

STAND PRODUCTIVITY: Some Considerations in Evaluating Genetic Improvement

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Abstract. The productivity of forest stands depends on the potential of their constituent abiotic and biotic elements. The patterns of stand and tree growth differ, and performance estimates based on free growing trees, which are mainly based on time, are not directly transferable to stands, where performance includes the additional dimension of space. The development of stands, whether from selected or unselected growing stock, will follow the classic growth curve and will be under the control of its determinants. Improving the rates of growth of the main biotic elements of stands will chiefly decrease the time required to reach the relatively fixed carrying capacity of the site. This improved rate will enable or require shorter rotations and more frequent thinnings to realize the genetic gains. The realities of these changes are briefly considered.

Additional Keywords: Carrying capacity; growth curves; stand dynamics.

INTRODUCTION

Stand productivity* is the focus of a diversity of disciplines associated with the forest resource. In forestry, it has traditionally been addressed by forest mensuration and has centered on the growth and yield of the utilized portion of the crop - wood. Such information has satisfied the practical needs of forest management, but it has not measurably contributed to an understanding of the productive processes of forest stands. The relationships between the biota and the environment that determine the productivity of stands has always been a challenge to practical ecologists such as silviculturist and agronomist (Baker 1950, Jenny 1980, Evans 1980). Fortunately, the early efforts of Moller (1945) and others in silviculture who attempted to quantify and understand these processes continues today. An understanding of the productive processes of forest stands is important now and in the future, as the forest is made more productive for mankind.

The success achieved by efforts in tree improvement during the last three decades requires an evaluation by those concerned with the

*The productivity of ecological systems can be expressed in various ways. Productivity is expressed here as either stem volume or basal area growth, the traditional terms used with forest stands.

productivity of forest stands. What will be the productivity and culture of stands composed of trees possessing improved growth rates, increased resin production, greater disease resistance, etc.? The following thoughts are restricted to the effects of improved rates of growth and do not consider any qualitative characteristics, although their importance and the contribution that genetic improvement has on their character is recognized. The relative compatibility of maximizing the potential of the individual tree and that of the stand is the principal thrust of these thoughts.

GENERAL CONSIDERATIONS

Forest Stands and Productivity

Forest stands are ecological systems, and their productivity is dependent on the potential of their biotic and abiotic elements and the interactions of these elements. The variation found in the productivity of forest stands is a reflection of the variation in these elements and their interactions. Foresters and others have tacitly recognized this variation and interaction by noting that the productivity of an area must be expressed in terms that are specific to a particular species.

The biotic and abiotic elements of forest stands are not equally amenable to management. The biotic elements are much more flexible and their modification and control constitutes the bulk of silvicultural practice, e.g. the control of composition, density, structure, etc. In comparison, the abiotic elements are relatively fixed and one has to mainly work within the confines of climate, soil, or whatever else is at hand. However, modification of the abiotic elements, either improving or degrading, is usually much more lasting.

Stand versus Tree Productivity

The productivity of forest stands is expressed in the behavior of the populations and communities that constitute the biotic elements assembled on an area. At the stand level productivity is expressed in terms of quantity per unit of time and space. In contrast, assessments of the productivity of individual trees usually ignore space. Thus, the growth patterns of trees and stands differ; the growth of the tree is continuous while the stand approaches a maximum quantity which is thereafter roughly maintained (Figure 1).

The growth rates of both trees and stands is also affected by the allotment of growing space. Increased growing space permits a greater expression of the potential of the individual tree. For example, beyond ten years wider spaced trees in loblolly pine plantations have twice as much basal area as closer spaced trees (Figure 1A). The effects of increased growing space on stand basal area is the reverse of that of the mean tree, since the stand includes considerations of population size and space. Increased growing space for the trees within the stand reduces the rate of approach of the stand to the maximum and constant levels which the site can apparently support. Thus, the stand with closer spacing reaches a rather constant level of basal area sooner than a stand with a wider spacing (14 years versus 22 years, Figure 1B).

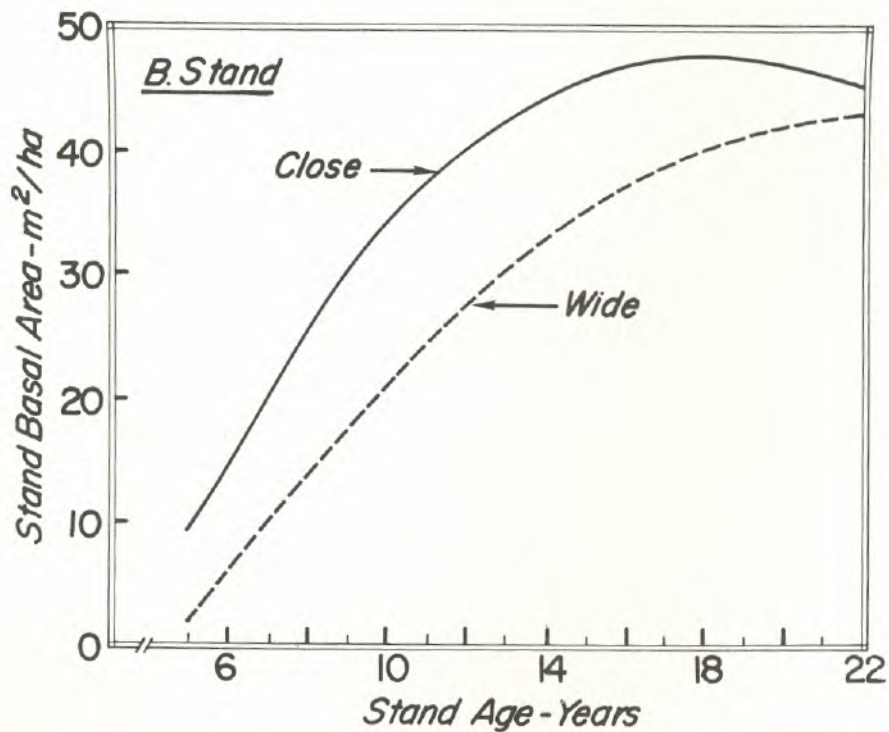
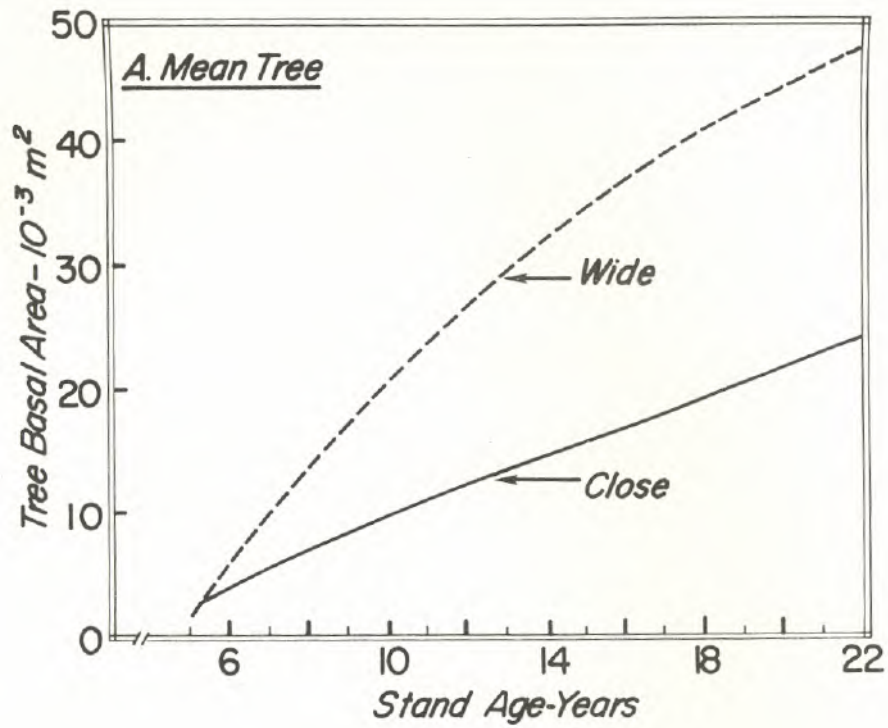


Figure 1. A comparison of the basal area development of the mean tree and the stand in loblolly pine plantations at wide (1200 trees/ha) and close (4300 trees/ha) initial spacings. The site index of the area is 29 m at 50 years.

The objectives of maximizing the potential of the individual tree and the stand are not compatible in forest management. Maximizing the potential of the individual involves performance in an unrestricted or "open grown" environment. In contrast, the objective in stand management is to maximize the productivity per unit of land area by optimizing the balance between the potential of the individual, the population, and the site. Therefore, assays of productivity based on free growing individual trees -- such as those arrived at in conventional progeny trials -- are not directly transferable to stands or populations which face the confines of space.

GROWTH CURVES AND SELECTION

Characteristics and Determinants

The previously described pattern of stand basal area growth is characteristic of the classic growth curve that applies to biologic populations in limited space and resources (Hutchinson 1978). The periods of population growth follow the common sequence of acceleration, linearity, deceleration, and constancy (Figure 2). This common pattern of behavior results from the integrated expression of the determinants of the growth curve identified as biotic potential, environmental resistance, and carrying capacity (K). Biotic potential is the inherent capacity for growth in an environment of unlimited resources and is a property of both individuals, populations, and communities. Carrying capacity is principally an expression of the limits of the relatively fixed abiotic elements of the environment to support life and is expressed in quantity per unit area. Environmental resistance is an

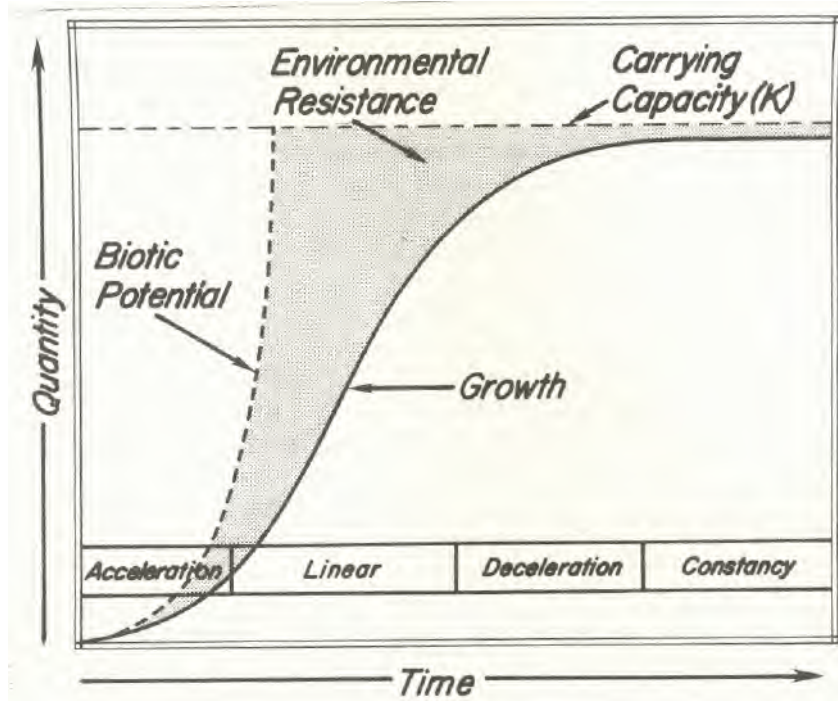


Figure 2. The periods of development and determinants of the classic growth curve.

expression of the opportunities for growth and is lowest during the early life of a stand when opportunities for growth are greater. It increases as time elapses and carrying capacity is approached.

During stand development conditions change from low levels of density and competition to high densities with more intense levels of competition. These changes bring about two types of selection in the life of the stand: r and K selection (MacArthur, 1972). r selection is independent of density and occurs early in the life of the stand when increased growth rates are favored by the low densities and temporal habitats offered before carrying capacity is reached. In contrast, K selection is density dependent and is expressed as the stand approaches and is at carrying capacity. K selection favors persistence at reduced growth rates and greater efficiency in the use of resources. These two types of selection have relevance in tree improvement since considerable selection effort is centered on improved rates of growth in low density environments (r selection). Little regard has been placed on increased efficiencies at the high densities associated with K selection. In addition, most of the species presently of interest in tree improvement are those which naturally preempt the low density and temporal habitats of the early stages of succession. Such species exemplify r selection.

Applications

The equations that mathematicians use to characterize population growth also recognize these determinants of behavior. The one used in the subsequent examples is that of Chapman and Richards (Pienaar and Turnbull 1973) where:

$$\text{Quantity} = KR$$
$$\text{and } R = (1 - e^{-a \text{ Time } b})$$

In this equation K is the carrying capacity of an area and is visualized as being constant. R is the degree of approach to K and is a function of biotic potential and time. It ranges from zero to one and is zero at time zero and approaches one as time increases and K is reached. When applied to forest stands K can be expressed by the various measures used to quantify stand properties such as basal area, volume, leaf area, and dry weight. However, for each of these expressions of K the level and rate of approach differs; the carrying capacity for foliage is achieved relatively early in the life of a stand while that of volume is much later. Two examples based on data from the literature are used to illustrate the expression of the growth curve determinants in forest stands. In the first example, carrying capacity varies and biotic potential is the same; in the second, biotic potential varies and carrying capacity is approximately the same.

The first example uses the performance of loblolly pine at the two limits of its observed productivity, i.e., site indices of 18 and 36 meters at 50 years (Figure 3A). The volume carrying capacities at these limits are 300 and 800 m³/ha, respectively. These carrying capacities differ by almost three-fold and represent the potential limits expressed

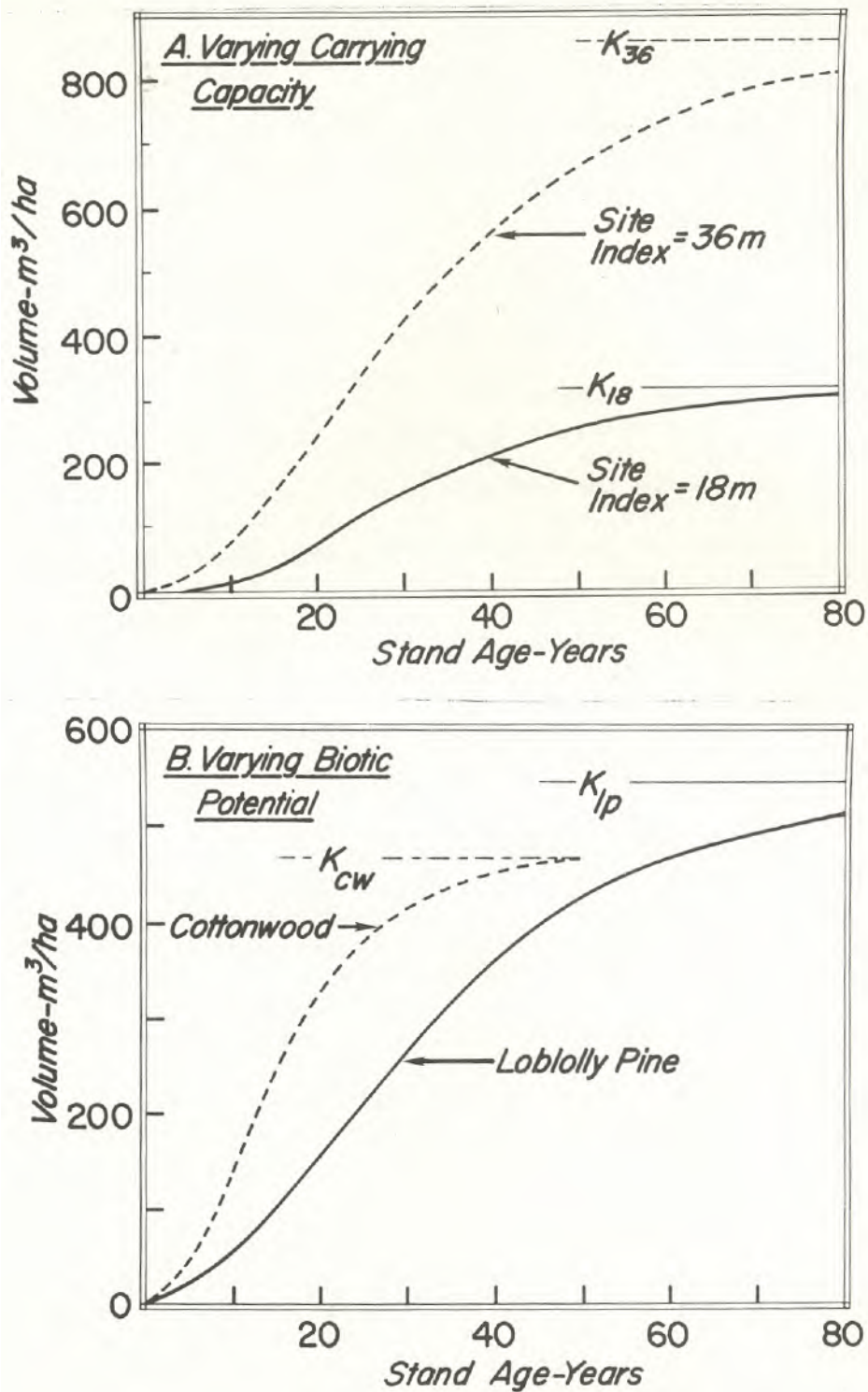


Figure 3. A comparison of the volume growth curves for: (A) varying carrying capacities and similar growth biotic potentials, and (B) varying biotic potentials and similar carrying capacities. The growth curves were fit with nonlinear regression using the Chapman-Richards equation. All data are based on site indices at 50 years and are from USDA (1929) for loblolly pine and Williamson (1913) for cottonwood.

by the species. In contrast, the values for R, considered to be an expression of the biotic potential of this species, are essentially the same for both carrying capacities. For example, at 40 years of age, 65 percent of K has been attained on both sites. This similarity of R on both sites indicates that the biotic potential of the species is the same. Thus, the difference between the two sites is principally the extent to which the carrying capacities have permitted the expression of biotic potential.

Cottonwood and loblolly pine are compared in thesecond example which considers comparable levels of K (around 500 m /ha)* and different levels of biotic potential (Figure 3B). This choice of species is perhaps a bit extreme but it usefully illustrates the point. The rate of approach to the "comparable" carrying capacities differs for the two species. For example, at 20 years the volume for the natural cottonwood stands is about 350 m /ha which is about 70 percent of K. At the same age the volume for the loblolly pine stands is only 150 m /ha or only 30 percent of K. Thus, there is more than a 2-fold difference in R at this age. Although two species were used here to demonstrate differences in R, genetic selection within a species can also result in increased biotic potential, though perhaps less than the 2-fold increases in this example. However, any gains in biotic potential will result in a shortening of the time required to reach K.

STAND DYNAMICS

Differentiation

The characteristics and determinants of the growth curve can be applied at both the individual tree and stand level. The growth curve of the stand is essentially a composite of the gains made by the growth of individual trees and the losses through tree mortality. However, the growth curves of the individual trees making up the stand are not the same, since the trees grow at different rates. Analysis of the growth of individual trees is very complicated since there can be as many patterns of growth as there are trees. However, the development of individual trees within a stand can be expressed by differentiating the stand population into size classes. The process of differentiation described here uses the distribution of height classes in loblolly pine plantations during the early years of development.

Differentiation commences early in the life of the stand and continues through the stand's development, although the rates diminish with age. For example, at planting there is a marked central tendency in height class distribution, and the range in heights is only 0.3 m (Figure 4). However with increasing age, differences in the rates of height growth within the population result in a widening of the distribution of heights, and by 4 years the range in heights has increased to

* Although these volume carrying capacities are about equal, the site indices are 41 m and 27 m for cottonwood and loblolly pine at 50 years, respectively.

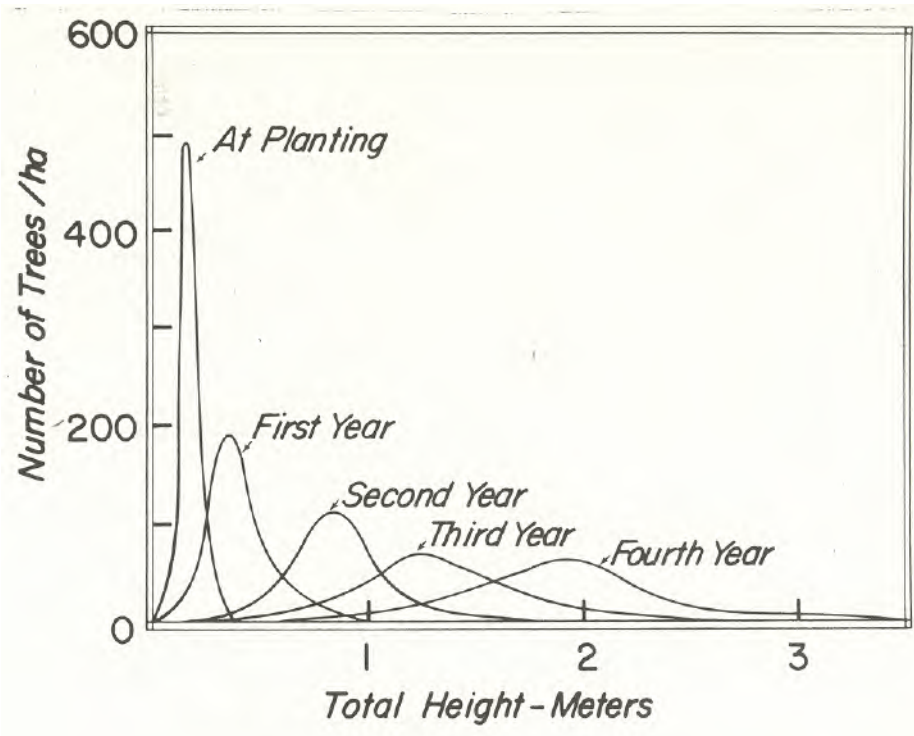


Figure 4. The distribution of height classes (3 cm) during the first 4 years of development of loblolly pine plantations planted with 1920 trees/ha and with a site index of 29 m at 50 years.

3 m. During these early years of development the leading edge of the distribution is growing at a rate about three times faster than that of the trailing edge. These early differences in growth rates occur before canopy closure and when the trees are relatively free growing. They are mainly attributable to the genetic makeup of individuals, micro-variation in the environment, and their interactions. Random variation also exerts an influence on differences in growth rates, since factors such as insect damage, top breakage, etc. are essentially random events. However, these early differences in growth rates are an expression of r selection and are a major criterion in advanced generation selection.

Subsequent Development

What are the implications of these early differences in rates of height growth on the subsequent development of the stand and its productivity? To resolve this, the performance of segments of the height distribution existing at 5 years in a loblolly pine plantation were followed through 20 years. The distribution at 5 years was grouped into ten segments of equal numbers (deciles). The first decile is the shortest 10% of the population and the tenth decile is the tallest. Repeated measurement of the trees permits tracking the development of each decile through time.

The current annual volume growth of trees through 20 years is strongly related to their decile at 5 years (Figure 5). The differences among deciles occur early in plantation development and increase through

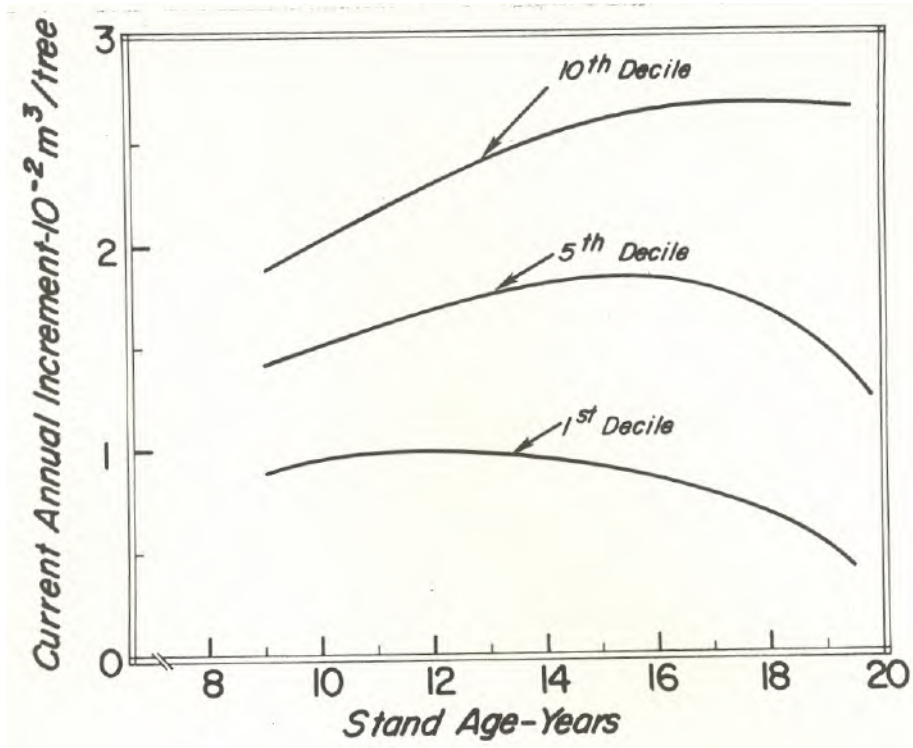


Figure 5. The patterns of current annual increment for the identified deciles in a loblolly pine plantation. The plantation was planted with 1920 trees/ha and has a site index of 29 m at 50 years. The deciles were identified from the height distribution at 5 years.

time. For example, at 8 years the tenth decile is growing twice as fast as the first decile. Further, this difference between these two deciles increases to five times by 20 years. Thus, the volume growth of the shortest trees at 5 years generally declines through time, while that of the tallest trees increases through 15 years and is maintained thereafter. The differences in the growth rates of the deciles are undoubtedly related to changes in the relative canopy positions of the trees. The trees in the lower deciles are constantly being shifted to subordinate positions within the canopy where their growth rates decline. In contrast, the superior canopy positions of the tallest trees enables them to maintain their high rates of growth.

The relative size of trees when the canopy closes is strongly related to their subsequent development. At 20 years the tenth decile trees are 60% greater in diameter than the first decile trees and have almost three times more volume (Table 1). The high rates of growth and low mortality of the tallest trees at 5 years enables them to make large contributions to the second decade volume growth (Table 1). Thus, the contribution to the total volume growth during the second decade is not equally distributed among the deciles. The tenth or tallest decile produces almost 25 times the volume growth of the first decile. In addition, the taller 50% of the trees at 5 years produces 70% of the second decade volume increment.

Table 1. The average properties at 20 years of the population deciles identified at 5 years and their percentage contribution to second decade volume increment.

Decile at 5 years	Twentieth year			Second Decade Volume Increment
	Mean DBH	Volume	Survival	
	-cm-	$10^{-2} \frac{3}{m}$	-%-	-%-
1	14	13	21	< 1
2	16	16	65	4
3	17	18	70	6
4	18	21	86	9
5	19	24	92	11
6	20	25	95	12
7	20	26	94	12
8	21	28	95	14
9	22	30	97	14
10	23	34	97	17

The trees in the lower deciles also have lower survival because of their subordinant canopy position. For example, only 20% of the trees in the first decile at 5 years are still living at 20 years, while the upper five deciles average 95% (Table 1). In addition, nearly 90% of the mortality from 5 to 20 years occurs in the shorter 50% of the trees at 5 years.

Components of Productivity

General Patterns. The volume and basal area increment of forest stands can be partitioned between gross, net, and mortality. Gross increment is the total productivity for a time period, net is the change in the standing crop during the period, and mortality is the loss for the period. Thus, net = gross - mortality. Mortality is a reality in natural populations whether they are from selected materials or not, although this phenomenon has been poorly quantified in past studies of stand performance. The pattern of mortality during stand development is important in shaping the growth curve of stands and is related to the four periods that characterize this curve (Figure 6).

During the acceleration period mortality is negligible and thus net increment is equal to the gross increment. The attainment of K during this period is low (< 20%) and the opportunities for growth are great. The trees have not fully occupied the site and thus the high rates of growth are a fair reflection of the biotic potential. The stand is also rapidly increasing in foliar mass, and at the end of the period maximum levels of foliage are achieved. During this period small increases in the approach to K result in large increases in the current annual increment. For example, with an increase from 5 to 10% of K, net increment increases by almost one-half. In contrast, an increase from 10 to 15% of K results in only a 10% increase in increment.

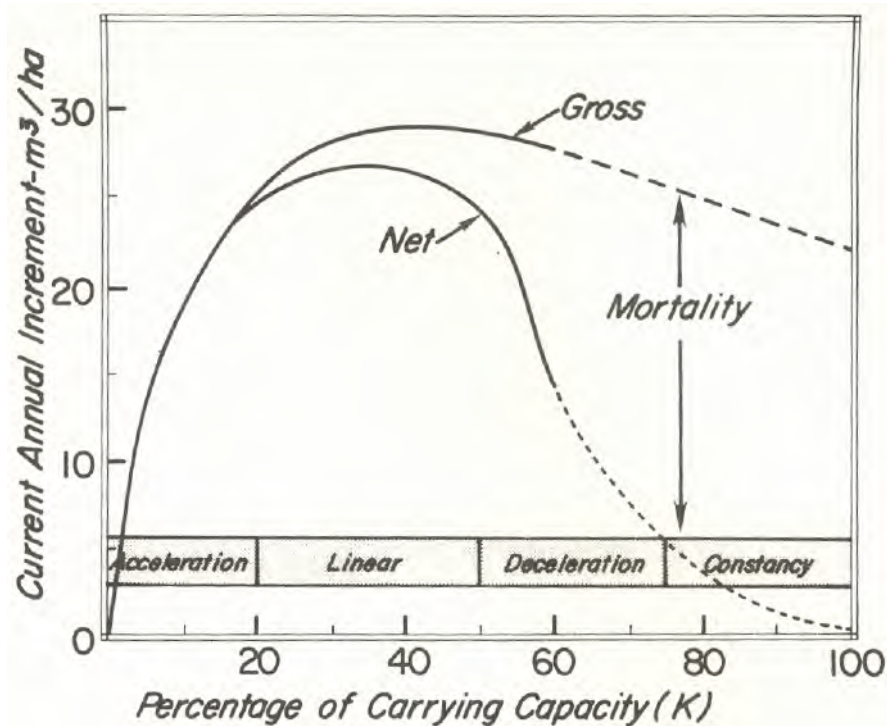


Figure 6. The relationship of the components of current annual volume increment and the volume of the standing crop expressed as a percentage of the sites carrying capacity (600 m³/ha). Data through 60% of K are from a loblolly pine spacing study, with a site index of 29 m at 50 years. The dashed portion of the curves are speculative.

The maximum rates of gross and net increment approach 25 m³/ha during the linear period, which extends from 20 to 50% of K. The foliar mass of the stand is maintained at constant levels during this period, and thus, increases in the crown size of individual trees are at the expense of its neighbors. As a consequence, mortality commences and the net increment falls below the gross increment.

The continued impress of mortality is reflected in the decline of net increment during the deceleration period, which extends from 50 to 80% of K. The increased rates of mortality result from the declining growth rates of the trees in the lower canopy, while those in the upper canopy continue to grow at high rates. The trees in the lower canopy are shifted to even lower positions, where they are unable to sustain life.

Since the carrying capacity is reached during the constancy period, net increment approaches zero, and thereafter, the standing crop is maintained at a constant level. Thus, a steady state exists where the gains from gross increment are offset by losses to mortality. In reality there are temporal fluctuations about the carrying capacity (Bormann and Likens 1979), and this value represents a longterm mean.

Implications. The improvement of growth rates realized from genetic selection will undoubtedly modify the behavior of population development. However, the growth of the population will still be restricted by the determinants of the growth curve. Within the current limits of forest management, the values of K are primarily fixed by the abiotic elements of the environment (Jenny 1980), while R is more flexible and can be modified by management techniques, such as using improved growing stock or varying the initial spacing.

A comparison of the effects of improved growth rates on the basal area development of loblolly pine plantations is illustrated in Figure 7. In this comparison, the improved growth rates achieved through the use of closer initial spacings are considered to be comparable to those attained by genetic selection. The stand with a closer spacing reaches full occupancy of the site earlier than that with a wider spacing. For example, the carrying capacity of the site (40-45 m²/ha) is reached at 13 years with the closer spacing while the wider spacing takes 19 years. This pattern of stand behavior is similar to that observed with improved growth rates in agronomic crops (Evans 1980) and is also anticipated in stands comprised of trees with improved growth rates.

As a result of the more rapid attainment of carrying capacity the gross increment of the closer spacing at 20 years is 25% greater than that of the wider spacing. However, the increased growth rate represented by the closer spacing intensifies the competition of trees for limited resources, and through 20 years, mortality is five times greater in the closer spacing than in the wider. Thus, at 20 years, mortality has offset the gains from increased growth and the net production of basal area at that age is the same for both spacings. Therefore, capitalization on improved rates of stand growth, whether from closer

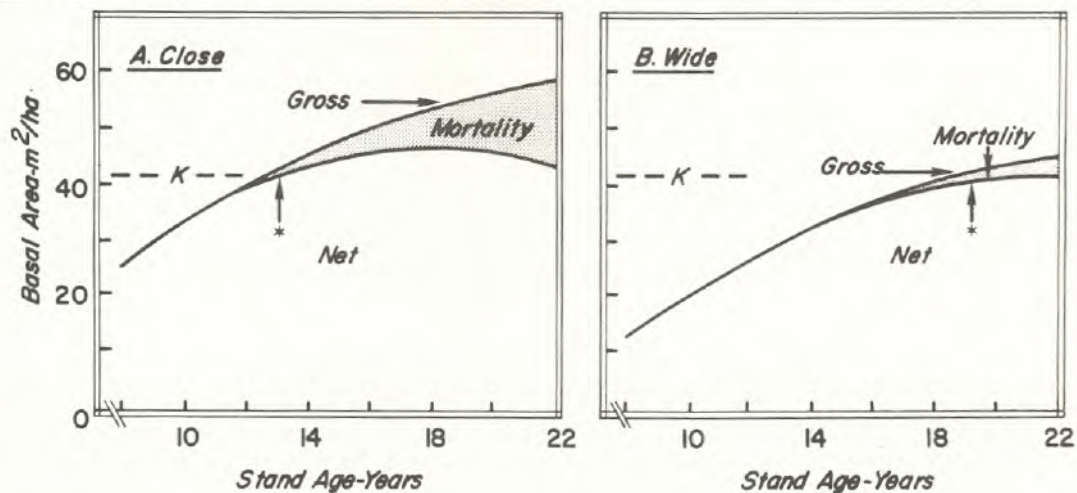


Figure 7. The components of basal area development in loblolly pine plantations at different initial spacings. (A) Close spacings (4300 trees/ha) represent improved rates of growth. (B) Wide spacings (1200 trees/ha) represent unimproved rates of growth. The starred arrows indicate when 90% of the sites carrying capacity is reached.

spacings or genetically improved growing stock, will require or enable the use of shorter rotations and frequent thinnings. These thinnings will lower the level of the standing crop below K and maintain the stand in the linear period of growth. Improved growth rates coupled with improved quality may also permit wider initial spacings in plantations, earlier achievement of desirable merchantable size, and a rapid realization of K.

CONCLUSIONS

The determinants of stand productivity are the relatively fixed abiotic elements and the comparatively flexible biotic elements. The flexibility of the biotic elements permits modification of their character through the silvicultural manipulation of stand structure, composition, density, etc. All of these stand properties are related to genetic character. The modification of the biotic elements requires effort and the application of skills. However, such efforts are not equal to those required to modify the relatively fixed abiotic elements, although such modifications, beneficial or detrimental, may be more lasting. The increased yields of present day agriculture have been achieved by simultaneously modifying both the biotic and abiotic elements (Pimentel et al. 1973) and are therefore not likely to be broadly applicable in forestry. The scale of time and area in forestry and the comparative value of forest crops sharply limits the wholesale transfer of such technology. Also, real crop yields in agriculture are often only about one-half to one-third of those attained under experimental conditions (Milthorpe and Moorby 1974). If the geometry and logistics of agriculture (Frink and Horsfall 1980) has this magnitude of influence on realized yields, what are the realities for forest management?

The determinants of the classic growth curve have implications in evaluating genetic improvement. Firstly, they indicate that evaluations of growth rates based on individual tree behavior are not applicable to stand conditions since they do not consider the limitations of space and/or resources (Ford 1976). Secondly, the determinants indicate that improved growth rates will enable or require the use of more intensive stand culture to realize the gains, i. e. shorter rotations, more frequent thinnings, etc. This requirement needs to be recognized and its desirability evaluated. Thirdly, if the experience with agronomic crops is valid for the forest (Evans 1980), the relatively fixed carrying capacity is not likely to be changed by selection based on improved rates of growth.

The results of our efforts to improve the performance of forest trees through applied genetics are generally real and in some cases noteworthy. However, the realities of using this improvement in the varied area of applied forest management has not been sufficiently evaluated. Until then, the traits that improve the quality of forest stands will undoubtedly be the most genuine improvements.

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