

Rapid capture of growing space by red maple

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Abstract: Red maple (*Acer rubrum* L.) is becoming increasingly dominant in forest stands throughout the eastern United States. To investigate the reasons for the increase, we examined the development of red maple and oak (*Quercus* spp.) seedlings and stump sprouts following the harvest of oak-dominated stands. Within 7 years after harvest, red maple seedlings were present in far greater numbers and captured more growing space than all oaks combined. Growing space occupied by red maple stump sprouts exceeded oak sprouts by a ratio of 3.5:1. Through stump sprouts alone, red maple fully recaptured the amount of growing space it had previously occupied in the overstory 7 years after harvest. Results from similar but older stands show that red maple dominance is sustained into the third decade of stand development. Red maple surpassed all oaks combined in rapid site capture through both seed-origin and sprout-origin regeneration. Red maple's superior ability to regenerate by sprouts is particularly favored by timber harvesting following a history of management and disturbance regimes that permit the accumulation of suppressed small-diameter red maple stems. Among the events and processes that promote stand conversion, timber harvesting may be the major proximal cause of the widespread, increasing dominance of red maple.

Résumé : L'érable rouge (*Acer rubrum* L.) devient de plus en plus dominant dans les peuplements forestiers de l'est des États-Unis. Pour déterminer les raisons de cette augmentation, nous avons étudié le développement de semis et de rejets de souche d'érable rouge et de chênes (*Quercus* spp.) après la coupe de peuplements dominés par le chêne. Au cours des sept premières années après la coupe, les semis d'érable rouge étaient beaucoup plus nombreux et occupaient plus d'espace de croissance que tous les chênes regroupés. L'espace de croissance utilisé par les rejets de souche d'érable rouge était 3,5 fois supérieur à celui qu'occupaient les rejets de souche de chêne. Au cours des sept premières années après la coupe, l'érable rouge a complètement réoccupé l'espace de croissance qu'il occupait précédemment dans le couvert dominant seulement à partir des rejets de souche. Les résultats provenant de peuplements de composition similaire, mais plus âgés, montrent que l'érable rouge est toujours dominant au cours de la troisième décennie du développement du peuplement. L'érable rouge surpasse tous les chênes combinés par sa rapidité à occuper l'espace de croissance avec sa régénération issue de graines et de rejets de souche. La capacité supérieure de l'érable rouge à se régénérer par rejets de souche est particulièrement favorisée par la récolte forestière effectuée à la suite d'un historique de régimes d'aménagement et de perturbations qui ont permis l'accumulation d'érables rouges opprimés et de petits diamètres. Parmi les événements et les processus qui favorisent la conversion des peuplements, la récolte forestière constitue probablement la principale cause rapprochée de la dominance fréquente et croissante de l'érable rouge.

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Introduction

Increases in red maple (*Acer rubrum* L.) abundance have been widely documented in eastern North America (Lorimer 1984; Abrams 1998; Fei and Steiner 2007). Red maple's increase often appears to have come at the expense of various oak (*Quercus*) species in stands where red maple was formerly a subordinate species but dominant in the understory and mid-canopy strata (Lorimer 1984; Abrams 1998). However, the phenomenon cannot be simply explained by endogenous factors, such as succession, because it appears to be unprecedented in the natural history of the region (Abrams 1998). Several exogenous factors have been implicated because they are known to affect the growth and survival of

red maple and associated species, and these factors have changed markedly during the twentieth century. For example, modern efforts to suppress fire in oak-dominated stands are believed to have contributed significantly to an increase in red maple and other late-successional species that are more sensitive to fire than oaks (Abrams 1992; Brose and Van Lear 1998; Hutchinson et al. 2008). Invasions of exotic species, such as gypsy moth (*Lymantria dispar* L.) and chestnut blight (*Cryphonectria parasitica* (Murrill) Barr), may have contributed to the increase in red maple through the invasive species' negative effects on oaks and other associated species (Woods and Shanks 1959; Fajvan and Wood 1996; Vandermaast et al. 2002). White-tailed deer (*Odocoileus virginianus* Boddaert) populations, which increased dramatically during the twentieth century, may also have contributed to the phenomenon because deer prefer oaks over red maple as browse (Kittredge and Ashton 1995). Other factors, such as climate change, modern land use, and forest management practices, may also have contributed to the expansion of red maple (Abrams 1998).

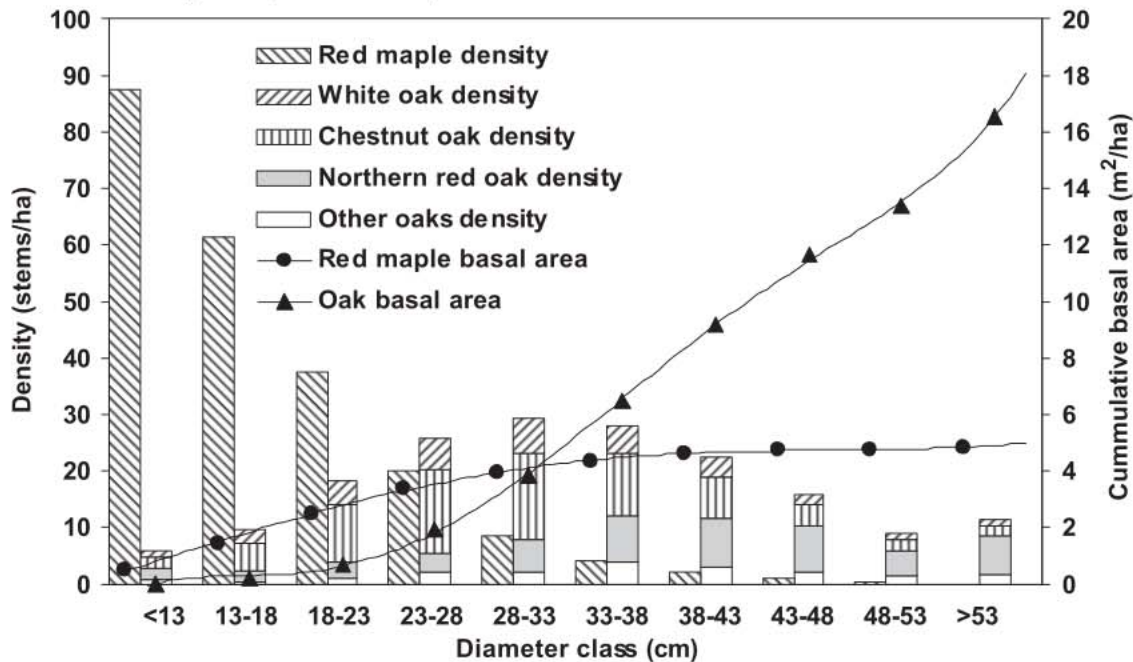
Research also has been conducted on the physiology of red maple. Red maple exhibits rather modest levels of leaf physiological response to various environmental conditions

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Fig. 1. Average stand level density and cumulative basal area for red maple and oaks by diameter classes based on data from 54 mature oak-dominated stands in Pennsylvania (ORSPA data set).



(Abrams 1998), and it has relatively low rates of net photosynthesis compared with other associated hardwoods (Reich et al. 1991; Sullivan et al. 1996; Turnbull et al. 2002). Abrams (1998) concluded that the expansion of red maple is due to its ability to act as a “super-generalist”, i.e., its ecological attributes enable it to compete successfully under a suite of changing environmental conditions. In this paper, we show that red maple, compared with its oak associates, exhibits advantages in regeneration that are likely enhanced by modern forest management regimes in oak-dominated forest stands. We studied the development of seed and sprout-origin regeneration of red maple in contrast to the dominant oak species in our study area: northern red oak (*Quercus rubra* L.), chestnut oak (*Quercus montana* Willd.), white oak (*Quercus alba* L.), black oak (*Quercus velutina* Lam.), and scarlet oak (*Quercus coccinea* Muenchh.).

Methods

Three data sets were used in this study. The first data set was collected before and after harvest in 54 stands measured from 1996–2006 as part of the Oak-forest Regeneration Study in Pennsylvania (ORSPA). The ORSPA data set was developed to examine stand composition and development following clear-cut or shelterwood harvests in stands containing a predominance of basal area in various oak species and a minority component of red maple (Fig. 1). The ORSPA stands are distributed over approximately the central third of Pennsylvania. Depending on stand size, 15–30 permanent plots with 8.02 m radii (0.05 acre) were systematically installed in each stand, and overstory composition and site attributes were measured for these plots. Four permanent subplots with 1.13 m radii (0.001 acre) were established within each plot for the purpose of measuring tree regeneration and vegetation competition. For this analysis, we used

data from a total of 5900 subplots. All stands were measured approximately 1 year before harvest, and a subset of the stands was remeasured 1 year (41 stands), 4 years (32 stands), and 7 years (16 stands) after harvest. For measurements taken before harvest, overstory trees on each plot were recorded by species and diameter at breast height (DBH) classes. Seed-origin tree seedlings (<5.1 cm in DBH) were tallied by species and height class on each subplot in each measurement period. In stands measured after harvest, species, total number of sprouts (if any), and height of the dominant sprout were also recorded for the stump closest to each subplot center.

Within each stand, basal area was used to calculate the relative dominance of overstory trees by species (basal area by species / total basal area × 100). Aggregate height (total height per unit area), a comprehensive measure of regeneration dominance that is analogous to basal area (i.e., a composite index of size × density, Fei et al. 2006), was used to calculate the relative dominance for understory seedlings by species (aggregate height by species / total aggregate height × 100). The three major oak species (white oak, chestnut oak, and northern red oak) were summarized by individual species, and other oak species were summarized as a group.

The aggregate height of seed-origin seedlings was also calculated for stands 1, 4, and 7 years after harvest. Seed-origin regeneration typically included both advance regeneration and a postharvest cohort. The species of dominant seedling (seed-origin) was recorded if a red maple or an oak seedling was taller (or larger, if the same height) than all other seedlings in each subplot. For each of the 16 stands remeasured 1, 4, and 7 years after harvest and for each species (red maple vs. oak), we calculated the average height of dominant seedlings and percentage of subplots dominated by

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that species within the stand. Paired *t* tests were used to test differences between means at each measurement period.

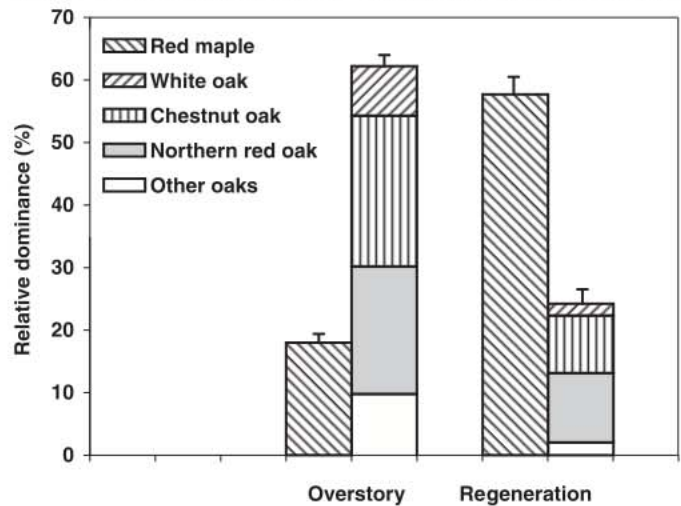
The percentage of stumps with one or more sprouts 1 year after harvest and survival probability 4 and 7 years after harvest were calculated within each stand by species and were summarized across all stands. The average number of sprouts per stump and mean height of the dominant sprout were calculated for white oak, chestnut oak, and northern red oak 1, 4, and 7 years after harvest. Averages for the three previously mentioned oak species were used for the small number of scarlet oaks and black oaks in the study. In addition, we used logistic regression models (GLIMMIX, SAS 9.1, SAS Institute Inc., Cary, North Carolina) to estimate sprouting probability as a function of diameter class for red maple ($n = 1037$ stumps) and all oaks combined ($n = 1160$ stumps). Stand was included in the models as a random effect variable to avoid the possibility of pseudo-replication arising from site effects.

Our second data set (ORSPA subsample) contains information about stump sprouting activity for red maple, white oak, chestnut oak, and northern red oak 4–6 years after harvest in a subset of six of the ORSPA stands. These data were collected by sampling stump sprout groups along transects, and for each sprouted stump in the sample, we recorded species, number of sprouts per stump, height of the dominant sprout, and diameter of the sprout-group's aggregate crown. A total of 152 stumps were surveyed in this data set (40 red maple, 7 white oak, 59 chestnut oak, and 46 northern red oak stumps). Crown diameters were measured from four orthogonal directions, and the measurements were averaged. The relationship between crown diameter and species and height of the dominant sprout was analyzed using GLIMMIX with the consideration of stand-induced random effects. Average crown areas at ages four and seven were then estimated based on this relationship, using average stump sprout height derived from the ORSPA data.

Preharvest canopy cover and postharvest stump-sprout cover percentages by species were then estimated for a hypothetical "average" stand with 100% stocking (full canopy cover, Gingrich 1967) based on average density and basal area of overstory species of all 54 ORSPA stands. The preharvest overstory cover percentage for each species was estimated based on its relative basal area in a stand by assuming that the percentage of crown cover of overstory trees was proportional to basal area (Gingrich 1967). The density of sprouting stumps after harvest was then calculated for each species by multiplying preharvest overstory stem density by sprouting probability and survival probability. Total crown coverage for each species was calculated by multiplying the number of stumps per hectare by the average crown area per stump at each development age. Cover percentage was then calculated using total crown coverage divided by total area in the hypothetical stand.

The third data set (FM-T-24), described by Gould et al. (2005), comes from 90 stands measured before harvest and again in the third decade of stand development following harvest by clear-cutting. Stand age at the time of the second measurement averaged 24 years (range 20–32). These stands were very similar, even almost identical on average, to ORSPA stands (Gould et al. 2006). Of the 90 stands, 23

Fig. 2. Average stand-level relative dominance and standard error of overstory trees (basal area by species / overall basal area \times 100) and understory regeneration (aggregate height by species / total aggregate height \times 100) for red maple and oaks based on data from 54 mature oak-dominated stands in Pennsylvania (ORSPA data set).



were measured more intensively to distinguish between seed-origin and sprout-origin of red maple and oak. From the FM-T-24 data set, we used data on the frequency distribution of diameter classes by species in the overstory to determine basal area and stocking by species and origin (seed vs. sprout).

Results

Preharvest stand composition

Oaks and red maple were the major components in the unharvested overstories of the 54 mature stands in the ORSPA data set and together made up an average of 80% of stand basal area. The average total basal area in these stands was 26.7 m²/ha, with 24.5% contributed by northern red oak, 20.1% by chestnut oak, 9.4% by white oak, 7.7% by other oak species, and 17.9% by red maple. Based on basal area, the overall relative dominance for all the oak species was 3.5 times that of red maple (Figs. 1 and 2). Although red maple had a relatively low basal area compared with oaks, average red maple density (222 stems/ha) was considerably higher than that of all oaks combined (156 stems/ha), because a majority of the red maple stems were in small diameter classes and individually contributed little to total basal area (Fig. 1).

In marked contrast to minor representation in overstory basal area, red maple was much more abundant than oak within the advance (preharvest) regeneration cohort (Fig. 2). Furthermore, with an average aggregate height of 0.7 m/m², relative dominance of red maple advance regeneration exceeded that of all oak species combined by a ratio of over 2:1 (Fig. 2). A high aggregate height of red maple advance regeneration was achieved primarily by a high density rather than large size. Red maple seedlings averaged about 63 000 stems/ha and about 12 cm in height, while oak seedlings averaged about 16 000 stems/ha and about 19 cm in height.

Fig. 3. Change of aggregate height (mean and standard error) by stand for seed-origin red maple and oak regeneration from before harvest (Pre) to 1, 4, and 7 years after harvest in 16 oak-dominated stands in Pennsylvania (ORSPA data set).

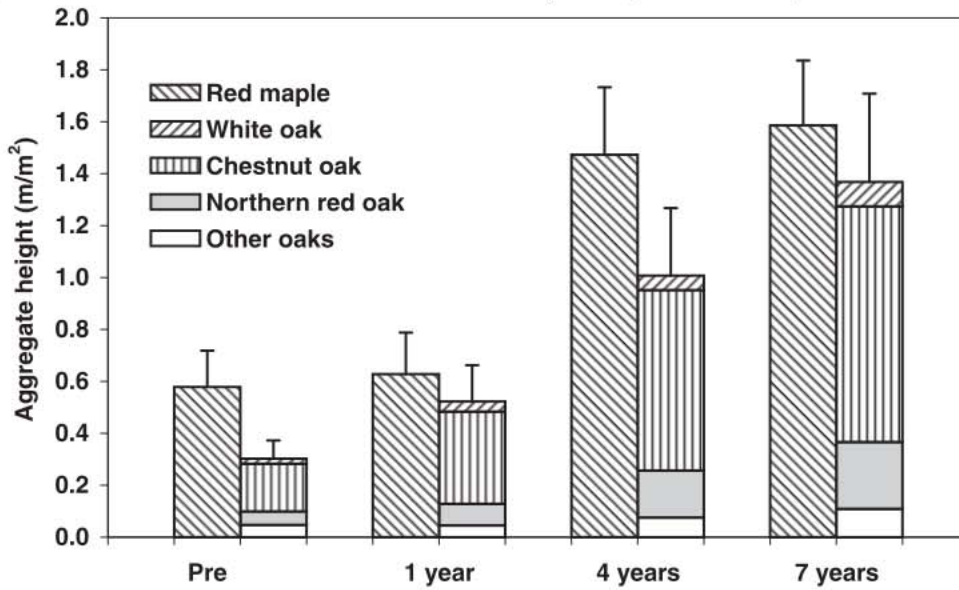
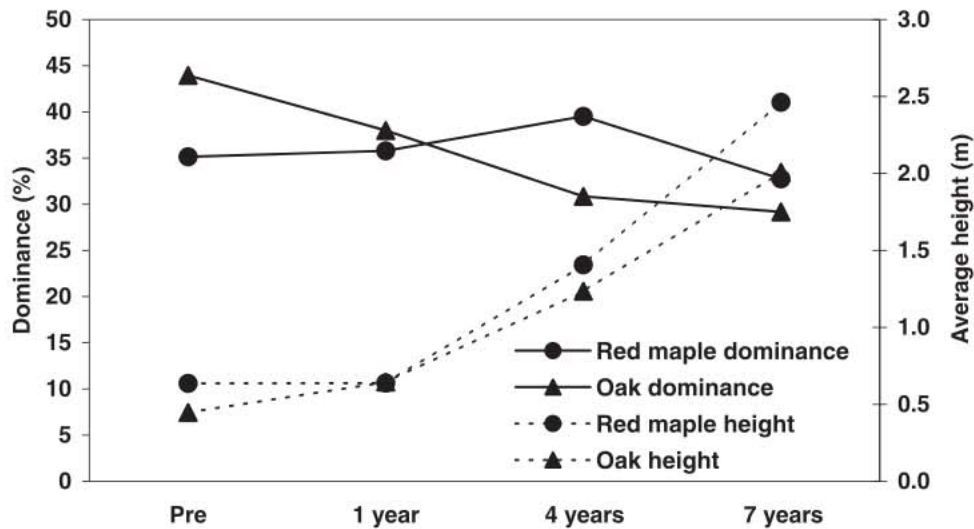


Fig. 4. Solid lines: percentage of plots whose dominant seedling was a red maple or any species of oak from before harvest (Pre) to 1, 4, and 7 years after harvest. Dashed lines: average height of dominant seedlings (ORSPA data set).



Postharvest stand development

Seed-origin regeneration

Following harvest, red maple retained its initial dominance over oak in seed-origin regeneration through the first 7 years of stand development based on the 16 stands for which we had measurements through age seven (Fig. 3). In these 16 stands, the average aggregate height of red maple increased from 0.58 m/m² before harvest to 0.63, 1.47, and 1.59 m/m² 1, 4, and 7 years after harvest, respectively, and was always at least 1.2 times higher than that of all oaks combined. Again, red maple's continued dominance in seed-origin regeneration within these stands is principally attributable to seedling density. There were 2–3 times as many red maple seedlings as oak seedlings at every sampling period except immediately after harvest, when the ratio fell to

1.8:1.0. Average red maple seedling density jumped markedly between stand ages one and four, reflecting the appearance of new (and small) seedlings, but most of this new recruitment did not survive to stand age seven.

Although the average height of red maple seedlings was less than that of oak seedlings, the tallest of the very abundant red maple seedlings were as tall, and as common, as the tallest of the oak seedlings (Fig. 4). By stand ages four and seven, slightly more subplots were dominated by a red maple seedling than by an oak seedling, although the difference between species was not statistically significant at any age ($P > 0.05$). By age seven, red maple was the largest tree seedling on 32.7% of all subplots and oak was the largest on 29.2%. At all ages, the average height of dominant red maple seedlings was greater than or equal to the average height of dominant oak seedlings.

Table 1. Mean attributes of stump sprouts by species and development age in the first 7 years (ORSPA data set).

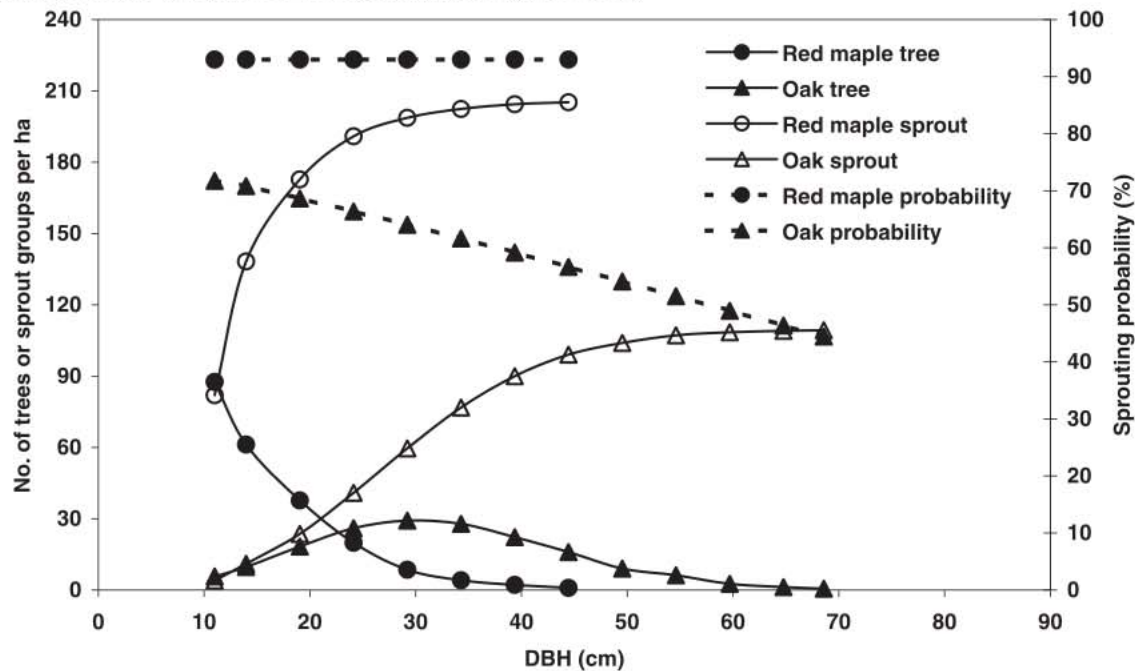
Species	1 year (n = 41)*			4 years (n = 32)*			7 years (n = 16)*		
	P (%)	No.	Ht (m)	Ps (%) [†]	No.	Ht (m)	Ps (%) [†]	No.	Ht (m)
<i>Acer rubrum</i>	91.5	23.9	1.3	90.0	15.9	3.4	95.4	11.0	5.5
<i>Quercus alba</i>	36.1	17.5	0.8	74.0	8.8	2.0	77.4	4.1	4.0
<i>Quercus montana</i>	67.2	20.5	1.1	84.0	15.6	2.6	84.3	7.9	5.0
<i>Quercus rubra</i>	58.3	16.6	1.1	74.6	12.1	2.8	88.5	8.0	4.6

Note: P, sprouting probability; No., mean number of sprouts per stump; Ht, mean height to the top of the dominant sprout from each stump; Ps, probability of survival of □ sprout/stump over the previous 3 years.

*Number of stands used to calculate the mean attributes.

[†]Percentage of stumps that survived through consecutive survey periods.

Fig. 5. Diameter distributions of oak and red maple trees in an “average” ORSPA stand (filled symbols, solid lines), probability of sprouting after harvest as a function of tree diameter at breast height (DBH) (filled symbols, dashed lines), and expected cumulative number of sprout groups as a function of parent tree DBH (empty symbols, solid lines).



Sprout-origin regeneration

Red maple generally exceeded each oak species by substantial margins for each aspect of sprout-origin regeneration (Table 1): percentage of cut stumps that produced live sprouts, number of sprouts per stump, average height of the dominant sprout, and percentage of sprouts surviving through stand age seven. While red maple stumps sprouted in excess of 90% regardless of diameter, the average rate of sprouting for all oak species in ORSPA stands was no greater than 74% at any diameter and declined significantly as diameter increased (Fig. 5; sprouting probability = $1/(1 + e^{-0.05+0.021 \times \text{DBH}}) \times 100$, where DBH is measured in centimetres).

Although crown areas for 7-year-old stumps were estimated using data based on 4- to 6-year-old sprouts, the average stump sprout height at age seven was within the range of data used to develop the height / crown-width relationship. Sprout-group crown diameter exhibited a simple linear relationship with height of the dominant sprout in a group

(Fig. 6). The linear relationships were not statistically different among species ($p > 0.05$), and a single generalized relationship between crown diameter (Cd) and height (Ht) was fitted for all species ($\text{Cd} = -0.04 + 0.76 \times \text{Ht}$, $1.5 \text{ m} < \text{Ht} < 7.6 \text{ m}$). On average, red maple stump sprouts were taller in height and wider in crown diameter than oak stump sprouts, and therefore red maple tends to occupy the upper right corner of Fig. 6.

Based on crown diameters and the average number of sprout groups per hectare (average number of overstory trees \times sprouting probability \times survival probability), red maple stump sprouts occupied 9.0% of the total potential growing space in the hypothetical stand after 4 years of stand development and 23.2% after 7 years, while stump sprouts from all oak species combined occupied 2.3% and 6.6%, respectively (Fig. 7).

Third decade stand composition

Before overstory removal in the 90 stands in the FM-T-24

Fig. 6. Relationship between sprout-group crown diameter and height of the dominant stem in sprout groups 4–6 years after harvest. Large, filled symbols represent the mean for each species (ORSPA subsample).

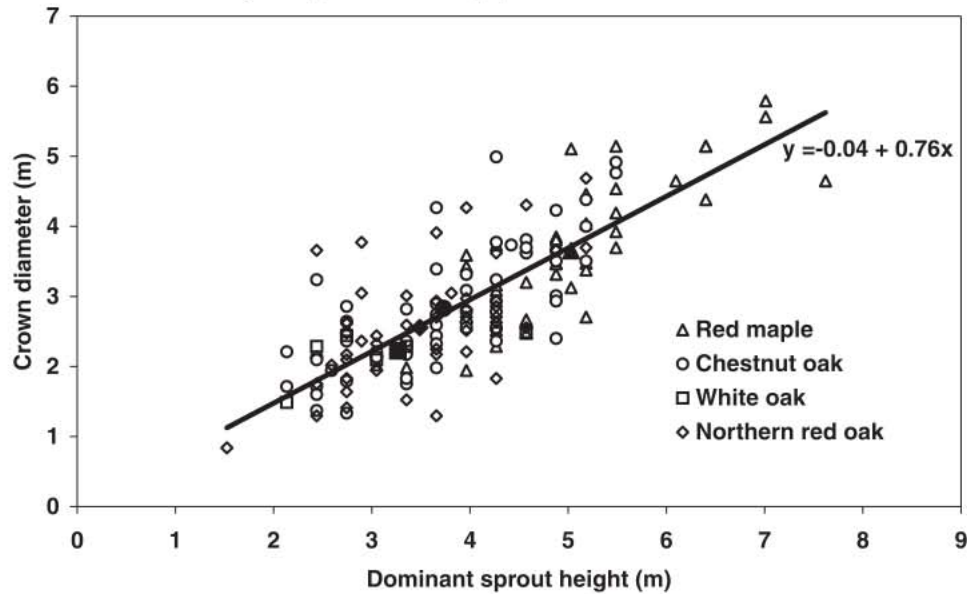
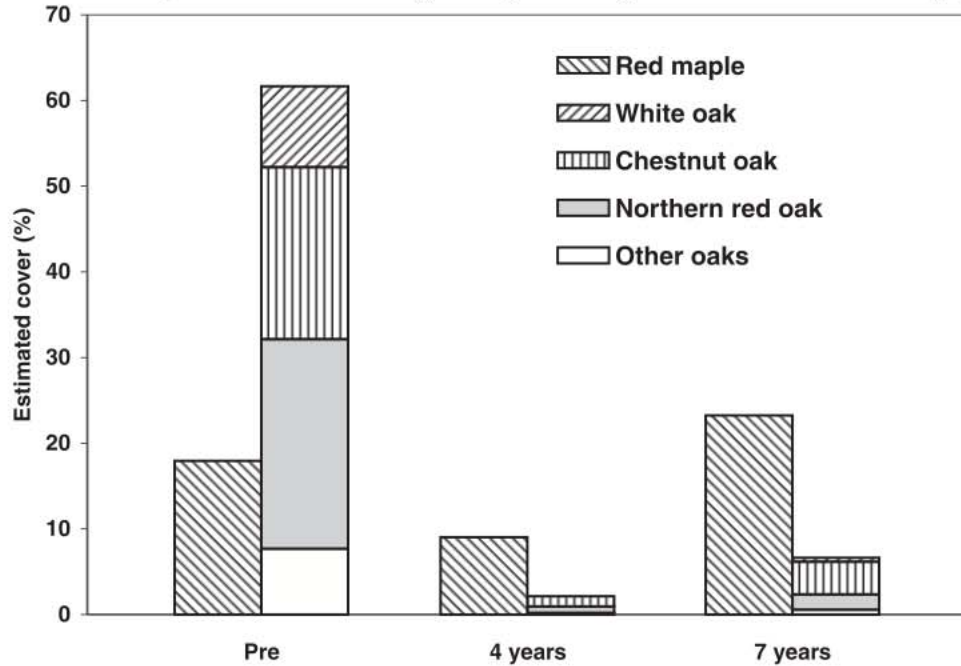


Fig. 7. Estimated cover percentage by species in a hypothetical stand for preharvest overstory tree (pre) and stump sprouts at age 4 and 7 years. The hypothetical stand composition is based on average density and average basal area from the ORSPA project.



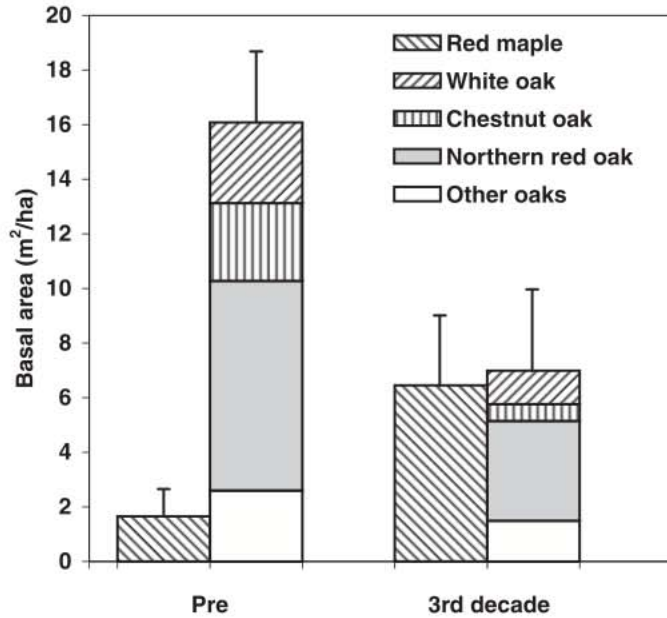
data set, average red maple basal area was 2.3 m²/ha or 10.4% of the total basal area and average oak basal area was 17.8 m²/ha or 81.2%. In 82 of these stands that had some level of regeneration three decades after harvest (eight stands failed to regenerate), average red maple basal area increased to 5.5 m²/ha or 35.0% of total basal area and oak decreased to 4.9 m²/ha or 31.4%. In 54 stands that reached >90% stocking by the third decade, average red maple basal area was 6.5 m²/ha or 32.6% of total basal area, while oak basal area was 7.0 m²/ha or 35.3% (Fig. 8). Based on the 23 stands in which a distinction was made between

seed-origin vs. sprout-origin regeneration, 50.5% of red maple basal area in the third-decade stands originated from stump sprouts and the balance from seedlings.

Discussion

The stands measured for this study were all dominated by oak species before they were harvested, but their exact composition varied according to the moisture regime of the site, soil parent material, topographic position, and stand history. The dominant oak species (as measured by basal area) was

Fig. 8. Basal area (mean and standard error) for red maple and oaks before (Pre) and three decades after overstory removal in stands that had >90% stocking in the third decade of stand development ($n = 54$) (FM-T-24 data set).



typically northern red oak and (or) chestnut oak, but some stands were dominated by white oak or black oak. Site conditions ranged from mesic to dry mesic, and the dominant non-tree understory plants varied according to the stand (Kaeser et al. 2008). The stands comprised by this study were representative in their variety of oak-dominated stands within the Ridge and Valley and Appalachian Plateau physiographic provinces of the central Appalachians.

Even though red maple was a subordinate component of preharvest overstories in all of our stands, red maple tree stems (≈ 5.1 cm DBH) were present in great abundance in most stands. In fact, red maple was the single most common tree species in 90% of all study stands, but most of the red maples were small compared with neighboring oaks (Fig. 1). In this respect, the stands examined for this study resemble many other oak stands in the eastern United States in which red maple, as either new regeneration or as suppressed remnants of the last stand replacement event, has become an important or dominant component of the understory and midstory during the twentieth century (Lorimer 1984; Abrams 1998).

This study focused on the contribution to regeneration of these numerous but relatively small red maples after stand harvest. Most seed-origin regeneration of both species originated as seedlings present in advance of harvest, and in our stands the advance regeneration cohort was dominated by red maple, with an average of nearly four times as many seedlings and twice as much aggregate height as was present for all oak species combined. This advantage in seed-origin regeneration is a natural outcome of certain life history characteristics of red maple (Abrams 1998), which has a seed production potential of at least one order of magnitude greater than that of oaks on a unit basal area basis (Clark et al. 1998).

Immediately following harvest in our study stands, the density of red maple regeneration substantially surpassed that of oaks in both seedling and sprout categories, an advantage that was greatly disproportionate to the relative dominance of red maple and oaks in the previous stands. Through the seventh year of stand development following harvest, red maple continued to maintain a distinct regeneration advantage over oak in the combination of density and growth of both seedlings and sprouts. Though typically small at the time of harvest, red maple seedlings were sufficiently abundant that they occupied a relatively large amount of growing space within the cohort of all tree regeneration, and their abundance ensured a strong presence even though thousands per hectare died during subsequent stand development. By age seven, seed-origin red maple continued to maintain an advantage in aggregate height, and the largest red maple seedlings were, on average, at least as numerous, and as tall, as the largest oak seedlings (Fig. 4). Similarly, in the category of sprout-origin regeneration, red maple sprouts maintained and even enhanced their initial advantage over oak sprouts by surviving in larger numbers and growing faster in height through the seventh year (Table 1).

Most significantly, in the hypothetical "average" stand, red maple sprout groups recovered and even surpassed the species' preharvest canopy area by age seven (Fig. 7). In other words, through stump sprouts alone, red maple fully recaptured in the new stands the canopy space it occupied in the old stands, and it did so by age seven. Furthermore, in 7-year-old stands, red maple sprouts dominated oak sprouts in site occupancy by a ratio of 3.5:1, which is a nearly exact inversion of the relative dominance of the two species prior to harvest.

Thus, the ORSPA data from stands as old as 7 years show a likely transition, occasioned by the event of stand harvest followed by regeneration, from dominance by oak to dominance by red maple. This outcome appears to be borne out by the long-term FM-T-24 data set derived from stands similar to those in the ORSPA data set. Data from third-decade stands indicate that the regeneration advantage achieved by red maple through age seven is sustained into the future, though the relative advantage diminishes by the third decade after harvest. Third-decade basal area in sprout-origin red maples alone was slightly greater than total red maple basal area in the overstory before harvest, further confirming that regeneration from stump sprouts is sufficient to recapture the growing space formerly occupied by red maple. Moreover, by the third decade, red maple regeneration had accumulated over twice as much basal area as the species had in the preharvest stands, while oak regeneration had accumulated less than half.

Although white-tailed deer browsing is an almost inescapable factor in stand regeneration under contemporary circumstances in Pennsylvania and other states, we do not consider browsing to have been a major factor in the outcome of this study. In fact, browsing (which tends to favor maple over oak) may have been an atypically minor factor in affecting the regeneration of these stands. The ORSPA stands were harvested operationally by the Pennsylvania Bureau of Forestry with no restrictions imposed by our research. Over 70% of those stands were fenced to exclude deer following harvest, and the remaining stands were not

fenced only because the supervising forester judged the local browsing pressure to be not limiting for oak regeneration. The long-term data set represents stands that originated under a higher, state-wide deer population than at present. However, by conservatively presenting data from only the 60% of stands in our database that regenerated to over 90% stocking, we have intentionally excluded a large fraction of stands where it appears that deer impacts along with other factors did indeed lead to various degrees of regeneration failure. This failure typically leads to even greater relative dominance by red maple in the new stand.

In its reproduction by both seedlings and stump sprouts, red maple achieves a distinct advantage in early site occupancy through the production of many more stems than will eventually survive to maturity. In the case of stump sprouts, the stems that fail will likely be displaced by others from the same sprout group rather than by oaks or other species. Under current regimes of land-use and forest management, sprouting behaviors alone will shift the canopy balance from oak to red maple within 7 years after harvest. The contribution of seedling regeneration, arising from the superior fecundity of red maple, further sets the stage for stand conversions to greater red maple dominance. In this respect, the stands in our study appear to mirror what is happening throughout most of the red maple range in the United States (Fei and Steiner 2007). Periodic, statewide forest inventories over the past 2 to 3 decades show that red maple has increased in importance value (relative density + relative volume) in almost every portion of its range.

A key to the reproductive success of red maple in this study was its disproportionate abundance as small trees, which contributed little to site occupancy prior to harvest but contributed greatly to sprout-origin regeneration after harvest. An abundance of small red maple trees is a range-wide phenomenon in the United States, where state by state the sapling size class (2.5–12.4 cm) accounts for 64%–95% of all trees of this species (Fei and Steiner 2007). Furthermore, successive forest inventories between 1980 and 2005 for all states in the red maple range show that the average density of this species relative to others within the region is increasing in all diameter classes (Fei and Steiner 2007). The evidence suggests that large numbers of red maples in the understory represent neither a transitory condition (i.e., a remnant and doomed cohort of small trees that failed to succeed during stand initiation) nor a permanent understory of trees incapable of reaching the canopy (Lorimer 1984). Although understory red maples may be as old as the overstory (Oliver and Stephens 1977; Tift and Fajvan 1999), it is capable of recruiting and persisting in the understory (Larsen 1953; Lorimer 1984; Cain and Shelton 1995), and suppressed red maples are capable of responding to crown release and of potentially reaching the canopy (Oliver and Stephens 1977; Lorimer 1980; Tift and Fajvan 1999). The relative density of red maple is increasing most rapidly in the sawtimber diameter classes (≥ 7.9 cm) (Fei and Steiner 2007), so it does not appear likely that this now ubiquitous species will remain largely relegated to the understory.

As discussed in the Introduction, a number of exogenous factors have plausibly strengthened red maples relative abundance as an understory tree. Among those factors, reduced frequency of fires during the past century (Lorimer

1985; Abrams 1992) seems to be most consistently associated with the red maple phenomenon. A twentieth-century decrease in the frequency of fires in oak-dominated stands, as inferred from historical data or from fire-scar frequencies in dendroecological reconstructions of old-growth stands, is often associated with a sharp increase in the recruitment of red maple and other shade-tolerant species, accompanied by a decrease in the recruitment of oak as understory light levels decline (Mikan et al. 1994; Shumway et al. 2001; Soucy et al. 2005). Furthermore, experimental applications of light ground fires can effectively discriminate against red maple regeneration in favor of oaks (Harmon 1984; Arthur et al. 1998; Hutchinson et al. 2005). Thus, widespread fire suppression during the twentieth century is likely a key factor in the modern emergence of an unprecedented abundance of shade-tolerant red maples in the understory and midcanopy strata of these stands (Abrams 1992, 1998).

We suggest that the proximal cause of the widespread increase in red maple dominance is the presence of a modern type of disturbance — logging. Others have suggested that the successional trend toward greater dominance by red maple in oak forests can be accelerated by small-scale canopy removals (Abrams and Downs 1990; Abrams and Nowacki 1992; Tift and Fajvan 1999). However, disturbance-mediated accelerated succession (Abrams and Scott 1989) does not describe the phenomenon we are reporting, which is contingent upon the sprouting capacity and fecundity of red maple rather than its ability to grow into the canopy stratum after decades of suppression. Logging does not merely accelerate stand conversion to red maple dominance by removing shade, it actively favors the regeneration of red maple over oak because of the red maple's superior capacity to sprout from dormant buds at the base of the tree and because of its vastly greater seed production. Although similar responses could occur as a result of some natural disturbances, such as windthrow, they would not occur on the same scale as a result of logging nor favor red maple to such a degree. Red maple's shade tolerance and ability to recruit and persist as a small understory tree in oak-dominated stands is a necessary, but not sufficient, condition for large-scale red maple dominance to occur. The absence of fire could be regarded as a predisposing cause, in the sense that frequent, light fires could reduce the component of red maple in small-size classes. However, it appears that harvesting will enhance the dominance of any component of red maple that is present in the stand. Harvesting clearly and directly favors red maple over oak in a manner, and to an extent, that would not have existed under natural disturbance regimes.

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