

Dynamics of the boreal forest south of James Bay

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Ordination models of approximate environmental and dynamic relationship between eight boreal tree species were constructed based upon principal components analysis and Kruskal's nonmetric multidimensional scaling. The assumptions inherent in these models are stated and discussed. The data consisted of 152 forest stands from the closed-crown boreal forest zone of Ontario and Quebec south of James Bay. Sequential forest succession, as demonstrated by similar techniques for a section of the Wisconsin evergreen–hardwood forest, is not common in the region of boreal forest studied. However, for those species in common between this and the Wisconsin study, similar dynamic pathways are indicated despite differences in sample size and field technique. Tree species developmental pathways, as indicated by 'succession vectors' on the ordination models are, for the most part, short and circular with the exception of *Abies balsamea* (balsam fir). This reflects the reestablishment of similar, relatively monospecific forest stands following catastrophic forest destruction by fire and (or) other agencies. Where catastrophe does not intervene, deciduous primary forest species may be succeeded by an understory of *A. balsamea* or by *Picea mariana* (black spruce). Equally, some forest stands of primary establishment may become decadent with little or no subsequent tree growth. These observations are discussed with respect to the general notion of forest succession.

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En se fondant sur l'analyse en composantes principales et sur la technique non-métrique multidimensionnelle de Kruskal, les auteurs ont construit des modèles d'ordination des rapports environnementaux et dynamiques entre huit espèces boréales arborescentes. Les hypothèses inhérentes à ces modèles sont énoncées et discutées. Les données consistent en 152 peuplements forestiers de la zone de la forêt boréale fermée de l'Ontario et du Québec au sud de la baie de James. Une succession forestière séquentielle, telle que celle démontrée par des techniques semblables pour une partie de la forêt mixte du Wisconsin, est rare dans la région étudiée. Cependant, les espèces communes à cette région et à celle étudiée au Wisconsin montrent les mêmes sentiers dynamiques, malgré des différences dans la taille des échantillons et dans les techniques de terrain. Les "sentiers de développement" des espèces arborescentes, tels que révélés par les "vecteurs de succession" dans les modèles d'ordination, sont surtout courts et circulaires, à l'exception de celui de l'*Abies balsamea*. Cela reflète de ré-établissement de peuplements forestiers semblables et relativement monospécifiques après une destruction forestière catastrophique par le feu et (ou) d'autres facteurs. Lorsqu'une telle catastrophe être succédées par une repousse d'*A. balsamea* ou par *Picea mariana*. Certains peuplements forestiers primaires peuvent aussi devenir décadents et les arbres présentent alors une croissance subséquente faible ou nulle. Ces observations sont discutées en rapport avec le concept général de succession forestière.

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Introduction

In broad descriptions of boreal forest vegetation, the spruce–fir association has often been regarded as the ultimate developmental stage (Shelford 1963; Eyre 1968; La Roi 1967; Oosting 1948). A monoclinal view has prevailed (Clements 1916) qualified by the understanding that a spruce–fir regional climax may rarely develop owing to the prior intervention by some catastrophic agency such as fire, insect attack, or windfall. Rowe (1961) has chal-

lenged this view and argues that the forests resulting from primary establishment in northwestern Alberta do not show a gradual transition to 'climax' types in the absence of external catastrophe. He (Rowe 1961) remarks: "Decadent forests do not return through an inevitable cycle to youth and an optimum phase but rather tend to remain open, ragged, and frequently brush-filled, awaiting the rejuvenating touch of fire, flood, or windfall-ploughing of the soil."

The same author goes on to stress the role of substrate in determining the path of forest development.

In addition to environmental features, these dynamic views must be taken into consideration when analyzing extensive boreal forest vegetation data. Conventionally, ordination methods are applied in attempts to identify the major gradients affecting vegetational composition. Such methods produce an ordering of species and (or) sites along axes by various criteria.

Principal components analysis (PCA) effects an ordering of species or sites along axes on the criterion of accounting for the maximal directions of total variance (Orloci 1975), and these may or may not correspond to recognizable environmental trends. Geometrically, however, the method may also be viewed as a means of reducing a set of points, representing species or stands in stand-species multidimensional space, to a few dimensions for ease of interpretation (Dale 1975). Nonmetric scaling methods extend this geometric view further by emphasizing a total point configuration within a defined number of dimensions at the expense of ordering species or stands along individual axes. Despite this different perspective, nonmetric methods have been shown to be effective at recovering environmental trends (Noy-Meir 1974; Austin 1976; Prentice 1977).

Principal components analysis has been widely used in vegetation research with some success at interpreting vegetation response to underlying environmental variables (Yarranton 1967; Austin 1968; Gittins 1969; Neal and Kershaw 1973). In general, however, this approach has met with poor success in forest vegetation studies. Bellefleur and Auclair (1972) have applied PCA to Quebec boreal forest data, both with and without the inclusion of environmental variables. They refute Whittaker's (1967) suggestion that vegetation characteristics provide a better approach to interpreting vegetation-environment relationships (indirect gradient analysis) than direct, environmental gradient analysis (Loucks 1962; Jeglum *et al.* 1971). Goff and Zedler (1972) make the cogent observation that the relationship between interpoint distance in ordination and ecological distance, as measured by spatial interspecific association, will be far more direct in communities composed of short-lived individuals such as grasslands, old fields, or aquatic vegetation than in forest communities where individuals may possess life spans of several centuries and enter the community at different points in time.

The ideal ordination model should be able to account for both environmental and dynamic

change as sources of variation in forest vegetation data. Goff and Zedler (1972) extend the geometric view of PCA to thinking not of sets of points in reduced euclidean space but to vectors possessing both magnitude and direction through ordination space, where each vector represents a tree species. Distance along each vector describes increasing tree girth and, by implication, tree age.

This study is concerned with boreal forest vegetation in the regions of Ontario and Quebec to the south of James Bay. The objective has been to provide a broad description of interspecies relations among trees, their distribution in relation to environment, and individual tree species dynamics across this regional landscape as a framework for presenting further results from the same research project at a later date. Multivariate techniques are useful in the detection of such major patterns and effectively summarize the results in succinct graphical form. For this reason, the method of Goff and Zedler (1972) has been applied to an extensive set of data on the trees and saplings within the study region. In addition, the contrasting notions of successional development toward a spruce-fir climax (Shelford 1963; Eyre 1968; La Roi 1967; Oosting 1948) in the absence of external catastrophe or toward a degraded, open and brush-filled forest (Rowe 1961) are considered on the basis of more empirical methods of data summary.

Description of Area

The boreal forest in North America extends in a wide latitudinal belt from Alaska-Yukon in the northwest to Newfoundland in the east (Rowe 1972). The central-eastern section of this zone extends south of James Bay where it reaches its narrowest latitudinal width owing to climatic compression between the cold, year-round influence of Hudson Bay to the north and the warmer, ameliorative effects of the Great Lakes to the south. The area of study occupies this zone of compression (Fig. 1) and is bounded in the west roughly by the Albany-Kenogami river system, while the eastern limit is formed by a line running south-southeast from Rupert House (51°29' latitude, 78°50' longitude) on James Bay to Ottawa (45°27' latitude, 75°48' longitude).

The area includes the southernmost section of the James Bay Lowlands, characterized by underlying Paleozoic rocks covered both by glacial and marine quaternary deposits. This section is marked by very little relief except where dissected by major river valleys such as those of the Moose River drainage system. The area also includes the whole of the Ontario and Quebec clay belt from Hearst,

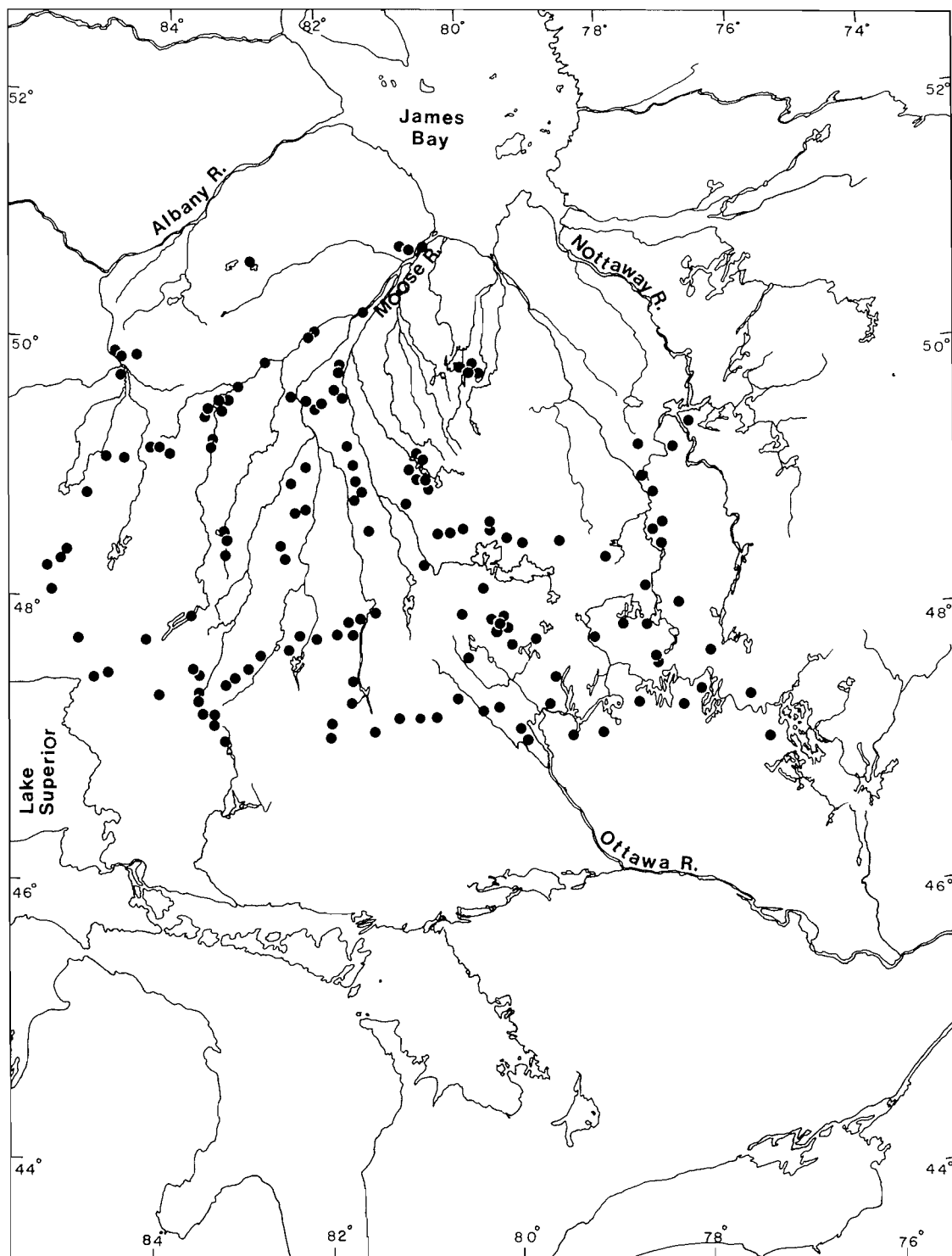


FIG. 1. Map of the study region showing the locations of 152 boreal forest stands.

Ontario, to Senneterre, Quebec. This section is typified by heavy clay deposits from glacial Lake Barlow-Ojibway underlain by archaic greenstones and crystalline rocks of the Precambrian Shield. Relief is poor in this region except where intrusions of rock project up through the clay or where esker ridges of gravel have been formed. Numerous glacial outwash sand plains are also present. On the western edge of the region, a small portion of the exposed Shield is included. This is characterized by rolling topography which becomes more vigorous as Lake Superior is approached.

Many of the forest communities are monospecific in dominance but a noticeable proportion are composed of mixtures of tree species. Much of the Lowlands section in the north supports 'open' or 'subarctic' woodland (Hare 1954). Only the river valleys, which possess a warmer microclimate and more favourable substrates, can support true closed boreal woodland and it is only this type of northern stand that is included in the analysis. Here *Picea glauca* (white spruce) and *Populus balsamifera* (balsam poplar) forests predominate. Further south, *Picea mariana* (black spruce) forests occupy a wide range of habitats from wet, lowland bogs to very dry rock outcrops. *Pinus banksiana* (jack pine) forms even-aged stands over large areas on outwash sand plains. In contrast, a well developed *Abies balsamea* (balsam fir) forest is relatively infrequent, usually found on moist, sandy soil in upland situations. This species, however, is abundant in a wide range of deciduous and mixed forests dominated by other tree species. These consist mostly of *Populus tremuloides* (trembling aspen) or *Betula papyrifera* (paper birch) forests. *Populus tremuloides* now covers extensive areas of the clay belt possibly owing to both postfire growth and the extensive human activity which has prevailed for the past 100 years. In contrast, *B. papyrifera* forests are more restricted to the well drained upland sites, most frequently on steep hillsides, and consequently are found more on the Precambrian Shield section of the study area.

Methods

Field Methods

One hundred and fifty-two forest stands were selected within the region of interest on the basis of criteria which were judged subjectively in the field. These consisted of relative continuity of forest canopy, no evidence of unnatural disturbance such as selective logging or grazing, apparent homogeneity over a minimal extent of 5 acres (1 acre = 0.405 ha), and uniformity of substrate characteristics and topography throughout.

In addition the compositional criterion that truly boreal tree species should constitute a sum of greater than 50% importance, as estimated by the importance value (see below), was adhered

to as an *a posteriori* decision for stand inclusion in the dataset. 'Boreal' trees were taken to be *Picea mariana*, *Abies balsamea*, *Picea glauca*, *Pinus banksiana*, *Larix laricina*, *Populus balsamifera*, and *Picea rubens* (cf. Marie-Victorin 1964). *Betula papyrifera* and *Populus tremuloides* were regarded as of neutral weight because they are very widespread in temperate North America. Species considered typical of the Great Lakes - St. Lawrence forest region (Rowe 1972) such as *Pinus strobus*, *Pinus resinosa*, *Thuja occidentalis*, *Tsuga canadensis*, *Fraxinus nigra*, *Betula lutea*, and *Acer rubrum* were regarded as compositional elements of antithetic value. These correspond to the floristic elements which typify the 'Regione Laurentienne' of Marie-Victorin (1964).

Data was collected for this study by the point-quarter method (Cottam and Curtis 1956) on both trees and saplings. The arbitrary division between these two classes was set at 12 in.² (77.4 cm²) basal area at breast height (BABH). Thirty points were laid by random siting (Orloci 1975, p. 12) within each stand.

Methods of Analysis

The conventional Wisconsin School summary statistics were calculated for each species in each stand (Curtis and McIntosh 1950). These consisted of relative density, relative frequency, and relative dominance for trees (basal area). These three relative values were then summed into an importance value for the tree data while only relative frequency and relative density were summed for a sapling index. Such composite indices have been criticized by Orloci (1975) in that their components are non-commensurable and nonindependent of one another. The criticism is valid for the comparison of species between different stands. As used here, where the main objective is to gain some idea of the status of tree representation in contrast with sapling representation within the same stand, the nonlinear nature of these importance values is less critical.

A second, adjusted relative density measure was calculated for each species by lumping tree and sapling data after first correcting for differences in absolute density between the two sets as estimated by the point-quarter method. To ensure that only significant species were included in the analysis, an arbitrary threshold of 5% adjusted relative density was chosen above which a tree species was considered present in a stand. Below this threshold, a species was considered absent. Table 1 shows tree species presence among 152 stands according to the threshold criterion. Those species present in 10 or more stands were included in the subsequent analysis. This restriction initially gave nine tree species for inclusion but *Thuja occidentalis* (white cedar) was rejected from the list as it did not occur as a leading dominant in any of the stands. The data matrix then consisted of an 8 × 152 table of presence-absence scores. This was used as the basis for calculating Cole's index (Cole 1949; Goff 1975) between species.

Reference Model Construction

The 8 × 8 similarity matrix was factored according to the method of principal components (PCA) such that the sum of squares of the species scores equalled the corresponding eigenvalue. A full account of the approach is presented by Goff and Zedler (1972). A criticism of this model is that it is nonorthogonal in euclidean space. It uses the R-mode form of the product-moment correlation coefficient or, in this case, a scaled form of it to perform a Q-mode analysis (Orloci 1967a). This action was justified by Goff and Zedler (1972) on the basis of ecological usefulness. For the purposes of comparison, the same approach has been adopted in the present analysis. By plotting the first two components as a scatter diagram, a two-dimensional reference model is produced.

An alternative, orthogonal, reference model was also produced by the method of principal coordinate analysis (PCORD).

TABLE 1. Tree species presence within 152 boreal forest stands. Threshold criteria for presence are outlined in text

Symbol	Species name	Presence
Pm	<i>Picea mariana</i>	96
Ab	<i>Abies balsamea</i>	83
Pib	<i>Pinus banksiana</i>	47
Pt	<i>Populus tremuloides</i>	47
Bp	<i>Betula papyrifera</i>	40
Pg	<i>Picea glauca</i>	34
Pba	<i>Populus balsamifera</i>	20
To	<i>Thuja occidentalis</i>	13
Ll	<i>Larix laricina</i>	11
Prp	<i>Prunus pensylvanica</i>	5
Fn	<i>Fraxinus nigra</i>	3
Ar	<i>Acer rubrum</i>	2
Prv	<i>Prunus virginiana</i>	2
As	<i>Acer saccharum</i>	1
Asp	<i>Acer spicatum</i>	1
Aln	<i>Alnus rugosa</i>	1
Pya	<i>Pyrus americana</i>	1
Pyd	<i>Pyrus decora</i>	1

The procedure is described by Pielou (1969). The full ranges of adjusted relative density values were used to calculate the euclidean distance with arcsine transformation between species (Orloci 1967b). The matrix of these distances was subjected to a Gower transformation (Gower 1966) followed by principal component factoring. The species loadings on the first two components gave a second, orthogonal reference model.

Each of these models produces a linear combination of the tree species along the maximum directions of initial and residual variance in the resemblance matrices. Much evidence has now appeared in the literature to indicate that linear models are too rigid in their extraction of trends from vegetation data (e.g., Swan 1970; Noy-Meir and Austin 1970; Gauch and Chase 1974).

As a means of improving the two-dimensional PCORD reference model, Kruskal's nonmetric multidimensional scaling was applied to the euclidean distance matrix. A full account of the procedure is given by Kruskal (1964) and Kruskal and Carmone (1971). This is an iterative approach which compares an estimated resemblance structure, within a defined number of dimensions, with the euclidean distance matrix until 'stress' between the two is minimized. Coordinates of the PCORD model were used as initial estimates of the resemblance structure in two dimensions. The procedure used assumes only that species responses are related in a globally monotonic fashion to underlying environmental variables. It was felt that the nonmetric multidimensional scaling model (MDSCAL) would give a reasonable reduction from eight to two dimensions and display environmental relations more efficiently than the linear approaches.

Succession Vector Construction

The lumped relative density figures were decomposed into five stem size classes for each species. In terms of basal area (square inches: square centimetres are parenthesized) at breast height (BABH) these were (class 1) < 12(77.4) ≤ (class 2) < 36(232.3) ≤ (class 3) < 72(464.4) ≤ (class 4) < 144(923.8) ≤ (class 5). This classification was arrived at empirically such that a reasonable number of stems were represented in each class across the whole data set. The correlation between the size classes of each species and each reference species were then calculated using Cole's index. With such information, it was possible to include the five stem size classes for each species

within the framework of the reference species models. This amounts to calculating the correlation between stem size classes and each axis of the model and then scaling to the appropriate axis lengths. As the included points represent changes in size and, by assumption, the age of tree species, they indicate directional trends in species relations through inferential time.

The assumptions in this method of analysis may be summarized as follows. (1) Individuals of different species of the same BABH are the same age. (2) There exists no difference in the growth potential of different sites for a given species, i.e., trees of the same species and the same age will be the same size regardless of their immediate environment.

Both of these are ecologically unreasonable. However, consistent trends in frequency between the different size classes point to obvious primary or secondary successional roles for the species involved. Using only presence data rather than specific BABH measurements, the PCA and MDSCAL models act to integrate the trends. As a consequence, the first assumption is not as serious as it seems. Furthermore, the use of presence data effectively reduces any bias in numbers which might occur through natural self-thinning.

To circumvent the second assumption, segregation of the stands into common environmental groups would be required followed by construction of a separate model for each group. Aside from the lack of an objective set of *a priori* criteria for stand segregation, this approach would lead to grossly inadequate sample sizes. As it is, the total number of stands (152) is not large for this type of analysis. Gross errors are only likely to appear for those tree species that are evenly distributed over a wide environmental spectrum.

All calculations for the analysis were performed on the University of Toronto IBM 370 computer. Principal component, principal coordinate, and nonmetric multidimensional scaling analyses were executed using the NTSYS74 programme package (Rohlf *et al.* 1974). The listing of a programme in Fortran IV, for the inclusion of stem size class data into a reference model, was kindly supplied by Dr. F. Glenn Goff of Oak Ridge National Laboratory. All other programmes necessary for the analysis were written in Fortran IV by the senior author.

Results and Discussion

A superficial grasp of the successional status of the major boreal tree species can be gained by looking at tree and sapling importance values across all stands. Figure 2 shows a simple, bivariate scatter plot of tree importance vs. sapling importance for *A. balsamea*. The sole occupation of the upper left half of the plot suggests that *A. balsamea* can be well represented in the sapling layer whether trees of this species are present in the stand or not. This accords with the general observation that *A. balsamea* is a shade-tolerant species which can successfully invade many boreal forest types. In contrast, a scatter for *P. banksiana* shows complete occupancy of the lower right half of the plot (Fig. 3). A strong dependence for high sapling representation upon high tree importance is indicated, suggesting an intolerant pioneer species. Indeed 'saplings' in the data are for the most part only marginally below the arbitrary threshold of 12 in.² (77.4 cm²) BABH for separation from trees. Stem BABH tends to uniformity in young, monospecific

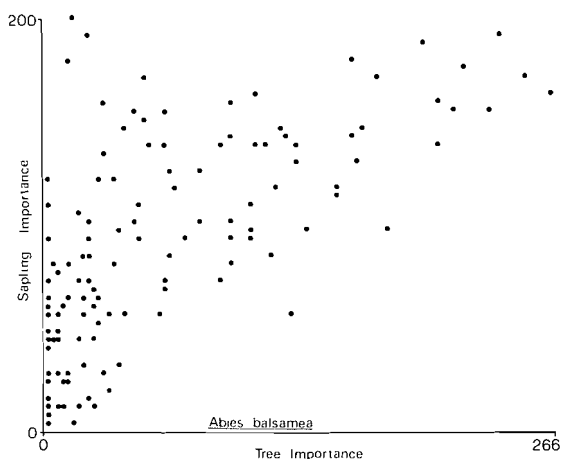


FIG. 2. Scatter plot of tree importance vs. sapling importance for *Abies balsamea* in each stand.

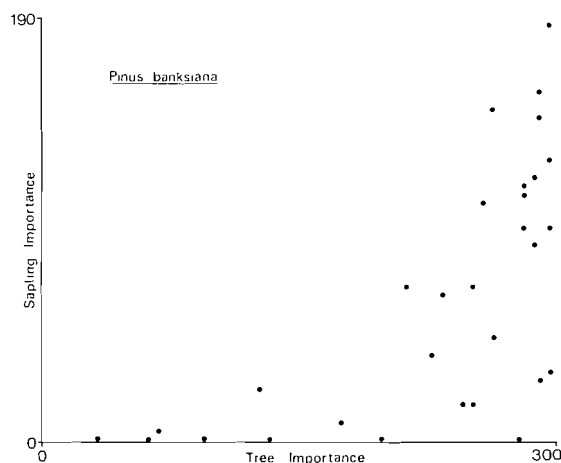


FIG. 3. Scatter plot of tree importance vs. sapling importance for *Pinus banksiana* in each stand.

stands of *P. banksiana* (Yarranton and Yarranton 1975), and all jack pine stands with a high pine sapling representation in the data are young. It is a restriction of the sampling scheme that pure stands of saplings are not included in the data.

The scatter plot for *Picea mariana* (Fig. 4) indicates a broad relationship between saplings and trees but variation around the central trend is very wide. A tight and linear relationship emerged in a similar plot for *Thuja occidentalis* trees vs. saplings (not illustrated). White cedar is well known to reproduce vegetatively from the branches of decumbent trees (Curtis 1959, p. 230). This form of sapling production is clearly dependent on the presence of mature trees. Similarly, Stanek (1961) reports on the layering of lower black spruce branches into mossy substrata in northern Ontario. Although reported for bog forests, the authors have observed

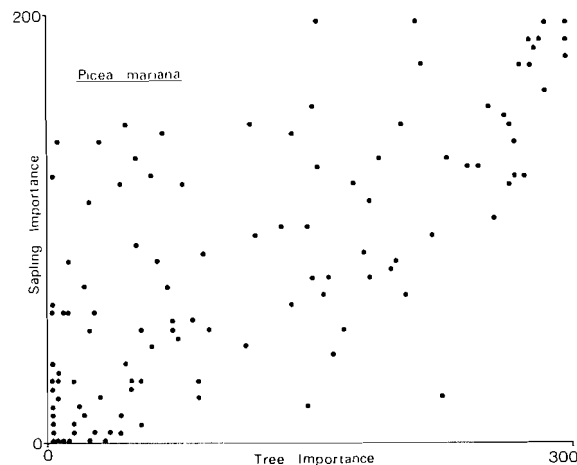


FIG. 4. Scatter plot of tree importance vs. sapling importance for *Picea mariana* in each stand.

the same habit of *P. mariana* on upland sites with a deep feathermoss mat in the understory.

Figure 4 also indicates that on certain deforested sites, *Picea mariana* can act as a primary colonist in a similar manner to *Pinus banksiana*. This seems to be the case in the more northern sections of the boreal forest region *sensu* Rowe (1972). Shafi (1972) indicates that postfire sites of the Cochrane clay belt in which patches of *Sphagnum* moss have survived provide the most favourable conditions for primary colonization by black spruce from seed. While jack pine is well known as a species possessing serotinous cones, releasing seed only after fire, black spruce is reported to be semiserotinous (Ahlgren 1974), i.e., some cones open at maturity to release seed while others are retained in a closed state next to the main axis of the tree crown.

Picea mariana is also seen (from Fig. 4) to behave as a shade-tolerant species which can invade beneath other tree canopies. However, this pattern is less pronounced than the similar pattern of *Abies balsamea* (Fig. 2).

Of the other significant boreal tree species, *Larix laricina*, *Populus balsamifera*, *Populus tremuloides*, *Betula papyrifera*, and *Picea glauca* all showed trees vs. sapling importance scatters of a more or less similar pattern to that for *Pinus banksiana*. This suggests that they are all species adapted to the colonization of open, nonforested sites. *Populus tremuloides* and *Betula papyrifera* can resprout fresh vegetative shoots following destruction by fire in addition to establishing on postfire sites by seed (Ahlgren 1974). *Larix laricina* invades sedge meadows and alder thickets by growth from seed. *Populus balsamifera* and *Picea glauca* invade newly exposed fluvial silts and some upland sites. Unlike black spruce, white spruce

sheds most of its annual seed crop shortly after cone maturity in early fall (Stiell 1976) and this corresponds with a time when river levels are at their lowest. In addition, saplings of *P. glauca* do appear in some upland stands often overlying a coarse, moist sandy substrate. However, these are always associated with one or two old white spruce trees in close proximity. This feature is most marked in jack pine stands close to Lake Superior where a 'blanket effect' from white spruce in the prevalent formation, an upland white spruce – paper birch – balsam fire mixture, occurs. Thus, white spruce seedlings and saplings are found in all forests of the area.

Reference Models

The reference species model by PCA is shown in Fig. 5. In overall character, it is very similar to that of Goff and Zedler (1972) for the Wisconsin data although far fewer species are involved. In their data, 26 taxa were used in model construction compared with 8 species in the present study. The boreal forest model is a triangular scatter with wet species (*L. laricina* and *P. mariana*), dry species (*P. banksiana*), and mesic species (*A. balsamea*) occupying the poles.

In contrast, the PCORD reference model was disappointing and is not shown. The majority of the species were clustered around the origin of the first axis with only three species, *L. laricina*, *P. banksiana*, and *P. balsamifera*, showing any separation. The point configuration of the first two axes of this model were input to the MDSCAL procedure as initial estimates. 'Stress' for this PCORD configuration was estimated at 0.960, an unacceptably high figure. After 14 iterations, 'stress' was reduced to 0.188, indicating a 'good' to

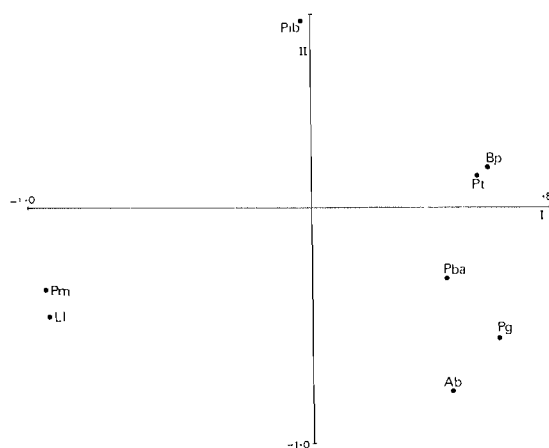


FIG. 5. Reference tree species ordination based upon the first two axes of a principal components analysis.

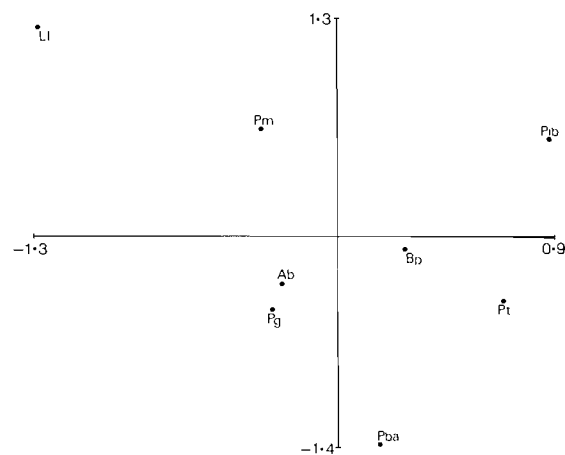


FIG. 6. Reference tree species model based upon nonmetric multidimensional scaling into two dimensions.

'fair' fit on the scale of Rholf *et al.* (1974). This remained constant for subsequent iterations.

The MDSCAL model (Fig. 6) improved the placement of intermediate species positions along both axes although species at the extremes remained the same as in the PCORD reference model. Projection of stand data into the species attribute space of the MDSCAL model produced a scatter diagram of stands within the two-dimensional ordination.

Figure 7 indicates a good visual correlation between the MDSCAL model and two substrate-related gradients. Stands overlying deep organic substrata, mostly bog peats, occupy the extreme left of the first dimension. The remaining scatter of stands, overlying inorganic substrata, exhibit a distinctive gradient of increasing moisture status from top right to bottom centre.

The distinction between shallow organic duff and deep organic peats was taken to be approximately 12 in. Thus the tree species which root in an inorganic substrate distribute along a broadly correlated moisture and decreasing substrate particle size gradient. The lowland conifer bog forests overlying deep wet peats do not form a continuous part of this joint gradient but represent a separate vegetation type on their own in which other environmental gradients, such as pH, conductivity, or nutrient availability, may be more important (Jeglum *et al.* 1971).

The MDSCAL reference model provides the best environmental interpretation and should be the only model to use as a basis for subsequent analysis and discussion. However, because the inclusion of succession vectors is of comparative interest between the PCA and MDSCAL models and because a PCA dynamic model is the best vehicle

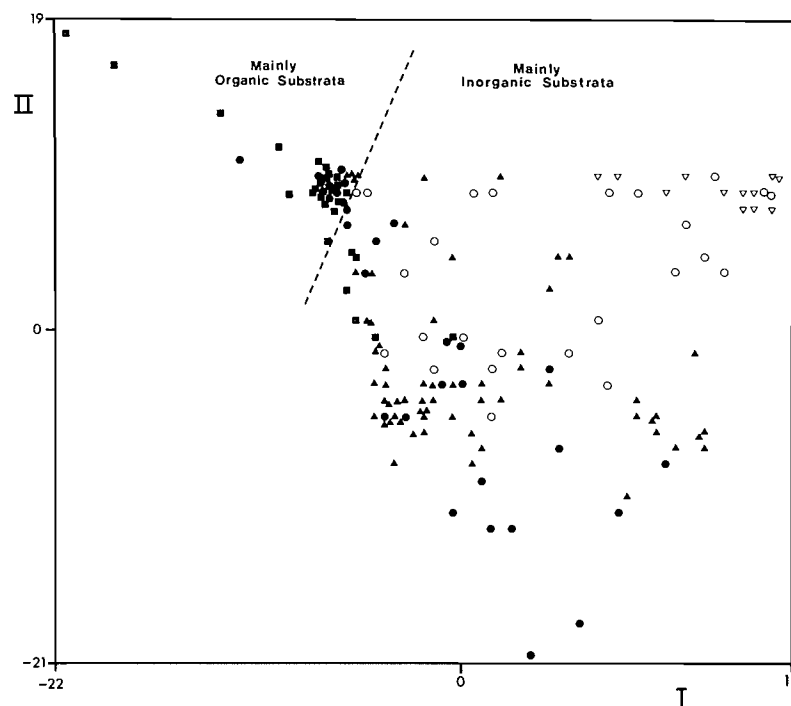


FIG. 7. Moisture status of stands projected into the nonmetric multidimensional scaling model. ▽, dry; ○, dry-mesic; ▲, mesic; ●, wet-mesic; ■, wet.

for comparison with the results of Goff and Zedler (1972), two succession vector plots have been constructed based on the PCA and MDSCAL reference models.

Dynamic Models

The size class points for each species are included in the PCA and MDSCAL models in Figs. 8 and 9. The points representing successive size classes are joined into directed vectors. Although the exact placement of each species 'succession vector' differs between models, the overall pattern of similarity in relative placement, vector magnitude, and direction shows a strong similarity. Because of this convergence between somewhat different reference models to similar dynamic schemes through the use of the same set of size class associations, the confidence which can be put into those associations is of prime importance to the interpretation of the dynamic models. The analysis is weak in this respect. Only 45% of all size class correlations attain significance at the 5% level. This is in marked contrast with the Wisconsin data of Goff and Zedler in which only a few of the larger size classes failed to attain significance. In their case, they substituted such nonsignificant correlations with those from the next smaller size class but clearly no such remedial action was possible with the boreal data. While the present study is based on

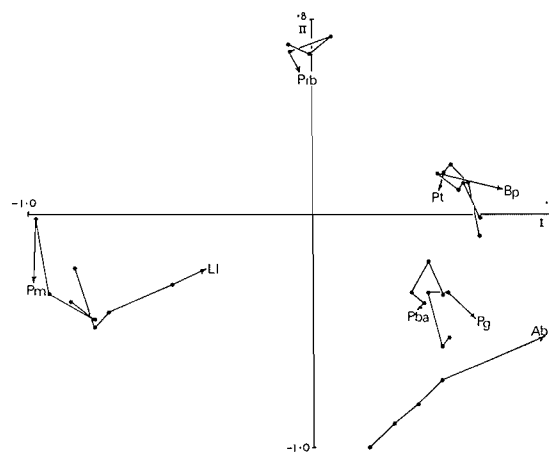


FIG. 8. Tree species succession vectors across the principal component ordination.

152 stands, the Wisconsin study was based upon data from 879 continuous forest inventory (CFI) plots.

Reexamination of the nonsignificant size class correlations in the boreal data confirmed that undersampling (i.e., few degrees of freedom), rather than some inconsistency within the data, was responsible for low levels of significance. This point, and the observation that species in common between the boreal data and the Wisconsin study tend

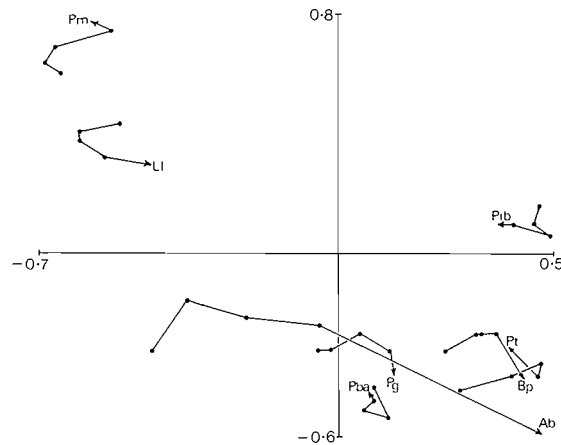


FIG. 9. Tree species succession vectors across the nonmetric multidimensional scaling model.

to show similar vector patterns, suggests that the boreal models do reflect true ecological relationships despite the low level of statistical confidence with which they can be viewed.

In general, the boreal species succession vectors tend to be short, circular, and divergent in their placement rather than long, linear, and convergent, that is, the species studied do not show any tendency to progress toward a single climax type. An exception which does show a continuous linear trend is *Abies balsamea*.

Larix laricina possesses a quasilinear vector in the PCA model where the two largest size classes extend toward the species of affinity to inorganic substrata. The sites supporting only smaller tamarack trees are mostly in the northern section of the region and have colder, more oligotrophic substrata. In contrast, the few southerly sites are associated with marginal locations subject to flushing by warmer, calcareous, and mineral-rich groundwater. While the sole associate species in the north is black spruce, further south mixed wet lowland forests of tamarack, balsam fir, white cedar, and black spruce frequently occur in which the trees grow considerably larger. Thus the vector for *Larix laricina* in the PCA model can be attributed more to environmental differences than to successional behaviour. The fortuitous linearity is more suppressed in the preferred MDSCAL model which also shows a longer vector for *Abies balsamea*.

In contrast with *Larix laricina*, the size class ranges for *Abies balsamea* are well represented in numerous upland stands, hence the size class correlations are considerably more robust. The vector represents a true successional pathway indicating unique affinity for balsam fir to no one tree species when young and associating primarily with white

spruce, balsam poplar, paper birch and trembling aspen in older phases of growth. The balsam fir vector is most easily interpreted as representing a species of establishment beneath a wide range of other tree canopies, in accordance with the bivariate scatter plot of Fig. 2, whose subsequent growth is most successful beneath canopies of the above four species.

Unlike the Wisconsin model (Goff and Zedler 1972), *A. balsamea* does not show any convergence toward other, more climax, species in the boreal models. Nor does *A. balsamea* seem to persist as a self-regenerating climax type. If it did, the ultimate size classes would then show some reversal in direction back toward the median size classes. In the model of Goff and Zedler (1972), this behaviour is shown very well by *Acer saccharum* and *Tsuga canadensis*. These might reasonably be regarded as self-perpetuating, climax species for the section of Wisconsin studied.

Examination of the specific data for those older stands in the data dominated by *Abies balsamea* indicates that all lack a sapling layer (i.e., fewer than 100 saplings per acre). Similarly, the recent work by Sprugel (1976) on wave regeneration in the fir forests of the Adirondacks confirms their ultimate dependence for regeneration upon destruction by external forces when growing as a monoculture.

Succession vectors for the remaining boreal tree species are short and more or less circular. The circularity accords with the bivariate scatter plots of tree vs. sapling importance which indicated that tree species adapted to establishment on deforested areas but goes further to indicate reestablishment by the same species on a site following catastrophic destruction.

As seen with *Abies balsamea*, the longer a succession vector the greater the proclivity for association with other species at the various phases of growth. The shortness of most of the species vectors indicates that interspecies association is neither strong nor does it change very much during stand history. However, this conclusion is also dependent upon vector position and here there is close agreement between both models. *Pinus banksiana* exhibits a short, circular vector which is isolated from other species. Extremely monospecific forests of jack pine are a common feature of the region and the efficient reestablishment from seed following fire was mentioned above.

The other species with short vectors seem to pair off on the ordination. Thus *Populus tremuloides* and *Betula papyrifera* lie close to one another, and although monospecific forests of these species are

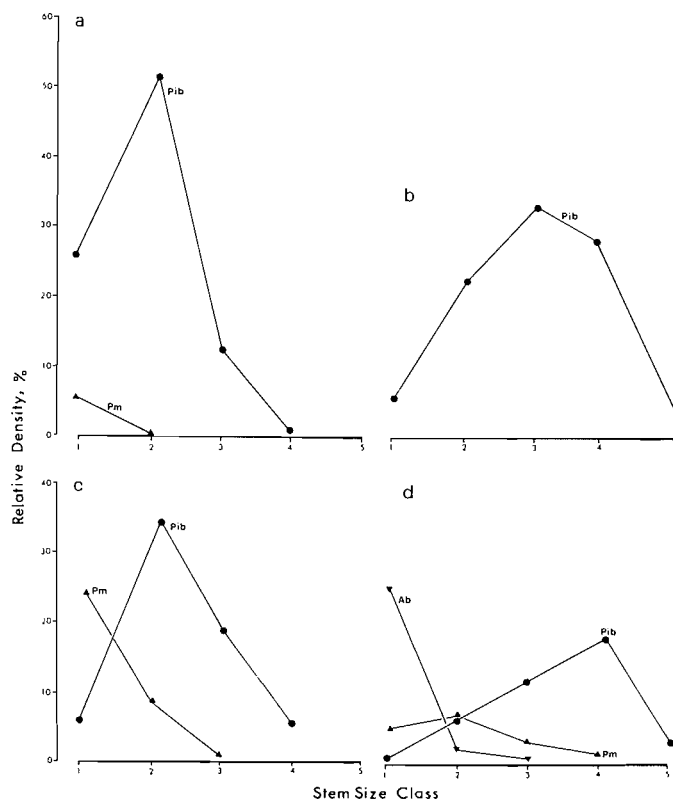


FIG. 10. Average size class spectra within the four major groups of stands dominated by jack pine: (a) young stands with no secondary understory; (b) older stands with no secondary understory; (c) older stands with a spruce understory; (d) older stands with a fir-spruce understory.

common, some admixture between them is not infrequent in the region. Similarly *Picea glauca* and *Populus balsamifera*, while growing mostly in monoculture on the higher and lower fluvial silt terraces of river bottoms, do frequently occur together in stands. *Picea mariana* and *Larix laricina* also tend to grow in association on those few wet, peaty sites in which tamarack occurs.

If recolonization following deforestation explains the vector schemes on the ordinations, the cause of such catastrophe must be viewed as a prime determinant of forest composition and structure equal in importance to macroclimate and substrate conditions. Windthrow, fire, hail storms, ice storms, and insect and fungal attack are all recognized as causes of major forest destruction in the region, but MacLean and Bedell (1955) point to fire as the prime agent. Bennett (1960) and Kourtz (1967) document the frequency of natural lightning strike as a cause of forest fire in Canada and the extent of its damage. However, certain forests are more susceptible to burning than others, notably those on dry or south-facing sites (Rowe and Scotter 1973). Similarly dead, dried-out standing timber

is more prone to burn than living trees in the same locale. In this way, the other agents of forest destruction mentioned above can presage fire to bring about the total deforestation of a site. The frequent occurrence of fire within a few years following a spruce budworm epidemic is well known. Similarly, the senior author has observed the natural burning of an extensive area of paper birch forest in the study region within 2 years of suffering birch dieback disease.

The wet lowlands dominated by *Picea mariana* and to a much lesser extent the *Larix laricina* forest also tend to exhibit short succession vectors. Such sites are less prone to fire than the uplands (Rowe and Scotter 1973). The situation is more complicated as cold groundwater and oligotrophic organic substrata tend to retard tree growth. While these forests do burn infrequently, changing hydrologic regimes may be more destructive than recurrent fire (Jeglum 1973). On the uplands, however, boreal forests seem to be mostly young and are generally composed of single tree species which are adapted to the postfire colonization of deforested sites. This may occur through seeding tactics in the conifers,

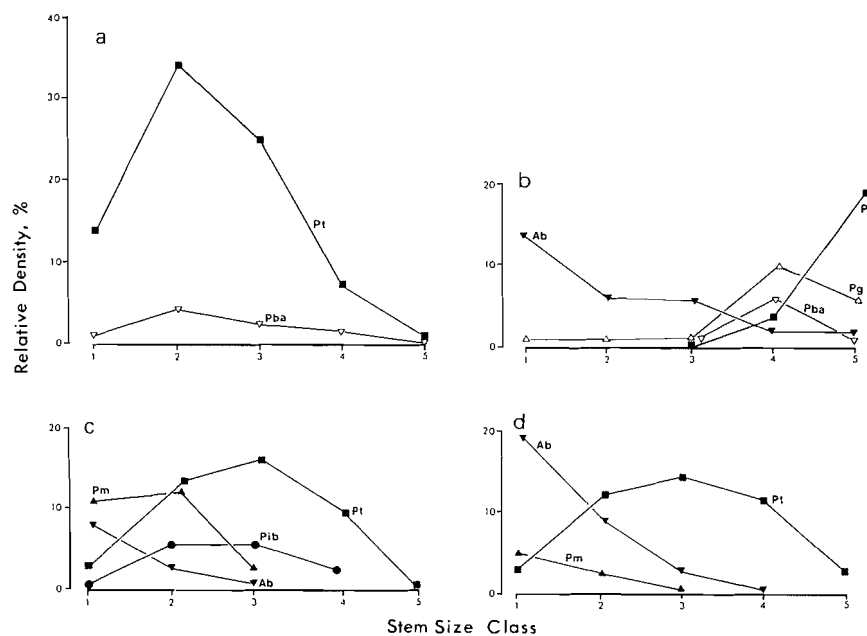


FIG. 11. Average size class spectra within the four major groups of stands dominated by trembling aspen: (a) young stands with little secondary understory; (b) old, decadent stands with delayed spruce and fir invasion; (c) older stands with a spruce-fir understory; (d) older stands with a fir-spruce understory.

as outlined above, and (or) by resprouting from persistent underground parts as is the case for trembling aspen and paper birch (Ahlgren 1974).

Potential for Secondary Forest Development

Although the succession vector models summarize the prevailing pattern of forest growth for each tree species, it is appropriate to examine the potential of sites dominated by species of primary establishment for subsequent development into stands of different composition. Stands dominated by jack pine, trembling aspen, and black spruce are by far the most abundant forests of primary establishment in the data.

Taking the highest importance value as an index of species dominance in a stand, those stands dominated by each of the above three species were selected from the data set. The size class spectra and environmental data were then examined and stands were grouped according to similar environmental, compositional, and structural features. In the case of jack pine and trembling aspen stands, four main classes could be identified: (a) young, monospecific stands with few saplings present; (b) old, decadent stands with poor reproduction; (c) stands of moderate age with a spruce sapling layer; and (d) stands of moderate age with a fir-spruce sapling layer.

Average structural spectra for stands within each

group are shown in Figs. 10 and 11 while Table 2 summarizes the numbers and proportion of stands in various structural classes within each group. Table 2 indicates that the largest percentage of stands dominated by jack pine correspond to class a (Fig. 10a) and are too young for secondary species to have invaded and established as saplings. A smaller group of stands, corresponding to class b, is dominated by the larger, intermediate size classes of jack pine but shows no secondary reproduction at all (Fig. 10b). In contrast, stand groups corresponding to classes c and d above (Figs. 10c and 10d) are also dominated by the larger jack pine stem sizes and yet they exhibit healthy sapling layers of black spruce or fir.

The pattern which emerges here for jack pine forest is rapid establishment as a monoculture over fire-prone sandy or rocky sites (cf. Cayford *et al.* 1967), with subsequent invasion and establishment in most cases by black spruce and (or) balsam fir. In approximately one-quarter of the older stands, however, no secondary species establish in the understory and these pine forests show signs of opening up to become savannahlike. The reasons for this might be either the destruction of an established seedling and sapling population by, for example, a ground fire or the inability of black spruce seedlings to establish in certain pine forests. During the examination of size class spectra, no

TABLE 2. Structural features of the groups of stands dominated by jack pine and trembling aspen

Stands dominated by jack pine				Stands dominated by trembling aspen			
Class	Description	No. stands	Percentage of total	Class	Description	No. stands	Percentage of total
<i>a</i>	Young, monospecific stands with no saplings	12	36	<i>a</i>	Young, monospecific stands with no saplings	7	32
<i>b</i>	Older, monospecific stands, open, savannah-like with no saplings	4	12	<i>b</i>	Older, decadent stands with dense tall shrub growth and some young balsam fir saplings	3	14
<i>c</i>	Moderate to older stands, monospecific or mixed with black spruce. Black spruce saplings abundant	8	2	<i>c</i>	Moderate-aged stands mixed with some conifer and abundant black spruce saplings	4	18
<i>d</i>	Moderate to older stands with abundant balsam fir and black spruce saplings	5	15	<i>d</i>	Moderate-aged stands with some conifer and abundant balsam fir saplings	5	23
<i>e</i>	Mixed tree layer with paper birch saplings	2	6	<i>e</i>	Mixed tree layer with no saplings	1	4
<i>f</i>	Mixed tree layer with white spruce saplings	1	3	<i>f</i>	Mixed tree layer with trembling aspen and paper birch saplings	1	4
<i>g</i>	Mixed tree layer with aspen birch and white spruce saplings	1	3	<i>g</i>	Mixed tree layer with trembling aspen saplings	1	4
Total		33		Total		22	

spruce- or fir-dominated stands in the data clearly derived from a previous jack pine forest could be found. This supports the pattern illustrated by the succession vector analysis.

Dix and Swan (1971) indicate that the vegetation may have 'adjusted' to the repetitive destruction of forest upon fire-prone sites such as the sand plains and rock outcrops dominated by jack pine (Rowe and Scotter 1973). The hypothesis of Mutch (1970), which suggests that selective forces have increased the flammability of species on fire-prone sites, might constitute one form of such adjustment. The prevalence of species which resprout (Ahlgren 1974) or whose buried seeds are stimulated to germinate following fire is another (Cushwa 1968). A less obvious, but nonetheless significant strategy of adjustment might be indicated by the appearance of older, open forests with no secondary species in the understory.

While an overdrained, depauperate substrate may cause a lack of reproduction, those jack pine stand groups with spruce and fir reproduction (classes *c* and *d*) also include sites of strong edaphic stress. More probable is either the lack of a spruce-fir seed source in the vicinity or a competitive inhibition of tree seedlings by understory species (Peterson 1965; Brown 1967; Brown and Mikola 1974) or a combination of these factors.

The younger stands dominated by trembling aspen with no conifer understory account for approximately one-third of the group (Table 2 and Fig. 11a). Stands of moderate age with either a

black spruce (Fig. 11c) or balsam fir (Fig. 11d) understory are very comparable in overall structure. Generally, a fir understory occurs beneath an aspen canopy in the more southern stands on relatively calcareous substrata while more northern stands on acid substrata favour the predominance of a black spruce sapling layer.

Older, decadent aspen stands (class *b* above) are of infrequent occurrence (Table 2) and a few black spruce and balsam fir stands elsewhere in the data have clearly derived from a previous trembling aspen forest. However, a few older, decadent stands do occur in which sapling regeneration, although not completely suppressed, does appear to be considerably arrested (Fig. 11b). The less fire-prone nature of aspen sites would suggest that there has been less 'vegetational adjustment' according to the proposition of Dix and Swan (1971). While distance from an appropriate seed source may explain the lack of reproduction, competition and shading by tall shrubs such as *Acer spicatum* (mountain maple) may be responsible for some more active role in this process (Vincent 1965; Post 1965).

As with the jack pine forests, the examination of structure in the trembling aspen stands largely confirms the pattern shown in the succession vector schemes. The preponderance of stands of younger to moderate ages (Table 2) suggests the recurrence of frequent catastrophic cycles in which trembling aspen establishes as a monospecific forest. Although other species may subsequently

invade and establish as saplings, few stands appear in a state of transition from aspen dominance to dominance by either spruce or fir.

The structural classes for forests dominated by black spruce are more varied than either of the above two examples (Table 3 and Fig. 12).

Classes *a* and *b* represent two upland stand groups which form contiguous phases in the development of upland black spruce forest. This appears mostly on some rocky knolls and well drained sandy sites in the region. Black spruce forest here seems to derive from primary establishment in association with a small amount of jack pine (Fig. 12*a*). As this forest type ages (Fig. 12*b*), the black spruce trees become larger, jack pine mortality proceeds and a wave of balsam fir saplings invade. Sites of this type supporting large, old black spruce are extremely infrequent in the study region. The only one present in the data was found on a sloping riverbank. This could indicate that the more exposed rocky and sandy sites are prone to frequent destruction by fire.

Classes *c* and *d* (Figs. 12*c* and 12*d*) represent the lowland, relatively oligotrophic bog forests. Group *c* is typified by larger trees and a continuous tree canopy, while group *d* possesses a discontinuous canopy and the trees are very small. These differences seem most attributable to the fertility of the site and the depth of *Sphagnum* peat, which is much greater in class *d*. In neither group are trees of greater than size class 2 well represented.

Of interest are classes *e* and *f* (Figs. 12*e* and 12*f*) which represent mixed lowland black spruce forest and often occur in marginal habitats subject to groundwater flushing. Figure 12*e* indicates that tamarack and black spruce may be primary colonizers in these marginal sites, followed by the influx of balsam fir and white cedar. In what may represent an older phase, Fig. 12*f* indicates an older profile for black spruce with vigorous establishment by younger balsam fir. Significantly, the larger size classes of black spruce are best represented in this habitat which is more fertile and productive than the upland or more oligotrophic lowland sites.

Thus in upland areas black spruce seems to behave in a manner which emulates jack pine and competition for sites may occur between these two species through the process of succession. In the wet lowlands, however, black spruce forest divides into several distinctive types in which succession to balsam fir forest is indicated on the more fertile sites while a vegetative regeneration through layering may enable black spruce to persist as a monoculture on the more oligotrophic sites.

TABLE 3. Structural features of the groups of stands dominated by black spruce

Class	Description	No. stands	Percentage of total
<i>a</i>	Dense, young upland forest with few saplings derived from secondary invasion	4	8
<i>b</i>	Older, upland black spruce forest with some secondary recruitment from balsam fir and black spruce saplings	6	12
<i>c</i>	Closed canopy lowland black spruce forest overlying wet peat	9	18
<i>d</i>	Open spruce bog forest with dense, small trees forming a discontinuous canopy	11	23
<i>e</i>	Marginal, wet mixed conifer forest overlying mostly vascular peat substrata	6	12
<i>f</i>	Black spruce - balsam fir mixed forest with shallow peat overlying fertile inorganic substrata	10	21
<i>g</i>	In wet flushed sites. Earlier tamarack forest succeeded to black spruce dominance	1	2
<i>h</i>	On mesic uplands. Previous trembling aspen forest succeeded to black spruce dominance	2	4
Total		49	

Successional Theory

Clementsian monoclimal theory can not adequately explain the scheme of succession vectors in the PCA and MDSCAL ordination models. No signs of a self-regenerating vegetation complex are apparent unless catastrophic destruction, mostly by fire, is viewed as an integral part of such regeneration (cf. Loucks 1970). Thus the emphasis in boreal forest dynamics focusses heavily upon the importance of forest fire. Well documented in the literature (e.g., Lutz 1956; Richie 1956; Cayford 1963; Dix and Swan 1971; Shafi and Yarranton 1973; Ahlgren 1960), this has been brought out by the PCA and MDSCAL models.

From the air, a boreal forest appears as a patchwork quilt, each 'patch' being sharply delimited by abrupt changes in tree composition or crown height. Dix and Swan (1971) invoke Odum's (1969) terminology to explain this pattern of vegetational response to fire by suggesting that a 'pulse strategy' maintains highly productive monoculture plant species populations near the starting point of succession. Odum's view ascribes strategy of development to the ecosystem as a whole. Colinvaux (1973) points out that selective processes do not choose between ecosystems, they choose between individual living things. When these individual liv-

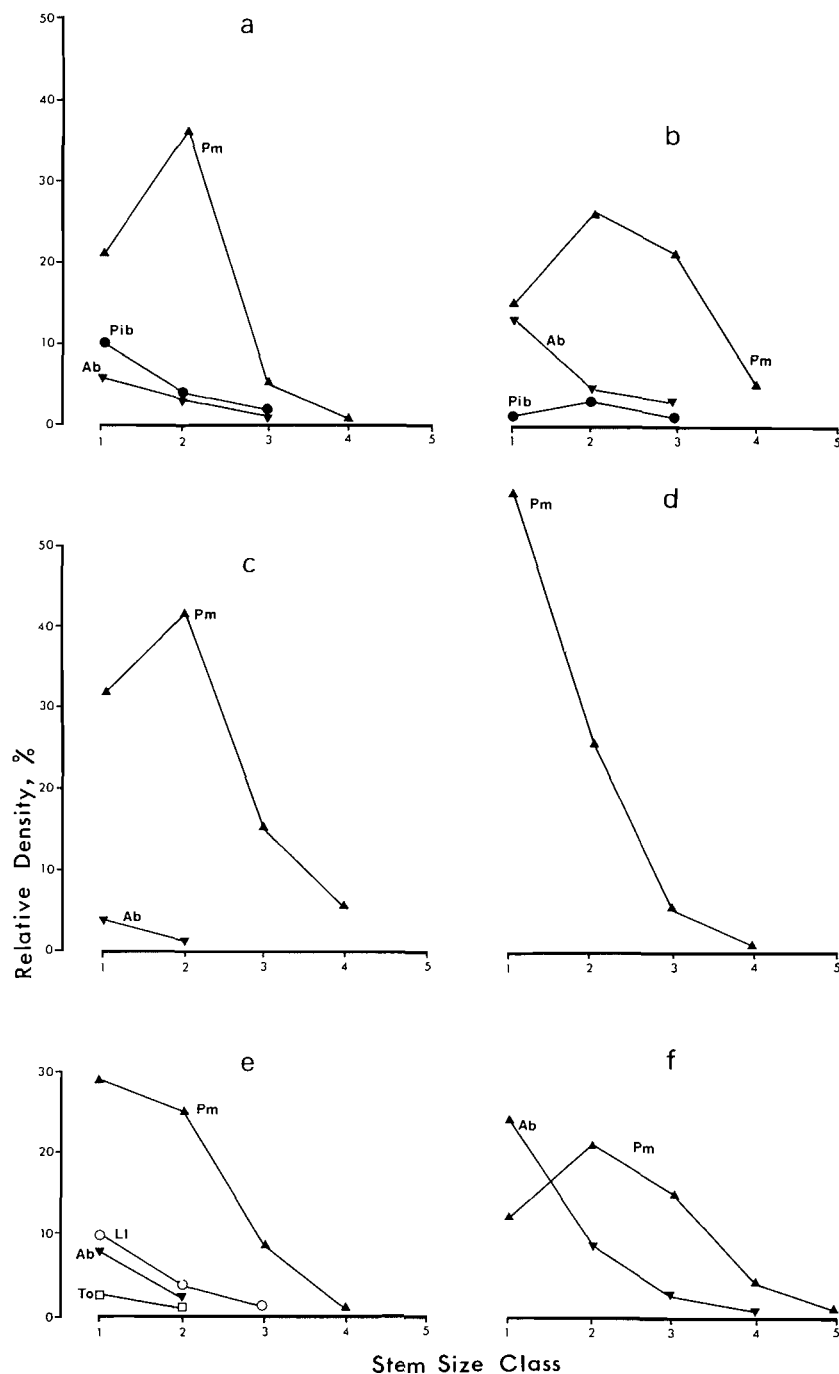


FIG. 12. Average size class spectra within the six major groups of stands dominated by black spruce. (a) young upland stands; (b) older upland stands; (c) closed-crown wet lowland stands; (d) open treed bog forests; (e) mixed stands of marginal wet sites; (f) mixed black spruce and balsam fir stands.

ing things are single tree species populations, however, the notion that a 'pulse strategy' can operate on the scale of a tract of forest becomes credible. More open to question, though, is the idea that an altruistic 'strategy' should exist to maximize any

macroscopic property, including the productivity of a spatial collection of plant individuals, rather than their own survival as a self-reproducing unit.

Colinvaux (1973) argues that all successions may be explained by the replacement of opportunistic,

generalist species of unpredictable environments by equilibrial specialists of more predictable environments, subject to the species list of a region including types along the continuum between extremes. This corresponds to the r - K selection continuum of the population ecologist (Jones 1976; Demetrius 1975; Pianka 1970). Whittaker's (1974) views on successional processes and the reviews by Drury and Nisbet (1973) and Horn (1976) converge to a similar general conclusion which emphasizes the rate of environmental change in comparison with the generation times of dominants.

The attractiveness of this view lies in its comprehensive explanation of species diversity, successional patterns, and breadth of environmental response while centering upon selection for survival and competitive success.

The paucity of tree species across most of the boreal zone may not simply represent a climatic limitation but also result from the unpredictable nature of the outbreak of fire and other catastrophes. The river bottoms of the James Bay Lowlands support forests of *Fraxinus nigra* (black ash) and *Ulmus americana* (white elm) found nowhere else in the main boreal zone. Although the local microclimate and substrate conditions are more favourable to growth, these sites are also free of recurrent fire. While subject to some seasonal flood damage, such sites are more predictable environments than the uplands and, consequently, can support a few more K -selected species. A wider potential species spectrum might exist along the r - K continuum throughout the zone, but against the background of uncertainty which fire and other dangers impose, those tree species which persist occupy the more opportunistic end of the spectrum. Thus the most equilibrial of the boreal upland tree species, *Abies balsamea*, only rarely attains dominance in a forest and its success is due mostly to its ability to establish beneath the canopies of a wide range of other forest stands.

Deforested sites in boreal regions become reforested far more rapidly and extensively than southern forest regions and the work of Shafi (1972) indicates some of the processes involved. Clearly the boreal tree species involved must be highly productive in their youth to gain a competitive advantage of height over shrub vegetation. In addition seed production and dispersal must occur at an early phase of tree growth before destruction recurs. The rapid reestablishment of highly vigorous tree populations following deforestation can, in this light, be viewed as a consequence of selection for survival and competitive success in an unpredictable environment rather than a macroscopic 'pulse strategy.'

In the absence of external catastrophe, some upland primary boreal forests seem to develop into secondary fir and (or) spruce forests. Also apparent, however, are old decadent forest stands typified by the complete absence of subsequent development or considerably delayed regeneration. Dix and Swan (1971) comment upon this feature in the uplands of Candle Lake, Saskatchewan: "Finally, poor reproduction in many stands suggests that a parkland (Rowe, 1961) may develop in the absence of disturbance..."

The independent observation of such checks to secondary forest development (Rowe 1961; Dix and Swan 1971) suggests that this is not a chance event in the boreal forests of Canada. Nor, as indicated here, does the process appear to be restricted to one forest type. Clearly the forces which operate to arrest forest succession are not perfectly effective because much change is also evident in the data presented here. Thus a suite of environmental conditions is envisaged which may tip the balance in favour of one process or the other. Whatever the mechanisms involved, a distinctive strategy can be ascribed to the arresting of succession beyond the phase of initial forest vegetation. Persistent exclusion of later successional tree species such as fir and spruce greatly increases the probability that the existent vegetation will recolonize a site following destruction by fire. Even if the mechanisms themselves are fairly weak in effect, a progressive elimination of fir and spruce seed sources could ensue over a period of several fire cycles, in turn consolidating the domination by a preliminary postfire forest.

The concept of a strategy operating at the level of the vegetation complex does, of course, reinvolve Odum's (1969) views that were criticized above. Concordant with this line of reasoning is the notion of vegetational adjustment to recurrent destruction by fire (Dix and Swan 1971). For reasons discussed above, it seems more credible that if the lack of advanced succession can be ascribed to the vegetation itself, then this must operate through the action of one or two abundant species. Such a process would accord more with the view of Sukachev (1925) who suggested the term 'edifikator' for species "which exert a strong influence on the environment of other species in the community" (Goodall 1966).

In view of the preceding discussion, it is clear that an interesting problem of forest development exists in the central boreal regions of North America. Considerably more circumstantial evidence that continuing forest succession is arrested should be sought and documented for various boreal forest types. In the more clear-cut instance

of *Pinus banksiana* forests, the underlying mechanisms for a lack of spruce or fir invasion should be sought. This aspect of the problem is at present under investigation.

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