THINKING ABOUT OAK FORESTS AS RESPONSIVE ECOSYSTEMS

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Abstract—Like all forests, oak forests are continually responding to disturbances originating from both within and outside the forest. Oaks (*Quercus* spp.) owe their very existence to disturbance. In this context, silvicultural and other management practices can be thought of as planned disturbances designed to direct forest change in specific ways. The internally (endogenously) controlled stages of stand development provide a useful framework for anticipating such changes together with an understanding of how external (exogenous) forces can further modify such changes.

INTRODUCTION

Because forests are "open systems," they are continually responding to forces originating from both within and outside the forest itself. Unlike a tree seedling in a growth chamber with precisely fixed growth conditions, trees and other organisms in a forest must continually adjust to changing conditions, many of which are unknown or only occur probabilistically. The list of factors that can change are indeterminate, i.e., they are so numerous and often unknown that we are unable to list all of them even for a single acre of forest. They include both physical and biological factors. Some factors produce effects that are sudden and result in major changes, while others operate more slowly and subtly. The only constant is the forest's continual response to relentless change.

TYPES OF RESPONSES

All forests respond to external (exogenous) and internal (endogenous) forces. Exogenous forces include, but are not limited to, wind, fire, insects, tree diseases, and human activity. Endogenous forces include crown closure, tree growth, tree mortality and associated self-thinning, and changes in species composition. In all cases, the forest "responds" to internally or externally induced changes. Because these changes are endless, an oak forest or savanna is therefore never "finished"–whether it is the product of human endeavor or of exclusively "natural" processes. Human activity, from an ecological and historical perspective, represents only one of the many forces that influence forests. Moreover, silvicultural and ecological restoration projects may not always produce their intended results. Forests are in effect "equal opportunity" responders to whatever forces and events come their way. We nevertheless need not be working blindly in achieving management goals. On the contrary, the manager can capitalize on a wealth of information on how oak forests respond to endogenously and exogenously caused changes.

Endogenous Change in Even-aged Oak Stands

Even-aged stands usually originate from sudden large-scale disturbances, natural or human-caused, that destroy all or most of the overstory of the previous stand. An even-aged stand thus consists of a group of trees comprising a single age class. This usually means that tree ages differ by no more than about 20 years.

Even-aged stands progress through a relatively predictable series of developmental stages until the next stand-initiating disturbance or some other severe disturbance occurs. These stages result from the internal dynamic of the stand itself. Defining these stages is useful in understanding the development of oak forests even though the duration of each stage and the accompanying changes in stand structure, density, and species composition may differ from stand to stand.

Although various terms have been used to define the stages of stand development, it is convenient here to follow the terminology of Oliver and Larson (1996) as modified by Oliver (1997). They defined four stages: (1) the stand initiation stage, (2) the stem exclusion stage, (3) the understory reinitiation stage, and (4) the complex stage (fig. 1). The complex stage of development also has been called the old-growth stage (Oliver 1981). These stages and their definitions provide a convenient conceptual framework for anticipating the inevitable changes in the ecological states that occur in oak forests.

The stand initiation stage—The development of an even-aged stand begins with the stand initiation stage (fig. 1). This stage typically lasts about 20 years in eastern oak forests. A brushy mass of woody vegetation comprised of thousands of trees and shrubs per acre, usually mixed with a luxuriant growth of vines and herbaceous plants characterizes this stage. It is a period of rapid change with intense competition among trees and other plants for growing space. Standing biomass is small relative to later stages of development, but the rate of biomass increase is high. During this stage, the quantity of dead biomass is often larger than during other stages of stand development. This results from the stand-initiating disturbance itself, which except when preceded by fire, usually leaves a large residue of tree boles and branches on the forest floor.

During the stand initiation stage, gaps in the new vegetative cover may persist for a decade or longer while new trees and other vegetation become established. New tree seedlings and herbaceous vegetation initially require little growing space. During this stage there are numerous microenvironments where seeds find the necessary conditions for germination and growth free from predators, competitors, and pathogens. Changes in the number, species, and size

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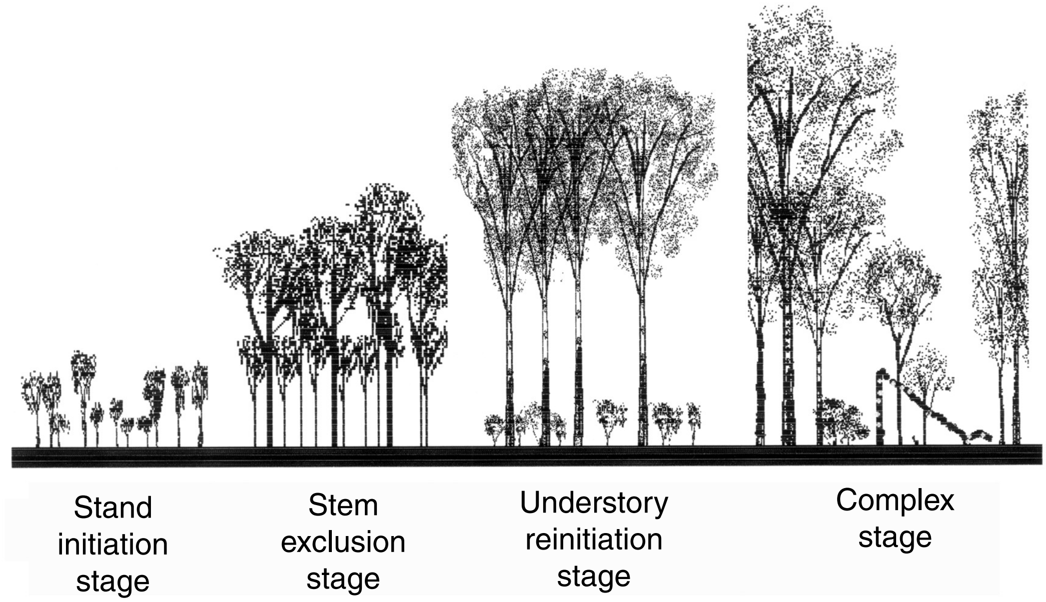

Figure 1—Stages of stand development occurring after a major disturbance that destroys all or most of the parent stand (from Johnson and others 2002).

of trees during the stand initiation stage are difficult to accurately predict. This is due to numerous essentially random events that influence the timing and spatial distribution of seed dispersal, germination, and seedling survival. Stand development during this period is subject to great natural variation, and predictions of stand development during this stage are usually only specifiable probabilistically (Dey and others 1996a, Johnson and others 2002). Future stand composition is heavily dependent on the amount and size of tree reproduction that is pre-established (i.e., occurring in "advance" of) the time of disturbance. Whether oaks are successful in attaining dominance during this stage largely depends on the number and size of oak seedlings and seedling sprouts present at the time of disturbance. In turn, this largely depends on site quality, the occurrence of prior disturbances such as fire or windthrow, or the natural development of overstory canopy gaps. Site quality combined with natural or silviculturally reduced stand densities during the stand initiation stage are closely connected to conditions that favor the development and accumulation of oak reproduction under the parent stand. This accumulation is more persistent on the poorer sites and where canopy closure is incomplete (Johnson and others 2002). Under those conditions, some of the oak reproduction can grow to a large size (fig. 2). When large advance oak reproduction is released from the inhibiting effect of the parent stand overstory it responds by producing one or more long flushes of terminal shoot growth in a single growing season (Johnson 1979, Johnson and others 2002). In turn, this imparts an initial growth advantage to the relatively shade-intolerant oaks.

The species composition of trees during the initiation stage is continually responding to the growth and maturation of the stand. Early theories of forest succession proposed that each species modifies the site to make it more favorable for the establishment and growth of succeeding species.

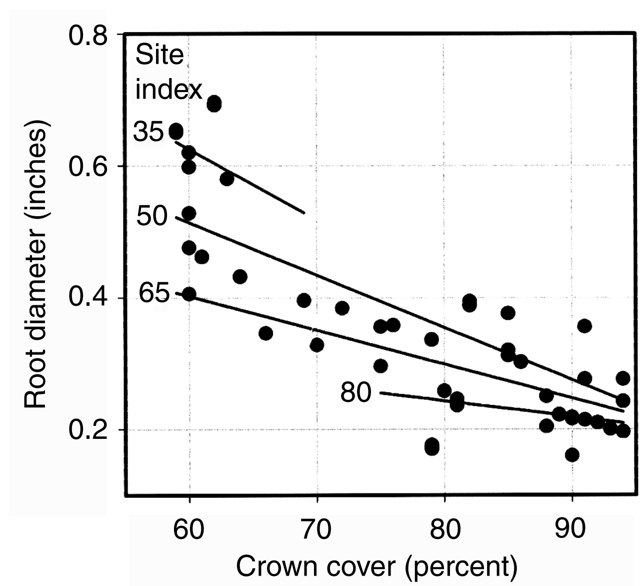

Figure 2—Diameters of roots of oak reproduction measured just below the root collar in relation to overstory crown cover and site index in West Virginia forests. The estimates represent the average of the scarlet, black, white, northern red and chestnut (*Quercus prinus* L.) oaks sampled. Estimates are based on a linear regression model that includes slope percent as a predictor; for this graph slope percent is held constant at 25. Each data point represents 7 to 10 trees (adapted from Matney 1974).

However, the actual processes can vary widely among the different types of oak forests. For example, in the Ozark Highlands of Missouri, the major tree species present at the time of disturbance become quickly stratified into crown classes through a process that could be described as competitive sorting. By the end of this stage, the initially abundant and ubiquitous sassafras (*Sassafras albidum*

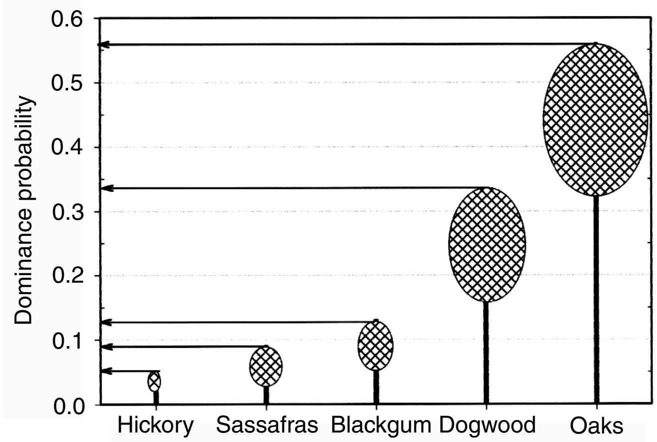

Figure 3—Dominance probabilities for advance reproduction (seedlings and seedling sprouts) of different species in the Ozark Highlands of Missouri. Dominance probability is defined here as the probability that advance reproduction of a given initial size will attain an intermediate-or-larger crown class 21 years after clearcutting. For each species, probabilities are for 6-foot-tall advance reproduction with 1-inch basal diameters growing on southeast- or northwest-facing mid-slopes. Probabilities differ by aspect and slope position. The five species groups shown are the predominant hardwoods occurring within this ecoregion. Probabilities were generated by the regeneration model *ACORn* (Dey and others 1996b).

(Nutt.) Nees), flowering dogwood (*Cornus florida* L.), blackgum (*Nyssa sylvatica* Marsh.), and hickories (*Carya* spp.) are largely relegated to the inferior crown classes. Black oak (*Quercus velutina* Lam.), white oak (*Q. alba* L.), scarlet oak (*Q. coccinea* Muenchh.) and other oaks by then usually predominate in the dominant and codominant crown classes. This competitive sorting process is reflected in each species' probability of attaining dominance. For a given species, this probability depends on a tree's size at the time of the stand initiating disturbance and site factors (fig. 3).

During the next two stages of stand development, few if any new trees are added to the overstory. Consequently, the composition of an even-aged stand at the end of the stand initiation stage is a good indicator of the species' richness of the future overstory. However, a species' relative abundance at this stage is often a poor indicator of its future importance. During the ensuing stem exclusion stage, species composition usually shifts toward the species that are best adapted to the site and able to attain and hold dominant or codominant crown positions. Dominance by oaks at the end of the stand initiation stage therefore does not always assure their continued dominance. The longer-term outcome varies among the many different types or classes of oak forests, and is often implicit in ecological classification systems (Johnson and others 2002).

The stem exclusion stage—In oak forests of the Eastern United States, crown closure is usually complete by the beginning of the second decade after a stand-initiating disturbance. By that time, trees have stratified into well-defined crown classes and natural mortality has changed the initially clumped spatial distribution of trees to a more random distribution (Rogers 1983). This stage of stand development is termed the stem exclusion stage because few, if any, new stems are added to the population of overstory trees (Oliver and Larson 1996). Mortality rates are high, especially among trees in intermediate and suppressed crown classes. The combined growth, competition, and mortality of trees during this stage produce spatial adjustments in the main canopy that maintain full utilization of growing space. It is usually not until after the stem exclusion stage begins that predictive growth and yield models are applicable. During this and subsequent stages, patterns of stand development and changes in species composition are more predictable than during the stand initiation stage.

If oaks are to maintain a position of dominance at this stage of development, they must outgrow their competitors. Oaks do this in three ways: (1) through inherently faster growth, (2) through an initially superior crown position, or (3) through greater persistence than their competitors. On some sites in the Ohio Valley, persistence may allow oaks to survive when other faster-growing species such as yellow-poplar (*Liriodendron tulipifera* L.) or red maple (*Acer rubrum* L.) succumb to drought (Hilt 1985). Persistence also may allow more oaks than other species to survive fires, or permit oaks to eventually grow taller than species of inherently small stature such as flowering dogwood, which may temporarily overtop the oaks.

As an even-aged stand matures, its diameter frequency distribution continually changes. For example, in 10-year-old upland oak stands of the eastern United States, diameter distributions form reverse J-shaped curves comprised of thousands of trees per acre. However, in the absence of exogenous disturbance, this diameter distribution may progressively transform itself into a bell-shaped diameter distribution comprised of few hundred trees per acre by the time the stand reaches a mean diameter of 8 inches in diameter at breast height (d.b.h.) (Schnur 1937). On sites of average quality, this occurs at approximately stand age 85, which is well into the understory reinitiation stage of development. In the absence of exogenous disturbance, numbers of trees decline with time through the process of self-thinning (Johnson and others 2002). During the stem exclusion stage, about 80 percent of trees die from crowding during self-thinning on average sites (Schnur 1937). Where markets for small trees exist, thinning stands during the stem exclusion stage thus can utilize many trees that would otherwise die from self-thinning. Moreover, the retained trees accelerate their growth in response to crown expansion, which in turn is facilitated by the increase in growing space available to them. Thinning during this stage also can be used to control species composition and the quality of future final crop trees.

When oak forests are subject to recurrent low-intensity disturbances (as in oak savannas maintained by periodic burning) they may not pass through the stem exclusion stage. In oak savannas, periodic burning maintains a relatively open overstory, which in turn maintains relatively high light intensities in the understory. Although the reproduction of oaks and other species is usually abundant under these conditions, its recruitment into the overstory is inhibited by recurrent topkill of reproduction unless there is a fire-free period of sufficient duration. Under these conditions, growth of oak reproduction into the overstory is limited more by the disturbance regime than by insufficient light. The fire-tolerant oak reproduction nevertheless responds to this disturbance regime by slowly accumulating beneath the savanna understory.

The understory reinitiation stage—During the understory reinitiation stage, tree reproduction becomes reestablished beneath the parent stand (fig. 1). In oak forests, this reproduction often becomes a major component of the new stand that develops after the next stand-initiating disturbance. Many factors influence which species become established in the understory and consequently which species are likely to dominate after a stand-initiating disturbance. In oak forests, light and soil moisture rank among the most important of these factors. This is also the stage of stand development when oak forests usually attain economic maturity. Consequently, it is a critical period in the development of an oak stand silviculturally. The reproduction that becomes established (naturally or by human design) largely determines future stand composition.

Compared to the stem exclusion stage, trees in the main canopy are larger and fewer in number during the understory reinitiation stage. At this stage of stand development, some main canopy trees periodically produce large quantities of seed. Large crowns are important determinants of acorn production and thus the establishment of oak seedlings and the availability of acorns to wildlife. Moreover, when large trees die they create larger canopy openings than those created during earlier stages of stand development. The crowns of large main canopy trees also expand more slowly than they did during earlier stages of stand development. Consequently, canopy gaps remain open for longer periods, and this often results in light intensities near the forest floor sufficient for seedling establishment and growth. The resultant spatial heterogeneity of the main canopy creates spatial variation in the amount of light that reaches the forest floor. This produces microenvironments favorable for the establishment of oak reproduction that can develop large root systems, which in turn are correlated with rapid height growth. Established trees in subordinate crown positions also benefit from the increased growing space when an overstory tree dies and creates a canopy opening.

The successional replacement of oaks by more-shade tolerant species is one of the most pervasive problems associated with oak silviculture on highly productive sites. The understory reinitiation stage is therefore a critical time for intervening silviculturally if the objective is to maintain or increase the proportion of oak in the future stand. However, not all oak forests are successional to non-oaks. In the Ozark Highlands of Missouri and similar dry oak forests in the Eastern United States, the successional displacement of oaks is limited by the inability of other hardwoods to persist in the superior crown classes. Although non-oaks may aggressively fill canopy gaps immediately after disturbance, their occurrence as canopy dominants is usually ephemeral. This limitation to persist as a canopy dominant is determined by each species' life-history, stature, and physiological responses to site conditions. Regardless of the spatial scale of disturbance, the non-oak hardwoods rapidly drop out of the stand or assume a subordinate canopy position as competition intensifies with crown closure (Dey and others 1996a).

Differential dropout rates among species are reflected in their probabilities of attaining an intermediate-or-better crown class after clearcutting. For a given initial (preharvest) basal diameter, these probabilities are higher for oaks than for other hardwoods 15 years after cutting. By that time, oaks dominate stands and species are stratified into well-defined crown classes. This outcome is the result of the collective influence of initial floristics, overstory inhibition, and competitive sorting processes that control secondary succession in oak-dominated ecosystems such as the Ozark Highlands and elsewhere where oak reproduction naturally (intrinsically) accumulates.

Reverse J-shaped diameter distributions are most often associated with uneven-aged forests, but they also occur in certain even-aged forests—including those beyond the stem exclusion stage of development. These stands often originate following the disturbance of stands comprised of both shade-tolerant and shade-intolerant species. In subsequent stages of stand development, reverse J-shaped diameter distributions may evolve through the recruitment of shade tolerant reproduction into the overstory. Meanwhile, the less tolerant oaks may develop a bell-shaped diameter distribution (Johnson and others 2002).

The complex stage—In the absence of timber harvesting or other exogenous disturbances that eliminate the overstory, even-aged stands progress toward the complex stage (Oliver 1997). During this stage, the natural mortality of large overstory trees creates canopy gaps, which occur irregularly in time and space. Gap size is typically equal to the crown area of one tree or a small cluster of trees. Because these gaps are relatively large, crown expansion of trees adjacent to a gap is insufficient to fill the gap. This lag in crown closure allows subcanopy trees and established reproduction to increase height growth and crown expansion to fill the canopy gap. As new canopy gaps occur, they are filled by new age classes of trees. If this gap-filling process continues in the absence of a stand-initiating event, an uneven-aged stand eventually evolves.

The complex stage of stand development includes old-growth forests, and Oliver and Larson (1996) originally termed this stage the old-growth stage. However, there is a basis for distinguishing between the two. All old-growth forests are complex, but not all complex forests are old-growth. Definitions of old-growth oak forests are usually based on overstory age, stand disturbance history, and structural characteristics such as the presence of old trees, snags, and down wood. The various definitions of old-growth all assume that human impact on forest development has been minimal. However, older second-growth forests (managed and unmanaged) may have complex structures that do not meet the strict definition of old-growth.

The Development of Uneven-aged Oak Stands

As even-aged stands advance toward the complex stage of development, trees initially comprising a single age class gradually evolve into a multi-aged population as a result of the successional processes accompanying stand maturation and gap formation and filling. As stands mature, canopy gaps become more numerous until the forest forms a mosaic of old trees and gaps filled with younger trees of various ages. As reproduction within gaps captures growing space, stand-wide diameter distributions gradually change. In the absence of a stand-initiating disturbance, the diameter distribution may change from bell-shaped to reverse J-shaped. Regardless of the shape of the diameter distribution, the normal evolution of stand structure from even- to uneven-aged eventually produces an uneven-aged collection of highly dispersed, even-aged groups of trees, each occupying a relatively small area. Eventually, the various tree age classes become visually indiscernible.

Although the overall diameter frequency distributions of old-growth forests containing oaks often form a reverse-J shape, the diameters of the oaks themselves may not conform to that distribution. The way a stand evolves structurally and compositionally largely depends on differences in the rates at which co-occurring species of tree reproduction are recruited into the overstory. Where non-oaks fill most of the canopy gaps created during the complex stage, those species will predominate among the smaller trees (e.g., the left tail of a reverse-J diameter distribution). Depending on the interaction of site factors with the biological characteristics of the non-oaks, the oaks may or may not ascend to dominance. The competitive capacity of the oaks largely depends on site quality and correlatively the tree species they are competing with. In the more productive oak forests, a bell-shaped diameter distribution of oaks embedded within an overall reverse J-shaped distribution reveals an oak population doomed to displacement by other species. A bell-shaped distribution for any given species reflects its failure to grow into the overstory. Oaks often lose this successional race to other long-lived species that are better adapted to establishment and survival under shade (e.g., sugar maple (*Acer saccharum* Marsh.)). Bell-shaped oak diameter distributions thus are harbingers of the oak's replacement unless there are disturbances that specifically favor oak regeneration.

In the Ozark Highlands of Missouri, crown stratification among the oaks persists into the complex stage (Shifley and others 1995). There, oaks are usually not successionally displaced by other tree species and the relative permanence of oaks is reflected by their relatively high abundance in the smaller diameter classes, even in old-growth stands. In mature, relatively undisturbed second-growth forests, the diameter frequency distributions of the oaks tend to peak in the smaller diameter classes. In these stands the diameter distributions of oaks approach the reverse-J shape characteristic of all-aged stands. Diameter distributions of all species combined (including non-oaks) clearly have a reverse J-shaped form because the smaller diameter classes are comprised of relatively large numbers of shade-tolerant species such as flowering dogwood and blackgum. However in that region, the predominant subcanopy species are largely relegated to the subcanopy (Dey and others 1996a). The relative permanence of the oaks is indicated by the persistence of diameter distributions that, under natural conditions, often approach a reverse-J shape. However, specific characteristics of diameter distributions in this ecosystem, and their natural occurrence and silvicultural maintenance, depend on species composition and stand density (Larsen and others 1999, Loewenstein and others 2000).

Exogenous Forces and Disturbance-Recovery Cycles

When forest disturbance is limited to gap-scale events, stand development follows the normal sequence (fig. 1). However, stand-initiating events that eliminate all or most of the overstory can occur during any stage of stand development. These events return stands to the stand initiation stage of development. In contrast, smaller-scale (incomplete stand-scale disturbances) may eliminate only a portion of the overstory and leave significant numbers of trees standing. Although incomplete stand-scale disturbances change the stage of stand development, they do not return the stand to the stand initiation stage. Rather, they create a mixed stage of stand development. Mixed-stage stands resulting from natural events often form mosaics of younger trees developing in large canopy openings interspersed with patches of older trees. They often form irregularly spaced tree populations of variable size and age structure. Mixed-stage stands also can result from various types of timber harvesting.

Stands in the mixed stage of development are distinguishable from stands in other stages by: (1) the spatial scale of disturbance, which is greater than gap-scale, and (2) stand density, which is often below average maximum density. Relatively young trees also may dominate mixed stage stands. Low density, highly disturbed stands of all descriptions therefore fall into the mixed stage of development. Examples of stands in the mixed stage include oak savannas, stands resulting from indiscriminate timber harvests, and some silvicultural practices. The latter include heavily thinned stands, shelterwoods, and some stands managed by group selection or single-tree selection cut to low or moderate densities. Oak forests in the mixed stage of development are ubiquitous because the exogenous forces that create them are so common.

The complete spectrum of forest developmental stages thus includes the mixed stage plus the four stages previously defined. Collectively they represent points in a potentially endless series of disturbance-recovery cycles initiated by stand-scale and gap-scale disturbances. These cycles follow specific sequences determined by the developmental stage of the stand at the time of disturbance and the type and spatial scale of disturbance. Disturbance and recovery cycles provide a conceptual framework for ecological process and silvicultural practice. However, control of stand composition and structure is often complicated by unpredictable natural disturbance events that often lie beyond the direct control of the forest manager. Even when forests are intensively managed, unplanned and unwelcome disturbances are a part of management reality.

Frequent stand-initiating disturbances can maintain a forest in the stand initiation stage indefinitely. Such disturbance regimes were common and extensive in many regions of North America before European settlement. For example, in the prairie-forest border region of southwestern Wisconsin, plant communities described as “oak scrub” failed to develop beyond the sapling stage because of frequent wildfires that persisted for centuries (Grimm 1984). As long as frequent fires occurred, the stands of oak scrub persisted. The fires arrested succession, and thus maintained stands in the stand initiation stage of development. But by the early twentieth century, wildfires were largely controlled and region-wide the oak scrubs quickly responded by developing into closed canopy forests so common in that region today (Curtis 1959).

SUMMARY AND CONCLUSIONS

A panoply of events and processes, predictable and unpredictable, represent the reality of managing oak forests. Our current management models are based largely on the sequence of changes occurring during the initiation stage through the reinitiation stage of stand development—with and without timber harvesting or other management practices. Superimposed on those changes are a myriad of possible unplanned exogenous disturbances that can abruptly redirect forest development at any time. Moreover, rapidly emerging interests include managing for old growth, wildlife and acorn production, biodiversity, various aesthetic values, and restoring savannas and the other historical plant communities associated with the oaks. A common denominator to all of these issues is the regeneration of oak forests, which ultimately determines the sustainability of the oaks for whatever end. However, the controlling ecological processes for all of these problems differ greatly among the various kinds of plant communities dominated by oaks. Understanding the likely responses of such communities to both endogenous and exogenous forces is central to formulating effective management practices and thus to minimizing unintended consequences.

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