VEGETATION OF THE MIMA MOUNDS, WASHINGTON STATE

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Abstract. The vegetation patterns on the undulating topography of the Mima Mounds, Washington, USA exist on at least three scales. At the smallest scale the distribution of individuals is determined primarily by microtopographic features which provide small, but significant habitat variation. An intermediate scale is dependent upon exposure and elevation. Mounds alter drainage and insolation to create moisture gradients to which all species respond. The largest scale involves the shift of species distributions with respect to mounds as one moves from the prairie to a zone of *Pseudotsuga menziesii* invasion. Conditions become more mesic as a consequence of reduced insolation and wind in this ecotone, resulting in an increase in mesophytes and a decrease in xerophytes.

Both ordination and classification methods are applied in this study. The analyses are complementary and provide insight into the nature of factors controlling vegetation. A method of detailed mapping is proposed which involves the description of a small sample of the area to be mapped, preliminary clustering, the application of discriminant analysis to perform reallocation of samples, and the construction of a key to the resultant associations. The key is used in the field to assign samples to the proper association.

Key words: Classification, vegetation; discriminant analysis; Mima Mounds; ordination, vegetation; prairies; succession; vegetation analysis; Washington.

INTRODUCTION

In the humid Puget Sound lowlands of Washington State, USA extensive prairies and woodlands exist under edaphic control (Lang 1961). The Mima Mound prairie is of particular interest because of the extensive and characteristic mounds which range from 0.5 to 2.1 m in height above the plain and which extend over many square kilometers. These mounds create microtopographic variety resulting in recurring vegetation patterns. The prairies are being invaded by *Pseudotsuga menziesii* and in places by *Quercus garryana*, a process which alters the relationship of the herb layer to the mound topography. In this paper we describe the vegetation pattern and examine the governing factors.

The Mima Mound prairie originated following the retreat of the Vashon glacier (ca. 12,000 Y.B.P.), which created a large gravelly outwash plain. Newcomb (1952) and Dalquist and Scheffer (1942) offer alternative hypotheses concerning mound origins. The controversy is unresolved, but the circumstantial evidence of Dalquist and Scheffer strongly suggests an origin due to large, mound forming gophers.

The gravelly outwash plains now occupy 67,200 ha in Pierce, Thurston, Lewis, Grays Harbor, and Mason counties of Washington State (C. W. Renny and R. S. MacLauchlan, 1957 unpublished progress report on adaptation of forage plants to Spanaway soils and Nisqually soils, Soil Conservation Service, Olympia, Wash.). The pollen record suggests that prairie vegetation became established on these coarse, glacial, outwash gravels early in the hypsithermal, ca. 9000 Y.B.P., at a time when tree seedlings could not become established (M. Tsukada, personal communication). Once established, they were maintained by the combination of prolonged summer drought (Lang 1961, Giles 1970), low soil fertility (Giles 1970), recurrent fires (Lang 1961), and competition. Due to the combined effects of grazing, physical disturbance for agriculture and military activities, and fire suppression the prairie was invaded by trees ca. 1850. Lang (1961) compared early and recent land survey maps and estimated that over one-half the original prairie was converted to forest by 1960.

No extensive portion of the prairie exists as it was prior to 1840. From relictual areas Lang (1961) concluded that the dominant species included: *Festuca idahoensis, Rhamnus californica, Carex pensylvanica, Luzula campestris var. multiflora, Dodecatheon hendersonii, Camassia quamash, Saxifraga integrifolia, Viola adunca, Zigadenus venenosus,* and *Balsamorhiza deltoidea,* a flora showing strong affinities with those of the climatically determined steppes of eastern Washington. Since 1850 this flora has been invaded by successive waves of European species which should be considered in current ecological research. *Hypochaeris radicata* was first collected in the region in 1904, *Hypericum perforatum* in 1930; *Cytisus scoparius* was introduced prior to 1900; *Aira caryophyllea* came with the first livestock in ca. 1840; and *Chrysanthemum leucanthemum* was established by 1900 (Lang 1961, and University of Washington herbarium records).

1 Manuscript received 2 June 1975; accepted 9 January 1976.
The Mima Mounds prairie is Washington State trust land, administered by the Washington Department of Natural Resources. Since 1965, when grazing leases were taken over by the Nature Conservancy, cattle grazing has ceased. The vegetation has been recovering from grazing, but in the absence of positive management efforts, it appears that the forest invasion now in progress will result in conversion to Douglas fir forest.

The purposes of this study were to: (1) establish a detailed baseline description upon which to judge future changes in the vegetation, (2) explore the environmental factors controlling these distributions, and (3) test a large scale mapping technique suggested by del Moral (1975).

**METHODS AND MATERIALS**

**Study site**

The study site is 2 km west of Littlerock, Thurston County, Washington, and includes the W 1/2 of Sec. 3 and the NW 1/4 of Sec. 10, T 16 N, R 3 W, at 60 m elevation (Figs. 1 and 2). The soils are included in the Spanaway series (Ness 1958) and consist of coarse sands and gravels. The study site lies in an incision through a terminal moraine.

Giles (1970) demonstrated that soil varies between mound and intermound areas. Intermound soil contains 69% gravel, but only 58% of mound material is as coarse. Of the 2-mm fraction, intermound material is 70% sand and 5% clay; mound material is 61% sand and 8% clay. Intermound material is wetter in spring due to poor drainage, but dries more quickly due to its reduced water-holding capacity. Giles' soil moisture tension data indicate that moisture gradients are not manifest until late June or July; however, growth begins in February.

Nutrient analyses from Giles (1970) are summarized in Table 1. Intermound soil is substantially less fertile than mound soil and north-facing slope soil is slightly more fertile than south-facing slope soil. Mound soil contains much more organic matter than intermound soil.

**Field methods**

*Microtransect.* A large representative mound was selected in the prairie and the distribution of mosses, lichens, and vascular plants was determined by means of a topograph (Boorman and Woodell 1966). Vascular plant nomenclature follows Hitchcock and Cronquist (1973), moss nomenclature follows Lawton (1971), and lichen nomenclature follows Howard (1950). Two transects were constructed and oriented SW to NE and SE to NW. Pins were lowered at 2 cm intervals to record both elevation and plant occurrence. A graphic display of microdistribution permits inferences concerning environmental requirements.

*Transect.* A 1-km transect from prairie to forest edge was sampled by means of 0.25-m² quadrats every 10 m. Frequency was determined from percent occurrence in 25, 5-×5-cm quadrats nested within the larger one. Percent cover was determined by summing cover estimates in each 5×5-cm quadrat.

Using data derived from this transect and following a cluster analysis, a detailed map of a representative portion of the prairie and ecotone was constructed. This was accomplished by establishing a grid 5×250 m and assigning the vegetation at each 1×1-m grid intersection (0.25-m² sample) to one of the clusters on the basis of a key to the vegetation. The position of the quadrat with respect to mound exposure and elevation was noted.
Quantitative methods

Data transformation. Transect data were relativized to produce importance values such that the sum in any quadrat totals 200. Double standardization of data was not attempted since Gauch and Whittaker (1972) found no advantage to this procedure.

Ordination. An indirect ordination of the transect data was carried out with a modification of the polar ordination method (Bray and Curtis 1957) termed similarity projection ordination (Gauch and Whittaker 1972) using percent difference of importance values and an internal association of 90%.

The first axis is defined by the two most dissimilar quadrats representing the extremes of an inferred environmental gradient. Ordination in two or more dimensions is accomplished by selecting additional pairs of end stands. We use the following criteria for such selection: (1) stands approximately equidistant from each end point, (2) stands maximally dissimilar to each other, (3) stands distant from the first axis, and (4) stands representing environmental extremes. The analysis was limited to two dimensions since attempts at a third dimension led to ordinations similar to one of the first two axes.

Clustering. Importance values were used to cluster transect data by mutual information (Oroloci 1969). Goldstein and Grigal (1971) provided the computing program MINFO. The analysis is agglomerative, polythetic, and hierarchical (Williams 1971); each sample is considered unique initially and on each cycle that pair which upon merger results in the minimum gain of information is joined. A dendrogram with a logarithmic axis results. In common with all clustering methods, the level of termination remains a difficult problem.

Reallocation. An approximate termination decision is possible by combining field observations and inspection of both the dendrogram pattern and individual samples. Uncertainty is always resolved in the direction of more associations rather than fewer. The provisional groups are subjected to stepwise discriminant analysis, SMDA (Dixon 1970). This classification method determines the order in which species are useful for separation of associations, provides tests for significant differences between groups, reallocates samples, and provides a graphic display of samples in canonical space. Canonical axes are strictly orthogonal axes in the discriminant space rotated to provide the maximum discriminatory power. Mathematical details and some ecological applications are given in Seal (1964), Horton et al. (1968), and Lee (1971). Use of discriminant analysis to reallocate ecological samples was suggested by del Moral (1975).

Results

Microtopography

The mound selected for study was 1.3 m above its immediate surroundings with a diameter from SW to NE of 13.0 m and from SE to NW of 13.1 m. The topograph transects were 18.9 m and 16.8 m long, respectively. The SW to NE transect is shown in Fig. 3 with only 13 of 33 encountered species shown. Many of these species have distinct patterns suggesting hypotheses concerning factors controlling their distribution.

Mosses. Rhacomitrium canescens var. ericoides and Polytrichum juniperinum are mosses of intermound and drier slopes where vascular plant biomass is often reduced. Dicranum scoparium and Eurhynchium oreganum are mosses of depressions in wetter portions of the mound.

Lichens. Cladonia chlorophaea is found primarily on the SW slope in microhummocks and is mutually exclusive with Rhacomitrium. Cladonia mitis dominates the northern midslope and mound top, often in a pure patch. It occurs in sites of intermediate moisture conditions.

Vascular plants. The most widely distributed dicot is Hypochaeris radicata. Unlike other rosette species on the prairie, it excludes species from beneath its leaves. Hypochaeris is always centered in microdepressions, suggesting strongly that seedling establishment in this biennial species is only successful in such "safe sites."

Chrysanthemum leucanthemum occurs primarily on upper mound areas and is negatively associated
Fig. 3. Microtopographic transect produced by the topograph. Species occurrence indicated by bar above point of occurrence. Original figure accurate to within 0.2 cm in the vertical and 1.0 cm in the horizontal.

Fig. 4. Distribution of samples in two dimensions determined by SIMPRO. Letter symbols refer to the associations determined by MINFO clustering followed by discriminant analysis.

with Hypochaeris. Hypericum perforatum is restricted to mound tops.

Agrostis diegoensis is an introduced grass found primarily on the western mound slopes. It appears to be a species of more xeric sites. Festuca idahoensis, a native dominant bunchgrass, is widely distributed. It dominates the upper and middle mound slopes and grows over a variety of microsites, but most clumps appear to be centered on depressions. On mound tops, Poa pratensis is dominant and excludes Festuca.

The most characteristic species of the prairie is Camassia quamash. It occurs sporadically throughout both transects, but in particular association with Rhaecomitrium.

The distributional patterns revealed by microtopographic study suggest two scales of interaction: the microtopographic scale in which depressions on the order of 1 cm are important for establishment and the mesotopographic scale (decimeters) in which conditions imposed by the entire mound (exposure and drainage) are critical. These scales interact and are complicated by biotic effects. However, the

Species coded as follows: (A) Rhaecomitrium canescens, (B) Polytrichum juniperinum, (C) Hypochaeris radicata, (D) Camassia quamash, (E) Agrostis diegoensis, (F) Cladonia chlorophaea, (G) Festuca idahoensis, (H) Chrysanthemum leucanthemum, (I) Dicranum scoparium, (J) Cladonia mitis, (K) Hypericum perforatum, (L) Poa pratensis, and (M) Erythronium oreganum.
topograph provides abundant data which can be used to generate and test numerous hypotheses about physiological capabilities, community characteristics, and the nature of smaller scale gradients.

**Ordination**

Figure 4 shows the similarity projection ordination of the samples from the transect. The ordination produced good sample separation in both dimensions which suggests at least two axes of variation.

The first ordination axis is defined by a sample from A (letters refer to categories to which samples were ultimately assigned by the cluster method) (*Rhacomitrium canescens-Polytrichum juniperinum*) and the one from K. However, this stand is devoid of herbs and J (*Poa pratensis/Isothecium stoloniferum*) stands represent the end point more accurately. Samples of type A occur on the lower south- to west-facing slopes. Type J is found primarily on mound tops. This axis appears to reveal an elevation gradient affecting moisture from lower, more mesic to higher, better drained sites.

The second ordination axis is defined by a sample of I (*Festuca idahoensis/Rhacomitrium canescens*) and one of M (*Camassia quamash/Dicranum scoparium-Eurhynchium oreganum*). This axis relates to exposure. Type I occurs in the lower to midmound regions on midslope southern exposures and on some isolated moundlets while M, L, and some H occur primarily on protected exposures and where mound drainage is reduced.

It is also possible that the first axis reflects soil fertility factors inasmuch as Giles (1970) found reduced soil fertility in the intermound compared to the mound. However, he did not look at gradients within the mounds. Fertility should increase from mound top to mound bottom due to drainage. We found no improved environmental interpretation or ordination by selecting alternative stands or additional axes.

**Clustering**

Clustering was pursued to permit microscale mapping of the mounds. MINFO resulted in the dendrogram shown in Fig. 5. The vertical scale is information content, which increases logarithmically as samples are joined.

Mergers were stopped arbitrarily at $10^3$ units. Inspection of the resultant groups suggested that the 13 resultant clusters were more than could be discerned in the field. Stands were reallocated and differences between groups were determined by stepwise discrim-
### Table 2. Species composition based on mean percent cover in associations and subassociations determined by MINFO. K is omitted

<table>
<thead>
<tr>
<th>Species</th>
<th>Association</th>
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<tbody>
<tr>
<td></td>
<td>A</td>
</tr>
<tr>
<td><strong>Rhacomitrium canescens</strong></td>
<td>92.4*</td>
</tr>
<tr>
<td><strong>Polystichum juniperinum</strong></td>
<td>3.1*</td>
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<tr>
<td><strong>Isoetes stolonifer</strong></td>
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</tr>
<tr>
<td><strong>Specularium scoparium</strong></td>
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</tr>
<tr>
<td><strong>Eryngium oreganum</strong></td>
<td>0</td>
</tr>
<tr>
<td><strong>Rhylidiadelphus triquetrus</strong></td>
<td>0</td>
</tr>
<tr>
<td><strong>Hypogymnia physoides</strong></td>
<td>0</td>
</tr>
<tr>
<td><strong>Petasites aphthosa</strong></td>
<td>0</td>
</tr>
<tr>
<td><strong>Cladonia chlorophaea</strong></td>
<td>1.3</td>
</tr>
<tr>
<td><strong>Cladonia furcata</strong></td>
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</tr>
<tr>
<td><strong>Cladonia mitis</strong></td>
<td>2.8</td>
</tr>
<tr>
<td><strong>Agrostis diegoensis</strong></td>
<td>1.9*</td>
</tr>
<tr>
<td><strong>Agrostis tenuis</strong></td>
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</tr>
<tr>
<td><strong>Aira praecox</strong></td>
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</tr>
<tr>
<td><strong>Festuca idahoensis</strong></td>
<td>0</td>
</tr>
<tr>
<td><strong>Holcus lanatus</strong></td>
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</tr>
<tr>
<td><strong>Poa pratensis</strong></td>
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</tr>
<tr>
<td><strong>Carex pensylvanica</strong></td>
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</tr>
<tr>
<td><strong>Brodiaea coronaria</strong></td>
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<td><strong>Campylopus quamae</strong></td>
<td>5.3*</td>
</tr>
<tr>
<td><strong>Zigadenus venosus</strong></td>
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<tr>
<td><strong>Achillea millefolium</strong></td>
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</tr>
<tr>
<td><strong>Campanula rotundifolia</strong></td>
<td>0</td>
</tr>
<tr>
<td><strong>Chrysanthemum leucanthemum</strong></td>
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</tr>
<tr>
<td><strong>Dodecatheon hendersonii</strong></td>
<td>0</td>
</tr>
<tr>
<td><strong>Hieracium cynoglycyodes</strong></td>
<td>0</td>
</tr>
<tr>
<td><strong>Hypericum perforatum</strong></td>
<td>0.9</td>
</tr>
<tr>
<td><strong>Hypochaeris radiata</strong></td>
<td>3.1*</td>
</tr>
<tr>
<td><strong>Ranunculus occidentalis</strong></td>
<td>0.3</td>
</tr>
<tr>
<td><strong>Rumex acetosella</strong></td>
<td>0.4</td>
</tr>
<tr>
<td><strong>Trifolium dubium</strong></td>
<td>0</td>
</tr>
<tr>
<td><strong>Viola adunca</strong></td>
<td>0</td>
</tr>
</tbody>
</table>

* Characteristic species.

The original MINFO clustering and discriminant analysis is quite high. The samples were reallocated as indicated by the table and the revised categories were used in constructing Table 2 and the vegetation key. Table 3 provides evidence concerning the relative closeness of each association. F-values indicate the degree of differences between associations. These values are useful in planning a keying strategy and in deciding whether or not to merge associations.

Discriminant analysis also results in an eigenvector analysis, often termed canonical analysis. In this instance the distribution of samples was similar to that performed by the ordination and is, therefore, not presented in detail. However, we note that the first canonical dimension (analogous to the first principal component) accounts for 82% of the total variation, while the remaining 11 dimensions for 18%. This suggests a single effective environmental variable, moisture, is controlling species distributions.

Groups A to F divide into two clusters, but it requires seven steps before A, D, and F are separated. This implies that these groups are closely related and that several species are required to distinguish them in the field. E is distinguished from D by the presence of Dodecatheon and Rumex acetosella and
by the absence of Festuca idahoensis. These are the 12th, 11th, and 9th species used in discrimination. Qualitatively, D and F are indistinguishable as are A to C. Thus, we represent them as subassociations. In the field B (Hypericum and Cladonia furcata) was noted only on the lower eastern portions of mounds A, (Cladonia mitis and Agrostis diegoensis) was found on lower southern exposures, and C in raised intermounds. This collection represents phases of the same group.

Groups G to M (except K) are closely related to each other, but can be qualitatively distinguished. G, H, and I are closely related while other groups are quite distinct. These groups are distinguished by several qualitative differences shown in the key.

The groups recognized above can be recognized in the field with the aid of the following key to the associations and subassociations. Since associations are conceptual and exist more in our minds than in the field, intergradations will result in less precision and more misclassifications than would be the case for a key to closely related species.

Key to the Associations of the Mima Mounds (Based on cover and presence or absence of characteristic species).

1. Rhacomitrium canescens var. ericoeides cover from 40 to 100%
2. Brodiaea coronaria cover exceeds 2%; Agrostis diegoensis, Rumex acetoella and Dodecatheon hendersonii all present............ Association E (Rhamtomitrium exceeds 70%; Poa pratensis absent)
22. Brodiaea coronaria usually rare, one or more species listed above absent
3. Agrostis tenuis always present Association D-F
33. Agrostis tenuis absent
4. Polytrichum juniperinum under 1%, Agrostis diegoensis and Canassia quashnash present and Hypochoeris radicata over 2% .................................. Association D-d
44. Polytrichum juniperinum over 1%, usually abundant
5. Agrostis diegoensis present
6. Festuca idahoensis present
.............. Association A-b
66. Festuca absent .... Association A-a
5. Agrostis diegoensis absent
6. Dicranum scoparium or Pelitgera aphthosa present
.............. Association A-b
66. Not as above, Aira praeccus usually present ........ Association A-c
11. Rhacomitrium canescens var. ericoeides cover under 40%, usually much less
2. Dominated by Pseudotoga menziesii, field layer lacking ..................................... Association K
22. Not as above, field layer well developed.
3. Rhacomitrium present or, if absent, then Cladonia mitis exceeds 40% cover
4. Cladonia mitis abundant, Canassia quashnash and Hypericum perforatum always present .................................. Association L
44. Cladonia mitis rare or lacking, Rhamtomitrium common, Hypericum perfomatum characteristic
5. Festuca idahoensis usually present; if absent, then Holcus lanatus present
6. Poa pratensis absent Association H
66. Holcus lanatus or Poa pratensis present .................................................. Association I
55. Festuca lacking, or if present then both Polytrichum juniperinum and Cladonia chlorophaeae present
............. Association G
33. Rhacomitrium absent
4. Dicranum scoparium common, Eurhyn-
chium oreganum and Camassia characteristic. Association M
44. Dicranum scoparium absent, Eriophorum virgatum rare or absent, Poa pratensis common .................................................. Association J

Habitat conditions and description of each association

Association A is divided and mapped as three subassociations (A, B, and C). Reference to Tables 2, 3, and 4 and to Fig. 4 indicate that the three subassociations are indeed similar. They are separated only with difficulty by the key and in the field. Association A is characterized by strong dominance by the moss *Rhacomitrium canescens* var. *ericoides* and the consistent occurrence of *Polytrichum juniperinum*, *Camassia quamash*, and *Hypochna radicata*. The association is found primarily in the raised intermounds and lower more exposed mound slopes.

Association D is divided and mapped as two subassociations, D and E, and is closely related to both association A and association F. They are characterized by *Rhacomitrium canescens* dominance, the consistent occurrence of *Hypochna radicata* and *Camassia quamash*, and grasses represented consistently by one, but not the other, species of *Agrostis.* D is characterized by *Agrostis diegoensis* and usually lacks *Polytrichum juniperinum*. This association was more common in the transect than in the region of the map. It appears to be located in intermound sites that are neither in depressions or local rises. It may be regarded as transitional between A and F.

Association F is also dominated by *Rhacomitrium*. It contains the following characteristic species: *Brodiaeae coronaria*, *Rumex acetosella*, and *Dodecatheon hendersonii*. This association is found in mesic depressions within the intermound areas.

The remaining associations are found on the mounds. They appear to represent different combinations of habitat variables which affect moisture conditions. Associations G, H, and I are intermediate in the first ordination axis and appear to have similar moisture relationships with increasing exposure from G to I. Association G is open and is characterized by *Rhacomitrium canescens*, various *Cladonia* species, *Hypochna*, *Hypericum perforatum*, and *Camassia*. Association G is to be found primarily on upper southern mound slopes.

Association H is characterized by limited *Rhacomitrium*, *Festuca idahoensis*, *Holcus lanatus*, and *Hypochna*. *Holcus* is the only consistent species unique to this type.

Association I, found primarily in mid-slope in more exposed areas, is characterized by substantial *Rhacomitrium*, *Festuca*, *Hypochna*, and *Hypericum*. As one might expect from the dominance of introduced species, this association lacks any unique, consistently occurring species.

Association J is confined to mound tops. It is characterized by the dominance by *Poa pratensis* and the absence of *Rhacomitrium*. Only *Isothecium stoloniferum* is also common in this association though it may not always occur.

Associations L and M occur intermixed on the more protected slopes of mounds. In association L *Cladonia mitis* is both characteristic and dominant. It provides sufficient cover so that *Rhacomitrium* may sometimes be found beneath it. *Camassia* and *Hypericum* are the only other consistent species. Association M is differentiated from L by the absence of *Cladonia* and the mixed dominance of *Dicranum scoparium* and *Camassia*. The way in which these two associations interdigitate suggests either strong competitive interactions between *Cladonia* and *Dicranum* or a very patchy soil situation to which these species respond.

Association K includes all samples dominated by *Pseudotsuga* and characterized by forest species, especially mosses, if any.

These distributional patterns are typical of the prairie proper, but are altered by the presence of *Pseudotsuga* in the ecotone. The trees increase shade and thereby decrease insolation. Wind is also reduced, thus decreasing evapotranspiration. Figure 6 compares maps of segments of the transect from prairie and from a portion of the ecotone surrounded by a cluster of three large *Pseudotsuga* individuals. This map is derived from 1,250 sample points and was drawn at a scale of 1 : 200. The most pronounced effect is the disappearance of association F within the shadow pattern. This suggests that the mesophytic dominants of F require greater sunlight or that they are susceptible to competitive replacement in the ecotone conditions. Association C is replaced by M, a case more easily understood; the mesophytic association finds its habitat expanded into the normally drier intermound region and thus it expands. Similarly, J expands on mound tops at the expense of more xerophytic G, H, or I.

**Discussion and Conclusions**

**Scale**

Patterns of vegetation may be examined on three scales in Mima Mounds topography. Microtopographic scale is important for highly competitive species whose abundance may be limited by germination sites. For example, *Hypochna radicata* individuals are strongly correlated with microdepressions on mounds suggesting that such depressions are "safe sites" for *Hypochna* germination. It occurs without respect to mound position or the invasion of trees. Other species, particularly *Rhacomitrium canescens*, appear to be influenced primarily by factors altered.
Table 4. Classification matrix derived from posterior probabilities calculated by discriminant functions after 32 steps. Probability that a sample occurs in each class is calculated and the sample is reclassified into that class of largest probability. Stands placed off the diagonal are judged to have been misclassified by the original classification.

<table>
<thead>
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<th>Classified from association</th>
<th>Number</th>
<th>Reclassified into</th>
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<tr>
<td></td>
<td>A</td>
<td>B</td>
</tr>
<tr>
<td>A-A</td>
<td>16</td>
<td>15</td>
</tr>
<tr>
<td>B</td>
<td>11</td>
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<tr>
<td>C</td>
<td>5</td>
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<tr>
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<tr>
<td>E</td>
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<td>J</td>
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<tr>
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<td>M</td>
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</table>

by the mounds themselves. Such species react strongly to changes in insolation and drainage which affect the effective moisture of a particular mound location. Even a species such as *Camassia quamash*, which is nearly ubiquitous on the prairie, displays changes in dominance with respect to the mound. It is not clear whether these responses are directly attributable to environmental factors or whether competitive interactions are involved.

The third level of scale involves the gradient from prairie to forest and is controlled primarily by the density of *Pseudotsuga menziesii*. On this level, mound topography is subordinated to mound position with respect to trees since the trees exert considerable influence on microclimate. In this study the influence of trees is revealed by shifts in species composition with respect to mounds and by the occurrence of species, such as *Pteridium aquilinum* and *Arctostaphylos uvaursi*, not found in the prairie. The mapping technique (Fig. 6) reveals these changes more efficiently than considerations of individual species. For example, association A, a relatively xerophytic assemblage, is replaced by the mesophytic moss dominated association M.

Classification

The construction of the key was facilitated by SMADA, but some liberties and selectivity were required to construct a functional key. This is due both to the fact that the classification and discrimination analyses were based on importance values, that is, the sum of two relative numbers, and to the logic of our key construction. It is exceedingly difficult to estimate importance value by merely looking at a quadrat since one must estimate the abundance and distribution of each species. Hence, the key is based on cover values obtained from the raw data.

The mapping method suggested here should be of great benefit when vegetation must be classified and mapped for utilitarian purposes and when trained personnel are scarce. We suggest that the trained ecologist devote most of his field time to the detailed description of the range of variation and prepare the classification and vegetation key. A larger number of assistants and surveyors, armed with the key and at least ad hoc taxonomic knowledge, can then map extensive areas in relatively short order.

Ordination

The similarity projection analysis reveals at least two axes of vegetation variation, drainage and insolation, related to mound position. Both reflect aspects of effective moisture with moisture decreasing with mound height and with increasing exposure to direct solar radiation. These interpretations will be subjected to experimental test in the future and should be viewed as tentative. Two factors provide additional reasons for this caution. The first is that association K is unique by virtue of lacking herbs and bears no relationship to any other sample; it is responsible for some distortion. The second is that there is a distinct "hump" in the ordination graph (Fig. 4) which suggests that the method has resulted in a distortion of a controlling axis (Gauch and Whittaker 1972). In this case one might be tempted to view the distortion as having resulted in the driest samples in the middle of the first projection. The effective moisture gradient may very well run from samples low on the mound or in the intermound (wet) to the exposed slopes (xeric) and back to protected slopes (mesic). Such distortions are relatively common in ordinations, but in this instance, it is more easily recognized by virtue of the classification prepared concurrently.
an understanding at some scale. The Mima Mounds may be viewed as a micromountain range. On the scale of a single mound (mountain), transects and ordination are most useful. Here the species change is gradual and patterns seldom reoccur. Ordination techniques are now recognized to be of considerable value under these conditions (Kershaw 1973). We believe that this is because the ordination results correspond to gradients in real space (habitats) when the range of variation is small. The prairie system (mountain ranges) is revealed with more clarity by the classification system since associations tend to reoccur in the same positions relative to the mounds. Classifications appear to be superior when gradients exist as nonlinear functions, where environmental combinations reoccur, or where floristic compositional change is large.

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LITERATURE CITED


