VARIABILITY OF YELLOW BIRCH IN THE WESTERN GREAT LAKES REGION[1]

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For the past several years, several of us have been involved with studies, directed by Professor Burton V. Barnes of the University of Michigan, of genecology of yellow birch (*Betula alleghaniensis* Britton) in the western Great Lakes region (Dancik 1967, 1969, and 1972; Dancik and Barnes 1971, 1972, and 1973) and the Appalachian Mountain region (Sharik 1970; Sharik and Barnes 1971; and Barnes, Dancik, and Sharik 1973). I would like to report on a small part of one of these studies, with special emphasis on a statistical technique, which I feel is particularly useful in genetic studies where the data included many measurements of many trees from many populations.

One objective of this study was to determine whether there was any relationship between leaf morphology and the characteristics of the sites upon which the populations of birches were growing. Leaves, instead of other organs or characters of the trees, were chosen because of their availability and ease of collection during a major portion of any year. I noted that the results of single character analysis often revealed significant differences among the populations, but only weak relationship to any environmental variable (Dancik 1972). The study of a complex of characters, however, might reflect a distinct adaptive pattern. One technique for analyzing many characters simultaneously is canonical variates analysis.

MATERIALS AND METHODS

Standard leaves (Dancik and Barnes 1973) were selected from 371 birches in 50 populations in Lower Michigan and eastern Upper Michigan (fig. 1). Thirteen measurements were made on each of 6 leaves from each tree according to the procedures of Dancik (1972). Means for each character of each tree were calculated. The first and second canonical variates of these tree means were then computed using a version of the U.C.L.A. Bimed program 7M. Canonical variates are transformations of the original data that are oriented orthogonally to one another in multivariate space, similar to principal components. The canonical variates, however, are derived from the variance-covariance matrix of the original data such that differences among the arbitrary input groups are maximized. The first canonical variate axis is inclined in the direction of greatest variability between the population means. The second axis is perpendicular to the first and inclined in the direction of next greatest variability between populations (Seal 1964; Blackith 1965; and Bartlett 1965). Means of the first two canonical variates of each population were plotted.

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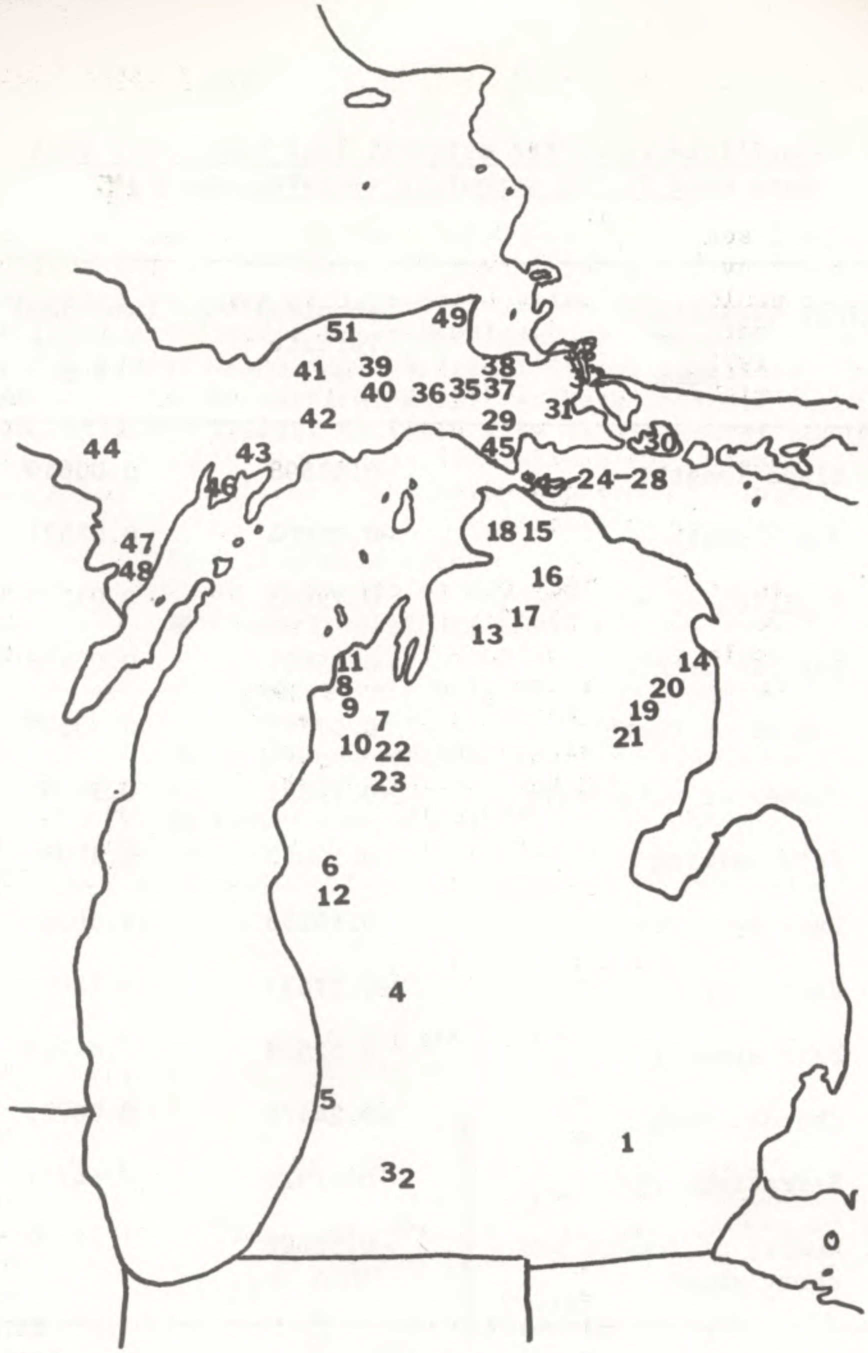


Figure 1.--Location of the 50 yellow birch populations.

RESULTS

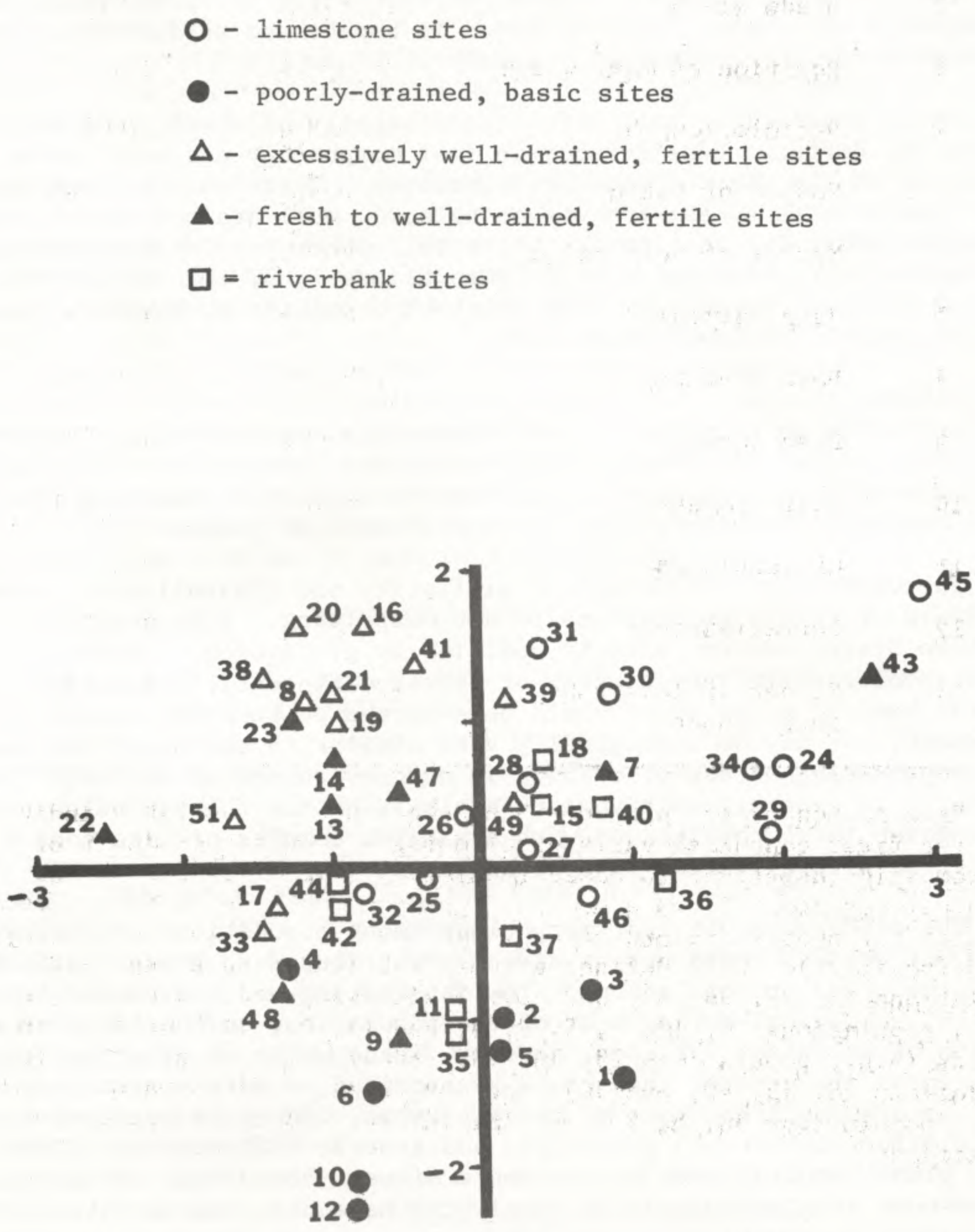
Canonical variates of the birches revealed that there was some separation and grouping of the populations that was related to the site types of the populations. The first two canonical variates of the 50 populations accounted for 44% of the total variance in the system. The first canonical variate was a rather complicated summation of several characters (table 1). The second canonical variate was largely derived from a number of leaves per short shoot, pair symmetry, and base symmetry, with a moderate input from serration type.

Table 1.--Coefficients of the original leaf characters that were used in the canonical variates analysis.

Original Variable #	Name	Canonical Variate #1	Canonical Variate # 2
1	Blade length	-0.07898	0.00639
2	Blade width	-0.01004	0.01521
3	Position of max. width	0.28965	0.07712
4	Petiole length	-0.05901	-0.00478
5	Number of teeth	0.02863	0.03309
6	Number of vein pairs	-0.37551	0.35563
7	Vein pairing	-0.10042	-0.38054
8	Base symmetry	0.10136	-1.56386
9	Base shape	-0.21653	-0.12600
10	Pair symmetry	0.52568	-1.84481
11	Chordateness	-0.24476	0.00772
12	Serration type	-0.21911	-0.64217
13	Number of leaves per short shoot	-0.50606	1.61198

Examination of the plot of these two canonical variates indicates that the first canonical variate following a moderate gradient of soil pH from acid (negative) to basic (positive) (fig. 2). The second canonical variate follows a moderate gradient of site drainage from undrained or poorly-drained sites (negative) to extremely well-drained sites (positive). Well defined groups from limestone sites (e.g., populations 24, 29, 34, 43, and 45); basic swamps and lake borders (e.g., populations 10, 12, 6, 5, 2, 3, and 1); fertile, well-drained uplands (e.g., populations 23, 14, 13, and 47); riverbank sites (e.g., populations 18, 15, 40, and 36); and dry, upland and outwash sites (e.g., populations 38, 8, 20, 21, 19, 16, and 41) can be easily identified.

Figure 2. Canonical variates of leaves of yellow birch in 50 populations in Lower and eastern Upper Michigan. Based upon 13 leaf characters of 371 trees. Canonical variate 1 is the horizontal axis; canonical variate 2 is the vertical axis. Numbers indicate numbers of the populations. Symbols indicate site conditions of populations:



DISCUSSION

The 50 Michigan populations of yellow birch exhibited natural groupings on the basis of their morphological leaf characteristics that followed discernible environmental gradients. As would be expected, some geographically proximate populations were morphologically similar, while others were very dissimilar. Some groups of populations, such as those from Bois Blanc Island (numbers 24 through 28 and 34) were similar in most leaf characters and the derived canonical variates. This could be explained on the basis of the relatively similar ecological sites upon which these populations were found. All of the populations from Bois Blanc Island came from sites with similar macro- and micro-climate, that had soils with a thick organic layer, little inorganic soil, and a limestone substrate. They differed in aspect and surface soil pH, but were otherwise ecologically similar.

Other populations that were geographically adjacent, such as numbers 43 and 46, differed considerably in leaf morphology and were quite widely dispersed on the plot of canonical variates. These populations, however, came from diverse sites; one was on an acid, well-drained sandy loam, while the other was on a basic, wet site. Other populations that were far apart geographically (such as populations 1, 3, 10, and 12) were similar in leaf morphology. All of these populations, however, came from similar, poorly-drained, basic sites.

Others, that are very similar morphologically (such as 22 and 51), were far apart geographically and, apparently, ecologically. The more southerly site of 22, however, was wetter and warmer than the site of 51, and these and other differences may cancel each other and make the two sites ecologically similar for the development of yellow birch.

The variety of morphological similarity and dissimilarity between proximate or remote populations is not surprising. This whole area of the Lake States was extensively modified by glaciation. Nearby sites may be ecologically very similar or vastly different. Similarly, sites several hundred miles apart would be expected to be ecologically quite different, but may be ecologically very similar to the plant because of the compensating effect of changes in one environmental variable for another. In general, multivariate analysis of the foliage helps to distinguish those populations with a similar complex of site conditions from those with different site conditions.

The differences in leaf morphology among populations of yellow birch, of course, could not be directly attributed to genetic differences among the trees or populations. The interesting and systematic, though complex, ecological arrangement of the populations on the basis of the results of canonical variates, however, leads me to believe that the differences are greater than could be ascribed to mere systematic, environmental modifications of the genotypes. There is evidence for the relationship between phenotypic and genetic differences in some woody plant species, even on proximate sites. Phenotypic and genetic differences in glaucousness of *Eucalyptus* have been demonstrated for populations within 1/2 mile and 400 feet elevation of one another (Barber and Jackson 1957). Similarly, genetic differences between nearby populations of white cedar (*Thuja occidentalis* L.) on upland and lowland sites have been demonstrated by Habeck (1958), As pointed out by Roche (1968), ".,.if populations in one type of habitat are regularly found to differ from those in another in any characteristic whatever, these differences have adaptive significance, and are due to the differential effect of selection in the two environments."

I believe that at least a portion of the differences in leaf morphology described here are due to genetic differences among the yellow birch individuals and populations associated with the ecological conditions of the sites they occupy. It seems likely that selective pressure could result in these differences, It would be premature and probably incorrect to assume that some of the morphological differences are directly related, for example, to the pH of the soil. Rather, it is likely that there are differences between populations on acid and basic sites that are related to a complex of environmental variables. One of these variables may be the observed variable, soil pH, or several whose variation parallels variation in soil pH.

Canonical variates seem to be biologically useful in studies of phenotypic or genetic variability. A complex of many characters can be synthesized into a few variables that may indicate a direct relationship to some environmental variables, Of particular importance, the method allows for partitioning of the within and among population variance. Mass collections of standard leaves of birches, and probably other species, appear to be useful in studies of genetic variability.

From a practical standpoint, the results indicate that yellow birch has different forms that are probably adapted to the different sites upon which they occur. Until further information is available, anyone wishing to plant yellow birch would be wise to collect seed from trees selected from sites similar to that of the planting site.

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DISCUSSION

Klein - Since the main components seem to be associated with pH and dryness, which could vary over a small area, by attributing this variation to genotypes, you are supposing genetic isolation in a small area. I would think there would be pollen flight across areas--across a gradient of pH and soil moisture so that I would look for a phenotypic response to the environment in that case.

Dancik - That involves the old argument: Are observed differences among phenotypes primarily due to differences among genotypes or to environmental modifications of the genotypes? There seem to be substantial arguments in favor of saying that phenotypic differences that are related to environmental gradients are genetically based (see Roche, L. 1968. Commonwealth Forestry Rev. 47:14-26; Heslop-Harrison, J. 1964. Advances in Ecol. Res. 2:159-247).

Klein - How can you maintain a genetic difference over a sharp gradient? How can you maintain a genetic isolation--genetic gradient over a small area in the presence of substantial gene flow?

Dancik - Natural selection appears to be working particularly rigorously here. Bradshaw's work with metal tolerance of grasses indicates that genetic differentiation can occur over a very small area where pollen flow among the populations could easily occur.

Gordon - You mentioned calcarous area--this thing might be resolved, Jerry, by deciding whether they were large homogeneous areas of calcarous material and the acid sites were well separated from this or were they in pockets in this calcarous basin where you could get pollen exchange?

Dancik - Several of the populations were on limestone sites. A few of the sites were on glacial morain sites.

Gordon - This has been investigated very extensively by Heimburger and Fowler's work with black spruce and upland and lowland types proved rather conclusively as far as genotypes. A few years ago there was quite a lot of discussion about white spruce by Mark Holst and Farrar on calcarous--well ecotypic variation. I rather think this is being inclusive again. I am not questioning this. I think the matter is still unresolved here because there is adaptive variation in spruce or whether these are site differences or real ecotypic variation.

Lester - Certainly the matter is unresolved, but there is a lot more to it than most people seem to be aware of. I would like to make several points: 1. pollen transfer or seed transfer do not necessarily constitute gene transfer; 2. we have done some work in Wisconsin with upland and lowland populations of white cedar and we find that in the space of a few hundred yards an elevational gradient of 30 or 40 feet can produce significant ecotypic variation; and 3. on the side of the interpretation Bruce is making, there is a comprehensive paper by Klaus Stern on Japanese birches in which he found that a pioneer species i.e., a species which corresponds to our B. papyrifera did not seem to show as close a genetic adaptation to environment as a climax species.

Gordon - We have a little experience, very old on that issue. I have some connection with yellow birch planting in Ontario, and the people seem to have a great reluctance, and this may be true all over North America, to decapitate hardwoods. The practice in Switzerland in planting *Fraxinus* is to plant the trees and chop them off at ground level and stand back. I noticed that where yellow birch is planted in Ontario by the thousands this way that nobody would cut them so they just died back--all of them died--by the thousands. In some trials we sort of stuck our noses in and interfered a little bit and chopped them right off as soon as the planters put them in the ground. We just took a pair of shears and chopped them right off. I think those trees are now growing as well as the average uncut trees. I noticed that the people working with hybrids in southern Ontario cut some of them, but it may be that with yellow birch you have to plant the tree from the nursery and then cut it right off at the ground. Certainly, white birch grows very well if you plant a tree, any tree, and you don't even have to be careful how you rip it out of the ground. You rip it out of the ground with a tractor or fork, stick it in the ground, chop it off, and it grows fine.

Valentine - You said that you didn't get a correlation between specific gravity and height growth.

Lee - The height-specific gravity correlation was slight but statistically significant at the 1% level.

Valentine - What did you use for your specific gravity study?

Lee - I used the growth increment (an increment core sample) formed during the 1969 growing season in my study.

Zsuffa - I would like to ask Dr. Lee how much variation in specific gravity was there within the provenances. And another question, if you have any explantation for the unusual higher specific gravity associated with faster growth?

Lee - There was greater variation in specific gravity within the provenances than between the provenances, although faster growing seedlots had higher specific gravity; but the difference associated with growth rate was not substantial.

Zsuffa - You said you analyzed only one tree per plot?

Lee - Right.

Dorn - I have a comment about cutting off yellow birch. We put in a planting this spring. We cut off all the trees in the two blocks out of four back to the ground line. On the way to this meeting I went around and looked at them and made a very brief observation. The ones that were cut off looked if anything better than the ones that were not cut off. I only found a couple of trees that hadn't sprouted. My own feeling is that they probably would have died anyway even if they hadn't been cut off. It looks quite promising. I had a question for Bruce concerning this study of leaf morphology of yellow birch. Did you find any that looked visually intermediate between yellow birch and paper birch?

The reason I ask this is because we planted several seedlots--50 or so--a few years ago, and I know the seed was from yellow birch, as I helped collect them myself. They were definitely from yellow birch trees, but now they look like paper birch to me, Has anyone got any comments on that sort of thing?

Dancik - Yes, Clausen found seedlings that appear to be hybrids between yellow birch and paper birch among the progeny from some of his yellow birch sources. These were generally from populations in the southwestern part of the yellow birch range where paper birch also existed. We have noted that in the southern part of the several birch ranges that flowering times of the different species often overlap and that natural hybrids appear to be much more frequent than elsewhere.

Dorn - I wonder how successful these so-called hybrids would be if they were outplanted?

Dancik - I suppose it would depend on the site used. Some of them look pretty good.

Fraser - Dr. Dancik, did you notice any special leaf characteristics typical of birch in various stages of decadence?

Dancik - No, most of the samples were restricted to a vigorous pole-sized or larger trees.

Garrett - I would like to hear that comment from Rhinelander.

Nienstaedt - From our range-wide provenance study of yellow birch, Knud Clausen has found that certain populations consistently will produce these hybrids. I recall several populations along the southern edge of the species. To answer your question about how they perform, Clausen lifted many of the hybrid seedlings out of the nursery bed. They 0 were quite easy to identify partly because they grow much faster than yellow birch, and partly because they are more susceptible to the leaf miner; you can spot them quite readily. And we planted the hybrids out separately because yellow birch grew much slower and required an additional year in the nursery.

Dorn - Have you reached any conclusion; I mean, have they survived?

Nienstaedt - As far as I know, they have survived and continue to grow well. Clausen hasn't remeasured them yet.

Gordon - When you mentioned the southern part of the range, what do you mean? Are you talking about outliers?

Nienstaedt - Yes, one of the selections I made for him is along the Rock River near Rockford, Illinois; it is very typical. It is one of the outliers for this species.

Gordon - Outplanted or natural? Were white birch present in the area?

Nienstaedt - It was a natural stand of hardwoods--white birch and "hybrids"--but the trees I collected seed from were of typical yellow birch type.