Survival and growth of understory trees in oak forests of the Hudson Highlands, New York[1]

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Mortality and growth rates of trees in various crown classes and size classes were analyzed from 40-year permanent plot records of slope and ravine forest dominated by chestnut oak (*Quercus prinus* L.) and northern red oak (*Quercus rubra* L.). Average 5-year mortality rates for suppressed trees ≥2.5 cm dbh of chestnut oak and red oak in the slope forest were 26 and 45%, respectively. None of the suppressed red oaks survived the 40-year period, compared with 14% of the chestnut oaks and 33% of the red maples (*Acer rubrum* L.). Mortality of oak trees in the intermediate crown class was less than half that of suppressed trees, but still much higher than that of maples and birches on the tracts. Survival was reasonably high for oaks as long as the top of the crown was receiving direct sunlight, but the expected 40-year survival rate of red oaks in such a position is only 20%, with an average growth rate of 1.0 mm in diameter per year. Curves and equations expressing average mortality and growth rates at various levels of competition are presented for each species.

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L'auteur a analysé le taux de mortalité et le taux de croissance d'arbres de diverses catégories de cime et de tige à partir d'observations étalées sur 40 ans dans des parcelles permanentes de forêt en pente et ravin, dominée par *Quercus prinus* L. et *Quercus rubra* L. Le taux moyen de mortalité quinquennale des arbres supprimés de ≥2.5 cm dhp s'élevait respectivement à 26 et 45% pour les deux espèces précitées. Aucun des sujets supprimés de *Q. rubra* n'a survécu 40 ans, comparativement à 14% pour *Q. prinus* et 33% pour *Acer rubrum* L. La mortalité des chênes de catégorie de cime intermédiaire était moins de la moitié de celle des arbres supprimés, mais bien supérieure à celle des érables et des bouleaux. Ce taux de survie des chênes était raisonnablement élevé, pour autant que le sommet de leur cime était exposé au soleil, mais le taux de survie anticipé (40 ans) des chênes rouges dans une telle situation n'est que de 20%, avec un taux moyen de croissance en diamètre de 1.0 mm/an. L'article renferme des courbes et équations exprimant les taux moyens de mortalité et de croissance de chaque espèce à divers niveaux de compétition.

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Most mature forests in humid regions are characterized by a rather high density of understory trees of shade-tolerant species. The ability of these suppressed trees to grow slowly under shade for long periods and then respond to sudden release upon the death of overstory trees may give them a competitive advantage over intolerant species in some situations. When a gap does occur, the tolerant transgressives may already be several metres high, whereas individuals of competing intolerant species must start from seed. Furthermore, if the understory trees are dense, they may cast enough shade that seedlings of intolerant species cannot survive. In the absence of disturbances such as fire that would be destructive to the understory, the subsequent stand is likely to be dominated by tolerant species whose understory trees are characterized by relatively high rates of survival and growth. Quantification of this potential in different forest types would aid in the prediction of successional trends and the effects of certain silvicultural practices such as selection cutting.

These relationships are not well understood for upland oak forests of eastern North America. Based on general observations of such traits as crown density, live crown ratio, seedling abundance beneath closed canopies, and response to release from suppression, most oak species have been considered intermediate in tolerance (Baker 1949; Spurr and Barnes 1973). Oaks clearly have the ability to maintain a vigorous understory in relatively open stands such as those of pine (Lutz and Cline 1947), and therefore intermediate status might seem warranted. White oak (*Quercus alba* L.) has been observed to respond to release from suppression, indicating a certain degree of tolerance (Minckler 1957), and black oak (*Quercus velutina* Lam.) seedlings have been found in oak and maple forests under conditions averaging more than 95% can-

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opy closure (Horn 1971). But the general ability of oak to survive beyond the sapling stage under closed-canopy forests or under small gaps is open to question. In Baker's (1949) tolerance survey, 32% of the silviculturists classified red oak (*Quercus rubra* L.) as intolerant. Similar opinions have been expressed by Zon and Graves (1911), Deters (1943) in Minnesota, Horton and Brown (1960) in Ontario, and Oliver (1978) in New England. Minckler and Woerheide (1965) reported that satisfactory growth of oaks in Illinois required openings that were at least as wide as three quarters of the height of the surrounding trees. Furthermore, the ability of white, red, and black oaks to resist displacement by the typically dense understory of shade-tolerant species is doubtful in many parts of their range (Schlesinger 1976; Anderson and Adams 1978; Stephens and Waggoner 1980).

One approach to quantifying shade tolerance is to monitor the survival and growth of trees in the suppressed and intermediate crown classes on permanent plots over a number of years. This approach is useful in that direct observations of mortality and growth are obtained under field conditions. The principal drawback is that environmental conditions are not controlled, and hence trees within and among species will not be growing under identical conditions.

Few permanent plot studies of oak sapling growth and survival have been reported to date. Good and Good (1972) observed seedling and sapling survival and growth over a period of 3 years in a New Jersey forest, and Christensen (1977) analyzed 22 years' change in a North Carolina oak–hickory forest. The latter study is particularly interesting with regard to oak tolerance since trees of oak (*Quercus* spp.) and hickory (*Carya* spp.) in the 2.5 to 10 cm diameter classes, many of which were probably suppressed, showed high mortality rates of 75–85% over the 22-year period.

This paper reports the results of analysis of survival and growth rates of trees in various crown classes in two stands of oak forest in the Hudson Highlands, New York, based on permanent plot records kept over a 40-year period. The stands are strictly even aged, and hence many of the suppressed trees were once in a dominant or codominant position. The aspect of shade tolerance investigated in this study is therefore the response among different species to progressive crowding or prolonged suppression.

Study areas

The two stands investigated are located on the Harvard Black Rock Forest in the Hudson Highlands of southern New York State. One stand is located in a broad ravine with 10–20% slopes at an elevation of 350 m and facing east-northeast. The second stand is located on a nearby middle slope with a 15–20% incline facing east-northeast at an elevation of 380 m. The soils in this area are clay loams developed from glacial till overlying granitic bedrock. A weak fragipan is found about 25 cm below the surface (Scholz 1931). Based on weather records at adjacent West Point, the mean annual precipitation is 105 cm. Mean January temperature is −3°C and mean July temperature is 22°C (Scholz 1931).

The two stands are of coppice origin, having developed after clear-cutting for fuelwood or charcoal near the turn of the century. Light precommercial thinnings were conducted in the late 1920's, but the stands have not been treated since that time. Age determinations of five dominant–codominant red oak trees in each stand in 1979 revealed an average age of 85 in the ravine forest (range 74 to 93), and an average age of 64 in the slope forest (range 58 to 74). The major dominant in both stands is chestnut oak, although some mesic species are intermixed in the ravine forest. In the last measurement periods (1973 and 1976), the composition of the overstory by principal species in the ravine forest was 33% chestnut oak (*Quercus prinus* L.), 22% sugar maple (*Acer saccharum* Marsh.), 15% yellow birch (*Betula alleghaniensis* Britt.), and 12% northern red oak. The slope forest at this time was 54% chestnut oak and 44% northern red oak. The stocking levels of these stands have been in the low to medium range of full stocking as indicated by the charts of Gingrich (1967) for upland central hardwoods. Stocking in the ravine forest has ranged from 65% in 1931 to 78% in 1973. The slope plots were slightly understocked (54%) in the first measurement period, but quickly achieved full stocking, reaching the 60% level in 1941 and the 73% level in 1976. Site index, based on height and age determinations of five red oaks in each stand and the site index curves of Schnur (1937), is 55 for both sites. This level of site quality is representative of stands at the Black Rock Forest, although in general SI 55 is considered only fair to average (Schnur 1937).

Methods

Two rectangular plots of 0.10 ha each were established in the ravine forest in 1931 by the Black Rock Forest staff.[3] Two plots of 0.04 ha each were established in the slope forest at the same time.[4] In 1936, two additional plots of 0.10 ha each were established in the slope forest.[5] Plots established in 1931

[3]Plots 4a-1 and 4a-lc, located along the stream connecting Arthurs Pond with Aleck Meadow Reservoir.

[4]Plots 4a-2 and 4a-2c, located 0.1 km southeast of the ravine plots on the same slope.

[5]Plots 9a-1 and 9a-1c, located along the Bog Meadow Road east-northeast of Arthurs Pond.

TABLE. 1. Mortality rates by species and crown class in the slope forest

Species	Avg. 5-year mortality*				40-year survival (%)			Avg. no. trees/ measurement period		
	S	S′	I	D–CD	S†	I‡	D–CD‡	S	I	D–CD
Chestnut oak	26.0	21.6	8.1	3.7	14.3	50.9	74.0	22	22	99
Northern red oak	44.8	—	18.0	2.4	0.0	20.4	82.3	29	21	64
Red maple	11.1	12.9	0.0	0.0	33.3	100.0	100.0	38	10	4

NOTE: S, all suppressed trees; S′, initial population of suppressed trees; I, intermediate; D–CD, dominant–codominant.

*Except for column S′, 5-year mortality rates are not restricted to the initial population of trees in 1936, but include periodic additions of trees to each crown class.

†Percent of original population of suppressed trees surviving 40 years.

‡Projected from 5-year mortality rates by Eq. 1.

were measured eight times at intervals ranging from 5 to 9 years over a period of 42 years. Those established in 1936 were measured at intervals of 5 to 10 years over a period of 40 years. All trees ≥2.54 cm were identified with painted numbers, and at each measurement period diameters were measured to the nearest 2.5 mm and trees assigned to dominant, codominant, intermediate, or suppressed crown classes following standard definitions (Smith 1962). The total number of trees in the record is 753.

Since there is some variation in the length of the measurement periods, mortality rates were calculated on a common 5-year basis using the equations of Hamilton and Edwards (1976), in which mortality rates are treated as negative compound interest rates. Thus

$$[1] \quad P_{n'} = 1 - (1 - P_n)^{n'/n}$$

where P_n = mortality rate based on an n-year measurement period and n' = length of period (years) for which mortality rate is desired.

Most measurements were made at the beginning of the growing season or after the end of the growing season in late fall or winter. In a few cases measurements were made in July, which makes it more difficult to calculate annual growth rates. In these cases the period up to July was considered to represent 0.5 of the total growing season.

The problem that individual trees in natural stands (and possibly species as well) are found under widely varying degrees of competition can be partly remedied by calculating a competition index for each tree and then relating mortality and growth rates to the level of competition. Numerous competition indices have been tested (Alemdag 1978; Martin 1978; Meldahl 1979) and many of these are distance-dependent indices that take spatial pattern as well as competitor sizes into account. Indices of this type cannot be used for the Black Rock data because stem maps are not available. However, there are indications that in fully stocked natural stands, simple distance-independent competition indices may be as highly correlated with growth rate as indices that take spatial pattern into account. A test of competition indices in upland red oak stands in Massachusetts (C. G. Lorimer, unpublished data) showed that a simple distance-independent size ratio such as $d/\bar{D}$, where d = diameter of subject tree and $\bar{D}$ = mean stand diameter of overstory trees, is as highly correlated with observed growth as some of the better distance-dependent indices such as that of Hegyi (1974). Similar conclusions have been reported by Martin (1978) for red pine plantations and Meldahl (1979) for hybrid poplar plantations. The index $d/\bar{D}$ has therefore been used in this study to compare species at similar levels of competition.

Results

Mortality rates

Most species showed great fluctuations in short-term mortality rates. Mortality of suppressed chestnut oak trees was as low as 0% in some measurement periods and as high as 65% in others. Mortality rates of suppressed red oak fluctuated from 23 to 94%. There seemed to be no general trend over time for mortality rates to increase or decrease as the stand became older. Long-term averages, however, reveal differences among some species that appear to be ecologically important. In the slope forest, suppressed chestnut oaks had more than double the mortality rate of red maple, and among trees of the intermediate crown class, the average 5-year mortality rate was 8% for chestnut oak and 0% for red maple. Red oak mortality, moreover, was approximately double that of chestnut oaks for suppressed and intermediate trees. None of the suppressed red oaks present in 1936 survived to 1976, compared with 14% for chestnut oak and 33% for red maple (Table 1).

In the ravine forest, suppressed oaks have been uncommon throughout the plot history even though the overstory has averaged about 45% oak. Of the four chestnut oaks that became suppressed from time to time, only two survived for 10 of the 40 years in the record, and none survived for 20 years. Mortality of chestnut oak in the intermediate crown class has also been fairly high (18%/5 years), especially when compared with the maples and birches, which had mean 5-year mortality rates ranging from 0.9 to 3.0% (Table 2). The few red oaks that became suppressed in the ravine forest also had high mortality rates. Only three suppressed red oaks were present, but none sur-

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TABLE. 2. Mortality rates by species and crown class in the ravine forest*

Species	Avg. 5-year mortality (%)				42-year survival (%)			Avg. no. trees/ measurement period		
	S	S′	I	D–CD	S	I	D–CD	S	I	D–CD
Chestnut oak	—	—	18.3	2.0	—	19.8	85.1	—	6	23
Sugar maple	13.0	16.3	2.9	2.0	22.5	79.0	85.1	33	7	18
American basswood†	—	—	—	11.1	—	—	39.0	—	—	18
Yellow birch	15.5	20.7	0.9	0.8	14.3	93.0	93.8	13	8	13
Northern red oak	—	—	—	2.7	—	—	80.3	—	—	11
Sweet birch‡	20.7	24.4	2.7	1.5	9.5	80.3	88.6	15	5	9
Red maple	20.1	27.9	3.0	5.6	6.4	78.4	63.1	22	6	7

*See footnotes, Table 1.
†*Tilia americana* (L).
‡*Betula lenta* (L.).

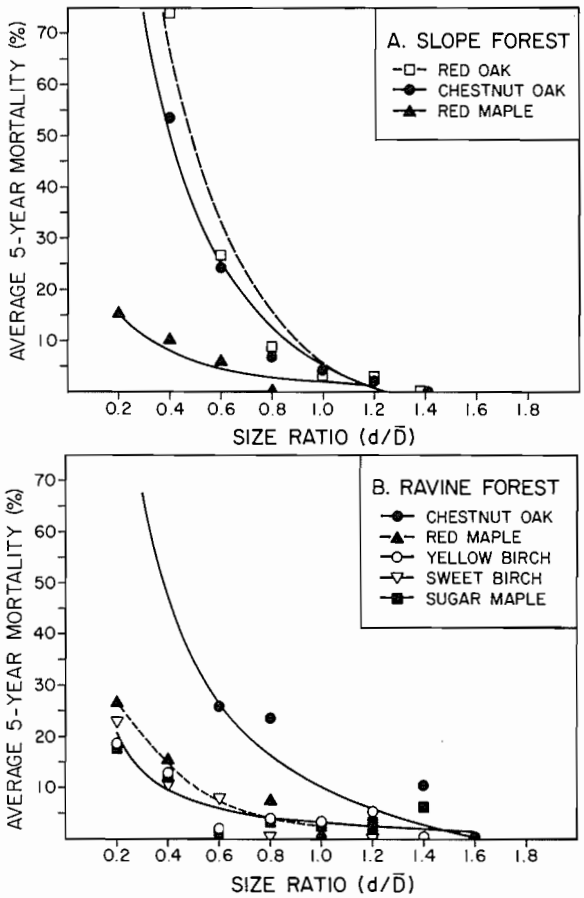


FIG. 1. Average 5-year mortality rates as a function of a distance-independent competition index $d/\bar{D}$, where d = diameter of subject tree and $\bar{D}$ = mean diameter of overstory trees (intermediate, codominant, and dominant crown classes). Equations and species parameters are shown in Table 3.

vived as long as 10 years. Red oaks of the intermediate crown class fared better, with four out of six surviving for at least 10 years and two out of six surviving for at least 20 years.

Average 5-year mortality rates among the maples and birches in the ravine forest do not widely differ from each other, but small differences may be important over a long time span. Thus, only 6% of the suppressed red maples (*Acer rubrum* L.) survived the entire 42-year period, compared with 22% of the sugar maples. The differences that do exist do not always follow the expected order of tolerance, although this could be due to other factors in addition to tolerance that affect mortality rates. Yellow birch in all crown classes had lower mortality rates than red maple, even though it is usually considered to be less tolerant.

Differences in mortality rates among species are also apparent when compared at similar competition levels (Fig. 1). For chestnut oak in the ravine forest, trees whose diameters are 50–70% of the mean overstory diameter have average 5-year mortality rates of 28%, compared with <3% for red maple, sugar maple, and yellow birch. The analysis by competition index class suggests that differences in mortality rates among the birches and maples are slight except in the lowest class (size ratio = 0.2), where red maple and sweet birch in the ravine have much higher mortality rates than sugar maple and yellow birch. The competition index analysis also seems to indicate that the differences in mortality rate between red oak and chestnut oak on the slope are confined to the lower classes (size ratio of 0.6 or less). Table 3 gives the parameters for equations fit by linear regression to the points in Fig. 1.

The probability of mortality for each suppressed tree is affected by the length of time it has been suppressed, but it is difficult to make accurate comparisons because of the variable lengths of the measurement periods. In the ravine forest, more than 70% of the suppressed trees had always been suppressed during the period of record. In the slope forest, however, more than 70% of

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TABLE. 3. Parameters for mortality and growth equations

	Mortality				Growth			
	Slope*		Ravine*		Slope†		Ravine‡	
Species	*a*	*b*	*a*	*b*	b_0	b_1	*a*	*b*
Chestnut oak	−25.7	30.6	−14.8	24.8	8.67	−1.45	1.52	2.91
Northern red oak	−36.0	41.6	—	—	11.8	−1.63	—	—
Yellow birch	—	—	−0.981	4.20	—	—	1.23	0.754
Sweet birch	—	—	−0.981	4.20	—	—	2.06	1.77
Red maple	−1.41	3.59	−3.25	5.96	3.32	−0.645	1.68	1.56
Sugar maple	—	—	−0.981	4.20	—	—	1.66	1.54

*For equation $y = a + b/x$, where y = mean 5-year mortality rate (percent) and x = size ratio $d/\bar{D}$.
†For equation $y = b_0\, e^{b_1/x}$, where y = mean yearly diameter growth (millimetres) and x = size ratio $d/\bar{D}$.
‡For equation $y = ax^b$, where y = mean yearly diameter growth (millimetres) and x = size ratio $d/\bar{D}$.

the suppressed oaks had recently lapsed into that class from the intermediate or codominant class. Except for chestnut oak, average 5-year mortality rates of the population of suppressed trees initially present in 1931–1936 were 16–38% higher than the figures for the suppressed population as a whole (columns 1 and 2, Tables 1 and 2).

Growth rates

Average diameter growth rates were similar among the maple and birch species, ranging from 0.1 mm/year at a size ratio of 0.2, to 0.8 mm/year at a size ratio of 0.6 (Fig. 2). Average growth rates of suppressed trees were 19–35% of the growth rates of dominant–codominant trees. Intermediate trees of the oak species grew at 36–40% of the rate of dominant–codominant trees, while intermediate birch and maple trees grew at 60–72% of the rate of dominant–codominant trees.

As expected, the more tolerant maples and birches had higher growth rates in the understory than the oaks, but lower growth rates in the overstory. The level of competition at which growth of the oaks equalled that of the birches and maples occurred at a size ratio of 0.8 to 1.0 (Fig. 2).

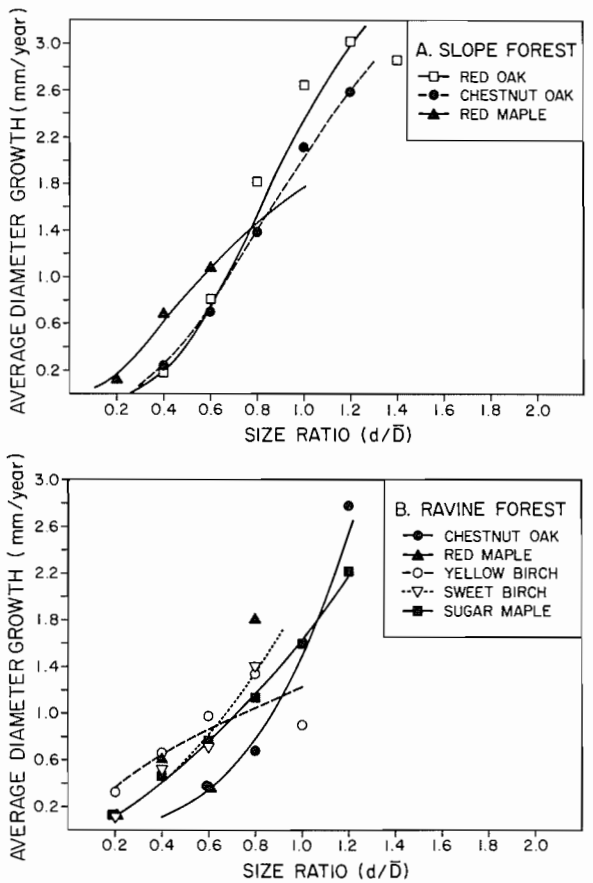


FIG. 2. Average yearly diameter growth as a function of the size ratio. Equations and species parameters are shown in Table 3.

Discussion

Chestnut oak and northern red oak seem to be considerably less tolerant on these upland clay loam soils than the four principal competing species of maple and birch even when compared with species usually classified as intermediate in tolerance. Although the lack of oak saplings in a forest understory can be partly attributed to such factors as destruction of acorns and seedlings by weevils, rodents, and deer (Marquis *et al.* 1976), the average 5-year mortality rate of 45% for suppressed red oak is so high that this factor alone is sufficient to preclude significant numbers of large saplings in the understory. It is possible that oak saplings originating under shade may be better adapted to understory conditions than those originating under full sun, but even saplings of the former type have been observed to undergo repeated top kill without substantial direct solar

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radiation (Sander 1972).

The exposure of even part of the crown to direct solar radiation has a dramatic influence on survival rates, as can be seen by comparing survival of trees in the intermediate crown class versus those in the suppressed class. The expected 40-year survival rate for intermediate chestnut oak is 51%, compared to 14% for suppressed trees. This effect is seen in all species (Tables 1 and 2), although it is most pronounced for the less tolerant oaks. With red oak, however, even trees of the intermediate crown class have a 40-year survival rate of only 20%.

The ravine forest is about 20 years older than the slope forest, but comparisons between the two are facilitated by the analysis of mortality and growth by competition index (Figs. 1 and 2). When the three species common to both sites are compared, it is evident that mortality rates are very similar for trees of size ratio 0.5 and higher. In the ravine forest, only red maple has sufficient numbers of trees of size ratio 0.5 or less to make comparisons between the two stands. For these smaller red maples, mortality seems to be considerably higher in the ravine site than on the slope.

Since sugar maple is generally considered much more tolerant than yellow birch, the similarity of mortality and growth at various competition levels may seem surprising. But the theory of shade tolerance predicts that photosynthetic rates and net assimilation rates of two species of differing tolerance must intersect at some point of moderate light intensity (Horn 1971; Larcher 1975) which may be the case here. In heavily shaded mesic hardwoods the relative response could be quite different. It is also possible that one or both species is outside the optimal range of environmental conditions on these upland sites.

The curves showing response of growth to the level of competition (Fig. 2) offer empirical support to the hypothesis that shade-tolerant trees, like other shade-tolerant plants, show higher net assimilation at low light intensities and lower net assimilation at high light intensities when compared to intolerant species (Horn 1971; Larcher 1975). The numerical scale for the size ratio is probably not linearly related to light intensity or root competition, which may account for the steepness of these curves. It is somewhat surprising, however, that the more tolerant species maintain an advantage of growth rate up to a size ratio of 0.8 to 1.0, corresponding to trees largely in the intermediate and codominant crown classes.

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