

Advance Reproduction and Other Stand Characteristics in Pennsylvania and French Stands of Northern Red Oak

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Abstract: The frequent scarcity of northern red oak (NRO) advance reproduction raises questions about its regeneration potential under prevailing stand conditions in eastern North America. In contrast, NRO plantations in France typically contain abundant advance reproduction. The purpose of this study was to document stand conditions in Pennsylvania (PA) and southwestern France (FR) that may be contributing to the difference in apparent regeneration potential. In each case, five mature stands or plantations were selected for study.

The density of NRO advance reproduction was 2,500/ha in PA and 271,300/ha in FR. NRO stems were taller and older on average in FR than in PA; 15% of the FR cohort but only 2% of the PA cohort had survived beyond the fifth growing season. Basal area for all species averaged about 27 m²/ha in both regions, but NRO composed only 49% of the basal area in PA as opposed to 98% in FR. Canopy cover in June was significantly greater in PA stands by an average of 5.3%. Herbaceous ground cover averaged much higher in PA than in FR; it appeared that the abundance of advance reproduction in FR effectively excluded competition by herbaceous vegetation. Unfragmented leaf litter in May (dry weight / m²) was over twice as great in FR than in PA. Results demonstrate that NRO can accumulate abundant advance reproduction under relatively undisturbed canopy, at least in FR. Among the factors measured in this study, lower accumulations of leaf litter in PA as compared to FR may suggest poorer conditions for overwinter survival and germination of acorns in PA. Lower herbivore pressure and marginally lower canopy shade levels in FR compared with PA probably contribute to the superior success of advance reproduction in FR.

INTRODUCTION

Oak (*Quercus*) species dominate forests in much of the eastern United States. Oak species were also important in presettlement forests of the region and were considered a climax type by early ecologists (Michaux 1853, Bromley 1935, Clements 1936, Braun 1950). Despite the fact that an occasional eastern oak forest contains abundant oak reproduction, much of the recent work indicates that oak regeneration failure is pervasive (Adams and Anderson 1980, Lorimer 1984, Host *et al.* 1987, Pallardy *et al.* 1988, Nowacki *et al.* 1990, Abrams and Downs 1990). However, low density of oak advance reproduction may be site dependent, being more apparent in mesic versus xeric forests (Abrams 1986, Nowacki and Abrams 1991). Thus, regeneration problems and

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probably successional replacement of the oak overstory are particularly evident in northern red oak (*Q. rubra* L.) forests, which tend to occur on mesic sites (Adams and Anderson 1980, Host *et al.* 1987, Crow 1988, Nowacki *et al.* 1990). It is economically significant that regeneration difficulties with northern red oak (NRO) appear to be especially severe in Pennsylvania, which has the largest concentration of NRO timber among states.

Numerous plantations of northern red oak have been established in southwestern and northeastern France since the late 1800's. The French plantations are managed for the production of lumber or low-grade veneer on rotations of 70-80 years (Lanier *et al.* 1980), which is considerably less than the >200-year rotations required for the more valuable but slower-growing native oaks (*Q. petraea* (Matt.) Liebl. and *Q. robur* L.). Harvested stands of NRO are regenerated in France by the release of advance reproduction, which is almost universally abundant in both portions of the country where the species is commonly grown (personal observation). The purpose of this study was to document stand conditions in Pennsylvania (PA) and southwestern France (FR) that may be contributing to northern red oak's apparently inferior regeneration potential in its native range.

MATERIALS AND METHODS

Study Sites

Five stands were selected for study in each region (Table 1). Stand selections in PA were coordinated through the Pennsylvania Bureau of Forestry, which manages 13% of the commercial forest land in the state. District offices were requested to identify stands with relatively abundant advance reproduction of NRO and a minimum of 70% stocking of NRO over an area of at least 1.2 ha. District offices identified 13 candidate stands. All stands fell short of the stocking criterion, and none had "abundant" advance reproduction. However, those selected for study had the highest reproduction densities and appeared *capable* of natural regeneration based upon maturity and canopy dominance of NRO over other species. All five are in central PA: two (Nook and Alan Seeger) in the Ridge and Valley physiographic province, and three in the Allegheny Plateau province.

Candidate plantations in FR were selected through the cooperation of M. Jean Timbal, Institut National de la Recherche Agronomique, who some years previously had surveyed all known plantations of NRO in that country for a growth and yield study. Site indices for FR plantations in Table 1 come from stem analyses that he performed and were extrapolated from base age 40 using Schnur's (1937) tables. From among 30 candidate plantations visited, five were selected for study primarily on the basis of relative freedom from previous or anticipated disturbance (thinning, harvesting, mowing, or seed collection). All but one of the 30 plantations had abundant NRO reproduction by PA standards, but the five study plantations are probably above-average in this regard. One plantation (Tournebride) is in the flat Landes Region immediately south of Bordeaux, and the other four are in the hilly countryside abutting the Pyrenees.

Measurements

The density of NRO advance reproduction was measured in mid-June 1990 (FR) and early June 1991 (PA) by counting understory stems within regularly spaced transect plots. Sampling consisted of 20 3-m² plots per study site in FR and 20 or 40, 20-m² or 5-m² plots per site in PA, depending upon the density of stems. All advance reproduction was counted regardless of height, which was sometimes as great as ca. 3.5 m in FR. In addition, at each of 20 plots per study site, the four NRO stems closest to the plot center were measured for height, and the root age of each

Table 1.—Locations and other characteristics of natural stands in Pennsylvania and northern red oak plantations in France used as study sites. Where appropriate, standard deviations are given in parentheses.

PENNSYLVANIA						
	Alan Seeger	Nook	Smith Road	Firebreak	Wykoff Branch	
Latitude	40°42'	40°31'	41°06'	41°08'	41°28'	
Longitude	77°45'	77°35'	78°33'	78°32'	77°59'	
Aspect	Northwest	Northwest		South	Southeast	
Slope	5°	9°		2°	2°	
Elevation (meters)	351	396	686	640	625	
Study area (hectares)	1.40	1.76	1.70	1.41	1.60	
Basal area, NRO (m ² /ha)	12.4 (0.57)	10.6 (0.60)	14.9 (0.62)	15.4 (0.94)	12.9 (0.78)	
Basal area, all species (m ² /ha)	26.9 (0.73)	26.6 (0.60)	22.0 (0.62)	31.9 (0.76)	28.9 (0.80)	
Site index (meters at age 50)	23.2	24.4	19.2	22.3	20.7	
Mean age of dominant NRO (years)	123	70	82	74	72	
Litter dry wt (g/m ²)	371 (31.3)	476 (77.1)	195 (17.6)	236 (17.3)	289 (23.3)	
NRO advance reproduction (#/ha)	70 (4.1)	520 (112)	8,660 (1,526)	2,300 (332)	1,150 (276)	

FRANCE						
	Vic-en-Bigorre	Ibos II	Bacqueieu I	Mixe II	Tournebride	
Latitude	43°24'	43°15'	43°44'	43°26'	44°39'	
Longitude	0°00'	0°02'W	0°03'E	1°09'W	0°44'W	
Aspect	East	East	West	Northwest	None	
Slope	1°	4°	2°	6°	0°	
Elevation (meters)	213	396	152	91	61	
Study area (hectares)	0.64	0.71	0.72	0.60	0.93	
Basal area, NRO (m ² /ha)	23.6 (0.55)	26.4 (0.57)	31.0 (0.73)	33.3 (0.76)	21.1 (0.46)	
Basal area, all species (m ² /ha)	same	same	same	same	23.4 (0.41)	
Site index (meters at age 40)	29.9	28.3	28.3	31.4	15.8	
Plantation age (years)	60	51	49	52	97	
Litter dry wt (g/m ²)	698 (71.4)	741 (53.4)	588 (27.3)	752 (60.4)	529 (20.5)	
NRO advance reproduction (#/ha)	239,190 (15,419)	256,240 (19,595)	253,770 (17,248)	211,520 (29,207)	395,610 (33,605)	

stem was determined by counting annual rings in a section taken immediately below the soil surface. However, because of the scarcity of advance reproduction on some PA sites, as few as 30 (as opposed to 80) stems were measured and aged in this manner. Current-year germinants were counted as age 0. At the same plot centers as above, overstory basal area was estimated with a basal area factor 10 prism.

On the same dates as above, percentage canopy cover was determined by photographing the canopy directly above 6 to 10 sample points per stand. A wide-angle lens and high contrast film were used. Photographs were enlarged to 8 x 10 inches and percentage of sky obscured by canopy was determined by means of a dot grid superimposed upon the photograph.

Also on the same dates, percentage ground cover by herbaceous and woody vegetation (excluding NRO stems) was determined from 20 sample plots per stand located by transect. Sample plots were 5-m² (PA) or 3-m² (FR) circles, and percentage ground cover by vegetation category was estimated using five classes: 0-5%, 6-25%, 26-50%, 51-75%, and 76-100%.

Quantity of mulch available for over-winter acorn protection was estimated from oven-dry weights of the unfragmented leaf litter persisting from autumn 1990 until mid-May 1991. At 15 (FR) or 22-30 (PA) transect points per study site, unfragmented leaf litter from 1990 was gathered by slicing the litter around the circumference of a 318-cm² aluminum sampling ring. Each sample was oven-dried at 80°C until the weight loss stabilized, and the samples were then weighed.

Observations in spring 1990 and 1991 indicated that over-winter soil turnover by earthworms may be a significant factor in burying acorns at most of the FR study sites. Piles of ca. 0.6-cm diameter castings are frequent at all FR sites except Tournebride, where the soil is exceptionally sandy and earthworms of this type seem to be absent. Casting piles may be as large as 25 cm in diameter and 8 cm in height. Nothing comparable was observed on PA sites. To estimate the extent of this phenomenon, we established sample plots at 7-8 systematically chosen locations on each study site in mid-November 1991. Each plot consisted of a 420-cm² plastic grid pinned to the soil surface underneath the leaf litter, which was then replaced. Each grid had 100 cells, and the fraction of these covered with new worm castings was determined 6 months later, in mid-May 1992.

RESULTS AND DISCUSSION

Stand basal areas averaged 27.3 and 27.5 m²/ha in PA and FR, respectively ($P > 0.05$), although stocking varied considerably from stand-to-stand within each region (Table 1). NRO composed an average of 49% of stand basal area in PA and all of the basal area in FR except at Tournebride, where there was a small component of *Pinus pinaster* Ait. and *Q. robur*. Non-oak species, principally maples, made up 35% of basal area stocking in PA stands. All five FR stands have been thinned at intervals, and their current stand density probably does not reflect full site occupancy. PA stands have not been treated silviculturally.

Site indices were almost uniformly higher in FR than in PA (Table 1), but the lowest site index in the study occurred at one of the FR study areas (Tournebride). Canopy cover in June averaged 5% greater ($P < 0.001$) in PA (range 84-95%) than in FR (range 83-89%). The greater canopy cover in PA was probably due in part to the presence in PA stands of maples and other species with a greater shade tolerance than NRO, and in part to the thinnings in FR mentioned above. Although one PA stand (Smith Road) was comparable in canopy cover to FR stands, it can be concluded that the understory in PA stands is generally more shaded than in these FR stands.

Despite the slightly greater canopy cover in PA than in FR, unfragmented leaf litter dry weight in May averaged less than half as much in PA (313 g/m²) as in FR (662 g/m²) ($P < 0.001$) (Table 1).

This discrepancy is likely due to the presence in the PA stands of a large component of maples and other non-oak species whose leaves tend to weather more rapidly than those of oaks (Kucera 1959, McClaugherty *et al.* 1985).

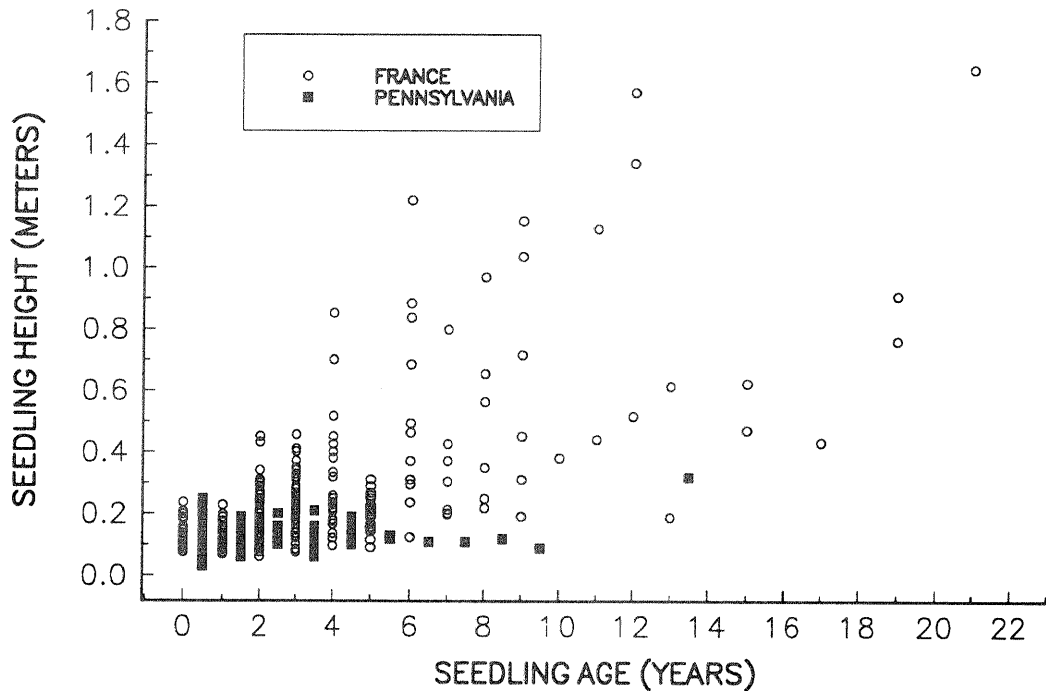


Figure 1. — Percentage of ground covered by herbaceous and woody vegetation other than northern red oak. Separate bars within a region apply to each of the five study sites, ordered from left to right in the same way as Table 1.

The percentage of ground cover by woody species other than NRO was comparable between PA and FR (ca. 6% and 8%, respectively), though somewhat variable among stands within each region (Figure 1). Herbaceous cover averaged much greater (36%) in PA than in FR (5%) but the difference was largely due to the abundance of hayscented or bracken fern at three of the PA sites. Two stands in PA had rather little herbaceous ground cover. Actually, the soil surface was probably more heavily shaded by understory vegetation in FR than in PA because of the presence in FR of an almost continuous "canopy" of NRO advance reproduction in those stands. As we show below, NRO was continuing to recruit into the advance reproduction in FR despite a very high density of woody stems in the understory. Although the heavy fern cover at three of the PA sites probably inhibits seedling establishment (Kolb *et al.* 1989, Scholz 1955, Smith and Vankat 1991), the relative absence of a woody understory in PA (including NRO advance reproduction) may more likely be the cause than the result of the generally more abundant herbaceous cover.

The greater abundance of unfragmented leaf litter in FR stands presumably contributes to better conditions for germination by protecting the acorns from desiccation (Korstian 1927) and hiding them from predators. In other research in these stands (Steiner, unpublished data) we have found the proportion of acorns in May that are exposed on top of the litter or soil to be several-fold higher in PA. Additionally, our estimates of soil turnover by earthworms indicate a surprising potential for burial through this phenomenon. On the four sites where we have seen castings, the percentage of soil surface that became covered with new castings between November and May varied from

2.3 (Mixe II) to 40.8 (Bacquieu I), with an average for all four sites of 16.6%. In addition, 4.4% of the surface at Mixe II was covered with fresh mole or rodent excavations. Although we have seen no such earthworm castings at Tournebride, its very sandy soil appears especially conducive to germination since fallen acorns tend to become at least partially buried over winter. Taken together, these conditions suggest that the forest floor in FR stands is generally more favorable for the over-winter storage and germination of acorns than it is in PA.

As noted already, the density of NRO stems was much higher in FR (271,300/ha) than in PA (2,500/ha) (Table 1). The fact that District Offices failed to find stands in PA with higher levels of advance reproduction suggests that stands with significantly higher levels are probably nonexistent on state forest lands in PA. Indeed, the density of NRO seedlings on our PA study sites is typical of densities found in other studies in upland oak stands in the eastern U. S. (Bowersox and Ward 1972, Good and Good 1972, Minckler and Jensen 1959, Nowacki *et al.* 1990, Nowacki and Abrams 1991, Dawson *et al.* 1989, Johnson *et al.* 1989, Kittredge and Ashton 1990, Tryon and Carvell 1958). We know of no reports on American stand conditions in which advance reproduction of upland oaks was even nearly as abundant as in the FR stands we studied, even after accounting for relative basal areas.

As expected, the numbers of stems of advance reproduction declined with stem age in both PA and FR stands, but the decline was much more rapid in PA (Figure 2). The relative frequencies of stems in different age classes was probably affected by the periodicity of acorn crops in previous years. For example, all five PA stands had moderate to heavy seed crops in the autumn prior to measurement, and current-year germinants (age class 0) were by far the most common class. Also, 2-year-old seedlings were the most common age class in FR probably because of a large acorn crop in autumn 1987. Thus, age-dependent survival is confounded with seed crop periodicity in Figure 2.

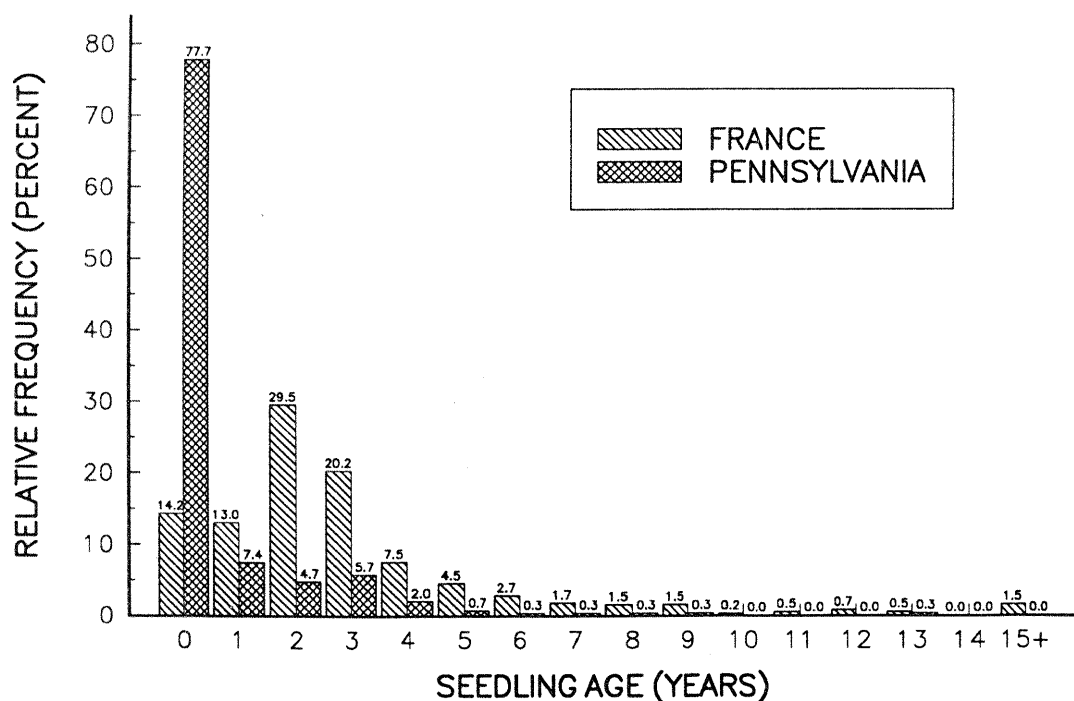


Figure 2. — Age-class distribution of stems of northern red oak advance reproduction in PA stands ($n = 296$ seedlings) and FR plantations ($n = 400$ seedlings), as sampled in June. Current-year germinants are age class zero. Numbers above bars are actual percentages.

Nevertheless, it seems apparent that advance reproduction is surviving longer in FR stands than in PA stands. Some 15% of FR stems had survived beyond the fifth growing season after germination, but only 2% of the PA seedlings had done so. Even an exceptionally large acorn crop in FR could hardly put half the stems in age class 0, and thereby reduce other age class frequencies by half. Likewise, even if there had been no autumn 1990 seed crop in PA, only 10% of PA stems present in spring 1991 would have been >5 years old. In contrast, other studies in the U.S. have shown better survival over time than appears to be occurring in our Pennsylvania stands. Good and Good (1972) observed only 16% mortality in each of the first two years for NRO seedling cohorts in a New Jersey woodland unaffected by deer browsing; survival after five seasons of growth would be 42% if the same annual rate continued. Beck (1970) found that 24% of NRO seedlings survived for 6 years under an overstory in North Carolina plots (see also Loftis 1988).

Although forest floor light levels can be limiting to NRO seedling survival and growth (Sander 1990), and overstory canopy cover was generally more dense in PA stands, we do not believe this accounts for the apparently more rapid mortality of seedlings in those stands as compared with FR. Regardless of overhead canopy, there was in FR stands a virtually complete "canopy" of NRO advance reproduction over the ground. The dominant portion of this understory consisted of a small proportion of larger seedlings and saplings, so most of those randomly sampled for aging were shaded by this canopy as well as by the overstory. As a result, the average seedling in FR was probably more heavily shaded than the average seedling in PA, though we have no data to document it. The faster mortality of PA seedlings is probably attributable to deer browsing, which can be severe in PA but is light in the FR stands we have observed.

The likelihood that NRO advance reproduction will actually contribute to regeneration following overstory removal is dependent upon seedling size (Loftis 1990, Sander 1971, Sander 1972, Sander *et al.* 1984). For example, Loftis (1990) used seedling size to predict the probability that an individual stem would produce a dominant or codominant tree at 20 years after harvest. None of the seedlings in PA stands were over 0.3 m in height (Figure 3), and Loftis' model suggests that no more than a very small percentage, if any, could actually contribute to stand regeneration. Although relatively few NRO stems in FR exceeded a meter in height (Figure 3), the absolute number per hectare was large (ca 4,700) due to the overall abundance of advance reproduction. None were represented in our samples, but most FR stands had many stems exceeding 2 m in height. Since NRO advance reproduction dominates the understory vegetation in these FR stands, there is little doubt that the stands would become fully restocked with NRO if harvested.

CONCLUSIONS

Seedling establishment in FR probably benefited from favorable conditions for overwinter storage of acorns, including relatively abundant leaf litter and the unusual soil turnover activity of large earthworms. This may help explain the abundance of seedlings in FR (though other factors such as acorn production and predation are probably also important), but it does not explain their persistence.

Overstory canopy density was slightly but significantly higher in PA than in FR, as was the mean percentage of forest floor occupied by herbaceous and woody plants other than NRO. However, two PA stands had light ground cover, and most of the sampled stems in FR were beneath a canopy of advance reproduction (since younger and thus smaller seedlings were much more frequent). Shade from ground vegetation probably does not account for the relative absence of regeneration in PA; in fact, the generally greater abundance of herbaceous ground vegetation in PA may instead be a consequence of the paucity of woody plant regeneration.

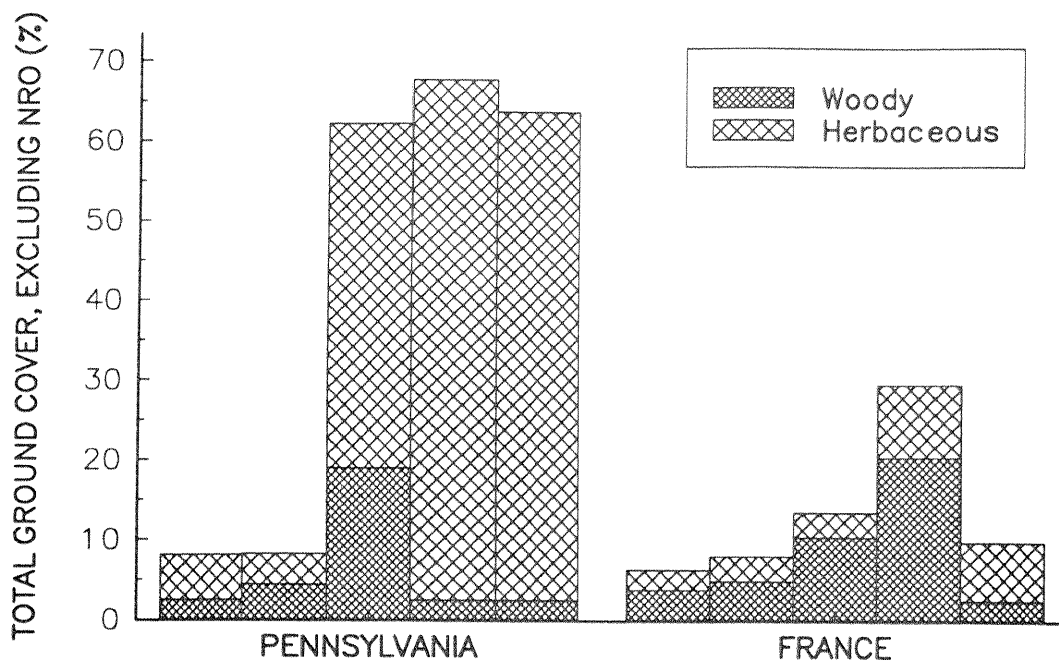


Figure 3. — Distribution of stem heights *versus* age for advance reproduction in PA and FR. PA stem ages were transformed to “age + 0.5” so that PA and FR symbols would not overlap on the plot.

The age-class distribution of seedlings in PA suggests rapid mortality with age. This tends to support the conclusion of Olson and Boyce (1971) that NRO does not persist as advance reproduction more than a few years. Similarly, Clark and Watt (1971) reported that all oak reproduction (species not indicated) died in a 70-year-old stand with overstory density of 23 m²/ha, but that advance reproduction was able to accumulate under an overstory of 18 m²/ha. However, the surveyed FR stands accumulated abundant advance reproduction under overstory densities of 21–33 m²/ha. Significant mortality appeared to be delayed until at least after the fourth growing season in FR, and FR plantations were continuing to recruit seedlings under the additional shade of the almost continuous understory canopy. We think it is more likely that deer browsing, rather than overstory shade, was the most significant factor in seedling mortality over time in PA.

Scholz (1952) suggested that NRO is more shade tolerant than normally believed, and that it is sufficiently tolerant and aggressive to occupy any natural openings where overhead light is available. The development of advance reproduction in FR stands certainly supports that judgment. NRO in these French stands is capable of persisting for several years under high (but unquantified) levels of shade at ground level. Frequent mild thinnings appear to have permitted some stems to persist even longer and accumulate appreciable growth. This class of “dominant” advance reproduction has effectively excluded most potentially competing vegetation.

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