

## CROWN MANAGEMENT AND STAND DENSITY

Thomas J. Dean, School of Forestry, Wildlife, and Fisheries, Louisiana Agricultural  
Experiment Station, Louisiana State University  
V. Clark Baldwin, Jr., USDA Forest Service, Southern Forest Experiment Station

### INTRODUCTION

Stand density management allows a forester to utilize mortality and promote individual tree vigor. However, even after four decades of spacing studies, planning for stand density management remains a difficult problem. Forest management approaches the problem with sophisticated analysis, but the heart of the analysis depends on statistical growth models fit to data from empirical field trials. Statistical growth-and-yield simulators interface poorly at times with modern forest management analyses (Chang 1984). Even though no better predictor of the next rotation exists than the performance of the previous rotation, historical data does not exist for every stand, and the combinations of species, density management, soils, and topography create a matrix too large to test with spacing studies. Furthermore, changes in cultural treatments, product specifications, and the physical environment diminish the predictive value of field trials. Theories are emerging from recent work to support density management planning. These theories focus on the dynamics of crown dimensions in relationship to stand development and average tree spacing and may aid in developing sound density management decisions and managing for desired stand qualities. In addition, they may aid in overcoming some of the deleterious effects climate change, air quality, and site degradation. Mechanistic linkages between the crown and the stem suggest new uses for traditional treatments that may stimulate productivity and improve value.

### FOLIAGE AND SIZE DENSITY RELATIONSHIPS

#### Foliage as an Indicator of Growing Space

The abstract concept of growing space embodies site limitations in resource supply in relation to silvics (Oliver and Larson 1990). Better sites supply more resources than poorer sites, and thus, provide a greater amount of growing space than poor sites. This definition expands the traditional association between growing space and the physical volume occupied by trees (see Smith 1986). Associating growing space with resource supply helps in understanding the stand recruitment and stem exclusion phases of stand development, dynamics of uneven-aged stands, the opposing nature of stand-level and tree-level growth, competition, and site occupancy.

Since growing space integrates the physical supply of resources and the resource requirements of species, quantifying growing space is impractical if not impossible. However, foliage should adequately represent growing space. Resource supply controls the rate of biomass accretion (Ingestad and Agren 1991), and biomass accretion closely follows leaf-area index (leaf area per occupied area) (Vose and Allen 1988). Other physiological processes also consume resources in proportion to leaf-area index. For example, leaf-area index approximates a linear relationship with transpiration (Whitehead et al. 1984).

During the course of stand development, leaf-area index peaks and either remains constant or declines slightly with age (Mohler et al. 1978, Long and Smith 1992). Maximum leaf-area index varies by species and site quality corresponding to the concept of growing space (Grier and Running 1977). Basically, a stand fully occupies the site (i.e. completely occupies the growing space) when it has accrued the maximum of leaf-area index that a site can support. During the interval a stand fully occupies a site, the scarcity of resources suppresses recruitment and reduces tree-level growth to a minimum through competition. Conversely, full-site occupancy results in maximum stand productivity because the stand consumes all the resources supplied by the site.

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## Size Density Relations During Full-Site Occupancy

Large trees grow more rapidly than small trees. Consequently, as a stand develops and trees grow larger, eventually the stand will require more resources than the site delivers. Since a finite amount of growing space exists, when a stand fully occupies the site, some trees must die to make growing space available for additional growth to occur. This mortality has been called self-thinning, suppression mortality, and competition-related mortality. Self-thinning depends on a range of competitive abilities within the stand; if trees compete equally within a stand, stagnation occurs.

Limited growing space creates a corresponding boundary in possible combinations between average tree size and numbers of trees per unit area that appears linear on log-transformed axes (Figure 1). The slope of the boundary is difficult to determine analytically (Westoby 1984, Weller 1987) largely because of the difficulty in truly identifying stands at the limit of growing space in natural conditions. Careful experiments with controlled conditions are required to correctly calculate the slope of the boundary (Lonsdale 1990). Such experiments are impractical for the size of trees relevant to forestry, however. The slope has been fitted by hand and is generally accepted as -1.5 or -0.625 for mean size expressed in terms of volume (Drew and Flewelling 1977) or diameter (Reineke 1933), respectively. During the interval that a stand fully occupies the available growing space, leaf-area index is constant; however, a slope of -1.5 between mean stem volume and trees per unit area indicates that the total stem volume per unit area increases as trees per unit area declines. In other words, to support leaf-area index at its site-specific maximum, stands with few trees need much more wood than stands with larger numbers of trees. The slope between average stand diameter and trees per unit area also indicates that more basal area is required to support maximum levels of leaf-area index as trees per unit area declines. Physical limitations of tree stems do not allow a stand to maintain maximum leaf-area indexes throughout its existence, causing leaf-area index to decline and the combination between mean size and trees per unit area to fall away from the size-density boundary.

## Density Indexes and Crown Properties

While the slope of the boundary between mean size and trees per unit area may vary, the existence of the boundary provides an easily measurable standard for quantifying stand density that is independent of age and site quality. Since the size density boundary is a tangible expression of growing space, the proximity of a stand to the boundary is a measure of site occupancy. This is supported by the linear relationship between leaf-area index and Reineke's stand density index, a mathematical combination of average stand diameter and trees per acre, (Figure 2). With an understanding of growing space, having a meaningful measure of site occupancy provides foresters with a firm foundation for prescribing treatments, understanding their effects, and replicating treatment effects in other stands.

As most foresters realize, many cultural treatments achieve their effects by modifying the crown environment. The size density boundary that is created when growing space is full is actually a fortunate manifestation of the crown environment at full site occupancy and the resultant effect on stem size. At face value, therefore, stand density indexes are convenient, empirical indicators of site occupancy and the crown environment. Recent research, however, shows that the relationship between the crowns and stand density index goes beyond simple statistical correlations.

Dean and Long (1986) showed that a cantilever beam analysis closely predicts the diameter of any cross section of lodgepole pine (*Pinus contorta* Douglas var. *latifolia* (Engel.) Critch.) stems. The important variables in this analysis were the "sail area" (leaf area) above the cross section and the amount of leverage exerted at the cross section. Similar analyses have been performed for diameter at breast height (DBH) for Japanese red pine (*Pinus densiflora* Sieb. & Zucc.) (Takahashi and Wakabayashi 1981), slash pine (*Pinus elliottii* var. *elliottii* Engelm.) seedlings (Dean 1991), and loblolly pine (Dean and Baldwin 1996a). The relationship developed by Dean and Long (1986),

$$\text{DBH} \propto (A_1 M_c)^{1/3},$$

where  $A_1$  = individual tree leaf area and  $M_c$  = the distance from breast height to the middle of the crown is called the constant-stress model of stem formation because it is based on the assumption that stem taper equalizes the bending stress generated within the stem by lateral wind action on the crown. Cannell and Dewar (1994) have concluded that

the constant-stress model is an adequate, though simplistic, description of tree taper: more precise and sophisticated models exist that are based on solid mechanics. Dean and Long (1992) used the constant-stress equation to predict average stand diameter based on stand averages of leaf area per tree and distance between breast height and the middle of the crown. The slope between average stand diameter calculated with the constant-stress model and actual average stand diameters was not significantly different from 1.00 (1.02,  $P=0.29$ ). This result indicates that stem diameter is functionally related to mean leaf per tree and the vertical distribution of that leaf area. Dean and Baldwin (1996a) substituted the constant-stress equation for average stand diameter in the equation for Reineke's stand density index (SDI) and were able to express SDI explicit in terms of foliage density ( $F$ ), and mean live-crown ratio ( $C_r$ ):

$$\text{SDI} \propto (F (1/C_r - 0.5))^{1/2}.$$

Foliage density is the average amount of leaf area per unit volume of space and is an important variable in light interception (Kuuluvainen 1992). This equation is an equilibrium equation indicating that foliage density and mean live-crown ratio are the principle variables that determine the value of SDI. As more growing space is utilized, foliage moves to the top of the crown and the ratio between the length of the crown and tree height decreases. The increased bending stress created by changes in foliage density and mean live-crown ratio stimulates diameter growth, resulting in increased values of SDI.

Growing space is species specific and causes the position of the size density boundary to vary. Different positions of the size density boundary are manifested as species-specific differences in maximum values of SDI. According to the equation developed by Dean and Baldwin (1996a), these differences should be reflected in maximum, attainable values of foliage density and minimum, sustainable values of live-crown ratio. However, when the canopy properties of loblolly pine and lodgepole pine (two species that have substantially different maximum SDI values) are compared, no significant differences are observed. If solid mechanics are indeed involved in determining the maximum values of SDI, and if no differences in foliage density or mean live-crown ratio exist, differences in the mechanical properties of stem should account for differences in maximum SDI values. Wood strength is closely related to specific gravity, and Dean and Baldwin (1996a) found that specific gravity accounts for 70 % of the variation in maximum SDI values for those species where both variables are known (Figure 3). Longleaf pine (*Pinus palustris* Mill.), which has the highest specific gravity of the southern pines, apparently does not require as much cross-sectional area at breast height to support similar values of foliage density and mean live-crown ratio as redwood, whose stemwood is among the lowest specific gravities measured.

## GROWTH GROWING STOCK RELATIONSHIPS

An old adage of density management is "room to grow: no room to spare." While a valid concept, it provides no basis for implementation nor any indication of achievement. Although foresters often speak of maximizing productivity, the relation between growing stock and growth is one of the most poorly understood concepts across the natural resource profession. Simply stated, the relation between growth and growing stock is this: for a given combination of species, age, and site, as a greater percentage of the growing space is utilized, total net primary productivity and gross-volume increment increase and average tree growth decreases (Figure 4). One area of concern for production ecologists that has immediate application is understanding how crown variables determine this classical silvicultural tradeoff.

Fundamentally, photosynthesis (the conversion of intercepted radiant energy to chemical energy) totally supports tree physiology, and while growth is but one of many physiological processes, intercepted radiant energy correlates strongly with total stand growth (DallaTea and Jokela 1991), suggesting that biomass increment consumes a large majority of the fixed energy. Correlations between leaf-area index and gross-volume increment logically follow (Waring 1983, Oren et al. 1987, Dean et al. 1988, Smith and Long 1989, Long and Smith 1992, Dean and Baldwin 1996b). At the individual tree level, mean leaf area per tree correlates well with individual tree growth (Long and Smith 1992). To emphasize total stand growth, the stand must be managed such that large values of leaf-area index are accumulated and maintained. Conversely, to emphasize individual tree growth, the stand must be managed to promote large crowns on individual trees. Both conditions are mutually exclusive.

The stage of stand development apparently affects the conclusions drawn from production ecology studies. Dean and Baldwin (1996b) analyzed growth--growing stock relationships and crown properties for a long-term, loblolly

pine, growth-and-yield study. They found that both gross-volume increment and mean-tree increment were generally correlated with crown properties for the 20-year duration of the study that began when the plantations were 17-years old. Both stand-level and tree-level growth lost their association with stand density after age 27 years, however. The age at which growth became independent of stand density corresponded to the age when crown structural variables such as crown length and live-crown ratio became independent of stand density. They concluded that while density management in this loblolly pine plantation would only be affective during the first 27 years, tree vigor during the later stages of plantation development depend on the maintenance of individual tree vigor by properly managing density during the early stages of plantation development.

## DENSITY MANAGEMENT

Within the context of the size density boundary, density management is simply identifying the distance from the size density boundary a particular stand should be managed. Usually the main factor involved in making this decision is the desired tradeoff between stand-level and tree-level growth. Intensive monitoring and tending would be required to implement this simple system, which, of course is impractical for most foresters. The process of planning density management based on the size density boundary is described in detail by Dean and Baldwin (1993). Basically, upper and lower limits of growing stock are selected that produce operational thinning yields. The upper growing-stock limit is chosen to obtain acceptable stand growth and individual tree vigor, and the lower growing-stock limit is chosen to maintain acceptable site occupancy. Levels of growing stock are generally constrained within stand densities corresponding to the threshold of self-thinning and canopy closure: 50-55 and 20-30 of maximum density, respectively. The upper growing-stock limit is generally between 40 and 55 % maximum density; and the lower growing-stock limit is generally between 25 and 35 % maximum density (Drew and Flewelling 1979, McCarter and Long 1986, Dean and Jokela 1992, Dean and Baldwin 1993). An example of a density-management plan is shown in Figure 5.

## ASSOCIATED RELATIONSHIPS

Forestry involves much more than managing the temporal and spatial patterns of productivity. Traditionally, foresters have been concerned with the suitability and quality of the raw material for various end products, wildlife habitat, forage production, recreational value, watershed yield, and protection from fire, insects, and pathogens. Other concerns and objectives include maximizing harvest index, simultaneous production of multiple crops, and promoting biological diversity. Crown manipulation through density management affects all of these concerns and objectives.

### Wood Quality

The quality and suitability of raw material is strongly related to crown management. A major problem in plantation management of coniferous species is the proportion of juvenile wood. The increase in the amount of juvenile wood formed in plantations is largely due to the wider spacings associated with plantation management compared to the close spacing of naturally regenerated stands. While many factors determine tracheid initiation and development, one factor influencing tracheid characteristics is the length of time between initiation and water conduction. High auxin concentrations hastens development producing short, thin-walled tracheids characteristic of juvenile wood. Auxin is produced by expanding buds and is exported down to the root system, creating a concentration gradient within the stem. Tracheids formed at the base of stem have a longer time to develop, resulting in long, thick-walled cells. Another term for juvenile wood is crown wood, and the longer a stem section develops within the crown, the greater that section will be comprised of juvenile wood. Therefore, the length of time between plantation establishment and canopy closure will have a large impact on the proportion of juvenile wood formed in the stem.

Intuitively, branch size has an obvious relationship to stand density, although quantifying the relationship can be difficult (Ballard and Long 1988). The formation of knot-free wood actually requires the stand to be maintained at extremely high densities and long rotations. The typical rotation length of southern pines does not provide enough time for dead branches to slough off, let alone producing clear wood over the branch stubs.

### Nontimber Objectives

Objectives such as multicropping and biodiversity involve the partitioning of growing space to other plant species capable of being members of the forest community. The diversity of insects and birds is correlated with the vertical diversity of foliage within the stand. Other species depend on the horizontal diversity of stand density across a landscape (Fiedler and Cully 1995). In order to promote vertical and horizontal diversity, the tree stand cannot utilize the entire growing space so that other plant species can establish. Consequently, to achieve these objectives, stand densities must be managed at values lower than traditional timber management and a range of stand densities must be established across a landscape. Multicropping and uneven-aged stand structure also require reallocation of growing space. Several strategies have been developed for allocating growing space for uneven-aged management (Smith 1986, Guldin 1991, Long and Daniel 1990).

### Harvest Index

Foresters have long been interested in duplicating the success of agronomists in manipulating allocation to the harvestable portion of crops, thereby increasing the harvest index. Allocation processes are difficult to follow in forests due to their dimensions and the extremely high variation and relatively low densities of their fine-root systems. In general, only about 35 % of a stand's biomass is utilized (Assmann 1970), depending on the use of the raw material. Studies and theory indicate that the harvest index increases with site quality, mainly due to the amount of mass allocated to the root systems (Davidson 1969, Keyes and Grier 1981, Haynes and Gower 1995). The differences in root allocation support the idea that root system need only be large enough to satisfy the water and nutrient requirements of the stand. Crown management should strongly influence the proportion of mass allocated to roots and therefore, affect the portion of harvestable biomass. The aboveground components of trees vary in concentration of mineral nutrients, most notably nitrogen. The concentration of nitrogen in the foliage, branches, and stems is approximately 1.3, 0.2, and 0.06 %, respectively (Switzer and Nelson 1972). As a stand increases in density, the growth of stemwood relative to other aboveground tissues increase. As a result, the relative demand for soil nitrogen decreases, which should reduce the required amount of root biomass.

### NOVEL TREATMENT OBJECTIVES

A more complete understanding of the relationship between crown properties and density management will lead to novel uses of conventional cultural treatments. For example, pruning is typically used to improve stem quality by restricting the size of the knotty core. However, the association of crown and wood properties indicates that live pruning may be used to reduce the size of the juvenile core by removing the influence of the crown on lower sections of the stem and to increase the harvest index by reducing the nutrient demand of the foliage and branches. The constant-stress model of stem formation indicates that live pruning can be used to reduce stem taper by artificially lifting the base of the live crown. Since live pruning also moves the crown's center of gravity up the stem, stem increment may be stimulated by increasing the bending stress generated in the stem.

The constant-stress model also suggests that light thinning will increase overall stand productivity. While thinning may increase the cumulative yield of a plantation, thinning reduces the net periodic annual increment of the residual stand because it removes leaf area. Within an unthinned stand, trees mutually support each other. Light thinning with the sole intention of removing a portion of this support, subjecting the crowns to greater wind action. The increased bending stress experienced by the stems stimulates diameter growth, resulting in a boost in net periodic annual increment.

### ENVIRONMENTAL IMPACTS

#### Air Chemistry

Changes in the wet and dry chemistry of the atmosphere have been shown to have deleterious effects on stand growth. High elevation red spruce subjected to acidic precipitation reduces its cold tolerance (Patton et al. 1991) and elevated ozone concentration reduces foliage longevity (Byres et al. 1992), increased ultraviolet radiation from the deterioration of stratospheric ozone shunts carbohydrate away from growth to produce protective, secondary compounds (Caldwell 1968), and increased concentrations of greenhouse gases will increase average air temperature if our current understanding of the system holds. If the impacts measured on individual trees and branches propagate through the stand, changes in air chemistry will change the crown properties of forest stands and, as a result, will affect density management. Conversely, with a better understanding of the effects of these impacts on crown

properties, changes in density management might aid in their mitigation. For instance, if tropospheric ozone concentrations lowers the amount of leaf area each tree can accumulate, managing the stand at higher densities might recover the productivity loss by restoring leaf-area index. Such a mitigation technique, however, will result in slower growth rates of individual trees and longer rotations to reach minimum diameter requirements. Growth--growing stock relationships will always extract a cost when density management is used to mitigate an environmental impact.

#### Long-Term Site Productivity

Multiple rotations on the same site have the potential of removing soil nutrients and reducing the available growing space for a species (Powers et al. 1990). Smaller growing space reduces the potential leaf-area index a stand can accumulate, reducing a species' growth potential. According the biomass allocation theory, degrading site quality will impact the harvest index disproportionately to the reduction in growing space. With a diminished supply of nutrients to the roots, more roots will be required to meet the growth demands of the aboveground portion of the tree. Such a diversion will reduce the proportion of biomass allocated to the stems. The simplest method for mitigating site degradation is conservation of site nutrients with careful harvesting techniques. The alternative may be increased stand densities to lower the demand for soil nutrients.

#### NEW OBJECTIVES FOR SPACING STUDIES

Although analyses of the relationship between crown properties and stand density suggest new methods for achieving management objectives and mitigating changes in the physical environment, these suggesting represent hypotheses that must be tested for viability. Since these new methods depend on density management, they will require the basic spacing study protocol. Typically spacing studies were used to determine appropriate planting densities and explore proper thinning timing and intensity. Spacing studies used as field trails are difficult to synthesize and have limited applicability. Empirical testing of predetermined hypotheses make spacing study results much more powerful and will help silvicultural technology to advance with a firm foundation.

#### LITERATURE CITED

- Assmann, E. 1970. *The Principles of Forest Yield Study*. Pergamon Press, Oxford. 506 pp.
- Ballard, L.A. and J.N. Long 1988. Influence of stand density on log quality of lodgepole pine. *Canadian Journal of Forest Research* 18: 911-916.
- Byres, D.P., T.J. Dean, and J.D. Johnson. 1992. Longterm effects of ozone and simulated acid rain on the foliage dynamics of slash pine (*Pinus elliotti* var. *elliotti* Engelm). *New Phytologist* 120: 61-67.
- Caldwell, M.M. 1968. Solar ultraviolet radiation as an ecological factor for alpine plants. *Ecological Monographs* 38: 243-268.
- Cannell, M.G.R and R.C. Dewar. 1994. Carbon allocation in trees: a review of concepts for modelling. *Advances in Ecological Research* 25: 59-104.
- Chang, S.J. 1984. A simple production function model for variable density growth and yield modeling. *Canadian Journal of Forest Research* 14: 783-788.
- Dalla-Tea, F. and E.J. Jokela 1991. Needlefall, canopy light interception, and productivity of young intensively managed slash and loblolly pine stands. *Forest Science* 37: 1298-1313.
- Davidson, R.L. 1969. Effects of soil nutrients and moisture on root/shoot ratios in *Lolium perenne* L. and *Trifolium repens* L.. *Annals of Botany* 33: 571-577.
- Dean, T.J. 1991. Effect of growth rate and wind sway on the relation between mechanical and waterflow properties in slash pine seedlings. *Canadian Journal of Forest Research* 21: 1501-1506.

- Dean, T.J. and V.C. Baldwin, Jr. 1993. Using a density-management diagram to develop thinning schedules for loblolly pine plantations. USDA Forest Service Southern Forest Experiment Station Research Paper, SO 275. 7 pp.
- Dean, T.J. and V.C. Baldwin, Jr. 1996a. The relationship between Reineke's stand density index and physical stem mechanics. *Forest Ecology and Management*. 81: 25-34.
- Dean, T.J. and V.C. Baldwin, Jr. 1996b. Growth in loblolly pine plantations as a function of stand density and canopy properties. *Forest Ecology and Management*. 82: 49-58.
- Dean, T.J. and E.J. Jokela. 1992. A density-management diagram for slash pine plantations in the lower coastal plain. *Southern Journal of Applied Forestry* 16: 178-185.
- Dean, T.J. and J.N. Long 1986. Validity of constant-stress and elastic instability principles of stem formation in *Pinus contorta* and *Trifolium pratense*. *Annals of Botany* 54: 833-840.
- Dean, T.J. and J.N. Long. 1992. Influence of leaf area and canopy structure on size-density relations in even-aged lodgepole pine stands. *Forest Ecology and Management* 49:109-117.
- Dean, T.J., J.N. Long, and F.W. Smith. 1988. Bias in leaf area sapwood area ratios and its impact on growth analysis in *Pinus contorta*. *Trees Structure and Function* 2: 104-109.
- Drew, T.J. and J.W. Flewelling. 1979. Stand density management: an alternative approach and its application to Douglas-fir plantations. *Forest Service* 25: 518-532.
- Guldin, J. M. 1991. Uneven-aged BDq regulation of Sierra Nevada mixed conifers. *Western Journal of Applied Forestry* 6: 27-32.
- Grier, C.C. and S.W. Running. 1977. Leaf area of mature northwestern coniferous forests: relation to site water balance. *Ecology* 58: 893-899.
- Haynes, B.E. and S.T. Gower 1995. Belowground carbon allocation in unfertilized and fertilized red pine plantations in northern Wisconsin. *Tree Physiology* 15: 317-325.
- Ingestad, T. and G.I. Agren. 1991. The influence of plant nutrition on biomass allocation. *Ecological Applications* 1: 168-174.
- Kuuluvainen, T. 1992. The effect of 2 growth forms of Norway spruce on stand development and radiation interception a model analysis. *Trees Structure and Function* 5: 171-179.
- Keyes, M.R. and C.C. Grier. 1981. Above and belowground net production in 40-year-old Douglas-fir stands on low and high productivity sites. *Canadian Journal of Forest Research* 11: 599-605.
- Lonsdale, W. M. 1990. The self-thinning rule: dead or alive? *Ecology* 71: 1378-1388.
- Long, J.N. 1985. A practical approach to density management. *Forestry Chronicle* 61: 23-27.
- Long, J. N. and Daniel T.W. 1990. Assessment of growing stock in uneven-aged stands. *Western Journal of Applied Forestry* 5: 93-96.
- Long, J.N. and F.W. Smith. 1992. Volume increment in *Pinus contorta* var. *latifolia*: the influence of stand development and crown dynamics. *Forest Ecology and Management* 53: 53-64.
- McCarter, J.B. and J.N. Long. 1986. A lodgepole pine density management diagram. *Western Journal of Applied Forestry* 1:6-11.

- Mohler, C.L., P.L. Marks, and D.G. Sprugel. 1978. Stand structure and allometry of trees during self-thinning of pure stands. *Journal of Ecology* 66: 599-614.
- Oren, R., R.H. Waring, S.G. Stafford, and J.W. Barrett. 1987. Twenty-four years of Ponderosa pine growth in relation to canopy leaf area and understory competition. *Forest Science* 33: 538-547.
- Oliver, C.D. and B.C. Larson. 1990. *Forest Stand Dynamics*. McGraw-Hill, Inc., New York. 467 pp.
- Patton, R.L., K.F. Jensen, and G.A. Schier. 1991. Responses of red spruce seedlings to ozone and acid deposition. *Canadian Journal of Forest Research* 21: 1354-1359.
- Powers, R.F., D.H. Alban, and R.E. Miller. 1990. Sustained site productivity in North American forests: problems and prospects. USDA Forest Service Southern Forest Experiment Station Proceedings Reprint. 79 pp.
- Reineke, L. H. 1933. Perfecting a stand density index for even-aged forests. *Journal of Agricultural Research* 46: 627-638.
- Smith, D.M. 1986. *The Practice of Silviculture*. John Wiley and Sons, New York.
- Smith, F.W. and J.N. Long. 1989. The influence of canopy architecture on stemwood production and growth efficiency of *Pinus contorta* var. *latifolia*. *Journal of Applied Ecology* 26: 681-691.
- Switzer, G.L. and L.E. Nelson. 1972. Nutrient Accumulation and cycling in loblolly pine (*Pinus taeda* L.) plantation ecosystems: the first twenty years. *Soil Science of America Proceedings* 36: 143-147.
- Takahashi, K and R. Wakabayashi. 1981. Stem sway and tree form of Akamatsu, Japanese red pine. *Journal of the Japanese Forestry Society* 63: 133-136.
- Vose, J.M. and H.L. Allen. 1988. Leaf area, stemwood growth, and nutrition relationships in loblolly pine. *Forest Science* 34: 547-563.
- Waring, R.H. 1983. Estimating forest growth and efficiency in relation to canopy leaf area. *Advances in Ecological Research* 13: 327-354.
- Weller, D.E. 1987. A reevaluation of the 3/2 power rule of plant self-thinning. *Ecological Monographs* 57: 23-47.
- Westoby, M. 1984. The self-thinning rule. *Advances in Ecological Research* 14: 167-225.
- Whitehead, D., W.R.N. Edwards, and P.G. Jarvis. Conducting sapwood area, foliage area, and permeability in mature trees of *Picea sitchensis* and *Pinus contorta*. *Canadian Journal of Forest Research* 14: 940-947.



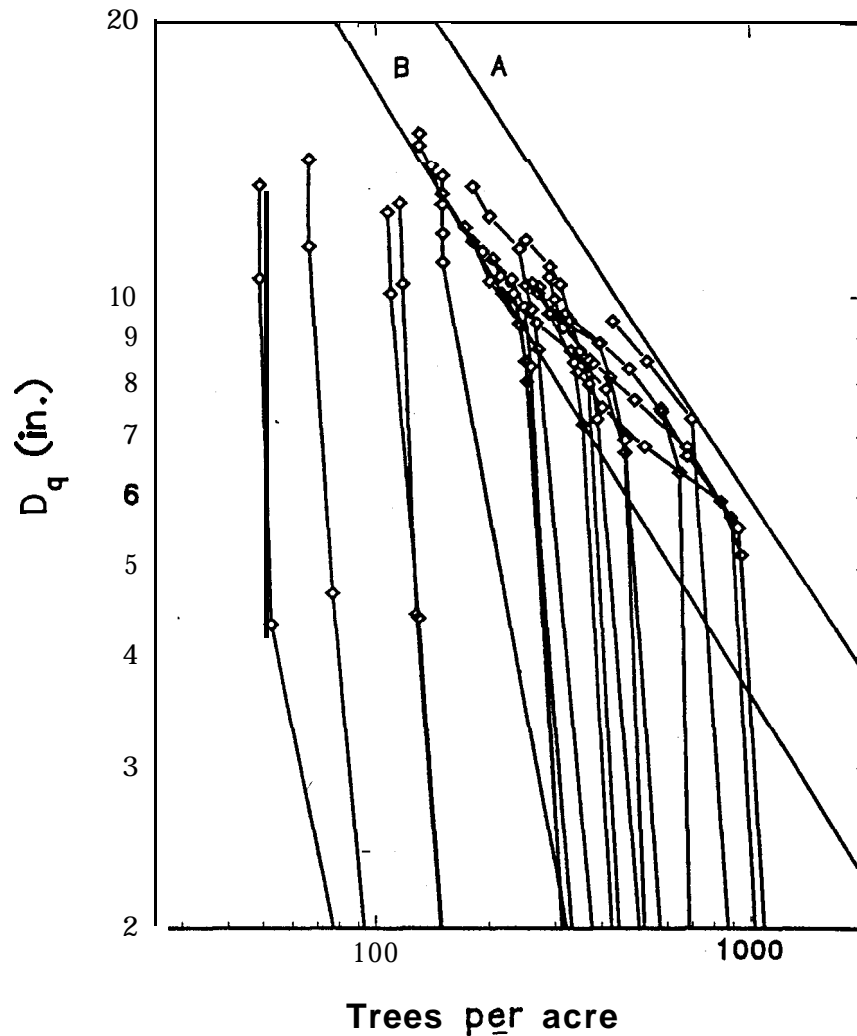


Figure 1. Change in average stand diameter ( $D_q$ ) and trees per acre in repeatedly measured plots. Line A represents the observed boundary between  $D_q$  and trees per acre, and line B represents the threshold of self-thinning. Data from growth-and-yield studies established in loblolly pine plantations by the USDA Forest Service Southern Forest Experiment Station in around Louisiana, USA (Dean and Baldwin 1993)

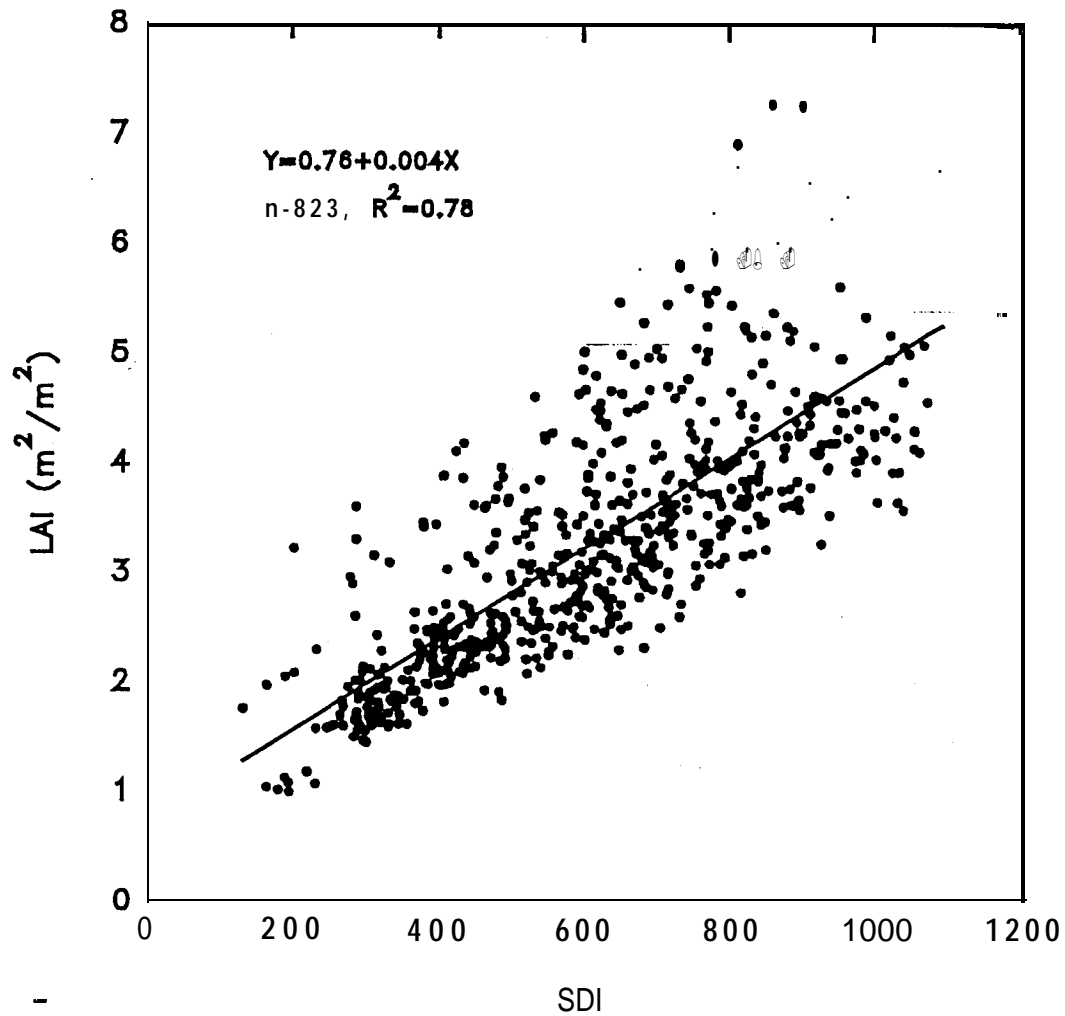


Figure 2. Scattergram of leaf-area index (LAI) and Reineke's stand-density index (SDI). Leaf area index calculated from mensurational data according to Dean and Baldwin (1996a). Data from growth-and-yield studies in loblolly pine plantations by the USDA Forest Service Southern Forest Experiment Station in and around Louisiana, USA. Line fitted with least-squares, linear regression.

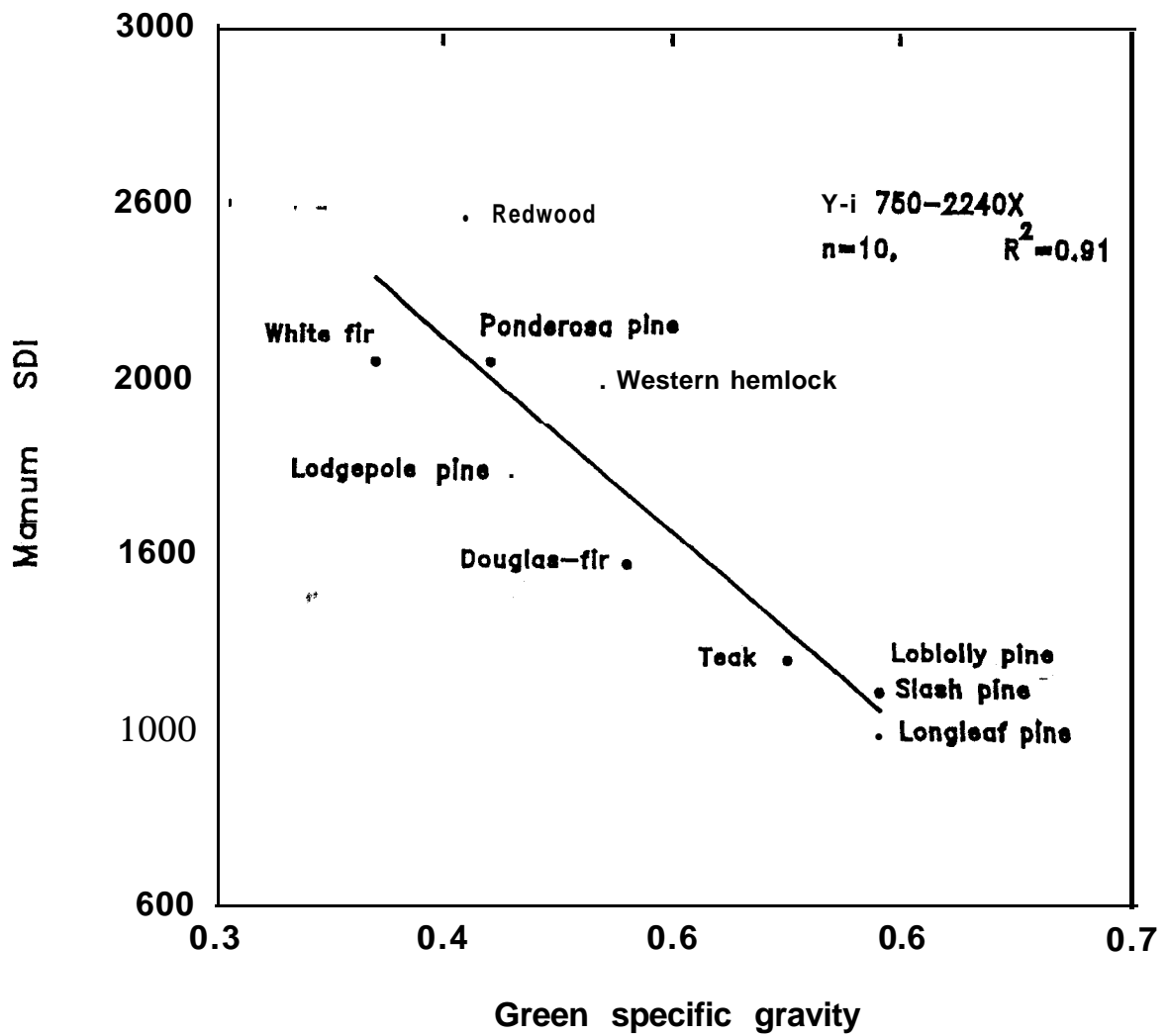


Figure 3. Maximum value of Reineke's stand density index (SDI) as a function green specific gravity of the stemwood for various species. Data are described in Dean and Baldwin (1996a). Line fitted with least-squares linear regression.

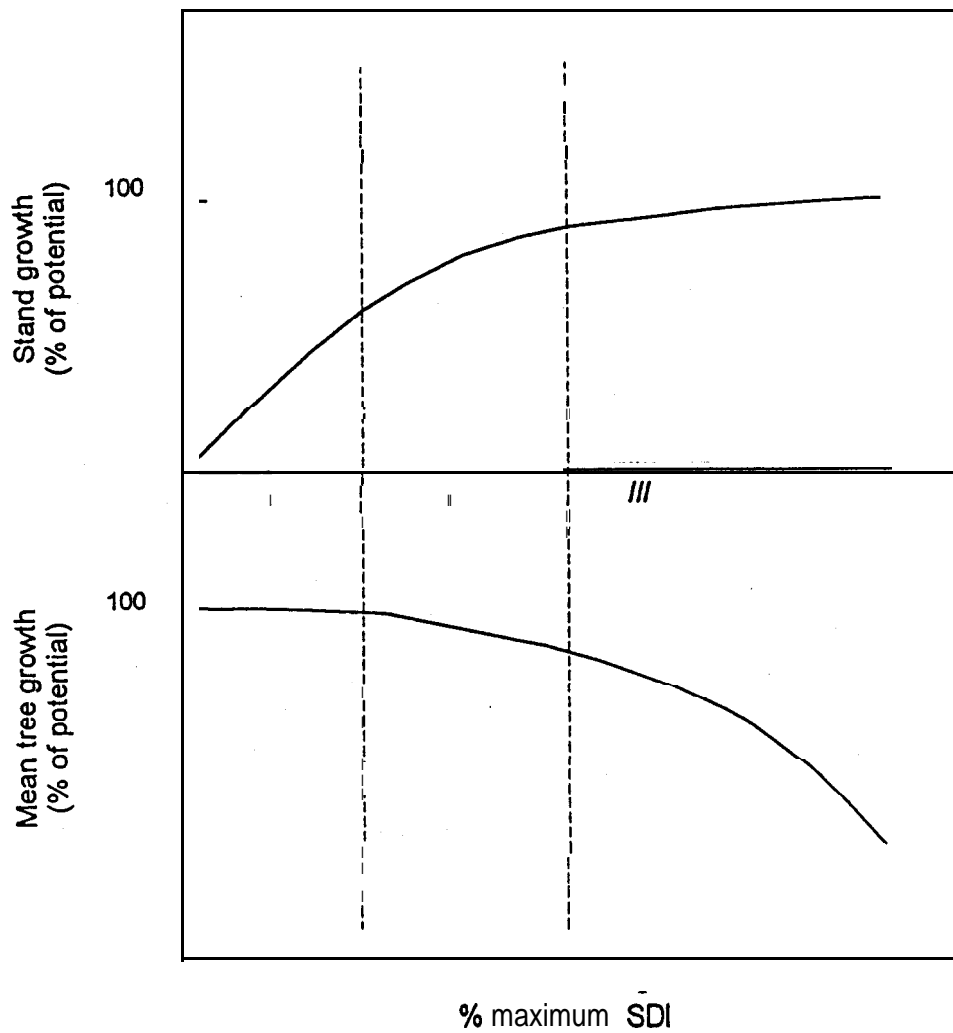


Figure 4. Hypothesized relationship between stand  $\bar{g}$  (gross) and percent maximum value of Reineke's stand-density index (SDI) (top) and between mean-tree growth and percent maximum SDI. Both stand growth and mean-tree growth are expressed in terms of percent of potential as defined for a particular combination of species, age, and site quality.

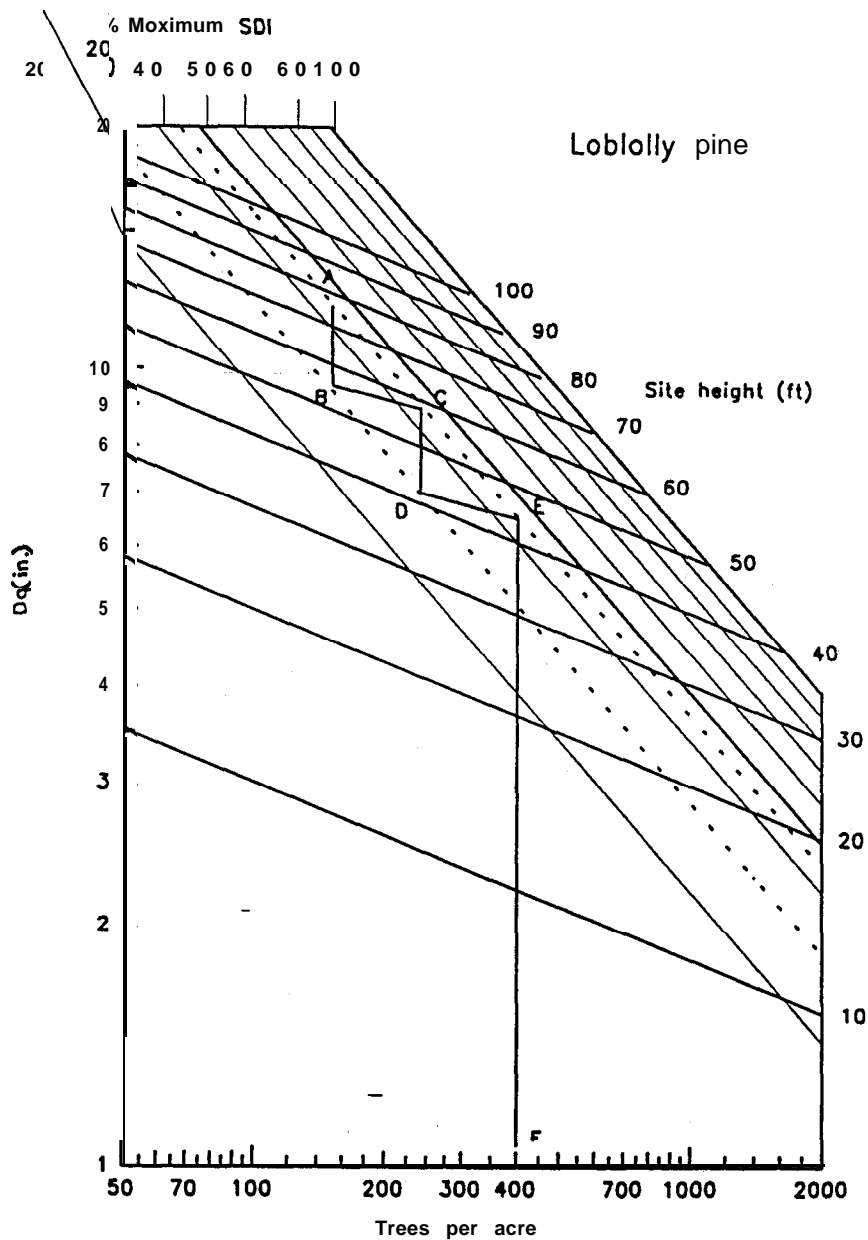


Figure 5. Density-management diagram for loblolly in the West Gulf region of the United States. Line within the figure represents one possible density-management plan. Dotted lines represent limits of upper and lower growing stock in which the plantation will be maintained. At points C and E the plantation is thinned back to points D and B, respectively. The slopes between DE and between BC are negative, representing the diameter lift caused by low thinning. Point A represents harvest, and point F represents the initial planting density. Figure from (Dean and Baldwin 1993).