OAK REGENERATION ECOLOGY AND DYNAMICS

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Abstract—The regeneration potential of oak following a disturbance or harvest that initiates stand regeneration is determined largely by the size structure of oak before the event. Collectively, regeneration from (1) seed, (2) advance reproduction, and (3) stump sprouts contribute to oak regeneration but vary in their competitive capacity. Oak regeneration potential is modified by site, competitor regeneration potential and management input. Prescribed fire is increasingly being used to promote oak regeneration with mixed results. Oak has many silvical traits that make it well adapted to fire. Fire can promote oak regeneration, but it also can reduce it, promote competing vegetation including invasive species, and retard oak recruitment into the overstory. Fire is a tool that can be used to sustain oak forests if it is applied judiciously with knowledge of oak forest ecology and stand dynamics, and with basic forest inventory information. Combining prescribed fire with thinning or harvesting can be effective in increasing oak regeneration potential and dominance in future stands.

INTRODUCTION

After 50 years of focused study on oak forests in eastern North America, managers still struggle to regenerate oak with certainty and scientists continue to research the oak regeneration problem (Fei and others 2011, Nowacki and Abrams 2008). We have made great advances in understanding oak biology and ecology, identifying drivers of oak regeneration problems, assessing silvicultural practices to promote oak, and modeling regeneration success. We know most about the commercially valuable oak species; more work is needed to discover basic information on the great diversity of oak species present throughout eastern North America. Valuable compilations and syntheses of what we know about oak ecology and silviculture have been published, e.g., Hicks (1998), Johnson and others (2009), and McShea and Healy (2002). This paper highlights our understanding of oak regeneration ecology and management with emphasis on the role that fire may play in sustaining oak forests through regeneration and recruitment into the overstory.

IMPORTANCE OF CURRENT FOREST COMPOSITION AND STRUCTURE

In eastern North American hardwood forests, initial floristics regulates future forest composition (Egler 1954, Johnson and others 2009, Loftis 2004); it is the current composition and size distribution of all trees from seedlings to mature trees that establishes the sources of regeneration and determines the competitiveness of individuals in a stand. In the East, oaks regenerate as newly germinated seedlings from acorns, advance reproduction, and stump sprouts. The abundance of mature dominant and codominant oak trees in the overstory defines seed production potential. The same holds true for many of oak's competitors, some of whom also may accumulate seed over the years in the forest floor, e.g., black cherry (*Prunus serotina* Ehrh.) and yellow-poplar (*Liriodendron tulipifera* L.). In general, total seed production for dominant/codominant oak trees increases with increasing diameter at breast height (dbh) to a threshold size beyond which it decreases, but this varies among the species (fig. 1) (Downs and McQuilken 1944). Consequently, the density of large (>10 inches dbh) oak trees in the upper crown classes is positively correlated with the abundance of oak advance reproduction in the understory (Fei and Steiner 2008, Johnson 1992), and density of large oak advance reproduction increases with decreasing overstory density (Johnson 1992, Larsen and others 1997). For advance reproduction, individual competitiveness following release by a regeneration harvest is directly related to the size of the seedling or sapling before harvest (fig. 2) (Dey 1991, Johnson and others 2009, Loftis 1990). The size and age of trees >2 inches dbh also determines the probability of stump sprout development after harvesting, which varies among oak species and their competitors (fig. 3) (Johnson and others 2009). Because initial floristics determines future forest composition, inventories of current forest overstory and understory tree populations can be used to predict the composition of future forests and aid in developing silvicultural prescriptions for oak regeneration (e.g., Brose and others 2008, Dey and others 1996, Vickers and others 2011).

SOURCES OF OAK REGENERATION

Johnson and others (2009) recognize three types of oak regeneration: seedlings, seedling sprouts, and stump sprouts. Any reproduction regardless of type that exists

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before a regeneration harvest or disturbance is known as advance reproduction. In oak seedlings, shoot and taproot are the same age, as the shoot has not experienced dieback yet. A seedling sprout arises from the root system after death of throot;e original stem; hence, the shoot is younger than the taproot. Stump sprouts are vegetative reproduction that arise from the stump or base of stems (≥2 inches dbh) cut during harvest, removed by an herbivore, or killed by fire or drought.

Seedlings

Oak seedlings are ephemeral because they either die or experience shoot dieback and sprouting thus becoming seedling sprouts. Seedling populations are most abundant following good to heavy acorn crops. Initial seedling growth is fueled by acorn reserves in the cotyledons and survival may be high even on productive sites in the dark of a mature forest understory. But, after the first season, seedling survival and growth depend on photosynthesis. Seedling cohorts are nearly eliminated within a decade (Beck 1970, Loftis 1983, Crow 1992) due to inadequate light (<5 percent full sunlight), a common condition in the understory on high quality mesic and hydric sites (Gardiner and Yeiser 2006, Lorimer and others 1994, Lhotka and Loewenstein 2009, Motsinger and others 2010, Parker and Dey 2008). Today, it is only on xeric sites that understory light levels are high enough (e.g., 10 to 25 percent of full sunlight) to permit the accumulation and development of large oak advance reproduction in the absence of management, including periodic fire (Blizzard and others 2013, Johnson and others 2009, Sander 1979). Oak seedlings exhibit slow juvenile shoot growth because carbon is preferentially allocated to the developing root system (Johnson and others 2009). Thus, they are not competitive and are easily suppressed by other vegetation under most situations in regenerating stands.

Seedling Sprouts

Oak advance reproduction as seedling sprouts are able to persist and develop large roots and high root:shoot ratios provided there is sufficient light to support a positive growth balance. It is by the cycle of shoot dieback and sprouting over decades that oak advance reproduction increases its competitive capacity (Spetich and others 2002) by enlarging its root system, as evidenced by increasing root collar diameter and root:shoot ratios (Canadell and Rhoda 1991, Dey and Parker 1997). The probability that a stem of oak advance reproduction survives and assumes dominance in a regenerating stand increases exponentially with increasing initial basal stem diameter (fig. 2) (Dey 1991, Johnson and others 2009, Loftis 1990). However, a dense overstory and complex vertical stand structure including multiple canopy layers of shade-tolerant species reduce available light to levels insufficient for most oak species (Parker and Dey 2008, Rebbeck and others 2011). Historically, the accumulation of large oak advance reproduction was promoted by factors that limited stand density and development of mid- and understory woody canopies such as cyclical drought, periodic fires, and site factors that limit tree growth. Available light levels over 20 percent of full sunlight promote growth of oak advance reproduction (Gardiner and Hodges 1998; Gottschalk 1985, 1987, 1994; Rebbeck and others 2011). Today, this may occur naturally in mature oak forests on low quality xeric sites located on south facing steep slopes and upper slope positions (Blizzard and others 2013), but elsewhere stand structure and density must be managed to increase available light in the understory. For example, in the Missouri Ozarks, Larsen and others (1997) found that the probability of having large oak advance reproduction increased with decreasing overstory density by timber harvesting, and they suggested that basal area be kept <65 ft^2/ac to promote development of large oak advance reproduction in these oak ecosystems.

Stump Sprouts

Stump sprouts arise from cut stems that are >2 inches dbh by definition (Johnson and others 2009). They are the fastest growing source of oak reproduction and hence are the most competitive in regenerating stands. In fact, Beck and Hooper (1986), Gould and others (2003), Morrissey and others (2008), and Swaim (2013) reported that 45 to 75 percent of dominant oak reproduction in developing clearcuts were stump sprouts by the time stands reached stem exclusion (20 to 35 years old) in southern Indiana, Pennsylvania, and the southern Appalachians of North Carolina. In most of these studies, oak stocking had declined substantially from preharvest levels in the former oak-dominated forests, and it would have been relegated to minor associate status were it not for the stump sprouts. The probability of an oak stump producing a sprout varies by species, diameter, age, and site quality (fig. 3). In general, sprouting capacity increases with increasing stem diameter to a threshold (e.g., 4 to 5 inches) beyond which it declines (Dey and others 1996, Weigel and Peng 2002, Weigel and others 2011). Chestnut oak (*Quercus prinus* L.) and the red oaks [black oak (*Q. velutina* Lam.), scarlet oak (*Q. coccinea* Muenchh.), northern red oak (*Q. rubra* L.)] have higher sprouting capacity and are more competitive than white oak (*Q. alba* L.). Sprouting capacity in oaks declines with increasing tree ages older than 50 years, and trees that are 100 years old have low potential to produce sprouts, regardless of species. Initially, oak stump sprouting potential increases with increasing site quality, but over time site quality has a negative correlation with oak sprout dominance probabilities because the intensity of competition is higher on productive sites. It is unlikely that oak stump sprout reproduction alone can maintain initial stocking levels in mature oak forests when they are regenerated because not all oak stumps produce sprouts, and some produce sprouts of low vigor. Therefore, the mantra of oak silviculture has become that success in sustaining oak stocking is reliant upon having adequate numbers of large oak advance reproduction (Clark and Watt 1971, Johnson and others 2009). Oak stump sprouts are important contributors to future oak stocking, but advance reproduction must be competitive to sustain stocking. This in essence is the crux of the oak regeneration problem; oak advance reproduction either is absent or is small with low competitive capacity in most of our eastern forests on higher quality sites. The problem is magnified as we try to regenerate our aging oak forests that are experiencing a decline in their stump sprouting capacity with concurrent development of shade tolerant midstory and understory canopies.

FIRE IN THE LIFE CYCLE OF OAK

Fire has long been associated with the widespread dominance of oak over the millennia in the East (e.g., Delcourt and Delcourt 1998, Delcourt and others 1998), and oak has numerous traits (e.g., thick bark and high vegetative sprouting ability) and reproductive strategies (e.g., seed caching in soil by animals, root-centric growth, accumulation of large advance reproduction) that favor it when the disturbance regime includes frequent fire. But prescribed burning alone has not always promoted oak regeneration (Brose and others 2013). Arthur and others (2012) identified stages of stand development and conditions in which fire may promote oak regeneration and recruitment into the overstory in their life cycle analysis of an oak forest. Brose and others (2008, 2013) have developed silvicultural prescriptions for oak regeneration using prescribed burning. There are times in the life of an oak forest when prescribed fire may benefit oak regeneration, and certain stand conditions that normally inhibit oak establishment and development that can be corrected by burning.

Preparing for and Establishing Oak Advance Reproduction

Regenerating a mature oak forest is a common objective for managers in the East, and often there is little to no oak advance reproduction. Burning is recommended to prepare the site for the next good acorn crop. In the absence of fire, litter layers may have accumulated to depths that create a barrier to the oak germinant rooting itself in soil. Low-intensity dormant-season fires are effective for reducing litter and facilitating oak seedling establishment. Reductions in leaf litter may persist for several years, but litter accumulates rapidly to pre-burn levels (Stambaugh and others 2006), which may necessitate a second burn in the absence of a good acorn crop. Fire can also destroy seed of competing species that is stored in the forest floor, but it may also stimulate the germination of seed that has thermal- or chemical-induced dormancy. However, new germinants and young seedlings of competing species arising after the initial fire are vulnerable to mortality in subsequent fires, and their growth will be suppressed under a fully stocked mature overstory. A final benefit of a low-intensity fire at this time is to increase understory light in advance of oak seedling establishment. Such a fire has little effect on overstory density but can reduce or eliminate the midstory canopy (if trees are predominantly <4 inches dbh) and increase understory light to about 10 to 15 percent of full sunlight (Dey and Hartman 2005, Green and others 2010, Lorimer and others 1994, Motsinger and others 2010, Waldrop and others 1992). The positive effect of midstory removal may last for several years (Parrott and others 2012), and maintaining an intact overstory canopy inhibits regrowth of competing tree and shrub sprouts (Dey and Hartman 2005). However, oak advance reproduction benefits from additional increases in light, and to achieve light levels >20 percent of full sunlight requires greater reductions in stand density. To affect this through prescribed burning requires more intense fires capable of killing larger trees, but this increases the risk of causing mortality of oak advance reproduction. Alternatively, chemical and mechanical thinning and harvesting can be used to more selectively remove trees, reduce mortality of oak advance reproduction, and in the case of chemical applications, limit sprouting of competitors. The need and timing of additional prescribed fires preceding a good acorn crop will be dictated by litter accumulation rates and regrowth of competing vegetation after the initial burn. But once acorns are on the ground, fire should be delayed or else most of the crop will be destroyed (Auchmoody and Smith 1993).

Promoting Oak Advance Reproduction

Another common condition in mature oak forests is for there to be thousands of small oak advance reproduction per acre. Burning these forests may be detrimental to oak regeneration because low intensity fires are capable of killing a high proportion of one-year-old oak seedlings (>50 percent) (Johnson 1974). In deciding to burn, consideration should be given to the number and size of oak advance reproduction. Size is an indication of the probability that a stem will survive a fire by sprouting, which increases exponentially with increasing basal diameter of oak seedlings. In general, oaks are better able to survive multiple fires than their competitors by sprouting and increasing root mass during fire-free periods under higher light regimes provided by midstory removal and random canopy gap formation (Brose and others 2013, Dey and Hartman 2005). But greater growth gains in oak advance reproduction are achieved when reproduction are growing in moderate to open light environments (i.e., >30 percent of full sunlight) (Gardiner and Hodges 1998; Gottschalk 1985, 1987, 1994). Benefits to oak advance reproduction when burning in mature oak forests are variable, and sometimes questionable according to studies conducted across eastern North America (Brose and others 2013). This is most likely due to the differences in initial size structure of advance reproduction for oak and its competitors, fire behavior, stand density, and presence of confounding factors such as deer (*Odocoileus virginianus* Zimmerman) browsing and competition from interference species such as hay-scented fern (*Dennstaedtia punctilobula* (Michx.) Moore). Fire effects can be more negative when oak seedlings are small (e.g., <0.25 inches basal diameter), fire intensity is moderate to high, and fires occur in a season when seedling physiological activity is on the rise. Low survival probabilities for small oak advance reproduction after burning may be offset by high densities, but it is less risky to use other means such as midstory removal by chemical or mechanical methods, or shelterwood harvesting to develop larger oak advance reproduction by increasing available light in the understory before burning.

Combining fire with thinning or harvesting is promising for developing larger oak advance reproduction. Hutchinson and others (2012) reported that multiple fires (three to five) beginning seven years before harvesting by the group selection method and ending in some cases a year or two after harvesting promoted the development of large white oak reproduction in southern Ohio. Brose and others (2013) recommended using the shelterwood method to increase light to oak advance reproduction and promote growth of small seedling sprouts before burning. Simply reducing stand density benefits oak advance reproduction for several years before the competition in the regeneration layer begins suppressing oak growth. During this time, oak advance reproduction seedlings are able to grow larger and increase their root mass (Brose 2008), thus increasing their probability of vigorously sprouting after a prescribed fire. If needed, prescribed fire may be used between the initial and final shelterwood harvest to release oak advance reproduction from encroaching competing vegetation that has also benefitted from improved light conditions. Alternatively, oak can be provided a second release by removal of the residual overstory. Several years after oak reproduction has been released by final overstory removal, fire can be used to favor oak development and dominance by periodically (e.g., every three to five years) setting back competing vegetation. This sequence may be repeated until the oak reproduction is capable of maintaining its dominance on its own.

Oak Recruitment into the Overstory

To sustain oak forests, the second most important process after regeneration is recruitment of oak saplings into the overstory (Dey 2014). Oaks eventually need a sufficiently long fire-free period to allow them to grow into the overstory by developing thick bark to resist topkill from any future fires. This may take 10 to 30 years to develop depending on source of oak regeneration, i.e., stump sprouts versus seedlings sprouts (Arthur and others 2012). Oaks that are in the dominant canopy position at the beginning of the stem exclusion stage have a high probability (>75 percent) of maintaining their dominance into maturity (Ward and Stephens 1994), but less dominant oaks have a high rate of attrition due to competition. Without release as saplings in the stem exclusion stage, oaks can be suppressed by yellow-poplar, red maple (*Acer rubrum* L.), black cherry and black birch (*Betual lenta* L.) (Brashears and others 2004, Groninger and Long 2008, Heiligmann and others 1985, Smith and Ashton 1993, Zenner and others 2012). Dominant oaks primarily remain at the end of stem exclusion; these are largely stump sprouts, especially on average and higher quality sites (Hilt 1985, Morrissey and others 2008, Zenner and others 2012). On xeric, lower quality sites, oaks are naturally more competitive and can rise to dominate stand basal area and volume at maturity. Crop tree release of codominant and lesser oak saplings early in the stem exclusion stage can significantly increase their persistence as dominants at maturity (Ward 2009, 2013). Fire is an ineffective tool for releasing oak saplings because it is indiscriminate in what trees are topkilled in the smaller diameter classes (<4 inches dbh); it may take out a smaller diameter oak as easily as a competitor. Fire's ability to topkill competing stems decreases as tree diameter increases, even for what are considered fire-sensitive trees. Hotter fires are needed to topkill larger trees of competing species and this increases the chances of removing oak saplings in the process. Prescribed burning affords little control over the spatial distribution of what trees are removed and hence the degree of release experienced by any individual oak. Fire may also scar residual trees, which has the potential to cause advanced decay in the butt log over decades if the wound does not heal rapidly (Marschall and others 2014). Alternative chemical and mechanical methods of crop tree release provide more control and certainty in releasing oak saplings and small poles.

CONCLUSION

Oak regeneration potential is a function of the collective contributions to future stand stocking from the main sources of oak regeneration, i.e., seed/seedlings, seedling sprouts (advance reproduction), and stump sprouts. The extent that oak regeneration potential contributes to stand regeneration potential determines if oak will dominate in the future after regeneration. Stump sprouts are no doubt the most competitive sources of oak regeneration and often comprise the majority of dominant oak in young stands following regeneration by even-aged methods. However, this in and of itself is an indictment of the failure of oak advance reproduction to contribute significantly to sustaining oak stocking in the future. Without contributions from oak advance reproduction, oak stocking will continue to decline through the generations. The focus of oak silviculture research has been the establishment and development of adequate densities of large, competitive oak advance reproduction. The shelterwood regeneration method has figured prominently in approaches to improve oak regeneration potential by increasing the role advance reproduction play in determining oak's future dominance. But midstory removal and the group selection method have also proven to enhance development of oak advance reproduction in conjunction with prescribed burning. Controlling competing vegetation before, during and after regeneration harvesting is an important, and sometimes overlooked, aspect of oak regeneration prescriptions. Prescribed fire is an effective tool to prepare the site for establishment of oak reproduction and to begin reducing competition and the regeneration potential of competing species. Care must be taken in determining the timing of prescribed burning to avoid destroying acorn crops or populations of small oak advance reproduction. After final overstory release, prescribed fire is effective in promoting oak dominance during stand initiation until the beginning of the stem exclusion stage. From this time until the next need for regeneration, the use of fire is problematic because it is a clumsy method for controlling stand density, composition, and spatial arrangement of trees, and because it can injure trees, which later leads to substantial loss of volume and value. Prescribed fire is another arrow in the quiver of the silviculturist who manages oak ecosystems.

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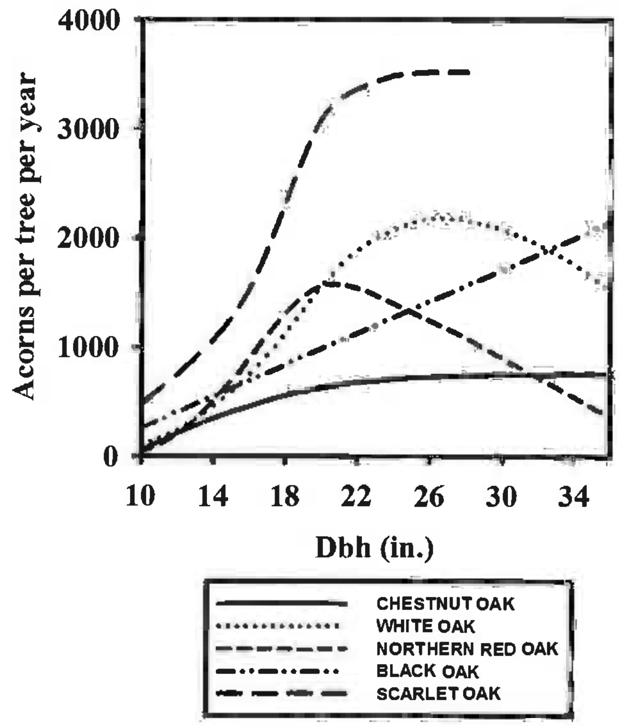

Figure 1—Average annual acorn production based on seven years of observations for five common oak species in eastern North America (adapted from Downs and McQuilken 1944).

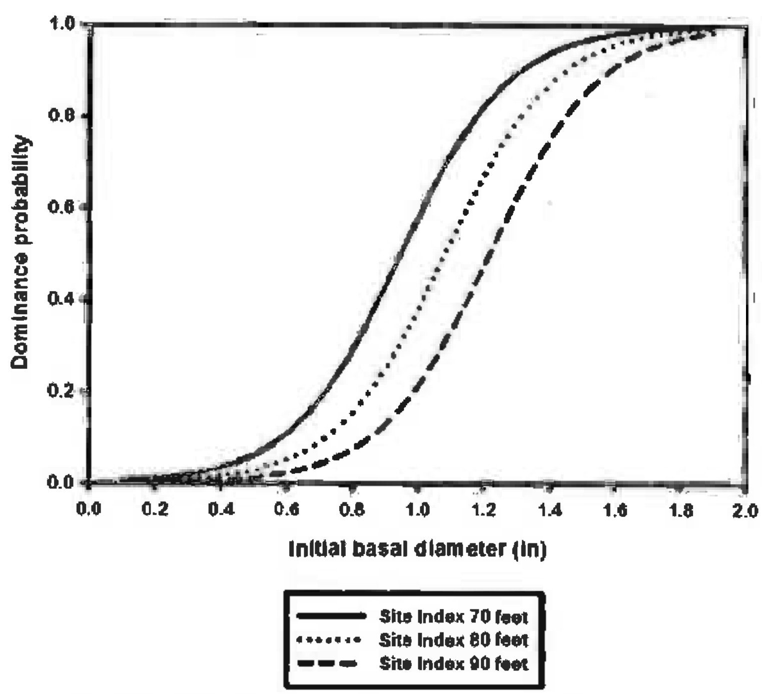

Figure 2—Probability of northern red oak advance reproduction becoming dominant/codominant stems eight years after clearcutting on various quality oak sites in the southern Appalachian Mountains (adapted from Loftis 1990).

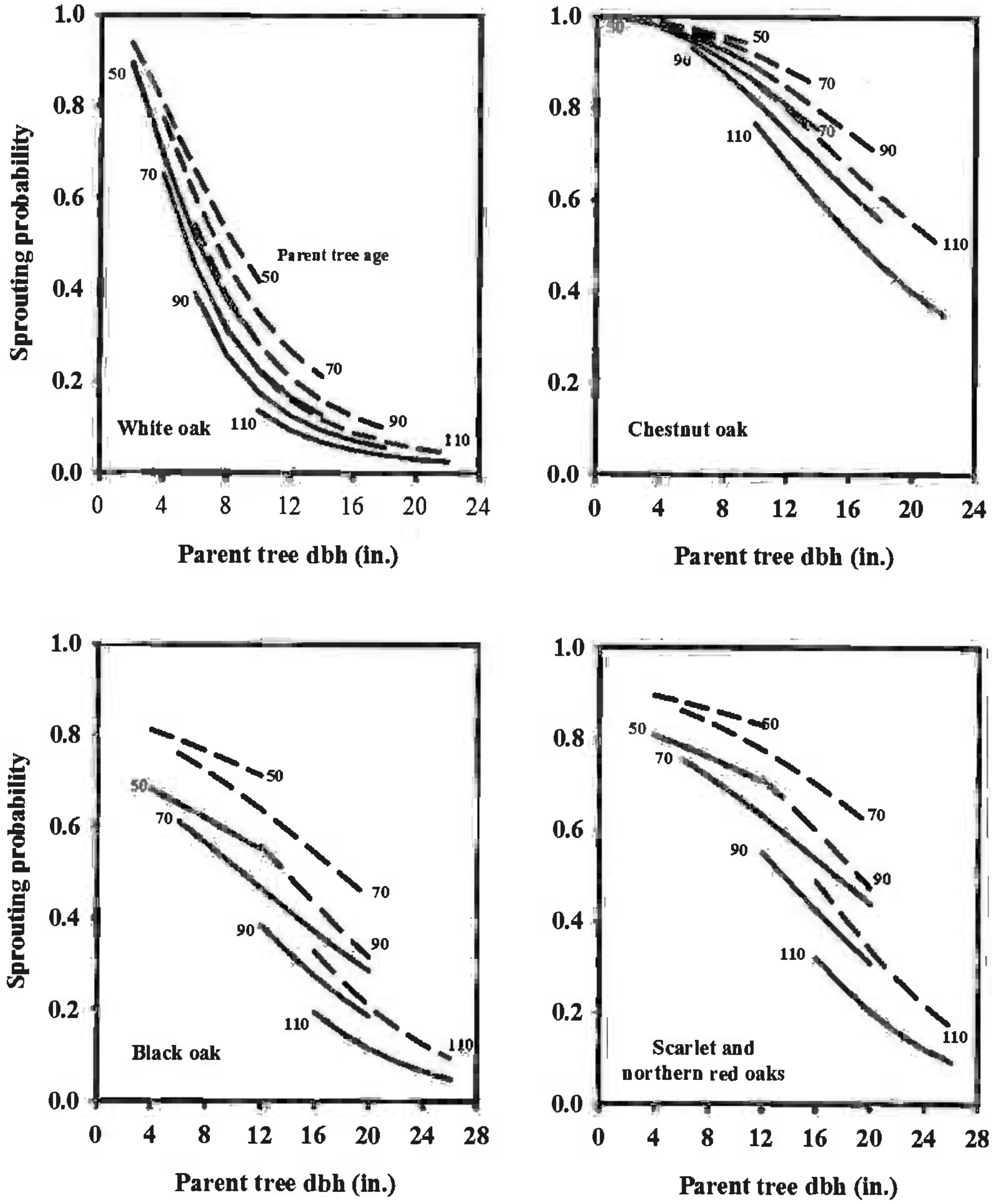

Figure 3—Probability that an oak will have at least one live sprout one year after harvest cutting in clearcuts of southern Indiana based on species, initial diameter breast height, tree age, and site quality (solid line = 59' oak site index, dashed line = 72' oak site index) (adapted from Weigel and Peng 2002).