trachycaulus (1), *Ambrosia artemesiifolia* (2), *Antennaria neglecta* (3), *Aster ciliolatus* (4) *Bromus kalmii* (5), *Campanula rotundifolia* (6), *Carex bebbii* (7), *Carex crawei* (8), *Carex launuginosa* (9), *Carex richardsonii* (10), *Carex rugosperma* (11), *Carex umbellata* (12), *Chaenorrhinum minus* (13), *Chrysanthemum leucanthemum* (14), *Danthonia spicata* (15), *Echium vulgare* (16), *Fragaria virginiana* (17), *Geranium bicknellii* (18), *Hedeoma hispida* (19), *Hieracium piloselloides* (20), *Hypericum perforatum* (21), *Melilotus species* (22), *Minuartia michauxii* (23), *Muhlenbergia mexicana* (24), *Panicum acuminatum* (25), *Panicum flexile* (26), *Panicum philadelphicum* (27), *Penstemon hirsutus* (28), *Poa pratensis* (29), *Potentilla recta* (30), *Rosa acicularis* (31), *Rhus radicans* (32), *Saxifraga virginiensis* (33), *Scutellaria parvula* (34), *Senecio pauperculus* (35), *Solidago nemoralis* (36), *Solidago ptarmicoides* (37), *Sporobolus heterolepis* (38), *Sporobolus vaginiflorus* (39), *Sisyrinchium montanum* (40), *Trichostema brachiatum* (41), *Verbascum thapsus* (42), *Viccia cracca* (43).

* Quadrats no. 6 and 54 were missed during sampling.

Appendix 1.3b.

Species frequencies in 51* quadrats sampled at Stone Road alvar, September 25-27, 1989. Data is given in condensed format (see Appendix 1.3a for explanation). Species names are given below.

```
STONE ROAD VEGETATION DATA 1989
(I4,10(I4,F3.0))                              10
   1  2 9.   9 3.  12 3.  16 1.  18 7.  19 9.  21 1.  24 7.  27 5.
   2  2 2.  18 8.  20 2.
   3  2 9.   9 9.  18 5.  19 9.  24 4.  27 1.
   4  2 9.   9 7.  18 7.  19 9.  27 2.
   5  2 9.   9 9.  12 1.  18 8.  19 9.  24 3.  27 6.
   6  2 9.   9 7.  11 1.  12 5.  18 6.  19 9.  21 4.  22 1.  24 7.  27 1.
   7  2 9.  18 9.  22 2.  24 4.  27 4.
   8  2 7.  18 8.  20 2.  24 4.  27 1.
   9  2 9.   9 3.  12 2.  18 1.  19 9.  21 1.  24 3.
  10  2 7.   8 1.   9 9.  12 2.  16 1.  19 9.  21 2.  22 1.  24 3.
  11  2 6.   7 2.   9 9.  19 9.  21 1.  22 1.  24 3.
  12  2 2.  14 2.  18 9.  19 3.  21 1.  22 3.  24 4.  27 9.
  13  2 9.   7 1.   9 3.  18 8.  19 9.  22 1.  24 2.  27 5.
  15 14 2.
  16 13 2.  14 9.  18 3.  27 2.
  17  9 2.  18 9.  27 8.
  18  2 3.  18 8.  22 2.  24 1.  27 9.
  19  2 6.  12 9.  18 9.  19 6.  21 4.  24 4.  27 1.
  20 13 1.  18 5.  26 2.  27 8.  28 3.
  21  2 8.   4 5.  10 2.  12 9.  18 9.  19 9.  21 8.  22 2.  24 1.  25 1.
  21 28 1.
  22  2 3.  13 3.  18 9.  21 1.  27 6.
  23 13 2.  14 5.  18 7.
  24  2 5.  18 7.  19 1.  21 2.  22 1.  28 1.
  25  2 9.   4 2.   9 4.  18 7.  19 9.  21 1.  24 4.  27 5.
  26  2 9.   9 9.  18 9.  19 5.  24 7.  27 8.
  27  2 5.  18 5.  21 2.  22 2.  24 3.  27 7.
  28  2 5.  13 2.  18 5.  24 1.  27 4.
  29  2 9.   4 1.   5 3.   9 7.  12 2.  16 1.  18 7.  19 9.  21 2.  24 6.
  29 25 1.  27 3.
  30 13 1.  18 3.  27 5.
  31  2 3.  14 1.  18 9.  19 6.  22 1.  23 4.  24 1.  27 8.  28 1.
  32 13 6.  18 3.  19 1.  27 2.
  33  2 9.  18 8.  19 7.  22 6.  24 6.  27 8.
```

```
 34  2 9.  4 1.  9 9.  12 1.  15 3.  17 7.  19 9.  24 1.
 35  2 4.  9 9.  17 3.  19 9.
 36  2 3.  13 4.  14 3.  18 4.  19 1.  27 6.
 37  2 9.  9 9.  17 3.  19 9.  24 1.
 38  2 9.  4 1.  9 9.  15 5.  17 6.  19 9.
 39  2 8.  17 3.  19 9.
 40  1 2.  2 1.  3 9.  6 2.  10 2.  19 9.  23 1.
 41  2 4.  3 9.  10 4.  17 3.  19 9.  21 2.  23 7.
 42  2 9.  3 7.  4 2.  17 9.  19 9.  23 9.
 43  1 4.  2 7.  3 9.  7 2.  19 9.  23 2.  27 1.
 44  2 2.  3 9.  6 2.  10 1.  19 9.
 45  1 3.  2 1.  3 9.  10 3.  19 9.  23 1.  24 1.
 46  1 6.  2 6.  3 9.  6 4.  7 4.  10 1.  19 9.
 47  2 5.  3 9.  10 1.  19 9.  23 6.
 48  2 4.  3 9.  9 5.  19 9.  23 3.
 49  2 7.  3 6.  4 1.  9 1.  10 1.  12 1.  17 1.  19 9.  23 9.
 50  2 4.  17 9.  19 9.  21 3.  23 6.
 51  2 3.  3 9.  10 6.  19 9.  21 2.  23 8.
 52  2 8.  13 8.  14 1.  18 1.  19 5.  22 1.  24 1.  27 5.
00
```

Agrostis gigantea (1), *Allium cernuum* (2), *Andropogon gerardii* (3), *Aster pilosus* (4), *Carex divulsa* (5), *Carex lanuginosa* (6), *Carex molesta* (7), *Clintonia vulgaris* (8), *Eleocharis compress* (9), *Fragaria virginiana* (10), *Geranium bicknellii* (11), *Hypericum perforatum* (12), *Juncus dudleyi* (13), *Leucospora multifida* (14), *Lotus corniculatus* (15), *Medicago sativa* (16), *Melilotus species* (17), *Panicum philadelphicum* (18), *Poa compressa* (19), *Portulaca olearca* (20), *Ratibida pinnata* (21), *Rumex crispus* (22), *Scirpus atrovirens* (23), *Scutellaria parvula* (24), *Setaria viridis* (25), *Sporobolus neglectus* (26), *Trichostema brachiatum* (27), *Verbena simplex* (28).

* Quadrat No. 14 was missed during sampling.

Appendix 1.3c.

Species frequencies in each quadrat sampled at La Cloche alvar, September 30 - October 2, 1989. Data given in condensed format (see Appendix 1.3a for explanation). Species names are given below.

```
LA CLOCHE VEGETATION DATA 1989
(I4,10(I4,F3.0))                                    10
   1   3 3.   5 3.  14 2.  17 2.  18 2.  23 9.  29 8.  31 5.  34 1.  35 1.
   1  37 1.  38 7.
   2   1 1.   3 3.  29 3.  38 9.
   3   3 9.  31 4.  38 9.
   4  29 2.  31 3.  33 1.  37 4.  38 9.  39 1.
   5   3 1.  24 2.  31 3.  33 9.  34 1.  37 2.  38 9.
   6  14 3.  18 3.  29 2.  31 3.  33 4.  38 8.  39 1.
   7  18 5.  20 1.  29 9.  31 9.  32 1.
   8   1 2.   3 1.  15 5.  18 2.  29 7.  31 3.  34 3.  38 1.
   9   8 1.   9 2.  11 4.  14 5.  33 3.  37 9.  38 3.
  10   9 5.  13 3.  14 3.  31 6.  33 6.  37 9.
  11   4 2.   9 1.  13 1.  14 1.  31 1.  37 9.
  12   7 8.   9 1.  11 1.  13 1.  37 7.
  13   4 2.   9 1.  14 2.  33 4.  37 9.
  14   9 1.  10 7.  33 4.  35 2.  37 7.
  15  10 6.  11 1.  14 2.  16 6.  31 2.  33 1.  37 9.  38 1.
  16   4 1.   8 1.   9 9.  11 8.  13 1.  14 8.  22 5.  27 6.  33 9.  38 1.
  17   4 2.   9 6.  14 2.  37 9.  38 5.
  18  10 5.  14 3.  21 1.  33 5.  37 4.  38 6.  39 2.
  19   9 7.  15 5.  37 9.  39 1.
  20   9 5.  15 5.  37 9.
  21   9 9.  15 5.  37 9.  38 7.
  22   4 2.   9 9.  15 2.  37 9.  38 8.
  23   3 1.  38 8.  39 4.
  24   9 8.  11 6.  22 1.  26 1.  33 9.  37 6.
  25   3 1.  38 9.  39 4.
  26   3 1.  25 5.  35 1.  37 4.  39 8.
  27   3 2.  25 4.  33 1.  38 8.
  28   3 1.  12 7.  25 1.  35 2.  38 4.
  29   1 1.   3 1.  12 4.  36 3.  38 5.
  30   3 3.  12 2.  38 9.
  31   1 7.   2 8.   9 9.  15 3.  34 1.  35 2.  38 9.
  32   1 9.   2 1.   7 6.  35 1.  38 9.
  33   1 2.   7 2.   9 3.  10 5.  25 1.  27 2.  33 2.  38 7.
```

```
 34  3 1.  7 5.  9 3.  38 9.
 35  2 8.  3 3.  7 9.  9 3.  28 7.  38 9.
 36  3 1.  15 1.  38 9.
 37  4 1.  9 8.  14 1.  18 1.  33 9.  36 4.  37 2.
 38  9 9.  14 7.  16 1.  21 2.  33 6.  36 7.
 39  4 1.  9 6.  14 4.  33 9.
 40  1 2.  4 2.  9 8.  14 5.  16 1.  19 2.  33 5.  36 1.  37 5.  38 1.
 41  6 1.  9 9.  14 7.  16 1.  17 1.  33 8.  37 2.
 42  8 5.  9 9.  14 7.  17 1.  30 3.  33 7.  35 1.  36 3.  37 1.
 43  4 2.  9 9.  14 9.  33 7.  37 1.
 44  9 9.  14 3.  18 1.  33 9.
 45  9 6.  12 3.  14 3.  33 7.  37 1.  38 4.
 46  4 3.  9 4.  11 5.  19 4.  31 2.  33 9.  37 9.
 47  14 2.  19 4.  25 2.  31 2.  33 1.  37 9.
 48  9 9.  14 1.  33 9.  37 7.
 49  4 1.  9 9.  14 1.  21 2.  31 1.  33 9.  37 9.
 50  6 3.  9 8.  14 8.  19 4.  31 1.  37 9.
00
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Agrostis scabra (1), *Allium schoenoprasum* (2), *Ambrosia artemisiifolia* (3), *Antennaria neglecta* (4), *Arabis hirsuta* (5), *Aster ericoides* (6), *Calamintha arkansana* (7), *Campanula rotundifolia* (8), *Carex crawei* (9), *Carex scirpoidea* (10), *Carex umbellata* (11), *Chaenorrhinum minus* (12), *Commandra umbellata* (13), *Danthonia spicata* (14), *Eleocharis compressa* (15), *Elymus trachycaulus* (16), *Fragaria virginiana* (17), *Geranium bicknellii* (18), *Geum triflorum* (19), *Hieracium piloselloides* (20), *Juncus dudleyi* (21), *Liatris cylindraceae* (22), *Lotus corniculatus* (23), *Medicago sativa* (24), *Minuartia michauxii* (25), *Muhlenbergia glomerata* (26), *Panicum acuminatus* (27), *Panicum philadelphicum* (28), *Poa compressa* (29), *Prunus vulgaris* (30), *Ranunculus fascicularis* (31), *Saxifraga virginiensis* (32), *Shizacyrium scoparius* (33), *Scutellaria parvula* (34), *Senecio pauperculus* (35), *Solidago ptarmicoides* (36), *Sporobolus heterolepis* (37), *Sporobolus vaginiflorus* (38), *Trichostema brachiatum* (39).

Appendix 1.3d.

Species frequencies in each quadrat sampled at Misery Bay, October 3-4, 1989. Data given in condensed format (see explanation in Appendix 1.3a). Species names are given below.

```
MISERY BAY VEGETATION DATA 1989
(I4,10(I4,F3.0))                                   10
   1   1 2.   6 3.  17 7.  20 1.  30 4.  35 1.  36 6.  38 8.
   2   6 4.  27 1.
   3   6 1.   8 1.  10 7.  14 2.  15 6.  28 2.  34 8.  36 2.  38 5.
   4   6 3.  11 8.  14 1.  17 2.  28 6.  34 6.  37 5.  38 2.
   5   6 3.  16 8.
   6   1 7.   6 9.  16 4.  17 3.  27 3.  34 2.  38 3.
   7   1 4.   2 1.   6 7.  11 1.  27 5.  30 6.  34 3.  36 2.  38 4.
   8   6 5.  16 3.  27 4.  34 1.  37 2.
   9   6 7.  16 2.  17 3.  38 4.
  10   4 1.  18 2.  27 1.  34 5.
  11   3 3.   4 2.  30 2.  33 4.
  12   4 1.  27 5.  34 5.
  13   6 6.   8 1.  20 1.  27 1.  28 6.  34 4.  35 5.  36 5.  38 2.
  14   1 1.   6 6.  11 1.  35 1.  36 1.  38 9.
  15   4 7.   6 8.  34 2.  38 4.
  16   1 1.   4 5.   6 5.  27 1.  34 4.  38 4.
  17   4 2.  21 1.  27 3.  30 1.  33 3.
  18   4 1.  15 1.  19 1.  21 2.  27 2.  34 1.  35 2.
  19   2 2.   3 3.   4 8.   7 1.  13 3.  20 2.  27 6.  29 9.  33 3.  35 2.
  20   1 3.   3 2.   6 2.  13 3.  18 2.  23 1.  27 6.  35 1.
  21   4 4.  17 1.  27 4.  33 2.  35 2.
  22   1 4.   6 4.  17 4.  36 2.  38 1.
  23   2 1.  16 6.  35 1.
  24   1 3.   2 2.  13 2.  14 1.  23 1.  30 2.  34 6.  38 2.
  25   1 4.  16 9.  23 3.  35 8.
  26   1 2.  16 9.  18 2.
  27   1 9.  16 7.  30 6.  31 2.
  28   1 6.  18 1.  30 1.  35 6.
  29   1 7.   9 7.  16 4.  18 3.  22 2.  23 5.  30 2.
  30   1 9.   5 4.  16 5.  17 1.  23 2.  31 3.
  31   1 1.  16 6.
  32   4 2.  18 4.  27 5.
  33   6 9.  20 1.  27 1.  29 9.
  34   6 9.  16 2.  20 8.  25 8.  29 9.  32 3.  33 1.  35 1.  40 1.
```

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 35  4 2.  16 1.  18 2.  21 3.
 36  6 3.  30 2.  38 9.
 37 15 1.  38 9.
 38  8 1.  38 9.
 39  8 8.  15 5.  36 1.  37 1.  38 9.  39 1.
 40  2 4.   4 4.   6 4.   7 3.  12 7.  18 1.  20 4.  27 4.  29 9.  33 3.
 40 34 3.
 41  1 5.   4 2.  27 2.  29 6.  33 3.  34 2.  38 2.
 42  6 3.   8 4.  17 3.  38 9.
 43  1 2.  16 8.
 44 38 9.
 45 24 8.  38 9.
 46  1 5.  38 9.
 47  1 6.   6 2.  16 9.  17 2.  35 3.
 48  1 2.   6 2.  16 9.  29 1.  35 9.
 49  1 1.   7 2.  10 2.  26 7.  38 6.
 50  1 2.   6 9.  16 2.  27 7.  33 2.  35 6.  38 4.
00
```

Ambrosia artemesiifolia (1), *Arabis hirsuta* (2), *Arenaria serpyllifolia* (3), *Artemisia campestris* (4), *Calamagrostis canadensis* (5), *Calamintha arkansana* (6), *Campanula rotundifolia* (7), *Carex crawei* (8), *Carex lanuginosa* (9), *Carex scirpoidea* (10), *Carex umbellata* (11), *Castillega coccinea* (12), *Cerastium arvense* (13), *Commandra umbellata* (14), *Danthonia spicata* (15), *Deschampsia cespitosa* (16), *Eleocharis compressa* (17), *Elymus trachycaulus* (18), *Festuca saximontana* (19), *Geranium bicknellii* (20), *Hymenoxys acaulis* (21), *Hypericum kalmii* (22), *Hypericum perforatum* (23), *Juncus balticus* (24), *Lepidium campestris* (25), *Liatris cylindracea* (26), *Minuartia michauxii* (27), *Panicum acuminatum* (28), *Panicum philadelphicum* (29), *Poa compressa* (30), *Potentilla norvegica* (31), *Rumex crispus* (32), *Saxifraga virginiensis* (33), *Schizachyrium scoparius* (34), *Scutellaria parvula* (35), *Senecio pauperculus* (36), *Solidago ptarmicoides* (37), *Sporobolus heterolepis* (38), *Sisyrinchium montanum* (39), *Verbascum thapsus* (40).

Appendix 1.4.

Soil depth, biomass and species richness values for each quadrat sampled at 4 alvar sites; (a) Burnt Lands, (b) Stone Road, (c) La Cloche and (d) Misery Bay. Soil depth is reported as the mean and standard deviation of 5 measures per quadrat. Also shown is the vegetation class assigned at the time of sampling; these were based on a visual approximation of above-ground biomass (class 1 has the lowest biomass; see Appendix 1.2).

(a) BURNT LANDS ALVAR

Quadrat No.	Vegetation Class	Soil Depth (cm)		Biomass (g/0.25m^2)	Species Richness (#/0.25m^2)
		Mean	St. Dev.		
1	2	3.2	0.1	5.78	2
2	3	7.9	1.1	8.60	11
3	3	10.4	2.3	49.91	8
4	1	0.1	0.2	0.02	1
5	1	0.6	0.5	3.18	2
7	3	10.6	0.6	35.30	13
8	5	9.8	1.0	25.78	4
9	5	12.8	0.6	29.67	5
10	5	10.9	1.2	33.13	8
11	5	8.4	2.6	22.68	4
12	5	12.8	1.8	21.56	5
13	2	2.4	0.6	6.36	4
14	3	8.4	1.4	13.80	10
15	3	12.7	1.3	25.69	9
16	4	9.3	3.2	21.83	8
17	4	2.4	1.2	15.12	9
18	4	5.1	2.2	21.88	10
19	4	6.3	1.6	29.44	8
20	4	3.4	1.3	17.93	4
21	1	0.3	0.3	0.18	1
22	3	16.1	2.0	33.76	9
23	2	5.2	2.1	11.05	9
24	3	8.3	0.9	28.97	12
25	2	3.1	2.1	10.67	4
26	3	4.2	1.3	14.36	9
27	2	4.3	1.9	4.45	9
28	2	0.7	0.3	5.29	2
29	1	0.3	0.4	0.14	1
30	1	0.2	0.3	0.07	1

31	1	0.9	0.9	5.14	3
32	3	4.7	0.8	9.45	6
33	2	3.0	2.0	6.96	8
34	5	9.4	2.3	29.31	4
35	5	11.7	2.2	32.78	7
36	3	4.2	1.3	14.03	8
37	3	3.2	0.8	16.49	4
38	3	2.9	1.8	12.27	9
39	5	6.1	1.2	25.19	6
40	3	4.0	1.8	10.76	9
41	2	3.8	1.7	9.20	4
42	1	0.2	0.3	0.30	1
43	4	1.5	1.1	30.92	10
44	4	2.6	2.6	17.00	14
45	4	4.6	1.1	28.49	5
46	4	3.9	1.2	26.36	5
47	4	4.3	1.9	20.11	10
48	4	4.1	2.3	27.08	7
49	2	2.8	0.5	3.26	6
50	1	0.1	0.2	0.00	0
51	1	2.0	2.9	0.64	1
52	2	2.6	1.2	5.02	3
53	2	1.7	1.1	13.20	6
55	3	10.9	1.3	27.13	7
56	1	0.6	0.5	1.15	5
57	1	0.5	0.4	5.10	3
58	5	6.7	0.8	37.75	6
59	3	13.5	1.5	48.60	10
60	3	6.0	2.6	36.30	6
61	1	0.9	0.5	0.45	1
62	3	9.8	1.7	12.90	12
63	2	3.8	1.1	7.52	3
64	3	5.2	2.1	14.20	8
65	3	6.7	1.1	13.25	9
66	1	0.6	0.5	1.98	2
67	3	11.6	0.8	26.37	9
68	1	1.7	1.1	6.70	6
69	1	1.1	0.4	3.42	3
70	5	11.5	1.2	29.01	6
71	2	1.8	0.9	6.78	5
72	5	11.4	2.7	34.21	6
73	5	10.8	0.8	27.39	6
74	5	7.2	0.9	23.77	4
75	5	17.9	4.0	28.50	7
76	5	16.6	3.1	39.61	3
77	5	12.4	1.7	39.05	5
78	5	10.7	1.6	35.26	3
79	5	9.8	0.5	30.89	3
80	5	12.2	1.0	37.39	5
81	5	12.7	4.3	43.62	7
82	1	1.2	0.5	4.59	3

83	2	2.3	1.5	5.25	2
84	2	1.7	1.1	5.37	3
85	2	4.2	1.4	5.69	6
86	2	5.2	1.0	10.50	10
87	2	2.1	1.3	6.16	4
88	2	0.9	0.4	2.31	5
89	2	2.7	1.2	4.00	3
90	1	0.9	0.6	3.17	4
91	1	1.8	1.0	6.63	3
92	4	8.2	3.2	17.75	9
93	4	4.9	1.6	17.05	12
94	4	3.1	1.4	15.51	10
95	4	4.2	1.7	14.21	6
96	4	5.5	1.9	17.82	10
97	4	6.5	0.5	24.40	6
98	4	4.1	2.5	7.35	11
99	4	5.7	1.7	14.93	8
100	4	5.9	1.1	13.14	7
101	4	5.5	2.4	9.02	10

(b) STONE ROAD ALVAR

Quadrat No.	Vegetation Class	Soil Depth (cm)		Biomass (g/0.25m^2)	Species Richness (#/0.25m^2)
		Mean	St. Dev.		
1	3	6.1	2.7	58.43	9
2	1	2.1	2.6	8.45	3
3	3	6.5	3.2	48.20	6
4	3	5.9	2.5	50.28	5
5	3	9.6	2.1	68.34	7
6	3	9.6	2.3	59.64	11
7	2	3.0	1.2	24.56	6
8	2	3.6	3.0	31.06	5
9	3	7.6	2.7	78.09	7
10	3	7.3	3.2	41.81	9
11	3	9.7	3.8	78.20	7
12	2	1.6	0.3	20.11	8
13	3	3.1	2.2	67.58	8
15	1	0.3	0.3	0.05	1
16	1	0.2	0.2	1.79	4
17	2	1.7	0.9	17.38	4
18	2	4.6	3.9	47.94	6
19	4	4.5	2.0	106.38	7
20	1	1.6	1.3	10.25	5
21	4	8.5	1.8	98.61	11
22	1	1.7	0.7	9.86	5
23	1	0.6	0.7	2.67	3
24	2	2.3	2.9	15.06	7
25	3	6.1	2.2	68.07	9

26	3	5.6	0.7	59.48	6
27	2	1.5	1.2	28.42	7
28	2	1.1	0.8	12.28	5
29	4	9.4	3.3	78.66	12
30	1	2.7	1.4	13.23	3
31	2	4.1	3.0	56.88	9
32	1	0.4	0.3	1.12	5
33	2	3.5	2.0	47.56	6
34	4	16.2	1.2	101.52	8
35	4	16.2	0.8	88.05	4
36	1	0.0	0.0	2.84	6
37	4	14.4	2.4	71.27	5
38	4	13.2	0.9	89.44	6
39	4	12.4	1.3	109.81	3
40	5	11.2	2.4	123.79	7
41	5	11.2	2.5	70.11	7
42	4	12.4	4.6	83.97	6
43	5	13.6	5.1	78.20	7
44	5	14.7	0.8	147.66	5
45	5	12.5	2.9	125.15	7
46	5	12.8	3.5	86.86	7
47	5	13.0	2.1	86.01	5
48	5	11.2	0.9	61.42	5
49	5	13.2	3.5	70.82	9
50	4	10.3	1.7	95.33	6
51	5	12.8	5.3	154.20	6
52	1	2.1	1.1	13.97	8

(c) LA CLOCHE ALVAR

Quadrat No.	Vegetation Class	Soil Depth (cm)		Biomass ($g/0.25m^2$)	Species Richness ($\#/0.25m^2$)
		Mean	St. Dev.		
1	2	3.9	1.0	25.04	12
2	1	2.4	1.5	2.97	4
3	1	2.4	1.5	6.15	3
4	2	2.5	0.6	10.65	6
5	2	2.6	2.1	11.06	7
6	1	5.1	1.4	6.20	7
7	2	3.7	2.3	12.88	5
8	3	4.0	1.9	13.98	8
9	5	4.4	2.1	18.42	7
10	5	6.8	1.7	34.89	6
11	5	6.6	1.2	23.16	6
12	4	6.0	1.1	14.16	6
13	4	6.1	6.4	27.30	5
14	4	4.8	4.1	30.32	5
15	5	4.7	2.9	36.71	8
16	4	4.7	3.2	20.22	11
17	5	8.4	5.4	32.99	5

18	4	5.9	3.0	17.77	7
19	5	7.5	4.9	38.13	4
20	5	4.2	2.8	33.78	3
21	5	6.0	2.1	42.73	4
22	5	5.8	3.6	18.54	5
23	1	1.8	1.1	1.45	3
24	4	4.3	2.9	32.68	6
25	1	0.8	1.0	4.39	3
26	1	1.5	0.9	3.67	5
27	1	1.9	0.7	2.39	4
28	1	1.5	1.3	2.10	5
29	1	0.5	0.7	3.61	5
30	1	0.9	1.3	4.76	3
31	2	3.7	2.1	4.67	7
32	2	2.8	3.6	6.59	6
33	2	2.6	1.3	5.14	9
34	2	6.0	1.8	6.88	4
35	2	3.2	2.0	6.35	6
36	2	0.6	0.6	8.56	3
37	3	6.8	2.5	10.23	7
38	3	2.3	1.4	16.57	6
39	3	3.9	3.5	23.05	4
40	3	4.3	3.9	25.98	10
41	3	2.2	1.9	16.39	8
42	3	-	-	8.25	9
43	3	2.6	2.7	13.48	5
44	4	1.7	1.3	14.45	4
45	3	2.4	1.3	15.95	6
46	4	11.4	2.2	43.66	7
47	4	8.5	2.8	11.81	6
48	4	7.7	2.2	27.78	4
49	4	7.2	3.1	22.87	7
50	5	24.4	0.8	41.66	6

(d) MISERY BAY ALVAR

Quadrat No.	Vegetation Class	Soil Depth (cm)		Biomass ($g/0.25m^2$)	Species Richness ($\#/0.25m^2$)
		Mean	St. Dev.		
1	5	9.8	3.0	19.11	9
2	1	0.2	0.3	0.54	3
3	4	3.5	5.9	18.41	9
4	3	2.0	2.6	14.66	8
5	2	0.3	0.7	2.80	2
6	3	6.0	3.0	12.50	9
7	3	6.6	3.8	10.35	9
8	1	1.6	1.6	2.94	5
9	2	0.6	0.8	3.64	4
10	1	0.2	0.2	2.02	4

11	1	0.4	0.4	1.82	4
12	1	0.2	0.4	5.05	5
13	3	5.8	2.6	5.19	10
14	4	8.2	3.9	14.10	6
15	2	0.7	0.8	3.67	4
16	2	1.5	2.4	6.65	6
17	2	0.5	0.7	1.88	5
18	1	0.6	1.3	3.61	7
19	2	3.5	1.3	8.99	12
20	2	2.0	0.8	6.60	10
21	1	0.8	1.1	3.58	6
22	4	2.0	1.8	3.40	5
23	4	0.1	0.2	11.79	6
24	3	2.1	1.7	9.60	9
25	4	5.0	4.5	16.45	5
26	5	6.3	2.4	62.14	3
27	3	2.3	1.4	16.26	4
28	2	0.5	0.5	5.82	4
29	4	5.3	1.5	21.55	7
30	5	4.2	1.8	27.41	6
31	1	0.3	0.6	4.33	2
32	1	0.2	0.3	3.02	3
33	2	3.5	1.1	7.03	5
34	2	3.5	0.6	11.11	10
35	1	0.6	0.7	2.05	4
36	5	10.8	4.2	22.49	3
37	5	8.6	3.3	19.13	3
38	5	6.6	4.8	34.28	3
39	5	15.1	5.8	27.40	6
40	3	3.3	1.1	9.80	12
41	3	2.0	3.7	5.43	9
42	4	2.3	1.7	11.37	4
43	3	2.0	0.7	4.16	2
44	5	7.3	3.8	92.48	1
45	5	5.9	1.4	54.82	2
46	5	5.9	2.6	45.18	2
47	4	5.7	4.3	14.90	6
48	4	6.0	2.6	13.17	5
49	4	1.7	1.5	21.03	5
50	4	2.2	1.6	5.63	7

Appendix 1.5a.

Vascular plant species sampled at Burnt Lands. Species are listed in order of decreasing frequency (frequency is the % of quadrats in which each occurred). Species listed below the dotted line had a frequency of less than 5% and were not included in the multivariate analysis. The species marked with an asterisk (*) is classified as provincially rare in Ontario (Argus *et al.* 1987).

Species	Frequency (%)
1. *Senecio pauperculus*	58.2
2. *Carex crawei*	44.9
3. *Danthonia spicata*	43.9
4. *Hieracium piloselloides*	39.8
5. *Panicum philadelphicum*	39.8
6. *Sporobolus vaginiflorus*	35.7
7. *Solidago ptarmicoides*	33.7
8. *Trichostema brachiatum*	25.5
9. *Scutellaria parvula*	23.5
10. *Sporobolus heterolepis* *	23.5
11. *Poa pratensis*	21.4
12. *Saxifraga virginiensis*	21.4
13. *Ambrosia artemesiifolia*	20.4
14. *Hypericum perforatum*	20.4
15. *Solidago nemoralis*	18.4
16. *Campanula rotundifolia*	17.3
17. *Minuartia michauxii*	17.3
18. *Fragaria virginiana*	12.2
19. *Chaenorrhinum minus*	8.2
20. *Potentilla recta*	8.2
21. *Carex bebbii*	6.1
22. *Carex richardsonii*	6.1
23. *Carex umbellata*	6.1
24. *Elymus trachycaulus*	6.1
25. *Panicum flexile*	6.1
26. *Hedeoma hispida*	5.1
....	
Carex lanuginosa	4.1
Carex rugosperma	4.1
Muhlenbergia mexicana	4.1
Rosa acicularis	4.1
Verbascum thapsus	3.1
Viccia cracca	3.1
Antennaria neglecta	2.0

Aster ciliolatus	2.0
Chrysanthemum leucanthemum	2.0
Echium vulgare	2.0
Geranium bicknellii	2.0
Melilotus spp.	2.0
Panicum acuminatum	2.0
Penstemon hirsutus	2.0
Bromus kalmii	1.0
Rhus radicans	1.0
Sisyrinchium montanum	1.0

Appendix 1.5b.

Vascular plant species sampled at all 4 Ontario alvar sites. Species are listed in order of decreasing frequency (frequency is the % of quadrats in which each occurred). Species listed below the dotted lines had a frequency of less than 5% and were not included in the multivariate analysis. Rare species are marked with an asterisk (* - provincially rare in Ontario (Argus *et al.* 1987); ** - rare in Canada (Argus and Pryor 1990).

Species	Frequency (%)
1. *Sporobolus heterolepis* *	31.5
2. *Panicum philadelphicum*	29.5
3. *Scutellaria parvula*	29.0
4. *Carex crawei*	27.0
5. *Poa compressa*	26.5
6. *Danthonia spicata*	24.5
7. *Ambrosia artemesiifolia*	23.5
8. *Trichostema brachiatum*	23.5
9. *Sporobolus vaginiflorus*	23.0
10. *Allium cernuum* *	22.0
11. *Senecio pauperculus*	21.0
12. *Schizachyrium scoparium*	19.5
13. *Eleocharis compressa*	17.5
14. *Minuartia michauxii*	17.0
15. *Calamintha arkansana*	14.0
16. *Solidago ptarmicoides*	13.5
17. *Hypericum perforatum*	13.0
18. *Saxifraga virginiensis*	11.0
19 *Hieracium piloselloides*	10.5
20. *Deschampsia cespitosa*	8.5
21. *Fragaria virginiana*	8.0
22. *Ratibida pinnata* **	8.0
23. *Elymus trachycaulus*	7.5
24. *Campanula rotundifolia*	7.0
25. *Geranium bicknellii*	7.0
26. *Artemisia campestris*	6.5
27. *Rumex crispus*	6.5
28. *Ranunculus fascicularis*	6.0
29. *Andropogon gerardii*	5.5
30. *Antennaria neglecta*	5.5
31. *Carex umbellata*	5.5
32. *Poa pratensis*	5.5
33. *Scirpus atrovirens*	5.5
34. *Juncus dudleyi*	5.0

35.	*Melilotus spp.*	5.0
36.	*Solidago nemoralis*	5.0

....

Chaenorrhinum minus	4.5
Aster pilosus	3.5
Agrostis scabra	3.5
Comandra umbellata	3.5
Leucospora multifida **	3.5
Panicum acuminatum	3.5
Arabis hirsuta	3.0
Carex lanuginosa	3.0
Carex scirpoidea	3.0
Agrostis gigantea	2.0
Carex molesta	2.0
Geum triflorum	2.0
Medicago sativa	2.0
Verbena simplex	2.0
Allium schoenoprasum	1.5
Arenaria serpyllifolia	1.5
Carex richardsonia	1.5
Cerastium arvense	1.5
Hymenoxys acaulis **	1.5
Liatris cylindraceae	1.5
Lotus corniculatus	1.5
Panicum flexile	1.5
Aster ericoides	1.0
Carex bebbii	1.0
Carex rugosperma	1.0
Hedeoma hispida	1.0
Penstemon hirsutus	1.0
Potentilla norvegica	1.0
Potentilla recta	1.0
Portulaca olearca	1.0
Setaria viridis	1.0
Viccia cracca	1.0
Aster ciliolatus	0.5
Calamagrostis canadensis	0.5
Castillega coccinea	0.5
Carex divulsa	0.5
Clintonia vulgaris	0.5
Echium vulgare	0.5
Festuca saximontana	0.5
Hypericum kalmianum	0.5
Juncus balticus	0.5
Lepidium campestris	0.5
Muhlenbergia glomerata	0.5
Muhlenbergia mexicana	0.5
Prunella vulgaris	0.5
Rosa acicularis	0.5
Sisyrinchium montanum	0.5
Sporobolus neglectus	0.5

Verbascum thapsus	0.5

Appendix 1.6a.

DCA scores for species (with ≥ 5% frequency; names given in Appendix 1.5a) and quadrats; within Burnt Lands. Eigenvalues for the first 4 axes are 0.72, 0.30, 0.35, 0.15.

SPECIES SCORES; WITHIN BURNT LANDS

SPECIES	AX1	AX2	AX3	AX4
1	158	25	155	185
2	0	178	58	205
3	103	125	309	294
4	127	165	271	224
5	386	57	187	163
6	280	63	23	161
7	86	245	286	82
8	297	204	187	333
9	274	241	196	172
10	-68	175	123	186
11	143	93	-60	146
12	536	212	145	138
13	299	293	61	367
14	227	345	213	318
15	96	307	293	124
16	83	249	205	121
17	445	297	90	381
18	131	290	147	14
19	330	329	225	0
20	125	342	-99	291
21	37	318	125	392
22	67	62	250	6
23	96	-26	417	308
24	265	-71	315	392
25	242	417	117	240
26	302	-165	211	76

QUADRAT SCORES; WITHIN BURNT LANDS

QUADRAT #	AX1	AX2	AX3	AX4
1	354	59	136	163
2	215	296	165	264
3	89	139	203	183
4	536	212	145	138
5	520	195	150	141
7	188	118	231	268
8	0	154	109	199
9	18	162	143	193
10	43	191	147	121
11	32	139	152	217
12	12	158	138	192

13	303	62	134	169
14	136	128	267	229
15	101	182	193	199
16	83	216	212	159
17	83	192	220	184
18	92	193	220	206
19	159	134	34	186
20	93	196	0	212
21	536	212	145	138
22	92	156	279	212
23	261	113	193	149
24	113	133	129	199
25	294	0	136	145
26	283	44	161	192
27	291	191	186	125
28	333	60	105	162
29	536	212	145	138
30	330	329	225	0
31	508	213	139	181
32	293	116	115	210
33	298	99	143	207
34	32	130	124	200
35	38	155	156	192
36	121	119	156	220
37	237	112	127	177
38	204	120	175	218
39	32	156	156	222
40	236	100	199	180
41	309	66	130	163
42	536	212	145	138
43	134	176	158	183
44	153	194	166	225
45	140	99	30	173
46	85	141	17	183
47	125	155	64	184
48	139	114	53	172
49	378	177	171	214
50*				
51	536	212	145	138
52	347	88	154	197
53	338	135	117	226
55	216	164	79	193
56	362	226	98	317
57	238	56	49	166
58	51	154	108	193
59	126	178	134	142
60	296	158	129	265
61	445	297	90	381
62	192	124	162	167
63	363	54	184	165
64	149	118	175	211

65	236	148	213	176
66	520	227	135	182
67	116	164	231	154
68	367	122	111	185
69	469	153	159	163
70	18	214	135	244
71	415	130	161	187
72	9	158	123	195
73	40	142	168	216
74	24	134	116	197
75	36	146	146	193
76	38	108	125	183
77	37	129	112	187
78	21	134	108	193
79	35	112	130	188
80	37	136	119	182
81	43	173	125	158
82	483	171	154	165
83	354	59	136	163
84	345	104	167	216
85	255	107	190	216
86	247	125	224	257
87	429	159	148	196
88	431	160	168	172
89	416	103	172	177
90	421	127	173	173
91	429	145	178	133
92	145	187	223	253
93	185	328	155	202
94	232	318	134	284
95	243	283	155	232
96	210	297	174	200
97	141	163	191	245
98	247	278	160	189
99	74	185	215	144
100	87	169	207	205
101	78	220	190	233

* quadrat 50 was omitted by DCA due to lack of vegetation data.

Appendix 1.6b.

DCA scores for species (with ≥ 5% frequency; names given in Appendix 1.5b) and quadrats; among sites. The letters B, S, M, and L in the quadrat names refer to sites (Burnt Lands, Stone Road, Misery Bay and La Cloche, respectively). Eigenvalues for the first four axes are 0.79, 0.51, 0.35, 0.28.

SPECIES SCORES; AMONG SITES

SPECIES	AX1	AX2	AX3	AX4
1	508	361	226	296
2	242	145	232	220
3	290	356	175	72
4	604	264	116	120
5	70	325	141	186
6	485	225	181	79
7	368	475	86	229
8	233	195	204	277
9	404	169	-24	385
10	51	293	200	178
11	423	199	98	110
12	562	285	325	222
13	179	362	125	216
14	368	102	399	218
15	395	432	351	173
16	446	190	133	-10
17	277	365	83	-6
18	300	0	300	125
19	426	150	78	-73
20	344	567	277	97
21	300	191	99	47
22	64	305	137	74
23	403	378	366	71
24	439	128	120	-33
25	340	278	282	142
26	374	81	491	133
27	127	299	276	137
28	397	349	30	353
29	-58	282	204	177
30	776	313	133	293
31	547	312	282	47
32	463	131	-19	-31
33	-54	273	217	179
34	216	234	327	330
35	-22	297	170	171

36	426	144	80	-73

QUADRAT SCORES; AMONG SITES

QUADRAT #	AX1	AX2	AX3	AX4
B1	292	152	154	271
B2	344	329	118	72
B4	300	0	300	125
B5	293	16	293	135
B7	410	252	158	121
B8	535	293	161	189
B10	452	261	147	141
B12	519	284	164	173
B15	487	243	131	64
B16	465	180	108	0
B18	473	202	119	31
B20	518	190	53	28
B23	340	246	151	125
B24	473	216	102	136
B27	318	169	194	122
B29	300	0	300	125
B31	306	29	311	148
B32	348	231	101	236
B33	331	207	144	229
B35	502	260	148	138
B37	376	239	82	196
B40	350	232	153	91
B44	394	221	100	64
B46	515	206	53	45
B48	480	189	44	135
B49	276	174	242	173
B53	311	178	144	279
B56	340	221	223	249
B58	491	284	145	191
B59	439	173	70	60
B61	368	102	399	218
B62	385	183	106	156
B65	362	204	166	107
B68	319	150	170	211
B71	273	109	243	209
B72	526	283	157	170
B74	517	279	152	177
B76	470	281	159	200
B78	519	281	150	181
B80	502	269	144	165
B82	287	53	287	161
B84	259	164	191	258
B86	346	236	189	118
B88	288	84	269	166
B91	264	89	258	183

B93	333	250	113	20
B95	323	252	98	146
B97	455	278	153	69
B99	481	186	110	3
S1	168	285	175	169
S2	204	175	226	212
S3	143	302	169	186
S4	132	279	176	203
S5	160	280	175	197
S6	163	306	166	149
S7	178	241	213	188
S8	184	241	208	179
S9	120	318	161	158
S10	130	332	153	162
S11	124	332	156	176
S12	200	234	207	199
S13	147	265	188	199
S15*				
S16	232	185	251	268
S17	231	189	209	244
S18	205	206	218	223
S19	181	286	162	128
S20	235	180	223	260
S21	154	284	161	126
S22	202	198	229	238
S23	236	165	253	244
S24	142	232	207	181
S25	151	275	181	191
S26	181	274	182	195
S27	181	243	206	190
S28	183	223	224	225
S29	159	293	170	172
S30	234	183	227	264
S31	150	233	203	212
S32	213	213	267	281
S33	165	263	204	185
S34	87	323	157	180
S35	95	330	148	194
S36	192	216	233	255
S37	94	325	157	187
S38	78	321	158	189
S39	49	308	169	181
S40	32	291	169	169
S41	31	285	174	160
S42	0	295	185	178
S43	21	295	183	184
S44	24	297	171	175
S45	54	290	166	160
S46	29	296	176	176
S47	11	292	183	176
S48	35	309	173	187

S49	25	296	181	172
S50	16	301	171	169
S51	47	278	170	153
S52	149	263	228	235
M1	334	337	172	202
M2	389	366	361	182
M3	512	284	238	184
M4	482	304	255	123
M5	358	530	297	118
M6	381	404	251	200
M7	363	325	250	202
M8	395	329	318	149
M9	376	418	268	202
M10	484	263	361	178
M11	261	102	308	142
M12	456	184	374	212
M13	420	315	241	157
M14	451	378	252	219
M15	425	287	372	188
M16	443	286	345	202
M17	313	88	358	164
M18	391	216	307	145
M19	322	128	334	165
M20	365	292	290	170
M21	333	139	357	155
M22	341	389	178	199
M23	336	537	263	94
M24	422	348	216	213
M25	322	456	187	98
M26	357	524	261	114
M27	279	463	162	176
M28	316	406	148	148
M29	319	438	167	121
M30	339	482	144	162
M31	348	554	250	116
M32	382	199	404	149
M33	322	279	297	195
M34	306	297	284	166
M35	380	297	398	101
M36	421	371	240	254
M37	506	348	221	274
M38	518	352	215	278
M39	529	287	171	172
M40	354	186	308	162
M41	355	223	255	208
M42	458	352	207	227
M43	349	548	239	124
M44	508	361	226	296
M45	508	361	226	296
M46	458	402	176	272
M47	333	482	204	148

M48	325	446	225	111
M49	477	322	187	215
M50	373	321	289	175
L1	311	289	93	239
L2	330	261	31	314
L3	388	327	31	315
L4	390	257	79	329
L5	462	268	141	297
L6	397	246	128	264
L7	265	304	133	225
L8	223	336	130	207
L9	509	283	197	195
L10	510	312	182	240
L11	544	337	187	271
L12	463	386	282	213
L13	553	319	226	245
L14	518	309	228	236
L15	467	338	238	209
L16	551	266	214	128
L17	531	281	135	252
L18	448	247	175	272
L19	451	323	167	221
L20	447	336	171	229
L21	458	287	118	251
L22	505	277	114	261
L23	349	200	55	340
L24	559	301	238	173
L25	353	198	49	343
L26	343	221	248	254
L27	400	200	127	309
L28	400	206	73	276
L29	414	210	41	236
L30	395	245	4	346
L31	448	239	66	229
L32	402	269	125	288
L33	461	234	129	271
L34	433	275	110	273
L35	381	279	167	246
L36	380	214	0	355
L37	550	268	209	155
L38	505	245	194	113
L39	570	268	224	166
L40	550	280	190	178
L41	537	269	208	147
L42	515	233	177	101
L43	564	264	194	151
L44	559	268	218	157
L45	530	252	174	207
L46	560	315	228	218
L47	477	306	224	261
L48	559	296	221	201

L49	536	298	219	223
L50	526	289	171	177

* Quadrat S15 was omitted by DCA due to shortage of vegetation data.

Appendix 1.7a.

Quadrats included in each of the 7 TWINSPAN groups (quadrat classification); within Burnt Lands.

TWINSPAN GROUP	QUADRATS INCLUDED
Tall Grassy Meadows	8 9 10 11 12 34 35 36 39 58 64 70 72 73 74 75 76 77 78 79 80 81
Tall Forb-Rich Meadows	3 15 16 17 18 20 22 24 43 45 46 48 59 67 90 100 101
Low Grassy Meadows	7 13 19 23 25 26 32 33 37 38 40 41 47 55 57 60 62 65 85 86 97
Low Forb-Rich Meadows	2 14 44 92 93 94 95 96 98
Dry Grassland	1 28 52 53 56 68 71 83 84
Rock Margin Grassland	5 31 69 82 87 88 90 91 27 49 63 89
Bare Rock Flats	4 21 29 30 42 51 61 66

Appendix 1.7b.

Quadrats included in each of the 8 TWINSPAN groups (quadrat classification); among sites.

TWINSPAN GROUP	QUADRATS INCLUDED
La Cloche Tall Meadows	B8 B10 B12 B72 B74 B76 B78 B80 M30 M37 M38 M39 M44 M45 L4 L5 L6 L9 L10 L11 L13 L14 L15 L16 L17 L18 L19 L20 L21 L22 L24 L37 L38 L39 L40 L41 L42 L43 L44 L45 L46 L47 L48 L49 L50
Burnt Lands Low Meadows	B7 B15 B16 B18 B20 B23 B24 B33 B35 B37 B40 B44 B46 B48 B58 B59 B62 B65 B86 B97 B99 L1 L23 L25 L29 L31
Misery Bay - La Cloche Low Meadows	B2 B32 M1 M5 M6 M9 M13 M14 M22 M24 M29 M30 M31 M36 M42 M43 M46 M47 M49 L2 L3 L12 L27 L28 L30 L32 L33 L34 L35 L36
Misery Bay Pavement	B61 M2 M4 M7 M8 M10 M12 M15 M16 M18 M20 M26 M32 M35 M40 M41 M50 L26
Mixed-Site Rock Flats	B4 B29 M11 M17 M21 L7
Burnt Lands Rock Margins	B1 B5 B27 B31 B49 B53 B56 B68 B71 B82 B84 B88 B91 S23 M19 M33 M34
Stone Road Dry Grassland	B93 B95 S1 S2 S3 S4 S5 S6 S7 S8 S9 S10 S11 S12 S13 S16 S17 S18 S18 S20 S21 S22 S24 S25 S26 S27 S28 S29 S30 S31 S32 S33 S36 S52 M23 M25 M27 M28 M48 L8
Stone Road Dry Prairie	S34 S35 S37 S38 S39 S40 S41 S42 S43 S44 S45 S46 S47 S48 S49 S50 S51

Appendix 1.8.

Ordination and classification of species; within Burnt Lands.

Results of the species ordination (Fig. a) and classification (Fig. b, Table a) show species relationships similar to the associations discussed in the quadrat classification discussed in chapter 1. *Sporobolus heterolepis*, and *Carex crawei*, had average loadings low on axis 1 (Fig. b), corresponding to sites with high biomass and deep soil (see Fig. 1.4). At the opposite extreme, where soil depth and plant biomass were low, *Saxifraga virginiensis* and *Minuartia michauxii* had the highest average loadings (Fig. a). Species weightings along the second axis are consistent with the potential moisture/disturbance gradient. At the lower end of this axis were species of moist or prairie grasslands (*Hedeoma hispida, Elymus trachycaulum* and *Carex umbellata*) whereas at the upper end were species of dry fields and disturbed sites (*Panicum flexile, Hypericum perforatum* and *Potentilla recta.* Species overlays presented in chapter 1 (see Fig. 1.5) illustrate the overall distribution of some of these species.

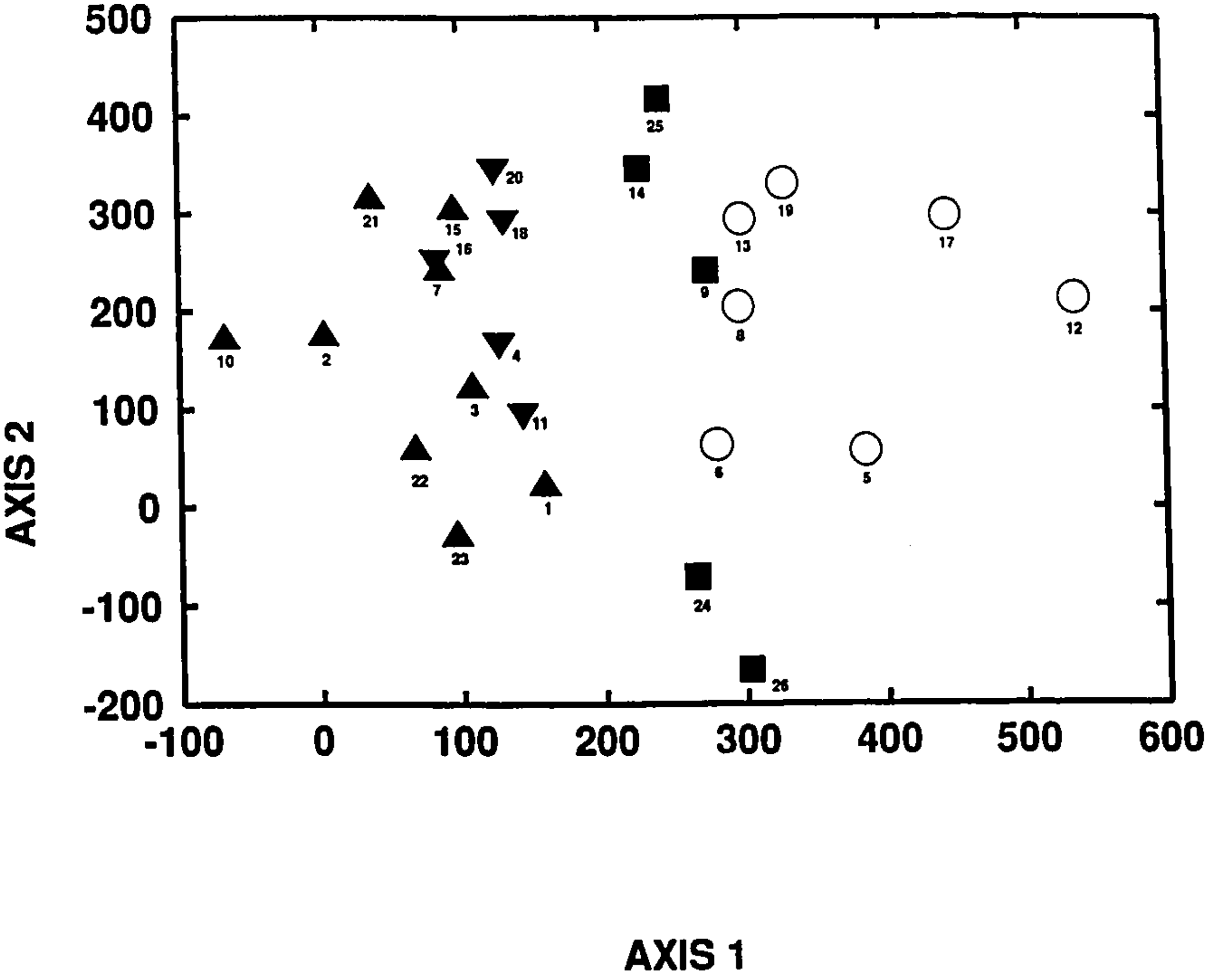
The main division, revealed by classification, was between rock flat and meadow species (Fig. b, Table a). The rock flat species (Group 1) included small annuals and stress-tolerant perennials. As mentioned, the evergreen perennials (*M. michauxii* and *S. virginiensis*) occupied the extremely shallow soil sites. These evergreen species are able to grow and flower early in the season before the summer drought. The other species in the group were all summer annuals which germinate in the spring when moisture and light are non-limiting (Baskin and Baskin 1985a). Two of these species (*P. philadelphicum* and *T. brachiatum*) are largely confined to alvars in Ontario (Catling *et al.* 1975).

The meadow species (Groups 1-3) occupied the intermediate to high biomass/soil depth sites (see Fig. 1.4). The second division split off a small group of 'old-field' species (Group 3) which occurred at intermediate soil depth sites. These species can be found in old-field habitats or disturbed grasslands. The annual *Panicum flexile* and the perennials *Hypericum perforatum* and *Scutellaria parvula* all occurred high on axis 2 (Fig. a).

The remainder of the meadow species were further separated into two groups. The 'alvar meadow species' (Group 1) occurred where soil depth was greatest and included sedges, perennial bunchgrasses and composites, all of which are important Canadian alvar species (Catling *et al.* 1975). The 'general grasslands' (Group 2) occurred where soil depth was slightly shallower and included a few species common to many grassland systems.

Appendix 1.8; Figure a.

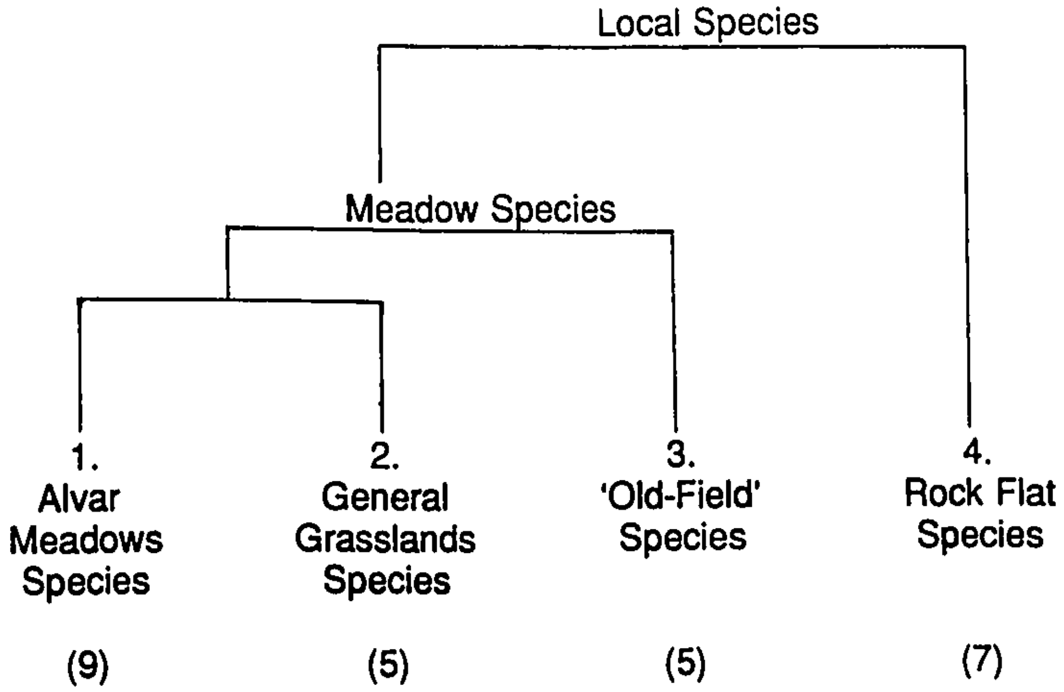
Within Burnt Lands species ordination. Species scores, as determined by DCA, are plotted on the ordination axes (1 vs. 2). Numbers correspond to species, as listed in Appendix 1.5a. Symbols refer to the four TWINSPAN species groups (see Fig. b and Table a in this Appendix): Alvar Meadow species (filled triangle up), General Grassland species (filled triangle down), Old-field species (filled square), and Rock Flat species (open circle).



Appendix 1.8
Figure a

Appendix 1.8; Figure b.

Within Burnt Lands dendrogram for species classification, as determined by TWINSPAN. The number of species in each group is shown in brackets (included species are listed in Appendix 1.8, Table a).



Appendix 1.8
Figure b

Appendix 1.8; Table a.

Species members in each of 4 TWINSPAN clusters; within Burnt Lands. The clusters were produced by classification of species at three levels of division (see Appendix 1.8, Fig. b).

Group 1	Group 2	Group 3	Group 4
Alvar Meadow Species	General Grassland Species	'Old-field' Species	Rock Flat Species
Carex bebbii	*Campanula rotundifolia*	*Elymus trachycaulus*	*Ambrosia artemesiifolia*
Carex crawei	*Fragaria virginiana*	*Hedeoma hispida*	*Chaenorrhinum minus*
Carex umbellata	*Hieracium piloselloides*	*Hypericum perforatum*	*Minuartia michauxii*
Danthonia spicata	*Poa pratensis*	*Panicum flexile*	*Panicum philadelphicum*
Senecio pauperculus	*Potentilla recta*	*Scutellaria parvula*	*Saxifraga virginiensis*
Solidago nemoralis			*Sporobolus vaginiflorus*
Solidago ptarmicoides			*Trichostema brachiatum*
Sporobolus heterolepis			

Appendix 1.9.

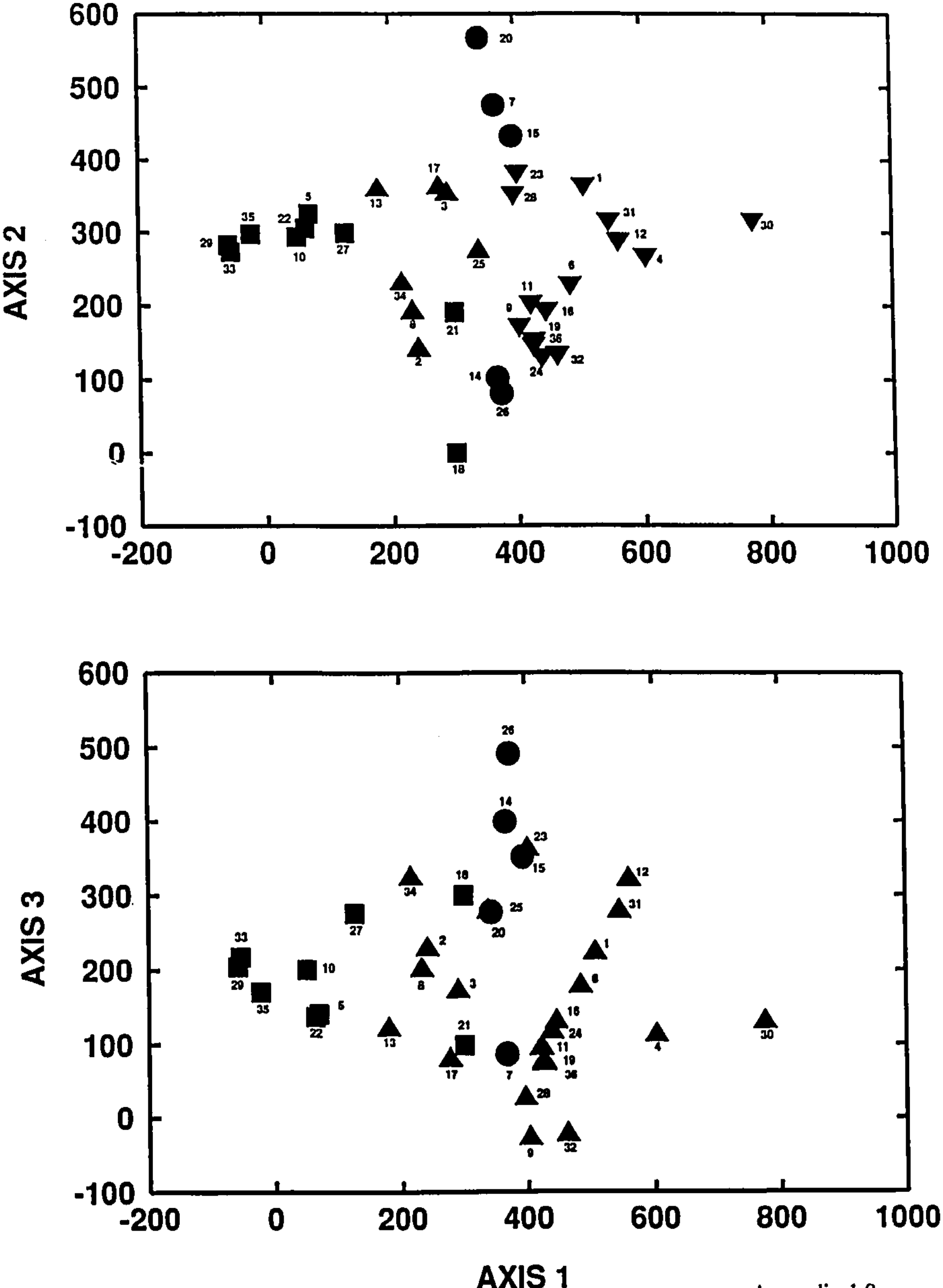
Ordination and classification of species; among sites.

Andropogon gerardii and *Scirpus atrovirens* had strong negative weights on axis 1 (Fig. a), corresponding to the high biomass, deep soil habitats of Stone Road (see Figs. 1.8 and 1.7). This is not surprising since these species occurred at none of the other 3 sites. At the extreme positive end of this axis was *Antennaria neglecta* (Fig. a), a rosette species which occurred mainly at La Cloche. Species overlays presented in chapter 1 (see Fig. 1.9) illustrate the overall distribution of some of these species.

The 4 TWINSPAN groups produced by species classification (Table a) were separated mainly along this first axis (Fig. b). These groups do not have any obvious ecological relationships but are associated, instead, by geographical distribution. At the high end of axis 1 was a large group (Group 1) consisting of species which occurred at Burnt Lands, La Cloche and Misery Bay. At the low end of this axis was a tight cluster (Group 4) of species (except *Fragaria* and *Saxifraga*) that were found only at Stone Road alvar, including two rare species: *Allium cernuum* and *Ratibida pinnata*. The other two TWINSPAN groups (Groups 2 and 3) consisted of species that are more general in distribution.

Appendix 1.9; Figure a.

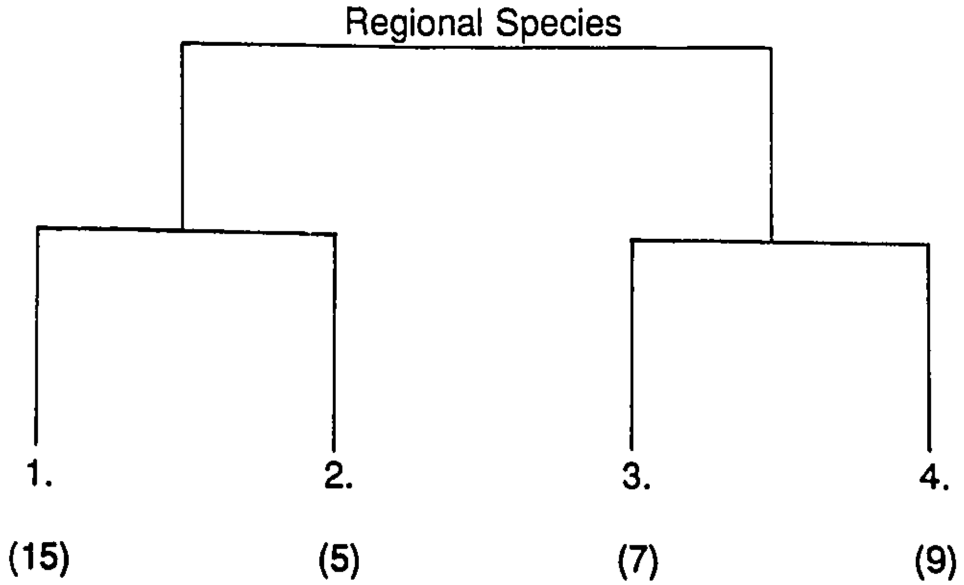
Among sites species ordinations. Species scores, as determined by DCA, are plotted on the ordination axes (1 vs. 2 and 1 vs. 3). Numbers correspond to species, as listed in Appendix 1.5b. Symbols refer to the four TWINSPAN species groups (see Appendix 1.9, Fig. b and Table a): Group 1 (filled triangle down), Group 2 (filled circle), Group 3 (filled triangle up) and Group 4 (filled square).



Appendix 1.9
Figure a

Appendix 1.9; Figure b.

Among sites dendrodgram for species classification, as determined by TWINSPAN. The number of species in each group is shown in brackets (included species are listed in Appendix 1.9, Table a).



Appendix 1.9
Figure b

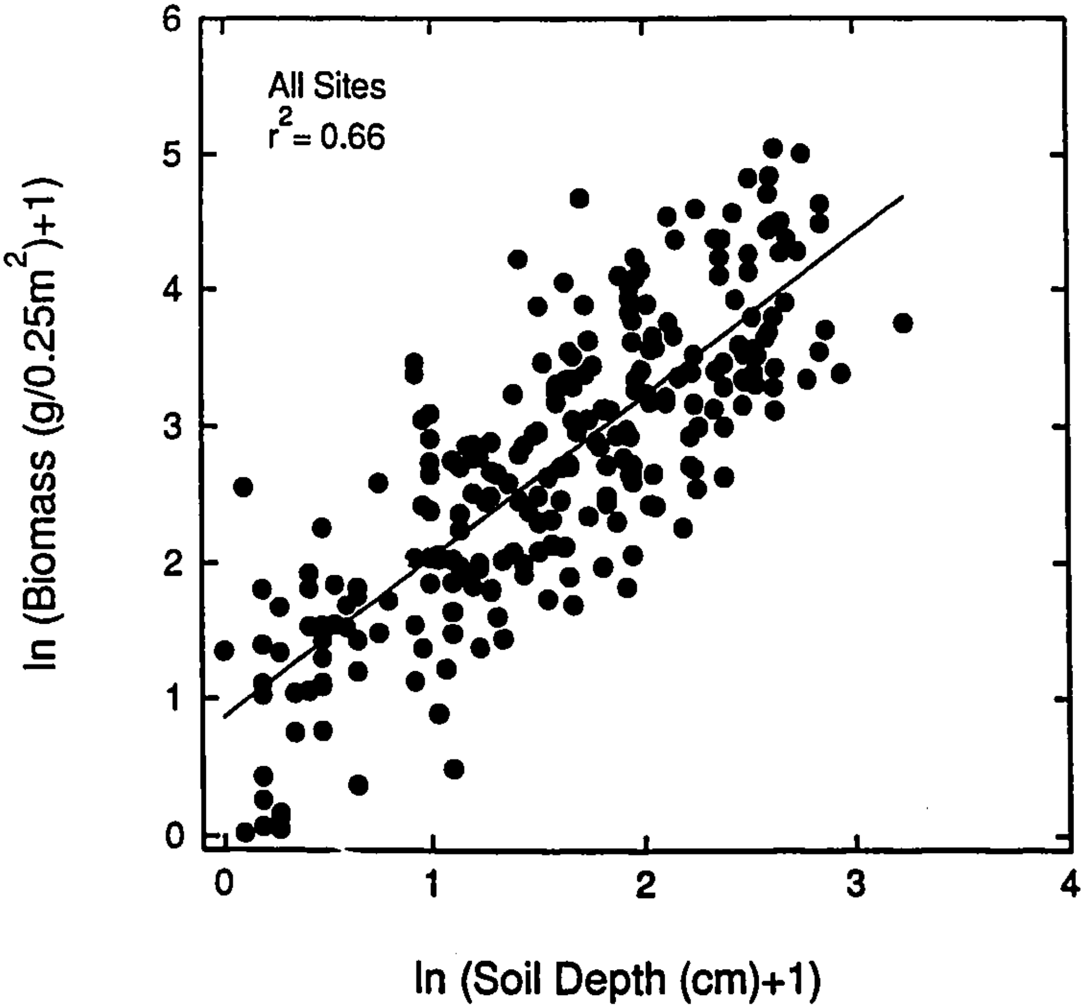
Appendix 1.9; Table a.

Species members in each of 4 TWINSPAN clusters; among sites. The clusters were produced by classification of species at two levels of division (see Appendix 1.9, Fig. b).

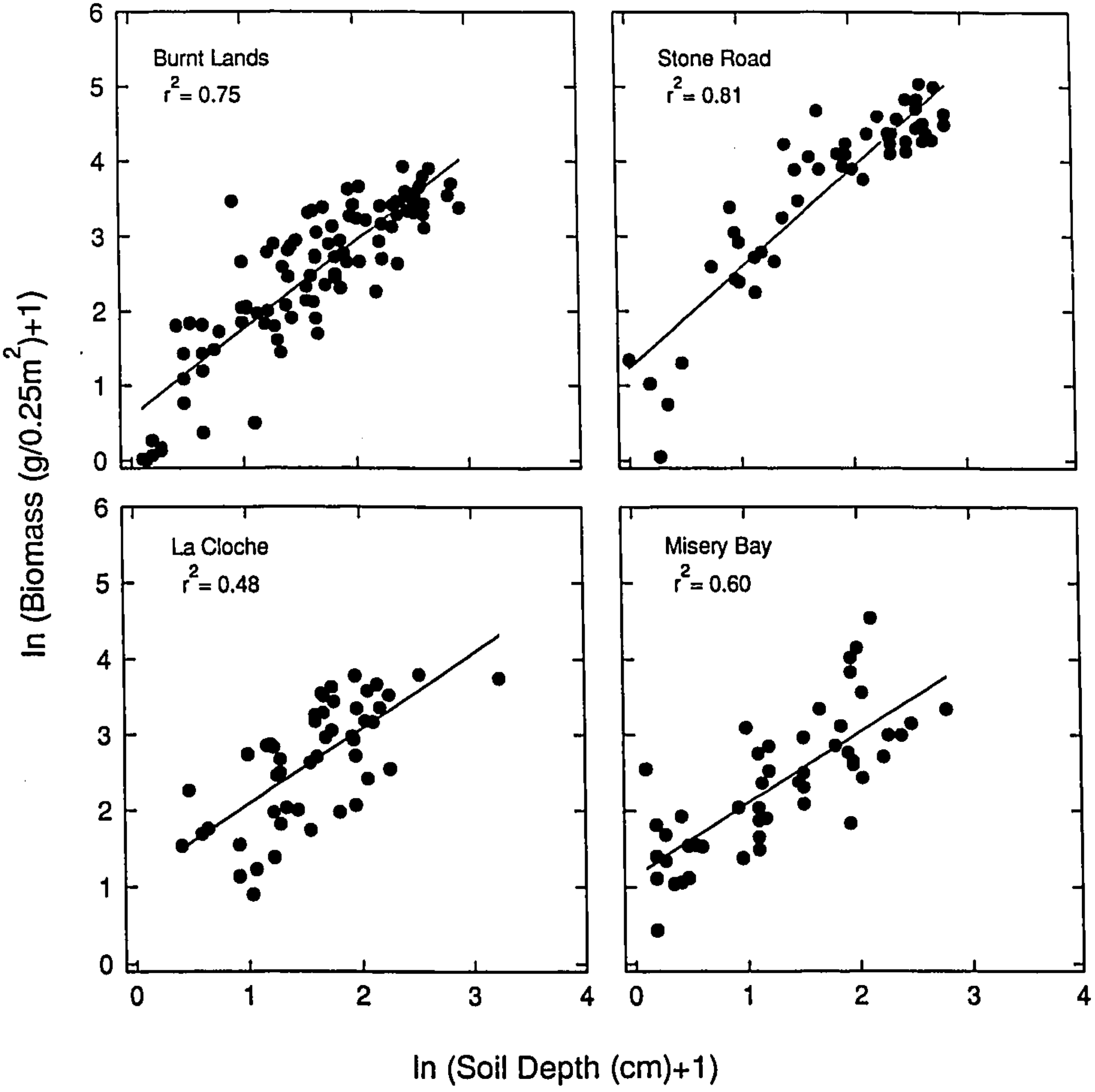
Group 1	Group 2	Group 3	Group 4
Antennaria neglecta	*Ambrosia artemesiifolia*	*Eleocharis compressa*	*Allium cernuum*
Carex umbellata	*Artemisia campestris*	*Geranium bicknellii*	*Andropogon gerardii*
Campanula rotundifolia	*Calamintha arkansana*	*Hypericum perfoliatum*	*Fragaria virginiana*
Carex crawei	*Deschampsia cespitosa*	*Juncus dudleyi*	*Melilotus spp.*
Danthonia spicata	*Minuartia michauxii*	*Panicum philadelphicum*	*Poa compressa*
Elymus trachycaulus		*Scutellaria parvula*	*Ratibida pinnata*
Hieracium piloselloides		*Trichostema brachiatum*	*Rumex crispus*
Poa pratensis			*Saxifraga virginiensis*
Ranunculus fascicularis			*Scirpus atrovirens*
Schizachyrium scoparium			
Senecio pauperculus			
Solidago nemoralis			
Solidago ptarmicoides			
Sporobolus heterolepis			
Sporobolus vaginiflorus			

Appendix 2.1.

Plot of biomass vs. soil depth on transformed scale for (a) all alvar sites and (b) each of the four sites. Regression equations are given in Table 2.2



Appendix 2.1a

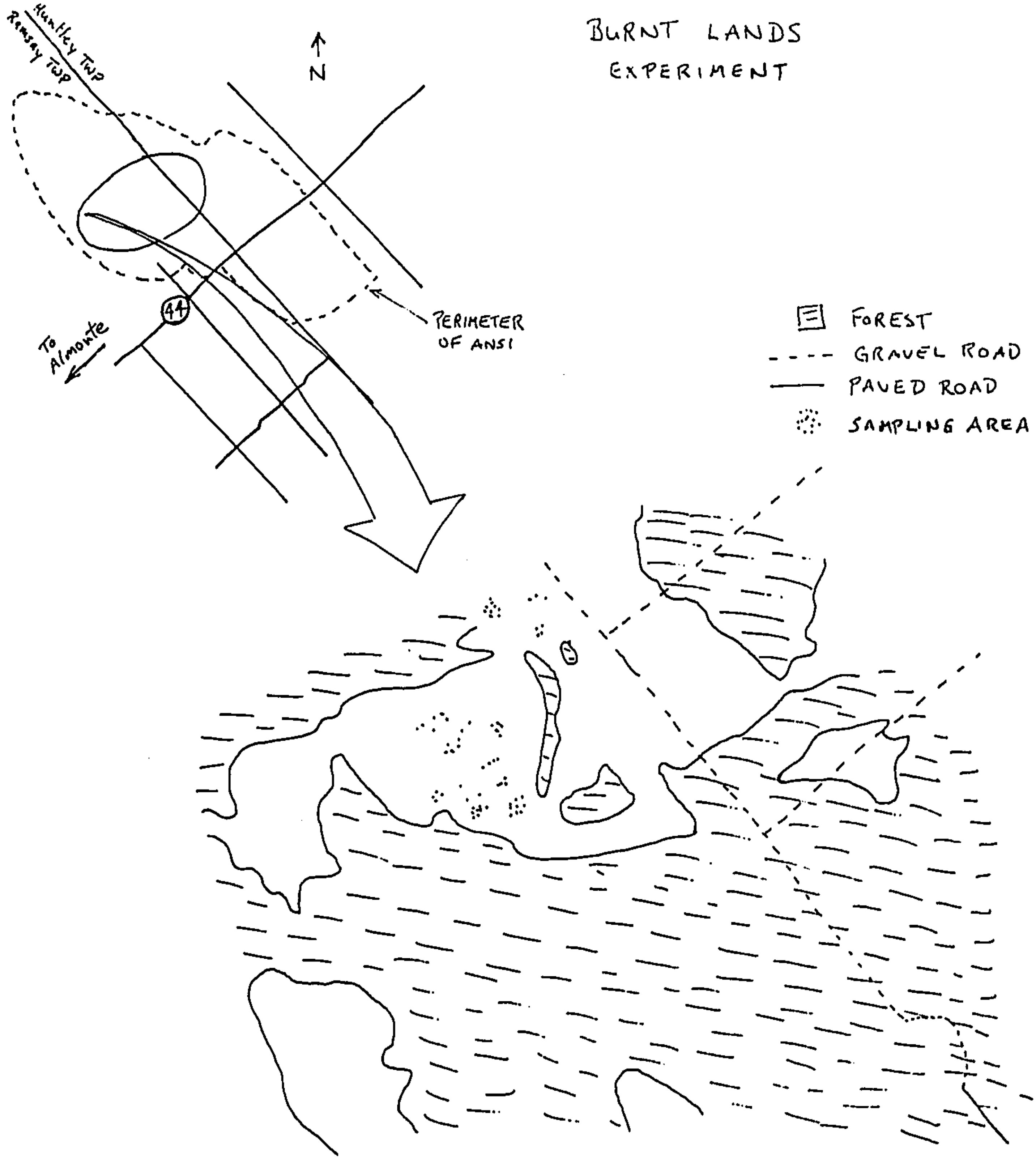


Appendix 2.1b

Appendix 3.1.

Map showing location of the Burnt Lands alvar in Eastern Ontario and the approximate locations of plots (stippled) in the competition experiment.

BURNT LANDS
EXPERIMENT



Appendix 3.1

Appendix 3.2.

Randomization scheme for plot treatments in the competition experiment. NN = no neighbours; NR = neighbour roots; NRS = neighbour roots and shoots and B = plot saved for fall biomass harvest. Also shown is the vegetation class assigned to the site (based on subjective estimate of biomass; 1 = low biomass, 5 = high biomass vegetation).

Sample	Vegetation Class	Treatment			
1	3	B	NR	NN	NRS
2	3	B	NN	NRS	NR
3	3	NN	NRS	NR	B
4	3	B	NN	NRS	NR
5	5	NN	NR	NRS	B
6	1	B	NN	NR	NRS
7	1	NN	NRS	NR	B
8	1	B	NN	NR	NRS
9	1	B	NN	NR	NRS
10	2	NN	NRS	NR	B
11	2	NN	NRS	NR	B
12	2	B	NRS	NR	NN
13	2	B	NR	NRS	NN
14	2	B	NR	NN	NRS
15	2	B	NRS	NN	NR
16	2	NR	NRS	NN	B
17	2	NN	NR	NRS	B
18	2	NN	NR	NRS	B
19	1	NRS	NN	NR	B

20	1	B	NN	NR	NRS
21	2	B	NN	NRS	NR
22	2	B	NR	NRS	NN
23	2	B	NRS	NR	NN
24	1	B	NN	NR	NRS
25	1	B	NN	NRS	NR
26	1	B	NN	NR	NRS
27	1	NR	NN	NRS	B
28	3	NRS	NR	NN	B
29	3	B	NRS	NN	NR
30	3	B	NRS	NN	NR
31	1	B	NN	NR	NRS
32	1	B	NRS	NN	NR
33	1	B	NR	NRS	NN
34	5	B	NRS	NN	B
35	5	B	NRS	NN	NR
36	3	B	NN	NRS	NR
37	3	NN	NRS	NR	B
38	3	B	NN	NR	NRS
39	3	B	NRS	NR	NN
40	4	B	NN	NRS	NR
41	4	B	NRS	NR	NN
42	4	B	NR	NN	NRS
43	4	NR	NN	NRS	B
44	5	B	NR	NRS	NN
45	5	NN	NR	NRS	B
46	4	NN	NRS	NR	B
47	4	B	NR	NN	NRS

48	4	B	NR	NN	NRS
49	5	B	NR	NRS	NN
50	5	NR	NN	NRS	B
51	5	B	NR	NN	NRS
52	5	B	NN	NRS	NR
53	5	NN	NRS	NR	B
54	5	B	NN	NRS	NR
55	5	NN	NR	NRS	B
56	5	B	NN	NR	NRS

Appendix 3.3.

Replacement dates for dead and dying seedling phytometers. Seedlings were replaced during the first two weeks of the competition experiment. Dates are shown for each treatment in the 56 experimental plots.

Sample	Treatment		
	NN	NR	NRS
1	06/17		
2	06/09;06/23		
3	06/23		06/09
4	06/09;06/23		
5	06/09		
6	06/09;06/28	06/09	06/09;06/28
7	06/09;06/28		06/09
8	06/17		
9	06/17;06/25		
10	06/09		
11	06/17		
12	06/17		
13	06/17		
14	06/17		
15	06/17		
16	06/17	06/23	
17	06/17		
18	06/17		
19	06/09;06/28	06/09	06/09
20	06/09	06/09	

21	06/17		
22	06/17		
23	06/17		
24	06/09;06/28		06/09
25	06/17		
26	06/09;06/17		
27	06/17		
28	06/23		
29	06/17		
30	06/23		
31	06/17		06/09
32	06/17		06/09;06/17
33	06/09;06/28	06/28	06/09
34	06/09;06/25	06/09	06/20
35	06/17		
36	06/23		
37	06/17		
38	06/09;06/23		
39	06/09		
40	06/17		
41	06/09;06/23	06/17	
42		06/17	06/17
43	06/09;06/23		06/17
44	06/17		
45	06/09;06/28		
46	06/09		
47	06/17		
48	06/09		

49	06/09;06/23		06/23
50	06/09;06/25		
51	06/09;06/23;06/25		
52	06/09;06/25		
53	06/09	06/17	
54	06/17;06/25		
55	06/09	06/09	
56	06/17		

Appendix 3.4.

Biomass and soil depth for each of the 56 experimental plots in the competition experiment. Biomass is given as actual mass harvested in the 25 cm x 25 cm sub-quadrat (g/0.0625m^2) and as calculated biomass per square metre (g/m^2). Biomass was harvested and soil depth measured on August 28 and 29, 1989.

Sample	Biomass (g/0.0625m^2)	Biomass (g/m^2)	Soil Depth (cm)
1	6.18	98.88	10.82
2	6.04	96.64	8.82
3	7.54	120.64	9.1
4	6.64	106.24	4.94
5	7.21	115.36	4.88
6	0.16	2.56	0.4
7	1.24	19.84	1.0
8	1.52	24.32	1.34
9	0.25	4.00	0.86
10	2.58	41.28	2.98
11	4.11	65.76	5.76
12	4.37	69.92	5.02
13	1.36	21.76	2.3
14	1.1	17.6	3.22
15	4.01	64.16	5.16
16	2.75	44.00	3.92
17	2.27	36.32	3.54
18	2.42	38.72	3.96
19	0.11	1.76	1.46
20	0.09	1.44	0.92
21	2.51	40.16	2.88
22	1.95	31.2	2.5
23	1.41	22.56	2.58
24	0.23	3.68	1.06
25	0.46	7.36	0.6
26	0.33	5.28	0.88
27	0.05	0.8	0.96
28	17.98	287.68	10.14
29	17.1	273.6	10.64
30	14.16	226.56	8.52
31	0.68	10.88	2.06
32	0.16	2.56	1.08
33	0.07	1.12	0.62
34	25.12	401.92	17.0
35	34.78	556.48	11.14
36	10.63	170.08	11.02

37	19.33	309.28	9.32
38	10.19	163.04	2.72
39	4.19	67.04	2.9
40	13.78	220.48	4.98
41	9.9	158.4	5.84
42	11.04	176.64	5.04
43	11.47	183.52	3.5
44	20.41	326.56	14.88
45	25.6	409.6	
46	20.2	323.2	9.56
47	16.22	259.52	13.14
48	22.61	361.76	11.38
49	35.2	563.2	11.04
50	25.75	412.00	9.96
51	22.05	352.8	10.54
52	20.95	335.2	11.32
53	26.38	422.08	16.76
54	17.07	273.12	11.94
55	25.03	400.48	15.42
56	6.0	96	16.54

Appendix 3.5.

Raw biomass (g) of phytometers in each of the three treatments (no neighbours, neighbour roots and shoots, neighbour roots) and calculated competitive intensity measures (total, root and shoot) for the competition experiment. Phytometers which did not survive are indicated by dashes; CI values could only be calculated for certain plots.

	Phytometer biomass (g) in treatment:			Competition Intensity		
SAMPLE	NN	NRS	NN	CIT	CIR	CIS
1	-	0.0701	-			
2	0.0438	0.1085	0.0444	-1.47716	-0.01369	-1.46347
3	0.1858	0.0302	-	0.837459		
4	0.0704	0.0603	-	0.143465		
5	-	0.0274	0.0249			
6	-	-	-			
7	-	-	-			
8	-	-	0.0859			
9	-	-	-			
10	-	0.0481	0.0889			
11	-	0.0487	0.0657			
12	0.0157	-	0.0327		-1.08280	
13	-	-	0.0562			
14	0.157	0.2125	-	-0.35350		
15	-	0.0891	0.1012			
16	0.0481	0.0799	0.026	-0.66112	0.459459	-1.12058
17	-	-	-			
18	-	-	-			
19	-	-	-			
20	-	-	-			
21	-	0.074	0.0533			
22	-	-	-			
23	-	-	-			
24	-	-	-			
25	-	-	-			
26	-	-	-			
27	-	-	-			
28	1.0782	0.0242	0.1208	0.977555	0.887961	0.089593
29	-	0.0367	0.0671			
30	0.04474	0.0727	0.0511	-0.62494	-0.14215	-0.48278
31	-	-	-			
32	-	-	-			
33	-	-	-			
34	0.0821	-	0.0091		0.889159	
35	0.0948	0.0118	0.0293	0.875527	0.690928	0.184599
36	-	-	-			

37	-	-	-			
38	1.2135	0.0188	-	0.984507		
39	-	0.0128	-			
40	-	0.2324	-			
41	1.719	0.0228	0.1155	0.986736	0.932809	0.053926
42	0.6086	0.0272	1.2824	0.955307	-1.10713	2.062438
43	0.7744	0.045	0.0464	0.941890	0.940082	0.001807
44	0.0535	0.0458	0.0094	0.143925	0.824299	-0.68037
45	0.1348	0.0041	0.0105	0.969584	0.922106	0.047477
46	-	0.0191	0.0099			
47	0.0074	0.0039	0.0082	0.472972	-0.10810	0.581081
48	-	0.0137	0.0128			
49	0.0724	0.0122	0.0052	0.831491	0.928176	-0.09668
50	0.2394	-	-			
51	0.1711	0.0214	0.0027	0.874926	0.984219	-0.10929
52	0.0259	0.0075	0.0133	0.710424	0.486486	0.223938
53	0.0843	0.0054	-	0.935943		
54	-	-	0.0098			
55	0.0324	0.1019	0.0101	-2.14506	0.688271	-2.83333
56	-	0.0095	0.0054			