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Development of the Red Maple Understory in Northeastern Oak Forests

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ABSTRACT. Permanent plot records ranging from 13 to 42 years in duration were used to study understory development in four upland oak forests in Massachusetts and New York. All tracts have a dense understory of shade-tolerant species dominated by red maple (*Acer rubrum* L.) but sparse representation of oak saplings. Mortality rates for red maple have been low compared to other species, and maples have increased in size and numbers on all tracts. For example, on one tract, 57 percent of the red maples in the 10-cm diameter class advanced two or more 2-cm classes over a 19-year period, and the number > 11 cm dbh increased from 30 to 80/ha. Diameter growth of red maple is highest among trees receiving substantial direct sunlight, and red maple may comprise a large proportion of the overstory on well-drained sites with a relatively low density of oak stems. There are currently no indications of decline of red maple canopy trees 80 years old, and growth rate shows a positive linear correlation with size. A severe drought of 1962–66 appeared to cause substantially higher mortality in the New York stands but had little impact on the Massachusetts stands. Drought did not cause a long-term setback in the red maple diameter distribution on any of the sites. FOREST SCI. 30:3–22.

ADDITIONAL KEY WORDS. Drought effects, forest succession.

A STRIKING FEATURE of most oak forests in the northeastern part of their range is the dense understory of shade-tolerant trees, of which red maple (*Acer rubrum* L.) is often most prevalent. The future significance of this understory is not clear, and there is much uncertainty as to whether red maple has the potential to become prominent in the canopy. Red maple is commonly believed to have a short to medium lifespan (Fowells 1965), and we have few stands in the oak region today in which red maple is the principal overstory species except in swamps. There is little indication that this situation was substantially different in presettlement times. Most early observers in central New England agreed with Smith (1616) that "Oke is the chiefe wood," and often mixed with chestnut (*Castanea dentata* Marsh.) and hickory (*Carya* spp.). Mesophytic species such as red maple, beech (*Fagus grandifolia* Ehrh.), and hemlock (*Tsuga canadensis* (L.) Carr.) were not mentioned as being prominent except in lowlands and wet sites (Kalm 1770, Whitney 1793, Dwight 1821).

The developmental potential of the red maple understory warrants careful evaluation nevertheless. First, the inherent ability of oaks to retain dominance on these sites is uncertain. Although oaks are potentially vigorous competitors and have the ability to overtop the more prevalent individuals of other species (Bey 1964, Oliver 1978), this appears to be likely only when vigorous oak saplings are already present in the understory, a situation that is not presently common (Gam-

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mon and others 1960, Monk 1961, Buell and others 1966). Investigators in the midwestern and southern United States have found that only the more vigorous oak 'seedling sprouts' are able to compete successfully with other species after heavy cutting (Beck 1970, Sander 1972, McQuilkin 1975, Johnson and Krinard 1976). Oak forests clearcut up to 25 years ago in southern Wisconsin have largely reverted to other species (Johnson 1976). In New England, it is clear that overstory oaks in many stands originated as vigorous saplings beneath old-field pine stands or as sprouts from coppice stands (McKinnon and others 1935, Lutz and Cline 1947). Historically, the origin of many present stands is unique and the conditions will not necessarily be repeated.

A second consideration is that fires may have played an important role in maintaining the presettlement oak forests. Morton (1637) wrote that the Indians of Massachusetts "set fire of the Country in all places where they come." Wood (1634) noted that the burning "consumes all the underwood, and rubbish, which would otherwise over grow the Country," and his statement that there were vast areas with "scarce a bush or bramble" is echoed in the writings of many early travelers (see Day 1953). These fires were probably often more intense than the conventional prescribed burns of today; Van der Donck (1656) stated that fire in the Hudson River area "frequently spreads and rages with such violence, that it is awful to behold . . . The outside of the bark is scorched three or four feet high, . . . [but] the trees are not killed." Whether this was a common practice farther inland is not well known, but oak savannas and fields with numerous small oak sprouts were described in western New York (Day 1953). Burning by later settlers was undoubtedly also a factor in favoring oaks and hindering maple (cf. Swan 1970). In an old-growth remnant on silt loam soil on the piedmont of New Jersey, detectable fire scars were present on a large white oak at approximately 10-year intervals between 1641 and 1711 (Buell and others 1954). Kalm (1770) reported annual burning of oak woods by settlers in New Jersey, and on a trip across the Allegheny Mountains in 1803, Harris (1805) stated that "For more than fifty miles, to the west and north, the mountains were burning." The prominent role of settlers' fires in southern Appalachian oak forests is well documented (Ayres and Ashe 1905, Reed 1905). Even in the present century, approximately 25 percent of the state of Rhode Island burned from 1930 to 1955 (Brown 1960). In view of past fire frequency along with heavy fuelwood cutting, it is not surprising that we have few stands in an advanced successional state. Certainly any hypothesis about the future development of oak stands must take the current maple understory into account.

For this study, an evaluation was made of changes in tree species populations in four tracts of upland oak forest in central Massachusetts and southern New York from permanent plot records spanning a period of 13 to 42 years. This period is not long enough to see major changes in the overstory, since the stands are even-aged and only recently approaching maturity. However, the period is sufficiently long to detect significant changes in the understory and the development of red maple in particular. Five plausible hypotheses on the developmental potential of red maple are considered in this paper:

1. The Permanent Understory Hypothesis
   Red maple in this hypothesis is considered to be more or less an obligate understory tree on uplands with little potential for overstory development, similar to *Ostrya virginiana* in northern forests, *Oxydendrum arboreum* in southern forests, and *Lithocarpus densiflorus* in parts of the Pacific Northwest. Scattered red maples could perhaps attain overstory status under favorable circumstances. The underlying causes of subordination could be inherently slow growth, high mortality rates, or possibly physiological inhibition under conditions of high exposure to sunlight.

In this and the other hypotheses that propose continued oak dominance, oak is assumed to have a competitive advantage over maple in multiple-tree gaps and large blowdowns or clearcuts.

2. The Transitory Red Maple Hypothesis
   Red maple is considered to be a somewhat opportunistic species that colonizes sites in the early stages of succession following fire, agricultural use, or heavy cutting, but which is unable to persist in high numbers in later stages of succession. In this respect it would be similar to black cherry (*Prunus serotina*) in southern Wisconsin oak forests (Auclair and Cottam 1971).
3. The Eradication by Drought Hypothesis
   This hypothesis would recognize that a potential driving force toward red maple dominance may exist, but is rarely achieved because of occasional severe droughts that cause widespread dieback of mesophytic trees on upland sites.
4. The Short Lifespan Hypothesis
   This hypothesis also allows for some progressive development in numbers and stem size of red maple, but development is assumed to be truncated by either the inherently short lifespan of red maple or its premature death from damaging storms. This hypothesis differs from #1 in that attainment of overstory status could be much more frequent. Overstory maples, however, would be short-lived, and oak would continue to be the predominant species through dominance of medium and large gaps.
5. The Red Maple Dominance Hypothesis
   The proportion of oak currently in the canopy is assumed to be unusually high because of past fires or heavy fuelwood cutting, and the current regime of less intense disturbance and sparse regeneration of oak is expected to result in diminished oak dominance and increased representation of maple. The density of understory trees would remain high over time, and suppressed and intermediate red maples would be capable of increased growth after the death of overstory trees. Red maple need not have a long lifespan, but its capacity for overstory development and its capacity to somewhat hinder the growth of young oak seedlings is assumed. This hypothesis might include the possibility of eventual replacement of red maple by more shade-tolerant species such as sugar maple and hemlock.

These hypotheses are treated separately for convenience, but it is recognized that combinations of several of these factors may actually be involved in red maple dynamics. A sixth hypothesis of alternation of species on the same site was not tested due to the lack of mature non-oak forests on upland sites.

STUDY AREAS

Two of the permanent plot areas are located on the Harvard Forest in central Massachusetts and two areas are located on the Harvard Black Rock Forest in the Hudson Highlands area of southern New York State. A summary of study area characteristics is shown in Table 1. All four sites support even-aged upland oak stands which at the time of the last measurement period in 1975 ranged from 52 to 85 years of age. The two Harvard Forest stands (Prospect Hill and Petersham Ridge) originated following clearcutting of old-field white pine (*Pinus strobus* L.) from 1895 to 1923. Attempts to regenerate the pine by clearcutting were not successful, and most of the current hardwood overstory trees were originally suppressed beneath the pines and released by the clearcuttings (Lutz and Cline 1947). A portion of the Prospect Hill tract (0.34 ha) was blown down in the 1938

TABLE 1 Summary of study area characteristics

	Black Rock ravine	Black Rock slope	Petersham Ridge (Harvard Forest)	Prospect Hill (Harvard Forest)
Location	Cornwall, N.Y. Ravine NE of Arthur's Pond	Cornwall, N.Y. Slope along Bog Meadow Rd.	Petersham, Mass. Compartment: Tom Swamp I	Petersham, Mass. Compartment: Prospect Hill I/VIII
Total plot area	0.20 ha	0.20 ha	0.56 ha	0.56 ha (13 yr) 2.90 ha (6 yr)
Elevation	350 m	380 m	320 m	350 m
Topography	10–20 percent slope	15–20 percent slope	Uniform 10 percent slope on high drumloidal ridge	7 percent slope rising away from swamp; variable microtopography
Aspect	E, NE	E	NW	SSW
Mean annual precipitation	105 cm	105 cm	107 cm	107 cm
Mean January temperature	−3°C	−3°C	−6°C	−6°C
Mean July temperature	22°C	22°C	21°C	21°C
Parent material	Glacial till on granite bedrock	Glacial till on granite bedrock	Granite, gneiss, schist in glacial till	Granite, gneiss, schist in glacial till
Depth to bedrock	(Not known)	(Not known)	1.8–3.0 m	1.5–2.0 m
Soil series	Rockaway	Rockaway	Paxton	Gloucester, Scituate, Norwell, Brockton
Soil drainage class	Well-drained	Well-drained	Well-drained	Variable; poorly to excessively drained
Soil texture	Clay loam (A & B)	Clay loam (A & B)	Fine sandy loam (A) Gravelly f.s. loam (B)	Sandy loam (A & B)
Depth to fragipan	0.5 m	0.5 m	0.5–0.8 m	0.5 m where present
Site index (red oak)	55	55	65	65
Stocking percent (1960)	80	72	87	70
Stand age (year as of 1975)	85	60	52 (east part) 60 (west part)	80
Stand history	Hardwood coppice origin. Thinning ca. 1930.	Hardwood coppice origin. Thinning ca. 1930.	Old-field white pine clearcut 1915–1923. Several early weedings of hardwoods. Thinning 1935, 1941.	Old-field white pine clearcut ca. 1895.

hurricane and was old-field white pine prior to the storm. The two Black Rock sites apparently have never been cleared for pasture or crops, and the current stands are of coppice origin following clearcutting of hardwoods about 1890 and 1910. Fire scars in some of the Black Rock oak stands were noted by Raup (1938).

Cultural treatments prior to plot establishment have had some influence on the species composition of the present stands. The Prospect Hill stand underwent a light thinning and improvement cut in the 1930's in which some gray birch (*Betula populifolia* Marsh.) and red maple were selectively removed to favor red oak (*Quercus rubra* L.) and yellow birch (*Betula alleghaniensis* Britt.). An experimental precommercial thinning was performed on part of the Black Rock plots about 1931, of which little is known. The Petersham Ridge tract received the most treatments and has detailed documentation in the Harvard Forest records and in Lutz and Cline (1947; cases 2, 4, 6). Of particular significance is that the hardwood understory was clearcut prior to overstory pine removal; slash was burned in piles resulting in some regeneration of paper birch (*Betula papyrifera* Marsh.); several weedings were made in the forest two decades after cutting which discriminated against hardwoods in an unsuccessful attempt to favor pine; and hardwood thinnings in 1935 and 1941 which attempted to favor white ash (*Fraxinus americana* L.) and discriminate against red oak, red maple, gray birch, and aspen (*Populus* spp.). No large gaps in the canopy were created in any of these cuttings, and as a result, the stand is still heavily dominated by red oak.

All four sites are at elevations of 300–400 m on slopes that are gentle to moderate in steepness. Soils on the Black Rock tracts are well-drained clay loams and those on the Harvard Forest tracts are sandy loams. Soils are well to excessively drained (hereafter called "dry") at Petersham Ridge and on parts of the Prospect Hill tract, but Prospect Hill has additional areas of moderately well-drained and somewhat poorly drained soils (hereafter called "moist") as well as some poorly drained soils (hereafter called "wet"). Dry soils are characterized by a lack of mottling in the surface 60 cm and rarely have a water table near the surface except for two to three days following heavy rains in the dormant season. Moist soils have brownish mottling at 20–60 cm and may have a water table at a depth of 30–60 cm in the dormant season. Wet soils are characterized by a water table near the surface except in summer and early fall, a surface layer high in organic matter, and mottling at 10–35 cm below the surface (Lyford 1978). Dry soils at Petersham Ridge and Prospect Hill are generally not more than 10 m in vertical elevation above nearby areas of moist or wet soil, which may result in a somewhat more favorable moisture regime than steep, excessively drained slopes (Husch 1958, Lyford 1964, Patric and Lyford 1980). A fragipan is present in the B horizon at all sites except the dry soils at Prospect Hill. These fragipans generally impede root penetration but can result in a perched water table at certain times of the year (Stout 1952, Lyford and others 1963). Site quality is about average for upland oaks on the Harvard Forest plots (site index 65, based on Schnur 1937) and below average on the Black Rock plots (SI 55).

METHODS

A total of 9 permanent plots ranging from 0.040 to 2.9 ha in size was established by E. M. Gould, Jr., W. H. Lyford, and H. H. Tryon of the Harvard Forest and Black Rock Forest staffs (Table 1). The Harvard Forest plots were gridded by string along compass lines and the locations of all trees $\geq$5.0 cm dbh estimated on maps of the subplots. Sizes of subplots are 6.1 × 6.1 m on the Prospect Hill tract and 3.0 × 3.0 m on the Petersham Ridge tract. These grids were reestablished at the time of each periodic measurement. Four remeasurements were made on the Petersham Ridge tract at approximately 5-yr intervals, and two remeasurements were made on the Prospect Hill tract. At the Prospect Hill tract, the initial plot size of 0.56 ha in 1962 was expanded to 2.9 ha in 1969.

On the Black Rock Forest plots, trees were identified by painting numbers on the stems, and all trees $\geq$2.5 cm dbh were measured. Measurements were begun in 1931 and 1936, and have been remeasured at intervals of 4 to 10 years.

On plots in both areas, diameters were measured to the nearest 0.1 inch (2.5 mm) and trees assigned to dominant, codominant, intermediate, and suppressed crown classes by standard definitions (Smith 1962). An exception to the crown classification procedure is the Petersham Ridge tract, where trees were classified as either overstory or suppressed. The overstory designation includes dominant, codominant, and intermediate trees.

The three principal soil drainage types on the Prospect Hill tract were mapped by soil scientist Walter Lyford based on numerous augur borings, soil pits, and from repeated observations of surface drainage patterns in all seasons over a period of 15 years (Lyford 1978).

To provide a broader basis of interpretation of species and site relations in the Harvard Forest, data from a 1956 timber cruise of all natural stands were compiled according to topographic position. Data for the 1956 cruise were obtained by proportional allocation of 962 variable-radius sample points according to stand area, using a basal area factor of 10 ft^2/acre (2.29 m^2/ha). All trees were tallied which covered the sighting angle, including understory trees. Board-foot timber volume to a 10 cm top was estimated for all trees $\geq$25 cm dbh.

Some evidence on presettlement forest composition is available from 191 boundary trees cited in the deeds of the 1738–99 metes and bounds surveys within the current boundaries of the Harvard Forest, obtained from the unpublished files of Raup and Carlson (1941). No evidence is available concerning possible bias in tree selection by these surveyors, and the data are considerably less detailed and systematic than those of the later rectangular surveys in other regions. Trees were used less frequently as boundary markers than other objects such as piles of stones. However, the properties were geometric in configuration and the boundaries cross many habitat types, indicating that there was probably not a systematic topographic bias in the location of property corners.

RESULTS

Present and Presettlement Forest Composition.—The almost universal occurrence of red maple on upland sites is illustrated in Table 2, which shows species composition of natural stands at the Harvard Forest segregated by topographic position. Red maple averaged 16–36 percent of the total stand basal area, but generally $<$10 percent of the timber volume of trees $>$25 cm dbh. The percentage basal area of red maple in the two Harvard Forest stands with permanent plots was 20 percent and 35 percent in 1956, indicating that they are representative of stands in their particular habitat types. Red maple in certain stands on convex slopes comprised 40–60 percent of the sawtimber volume, but this occurred only in stands where white pine rather than red oak was one of the principal canopy dominants.

Red oak is the most widespread overstory dominant on the higher convex slopes (300–400 m), averaging 24–68 percent of the sawtimber volume in 1956. In the two Harvard Forest stands with permanent plots it comprises 60–80 percent of the basal area. Hemlock is also abundant as an overstory tree in certain habitats, and may heavily dominate stands in ravines, stream gorges, and on flats and gentle slopes near swamps and lakeshores. However, hemlock is not presently abundant on the higher convex slopes where red oak is prominent. Beech and sugar maple are currently nowhere abundant in either overstory or understory (see also Tables

TABLE 2. Average species composition (percent) of natural stands on upland loamy soils in the Harvard Forest, based on the 1956 cruise. Only major species shown. Total basal area figures are for all overstory and understory stems >1.6 m tall. Volume figures are based on merchantable board-foot volume for trees >25 cm dbh.

	Red oak		Red maple		Yellow birch		Sweet birch		White pine		Sugar maple		Beech		Hemlock	
Habitat	Basal area	Volume	Basal area	Volume	Basal area	Volume	Basal area	Volume	Basal area	Volume	Basal area	Volume	Basal area	Volume	Basal area	Volume
W and SW slopes 200–300 m	20.2	23.5	16.3	3.8	4.0	0.8	6.1	1.8	10.4	19.0	1.8	0.2	2.2	0.9	22.4	44.1
W and SW slopes 300–400 m	20.9	45.6	36.3	10.8	2.1	0.2	1.5	1.6	11.3	29.3	3.8	2.5	0.2	0.0	1.3	1.2
E and SE slopes 200–300 m	18.0	40.1	18.0	6.1	0.6	0.8	8.2	2.9	9.7	17.4	4.3	2.1	3.2	4.0	18.9	22.2
E and SE slopes 300–400 m	39.8	67.8	22.7	2.0	11.0	3.4	1.3	0.0	2.3	4.7	0.3	0.0	3.2	2.9	5.8	10.7
N and NW slopes 300–400 m	30.3	40.1	26.1	0.6	2.5	1.2	1.4	0.0	2.5	0.9	2.5	0.2	0.1	0.0	1.7	16.3
Lakeshores and flats near bogs and ponds 200–300 m	14.4	20.2	14.5	2.3	3.2	0.9	3.0	1.2	13.7	23.4	0.8	2.2	0.5	0.0	33.6	45.6
Lakeshores and flats near bogs and ponds 300–400 m	5.4	7.9	20.6	4.1	1.0	0.2	1.0	0.2	9.7	2.2	0.0	2.4	0.3	0.0	49.4	77.5
Ravines 200–400 m	13.6	11.8	18.4	5.7	5.7	1.0	4.3	0.8	20.0	48.0	0.5	0.7	2.4	0.3	23.3	28.1

TABLE 3. Percentage density of dominant-codominant trees of each species in first and last measurement periods.

	Black Rock, ravine		Black Rock, slope		Petersham Ridge[a]		Prospect Hill, dry/moist soils		Prospect Hill, wet soils	
Species	1931	1973	1936	1976	1956	1975	1962	1975	1962	1975
Red oak (*Quercus rubra*)	11.9	11.7	41.0	44.0	32.4	40.3	64.2	68.2	8.3	8.5
Chestnut oak (*Q. prinus*)	21.4	33.3	55.1	53.6	–	–	–	–	–	–
White oak (*Q. alba*)	–	–	2.6	1.2	–	–	–	–	–	–
Black oak (*Q. velutina*)	–	–	–	–	0.2	0.2	–	–	–	–
Red maple (*Acer rubrum*)	4.8	3.3	1.3	1.2	9.6	11.6	20.2	17.7	61.4	63.1
Sugar maple (*A. saccharum*)	18.2	21.7	–	–	1.1	1.5	–	–	–	–
Yellow birch (*Betula alleghaniensis*)	14.3	15.0	–	–	–	–	7.4	5.6	24.8	25.5
Sweet birch (*B. lenta*)	6.4	8.3	–	–	5.3	5.1	0.9	0.9	2.7	2.8
Paper birch (*B. papyrifera*)	–	–	–	–	31.1	29.8	–	–	–	–
White ash (*Fraxinus americana*)	1.6	0.0	–	–	16.4	7.6	0.9	0.9	–	–
White pine (*Pinus strobus*)	–	–	–	–	0.6	0.8	–	–	–	–
Red pine (*P. resinosa*)	–	–	–	–	1.3	1.5	–	–	–	–
Basswood (*Tilia americana*)	19.8	5.0	–	–	–	–	–	–	–	–
Pignut hickory (*Carya glabra*)	1.6	1.7	–	–	2.0	1.7	–	–	–	–
Eastern hemlock (*Tsuga canadensis*)	–	–	–	–	–	–	0.9	0.9	–	–
Bigtooth aspen (*Populus grandidentata*)	–	–	–	–	–	–	1.8	0.9	–	–
American beech (*Fagus grandifolia*)	–	–	–	–	–	–	2.8	3.7	–	–
Black cherry (*Prunus serotina*)	–	–	–	–	–	–	0.9	0.9	–	–
Gray birch (*Betula populifolia*)	–	–	–	–	–	–	–	–	2.7	0.0
Number of trees/hectare	630.0	300.0	780.0	420.0	1,119.6[a]	846.4[a]	261.2	256.3	258.4	251.3

[a] Includes intermediate crown class.

3–5). Thus there is little indication that hemlock, beech, or sugar maple will increase markedly in oak stands in the near future, an assessment shared by Stephens and Waggoner (1980) for similar upland sites in Connecticut. However, these species are prominent in the understory of oak stands on some sites in the region (Lutz 1928, Forman and Elfstrom 1975).

At the Black Rock Forest, as at the Harvard Forest, red maple is the only abundant understory tree on the slopes (Table 5). The Black Rock stands have

TABLE 4. Percentage density of intermediate trees of each species in first and last measurement periods.

	Black Rock, ravine		Black Rock, slope		Prospect Hill, dry/moist soils		Prospect Hill, wet soils	
Species	1931	1973	1936	1976	1962	1975	1962	1975
Red oak	—	—	54.0	14.8	33.9	29.8	—	—
Chestnut oak	13.8	0.0	22.4	51.8	—	—	—	—
White oak	—	—	5.3	0.0	—	—	—	—
Red maple	20.6	22.7	14.5	22.2	49.1	56.7	54.5	60.0
Sugar maple	31.0	18.2	1.3	0.0	—	—	—	—
Yellow birch	10.3	27.2	—	—	13.2	10.8	31.8	40.0
Sweet birch	17.2	22.7	1.3	7.4	—	—	4.6	0.0
Basswood	6.9	9.1	—	—	—	—	—	—
Pignut hickory	—	—	1.3	0.0	—	—	—	—
Eastern hemlock	—	—	0.0	3.7	—	—	—	—
Bigtooth aspen	—	—	—	—	1.9	2.7	—	—
American beech	—	—	—	—	1.9	0.0	—	—
Gray birch	—	—	—	—	—	—	9.1	0.0
Number of trees/hectare	143.3	108.7	268.0	95.3	127.0	88.7	157.1	107.0

closer affinities with the former oak-chestnut type of the central and southern Appalachians (cf. Raup 1938, Braun 1950), and chestnut oak (*Quercus prinus* L.) commonly shares dominance of both slope and ravine sites with red oak. Sugar maple and yellow birch are locally abundant in ravines as both overstory and understory trees (Table 3).

The nature of the presettlement metes and bounds surveys does not allow close comparison with the present forest, but there seems to be little indication that hemlock, beech, sugar maple, and red maple were substantially more or less prevalent in the mid 1700's than today. On the higher lands of the Harvard Forest (300–400 m elevation), hemlock comprised 4 percent of the boundary trees, beech 4 percent, and maple 10 percent. Boundary trees in the lower Tom Swamp area (200–300 m elevation) included 16 percent hemlock, 10 percent maple, and 7 percent beech. The proportion of oak and chestnut on the higher lands was each 27 percent, and on the lower lands it was 18 percent and 8 percent, respectively. Russell (1981) also found that trees marked in 18th century surveys of northern New Jersey, not far from the Black Rock Forest, were predominantly oak and hickory with little beech, hemlock, or maple.

Changes in Species Composition Over Time.—Substantial reductions in the number of dominant and codominant trees/ha have occurred on most of the permanent plots during the period of measurement, as would be expected for even-aged stands progressing through the "pole stage" toward maturity. However, most species, including red maple, have remained remarkably stable in terms of their relative abundance in the canopy (Table 3). Exceptions are the dieback of white ash (*Fraxinus americana* L.) on the Petersham Ridge tract and basswood (*Tilia americana* L.) in the Black Rock ravine. Chestnut oak and red oak show a corresponding relative gain on these two sites, but otherwise the faster growth of oaks has not resulted in marked increase in oak dominance on these tracts during the period of record.

In trees of even-aged stands, the intermediate crown class is often a rather transient state, most trees lapsing into that class from the codominant class, and often becoming subsequently suppressed. The total number of intermediate trees

TABLE 5. Percentage density of suppressed trees of each species in first and last measurement periods.

	Black Rock, ravine		Black Rock, slope		Petersham Ridge		Prospect Hill, dry/moist soils		Prospect Hill, wet soils	
Species	1931	1973	1936	1976	1956	1975	1962	1975	1962	1975
Red oak	1.8	1.8	25.4	6.3	6.4	2.0	18.8	13.3	1.5	0.0
Chestnut oak	1.8	0.0	34.3	15.5	—	—	—	—	—	—
White oak	—	—	3.0	0.0	4.1	0.0	—	—	1.5	0.0
Scarlet oak	—	—	1.5	0.0	—	—	—	—	—	—
Red maple	24.8	18.2	31.3	68.3	19.6	49.2	60.9	67.2	64.6	65.3
Sugar maple	38.9	32.7	0.0	0.7	4.4	6.2	1.6	1.3	—	—
Yellow birch	11.5	34.6	0.0	0.7	0.2	0.8	7.4	6.6	16.9	18.4
Sweet birch	18.6	5.4	4.5	6.4	10.8	9.0	2.7	3.5	1.5	2.0
Paper birch	—	—	—	—	11.3	2.5	—	—	—	—
White ash	—	—	—	—	17.8	0.8	2.0	0.0	1.5	0.0
White pine	—	—	—	—	19.6	25.6	2.7	4.4	1.5	4.1
Red pine	—	—	—	—	3.9	1.1	—	—	—	—
Basswood	2.6	1.8	—	—	0.2	0.0	—	—	—	—
Pignut hickory	—	—	—	—	1.2	1.4	—	—	—	—
Eastern hemlock	0.0	1.8	0.0	1.4	—	—	0.4	2.2	3.1	8.2
American beech	—	—	—	—	—	—	0.8	0.9	0.0	2.0
Black cherry	—	—	—	—	0.2	0.3	0.4	0.4	—	—
Gray birch	—	—	—	—	—	—	0.8	0.0	6.1	0.0
American elm	—	—	—	—	—	—	—	—	1.5	0.0
American chestnut	0.0	3.6	0.0	0.7	0.0	0.3	—	—	—	—
Number of trees/hectare	558.2	271.6	236.5	501.1	1,091.2	635.7	613.3	541.5	463.7	349.6

has also undergone a substantial reduction on most tracts, indicating that a kind of self-thinning process occurs in this stratum as well. In most cases, oaks have undergone a relative reduction in this class, and red maple has made slight relative gains (Table 4).

Reductions in the number of suppressed trees per unit area have also occurred on most tracts (Table 5). Since most of the larger suppressed trees in these stratified forests are generally the same age as the overstory (Oliver 1978), and few openings occur in the overstory that could release suppressed trees, a progressive attrition in numbers is understandable. However, large gains in both the absolute and relative sense have occurred for red maple on some sites, particularly the driest and most exposed sites. Red maple increased from 31 to 68 percent of the suppressed trees in 40 years on the Black Rock slope and from 20 to 49 percent in 19 years at Petersham Ridge. These represent absolute gains as well, from 75 to 342/ha and from 214 to 312/ha, respectively. On the dry and moist soils of the Prospect Hill tract, where red maple already comprised 61 percent of the understory in 1962, a slight relative increase took place over 13 years.

Diameter Transition Probabilities of Red Maple.—A more detailed examination of the dynamics of red maple can be obtained by calculating the percentage of trees in each diameter class that have either died, remained in their original class, or advanced one or more classes during the span of measurement. Diameter transition probabilities for red maple on the Petersham Ridge and Prospect Hill tracts are shown in Tables 6 and 7. These data indicate clearly that the red maple

TABLE 6. 19-year diameter transition probabilities for red maple on the Petersham Ridge tract, Harvard Forest, central Massachusetts.

Diameter class (cm)	Initial number 1956[a]	Died	No change	1 Class	2 Classes	3 Classes	4 Classes	Final number 1975
6	100	0.17	0.22	0.48	0.13	0.00	0.00	102
8	45	.15	.15	.49	.18	.02	.00	73
10	21	.00	.05	.38	.43	.14	.00	40
12	11	.09	.00	.36	.46	.09	.00	17
14	4	.00	.00	.00	.75	.00	.25	14
16	2	.00	.00	.50	.50	.00	.00	8
18	0	—	—	—	—	—	—	4
20	0	—	—	—	—	—	—	1
22	0	—	—	—	—	—	—	1

[a] On 0.56 hectare.

understory is not in a state of dynamic equilibrium due to rapid turnover, but rather is showing a progressive development in its diameter distribution over time. For example, at Petersham Ridge none of the red maples in the 10-cm class died over the 19-year period, 38 percent advanced one 2-cm diameter class, 43 percent advanced two classes, and 14 percent advanced 3 classes (Table 6). Mortality rates of understory trees have been low and growth rates relatively high compared to other species. At Petersham Ridge, the 19-year mortality rate for suppressed red maple was 16 percent, compared to 90 percent for red oak, 100 percent for white oak, 30 percent for sugar maple, and 65 percent for sweet birch. Furthermore, survival rates and growth rates show a progressive increase with tree size, and the larger the tree, the greater was its chance of advancing 2 or more classes (Tables 6 and 7).

A comparison of 'initial' and 'final' diameter distributions shows substantial

TABLE 7. 13-year diameter transition probabilities for red maple on the Prospect Hill tract, Harvard Forest.[a]

Diameter class (cm)	Initial number 1962[b]	Died	Cut	No change	1 Class	2 Classes	3 Classes	Final number 1975
6	87	0.22	0.00	0.44	0.32	0.02	0.00	62
8	62	.22	.00	.42	.34	.02	.00	55
10	27	.07	.00	.33	.52	.07	.00	31
12	29	.03	.00	.35	.48	.14	.00	23
14	24	.08	.00	.25	.54	.13	.00	23
16	18	.11	.00	.22	.44	.17	.06	21
18	13	.23	.00	.15	.23	.39	.00	13
20	6	.17	.00	.17	.33	.00	.33	7
22	4	.00	.25	.00	.25	.00	.50	8
24	8	.12	.00	.12	.25	.50	.00	2
26	5	.00	.00	.00	.00	1.00	.00	6
28	0	.00	.00	.00	.00	.00	.00	5
30	1	.00	.00	.00	.00	1.00	.00	5
32	1	.00	.00	.00	1.00	.00	.00	0
34	0	.00	.00	.00	.00	.00	.00	2

[a] Data for wet, moist, and dry soils are similar and have been pooled.

[b] On 0.56 hectare.

net gains by red maple, especially in the larger size classes. At Petersham Ridge the number of red maples ≥15 cm dbh has increased from 3.6/ha to 25.0/ha; at Prospect Hill the number ≥25 cm dbh has increased from 12.5/ha to 32.1/ha (Tables 6 and 7).

There are insufficient numbers of red maples on the Black Rock Forest plots to calculate 40-year transition probabilities for individual classes, but overall trends can be briefly summarized. Of 39 red maples on the slope ≥2.0 cm dbh in 1936, 56 percent had died by 1976, 5 percent remained in their original diameter class, 20 percent advanced one class, 5 percent advanced 2 classes, 8 percent advanced 3 classes, 3 percent advanced 4 classes, and 3 percent advanced 5 classes. On the whole, it is evident that red maple has not made dramatic gains in the larger size classes on the Black Rock slope in 40 years. Mortality has been much higher there than on the Harvard Forest tracts, possibly because of more xeric site conditions. The total number of red maples ≥9 cm dbh is still only 28/ha. However, the initial density of red maple on the Black Rock slope was considerably less than on the Harvard Forest tracts, and the relative gain over 40 years is still substantial. The total number of red maples has increased 154 percent and the number ≥11.0 cm dbh has increased from 3.5/ha to 21.2/ha, an increase of more than 500 percent. The dramatic increase in the number of suppressed red maples from 75 to 342/ha suggests a potential for increased importance.

Potential of Red Maple for Overstory Development.—In even-aged stands that develop after clearcutting, red maple tends to become quickly overtopped by faster growing species such as red oak, so that in mature stands it is not well represented in the canopy layer (Oliver 1978). This is the case on most of the Harvard and Black Rock plots. However, the density of overstory red maple trees is higher than would be anticipated from the Permanent Understory hypothesis. The number of dominant, codominant, and intermediate red maples at Petersham Ridge was 107/ha in 1956 (9.6 percent of the total overstory), even though red maple was heavily discriminated against in the early thinnings (Lutz and Cline 1947, Patric 1956). The 80-year-old stand on moist soils at Prospect Hill had 86 dominant-codominant red maples per ha (30 percent of the total) and 77 intermediate red maples per ha in 1975. Even on the dry soils there were 31 dominant-codominant and 60 intermediate red maples/ha.

The higher proportion of overstory red maples on moist sites compared to dry sites is consistent with data obtained by Hicock and others (1931) and Patric (1956). The total density of red maple stems of all crown classes, however, is similar on both soils (630/ha on dry, 615/ha on moist soils), but a larger proportion of the red maple stems on moist sites are overstory trees. This does not appear to be due to faster growth of red maple on moist soil. Patric's (1956) data indicate that the ratio of heights of dominant-codominant red maple to that of red oak at Petersham Ridge was similar on moist and dry soils (ratio of ~0.78), and the Prospect Hill permanent plot data indicate little difference in diameter growth rates of red maple on the two drainage classes. Red oak appears to have a clear competitive advantage on both soil types. It seems more likely that the higher proportion of red maple overstory trees on moist soils is due to fewer red oaks becoming initially established on such sites. During the period of record, red oaks have been less numerous on moist soils than on dry soils.

The importance of the initial density of red oak in influencing the number of red maple overstory trees is illustrated by the stand which developed after the 1938 blowdown of the former old-field pine stand on part of the Prospect Hill tract with dry soils. At age 37 (in 1975), this stand had 90 dominant-codominant red oaks/ha and 26/ha of other oak species. This is far less than the 194 dominant-codominant red oaks/ha present in the adjacent 80-year-old stand on the same soil type or the 363/ha at Petersham Ridge at age 36. The density of dominant-codominant red maples on the blowdown area at age 37 is correspondingly much greater than on other areas (215/ha or 49 percent of the total).

Dominant-codominant trees of red maple at Prospect Hill were growing at an average rate of 2.0 mm diameter/yr on dry soils and 2.2 mm/yr on moist and wet soils. This compares with 3.4, 3.3, and 3.9 mm/yr for red oak on dry, moist, and wet soils. respectively. On dry soils, intermediate and suppressed trees of red maple grew at average rates of 1.7 and 0.9 mm/yr, respectively. Thus, while red maple overstory trees grew more slowly than those of red oak, their growth rates were comparable to those of other shade-tolerant overstory species, and the dominant-codominant red maples grew faster on the average than intermediate or suppressed trees. These results do not support the idea that red maple on well-drained sites is physiologically inhibited at higher light intensities. It is probable that most of the red maples currently in the overstory have been in that position for many decades, for at the current average rate of 2 mm diameter/yr it would require the entire period of stand development (80 years) to produce trees 16 cm dbh.

Further analysis indicated that red maple diameter growth shows a positive linear correlation with the initial diameter of the tree and a negative curvilinear relationship with Hegyi's (1974) competition index, a distance-dependent index for individual trees. The equations obtained by linear regression are

$$\mathrm{DI} = 0.270 + 0.0745\mathrm{D} \qquad (P < 0.01)$$
$$\mathrm{DI} = 2.05 - 0.129\mathrm{CI} + 0.0028\mathrm{CI}^2 \qquad (P < 0.01)$$

where DI = average diameter increment (mm/yr), D = dbh of the tree in cm, and CI = Hegyi's competition index using a radius of competition of 10 m. Although these regressions are highly significant, there is much scatter ($r^2 = 0.18$ and 0.13, respectively), a phenomenon that appears to be related to the shade tolerance of maple. Red oak on the same tract has an r^2 value of 0.70 using regressions of the same format, and yellow birch has an intermediate value of 0.51. Sugar maple, a very tolerant species, has r^2 values generally <0.35 for such relationships in the northern hardwood region of Wisconsin and Michigan (Lorimer and Frelich, unpublished data).

Effects of Drought on Mortality.—The occurrence of an unusually severe drought throughout New England and New York in 1962–66 provided an opportunity to test the hypothesis that much of the tolerant understory would be eradicated during infrequent severe droughts. At the Black Rock Forest, precipitation from April through September was an average of 22 percent below normal from 1962 to 1966 (Karnig and Lyford 1968). At the Harvard Forest, mean annual precipitation averaged 27 percent below normal from 1961 to 1966, with the driest year in 1965 (42 percent below normal), and the driest summer in 1964 (6.8 cm in July and August). A climatic reconstruction of the Hudson Valley region was recently completed by Cook and Jacoby (1979) based on tree ring series from several species. Their reconstruction suggested that severe July droughts (Palmer Drought Index of -3.0 or less) have occurred 10 times in the last 272 years, but that the drought of 1962–66 was slightly more severe (Drought Index <-5.0) than any other drought since 1700.

Tables 8 and 9 show average and maximum mortality rates before the drought compared to mortality rates after the drought. It is not possible to prove whether or not drought is the cause of high mortality in any given period, yet the comparisons are informative and direct observations of increased mortality at the Black Rock Forest due to this drought have been recorded (Karnig and Lyford 1968). In the Black Rock ravine, there was little difference in the mortality rates

TABLE 8. *Mortality rates of suppressed trees before and after the severe drought of 1962–66.*

	Average 5-yr mortality (percent)[a]													
	Black Rock ravine				Black Rock slope				Petersham Ridge			Prospect Hill (dry/ moist), 1962–75	
	1931–61		1962–73		1936–54		1955–76		1956–60 (one period)	1961–75			
Species	Average	Maximum	Average	Maximum	Average	Maximum	Average	Maximum		Average	Maximum	Average	Maximum
Red oak	—	—	—	—	35.8	53.4	57.7	86.2	33.1	38.6	54.5	19.7	19.9
Chestnut oak	—	—	—	—	25.3	45.8	23.0	46.5	—	—	—	—	—
White oak	—	—	—	—	—	—	—	—	29.0	50.5	100.0	—	—
Red maple	14.1	33.8	35.3	38.3	4.1	8.8	18.1	37.2	3.1	4.6	7.0	5.5	7.0
Sugar maple	11.2	21.4	17.4	18.7	—	—	—	—	4.6	9.3	16.3	—	—
Yellow birch	15.7	22.0	15.0	21.2	—	—	—	—	—	—	—	17.7	26.8
Sweet birch	14.1	31.2	37.1	38.3	—	—	—	—	5.6	25.3	43.9	0.0	0.0
Paper birch	—	—	—	—	—	—	—	—	19.2	44.9	64.3	—	—
White ash	—	—	—	—	—	—	—	—	18.9	51.4	94.0	100.0	100.0
White pine	—	—	—	—	—	—	—	—	7.2	13.8	17.0	12.1	12.2
Pignut hickory	—	—	—	—	—	—	—	—	17.5	9.4	14.1	—	—
Red pine	—	—	—	—	—	—	—	—	20.4	41.4	43.9	—	—
Witch hazel	—	—	—	—	—	—	—	—	—	—	—	11.8	12.7

[a] Mortality rates in all measurement periods converted to 5-yr rates by the equation of Hamilton and Edwards (1976).

of understory sugar maple and yellow birch before or after the drought, but the average 5-yr mortality of suppressed red maple increased from 14 to 35 percent. Red maple mortality on the slope was lower, but still showed a 4-fold increase over pre-drought averages (Table 8). Mortality also increased among overstory trees. In the ravine, there was no mortality of dominant/codominant red maples from 1931 to 1965, but 28 percent died between 1965 and 1973. Overstory sugar maple and yellow birch were not affected (Table 9).

The apparent impact of the drought on red maple at the Harvard Forest was small. At Petersham Ridge, average 5-yr mortality of suppressed red maples in the three measurement periods after the drought was only 4.6 percent with a maximum of 7 percent. At Prospect Hill, the equivalent 5-yr mortality rates were 6 percent and 7 percent in the two measurement periods after the drought. These rates are considerably lower than most other species (Table 8). Mortality rates of red maple overstory trees were also low; the highest rate at Petersham Ridge was 5 percent from 1966 to 1969 and 5 percent at Prospect Hill from 1969 to 1975 (Table 9).

DISCUSSION

The Permanent Understory Hypothesis.—The increase in the numbers of red maple on all tracts, the progressive development of the diameter distribution, and the current prominence of red maple in the overstory of some stands all suggest that the Permanent Understory hypothesis is probably an unsuitable hypothesis for stands in this region. Red maple grows most rapidly when it is in an overstory position, and the fact that such a large proportion of the red maple stems are suppressed can be more adequately explained by the superior growth of red oak under open conditions (Oliver 1978). Red maple comprises a large proportion of the overstory on well-drained sites in areas where oak density is relatively low. Suppressed red maples have been found to be capable of greatly increased growth and attainment of canopy status following release from suppression in New England (Oliver and Stephens 1977) and the southern Appalachians (Lorimer 1980). In a 300-year-old white oak forest in Michigan, red maple was the only species which responded with increased growth following partial cutting (Gerrard 1969).

The Transitory Red Maple Hypothesis.—The evidence does not appear to support the concept of red maple as an opportunistic, early successional species. The density of the red maple understory has been increasing over time, not decreasing, and the mortality rates of suppressed red maple are lower and growth rates higher than most other species. Mortality of overstory red maples has also been very low. There is evidence of continued recruitment on these and other tracts. At Petersham Ridge, large numbers of small red maple saplings <2.5 cm dbh are present beneath the red maple subcanopy, averaging 609/hectare, suggesting that dominance of the understory by red maple will continue. Continued seedling establishment of red maple over time has been documented in unmanaged oak stands in Connecticut by Stephens and Waggoner (1980) and after partial cutting in a Michigan oak stand by Rudolph and Lemmien (1976). The persistence of red maple in old-growth oak stands in New Jersey is evident from the data of Forman and Elfstrom (1975), in which red maple averaged 19 percent of the stems ≥ 10 cm dbh of species capable of attaining canopy status in eight stands on well-drained soils.

The Eradication by Drought Hypothesis.—The unusually severe drought of 1962–66 seems to have had a substantial adverse effect on red maple at the Black Rock Forest but negligible effect at the Harvard Forest. The Black Rock Forest, in view of the admixture of chestnut oak, is probably a warmer and drier site. Even at

TABLE 9. Mortality rates of dominant-codominant trees before and after the severe drought of 1962–66.

	Average 5-yr mortality (percent)[a]													
	Black Rock ravine				Black Rock slope				Petersham Ridge[b]			Prospect Hill (dry/moist), 1962–75	
	1931–61		1962–73		1936–54		1955–76			1961–75			
Species	Average	Maxi-mum	Average	Maxi-mum	Average	Maxi-mum	Average	Maxi-mum	1956–60 (one period)	Average	Maxi-mum	Average	Maxi-mum
Red oak	1.5	5.9	4.4	13.1	1.3	3.9	4.3	6.6	0.6	2.1	2.6	0.6	1.2
Chestnut oak	1.9	7.4	2.1	6.2	2.8	7.6	4.8	8.2	—	—	—	—	—
Red maple	0.0	0.0	9.3	27.9	—	—	—	—	0.0	3.8	8.5	3.8	4.2
Sugar maple	3.6	10.5	0.0	0.0	—	—	—	—	0.0	0.0	0.0	—	—
Yellow birch	1.3	5.4	0.0	0.0	—	—	—	—	—	—	—	5.3	10.5
Sweet birch	1.9	7.5	0.0	0.0	—	—	—	—	7.5	9.2	15.6	—	—
Paper birch	—	—	—	—	—	—	—	—	2.6	9.4	14.4	—	—
White ash	—	—	—	—	—	—	—	—	0.0	23.7	53.0	—	—
Pignut hickory	—	—	—	—	—	—	—	—	0.0	11.7	28.7	—	—
American basswood	3.3	7.7	21.5	23.3	—	—	—	—	—	—	—	—	—

[a] Mortality rates in all measurement periods converted to 5-yr rates by the equation of Hamilton and Edwards (1976).

[b] Includes intermediate trees.

the Black Rock Forest, however, the drought really only slowed the progressive development of red maple rather than causing a long-term setback. In Pennsylvania, McIntyre and Schnur (1936) likewise found that the severe drought of 1930 had little adverse effect on red maple, although it caused substantial dieback of some species such as hemlock and white pine. Little effect of the 1962–66 drought could be detected in the Connecticut stands studied by Stephens and Waggoner (1980). Thus, while drought may have some adverse effect on red maple development in some cases, the impact does not appear sufficient to preclude progressive development into the overstory.

The Short Lifespan Hypothesis.—The idea that red maple is a relatively short-lived tree in the oak region may be reasonable but published evidence is meager. It is commonly believed that the maximum age may be limited by internal decay which renders the trees susceptible to stem breakage. However, Gruschow and Trousdell (1958) and Bryan (1960) implied that past fires may have been an important cause of decay in stands which they studied. Ice storms may be a more important cause of defect in areas of low fire frequency (Campbell 1937, Downs 1938). However, in the oldest stands in the present study (Black Rock ravine and Prospect Hill, both about 80 years), there is as yet no evidence of a decline among the larger trees and growth rate is positively correlated with size. Over half of the red maples in an ecotonal oak-northern hardwood forest (near Hearts Content) in Pennsylvania were >180 years old, and among these older red maples, ages were well distributed up to a maximum of 290 years (Hough and Forbes 1943). Some 150-year-old red maples were present in a Harvard Forest stand of that age analyzed by Oliver and Stephens (1977).

Even if red maple has a comparatively short lifespan, many gaps created by dying trees would probably be filled by understory red maples rather than red oak (Ehrenfeld 1980), especially where oak advance regeneration is sparse. Thus it is questionable whether a short lifespan of red maple would by itself facilitate continued regeneration and dominance of oak. Destruction of existing stands by wind or heavy cutting would be expected in some cases to result in oak-dominated stands, but only where oak advance regeneration had been present.

The Red Maple Dominance Hypothesis.—The data gathered in this study of maturing stands appear to be consistent with this hypothesis, but the degree to which maple might be represented in future stands is partly dependent upon growth and mortality rates of older maples and on competitive relationships between oak and maple under gaps in older stands. In mature and old-growth stands where oak seedling sprouts are sparse, the evidence does suggest a trend toward increased importance of maple and other species, especially on reasonably moist sites. The finding in several regions that red oak seedlings germinating after a disturbance are generally unable to compete with advance regeneration appears to hold true in New England as well (Hibbs 1983). Gaps in 50 to 150-year-old oak forests caused by gypsy moth defoliation were dominated by red maple, beech, and sweet birch after 7 years (Ehrenfeld 1980). Red maple has been increasing in an old-growth forest in New Jersey, and despite numerous canopy gaps and small oak seedlings, no oak saplings were observed in measurement periods spanning 29 years (Davison 1980). Even small oak saplings are often sparse in old-growth stands (Lutz 1928, Toumey 1932, Monk 1961, Lorimer 1980).

Where vigorous oak advance regeneration is reasonably abundant, the outcome of competition between species will be influenced by gap size. There is little reason to doubt that red oak could maintain its dominance after clearcutting or large-scale windthrow on sites where vigorous oak seedling sprouts were already common prior to the disturbance. In openings of less than one tree height in width, however, red maple appears to grow faster in height than red oak (Hibbs 1982).

Competitive relationships are probably also site-dependent; on a fairly dry site in Michigan dominated by black oak, there was nearly an equal mixture of red maple and oak saplings >6 m tall in 0.04 ha openings 21 years after group selection cutting (Rudolph and Lemmien 1976). Additional evidence on the fate of oak seedlings on various sites in the Northeast and data on growth and mortality of individual trees in gaps of old-growth stands would be helpful in evaluating this hypothesis further.

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Effect of a Prescribed Fire on Herbage Production in Southwestern Ponderosa Pine on Sedimentary Soils

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ABSTRACT. An area burned by prescription in 1977 and a nearby unburned area were measured in 1974 and 1980 to determine effects of the burn on herbage and forage production. Herbage production on the burned area increased significantly in 1980 over its 1974 level, in addition to being greater than the 1980 control production. However, the proportion of forage production to total herbage production in 1980 on the burned area decreased after the burn, and was significantly less than the control area forage production. This reduction in forage production can be attributed to the increase of nonforage species, notably bracken fern.

Increases in total herbage production on both burned and unburned areas between 1974 and 1980 are attributed to a number of factors, including increased soil moisture availability during the 1980 growing season which had 50 percent more precipitation than the historical average. FOREST SCI. 30:22–25.

ADDITIONAL KEY WORDS. *Pinus ponderosa,* forage production.

FIRE SUPPRESSION in southwestern ponderosa pine has been blamed for a host of negative environmental impacts including decreased forage production, increased fuel loads, and increased severity and destructive potential of wildfires (Weaver 1974). In an attempt to alleviate the wildfire severity problem, land managers are using prescribed burning to reduce these heavy fuel loads.

Little is known about the impact of prescribed fire on understory production in southwestern ponderosa pine. Ffolliott and others (1977) found a 13 fold increase (from 3.4 to

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