



## Linkages between silviculture and ecology: examination of several important conceptual models

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### Abstract

Responses to most silvicultural practices result from their influence on the amount of resources potentially available for growth, the ability of crop trees to acquire those resources, and the distribution of resources among components of the population. We review several conceptual models useful in accounting for important tree- and stand-level responses to a variety of silvicultural treatments. These conceptualizations of stand dynamics and production ecology do not directly associate growth response to resources, such as water and nutrients; but they facilitate the use of leaf area as an integrator of the ecological processes being silviculturally manipulated. We discuss several common silvicultural practices, including early competition control, soil manipulation, thinning, and fertilization, in the context of their influence on the amount, distribution, and net efficiency of leaf area.

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### 1. Introduction

Foresters use an extensive array of silvicultural practices to accomplish a wide range of objectives such as producing fiber, creating wildlife habitat, and enhancing recreational opportunities. Whether practices

involve site preparation prior to the establishment of a new stand or thinning of an established stand, silvicultural practices are commonly intended to directly or indirectly influence tree growth. Ecophysiologicals and production ecologists study how trees and stands respond to a range of environmental factors, but the resulting mechanistic detail is often difficult to translate into silvicultural application. Foresters, on the other hand, often make fairly accurate empirically based

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predictions about responses to various treatments, but commonly do so in the absence of detailed knowledge of the processes driving these responses.

The ability to explicitly link the objectives of silvicultural practices with the processes underlying their effects should enhance the efficacy of silvicultural prescriptions. This is especially important in the design of silvicultural systems involving novel species compositions and complex stand structures. Foresters are increasingly being challenged with new, often complicated, stand management objectives requiring the use of silvicultural approaches outside the realm of common experience (O'Hara et al., 1994; Kohn and Franklin, 1997). Being able to explicitly link particular practices with the ecological processes they affect offers considerable benefit, not only where empirical experience is lacking, but also where considerable practical experience exists. For example, Morris and Lowery (1988) argue that recognizing and separating soil manipulation

effects from those resulting from competition control can improve the effectiveness of site preparation on seedling survival and growth.

While no single model accounts for the diversity of ecological processes potentially influenced by silvicultural treatments, several useful conceptualizations incorporate important aspects of population dynamics and production ecology. We review these models and illustrate that collectively they can explain important tree- and stand-level responses to a variety of silvicultural treatments, including site preparation, release, thinning, and fertilization. The key driver of responses to these practices is their effect on the amount, distribution, accumulation rate, and net efficiency of leaf area within a stand. Foresters recognize that both tree and stand growth are functions of photosynthesis, which occurs almost exclusively in foliage. They also intuitively understand that in actions such as thinning they are manipulating the canopy and its leaf area. We

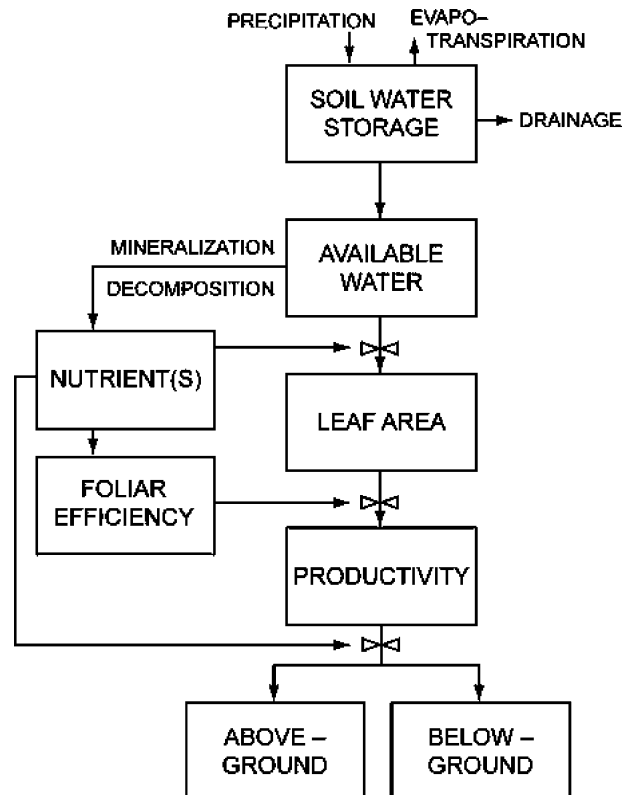


Fig. 1. Relationships between foliage, production and the availability of water and nutrients (after Grier et al., 1990).

argue that most silvicultural practices, not just thinning, produce their effects through direct or indirect influences on leaf area.

## 2. Conceptual models of processes and dynamics

### 2.1. Leaf area and stand production

Our underlying contention is that stand production is a function of resource availability, and that leaf area is the best integrator of the ecological processes affecting resource capture and carbon assimilation. The relationship between growth and resource availability has been demonstrated in a variety of studies. Ingestad and Lund (1986) demonstrated that the relative growth rate of tree seedlings maintained in tightly controlled environments could be increased or decreased by varying nutrients to the root system. Switzer and Nelson (1972), working with a 20-year chronosequence of loblolly pine (*Pinus taeda* L.) plantations, demonstrated that nutrient requirements increased with stand age. Forest nutrition studies have commonly shown a link between soil resource availability and stand growth (Brix and Ebell, 1969; Bolstad and Allen, 1987; Fisher and Garbett, 1980). Reich et al. (1997), compiling data from several forest types, found a linear relationship between the rate of nitrogen mineralization and stand growth. Dicus (2000) found a similar correlation between nitrogen uptake and growth in mid-rotation plantations of loblolly pine and slash pine (*Pinus elliottii* Engelm.). Dalla-Tea and Jokela (1991) demonstrated a linear relationship between stand growth and light interception in young loblolly and slash pine plantations in northern Florida.

Some of the connections between resource availability, growth, and leaf area are illustrated in Fig. 1. An upper limit to leaf area in fully occupied stands (Fig. 2b) is associated with site limitations in resource availability, including soil moisture and nitrogen availability (Mar Möller, 1947; Turner and Long, 1975; Mohler et al., 1978; Grier and Running, 1977; Waring et al., 1978; Hebert and Jack, 1998; Vose et al., 1994). The upper limit to leaf area is an emergent property of stand dynamics in that it is associated with the continued increase in leaf area of individual trees (Fig. 2a). This somewhat counter-intuitive relationship between stand- and tree-level

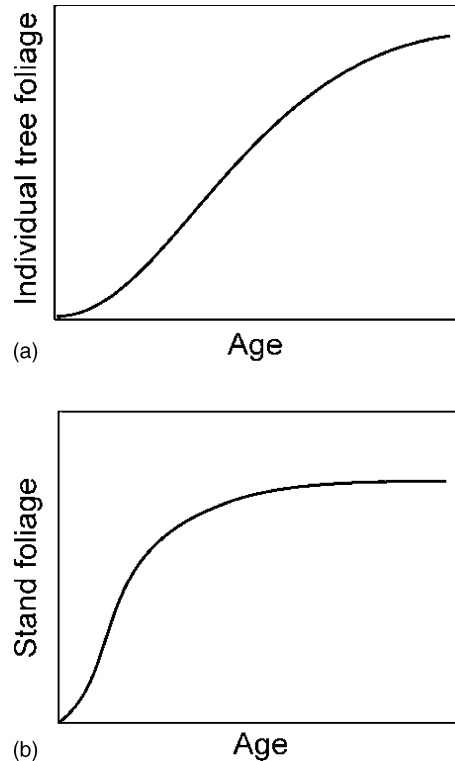


Fig. 2. Accumulation of foliage with age for individual tree (a) vs. a population (b).

leaf areas illustrates the importance of explicitly recognizing individual tree versus stand attributes (Smith and Long, 2001).

Growth increases associated with greater stand leaf area have been supported by studies conducted across natural gradients of site quality, and by manipulative studies amending nutrients and water. Gholz (1982) found that maximum leaf area index and net primary production across Oregon and Washington were strongly correlated with site-water balance. Fertilizer applications to both loblolly pine and slash pine plantations have resulted in corresponding increases in stand-level leaf area and stand growth (Vose and Allen, 1988; Colbert et al., 1990; Albaugh et al., 1998; Will et al., 2002). Gower et al. (1992) reported similar results with natural stands of Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco). Jokela and Martin (2000) were able to increase and maintain steady-state values of foliage mass with annual fertilization in both loblolly pine and slash pine. Foliage mass fell when fertilization was stopped. Gholz et al. (1985) found

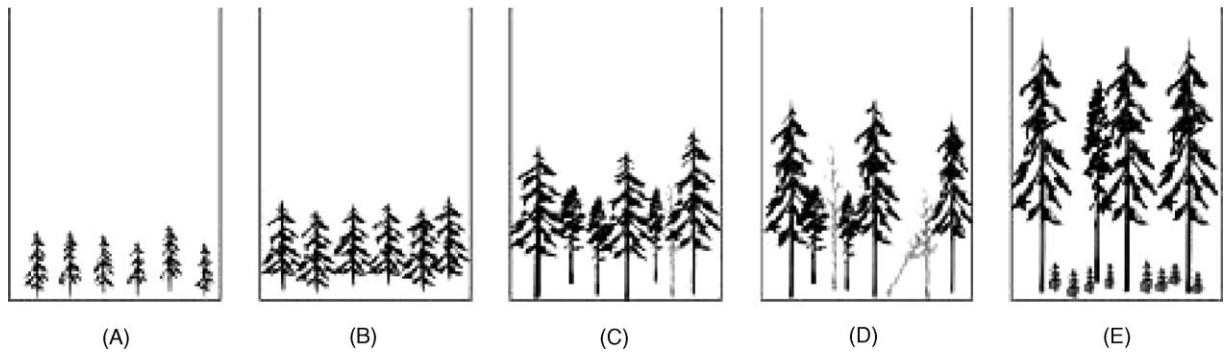


Fig. 3. Stages of stand development for an idealized even-aged stand. (A) Trees are free-to-grow; (B) onset of competitive interaction; (C) full site occupancy; (D) self-thinning; (E) stem reinitiation (after Long and Smith, 1984).

that peak nutrient uptake coincided with peak leaf area in a 34-year chronosequence of slash pine plantations. These results are all consistent with the use of leaf area as an index of resource availability; this minimizes the need to directly associate growth responses with the capture of light, water, and nutrients in order to understand how silvicultural practices work.

## 2.2. Stand development and size–density relations

Even-aged stands develop from a collection of individual, free to grow trees through the onset of competition, to full site occupancy, self-thinning, and the eventual development of multicohort stand structures (Long and Smith, 1984; Oliver and Larson, 1990; Smith and Long, 2001) (Fig. 3). The relationship between tree size and stem density in developing stands has a central place in population dynamics and quantitative silviculture (Jack and Long, 1996). Stand development is commonly displayed as a trajectory of increasing mean tree size with decreasing stand density (Fig. 4), and many widely used indices of relative density (e.g., Reineke's stand density index, crown competition factor, Curtis' RD) are based on the combination of mean tree size and stand density (Curtis, 1970; Jack and Long, 1996). Different combinations of mean size and density can represent the same relative density—for example, many small trees can have the same relative density as fewer, but larger trees.

The different ways in which stand-level leaf area might be distributed among individual trees can be considered in the context of changes in mean size and density during stand development. At lower relative

densities (i.e., combinations of mean size and density below the threshold for competition—stage A in Figs. 3 and 4) individual trees carry large amounts of leaf area compared to trees of the same age growing in denser stands. At such low relative densities, however, stand-level leaf area is substantially below the upper limit, and stand growth, therefore, is substantially below potential for the species, site quality and stand age. At higher relative densities (e.g., stage C in Figs. 3 and 4), individual tree leaf area, and thus tree growth,

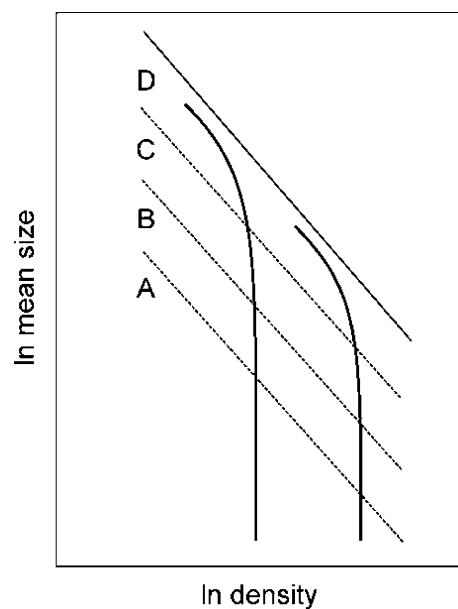


Fig. 4. Mean size–density trajectories for two hypothetical even-aged stands: one with low and the other with high, initial density. A–D indicate combinations of mean size and density corresponding to stages of stand development illustrated in Fig. 3.

is much lower than that of open grown trees of the same species and age on the same site. Stand-level leaf area, however, is close to its upper limit and, for practical purposes, stand growth is at its potential (Smith and Long, 2001). At full site occupancy, or stage C of stand development (Fig. 3), the specific combination of tree size and density determines how a fixed amount of stand foliage is distributed among trees in the stand. As the stand progresses through stage C, the stronger competitors continue to accumulate more foliage at the expense of weaker competitors. The process of self-thinning (stage D in Figs. 3 and 4) is, in effect, the natural redistribution of a fixed amount of total leaf area onto progressively fewer, and eventually larger, individuals.

Measures of relative density have considerable utility in the design and application of silvicultural treatments. One reason for this is that site quality does not typically have an appreciable affect on the nature of the size–density trajectory during stand development (White and Harper, 1970; Westoby, 1984; Harms et al., 2000). Site quality does, of course, substantially influence the rate at which a stand moves along its trajectory. On high quality sites, leaf area of both individual trees and the stand accumulates more rapidly. This, in turn, results in greater potential tree and stand growth. Given the same initial density, stands on more productive sites will reach the onset of competition, canopy closure, full site occupancy, and self-thinning more rapidly than stands on poorer sites. Thus, while basic size–density relations are largely independent of site quality, the rate of stand development is very much dependent on site quality.

In some circumstances, silvicultural practices can have very long lasting influences on site quality—for example, drainage of excessively wet sites, or fertilization on phosphorus deficient sites. In these limited situations, stand development and the rate at which stands move along the size–density trajectory may, for all practical purposes, be permanently changed. Much more commonly, however, silvicultural treatments result in temporary increases in site growth potential. For example, a single application of nitrogen generally results in a growth response of relatively few years duration. The effects of most treatments can therefore be conceptualized as a temporary boost in the rate of stand development. The result, in effect, is an acceleration of the stand along the size–density trajectory

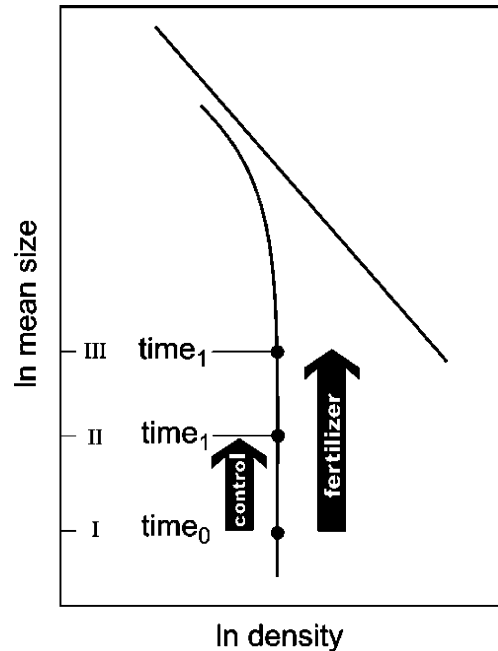


Fig. 5. Normal progression of a stand from mean size I to mean size II (arrow on left). Accelerated progression of the stand to mean size III (arrow on right). The time taken to progress to either II (control) or III (fertilizer) is the same. Stand at mean size III is the same age as at mean size II, but is more developed and appears to be older.

for a few years, after which the rate of stand development returns to normal. An extremely important result, however, is that the leap ahead is usually permanent. Stand dynamics and structure are such that the stand appears more mature than its actual age, i.e., it is further along the size–density trajectory (Fig. 5). And while the stand may be further ahead in growth and leaf area accumulation, it is also further ahead in self-thinning. Miller (1981) referred to this phenomenon as the bootstrap effect. Possibly the most important practical result of such temporary accelerations in stand development is a shortened rotation (Miller, 1981).

### 2.3. Growth–growing stock relations

The relationship between tree and stand growth and level of growing stock is another conceptual model fundamental to understanding responses to silvicultural practices. Growth–growing stock relations (Fig. 6) illustrate important considerations in the management of stand density. Simply stated, stand

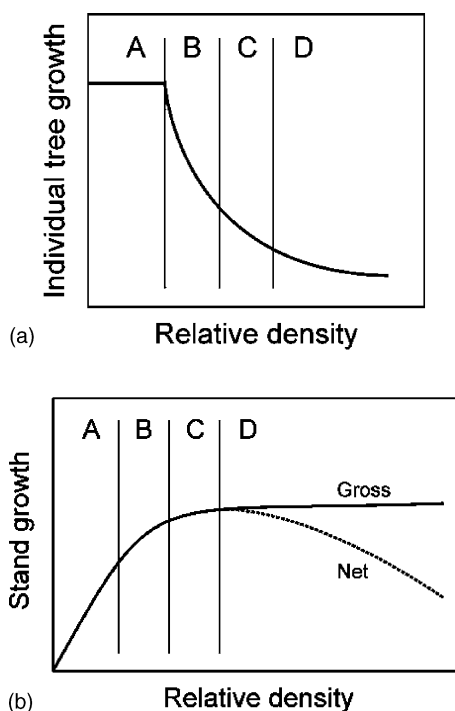


Fig. 6. The generalized relation between individual tree growth and relative density (a) and between stand growth and relative density (b). A–D correspond to stages of stand development illustrated in Fig. 3.

density can be managed to maximize stand growth (Fig. 6b), managed to maximize individual tree growth (Fig. 6a), or managed as a compromise between the two. Stand density cannot, however, be managed to simultaneously maximize stand growth and individual tree growth. These two fundamentally different growth–growing stock relationships (Fig. 6) are central to stand density management. At low relative densities, i.e., in the absence of competition (stage A in Figs. 3 and 4), tree growth is maximized because individual tree leaf area is at its maximum as determined by species, age, and site quality. At these low relative densities, however, stand growth is substantially below its potential because stand-level leaf area is below its upper limit. At high relative densities, stand leaf area is near its upper limit, and therefore stand growth approaches its potential. However, at these high relative densities, trees are crowded and have relatively low leaf areas and individual tree growth. With the possible exception of truly stagnated

stands, gross stand growth continues to increase across the entire range of relative densities (Long and Smith, 1990). At relative densities above the threshold of self-thinning, net stand growth often declines with further increases in relative density due to increasing mortality.

#### 2.4. Canopy structure and efficiency

Gross stand production typically continues to increase, albeit often slightly, with continued increases in relative density (Fig. 6b) even though the increases in relative density are associated with near constant amounts of stand foliage. This is consistent with the common observation that relatively small trees in crowded populations occupy space more efficiently than relatively large trees in less crowded populations (Assmann, 1970; Long and Smith, 1990; Jack and Long, 1992; Roberts et al., 1993; Smith and Long, 2001; Seymour and Kenefic, 2002; Will et al., 2002). In production forestry at least, “wolf trees” are undesirable not only because they have poor form (e.g., large branches, excessive taper) but also because they are “space robbers”. While growth of an individual wolf tree with its large leaf area is relatively high, growth per unit of ground area of a population of such trees would be substantially less than a dense population of smaller trees (Assmann, 1970). Efficiency differences associated with canopy structure can fundamentally influence the design of density management regimes in silvicultural systems (Smith and Long, 1989).

### 3. Evaluation of several practices

The conceptual models described above are useful in organizing and accounting for important tree- and stand-level responses to a variety of silvicultural treatments. Ultimately, responses to most silvicultural practices result from their influence on the amount of resources potentially available for growth, the ability of trees to acquire those resources, and the distribution of resources among population components. The conceptual models of stand dynamics and production ecology that we have presented do not directly associate growth responses with resources (e.g., water and nutrients) and resource acquisition. They do, however,

facilitate the use of foliage as an integrator of the ecological processes being manipulated. We evaluate some common silvicultural practices in the context of their potential influence on the amount, distribution, and net efficiency of leaf area.

As discussed previously, the rate at which trees accumulate foliage prior to canopy closure, and the eventual upper limit to stand-level leaf area after canopy closure, is primarily a function of site water balance and secondarily a function of available nutrients (Fig. 1). With few exceptions, such as heavy fertilization on the poorest of sites or continuously re-fertilizing more typical sites (Fisher and Binkley, 2000), little can be done silviculturally to permanently increase the upper limit of stand-level leaf area. However, silvicultural practices can have considerable influence on the rate at which individual trees accumulate leaf area and how rapidly populations approach the upper limit of stand-level leaf area. Equally important, silviculturists have considerable control over the distribution of leaf area among individual trees—a fixed amount of foliage can be distributed among many small crowned trees or fewer large crowned trees. Such choices have tremendous influence on stand structure, total stand growth, future tree size, and the ultimate value of the stand.

### 3.1. *Site preparation and early stand tending*

Stand regeneration practices are usually intended to create conditions that favor early dominance by one or more desired species comprising the new age class to be established. These conditions are created by the combination of a regeneration method and site preparation practices. The prescribed regeneration method (e.g., clearcutting, shelterwood, group selection) creates an advantageous light environment for the target species. Site preparation and early release treatments focus on the quality of the microenvironment by improving soil physical and chemical properties, controlling competing vegetation, creating suitable seedbeds, and providing access to planters.

Site dominance implies preferential resource capture and use, and can be effectively represented by the accumulation of leaf area (Figs. 1 and 2). During the initial stages of stand regeneration, accumulation of leaf area by seedlings and sprouts is dependent on the availability of nearby resources for rapid development

of a shoot system. Accumulation of leaf area is related to both the absolute amount of resources and their relative availability as influenced by competing vegetation. Which species eventually dominate a site typically depends on how quickly trees or competing vegetation establish, or reestablish, shoot systems. Thus, species dominance after disturbance often depends on complex ecological interactions between viable seeds and residual vegetation (Oliver and Larsen, 1990). Undamaged understory trees and shrubs are more likely to dominate a site than individuals that must reestablish a shoot system from stump sprouts or root suckers. Trees and shrubs regenerating from sprouts or suckers are, in turn, more likely to dominate a site than individuals that must establish both roots and shoots from seed. And finally, seedlings germinating from residual seed are often more successful than species whose seed must come from outside the site. Much of site preparation and early release, therefore, focuses on favoring the initiation of shoot systems, and therefore the accumulation of leaf area, of desired species.

In plantations, site preparation practices can be grouped into two categories—those that manipulate the soil's physical properties and those that control competition (Morris and Lowery, 1988). Treatments that manipulate the soil include plowing, harrowing, mounding, bedding, and subsoiling and mainly serve to increase the volume of soil available for root exploration and the speed in which growing space is captured by the crop species. Treatments to control competition primarily involve applying herbicides, and to a lesser degree include scalping, root raking, shearing, chopping, harrowing, burning, dragging, and mulching. Competition control reallocates growing space to desired species, and can be applied prior to planting or as a release treatment after planting. Treatments of either category applied singularly or in combination are known to increase growth and survival when compared to no site preparation (Derr and Mann, 1970; Williams, 1974; Cain, 1978; Haywood and Tiarks, 1990; Sutton, 1993; Varelides and Kritikos, 1995; Weber et al., 1996; Haywood et al., 1997; Querejeta et al., 2001; Li et al., 2003). As a result, application of these treatments often assures that the crop species will dominate the site. The expertise required of foresters involves selecting the most cost effective combination of site preparation

and release treatments for a specific set of site conditions given the prevailing economic environment (e.g., Archibald et al., 2000).

Proper site preparation also promotes site dominance when a new age class is established with either natural regeneration or direct seeding. The keys for achieving site dominance using seed are a cooperative climate and the availability of large numbers of seeds falling on favorable seedbeds and escaping depredation (Cain, 1991). Consequently, in addition to manipulating soil physical properties and controlling competition, site preparation prescriptions for natural regeneration and direct seeding must take into account the additional factors of seed production, seed predation, availability of suitable microsites, and seedbed conditions. In most situations, sufficient establishment of seedlings for site domination is only possible during good seed years and on properly prepared seedbeds. For seeds needing exposed mineral soil for rapid germination and establishment, practices that scarify the soil such as dragging, scalping, or broadcast burning are used. For seeds needing burial within a litter layer, soil scarification must be restricted to the extent possible. Early site dominance by the crop species, while obviously desirable, often requires subsequent thinning to avoid restricted tree growth.

There are objectives for site preparation that are, at most, only indirectly related to the rapid accumulation of leaf area by crop trees. Most notable maybe are slash treatments intended to improve site access for tree planters. Increasing site access may not directly add to the growth of the crop species, but any treatment that increases the depth that the seedling is planted and improves contact between the root system and the soil increases the probability of seedling survival and future site domination. In commercial operations in the southeastern United States, hand planters spend less than 15 s planting each seedling. Within that brief period, the planter moves to the position, selects a microsite, digs the hole, plants the seedling, and packs the soil around it. Better access and planting conditions increase the chances that the seedling will be planted correctly and survive. The effectiveness of site preparation in accelerating eventual site capture and dominance by the crop species is substantially influenced by actions and decisions that occur within the few seconds that a seedling is planted.

### 3.2. Thinning

Foresters intuitively know that when thinning a stand they are manipulating the canopy and its leaf area (Fig. 7). There are two critical components to this manipulation—an immediate reduction in stand-level leaf area, followed eventually by increases in the leaf area of residual trees. In the short-term, thinning clearly reduces canopy leaf area and thus gross stand growth. The time necessary for stand-level leaf area to return to prethinning levels is a function of stand age, site quality, and the intensity of thinning. At one extreme, an older stand on a poor site might take decades to regain the foliage lost in a heavy thinning. A young stand on a good site, however, might return to prethinning foliage levels within a few years following a light thinning. The amount of reduction in stand-level leaf area, and the time required to regain that leaf area, represent foregone potential stand growth. In practice, thinning inevitably results in lower stand growth (Zeide, 2001), and a regime based on few heavy thinnings (Fig. 7a) will result in greater reduction in potential stand growth than a regime based on

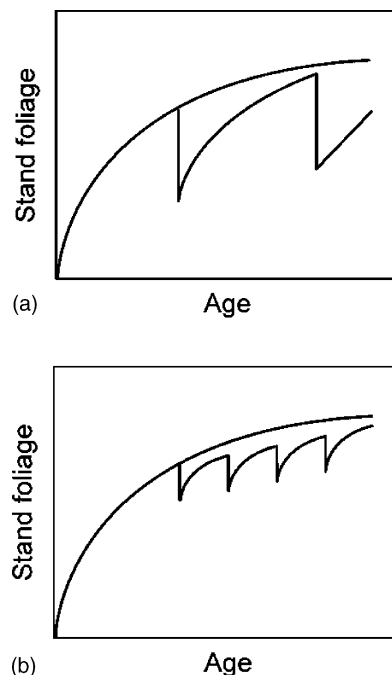


Fig. 7. Influence of heavy (a) and light thinnings (b) on stand foliage.



frequent light thinnings (Fig. 7b). There are, of course, other factors to be considered in choosing a thinning regime. For example, frequent thinnings may adversely affect advanced regeneration.

The second critical component of canopy manipulation is that thinning, over time, acts to “reallocate” leaf area onto residual trees—similar to but more drastic than self-thinning. Post-thinning recovery of stand-level foliage results from increases in individual tree leaf area that occurs more rapidly than it would in dense stands (Fig. 8). The increase in individual tree leaf area is associated with increased individual tree growth. Thus, temporary reductions in stand foliage (Fig. 7) inevitably result in the loss of at least some potential stand growth, but increases in individual tree growth. This is the tradeoff associated with allocating leaf area onto fewer, eventually larger trees (Fig. 8). In the context of growth–growing stock relations (Fig. 6), thinning represents a reduction in relative density resulting in an immediate reduction in stand leaf area (Fig. 7) and growth (Fig. 6b), and an eventual increase in individual tree leaf area (Fig. 8) and growth (Fig. 6a). In practice, of course, thinning is not done to increase stand production, but rather to increase overall stand value (Assmann, 1970). Definition of value clearly depends on management objectives; but whether objectives involve thinning for future nest trees for Northern goshawks (e.g. Lilieholm et al., 1993) or the maximization of land expectation value (e.g., Dean and Chang, 2002), they almost always translate into an emphasis on individual tree growth at the expense of stand growth. Even where stand growth is strongly emphasized, such as with pulpwood regimes, it is still necessary for trees to achieve a

critical minimum size and it is therefore necessary to focus some attention on the growth of individual trees.

Size–density relations (Fig. 4) are an important part of thinning theory and are the basis of many practical thinning tools (Jack and Long, 1996). Size–density relationships have been incorporated into a variety of density management diagrams (DMDs) (Ando, 1962; Drew and Flewelling, 1979; McCarter and Long, 1986). DMDs are exceedingly valuable for conceptualizing stand dynamics (Jack and Long, 1996), and are useful in the practical design of thinning prescriptions and displaying density management alternatives for a wide variety of objectives (Anhold et al., 1996; Dean and Baldwin, 1993; Smith and Long, 1987; Sturtevent et al., 1996).

### 3.3. Fertilization

Increases in productivity associated with fertilization result from increases in the total amount of leaf area, the rate of leaf area accumulation, and the growth efficiency of the leaf area (Gholz et al., 1991; Gower et al., 1992; Albaugh et al., 1998; Fisher and Binkley, 2000). From a silvicultural standpoint, increases in total leaf area and how rapidly it develops are most important.

For individual trees, the response to fertilization is typically an increase in the rate at which leaf area is accumulated (Fig. 1). Increasing leaf area on individual trees is eventually constrained as stand-level limits to leaf area are approached, although there is often an increase in total foliage beyond the inherent “carrying capacity” for the species and site. In some cases, such as phosphorus fertilization on severely P deficient sites, this increase in foliage carrying capacity may be more or less permanent (Albaugh et al., 1998). More commonly, however, increases in the limits of stand-level leaf area are temporary, and leaf area eventually returns to its original level (Mitchell et al., 1996; Jokela and Martin, 2000). The growth response to increased leaf area is effectively illustrated using size–density relationships—the stand follows the same trajectory, but with an increased rate of development (Fig. 5). Dean and Jokela (1992) found that fertilization did not affect the maximum values of stand density obtained by slash pine plantations in northern Florida, suggesting that accelerated stand development does not change the stand densities

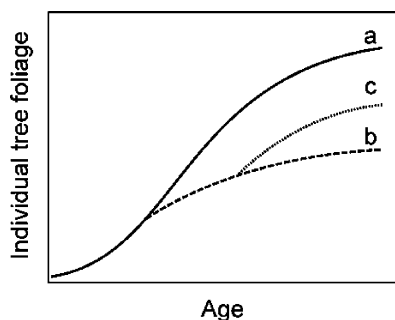


Fig. 8. Accumulation of foliage by an individual tree in a stand with low relative density (a), in a stand with high relative density (b), and in the high relative density stand after thinning (c).

associated with the various stages of stand development.

It typically makes little sense to fertilize stands already carrying maximum leaf area, i.e., fully stocked stands, as the ability of individual trees to add leaf area in such circumstances is limited. Fertilization in fully stocked stands has even been observed to result in the acceleration of self-thinning where site resources were not capable of supporting the increases in stand-level leaf area (Mitchell et al., 1996). It is generally more efficient to fertilize stands carrying less than maximum leaf area, which is why fertilization is commonly prescribed in conjunction with thinning. Increasingly, fertilization is being prescribed early in stand development to accelerate crown closure. It is sometimes used to accelerate growth so that young trees can more quickly grow beyond the reach of herbivores (e.g., Auchmoody, 1982). In each case, the result is a shortening of the time required to attain or regain maximum leaf area (Albaugh et al., 1998; Brix, 1983; Mitchell et al., 1996; Will et al., 2002).

Stand response to fertilization can be either long-term or short-term. Long-term responses occur when a slowly soluble nutrient such as phosphorus is amended. Such long-term responses have been documented to last over 50 years following phosphorous fertilization in a *Pinus radiata* plantation (Turner et al., 2002). Long-term responses also occur when nutrient additions are large relative to the total available pool. Albaugh et al. (1998) sustained long-term growth increases in loblolly pine plantations planted on deep, impoverished sands with annual additions of a carefully prescribed mixture of macro- and micro-nutrients. For practical purposes, such amendments changed the quality of this site.

The second, and more common response to fertilization is of fairly short duration, e.g., 4–8 years. This type of response is typical of a single application of nitrogen fertilizer. In contrast to phosphorous, application rates of nitrogen are usually relatively modest compared to the total pool of available nitrogen (Fisher and Binkley, 2000). This is true even on sites where nitrogen availability substantially limits growth (Fisher and Binkley, 2000; Miller, 1981). Thus, while the response to phosphorous fertilization is analogous to an increase in site quality, the short-lived response typical of nitrogen fertilization is essentially a temporary increase in stand development—analogueous to

the stand “leap-frogging” ahead along the size–density trajectory (Fig. 5). However, while the direct effect of fertilization on stand development can be characterized as a short-lived increase in the rate of movement along the size–density trajectory (Fig. 3), the gains in stand development during this period of accelerated leaf area production and growth are generally permanent. This ghost of fertilization past is the reason that Miller (1981) characterizes nitrogen fertilization as generally benefiting trees, and not the site.

Whether response to fertilization lasts a few years or for decades, the effective result is a shortening of the rotation. Fertilization accelerates leaf area development, increases the growth rate of trees, and reduces the number of years required to reach culmination of both current and mean annual increment (Smith and Long, 2001). Fertilization can thus improve the economics of a rotation in two ways—less time is required to reach a target tree size, and the number of years that the cost of fertilization (or other) treatments must be carried is reduced. Indeed, the historical motivation for fertilization late in a rotation has much to do with the tyranny of compound interest.

#### 4. Summary

Responses to a wide range of silvicultural practices result from their influences on the amount of resources potentially available for growth, the ability of trees to acquire those resources, and the distribution of resources among different population components. Given the paucity of specific information directly associating growth responses with resource uptake, foliage can be an effective integrator of the ecological processes responsible for carbon assimilation and potential productivity.

A suite of simple conceptual models can be used to effectively organize and account for important tree- and stand-level responses to a variety of silvicultural treatments, including competition control, soil manipulation, thinning, and fertilization. These models incorporate important aspects of population dynamics and production ecology. They relate the influence of water and nutrients on the amount and efficiency of leaf area, stand-level limits to leaf area and its distribution to individual trees, the relationship between tree size and stand density in crowded populations, the

relationship between tree- and stand-level growth and stand density, and the influence of canopy structure on foliar efficiency. Explicitly linking silvicultural objectives and practices to the processes underlying expected responses makes silvicultural prescriptions more effective. This linkage will be especially important as foresters are increasingly challenged by stand management objectives requiring the design of novel silvicultural systems.

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