United States Department of Agriculture

Forest Service

North Central Forest Experiment Station

Research Paper NC-310

Synecological Coordinates As Indicators Of Variation In Red Pine Productivity Among TWINSPAN Classes: A Case Study

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Manuscript approved for publication October 14, 1992
1992

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During the past 10 to 15 years, there has been an increasing effort in the Great Lakes region of North America to classify forest ecosystems. The classes identified are expected to provide a unifying framework for land management and planning. Knowledge gained about managing forests (*e.g.*, growth and yield, risk of damage from insects or disease, regeneration success) in one location should apply to other locations in the same class.

Knowledge of overstory productivity is needed for many forest management decisions. Quantifying overstory productivity is time consuming and expensive because destructive sampling or long-term remeasurement of permanent plots is essential for suitable accuracy. A method is needed to inexpensively determine which classes differ in overstory productivity, thereby eliminating the necessity to analyze all classes. In this paper we evaluate a simple method for identifying such classes.

Not all classes identified have different productivities. Cleland *et al.* (1985), in their classification of upland ecosystems in Michigan, describe 10 classes with four distinct levels of mean annual increment. They also found that two or three classes generally had similar site indices. Reporting on a further refinement of the Cleland *et al.* classification, Host *et al.* (1988) found differences in mean annual biomass increment among some classes but not among others. Their nine classes contained four levels of mean annual biomass increment. Hix (1988) developed 11 classes for upland ecosystems of southwestern Wisconsin. The classes represented, with some overlap, four levels of northern red oak (*Quercus rubra* L.) site index. Mueller-Dombois (1964) produced seven classes of jack pine (*Pinus banksiana* Lamb.) representing four site index levels and four classes of black spruce (*Picea mariana* Mill.) distributed among two site index levels.

Ecologists use different methods to distinguish areas that are ecologically similar. Some focus on vegetation (Coffman *et al.* 1983 and Kotar *et al.* 1988), while others use a multifactor approach that explicitly includes physiography and soils, as well as vegetation (Barnes *et al.* 1982, Host and Pregitzer 1991, and Hix 1988). Regardless of the approach, vegetation is always considered. Whether vegetation is the sole factor, or one among several, the TWINSPAN computer program (Hill 1979), is a widely used classification tool in the Great Lakes region (Host and Pregitzer 1991, Hix 1988, Jones 1984, Jeglum *et al.* 1982, and Kotar *et al.* 1988).

TWINSPAN (Hill 1979) classifies sample plot floristic data (either presence-absence or species abundance) by using a polythetic divisive technique. Polythetic techniques use

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all the species recorded; and divisive techniques start with all plots as a group and progressively divide them into groups with fewer members (Gauch 1982). The approach is computationally efficient and can be used to analyze large data sets (Gauch 1982). Because of its many desirable features, TWINSPAN is commonly used for classifying floristic data (Jongman *et al.* 1987, p. 193).

Although TWINSPAN classifies sampling units that are floristically dissimilar, the classes do not necessarily represent different environmental conditions (Kurmis *et al.* 1986). Plant composition depends not only on the relatively stable environmental conditions that affect plant growth and survival, but also on non-environmental factors such as natural disturbance (fire, windthrow, etc.), human disturbance (logging, grazing, etc.), and time (Carleton *et al.* 1985). Depending on the extent that vegetational classes are determined by non-environmental factors and productivity is determined by environmental factors, there will be a mismatch between the classes and productivity.

Because Bakuzis' (1959) method of synecological coordinates uses vegetation to quantify environmental factors (moisture, nutrients, heat, and light) of a sampling unit, we tested it as a method capable of distinguishing classes that differ in productivity. His approach is simple to apply and requires only a list of plant species present on the sampling unit and synecological coordinates for each species. Coordinates for a particular species may range from 1 (low intensity of the factor) to 5 (high intensity of the factor), depending on its prevailing occurrence when growing in competition with other plants. For example, species occurring primarily in very dry habitats would have a moisture coordinate of 1. Synecological coordinates do not directly measure the physiological requirements of a species (Kurmis *et al.* 1986).

Values of synecological coordinates for species growing in a region are determined by a two-step process (Bakuzis 1959, Brand 1985, Gutiérrez-Espeleta 1991). Species synecological coordinates are first estimated from the botanical literature. Second, a field reconnaissance covering a wide range of environmental conditions is conducted, and the initial coordinates are adjusted based on the species composition of the sample plots. For example, red pine (*Pinus resinosa* Ait.), described by Fernald (1950) as growing in dry woods, was given a moisture coordinate of 2 by Bakuzis (1959). After a reconnaissance in Minnesota, the moisture coordinate of red pine was adjusted to 1 (Bakuzis 1959). The adjustment process, originally done manually, has now been coded into a computer program (Gutiérrez-Espeleta 1991).

Synecological coordinates for a plot are the average adjusted synecological coordinates of species present on the plot. Because plot synecological coordinates express the level of environmental factors present, they may also indicate overstory productivity. The objective of this paper is to evaluate whether synecological coordinates are useful in identifying TWINSPAN vegetation classes that have different overstory productivities. Specifically, we hypothesize that those classes with different moisture (M) or nutrient (N) synecological coordinates will also differ in productivity.

METHODS

The study area is located within the Chippewa National Forest of north-central Minnesota, at approximately 47° 33' N latitude and 94° 6' W longitude. The regional climate is continental, with average winter temperature of 11°F, average summer temperature of 65°F, and 26 in. of annual precipitation that falls mostly from April through September (Nyberg 1987). The study area occurs on nearly level to rolling outwash of the Bemidji Sand Plain (Minnesota Soil Atlas 1980), which was deposited primarily by the wastage of the St. Louis sublobe, sometime after its maximum advance about 12,000 B.P. (Wright 1972). The soils have a loamy coarse sand texture and are classified as Typic Udipsamments (Menahga series) or Alfic Udipsamments (Graycalm series, Nyberg 1987). Although these sands tend to be low in fertility and droughty, there are deep, underlying, clay lenses (Bay and Boelter 1963) that may provide additional moisture and nutrients to the trees (Hannah and Zahner 1970). The original vegetation was described as jack pine/red pine barrens (Marschner 1974), which developed in the region after about 3,000 B.P. (Almendinger 1985).

In 1949, the Forestry Sciences Laboratory of the USDA Forest Service, North Central Forest Experiment Station in Grand Rapids, MN established two studies within a 400-acre area to evaluate the growth and yield of an 80-year-old red pine/jack pine stand of fire origin. Approximately 148 acres of the area were assigned to various treatments, and the response was measured with 135 circular 1/5 acre plots. Plot locations minimized variation in overstory composition and density. For our analysis we selected the 39 plots that were periodically thinned from below to 100 ft^2/acre. D.b.h. of each live tree > 3.5 inches at each measurement was recorded. Also, for each measurement after 1955, the total heights of two to seven dominant or codominant red pine on each plot were measured. The year trees were cut or died was also recorded.

The data collected allowed us to calculate two measures of productivity: site index (SI) and gross basal area growth including ingrowth (GG+I). Site index indicates the ability of a tree to grow vertically (a primary determinant of volume and biomass). From tree heights, stand age, and the Lundgren and Dolid (1970) red pine equation we computed SI for each tree. Plot site index was the average of all tree site index estimates.

Basal area growth measures change in girth (the other determinant of volume and biomass). GG+I, which includes the total basal area produced during a period, is defined by Husch *et al.* (1982):

$$[1] \qquad GG{+}I = BA_f + BA_m + BA_c - BA_i$$

where BA_f, BA_m, BA_c, and BA_i are the basal area values of trees alive at the end of the period, dying during the period, cut during the period, and alive at the beginning of the period, respectively. GG+I, like other measures of growth, varies with stand age. Therefore, comparing GG+I calculated with growth periods obtained at different stand ages includes the effect of stand age as well as site.

To minimize the effect of species composition on GG+I, we used 1959-1961 measurements as our starting points (all overstory jack pine had been cut by this time). The ending point was measurements taken in 1985 or 1986. Because the period of measurement differed slightly (ranging from 24 to 27 years), we calculated an annual GG+I.

A 10-m by 10-m vegetation plot was established within each overstory plot during the summer of 1989. The vegetation was recorded using a slightly modified relevé methodology (Almendinger 1988) that employs the standard Braun-Blanquet cover and abundance scale to estimate plant abundance (Mueller-Dombois and Ellenberg 1974), and Küchler's physiognomic system (Küchler 1967) to describe vegetation structure. The midpoints of the Braun-Blanquet cover classes were used for TWINSPAN analysis, and coverages of 1, 3, and 5 percent were assigned to the r (single individual), + (few individuals), and 1 (numerous individuals) abundance classes, respectively. Woody species in height classes 0 - 2 m, 2 - 10 m, >10 m, representing seedlings, saplings, and canopy trees, respectively, were treated as distinct taxa in the TWINSPAN analysis. Because TWINSPAN will continue to produce dichotomies until encountering an arbitrary stopping rule, the number of "significant" classes becomes subjective. We recognized those classes that appeared to be vegetatively different based on physiognomic differences in the shrub layer and the preferential occurrence of some ground layer species.

Synecological coordinates for moisture and nutrients were calculated for each plot based on the species present. Values for most forest species of trees, shrubs, ferns, and herbs growing in Minnesota have been computed and tabulated (Bakuzis and Kurmis 1978). Plot synecological coordinates are the average synecological coordinates of species present on the plot. These average values for moisture, nutrients, heat, and light provide an estimate of the environmental factors for a plot. We used moisture and nutrient coordinates because they represent the edaphic conditions of a site.

Overstory productivity is affected by site conditions, climate, and the composition and structure of the overstory. Before the difference in overstory productivity among ecological classes can be evaluated, the effect of climate and overstory must be removed. The 39 plots sampled were within a 400-acre area and were measured during the same period. Therefore, it is reasonable to assume that all sample plots have received essentially the same climatic input. The overstory composition of the sample plots was nearly pure red pine by 1960. The age dependence of GG+I is not a factor in this data set because the age of the overstory is the same for all samples. Although site index is relatively insensitive to stand density and tree size, basal area growth does depend on stand density and tree size.

A fixed effects analysis of variance (ANOVA) was used to determine if TWINSPAN classes have different synecological coordinates (Snedecor and Cochran 1980). Because there are few samples, we also corroborated the ANOVA tests with the nonparametric Kruskal-Wallis test (Conover 1971). When synecological coordinates differed, we used the Newman Keuls Studentized range test to determine which classes were different (Snedecor and Cochran 1980). This test fully implements the statistical notion of experiment-wise error for all paired comparisons without sacrificing the power to detect differences. Because classes contained different numbers of plots, we used the harmonic mean class size in computing the test statistic. Similar classes were grouped to form new classes. These new classes were tested for differences in site index and GG+I. Analysis of variance provided a test of differences in site index. Using an analysis of covariance, we accounted for the effect on GG+I of stand density with initial (1959-1961) plot basal area (BA) and the effect of tree size with quadratic mean d.b.h. (Dq).

RESULTS AND DISCUSSION

Based on the criteria mentioned above, the 39 plots were divided into four TWINSPAN classes (table 1). We chose these classes without knowing their overstory productivity.

The first TWINSPAN division (table 1) separates six plots (class D) from the remaining 33 plots (class ABC). Plots in class D are characterized by an extremely open understory, lacking any significant woody cover taller than 0.5 m. Particularly characteristic of class D are the high cover of *Vaccinium angustifolium* and *Gaultheria procumbens*; the comparatively high constancy of *Melampyrum lineare*, *Epigaea repens*, and *Prunus pumila*; and the presence of *Aster ciliolatus*, *Pyrola secunda*, and *Danthonia spicata*. In contrast to class D, class ABC has a well-developed shrub layer.

Much of the rationale for considering further subdivision as significant was based on differences in the composition of the shrub layer, particularly where these differences are supported by the fidelity of some ground layer species (table 1). The second TWINSPAN division segregates plots with *Abies balsamea* saplings (class AB) from those that generally lack *A. balsamea* (class C). This split is supported by the presence of *Pyrola chlorantha*, *Uvularia sessilifolia*, and *Lycopodium complanatum* in class AB and the abundance of *Rubus* (Flagellares section), *Fragaria virginiana*, and *Amelanchier* in class C. The assumed significance of the TWINSPAN division between classes A and B (level 3) is based on the observation that *Pinus strobus* saplings and *Quercus ellipsoidalis* seedlings are particularly characteristic of class B. Several woody species are either more abundant (*Vaccinium angustifolium*, *Amelanchier*, and *Rosa accicularis*) or occur more frequently as tall shrubs (*Corylus cornuta* and *Alnus crispa*) in class B. The low frequency of *Betula papyrifera* saplings in classes B and D was also considered significant.

The uniform site and overstory conditions of the study area are evident in the small range in the variables measured on the plots (table 2). Regardless, statistically significant ($P < 0.05$) differences were found in both mean moisture and nutrient synecological coordinates among the TWINSPAN classes with a fixed effects ANOVA (table 3). Although assumptions for ANOVA were not violated, the small number of samples prevented us from being certain that the errors were normally distributed. Applying the Kruskal-Wallis test relaxes the distributional requirements and requires only ordinal scale measurement of the response variable. With this test we also found a statistically significant difference among classes for nutrient coordinates ($P = 0.002$) but not for moisture coordinates ($P = 0.053$). Although the two tests did not produce consistent statistical inferences for moisture, we conclude that both moisture and nutrient coordinates differ among the four classes.

Table 1.—*Cover, constancy by class (A, B, C, D), and synecological coordinates for moisture (M) and nutrients (N) for species that are indicators or strong preferentials in the TWINSPAN divisions*

Div. 1
Div. 2
Div. 3

Species	Cover	A	B	C	D	M	N
		- - - - - - - - - - - - *Percent* - - - - - - - - - - -					
Division 1 [ABC(33)[a]/D(6)]							
Betula papyrifera Marsh. [b]	> 0	44	15	55	0	3	2
Galium aparine L.	> 0	56	31	55	0	3	4
Diervilla lonicera Mill.	> 0	67	38	73	0	1	2
Rubus strigosus Michx.	> 0	11	46	45	0	3	2
Aster macrophyllus L.	> 0	100	77	91	50	2	2
Gaultheria procumbens L.	> 5	33	38	27	100	1	1
Melampyrum lineare Desr.	> 0	0	31	18	100	1	1
Epigaea repens L.	> 0	0	23	36	83	1	1
Prunus pumila L.	> 1	0	8	18	100	1	2
Arctostaphylos uva-ursi (L.) Spreng.	> 0	0	15	0	67	1	1
Vaccinium angustifolium Ait.	> 50	0	0	18	67	1	1
Danthonia spicata L.	> 0	0	0	9	50	-	-
Aster ciliolatus Lindl.	> 3	0	0	0	33	2	2
Pyrola secunda L.	> 0	0	0	0	50	2	2
Division 2 [AB(22)[a]/C(11)]							
Alnus crispa (Ait.) Pursh.[b]	> 0	22	46	9	0	2	1
Abies balsamea (L.) Mill.[b]	> 0	100	85	9	17	4	2
Abies balsamea (L.) Mill.[c]	> 3	89	62	0	17	4	2
Pyrola chlorantha Sw.	> 0	56	23	0	33	2	3
Uvularia sessilifolia L.	> 0	22	38	0	0	2	4
Lycopodium complanatum L.	> 0	44	69	9	100	2	2
Rubus (Flagellares section)	> 5	33	8	64	17	1	3
Fragaria virginiana Duchesne.	> 3	22	15	73	67	2	2
Amelanchier spp.[c]	> 1	11	54	91	100	3	2
Division 3 [A(9)[a]/B(13)]							
Pinus strobus L.[b]	> 1	11	62	27	0	2	2
Vicia americana Muhl.	> 0	0	54	27	33	3	3
Quercus ellipsoidalis E.J. Hill[c]	> 3	22	77	18	17	1	2
Corylus cornuta Marsh.[b]	> 0	33	77	27	50	2	1
Vaccinium angustifolium Ait.	> 5	44	100	91	100	1	1
Amelanchier spp. [c]	> 1	11	54	91	100	3	2
*Rosa acciculari*s Lindl.	> 3	0	62	82	0	1	2

[a] Numbers in parentheses are the number of plots in each class.
[b] between 2 m and 10 m (saplings).
[c] ≤ 2 m tall (seedlings).

Table 2.—*Minimum, maximum, mean, and standard deviation for selected attributes of the 39 study plots*

	Minimum	Maximum	Mean	s
Initial BA ($ft^2\ ac^{-1}$)	81.2	110.3	98.2	6.2
Initial Dq (in)	9.4	14.9	12.6	1.1
M coordinate	1.41	2.06	1.83	.13
N coordinate	1.79	2.42	2.07	.14
Number of species on plot	19	36	29	3.8
SI (ft)	45.0	53.0	49.8	2.1
GG+I ($ft^2\ ac^{-1}\ yr^{-1}$)	1.36	2.31	1.79	.22

Table 3.—*ANOVA for moisture and nutrient coordinates among four TWINSPAN classes (A, B, C, D)*

		M coordinate			N coordinate		
Source	df	SS	F	P	SS	F	P
Class	3	0.1528	3.49	0.026	0.2810	6.48	0.001
Error	35	.5104			.5060		

The Newman Keuls Studentized range test allowed us to determine which classes were causing the difference in moisture and nutrient coordinates. The test shows a statistically significant ($P < 0.05$) difference between class D and the other classes for both moisture and nutrients (table 4). Differences do not appear for any other pair of classes. We conclude that synecological coordinates of class D are different from those of classes A, B, and C. Therefore, classes A, B, and C belong together in a single class, ABC. Class D has smaller moisture and nutrient coordinates than class ABC (table 5).

Site index is significantly different between the two classes (table 6). An analysis of covariance with BA and Dq as covariates showed that GG+I does not depend on initial basal area ($P = 0.232$), but it does depend on Dq ($P = 0.003$). After we account for Dq, the adjusted GG+I means for classes ABC (1.82 $ft^2\ ac^{-1}\ yr^{-1}$) and D (1.61 $ft^2\ ac^{-1}\ yr^{-1}$) are significantly different (table 7). The interaction between Dq and class was found to be insignificant ($P = 0.234$), thus confirming the homogeneity of slopes. Class D is less productive than class ABC.

GENERAL DISCUSSION

The statistical analysis shows that TWINSPAN classes with different moisture and nutrient synecological coordinates differ in overstory productivity. Although the differences in mean site index and GG+I between the two classes (ABC and D) are small (table 5), variation in factors that cause differences in productivity (climate, tree age, species composition, density, and disturbance) is also small. Recall, all plots were located within a 400-acre area and were measured about the same time so precipitation and temperature histories are probably similar for each plot. Ages of the trees on the plots are similar because the plots are within an area burned by wildfire in 1870. Although the species composition and density of the regenerated forest varied, study plots were located to minimize this variation.

Table 4.—*Moisture (M) and nutrient (N) synecological coordinate means and rank sums for the four TWINSPAN classes*

Class[a]	n	Mean M	Mean N	Rank sum M	Rank sum N
A	9	1.87a	2.17a	217	259
B	13	1.87a	2.05a	298	252
C	11	1.82a	2.10a	211	232
D	6	1.69b	1.90b	54	37

[a] Classes with mean M and mean N followed by different letters are significantly different (P < 0.05) according to the Newman Keuls Studentized range test.

Table 5.—*Minimum, maximum, mean, and standard deviation for selected attributes of the two TWINSPAN classes with different synecological coordinates*

	Minimum	Maximum	Mean	s
		Class ABC		
Initial BA (ft^2 ac^{-1})	81.2	110.3	98.7	5.9
Initial Dq (in)[a]	10.2	14.9	12.8	1.0
M coordinate	1.58	2.06	1.86	.11
N coordinate	1.79	2.42	2.10	.13
Number of species on plot	19	34	28.3	3.5
SI (ft)	46.0	53.0	50.3	1.7
GG+I (ft^2 ac^{-1} yr^{-1})	1.36	2.31	1.80	.21
		Class D		
Initial BA (ft^2 ac^{-1})	84.7	100.9	95.6	7.3
Initial Dq (in)	9.4	12.4	11.5	1.1
M coordinate	1.41	1.84	1.69	.15
N coordinate	1.81	1.97	1.90	.07
Number of species on plot	22	36	30.5	5.2
SI (ft)	45.0	52.0	47.5	2.9
GG+I (ft^2 ac^{-1} yr^{-1})	1.45	2.15	1.73	.29

[a] Quadratic mean diameter.

Table 6.—*ANOVA for site index among two TWINSPAN classes (ABC, D)*

Source	df	SS	F	P
Class	1	39.03	10.94	0.002
Error	37	132.04		

Table 7.—*Analysis of covariance for GG+I among two TWINSPAN classes (ABC, D)*

Source	df	SS	F	P
Class	1	0.1736	4.32	0.045
Dq	1	.4438	11.03	.002
Error	36	1.4479		

Class	Adjusted mean GG+I
ABC	1.82 ft^2 ac^{-1} yr^{-1}
D	1.61 ft^2 ac^{-1} yr^{-1}

In addition, all plots were periodically thinned from below, which further increased their homogeneity.

Site index is more strongly related to TWINSPAN classes with different moisture and nutrient coordinates (tables 6 and 7) than gross growth plus ingrowth. Pluth and Arneman (1965), however, found no significant correlation between the site index of red pine, jack pine, or quaking aspen (*Populus tremuloides* Michx.) and moisture and nutrient synecological coordinates. Total basal area and moisture and nutrient coordinates were correlated on their plots. It is not clear if this correlation was due primarily to differences in the environment. It may have been due to differences in overstory composition because species composition of the overstory on a given site also directly influences overstory growth (Alban 1985, Frederick and Coffman 1978, Schlaegel 1975, Spurr and Barnes 1980).

Sampling units in this study are similar in climatic history, stand conditions, and disturbance history. Under these conditions, synecological coordinates differentiated

TWINSPAN classes with different productivities. Whether this method can be applied to a broader range of conditions needs to be determined. If it can be applied in this way, then fewer TWINSPAN classes would require expensive mensurational studies to quantify their overstory productivity.

Acknowledgment

We thank the personnel of the USDA Forest Service, North Central Forest Experiment Station, Silvicultural Project (NC-4101), in Grand Rapids, Minnesota, for installing, measuring, and maintaining the silvicultural studies that provided the mensurational data for this analysis. They also provided historical information and the data in electronic form. We especially appreciate the help of Robert G. Barse (NC-4101) in finding the plots and David Shadis of the Chippewa National Forest in arranging for collection of the floristic data. Ronald E. McRoberts, David J. Rugg, and Anne Steuer, of the North Central Forest Experiment Station, St. Paul, Minnesota, provided helpful advice on the appropriate statistical procedures. Three others provided helpful review comments: David F. Grigal, University of Minnesota; George E. Host, Natural Resources Research Institute; and David D. Reed, Michigan Technological University,

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KEY WORDS: Floristic classes, ecological classes, basal area growth, site index, Minnesota.