PHYSIOLOGICAL CHARACTERISTICS OF LOBLOLLY PINE SEEDLINGS IN RELATION TO FIELD PERFORMANCE

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Abstract. The physiological processes of pine seedlings are important because they are the machinery through which heredity and cultural practices operate to determine seedling quality. The physiological effects of nursery location and of cultural practices such as seedling density, fertilization, irrigation, and wrenching are discussed briefly and some research needs are indicated. More careful monitoring of water and mineral status in the nursery and of oxygen and ethylene concentration in storage seems desirable. There also is need for a better understanding of the physiology and biochemistry of shoot dormancy and its relationship to root growth potential. This will require basic research on the accumulation of food and growth regulators and their translocation in relation to the onset and breaking of shoot dormancy and to changes in root growth potential. Such an understanding is complicated by evidence of significant differences among families and provenances within a species as well as by differences among species.

Additional key words. Southern pines, seedling physiology, root growth potential, shoot and root dormancy, research needs

INTRODUCTION

Hundreds of millions of southern pine seedlings are grown in nurseries and outplanted every year, usually with mixed survival results. Even a small increase in the percentage of survival would be economically advantageous, but according to Weaver et al. (1980) and Venator (1981) there was a decrease in survival from 1976 to 1981. It is not clear whether this resulted from deterioration in seedling quality, from unfavorable weather or from other causes such as planting on less favorable sites or less severe culling of seedlings. In 1982 Johnson et al. did a problem analysis of pine seedling production in the South. From this survey of 114 people associated with southern nursery operations and research, one of the results pointed to the need for more information on seedling physiology. First priority was given to the need for more information concerning the effects of cultural practices in the nursery on seedling quality as indicated by survival and performance in the field. The second priority was the need for more information concerning the effects of various fertilizer practices.

Most of the improvement in seedling quality that has occurred over the years has been made empirically by trial and error. However, the trial and error process probably has gone as far as it can, and it is time to find a more logical basis for improving nursery practices, based on the physiological requirements of seedlings. Even today quality of seedlings often is judged on size and other morphological characteristics, although nearly 40 years ago Wakeley (1948) pointed out that morphological grades are not a reliable indicator of survival in the field and asked for a physiological indicator of seedling quality. The quality of seedlings depends in part on physiological characteristics that cannot be evaluated by visual inspection. Unfortunately we have made little progress during the 40 years since Wakeley stated the problem.

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The physiological processes of seedlings are the machinery through which their hereditary potentialities and their environment interact to produce seedlings of good or poor quality (see Fig. 1). If there are differences in the success of different genetic families, it is because their physiological processes react differently to the environment in which they are grown. Likewise if different cultural or storage conditions affect seedling quality, it is because they affect the physiological processes that control the quantity and quality of growth.

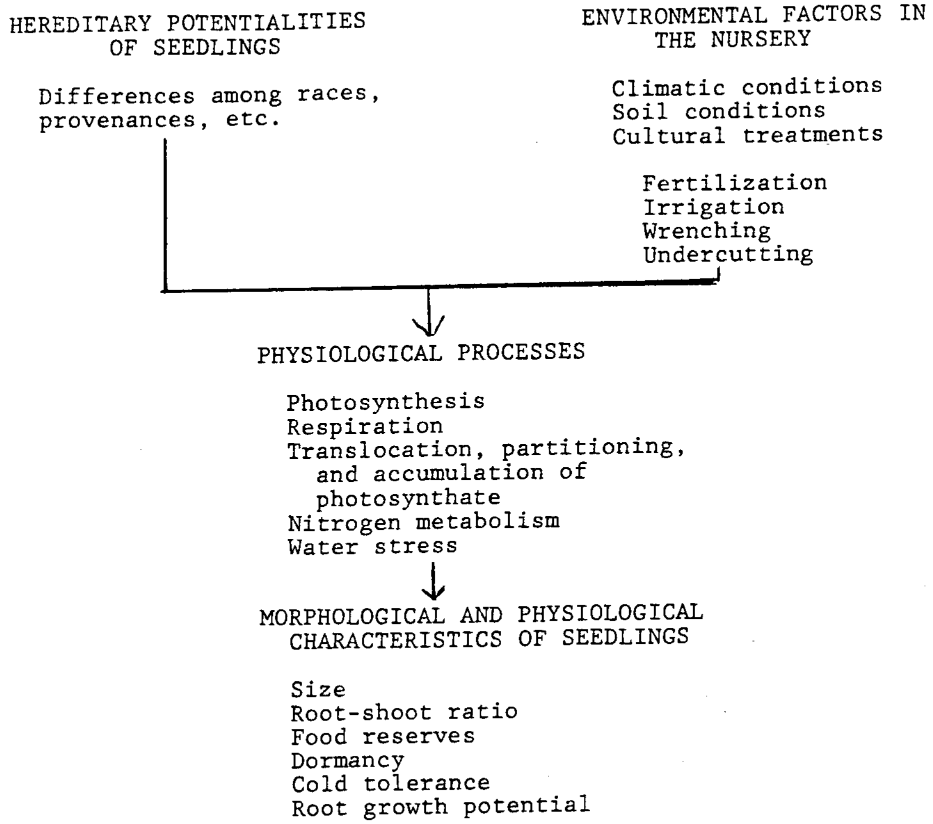

Fig. 1. Hereditary potentialities and environmental factors operate through physiological processes to control seedling characteristics.

Tree seedlings can be regarded as complex biochemical factories which, unlike industrial factories, build themselves out of a few raw materials or reagents available in their environment. The basic physiological processes of these plant factories include photosynthesis and the translocation, partitioning, and accumulation of photosynthate; respiration, carbohydrate and nitrogen metabolism; and plant water stress, which is controlled by the relative rates of water absorption and loss.

Growth regulators and enzymes play an important but poorly understood role in the seasonal changes between growth and dormancy, the seasonal variations in root growth potential, and the partitioning of photosynthate between roots and shoots during storage and after outplanting. The environmental requirements for growth are relatively simple: light and CO_2 for photosynthesis, oxygen for respiration, mineral nutrients and nitrogen as raw materials in the synthesis of various compounds, water as a reagent and to maintain the cell turgor necessary for growth, and a suitable temperature for the physiological and biochemical processes to operate efficiently.

The success or failure of nursery practices really depends on the extent to which they promote favorable physiological processes. All successful nursery practices favor beneficial physiological conditions in seedlings, but they are often used without fully realizing *why* they are successful. Nursery managers tend to judge their cultural practices by the end result in seedling quality without realizing that the physiological processes of the seedling are the intermediate step between cultural practices and seedling quality. The role of plant physiology in the production of tree seedlings is to identify the physiological processes that most often limit seedling growth and quality and determine which environmental factors most often limit these processes. This information should aid nursery managers to modify cultural practices, compensate for varying environmental conditions in a logical manner, and achieve greater success in seedling field performance (Duryea and McClain, 1984).

The numerous factors that interact to affect seedling quality are shown in Figure 2. The endogenous factors of this diagram include both the genetic potentialities and the physiological processes and conditions of Figure 1, while the exogenous factors are the environmental factors of that figure, presented in more detail. For this paper we will divide our discussion into five major headings: nursery conditions, condition of seedlings at lifting, storage conditions, conditions at and after planting, and research needs. Emphasis is placed on the physiological processes that are affected at each stage of seedling production and after planting.

NURSERY CONDITIONS THAT AFFECT SEEDLING QUALITY

Wakeley (1948) suggested that differences in such nursery practices as fertilization, watering, and use of fungicides explained some of the differences in seedling quality that he observed. The possible effects of nursery location and nursery practices on physiological processes also will be discussed in this section.

Nursery Location

There are certain basic considerations such as climate, physical properties of the soil and good drainage that should be dominant factors in nursery site selection. Unfavorable soil conditions operate by inhibiting the physiological processes involved in root growth while climatic effects of nursery location can operate through temperature and photoperiod effects on seedling physiology, mycorrhizal association, and susceptibility to disease.

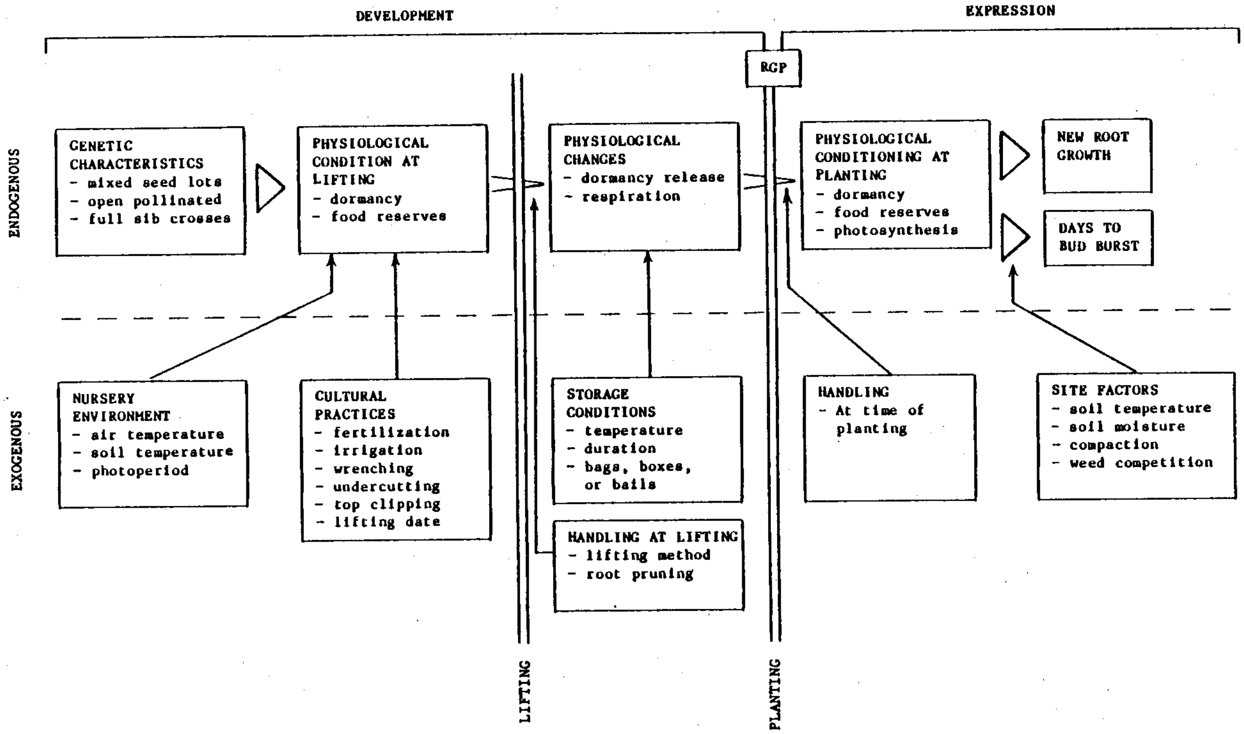

Fig. 2. Factors affecting seedling development, root growth potential, and time to bud burst. (Adapted from Ritchie and Dunlap, 1980.)

Elevation is an important site factor in nurseries in the western United States where some species require an accumulation of cool nights to develop good root growth potential (Krugman and Stone, 1966) and interruption by periods of warm weather in the autumn is unfavorable to this process. As a result, some low altitude nurseries in California are said to consistently produce seedlings of such species as the true firs (*Abies concolor* and *A. magnifica*) with low root growth potentials (Stone *et al.*, 1963; Stone and Norberg, 1979).

In the eastern United States most nurseries for southern pines are in the Coastal Plain or lower Piedmont where the differences in temperature accompanying the minor differences in elevation are small. However, phytotron experiments indicate that the lower the night temperature relative to the day temperature, the greater the height growth of loblolly pine seedlings (Kramer, 1957). For example, with a day temperature of 23°C reducing the night temperature from 23° to 17° increased height growth 58%, or 1.5 cm per degree. Cooler nights reduce respiration relative to photosynthesis and also increase the partitioning of photosynthate to root growth. In view of the large effects of a small decrease in night temperature, temperature differences among nurseries may be more important than generally supposed. It appears that more experiments on the effects of nursery location, similar to that described earlier in this volume by Rose, are needed. Although there are significant differences in latitude, photoperiod, and the number of chilling hours between nurseries in the Carolinas and Florida, this does not seem to be a limiting factor to seedling production. McGregor *et al.* (1961) reported that long days increased the growth of loblolly pine seedlings from Florida more than growth of Georgia seedlings, but there was no difference in rates of photosynthesis or respiration per unit of leaf tissue. Barney (1951) found little difference in the effect of temperature on root growth of loblolly pine seedlings grown from North Carolina and Louisiana seed and Carlson (1985a) found no differences in the numbers of new roots produced between North Carolina Coastal Plain and Piedmont families of loblolly pine treated similarly. However, he did find wide differences in time to bud break among seedlings of families from different areas of the Southeast when lifted after 207 h of chilling below 8°C and placed in a warm humid environment. Seedlings from Alabama and Mississippi families broke dormancy sooner than those from the North Carolina Piedmont families, and there were small differences between North Carolina Coastal and Piedmont families. It is not uncommon for a single nursery to raise loblolly seedlings from a diverse assortment of seed sources collected over a wide geographical range. However, Wakeley (1944) reported that loblolly pine trees grown at Bogalusa, Ga., from local seed were much larger and healthier after 15 years than trees grown from seed collected in other states. It seems that seedlings grown from seed from different geographic sources ought to be kept separate.

Seedbed Density

The preferred density of seedlings in the seedbed has varied over the years and in different nurseries. Nursery managers often favor high density for economic reasons, but there is considerable evidence that too high a density decreases seedling size and probably seedling quality (Duryea and McClain, 1984). It certainly results in slender seedlings with small stem diameters, less photosynthetic surface, and smaller root volumes. More than 20 years ago Switzer and Nelson (1963) observed that the height growth of loblolly pine seedlings was increased for three years after outplanting by decreased density and heavier fertilization while in the nursery bed. Wearstler (1979) grew 17 families of loblolly pine at three densities. The general relationship of increasing size with decreasing density held for all components of total seedling dry weight, including root/branch-stem/foliage. Figure 3 shows the relationship between dry weight and density for several families having different growth rates. A unique aspect of this experiment was the testing of the null hypothesis that there are no differences in slope of the maximum dry-weight/diameter-density relationships for different loblolly pine families. The attempt was moderately successful and supports the basic concept of the -3/2 power law currently being applied to modeling the growth of timber stands. That law was mentioned earlier by Cannell and the effects of density are discussed in several other papers in this volume.

Fertilization

Fertilization practices seem relatively satisfactory today in contrast to past times when some foresters mistakenly thought they could produce hardier seedlings by restricting the supply of mineral nutrients. Deficiencies of mineral nutrients severe enough to seriously disturb physiological processes are seldom seen in modern forest nurseries. However, better control of fertilization is desirable, both economically and physiologically, and better methods of monitoring the fertilizer supply are needed. Foliar diagnosis, based on analysis of the chemical composition of leaves has been used on a variety of horticultural and agronomic crops and probably can be adapted for use

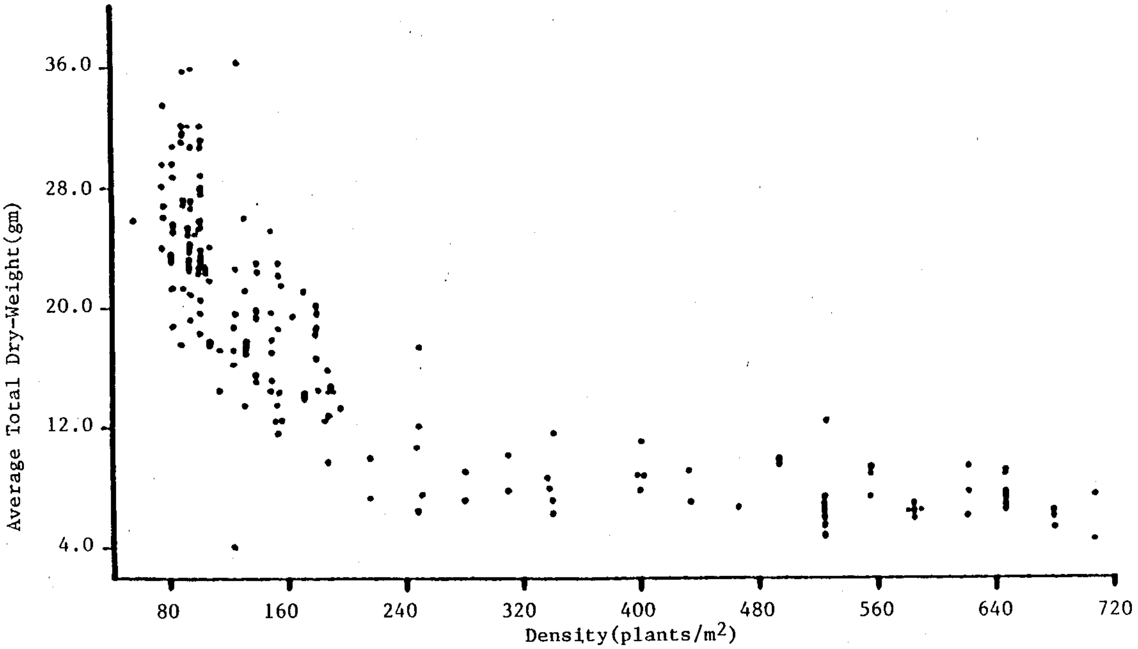

Fig. 3. Scatter diagram of average dry weight per seedling after two growing seasons at various plant densities. (From Wearstler, 1979.)

in nurseries (van den Driesche, 1974). Nitrogen supply needs close attention because it affects needle growth, root-shoot ratio, drought tolerance, and length of growing season. There appears to be an interaction between nitrogen supply, growth, and drought injury such that too much nitrogen can increase the severity of injury (Pharis and Kramer, 1964), but this problem needs more research. Heavy fertilization with nitrogen late in the growing season can postpone the onset of dormancy and cold tolerance, resulting in frost injury. However, where mineral nutrition is marginal fertilization after top growth has ceased might increase photosynthesis in the autumn and early winter and increase the supply of reserve food. This situation should be investigated. Many investigators have emphasized the important interactions between fertilization and other nursery practices such as seedling density, irrigation, and wrenching, but no consistent relationship between mineral nutrition and seedling quality has been established in the absence of severe deficiencies (Duryea and Landis, 1984).

Irrigation

Water stress affects both the physiology and morphology of seedlings as pointed out in an earlier paper in this volume. Drought during the growing season reduces growth directly by inhibiting cell expansion and indirectly by causing stomatal closure, reduction in photosynthesis, and disturbance of processes such as carbohydrate and nitrogen metabolism (also see Johnson _et al_. in this volume). Excessive rain or irrigation can leach out fertilizer and create local soil aeration problems. Cleary and Zaerr (1980) recommended frequent irrigation of Douglas fir (_Pseudotsuga menziesii_ (Mirb.) Franco) and ponderosa pine (_Pinus ponderosa_ Laws) seedlings until midsummer to encourage good growth and less frequent irrigation in late summer and fall to encourage development of dormancy. Probably the same general principle applies to management of irrigation of southern pines.

In agriculture, the timing of irrigation is controlled by measurements of soil water stress, plant water stress, or from evaporation data combined with knowledge of the water holding capacity of the soil, sometimes termed the water budget method (Kramer, 1983, pp. 111-115). Seedlings themselves really are the best instruments to monitor water status because they integrate soil and atmospheric moisture conditions. Whitehead (1980) suggested monitoring seedling water status by measurements of stomatal conductance with a diffusion porometer and water potential with a pressure chamber. Cleary and Zaerr (1980) described use of the Scholander pressure chamber to monitor water stress in western conifer seedlings and reported that water potentials below -10 bars reduced photosynthesis of Douglas fir. The same general principles apply to irrigation of southern pine seedlings, but more specific information is needed. Furthermore, irrigation scheduling in the Southeast is complicated by the unpredictability of summer rainfall.

It is widely believed that exposure to moderate water stress will "harden" seedlings so they will be more tolerant of drought after transplanting than unstressed seedlings. The increase in drought tolerance often is attributed to development of a larger root-shoot ratio in stressed seedlings. However, Rook (1973) found that although water stress reduced the overall size of _Pinus radiata_ seedlings it did not change the root-shoot ratio, but increases have been reported in herbaceous plants (Sharp and Davies, 1979). According to Rook (1973) the needles of stressed seedlings had a thicker cuticle and more responsive stomata than those of unstressed seedlings, but the latter acclimated rapidly to drier conditions after transplanting. Seedlings watered weekly and therefore moderately stressed prior to transplanting made more root growth during the first 18 days after transplanting than those watered more or less frequently, but this difference had disappeared by 40 days after transplanting. McNabb (1985) also reported that repeated moderate stress cycles are better than a prolonged period of severe stress in conditioning slash pine (_Pinus elliotti_, var. _elliotti_) seedlings. Bacon and Bachelard (1978) also reported evidence of physiological conditioning of Caribbean pine (_Pinus caribaea_) seedlings. This probably is because moderate stress "conditions" stomata to become less responsive to stress and allows osmotic adjustment to occur (Hennessey and Dougherty, 1984; Johnson _et al_., this volume). The physiological basis of "hardening" by moderate water stress needs more study.

Water stress applied too early in the season is likely to cause an undesirable reduction in growth while water stress toward the end of the growing season will hasten the development of dormancy but might reduce photosynthesis and accumulation of food reserves. More research on the effects of water stress at various stages of development of southern pine seedlings might provide a better basis for the timing of irrigation.

Undercutting, and Wrenching

It has long been the practice in nurseries to cut off all roots extending deeper into the soil than 12 to 20 cm by running a cutting bar under the seed bed before lifting seedlings. This produces seedlings with shallow, but more extensively branched root systems that are easier to lift. Root pruning of *Pinus radiata* seedlings after lifting, but before replanting sharply reduced stomatal conductance, photosynthesis, and transpiration, and the rate of photosynthesis was only 60% of the initial rate 30 days after root pruning (Stupendick and Shepherd, 1980). McNabb (1985) reported that repeated undercutting of seedlings of slash pine (*Pinus elliottii*, var. *elliottii* in November and December resulted in increased root growth and survival over controls after outplanting in January. Another nursery practice is "wrenching" which involves loosening the soil, temporarily decreasing the contact between soil and roots. This temporarily increases seedling water stress, but it also increases the production of secondary roots, resulting in a more fibrous root system and usually a larger root-shoot ratio (Rook, 1971; van Dorsser and Rook, 1972; Nambiar *et al*., 1979). Tanaka *et al*. (1976) compared wrenched and non-wrenched loblolly seedlings when outplanted and reported that the wrenched seedlings had significantly larger root-shoot ratios and higher survival. Lateral roots made up 60% of each root system (dry weight basis) of wrenched seedlings versus 43% for non-wrenched seedlings. Similar increases in number of fine roots were reported for loblolly pine by Dierauf (1984) and for slash pine by McNabb (1985). Miller *et al*. (1984) found that wrenching during the growing season reduced total starch content of roots at lifting in January compared with non-wrenched seedlings. The reduction in starch content after wrenching probably resulted from reduction in photosynthesis, but the benefit from a more fibrous root system seems to outweigh any detrimental effects from reduction in starch content. Perhaps an evaluation should be made of the relative importance of wrenching on root system morphology compared to its transient effect through seedling water stress, as suggested by Bacon in this volume.

Shoot Pruning

Clipping off part of the foliage is another method of increasing the root-shoot ratio and partially compensating for loss of roots during transplanting, thereby maintaining a better balance between absorbing and transpiring surfaces. Allen (1955) reported that clipping the foliage of longleaf pine seedlings to a length of 10 to 12.5 cm near the time of lifting increased survival the first year by 10 to 30% in various experiments. Clipping of longleaf pine should be done no earlier than November, or it may reduce the accumulation of carbohydrates. Miller *et al*. (1984) reported that although wrenching reduced seedling size and starch content of roots there was no significant interaction between top pruning and wrenching of loblolly pine seedlings with respect to characteristics such as seedling height, diameter, root-shoot ratio or needle nutrient level.

Special Techniques

Some special techniques deserve at least brief mention. Among these are container-grown seedlings, use of tissue culture plantlets, and inoculation to produce mycorrhizae.

Container-Grown Seedlings. In recent years there has been increasing interest in growing seedlings in containers. This is at least in part because

use of containers permits producing a crop at any time of year and use of container-grown seedlings lengthens the planting period. Also because of more uniform growing conditions seedlings are more uniform and there are fewer culls. Container-grown seedlings are subjected to the same stresses as nursery grown seedlings when outplanted, and in general the same morphological and physiological characteristics are important for both types of seedlings. Experience with container-grown seedlings was summarized by Barnett in Duryea and Brown (1984) and discussed in several papers in this volume. One factor not discussed by these authors is the possible beneficial effects of increasing the CO_2 concentration of the air in enclosures where seedlings are grown in containers. Experience in the Duke University phytotron indicates that increasing the CO_2 concentration causes increased height and diameter growth in loblolly pine seedlings (Sionit, et al., 1985).

Tissue Culture Plantlets. The production of plantable seedlings by tissue culture methods is of increasing interest. Many of the concepts applied to growing nursery seedlings will apply to the production of seedlings from tissue culture plantlets and it can be anticipated that many of the same problems and questions will develop. Some of what is being discovered about tissue culture plantlets may be useful for improving our understanding of pine seedling physiology.

Wisniewski et al. (1983) grew tissue culture plantlets, rooted hypocotyls, excised embryos, and seedlings from seed of loblolly pine in the nursery and greenhouse. Survival of all four plant types in both environments was excellent. After the fourth month, nursery performance was better than greenhouse performance of all four plant types with respect to height growth. McKeand and Allen (1984) compared mineral nutrition and root development of tissue culture plantlets of loblolly pine with that of seedlings. Plantlets had lower concentrations of nitrogen and phosphorus per gram of shoot dry weight, but the main difference between plantlets and seedlings was in root system morphology. The plantlets had thick, unbranched roots and this appeared to reduce nutrient uptake. Root pruning appeared to have the same beneficial effects on loblolly tissue culture plantlets as on seedlings from seed. Frampton (1984) found that August root pruning reduced plantlet and seedling October heights equally relative to the non-pruned plants. The pruned plantlets grew 25.9 cm the first season after outplanting versus 4.3 cm for the non-pruned plantlets. Some of the possibilities and problems of propagation by tissue culture are discussed in Duryea and Brown (1984) and vegetative propagation is discussed in other chapters of this volume. Increasing the concentration of CO_2 probably will be beneficial in the production of tissue culture plantlets.

Mycorrhizae. The importance of mycorrhizae in relation to mineral and water absorption and as protection against certain soil pathogens has been recognized for many years and discussed in hundreds of papers. Marx and Artman (1978) reported large increases in fresh weight of loblolly pine seedlings inoculated with mycorrhizal-forming fungi and Reid et al. (1983) and Rygiewicz and Bledsoe (1984) discussed their role in mineral absorption. Although seedlings usually are naturally infected from fungi in the soil, nursery bed fumigation often eliminates such fungi. This suggests that artificial inoculation of seedlings might sometimes be beneficial. This problem was discussed by Mexal (1980) who pointed out the potential advantages and the uncertainties related to inoculation.

SEEDLING CONDITIONS WHEN LIFTED

The objective of treatments in the nursery bed is to produce seedlings as economically as possible with the highest possible probability of survival when transferred to the field. Survival and growth depend on both the morphological and physiological characteristics of the seedlings at the time of planting and this depends on both the condition when lifted and the effects of storage between lifting and planting.

Morphological Characteristics

Much has been written about seedling grades since Wakeley's book, Planting the Southern Pines (1954) appeared. It is widely accepted that a good loblolly seedling is 20 to 25 cm in height with a woody stem 4 to 5 mm in diameter, a fibrous root system, well developed terminal buds, and a good distribution of needles. Measuring such traits is easy and straight forward. In the nursery, morphological characteristics often are linked to physiological characteristics and size and physical ratios are often regarded as being indirect indicators of physiological vigor. The tendency is to assume that physiological needs of the seedlings have been met if the morphological characteristics fall within a pre-determined set of grading guidelines. However, most nurserymen will agree that the above assumption often is invalid, a point made nearly 40 years ago by Wakeley (1948) and more recently by others. The problem is that a seedling that is vigorous in appearance does not necessarily have the physiological characteristics necessary to survive storage and resume growth when outplanted. These characteristics will be discussed later.

Carlson (1985b) emphasized the positive relationship of initial root volume to new root growth because a large volume of roots provides more absorbing surface and more sites for production of new roots. Loblolly seedlings with 3.5 ml volume root systems had hydraulic conductivities 7 times higher than 1 ml volume root systems. After root elongation, the larger root system had 1.9 times more roots capable of conducting 2.1 times more water than the smaller root system. Lopushinsky and Beebe (1976) reported that seedlings of Douglas fir and ponderosa pine with large root systems survived and grew better than those with small root systems. Although Cleary et al. (1978) agree that seedlings with high root-shoot ratio are more likely to survive on dry sites, they warn that root-shoot ratio should not be used alone as an indicator of survival potential.

Important Physiological Characteristics of Seedlings

Probably the most important physiological characteristics of seedlings are the ability to resume root growth promptly after transplanting and enough reserve food to support this growth. Most deaths of transplanted seedlings apparently result from dehydration, caused by root systems inadequate to supply the water required for the maintenance of turgidity. Although pine seedlings absorb water through suberized roots (Kramer and Bullock, 1966), dangerous dehydration can be avoided only if new roots begin to occupy a large volume of soil immediately after outplanting, especially during droughts. Cold tolerance also may be important for early planting.

Root Growth Potential

The ability of seedling root systems to resume growth when transplanted is termed the root growth potential, generally abbreviated as RGP. It usually is tested by planting seedlings in a favorable environment such as a greenhouse or growth chamber and after 30 or more days excavating them and observing the percentage of seedlings that show root elongation and the number of elongating roots per seedling (Ritchie and Dunlap, 1980). Sometimes RGP is measured by the total length of new roots formed rather than by the number. According to Ritchie and Dunlap (1980, p. 220), in Douglas fir the peaks for number, length, and rate of growth of new roots do not coincide. They suggested that RGP be expressed as the number of new roots produced. According to Dewald _et al_. (1984) and Rose and Whiles (1984), the RGP of southern pine seedlings can be evaluated by growing them hydroponically in a nutrient solution for only 15 to 20 days. It has been questioned whether testing for RGP under favorable conditions in a greenhouse is a good indicator of behavior in the field. However, Rook (1973) found the same relative RGPs among seedlings of various past treatments when transplanted and grown with various degrees of water stress.

Among the early studies of RGP were those of Stone and his colleagues on western conifers, including Douglas fir, the true firs, and ponderosa pine. These showed large seasonal differences in RGP of seedlings, with the lowest potential in the summer, increase during the autumn to a peak in the winter, and then decrease during the spring to the summer's low. This cycle applied both to the elongation of existing lateral roots and to the initiation of new roots (Stone, 1955; Stone and Schubert, 1959; Stone _et al_., 1962; Stone and Jenkinson, 1971). However, initiation of new roots seemed to lag behind elongation of existing lateral roots (Stone and Schubert, 1959).

Unfortunately, there seem to be few systematic evaluations of seasonal variations in RGP of southern pines. However, it is well documented that some root growth occurs in the field on loblolly and shortleaf pine plantations in every month of the year. Reed (1939) observed root growth every month of the year on 6 year old trees of these two species in a plantation at Durham, North Carolina and growth of roots was observed in every week of the year for two years in a nursery in Arkansas by Turner (1936). Both investigators reported that growth in the winter was reduced by cold soil and in the summer by dry soil, and most rapid growth occurred in the spring when both temperature and soil water conditions were favorable. Although these data indicate that root elongation can occur throughout the year, they do not provide any information concerning endogenous seasonal variations in ability to produce new roots independent of environmental factors. As mentioned earlier, the extensive data of Carlson (1985a) (see Fig. 4) indicate differences in seasonal RGP among families of loblolly pine, but more data are needed.

Control of Root Growth Potential. Root growth potential seems to be controlled by physiological factors which are poorly understood. We still need to know what stimulates embryonic regions to resume cell division and become sinks for food. Ritchie and Dunlap (1980), in their extensive review of the topic, concluded that initiation of new roots depends on a stimulus from the shoot that may originate in buds or leaves, or both. It probably is translocated downward in the phloem because girdling reduces or stops root growth in loblolly pine (Gilmore, 1961) and some other conifers. Richardson (1958) suggested that it might be the same substance that causes initiation of cambial activity, probably auxin. The role of other growth regulators such as gibberellins, cytokinins, abscisic acid, and ethylene remain uncertain (Ritchie and Dunlap, 1980, pp. 222-223). Zaerr and Lavender (1980) predicted that development of new analytical techniques would increase our knowledge of the role of growth regulators but little progress has been made. There appears to be some relationship between bud dormancy and root growth in trees native to cool climates, and both Krugman and Stone (1966) and Ritchie and Dunlap (1980) state that cool weather in the autumn hastens the increase of RGP of western conifers. Ritchie and Dunlap (1980; pp. 224-227) cite other observations indicating that as chilling breaks physiological shoot dormancy, RGP increases in a number of species. However, significant differences among families and provenances of a species and among species make generalizations difficult.

According to W. C. Carlson (1985a), chilling in storage hastens bud break in loblolly pine seedlings as effectively as natural chilling, but there are significant differences among families and provenances in response to chilling. The effect of chilling on RGP was somewhat less than the effect on bud break, although RGP tended to increase as days to bud burst decreased (Figure 4). Carlson also observed that root growth potential of seedlings lifted in late November was reduced by 500 h in cold storage, but storage had little effect on seedlings lifted in January. Johnson (1984) found that exposing loblolly seedlings in storage to 8 or 16 hour photoperiods accelerated bud activity during the first two months after planting, but little information is available concerning effects of illumination during storage.

Food Reserves. Another requirement for successful establishment of seedlings is a food reserve sufficient to maintain them through storage and planting, until they can reestablish normal photosynthesis. Data are needed on the time required for resumption of normal rates of photosynthesis after transplanting. Recovery probably is slow as Stupendick and Shepherd (1980) reported that photosynthesis of *Pinus radiata* seedlings was only beginning to recover 12 days after root pruning and transplanting, although leaf water potential was back to normal in 8 days. According to McNabb (1985) slash pine seedlings resume normal physiological functioning in two to four weeks after outplanting if the water supply is adequate.

A number of attempts have been made to correlate seedling success with carbohydrate reserves, but with conflicting results (Duryea and McClain, 1984, pp. 104-105). Gilmore (1961) reported that shading in the seedbed and in storage both reduced the starch content of loblolly pine seedlings and that in some experiments, survival of transplanted seedlings was correlated with starch content. In later experiments with unshaded seedlings he found no correlation between carbohydrate reserves and root growth or survival

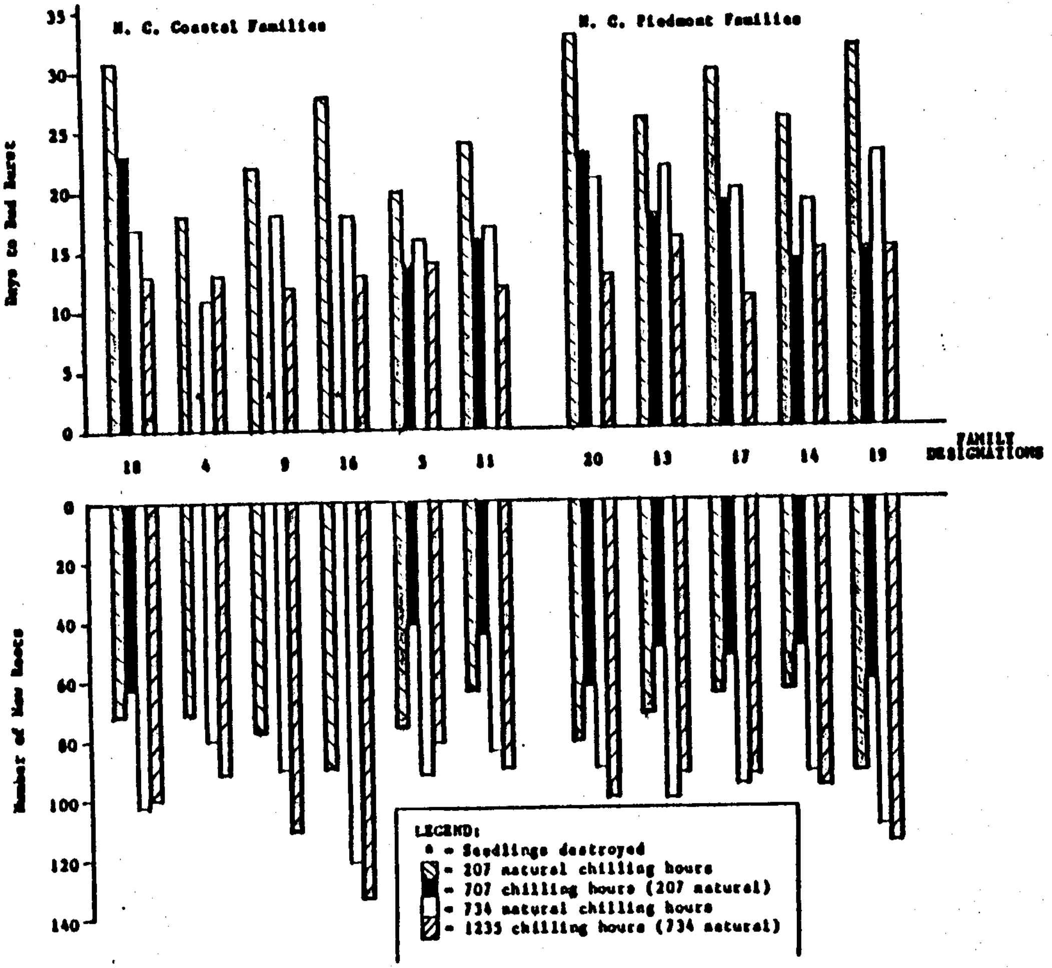

Fig. 4. Effect of length of chilling on days to bud burst and on numbers of new roots produced by various families of loblolly pine. (Adapted from Carlson, 1985a.)

(Gilmore, 1964). Hellmers (1962) stated that the starch content of seedlings of ponderosa and Jeffrey (Pinus jeffreyi) pine could be a good indication of their physiological condition. He also noted that starch is used up first from the top of the plant, and then from the roots and the location of the starch as well as the amount present might indicate the general condition of the planting stock. He was careful to point out that a starch test would not assess other harmful conditions imposed on the seedlings. Rose and Whiles (1984) found that the starch content of lateral roots was not a good indicator of RGP of loblolly pine seedlings. Ronco (1973) did not find any correlation between carbohydrate reserves and field survival of Englemann spruce, and Ritchie (1982) found that the food reserves of Douglas fir seedlings in storage were decreasing while RGP was increasing. It is doubtful if lack of food is often a limiting factor on resumption of root growth of healthy seedlings (Duryea and McClain, 1984; McNabb, 1985). Nevertheless, some minimum amount of reserve food is essential for the establishment of outplanted seedlings. Perhaps, as suggested by Ronco (1973), so long as the carbohydrate content does not fall below some critical level, it does not become a limiting factor. Further research is needed on starch, soluble carbohydrates and lipids and the enzymes involved in their metabolism in both roots and shoots.

Conifers accumulate food reserves in the form of carbohydrates and lipids (Glerum, 1980), but most emphasis has been placed on carbohydrates because starch is the chief reserve food in roots. However, according to Ziegler tree (1964) roots have the potential to produce lipids and do so when subjected to low temperatures. Perhaps more attention should be given to lipid reserves in conifers. Southern pines accumulate most of their reserve carbohydrates during the autumn and winter, after shoot growth has ceased (Kramer and Kozlowski, 1979, pp. 268-277). In fact Hepting (1945) found that carbohydrate concentration in roots of shortleaf pine trees reached its maximum in early spring and McNabb (1985) found the sugar concentration in both roots and shoots of slash pine to be higher in the winter than in the summer. This means that it is important to maintain conditions in the nursery favorable for photosynthesis late in the season. It also is important not to lift seedlings too early in the autumn, before they have accumulated sufficient reserves to support metabolism and growth, if they are to be held in cold storage.

In summary, at lifting seedlings that are to be stored should be physiologically dormant with respect to shoot growth and contain enough reserve food to maintain essential physiological processes through storage and recovery from outplanting. However, reserve food probably is seldom a limiting factor for southern pine seedlings. The condition of seedlings at lifting has such an important effect on their success that some indicator of dormancy is needed. Perhaps a combination of mitotic activity in buds and the amount of starch accumulation would be useful. Observation of the accumulation of chilling hours also might be useful in predicting dormancy. Seasonal variations in mitotic activity of stem tips as an indicator of dormancy were discussed earlier in this volume by Carlson.

According to Garber and Mexal (1980) southern pine seedlings should be lifted between late December and early February, and lifting in mid-March resulted in poor survival. However, the timing certainly will vary from year to year with differences in weather, and it varies among families. Jenkinson (1984) reported that in one California nursery the safe period or "window" for lifting Douglas fir seedlings ranged from 7 to 18 weeks for different seed sources. Perhaps the timing of lifting southern pine seedlings deserves further study.

STORAGE CONDITIONS

The ideal procedure would be to plant seedlings as soon as possible after they are lifted, but soil conditions, weather, logistics, and other considerations often require that they be stored for weeks or even months. Successful storage depends on meeting certain physiological requirements of the seedlings such as a chilling hour requirement, avoidance of dehydration, and the maintenance of a low rate of respiration to conserve stored carbohydrates. Cleary and Zaerr (1980) reported that in Oregon lifted seedlings lose water rapidly during processing and suggested sprinkling seedlings after lifting to prevent dehydration during processing. Sprinkled seedlings survived competition better and made more growth on poor sites than unsprinkled seedlings.

There is general agreement that seedlings need to be physiologically dormant before placing them in storage. Date of lifting and storage experiments tend to show that the field performance of early lifted seedlings is seldom as good as that of seedlings lifted after they are fully dormant. However, Boyer and South in this volume question if the chilling requirement must be fully satisfied before lifting and Carlson (1985a) stated that it could be satisfied in storage. As indicated earlier there is need for a method for determining the peak physiological condition at which to lift and store seedlings. Another primary concern is to find a method for determining prior to planting if the seedlings coming out of storage are physiologically ready to grow. At present the best indicator seems to be the RGP discussed earlier. Proper storage conditions in coolers are well worked out and several researchers spanning a 25 year period (Dierauf, 1984; Kahler and Gilmore, 1961; Williston, 1974) have reported storing loblolly seedlings for periods from 30 to 90 days without decrease in survival when outplanted. Perhaps most loss in RGP during storage occurs because seedlings were placed in storage before they were physiologically ready.

Maintenance of seedlings in a cool (1°C or 34°F), moist (RH>90%) environment is desirable to preserve food reserves by reducing respiration and to prevent dehydration, but other problems can develop that reduce quality. Occasionally, fungi and bacteria cause injury, and oxygen deficits can develop where large masses of seedlings are inadequately ventilated. Ethylene gas tends to accumulate wherever large amounts of plant material are confined in a small space. Stumpff (1984) showed a general trend of increasing ethylene concentrations in K-P bags of stored loblolly seedlings lifted from November through February. Ethylene concentration was significantly affected by the month the seedlings were lifted from the nursery. February-lifted seedlings produced the highest concentrations of ethylene (0.434 ppb/g dry wt.). Stumpff (1984) suggested that ethylene production rates may be related to the level of dormancy of the seedlings, with the peak in production corresponding to fulfillment of the chilling requirement. She reported that exposure of seedlings to concentrations of ethylene as high as 4 ppm for 6 weeks resulted in increased root growth. In contrast, Barnett (1980) reported that addition of an ethylene absorbent to bags of loblolly pine seedlings held in storage for 6 weeks improved their RGP over controls exposed to ethylene, and Hinesley and Saltveit (1980) reported that exposure of Fraser fir seedlings to the high concentration of ethylene found in apple storage chambers (17.5 ppm) reduced growth after planting. The effects of ethylene on seedlings in storage is discussed in this volume by Elam. In view of the inconsistent results reported by different investigators the effects of ethylene in storage deserve more investigation.

CONDITIONS AFTER PLANTING

It is recognized that seedlings of poor quality planted under favorable conditions often survive and become established while under the worst conditions it may be unfair to expect the best quality of seedlings to survive. It must be admitted that there is considerable "luck" with respect to weather and soil conditions in the planting of southern pines.

Seedlings usually are subjected to a period of physiological stress when outplanted. Water stress develops because rapid transpiration during a period when roots are functioning poorly results in temporary dehydration. This inhibits photosynthesis and cell expansion. During this period seedlings are largely dependent on their food reserves. After water stress is relieved and photosynthesis is resumed the seedlings become physiologically independent and growth is resumed. Thus seedling survival seems to depend primarily on development of enough new roots to prevent prolonged water stress. The time after outplanting until root growth is resumed will vary widely with soil temperature and moisture conditions, but usually will be several weeks. McNabb (1985) reported that normal accumulation of carbohydrates was resumed in two to four weeks after outplanting of slash pine seedlings in northern Florida.

Development of new root systems on transplanted seedlings involves both the extension of existing laterals and initiation of new branch roots. The former probably is most important at first and possession of a large number of healthy lateral roots seems important as a base for root extension (Stone *et al.*, 1962; Ritchie and Dunlap, 1980). According to Bushey (1957) seedlings of species such as elm which lose few roots during transplanting survive better than oaks which lose many fibrous roots. Development of root systems of coniferous seedlings was discussed in detail by Sutton (1980). In general, development of new roots depends on the establishment of active meristematic regions at many sites on existing root systems. Continued root growth also depends on the new meristematic regions becoming strong "sinks" to which food is translocated. All of these complex physiological processes benefit from a favorable soil environment.

Environmental Limitations on Root Growth

The most common environmental limitations on the resumption of root growth are cold soil and drought, but occasionally soil flooding causes oxygen to become limiting to root growth. The effects of water deficits require no further discussion, but the effects of cold soil are often neglected. Low soil temperature is an important limitation on root growth of seedlings planted early in the season. It is well established that temperatures below 15°C not only reduce root growth (Barney, 1951; Carlson, 1985b; Stupendick and Shepherd, 1979), but also significantly reduce water absorption through the existing roots (Kramer and Kozlowski, 1979, p. 461). Soil temperatures in the root zone often are far below 15°C in late winter and early spring. Root growth potential usually is tested at 20 to 25°, but perhaps more attention ought to be given to selection of families with a good RGP at low temperatures for early planting. Figure 5 from work by Carlson (1985b) shows considerable differences among families in this respect, suggesting the existence of genetic variability.

Another limitation on seedling growth is soil aeration. Heavy rains sometimes saturate heavy soils, displace the air, and reduce the oxygen supply below the level essential for respiration and root growth. This prevents the rapid resumption of root growth so important for shoot growth, and if prolonged can even kill the roots. Unfortunately, the young roots so important for absorption of water and minerals are most likely to be killed by inadequate aeration. The effects of flooding on woody plants were reviewed by Kozlowski (1984, Chap. 4).

The physiological quality of seedlings is especially important when conditions are unfavorable for planting and growth. No one can predict whether there will be a drought during the planting season or if flooding or the unavailability of planting crews will necessitate keeping some seedlings in storage longer than is desirable. Since there is no way to insure favorable conditions the best insurance against planting failures is to produce seedlings that are most capable physiologically of becoming established under the worst conditions.

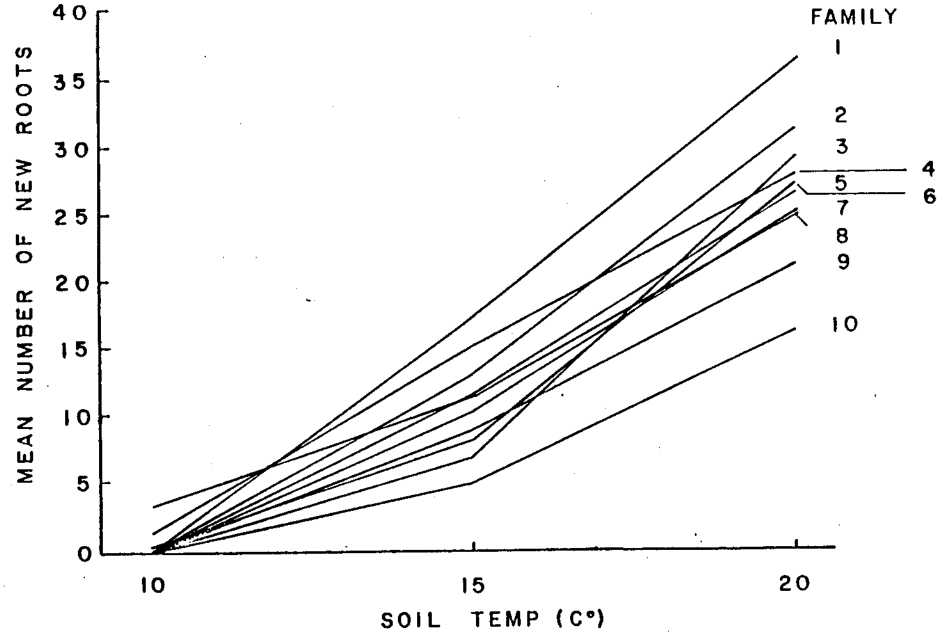

Fig. 5. Differences in effects of soil temperature on root growth of ten families of loblolly pine. Carlson, 1985b.

DISCUSSION OF FUTURE RESEARCH NEEDS

We seem to have a fairly clear picture of the kind of seedlings that are needed to result in good survival in the field. Morphologically they should be 20 to 25 cm high with stems 4 to 5 mm in diameter, a much branched, fibrous root system, and a large needle surface. The physiological importance of a large leaf area for photosynthesis exceeds the disadvantage of the large transpiring surface. An extensive, fibrous root system provides more absorbing surface and more possibilities for development of new roots. Physiologically, seedlings when outplanted should have lost their winter shoot dormancy, have a high potential to produce new roots after planting, and enough stored food to support root growth until a normal rate of photosynthesis is absorbed. Although we know the kind of seedlings we need we do not know how to consistently produce these seedlings. Part of the inconsistency in results arises from normal variations in weather and in the genetic potential of the seed.

Weather. No two growing seasons are identical and the existence of unpredictable variations in temperature, sunshine, and rainfall means that a given cultural regime will not necessarily produce the same results in successive years. This emphasizes the need for giving more attention to diagnostic tests that monitor seedling conditions with respect to water and mineral nutrition from time to time in order to insure that proper compensation is made in such cultural procedures as watering and fertilization for year to year variations in weather. The desirability of more uniform environmental conditions may be an argument in favor of growing seedlings in containers.

Genetic Variability. There is so much genetic variability in the seed planted in the average nursery that not all seedlings can be expected to react in the same way to a given cultural regime. This problem will be alleviated as the genetic uniformity of seed sources increases. For the most part selection has concentrated on tree form and growth rate, but perhaps more attention should be paid to seedling success as well as to desirable types of trees. Perhaps selection for success after transplanting is almost as important as subsequent growth and more attention should be given to combining desirable seedling characteristics with desirable characteristics in mature trees. If these do not exist in the same family the genetic engineers probably can produce the desired combinations.

Figure 6 indicates some of the important processes occurring during the development and loss of dormancy in tree seedlings. The processes shown on this figure all play important roles in determining seedling quality and success after outplanting, and are subjects that deserve further investigation. It seems likely that the most important contributions to seedling quality will come from a better understanding of how root growth potential is related to shoot dormancy.

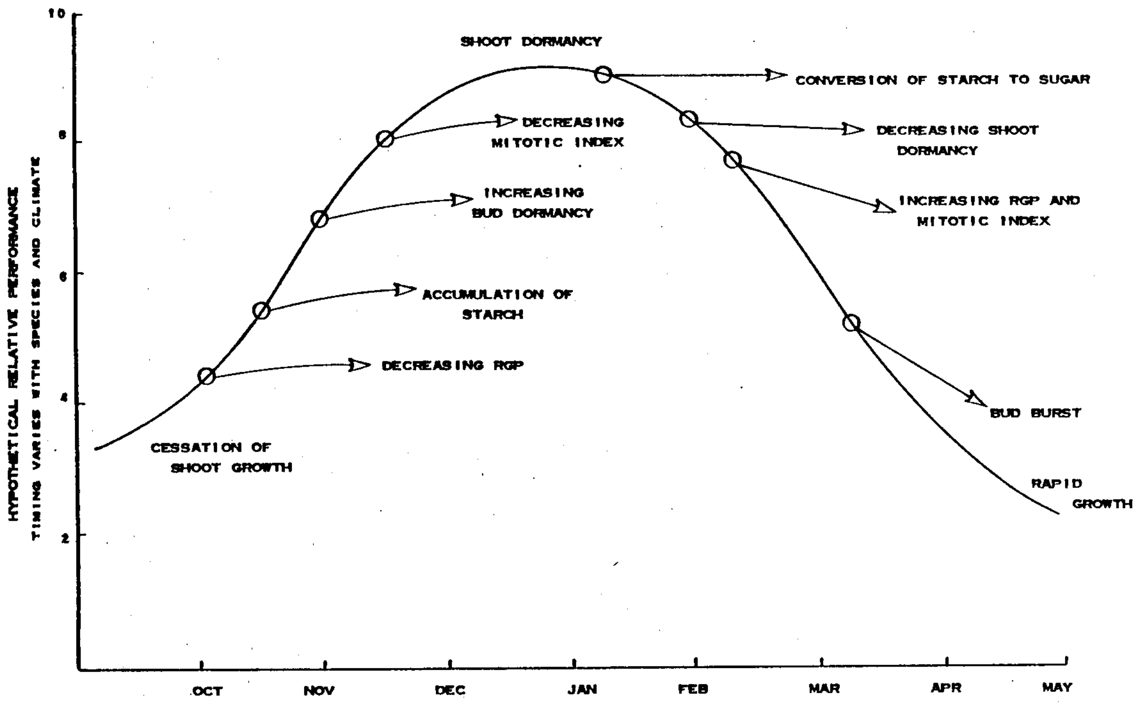

Fig. 6. The annual cycle in shoot dormancy, carbohydrate reserves, and root growth potential

Height growth typically is very rapid in the spring, slows down in late summer, and ceases in the autumn before temperatures are low enough to be limiting (Kramer, 1957, Fig. 1). Loblolly pine does not grow continuously during the growing season, but makes several flushes of growth separated by short periods of no growth. The reasons for this intermittent growth are unknown, but these temporary cessations in growth probably have some relationship to the permanent cessation that occurs later in the season when true dormancy develops. The whole problem of the causes for development of shoot dormancy deserve more study.

In summary, we will list some of the problems that seem to deserve consideration:

Effects of nursery location in terms of temperature and photoperiod
Better monitoring of water and mineral status of seedlings
Effects on seedling quality of water stress at various times during the growing season
Effects of enhanced CO_2 concentration on container seedlings and tissue culture plantlets
A good indicator of physiological shoot and root dormancy
Relationship between shoot dormancy and root growth potential (RGP)
A quick test for root growth potential
What controls root initiation and sink strength for food
Possibility of selection for rapid resumption of root growth
Possibility of selection for root growth in cold soil

Effective research on these and other problems bearing on seedling quality will require good collaboration between scientists working in nurseries and those working in greenhouses and laboratories. Because of recent improvements in instrumentation progress should be much more rapid in the future than it has been in the past.

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