# Alvar vegetation in Canada: a multivariate description at two scales

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Alvars are areas with a distinctive dry grassland vegetation growing in thin soil over level limestone, and they are documented in Scandinavia, the eastern United States, and central Canada. Ordination and classification analysis techniques were used to describe alvar vegetation in Canada at two scales: within one alvar and among four alvar sites. Within one alvar, 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. Among alvars, species composition was related primarily to geographic location. The southern site was distinct from the eastern and northern sites. Relationships between soil depth, plant biomass, and vegetation could also be detected. At within and among alvar 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. Our results describe Canadian alvar vegetation and illustrate important differences among alvar sites, showing that a number of these sites need protection to conserve alvar vegetation.

*Key words*: grassland, drought, soil depth, species richness, biomass, conservation.

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Les alvars sont des endroits où on retrouve une végétation herbacée carctéristique de prairies sèches, poussant dans des sols minces sur des roches calcaires étalées; on les a signalés en Scandinavie, dans l'est des États-Unis et au centre du Canada. Les techniques d'analyse par ordination et classification ont été utilisées pour décrire, à deux echelles, la végétation d'alvars : à l'intérieur d'un même site d'alvar et entre quatre sites d'alvar. À l'intérieur d'un alvar, les changements de la composition en espèces correspondent à des changements de la profondeur du sol et de la biomasse. On retrouve deux types principaux de végétation : (*i*) la prairie d'alvar montrant une couverture complète de végétation et (*ii*) des rochers aplatis où on trouve un couvert de végétation incomplet sur roches calcaires. Parmi les alvars, la composition en espèces dépend surtout de la localisation géographique. Le site méridional est différent des sites situés à l'est et au nord. On peut également déceler des relations entre la profondeur du sol, la biomase végétale et la végétation. Aux échelles à l'intérieur et entre les alvars, des graminoïdes pérennes de fortes dimensions dominent les sites sur sols profonds, alos que de petites espèces annuelles et des espèces pérennes tolérantes aux stress dominent sur les sites à sols peu profonds. Il existe une forte corrélation positive entre la biomasse moyenne et la profondeur du sol parmi les types de végétation. La richesse moyenne en espèces montre une relation curvilinéaire avec la biomasse. Les résultats décrivent la végétation d'alvar au Canada et illustrent les différences importantes entre les sites d'alvar, montrant qu'un nombre de ces sites ne saurait maintenir une végétation d'alvar sans protection particulière.

*Mots clés* : prairie, sécheresse, profondeur du sol, richesse en espèces, biomasse, conservation.

[Traduit par la rédaction]

## Introduction

Alvar refers to a naturally occurring system of dry grassland vegetation growing in thin soil over level limestone rock (e.g., Petterson 1965; Catling et al. 1975). In the Baltic region alvars occur on the islands of Gotland and Öland in southern Sweden and in Estonia (Petterson 1965; Sjogren 1988). In North America this system occurs in the eastern United States, where it is generally known as cedar glades (e.g., Freeman 1933; Baskin and Baskin 1985*a*) and in central Canada within the province of Ontario only (Catling et al. 1975).

In alvars, 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).

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 focussed on assigning plant associations to taxonomic units (Krahulec et al. 1986; Bengtsson et al. 1988) and on the development of a guild classification for the alvar vegetation (van der Maarel 1988). Many United States cedar glades have also been described (e.g., Harper 1926; Freeman 1933; Erickson et al. 1942; Baskin and Baskin 1978, 1985*a*, 1985*b*). Baskin and Baskin (1985*a*) 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 characteristic 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: (*i*) the Manitoulin Island region (northern Lake Huron), (*ii*) Pelee Island in southern Ontario, and (*iii*) and region of Precambrian rock contact east of Lake Huron in Ontario (P. M. Catling, personal communication). These alvars include some large and virtually 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

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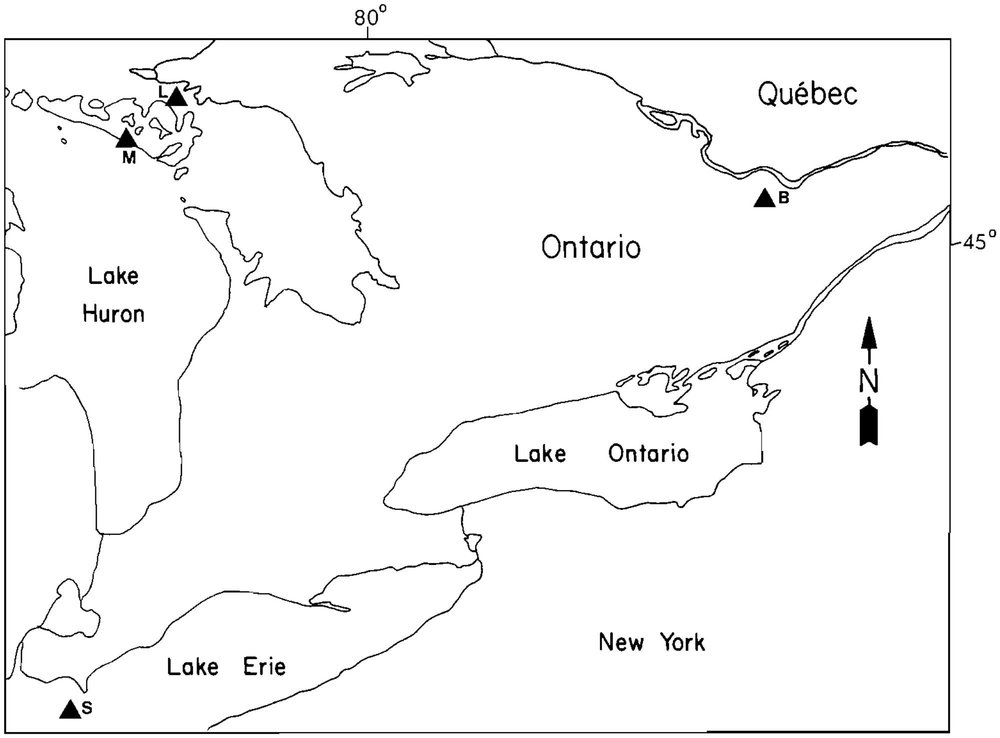


FIG. 1. Locations of study sites in Ontario. Study sites are Burnt Lands alvar (B), Stone Road alvar (S), La Cloche alvar (L), and Misery Bay alvar (M).

and Keddy 1992). Our intention was to provide a basic description of alvar vegetation to serve as a baseline for future work on environmental gradients and conservation biology.

We studied four alvar sites that represent examples from each of the phytogeographic groups. At each site we examined species composition, soil depth, plant biomass, and species richness. Our general objective was to describe Canadian alvar vegetation in detail by the within-alvar scale and more generally by the among-alvar scale. Our specific objectives were (*i*) to describe species composition, (*ii*) to examine species relationships, and (*iii*) to 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, we aimed to increase the generality of our description and to develop some predictive relationships (Rigler 1982; Keddy 1989).

## Methods

*Study sites*

Four alvars in Ontario were sampled (Fig. 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. 2*a*). 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 those at the other sites. For this reason, sampling was carried out at six subsites 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. Thus, vegetation here is more rigidly restricted to surface cracks (Fig. 2*b*).

*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) (see Belcher 1992 for more details). To ensure even sampling across the gradient, we identified five 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. In each class, an approximately equal number of 0.25-m$^2$ (0.5 × 0.5 m) quadrats were randomly located for a total sample size of $n$ = 99 at Burnt Lands and $n$ = 50 at Stone Road, at La Cloche, and Misery Bay.

Species composition of vascular plants was determined at each location by recording species presence in each of nine subquadrats, thereby obtaining a frequency, out of nine, for each species encountered. 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 was the mean of five measurements (four corners and the centre of the quadrat) taken with a 4-mm diameter pin.

*Analysis*

Multivariate analysis was employed at two levels: within a single site and among all four sites. Within-site analysis was conducted on the entire Burnt Lands data set ($n$ = 99). For the among-alvar analysis, data from all four sites were combined; half of the Burnt Lands data was used (10 samples from each of the five vegetation classes) so that sample sizes would be equivalent ($n$ = 50 for all sites).

Species that occurred in less than 5% of the quadrats were omitted from the analysis, leaving data matrices of 26 species by 99 quadrats for the within-site (Burnt Lands) set and 36 species by 200 quadrats for the among-site set. The data sets were explored with detrended

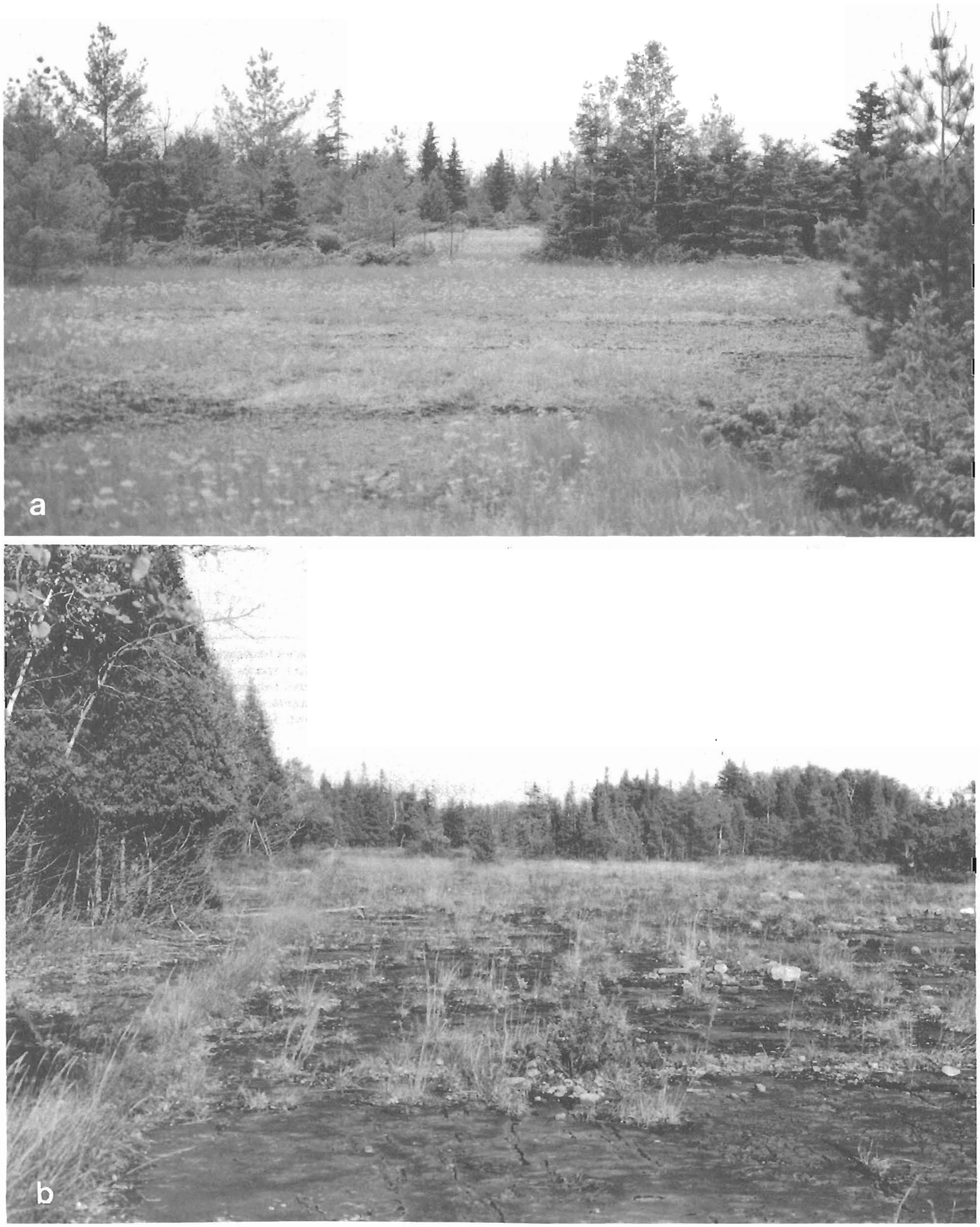


FIG. 2. (*a*) Burnt Lands alvar: vegetation occupies shallow soil over limestone. (*b*) Misery Bay alvar: soil and vegetation are largely restricted to cracks in the harder dolomite limestone.

TABLE 1. Frequency of occurrence of alvar species within the Burnt Lands site

| | | TWINSPAN group | | | | | | |
|---|---|---|---|---|---|---|---|---|
| Species | Overall frequency (%) | 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 no. of species | 26 | 20 | 19 | 25 | 20 | 7 | 12 | 3 |
| Total no. of plots | 98 | 22 | 17 | 21 | 9 | 9 | 12 | 8 |

NOTE: Shown is the overall frequency (percentage of quadrats in which each species occurred) and the average species frequencies (average number of subquadrats, out of nine, in which each species occurred) in each TWINSPAN group. For each group the frequency of the dominant species is indicated in boldface, and the total number of species and plots included is shown at the bottom of the table. The following 17 species that had an overall frequency of less than 5% were omitted from the analysis: *Antennaria neglecta*, *Aster ciliolatus*, *Bromus kalmii*, *Carex lanuginosa*, *C. rugosa*, *Chrysanthemum leucanthemum*, *Echium vulgare*, *Geranium bicknellii*, *Melilotus* spp., *Muhlenbergia mexicana*, *Panicum acuminatum*, *Penstemon hirsutus*, *Rhus radicans*, *Rosa acicularis*, *Sisyrinchium montanum*, *Verbascum thapsus*, *Viccia cracca*. Nomenclature follows Morton and Venn (1990).

correspondence analysis (DCA) and classified using two-way indicator analysis (TWINSPAN). Average species frequencies and measured variable data were summarized within TWINSPAN groups. DCA and TWINSPAN were conducted using CANOCO (Ter Braak 1988) and ECOSURVEY (Carleton 1985), respectively.

## 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). The first four axes extracted by DCA had eigenvalues of 0.72, 0.30, 0.25, and 0.15. Figure 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. 4). There were no evident trends along the second axis.

#### *Species overlays*

The distribution of eight significant alvar species (Catling et al. 1975) within one alvar was illustrated by comparing their frequencies in the ordination space (Fig. 5) with the measured variable diagrams (Fig. 4). *Sporobolus heterolepis* and *Carex crawei* (Figs. 5*a*, 5*b*) were restricted to deep soil, high biomass locations. *Senecio pauperculus* and *Solidago ptarmicoides* (Figs. 5*c*, 5*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* (Figs. 5*e*, 5*f*) were widely distributed in intermediate to shallow soil sites, while *Minuartia michauxii* and *Saxifraga virginiensis* (Figs. 5*g*, 5*h*) occurred only in extreme shallow soil, low biomass locations.

#### *Classification*

The variation in species composition was generally continuous within the ordination space (Fig. 3), but this variation can be summarized by examining average species composition (Table 1) and measured variable levels (Table 2) within quadrat groups. At three levels of division, classification analysis produced seven quadrat groups (Fig. 6), as shown on the ordination diagram (Fig. 3). The first division separated the meadows from the rock flats. The meadows had dense, continuous vegetation cover while the rock flats occurred on limestone outcrop or gravelly surfaces and had sparse or discontinuous vegetation cover (personal observation). The meadows and rock flats were further divided into tall meadows

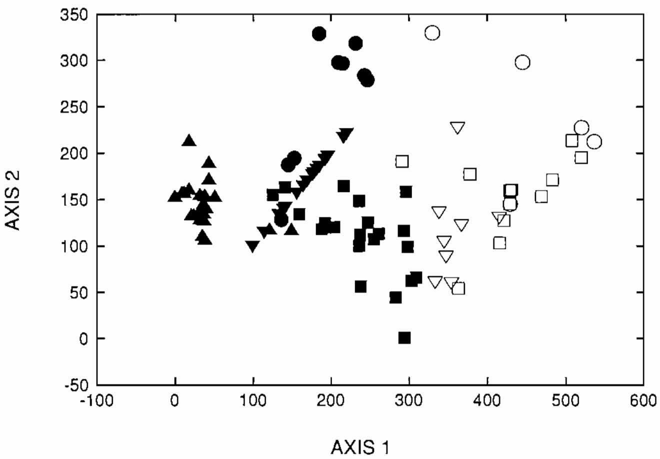


FIG. 3. Within Burnt Lands quadrat ordinations for axes 1 vs. 2. Symbols refer to seven TWINSPAN vegetation types (see Tables 1 and 2; Fig. 6) as follows: ▲, tall grassy meadows; ▼, tall forb-rich meadows; ■, low grassy meadows; ●, low forb-rich meadows; ▽, dry grasslands; □, rock margin grasslands; and ○, bare rock flats.

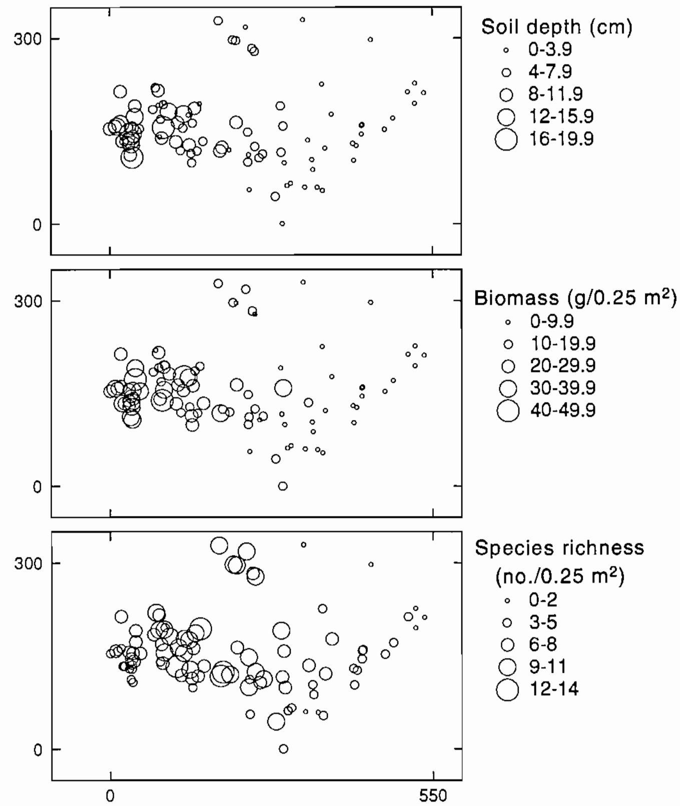


FIG. 4. Variable overlays within Burnt Lands. For each quadrat on the ordination diagram, the level of three variables (soil depth, biomass, and species richness) is indicated by circle size.

and low meadows, and rocky grasslands and bare flat rocks, respectively (Fig. 6). Soil depth and biomass levels decreased across these groups (Table 2). The seven third-level groups (Fig. 6) differed in species composition and variable levels.

The meadows occurred in deeper soil and had relatively high biomass and species richness (Table 2). They included species like *Carex crawei*, *Danthonia spicata*, *Senecio pauperculus*, *Solidago ptarmicoides*, and *Sporobolus heterolepis* that 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 that were dominated by *Sporobolus heterolepis*, a tall, perennial bunchgrass, and by the sedge, *Carex crawei* (Table 1). Also important was *Senecio pauperculus*, a rosette, evergreen perennial that 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 2). *Carex crawei* was the dominant species. This group had higher species richness than the previous group (Table 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 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 2). The low forb-rich meadows represented a small group with maximum species richness (Table 2), and most of the included quadrats occurred high on the second ordination axis (Fig. 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).

In contrast with meadows, the three groups of rock flats (Fig. 6) had low biomass, low species richness, and shallow soil (mean depth <2 cm; Table 2). The dry grassland had a sparse but continuous vegetation cover and occurred in relatively large areas that had thin soil over a gravelly surface (personal observation). 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 was transitional to the low meadows groups. The rock margin grassland 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.

### *Among sites*

#### *Ordination*

Among the four alvars sampled, 67 species were encountered, but only 36 of these occured in at least 5% of the quadrats (Table 3). The first four axes extracted by DCA had eigenvalues of 0.79, 0.51, 0.35, and 0.28. Figure 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 partially separated through the second and third dimensions of the ordi-

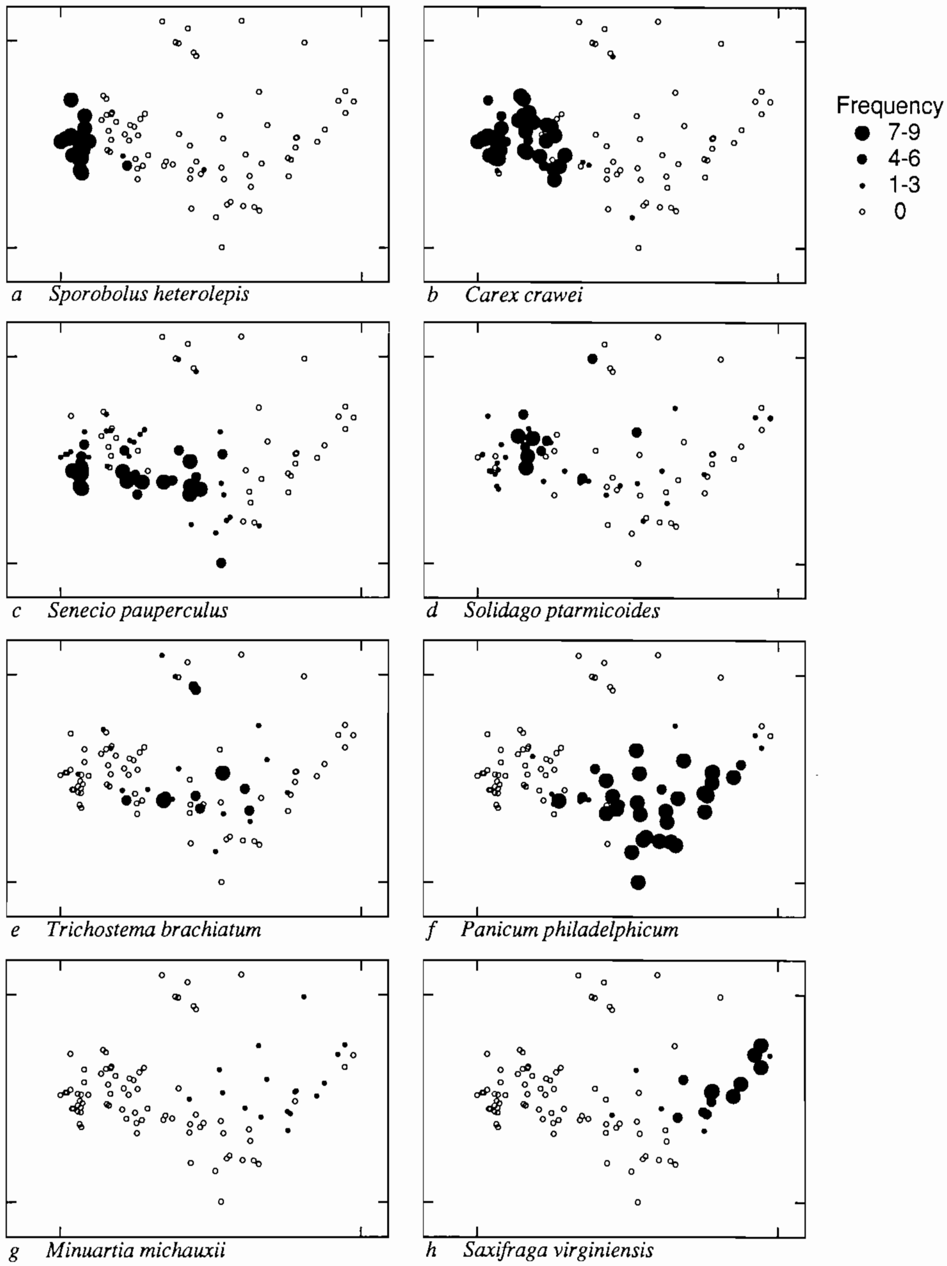


FIG. 5. Species overlays within Burnt Lands. For each quadrat on the ordination diagram (Fig. 2), the frequency of occurrence of eight species is indicated by circle size.

nation, i.e., 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. 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 three alvar sites (cf. Fig. 7). Species richness did not appear to be related to the ordination axes either (Fig. 8*d*), although there were more rare species along the lower one-third of axis 1 where Stone Road sites occurred and one or less species occurred in quadrats at the other sites (cf., Figs. 7 and 9*d*).

*Species overlays*

The distribution of species among alvars was illustrated by comparing their frequencies within the ordination space (Fig. 9) to diagrams showing sites (Fig. 7) and measured variables (Fig. 8). *Sporobolus heterolepis*, *Carex crawei*, *Senecio pauperculus*, and *Solidago ptarmicoides* (Figs. 9*a*–9*d*) had similar distributions but did not occur at Stone Road (cf. Fig. 7). *Minuartia michauxii* and *Saxifraga virginiensis* (Figs. 9*e*, 9*f*) were distributed in the centre of the ordination, corresponding with shallow soil, low biomass sites (cf. Figs. 8*a*, 8*b*), mainly at Burnt Lands and Misery Bay. *Trichostema brachiatum* and *Panicum philadelphicum* (Figs. 9*g*, 9*h*) were widely distributed. Rare species were more site specific: *Hymenoxys acaulis* (Fig. 9*l*) occurred frequently and only at Misery Bay in shallow soil locations; *Allium cernuum*, *Ratibida pinnata*, and *Leucospora multifida* (Figs. 9*i*–9*k*) occurred only at Stone Road; *Allium cernuum* was most abundant, and *Leucospora multifida* occurred infrequently and was restricted to shallow soils.

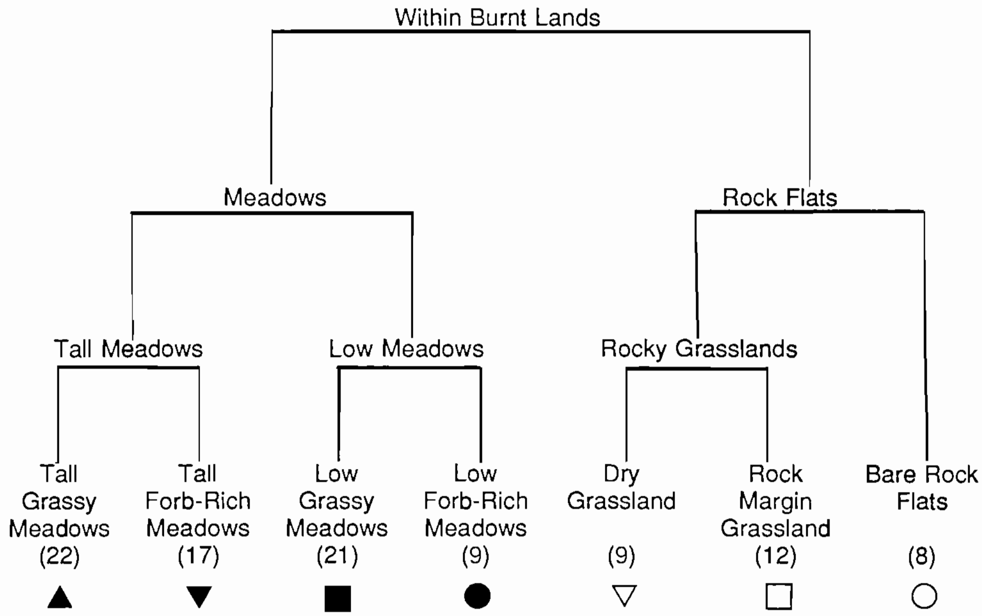


FIG. 6. Dendrogram for plot classification within Burnt Lands. Number of quadrats in each group is shown in parentheses; symbols correspond to Fig. 3.

TABLE 2. Average value for three measured variables (soil depth, biomass, and species richness) in each TWINSPAN group at the Burnt Lands site

| 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/0.25 $m^2$) | 29.8 | 25.9 | 16.6 | 14.3 | 6.1 | 4.5 | 0.5 |
| Richness (no./0.25 $m^2$) | 5.5 | 8.2 | 7.4 | 10.1 | 3.8 | 4.0 | 1.1 |

*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 3) and average variable levels (Table 4) in TWINSPAN groups. At three levels of division, classification analysis produced eight quadrat groups (Fig. 10), as shown on the ordination diagram (Fig. 11). 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 Bay – La Cloche, Burnt Lands mix, and Stone Road groups.

Biomass and soil depth levels at the northern and eastern sites were intermediate compared with the groups discussed above (Table 4). Stone Road quadrats were absent in this group but 80% of the quadrats from the other three sites were present (Table 3). The presence of *Sporobolus heterolepis* in this set is the main floristic difference from the southern and eastern sites (Table 3).

The Burnt Lands – La Cloche groups had intermediate soil depth and biomass levels (Table 4). Important species included *Carex crawei* and *Danthonia spicata*. The La Cloche tall meadows group (69% of the included quadrats were from La Cloche; Table 3) had higher biomass and deep soil (the highest levels of these variables outside of Stone Road). Dominant species were *Sporobolus heterolepis* and *Carex crawei* (Table 4). 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 3) and species richness was highest (Table 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 to intermediate levels of biomass and soil depth (Table 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 3). The Misery Bay pavement occurred in shallow soil and *Minuartia michauxii* was the most abundant species (Table 3).

Based on biomass and soil depth (Table 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 4). These sites included the stress-tolerant perennials *Saxifraga virginiensis* and *Minuartia michauxii* (Table 3). The small, mixed-site rock flats included quadrats at Burnt Lands, Misery Bay, and La Cloche (Table 3). Soil depth, biomass, and species richness levels

TABLE 3. Frequency of occurrence of alvar species among four sites

| Species | Overall frequency (%) | TWINSPAN group: 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 grassland | Stone Road dry prairie |
|---|---|---|---|---|---|---|---|---|---|
| *Allium cernuum* | 22.0 | 0 | 0 | 0 | 0 | 0 | 0 | 4.5 | 5.4 |
| *Ambrosia artemesiifolia* | 23.5 | 0 | 0.8 | 2.7 | 1.0 | 0 | 0.4 | 0.6 | 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 | **3.0** | 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 no. of species | 36 | 24 | 25 | 21 | 21 | 9 | 20 | 21 | 11 |
| No. of plots 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 no. of plots | 199 | 45 | 26 | 30 | 18 | 6 | 17 | 40 | 17 |

NOTE: Shown is the overall frequency (percentage of quadrats in which each species occurred) and the average species frequencies in each TWINSPAN group (mean number of subquadrats, out of nine, in which each species occurred). For each group the frequency of the dominant species is indicated in boldface, and the total number of species and plots, and the number of plots from each site, are shown at the bottom of the table. The following 49 species that had an overall frequency of less than 5% were omitted from the analysis: *Agrostis gigantea*, *A. scabra*, *Allium schoenoprasum*, *Arabis hirsuta*, *Arenaria serpyllifolia*, *Aster ciliolatus*, *A. ericoides*, *A. pilosus*, *Calamagrostis canadensis*, *Carex bebbii*, *C. divulsa*, *C. lanuginosa*, *C. molesta*, *C. richardsonii*, *C. rugosperma*, *C. scirpoidea*, *Castilleja coccinea*, *Cerastium arvense*, *Chaenorrhinum minus*, *Clintopodium vulgare*, *Comandra umbellata*, *Echium vulgare*, *Festuca saximontana*, *Geum triflorum*, *Hedeoma hispida*, *Hymenoxys acaulis*, *Hypericum kalmianum*, *Juncus balticus*, *Lepidium campestris*, *Leucospora multifida*, *Liatris cylindracea*, *Lotus corniculatus*, *Medicago sativa*, *Muhlenbergia glomerata*, *M. mexicana*, *Panicum acuminatum*, *P. flexile*, *Penstemon hirsutus*, *Portulaca olearcea*, *Potentilla norvegica*, *P. recta*, *Prunella vulgaris*, *Rosa acicularis*, *Setaria viridis*, *Sisyrinchium montanum*, *Sporobolus neglectus*, *Verbascum thapsus*, *Verbena simplex*, *Viccia cracca*. One quadrat was omitted from the analysis due to insufficient vegetation data. Nomenclature follows Morton and Venn (1990).

were lowest in this group (Table 4). The dominant species were *Saxifraga virginiensis* and *Poa compressa* (Table 3). The Burnt Lands rock margins, which included mainly sites from the Burnt Lands (Table 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 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 3). The Stone Road dry grassland (which also included a few quadrats from

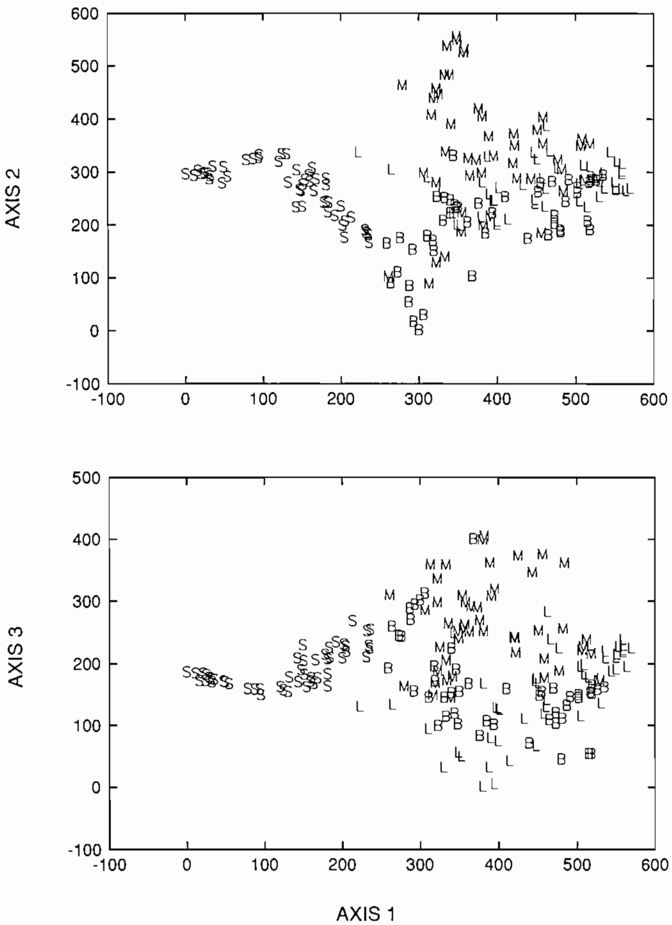


FIG. 7. Among alvar quadrat ordinations for axes 1 vs. 2 and 1 vs. 3. Letters represent the four study sites: B, Burnt Lands; S, Stone Road; L, La Cloche; and M, Misery Bay.

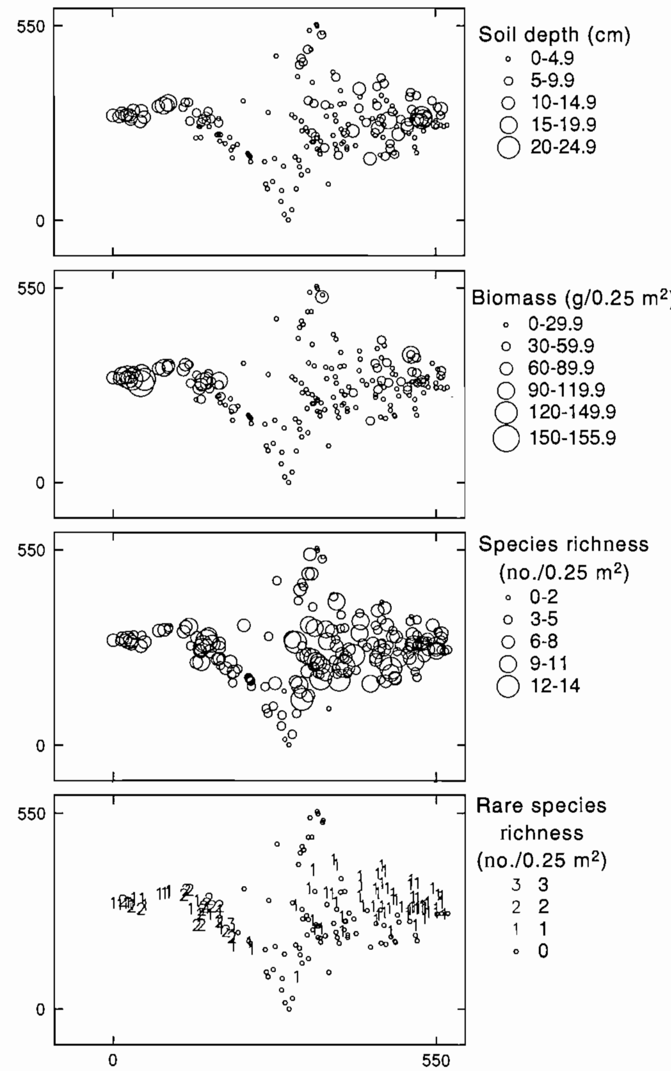


FIG. 8. Variable overlays among alvars. For each quadrat on the ordination diagram (axes 1 vs. 2) the level of four variables (soil depth, biomass, species richness, and rare species richness) is indicated by circle size or number.

other sites; Table 3) had slightly lower biomass and occurred in shallower soil (Table 4). It was dominated by *Panicum philadelphicum*. The Stone Road prairie had the highest overall biomass and soil depth (Table 4). This group was dominated by *Poa compressa*, which had an average frequency of 100% (Table 3), and *Andropogon gerardii*, a tall-grass prairie bunchgrass that occurred only in this group.

## 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. 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. 3), were situated where elevation was higher (personal observation) and drainage may have been greater. Also, there was evidence of past disturbance (possibly an old building site; personal observation) at the same location. The dominant species of this group (Table 1) were *Panicum flexile*, a species often found in disturbed sites in cedar glades (Baskin and Baskin 1985*a*) and *Hypericum perforatum*, a wide-ranging 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 that 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). We 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 (*i*) tall, perennial graminoids (e.g., *Sporobolus heterolepis*, *Carex crawei*), through (*ii*) perennial forbs (mainly family Asteraceae, e.g., *Senecio pauperculus*, *Solidago ptarmicoides*), (*iii*) small annual grasses (e.g., *Panicum flexile*, *Sporobolus vaginiflorus*), and (*iv*) small annual forbs (e.g.,

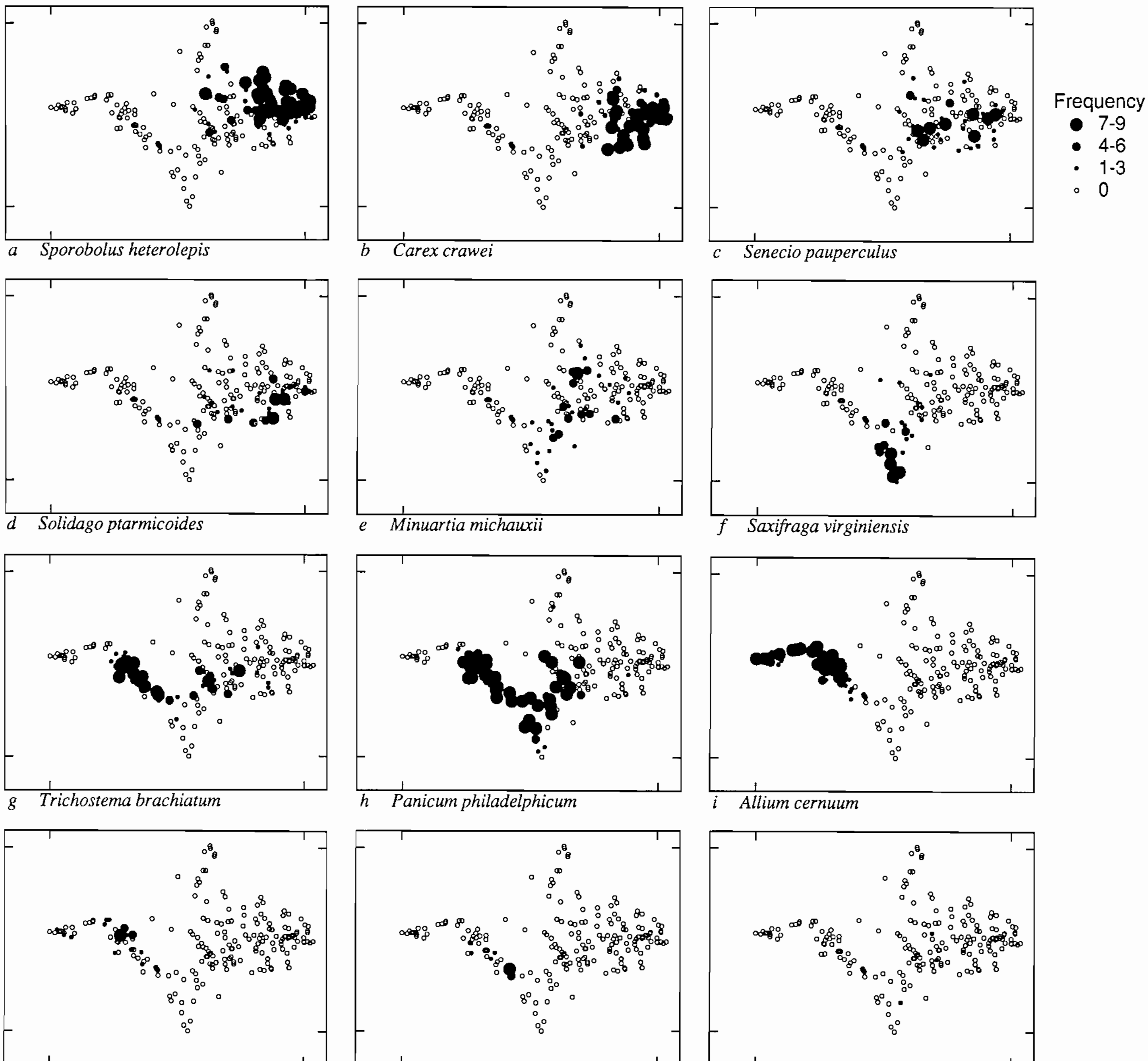


FIG. 9. Species overlays among alvars. For each quadrat on the ordination diagram, the frequency of occurrence 12 species is indicated by circle size. Included are five rare species: rare in Ontario (*a–i*; Argus et al. 1987) and rare in Canada (*j–l*; Argus and Pryer 1990).

*Trichostema brachiatum*, *Chaenorrhinum minus*) to (*v*) small, evergreen perennials (e.g., *Minuartia michauxii*, *Saxifraga virginiensis*).

The perennial graminoids and forbs that occurred in the deepest soils may be competitive dominants (Grime 1977) that exclude smaller species by competition. Wilson and Keddy (1986) have shown that small stress-tolerators are competitively excluded from fertile habitats. In the Burnt Lands alvar, competition did occur and was primarily for belowground resources (Belcher 1992).

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 1985*a*); therefore, they 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 outcrops 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, for

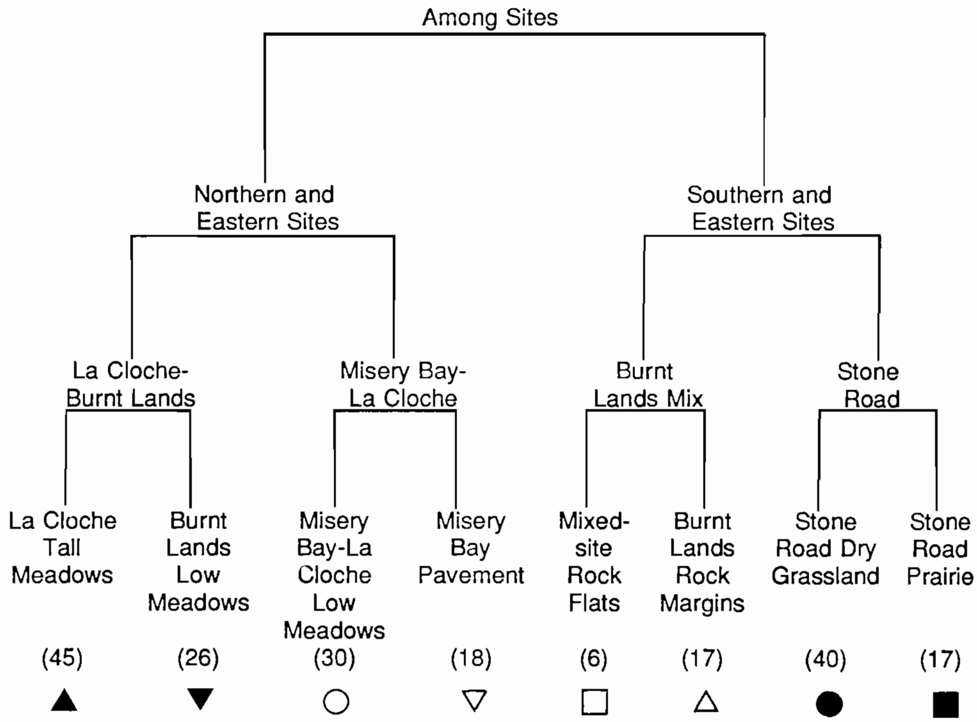


FIG. 10. Dendrogram for quadrat classification among alvars. Number of quadrats in each group is shown in parentheses; symbols correspond to Fig. 11.

TABLE 4. Average value for four state variables (soil depth, biomass, species richness, and rare species richness) in each TWINSPAN group (regional scale)

| Variable | La Cloche tall meadows | Burnt Lands low meadows | Misery Bay – La Cloche meadows | Misery Bay pavement | Mixed-site rock flats | Burnt Lands rock margins | Stone Road dry grassland | 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/0.25 $m^2$) | 27.2 | 19.3 | 10.9 | 8.2 | 3.4 | 5.6 | 35.8 | 96.7 |
| Richness (no./0.25 $m^2$) | 5.6 | 8.1 | 5.4 | 5.8 | 3.7 | 5.1 | 6.6 | 6.1 |
| Rare species richness (no./0.25 $m^2$) | 0.9 | 0.2 | 0.4 | 0.5 | 0.2 | 0.1 | 1.1 | 1.2 |

example, 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), and slow-growing evergreens in arctic alpine and subalpine communities (e.g., del Moral 1983).

Additionally, we identified eight candidate species that could serve as indicators of healthy (sensu Rapport 1989) alvar vegetation (Fig. 5). These included *Sporobolus heterolepis*, a provincially rare species (Argus et al. 1987), and seven significant alvar species (listed in Catling et al. 1975). All eight were dominant in at least one vegetation type (Table 1). Moreover, the limited distribution of *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. 7) that did not correspond to simple variables (Fig. 8). We 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 that were based mainly on geographic location but that also revealed some ecological relationships, specific habitat types, and interactions between geographic and ecological sites.

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 4) and was the only type with the tall-grass prairie species *Andropogon gerardii*. The Stone Road dry grassland included the

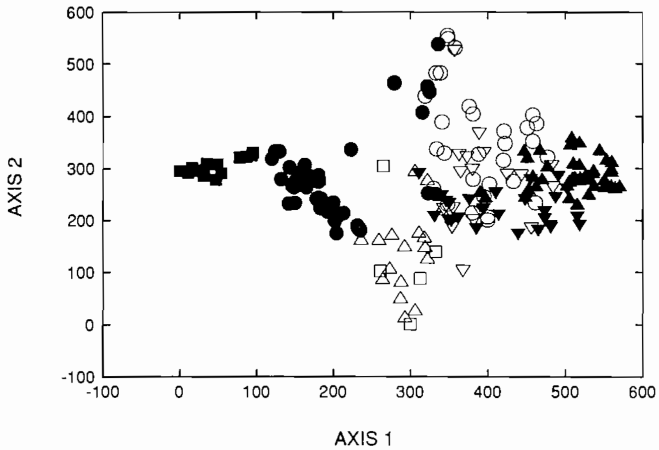


FIG. 11. Among site quadrat ordination showing symbols for each TWINSPAN vegetation groups (see Tables 2 and 3; Fig. 10) as follows: ▲, La Cloche tall meadows; ▼, Burnt Lands low meadows; ○, Misery Bay – La Cloche low meadows; ▽, Misery Bay pavement; □, mixed-site rock flats; △, Burnt Lands rock margins; ●, Stone Road dry grassland; and ■, Stone Road prairie.

remainder of the Stone Road quadrats that occurred in shallower soil (Table 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 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 3, 4). Meadow habitats at Misery Bay and La Cloche were similar in slightly shallower soil (Misery Bay – La Cloche groups; Tables 3, 4).

We examined the among-site distribution of the same eight indicator species examined within Burnt Lands (Figs. 9*a*–9*h*). Their distributions were closely related to the classification patterns. Tall meadow species (Figs. 9*a*–9*d*) (e.g., *Sporobolus 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 (Figs. 9*e*–9*f*) (e.g., *Saxifraga virginiensis*) were also absent from Stone Road. Here, the rare species *Leucospora multifida* (Fig. 9*k*) occupied the rock flat habitat instead (personal observation). 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. 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. 12B). This agrees with the model proposed by Grime (1973) that 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. Alvar species richness patterns were examined in greater detail elsewhere (Belcher 1992).

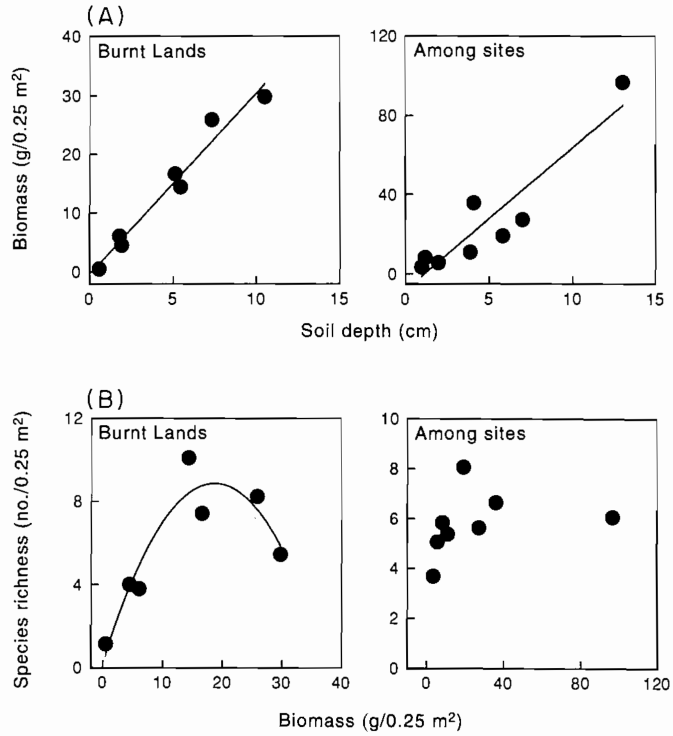


FIG. 12. The relationships among measured variables. Plotted points are mean values for these variables in each vegetation type within Burnt Lands (Table 2) and among alvars (Table 4). (A) Biomass increased linearly with soil depth by both within-alvar and among-alvar scales (within Burnt Lands: $r^2 = 0.96$, $P < 0.001$, $y = -0.4 + 3.1x$; 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 ($r^2 = 0.40$, $P > 0.05$).

This paper 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, we know that the flora varies not only among Canadian alvars but also among sites globally; there is apparently little species overlap between alvars in Canada and elsewhere (e.g., Baskin and Baskin 1985*b*; 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 1992) and that management (if any) is likely to involve maintaining a variety of soil depth gradients in the absence of anthropogenic disturbance.

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