A test of the accuracy of shade-tolerance classifications based on physiognomic and reproductive traits

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Traits such as live crown ratio and understory stem density are often used subjectively as a guide to grouping tree species into shade tolerance classes. The accuracy of this approach was tested on nine species in an upland oak forest by comparing a tolerance index based on measurements of live crown ratio and understory stem density with observed survival and growth rates of suppressed trees obtained from 19-year permanent plot records. A high correlation ($r = 0.93$) was found between predicted and observed tolerance indices. The observed tolerance of several species differs from traditional classifications but was correctly predicted by the tolerance index.

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Des caractéristiques comme le rapport de la longueur de cime verte sur la hauteur de l'arbre et la densité des tiges dans le sous-bois sont souvent utilisées comme guides subjectifs pour répartir les espèces arborescentes en classes de tolérance à l'ombre. La justesse de cette approche a été évaluée dans une chênaie, en comparant un indice de tolérance reposant sur les mesures du rapport cime verte:hauteur et sur la densité des tiges dans le sous-bois, à des observations sur la survie et le taux de croissance d'arbres réprimés; ces dernières observations ont été extraites de données obtenues pendant 19 ans dans des quadrats permanents. Il y a une corrélation élevée ($r = 0{,}93$) entre les indices de tolérance prévus et observés. La tolérance de plusieurs espèces diffère de celle qu'on leur reconnaît dans les classifications traditionnelles mais elle est correctement prédite par l'indice de tolérance.

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Introduction

Shade tolerance in forest trees, defined by Spurr and Barnes (1980) as the ability of trees to survive and grow beneath a forest canopy, is difficult to evaluate numerically in the absence of long-term permanent plot records. Quantification of shade tolerance on the basis of physiological and anatomical factors has also proved to be difficult. In recent reviews of this problem, investigators have indicated that shade tolerance appears to result from a complex of physiological and anatomical factors, and no one or two causal factors seem to be useful for diagnostic or classification purposes (Boardman 1977; Pereira and Kozlowski 1977; Kramer and Kozlowski 1979). Most tables of shade tolerance of forest trees are therefore based on subjective assessments of factors believed to be correlated with survival and growth under low light conditions (Baker 1949; Trimble 1975; Spurr and Barnes 1980). The most common factors used in assessing tolerance are relative density of live suppressed trees beneath the forest canopy, foliage density, live crown ratio (ratio of crown length to total tree height), proportion of total branch length with live foliage, and the ability to respond to release from suppression (as indicated by radial growth patterns). More precise classifications of shade tolerance would be desirable for interpreting successional trends and for use in forest growth and succession models (Botkin *et al.* 1972; Ek and Monserud 1974; Phipps 1979; Shugart *et al.* 1981).

Graham (1954) appears to have been the first to try to quantify the kinds of physiognomic and reproductive traits ordinarily used in making the subjective tolerance classifications. His method does not require actual measurements of trees but rather a subjective scoring of each trait on a three-point scale for each species. Four traits are evaluated, resulting in a final scale of relative tolerance ranging from 0 (intolerant) to 10 (very tolerant). The procedure is simple and applicable to any region, but how accurate are the results? This study was undertaken to compare the relative tolerance scale obtained from measurements of physiognomic and reproductive traits with actual mortality and growth rates of understory trees obtained from permanent plot records.

Study area

The study area is an even-aged mixed hardwood stand in the Harvard Forest, central Massachusetts, that developed following clear-cutting of a seral stand of white pine (*Pinus strobus* L.). Portions of the stand were cut sequentially in 1915, 1917, and 1923 (Lutz and Cline 1947; cases 2, 4, 6). The stand is located on a gentle northwest slope on a drumlin at an elevation of 320 m. The soil is a fine sandy loam with a fragipan at a depth of 0.5–0.8 m (Lyford *et al.* 1963). Site quality is average for upland sites in the region, with a site index of 65 (feet (1 foot = 0.3048 m)) for red oak (*Quercus rubra* L.) at a base age of 50 years. The stand is especially suitable for a study of comparative shade tolerance because of the high species diversity. Principal overstory dominants and their percent density of canopy (nonsuppressed) stems in 1956 were red oak (32%), paper birch (*Betula papyrifera* Marsh.; 31%), white ash (*Fraxinus americana* L.; 16%), red maple (*Acer rubrum* L.; 10%), and sweet birch (*Betula lenta* L.; 5%). The stand is relatively dense according to the criteria of Gingrich (1967), classified at the 75% level of full stocking in 1956 and the 105% level in 1975 (1120 overstory stems/ha in 1956 and 846 in 1975; 15.9 m^2/ha basal area in 1956 and 25.5 in 1975).

Methods

Two permanent plots, each 30.5 × 91.4 m, were established in the study area in 1956 by the Harvard Forest staff. Each plot was gridded with string along compass lines into three-hundred 3.0 × 3.0 m subplots, and the location of each tree ≥5.0 cm diameter at breast height (dbh) was estimated on a map of the subplot. Trees were classified by crown position as either understory (completely suppressed beneath the forest canopy) or overstory (receiving at least some direct sunlight). Diameter measurements were made at breast height to the nearest 0.1 in. (2.54 mm) with a diameter tape. Four remeasurements of the plots by staff members were made over a period of 19 years. Although numbers were not painted on the stems, no problems were encountered in locating even the small trees during an examination of all suppressed trees on the plots by the author in 1977.

Two physiognomic and reproductive traits were selected for evaluation: average live crown ratio of the dominant–codominant trees and number of suppressed trees per unit area. Of the traits considered to be correlated with shade tolerance, these are the most easily quantified. Live crown ratio reflects the degree to which the lower live branches of overstory trees are retained or shed in the shaded environment beneath the upper canopy surface. The density of suppressed trees, although influenced by several factors including germination requirements, is generally considered to be correlated with shade tolerance since tolerant species classified by other criteria usually have abundant saplings beneath the canopy and intolerant species do not. In the present study area, most of the suppressed trees >5.0 cm dbh were initially in a dominant position but were subsequently overtopped by faster growing trees (cf. Oliver 1978). For all species suited to a particular site and having no barriers to initial establishment, the number of large suppressed saplings at any time is hypothesized to be correlated with the survival rate beneath the canopy.

Density of suppressed trees was obtained directly from the permanent plot records. Live crown ratios were calculated from height measurements by the author of 15–18 trees of each species. Twenty-three random points were established in the stand, and the two nearest dominant or codominant trees of each species within a 20-m radius were measured (when present) for crown length and total height with a Haga altimeter. Measurements were made after budbreak in early spring, and at that time no difficulties were encountered in obtaining views of the crowns along a base line of 15–25 m if several vantage points were checked. The base of the live crown was defined by an imaginary horizontal plane passing through the lowest mass of foliage originating from a branch at least 1.0 m long.

The mean values of each trait for each species were then converted to a relative scale of 0 to 10. For the density of suppressed stems, for which the distribution of values was greatly skewed, the logarithm of stem density was used as the basis for the relative scale. The "predicted" tolerance index was then defined to be the mean relative value for the two traits live crown ratio and logarithm of understory stem density.

The "observed" tolerance of each species, following the definition of Spurr and Barnes (1980), is based on the relative survival and relative growth of suppressed trees. In the absence of objective criteria for a differential weighting of these two factors, the "observed" tolerance index was computed to be the arithmetic mean of relative survival and relative growth, also on a 0–10 scale. In all cases, relative scores were computed by the following formula: $R_i = 10((x_i - x_{\min})/(x_{\max} - x_{\min}))$, where R_i = relative score for species i; x_i = observed mean value for species i; and $x_{\max}$ and $x_{\min}$ are the highest and lowest observed mean values, respectively.

Results and discussion

A wide range of survival and growth rates of suppressed trees among different species was observed. Nineteen-year survival among the population of suppressed trees ranged from 2% in white ash to 84% in red maple. Mean annual diameter growth showed a similar wide range, from 0.11 mm in red pine (*Pinus resinosa* Ait.) to 0.98 mm in red maple (Table 1). Although mean survival and growth rates among species were correlated (r = 0.78), certain species had relative survival rates dissimilar to the relative growth rates. Pignut hickory (*Carya glabra* (Mill.) Sweet), for example, had a high survival rate but only moderate growth rate, and red oak had a low survival rate but moderate growth rate.

A comparison of the predicted tolerance index with the observed tolerance index (Table 2) indicated that the two are highly correlated (r = 0.93). The predicted tolerance index correctly grouped white ash (generally considered a midtolerant species) with intolerant species such as red pine and paper birch. At least on this upland site, all three species had high mortality rates and low growth rates with observed tolerance indices of <1.5. The procedure also resulted in an accurate classification of pignut hickory (predicted index, 5.6; observed, 6.0), a species whose tolerance classification has been highly uncertain (Baker 1949). The relatively high tolerance of white pine was predicted fairly closely. The index also anticipated a somewhat lower tolerance of sugar maple (*Acer saccharum* Marsh.) compared with red maple; although this would not be the expected order of tolerance for the two species in mesic northern hardwood forests, it is in fact in accordance with the data obtained from permanent plots on this upland oak site. In a few cases the predicted ordering of species is different from what was observed, at least for this specific 19-year period. The reversal of sweet birch and

TABLE 1. Survival and growth rates of suppressed trees ≥5.0 cm dbh on the study area, 1956–1975

Species	19-year survival (%)	Mean diameter growth rate (mm/year)	Initial no. trees (1956)	Average dbh in 1960 (cm)
White ash (*Fraxinus americana* L.)	1.8	0.20	111	6.8
Red oak (*Quercus rubra* L.)	10.0	0.48	40	7.5
Paper birch (*Betula papyrifera* Marsh.)	11.4	0.21	70	6.7
Red pine (*Pinus resinosa* Ait.)	16.7	0.11	24	9.1
Sweet birch (*Betula lenta* L.)	34.8	0.64	66	7.4
White pine (*Pinus strobus* L.)	59.5	0.76	121	8.4
Sugar maple (*Acer saccharum* Marsh.)	70.4	0.67	27	7.0
Pignut hickory (*Carya glabra* (Mill.) Sweet)	71.4	0.41	7	7.4
Red maple (*Acer rubrum* L.)	83.6	0.98	122	6.8

TABLE 2. A comparison of predicted vs. observed tolerance indices

Species	No. suppressed trees/ha (1975) (1)	Live crown ratio (%) (2)	Relative scores (3)[a]	Relative scores (4)[b]	Predicted tolerance index[c] (5)	Observed tolerance index[d] (6)	Tolerance class (observed)[e] (7)
White ash	5.4	36.0	0.0	0.0	0.0	0.5	Intolerant
Red pine	7.1	41.8	0.8	2.0	1.4	0.9	Intolerant
Paper birch	16.1	44.3	2.8	2.9	2.8	1.2	Intolerant
Red oak	12.5	54.8	2.0	6.6	4.3	2.6	Low midtolerant
Sweet birch	57.1	61.6	5.8	9.0	7.4	5.1	High midtolerant
Pignut hickory	8.9	64.5	1.2	10.0	5.6	6.0	High midtolerant
White pine	162.5	46.3	8.5	3.6	6.0	7.3	Tolerant
Sugar maple	39.3	62.8	5.0	9.4	7.2	7.4	Tolerant
Red maple	312.5	62.1	10.0	9.2	9.6	10.0	Very tolerant

[a]$\log_e$ of column 1.
[b]Relative scope of column 2.
[c]Mean of columns 3 and 4.
[d]Mean of relative 19-year survival and relative mean annual diameter growth of suppressed trees (Table 1).
[e]These classifications are understood to apply only to upland oak stands of fairly high density in central Massachusetts. Point values of boundaries between classes follow those established by Graham (1954).

white pine is a case in point. Given that perfect ordering of species is not likely to result from any predictive method, the most reasonable approach is probably to arrange species into five two-point tolerance classes as was done by Graham (1954), realizing that errors of ± two points can be expected for some species. Nevertheless, the test reported here indicates sufficiently close agreement with observed and predicted relative tolerance in most cases so that this method of classification may be useful in areas where permanent plot records are not available. Accuracy in such cases would be improved if growth rates of suppressed trees, determined from increment cores or stem cross sections, were to be included as a component of the predicted index.

It should be emphasized that ratings obtained by this method, and observed tolerance as well, should be expected to vary according to geographic location, habitat type, species composition of the canopy, and stand density. To avoid confusion, ecologists would be advised to specify the tolerance of a species in relation to specific habitats. Thus red oak saplings may be able to survive under a canopy of certain pine species (e.g., Lutz and Cline 1947) but not under a canopy of red oak (Lorimer 1981; present study). The method described here is most likely to be successful when data are available from a large number of species of widely differing shade tolerance from a fairly homogeneous forest environment. In most forest types, this method would probably be best applied to stands over 50 years of age, after crown differentiation has become pronounced and suppressed trees have been in a subordinate position for a number of years.

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