Boreal Vegetation Of A Lacustrine Surficial Sand Belt, Elk Lake, Ontario: Types And Environmental Gradients

Norman Charles Kenkel

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BOREAL VEGETATION OF A LACUSTRINE
SURFICIAL SAND BELT, ELK LAKE,
ONTARIO: TYPES AND ENVIRONMENTAL
GRADIENTS

by

Norman Charles Kenkel

Department of Plant Sciences

Submitted in partial fulfillment
of the requirements of the degree of
Doctor of Philosophy
The University of Western Ontario
London, Ontario

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ABSTRACT

This study addresses the problem of relating compositional variation in boreal vegetation to underlying deterministic (environmental) and probabilistic (primarily historical) influences. The problem of determining plot size is addressed, and a statistical optimization procedure outlined. Alternative ordination strategies are compared (using simulated data), and the advantages of non-metric multidimensional scaling discussed.

The vegetation studied occurs along the southern fringe of the boreal forest near Elk Lake, Ontario. Lacustrine sand deposits are characteristic, but rocky hills overlain by finer soils and small rock outcrops also occur. Accumulation of peat typifies low-lying areas.

The study area, comprising 90 km², was intensively sampled using a restricted random strategy, vegetation and environmental data being obtained from 431 plots. Multivariate methods were used to summarize and interpret the data: cluster analysis to delineate vegetation types and species groupings, and ordination to summarize trends in vegetational composition, to examine interspecific associations of species, and to summarize relationships between delineated types and species groupings.

Initial analyses led to the recognition of two distinct groupings: wetlands (132 plots) and uplands (299 plots). Within the wetlands, nine distinct vegetation types were recognized. Ordination results indicated the importance of nutrient status, and factors related to nutrient availability, in determining vegetation composition. Analyses of the upland sites indicated the importance of moisture availability. In xeric, oligotrophic habitats, ten vegetation types dominated by jack pine were recognized, and a continuum related to moisture availability indicated. In mesic, mesotrophic
upland habitats, seven types, related to substrate type and moisture status, were delineated. The influence of fire history in determining vegetation composition is also discussed.
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I extend my thanks to my supervisor, Prof. L. Orlóci, who contributed so much to my scientific education, and gave me the freedom to pursue this project as I saw fit.

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# TABLE OF CONTENTS

<table>
<thead>
<tr>
<th>Section</th>
<th>Page</th>
</tr>
</thead>
<tbody>
<tr>
<td>CERTIFICATE OF EXAMINATION</td>
<td>ii</td>
</tr>
<tr>
<td>ABSTRACT</td>
<td>iii</td>
</tr>
<tr>
<td>ACKNOWLEDGEMENTS'</td>
<td>v</td>
</tr>
<tr>
<td>TABLE OF CONTENTS</td>
<td>vi</td>
</tr>
<tr>
<td>LIST OF TABLES</td>
<td>xii</td>
</tr>
<tr>
<td>LIST OF FIGURES</td>
<td>xv</td>
</tr>
<tr>
<td>LIST OF APPENDICES</td>
<td>xxii</td>
</tr>
<tr>
<td>CHAPTER 1 - INTRODUCTION</td>
<td>1</td>
</tr>
<tr>
<td>CHAPTER 2 - APPROACHES AND METHODS IN VEGETATION</td>
<td></td>
</tr>
<tr>
<td>ANALYSIS</td>
<td>4</td>
</tr>
<tr>
<td>2.1 Views of the Medium</td>
<td>4</td>
</tr>
<tr>
<td>2.1.1 The Organismal Viewpoint</td>
<td>4</td>
</tr>
<tr>
<td>2.1.2 The Taxonomic Viewpoint</td>
<td>5</td>
</tr>
<tr>
<td>2.1.3 The Individualistic Viewpoint</td>
<td>6</td>
</tr>
<tr>
<td>2.1.4 The Integrated Plant Community</td>
<td>7</td>
</tr>
<tr>
<td>2.1.5 Discussion</td>
<td>7</td>
</tr>
<tr>
<td>2.2 Phytosociological Approaches</td>
<td>8</td>
</tr>
<tr>
<td>2.2.1 The Physiognomic Approach</td>
<td>8</td>
</tr>
<tr>
<td>2.2.2 The Floristic Approach</td>
<td>9</td>
</tr>
<tr>
<td>2.2.2.1 The Classification Tradition</td>
<td>9</td>
</tr>
<tr>
<td>Section</td>
<td>Page</td>
</tr>
<tr>
<td>-------------------------------------------------------------------------</td>
<td>------</td>
</tr>
<tr>
<td>2.4.5 On Choosing an Ordination Technique</td>
<td>40</td>
</tr>
<tr>
<td>2.4.6 Metric and Nonmetric Multidimensional Scaling</td>
<td></td>
</tr>
<tr>
<td>A Comparison</td>
<td>41</td>
</tr>
<tr>
<td>2.4.6.1 Introduction</td>
<td>41</td>
</tr>
<tr>
<td>2.4.6.2 Comparison</td>
<td>43</td>
</tr>
<tr>
<td>2.5 Sampling Theory, With Ecological Applications</td>
<td>54</td>
</tr>
<tr>
<td>2.5.1 Objectives of Sampling in Phytosociological Surveys</td>
<td>54</td>
</tr>
<tr>
<td>2.5.2 Preferential Sampling</td>
<td>55</td>
</tr>
<tr>
<td>2.5.3 Statistical Sampling</td>
<td>55</td>
</tr>
<tr>
<td>2.5.4 Methods of Statistical Sampling</td>
<td>56</td>
</tr>
<tr>
<td>2.5.4.1 Simple Random Sampling</td>
<td>56</td>
</tr>
<tr>
<td>2.5.4.2 Stratified (Restricted) Random Sampling</td>
<td>56</td>
</tr>
<tr>
<td>2.5.4.3 Systematic Sampling</td>
<td>57</td>
</tr>
<tr>
<td>2.5.4.4 Two-stage Sampling</td>
<td>57</td>
</tr>
<tr>
<td>2.5.4.5 Cluster Sampling</td>
<td>58</td>
</tr>
<tr>
<td>2.5.5 On Choosing a Sampling Strategy</td>
<td>61</td>
</tr>
<tr>
<td>2.5.6 Some Aspects of Quadrat Determination</td>
<td>61</td>
</tr>
<tr>
<td>2.5.6.1 Quadrat Shape</td>
<td>61</td>
</tr>
<tr>
<td>2.5.6.2 Quadrat Size</td>
<td>62</td>
</tr>
<tr>
<td>CHAPTER 3 - THE BOREAL FOREST ECOSYSTEM</td>
<td>79</td>
</tr>
<tr>
<td>3.1 Introduction</td>
<td>79</td>
</tr>
<tr>
<td>3.2 Studies of the Boreal Forest Vegetation</td>
<td>79</td>
</tr>
<tr>
<td>3.3 Major Tree Species of Boreal North America</td>
<td>80</td>
</tr>
<tr>
<td>3.3.1 <em>Picea mariana</em> (Black Spruce)</td>
<td>81</td>
</tr>
<tr>
<td>Section</td>
<td>Page</td>
</tr>
<tr>
<td>------------------------------------------------------------------------</td>
<td>------</td>
</tr>
<tr>
<td>3.3.2 <em>Larix laricina</em> (Eastern Larch)</td>
<td>82</td>
</tr>
<tr>
<td>3.3.3 <em>Pinus banksiana</em> (Jack Pine)</td>
<td>82</td>
</tr>
<tr>
<td>3.3.4 <em>Picea glauca</em> (White Spruce)</td>
<td>83</td>
</tr>
<tr>
<td>3.3.5 <em>Abies balsamea</em> (Balsam Fir)</td>
<td>84</td>
</tr>
<tr>
<td>3.3.6 <em>Thuja occidentalis</em> (Eastern White Cedar)</td>
<td>85</td>
</tr>
<tr>
<td>3.3.7 <em>Populus tremuloides</em> (Trembling Aspen)</td>
<td>85</td>
</tr>
<tr>
<td>3.3.8 <em>Betula papyrifera</em> (White Birch)</td>
<td>86</td>
</tr>
<tr>
<td>3.4 Boreal Forest Dynamics</td>
<td>86</td>
</tr>
<tr>
<td>3.5 Boreal Soils</td>
<td>88</td>
</tr>
<tr>
<td>3.6 Environmental Factors Influencing Boreal Vegetation</td>
<td>89</td>
</tr>
<tr>
<td>3.6.1 Climate</td>
<td>89</td>
</tr>
<tr>
<td>3.6.2 Fire</td>
<td>90</td>
</tr>
<tr>
<td>3.6.3 Moisture</td>
<td>90</td>
</tr>
<tr>
<td>3.6.4 Light</td>
<td>91</td>
</tr>
<tr>
<td>3.6.5 Nutrients</td>
<td>92</td>
</tr>
<tr>
<td>3.6.6 Biotic Factors</td>
<td>93</td>
</tr>
</tbody>
</table>

CHAPTER 4 - THE ELK LAKE STUDY AREA - DESCRIPTION AND SURVEY DESIGN

<table>
<thead>
<tr>
<th>Section</th>
<th>Page</th>
</tr>
</thead>
<tbody>
<tr>
<td>4.1 The Study Area</td>
<td>95</td>
</tr>
<tr>
<td>4.2 Sampling Method</td>
<td>104</td>
</tr>
<tr>
<td>4.3 Quadrat Size Determination</td>
<td>105</td>
</tr>
<tr>
<td>4.4 Data Collected</td>
<td>115</td>
</tr>
</tbody>
</table>
CHAPTER 5 - THE ELK LAKE STUDY AREA - VEGETATION TYPES

AND ENVIRONMENTAL GRADIENTS

<table>
<thead>
<tr>
<th>Section</th>
<th>Page</th>
</tr>
</thead>
<tbody>
<tr>
<td>5.1 Initial Subdivision of the Data</td>
<td>117</td>
</tr>
<tr>
<td>5.2 Data Analysis</td>
<td>121</td>
</tr>
<tr>
<td>5.2.1 Strategies</td>
<td>121</td>
</tr>
<tr>
<td>5.2.2 Choice of Methods</td>
<td>121</td>
</tr>
<tr>
<td>5.2.3 Data Standardization</td>
<td>122</td>
</tr>
<tr>
<td>5.3 Species Nomenclature</td>
<td>123</td>
</tr>
<tr>
<td>5.4 Analysis of the Wetland Sites</td>
<td>124</td>
</tr>
<tr>
<td>5.4.1 Choice of Clustering Strategy</td>
<td>125</td>
</tr>
<tr>
<td>5.4.2 Classification of Sites</td>
<td>130</td>
</tr>
<tr>
<td>5.4.3 Site Relationships and Environmental Characterization</td>
<td>143</td>
</tr>
<tr>
<td>5.4.4 Ordination of Sites</td>
<td>151</td>
</tr>
<tr>
<td>5.4.5 Species Classification</td>
<td>155</td>
</tr>
<tr>
<td>5.4.6 Species Ordination</td>
<td>159</td>
</tr>
<tr>
<td>5.4.7 Ecological Relationships</td>
<td>162</td>
</tr>
<tr>
<td>5.4.8 Discussion</td>
<td>169</td>
</tr>
<tr>
<td>5.5 Analysis of the Upland Sites I. Full Data Set</td>
<td>170</td>
</tr>
<tr>
<td>5.5.1 Classification of Sites</td>
<td>170</td>
</tr>
<tr>
<td>5.5.2 Ordination of Sites</td>
<td>178</td>
</tr>
<tr>
<td>5.5.3 Classification of Species</td>
<td>182</td>
</tr>
<tr>
<td>5.5.4 Species Ordination</td>
<td>186</td>
</tr>
<tr>
<td>5.5.5 Ecological Relationships</td>
<td>186</td>
</tr>
<tr>
<td>5.6 Analysis of the Upland Sites II. Xeric Upland Habitats</td>
<td>191</td>
</tr>
<tr>
<td>5.6.1 Classification of Sites</td>
<td>192</td>
</tr>
</tbody>
</table>
# List of Tables

<table>
<thead>
<tr>
<th>Table</th>
<th>Description</th>
<th>Page</th>
</tr>
</thead>
<tbody>
<tr>
<td>2.1</td>
<td>Description of the eight methods used in the comparison of ordination techniques</td>
<td>46</td>
</tr>
<tr>
<td>2.2</td>
<td>Results of procrustes analysis (sums of squares values) for the ordination methods outlined in Table 2.1, using simulated data (see text)</td>
<td>52</td>
</tr>
<tr>
<td>2.3</td>
<td>Population parameters and corresponding unbiased estimates in cluster sampling (modified from Cochran 1977)</td>
<td>60</td>
</tr>
<tr>
<td>2.4</td>
<td>Variance table for the determination of optimal quadrat size using cluster sampling</td>
<td>70</td>
</tr>
<tr>
<td>4.1</td>
<td>Results of the univariate optimal quadrat size determinations for the jack pine and black spruce dominated systems. Maximum relative efficiency values (see text and Table 2.4) are given, and the size of the grid units for this maximal comparison is indicated</td>
<td>108</td>
</tr>
<tr>
<td>Table</td>
<td>Description</td>
<td>Page</td>
</tr>
<tr>
<td>-------</td>
<td>------------------------------------------------------------------------------</td>
<td>------</td>
</tr>
<tr>
<td>5.1</td>
<td>Generalized distance assignments of the 13 differently assigned quadrats to</td>
<td>129</td>
</tr>
<tr>
<td></td>
<td>the 9 groupings of the wetland habitats at Elk Lake, Ontario, and the number</td>
<td></td>
</tr>
<tr>
<td></td>
<td>of incorrect assignments made for each of the five clustering methods tested.</td>
<td></td>
</tr>
<tr>
<td>5.2</td>
<td>Means, variances, and frequencies of the 114 most common species in each of</td>
<td>134</td>
</tr>
<tr>
<td></td>
<td>the nine vegetation types (I - IX) described for the wetland habitats at</td>
<td></td>
</tr>
<tr>
<td></td>
<td>Elk Lake, Ontario.</td>
<td></td>
</tr>
<tr>
<td>5.3</td>
<td>Pairwise compositional divergences (using the 2I statistic) for the 9 wetland</td>
<td>145</td>
</tr>
<tr>
<td></td>
<td>types.</td>
<td></td>
</tr>
<tr>
<td>5.4</td>
<td>Physiognomic - environmental characterization of the 9 wetland types.</td>
<td>148</td>
</tr>
<tr>
<td>5.5</td>
<td>Correlations of the concentration analysis scores for the 9 wetland types</td>
<td>167</td>
</tr>
<tr>
<td></td>
<td>with selected environmental parameters.</td>
<td></td>
</tr>
<tr>
<td>5.6</td>
<td>Means, variances, and frequencies of the 79 most common species in each of</td>
<td>176</td>
</tr>
<tr>
<td></td>
<td>the eight vegetation groupings (I - VIII) described for the upland habitats</td>
<td></td>
</tr>
<tr>
<td></td>
<td>at Elk Lake, Ontario.</td>
<td></td>
</tr>
<tr>
<td>5.7</td>
<td>Means, variances, and frequencies of the 67 most common species in each of</td>
<td>196</td>
</tr>
<tr>
<td></td>
<td>the ten vegetation types (I - X) described for the xeric, jack pine</td>
<td></td>
</tr>
<tr>
<td></td>
<td>dominated habitats at Elk Lake, Ontario.</td>
<td></td>
</tr>
<tr>
<td>5.8</td>
<td>Pairwise compositional divergences (using the 2I statistic) for the 10</td>
<td>207</td>
</tr>
<tr>
<td></td>
<td>xeric upland types. Values of chi-square, degrees of freedom, and the</td>
<td></td>
</tr>
<tr>
<td></td>
<td>standard normal deviate are given.</td>
<td></td>
</tr>
<tr>
<td>Table</td>
<td>Description</td>
<td>Page</td>
</tr>
<tr>
<td>-------</td>
<td>------------------------------------------------------------------------------</td>
<td>------</td>
</tr>
<tr>
<td>5.9</td>
<td>Physiognomic – environmental characterization of the 10 xeric upland types.</td>
<td>209</td>
</tr>
<tr>
<td>5.10</td>
<td>Correlations of the concentration analysis scores for the 10 xeric upland types with selected environmental parameters.</td>
<td>231</td>
</tr>
<tr>
<td>5.11</td>
<td>Means, variances, and frequencies of the 53 most common species in each of the seven vegetation types (I – VII) described for the mesic upland habitats at Elk Lake, Ontario.</td>
<td>239</td>
</tr>
<tr>
<td>5.12</td>
<td>Pairwise compositional divergences (using the 2I statistic) for the 7 mesic upland types. Values of chi-square, degrees of freedom, and the standard normal deviate are given.</td>
<td>247</td>
</tr>
<tr>
<td>5.13</td>
<td>Physiognomic – environmental characterization of the 7 mesic upland types.</td>
<td>249</td>
</tr>
<tr>
<td>5.14</td>
<td>Correlations of the concentration analysis scores for the 7 mesic upland types with selected environmental parameters.</td>
<td>268</td>
</tr>
</tbody>
</table>
# LIST OF FIGURES

<table>
<thead>
<tr>
<th>Figure</th>
<th>Description</th>
<th>Page</th>
</tr>
</thead>
<tbody>
<tr>
<td>2.1</td>
<td>Results of ordination strategies applied to artificial coenoplane data of varying degrees of species turnover, measured in half-change (HC) units: (a). 1.5 x 1.5 HC (b). 1.5 x 4.5 HC (c). 4.5 x 4.5 HC (d). 4.5 x 9.0 HC. Individuals are points connected by grid lines.</td>
<td>49</td>
</tr>
<tr>
<td>2.2</td>
<td>A simple artificial example to illustrate the utility of cluster sampling in the determination of optimal quadrat size. The relative efficiency values are shown for each of step.</td>
<td>68</td>
</tr>
<tr>
<td>2.3</td>
<td>Maps of a portion of an artificial data set containing four species A – D. The shaded areas represent areas where the species occurs. The seven quadrat sizes used to sample the data set are also shown.</td>
<td>73</td>
</tr>
<tr>
<td>2.4</td>
<td>Plot of the largest eigenvalue versus quadrat size for the data set of Figure 2.3.</td>
<td>75</td>
</tr>
<tr>
<td>2.5</td>
<td>Plot of (a) the largest eigenvalue, and (b) the sum of the two largest eigenvalues, versus quadrat size for the London, Ontario weed community data.</td>
<td>77</td>
</tr>
<tr>
<td>Figure</td>
<td>Description</td>
<td>Page</td>
</tr>
<tr>
<td>--------</td>
<td>-----------------------------------------------------------------------------</td>
<td>------</td>
</tr>
<tr>
<td>4.1</td>
<td>Map of Ontario, Canada showing the location of the Elk Lake study area</td>
<td>97</td>
</tr>
<tr>
<td>4.2</td>
<td>Outline of the sampling frame of the Elk Lake study area (shaded), showing</td>
<td>99</td>
</tr>
<tr>
<td></td>
<td>the general drainage pattern of the area. The limits of the surficial</td>
<td></td>
</tr>
<tr>
<td></td>
<td>lacustrine sand deposits of the region are also shown.</td>
<td></td>
</tr>
<tr>
<td>4.3</td>
<td>A detailed map of the Elk Lake study area. The three sampling strata are</td>
<td>101</td>
</tr>
<tr>
<td></td>
<td>also shown. Codes are: 1 - lowlands (areas in which the water table is at</td>
<td></td>
</tr>
<tr>
<td></td>
<td>or near the surface). 2 - uplands (flat or gently rolling land above the</td>
<td></td>
</tr>
<tr>
<td></td>
<td>water table). 3 - highlands (rocky promotoriums). The location of the</td>
<td></td>
</tr>
<tr>
<td></td>
<td>Indian Chute weather station is also shown.</td>
<td></td>
</tr>
<tr>
<td>4.4</td>
<td>Environmental data for Indian Chute, Ontario (1941 - 1970)</td>
<td>103</td>
</tr>
<tr>
<td>4.5</td>
<td>Plots of the largest eigenvalues versus quadrat size for the (a) black</td>
<td>111</td>
</tr>
<tr>
<td></td>
<td>spruce and (b) jack pine sites at Elk Lake, Ontario.</td>
<td></td>
</tr>
<tr>
<td>4.6</td>
<td>The two-stage sampling procedure used in the study of the Elk Lake</td>
<td>114</td>
</tr>
<tr>
<td></td>
<td>vegetation.</td>
<td></td>
</tr>
<tr>
<td>Figure</td>
<td>Description</td>
<td>Page</td>
</tr>
<tr>
<td>--------</td>
<td>-------------</td>
<td>------</td>
</tr>
<tr>
<td>5.1</td>
<td>(a). Correspondence analysis (CA) of the full data set (431 quadrats), showing the separation of the 19 grass-sedge meadow quadrats from the others (strong hatched line). (b). CA of the 412 quadrats (following removal of the 19 grass-sedge meadow quadrats), the strongly hatched line showing the two groups (upland and wetland areas) delineated by the TWINSPLAN program.</td>
<td>119</td>
</tr>
<tr>
<td>5.2</td>
<td>Sum of squares agglomeration dendrogram of the 132 quadrats from wetland habitats at Elk Lake, Ontario. The nine vegetation types (I - IX) are also indicated.</td>
<td>132</td>
</tr>
<tr>
<td>5.3</td>
<td>Nonmetric multidimensional scaling ordination (two-dimensional solution, utilizing chord distance) of the 132 quadrats of the wetland habitats at Elk Lake, Ontario.</td>
<td>153</td>
</tr>
<tr>
<td>5.4</td>
<td>Sum of squares agglomeration dendrogram of 114 species from the wetland habitats at Elk Lake, Ontario. The seven ecological species groups A - G are also indicated.</td>
<td>157</td>
</tr>
<tr>
<td>5.5</td>
<td>Nonmetric multidimensional scaling (two-dimensional solution, utilizing chord distance) of the common 114 species of wetland habitats at Elk Lake, Ontario.</td>
<td>161</td>
</tr>
<tr>
<td>Figure</td>
<td>Description</td>
<td>Page</td>
</tr>
<tr>
<td>--------</td>
<td>-------------</td>
<td>------</td>
</tr>
<tr>
<td>5.6</td>
<td>Three-dimensional concentration analysis ordinations of the nine vegetation types (I - IX) and seven species ecological groups (A - G) of the wetland habitats at Elk Lake, Ontario.</td>
<td>165</td>
</tr>
<tr>
<td>5.7</td>
<td>Sum of squares agglomeration dendrogram of the 299 quadrats from upland habitats at Elk Lake, Ontario. The two major groupings resulting from the first dichotomy are labelled 1 and 2. The eight vegetation groups (I - VIII) are also indicated.</td>
<td>172</td>
</tr>
<tr>
<td>5.8</td>
<td>Principal components analysis (utilizing a covariance matrix between species) of the 299 quadrats of upland habitats at Elk Lake, Ontario. Symbols correspond to the vegetation groupings. (a) axis I vs. axis II. (b) axis I vs. axis III.</td>
<td>181</td>
</tr>
<tr>
<td>5.9</td>
<td>Sum of squares agglomeration dendrogram of the 79 most common species of upland habitats at Elk Lake, Ontario. The six species ecological groupings (A - F) are also indicated.</td>
<td>184</td>
</tr>
<tr>
<td>5.10</td>
<td>Nonmetric multidimensional scaling (two-dimensional solution, utilizing chord distance) of the 79 most common species of upland habitats at Elk Lake, Ontario.</td>
<td>188</td>
</tr>
<tr>
<td>Figure</td>
<td>Description</td>
<td>Page</td>
</tr>
<tr>
<td>--------</td>
<td>---------------------------------------------------------------------------------------------------------------------------------------------------------------------------</td>
<td>------</td>
</tr>
<tr>
<td>5.11</td>
<td>Three-dimensional concentration analysis ordinations of the eight vegetation types (I - VIII) and six species ecological groupings (A - F) of the upland habitats at Elk Lake, Ontario.</td>
<td>190</td>
</tr>
<tr>
<td>5.12</td>
<td>Sum of squares agglomeration dendrogram of the 180 quadrats of xeric, jack pine dominated upland habitats at Elk Lake, Ontario. The ten vegetation types (I - X) are also indicated.</td>
<td>194</td>
</tr>
<tr>
<td>5.13</td>
<td>Nonmetric multidimensional scaling ordination (two-dimensional solution, utilizing chord distance) of the 180 quadrats of xeric, jack pine dominated upland habitats at Elk Lake, Ontario.</td>
<td>214</td>
</tr>
<tr>
<td>5.14</td>
<td>Soil particle size values superimposed on the nonmetric multidimensional scaling scattergram (Figure 5.13) of the 180 xeric, jack pine sites.</td>
<td>217</td>
</tr>
<tr>
<td>5.15</td>
<td>Relative elevation (arbitrary five point scale) values superimposed on the nonmetric multidimensional scaling (Figure 5.13) of the 180 xeric, jack pine dominated upland sites.</td>
<td>219</td>
</tr>
<tr>
<td>5.16</td>
<td>Sum of squares agglomeration dendrogram of the 60 most common species of xeric, jack pine dominated upland habitats at Elk Lake, Ontario. The five species ecological groupings (A - E) are also indicated.</td>
<td>222</td>
</tr>
<tr>
<td>Figure</td>
<td>Description</td>
<td>Page</td>
</tr>
<tr>
<td>--------</td>
<td>-------------</td>
<td>------</td>
</tr>
<tr>
<td>5.17</td>
<td>Nonmetric multidimensional scaling (two-dimensional solution, utilizing chord distance) of the 60 most common species of xeric, jack pine dominated upland habitats at Elk Lake, Ontario.</td>
<td>226</td>
</tr>
<tr>
<td>5.18</td>
<td>Three-dimensional concentration analysis ordinations of the ten vegetation types (I - X) and five species ecological groupings (A - E) of the xeric, jack pine dominated uplands at Elk Lake, Ontario.</td>
<td>228</td>
</tr>
<tr>
<td>5.19</td>
<td>Sum of squares agglomerative dendrogram of the 119 quadrats of the mesic upland habitats at Elk Lake, Ontario. The seven vegetation types (I - VII) are also indicated.</td>
<td>237</td>
</tr>
<tr>
<td>5.20</td>
<td>Nonmetric multidimensional scaling (two-dimensional solution, utilizing chord distance) of the 119 quadrats of the mesic upland habitats at Elk Lake, Ontario.</td>
<td>253</td>
</tr>
<tr>
<td>5.21</td>
<td>Soil particle size values superimposed on the nonmetric multidimensional scaling of the 119 mesic upland habitats of Figure 5.20.</td>
<td>256</td>
</tr>
<tr>
<td>5.22</td>
<td>Sum of squares agglomerative dendrogram of the 52 most common species of the mesic upland habitats at Elk Lake, Ontario. The four species ecological groups (A - D) are also shown.</td>
<td>260</td>
</tr>
<tr>
<td>Figure</td>
<td>Description</td>
<td>Page</td>
</tr>
<tr>
<td>--------</td>
<td>-------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------</td>
<td>------</td>
</tr>
<tr>
<td>5.23</td>
<td>Nonmetric multidimensional scaling (two-dimensional solution, utilizing chord distance) of the 52 most common species of the mesic upland habitats at Elk Lake, Ontario.</td>
<td>263</td>
</tr>
<tr>
<td>5.24</td>
<td>Three-dimensional concentration analysis ordinations of the seven vegetation types (I - VII) and four species ecological groupings (A - D) of the mesic upland habitats at Elk Lake, Ontario.</td>
<td>266</td>
</tr>
</tbody>
</table>
# LIST OF APPENDICES

<table>
<thead>
<tr>
<th>Appendix</th>
<th>Description</th>
<th>Page</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td>Scattergrams resulting from the comparison of metric and nonmetric multidimensional scaling ordination strategies based on artificial data sets (coenoplanes) of varying degrees of species turnover (measured in half-change (or HC) units). Points represent individuals, which are connected by grid lines. Half-change units for the eleven different coenoplanes are indicated in each case.</td>
<td>279</td>
</tr>
<tr>
<td>2</td>
<td>The determination of soil particle size and soil water-holding capacity.</td>
<td>302</td>
</tr>
<tr>
<td>3</td>
<td>Raw data for the wetland habitats at Elk Lake, Ontario. Species occurring with a frequency of less than 10 are not included. The relevés have been sorted and grouped according to the sum of squares agglomerative dendrogram shown in Figure 5.2, while sorting and grouping of species is based on the dendrogram results presented in Figure 5.4.</td>
<td>305</td>
</tr>
</tbody>
</table>
Appendix | Description | Page
--- | --- | ---
4 | Species performance plots for the wetland habitats at Elk Lake, Ontario. Symbols corresponding to percent cover of a given species are superimposed on the nonmetric multidimensional scaling scattergram shown in Figure 5.3. | 310
5 | Raw data for the xeric, jack pine dominated upland habitats at Elk Lake, Ontario. Species occurring with a frequency of less than 10 are not included. Releves are sorted and grouped according to the sum of squares agglomeration dendrogram shown in Figure 5.12. Species have been sorted and grouped according to the dendrogram in Figure 5.16. | 322
6 | Species performance plots for the xeric, jack pine dominated upland habitats at Elk Lake, Ontario. Symbols corresponding to percentage cover of a given species are superimposed on the nonmetric multidimensional scaling scattergram shown in Figure 5.13. | 329
7 | Raw data for the mesic upland habitats at Elk Lake, Ontario. Species occurring with a frequency of less than 10 are not included. Releves are sorted and grouped according to the sum of squares agglomerative dendrogram shown in Figure 5.19. Species have been sorted and grouped according to the dendrogram in Figure 5.22. | 339
<table>
<thead>
<tr>
<th>Appendix</th>
<th>Description</th>
<th>Page</th>
</tr>
</thead>
<tbody>
<tr>
<td>8</td>
<td>Species performance plots for the mesic upland habitats at Elk Lake, Ontario. Symbols corresponding to percentage cover of a given species are superimposed on the nonmetric multidimensional scaling scattergram shown in Figure 5.20.</td>
<td>344</td>
</tr>
<tr>
<td>9</td>
<td>Selected aerial photographs of the Elk Lake study area.</td>
<td>354</td>
</tr>
<tr>
<td>10</td>
<td>Photographic plates, showing various sites in the Elk Lake study area.</td>
<td>359</td>
</tr>
</tbody>
</table>
CHAPTER 1

INTRODUCTION

The science of phytosociology has its roots in the early descriptive accounts of vegetation by European field naturalists exploring both their own continent and more exotic areas. This descriptive tradition has continued to this day, and serves a useful purpose of documenting, in very general terms, the plant geography of various parts of the globe. It was not until this century, however, that workers began to place greater emphasis on the structural and functional aspects of the vegetation, and in particular on the relationship between plants growing in a given area and the corresponding environmental conditions found there. A number of schools of thought have developed from this basic idea, with some emphasizing a purely descriptive approach, others structural-functional relationships, or more often a synthesis of the two. In recent years there has been a trend toward methods of collecting and analyzing vegetation data which can claim a greater degree of objectivity than the earlier approaches. Plant ecologists have turned to sampling theory in defining objective methods of collecting data, and have in recent years begun to use statistical, and particularly multivariate, procedures in the analysis of quantitative vegetation data. It is hardly surprising, therefore, that there remains a high degree of methodological diversification in the field, attributable not only to the different phytosociological traditions but also to differences in objectives. Indeed, it can be said that it is largely the basic misunderstanding of objectives of different schools which has lead to differences in opinion regarding the nature of vegetation and its analysis.

In all but the most poorly described parts of the world, there has been an historical trend from very subjective, broad scale vegetation descriptions to more detailed vegetation studies employing statistical sampling methods in the analysis of vegetation and environmental
correlations. This trend is well documented for the boreal forests of Canada, beginning with the descriptive accounts of early explorers and naturalists (as documented in Larsen 1980) and culminating in recent studies emphasizing more objective methods of data collection and analysis (e.g., Carleton and Maycock 1978; Orlóci and Stanek 1979; Bergeron and Bouchard 1983). Nonetheless, many areas of the boreal forest remain poorly described, and many of the statements regarding vegetation-environmental relationships remain somewhat speculative. Indeed, it can be said that much work, even at the most fundamental level, still needs to be done in describing and analyzing the structural-functional aspects of the boreal ecosystems of Canada. The extent of such forests, and the economic importance of this vast natural resource, underlies the need for detailed objective vegetation studies of such areas.

Relatively few studies of the boreal forest at a small scale level are available. This is probably attributable in large part to the lack, until recently, of even broad-scale surveys of these forests. Recently some detailed work has been done on the vegetation of lacustrine clay deposits in northern Ontario and Québec (Carleton and Maycock 1978; Gaudreau 1979; Jones et al. 1983; Bergeron and Bouchard 1983), but the vegetation of sandy soils, which are quite common in the boreal regions (Rowe 1972), has received comparatively little attention. Most workers have been satisfied with very general descriptions of the vegetation on these coarse surficial deposits. Mueller-Dombois (1964, 1965) describes typical forest types, using methods similar to the traditional European approaches, of predominantly sandy soils in south-eastern Manitoba. More recently Carroll and Bliss (1982) described community types of the extensive sandy deposits in northern Saskatchewan. A detailed analysis of the vegetation of lacustrine sand deposits in Ontario emphasizing both objective sampling methods and analytical strategies has yet to be undertaken, however.

This dissertation is concerned with the vegetation of a small area of the southern boreal forest at Elk Lake in northeastern Ontario dominated
by surficial deposits of lacustrine sands. The purpose was to sample intensively this small portion of the boreal ecosystem, in order to provide an adequate and substantial base for the analysis of the full range, and small-scale variation, of vegetation in the area. In analyzing the data, trends were sought and groupings of vegetation were delineated and described. An attempt was made to examine vegetation trends and their correspondence to underlying environmental factors in determining the primary factors responsible for vegetational variation in the area. In outlining the study, questions arose regarding the implementation of an appropriate sampling design and the approach to use in analyzing the data collected. The dissertation therefore begins with a brief history of phytosociological traditions and views of the medium. Following this, a review of available classification and ordination procedures is presented. This includes a discussion of the two major alternative methodologies in ordination, eigenanalysis (or metric multidimensional scaling) and non-metric multidimensional scaling, and a discussion and comparison of their usefulness. Alternative sampling procedures are outlined next, and their application to phytosociological studies is discussed. The problem of quadrat size determination is also outlined, and alternative strategies for choosing an appropriate quadrat size are discussed and a new approach is presented. The final portion is devoted to the analysis of the vegetation data collected at Elk Lake, Ontario. Vegetation types and species ecological groupings are delineated and described, trends are summarized, and ecological relationships discussed for the highly diverse vegetation of the study area. The final portion of the thesis summarizes the information presented and offers some concluding statements regarding both spatial and temporal processes in this complex ecosystem.
CHAPTER 2

APPROACHES AND METHODS IN VEGETATION ANALYSIS

2.1 Views of the Medium

The conceptualization of vegetation structure will dictate to a large degree the approach taken to its study. Vegetation is a complex of spatial and temporal variation, being influenced by a number of interacting environmental influences. Goodall (1963) has pointed out that in gaining insights into the vegetation we must consider the evolutionary aspects of both the composite species and the plant communities themselves. While this is in theory possible to do, it is in practice an insurmountable task, and for this reason there is no general consensus as to how vegetation should be viewed. Undoubtedly the view taken is somewhat dependent upon the nature of the vegetation being examined (Margalef 1968), the scale at which it is examined, and the objectives of the study. With these points in mind, the major views which have been advanced are outlined below.

2.1.1 The Organismal Viewpoint

Clements (1916) examined vegetation from a temporal standpoint (following Cowles 1899), popularizing the concept of vegetational succession. Temporal change was seen as a directional process, with seral vegetation units modifying a given region, and thereby rendering it favorable to successive units. The final, or climax, vegetation was felt to consist of discrete, recognizable units whose manifestation is dictated by the prevailing macroclimate - this is known as the monoclimax theory. He also suggested an organismal analogy, claiming that vegetation too is conceived, grows, and finally dies. Such a model presupposes the existence of successive, clearly defined stages of an organic entity which can be followed through time along a set path, and is by definition deterministic. Moss (1910)
presented a similar viewpoint, but emphasized edaphic rather than climatic factors. Tansley (1939; following Schimper 1890) modified these viewpoints, recognizing that both macroclimate and other factors were important in classifying vegetation.

The organismal viewpoint has been challenged on a number of counts. It is generally recognized that Clements placed far too much emphasis on biotic modifications as succession proceeds (Johnson 1979). In particular, he failed to consider the resident diasporal population at a given site and other factors which render succession a probabilistic rather than deterministic phenomenon. Furthermore, many contemporary workers seriously question the assumption of recognizable, discrete vegetational units and stages as the successional process proceeds (Drury and Nesbit 1973, Colinvaux 1973).

2.1.2 The Taxonomic Viewpoint

This viewpoint, which has been championed with particular vigour by Braun-Blanquet (1932) and other European workers, assumes that vegetation consists of spatially repeating, structurally definable entities which show some degree of overall internal homogeneity. These units are thought to occur naturally, though they are generally described as abstractions. An hierarchical relationship of these vegetation units is assumed, implying some degree of internal species interrelationships which serve to define the hierarchy. This viewpoint, unlike the previous, places little emphasis on the temporal aspects of vegetation. It is instead a classificatory strategy which presupposes the existence of discrete vegetational units which are defined, delineated, and described by the worker.
2.1.3 The Individualistic Viewpoint

This viewpoint, apparently advanced independently by Ramensky (1930) and Gleason (1917, 1927), conceives of vegetation as resulting from the selective forces of spatially and temporally fluctuating environmental factors on immigrant diasporopopulations. Both workers developed the idea of species individuality, which states that each species responds uniquely to a complex of environmental factors, thereby coming to occupy a unique niche. Gleason also advanced the idea of community continuity, arguing that species show optimal responses which are distributed in such a way that competition is minimized. This in turn implies that any species interrelationships observable in the field (which according to Gleason will arise only through chance occurrences of species with overlapping ecological requirements) will fail to have the obligate biotic interactions necessary for the organization of species into recognizable vegetation units. Vegetation discontinuities were attributed to strong environmental discontinuities rather than species coevolution.

More recently Whittaker (1951, 1967) has readdressed this problem. His studies suggest that a more complete survey of vegetation over a large area, and its subsequent synthesis, will invariably show continuity. In particular, he concluded that wherever there is a continuous change in one or more environmental variables (such as an elevational gradient), a continuous change in the vegetation will also be seen, with species optima distributed at random along the gradient. Daubenmire (1968), however, argues that such an approach may obscure the recognition of distinct units.

2.1.4 The Integrated Plant Community

Goodall (1963) has pointed out that the individualistic and organismal-discrete viewpoints are opposite and mutually exclusive extremes, stating that the true nature of vegetation likely lies somewhere in between. He argues strongly for what he calls the integrated plant community, using
as a basic premise the idea that both biotic and abiotic factors serve to
determine whether or not a given species can occupy a site. Competition
is seen as a strong determining force, exerting mutual influences and
ultimately leading to the cooperative interaction of species occurring in a
given habitat. This in turn leads to an integration of the species occupying
a given niche-space, maintained by a 'positive feedback' mechanism (Margalef
1968). The community is therefore seen as consisting of a complex of species
evolving in close proximity for extended periods of geological time, with
strong selection pressures which include the interrelationships of
constituent species. The net result is a community which evolves as a whole.
A similar viewpoint has been advocated by a number of other workers (see
Miles 1979).

2.1.5 Discussion

In discussing the alternative viewpoints, Goodall (1963) developed a
useful spatial analogy in which species are axes and relevés points in this
'vegetational space'. In such a model, a continuum of points would support
the individualistic viewpoint. The existence of reasonably discrete clusters,
however, may arise either because certain combinations of environmental
factors, or certain species combinations, fail to occur. In either case, such
clusters should not be recognized as true vegetation types but as artifacts
reflective of a discontinuous environment. However, the existence of discrete
clusters resulting from the stability of certain species groups in the
presence of a continuous environment is evidence for the integrated plant
community. The problem, then, lies in determining whether species
assemblages occurring in the field are attributable to environmental
discontinuities or coevolutionary factors. In any case, it seems unlikely that
the extreme viewpoints advocated by earlier workers will be confirmed.
Vegetation is a complex phenomenon, making it unlikely that a simple
explanation of its structure will suffice.
2.2 Phytosociological Approaches

In recent years there has been a proliferation of methodological approaches for studying vegetation. Some methods are principally for the description and summarization of a body of vegetation data, while others were developed to allow for the more detailed analysis of the relationship between vegetation and environment. The approach taken is dependent to a large degree on the objectives of the study and the view of the vegetation taken. A brief overview of the alternative approaches is given below.

2.2.1 The Physiognomic Approach

Physiognomy is defined here as the form and structure of vegetation, as manifested by overall appearance resulting from dominant growth forms (Cain and Castro 1959). Physiognomic descriptions have been used primarily in large-scale surveys where it is important to compare the overall structure of vegetation from different parts of the world. Features which contribute to the physiognomy of the vegetation include structural aspects such as dominant growth form and the height and density of individuals, strictly physiognomic aspects such as seasonality and colour, functional aspects (species longevity), and diversity.

Various methods for the physiognomic description of vegetation have been suggested. Warming (1909) presented a complex, all-encompassing physiognomic-function classification of great theoretical interest which is unfortunately burdened by a large number of categories and a complicated terminology. More recent work in Europe (Rubel 1930, Du Reitz 1930, Ellenberg 1956) has emphasized much simpler systems incorporating both environmental and ecological considerations. Raunkier (1934) developed a classificatory system for plants based on physiognomy. He chose as a criterion the adaptation of plants to survival under unfavourable conditions, in particular the position of perennating buds. Later attempts to consider the degree of bud protection were somewhat less successful, as was an
alternative approach based on leaf size. Davis and Richards (1933) suggested the use of profile diagrams, which involve drawing to scale a typical cross-section of the vegetation. Stamp (1934) used a similar approach, but used symbols to represent the profile. Later, Kuchler (1949) and Dansereau (1957) independently developed a symbolic approach using structural and functional characteristics to represent the vegetation of an area.

2.2.2 The Floristic Approach

In this, the most widely used approach, the vegetation is characterized by its constituent species. The justification for this is that the biological species, as the basic evolutionary unit, will most accurately reflect prevailing habitat conditions, and that species with similar ecological requirements will tend to occur together at a given site.

A number of schools have arisen which utilize floristic criteria in describing the vegetation of an area. These reflect differences in both objectives and the presupposed viewpoint taken as to the nature of the vegetation.

2.2.2.1 The Classification Tradition

Vegetation classification has had a long and sometimes volatile history in Europe. The historical aspects are discussed by Shimwell (1971) and in the review papers in Whittaker (1978). There has been a tendency in recent years toward a general consensus in classificatory strategies, the diversification of ideas and concepts prevalent in the first half of the century giving way to an approach which is more general and all-encompassing. The main European schools are discussed briefly below.

1. The Zürich-Montpellier Tradition. This school, whose basic tenet is that vegetation is readily classifiable into discrete units termed associations, has enjoyed widespread use in the past and is currently the preferred method for describing vegetation in continental Europe. Its main proponent was
Braun-Blanquet (1932), who defined the plant association as a community of specific floristic composition and uniform physiognomy growing under relatively uniform environmental conditions. The association itself, however, is an abstraction which is never actually seen in the field, though it is based on field data. Details of the procedures and theory underlying this school of vegetation study are given in Shimwell (1971), Mueller-Dombois and Ellenberg (1974), and Westhoff and van der Maarel (1978), among others. The procedure begins with the investigator preferentially delimiting a stand which is considered typical of the vegetation to be described. A complete enumeration of the plant species occurring in the stand is undertaken, and estimates of their abundance (usually employing a 'cover-abundance' scale) are made. The description of the plant association is then made based on the composite information obtained from one or usually more 'typical' stands. This is obtained through a complicated procedure involving field descriptions, tabular rearrangement of vegetation tables, further checking of the 'ecological reality' of tentatively described types, and the final characterization and description of associations based on the concepts of species fidelity and constancy. Species showing a high degree of fidelity (that is, characteristic of a particular vegetation unit), are termed characteristic species and are used to describe the associations. A major criticism of this approach is the circularity of argument which renders the method somewhat self-serving (Poore 1955).

2. The Uppsala Tradition. This Scandinavian school was for a considerable time the chief rival of the Zürich-Montpellier school for supremacy in the description of European vegetation. Like the Zürich-Montpellier school, it was assumed that the vegetation could be readily described in terms of discrete units, and that these could in turn be defined by characteristic species. However, the units were considered to be elements of certain minimal area which could be recognized in the field (Du Reitz 1930). The historical aspects of this tradition are reviewed by Shimwell (1971), who points out that during the 1930's and since there has been a convergence toward the
3. The British Tradition. This approach stemmed from the work of Clements (1916), who described and classified vegetation using the analogy of a functional organism. His descriptions were based on the presumed monoclimax vegetation at a given site. However, consideration was also given to 'local stops', or seres, in the presumed temporal sequence. Cooper (1926) also stressed a dynamic approach but placed little emphasis on classification per se. Tansley (1939) modified the Clementsian approach somewhat, recognizing that the idea of the functional organism was an oversimplification, and that factors other than macroclimate (in particular edaphic considerations) were important in determining the climax vegetation of a given area. The tendency in Britain in recent years has been to deemphasize classification, stressing instead the elucidation of trends of variation (Greig-Smith 1982).

4. Numerical Classification. The term numerical classification was coined by Goodall (1978) to describe classificatory strategies which involve a formal algorithm to define groupings. These methods fall under the general name of 'cluster analysis', and a large number of algorithms have been described. The current trend in classification of vegetation has been toward the use of these objective strategies in conjunction with the incorporation of randomization in the sampling strategy. Some of the available clustering techniques are briefly outlined in Section 2.3.

2.2.2.2 The Vegetation Continuum

While the utility of classification for the description and summarization of vegetation has long been recognized, the validity of the units so described has often been questioned (Gleason 1939, Whittaker 1967). In both North America and Britain, recent interest has centered on studying vegetation as a continuum, in particular the changes in vegetational composition along gradients of environmental variation. Such studies may be either direct, in which vegetation data is collected from a transect along a clearly defined
environmental gradient, or indirect, where vegetation data is first collected and summarized in examining correlations with environmental variation. In either case emphasis is placed on the elucidation of trends rather than the pigeonholing of stands into homogeneous groupings. Some suggested strategies for the analysis of trends in vegetational variation are outlined below.

1. **The Direct Strategy.** In this strategy, a number of transects are enumerated along a clearly demarcated complex environmental gradient (or ecocline), such as elevation. Quadrats from a given level along the gradient are normally pooled to obtain an average, thereby minimizing errors attributable to random variation (Whittaker 1967). A number of methods have been suggested to summarize such data. Whittaker (1967) presented elevational transects as smoothed curves representing species performances. Curtis and MacIntosh (1951) used a weighted averages technique, in which species are weighted according to an environmental classification - for example, species may be classified as being mesic, submesic, or xeric if a moisture criterion is used. The presence of species in quadrats is noted, and the stands are ordered along a moisture gradient according to their constituent species. The method cannot be recommended because of the circularity of argument involved (Orlóci 1978). Bray and Curtis (1957) developed a geometric method for arranging stands on the basis of their vegetational composition which assumes that the endpoints of the gradient are known *a priori*.

2. **The Indirect Strategy.** Whenever a clear-cut environmental gradient is not present an indirect strategy must be employed. In this, stands are compared to reveal trends corresponding to underlying environmental gradients. Whittaker (1967) and Orlóci (1978) discuss the various methods available for unfolding complex data sets to reveal such trends.

   Matrix rearrangement involves the calculation of a matrix of similarity or distances between stands, followed by the shuffling of the rows and
columns to reveal overall trends in similarity. These matrices may be difficult to interpret, however, particularly when the number of stands is large. Gale et al. (1984) have developed an objective method for optimizing structure in these sorted matrices.

Plexus diagrams involve the arrangement of stands in a two-dimensional non-euclidean space. Bars whose thickness indicate degree of similarity connect the stand points. The method is limited in the number of stands which can be accommodated, and it may be difficult to obtain a parsimonious placement of points. Matthews (1978) has developed an objective procedure which uses a nonmetric scaling procedure to obtain an efficient placement of points.

Indirect ordination is by far the most widely used procedure for unfolding continuous vegetational variation to reveal trends in the data. Goodall (1954, after Ramensky-1930) defined ordination as the arrangement of stands in a uni- or multi-dimensional order, and introduced to biology the method of principal components analysis from the statistical literature. However, the lack of computational facilities and a general distrust and lack of understanding among vegetation scientists ensured that the strategy laid dormant in the literature until revived by Orlić (1966). In the interim, computationally less rigorous strategies were developed, and the method of Bray and Curtis (1957) enjoyed widespread use. The trend in recent years has been toward the use of metric multidimensional scaling procedures, otherwise known as eigenvector methods. Nonmetric multidimensional scaling, originally developed by psychometricians, has in recent years been increasingly used by biologists. These and other ordination methods are described in Section 2.4.
2.2.2.3 Current Trends in Floristic Investigations

The trend in recent years, particularly in North America and Britain, has been toward greater objectivity in the study of vegetation. The question of whether vegetation is classifiable, while still of great theoretical interest, is no longer of primary concern. Recent workers (Lambert and Dale 1964, Anderson 1965, Orlóci 1978, Greig-Smith 1982) have stressed the utility of both classificatory and ordination strategies in the exploration of data structure. It has been realized that little progress in vegetation science can be made if workers continue to merely classify vegetation or describe clearly apparent trends. Instead, efforts should be made to examine the complexities of vegetational interaction, which can only be accomplished through the development of an objective and clearly defined strategy.

2.3 Numerical Classification

Numerical methods of classification come under the general heading of cluster analysis. The suitability of a classificatory strategy is clearly dependent upon the underlying structure of the data. If continuous, numerical methods will produce a dissection. As Kendall (1966) has pointed out, all data sets can be dissected but only some are truly classifiable. If areas of high density, or structure, occur in the data, then questions as to the appropriate number of classes, the manner in which these are delineated, and the strategy utilized in allotting individuals to classes, must be addressed (Goodall 1978). Whereas considerable attention has been given to the question of cluster definition, comparatively little work has been undertaken concerning the number of clusters to recognize. Even the definition of the cluster is somewhat problematic. Williams (1971) points out that any definition based on internal properties of the cluster is weak. In general a cluster is defined as containing members which have one or more characteristics in common which set them apart from others (Cormack 1971, Greig-Smith 1982). To Williams (1971), the members of a cluster are related internally but separated by comparatively negative relationships.
from other clusters.

The objectives of cluster analysis in phytosociology are various, but generally involve problem solving, hypothesis generation, and data reduction (Orličić 1978). Cormack (1971), however, points out that it is not valid to test hypotheses of the existence of clusters which a method finds, as this involves some degree of circular reasoning (see also Pielou 1977).

In general, any numerical classification strategy should meet the general requirements of objectivity, stability, predictivity, and robustness (Cormack 1971). An objective classification is a repeatable one (given the same data set and algorithm), while stability implies consistent clustering in the light of new data. A predictive classification permits assignment of new individuals to previously-defined groups, while robustness implies that only small changes in the classification result from small changes in the data set.

Most clustering techniques have been developed as algorithms, and in most cases a cluster is defined only by the algorithm (Gower 1967). It is hardly surprising that different algorithms imply different bases for cluster recognition. In some cases, internal cohesion is stressed, accepting into the same cluster only individuals showing a specific degree of similarity. Alternatively, external cohesion may be stressed, in which case similar individuals will not be placed in different classes. Most algorithms offer a compromise between these two strategies.

2.3.1 Definitions

In theory a clustering strategy will show maximal efficiency if both group homogeneity and hierarchical efficiency can be simultaneously maximized. However, few methods actually search for discontinuities. To Goodall (1978), an optimal classification results if the classes so defined predict attribute values better than any other dissection would (see also Gower 1974).
A classificatory strategy may be hierarchical or non-hierarchical. An hierarchy is of interest when concern lies with the paths of fusion, since it offers a summary of the interrelationships of \( n \) entities by \((2^{n-1})\) clusters. Non-hierarchical methods, by contrast, offer a parsimonious representation of the \( n \) individuals in \( k \) partitioned classes, thereby optimizing group structure.

An hierarchical classification may be either agglomerative or divisive. An agglomerative strategy starts with the \( n \) individuals, progressively fusing them by some criterion of decreasing within similarity. Williams (1971) sees two potential disadvantages of such a strategy. It is computationally inefficient, since the majority of calculations are performed at lower fusion levels which are normally of little importance to the investigator (note, however, that the calculation of the similarity matrix itself is normally the most time-consuming step). He also claims that such a strategy is prone to some degree of misclassification, since the probability of error is greatest at lower fusion levels (see also MacNaughton-Smith et al. 1964). Cormack (1971) comments that such a criticism is unjustified since no common error structure can be assumed for the individuals. The alternative is a divisive strategy, which successively dichotomizes the full data set into hierarchically related groups. This has the major disadvantage that existing groups may be dismembered at each dichotomy (Gower 1974). A major advantage of such a strategy is that cut-off levels are more readily defined, particularly when a statistical criterion in involved in the clustering (Goodall 1978, Greig-Smith 1982).

In a monothetic divisive strategy, division is made on the basis of the presence or absence of a single variable (a monothetic agglomerative strategy is undefined). A polythetic strategy uses, at least potentially, the full set of variables in deciding on an agglomeration or division. To Williams (1971), a monothetic strategy has some advantages in producing clear groups for which a key can be readily produced. However, the strategy may also lead to serious misclassifications, since the chance presence or absence of
a variable in an individual which is otherwise very similar to others may be misclassified (Gower 1967).

Lance and Williams (1967) present an interesting classification of agglomerative methods based on the changing properties of the space occupied by individuals as clustering proceeds. In space-conserving (or space-indifferent) methods, intergroup distances define a space with the same properties as the initial configuration (based on initially calculated similarities) as groups are formed. A strategy is said to be space contracting if individuals show a tendency to be added to existing groups rather than acting as the centres of a new one. Dendrograms resulting from such a strategy often show some degree of chaining. Finally, in space-dilating methods individuals show a distinct tendency to act as a focal point for a new group rather than becoming the member of a group already defined. This results in a strongly-structured dendrogram of similar-sized groups.

2.3.2 Clustering Algorithms

A large number of algorithms for cluster analysis have been suggested, and many have been applied in biological investigations. The choice of a strategy from the bewildering array available is made more difficult by the lack of objective comparisons of the methods. Reviews of available methods written for biologists include Jardine and Sibson (1970), Cormack (1971), Williams (1971), Orlóci (1978), Goodall (1978), and Greig-Smith (1982). The following review discusses some of the alternative algorithms, with emphasis on strategy rather than mathematical theory.

3.3.1 Hierarchical Agglomerative Methods

The majority of clustering algorithms are of this type, and a perusal of the literature suggests that this strategy is the most widely used. The following discussion, while not complete, surveys the major strategies suggested.
1. **Combinatorial Methods**: These methods begin with a matrix of distances or similarities between individuals. The first step involves the fusion of the two most similar individuals. The next fusion is dependent upon the method used to measure distances between groups. Those commonly suggested include:

1. **Nearest Neighbour** - the distance between groups is measured as the shortest distance between two individuals, one from each group. This method is strongly space-contracting.

2. **Furthest Neighbour** - as above, but the furthest rather than the nearest individuals are used. This strategy is strongly space-dilating.

3. **Centroid or Average** - in this method individuals within a group are replaced by their centroid, and the fusion criterion uses the minimal centroid distance. A space-conserving strategy results.

4. **Median** - as above, but replaces individuals in a group by their median rather than arithmetic centroid.

5. **Group-average** - the average distance between all possible pairs of stands, one from each group, is minimized.

6. **Weighted-average** - as above, but the method uses the mean similarity to all members of the potential cluster as the fusion criterion.

A number of other measures of group distance are of course conceivable. Lance and Williams (1967) have shown that these methods are related by a common combinatorial formula. They consider two groups i and j (of size \( n_i \) and \( n_j \) respectively) at distance \( d_{ij} \) apart. These are fused to form a new group \( k \) of size \( n_k = n_i + n_j \). Consider now a third group \( h \). If \( d_{kh} \) can be calculated from \( d_{hi} \), \( d_{hj} \), \( d_{ij} \), \( n_i \) and \( n_j \), then the clustering algorithm is of the combinatorial type, implying that the original data need not be consulted once the initial interstand distances have been computed. The
combinatorial formula has the form:

\[ d_{hk} = \alpha_i d_{hi} + \alpha_j d_{hj} + \beta d_{ij} - \gamma d_{hi} - d_{hj} \]

The parameters \( \alpha_i, \alpha_j, \beta, \) and \( \gamma \) depend upon the definition of intergroup distances. Tabulated values are given by Cormack (1971) and Greig-Smith (1982). Lance and Williams (1967) suggest the use of flexible clustering, in which the user chooses the values of the coefficients (within certain constraints). While this may be very useful, there is some degree of arbitrariness in such parameter manipulation.

2. **Sum of Squares Clustering**: This method was first described by Ward (1963) under the name minimum variance clustering. Orlóci (1967a) independently described the same algorithm in an ecological application. The basic idea involves minimizing the within group sum of squares at each fusion. The algorithm implies the use of an euclidean matrix in defining interstand distances. The method is space-dilating and produces tight, even-sized clusters. Goodall (1978) recommends the method for ecological applications since it considers intra-class variances in producing groups. It must be remembered, however, that optimization at each agglomerative step does not necessarily imply that the final groups will be optimal. Sum of squares clustering is also a combinatorial method and thus easily programmed.

3. **Clustering by Heterogeneity**: Hall (1970) developed a space-contracting method which uses a 'heterogeneity function' to express the divergence of intergroup variable values. This is defined as the relative contribution of a species, weighted by its average presence in the group expressed in proportion to its average presence in all samples. The function is minimized at each fusion step.

4. **Information Clustering**: Orlóci (1970) suggested using information criteria, which are convenient to work with since they are based on an additive model. A number of alternative fusion strategies exist (Orlóci 1978,
Feoli *et al.* 1984), though all minimize the increase in information content at each fusion. Goodall (1978) points out that an information criterion will be suboptimal when applied to quantitative data, but suggested its use in analyzing binary data.

2.3.2.2 Hierarchical, Divisive, Monothetic Methods

These methods are mainly of historical interest, since it is generally accepted that they are subject to severe misclassification (Goodall 1978, Orlóci 1978). They are nonetheless of considerable theoretical interest, and are included here for completeness.

1. Association Analysis: The idea here is that a homogeneous grouping is one lacking interspecific correlations between species, suggesting an algorithm which divides the sample to minimize such within-group correlations. Goodall (1953) devised the original strategy, which begins by testing each pair of interspecific correlations. Based on these, the most common species showing a high degree of association are used to divide the individuals into two groups, one containing this species and the other lacking it. The former group is then reexamined, performing the same procedure until no further significant correlations are present. The 'absence' individuals are then pooled, and the same procedure repeated on them. After all groupings had been found, they are successively recombined in pairs. If no associations reemerged, the groups are recombined.

Williams and Lambert (1959, 1960) examined this strategy and suggested a number of improvements. They no longer performed tests of homogeneity, choosing instead a fixed chi-square quantity beyond which no further subdivisions were made. Division was based on the species producing the smallest amount of overall association between the groupings, utilizing a maximum sum of chi-square criterion. A number of alternatives were suggested, including the use of information rather than chi-square (Lance and Williams 1968). Finally, the method was made strictly hierarchical. A
similar method was later developed by Crawford and Wishart (1967). Greig-Smith (1982) discusses the major disadvantages of association analysis: the chi-square quantity implicitly standardizes each species to unit variance (emphasizing rare species), the data is restandardized after each fusion, and the method, being monothetic, is influenced by the chance presence or absence of a species.

2.3.2.3 Hierarchical, Divisive, Polythetic Methods

These strategies are, at least potentially, the least prone to misclassification (Williams 1971), but until recently computational problems rendered them unfeasible for all but the smallest data sets. More recently developed methods show much greater robustness in this regard.

1. Sum of Squares Analysis: Edwards and Cavalli-Sforza (1965) suggested a method which begins by examining all possible dichotomous splits of the data, choosing the division which minimizing the within sum of squares. This strategy is then repeated for the two subgroups, continuing until sufficient within groups homogeneity is acheived. The method is of great theoretical interest since a working definition of optimality is implied (Goodall 1978). Unfortunately, it is computationally demanding, and becomes logistically impossible above about 25 individuals. Orlóci (1978) suggests that information be used in place of sum of squares.

2. Dissimilarity Analysis: McNaughton-Smith et al. (1964) developed a divisive strategy, applicable to large data sets, which begins by finding the individual most dissimilar to all others in the sample. A group is formed about this individual by adding to it those individuals which show greater similarity to it than to individuals which are not part of the group. Two groups result (the 'fusion' group and a 'residual' group), and the method is repeated for each of these. This continues until sufficient internal group homogeneity is acheived. The method appears to have been little used, though Goodall (1978) recommends its use.
3. Axis Analyses: These methods utilize the location of individuals on an eigenvector axis as a divisive criterion. Lambert et al. (1973) described a method in which all possible \((n-1)\) splits of individuals located on the first principal component axis are considered. The split which minimizes the within group sum of squares (or, alternatively, information) is chosen. Provision is also made for subsequent relocation of individuals by examining higher axes. Hill et al. (1975) described a similar method under the name indicator species analysis. This method partitions an eigenvector axis from a correspondence analysis, followed by involved though straightforward steps to produce a series of dichotomies characterized by a set of indicator species which can be used to key out individuals.

2.3.2.4 Non-Hierarchical Methods

If the investigator is interested in optimizing group structure, and is not concerned with paths of fusion of the groups, a non-hierarchical strategy may be appropriate. Many of these strategies have the further theoretical advantage of searching for discontinuities in the data, and in some cases will fail to produce groups unless the data is sufficiently structured.

1. Iterative Reallocation: Jancey (1966) suggests a method in which the user states \(a \text{ priori}\) the \(k\) number of groups required. This number of points is then injected, randomly or at regular intervals, into \(p\)-dimensional space, where \(p\) is the number of variables. Individuals are then assigned to the nearest point, and a new set of \(k\) points are defined as the centroids of the nearest neighbours. The process is continued until convergence is achieved. Lance and Williams (1967) suggest that such a strategy offers considerable advantages over hierarchical methods. The principle drawback is the requirement for specifying the number of groups required.

2. Maximal Predictive Classification: Gower (1974) presents an interesting algorithm which attempts to simultaneously meet the
requirements of internal homogeneity, while maximizing distances between classes, in the partitioning of \( n \) individuals into \( k \) groups. The method shuffles elements between groups, calculating at each stage the mismatches with respect to a binary predictive vector. This is computationally demanding, but Gower suggests a local optimization algorithm to overcome the problem. This, however, may lead to a local rather than a globally optimal solution. The method is restricted to use with binary data.

3. **Function-point Cluster Analysis**: This method, also known as gradient analysis, utilizes a gradient method to examine the density phases of points in space (Katz and Rohlf 1973). Areas of high density are taken as cluster centroids, and individuals are 'gathered up' from the slopes of respective centroids. The method tends to be relatively insensitive to outliers. An hierarchy can be produced by varying parameters, but it may not be nested.

4. **Clustering by Neighbourhoods**: Orlóci (1976, 1978) developed an algorithm which hypothesizes the existence of discontinuities which subdivide the sample. The method will fail to produce clusters if such discontinuities are not found. A group is discontinuous with others if none of its 'neighbourhoods' (of a given radius) overlap with any others of another group.

5. **Nodal Analysis**: This method utilizes non-centred principal components analysis to seek clusters in a data set. It is dependent upon the existence of discontinuities, or at least well-defined density phases, in the data set. The data matrix is in fact 'partitioned', via unipolar components, into a series of submatrices, each representing a single group. Examples of its application in ecology include Noy-Meir (1971) and Carleton (1979, 1980). Feoli (1977) discusses the general properties of non-centred component analysis.
2.3.3 On Choosing a Clustering Strategy

To Williams and Dale (1964), a biologically useful clustering algorithm should be open-ended, and should produce non-overlapping groups whose elements share at least one thing in common. In addition to these fundamental criteria, Hill et al. (1975) list a number of practical considerations in choosing a clustering algorithm for use in ecological work. To them a method should be successful in classifying a heterogeneous data set into ecologically interpretable clusters, and should not be prone to serious misclassification. Jardine and Sibson (1970), stressing axiomatic properties, concluded that only single linkage clustering is theoretically justifiable. Lance and Williams (1967; also Williams 1971, Orlóci 1978), however, consider the choice of an algorithm to be a more pragmatic decision, based upon biological considerations and the nature of the problem to be solved. They suggest that space-contracting methods such as single linkage clustering obscure boundaries between groups, and therefore cannot be recommended. On the other hand, space-dilating methods may lead to intense clustering, but may produce groups whose elements share only the property that they are unlike any others. Greig-Smith (1982) stresses the advantages of the combinatorial algorithms, and suggests avoiding methods which can lead to reversals. Like Tukey (1962) and Williams (1971), he stresses context, in particular the nature of the variation and the purpose of the analysis. He further suggests that methods appropriate to numerical taxonomy should not be applied uncritically to vegetation data. Goodall (1979) recommends polythetic methods, and in particular sum of squares agglomeration, for quantitative data and information clustering or the method of McNaughton-Smith et al. (1964) for binary data. Monte Carlo studies (e.g. Kuiper and Fisher 1975) have also suggested the superiority of the sum of squares strategy. It would be difficult, however, to recommend a single method for use under all circumstances, as due consideration must always be given to the nature of the problem and the characteristics of the data being analyzed (Orlóci 1978).
In conclusion, the choice of a clustering strategy is necessarily subjective, but it should not be made in ignorance. The user should be familiar with the available methods, their properties, the objectives of the analysis, and the underlying nature of the data being analyzed. This implies experience with both the statistical and biological aspects of the questions being posed. Given this background, the investigator can choose a clustering strategy which will suit his or her particular needs under specific circumstances.

2.4 Ordination Techniques

Ordination strategies have been favoured by workers whose view of vegetation presupposes a continuum model. However, as Cormack (1971), Goodall (1978), and Orióci (1978) have pointed out, an ordination strategy can equally be applied to both continuous and discontinuous data. Nevertheless, ordination does represent a designation by coordinates as opposed to category (Goodall 1978), and will therefore place greater emphasis on underlying continuity in the data set.

Dale (1975) stresses three major objectives of ordination: the arrangement of stands along an environmental gradient, factor revelation or path seeking, and dimensionality reduction. There has been a tendency toward convergence of the latter two objectives (Nichols 1977), and to Austin (1976) the two are irrevocably linked. In any case, the divergence of objectives renders the comparative assessment of various ordination strategies difficult. Most workers have stressed path-seeking, following the work of Gauch and Whittaker (1972a,b).
2.4.1 Ordination Algorithms

There exist three major groups of ordination techniques used in the ecological literature: geometric projective methods, eigenvector or metric scaling procedures, and nonmetric scaling strategies. Projection methods were introduced by ecologists, while the eigenvector procedures were developed by statisticians and later adapted for ecological use. Nonmetric scaling methods were first developed by psychometricians, but because of computational problem were not until recently applied by biologists. Since some of the techniques do not fit easily into these categories they are described separately.

2.4.1.1 Polar Ordination

This geometric method, described by Bray and Curtis (1957), projects individuals in Euclidean space (Orlóci 1974), although many workers have failed to appreciate the significance of this. User-selected endpoints define the direction and length of the axis on which the projection is accomplished. Dale (1975) points out that there is little evidence to suggest that such external endpoints can provide an adequate redescription of an entire data set. The method has been criticized on a number of other grounds, including the subjectivity of end-point selection, the oblique and non-intersecting nature of the derived axes, the inefficiency of summarization (Austin and Orlóci 1966), and the use of non-Euclidean metrics in a geometric model. The subjectivity of axis endpoint selection is particularly critical, since an inappropriate choice will normally produce suboptimal, uninterpretable results (Anderson 1974, Orlóci 1974, Dale 1975). Noy-Meir and Whittaker (1977) have discussed this problem and suggested some remedies, but it seems best to restrict use of the method to direct ordination studies where endpoints are known a priori.

A number of alternative procedures have been suggested to alleviate some of the disadvantages of polar ordination (reviewed by Noy-Meir and
<table>
<thead>
<tr>
<th>Parameter</th>
<th>Population Value</th>
<th>Estimator</th>
</tr>
</thead>
<tbody>
<tr>
<td>Cluster Mean</td>
<td>( u_j = \frac{1}{M} \sum_{i=1}^{M} x_{ij} ) ( j = 1 \ldots M )</td>
<td></td>
</tr>
<tr>
<td>Population Mean</td>
<td>( \bar{u} = \frac{1}{(NM)} \sum_{i=1}^{N} \sum_{j=1}^{M} x_{ij} )</td>
<td>( \bar{x} = \frac{1}{n} \sum_{i=1}^{n} u_i )</td>
</tr>
<tr>
<td></td>
<td>( = \frac{1}{N} \sum_{i=1}^{N} u_i )</td>
<td></td>
</tr>
<tr>
<td>Mean Square between elements of</td>
<td>( V_1 = \frac{1}{(M-1)} \sum_{j=1}^{M} (x_{ij} - u_j)^2 )</td>
<td></td>
</tr>
<tr>
<td>within clusters Mean Square</td>
<td>( V_w = \frac{1}{N} \sum_{i=1}^{N} x_{ij} )</td>
<td>( s^2_w = \frac{1}{n} \sum_{i=1}^{n} V_{ij} )</td>
</tr>
<tr>
<td>Mean square between cluster means</td>
<td>( V_b = \frac{1}{(N-1)} \sum_{i=1}^{N} (u_i - \bar{u})^2 )</td>
<td>( s^2_b = \frac{1}{(n-1)} \sum_{i=1}^{n} (u_i - \bar{x})^2 )</td>
</tr>
<tr>
<td>Population Variance</td>
<td>( V_X = \frac{1}{(NM-1)} \sum_{i=1}^{N} \sum_{j=1}^{M} (x_{ij} - u_j)^2 )</td>
<td>( s^2_X = (1/M)(H-N-1)s^2_B + (1/M)(N-M-1)s^2_W )</td>
</tr>
<tr>
<td></td>
<td>( = (1/(NM-1))(M(N-1)V_b + N(M-1)V_w) )</td>
<td>( = (1/M)(MS^2_B - (M-1)s^2_W) ) (large ( N ))</td>
</tr>
<tr>
<td>Sampling Variance</td>
<td>( V_X = (N-n)/nV_b )</td>
<td>( s^2_X = ((N-n)/Nn)s^2_b )</td>
</tr>
</tbody>
</table>


2.5.5 On Choosing a Sampling Strategy

Systematic sampling has considerable advantages in terms of efficiency, since sample positions are readily located in the field. Furthermore, the method is particularly suited to the mapping of vegetation and in environmental transect studies. Its major disadvantage is the lack of an estimate of the precision of parameter estimates. Such an estimate can be obtained from simple random sampling, but this strategy tends to be relatively imprecise because of its highly uneven coverage of the frame. Stratification prior to random sampling is probably the best strategy for general vegetation survey use: strata can be defined by the investigator to give more even coverage of the frame, thus increasing precision, and unbiased estimates of precision are still available. Subsampling may be utilized when vegetational stratification is evident.

2.5.6 Some Aspects of Quadrat Determination

This section reviews and comments on previous work on the determination of quadrat size and shape in phytosociological contexts. Alternative strategies and objectives in quadrat size choice are discussed, and a new method is described.

2.5.6.1 Quadrat Shape

When the objective lies solely in the estimation of population parameters (for example, the total number of trees per hectare in a given stand), a rectangular quadrat oriented against an underlying gradient or trend (for example, elevation) has often been found to give more precise estimates (Bormann 1953; see also discussions in Greig-Smith 1982). Unfortunately, rectangular quadrats are more prone to 'edge effect'. This is defined as the problem of including or excluding in the enumeration an individual occurring along the quadrat edge. This problem has been particularly well studied in agricultural yield estimation (reviewed by
Whittaker 1977 and Orloci 1978), but all require subjective endpoint selection.

2.4.1.2 Principal Components Analysis

This is a widely-used eigenvector method of ordination first suggested by Goodall (1954) as being useful in phytosociological investigations. Dale (1975) states that it offers an efficient redesription of a complex data set, recommending its use in dimensionality reduction whenever certain basic assumptions, discussed below, are met. The procedure examines a coefficient matrix in cross-products form, and working in this Euclidean space uses an eigenanalysis procedure to summarize linear trends of variation. Geometrically, planes which summarize directions of maximal variation are fitted to the set of $n$ points in variable space. Axes are orthogonal, the first depicting the main direction of linear variation, the second the main residual variation after removal of the trended linear variation accounted for by the first, and so forth. This implies that the method does not produce a reduction in dimensionality per se, but merely rotates axes rigidly to produce a more parsimonious representation.

Mathematically, a cross products matrix $S$ represents a transformation of individual vectors in Euclidean space. The objective of component analysis is to find a new direction $b_i$ in this space, such that $b_i$ is transformed by $S$ into a multiple of itself:

$$Sb_i = \lambda_i b_i; i = 1, ..., p$$

This can also be written as:

$$(S - \lambda_i I)b_i = 0$$

Since we wish to solve this equation for the non-trivial case ($b_i \neq 0$), the determinantal form is utilized (Green 1976):

$$|S - \lambda_i I| = 0$$
The eigenvalues (λ) so obtained can be substituted to find their corresponding eigenvectors (b). Eigenvector elements are direction cosines which serve as ‘weights’ of the variables on the new derived axis, while the corresponding eigenvalue measures its variance. The new axis therefore represents a linear composite of the original variables, and a simple transformation produces the individual scores.

Because the cross-products structure represents a linear transformation in Euclidean space, component analysis summarizes only linear variation in the data (Orlóci 1978). Non-linear trends will therefore be represented as distortions in higher dimensions. Because the model is a linear additive one (Dale 1975), the axes so derived may not be interpretable ecologically (Feoli 1977).

The method described above will handle only correlation and covariance matrices. Torgerson (1958) first considered methods to handle more general cases of the cross-products form. The strategy was examined in greater detail by Gower (1966) and Orlóci (1966, 1967b). They showed that in general a meaningful eigenanalysis can be performed on any resemblance matrix which shows an underlying correspondence to a metric euclidean distance. Gower (1966) suggested the name principal coordinates analysis (P-Co-A) for the steps involved. These authors also showed that the principal components of a raw data matrix X can be obtained directly from an eigenanalysis of X'. This duality is particularly important when the number of individuals greatly exceeds the number of variables. P-Co-A has the same basic restrictions as component analysis, though it does permit a wider choice of resemblance functions. This is important since some inherent non-linearity in the data structure may be transferred to an appropriately-chosen coefficient (Dale 1975).
2.4.1.3 Factor Analysis

Whereas component analysis partitions a generalized variance structure, factor analysis considers also the covariances, extracting axes subject to the reduction in residual covariances (Dale 1975). It is assumed that the observed variances can be partitioned into additive components, specifically the error, the variance specific to the variable, and the variance held in common with other variables. The assumptions are thus more restrictive than the simpler component analysis model, and may therefore be of limited use except with linear homogeneous data sets in which the assumptions are most likely to be met (Gower 1966). The number of factors to extract must be specified a priori, and the method is restricted to the analysis of a correlation matrix. The heterogeneous nature of most biological data sets suggests that the method is of limited utility, though its use has been strongly advocated by Dagnelie (1978).

2.4.1.4 Correspondence Analysis

This method can be thought of as a variant of component analysis which extracts eigenvalues from a cross-products matrix derived from uncentred, doubly standardized (normalization by the square root of the row and column totals) data. A post-normalization of eigenvector elements is also involved (Orlóci 1978). Hill (1973) presents a computationally efficient iterative algorithm which avoids an eigenanalysis. The method in fact treats the raw data as a contingency table, producing a factorial partitioning of the contingency table chi-square, and therefore implicitly assumes discrete data (Hill 1974, Feoli and Orlóci 1979). Some authors therefore suggest that it be restricted to use with binary data (Jeffers 1982).

The method has been shown to be efficient with highly heterogeneous data (Gauch et al. 1977), but has the disadvantage that higher axes, while orthogonal and uncorrelated, are normally not independent. To overcome this problem, Hill and Gauch (1980) suggested an empirical method of
'detrending' to render the axes independent. A more persistent problem is
the sensitivity of the method to rare species and anomalous quadrats, and
particularly their combination. The method will readily isolate these
'distinctive nodes' at the expense of obscuring trends in the remaining
individuals.

2.4.1.5 Canonical Correlation Analysis

This model assumes that two sets of variables, for example \( p_1 \)
environmental factors and \( p_2 \) species, are recorded for each of \( n \) individuals.
The resultant \( p \)-dimensional correlation matrix is therefore partitioned:

\[
S = \begin{pmatrix}
S_{yy} & S_{yx} \\
S_{xy} & S_{xx}
\end{pmatrix}
\]

\( S_{yy} \) represents the within set correlations for the first variable set, \( S_{xx} \)
the same for the second set, and \( S_{xy} = S_{yx} \) the cross-set correlations. The
objective is to find a linear additive model (as in component analysis) for
the \( Y \)-variables, and one for the \( X \)-variables, subject to the constraint that
the correlation between scores of the individuals on these two axes is
maximized. This is accomplished by an eigenanalysis of

\[
(S_{xx}^{-1}S_{xy}S_{yy}S_{yx}^{-1}S_{xy} - \lambda I)b_1 = 0
\]

with the added constraint that \( b_1^T S_{xx} b_1 = 1 \). As in component analysis, axes
are extracted in order of decreasing variance.

Other models can be envisaged from this general one. If, for example,
one set of variables is quantitative (such as records of species abundance),
while the second set uses \( k-1 \) dummy variables to code group affinity of
individuals to \( k \) groups (defined \( a \ priori \)), the method is known as multiple
discriminat analysis or canonical variates analysis. Alternatively, consider
a \( q \) by \( t \) contingency table whose elements total to \( n \). This can also be
represented in a canonical model by defining two sets of dummy variables,
where $p_1 = q - 1$ and $p_2 = t - 1$. Entries in the raw data would then describe the row and column affinity for each of the $n$ individuals of the original contingency table. This is in fact the model for correspondence analysis (Section 2.4.1.4).

Canonical procedures have problems similar to those of component analysis. Since a linear additive model is assumed, non-linear relationships between the two batteries of variables will go undetected. Multiple discriminant analysis makes the further assumption of equal covariance matrices. A comprehensive review is given by Gittins (1979), while Rohlf (in Legendre and Legendre 1983) offers some sobering comments regarding their biological applications.

### 2.4.1.6 Gaussian Ordination Models

These models fit a matrix of raw data to a Gaussian model, under the assumption that the underlying response to a complex environmental factor is bell-shaped and symmetrical in form. Gauch et al. (1974) developed a strategy appropriate to data with a single dominant underlying trend and relatively high species turnover. Axis position must be stated a priori, and the Gaussian model is fitted even when it is inappropriate. Ihn and von Groenevoud (1975) suggested an eigenvector procedure which also assumes Gaussian responses. Furthermore, it is assumed that the species have the same standard deviation, that their modes are independently and uniformly distributed, and that the number of species in a stand is constant. While of great theoretical interest, such severe assumptions render the method of little practical use. Johnson and Goodall (1979), using a maximum likelihood approach, iteratively improve an initial configuration derived from polar ordination. The Gaussian response is assumed, and the method as described is appropriate only for a single predominant gradient. They later (Johnson and Goodall 1982) developed a model appropriate for analyses in several dimensions.
Prentice (1980) has pointed out that forcing data to conform to an underlying Gaussian model is no better than the linear assumption. Furthermore, linear methods are much simpler in their conception, implementation, and interpretation.

2.4.1.7 Polynomial Ordination

McDonald (1962) described a method for overcoming the linearity assumption of component analysis which involves finding a polynomial which best relates the inherent non-linearity of the data to extracted principal components, followed by axis rotation to maximize the polynomial fit. The chief drawback of the method is the requirement for specifying a priori the underlying form of the non-linearity. Phillips (1978) suggested a more straightforward algorithm which fits a polynomial to a scattergram directly.

2.4.1.8 Nonmetric Multidimensional Scaling

This procedure, based on the rankings of distances between points, was first suggested by Shepard (1962), while Kruskal (1964a,b) developed a more stringent algorithm with an objective optimization criterion. It is of great theoretical interest since it circumvents the linearity assumption of eigenanalysis procedures.

The basic idea is intuitively (though not computationally) simple: an arrangement of individuals is sought in a reduced Euclidean space such that the distances in this reduced space are as closely monotonic as possible to the original distances calculated in variable space. The monotonicity requirement originally suggested was the tetrad inequality, that \( d_{ij} = d_{kl} \) whenever \( \sigma_{ij} = \sigma_{kl} \). Here \( \sigma \) represents distances in variable space, and \( d \) distances in reduced space. Sibson (1972) termed this global order equivalence, and suggested as an alternative a triad inequality (or local order equivalence) criterion, such that \( d_{ij} = d_{ik} \) whenever \( \sigma_{ij} = \sigma_{ik} \). He
stated that these two monotonicity requirements differ little in practice, but that local order may place some individuals more haphazardly.

The algorithm, while simple in theory, is difficult and computationally demanding to implement in practice. A method of iterative successive approximation is involved, and although the algorithm normally converges to an optimal solution, local (non-optimal) solutions are also possible. In practice, a number of different starting configurations should be tried, and the solution minimizing stress (a measure of deviation from monotonicity) chosen. Random starting configurations will likely minimize the local minima problem (Fasham 1977), although some workers (e.g. Anderson 1971, Gauch et al. 1981) suggest a starting configuration derived from an eigenanalysis procedure. However, this may severely constrain the algorithm to a local optimum similar to the eigensolution.

The method requires the user to specify the number of dimensions of the solution, which brings up the problem of choosing the appropriate dimensionality. Psychometricians have tended to follow Kruskal’s (1964a) guidelines and choose a solution which reduces stress to a sufficiently small value. More recently Shepard (1974) has argued strongly for solutions in two, or at most three, dimensions, as these are more readily interpretable. It should be noted that the K-dimensional solution obtained in a nonmetric scaling is not a projection of a solution in higher dimensions as in the metric scaling procedures.

Kendall (1969) argues that nonmetric scaling is superior to metric procedures since it is based on fewer assumptions. Gower (in Sibson 1972) has questioned this, arguing that computational expense is a more important consideration, particularly if metric and nonmetric methods tend to converge to a common solution. Nonmetric scaling has the advantage that, because only rank order is used, the method can accept as input a large array of distance and similarity coefficients. In fact, any measure related to distance by a monotonic function can be utilized.
2.4.1.9 Parametric Mapping

Also known as continuity analysis and catenation (Noy-Meir 1974), this method seeks the maximum number of dimensions required to have all variables related by functions which are as smooth as possible. The functional form of the response surface is not specified. Shepard and Carroll (1966) first described the algorithm as a method for preserving local continuity rather than rank order, by emphasizing local rather than global relationships. Kruskal and Carroll (1969) encountered computational difficulties, as well as problems in parameter choices and specification of dimensionality, in applying the method. In an ecological application, Noy-Meir (1974) had similar problems but concluded that the method was useful in examining ecological gradients. Orlóci (1978) states that the method is sensitive to discontinuities.

A similar method known as multidimensional unfolding operates directly on a raw data matrix, using the ranking criterion that \( d_{ik} = d_{jk} \) whenever \( X_{ik} = X_{jk} \). Carroll (1972) suggests that such a general model, with few external constraints, increases the chance of a trivial solution. Dale (1975) and Prentice (1980) discuss possible ecological applications.

2.4.1.10 Individual Differences Scaling

Carroll and Chang (1970) developed a method for the simultaneous analysis of a series of resemblance matrices. An overall ordination of individuals is produced, as well as an ordination of variables. Dale (1975) suggests that such a strategy may have considerable biological applications, but it appears to have been little used.
2.4.2 The Problem of Non-linearity in Ordination

Whenever species show a monotonic increase to a maximum followed by a monotonic decrease along a predominant gradient, curvilinear distortion of the scattergram will result if a linear metric scaling procedure is applied. This problem was first discussed in detail by van Groenewoud (1965) and Shepard and Carroll (1966). Kendall (1971) noted the problem in archeological seriation, terming it the 'horseshoe effect'. Whittaker (1956) first noted the non-linear response of species along environmental gradients, and while the exact form of this response has been questioned (Austin 1976, 1980), most workers have accepted that it is generally bell-shaped or Gaussian in form.

Curvilinear distortion is actually attributable to two factors. The first, already mentioned, is that a linear model will distort non-linear trends into intrinsically higher dimensions. The second and potentially more detrimental problem is that measures of similarity or distance between individuals are normally not linear functions of their separation along an environmental gradient (Gauch 1973). This is particularly problematic if species turnover is high, since individuals with little or nothing in common are not comparable except in the trivial sense that they are fundamentally different. It then becomes difficult to order individuals along the gradient.

Component analysis and other metric scaling procedures are theoretically appropriate only when the variation of variables shows a linear dependence on a set of underlying environmental factors. If this is not the case, a greater number of intrinsic dimensions will be required to recover the data structure, and the summarization will not be optimally parsimonious (Orlóci 1978).
2.4.3 Comparison of Ordination Techniques - Methods

In ecology, the comparison of ordination techniques has generally involved the use of artificial data sets with underlying Gaussian species responses to a single environmental gradient (coenocline), or two or more independent, uncorrelated gradients (coenoplanes or coenocubes). The model first described by Gauch and Whittaker (1972a, 1976) has generally been applied. It implicitly assumes that the objective is to optimize path-seeking rather than data reduction. Orliči (1978) and Feoli and Feoli-Chiapella (1980) have stressed that this places undue emphasis on the recovery of environmental axes while ignoring the more fundamental consideration of data summarization.

Austin (1976) points out that before ordinations can be compared objectively, a greater understanding of the complex structure and patterning of plant communities is required. He found many examples in the literature suggesting that the pure Gaussian form is more an exception than the rule, and that skewed and even bimodal responses can be anticipated. In a later paper (Austin 1980) he suggests that tests of the effectiveness of ordination methods are highly dependent upon the model used to generate the data, and seriously questions the validity of the purely Gaussian model so often used (see also Orliči 1974, 1978). Another problem is that these models rarely incorporate considerations of sampling error, which is so characteristic of field data (Goodall 1970). A model incorporating 'noise' has been suggested by Gauch and Whittaker (1976), but its ecological reality is open to question.

In Gauch and Whittaker's model species modal positions are distributed at random along an environmental gradient, following the field observations of Whittaker (1956) on the distribution of trees along an elevational transect. The reality of random species distributions, particularly when the shrub and understory layers are also considered, must be seriously questioned in light of the discussions by Goodall (1963) and others on species
interaction.

The most serious drawback of the model, however, has to do with sampling and the frequency of different environmental conditions in the field. The model implicitly assumes that a gradient is sampled at regular intervals, and that all portions of it are sampled with equal frequency. Except in the case of direct gradient analysis (for example systematic sampling along an elevational gradient), it is extremely unlikely that these assumptions will be met. In the majority of field investigations, a number of complex environmental gradients are present. However, only certain combinations of factors are manifested, resulting in a discontinuous data structure in which high density phases alternate with low ones. Furthermore, the environmental combinations which are present will rarely occur with equal frequency. Finally, strictly continuous environmental gradients are uncommon in the field. Instead, sharp discontinuities may occur, and these can be expected to lead to corresponding discontinuities in the vegetation. All these arguments suggest that a coenoplane model with regularly-spaced sample points along continuous, non-interacting environmental gradients is unlikely to reflect, even approximately, the true nature of most vegetation survey data. Van der Maarel (1980) and others have noted that the linearity problem, which has been demonstrated so well in simulation studies, rarely manifests itself in vegetation studies. He attributes this to the inappropriateness of the Gaussian response, and to the low species turnover rate of most studies. However, it is more likely attributable to the unrealistic model, as discussed above. Despite these remarks, it must be pointed out that the Gaussian model, while unrealistic, is useful in demonstrating the problem of non-linearity in ordination. But as Dale (1975) has pointed out, ecologists must assume that such simulated data reflects completely the inherent structure of real data before the comparative studies themselves can be assessed.
2.4.4 Comparison of Ordination Techniques - Results

Orlóci (1974, 1978) has pointed out that most comparisons of ordination techniques have confounded three things: the methodological algorithm, the similarity measure employed, and the standardization used. Indeed, the comparison of methods is made more difficult by the fact that many techniques will permit only certain coefficients, and that different standardizations are implicit in these. Objectives have also been confounded, with greater emphasis being placed on path-seeking than data reduction.

The need for assessing and comparing ordination techniques was first stated by Austin and Greig-Smith (1968). Swan (1970) and Austin and Noy-Meir (1971) described involution and the production of spurious axes in component analysis when applied to non-linear data, attributing this to the application of a linear model to non-linear data structure. The latter authors found that different standardizations could alleviate somewhat the degree of distortion. Gauch and Whittaker (1972b) compared polar ordination (PO, using various metric and nonmetric similarity coefficients) and component analysis (PCA, similarity measure not specified), using as a criterion for comparison the ability to recover a cenocline. They concluded that polar ordination utilizing the nonmetric Czekanowski coefficient gave the best results, while PCA showed serious involution (implying distortion into higher dimensions) even at moderate rates of species turnover. These authors chose the a priori known endpoints of the simulated cenocline in obtaining projections. Many workers have pointed out that this biased their results in favour of polar ordination (Prentice 1977, Phillips 1978).

Anderson (1971) found that polar ordination led to severe distortion when applied to real data sets. Austin and Orlóci (1966), stressing a data reduction objective, concluded that component analysis was vastly superior to polar ordination. Later papers from Cornell (e.g., Kessell and Whittaker 1976, Gauch et al. 1977) generally repeated the original paper of Gauch and Whittaker (1972b). It must be emphasized that their conclusions are based...
on the assumption of a direct ordination in which endpoints are known, and may not apply for the indirect case.

More recent papers have used the same general strategy in comparing correspondence analysis (CA), nonmetric multidimensional scaling (NMDS), and some other less well-known techniques. Gauch et al. (1977) found correspondence analysis to be superior to both PO and PCA, again assuming coenocline and coenoplane recovery to be of principal importance. However, Greig-Smith (1982) points out that CA is merely a variant of component analysis, suggesting that the differences in results are attributable to standardization differences rather than algorithm differences per se. In practice the simultaneous double standardization implicit in the CA algorithm may lead to an undue emphasis on outliers (Hill and Gauch 1980, Noy-Meir et al. 1975), though this is not readily apparent from the analysis of artificial simulated data where a smooth, continuous structure is present.

Nonmetric scaling (NMDS) has invariably performed well in these comparative tests. Noy-Meir and Whittaker (1977) and Dale (1975) recommend its use, notwithstanding the computational burden. Some workers (e.g., Anderson 1971; Gower in Sibson 1972; Gauch et al. 1981) noted that NMDS produces results similar to metric scaling strategies, and questioned the worth of a much less efficient algorithm in achieving the same end. However, this similarity may be artifactual, since these authors used the PCA output as the starting configuration for NMDS, which may have constrained the solution. Fasham (1977) stressed the importance of coefficient choice when using NMDS, and found that the cos theta function (Anderberg 1973) gave results which were superior to metric scaling procedures. Prentice (1977, 1980) suggested the use of Sibson's (1972) local variant method in conjunction with a coefficient suggested by Kendall (1969). He found that such a strategy gave results superior to metric scaling methods when applied to both real and artificial data sets. Gauch et al. (1981) concluded that nonmetric scaling methods were often superior to metric strategies, though this depended on the data set analyzed.
2.4.5 On Choosing an Ordination Technique

In choosing an ordination strategy, primary consideration must be given to the objectives of the study. If the purpose is to perform a direct ordination (to reproduce a clear-cut gradient, or set of independent gradients), methods which permit endpoint selection and direct ordering of stands are appropriate (Dale 1975). These include polar ordination and other methods discussed in Section 2.2.2.2 and in Whittaker (1978). In most vegetation studies, however, indirect ordination is implied, the objective being to summarize the data in a few readily interpretable dimensions. Component analysis and its variants can be recommended if the underlying data structure is at least approximately linear. This will be the case if species turnover is low to moderate. In the presence of non-linearity and higher species turnover, theory suggests that nonmetric scaling may be more appropriate, particularly if used in conjunction with a suitably chosen similarity coefficient.

Flexibility is also important. All eigenanalysis procedures are straightjacketed by the linearity assumption. Nonmetric scaling methods offer much greater flexibility since fewer assumptions regarding the underlying data structure are made. Because the method maps individuals into lower intrinsic dimensions using a monotonicity criterion, various similarity coefficients can be chosen to effectively "absorb" inherent non-linearity (Kendall 1974). In this regard Sibson (1972) points out that in defining similarities between individuals, all information about variable relations is lost. Therefore one must carefully consider the mathematical properties of both the similarity function, and the algorithm to which it is applied (Orlóci 1974).
2.4.6 Metric or Nonmetric Multidimensional Scaling - A Comparison

2.4.6.1 Introduction

Eigenanalysis procedures are also known as metric multidimensional scalings (Torgerson 1958), referring to the family of methods which extract linear trends from a matrix of cross-products. Principal components analysis (PCA), principal coordinates analysis (P-Co-A), correspondence analysis (CA), and canonical correlation analysis are all included under this general heading. Although many workers have stressed the differences between these algorithms, it is enlightening to consider them all as derived from the general canonical form (Gittins 1979). Conversely, nonmetric multidimensional scaling uses only the rank order relationships of individuals in deriving a configuration. It is nonlinear in the sense that it is not restricted by an eigenanalysis procedure.

The strategies of metric and nonmetric scaling are therefore fundamentally different, and it is important to consider their potential applications from an ecological perspective. Psychometricians developed nonmetric methods for the examination of data sets in which 'similarities' were defined as pairwise ratings on arbitrary ranked scales, which violated the cross-products form required by metric methods. Nonmetric methods relax this cross-products requirement. In ecology, data are normally quantitative, so that resemblance structures of the general cross-products form are readily obtainable. The utility and meaning of cross-products in an ecological context must be seriously questioned, however. Is vegetational variation best described and examined in cross-products form, with its linearity and additivity constraints? Does the extraction of linear components of variance have any ecological meaning? (Dale 1975). These problems have been discussed by Prentice (1980), who suggests that order invariant (nonmetric) methods reflect better our current understanding of vegetation than methods implying more restrictive assumptions. To Kendall (1969) and Dale (1975), the mapping of a distance configuration into lower
dimensions is logically of greater appeal than an eigenanalysis.

This is not to suggest that nonmetric scaling procedures are not without problems. The foremost one cited, that of computational expense, has been largely alleviated by more efficient algorithms (reviewed by Gauch et al. 1981) and the advent of high-speed computers. The non-uniqueness of the final configuration is more serious, though this is normally only a problem when the number of individuals is small (less than 30) or when the data is highly redundant (Shepard 1974). Still, the investigator must be careful to avoid local minima (a suboptimal solution). In practice, reasonably well structured data will tend to converge to an optimal solution quite readily, though more than one starting configuration may be required to achieve it. In some cases a few points may be badly misplaced.

To Gauch et al. (1981), the requirement for specifying a resemblance coefficient is also a drawback. While it is certainly true that this will require further input and thought on the part of the investigator, it is exactly this flexibility which renders the method of greater utility (Orlóci 1979).

Some workers have suggested that the requirement for specifying the number of dimensions of the reduced solution is a disadvantage, arguing that unless the number of intrinsic dimensions is known a priori the decision is necessarily arbitrary. However, the stress quantity can aid in determining the intrinsic dimensionality, and a plot of stress versus the number of dimensions can certainly help in this regard. Shepard (1974) has argued that an investigator should always aim for a two-dimensional solution, since the resultant scattergram summarizes inherent structure in a readily interpretable and easily presentable way. In this respect NMDS has a potential advantage over eigenanalysis methods which seems to have been overlooked by most ecologists. Because eigenanalysis procedures merely rotate axes to accommodate maximal variation, nonlinear trends will tend to be distorted into higher dimensions. Furthermore, because a lower
dimensional solution is merely a projection of a solution in higher dimensions, the presentation of a two-dimensional scattergram, or even a three-dimensional structure (ecologist rarely interpret or present the coordinates of the fourth or higher axes), will ignore certain components of trended variation inherent in the data. This variation may or may not be ecologically meaningful, but in any case it is lost. Conversely, NMDS will constrain the solution into the number of dimensions specified by the user, presenting the most parsimonious solution possible in that space. In other words, the entire set of trended variation is summarized in the reduced space. Thus for data summarization and subsequent interpretation of a complex data structure, NMDS may in practice be superior to eigenanalysis strategies.

2.4.6.2 Comparison

The importance of the choice of coefficient and standardization on the results of eigenanalysis strategies was examined in detail by Austin and Noy-Meir (1971). They concluded that both standardization and coefficient choice had some influence on ordination results, and in some situations considerably lessened the degree of distortion attributable to non-linear variation. Corresponding studies of nonmetric scaling strategies are less complete. Fasham (1977) did test a number of similarity coefficients in NMDS, though they appear to have been arbitrarily chosen. He found that the cos-theta coefficient gave the best results in tests with coenoplane data, but failed to discuss the reasoning and consequences of his findings. Most other workers (e.g. Anderson 1971; Austin 1976; Prentice 1977,1980; Gauch et al. 1981) have been satisfied with using a single similarity coefficient in conjunction with NMDS, and comparing the results so obtained with the standard eigenanalysis algorithms. Fewster and Orloci (1983) took a different approach, examining the effect of changing the criterion for monotonic fitting in the NMDS algorithm to reflect the underlying data structure. Their results stress the flexibility of NMDS in accommodating different types of nonlinear data structure. Later work by Orloci et al. (1984) stresses
the importance of accounting for inherent nonlinearity in the definition of the original resemblance structure, and suggests the use of chord distance (Orlóci 1967b) for achieving this.

The purpose of this investigation is to compare metric and nonmetric scaling procedures using the coenoplane model. The limitations of this model have already been discussed, but the strategy was felt appropriate in rendering the study comparable with previous work. Furthermore, the method does provide information about the behaviour of the methods under fixed conditions, permitting an objective comparison of results.

To minimize the confounding of algorithm, similarity measure, and standardization, only euclidean distance measures were used, in each case utilizing the raw data, data standardized by stand norm, and simultaneous double standardization. Table 2.1 presents the comparisons which were made. The emphasis is on comparing the metric and nonmetric scaling methods directly; thus, the P-Co-A using chord distance (euclidean distance after standardization by stand norm) is directly comparable to NMDS using the same distance function. Correspondence analysis (CA) and the 'detrended' form (DCA, Hill and Gauch 1980) have been performed for the sake of completeness, as these methods have been reported to be least susceptible to distortion when applied to simulated coenoplane data. These methods, which involve a simultaneous double standardization of the data, are in some ways comparable to P-Co-A and NMDS based on doubly-standardized data, but their are some differences which negate a direct comparison.

To produce the coenoplane simulation data, a program was written based on the model presented by Gauch and Whittaker (1976). It is similar to the program CEP-21 published by Gauch (1977), but permits greater flexibility in the positioning of species modal positions. The program was first tested by producing four data sets similar to those used by Gauch et al. (1976) and Fasham (1977). Each consists of 40 stands, positioned at regular intervals on a 5 by 8 grid representing two independent environmental gradients,
Table 2.1  Description of the eight methods used in the comparison of ordination techniques.
<table>
<thead>
<tr>
<th>Principal Coordinates Analysis (Gower 1966)</th>
<th>1. Euclidean distance</th>
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</thead>
<tbody>
<tr>
<td></td>
<td>2. Euclidean distance, standardization by stand norm (chord distance)</td>
</tr>
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<td></td>
<td>3. Euclidean distance, simultaneous double standardization</td>
</tr>
<tr>
<td>Nonmetric Multidimensional Scaling (Shepard 1962, Kruskal 1964 a,b)</td>
<td>4. Euclidean distance</td>
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<td></td>
<td>5. Euclidean distance, standardization by stand norm (chord distance)</td>
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<td></td>
<td>6. Euclidean distance, simultaneous double standardization</td>
</tr>
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<td>Correspondence Analysis (Hill 1974; Hill and Gauch 1980)</td>
<td>7. unmodified version</td>
</tr>
<tr>
<td></td>
<td>8. detrended version</td>
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</table>
and 30 species each showing a Gaussian distribution. Whereas in the original data sets these species were spaced at regular intervals, the data used here was obtained by placing species modal positions in a stratified random manner. This was felt to be more realistic and representative of 'noise' in the data than the method suggested by Gauch and Whittaker (1976). The four data sets showed different levels of species turnover on the two gradients, measured in half-changes (Gauch and Whittaker 1972; calculated using the procedure suggested by Fasham 1977). The values are: 1.5 by 1.5 HC; 1.5 by 4.5 HC; 4.5 by 4.5 HC; and 4.5 by 9.0 HC. The data sets were analysed using CA, DCA, and NMDS (with chord distance), and the resultant scattergrams are presented in Figure 2.1. The results for CA are similar to those presented by Fasham (1977), but with slightly greater distortion. This is attributable to the different method of placement of species modal positions. DCA improves the results of the 1.5 by 4.5 HC coenoplane, which has been observed by Hill and Gauch (1980). The results of NMDS using chord distance are similar to the results obtained by Fasham (1977) for the costheta similarity function. This results since these functions are inversely monotonically related (Orlović 1978). The close similarity between the results presented here and those published by Fasham (1977), who used the CEP-21 program, suggests that the program written for the analysis presented here reflects the same model.

The methods outlined in Table 2.1 were applied to eleven simulated coenoplane data sets. In all cases two independent environmental gradients were assumed, and 36 stands were placed at regular intervals on a 6 by 6 grid. Species modal positions were located in a stratified random manner, with a total of 36 species used. Heights of species surfaces were normally distributed within the 60-100 range (representing percent cover values). The eleven data sets differed in the amount of species turnover on the two gradients. Half-change (HC) values on the coenoplane are: 1 - 2.65 x 2.65 HC; 2 - 2.65 x 3.05 HC; 3 - 2.65 x 3.75 HC; 4 - 2.65 x 5.30 HC; 5 - 3.05 x 3.05 HC; 6 - 3.05 x 3.75 HC; 7 - 3.05 x 3.75 HC; 8 - 3.75 x 3.75 HC; 9 - 3.75
Figure 2.1  Results of ordination strategies applied to artificial coenoplane data of varying degrees of species turnover, measured in half-change (HC) units: (a) 1.5 x 1.5 HC. (b) 1.5 x 4.5 HC. (c) 4.5 x 4.5 HC. (d) 4.5 x 9.0 HC. Individuals are points connected by grid lines.
The results of the analyses were assessed both by visual inspection (plotting the ordination obtained) and using the method of Procrustes analysis (Schönemann and Carroll 1970). This method uses the 6 by 6 regular spacing of stands on the coenoplane as a target matrix, minimizing the sum of squares residuals in a rigid rotation of the resultant ordination configuration with respect to this target. The sum of squares quantity thus measures goodness of fit: the smaller the value, the more successful the ordination is in recovering the original structure of the data.

The resultant ordination plot, with grid lines connecting the points, are presented in Appendix 1. The salient features are apparent upon visual inspection and from the Procrustes residual values presented in Table 2.2. The results are summarized and discussed below as a series of observations:

1. Regardless of the method used, the ability to recover the underlying data structure decreases as species turnover increases. This is in keeping with the well known fact that as the percentage of zeros in the data increases, the data becomes less structured (Swan 1970). Complete species turnover (when at least some stands have no species in common) occurs at approximately 4.5 HC (Gauch 1982), and above this value structure begins to collapse since many stand comparisons become trivial.

2. Standardization has important effects on the ordination results. Both standardization by stand norm and simultaneous double standardization were superior to the use of raw data when P-Co-A was applied, though severe distortion was nonetheless present even at moderate species turnover. The results of NMDS and P-Co-A were similar when unstandardized data was used. On the other hand, NMDS after stand norm standardization gave results which were consistently superior to all the other strategies, and far superior to the P-Co-A results with the same standardization. NMDS
Table 2.2  Results of procrustes analysis (sums of squares values) for the eleven data sets (see Section 2.4.6.2 for details) applied to the ordination methods outlined in Table 2.1.
<table>
<thead>
<tr>
<th>Data Set</th>
<th>Method 1 - PCAE</th>
<th>Method 2 - PCAC</th>
<th>Method 3 - PCAD</th>
<th>Method 4 - MDSE</th>
<th>Method 5 - MDSC</th>
<th>Method 6 - MDSD</th>
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<td>11</td>
<td>9.2348</td>
<td>4.6590</td>
<td>8.9880</td>
<td>10.5699</td>
<td>0.2668</td>
<td>10.7417</td>
<td>1.7128</td>
<td>7.5229</td>
</tr>
</tbody>
</table>
with simultaneous double standardization, by contrast, was somewhat sensitive to outliers and anomalies in the data, though results were somewhat superior to using unstandardized data up to about 4.0 HC. Results of CA and DCA were similar except where considerable differences in species turnover on the two gradients occur, in which case DCA performs better. The results were similar, though inferior, to NMDS using the stand norm standardization, and were more sensitive to higher species turnover rates.

3. The detrended version of CA was found to collapse and distort the structure at high levels of species turnover. It would therefore be difficult to recommend this empirical strategy unequivocally, though it may be useful after careful inspection of a CA scattergram indicates a definite dependence between axis scores.

4. The differences between CA and P-Co-A with simultaneous double standardization underly the importance of the differences in the definition of the cross-products form, and post-normalization of eigenvector elements, between these metric strategies. Thus the simultaneous double standardization implicit in the CA algorithm, while it may be important, is not the sole reason for the superiority of CA over PCA in recovering the underlying data structure of simulated coenoplane data.

5. The results of NMDS and P-Co-A were very similar when the raw data were analyzed directly, whereas standardization by stand norm, while it improved the results of P-Co-A to some extent, was much more effective when applied to the NMDS algorithm. This suggests the greater potential utility of nonmetric scaling strategies in recovering nonlinear variation. The metric methods are tied into the constaints of an eigenanalysis, whereas NMDS has no such restrictions. In other words NMDS appears to have a much greater flexibility in allowing for inherent nonlinearity to be accounted for by an appropriate definition of the resemblance structure. This follows directly from the fact that the algorithm
involves a simple mapping of resemblance structure into lower dimensions without a linear constraint. The fact that the solution at a given dimensionality is not a projection of one in higher dimensions, as in metric strategies, is undoubtedly also important.

6. Standardization by stand norm appears to be able to account for nonlinearity in data structure, at least for simulated coenoplane data. This was also noted by Austin and Noy-Meir (1971) for PCA, but the effect is much more pronounced when applied to the NMDS algorithm. Interestingly, this standardization was advocated by Noy-Meir et al. (1975) as a generally useful strategy, having certain desirable ecological properties. Orloci (1979, 1980) has presented a theoretical justification of the chord distance when nonlinear species responses are anticipated.

2.5 Sampling Theory, With Ecological Applications

Sampling theory was developed by statisticians to find objective criteria for the description of a population based on the enumeration of a small subset of member individuals. Many of the theoretical aspects are of considerable importance to ecologists seeking objectivity in their science (Goodall 1970), and these are reviewed in this chapter. In addition, sampling problems unique to the field of vegetation science are discussed, with particular reference to the problem of quadrat size determination.

2.5.1 Objectives of Sampling in Phytosociological Surveys

Sampling theory presupposes that estimation of a variable value is the principal objective of sampling. Consequently emphasis has been placed on the development of strategies to increase precision in the estimation of population parameters. In phytosociological surveys, however, the sampling objectives are often two-fold: the delineation of recognizable groups or types (typification), and the estimation of the parameters of the multivariate species population making up each type. In such cases a single
survey must satisfy these potentially conflicting dual objectives. The sample should simultaneously maximize precision within types (that is, minimize the sampling variance within each type) while maximizing the distinctiveness of the types (maximize the variance between types). The problem, of course, is that the types are normally not known a priori. In attempting to achieve these two objectives, consideration must be given to both the sampling strategy employed and the quadrat size used.

2.5.2 Preferential Sampling

Orioci (1978) coined the term 'preferential sampling' to characterize vegetation surveys in which samples are located in areas deemed by the investigator to be typical and homogeneous. This strategy has been widely used, especially in Europe. As a purely descriptive approach, it may have some advantages, particularly when the investigator is familiar with the vegetation being examined (Knapp 1984). It must be remembered, however, that such a sample is biased in some unknown way, since the probability of obtaining it is unknown (Green 1977). This implies that statistical methods cannot strictly speaking be applied to data resulting from a preferential sample (Goodall 1970). Furthermore, such a sampling strategy tends to be self-serving, making it difficult to recommend in objective studies which go beyond mere tabulation and description.

2.5.3 Statistical Sampling

In any sampling procedure, the objective is ultimately to make inferences about the underlying population from a sample. Sampling theory has been developed to designate criteria by which a sample can accomplish this. The most important criteria are that sample selection be based on a random component, and that any given sample must have a known, and nonzero, chance of being selected. By meeting these fundamental criteria, statistical methods can be developed to allow for the estimation of population parameters and corresponding confidence limits based on a
2.5.4 Methods of Statistical Sampling

A number of statistical sampling strategies have been developed, primarily in response to the need for greater precision and ease in collecting data. Statistical aspects are discussed by Raj (1968) and Cochran (1977), while Sampford (1962) discusses some biological applications. Methods most useful to vegetation ecologists are discussed below.

2.5.4.1 Simple Random Sampling

This, the simplest of statistical sampling strategies, involves the location of stand positions by random coordinates, and implies that any point within the sampling frame has an equal chance of being selected. Samples obtained in this way normally result in a high sampling variance (Goodall 1970; Ordoc 1978), implying low precision in parameter estimation. Furthermore, certain areas of the sampling frame will tend to be underrepresented unless sample size is very large. Unbiased estimates of both the mean and its precision are obtainable.

2.5.4.2 Stratified (Restricted) Random Sampling

This method, which was developed to increase sampling precision, is accomplished by dividing the population into k non-overlapping subgroups or strata, and sampling each stratum randomly. The number of individuals sampled within a given strata is normally made proportional to stratal size, although this is not necessary. Stratification has two important advantages over simple random sampling: the sample will tend to be more evenly distributed over the population, and estimates of population parameters will generally be more precise, particularly if within-stratal variance is minimized and between-stratal variance maximized. In phytosociology, strata are normally defined by an external criterion, for example elevational
example elevational groupings. They should not be based on the vegetation itself if the objective is typification, however, as this would involve a circularity of argument (Orloci 1978; Greig-Smith 1982). Unbiased estimates of the mean and its precision are obtainable for the strata and the whole population.

2.5.4.3 Systematic Sampling

This method differs from those already described in that only the starting or pivotal point is selected at random: subsequent sample positions are taken at regular intervals from this pivot. The primary advantages of this strategy are the ease in locating points, and the even coverage of the sampling frame obtained. For these reasons the method is widely used by vegetation ecologists (Goodall 1954). The major disadvantage of the strategy is that an unbiased estimate of the precision of the mean is not obtainable. It has been inferred, however, that because the method leads to an even coverage of the frame the mean estimate can be expected to be very precise. Cochran (1977) however has shown that this is dependent upon underlying trends in the population, with a consistent monotonic trend leading to greater precision when sampling systematically. Like random sampling, a systematic setup assumes that all individuals have an equal chance of being represented (Greig-Smith 1964).

2.5.4.4 Two-stage Sampling

Two-stage sampling, or subsampling, often arises in phytosociological investigations of stratified vegetation. Typically, different quadrat sizes are used to characterize tree and understory strata. In a statistical context, two-stage sampling involves the location of a large quadrat at random (for estimation of tree biomass), followed by the enumeration of $m$ small quadrats located randomly or systematically within the large one, for estimation of understory vegetation. Cochran (1977) shows that both random and systematic location of small quadrats yields unbiased estimates of both the
mean and its precision.

2.5.4.5 Cluster Sampling

This method, though rarely discussed in the biological literature, may be of considerable use (Green 1979). The method is similar to simple random sampling, but the sampling unit is envisioned as a group or cluster of individuals rather than the individuals themselves. Interestingly, a quadrat of given size can be thought of as a cluster, consisting of a group of very small units or ‘individuals’, and for this reason the statistical theory of cluster sampling is of considerable interest to phytosociologists.

Consider a population consisting of \( N \) clusters each containing \( M \) individuals (or equivalently, \( N \) ‘large quadrats’ each containing \( M \) ‘small quadrats’). Population size is therefore \( NM \), and a given individual is represented by \( x_{ij} \), \( i = 1, \ldots, N; j = 1, \ldots, M \). Sampling would involve the enumeration of all \( M \) individuals within each of \( n \) clusters selected at random, for a total sample size of \( nM \). Table 2.3 shows the population values and corresponding unbiased estimates. This information can be used to compare the relative precision of cluster and random sampling. In this context the sampling variance for simple random sampling can be written as:

\[
S^2_x = \frac{(NM-nM)/NM}{MS^2_x/nM}
\]

The relative efficiency (R.E.) of random versus cluster sampling is the ratio:

\[
R.E.(\text{random/cluster}) = \frac{S^2_x}{MS^2}
\]

This implies that cluster sampling will be most efficient if the variance between cluster means is small relative to that within clusters (in other words, clusters should be heterogeneous within and homogeneous among).
Table 2.3 Population parameters and corresponding unbiased estimates in cluster sampling (modified from Cochran 1977).
Sampford 1962). Edge effect is minimal for circles, although an increase of only 11% results from using a square of the same area. Many agricultural and other studies suggest that rectangular quadrats are often easier to work with, however. Edge effect is particularly problematic for small quadrat sizes where the area:perimeter ratio is relatively small.

When the objectives include typification, the orientation of rectangular quadrats against a major environmental gradient will obscure the recognition of types, since such an arrangement increases the likelihood of the quadrat including components of two or more vegetation types. For the recognition of types, it would therefore be beneficial to orient rectangular quadrats perpendicular to a major environmental axis perceived in the field.

For studies in which vegetation estimation and typification are dual goals, it is probably advantageous to utilize square or circular quadrats. In this way the problem of edge effect is minimized, and the problem of quadrat orientation, which is necessarily subjective, does not arise. Furthermore, this will minimize the probability of the quadrat including components from more than one distinctive type, making the delineation of distinct groupings more likely.

2.5.6.2 Quadrat Size

The choice of quadrat size has until recently been highly subjective, and remains so in many textbooks treating the subject (e.g. Gauch 1982). The objectives of the study are of primary consideration in choosing an appropriate size. In studies where logistic considerations dictate the maximum biomass harvestable (for example, seed bank studies where a fixed volume of soil can be analyzed), the smallest possible quadrat (or soil core) should be used to obtain maximal coverage over the field, as this will normally minimize sampling variance (Stuart 1976). In yield studies, edge effect must also be considered, and a compromising size must therefore be
found (Sampford 1962). In phytosociological studies where this constraint normally does not exist, different statistical and biological criteria are important. Greig-Smith (1982) suggests the following considerations:

1. Small quadrat sizes should be avoided to minimize edge effect problems.

2. Sampling variance within a given vegetation type should be minimized, suggesting a quadrat size which minimizes between-quadrat variance within a type.

3. Symmetry of species frequency distributions should be sought. As Greig-Smith (1964) has pointed out, a small quadrat size tends to give low species mean values, implying assymmetric species distributions. Rice (1967) examined this problem in a grassland community, and found that reasonable symmetry was achieved at 0.4 m² quadrats for common species, but that a much larger quadrat size was required for the rare ones.

Quadrat size will influence the detection of pattern of species and the level at which the pattern is detected. Furthermore, the degree and nature of association between species is highly dependent upon quadrat size choice (Pielou 1977; Greig-Smith 1983). This implies that the detection and characterization of vegetation types will depend upon the quadrat size chosen.

Phytosociologists have long been concerned with the characterization of the 'minimal area' of a plant community. This has been variously defined, reflecting the different viewpoints of investigators. To Goodall (1961), the minimal area is the smallest area for which an expected (probabilistic) change in species composition between replicate quadrats ceases to be a function of their distance apart. European phytosociologists have defined it in more general terms as the area required to adequately describe the species composition of a given plant community (Westhoff and van der Maarel 1978). The traditional method interprets species-area or frequency-area
curves, which plot number of species against quadrat area and species frequency against area respectively (Mueller-Dombois and Ellenberg 1974). In practice species number seldom reaches a saturation level, but continues to increase, making the determination of cut-off level difficult (McIntosh 1967). Furthermore, the methods suggested for determining cut-off level depend on the total area sampled (Rice and Kelting 1955). More recently similarity analysis (Gonot and Calleja 1962, Moravec 1973) has been suggested as an alternative. In this quadrats of increasing size are randomly located, with minimal area defined as the area for which the average of a binary similarity coefficient (generally the Sorensen variant) between plots exceeds a given percentage (Gonot and Calleja, working in a Brachypodium grassland, used 4 plots and an 80 percent level). The idea has been further examined by Roux and Rieux (1981) for saxicolous lichens communities, and by Dierendorst et al. (1982) in a phytosociological context. The latter authors concluded that the determination of minimal area by similarity analysis is possible and useful though tedious, and suggested using quantitative rather than binary data. Juhasz-Nagy and Podani (1983) have taken a different approach, arguing that multivariate methods are most efficient when quadrats are defined so as to be maximally distinct. Working from this premise, they utilized concepts of information theory to find quadrat sizes at which various entropy quantities were maximized. Their graphs of entropy versus quadrat area generally showed a unimodal response. Such a strategy is useful if the objective is to assess the inherent variability in what is considered to be a single community. However, if the objective is to obtain maximally precise estimates of community composition, their strategy cannot be recommended.

Greig-Smith (1982) has pointed out that minimal area is generally defined in a descriptive sense and is therefore not related to the determination of a suitable quadrat size for the statistical determination of community characteristics such as species means, degree of variability, and so forth. This has not always been appreciated. Minimal area is most...
useful in descriptive inventory studies, whereas optimal area is defined in a statistical sense as the area which maximizes sampling precision.

Returning to the criteria set out by Greig-Smith (1982), we note that both the edge-effect and distributional symmetry problems can be largely alleviated simply by utilizing a sufficiently large quadrat. The optimization of precision has received surprisingly little consideration despite its fundamental importance. If species distributions are completely random and independent (which will rarely if ever occur), quadrat size will not influence the sampling variance in any way. If however contiguous species distributions are present quadrat size will have an effect. For frequency data, variance will approximately equal the mean if quadrat size is smaller than the patch size of a species. If quadrat and patch size are of the same order, the variance will be substantially greater than the mean, implying imprecise estimates. A further increase in quadrat size will decrease the variance again. Further trends will depend upon the distribution of the patches themselves (Pielou 1977; Greig-Smith 1964, 1982). These facts were used by Greig-Smith (1952; also Kershaw 1958, 1959) in the analysis of univariate species pattern, utilizing variance criteria at various quadrat sizes to detect the scale and extent of species pattern in plant communities. Noy-Meir and Anderson (1971) suggested a multivariate analogue called multiple pattern analysis. This involves the calculation of covariance matrices for block sizes derived from a contiguous grid of quadrats. These matrices are pooled to form a combined matrix which is subjected to an eigenanalysis. Each eigenvalue is subsequently partitioned into contributions from the various block sizes. Goodall (in Noy-Meir and Anderson 1971) has summarized and discussed the problems of methods of pattern analysis in general. These include the constraint of analysis to only integer multiples of the basic unit size, the unequal divisions of degrees of freedom (which is particularly problematic at larger scales), the dependence of variance estimates (thus precluding statistical significance tests), the dependence of pattern level on where the initial quadrat is
positioned (see also Errington 1973), and the inverse pattern problem discussed by Pielou (1977).

The statistical aspects of cluster sampling discussed in Section 2.5.4.5 can be utilized to obtain an objective method for optimal quadrat size determination in the univariate case. This would begin with the enumeration of a series of gridded contiguous quadrats. A simple artificial example is shown in Figure 2.2. The analysis would begin with the calculation of a variance table as shown in Table 2.4 (values are calculated as in Section 2.5.4.5). The between small quadrats variance is simply the variance of the smallest grid units. The large quadrat data is obtained by pooling two adjacent small grid units in the same way originally suggested by Greig-Smith (1952). The efficiency index (R.E.) indicates whether the large or small quadrat size gives samples with greater precision. The next step depends on the value of R.E. If less than one, greater precision of the smaller quadrat size is indicated, and this size would be compared with the size obtained by pooling four adjacent to give a square. If greater than one, the larger would be compared with the four adjacent poolings. The procedure continues until too few large quadrats remain. The steps are illustrated in Figure 2.2 for the example; a quadrat four times the size of original grid unit is suggested to achieve maximal precision.

This method of maximizing sampling precision is not new. A similar strategy was suggested by Clapham (1932; see also Bormann 1953), although the underlying theoretical and statistical basis was not discussed. The method outlined here stresses the statistical derivation and shows the close relationship between cluster sampling and the determination of optimal quadrat size.

This strategy suffers from the same drawbacks as pattern analysis using gridded contiguous quadrats. Furthermore, the method as outlined is appropriate only for univariate data. In principal the method could probably be rendered multivariate, but this is not pursued here, although an
Figure 2.2  A simple artificial example to illustrate the utility of cluster sampling in the determination of optimal quadrat size. The relative efficiency values are shown for each of the steps (a) – (e).
<table>
<thead>
<tr>
<th>a</th>
<th>b</th>
</tr>
</thead>
<tbody>
<tr>
<td>0 8 0 7 0 8 0 8</td>
<td>8 7 8 8</td>
</tr>
<tr>
<td>0 0 1 0 0 0 0 0</td>
<td>0 1 0 0</td>
</tr>
<tr>
<td>0 7 0 8 0 9 0 8</td>
<td>7 8 9 8</td>
</tr>
<tr>
<td>0 0 0 0 0 0 1 0</td>
<td>0 0 0 1</td>
</tr>
<tr>
<td>0 7 0 9 0 7 0 8</td>
<td>7 9 7 8</td>
</tr>
<tr>
<td>1 0 0 1 0 0 0 0</td>
<td>1 1 1 0</td>
</tr>
<tr>
<td>0 8 0 8 0 8 0 7</td>
<td>8 8 8 7</td>
</tr>
<tr>
<td>0 0 1 0 1 0 0 0</td>
<td>0 1 1 0</td>
</tr>
</tbody>
</table>

<table>
<thead>
<tr>
<th>c</th>
<th>d</th>
</tr>
</thead>
<tbody>
<tr>
<td>8 8 8 8</td>
<td>16 16</td>
</tr>
<tr>
<td>7 8 9 9</td>
<td>15 15</td>
</tr>
<tr>
<td>8 0 7 8</td>
<td>18 15</td>
</tr>
<tr>
<td>8 9 9 7</td>
<td>1% 16</td>
</tr>
</tbody>
</table>

1. R.E. (a, b) = 1.56
2. R.E. (b, c) = 40.69
3. R.E. (c, d) = 0.99
4. R.E. (c, e) = 0.68
Table 2.4 Variance table for the determination of optimal quadrat size using cluster sampling.
<table>
<thead>
<tr>
<th>Variance</th>
<th>d.f.</th>
<th>Mean square</th>
<th>Relative Efficiency</th>
</tr>
</thead>
<tbody>
<tr>
<td>Between large quadrats</td>
<td>(n-1)</td>
<td>$\frac{MS_B}{MS_B}$</td>
<td>$R.E. = \frac{S_X^2}{MS_B}$</td>
</tr>
<tr>
<td>Between small quadrats</td>
<td>n(M-1)</td>
<td>$S_W^2$</td>
<td></td>
</tr>
<tr>
<td>within large ones</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Between small quadrats</td>
<td>nM-1</td>
<td>$S_X^2$</td>
<td></td>
</tr>
</tbody>
</table>
alternative multivariate strategy is discussed below. It seems likely that different species would show different optimal quadrat sizes, so that any multivariate method must necessarily be a compromise.

An alternative univariate model for determining optimal quadrat size in an homogeneous vegetation would be to plot species variance against plot size based on data collected from randomly located quadrats of various sizes. The quadrat size for which variance is minimal would then be chosen. In a multivariate model, the covariance between species must also be considered. Goodall (1953) has stressed the need to minimize interspecific associations in delineating a vegetation type. Thus, given a species covariance matrix $S$ derived from random data at a given quadrat size, the objective is to minimize both the diagonal elements (that is, to minimize the variance and thus maximize precision) and the off-diagonals (the covariances, which measure interspecific association). The requirement then is to derive a parameter which summarizes the structure of a covariance matrix, so that covariance matrices derived from different quadrat sizes can be readily compared. This immediately suggests an eigenanalysis procedure. The sum of the eigenvalues is directly related to the diagonal elements of the covariance matrix by the relationship:

$$\Sigma \lambda_i = \Sigma S_{ii}^2, i = 1, \ldots, p$$

Furthermore, the magnitude of the first eigenvalue will increase as the absolute value of the off-diagonal cells increase. Therefore, given the objective of finding a quadrat size which minimizes the structure of a covariance matrix, and a set of $q$ covariance matrices (from random samples using $q$ different quadrat sizes), we would choose that quadrat size giving the smallest first (supremum) eigenvalue. Note that in order for the eigenvalues to be directly comparable, it must be assumed that the same sample size is used for each quadrat size. Furthermore, the analysis must be based on a proportional quantity of species abundance such as percent cover.
Figure 2.3: Maps of a portion of an artificial data set containing four species A – D. The shaded areas represent areas where the species occurs. The seven quadrat sizes used to sample the data set are also shown.
Figure 2.4  Plot of the largest eigenvalue versus quadrat size for the data set of Figure 2.3.
Figure 2.5  Plot of (a) the largest eigenvalue, and (b) the sum of the two largest eigenvalues, versus quadrat size for the London, Ontario weed community data (courtesy of S. S. Shaukat).
It could be argued that data obtained by increasing plot size at a
given point, as advocated here, renders the resulting covariance matrices
statistically dependent. However, independent random samples for each
quadrat size would confound the results by adding a second source of
sampling error. Alternatively, the covariance matrices could be partitioned
into common and specific components, but the meaning of these from a
sampling standpoint is unclear.

To illustrate the method, an artificial data set consisting of two highly
associated species dispersed as regular clumps and surrounded by two other
associated species was created; a portion of the vegetation map is reproduced
in Figure 2.3, along with the quadrat sizes which were used. The plot of
first (largest) eigenvalue versus plot size is shown in Figure 2.4. The
eigenvalues appear to level out strongly at a quadrat size which is somewhat
greater than the average clump size, as would be expected.

The method was also tested using field data from a homogeneous weed
community near London, Ontario. This was kindly provided by S. S. Shaukat.
Twenty positions were located within the area, and the percentage cover
estimates were made for 26 species in each of seven rectangular quadrats.
The quadrat sizes are: 1 = 0.5 x 0.25 m, 2 = 0.70 x 0.35 m, 3 = 1.0 x 0.5 m;
4 = 1.41 x 0.71 m, 5 = 2.0 x 1.0 m, 6 = 2.84 x 1.41 m, 7 = 4.0 x 2.0 m. The
results of the analysis are presented in Figure 2.5, which shows plots of
both the maximum eigenvalue for each quadrat size and the sum of the
two largest eigenvalues. The results for the maximum eigenvalue suggest
that quadrat sizes 4, 5, and 6 are optimal. In practice one would probably
choose the smallest size. If the sum of the two largest eigenvalues is
considered, the results suggest that quadrat size 6 would be the best choice.

The results using both artificial and real data sets suggest the utility
of this method of determining optimal quadrat size in a multivariate context.
The method is also used later in examining data collected from the Elk
Lake study area.
CHAPTER 3

THE BOREAL FOREST ECOSYSTEM

3.1 Introduction

The study area lies on the southern fringe of the boreal forest. The primary factor determining boreal climate is the nature and movement of the continental air masses (Barry 1967). Short, warm to relatively cool summers and long, cold winters are characteristic (Hare 1954). The northern limit of this ecosystem is the forest-tundra ecotone, which corresponds closely to the July 13°C isotherm except in areas of oceanic or montane influence. The southern limit is less well-defined except in the prairie regions where the forest-grassland ecotone is the generally accepted boundary. The southern border is particularly poorly defined in Ontario (Thaler and Plowright 1973), though it follows very generally the July 18°C isotherm.

3.2 Studies of the Boreal Forest Vegetation

There exists a fairly extensive literature on the description of boreal vegetation, and it is beyond the scope of this dissertation to summarize all the studies. The North American literature has been reviewed by Larsen (1980). The Eurasian literature is generally in Russian and unfortunately remains largely untranslated. Frey (1978) and Trass and Malmer (1978) have reviewed the northern European approaches to the classification of boreal vegetation, while Aleksandrova (1978) discusses the approaches used by the Russians. Other useful reviews include Sukachev (1928), Sukachev and Dylis (1964), Kujala (1952), and Tseybyae (1965).

The majority of boreal vegetation studies have been largely descriptive, and have concentrated on broad, extensive and general studies rather than more detailed examinations of the vegetation of a small area. This is undoubtedly attributable to the extent of the boreal ecosystem, its relative
uniformity, and the lack until recently of even broad, general descriptions of vegetation structure and dynamics.

General broad-scale descriptions of North American boreal ecosystems are given by Raup (1946), Hustich (1949), Moss (1953a,b, 1955), Ritchie (1956), and many others (see Larsen 1980 for a comprehensive review). An interesting paper by LaRoi (1967; also LaRoi and Stringer 1976) examined regional variation in boreal forest composition in Canada, recognizing five reasonably well defined floristic discontinuities along an east-west transect. Swan and Dix (1966) examined the vegetational structure in a forest-grassland area in central Saskatchewan, while Carleton and Maycock (1978, 1980) and Bergeron and Bouchard (1983) examined vegetation composition in northern Ontario and adjacent Québec. Mueller-Dombois (1964, 1965) described vegetation types in southeastern Manitoba. Orloci and Stanek (1979; also Nimis 1981) undertook an extensive survey of boreal-taiga vegetation along the Yukon portion of the Alaska highway. Achuff and La Roi (1977) describe the vegetation of highland areas in Alberta. The boreal-northern hardwood ecotone in Minnesota and Wisconsin has been particularly well studied (Maycock and Curtis 1960; Buell and Niering 1957; Curtis 1959). Boreal wetlands have also received some attention (Heinselman 1963, 1970; Jeglum 1971; Jeglum et al. 1974; Wells 1981; Zoltai and Pollett 1983).

3.3 Major Tree Species of Boreal North America

The dominance of trees in boreal ecosystems is well documented, and considerable attention has been paid to the tree stratum in general descriptive studies. The wide distribution of most tree species, their distinct environmental requirements, and their economic value underly their importance in boreal ecosystems. Kornas (1972) discusses the ecology of major boreal tree taxa, with particular emphasis on the similarities and differences between North American and Eurasia representatives. The following review is derived from various sources, and highlights the distributional and ecological features of the major tree species encountered in boreal North
America, with emphasis on species common to Ontario.

3.3.1 *Picea mariana* (Black Spruce)

This widely distributed species occurs on all portions of the Canadian boreal forest from Alaska to Newfoundland. The species generally occurs on oligotrophic sites, being particularly abundant in both boggy, acidic substrates and on dry, nutrient-poor substrates such as rock outcrops and sandy uplands (Maycock and Curtis 1960). In Alaska, where the species is locally dominant in lowlands, Heilman (1966, 1968) found evidence for succession from black spruce dominated forest to more open sites dominated by *Sphagnum*. He attributed this to the decreasing availability of nitrogen and phosphorus. In the northern MacKenzie area Black and Bliss (1978) found that black spruce muskeg forest dominates on north slopes and other areas where permafrost is high (see also Johnson 1981). Moss (1953) describes interesting black spruce-feathermoss forests on upland sites in northern Alberta, and also notes that black spruce-*Sphagnum* muskeg is particularly common in the area. In the Canadian shield region of central Canada, black spruce becomes more common further northward, forming extensive lowland muskeg on the poorly drained lowlands around Hudson Bay and the Ontario Clay Belt. In northern Ontario, Wisconsin, and Minnesota, extensive black spruce muskegs occur, but in addition the species is also found on xeric upland sites. In the Gaspé black spruce is particularly abundant on mountain sides, often forming open forests at higher elevations. Extensive stands also occur on rolling, poorly drained landscapes in northern Québec and Labrador.

Cones are produced in great profusion at the tops of trees and are semi-serotinous (Larsen 1980), which may account for the persistence of this species on dry sites. The species also reproduces vegetatively by layering, and although foresters have questioned the importance of this characteristic (see Stanek 1961), there seems little doubt that layering is an important strategy in perpetuating the species, particularly on organic
substrates, which are poor seedbeds. The species also develops a shallow-root system, which may account for its success in colonizing permafrost areas and oligotrophic sites.

3.3.2 *Larix laricina* (Eastern Larch)

This species is widely distributed in North America, though it is absent from Alaska and is very rare in the Yukon. It is highly shade intolerant (Beefink 1960) and generally occurs on organic substrates where slow water movement or underground percolation increases nutrient availability (Heinselman 1963). In northern Alberta Moss (1953) found that larch bogs were more frequent in the east, and were generally floristically similar to black spruce bogs. However, the species occurred in areas subject to flooding or along drainageways in extensive muskeg bogs. In the Canadian shield region, the species typically occurs in poorly drained sites, typically *Sphagnum* dominated peatlands of higher nutrient status than those dominated by black spruce. Mixed larch-black spruce bogs also occur, particularly in north-eastern Québec and Labrador. Devastating attacks by the larch sawfly during the 1920s have considerably lessened the importance of this species over much of the boreal forest (Baldwin 1958).

3.3.3 *Pinus banksiana* (Jack Pine)

This species occurs in all areas of the boreal forest except the far western regions (where it is replaced by *Pinus contorta*, a species with similar ecological requirements) and Labrador. It is characteristic of nutrient-poor, very dry upland sites, and is the characteristic species of coarse sandy outwash plains. On such sites it is generally considered to be a pyric-edaphic climax species, its persistence being attributable to the serotiny of its cones. The species is rare on the sandy outwash plains south and east of Great Slave Lake, being replaced by black spruce. In the southern boreal areas of Alberta, and extending to the Yukon border, the species typically occurs on sandy hills and ridges and granitic rock
outcrops. On the Canadian shield, jack pine occurs with black spruce on rock outcrops, and forms even-aged, monospecific stands on sandy soils (Mueller-Dombois 1964, 1965). In central Canada the species becomes more important in northern areas. On the expansive sand deposits of northern Saskatchewan it is often the only tree species, being maintained by recurrent fires (Carroll and Bliss 1980). In northern Ontario and Québec even-aged monotypic stands of jack pine are typical of coarse sandy plains (Carleton and Maycock 1978).

This species is well adapted to growth on xeric, oligotrophic sites, producing a deep taproot to the underlying water table, and an extensive surface root system which competes with the understory species for percolating water and limited nutrients. The understory of jack pine stands is floristically poor, the surface characterized by highly flammable, poorly decomposed organic matter and fruticose lichens. Severe fires open the serotinous cones and expose inorganic soil, permitting germination and establishment of jack pine in the same season.

3.3.4 *Picea glauca* (White Spruce)

This species is widely distributed throughout the boreal forest, though it is much more common in the western regions. Lutz (1956) speculated that it is the predominant climax species in the Alaskan interior, invading birch-aspen stands which establish following fire. In the Yukon white spruce is restricted to shorelines, islands, and deltas of the Mackenzie River and south-facing slopes. In northern Alberta it is common on well-drained uplands and along rivers, forming dense, dark stands with a feathermoss understory which are generally considered to be climax stands (Moss 1953; Raup 1946). It may also occur on rock outcrops. In highland regions of boreal Alberta, mixed *Picea glauca* - *Abies balsamea* stands are common (Achuff and La Roi 1977). In the Canadian shield region and the eastern provinces, the species is generally restricted to favourable locations (richer soils and less severe microclimate) such as alluvial sites, valleys, and river edges.
In such areas it often occurs with *Abies balsamea*. In northern Ontario and Quebec white spruce is restricted to river valleys, where it is usually associated with *Populus balsamifera* (Carleton and Maycock 1978, Bergeron and Bouchard 1983).

In the eastern boreal forest, white spruce is often found growing with *Populus tremuloides*, *Betula papyrifera*, and *Abies balsamea* on well-drained moist silty soils (Larsen 1980). Pure stands are rare. The species is highly shade tolerant, and this has often been cited as evidence that it is a climax species.

3.3.5 *Abies balsamea* (Balsam Fir)

This is primarily an eastern boreal species, although it does occur as far west as Alberta. On the Canadian shield, balsam fir is restricted to well-drained, silty soils in the more southerly regions, often occurring with *Picea glauca*. In northern Wisconsin and western Ontario, forests dominated by balsam fir are typical, and there is some evidence of invasion of jack pine forests by balsam fir and white spruce in the absence of fire (Buell and Niering 1960). Swan and Dix (1966) noted that in Saskatchewan the species rarely dominates a stand, but is the principal tree in the understorey. Similar observations were made by Carleton and Maycock (1978) in northern Ontario. They found it mixed with *Betula papyrifera* and *Populus tremuloides* in mesic, mesotrophic habitats. In the Gaspe, balsam fir is restricted to sloping, well-drained upland sites.

This is by far the most shade-tolerant of the North American boreal trees, reproducing well in shade even on relatively poor seedbeds. Seedlings are generally numerous in mixed stands greater than 50 years of age on fine-textured upland soils, which led Carleton and Maycock (1978) to suggest that many of these sites will eventually reach an *Abies balsamea - Picea glauca* climax in the absence of disturbance. Balsam fir is poorly adapted to fire, and is therefore often restricted to moist, fire-resistant sites in
areas with a history of recurrent burning. In recent years spruce budworm infestation has destroyed vast tracts of balsam fir forest, particularly in New Brunswick, Québec, and Ontario. In such areas the understory is generally dominated by healthy *Abies* seedlings which grow quickly upon opening of the canopy. Spreiegel (1976) describes 'regeneration wave' sequences in *Abies*-dominated forests, in which a cyclical dying-off and subsequent regeneration attributable to microclimatic influences occurs.

3.3.6 *Thuja occidentalis* (Eastern White Cedar)

Though not strictly a boreal species, this tree is locally abundant in the southern boreal regions of Ontario and Québec, generally in swampy seepage sites, along riverbanks, and occasionally bordering lakes (Baldwin 1958). It forms small, localized stands in areas associated with nutrient-rich highly decayed organic soil. The species may occasionally be found in more acidic sites, but here growth is slow and trees are depauperate.

3.3.7 *Populus tremuloides* (Trembling Aspen)

This species shows an ubiquitous distribution, and has probably become more abundant following the exploitation of boreal forests by man (Larsen 1980). A highly shade intolerant species, it is normally absent from the understory. It is well adapted to fire, resprouting readily from rootstock following all but the most severe fires. In addition, it produces large quantities of light, wind-dispersed seeds which readily germinate in recently burned or logged areas. Throughout the boreal forest this species, along with *Betula papyrifera*, typically colonizes all but the driest upland sites following fire, and it has therefore been regarded as a successional species. In areas of recurrent fire, however, it may form a pyric climax. In the absence of disturbance, trembling aspen stands may be eventually invaded by shade-tolerant coniferous species, particularly *Abies balsamea* and *Picea glauca* (Curtis 1959), though the reality of such a successional sequence has been questioned (Carleton and Maycock 1978; Rowe 1961). Mixed forests
of *P. tremuloides*, *B. papyrifera*, and either *P. glauca* (in western areas) or *A. balsamea* (principally in the eastern portions) are characteristic of many boreal ecosystems, reflecting the importance of disturbance factors.

3.3.8 *Betula papyrifera* (White Birch)

Like trembling aspen, this species is widely distributed throughout North American boreal regions, and in many respects the two species are ecologically similar. A shade intolerant species, white birch is an early colonizer following fire, growing on well-drained sandy or silty soil, as well as on rocky slopes and outcrops. It resprouts readily from the base following fire, and also produces wind dispersed seeds which readily germinate in disturbed areas. Like trembling aspen, it is generally considered to be a successional species, and the two in fact often occur together. Ritchie (1956) discusses the ecological requirements of these species, concluding that white birch typically colonizes rocky areas of lower insolation, whereas trembling aspen forms pure stands on more mesic, mesotrophic sites of higher insolation.

3.4 Boreal Forest Dynamics

The reality of the concept of succession in boreal ecosystems has been hotly debated, but there is little evidence to support any of the theories as most have been based on observation rather than long-term studies. As Maycock and Curtis (1960) have pointed out, the existence of a dense sapling population of a given tree species does not necessarily imply its increased representation at a later date. Indeed, until long-term studies are instigated and reported on, aspects of boreal forest dynamics must remain speculative, though it is probably safe to say that carefully planned observational studies can suggest working hypotheses regarding forest dynamics.

Successational trends on upland sites have been examined in many areas of the boreal forest. Lutz (1956), working in Alaska, concluded that a general
sequence following fire involved the gradual replacement of white birch and trembling aspen by white spruce, which was considered the climax species. In northern Alberta, Ritchie (1956) found evidence for a similar sequence, but ending in a black spruce-feathermoss forest. Achuff and La Roi (1977) concluded that a mixed white spruce-balsam fir forest is the climax in the highlands of Alberta. Curtis (1959) suggested that a mixed white spruce-balsam fir forest is the climax in northern Wisconsin, though he recognized also the edaphic-pyric climax of jack pine on coarse sandy soils (see also Raup 1946). Others have emphasized disturbance aspects, arguing that the combined effect of fire, windthrow, and insect infestation implies that the concept of succession, in the neo-classical Clementsian sense, is not applicable to boreal forests. This viewpoint has been particularly strongly advocated by Rowe (1961), who argued that boreal forests, far from being self-perpetuating, instead becomes open and 'ragged', awaiting a catastrophic event (such as a fire) to 'rejuvenate' the system (see also Carleton and Maycock 1978). A similar conclusion was reached by Swan and Dix (1966; also Dix and Swan 1971) regarding the forests at Candle Lake, Saskatchewan. They concluded that the area has undergone "...an infinite number of vegetational readjustments...", and that succession was unimportant. Curtis (1959) also stressed the adaptation of boreal ecosystems to catastrophe, arguing that the trend of destruction and subsequent replacement best accounts for the occurrence of even-aged, often monotypic stands so characteristic of the boreal forest.

Working in Alaskan wetlands, Lutz (1956) concluded that black spruce muskeg is a pyric-edaphic climax, with regeneration after fire made possible by the serotiny of the species. Heilman (1968,1969) cited evidence for palidification in these same forests, with fire leading back to increased dominance of black spruce over Sphagnum. Working in Alberta, Moss (1959) concluded that the shade-intolerant larch, in the absence of fire, is gradually replaced by black spruce in boggy habitats. By contrast, Heinselman (1970) concluded that Minnesota wetlands show little evidence of
progressive change to a self-perpetuating climax, but rather undergo small, random fluctuations in species composition and structure in response to changing environmental conditions (particularly drainage patterns). He also concluded that peatlands, which restrict drainage and tie up nutrients in poorly decomposed organic matter, are highly stable systems.

In conclusion, the concept of the hypothetical, classical (sensu Clements 1916) climax probably has little meaning in boreal systems, which are subjected to recurrent catastrophe whose frequency of occurrence are often of the same order as the lifespan of the trees. Thus boreal regions are characterized by disturbance forests in a continual state of flux, showing no progressive change to a self-perpetuating and stable climax vegetation. There is, however, considerable evidence for pyric and/or edaphic climax types.

3.5 Boreal Soils

Boreal soils in upland habitats are generally podzolic in nature, and are derived from sands or coarse-grained rock (generally granitics). In some areas, including northern Ontario, extensive lacustrine clay deposits occur, and rock outcrops are also common. Lowlands are almost invariably organic peats.

Podzolization involves the movement of iron, aluminum, and various organics by acid-chelating substances from the upper A-horizon to the lower B-horizon, where the higher pH leads to the breakup of chelators. This phenomenon is particularly intense in acidic, sandy glacial deposits, leading to a bleached, ash-grey Ae-horizon overlying a brown-red, anaerobic B-horizon. This reddish tinge is attributable to the development of a colloidal skin on quartz grains. As a result of podzolization, solubles such as calcium, sodium, and potassium are rapidly washed into the lower horizons by percolating water, which leads to a further decrease in pH in the upper horizons. This, combined with low temperatures, hinders the breakdown of
proteinaceous compounds to usable nitrogen by fungi and bacteria, leading to the accumulation of litter and raw humus on the soil surface. Nutrients (primarily nitrogen and phosphorus) are thus largely tied up in unassimilated organics. Nitrification is generally unimportant in boreal soils, but nitrogen-fixation may be. The Fabaceae are poorly represented in the boreal flora, but other nitrogen-fixers such as Alnus, Myrica gale, Hippophae (an Eurasian genus), Eleagnus, and Shepardia may be important components of some communities. The bacterium Clostridium is also characteristic of boreal soils. Crittenden and Kershaw (1979) stress the importance of nitrogen fixation by certain lichen genera (for example Stereocaulon and Peltigera).

Weetman and Weber (1972) studied in detail nutrient availability in mor humus, which is organic matter for which decomposition is incomplete. They found that nitrogen was the primary limiting factor, with only a very small proportion (two percent or less) of the total nitrogen pool available. Availability was found to be somewhat dependent upon the rate of decomposition and the type of humus, with rate of decomposition varying monotonically with pH. Christensen and Cook (1970) have examined the microbiological ecology of these poorly decomposed organics.

3.6 Environmental Factors Influencing Boreal Vegetation

3.6.1 Climate

Climatic variation is substantial in boreal systems, particularly along a general north-south gradient. Ritchie (1962) discusses the strong correlation between vegetation and climate along such a gradient, from tundra to forest-tundra transition to open coniferous forest, finally giving way to a closed coniferous forest (see also Hare 1950). The general sequence is not seen in Alaska due to topographic interaction, and is largely obscured in northern Ontario by edaphic factors, particularly the marine deposits surrounding James Bay and the lacustrine clays further inland. Ritchie (1956) has described the vegetation trend in Manitoba, attributing changes in
vegetational composition to corresponding changes in the length of growing season, mean daily temperature, and other macroclimatic factors.

3.6.2 Fire

Of all the environmental events influencing boreal vegetation, fire is undoubtedly the most important, frequent, and widespread (Rowe and Scotter 1973). The vegetation is generally well adapted to fire (Shafi and Yarranton 1973; Carleton and Maycock 1978), and some ecosystems are in fact dependent upon repeated, intense burning for their perpetuation (Raup 1946). Adaptations include rapid diaspore germination and subsequent establishment, rapid initial growth, the perennial habit, the presence of underground perennating organs, rapid and efficient vegetative reproduction, and the ability to mature and successfully reproduce before the next fire (which is particularly important for long-lived tree species). All major tree species with the exception of *Picea glauca* and *Abies balsamea* are adapted in some way to fire, and most understory species are able to resprout following all but the most intense fires. Fire therefore appears to be all-pervasive in its effects, and extremely important ecologically. Sharp boundaries and discontinuities in boreal forests often represent the extent of a given fire. To Rowe (1961), fire is of primary importance in the perpetuation and maintenance of healthy stands of vegetation. Recovery sequences following fire are difficult to generalize, however, as they depend upon burning intensity, proximity of diaspore source, and type of substrate (Wright and Heinselman 1973).

3.6.3 Moisture

Rowe (1956) rated boreal species according to their preferred moisture class, recognizing that although most species show a wide moisture tolerance, they generally show an apparent optimum. Jeglum (1971) used a similar strategy, ordering species along a 'moisture availability' index, using depth to water as a criterion. Other workers have recognized a strong
correlation between vegetation composition and moisture status. Maycock and Curtis (1960) concluded that a complex of factors dictating moisture conditions were important determinants of species distributions. Carleton and Maycock (1978) found that trees growing on inorganic substrates could be ordered along a moisture-soil particle size gradient, but that on organic peats other factors such as nutrient availability were important. To Baldwin (1958), drainage is the most characteristic environmental factor influencing the structure and composition of boreal vegetation.

3.6.4 Light

Rowe (1961) has suggested that while moisture is of primary importance in determining overall community composition, light is an important factor in determining the composition and structure of the understory. Of course the factors moisture and light are correlated and somewhat synergistic in their effects. For example, an open canopy may be characteristic of a dry site, which will in turn increase the amount of light reaching the ground, thereby increasing evapotranspiration. Swan and Dix (1966) also recognized the importance of light, noting that an understory dominated by feathermosses and few vascular plants is characteristic of closed black spruce and balsam fir forests in western Canada. This thick moss layer may act as an insulation (maintaining low soil temperatures), and it may inhibit the germination and establishment of tree seedlings. Conversely, a rich understory dominated by vascular plants develops beneath more open canopies dominated by jack pine, white birch, or trembling aspen. Seasonality is also important to an understory occurring beneath deciduous trees.
3.6.5 Nutrients

Soil fertility has often been cited as being important in the establishment and growth of boreal species. Most studies have concentrated on tree species, presumably because of their economic importance. Pierce (1953) correlated ground water oxidation-reduction potential to growth of black spruce. Gerloff et al. (1966), examining foliar nutrient concentrations in black spruce and jack pine, found that nitrogen, phosphorus, and some of the trace element levels were near or even below deficiency levels. Similarly, Small (1972) found low foliar concentrations of nitrogen and phosphorus in bog species. Reader (1982) found shoot productivity of bog species to be correlated most strongly with nutrient levels, depth to water table, and heat sum.

Jeglum (1971), using pH as a gross measure of overall fertility in the upper soil horizon, ordered species according to nutrient-phases. Heinselman (1963, 1970) examined in detail the nutrient status of sloping bogs in Minnesota. He showed that rich swamp forests dominated by black spruce, larch, eastern white cedar, and Alnus rugosa develop downslope from mineral "islands", while adjacent areas support depauperate black spruce and ericaceous shrubs. Belts of rich swamp forest marking the course of mineral-bearing ground water were clearly apparent. Foliar analyses verified these observations. He suggests that nutrient status is of primary importance in determining species composition in wetlands (see also Carleton and Maycock 1978).

Foster (1974; also Foster and Morrison 1976) studied in detail nutrient input into a jack pine stand, concluding that tree litter contributes the majority of nitrogen, phosphorus, calcium, and magnesium while leaf-wash was the most important source of potassium. Relatively little nutrient input from precipitation was evident, underlying the importance of nutrient cycling in this ecosystem. Larsen (1980) cites other such studies.
Nutrients are often tied up in undecomposed detritus in boreal soils. Light fires will tend to release these, making them available to the resprouting vegetation and thus enhancing its development. After a very severe fire, however, nutrients may be lost before they can be utilized by colonizing species.

3.6.6 Biotic Factors

1. Competition. Interspecific competition is an extensive, complicated subject, and justice cannot be done to it here. Few studies of competition are available in boreal vegetation, though it is undoubtedly important. For example, Steill (1970) and a number of Russian workers (eg. Karpov, cited in Larsen 1980) have stressed the importance of root competition. Competition here is for both nutrients and water, which may both be limiting factors on upland sites.

2. Mycorrhizae. Mycorrhizal associations have in recent years been shown to be important to the establishment and survival of vascular plants (Malloch et al. 1980). However, such associations have until recently been poorly studied in boreal species. The work of Malloch and Malloch (1981, 1982) has demonstrated the presence of mycorrhizae in many common boreal species. They stress that further work needs to be undertaken concerning the role and importance of these associations to the functioning of boreal ecosystems.

3. Insects. The population dynamics of defoliating insect populations generally shows considerable fluctuation, with sudden explosions followed by catastrophic dieoffs. During these recurrent infestations such species can cause considerable damage to boreal tree species. Baldwin (1950) cites the severe defoliation of deciduous trees (primarily trembling aspen) by forest tent caterpillars (Malacosoma disstria) in the Ontario Clay Belt in 1952. Larch sawfly infestations since the 1920’s have been implicated in the change from a mixed black spruce-larch muskeg to stands dominated by black spruce
in Ontario (Baldwin 1958). In recent years the most devastating insect has undoubtedly been the spruce budworm (*Choristoneura fumiferana*), which attacks *Abies balsamea* and may destroy mature stands of this economically important species. Infestations are cyclical in nature, and are associated with the maturity of the trees (Ghent 1958).

4. Mammals. Herbivorous mammals may influence vegetation composition to some degree. A moose can consume 20-30 kgs of vegetation per day, and although overgrazing is rare it has been reported (Sukachev and Dylis 1964). The species is a generalist herbivore; a detailed study of its food preferences is given by Belovsky (1981). Black and grizzly bear are primarily vegetarian (Juniper 1978), but their most conspicuous influence on vegetation results from local but severe girdling of trees. Porcupines, whose main diet is coniferous bark, may also damage trees. The most important mammal (aside from man) is undoubtedly the beaver. It has been estimated that considerable tracts of marketable timber are lost annually as a result of beaver dam flooding. Furthermore, the felling of trees, in particular trembling aspen, may be locally devastating. It seems likely that these effects are of great importance in the long term vegetation dynamics of boreal ecosystems, but this has yet to be examined.
CHAPTER 4

THE ELK LAKE STUDY AREA - DESCRIPTION AND SURVEY DESIGN

4.1 The Study Area

The Elk Lake study area lies approximately between 47°45' - 48°00' N and 80°25' - 80°35' W (Figure 4.1). It lies west of the Québec border, just south of both the height of land and the 'clay belt' region, and along the southern edge of the boreal forest as delineated by Rowe (1972). Elevation ranges between 300-400 meters. A flat relief is characteristic, although occasional rocky hills also occur, with most rising 50-100 m above the surrounding terrain. Surficial sand deposits predominate on the flat areas, while finer soils often occur in rocky and hilly areas. Local rock outcrops are also common. The region is drained by the Montreal River watershed (Figure 4.2) which flows into the Ottawa River drainage basin. Nevertheless, some poorly drained areas occur, attributable primarily to the accumulation of peat in low-lying areas (see aerial photos, Appendix 9). Geologically the region is characterized by felsic and mafic intrusive rock, with granitic diabase and dikes predominating (Boissonneau 1968).

Climatic parameters for northern Ontario are given by Chapman (1953). In the Elk Lake area, the growing season (from when the mean daily temperature reaches 5.6°C until it falls below this level) extends from May 3 - October 11, or an average of about 160 days. Potential evapotranspiration is in the range of 40 - 50.5 cm, which is high for the boreal forest (Larsen 1980). Thunderstorms, which are important in igniting forest fires, average 15 per year. Climate data for Indian Chute (47°51' N, 80°27' W, elevation 293 m), which lies within the study area (see Figure 4.3), is summarized in Figure 4.4. The data indicates that the area is characterized by a rather short, warm summer and a long, cold winter. Precipitation is greatest in the summer months, with just over 50% falling between May
Figure 4.1: Map of Ontario, Canada showing the location of the Elk Lake study area.
Outline of the sampling frame of the Elk Lake study area (shaded), showing the general drainage pattern of the area. The limits of the surficial lacustrine sand deposits of the region are also shown.
Figure 4.3  A detailed map of the Elk Lake study area. The three sampling strata are also shown. Codes are: 1 - lowlands (areas in which the water table is at or near the surface). 2 - uplands (flat or gently rolling land above the water table). 3 - highlands (rocky hills). The location of the Indian Chute weather station is also shown.
Figure 4.4  Environmental data for Indian Chute, Ontario (1941 - 1970). Shaded area represents proportion of precipitation falling as snow.
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and September.

An extensive and severe fire swept through this area in the early 1920's (Donnelly and Harrington 1978), and as a result most stands are of a uniform age of about 60 years. Some recently felled *Thuja occidentalis* specimens, however, were aged at greater than 250 years.

An analysis of aerial photographs (see Appendix 9) and a general reconnaissance undertaken in the fall of 1980 suggested that drainage is of principal importance in determining vegetation composition and structure in the area. Flat-sandy plains above the water table are generally dominated by monospecific jack pine or trembling aspen stands. On finer soils over rock, mixed forests of balsam fir, black spruce, jack pine, trembling aspen, and white birch occur. Lowland clay deposits along rivers, which is a very rare habitat in the area, support stands of *Populus balsamifera* or *Picea glauca* along with some of the species mentioned above. Silty, periodically flooded terraces along the meanders of the Montreal River below Indian Chute are dominated by stands of *Fraxinus nigra*. *Thuja occidentalis* occurs along riverbanks, some lakeshores, and in seepage areas where considerable deposits of well-decomposed organic muck occur. On poorly decomposed peats *Picea mariana* generally occurs, while *Larix laricina* predominates along water-tracks in boggy areas. Marshy areas along Whiskey Jack Creek are dominated by species of *Carex*, while grass-sedge meadows occur along meandering creek banks subject to regular flooding.

### 4.2 Sampling Method

The strategy employed has been to intensively sample a small, relatively homogeneous stand of vegetation, as advocated by Goodall 1970. Surficial geology was used as a homogeneity criterion (the region is predominantly lacustrine sand deposits; see Figure 4.2). Other criteria used in delineating the sampling frame included accessibility and lack of disturbance; the boundaries are shown in Figure 4.3.
Stands were located using a stratified random procedure, with three strata defined on the basis of relative elevation (above the perceived water table). Stratal boundaries were delineated with the aid of aerial photographs and contour maps. The stratal boundaries are shown in Figure 4.3. The number of stands within a given strata was made proportional to stratal area.

Within each stratum, stands were located at random and marked on aerial photographs and contour maps. Stand positions were subsequently located in the field as well as possible. From this point, a random direction (one of eight compass point directions) and distance (ranging between 0 - 50 paces) were taken, and this position was taken as the centre of the quadrat. This latter set of steps were undertaken to ensure objectivity in the positioning of stands. If the area proved to be vegetationally heterogeneous, more than one stand was enumerated at the same location. While this undermines somewhat the statistical objectivity of the sampling procedure, it was felt appropriate in obtaining an adequate sample size for the accurate description of some of the rare community-types.

A total of 400 stands were located in the stratified random manner outlined above. Of these, 19 proved to be located in highly disturbed sites and were therefore excluded from enumeration. At 44 of the positions, more than one stand was enumerated. In total data from 431 quadrats was obtained.

4.3 Quadrat Size Determination

Various strategies have been used in sampling boreal forest vegetation. Carleton and Maycock (1978) used plotless sampling (point-centred quarter method) for the enumeration of trees and tall shrubs, locating 30 points in each stand. The understory vegetation was examined at alternate points using one meter square quadrats. Dix and Swan (1966) employed a similar strategy, but their understory quadrats were half as wide. Plotless sampling has some advantages, primarily in removing the edge effect problem.
However, unbiased estimates are not obtained unless the trees are randomly distributed (Pielou 1977). Furthermore, plotless methods are useful only in broad-scale site descriptions, since at least 20 points are required to obtain an adequate description of an area. Because interest in this study lies in small-scale vegetational variation and the obtaining of unbiased estimates, quadrats were used to enumerate the tree stratum. This has the further advantage of allowing the principles of two-stage sampling to be applied.

The problem then arose of determining appropriate quadrat sizes for the description of the tree and understory strata. Two sites were chosen to examine this problem, and two alternative strategies (discussed in Section 2.5.6.2) were used. The first site was a closed jack pine stand on sandy uplands, and the second an open black spruce stand on poorly decomposed peat.

1. **Contiguous Quadrat Method.** To enumerate the tree stratum at each of the two sites, a 64 square meter area laid out as a grid of 2 meter square units was located in the field. The number of trees (over 3 meters in height) were recorded in each of the small units. For the understory, a 16 meter square block divided into half-meter square units was used, and percentage cover was recorded. Univariate optimal quadrat size analyses were then carried out for the most common species, and the results are presented in Table 4.1. Not surprisingly, different optimal sizes are suggested for the different species. For the tree stratum, a larger quadrat size is suggested for the black spruce site. Furthermore, the R.E. value for the jack pine site is quite low, suggesting that this species may be more or less randomly distributed. Nevertheless, the results do suggest an optimal size of between 10 and 20 meters square. Similarly, the results for the understory are variable. At both sites, there is a tendency for smaller species (*Sphagnum, Pleurozium schreberi, Vaccinium*) to show a smaller optimal size than the larger shrubs and saplings. This difference indicates patterning at different scales in the communities, reflecting the influence of both abiotic and biotic (competitive) factors. It is clear that in choosing a quadrat size for the
Table 4.1 Results of the univariate optimal quadrat size determinations for the jack pine and black spruce dominated systems. Maximum relative efficiency values (see text and Table 2.4) are given, and the size of the grid units for this maximal comparison is indicated.
<table>
<thead>
<tr>
<th>Species</th>
<th>Optimal Size (meters)</th>
<th>Relative Efficiency</th>
</tr>
</thead>
<tbody>
<tr>
<td>1. Tree Stratum</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Pinus banksiana</td>
<td>8 x 16</td>
<td>R.E. (8,8;16,16) = 1.102</td>
</tr>
<tr>
<td>Picea mariana</td>
<td>16 x 16</td>
<td>R.E. (8,8;16,16) = 1.342</td>
</tr>
<tr>
<td>2. Jack Pine Understory</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Liriodendron tulipifera</td>
<td>4 x 2</td>
<td>R.E. (1,1;4,2) = 1.10</td>
</tr>
<tr>
<td>Vacecum myrtillioides</td>
<td>2 x 2</td>
<td>R.E. (.5,.5;2,2) = 1.012</td>
</tr>
<tr>
<td>V. angustifolium</td>
<td>2 x 2</td>
<td>R.E. (.5,.5;2,2) = 1.43</td>
</tr>
<tr>
<td>Pseudotsuga echinata</td>
<td>0.5 x 0.5</td>
<td>R.E. (.5,.5;4,4) = 0.874</td>
</tr>
<tr>
<td>Cornus canadensis</td>
<td>4 x 4</td>
<td>R.E. (1,2;4,4) = 1.026</td>
</tr>
<tr>
<td>Prunus pensylvanica</td>
<td>8 x 4</td>
<td>R.E. (2,2;4,8) = 2.423</td>
</tr>
<tr>
<td>3. Black Spruce Understory</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Sphagnum magellanicum</td>
<td>2 x 2</td>
<td>R.E. (.5,.5;2,2) = 1.118</td>
</tr>
<tr>
<td>S. angustifolium</td>
<td>1 x 1</td>
<td>R.E. (.5,.5;8,8) = 0.894</td>
</tr>
<tr>
<td>S. fuscum</td>
<td>2 x 2</td>
<td>R.E. (1,2;2,2) = 1.123</td>
</tr>
<tr>
<td>Ledum groenlandicum</td>
<td>4 x 4</td>
<td>R.E. (1,2;4,4) = 1.342</td>
</tr>
<tr>
<td>Liriodendron tulipifera</td>
<td>4 x 4</td>
<td>R.E. (2,4;4,4) = 1.121</td>
</tr>
</tbody>
</table>
understory a compromise must be sought, since no clear trends are indicated by the data.

The chief drawback of this method is that it examines the species separately, treating each as an independent, univariate population. This is clearly unrealistic, as it implies that the multivariate population consists of noninteracting species.

2. Eigenvalue Method. This method involves the extraction of the principal eigenvalue from a series of covariance matrices obtained from different quadrat sizes. The sites used above were sampled again, this time defining 20 random points within each. These points formed the centroids of a series of square quadrats of various size. Only the understory was examined since the tree stratum represents a univariate population at each site. The quadrat sizes employed were: 0.5, 1, 2, 3, 4, and 5 meters square. In both sites, percent cover estimates were obtained for the common species at each quadrat size at each of the 20 random points. The resultant covariance matrices were subjected to eigenanalysis and the largest eigenvalue extracted. These were then plotted against quadrat length (Figure 4.5). For the black spruce stand, the largest quadrat size produced the smallest primary eigenvalue, though the general trend suggests a drop up to the 3 meter size followed by a levelling off. The results for the jack pine stand are less trended, although lowest eigenvalues occur at the 3 and 4 meter sizes.

For the overstory data, the contiguous quadrat method suggests an optimal quadrat size somewhere in the range of 10–20 meters square. The R.E. value for black spruce is relatively high, suggesting a reasonably clumped distribution of this species. This was apparent in the field, with clumps on the order of 5–8 meters apart. Clearly the optimal quadrat size should be somewhat larger than this clump size (Section 2.5.6.2).

The results for the understory data are more difficult to interpret, primarily because of the large number of species involved. While the
Figure 4.5  Plots of the largest eigenvalues versus quadrat size for (a) black spruce and (b) jack pine sites at Elk Lake, Ontario.
contiguous quadrats method showed a greater deal of variation in optimal size, the results of the eigenvalue procedure were much more interpretable, suggesting an optimal quadrat size on the order of three meters square.

In choosing a quadrat size, consideration must also be given to logistics. A very large quadrat will be more difficult to enumerate, while a small one may not be representative of a site. Other factors such as edge effect and distributional symmetry argue strongly for a larger size.

For enumeration of sites, a two-stage sampling systematic strategy was decided upon, in which small understory quadrats are placed systematically within the larger overstory quadrat. A further requirement therefore is that the width of the large quadrat be an integer multiple of the small quadrat.

After considering the results from the contiguous quadrats method and the logistic limitations imposed by quadrat sampling, a 12 meter square quadrat was chosen for enumerating the overstory, and a 3 meter square one for the understory. The eigenvalue method was not developed until after the survey was completed. Interestingly, the results of this method confirm that the choice of understory quadrat size was a good one. In the two-stage-systematic strategy, four of the understory quadrats were placed within each of the large quadrats, giving a 25% enumeration. The pivotal point was chosen by selecting randomly a pair of numbers, either 1 or 2, and using the north-west corner of the quadrat as a reference (see Figure 4.6 for clarification). The systematic strategy is unbiased with respect to precision estimates (Cochran 1977), and has the further advantage of ease of location.
Figure 4.6  The two-stage sampling procedure used in the study of the Elk Lake vegetation. The 12 x 12 m large quadrat was used to enumerate the tree stratum. This was divided into sixteen 3 x 3 m units as shown. Four of these, chosen systematically, were used to sample the understory vegetation. In the example shown, the pivotal point is 1,2 (with respect to the north-west corner of the quadrat), which results in the enumeration of the shaded units.
4.4 Data Collected

For the tree stratum (large quadrat), percent cover was recorded for each species. The number of trees of each species was also recorded, and their height and DBH measured. In some cases, sample cores were taken (at DBH level) to obtain estimates of tree age. Within each of the four understory quadrats, percentage cover estimates were made for each species. The data for the four quadrats were subsequently pooled and a mean cover obtained for the stand.

In upland sites a soil pit was dug near the centre of the large quadrat. Depth of the organic layer, the leached A-horizon, the colour and general texture of the soil, and the amount of gravel and/or rock, were recorded. In addition, a soil sample was taken from just below the leached layer and air dried for later determination of particle size. The method used to determine soil particle size is outlined in Appendix 2, which also examines the relationship between soil particle size and water-holding capacity. No nutrient analyses were undertaken following the suggestion by Carleton and Maycock (1978) and many others that drainage and moisture rather than nutrients are important determinants of vegetational composition in upland boreal sites. Subjective estimates of overall nutrient status were made using a five-point scale from very oligotrophic to very eutrophic.

In the wetland habitats, depth to water table (obtained by digging a pit when necessary), degree of decomposition of organic matter (if present), and estimated nutrient status (using the five-point scale of Jeglum et al. 1974) were recorded. Field recordings of pH were obtained at selected sites. Degree of groundwater movement was estimated before visiting sites, based on drainage patterns suggested by aerial photographs and local topography. Periodicity and degree of flooding were also recorded, based on field observations at various times of the year.

At all sites, the general physiognomy, topography and substrate type of the area were recorded, and slope and aspect were noted. Drainage class
was also recorded, using the scale: 1—very xeric; 2—xeric, 3—mesic/xeric,
4—mesic, 5—mesic/hydric, 6—hydric. Classification was initially made on the
basis of relative elevation (height above water table, determined from the
examination of aerial photographs and topographic maps) before visiting
the site. At the site, modifications were made if necessary using topographic
and soil criteria (texture, presence of rock and/or gravel). To minimize the
'circularity of argument in correlating vegetation with drainage, the
vegetation was not used as a criterion. Finally, the nature and degree of
variability of vegetation in the immediate area, and disturbance features,
were also noted.
CHAPTER 5

THE ELK LAKE STUDY AREA -
VEGETATION TYPES AND ENVIRONMENTAL GRADIENTS

5.1 Initial Subdivision of the Data

Data sets collected by phytosociologists are typically large, with respect to both the number of individuals (quadrats) and the number of variables (species and/or environmental parameters). The data set examined here consists of 217 species in 431 quadrats.

Large data sets are characteristically diverse, containing quadrats from a number of ecologically distinct areas of differing species composition. In such a case, an objective partitioning into smaller, more manageable and homogeneous units has often been suggested (Hill et al. 1975; Orlić 1978; van der Maarel 1980; Peet 1980). This strategy, which is followed in the present study, permits a more detailed analysis of structure and trends in the data set. Indeed, the analysis of smaller units has the advantage of greater homogeneity, giving the data a structure more amenable to analysis using multivariate statistical methods. Furthermore, computations which may be difficult or computationally burdensome when applied to large data sets are more readily applied to modest-sized ones, permitting more detailed and diversified analyses.

The requirement then is to find a computationally efficient algorithm for the objective partitioning of a large data set. For this purpose, the TWINSPLAN program (Hill et al. 1975; Hill 1979) was used. The first division of the data separated out a small group of 19 quadrats characterized by the presence of Calamagrostis canadensis, Potentilla palustris, Carex rostrata, C. aquatilis, Campanula uliginosa, and Chamaedaphne calyculata. The correspondence analysis for the full data set is shown in Figure 5.1a,
Figure 5.1  (a). Correspondence analysis (CA) of the full data set (431 quadrats), axes I and II, showing the separation of the 19 grass-sedge meadow quadrats from the others (strong hatched line). The three groups delineated correspond to the groups formed in the first two subdivisions of the TWINSPLAN program. Quantities represent numbers of quadrats in each group.

(b). Correspondence analysis of the 412 quadrats (following removal of the 19 grass-sedge meadow quadrats), the strong hatched line showing the two groups (upland and wetland areas) delineated by the TWINSPLAN program.
which makes clear the separation of these 19 from the others on the first axis. This small group consists of grass-sedge meadows occurring on periodically flooded lowlands (their ecology and species composition are discussed in Section 5.4.2). The next division partitions the remaining 412 quadrats into two groups, on the basis of the positive 'indicator' species *Sphagnum magellanicum* and *Carex trisperma*, and the negative 'indicator' species *Pinus banksiana*, *Diervilla lonicera*, *Vaccinium angustifolium*, and *Populus tremuloides*. In determining assignment, the presence of any of these six species is noted within a given quadrat, and a score (positive or negative, depending on which group it belongs to) is recorded. For example, a quadrat containing *D. lonicera* and *P. banksiana* would score -2. Quadrats with a zero or positive score are assigned to the positive group, while a negative score indicates assignment to the negative group. The negative group contained 299 quadrats characteristic of drier, upland sites on mineral soil. The positive group, containing 113 quadrats, are wetland habitats which are either periodically flooded or occur on poorly to well-decomposed organics. The correspondence analysis for the 412 quadrats (after removal of the 19 grass-sedge meadow group) is shown in Figure 5.1b. A clear subdivision of the two groups is indicated along the first axis. Note also that another distinct group is separated along the second axis. However, since the division is made along the first axis only, this set of quadrats is lumped in with the wetlands group (it is separated out in later subdivisions, however).

Further subdivisions were found to be less clear and somewhat ambiguous, and were deemed unnecessary at this stage. Three groups therefore exist: two large ones consisting of upland and wetland habitats, and a small group of 19 wet meadow quadrats. It was decided to include this small group with the other wetland habitats, giving a wetland group containing 132 quadrats and permitting the examination of the relationship and affinity of the meadows to the other wetland habitats. While this decision is somewhat subjective, reference to Figure 5.1b indicates the
greater affinity of the meadow quadrats to the wetlands group. Ecological considerations also indicate that the assignment is a good one.

In subsequent analyses these two groups (the 299 drier upland sites on mineral soil and the 132 wetland sites) are examined separately.

5.2 Data Analysis

5.2.1 Strategies

In analyzing the data a dual classification and ordination strategy was used (Orléci 1978). Classification of relevés was performed for utilitarian purposes, with the objectives of describing the composition, structure, and relationships of the vegetation. Ordination of relevés was undertaken to examine and emphasize the continuous nature of the vegetation, and for analyzing the correlation of the vegetation with environmental factors. To examine structure further, ordination and classification of the common species was also undertaken. Classification was again used as an utilitarian strategy. Species ordinations summarize overall trends in interspecific associations, permit examination of the correlation of these associations with environmental trends, and serve a complementary function in the interpretation of quadrat ordinations.

Most of the analyses were carried out using the package of Wildi and Orlécí (1983). Some analyses used the Cornell Ecology Program series (Gauch 1977, Hill 1979). Nonmetric multidimensional scaling was accomplished using a modification of the program described by Brambilla and Salzano (1981).

5.2.2 Choice of Methods

A plethora of available classification and ordination strategies were reviewed in Chapter 2. It was decided to classify using a numerical strategy, but even so considerable alternative methods are available. Because of the large size of the data set, and because many methods have been rarely
applied in a phytosociological context, only the following methods were examined for their overall utility: two-way species indicator analysis, agglomerative sum of squares, single linkage agglomeration, and complete linkage agglomeration. While the primary objective of this dissertation is not to compare alternative classificatory strategies, some comparisons are required since no one method has been shown to be superior under all circumstances (Orlóci 1978). The methods are compared in Section 5.4.1, using the wetlands data.

For the agglomerative methods, the choice of an appropriate resemblance measure remains. In theory and practice, metric measures have considerable advantages (Anderberg 1973, Orlóci 1974), and are in fact required by the sum of squares algorithm. Therefore, euclidean distance was used, applied to both the raw data and after standardization by stand norm (equivalent to the chord distance of Orlóci 1967b). This standardization has been advocated by Noy-Meir et al. (1975).

Nonmetric multidimensional scaling, using chord distance and specifying a two-dimensional solution, was used for both the quadrat and species ordinations. In addition, principal components analysis and correspondence analysis were applied for comparative purposes. The relationships between quadrat and species groupings obtained from classification was examined using concentration analysis (Feoli and Orlóci 1979; also Orlóci 1980). This is similar to a correspondence analysis, but uses group structuring in two-way tables in analyzing trends of variation. The method gives simultaneous ordinations of quadrat and species groups.

5.2.3 Data Standardization

The standardization of raw abundance data has a long history in phytosociology, being implicit in the cover-abundance scales used in the European schools (reviewed by Mueller-Dombois and Ellenberg 1974). For example, the Braun-Blanquet cover-abundance scale (Braun-Blanquet 1928)
is similar to a cube root transformation of raw abundance data. The rationale of data standardization is that greater emphasis should be given to minor species with low cover, for otherwise analyses (particularly objective numerical methods) will tend to emphasize dominant species at the expense of the less dominant ones. Dominance refers here to large species having consistently high cover when present. In this study, extensive analyses were initially performed utilizing the unstandardized cover estimates. Later attempts to interpret these results showed that the analyses were largely dominated by species of high cover, making the ecological interpretation of the results difficult. It was decided to reanalyze the data after first performing a square root transformation to deemphasize somewhat the dominant species (a cube root transformation was felt to be too severe). Bartlett (1936, 1947) has advocated using the square root transformation for frequency data, since it will render the variance more independent of the mean. While no such theoretical justification can be claimed for abundance data, the standardization was used here for utilitarian rather than statistical reasons.

5.3 Species Nomenclature

Nomenclature for vascular plants follows Gleason (1968), for mosses Crum and Anderson (1981), and for lichens Hale (1979). In some cases, the species epithets was not readily assignable in the field, or two closely related species were not readily separable. In these cases, the following assignments were used:

*Sorbus decora* may include *S. americana.*

*Prunus pensylvanica* may include *P. virginiana.*

*Amelanchier* spp.: no species assignments were attempted for this genus.

*Kypros* spp.: includes *H. lindbergii* and *H. pratense.*

*Viola* spp.: includes *V. incognita, V. renifolia,* and *V. septentrionalis.*

*Callitriche* spp.: mainly *C. palustris.*

*Sphagnum cuspidatum* may include *S. majus.*

*Mnium punctatum* includes *M. pseudopunctatum* and *M. spinulosum.*
Calliergon cordifolium includes C. giganteum.

Brachytrium salebrosum may include B. curtum and B. reflexum.

5.4 Analysis of the Wetland Sites

This section analyzes the 132 quadrats which occurred either in periodically flooded environments or on poorly to well decomposed organic substrates (Section 5.1). The raw data, for species occurring with a frequency of 10 or more, is presented in Appendix 3.

Wetland sites in the Ontario Clay belt have been described in the subjective classification of Jeglum et al. (1974), and some (predominantly treed) sites have been described by others (e.g. Carleton and Maycock 1978; Bergeron and Bouchard 1983). Nonetheless, relationships among the wetland vegetation types are poorly understood. Heinzelman (1963, 1970) concluded that on organic substrates in wetlands nutrient status is the primary determinant of vegetation structure and composition. Jeglum (1971) ordered boreal wetland species along a nutrient gradient, using field measurements of pH as a general indicator of nutrient status. The vast majority of species were found to show a definite peak along this gradient, though many showed a wide tolerance. In a more recent study by Stanek et al. (1977), the classification of Jeglum et al. (1974) was reexamined with respect to nutrient status of the organic substratum. In general, considerable differences in the nutrient status of the various wetland types were found. The recent review of Zoltai and Pollett (1983) classifies Canadian wetlands with emphasis on nutrient status and other environmental factors which characterize the groupings.

In this chapter, the wetland sites are first classified using a number of different clustering methods. These methods are then compared to determine the most parsimonious strategy for partitioning the data set. The chosen method is used in this and subsequent chapters in delineating groups and presenting the results of classification. Relationships and trends in
wetland habitats are presented next, using an ordination strategy. Following this, species are classified and ordinated to determine their interspecific relationships and trends in variation. Finally, the ecological relationships of the species and quadrat groups are analyzed, and overall trends are summarized.

5.4.1 Choice of Clustering Strategy

As Goodall (1978) has pointed out, the objectivity of numerical classification lies in the repeatability of the results of a given data set when applied to a given algorithm, and not in the choice of the algorithm; this is a more pragmatic decision. Since no straightforward, ubiquitous method is available for choosing an appropriate algorithm, and since the suitability of a given method is somewhat dependent upon the underlying data structure, the decision must be based on the direct comparison of the results obtained from real data.

The judgement of which method gives the most 'ecologically meaningful' results is necessarily a subjective one, though it must be remembered that the experience and additional knowledge of the investigator can be used in a 'quasi-objective' manner (Williams, 1971; also Goodall, 1970). The choice of methods tested here is based on the recommendations of workers in plant ecology. Gauch and Whittaker (1981) recommend two-way species indicator analysis, a polythetic divisive technique. The sum of squares agglomerative strategy was recommended by Goodall (1978) and Orłoci (1978) for quantitative data. Jardine and Sibson (1970) recommend, on the basis of mathematical criteria, the single linkage clustering strategy. Finally, a number of workers in the field of numerical taxonomy (e.g., Sneath and Sokal 1973) suggest the use of space-indifferent agglomerative strategies such as average linkage, and the space-dilating complete linkage method.

A total of five clustering strategies were employed:
1. **TWINSPAN**: Two-way indicator species analysis (Hill et al. 1975).

2. **SSA-E**: Sum of squares agglomeration with euclidean distance.

3. **SSA-C**: Sum of squares agglomeration with chord distance.

4. **SLA-C**: Single linkage agglomeration with chord distance.

5. **CLA-C**: Complete linkage agglomeration, with chord distance.

For the agglomerative techniques the same distance measure was used in each case to prevent confounding of clustering strategy and measure. A metric distance measure was used following the recommendations of Orlóci (1974; see also Anderberg 1973). Chord distance (euclidean distance after standardization by stand norm) was chosen following the recommendation of Noy-Meir et al. (1975). To compare the results of standardized and unstandardized data, sum of squares agglomeration was performed using both euclidean and chord distance.

The classifications produced by these five strategies each suggest the existence of nine relatively distinct, ecologically meaningful groups. Note however that the level of group recognition in clustering is necessarily arbitrary (Goodall 1978); in this case, the nine groups were recognized on the basis of somewhat subjectively defined ecological criteria. As will be seen later, the nine groups so defined are internally homogeneous and ecologically distinct.

Although the methods suggested the existence of nine major ecological groupings, there was some discrepancy in the group assignments. A total of 13 of the 132 quadrats were assigned differently by at least one of the methods. This nevertheless represents a high consistency of group recognition, suggesting that the data is well structured (Orlóci 1978, Green 1979). The fact that some of the individuals were assigned differently suggests that they are somewhat intermediate in their characteristics, with the various algorithms stressing different aspects of the data structure.
in determining assignments.

To compare the results of each clustering method, the 13 differently assigned quadrats were removed and group centroids calculated for each of the nine groups, based on group affinities of the remaining 119 quadrats. Following this, the euclidean generalized distance (Rao 1952; Orloci 1978) was calculated between the group centroids and each of the 13 'unassigned' individuals, and assignment to the group for which the generalized distance was minimal was made. The results are shown in Table 5.1. The method showing the greatest number of correct initial assignments can be inferred to be the strategy of greatest overall utility and flexibility. Table 5.1 indicates that the sum of squares agglomeration (using chord distance) results agree most closely with the generalized distance assignments. Complete linkage and indicator species analysis also performed fairly well. Single linkage produced the most disappointing results.

In this and subsequent chapters, only the numerical classifications based on sum of squares agglomeration using chord distance are presented and interpreted, although all the strategies mentioned above were in fact performed on all data sets. This will render the presentation more succinct, admittedly at the cost of potential imprecision and misclassification in some cases. However, the recommendation of Goodall (1979), and the results of Monte Carlo analyses (e.g. Kuiper and Fisher 1975), suggest that the choice of sum of squares is a good one, producing tight, homogeneous groups and few outliers. This is certainly useful when the objective is the utilitarian summarization of complex data structure. A further advantage is that the fusion sum of squares can aid in determining the degree of structure in the data, suggesting a cut-off level for the delineation of groups (Goodall 1973; Orloci 1978). The ratio of the between to the total sum of squares at a given level (the 'classification efficiency' of Orloci and Stanek 1979) is used here.
Table 5.1  Generalized distance assignments of the 13 differently assigned quadrats to the 9 groupings of the wetland habitats at Elk Lake, Ontario, and the number of incorrect assignments made for each of the five clustering methods tested.
<table>
<thead>
<tr>
<th>Individual</th>
<th>Assignment</th>
<th>TWINSPAN</th>
<th>SSA - E</th>
<th>SSA - C</th>
<th>SLA - C</th>
<th>CLA - C</th>
</tr>
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<tbody>
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<td>I</td>
<td>+</td>
<td>+</td>
<td>+</td>
<td>-</td>
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<td>+</td>
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<td>-</td>
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<td>+</td>
<td>-</td>
<td>-</td>
<td>+</td>
<td>+</td>
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<tr>
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<td>+</td>
<td>+</td>
<td>+</td>
<td>+</td>
<td>-</td>
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<td>+</td>
<td>+</td>
<td>-</td>
<td>-</td>
</tr>
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<td>+</td>
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<tr>
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</tr>
<tr>
<td>10</td>
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<td>-</td>
<td>+</td>
<td>-</td>
<td>-</td>
<td>+</td>
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<td>12</td>
<td>III</td>
<td>+</td>
<td>+</td>
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</tr>
<tr>
<td>13</td>
<td>II</td>
<td>-</td>
<td>-</td>
<td>+</td>
<td>-</td>
<td>+</td>
</tr>
</tbody>
</table>

Number incorrectly assigned: 5 6 2 10 5
5.4.2 Classification of Sites

The sum of squares agglomerative dendrogram is given in Figure 5.2. A subjective examination of dendrogram structure, coupled with a plot of fusion sum of squares versus number of groups, suggested the presence of nine ecologically distinguishable groups, giving a classification efficiency of 71.7%. For each group, the frequency, mean, and variance were calculated for the common species (those occurring with a frequency of 10 or more in the data set; see Table 5.2). The nine groups, which are labelled in Figure 5.2, are described below with respect to their species composition, general habitat factors, physiognomy, and ecology. In addition, their relationship to sites and habitats described by other workers is discussed. The neutral term 'vegetation type' (sensu Orlić and Stanek 1979) is used for these groups, which are named for their major constituent species.

I. *Picea mariana* - *Ledum groenlandicum* dry bog

The topography of these sites is very gently rolling and somewhat hummooky. Major constituent species include *Picea mariana* in the overstory, and the shrub *Ledum groenlandicum* in the understory. Both species occur as constants. The mosses *Sphagnum recurvum*, *S. magellanicum*, *S. fuscum*, *S. nemoreum*, and *Pleurozium schreberi* are common understory components. Other vascular shrubs occurring with high frequency in this type include *Kalmia angustifolia*, *Caultheria hispidula*, *Vaccinium myrtillusoides*, *Carex trisperma*, and *Coptis groenlandicum*. *Picea mariana* forms pure stands in these sites, readily layering and reaching a cover of just under 50%. *Larix laricina* saplings occur very sporadically. The relative openness of the canopy undoubtedly favours the establishment of understory shrubs.

Three subgroups within this type can be recognized (see Figure 5.2). The first, consisting of 6 quadrats, is characterized by higher black spruce cover, low cover of *L. groenlandicum*, and high cover of *S. magellanicum*. The second is a larger block of 13 quadrats with high cover of *L. groenlandicum*. The third subgroup contains 8 quadrats, and has the lowest
Figure 5.2  Sum of squares agglomeration dendrogram of the 132 quadrats from wetland habitats at Elk Lake, Ontario. The nine vegetation types (I - IX). The quantities along the bottom of the dendrogram represent the number of individuals belonging to the respective branches; lower bifurcations are not shown.
Table 5.2 Means (M), variances (V), and relative frequencies (F) of the 114 most common species in each of the nine vegetation types (I - IX) described for the wetland habitats at Elk Lake, Ontario.
<table>
<thead>
<tr>
<th></th>
<th>ALL (132)</th>
<th>I (27)</th>
<th>II (11)</th>
<th>III (15)</th>
<th>IV (17)</th>
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</thead>
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Table 52: Continued.
black spruce cover. *Alnus rugosa* also occurs occasionally here, indicating more mesotrophic conditions.

This vegetation type occurs over a thick mat of poorly decomposed organic peat. This, and the presence of ericaceous shrubs and *Sphagnum*, suggest the oligotrophic nature of this habitat. This type is somewhat similar to the ‘shrub-rich treed bog’ of Jeglum *et al.* (1974), who suggest that such sites are still influenced to a small degree by mineral soil waters. This was apparent at Elk Lake, as these sites invariably occurred in lowlands in which aerial photographs indicated slow drainage patterns. This is the driest of the black spruce bog types described (types I–III), with the water table greater than 0.5 meters below the surface at most of the sites. The presence of *Kalmia angustifolia*, *Ledum groenlandicum*, and *Pleurozium schreberi*, and the relatively high cover of black spruce, indicate the relative driness of this type. See photo, Appendix 10.

II. *Picea mariana - Chamaedaphne calyculata - Sphagnum bog*

This is a small group of 11 quadrats in which black spruce occurs alone in the tree stratum, though with low cover (just under 20% on average). The substratum, like the previous type, is deep poorly decomposed organic peat. Constants in this vegetation type include *Ledum groenlandicum* and *Chamaedaphne calyculata*, the sedges *Carex oligosperma* and *Eriophorum spissum*, and the mosses *Sphagnum fuscum*, *S. magellanicum*, and *S. nemoreum*. The microtopography is characterized by small high hummocks and hollows. *S. fuscum* occurs at the tops of the hummocks and the other two Sphagnidae, along with *S. recurvum*, in the depressions. Other species of importance include *Vaccinium oxyccoccus*, *Carex pauciflora*, *Ptychidium juniperinum*, *Mylia anomota*, and *Eriophorum angustifolium*. Most trees show extensive layering and tend to be concentrated on higher mounds. The water table is much higher than in the previously-described type, and in late summer may be just below the surface of low hollows.
This type is very similar to the 'graminoid-rich treed bog' of Jeglum *et al.* (1974); a similar type is also described by Gaudreau (1979). The former authors described these sites as very weakly minerotrophic, and described two variants. The type described here is similar to their second variant, which is characterized by the presence of *Eriophorum* species and *Carex pauciflora*, indicating a poor nutrient status. See photo, Appendix 10.

III. *Chamaedaphne calyculata* - *Sphagnum* open bog

This is an homogeneous group of 15 quadrats occurring on deep, poorly decomposed peat deposits. The terrain is very hummocky, and water is often present in the hollows, particularly after a rainfall and following snowmelt. Low stunted black spruce occurs with low cover (just over 10%), the trees restricted to higher, drier regions. These small trees show extensive layering and often very high cone production, which may indicate an unfavourable habitat (see also Larsen 1980). *Chamaedaphne calyculata* is the community dominant, while other ericaceous shrubs such as *Ledum groenlandicum*, *Kalmia polifolia*, and *Andromeda glaucophylla* occur with high frequency. *Sphagnum fuscum* is characteristic of the hummocks, while *S. magellanicum* and *S. recurvum* occur at lower levels. In wet hollows the hydric species *S. cuspidatum* occurs. *Sarracenia purpurea* is also common, typically growing with *S. fuscum* on the hummocks.

The low cover of black spruce, together with the dominance of ericaceous species, indicates the hydric, very oligotrophic conditions predominating here. *Chamaedaphne calyculata* and *Kalmia polifolia*, in particular, are indicative of these conditions (Jeglum 1971; Segadas-Vianna 1955). This type has some affinity with the 'low shrub bog' of Jeglum *et al.* (1974). They state that *L. groenlandicum* occurs in somewhat drier areas, while *A. glaucophylla* is a good indicator of weakly minerotrophic sites where the water table is at or very near the surface. Similar types are also described by Hustich (1957) and Dansereau (1959).
IV. *Alnus rugosa - Viola pallens* thicket

This is an homogeneous group of 17 quadrats occurring on intermittent streambeds subject to periodic flooding. Pools and channels may be present. The soil is typically black, well decomposed organic muck, up to 1 m or more in depth, often alternating with layers of silt. Tall, robust specimens of *Larix laricina* occur here, but the dominant species is *Alnus rugosa*, which forms dense impenetrable thickets. This species may attain a height of 4 m or more at these sites. *Salix discolor*, which may attain a height of 12 m, also occurs in some stands. The understory is generally very rich, consisting of herbaceous species which are otherwise uncommon in the boreal forest. In addition to the rich herb layer clumps of moss and occasional *Sphagnum* mounds are typical. Species of high frequency include *Sphagnum girgensohnii*, *Viola pallens*, *Caltha palustris*, *Rubus pubescens*, *Eupatorium maculatum*, *Galium asprellum*, *Thalictrum polygamum*, *Athyrium felix-femina*, *Carex intumescens*, and *Brachythecium salebrosum*. See photo, Appendix 10.

This type shows some similarity to the 'thicket swamp' of Jeglum et al. (1974), which they describe as a mesotrophic-eutrophic, mesic to hydric habitat. They suggest that this type is maintained by periodic flooding, and hypothesize a successional sequence to a hardwood or coniferous swamp (dominated by *Fraxinus nigra* and *Thuja occidentalis* respectively). This is difficult to substantiate, however, and in this study there was little evidence to suggest such a sequence.

Interestingly, this vegetation type is often associated with beaver dams, usually occurring below the dam in the gully draining the area. One could hypothesize that this type is maintained by the action of beavers, but this would require further and more detailed examination.

V. *Larix laricina - Alnus rugosa* swamp

The 13 quadrats characterizing this type are dominated by *Larix laricina* in the overstory and *Alnus rugosa* in the shrub layer. *Picea mariana*
is also present, usually as saplings or small, actively layering trees. The dominant shrub is *Ledum groenlandicum*, while the ground vegetation is dominated by *Sphagnum magellanicum*, *S. russowii*, and *S. girghensohnii*. *Smilacina trifolia*, *Carex trisperma*, *C. canescens*, *Lycopodium annotinum*, *Equisetum fluviatile*, and *Viola pallens* occur with high frequency in the understory.

These sites are characterized by an uneven surface of low hummocks interrupted by shallow pools and water channels, indicating groundwater and some surface water movement. Peat accumulation is extensive, and it is often reasonably well decomposed. In some areas a black, well decomposed black organic, muck may occur. All these factors indicate more mesotrophic conditions than exist in black spruce dominated bogs (types I–III). Fallen logs, covered with *Sphagnum* and feathermosses, are also common at these sites, suggesting a possible disturbance origin. This type typically occurs along the edge of open black spruce bogs, or in areas draining into boggy land. This has also been noted by Heinselman (1969).

This type shows similarity to both the 'tamarack-speckled alder' and 'black spruce-speckled alder' groupings of Jeglum *et al.* (1974). They characterize these sites as generally mesotrophic, bordering other swamp or upland sites and typically forming along slow drainageways. Raup (1946) has cited evidence suggesting that stands of *L. laricina* will, if left undisturbed, be eventually succeeded by *Picea mariana*. Although the presence of black spruce saplings suggests this possibility, it should be noted that active regeneration of larch was also occurring at most of the sites (generally in more open, unshaded areas). Recurrent fires may also perpetuate this type.

VI. *Fraxinus nigra* hardwood swamp

These 16 stands occurred mostly below Indian Chute on the low, annually flooded silty banks of the meandering Montreal River. These floodplains are generally no more than 1–1.5 m above summer river water levels. The tree
stratum is dominated by *Fraxinus nigra*, and occasionally *Ulmus americana* (generally saplings), *Populus tremuloides*, and *P. balsamifera*. A rich shrub layer consisting primarily of *Abies balsamea-*saplings, *Cornus stolonifera*, *Frunus pensylvanaica*, and *Viburnum edule* is characteristic. The understory is also rich in species, and includes *Thalictrum polygamum*, *Eupatorium maculatum*, *Fragaria vesca*, *Pyrola asarifolia*, *Rubus pubescens*, *Smilacina racemosa*, *Cimna latifolia*, *Elymus virginiana*, *Equisetum sylvaticum*, and a number of other species. See photo, Appendix 10.

The species composition of this type indicates an eutrophic habitat (Baldwin 1958). Very fine silty deposits are typical, and drainage channels running parallel to the river are common, creating an undulating topography. The organic layer is thin, probably the result of annual flooding.

Hardwood swamps have been well documented in the literature (Baldwin 1958; Jeglum *et al.* 1974; Bergeron and Bouchard 1983) as seasonally flooded, eutrophic, mesic sites. They are amongst the richest habitat types in the boreal forest, and contain a number of species unique to such areas. Despite the presence of *A. balsamea* seedlings, this type is probably an edaphic climax. Many of the hardwood swamp sites at Elk Lake showed some evidence of disturbance, probably natural in origin. Dead *U. americana* trunks were also observed, probably the victims of Dutch elm disease. However, a number of small trees of this species were seen, suggesting that it may become a more important component in future generations.

**VII. Thuja occidentalis - Sphagnum swamp**

The 14 sites defining this vegetation type are typified by monospecific stands of *Thuja occidentalis* occurring on well decomposed organic muck. Such sites, which show considerable seepage of mineral soil deposits, occur along lake shores (where the lake drains into bogs or swampy land), along riverbanks, or more typically in low-lying seepage areas. These stands are normally not extensive, though at one site at least 300 trees occurred. The
organic muck is mostly covered with *Sphagnum*, except where drainage channels or pools occur. Species typical of the rich understory include the shrub *Alnus rugosa*, *Viola pallens*, *Carex disperma*, *C. leptalea*, *C. trisperma*, *Glyceria striata*, *Cinna latifolia*, *Onoclea sensibilis*, *Nemetha arvensis*, *Lycopus uniflorus*, *Rhamnus alnifolia*, *Rhytidiadelphus triquetrus*, *Climacium dendroides*, and *Ptilidium ciliare*. The presence of a well-decomposed muck, and the species characteristic of this type, indicate the mesic-hydric, eutrophic nature of these sites. Surface topography is typically irregular, with drainage pits and channels alternating with *Sphagnum* mounds (chiefly *S. girgensohnii*, *S. magellanicum*, and *S. wulfianum*) and moss-covered fallen trunks. *Hninum punctatum* and *Drepanocladus uncinatus* are characteristic of the wet depressions. Ring counts of recently-felled trees at one site indicated ages in excess of 250 years, indicating the fire resistance of these sites. See photo, Appendix 10.

Similar vegetation types have been described by Hustich (1957) and Jeglum *et al.* (1974). The latter authors state that *Thuja* stands are characteristic of drainage areas where an abundance of nutrients and oxygen are available. They also suggest a probable succession to a rich black spruce swamp as peat accumulates and nutrients are depleted.

VIII. *Betula pumila* – *Chamaedaphne calyculata* fens

This is a small group characterized by 5 quadrats occurring along very slow moving water courses through or draining acidic boggy land. The terrain is generally somewhat hummocky. The shrubs *Betula pumila* and *Chamaedaphne calyculata* are the type dominants. Other species of importance include *Potentilla palustris*, *Calamagrostis canadensis*, *Campanula uliginosa*, *Hyrica gale*, *Spiraea alba*, *Salix serissima*, *Carex stricta*, and *Tomenthyponium nitens*. The substratum is poorly to moderately decomposed peat, and the water table is at or near the surface.
Jeglum et al. (1974) describe a 'low shrub fen' which has some affinities with the type described here. They characterize such fens as occurring on at least 30 cm of moderately to poorly decomposed peat, with a mesotrophic to oligotrophic nutrient status. Ritchie (1960) describes similar shrub fens on organic substrates, and Dansereau (1959) describes fens dominated by Myrica gale and Spiraea alba. The presence of Salix in some of the quadrats suggests the paludified bog of Jeglum et al. (1974).

IX. Carex - Calamagrostis canadensis marsh

The 14 quadrats making up this type occur along slow, meandering creeks in low-lying, frequently flooded areas. Such sites are generally silted, and well decomposed organic mucks are typical. Low slightly hummocky terrain is characteristic. Typical species include Carex aquatilis, C. rostrata, Calamagrostis canadensis, Glyceria striata, Potentilla palustris, and Lysimachia terrestris. Physiognomically this type resembles a grass-sedge meadow. Two subgroups can also be recognized (see Figure 5.2). The first is dominated by Carex aquatilis, the second by C. rostrata. See photo, Appendix 10.

This type shows affinities to both the 'meadow marsh' and 'graminoid fen' types of Jeglum et al. (1974), which they describe as being physiognomically similar. These are characterized by a closed tussocky graminoid cover, with little if any open water. Frequent flooding and silting are characteristic, making such sites eutrophic to mesotrophic. Similar sites are described by Baldwin (1958). The high, fluctuating water table probably precludes the establishment of trees on these sites.

5.4.3 Site Relationships and Environmental Characterization

Compositional divergence (using an information criterion) of the nine types was assessed using the relative frequencies of their constituent species (see Orlóci and Stanek 1979 for formulae). The pairwise comparisons (Table 5.3) summarize in matrix form the interrelationships between types.
Table 5.3. Pairwise compositional divergences (using the 2I statistic) for the 9 wetland types. Values of chi-square ($\chi^2$), degrees of freedom (DF), and the standard normal deviate (Z) are given.
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The relative similarities of types I – III (and particularly types II and III), which is suggested by the dendrogram, is reconfirmed here. Type VIII shows some affinity for type III, as does type V for type I. Types VIII and IX also show relatively low divergence. Types IV, V, and VII show some affinity, while type VI forms a relatively isolated group showing high divergence in all pairwise comparisons. Note that these values serve a strictly utilitarian purpose, and should not be interpreted in a statistical sense (see Orióci 1978).

A physiognomic-environmental characterization of the nine types is presented in Table 5.4. Dominant species are defined as those contributing the greatest biomass and/or cover at the sites, while the physiognomic descriptions generally follow Jeglum et al. (1974). Terrain type, nature of the substratum, depth to water table, degree of groundwater movement, flooding periodicity, and site productivity were measured at each plot. Measurements of pH (expressed here using a 5-point scale, see also Jeglum et al. 1974) were obtained only at selected sites. Estimates of nutrient status were obtained subsequent to the delineation of types. This involved using the classification of Jeglum (1971), which ordered boreal wetland species into five nutrient status categories, in conjunction with observed species frequencies within the nine types. His five nutrient groups were coded as 1 = very oligotrophic; 2 = oligotrophic; 3 = mesotrophic; 4 = eutrophic; 5 = very eutrophic, and the formula:

\[ NS = \sum p_i q_i \]

where \( p_i = f_i/f_{..} \) (the proportional frequency of species \( i \)), and \( q_i \) = coded nutrient status group for species \( i \), was used to obtain a composite index of overall nutrient status. Note that the NS value obtained (a decimal quantity) has been reexpressed using the original code. Species not included in the original paper of Jeglum were coded based on data from other source references (Jeglum et al. 1974, Gaudreau 1979, Bergeron and Bouchard 1983). A similar strategy has been advocated recently by Persson (1981).
Table 5.4. Physiognomic – environmental characterization of the nine wetland types.
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<td>irregular, with small high hummocks</td>
<td>irregularly flat, with hummocks</td>
<td>levels, occasionally; hummocky</td>
</tr>
<tr>
<td><strong>Depth to Water Table (meters, late summer)</strong></td>
<td>0.5 - 2</td>
<td>0 - 0.5</td>
<td>0 - 0.25</td>
<td>0.5 - 2</td>
</tr>
<tr>
<td><strong>Groundwater Movement</strong></td>
<td>poor</td>
<td>very poor</td>
<td>very poor</td>
<td>moderate to good</td>
</tr>
<tr>
<td><strong>Flooding Periodicity</strong></td>
<td>-</td>
<td></td>
<td></td>
<td>spring, occasionally</td>
</tr>
<tr>
<td><strong>Nutrient Status</strong></td>
<td>oligotrophic - oligotrophic/mesotrophic</td>
<td>very oligotrophic - oligotrophic</td>
<td>very oligotrophic - oligotrophic</td>
<td>eutrophic</td>
</tr>
<tr>
<td><strong>pH</strong></td>
<td>acidic</td>
<td>highly acidic - acidic</td>
<td>highly acidic - acidic</td>
<td>slightly acidic</td>
</tr>
<tr>
<td><strong>Productivity</strong></td>
<td>Black spruce DBH 15 - 25 cm; height 9 - 12 m</td>
<td>Black spruce DBH 10 - 20 cm; height 3 - 10 m</td>
<td>Black spruce DBH 10 - 15 cm; height 4 - 6 m</td>
<td>Specified elder height 2' - 3'</td>
</tr>
</tbody>
</table>
Table 5.4. Continued.
<table>
<thead>
<tr>
<th>VI</th>
<th>VII</th>
<th>VIII</th>
<th>IX</th>
</tr>
</thead>
<tbody>
<tr>
<td>Dominant Species</td>
<td>F. nigra</td>
<td>T. occidentalis</td>
<td>B. pumila</td>
</tr>
<tr>
<td>Physiognomy</td>
<td>hardwood swamp</td>
<td>conifer swamp</td>
<td>low shrub fen</td>
</tr>
<tr>
<td>Nature of Substrate</td>
<td>silt and clay</td>
<td>well decomposed organic peat</td>
<td>poorly to moderately decomposed peat</td>
</tr>
<tr>
<td>Terrain Type</td>
<td>level floodplain, occasional ditches</td>
<td>irregular, hummocky with water courses, pools</td>
<td>level, or slightly hummocky</td>
</tr>
<tr>
<td>Depth to Water Table (meters, late summer)</td>
<td>1 – 1.5</td>
<td>0 – 0.25</td>
<td>0 – 0.5</td>
</tr>
<tr>
<td>Groundwater Movement</td>
<td>good – very good</td>
<td>very good</td>
<td>good</td>
</tr>
<tr>
<td>Flooding Periodicity</td>
<td>spring</td>
<td>continuous percolation</td>
<td>spring</td>
</tr>
<tr>
<td>Nutrient Status</td>
<td>eutrophic – very eutrophic</td>
<td>mesotrophic – eutrophic</td>
<td>oligotrophic – mesotrophic</td>
</tr>
<tr>
<td>pH</td>
<td>neutral – slightly basic</td>
<td>slightly acidic</td>
<td>acidic – slightly acidic</td>
</tr>
<tr>
<td>Productivity</td>
<td>Black Ash DBH 20 – 30 cm, height 10 – 15 m.</td>
<td>Eastern White Cedar DBH 25 – 50 cm, height 9 – 12 m.</td>
<td>low shrubs height 1 – 2 m.</td>
</tr>
</tbody>
</table>
The results indicate that each type is characterized by a unique combination of environmental factors which can be expected to influence overall species composition, physiognomy, and site productivity. Relationships between the types and the nature of underlying environmental influences are explored further in the next few sections.

5.4.4 Ordination of Sites

Three ordination techniques were applied to the wetlands data: principal components analysis (PCA), correspondence analysis (CA) with rare species downweighting, and nonmetric multidimensional scaling (NMDS) using chord distance and specifying a two-dimensional solution. The results of CA (not shown) were disappointing, separating out one group while obscuring any trends in the others. While this may be useful in delineating groups (Hill et al. 1975, Peet 1980), such a strategy is clearly disadvantageous if the objective is data summarization and the examination of underlying trends. The PCA results (not shown) suggested that 3 dimensions were necessary to summarize the data structure with respect to the group affinities defined by the cluster analysis. This is not surprising given the high diversity of the data set analyzed.

The result of NMDS proved to be the most readily interpretable in two dimensions (Figure 5.3). Although the stress value is high (17.3%), the results suggest that the representation is a parsimonious one. Convergence to this same general solution was obtained using different random starting configurations, suggesting that the solution is a global and not a local minimum. By Kruskal's (1964) criteria, this stress value indicates a 'poor' fit. However, as Shepard (1974) has pointed out, the actual value of the stress quantity is of much lesser importance than the interpretability of the results. He suggests obtaining two-dimensional solutions whenever possible, as they are more readily presentable and interpretable than higher dimensional ones. If the results are readily interpretable, the solution is deemed a parsimonious one. This line of reasoning is of particular use to
Figure 5.3 Nonmetric multidimensional scaling ordination (two-dimensional solution, utilizing chord distance) of the 132 quadrats of the wetland habitats at Elk Lake, Ontario. The symbols correspond to the vegetation types. The stress value is 17.3%.
the vegetation ecologist when the objective is to obtain a simple, parsimonious summarization of a complex data set.

Examination of the two-dimensional NMDS solution reveals some interesting trends, and indicates the strength of the groupings produced by the cluster analysis. The *Fraxinus nigra* swamps form a very distinctive group in the upper right of the scattergram. The *Betula pumila* fens and *Carex-Galamagrostis* marsh also form distinctive groups, occurring at the bottom right of the ordination. The *Thuja occidentalis* swamp sites form a rather distinct group in the upper left, but show some affinity to both the *Larix laricina* swamps and the *Alnus rugosa* thickets. These latter two groupings are also rather distinctive, though they show some tendency to intergrade. The three site groupings dominated by *Picea mariana* (types I–III) show more or less continuous intergradation, suggesting that the groupings produced by the cluster analysis, while useful and meaningful, may be somewhat artificial. Interestingly, there is some evidence of intergradation of the *Larix laricina* swamp and the *Picea mariana* – *Ledum groenlandicum* dry bog.

Some interesting environmental trends are indicated from perusal of the scattergram (refer back to Table 5.4). A gradient from acidic, oligotrophic sites to basic, eutrophic conditions occurs from lower left to upper right, indicating the importance of nutrient status in determining species composition in these boreal wetland habitats. A 'drainage' gradient is also seen, with poorly drained sites at the left, and periodically flooded sites at the right.

In conclusion, oligotrophic acidic sites of low groundwater flow on poorly decomposed organic substrates, which are dominated by black spruce, occur at the left of the scattergram. Three variants have been recognized on the basis of depth to water table, and these are reflected in the scattergram. To the right of the black spruce sites stands dominated by larch occur. These are also acidic sites on organic substratum, but generally
have some groundwater flow indicative of somewhat higher nutrient conditions. Above the larch stands occurs the *Thuja occidentalis - Sphagnum* swamp type, which has still greater groundwater flow and also surface seepage, suggesting relatively nutrient rich conditions. The affinity of this group to the larch stands is probably attributable to a similar substratum, although cedar normally occurs on more highly decomposed organic soil. To the right of the larch stands, the *Alnus rugosa - Viola pallens* thickets occur. These are found on well-decomposed organic muck subject to periodic flooding, and represent a more mesotrophic-eutrophic trend. At the far right, the highly eutrophic *Fraxinus nigra* swamps occur, which are characteristic of seasonally flooded silty plains. The *Betula pumila - Chamaedaphne calyculata* fens occur to the right of the *C. calyculata - Sphagnum* open bog. These sites occur on more decomposed acidic organic peats, showing higher nutrient status than the open bogs. The *Carex - Calamagrostis* marsh sites form a distinctive group at the lower left of the scattergram, showing little affinity with the other groups except the birch fens. These graminoid marshes are characterized by periodic flooding and silting in areas of relatively high nutrient status. Note also that the relationships between the types in the ordination scattergram agree well with the compositional divergence values presented in Table 5.3.

Performance values for selected common species were plotted on the ordination scattergram, and are shown in Appendix 4. The trends in species composition and performance generally show distinct preferences along the nutrient status gradient (see also Jeglum 1971), reenforcing the description of trends outlined above.

5.4.5 Species Classification.

The cluster analysis of species (sum of squares agglomeration, chord distance) from the wetland sites is shown in Figure 5.4. Before performing the analysis, species occurring with a frequency less than 10 were removed, since it was felt that rare species contained insufficient information as
Figure 5.4 Sum of squares agglomeration dendrogram of 114 species from the wetland habitats at Elk Lake, Ontario. The seven ecological species groups A–G are also indicated.
to their interspecific affinities. Species 'ecological groups' (c.f. Bergeron
and Bouchard 1983) were defined with the aid of a sum of squares versus
number of groups plot. Again, these groups have primarily a utilitarian
purpose, and the choice of the number of groups was made primarily on
the basis of ecological considerations. The sum of squares plot indicates
the existence of seven distinct groups, giving a classification efficiency
of 36.1%. The descriptions of nutrient status and moisture level, which follow
 Jeglum (1971; also Jeglum et al. 1974), are based on field observations.

A. This group of species is generally associated with drier black
spruce stands on poorly decomposed organic peats. Although there
may be some mineral soil water, these are species characteristic
of acidic, oligotrophic, very moist habitats.

B. These are somewhat minerotrophic species which show high
association with *Larix laricina*. They prefer somewhat acidic,
mesotrophic, wet sites.

C. These species are characteristic of low, acidic bogs with low tree
cover. Such habitats are oligotrophic or even ombrotrophic, and
very wet.

D. These species occur on black, well-decomposed organic muck in
riparian areas subject to periodic flooding (intermittent water
courses), usually in association with a tall shrub *Alnus rugosa*
overstory. These sites are slightly acidic to neutral, eutrophic, and
very moist.

E. These species occur together on annually flooded low alluvial silty
ground, typically associated with *Fraxinus nigra*. These sites are
neutral to weakly basic, very eutrophic, and moist.

F. These species occur on moderately decomposed organic soils, or well
decomposed mucks, in wet areas subject to regular periodic flooding.
Surface water is generally always present except in high summer.
These habitats are weakly acidic, mesotrophic, and very wet.

G. These species occur in seepage areas and along riverbanks on well decomposed organic muck; typically in association with *Thuja occidentalis*. These sites are very moist to wet (often with surface water), and are mesotrophic to eutrophic.

The description of these ecological species groupings suggest the existence of definite patterns of interspecific association in response to nutrient status and depth to water table.

5.4.6 Species Ordination

The two-dimensional nonmetric multidimensional scaling (using chord distance) is shown in Figure 5.5. Again, those species occurring with a frequency of less than 10 were first removed, as they contained insufficient information. The 22.1% stress value is high, but repeating the analysis using different random starting configurations produced very similar solutions, indicating a stable structure. This structure reveals the overall trends in interspecific associations between species as related to trended variation in environmental influence.

Clear trends attributable to changing nutrient status, acidity, nature of the substrate, and depth to water table are again indicated. Species tolerant of low nutrient levels and occurring on wet, poorly decomposed organic substrates are located at the top right of the scattergram. Species occurring on the same substratum but under somewhat drier conditions occur lower down. At the bottom right, species occurring in marshy, flooded habitats of high nutrient content occur. To the left of these occur species associated with *Thuja occidentalis* on well decomposed organic muck in seepage areas. The bottom left of the scattergram contains species associated with *Fraxinus nigra* on lowland spring flooded silty alluvial plains. In the left centre are species found growing in periodically flooded sites with a well decomposed organic muck substrate. Species occurring in
Figure 5.5  Nonmetric multidimensional scaling (two-dimensional solution, utilizing chord distance) of the common 114 species of wetland habitats at Elk Lake, Ontario. Codes correspond to the species names (the first four letters of the genus, and the first three of the species epithet). Exceptions: CARE PAP = Carex paucervulca, CARE LEN = C. leptanervia. The stress value is 18.7%.
fen habitats (wet, mesotrophic to oligotrophic sites) occur at the top centre of the ordination.

The general trend of increasing nutrient status from top right to bottom left was quantified by correlating species axis scores with their corresponding nutrient status categories (Jeglum 1971; see also Section 5.4.3). Such a strategy has been advocated by Persson (1981). The coefficients ($r_1 = -0.655$, $r_2 = -0.564$, $R^2 = 0.503$) suggest that nutrient status (a composite index related to acidity, decomposition of organic material, substratum, and degree of ground water flow) is of considerable importance in determining species composition of boreal wetlands. In the lower part of the ordination there is a trend from wet, periodically flooded and seepage habitats to seasonally flooded habitats, from right to left.

5.4.7 Ecological Relationships

Feoli and Orlóci (1979; also Bergeron and Bouchard 1983) have stressed the need for examining the relationships between vegetation types and species groups in obtaining a further understanding of the ecological relationships of the vegetation. In the present context, this would involve determining relationships between the nine vegetation types and the seven species groupings. This allows further insight to be made regarding the structuring of the data, and also permits examination of relationships within the vegetation types, within the species groupings, and between these classifications.

A number of multivariate strategies are available for examining intergroup relationships (reviewed by Orlóci 1978; also Legendre and Legendre 1983). The recently developed method of stratification analysis (Feoli and Orlóci 1979) is used here. This method begins with an ordered (by quadrat and species groupings) table. Within each block, the number of occurrences of the species of a given group within each vegetation type is recorded. This results in a $\varphi$ by $\ell$ contingency table, where $\varphi$ the number of species
groups, and 2 the number of vegetation types. This table is then examined as in correspondence analysis, after adjustment to equal block sizes. The result is a simultaneous ordination of vegetation types and species groupings.

The results of the analysis are shown in Figure 5.6. Statistical tests of significance of the chi-square quantities may be tempting, but the pertinence of this has been questioned (Kendall and Stuart 1973; Hill 1974). Since the purpose of the analysis in this context is strictly utilitarian, no such analyses were undertaken. The results show that 85.5% of the partitioned chi-square is accounted for by the first three ordination axes, while the relative sharpness of group structure (Orlóci and Staněk 1979) is 21.3%. The three dimensional ordination plots of the vegetation types and the species groups, which are shown in Figure 5.6, have a one-to-one correspondence, indicating trends in the relationships between site types and species groupings.

The trends represented by the ordination of vegetation types were examined by correlating the first 3 sets of axis scores with selected environmental factors, the results of which are shown in Table 5.5 (unfortunately, nature of substratum, terrain type, and flooding periodicity were not quantifiable). The results suggest that the first axis reflects a strong nutrient gradient, with type VI (eutrophic) and types II and III (oligotrophic) representing the endpoints. The other factors (pH, depth to water table, and groundwater movement) are also relatively highly correlated with this first axis. Depth to water table and groundwater movement are most highly correlated on the second axis, which separates the marsh and fen types (VIII and IX) from those sites dominated by trees and shrubs. It therefore indicates an overall physiognomic trend. Correlations on the third axis are relatively low. This axis serves primarily to distinguish Fraxinus nigra dominated stands (type VI) from those dominated by Alnus rugosa (type IV) and Thuja occidentalis (type VII). The multiple correlation values (Table 5.5) reenforce earlier suggestions that
Three-dimensional concentration analysis ordinations of the nine vegetation types (I - IX) and seven species ecological groups (A - G) of the wetland habitats at Elk Lake, Ontario. These ordinations have a one-to-one correspondence. The partitioning of chi-square (d.f. = 48) is also given.
<table>
<thead>
<tr>
<th>Canonical variate (i)</th>
<th>Canonical correlation ($R_i$)</th>
<th>Chi-Square</th>
<th>Percentage</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td>0.7327</td>
<td>1432.40</td>
<td>40.78</td>
</tr>
<tr>
<td>2</td>
<td>0.6592</td>
<td>1159.51</td>
<td>33.01</td>
</tr>
<tr>
<td>3</td>
<td>0.3923</td>
<td>410.53</td>
<td>11.69</td>
</tr>
<tr>
<td>4</td>
<td>0.3057</td>
<td>249.41</td>
<td>7.10</td>
</tr>
<tr>
<td>5</td>
<td>0.2409</td>
<td>154.87</td>
<td>4.41</td>
</tr>
<tr>
<td>6</td>
<td>0.1992</td>
<td>105.91</td>
<td>3.01</td>
</tr>
</tbody>
</table>

Total $\chi^2 = 3412.62$ 100.00
Table 5.5. Correlations of the concentration analysis scores for the 9 wetland types with selected environmental parameters.
<table>
<thead>
<tr>
<th></th>
<th>$r_1$</th>
<th>$r_2$</th>
<th>$r_3 \beta$</th>
<th>$R^2$</th>
</tr>
</thead>
<tbody>
<tr>
<td>Nutrient Status</td>
<td>-0.992</td>
<td>0.075</td>
<td>-0.052</td>
<td>0.961</td>
</tr>
<tr>
<td>pH</td>
<td>-0.724</td>
<td>0.297</td>
<td>0.307</td>
<td>0.773</td>
</tr>
<tr>
<td>Depth to Water</td>
<td>-0.606</td>
<td>-0.450</td>
<td>0.348</td>
<td>0.628</td>
</tr>
<tr>
<td>Groundwater Movement</td>
<td>-0.693</td>
<td>0.468</td>
<td>0.053</td>
<td>0.740</td>
</tr>
</tbody>
</table>
nutrient status is the principle environmental factor influencing species composition in boreal wetlands.

Similar trends are also shown in the species group ordination. The first axis reflects species changes in nutrient tolerance, with species groups at the right characteristic of more oligotrophic sites. The second axis separates out species group F, which is characteristic of flooded sites on well decomposed organic substrates. The third axis serves to refine some of these relationships.

Interesting trends in the relationships of vegetation types and species groupings are also apparent. Types II and III show strong affinity to species group C, characteristic of highly oligotrophic, wet sites, and to a lesser extent group A, characterized by species of oligotrophic but somewhat drier sites. Type I is highly associated with this species group. Type V (larch stands) shows high affinity with species group B, characteristic of poorly to moderately decomposed organic peats and more mesotrophic conditions than groups A and C. Close one-to-one correspondence occurs between the following vegetation types and species groupings: VII (cedar swamp) and G (mesotrophic to eutrophic, very moist seepage area species), IV (Alnus rugosa thicket) and D (species on well decomposed organic muck, eutrophic riparian sites), and VI (Fraxinus nigra swamps) with E (species on low alluvial plains of high nutrient status). The fen and marsh habitats (types VIII and IX) show strong association with species group F (species adapted to wet areas and recurrent flooding), although type VIII (Chamaedaphne fens) also show some affinity with species group C on the third axis.

There appears to be strong affinities between the species grouping and the vegetation types, suggesting strong group structure in these wetland habitats. This is likely attributable to unique combinations of environmental factors (soil type, nutrient status, depth to water table, groundwater flow rate, and so forth) at a given site and the development of strong species affinities for these combinations of site conditions (c.f.
5.4.8 Discussion

The examination of ecological relationships between the nine vegetation types and the seven species groupings has proved highly revealing. The close one-to-one correspondence of many of the type-group relationships suggests a strongly structured data set, which in turn implies a discontinuous environment in which specialized environmental sites harbour a characteristic assemblage of species. Those types showing some degree of overlap in species group affinities, particularly the black spruce types (I–III), were fused at fairly low levels in the sum of squares dendrogram (Figure 5.2), suggesting some ambiguity in their definition. Nevertheless, the ability of NMDS to recover the structure revealed by the classification indicates the utility of the delineated groups.

On the basis of the results presented here, as well as previous work, a strong correlation between vegetation composition and nutrient status is indicated. The fertility of a given site is dictated by a number of factors, including acidity, type of substrate (organic or inorganic), degree of decomposition of organic substrata, degree of flooding, and groundwater flow. Thus nutrient status represents a complex environmental gradient sensu Whittaker (1956, 1967). However, the results presented here must remain tentative until detailed analyses of these sites are undertaken to actually determine nutrient levels. In this respect the strategy employed here is an hypothesis-generating one. Unfortunately, collecting accurate quantitative data on the nutrient status of boreal wetlands is difficult (Heinselman 1963, 1970; Jeglum 1971; Jeglum et al. 1974; Stanek et al. 1977). Nonetheless, progress in understanding the complexity of boreal wetland habitats can only be accomplished through the detailed study of underlying environmental factors. This will aid not only in understanding the variation in vegetational composition, but may also be useful in elucidating the nature of interspecific associations between species. A fuller understanding of the evolution of
vegetation types and possible successional sequences would then be forthcoming, which may in turn suggest more sound management practices.

5.5 Analysis of the Upland Sites I. Full Data Set

There are a total of 299 quadrats belonging to upland habitats, characterized as sites on inorganic soil or rock above the water table which are not periodically flooded. A perusal of this data showed it to be highly heterogeneous, which is hardly surprising given the corresponding environmental heterogeneity of upland sites. This, coupled with the unwieldy size of the data set, suggests the usefulness of subdividing it into still smaller groups. First, however, initial analyses are undertaken to elucidate the overall structure and relationships of upland sites. Following this, the data set is subdivided into two groups using objective criteria, and each are analyzed in more detail.

5.5.1 Classification of Sites

Sites were classified using sum of squares agglomeration (SSA) with chord distance; the resultant dendrogram is shown in Figure 5.7. The following clustering strategies were also performed: complete linkage, single linkage (both using chord distance), and two-way indicator species analysis. The results from these analyses were felt to be less interpretable ecologically and are not presented here.

The results reveal a major dichotomy in the data, labelled 1 and 2 in Figure 5.7. These are characterized as follows:

1. These are xeric sites on well-drained sand flats or dune systems, and occasionally dry rock outcrops. *Pinus banksiana* predominates here.

2. These are mesic to mesic-xeric sites on various substrates, from finer sands to clays and silts to extensive rock outcrops covered
Figure 5.7. Sum of squares agglomeration dendrogram of the 299 quadrats from upland habitats at Elk Lake, Ontario. The two major groupings resulting from the first dichotomy are labelled 1 and 2. The eight vegetation groupings (I - VIII) are also indicated. The quantities along the bottom of the dendrogram represent the number of individuals belonging to the corresponding branches; lower level bifurcations are not shown.
with soil. Gravelly and rocky soils also occur. Monospecific stands of *Populus tremuloides* occur on fine sands and gravelly sites, while a mixed forest containing any or all of *Abies balsamea, Picea mariana, P. tremuloides, Betula papyrifera, Pinus banksiana*, or a few other less common tree species, tend to occur on less coarse soils, sometimes associated with rock.

These therefore appear to be ecologically distinct units, and it would appear legitimate to divide the data into these two groups for further analysis. These two groupings are certainly recognizable in the field, though there may be some ambiguity in their definition. The two-level groupings resulting from SSA were therefore compared with the corresponding results obtained from two-way indicator species analysis (TWINSPAN). The two groupings were remarkably similar, but differed in the assignment of 22 quadrats dominated by black spruce in mesic habitats on coarse sand. These were assigned to group 1 by SSA, while TWINSPAN assigned them to group 2. Before proceeding any further, it would be useful to determine to which group these 22 quadrats are best assigned. This was accomplished using program IDEN (Wildi and Orlofi 1983), which finds the nearest neighbour of the unassigned individuals as a basis for group assignment. Distances were calculated using both euclidean and chord distances. The results are not worth presenting here in detail, since in all cases assignment to group 1 was indicated. This suggests that the subdivision produced by SSA is the more parsimonious one.

Before analyzing these subgroups in more detail, the next few sections are devoted to the examination of overall trends in the upland vegetation at Elk Lake. Reference to Figure 5.7, and ecological considerations, suggest the recognition of eight broadly-defined vegetation groups (vegetation types are described in Sections 5.6 and 5.7). Five of these represent subdivisions of the group 1, while group 2 is represented by three subdivisions. A brief description of these general upland vegetation groups is given below. As in the previous chapter, these are named according to
their major constituent species. Because detailed analyses of vegetation types will be undertaken when analyzing the two groups described above separately, the presentation here is more general and descriptive in nature, serving as an introduction to the vegetation of upland sites. Means, variances, and frequencies for the constituent species in the groups are presented in Table 5.6.

1. *Pinus banksiana - Vaccinium angustifolium*

The 30 quadrats of this grouping occur on excessively drained coarse sand (particularly dune systems), and on exposed very dry rock outcrops. They are characteristically very xeric and highly oligotrophic. The only tree occurring on such sites is *Pinus banksiana*. *Vaccinium angustifolium* forms a characteristic shrub cover, while *Cladina rangiferina*, *C. mitis*, *C. stellaris*, *Dianthus polysetum*, and species of the genus *Cladonia* form a distinctive ground layer. The shrub *Comptonia peregrina*, which is characteristic of highly xeric sites, also occurs here.

II. *Pinus banksiana - Kalmia angustifolia*

This group, characterized by 28 quadrats, typically occurs on gravelly sands or gravelly boulder flats. It also includes quadrats from very open jack pine forest on very coarse sandy flats which appear to have a fire origin. The dominant tree is *Pinus banksiana*, although *Populus tremuloides* also occurs here, often as stunted or dying individuals showing active root resprouting. The shrubs *Kalmia angustifolia*, *Comptonia peregrina*, and *Vaccinium angustifolium* occur with high frequency and cover. *V. myrtylloides* also occurs in many sites, as does the tall shrub *Salix humilis*. The chief ground layer constituents, which rarely reach high cover, include *Cladina rangiferina*, *Dianthus polysetum*, and *Pleurozium schreberi*. The species composition suggests xeric, oligotrophic conditions, although the presence of *P. tremuloides*, *V. myrtylloides*, and *S. humilis* suggest less xeric conditions than group I.
<table>
<thead>
<tr>
<th></th>
<th>ALL (299)</th>
<th>I (30)</th>
<th>II (28)</th>
<th>III (61)</th>
<th>IV (22)</th>
</tr>
</thead>
<tbody>
<tr>
<td>F</td>
<td>M</td>
<td>V</td>
<td>F</td>
<td>M</td>
<td>V</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Picea glauca</td>
<td>3.12</td>
<td>2.10</td>
<td>2.03</td>
<td>2.46</td>
<td>2.19</td>
</tr>
<tr>
<td>Betula papyrifera</td>
<td>3.61</td>
<td>3.43</td>
<td>3.42</td>
<td>3.47</td>
<td>3.50</td>
</tr>
<tr>
<td>Alnus incana</td>
<td>3.61</td>
<td>3.83</td>
<td>3.51</td>
<td>3.67</td>
<td>3.70</td>
</tr>
<tr>
<td>Populus tremuloides</td>
<td>4.00</td>
<td>4.00</td>
<td>3.90</td>
<td>4.00</td>
<td>4.00</td>
</tr>
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<td>Salix alba</td>
<td>3.72</td>
<td>3.72</td>
<td>3.72</td>
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</tr>
<tr>
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Table 5.1: Means (M), variances (V), and relative frequencies (F) of the 79 most common species in each of the eight vegetation types (I - VIII) described for the upland habitats at Elk Lake, Ontario.
III. **Pinus banksiana - Pleurozium schreberi**

This is a large group of 61 quadrats characterized by closed monospecific stands of jack pine on level lacustrine deposits of coarse sand. Soils show extensive podzolization, indicative of relatively oligotrophic conditions. This group, though xeric, is less so than groups I and II described above, and is able to support relatively dense stands of jack pine (average cover just over 50%). A dense carpet of *Pleurozium schreberi* is characteristic, along with the presence and high cover of *Kalmia angustifolia*. Other important constituents of the shrub layer include *Vaccinium angustifolium, V. myrtilloides, Cornus canadensis, Linnaea borealis, Maianthemum canadense*, and *Diervilla lonicera*. *Cladina rangiferina* and *Dicranum polysetum* occur in many of the sites with *P. schreberi* on the forest floor.

IV. **Picea mariana - Pleurozium schreberi**

The 22 quadrats making up this group occur at low elevations (relative to the water table) bordering black spruce bogs, either on coarse sand deposits or rock outcrops covered by a layer of sand. The presence and abundance of *Picea mariana* and especially *Ledum groenlandicum* underly the more mesic conditions prevailing at these oligotrophic sites. Nonetheless, species characteristic of the xeric sites described above are also common here, particularly *Pinus banksiana* and the shrubs *Kalmia angustifolia, Cornus canadensis*, and *Vaccinium myrtilloides*. Species characteristic of very xeric sites do not occur here, however. The ground is covered by a relatively dense mat of *Pleurozium schreberi*, interspersed with clumps of *Dicranum polysetum* and *Cladina rangiferina*. *Sphagnum* species are infrequent.

V. **Pinus banksiana - Alnus crispa**

The 39 quadrats making up this group are typically found on coarse sand near river courses, where the water table is relatively high. *P.
**banksiana** is the major overstory species, reaching almost 56% mean cover. *Betula papyrifera* also occurs with high frequency though generally low cover, and saplings or small trees of *Picea mariana* are commonly encountered. The shrub *Alnus crispa* is characteristic of these sites, sometimes forming dense thickets. Common understory shrubs include *Diervilla lonicera, Cornus canadensis, Kalmia angustifolia, Vaccinium myrtillusoides, and V. angustifolium*. The ground layer is predominantly *Maianthemum canadense* and *Pleurozium schreberi*, although *Dicranum polysetum* also occurs. Because of the relatively high water table, this group is somewhat less xeric and oligotrophic than other jack pine dominated stands.

VI. **Abies balsamea - Picea mariana - Clintonia borealis**

This is a large group of 52 quadrats which characteristically occur on fine silt or clay deposits, often over rock. Occasionally, the substratum is a hardpan on poorly drained river terraces. In such areas *Picea glauca*, which is rare within the study area, may occur. Most stands are dominated by a mixture of *A. balsamea, P. mariana, Betula papyrifera*, and *Populus tremuloides*. *Clintonia borealis* is characteristic of the understory, usually occurring with *Aralia nudicaulis, Maianthemum canadense*, and *Trientalis borealis*. The disturbance nature of these forests is indicated by the common occurrence of rotting logs and stumps. Spruce budworm decimation of *A. balsamea* was evident at many of the sites, though considerable regeneration of this species was also seen.

VII. **Populus tremuloides - Diervilla lonicera**

This group of 34 quadrats occurs on upland sites with fine sandy deposits, often with some gravel mixed in. *Populus tremuloides* is the dominant in the tree stratum, usually forming monotypic stands. Tall shrubs are also characteristic, with *Alnus crispa* predominating. Typical understory constituents include *Diervilla lonicera, Aster macrophyllus, Clintonia borealis, Vaccinium myrtillusoides, Maianthemum canadense, Cornus*
canadensis, and Aralia nudicaulis. The ground layer is primarily decaying leaf litter; mosses and particularly lichens are uncommon.

VIII. Populus tremuloides - Betula papyrifera - Corylus cornuta

The 33 quadrats making up this group typically occur either on rocky slopes or bouldery to gravelly sloping ground. P. tremuloides and B. papyrifera are characteristic of the overstory, and a dense tall shrub layer dominated either by C. cornuta or Acer spicatum often occurs. Typical understory constituents include Aster macrophyllus, Clintonia borealis, Pteridium aquilinum, Lycopodium obscurum, and Aralia nudicaulis. Physiognomically, the tree canopy is more open than that of group VII, permitting the establishment and persistence of a tall shrub layer. There is some evidence to suggest that this vegetation is of disturbance origin, resulting from the selective cutting of trees. Saplings of both Abies balsamea and Picea mariana are of common occurrence.

5.5.2 Ordination of Sites

The large number of quadrats precludes an analysis using a nonmetric scaling strategy. Therefore only principal components analysis (PCA, using a covariance matrix) and correspondence analysis (CA, with downweighting of rare species) were performed. The results of these analyses were similar, although CA proved to be more sensitive to outliers. The PCA solution in the first three dimensions is shown in Figure 5.8, with group affinities plotted. It is clear that three dimensions are required for the summarization of the group structure imposed by the SSA classification. The jack pine dominated stands are separated from the others along the first axis, indicating a very general trend to more xeric and oligotrophic conditions from left to right. A similar trend is seen along the second axis, particularly with respect to the jack pine stands. The most xeric sites with jack pine occur on the negative side of the second axis, while the most mesic Picea mariana - Pleurozium schreberi sites occur on the positive side. The third
Figure 5.8  Principal components analysis (utilizing a covariance matrix between species) of the 299 quadrats of upland habitats at Elk Lake, Ontario. Symbols correspond to the vegetation groupings. (a) axis I vs. axis II. (b) axis I vs. axis III. These first three components account for 32.84, 10.72, and 8.99 percent of the total variance respectively.
axis serves primarily to distinguish more clearly some of the groups, particularly the *Populus tremuloides* - *Diervilla* group from the *P. tremuloides* - *Betula papyrifera* - *Cornus cornuta* stands.

The ordination results suggest that moisture status may be an important determinant of species composition in upland boreal forest on inorganic substrates, which concurs with the results of Carletón and Maycock (1978) and numerous others. This is not to say that nutrient status is not also important. In fact, workers have generally recognized that moisture and nutrient status are often positively correlated in upland habitats (e.g., Bergeron and Bouchard 1983). For example, podzolization, which leads to nutrient leaching and depletion, is strongest on dry sandy substrates. Thus the first axis serves to separate out more mesic, mesotrophic sites from the xeric, oligotrophic stands on coarse sandy podzols dominated by jack pine. Similar trends are also apparent on subsequent axes. They are examined in more detail in Section 5.5.5.

### 5.5.3 Classification of Species

Species were classified using sum of squares agglomeration with chord distance, after first removing species of frequency less than ten. The resulting dendrogram is shown in Figure 5.9. A plot of sum of squares versus number of groups strongly suggested the existence of 6 species groupings, giving a classification efficiency of 31.2%. These are discussed below with respect to the habitat characteristics preferred by the species.

A. This is a large group of 24 species which occur in association with a deciduous canopy (*Populus tremuloides* and *Betula papyrifera*). Site conditions are mesic to mesic-xeric, attributable to the relatively fine-textured soil and the dense canopy. A moderately decomposed, somewhat acidic leaf litter layer is characteristic, suggesting a mesotrophic nutrient status. The soil generally shows weak to moderate podzolization. Most understory species root near the soil surface where nutrients are more readily available. This
species group is somewhat heterogeneous, containing more oligotrophic and xeric species such as *Lycopodium obscurum*, *Cornus canadensis*, *Diervilla lonicera*, and *Aster macrophyllus* as well as more nutrient demanding mesic species such as *Streptopus amplexifolius*, *Pyrola asarifolia*, *Rosa acicularis*, and *Lycopodium* species (Bergeron and Bouchard 1983). Perusal of the dendrogram reveals that such trends are revealed at lower fusion levels.

B. This is a small group of 7 species associated with fine clay or silt deposits in low-lying areas. A well decomposed humus layer also occurs. These species are associated with an overstory of *Populus balsamifera*, *P. tremuloides*, and/or *Picea glauca*. These are hydric habitats of high nutrient status (mesotrophic to eutrophic).

C. These 13 species generally occur on fine sand or silty soils, often over rock. Conditions are mesic to xeric-mesic, and nutrient levels mesotrophic to mesotrophic-oligotrophic. These species are generally associated with a mixed overstory dominated by conifers.

D. These 17 species are characteristic of the somewhat xeric, oligotrophic conditions of closed jack pine stands on coarse sandy flats. High acidity and extensive podzolization renders these sites nutrient poor, while the coarse sand and relative openness of the canopy create relatively xeric conditions near the surface.

E. The 6 species of this group occur on shifting to somewhat stable coarse sand on dunes or sandy slopes. There is typically little if any organic accumulation, and the soil has little profile. These factors suggest highly xeric, oligotrophic conditions.

F. This grouping of twelve species is characteristic of highly xeric rocky habitats. Species are generally found growing directly on rock or on thin deposits of poorly decomposed organic matter over rock. This suggests low nutrient status and highly xeric conditions.
5.5.4 Species Ordination

The two-dimensional species ordination using NMDS, after removal of species with frequencies less than ten, is shown in Figure 5.10. Species associated with xeric, oligotrophic sites dominated by jack pine occur in the lower portion of the ordination. Those species occurring in more mesic sandy sites dominated by a mixture of jack pine and black spruce occur in the left-centre of the scattergram. Those characteristic of more mesic, mesotrophic conditions occur at the top-centre, while species with even higher nutrient demands occur at the top right. Finally, species of relatively mesic, mesotrophic sites dominated by a deciduous overstory occur in the centre and right-centre of the scattergram.

A general trend from xeric, oligotrophic species in the lower left to mesic, mesotrophic-eutrophic species in the upper right is therefore indicated. The results therefore suggest that both moisture regime and nutrient status may be important determinants of species habitat preferences and overall interspecific associations in upland boreal habitats.

5.5.5 Ecological Relationships

Concentration analysis was performed to examine the interrelationships of the previously defined quadrat and species groupings. The resultant three-dimensional scattergrams are presented in Figure 5.11. The first three axes account for 97.4% of the partitioned chi-square, and the relative sharpness is 10.64%. For the quadrat groupings, the first axis appears to represent a xeric-oligotrophic to mesic-mesotrophic trend, separating the jack pine dominated stands from the mixed forests. This was quantified by correlating mean drainage class (Section 4.4) for each group with their axis scores. The results ($r_1 = -0.95$, $r_2 = -0.16$, $r_3 = 0.23$, $R^2 = 0.97$) confirm that the first axis reflects a moisture gradient, though higher axes show poor correlation with this environmental factor. Vegetation group I is separated from the other jack pine dominated types on the second axis.
Figure 5.10 Nonmetric multidimensional scaling (two-dimensional solution, utilizing chord distance) of the 79 most common species of upland habitats at Elk Lake, Ontario. Codes correspond to species names (the first four letters of the genus, and the first three of the species epithet). The stress value is 19.2%.
Three-dimensional concentration analysis ordinations of the eight vegetation types (I – VIII) and six species ecological groupings (A – F) of the upland habitats at Elk Lake, Ontario. These ordinations have a one-to-one correspondence. The partitioning of chi-square (d.f. = 35) is also given.
<table>
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<tr>
<th>Canonical variate (i)</th>
<th>Canonical correlation ($R_i$)</th>
<th>Chi-Square</th>
<th>Percentage</th>
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<td>65.33</td>
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<td>615.41</td>
<td>20.43</td>
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<tr>
<td>4</td>
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<td>2.63</td>
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<tr>
<td>Total</td>
<td></td>
<td>$\chi^2 = 3012.06$</td>
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</table>
Groups II and III, are similar, as are groups IV and V, though these latter two are separated on the third axis. They are also the most mesic of the jack pine stands, showing some affinity with groups VII and VI.

A similar general trend is seen for the species groups, the first axis separating out species adapted to very xeric, oligotrophic habitats from those demanding higher nutrient levels and more mesic conditions.

Associations between the quadrat and species groupings are quite revealing. Vegetation type I shows a close one-to-one correspondence with species group E, indicating the unique nature of these very xeric, oligotrophic habitats of sand dunes and dry rock outcrops. Vegetation types II and III both show affinity to the two species groupings D and F, indicating the xeric oligotrophic conditions prevailing in these dry jack pine dominated stands. The remaining vegetation types show varying degrees of affinity to species groups A, B, and C. Type VII (Populus tremuloides - Biervilla lonicera) shows very high affinity to species group A. Type IV (upland Picea mariana - Pleurozium schreberi) shows some affinity to species groups C and D, while type V shows greater affinity for species groups A, D, and E. Finally, type VIII shows highest affinity for species groups A, B, and C.

5.6 Analysis of the Upland Sites II: Xeric Upland Habitats

A total of 180 quadrats make up this group. These generally occur on flat, upland coarse sand lacustrine deposits, dune systems, or localized rock outcrops. A well developed podzol is often characteristic, indicating the xeric and generally oligotrophic conditions prevailing in such habitats, which prevail in about 40% of the study area. Pinus banksiana is the dominant tree at most sites, suggesting a vegetation well adapted to recurrent fires. The raw data for these quadrats is given in Appendix 5.

These ecosystems, which are quite simple floristically, have rarely been studied in detail. Mueller-Dombois (1964, 1965) examined jack pine dominated
stands in southeastern Manitoba, emphasizing silvic characteristics and forest potential. Carroll and Bliss (1982) examined the extensive jack pine stands in northern Saskatchewan, which are characterized by regular, recurrent fires (averaging every 28-54 years at a given site) and a very depauperate flora. They recognized four vegetation types using cluster analysis and polar ordination. Most workers in Ontario and Quebec (e.g. Carleton and Maycock 1978; Bergeron and Bouchard 1983) have described jack pine stands in a much broader context. The high intensity of sampling undertaken here will permit a more detailed examination of the structural and compositional aspects of jack pine dominated vegetation.

5.6.1 Classification of Sites

The dendrogram resulting from sum of squares agglomeration (SSA) using chord distance is shown in Figure 5.12. While other clustering strategies were also attempted, the results are not presented here.

A plot of the sum of squares versus the number of groups, together with ecological considerations, suggest the recognition of 10 groups, giving a classification efficiency of 53.6%. The types are described below with respect to their species composition, physiognomic structure, and habitat characteristics. Types are named by their major constituent species. The mean, frequency, and variance of major constituent species in each of the ten vegetation types is given in Table 5.7.

1. *Vaccinium angustifolium* - *Arctostaphylos uva-ursi*

The 10 quadrats making up this type occur on coarse, loose, sometimes shifting sand, typically on south-facing dune slopes. Soil development is poor or non-existent. *Pinus banksiana* occurs with an average cover of less than 10%, and the type is dominated by lichens and low shrubs adapted to highly xeric, oligotrophic conditions. The dominant shrubs are *Arctostaphylos uva-ursi*, *Vaccinium angustifolium*, *Comptonia peregrina*, *Prunus pumila*, *Pteridium aquilinum*, and *Gaultheria procumbens*. Grasses of
Figure 5.12  Sum of squares agglomeration dendrogram of the 180 quadrats of xeric, jack pine dominated upland habitats at Elk Lake, Ontario. The ten vegetation types (I – X) are also indicated. The quantities along the bottom of the dendrogram represent the number of individuals belonging to the corresponding branches; lower level bifurcations are not shown.
Table 5.7  Means (\( M \)), variances (\( V \)), and relative frequencies (\( f' \)) of the 60 most common species in each of the ten vegetation types (I, X) described for the xeric, jack pine dominated habitats at Elk Lake, Ontario.
Table 5.7  Continued.
the genus Oryzopsis (mainly O. punigens) are also scattered throughout the site, though they never attain high cover. An extensive lichen mat occurs, which includes Cladina rangiferina, C. mitis, C. stellaris, C. arbuscula, Lecidea granulosa, and a number of species of the genus Cladonia. There is little accumulation of surface organic matter, the lichens often growing directly on the sand (see photo, Appendix 10). In very dry, sloping areas, the sand is often covered with a thin crust of Lecidea granulosa, which may stabilize the sand and prevent erosion. Mueller-Dombois (1964) has termed this an ‘insect crust mor’ because of the action of ants and Arthropods. These were clearly in evidence at the present site.

This type bears some resemblance to both the ‘very dry Cladonia’ and ‘dry Arctostaphylos-Cladonia’ types described by Mueller-Dombois (1964). The former is characterized as occurring on aeolian regosol soils on high dunes, showing minimal podzolization or soil formation. The latter occurs on high beach deposits, showing minimal podzolization and a shallow, continuous humus layer with abundant insect activity. He places the water table 2.5 – 3 m below the surface at his sites, and considers jack pine to be an edaphic climax species in this environment.

This type is characteristic of very xeric, highly oligotrophic sites. Evidence for such conditions include the coarse sand substratum and the lack of soil formation. Physiognomically, such sites are characterized by scattered jack pine, a low discontinuous shrub layer, and a lichen dominated ground layer.

II. Pinus bankstana - Vaccinium angustifolium - Cladina rangiferina

This vegetation type, characterized by 20 quadrats, occurs either on dry rock outcrops or on coarse sand flats overlying a loose stone-gravel mix. As in the above vegetation type, very xeric and oligotrophic conditions prevail. Organic accumulation is generally greater at these sites, however, particularly on rock where pockets of poorly decomposed humus are often characteristic. The flat, coarse sand sites typically have a continuous poorly
decomposed humus layer 1 - 3 cm in depth;

*Pinus banksiana* is the characteristic tree of this type, reaching almost 40% mean cover. On the rock outcrops, *Picea mariana* may also occur, and occasionally saplings of *Pinus strobus* were also noted. The characteristic shrub is *Vaccinium angustifolium*, with *V. myrtillus* and *Comptonia peregrina* occurring with much lower frequency and cover. The lichen *Cladina rangiferina* is the most common forest constituent, although the mosses *Pleurozium schreberi* and *Dicranum polysetum* also occur. Other species characteristic of the ground layer include *C. mitis*, *C. stellaris*, *Ptilidium ciliare*, and a number of species of the genus *Cladonia*.

Examination of the dendrogram suggests the recognition of 4 subtypes (see Figure 5.12). The first are quadrats occurring on north slopes of low dunes or flats of coarse sand, and are characterized by relatively high jack pine cover. The second group occurs on very coarse sandy flats overlying a boulder-gravel matrix. *Prunus pumila* achieves high cover here. The latter two subgroups are characteristic of rock outcrops. The second is distinguished from the first by occurring on more exposed rock.

The sites occurring on rock are similar to those described by Jones *et al.* (1983). Little mineral soil accumulation is characteristic, though extensive pockets of poorly decomposed organic matter often occur (see photo, Appendix 10). Trees generally root in fissures and cracks in the rock, and windthrows are common. The sites occurring on very coarse sands show some affinity with the 'dry Arctostaphylos-Cladonia' type of Mueller-Dombois (1964). Commercial gravel excavations near these sites revealed that below a 2 - 3 meter layer of coarse sand a layer of boulders and gravel occurs, indicating excessive site drainage. This and the oligotrophic nature of the sites are indicated by the poorly-developed understory dominated by lichens and *V. angustifolium*.

III. *Pinus banksiana* - *Kalmia angustifolia* - *Populus tremuloides*
This type is defined by a small group of 9 quadrats. The sites are characterized by a gravelly-bouldery substratum, intermixed with small pockets of fine silty soil. These sites all occurred near the Montreal River, suggesting that they may have originated during lacustrine and riparian remodelling phases. Trees are fairly widely spaced, with large specimens of *Pinus banksiana* predominating. *Populus tremuloides* occurs as small, depauperate, and actively respouting individuals. A number of dead trunks of this species were also evident, suggesting that this species is here at its limit of tolerance. These trees may have died following a particularly dry summer (see discussion in Yarranton and Yarranton 1975). Shrub species predominant in the bouldery understory include *Kalmia angustifolia*, *Vaccinium myrtillus*, *Aster macrophyllus*, *Cornus canadensis*, *Comptonia peregrina*, *Maianthemum canadense*, *Salix humilis*, and *Linnaea borealis*. Lichens are rare, but the mosses *Pleurozium schreberi* and *Dicranum polysetum* do occur. This is an interesting combination of species, indicating relatively xeric but somewhat less oligotrophic conditions than the two types described above. This is probably attributable to the fine silt and clay deposits found here. However, the bouldery-gravelly nature of the site leads to excessive drainage, favouring species adapted to xeric conditions.

Physiognomically this type is an open forest of tall, healthy but widely spaced jack pine and smaller, depauperate specimens of trembling aspen. White birch occasionally occurs, and black spruce saplings were found in some of the quadrats. The understory is generally low, although tall shrubs such as *Salix humilis*, *Amelanchier* spp., and *Prunus pensylvanica* do occur sporadically. See photo, Appendix 10.

IV. *Pinus banksiana* - *Comptonia peregrina* - *Vaccinium angustifolium*

This type is defined by a group of 19 quadrats which forms three distinct subgroups (see Figure 5.12). The first occurs on steep, stable dune faces characterized by high cover of *Pteridium aquilinum*. The second occurs on flat, coarse sand plains, and is characterized by high cover of *Comptonia*
*peregrina*, *Vaccinium angustifolium*, and *Cladina rangiferina* (see photo, Appendix 10). The final grouping is characteristic of very gravelly, coarse sandy soils which are probably the result of lacustrine sorting of fluvioglacial deposits.

These sites are characterized by low jack pine cover (averaging less than 20%) and an almost continuous shrub layer dominated by the low shrubs *Kalmia angustifolia*, *Vaccinium angustifolium*, *Comptonia peregrina*, and *V. myrtilloides*. *Populus tremuloides* also occurs in the overstory, though it is generally small and depauperate in form, much as in type III. *Cladina rangiferina*, *Pleurozium schreberi*, and *Dicranum polysetum* are characteristic of openings in the shrub layer, while *Salix humilis* and *Prunus pensylvanica* are the most common tall shrubs. *Diervilla lonicera* and the small annual *Melampyrum lineare* occur in about half the quadrats.

The substrate predominating in this type (coarse and/or gravelly sands) suggests an excessively drained habitat, and this is confirmed by the species composition. Conditions are probably similar to type III (xeric, oligotrophic), but are somewhat less xeric than types I and II.

V. *Pinus banksiana* - *Pleurozium schreberi* - *Cladina rangiferina*

The 23 quadrats making up this type occur on coarse sandy flats, or occasionally on coarse sand over rock. *Pinus banksiana* is the dominant tree species, achieving a mean cover of just over 30%. The understory is dominated by the low shrubs *Kalmia angustifolia*, *Vaccinium angustifolium*, *V. myrtilloides*, *Diervilla lonicera*, *Comptonia peregrina*, and *Gaultheria procumbens*. *Pleurozium schreberi* is the dominant species of the ground layer, although *Cladina rangiferina* and *Dicranum polysetum* also occur. The tall shrubs *Prunus pensylvanica*, *Alnus crispa*, and *Salix humilis* often occur in more open areas of the canopy.

The openness of the forest and the species composition suggest the xeric, oligotrophic conditions prevailing in this type. Drainage conditions
are likely similar to types III and IV, but the general phytograpy and substratum are different in this type. Strong podzolization is characteristic of these sites.

VI. Pinus banksiana - Pleurozium schreberi - Kalmia angustifolia - Ledum groenlandicum

The 16 quadrats making up this type are characterized by a dense jack pine overstory (averaging just over 70% cover) with saplings or small trees of Picea mariana commonly occurring at a lower stratal level. These are sandy sites with a well-developed podzol, occurring along the fringe of black spruce bogs, 0.5 - 2 meters above the water table. Thus the conditions here are somewhat more mesic than types I-V, although oligotrophic conditions still likely prevail. Kalmia angustifolia is the dominant shrub, although Ledum groenlandicum is also typical. This latter species, along with Coptis groenlandicum, Gaultheria hispidula, and Kainantheum canadense, are good indicators of the more mesic status of this type. The forest floor is dominated by thick mats of Pleurozium schreberi, with occasional clumps of Dicranum polysetum. Sphagnum species do occur, but are uncommon. Other shrubs occurring in this type include Vaccinium myrtilloides, V. angustifolium, and Corus canadensis, the latter achieving a cover of over 12%.

The prevalence of small black spruce trees in the lower tree strata is probably attributable to the relatively high water table, the oligotrophic conditions, and the proximity of bogs, which provide a ready seed source. In the absence of fire it would seem likely that black spruce would succeed jack pine on these sites, but this is somewhat hypothetical since a fire would be expected before such a succession could be completed, reestablishing jack pine.

VII. Pinus banksiana - Pleurozium schreberi - Kalmia angustifolia - Vaccinium myrtilloides
The 22 quadrats defining this type occur on flat upland sandy sites. These sands are generally of finer texture than those of physiographically similar areas described above. Strong podzolization is in evidence, suggesting relatively dry, oligotrophic conditions. Monospecific jack pine stands are characteristic, attaining just over two-thirds cover. The understory is dominated by *Kalmia angustifolia*, although the shrubs *Vaccinium myrtillus*, *Cornus canadensis*, *Linnaea borealis*, *V. angustifolium*, *Maianthemum canadense*, *Gaultheria procumbens*, and *Diervilla lonicera* are also common. The ground layer is dominated by *Pleuridium schreberi*. The tall shrubs *Prunus pensylvanica*, *Salix humilis*, and *Amelanchier* spp. each occur with about 50% frequency within this type, forming a minor understory component of low cover. Seedlings or small trees of both *Abies balsamea* and *Picea mariana* are occasional though uncommon.

This type is a more upland, less mesic version of type VI, physiognomically similar though lacking some species characteristic of a higher water table. The more mesic conditions here compared with types I-V are indicated by the increased dominance of jack pine, the higher cover of small ericaceous species, and the decreased abundance of lichens, particularly *Cladina rangiferina*. Also, the presence of *Linnaea borealis*, *Diervilla lonicera*, and *Cornus canadensis*, and the increased importance of *Prunus pensylvanica*, *Salix humilis*, *Amelanchier* spp., and occasionally *Alnus crispa* are all good indicators of less xeric conditions.

Two subgroups of this type can be recognized (see Figure 5.12). The first is a drier subtype, showing lower cover of such mesotrophic species as *Cornus canadensis* and *Vaccinium myrtillus*.

VIII. *Picea mariana - Pleuroziunm schreberi - Ledum groenlandicum*

The 22 quadrats making up this type are invariably found on flat or gently sloping sandy substrates just above the water table, typically bordering boggy land or slow-moving watercourses showing some peat accumulation. Some of these low-lying sites are characterized by rock.
overlain by sandy soil 0.5 – 1 meter in depth. Soils are generally poorly podzolized, and the sand is often saturated at depths greater than 50 cm. *Picea mariana* is the dominant species of the tree stratum, achieving an average cover of over 55%. *Pinus banksiana* also occurs, with an average cover of just under 25%. Because of the active layering and consequent local shading and smothering by black spruce, the understory is of relatively low cover. *Ledum groenlandicum* and *Kalmia angustifolia* predominate in the shrub layer, although *Cornus aquadensis*, *Vaccinium myrtillus*, and *Gaultheria hispidula* are also characteristic. The ground layer is dominated by thick carpets of *Pleurozium schreberi*, interspersed with small clumps of *Cladina rangiferina* and *Dieranum polysetum*. Species of *Sphagnum* are of rare occurrence.

*L. groenlandicum* and *C. hispidula* are indicative of the mesic conditions prevailing at these sites. Nevertheless, more xeric conditions are indicated by the presence of *P. schreberi* and *C. rangiferina*. This is probably attributable to the physiognomic structure of these sites. Unlike jack pine, black spruce trees taper strongly and are profusely branched near the base where layering is active. As a result the canopy is actually quite open, leading to higher insolation and evapotranspiration at the surface, which may favour those species adapted to xeric conditions.

**IX. Pinus banksiana – Pleurozium schreberi – Alnus crispa**

This group of 20 quadrats characterizes a relatively heterogeneous type. The substratum is generally a coarse to relatively fine sandy soil, often associated with rock. While jack pine forms the major component of the tree stratum, black spruce also occurs with high frequency (often as small trees), and *Betula papyrifera* and *Acer rubrum* occur in some sites. *Alnus crispa* is a common tall shrub in this type. The understory is of relatively low cover and not strongly dominated by any one species. The most commonly encountered small shrubs are *Kalmia angustifolia*, *Vaccinium myrtillus*, *Cornus canadensis*, *V. angustifolium*, and *Diervilla lonicera*. 
The ground layer is dominated by *Pleurozium schreberi*, although *Dicranum polysetum* also occurs.

Four major subgroups can be delineated (see Figure 5.12). The first occurs on fine sands overlying rock, and includes *Betula papyrifera* and *Acer rubrum* in the overstory. The second occurs on somewhat rocky sites with some sand or silt deposition. Black spruce occurs in the tree stratum, and *Pteridium aquilinum* is a typical understory species. The third is characterized by high cover of the tall shrub *Alnus crispa*. These sites are quite mesic, often occurring near rocky streams. A coarse sandy soil over rock is characteristic. The final subgroup is characteristic of somewhat rocky sites overlain by sandy soil, often in mesic conditions similar to the third subgroup. Both black spruce and *Alnus crispa* occur here.

X. *Pinus banksiana - Corylus cornuta - Alnus crispa*

These 19 quadrats form a group characteristic of riparian sites on coarse sand along the Montreal River and lower Sydney Creek. The type is therefore mesic and probably mesotrophic, the water table normally occurring no more than a meter below the sandy substrate. Jack pine is dominant in the tree stratum, although *Betula papyrifera* also occurs with high frequency but low cover. The tall shrubs *Alnus crispa* and *Corylus cornuta* occur with high frequency and cover, often forming dense impenetrable thickets. The shading of this tall shrub layer inhibits the development of a dense lower understory. Dominant low shrubs include *Diervilla lonicera*, *Aster macrophyllus*, *Vaccinium myrtilloides*, *V. angustifolium*, *Maianthemum canadense*, and *Kalmia angustifolia*. *Pleurozium schreberi* occurs on the ground layer with relatively low cover.

The occurrence of *D. lonicera* and *A. macrophyllus* in the understory is interesting, as these species are more characteristic of a deciduous canopy (particularly one dominated by *Populus tremuloides*). It seems likely that the two dominant tall shrubs may produce the necessary shade and deciduous litter for the establishment and persistence of these species. The relatively
mesic, mesotrophic conditions undoubtedly have some influence also. The occurrence of *A. crispa* and *C. cornuta* are reflective of a high water table and more mesotrophic conditions (Mueller-Dombois 1964; Gleason 1969).

5.6.2 Site Relationships and Environmental Characterization

Pairwise compositional divergences for the ten types (using an information criterion, see Section 5.4.3) are presented in Table 5.8. The results indicate some interesting overall relationships between types (based on their marginal species frequencies). Type I forms a relatively isolated groups which shows highest affinity for types II, IV, and V. Types VI and VIII (sites bordering boggy lowlands) are similar, as are types IX and X (jack pine stands with a significant tall shrub component). Types IV, V, and VII (dry upland jack pine stands) show relatively low divergence, while type III shows highest similarity with type VII. Note that values presented here are generally less divergent than those obtained for the wetland sites (Section 5.4.3). This is undoubtedly attributable to the greater degree of floristic and environmental homogeneity of these upland sites. Again, these values are presented for utilitarian purposes and should not be interpreted in a strict statistical sense.

Table 5.9 presents a physiognomic-environmental characterization of the ten types. Dominance is defined as in Section 5.4.3. Substrate and terrain type, productivity, soil characterization, and drainage class (Section 4.4) were estimated at each site. Particle size class was determined from soil samples collected at each site (see Appendix 3); the values presented in the table are expressed using a four-point scale from very coarse to fine. Nutrient status (using the five-point scale of Jeglum *et al.* 1974) are synthetic estimates based on the results of previous workers (particularly Mueller-Dombois 1964, and Bergeron and Bouchard 1983) and considerations of site drainage, depth to water table, and the nature of the groundwater. The values must therefore be regarded as tentative; measurements of pH, conductivity, or concentration of selected minerals would be required to
Table 5.8. Pairwise compositional divergences (using the ZI statistic) for the ten xeric upland types. Values of chi-square ($\chi^2$), degrees of freedom (DF), and the standard normal deviate (Z) are given.
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Table 5.9  Physiognomic – environmental characterization of the 10 xeric upland types.
Table 5.9 Continued.
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<th>VIII</th>
<th>IX</th>
<th>X</th>
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<td></td>
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<td></td>
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<td>strong podsol</td>
<td>moderate podsolization</td>
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<td>tree cover 70%</td>
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<tr>
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<td>Jack pine</td>
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<tr>
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<td>height 15 - 18 m</td>
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</table>
substantiate the claims made here.

The table indicates substantial environmental divergence of the types. Significant differences in drainage (related to substrate and terrain type) are apparent, suggesting the possible importance of this environmental factor in determining vegetation on upland sites. This is further investigated in the next few sections.

5.6.3 Ordination of Sites

Ordinations were performed using principal components analysis (PCA, covariance matrix), correspondence analysis (CA), and nonmetric multidimensional scaling (NMDS, chord distance and two-dimensional solution). The results of correspondence analysis were disappointing, being overly sensitive to outliers. The results of PCA were interpretable in three dimensions, but are not presented here since NMDS was able to represent essentially the same structure in two dimensions, which is much more readily interpretable. The resultant scattergram (Figure 5.13) is discussed and interpreted here.

In general the group structure imposed on the data set by the sum of squares agglomerative clustering is reproduced well by the ordination, although a continuum is suggested. This in turn suggests that the ten types defined in the previous section may in fact represent a continuum in vegetational (and presumably environmental) space, and that the divisions imposed, while objective, are perhaps somewhat arbitrary. This conclusion is hardly surprising given the relative homogeneity of these sites in terms of both vegetation and environment. Nonetheless, the types described do serve the utilitarian purpose of providing a comprehensive description of the vegetation, and the ability to interpret the results in an environmental context (Section 5.6.2) suggests that they are ecologically meaningful.

There appears to be a general trend from highly xeric sites in the lower right to more mesic sites in the upper left of the scattergram. To
Figure 5.13  Nonmetric multidimensional scaling ordination (two-dimensional solution, utilizing chord distance) of the 180 quadrats of xeric, jack pine dominated upland habitats at Elk Lake, Ontario. Symbols correspond to the ten vegetation types (I - X). The stress value is 21.3%.
examine this further, values of soil particle size were superimposed on the scattergram (Figure 5.14). These results clearly indicate a trend from coarse soils (and rock outcrops) in the lower right to more finely particulate soils in the upper left of the ordination, indicating an overall decrease in drainage in this direction. If drainage class (on a five point scale, Section 4.4) is also considered (see Figure 5.15), this moisture gradient is further reinforced.

The relationship of the types (that is, their relative placement on the scattergram) generally reflects their fusion relationships in the SSA dendrogram (Figure 5.12). For example, types I and II, which fuse at a low level but as a group unite with the other types only at the final fusion, occur in close proximity in the scattergram. Similar observations can be made for the other types. However, cluster analysis is suboptimal for the representation of interspecific relationships. For example, a relatively close relationship between types II and V, and the relative dissimilarity of types II and III, is indicated by the ordination scattergram but not from the paths of fusion in the dendrogram. This reflects a difference in objectives: cluster analysis defines and imposes group structure, whereas ordination summarizes continuous trends.

Trends in the ordination were examined further by plotting species abundance values on the scattergram for selected common species. The results are presented in Appendix 6. Most of the species show some relationship to the proposed moisture gradient. Species appearing to show optimal abundance at the mesic end include _Maianthemum canadense_, _Diervilia lonicera_, _Cornus canadensis_, _Ledum groenlandicum_, _Alnus crispa_, and _Picea mariana_. The following species show preference for xeric conditions: _Cladina rangiferina_, _Comptonia peregrina_, and _Vaccinium angustifolium_. Species showing optima near the centre of the scattergram, indicating intermediate xeric-mesic preferences, include _Pleurozium schreberi_, _Dicranum polysetum_, _Vaccinium myrtillus_, _Kalmia angustifolia_, _Salix humilis_, and _Pinus banksiana_. 
Figure 5.14 Soil particle size values superimposed on the nonmetric multidimensional scaling scattergram (Figure 5.13) of the 180 xeric, jack pine sites. Larger particle sizes are indicated by larger circles. A slash through the circle indicates the presence of gravel or stones. R = on rock, no soil sample available. D = site located on dune.
Figure 5.15 - Relative elevation (arbitrary five point scale) values superimposed on the nonmetric multidimensional scaling (Figure 5.13) of the 180 xeric, jack pine dominated upland sites.
In summary, moisture status (related to terrain and substrate type) appears to be the primary factor determining variation in vegetation composition in upland jack pine dominated habitats. This apparently concurs with the conclusions of Carleton and Maycock (1978), which were made in a more general context. Nutrient analyses should also be undertaken, however, to determine the importance of this factor. If, as expected, nutrient status is highly correlated with moisture status, the moisture gradient elucidated here may be better described as a composite moisture-nutrient gradient from very xeric, highly oligotrophic sites to mesic, mesotrophic ones. Other factors such as fire history, biotic influences, slope, and aspect must of course also be considered.

5.6.4 Species Classification

The delineation of species ecological groups was undertaken using sum of squares agglomeration (with chord distance) after first removing those species occurring with a frequency of less than 10. The resultant dendrogram is shown in Figure 5.16. A plot of sum of squares versus number of groups, and ecological considerations, suggest the recognition of 5 groups, giving a classification efficiency of 27.2%. These are described below:

A. These 8 species form a distinctive group restricted to dune slopes of unstable, coarse sand. Such sites are highly xeric and oligotrophic. These species characteristically grow directly on sand, since surface organic accumulation is virtually nonexistent.

B. These 15 species grow in very xeric, oligotrophic habitats, occurring either on dry rock outcrops or on coarse sandy flats. Such areas generally have some accumulation of poorly decomposed humus. Species may grow directly on rock (*Stereocaulon paschale*, *Cladina*, and *Cladonia* species), on humus layers over rock (*Dicranum polysetum*, some *Cladonia* species), or in small pockets of mixed organic and inorganic matter (*Vaccinium angustifolium*, *Ptilium ciliare*, *Potentilla tridentata*, *Oryzopsis pungens*, *Polytrichum*...
Figure 5.16  Sum of squares agglomeration dendrogram of the 60 most common species of xeric, jack pine dominated upland habitats at Elk Lake, Ontario. The five species ecological groupings (A – E) are also indicated.
C. The 12 species of this group require more mesic and mesotrophic conditions, being found on sand or gravelly sand in riparian habitats, particularly along the Montreal River and the lower arm of Sydney Creek. In such areas the water table is no more than a meter or so from the surface, providing some nutrient enrichment through groundwater flow.

D. These 6 species are characteristic of mesic, oligotrophic habitats, occurring in upland sites bordering acidic black spruce bogs. The water table is generally no more than a meter or so from the surface, implying mesic conditions. Overall oligotrophic conditions persist because of the proximity of acidic bogs.

E. This is a large group of 19 species characteristic of flat upland sandy sites dominated by a jack pine canopy. The vegetation represents a pyric/edaphic climax, the species forming a distinct ecological group adapted to the xeric to xeric-mesic, oligotrophic conditions prevailing at such sites. The soils show strong podzolization and a relatively thick but poorly decomposed litter layer. These species are typically well adapted to fire, with many having the ability to resprout from underground roots after a relatively light fire, and to rapid colonization of more severely burned areas.

Two subgroups can be readily recognized (see Figure 5.16). The first group represents species adapted to growing in more shaded areas, whereas the latter group generally prefers higher insolation, occurring in gaps in closed forest or beneath more open canopies.
5.6.5 Species Ordination

The nonmetric multidimensional scaling (using chord distance) two-dimensional scattergram is shown in Figure 5.17; species of frequency less than 10 were first removed from the data set. *Pinus banksiana* occurs at the centre of this ordination, with various trends emanating from it. Species adapted to highly xeric, oligotrophic conditions occur at the lower right (species group A). Those species characteristic of dry rock outcrops occur in the same area on the scattergram, but slightly to the left. Species characteristic of mesic, mesotrophic riparian sites (species group C) occur in the middle left, while those adapted to mesic, oligotrophic conditions (species group D) are found at the upper left of the scattergram. Members of species group E, adapted to growing under a jack pine canopy on coarse sand flats, occur near the centre of the scattergram. Species occurring in gravelly or bouldery sites occur at the upper right.

A xeric-mesic trend in the species ordination, from lower right to upper left, is clearly apparent, underlying the importance of moisture conditions to the development of interspecific associations. A trend of increasing nutrient status is also indicated from the centre to the lower left of the scattergram, but more information on soil nutrients would be required to substantiate this claim.

5.6.6 Ecological Relationships

Concentration analysis was performed to summarize trends in the 10 vegetation types and 5 species groupings, and to examine the interrelationships between these two classifications. The results are summarized in Figure 5.18, which shows the three-dimensional scattergrams. These first three axes summarize 93.1% of the partitioned chi-square; the relative sharpness is 16.5%.

The trend in the species group ordination indicates a moisture gradient along the first axis, from the highly xeric group A to the more mesic groups
Figure 5.17  Nonmetric multidimensional scaling (two-dimensional solution, utilizing chord distance) of the 60 most common species of xeric, jack pine dominated upland habitats at Elk Lake, Ontario. Codes correspond to species names (the first four letters of the genus, and the first three of the species epithet). The stress value is 16.2%.
Figure 5.18. Three-dimensional concentration analysis ordinations of the ten vegetation types (I - X) and five species ecological groupings (A - E) of the xeric, jack pine dominated uplands at Elk Lake, Ontario. These ordinations have a one-to-one correspondence. The partitioning of chi-square (d.f. = 36) is also given.
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<td></td>
<td>$\chi^2 = 2059.53$</td>
<td><strong>100.00</strong></td>
</tr>
</tbody>
</table>
The second axis serves to separate the mesic, oligotrophic species group D from groups B, C, and E which are characteristic of somewhat drier conditions; it therefore represents a secondary moisture-nutrient status gradient. The third axis serves mainly to separate the species of group C, which require more mesic conditions, from groups B and E.

The ordination of the vegetation types suggests four major groupings. Vegetation type I is an outlier, forming its own group. It shows very high affinity with species group A, underlying the characteristic highly xeric and oligotrophic conditions prevailing on these unstable sand dune systems. Types VI and VIII, which are both characteristic of low lying areas on coarse sand adjacent to boggy land, show high affinity for species group D. Conditions here are more mesic than the upland jack pine forests, but are probably still oligotrophic. A third general category includes types II, III, IV, V, and VII. These are all jack pine dominated ecosystems in xeric to xeric-mesic, oligotrophic habitats. Types II and IV show highest affinity for species group B, indicating xeric conditions on rock or very coarse sand. By contrast, types III, V, and VII are most highly associated with species group E, indicating somewhat less xeric conditions (medium to coarse, well drained sands). The final category (to which type VIII shows some affinity) consists of types IX and X, which are characteristic of more nutrient rich jack pine dominated stands. These stands characteristically have a well-developed secondary tall shrub canopy of nutrient and moisture demanding species such as Alnus crispa, Corylus cornuta, and Acer spicatum. These types show highest affinity for species group C.

Overall trends in the scattergram of the ten types have been summarized by correlating quantifiable environmental factors (drainage, estimated nutrient status, and soil particle size) with the axis scores. The results, presented in Table 5.10, indicate a strong moisture-nutrient gradient along the first axis (which accounts for over 60% of the total chi-square). This reaffirms the conclusion reached earlier with regard to the NMDS scattergram of the 180 quadrats. The multiple correlation values further
Table 5.10 Correlations of the concentration analysis scores for the 10 xeric upland types with selected environmental parameters.
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reenforce this. The second and third axes are rather poorly correlated with these factors, however. These axes may indicate trends in unmeasured environmental factors, or may represent trends in floristic variation attributable to biotic and/or historical factors.

In conclusion, concentration analysis has summarized trends in variation in the species and vegetation groupings, and has shown patterns of affinity between these groups. A strong trend attributable to moisture availability (based on soil particle size and substrate considerations) is indicated. Stands on coarse sands adjacent to black spruce bogs form a distinctive grouping, indicating the more mesic but nonetheless oligotrophic conditions prevailing here. The proximity of a seed source may also explain the presence of species such as Picea mariana and Ledum groenlandicum at such sites. Stands on open, coarse sand dune systems form a very distinct group in the ordination, indicating the unique habitat conditions prevailing there. The other groups are more closely related, but even here some strong trends attributable primarily to moisture availability and nutrient status are indicated, with stands in more mesotrophic, mesic situations (primarily riparian sites) typically developing a secondary tall shrub stratum. Mueller-Dombois (1964) has indicated that the presence of such a stratum on sandy soils is a good indication of increased nutrient and moisture availability.

5.6.7 Discussion

The results have clearly demonstrated the importance of moisture status on species composition in upland, jack pine dominated boreal habitats. There is some evidence that nutrient status is also important, though more data would be required to substantiate this claim. Moisture status was evaluated using a general composite index of soil particle size, presence of gravel, boulders, and/or rock, the estimated level of the water table, and slope and aspect considerations. The moisture gradient so defined in therefore a complex environmental gradient (c.f. Whittaker 1967).
*Pinus banksiana* on coarse sand deposits is generally considered to be an edaphic/pyric climax, with recurrent fires perpetuating the ecosystem. In many boreal areas, man is actively preventing the spread of fires in such habitats, and in future generations it may be possible to examine the successional sequence occurring under these rather unnatural conditions. Jack pine is shade intolerant, and the cones are generally (though not exclusively) serotinous. Also, seedlings require an inorganic substrate for establishment. Many of the jack pine stands (with the exception of the very xeric sites) had *Picea mariana* and occasionally *Abies balsamea* saplings or small trees in the understorey, which lends credence to the hypothesis that either or both of these species will eventually dominate the tree stratum as the jack pine dies off (Ritchie 1956, Moss 1953a, Curtis 1959). Alternatively, Carleton and Maycock (1978) have suggested that the vegetation may become 'parklike'. Such areas do occur within the study area. Whether they are the result of xeric conditions, light fires, or a true successional sequence in not apparent; however, a combination of xeric conditions and a light fire a few years after the severe fire of the early 1920's seems the most likely candidate. Such a light fire would kill the young jack pine saplings, but would not severely damage the underground perennating sprouts of fire adapted shrubs, which would have also established at the sites. This, coupled with the lack of a seed source for jack pine, could lead to these open parklands (dominated by ericaceous shrubs and *Pleurozium schreberi*, with occasional scattered jack pine and black spruce). A light fire of this sort did occur in an open, mature jack pine stand in the summer of 1981. Shrub and herbaceous vegetation readily resprouted in the same season, and active root sprouting of the killed trembling aspen was observed. The mature jack pine were also killed, and only limited seed germination was seen (mainly in more severely burned areas beneath parent trees). Many of these seedlings were being smothered by encroaching understorey vegetation, however. These light burns also killed all mosses and lichens.

There is some evidence for site competition between jack pine and
trembling aspen, particularly on less coarse sands of upland plains. These species do show somewhat different habitat preferences; while jack pine prefers very coarse sand outwashes and lacustrine deposits, trembling aspen prefers well drained but somewhat finer sands. Nonetheless, there is considerable overlap in habitat preferences. Past history seems important in determining which species occurs in a given upland sandy habitat. Trembling aspen, once established on such a site, may be difficult to eradicate because of its remarkable ability to resprout from root suckers following all but the most severe fires. Conversely, jack pine will always reestablish after a severe fire if it already exists at a site because of cone serotiny; seedlings will have a chance to become well established in the same season, thereby outcompeting other species. These observations have interesting implications for the logging industry. If a jack pine stand is logged and the slash not burned to open the cones, an inorganic substratum conducive to the establishment of trembling aspen and unwanted shrub species results. Furthermore, if even occasional trembling aspen existed in the logged stand, the cutting of the tree will result in extensive resprouting. This has been confirmed from observations of logged jack pine forests to the east of the study area. Unless steps are taken to replant these sites, they will undoubtedly develop into less desirable trembling aspen scrub.

Management of fire adapted ecosystems has until recently been poorly studied, and the strategies developed in pine barrens in the United States have apparently not been applied to boreal forests. Only through sound management practices can these economically desirable and recreationally important forest stands be perpetuated.

5.7 Analysis of Upland Sites III. Mesic Upland Habitats

The 119 quadrats making up this grouping characteristicly occur on more finely textured inorganic soils than the jack pine dominated stands described above. The substrata are various, including fine lacustrine sand deposits, clay hardpans, clay-silt deposits over rock, gravelly deposits, rocky slopes, and rock outcrops. At Elk Lake, the major constituents of
these habitats are *Abies balsamea*, *Picea mariana*, *Populus tremuloides*, and *Betula papyrifera*. Trees of minor importance include *Pinus banksiana*, *Picea glauca*, *Acer rubrum*, and *Populus balsamifera*. The raw data for these quadrats are presented in Appendix 7.

Carleton and Maycock (1978) and Bergeron and Bouchard (1983) have previously described mixed forest stands in the Ontario clay belt area. The sites described here are not on lacustrine clay deposits, however, occurring instead on less finely textured soils. Their vegetational composition can therefore be expected to differ considerably from the clay belt sites.

5.7.1 Classification of Sites

The sum of squares agglomeration (using chord distance) dendrogram is shown in Figure 5.19. Reference to a sum of squares versus the number of groups plot, and ecological considerations, suggest the recognition of seven vegetation types, giving a classification efficiency of 40.5%. The species composition, physiognomic structure, and habitat characteristics of each of these types are described below. Calculations of the mean, frequency, and variance of constituent species in each of the types are presented in Table 5.11. Types have been named according to their major constituent species.

I. *Picea mariana - Betula papyrifera - Abies balsamea*

The 17 quadrats of this type typically occur on gently to moderately sloping rocky substrates with a surface accumulation of fine sand and silt of variable depth. These are typical habitats of the rocky hills found in the study area. The tree stratum is of mixed composition, dominated by *Picea mariana*, *Betula papyrifera*, *Pinus banksiana*, and *Abies balsamea*. Balsam fir seedlings are a very common feature in the ground layer. The tall shrubs *Acer spicatum* and *Alnus crispa* occur with relatively high frequency. The low shrub-herb layer is dominated by *Clintonia borealis*, *Maianthemum canadense*, and *Aralia nudicaulis*, with *Vaccinium myrtillus*, *Coptis*
Figure 5.19  Sum of squares agglomeration dendrogram of the 119 quadrats of the mesic upland habitats at Elk Lake, Ontario. The seven vegetation types (I - VII) are also indicated. The quantities along the bottom of the dendrogram represent the number of individuals belonging to the corresponding branches; the lower level bifurcations are not shown.
Table 5.11 Means (M), variances (V), and relative frequencies (F) of the 52 most common species in each of the seven vegetation types (I - VII) described for the mesic upland habitats at Elk Lake, Ontario.
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<td>4.8</td>
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Table 5.1. Continued.
*groenlandicum,* and *Trientalis borealis* also occurring though with lower frequency and cover. Lichens are uncommon except as epiphytes. *Dicranum fuscescens,* a moss characteristic of rotted wood, is common. Most of these quadrats have rotted logs on the forest floor, and occasionally balsam fir individuals recently killed by spruce budworm are evident. In such areas this has opened up the canopy considerably.

Relatively mesic conditions prevail at these sites, attributable to the finely textured soils. Drainage is moderate to good, however, because of the sloping and rocky nature of these habitats. The presence of *Acer spicatum* and *Betula papyrifera* are both good indicators of these conditions, and of the disturbance nature of these habitats (Vincent 1965, Bergeron and Bouchard 1983).

Soil profiles are difficult to obtain because of the excessively rocky nature of the terrain. Where a good profile is obtained, weak podzolization is apparent below a 5-10 cm accumulation of poorly to moderately decomposed organic matter.

II. *Picea mariana - Populus tremuloides - Abies balsamea*

This type, which is defined by a group of 21 quadrats, is characteristic of flat to rolling, rocky, well drained terrain and fine textured soils. Habitats include rocky sites overlain with silty soil of variable depth, and compacted gravelly hardpans along the Montreal River. In some sites bordering lakes, a bouldery substratum with interspersed silt deposits occurs.

The canopy is dominated by a mixture of *Picea mariana,* *Abies balsamea,* and *Populus tremuloides,* though *Pinus banksiana* and *Betula papyrifera* also occur. At many sites mature balsam fir recently killed by spruce budworm are in evidence, underlying the disturbance nature of these communities. However, balsam fir seedlings are fairly common at most sites. Other major understory constituents include *Clintonia borealis,* *Cornus*
canadensis, Maianthemum canadense, Kalmia angustifolia, Aralia nudicaulis, and Trientalis borealis. Dicranum fuscescens grows on the rotting logs characteristic of these sites.

This type is quite similar to type I, differing primarily in its occurrence on rocky flats or rolling land rather than sloping situations. Conditions here are probably slightly more xeric (less soil and more rock), though nutrient status is likely similar. The dendrogram indicates that types I and II, which fuse at a fairly low level, together form a distinctive group which unites with the remaining types only at the final fusion.

III. *Populus tremuloides* - *Ailus crispa* - *Diervilla lonicera*

This grouping of 13 quadrats is characteristic of gravelly sands on upland sites along the Montreal River and upper Sydney Creek, often near monospecific stands of jack pine. *Populus tremuloides* forms a relatively open canopy, *Pinus banksiana* and *Betula papyrifera* also occur with high frequency though lower cover. *Ailus crispa* commonly occurs in the tall shrub layer, with *Corylus cornuta* also contributing. *Diervilla lonicera* is the dominant species of the low shrub layer. Other species include *Kalmia angustifolia*, * Vaccinium myrtillusoides*, *Cornus canadensis*, *Maianthemum canadense*, *Clintonia borealis*, *Aster macrophyllus*, *Aralia nudicaulis*, and *Linnaea borealis*. The tall fern *Pteridium aquilinum* occurs in about half the quadrats. Mosses and lichens are infrequent.

The gravelly nature of the substrate implies relatively xeric conditions. Further evidence for this, and for the relatively oligotrophic conditions, comes from the presence of jack pine, *Kalmia angustifolia*, and other species characteristic of dry uplands. Vegetationally this type has some affinities with the "*Corylus - Linnaea*" type of Mueller-Dombois (1964).

Two subgroups (see Figure 5.19) of this type are distinguished by habitat. The first occurs on gravelly sands along the rapids of Sydney Creek. These sites are characterized by high cover of tall shrubs and the presence
of *Pteridium aquilinum*. The second occurs on gravelly clay or pebbly sand. Here the canopy is typically a mixture of trembling aspen, jack pine, and white birch, and the tall shrub understory is less prevalent.

IV. *Populus tremuloides* – *Corylus cornuta* – *Aster macrophyllus*

The 27 quadrats making up this type are characteristic of well drained flat upland sites with finely textured sands or somewhat gravelly, fine sands. A relatively closed, monospecific tree stratum of trembling aspen is typical. Soil profiles show moderate podzolization, with a surface layer of moderately well decomposed leaf litter 5-15 cm in depth. A relatively dense tall shrub understory dominated by *Corylus cornuta*, and to a lesser extent *Alnus crispa*, develops beneath the tree canopy. *Aster macrophyllus* and *Diervilla lonicera* dominate in the lower shrub layer; other common constituents include *Clintonia borealis*, *Vaccinium myrtillusoides*, *Aralia nudicaulis*, *Maianthemum canadense*, and *Lycopodium obscurum*.

These sites are generally well drained, though they are more mesic than jack pine dominated stands on uplands with coarser soils. The decomposing leaf litter of these forests probably leads to more mesotrophic conditions, as reflected by the composition of the understory. However, further detailed studies would be required to substantiate this statement.

It seems likely that such sites may also support stands of jack pine. In fact, adjacent sites with very similar edaphic conditions were often found to support very different vegetation types, jack pine dominating on one and trembling aspen on the other. Thus historical factors may be more important than edaphic ones in dictating the vegetation occurring on sandy uplands. Subsequent microsite modification by these trees is also very important. Jack pine forms a relatively open canopy allowing considerable light penetration, which increases surface evapotranspiration and results in highly xeric conditions. Furthermore, the high acidity of jack pine litter leads to acidic conditions in the upper soil horizon, increasing podzolization and resulting in more oligotrophic conditions. Trembling aspen, by contrast,
forms a more closed canopy, resulting in lower light levels and decreased evapotranspiration, which in turn implies less xeric conditions. Furthermore, the leaf litter of this species is much less acidic than conifer needles (Bergeron and Bouchard 1983), and is in turn more readily decomposed by microorganisms, thus increasing nutrient availability. Thus jack pine modifies the habitat toward highly xeric and oligotrophic conditions (which are highly conducive to the spread of hot fire to which the species is so well adapted), whereas a trembling aspen canopy leads to more mesic, mesotrophic conditions. It is hardly surprising that the understory vegetation beneath these two canopies is so different.

V. *Betula papyrifera* - *Populus tremuloides* - *Corylus cornuta*

The tree canopy of the 24 quadrats making up this vegetation type is dominated by *Betula papyrifera* (just over 40% mean cover), although *Populus tremuloides* also occurs with lower cover (mean cover of 23%). *Abies balsamea* and *Picea mariana* also occur, both as saplings and trees. The tall shrubs *Corylus cornuta* and *Acer spicatum* are also characteristic, as is the tall, clonal fern *Pteridium aquilinum*. Together the tree and tall shrub strata form a relatively closed canopy (see photo, Appendix 10). Characteristic understory shrubs include *Aster macrophyllus*, *Clintonia borealis*, *Diervilla lonicera*, *Aralia nudicaulis*, *Maianthemum canadense*, *Trientalis borealis*, and *Lycopodium obscurum*. Mosses and lichens are uncommon.

This type is typical of slightly to moderately sloping rocky hillsides (other than south aspects) with some accumulation of fine-textured soil over the rock. Site conditions are characteristically xeric-mesic and probably oligotrophic to mesotrophic.

VI. *Populus tremuloides* - *Corylus cornuta* - *Acer spicatum*

This is a very homogeneous grouping of 12 quadrats characteristic of lowland sand deposits. *Populus tremuloides* forms a closed, monotypic
cover, achieving over 75% mean cover. A dense tall shrub layer is characteristic, dominated by *Corylus cornuta* (averaging about 50% cover) and *Acer spicatum* (just under 25% mean cover). The understory is similar to that of type IV, with *Aster macrophyllus* and *Clintonia borealis* predominating, and *Lycopodium obscurum*, *Aralia nudicaulis*, *Trientalis borealis*, and *Pteridium aquilinum* also achieving some importance (see photo, Appendix 10).

The dense overstory and tall shrub layer suggest more mesic conditions than those of type IV, to which this type shows some affinity in terms of species composition. This type tends to occur on somewhat finer soils, however, typically at relatively low elevations at the base of steep slopes.

**VII. *Populus balsamifera - Corylus cornuta***

This is a rare habitat within the study area, occurring in low lying areas along the Montreal River which are characterized by fine, silty soil. It is represented by 5 quadrats. A thick well-decomposed organic layer over a mineral substrate is characteristic. Such sites are therefore hydric and quite eutrophic (see also Bergeron and Bouchard 1983). The tree stratum is dominated by *Populus balsamifera* (averaging 55% cover), although *P. tremuloides* and *Picea glauca* also occur. Occasional saplings of *Abies balsamea*, *Picea glauca*, and *Picea mariana* are also present. The tall shrubs *Corylus cornuta* and *Acer spicatum* usually contribute to the upper understory. The understory is dominated by species demanding eutrophic, mesic - hydric conditions. These include *Streptopus roseus*, *S. amplexifolius*, *Viola pallens*, *Dryopteris austriaca*, *Osmunda claytoniana*, *Mitella nuda*, and *Coptis groenlandicum*. Less nutrient demanding species also occur, including *Rosa acicularis*, *Clintonia borealis*, and *Trientalis borealis*.

Bergeron and Bouchard (1983) state that the basic litter of balsam poplar leads to eutrophic conditions at such sites. They also note that sites dominated by this species generally have charcoal and burned stumps indicating a fire origin. This was noted at the sites described here.
5.7.2 Site Relationships and Environmental Characterization

Compositional divergences (see Section 5.4.3) for the seven types are presented in Table 5.12. The results indicate a close relationship between types I and II (and their relative isolation from the other five types), which is also apparent from the dendrogram structure (Figure 5.19). Interestingly, type IV shows highest affinity with type I, although it also shows relatively low divergence for all others except type VII. Types III and IV show low divergence, while type VII form an isolated group showing highest affinity with type VI. Overall the values reflect well the relationships implicit in the dendrogram structure. Again, the values are not meant to be treated in a strict statistical sense.

The types have also been characterized using physiognomic and environmental criteria (Table 5.13). This information was obtained as explained in Section 5.6.2. Again, nutrient status values are synthetic estimates and as such are tentative. Environmentally, types I and II are shown to be very similar, suggesting that they perhaps represent variants of the same mixed forest type. For the other types, environmental divergence is apparent, particularly with respect to substrate, drainage class, and soil particle size (all of which are related to moisture status). The importance of these environmental parameters to the vegetation is further examined in the next few sections.

5.7.3 Ordination of Sites

Principal components analysis (covariance matrix), correspondence analysis, and nonmetric multidimensional scaling (chord distance, specifying a two-dimensional solution) were all performed on the data set. The results were essentially similar, though the NMDS appeared to give the most parsimonious representation in two dimensions. Therefore only these results are discussed and presented here (Figure 5.20).
Table 5.12  Pairwise compositional divergences (using the 2I statistic) for the 7 mesic upland types. Values of chi-square ($\chi^2$), degrees of freedom (DF), and the standard normal deviate (Z) are given.
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<th>Substrate Type</th>
<th>Terrain Type</th>
<th>Drainage Class</th>
<th>Nutrient Status</th>
<th>Particle Size Class</th>
<th>Soil</th>
<th>Productivity</th>
</tr>
</thead>
<tbody>
<tr>
<td>Picea mariana</td>
<td>mixed conifer - deciduous forest. Poorly developed understory</td>
<td>rocky, with silt accumulation</td>
<td>sloping rocky hillside and hillocks</td>
<td>mesic</td>
<td>mesotrophic</td>
<td>fine</td>
<td>fine sand - silt</td>
<td>tree cover 35%</td>
</tr>
<tr>
<td>Pseudotsuga menziesii</td>
<td>mixed conifer - deciduous forest. Poorly developed understory</td>
<td>usually rocky, Silt and gravel</td>
<td>rolling, rock outcrops common, clay hardpan</td>
<td>mesic</td>
<td>xeric/mesic</td>
<td>coarse-fine</td>
<td>fine sand - silt</td>
<td>tree cover 50%</td>
</tr>
<tr>
<td>Abies balsamea</td>
<td>open deciduous forest, some conifers</td>
<td>gravelly sands</td>
<td>very gently slopes</td>
<td>xeric/mesic</td>
<td>mesotrophic</td>
<td>medium-fine</td>
<td>sandy</td>
<td>tree cover 55%</td>
</tr>
</tbody>
</table>
|                  | closed deciduous forest, tall shrubs | fine sand, some gravel | level | mesotrophic | oligotrophic/mesotrophic coupled
|                  | closed mixed deciduous forest | rock, overlain with fine sand or silt | sloping hillside (not facing) | xeric/mesic | xeric/mesic | fine | sand - silt |
|                  |                        |                        |                |                |                |                  |      |
|                  |                        |                        |                |                |                |                  |      |

Productivity:
- Tree cover 35%
- Black spruce DBH 10 - 15 cm height 8 - 12 m
- Balsam fir DBH 15 - 25 cm height 8 - 12 m
- White birch DBH 15 - 20 cm height 8 - 10 m

Tree cover 50%
- Black spruce DBH 10 - 15 cm height 10 - 14 m
- Balsam fir DBH 15 - 25 cm height 10 - 14 m
- Trembling aspen DBH 15 - 20 cm height 8 - 14 m

Tree cover 55%
- Trembling aspen DBH 10 - 16 cm height 8 - 12 m
- DBH 25 - 40 cm height 12 - 16 m

Tree cover 75%
- Trembling aspen DBH 10 - 20 cm height 8 - 14 m
- DBH 15 - 20 cm height 8 - 12 m

NOTES: A critical review of the conifer canopy type tree cover 35%
Table 5.13  Continued.
<table>
<thead>
<tr>
<th>VI</th>
<th>VII</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Dominant Species</strong></td>
<td><em>Populus tremuloideae</em></td>
</tr>
<tr>
<td></td>
<td><em>Corylus cornuta</em></td>
</tr>
<tr>
<td></td>
<td><em>Acer spicatum</em></td>
</tr>
<tr>
<td></td>
<td><em>Aster macrophyllus</em></td>
</tr>
<tr>
<td></td>
<td><em>Climax borealis</em></td>
</tr>
<tr>
<td><strong>Physiognomy</strong></td>
<td>closed deciduous forest, dense tall shrub</td>
</tr>
<tr>
<td><strong>Substrate Type</strong></td>
<td>fine sand</td>
</tr>
<tr>
<td><strong>Terrain Type</strong></td>
<td>level, or gentle slope</td>
</tr>
<tr>
<td><strong>Drainage Class</strong></td>
<td>mesic</td>
</tr>
<tr>
<td></td>
<td>mesic/hydric</td>
</tr>
<tr>
<td><strong>Nutrient Status</strong></td>
<td>mesotrophic</td>
</tr>
<tr>
<td></td>
<td>mesotrophic/eutrophic</td>
</tr>
<tr>
<td><strong>Particle Size Class</strong></td>
<td>medium-fine</td>
</tr>
<tr>
<td><strong>Soil</strong></td>
<td>sandy</td>
</tr>
<tr>
<td></td>
<td>O: 20 - 25 cm</td>
</tr>
<tr>
<td></td>
<td>A: 15 - 25 cm</td>
</tr>
<tr>
<td></td>
<td>poor - moderate podzol</td>
</tr>
<tr>
<td><strong>Productivity</strong></td>
<td>tree cover: 75%</td>
</tr>
<tr>
<td></td>
<td>Trembling aspen</td>
</tr>
<tr>
<td></td>
<td>DBH: 25 - 45 cm</td>
</tr>
<tr>
<td></td>
<td>height: 12 - 20 m</td>
</tr>
<tr>
<td></td>
<td>Trembling aspen</td>
</tr>
<tr>
<td></td>
<td>DBH: 30 - 35 cm</td>
</tr>
<tr>
<td></td>
<td>height 15 - 20 m</td>
</tr>
</tbody>
</table>
Figure 5.20 Nonmetric multidimensional-scaling (two-dimensional solution, utilizing chord distance) of the 119 quadrats of the mesic upland habitats at Elk Lake, Ontario. Symbols correspond to the seven vegetation types (I-VII). The stress value is 17.1%.
The horizontal axis serves primarily to distinguish sites dominated by a coniferous canopy from those dominated by a deciduous one. Interestingly, this was also the fundamental division of the sum of squares dendrogram (Figure 5.19). Rocky sites occur at the top right of the scattergram, while those occurring on sandy or silty flats occur at the far left. To aid in further interpretations, soil particle size values, and the presence of rock, were plotted on the scattergram (Figure 5.21). A general trend of coarser to more finely textured soil from lower left to upper right is indicated, and the increased frequency of rocky sites at the upper right is also apparent. A major trend in the vegetation, therefore, occurs from sandy upland flats to sloping, rocky areas overlain with clay and silt deposits. It would be difficult to establish this as a moisture gradient, since all these sites would be classified (with the exception of type VII) as well drained habitats (see also Bergeron and Bouchard 1983). On the sandy plains good drainage is attributable to the coarse texture of the soil, whereas the sloping, rocky nature of the other sites results in moderate drainage. Therefore, rather than referring to a moisture gradient, the trend is referred to here as an edaphic gradient. The presence of the hydric *Populus balsamifera* type in the upper left of the scattergram, however, suggests increasing moisture conditions from lower right to upper left. To investigate this further, performance values for selected common species were plotted over the scattergrams (Appendix 8). Species characteristic of the more rocky, sloping sites include *Dicranum fuscescens*, *Abies balsamea*, and *Betula papyrifera*. The following species are typical of the sandy upland flats: *Populus tremuloides*, *Aster macrophyllus*, *Dierovilla lonicera*, *Vaccinium myrtilloides*, *Alnus crispa*, and *Corylus cornuta*. In the lower right of the ordination *Pinus banksiana*, *Kalmia angustifolia*, *Picea mariana*, and *Cornus canadensis* are most common, while *Acer spicatum* is more frequent in the upper left. Species showing no overall clear-cut trend include *Clintonia borealis*, *Aralia nudicaulis*, *Lycopodium obscurum*, *Maianthemum canadense*, and *Pteridium aquilinum*. There appears, therefore, to be a trend from more xerio and oligotrophic conditions in the lower right (characterized by *P.*
Figure 5.21  Soil particle size values superimposed on the nonmetric multidimensional scaling of the 119 mesic upland habitats of Figure 5.20. Larger particle sizes are indicated by larger circles. A slash through the circle indicates the presence of gravel and/or stones. R = on rock, no soil sample available.
banksiana, K. angustifolia, and P. mariana) to more mesic, eutrophic sites at the upper right (indicated by the presence of Acer pseudosie (see Hosie 1979) and P. balsamifera stands).

The relationships between types summarized by the scattergram reveal some interesting trends. The somewhat arbitrary division between types I and II indicate that it may be better to recognize these types as a single mixed forest continuum. The overall similarity in their vegetational composition (Section 5.7.2), coupled with their low level of fusion in the dendrogram (see Figure 5.49) also suggest this. However, these two types are distinguishable in general terms on the basis of habitat (occurring on rocky hills and on bouldery, or rocky flats respectively), suggesting that they do have some ecological meaning. The proximity of types I and V appears to be attributable largely to the mutual presence of Betula papyrifera. The affinity of types II and III is attributable to somewhat similar habitat conditions, these groupings being characteristic of gravelly and bouldery sites respectively, which are both well drained substrates. Types IV and VI are also shown to be highly associated, although this is not readily apparent from the path of fusions of the dendrogram.

In conclusion, general trends in edaphic characteristics and moisture status are indicated. The most mesic types (VII, VI, and IV) occur at the far left. The other types are more xeric, though this is manifested in different ways. Types I and V are characteristic of upland rocky slopes with some soil accumulation, whereas types II and III are characteristic of well drained flatlands (gravel or rock in a matrix of fine textured soils). The dominance of coniferous versus deciduous tree species may be attributable more to historical factors than underlying habitat differences. Betula papyrifera, for example, will reestablish rapidly on rocky slopes following severe fire, and is able to resprout from burned stumps. Similarly, P. tremuloides produces small, wind-blown seeds and is able to regenerate from rootstock. Picea mariana cones are often serotinous, permitting the reestablishment of this species following a fire. These facts indicate the
importance of regeneration at a site following disturbance (primarily by fire) once a species is established there. Rowe (1961) has in fact stressed this point in discussing the concept of succession in boreal ecosystems. He argues eloquently that disturbance factors as well as environmental effects are important in determining vegetation composition in many boreal sites.

5.7.4 Species Classification

A classification into species ecological groups was performed using sum of squares agglomeration (SSA, with chord distance). The resultant dendrogram is shown in Figure 5.22. The existence of four groups is suggested, giving a classification efficiency of 35.4%. These groups are discussed below with regard to their habitat preferences.

A. This group of 17 species, which includes *Abies balsamea* and *Picea mariana*, is characteristic of the conifer dominated sites or rock-clay hillsides and bouldery flats. Two subgroups are recognizable, the first consisting of species adapted to drier conditions than those of the second. Overall these species are adapted to mesotrophic, mesic conditions.

B. This is a small group of 7 species requiring eutrophic, mesic conditions. They typically occur on low-lying silt or clay deposits, often beneath a canopy of *Populus balsamifera*.

C. This group of 14 species characterizes sandy or gravelly flats dominated by a closed deciduous canopy (*Populus tremuloides* and *Betula papyrifera*). Conditions are generally mesic (attributable in large part to the closed canopy) and mesotrophic (from the annual rain of nutrient-rich leaf litter).

D. This group consists of 14 species adapted to more xeric conditions than group C, typically occurring on well drained coarse sandy and gravelly sites. Two major subgroups can be delineated. The first is characteristic of xeric, oligotrophic conditions occurring on sand
Figure 5.22  Sum of squares agglomeration dendrogram of the 52 most common species of the mesic upland habitats at Elk Lake, Ontario. The four species ecological groups (A - D) are also shown.
uplands (and showing strong association with jack pine). The second is similar, but these species often prefer a somewhat more open canopy (increased insolation).

5.7.5 Species Ordination

Nonmetric multidimensional scaling (utilizing chord distance, and specifying a two dimensional solution) was used to summarize interspecific species associations, after first removing species occurring with a frequency of less than ten. The resultant scattergram is shown in Figure 5.23. A general trend from species adapted to xeric and oligotrophic conditions to those requiring eutrophic and mesic conditions is indicated (from left to right in the scattergram). The species occurring at the far left are strongly associated with jack pine (indicating drier conditions), while those at the far right typically occur beneath a *Populus balsamifera* canopy (indicative of nutrient rich, mesic to hydric conditions). Species near the center of the scattergram are somewhat intermediate in their moisture and nutrient requirements. A trend from species adapted to rocky, conifer dominated sites to those found on sandy to somewhat gravelly soils dominated by a deciduous canopy is also indicated, from the bottom to the top of the ordination. This may indicate a general trend from oligotrophic to more mesotrophic conditions, but further work would be required to substantiate this claim.

To summarize, the results suggest that interspecific associations develop largely in response to moisture (and perhaps nutrient) status. There is also some evidence to indicate understory-canopy affinities leading to the development of strong interspecific associations, particularly as regards the distinction between coniferous and deciduous canopies. Other workers, however, have found that in temperate forests such affinities are normally only weakly developed (Dix and Swan 1971; Carleton and Maycock 1981; Antos and McCune 1981).
Figure 5.23  Nonmetric multidimensional scaling (two-dimensional solution, utilizing chord distance) of the 52 most common species of the mesi upland habitats at Elk Lake, Ontario. Codes correspond to species names (the first four letters of the genus, and the first three of the species epithet). The stress value is 16.3%. 
5.7.6 Ecological Relationships

To summarize the overall trends in the 7 vegetation types and 4 species groupings, and to examine the interrelationships between the two classifications, an analysis of concentration was performed. The results are presented as three dimensional ordinations and are reproduced in Fig. 5.24. The first three axes account for the entire partitioned chi-square, while the relative sharpness is 9.37%.

Interesting trends are revealed from the ordination of the vegetation types. The first axis separates out types VII and VI, characteristic of more mesic deciduous situations, from the types which are typical of somewhat drier habitats. The second axis serves primarily to distinguish the coniferdominated forests from those with a primarily deciduous dominated canopies. The third axis distinguishes the more mesic deciduous vegetation types (V and VI) from the drier ones (III and IV). Environmental trends were examined by correlating axis scores for the seven types with quantifiable environmental factors (drainage class, soil particle size, and estimated nutrient status); see Table 5.14. Drainage class and nutrient status are highly correlated with the first axis (which accounts for 66% of the total chi-square), indicating a strong moisture-nutrient gradient. This is indicated by the multiple correlation values. The second axis is correlated somewhat with soil particle size, while the third axis shows poor correlation with these factors. The suggestion that nutrient status is important must remain tentative until detailed soil nutrient analyses are undertaken.

The ordination of species groups summarizes well the major trends indicated earlier. The first axis (representing the moisture-nutrient gradient), has groups A and D (oligotrophic, xeric-mesic) occurring at one end and group B (eutrophic, hydric) at the other. Group C, consisting of species adapted to more mesic conditions, is somewhat intermediate. The second axis serves mainly to distinguish the oligotrophic group A from...
Figure 5.24  Three-dimensional concentration analysis ordinations of the seven vegetation types (I - VII) and four species ecological groupings (A - D) of the mesic upland habitats at Elk Lake, Ontario. Note that these ordinations have a one-to-one correspondence. The partitioning of chi-square (d.f. = 36) is also given.
<table>
<thead>
<tr>
<th>Canonical variate (i)</th>
<th>Canonical correlation ($R_i$)</th>
<th>Chi-Square</th>
<th>Percentage</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td>0.4317</td>
<td>420.95</td>
<td>66.30</td>
</tr>
<tr>
<td>2</td>
<td>0.2493</td>
<td>140.44</td>
<td>22.12</td>
</tr>
<tr>
<td>3</td>
<td>0.1804</td>
<td>73.56</td>
<td>11.58</td>
</tr>
</tbody>
</table>

| Total               | $\chi^2 = 634.95$            | 100.00     |
Table 5.14  Correlations of the concentration analysis scores for the 7 mesic upland types with selected environmental parameters.
<table>
<thead>
<tr>
<th></th>
<th>$r_1$</th>
<th>$r_2$</th>
<th>$r_3$</th>
<th>$R^2$</th>
</tr>
</thead>
<tbody>
<tr>
<td>Drainage Class</td>
<td>0.927</td>
<td>0.151</td>
<td>0.174</td>
<td>0.927</td>
</tr>
<tr>
<td>Nutrient Status (estimated)</td>
<td>0.952</td>
<td>0.021</td>
<td>0.146</td>
<td>0.944</td>
</tr>
<tr>
<td>Soil Particle Size</td>
<td>0.350</td>
<td>0.687</td>
<td>−0.334</td>
<td>0.685</td>
</tr>
</tbody>
</table>
mesotrophic groups C and D. The third axis serves mainly to separate groups C and D, which fuse early on in the dendrogram (Figure 5.22).

Associations between the two ordinations are very revealing of the principle trends. Species group B is very strongly associated with type VII, and strongly isolated from the other groups. This underlies the much moister, nutrient rich status of these sites compared with the others. Vegetation type II shows high affinity with species group A, indicating the oligotrophic-mesotrophic, relatively mesic conditions occurring here. By constrast, type I shows an affinity for both species group A and D. This indicates mesotrophic but more xeric conditions than those of type II. The remaining types show highest affinities for species groups C and D, but with some interesting and revealing trends. Type V shows the highest affinity for group C, characterizing the more mesic, mesotrophic conditions prevailing here. Type VI shows an affinity for species group C and to some extent the more eutrophic, hydric group B, indicating even higher moisture and nutrient status at these sites. Both types III and IV show highest affinity for the drier species group D, underlying the more xeric conditions occurring here. However, type III also shows some affinity with species group A, indicating a tendency toward more oligotrophic conditions. By contrast, type IV shows greater affinity for the more mesic species group C, indicating less excessive drainage.

In conclusion, a trend attributable to changing moisture status appears to be of primary importance. This is confirmed by the analysis of soil particle size and considerations of substrate. A nutrient status trend is also indicated, but studies of soil fertility would be required to substantiate this.
5.7.7 Discussion

The results presented here have summarized the vegetational composition on upland sites in areas not dominated by jack pine. Two general subgroupings of stands are recognizable: the first is characterized by a canopy dominated by coniferous species, the second by a deciduous canopy. It is suggested that, at least within the study area, the existence of these canopies at a given site is dependent upon historical factors as well as environmental (primarily edaphic) ones. Closed stands of trembling aspen, for example, are characteristic of fine sand or somewhat gravelly flat plains. On rocky sites with some soil accumulation, any or all of the following tree species may occur: *Abies balsamea*, *Picea mariana*, *Betula papyrifera*, *Populus tremuloides*, and *Pinus banksiana*. *Betula papyrifera* appears to prefer somewhat sloping rocky sites, whereas *Abies balsamea* prefers flatter areas with greater soil accumulation. *Picea mariana* shows wide tolerance, occurring on xeric rock outcrops as well as in more mesic habitats.

It seems likely that the exact composition at a given locality will be dictated by three major factors: the environment, historical considerations, and chance. In broad scale, general surveys (e.g., Bergeron and Bouchard 1983) environmental considerations will be of primary importance, but in smaller scale, more detailed surveys the other factors take on some importance. Despite this, some general trends in the vegetation at Elk Lake can be related to environmental factors. Moisture status (related to particle size, presence or absence of rock and gravel, etc.) appears to be important, and nutrient status has been implicated as being important also.

By the criteria given by Bergeron and Bouchard (1983), the types described here, with the exception of type VII (*Populus balsamifera*), are all xeric and oligotrophic variants of vegetational groupings they described for Québec clay belt vegetation. This is hardly surprising given that the Elk Lake study area was chosen to incorporate only dry upland habitats.
The results of this section also support Rowe's (1961) contention that boreal vegetation consists primarily of 'disturbance forest', constantly adapting to onslaughts of various perturbatory influences. On these upland sites two catastrophic forces appear to be very important in vegetation structure and dynamics. The first is of course fire. The existence and persistence of *Populus tremuloides*, *P. balsamifera*, and *Betula papyrifera* are most certainly attributable to recurrent and regular fires, since these species are all highly shade intolerant. All three species produce profuse amounts of tiny, wind-blown seeds which readily germinate on the inorganic substrates following a burn. In addition, these species will resprout readily from rootstock. The second factor, particularly noticeable in recent years, is the effect of spruce budworm on mature stands of *Abies balsamea*. In some areas where balsam fir is particularly common, extensive defoliation and subsequent death of this species is apparent. Paradoxically, this effect may be most beneficial to balsam fir, since already established saplings develop and grow rapidly following opening of the canopy. Other species have difficulty establishing because little organic soil is exposed (as there would be after a fire), and even if they did establish they would likely be shaded out by the larger *Abies* saplings and other understory species. Nonetheless, some shade intolerant deciduous species may establish in gaps resulting from the budworm infestations, resulting in the 'disturbance climax' forest (that is, a mixture of so-called successional, shade intolerant tree species and more shade tolerant ones). Fire will serve to further perpetuate such a canopy structure. Fires will of course also give rise to monotypic stands of pyric species such as jack pine and trembling aspen, particularly in relatively uniform, xeric habitats.
CHAPTER 6

GENERAL DISCUSSION

This dissertation has contributed new information to three important topics in quantitative plant ecology. The first, that of determining an appropriate plot size in field enumeration, has been addressed from a statistical viewpoint. The strategy suggested involves minimizing the structure of a species covariance matrix obtained from the enumeration, using different plot sizes, of an homogeneous area. The plot size minimizing covariance structure will optimize type description by maximizing precision while minimizing interspecific associations within a type.

The second topic concerns the problem of determining the most suitable ordination technique for use in summarizing complex ecological data. Theoretical considerations suggest that non-metric multidimensional scaling has a number of advantages over eigenanalysis, relaxing the linearity assumptions of metric (eigenanalysis) strategies and offering much greater flexibility in the choice of a resemblance coefficient. The requirement of specifying the dimensionality of the final solution, often considered a detriment, may also offer some advantages, particularly in the summarization of complex data structure. A comparative assessment of ordination methods using simulated data suggests that inherent non-linear data structure can most effectively be summarized using non-metric multidimensional scaling in conjunction with an appropriately chosen resemblance function. It is concluded that the greater flexibility in coefficient choice, together with the relaxation of a priori assumptions, renders non-metric strategies of considerably greater utility in offering a parsimonious representation of non-linear data structure than more conventional metric methods.

The major portion of the thesis is devoted to the detailed quantitative examination of vegetation of a rather poorly-known boreal ecosystem. The study of vegetation structure and composition at Elk Lake, Ontario has
indicated a high degree of vegetational heterogeneity over a relatively small area. The vegetation has an overall mosaic or patchy appearance, with strong discontinuities between regions of relatively strong structural and compositional uniformity. Moisture status appears to be an important and fundamental environmental factor influencing the vegetation, with a strong dichotomy between wetland sites (habitats with the water table at or near the surface, either on organic substrates or on periodically flooded mineral soils) and those of upland habitats (on mineral soil above the water table, and on rock outcrops).

In wetland habitats, the nature of the parent substratum (organic or mineral), the extent and frequency of flooding, the degree of lateral ground water movement, and the degree of decomposition of organic substrates all appear to be important factors determining vegetation composition. Unique combinations of these factors at different sites lead to interspecific species associations which give rise to characteristic vegetation types. The results of the analyses undertaken here suggest strong group structure in the boreal wetlands at Elk Lake, and a strong correspondence between vegetation types and ecological species groupings. This appears to be the result of discontinuities in environmental space. Overall, the nine vegetation types recognized appear to develop in response to complex, synergistically interacting environmental gradients related to surface moisture and nutrient status (specifically pH, water conductivity, and nutrient availability). This agrees with previous studies of boreal wetland habitats (e.g. Heinselman 1963, 1970). However, more detailed studies of the nutrient status of the sites would be required to substantiate and quantify this conclusion. The role of historical (probabilistic as opposed to deterministic) factors should also be considered.

The upland habitats at Elk Lake are also highly diverse. It appears that drainage class, soil particle size, depth to water table, and possibly nutrient status, are important factors in determining vegetation composition in these habitats. A general trend from xeric - oligotrophic
to mesic - mesotrophic conditions is indicated, suggesting that the vegetation responds most strongly to a complex moisture - nutrient gradient. This is in keeping with the results of Carleton and Maycock (1978, 1980) and many others. There is some indication that historical and other factors (e.g. fire, diaspore source, previous site history) may also have some influence on the present-day vegetation, however.

A major dichotomy exists in the upland sites, with xeric, oligotrophic stands dominated by typically monospecific stands of Jack pine distinguished from those upland sites dominated by other species. Within the Jack pine group ten vegetation types were recognized, with trends attributable mainly to moisture status (soil particle size and depth to water table), substrate type, and possibly nutrient status. A vegetational continuum is suggested, however, indicating a corresponding continuous change in soil moisture conditions in these habitats. The remaining upland forests are quite heterogeneous. An important distinction exists between stands dominated by coniferous species (primarily Abies balsamea and Picea mariana) and those with a deciduous overstory (Populus tremuloides and/or Betula papyrifera). The seven vegetation types recognized appear to develop in response to moisture and perhaps nutrient status, with substrate type playing a particularly important role. Monospecific stands of trembling aspen are typical of upland flat sandy deposits, while the coniferous mixed forests predominate on finer soils usually associated with rock. White birch typically occurs in well-drained sites, including rocky slopes of relatively low insolation and on gravelly soils. As in the Jack pine dominated uplands, a vegetational continuum is indicated corresponding to continuously changing environmental conditions.

To summarize, the following environmental factors appear to be most important in determining spatial distributions in the vegetation at Elk Lake:

1. Substrate type - A fundamental distinction is made between organic and mineral substrates. The degree of decomposition of organic
material is also important. For inorganic substrates, soil texture and the presence of gravels, boulders, or exposed rock, are important.

2. Moisture status - On mineral substrates in upland habitats soil particle size, depth to water table, and extent of drainage (as related to slope and presence of rock, boulders, and/or gravels) are important determinants of moisture availability.

3. Nutrient Status - This factors appears to be particularly important in wetland habitats. Annual or regular flooding results in the deposition of silt which increases nutrient status, while lateral surface or ground water flow may also enrich a site, particularly those occurring on organic substrates. In upland habitats, soil parent material and degree of podzolization will affect soil nutrient status and availability.

Combinations of these factors lead to a unique habitat at a given site, and a corresponding species assemblage characteristic of such a habitat. The wetlands data suggests relatively well developed environmental discontinuities, leading to unique habitats with a corresponding species assemblage showing strong group structure. Upland habitats are by contrast more continuous in environmental characteristics, leading to a continuum in vegetational composition.

Any discussion of vegetation structure and composition in the boreal forest must also consider the role of historical and biotic factors. Such influences add a probabilistic component to the study of vegetation. In both a spatial and temporal context, fire plays an integral role in determining vegetation structure and composition at a given site. In fact, fires are so frequent and influential that considerations of fire-free successional sequences must remain no more than hypothetical. For example, Dix and Swan (1971) found that trees at Candle Lake, Saskatchewan were no more than 120 years old, and that most stands were much younger. Similar observations
were made by McLean and Bedell (1955) for the Ontario clay belt.

Dix and Swan (1971; also Rowe 1961, Carleton and Maycock 1978) have evoked the 'pulse strategy' of Odum (1969) to explain temporal dynamics in boreal ecosystems. By this strategy fire maintains healthy, productive stands near the early stages of an hypothetical successional sequence. Similarly, Loucks (1970) cites the high incidence of fire as resulting in a randomly perturbed cyclical pattern of development in boreal ecosystems. The degree of occurrence and severity of fire is important in determining, quite independently of deterministic factors such as substrate conditions, the vegetation at a given site. The observation of Ritchie (1956) that upland sites of apparently identical topographic and substrate conditions may support floristically different species compositions is undoubtedly attributable to historical factors related to fire. Specifically, the vegetation which was present before a fire will often reestablish at the same site. This is particularly true of sites dominated by jack pine, trembling aspen, white birch, and balsam poplar (Dix and Swan 1971). Thus in addition to substrate and related influences, which are deterministic in nature, the vegetation at a given site is determined also by a probabilistic or chance component related to fire and fire history. On balance, the following factors appear to be important in determining the vegetational composition at a given site:

1. Nature of the substrate.

2. Soil moisture conditions.

3. Fire history (severity, and frequency of occurrence).

4. Nature of the vegetation at the time of a fire.

5. Nature of the adjacent vegetation (as a diaspore source).

McIvor (1970) has hypothesized that species of pyric ecosystems have adapted by increasing their flammability, sacrificing the individual for the
benefit of the species as a whole. In addition, pyric species are adapted to survival and competition in the presence of recurrent fires. Carleton and Maycock (1978) have termed a fire ecosystem an unpredictable environment, but this is somewhat misleading. While the exact timing of a fire is largely unpredictable, fire is a recurrent phenomenon to which boreal species are well adapted. Thus, in an evolutionary context recurrence implies that a fire ecosystem is a highly predictable one. Species adaptations to an unstable pyric boreal ecosystem include:

1. **Effective regeneration following fire.** This may be manifested in a number of ways: resprouting from underground perennating organs (eg. trembling aspen and white birch, Ahlgren 1974; and many ericaceous and other shrubs, Carleton and Maycock 1978), serotiny (eg. jack pine) or semi-serotiny (eg. black spruce, Larsen 1980), and long distance dispersal (eg. the wind-blown diaspores of trembling aspen, white birch, *Salix*, lichens, etc; also, bird and mammal dispersed propagules).

2. **Rapid growth and reproduction within the timespan of mean fire recurrence** (Shafii and Yarranton 1973; Dix and Swan 1971).

3. **Rapid diaspores establishment.** Opportunistic species are therefore favoured (Shafii and Yarranton 1973; Carleton and Maycock 1978).

4. **Adaptations to colonizing open, exposed sites with high light levels and mineral seed beds** (eg. jack pine, trembling aspen).

5. **Fire stimulated seed germination** (Carleton and Maycock 1978).

Dix and Swan (1971) examined the successional status of common boreal tree species in upland habitats. They concluded that fire rather than a successional sequence is important in the temporal dynamics of boreal ecosystems. Species such as jack pine, trembling aspen, white birch, balsam poplar, and white spruce were found to be primarily pioneer species after fire, rarely occurring in the lower tree understory layer in stands at Candle
Lake. Black spruce was found to have some invasion ability until about 20 years after the original disturbance. Interestingly, they found that balsam fir has little pioneer status. Indeed, this species was found to establish and reproduce beneath previously established canopies. Spreugel (1976; also Carleton and Maycock 1978) cite evidence that the perpetuation of this species is dependent upon catastrophic events. Evidence from the present study supports this, as extensive regeneration of balsam fir was observed following opening of *Abies balsamea* canopies by spruce budworm.

Carleton and Maycock (1978; after Dix and Swan 1971) have suggested that upland boreal vegetation may be held in "check," with succession arrested after the initial invasion of tree species due to a lack of a lower tree canopy. This may be attributable to a lack of seed source of shade tolerant species, edaphic factors, or competition from understory shrubs. There is good evidence for this at Elk Lake, as many stands showed poor tree regeneration in the understory. This was not true at all sites, however, and it would be misleading to make any generalizations regarding overstory replacement (or lack of it) without examining the question in greater detail and over a wider range of sites.

Future work in boreal ecosystems should concentrate on the collection of detailed quantitative environmental data. This will help elucidate which environmental factors are most important in determining the vegetation at a given site, and will also indicate those factors most limiting to the ecosystem. Indirectly such a strategy may also help determine the relative importance of deterministic versus probabilistic phenomena in dictating the vegetational composition of a site.
APPENDIX 1

Scattergrams resulting from the comparison of metric and nonmetric multidimensional scaling ordination strategies based on artificial data sets (coenoplanes) of varying degrees of species turnover (measured in half-change (or HC) units). Points represent individuals, which are connected by grid lines. Half-change units for the eleven different coenoplanes are indicated in each case. Symbol codes for the ordination strategies are as follows:

CAE - Principal co-ordinates analysis, euclidean distance.
CAAC - Principal co-ordinates analysis, chord distance.
CAOD - Principal co-ordinates analysis, simultaneous double standardization and euclidean distance.
MDSE - Nonmetric multidimensional scaling, euclidean distance.
MDSC - Nonmetric multidimensional scaling, euclidean chord distance.
MDSD - Nonmetric multidimensional scaling, simultaneous double standardization and euclidean distance.
CA - Correspondence analysis.
DCA - Detrended version of correspondence analysis.
APPENDIX 2

The determination of soil particle size and soil water-holding capacity.
Soil particle size was determined for all of the soil samples collected. Each sample was first air dried for 24 hours. Following this, the sample was sorted into six fractions by passing it through a series of sieves with the following mesh diameters: 1.0, 0.5, 0.212, 0.105, and 0.053 mm. The fraction which failed to pass through the largest sieve size was not considered in subsequent analyses. The remaining five fractions have the following mean particle diameters: $1 = 0.75$ mm, $2 = 0.356$ mm, $3 = 0.1585$ mm, $4 = 0.079$ mm, and $5 = 0.039$ mm. Note the multiplicative nature of this series, with each value approximately half the previous one. These mean diameters were calculated as the average of the mesh diameters within which the fraction falls; for example, soil which passes through the 0.5 mm sieve but not the 0.212 mm one has an average diameter of $(0.5 + 0.212)/2 = 0.356$ mm. Each of the resulting five fractions were weighed to the nearest 0.1 grams, and then converted to proportions of the total sample weight.

Soil particle size was calculated after first linearizing the multiplicative scale of the mean particle diameter values:

$$X = \left[p_1 \log_{10}(0.75\text{ mm}) + \ldots + p_5 \log_{10}(0.039\text{ mm})\right]$$

Note that $p_1$ is the proportional weight of fraction 1, $p_2$ the same for the second fraction, and so forth. Soil particle size is then given by $Y = 2^X$.

To test the relationship between soil particle size and water-holding capacity, 65 of the samples were chosen to determine their water-holding capacity using the method of Cox (1976). One hundred grams of air dried soil was placed in a tin can with a hole and a piece of filter paper at the bottom. The can, after being tapped to settle the soil, was placed in 4 cm of water for 3 hours to ensure saturation. It was then placed on paper towelling for 3 hours and allowed to drain. The can was then weighed (saturated weight) and then placed in an oven at 105°C for 24 hours, after which it was weighed again (dry weight). Water-holding capacity is given by the formula:

$$\text{Capacity (\%)} = \left(\frac{\text{saturated weight} - \text{dry weight}}{\text{dry weight}}\right) \times 100$$

The scattergram of the water-holding capacity versus soil particle size is presented on the next page. The fitted linear regression equation is highly significant ($F = 61.55$, p. less than 0.01).
APPENDIX 3

Raw data for the wetland habitats at Elk Lake, Ontario. Species occurring with a frequency of less than 10 are not included. The relevés have been sorted and grouped according to the sum of squares agglomerative dendrogram shown in Figure 5.2, while sorting and grouping of species is based on the dendrogram results presented in Figure 5.4.
APPENDIX 4

Species performance plots for the wetland habitats at Elk Lake, Ontario. Symbols corresponding to percent cover of a given species are superimposed on the nonmetric multidimensional scaling scattergram shown in Figure 5.3. The symbols are circles of increasing size corresponding to increasing cover, using the following code (1 - smallest circle, 9 - largest one) which approximates a square root transformation:

<table>
<thead>
<tr>
<th>Code</th>
<th>Cover Range</th>
</tr>
</thead>
<tbody>
<tr>
<td>-</td>
<td>absent</td>
</tr>
<tr>
<td>1</td>
<td>1 - 2</td>
</tr>
<tr>
<td>2</td>
<td>3 - 6</td>
</tr>
<tr>
<td>3</td>
<td>7 - 12</td>
</tr>
<tr>
<td>4</td>
<td>13 - 20</td>
</tr>
<tr>
<td>5</td>
<td>21 - 30</td>
</tr>
<tr>
<td>6</td>
<td>31 - 45</td>
</tr>
<tr>
<td>7</td>
<td>46 - 60</td>
</tr>
<tr>
<td>8</td>
<td>61 - 75</td>
</tr>
<tr>
<td>9</td>
<td>greater than 75</td>
</tr>
</tbody>
</table>
Alnus rugosa

Rubus pubescens
Thalictrum polygamum

Gaultheria hispidula
Carex trisperma

Spinae x girosehoni
Larix laricina

Thuja occidentalis
Smilacina trifolia

Vaccinium oxyccoccus
APPENDIX 5

Raw data for the xeric, jack pine dominated upland habitats at Elk Lake, Ontario. Species occurring with a frequency of less than 10 are not included. Releves are sorted and grouped according to the sum of squares agglomeration dendrogram shown in Figure 5.12. Species have been sorted and grouped according to the dendrogram in Figure 5.16.
APPENDIX 6

Species performance plots for the xeric, jack pine dominated upland habitats at Elk Lake, Ontario. Symbols corresponding to percentage cover of a given species are superimposed on the nonmetric multidimensional scaling scattergram shown in Figure 5.13. Symbol codes correspond to those used in Appendix 4.
Betula papyrifera

Populus tremuloides
<table>
<thead>
<tr>
<th>Ploca varians</th>
<th>Diervilla lonicera</th>
</tr>
</thead>
</table>

[Graph showing distribution of Ploca varians and Diervilla lonicera species]
Ledum groenlandicum

Kalmia angustifolia
APPENDIX 7

Raw data for the mesic upland habitats at Elk Lake, Ontario. Species occurring with a frequency of less than 10 are not included. Releves are sorted and grouped according to the sum of squares agglomerative dendrogram shown in Figure 5.19. Species have been sorted and grouped according to the dendrogram in Figure 5.22.

APPENDIX 8

Species performance plots for the mesic upland habitats at Elk Lake, Ontario. Symbols corresponding to percentage cover of a given species are superimposed on the nonmetric multidimensional scaling scattergram shown in Figure 5.20.
APPENDIX 9

Selected aerial photographs of the Elk Lake study area.
North occurs at the top in each case.

Page

355 Stabilized dune system, northeastern portion of the study area. Monospecific jack pine stands at lower left and on dune ridges (dark areas). Chamaedaphne - black spruce bog at centre, and in dune slacks. Balsam fir - black spruce - trembling aspen stands occur at lower right.

356 North-central portion of study area, showing Montreal River and powerline-road cut. Marsh near centre of photo. White birch - trembling aspen - jack pine stands at lower left. Monospecific jack pine stands at upper left, with some stands of mixed jack pine - trembling aspen (on gravel) at top left and lower right.

357 Central portion of study area. Montreal River and Sydney Creek (extreme lower right) are shown, along with powerline and road cuts. Monospecific stands of jack pine predominate at lower right. Open jack pine stands (the result of local fire?) at centre. Black spruce bogs at lower left. Rocky hill with mixed forest of balsam fir, black spruce, and white birch occur at the top centre.

358 Lower - central portion of study area, showing lower Sydney Creek (flowing into Montreal River at extreme top centre). Central area dominated by monospecific stands of trembling aspen. Monospecific jack pine stands occur in most other areas. Note the open jack pine stands at the lower right, and small pockets of trembling aspen surrounded by jack pine just above this (trembling aspen shows as a lighter shade).
APPENDIX 10

Photographic plates, showing various sites in the Elk Lake study area.


C. Wetlands. Type II. *Picea mariana* - *Chamaedaphne calyculata* - *Sphagnum* bog. p. 137.


G. Wetlands. Type IV. *Alnus rugosa* - *Viola patens* thicket. p. 139.

H. Wetlands. Type IX. *Carex* - *Calamagrostis* marsh. p. 143.

I. Wetlands. Type VI. *Fraxinus nigra* hardwood swamp. p. 140.

J. Xeric uplands. Type II. *Pinus banksiana* - *Vaccinium angustifolium* - *Cladina rangiferina*. p. 197.

K. Wetlands. Type VII. *Thuja occidentalis* - *Sphagnum* swamp. p. 141.

REFERENCES


Gleason, H. A. (1917). The structure and development of the plant association. 


Hare, F. K. (1950). Climate and zonal divisions of the boreal forest formations in eastern Canada. Geogr. Rev. 40: 615 - 635.


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