PHYSIOLOGY OF SOUTHERN PINE SEEDLINGS

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Abstract. An overview is given of some aspects of the physiology of southern pine seedlings during three stages of their development, with regard to the climate of the southeastern USA, the literature on southern pines, and current concepts in tree biology. First, with reference to the period of rapid seedling growth after germination, points are made concerning (i) the effects of seed size on early growth rates, and seedling size, (ii) mineral nutrition, (iii) responses to water stress, and (iv) responses to competition. Second, with reference to the period of growth cessation and autumn hardening, points are made concerning (i) shoot growth cessation, (ii) dormancy onset, and (iii) frost hardening. Third, with reference to the period of overwintering and regrowth in spring, points are made concerning (i) the loss of shoot bud dormancy and potential shoot growth, and (ii) actual and potential growth of the roots. It is suggested that models of changes with time in the growth and physiological status of seedling roots and shoots could be constructed to serve as tools for both researchers and nursery managers.

INTRODUCTION

The purpose of this review is to highlight some of the more important aspects of the physiology of southern pine seedlings, from the time they germinate in the nursery to the time they are planted in the forest. This period normally spans a maximum of one year, from about April to March. Most of the discussion will refer to published information on loblolly pine (Pinus taeda L.) and slash pine (Pinus elliottii Engelm. var. elliottii), but some general points are made from the current literature on tree physiology, and from recent reviews on the physiology of nursery seedlings of other species (Gadgil and Harris, 1980; Duryea and Landis, 1984). Some points will be relevant to the production of container seedlings, but I mostly have in mind the production of bareroot southern pine seedlings (1.3 billion/yr) in open nurseries as described by Wakeley (1954) and Boyer and South (1984).

To provide a framework, I shall consider three phases of seedling development. These phases are shown at the top of Figure 1 in relation to the climate at Montgomery, Alabama. Phase I spans the period from germination in March-April to the time when growth is slowed by competition. Phase II spans the August-November period of height growth cessation, dormancy onset and frost hardening. And Phase III covers the winter and early spring periods when there are changes in dormancy status and in the actual and potential growth rates of the shoots and roots.

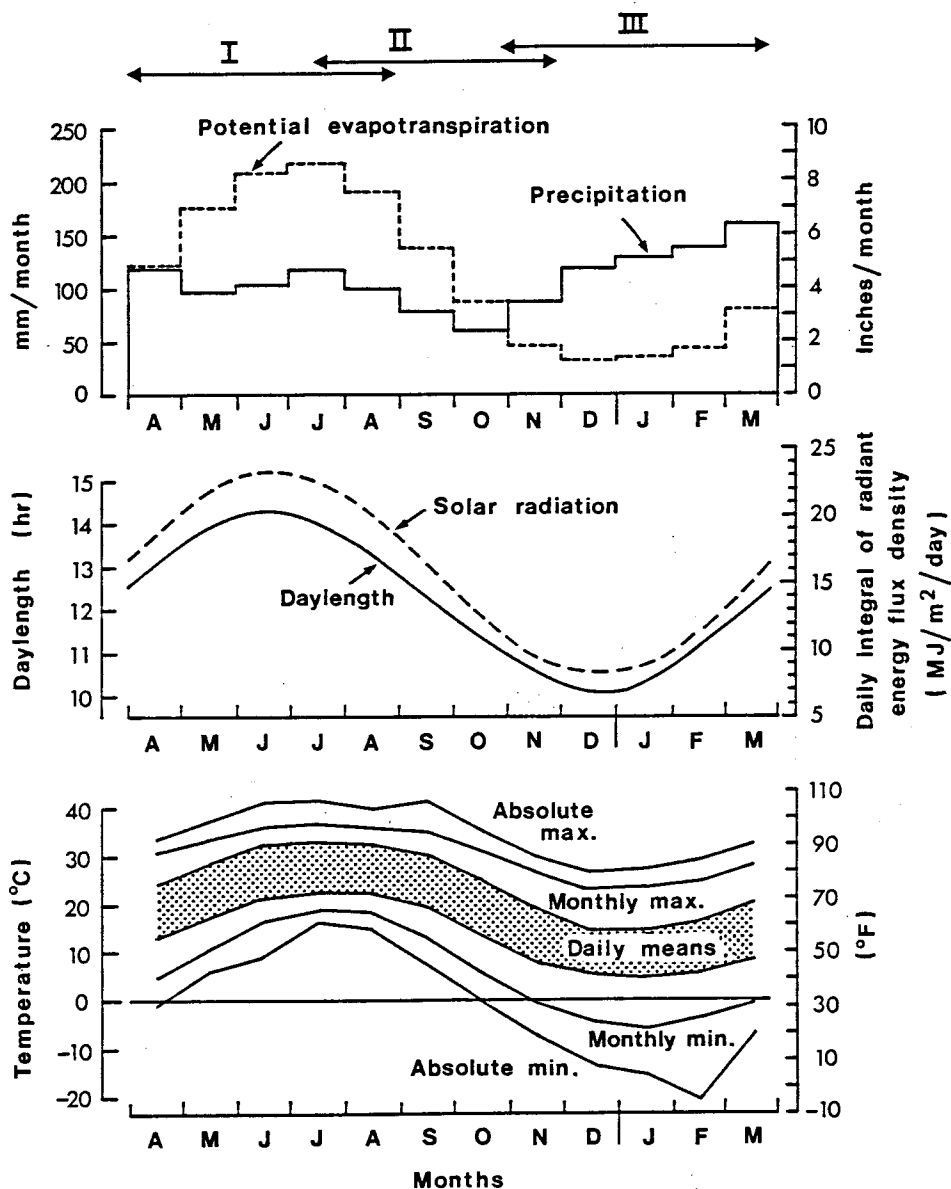[1]/Institute of Terrestrial Ecology, Bush Estate, Penicuik, Midlothian EH26 0QB, Scotland.

Figure 1. The climate of Montgomery, Alabama (32°23'N, 86°18'W, 61m).
Temperature and precipitation data were taken from Anon (1958)
based on the period 1872-1948; daylengths were taken from
Smithsonian Institution tables; daily solar radiation was
derived from latitude using equation 3.4 of Charles-Edwards
(1982); potential evapotranspiration was derived from
temperature and solar radiation using equation 10.22 of Campbell
(1977). I, II and III refer to the three phases of seedling
development that form the framework for the text.

The climatic factors shown in Figure 1 illustrate seasonal changes in the conditions for growth (temperatures, light and water), in the environmental stresses that must be avoided or endured (water stress and frost) and in the environmental information that may be used by the seedlings to phase their development (daylengths, chilling and water stress). I shall assume that the climate at Montgomery is, in many respects, typical of that of the southern pine region.

PHASE I. RAPID SEEDLING GROWTH

From germination to about July-August, the seedlings grow rapidly in size and weight. They experience increasing and high temperatures (15-30 °C), high levels of solar radiation, daylengths greater than 12 hours, and levels of potential evapotranspiration which greatly exceed rainfall (Fig. 1). It is during this phase that we might be most concerned with physiological factors that affect seedling size. These factors include (i) seed size and initial growth rates, (ii) responses to water stress, (iii) mineral nutrition, and (iv) responses to interseedling competition in the nursery bed.

Seed size and seedling growth rate relationships

About 80% of the weight of a southern pine seed is haploid maternal tissue and diploid sporophytic seed coat tissue. The weight of these tissues is determined by the genotype of the maternal parent and the environment in which the seed develops (Perry, 1976). Loblolly pine seeds with large amounts of these tissues (a) tend to be less dormant than smaller seeds and hence to germinate sooner, and (b) tend to produce larger hypocotyls and larger seedlings (Dunlap and Barnett, 1983; Barnett and McLemore, 1984) which may remain larger for several years after planting, sometimes masking inherent differences contained in the original embryos (e.g. Robinson et al., 1984). There has, consequently, been considerable speculation about the effect of seed size on seedling performance.

Theoretically, there can be numerous relationships between seed weights, seedling sizes, seedling growth rates and seedling relative growth rates, depending on the contribution of the maternal and embryo tissues. However, two 'expected' relationships might be those illustrated in Figure 2, in which it is assumed that large seeds germinate first. In Figure 2A the three seedlings have the same exponential relative growth rates (cm/cm/wk or g/g/wk) at all times, but at time T there are positive relationships between seed weights and both seedling sizes and absolute growth rates (cm/wk or g/wk). More realistically, in Figure 2B, the seedlings do not maintain exponential growth for more than a short period after germination. Consequently, their absolute growth rates become similar, and their relative growth rates become negatively related to seed weights. However, seedling sizes are still positively related to seed weights (Fig. 2B).

[1]Many authors now prefer the term 'specific growth rate', which is in common use in zoology and microbiology, the word 'specific' meaning 'divided by mass'.
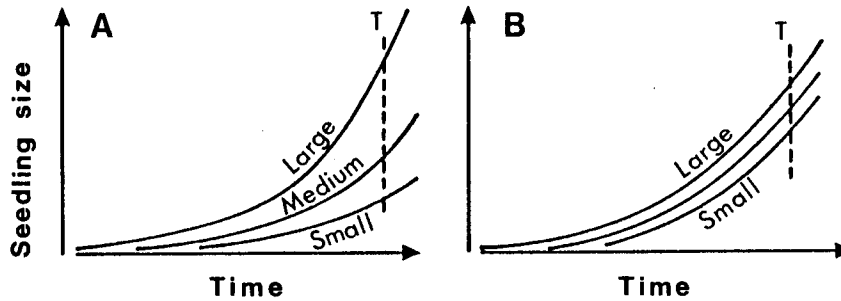
Figure 2.   Relationships between seed weights (large, medium and small)
            and the size and growth rates of seedlings at time T, assuming
            that large seeds germinate before small ones.   A. The
            seedlings maintain constant relative growth rates to time T.
            B.   The seedlings have similar absolute growth rates at time
            T (see text).

An example of the situation in Figure 2B is illustrated in Figure 3,
taken from Cannell et al. (1978), referring to the means of 16 North
Carolina families of loblolly pine, with family mean seed weights in the
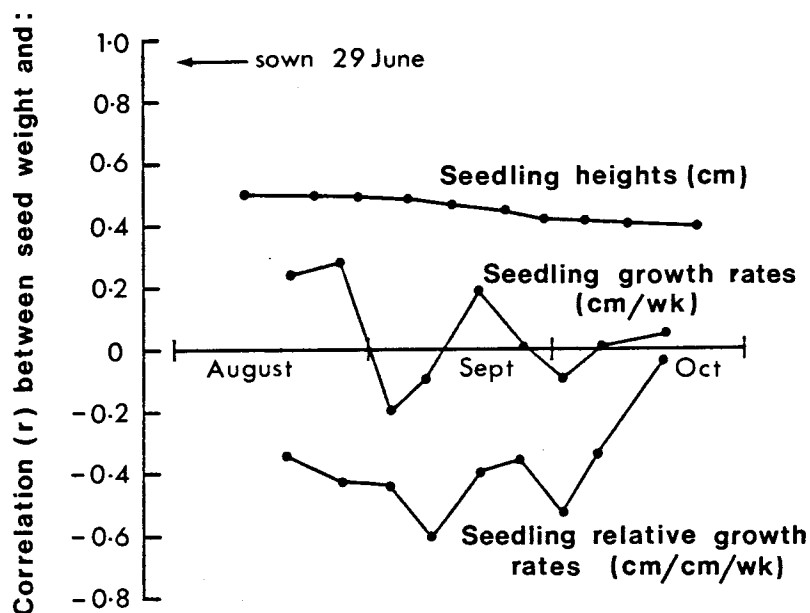range 28-48 mg/seed.

Figure 3.   Correlations between mean seed weights of 16 families of
            loblolly pine and the heights, growth rates and relative
            growth rates of the seedlings about 5-15 weeks after
            germination in 164 cm^3 'Leach' tubes.   Taken from Cannell et
            al. (1978).

Mineral nutrition

During the last decade it has been possible to obtain a more dynamic description of the mineral nutrition of plants than hitherto, using flowing or mist circulating culture systems which supply nutrients to plants at known rates (e.g. Ingestad and Lund, 1979). Over the same period, there has been increasing research on mycorrhizas and root physiology (e.g. Atkinson et al., 1983). The outcome has been to emphasize two factors controlling the rate of ion uptake: (a) the plant's demand for nutrients, and (b) the ability of plants to access nutrients by producing new roots or mycorrhizas as with hyphal webs that permeate the soil.

Growth demand. Formerly, it was thought that the inherent attributes of root cells and their ion transport systems controlled the rate of ion absorption by plants. Now, it has been shown for a number of plants, including trees, that the rate of ion uptake is closely tuned to the growth demand which, in some rapidly growing plants, can be linearly related to their internal N concentration, up to maximum level (Clarkson and Hanson, 1980; Ingestad, 1982). Thus, maximum growth is achieved (within limitations imposed by temperature, water, CO_2 and light conditions) when nutrients are supplied or accessed at a rate required to maintain tissues nutrient concentrations at an optimal level. Using exponentially growing young seedlings of Betula pendula Roth., Ingestad (1982) found linear relationships between percent N in the tissues, seedling relative growth rates and relative rates of nitrogen supply, up to a maximum level.

Consider B. pendula seedlings that are growing exponentially. According to Ingestad (1982), if their relative growth rates and internal N concentrations are to be maintained, there must be an exponential increase in the rate of N supply - which might occur with an exponentially increasing root system (Fig. 4, broken line). If N is supplied at a constant rate, the relative growth rates and internal N concentrations of the seedlings will decline (Fig. 4, continuous line).

This theory may not apply totally to southern pine seedlings, which grow exponentially for only a short period and may or may not exhibit linear relationships between tissue N concentrations and relative growth rates. However, the principle is important, that to maximize seedling growth rates, fertilizers must be supplied so that the nutrient delivery capacity of the soil (and the 'nutrient flux densities' to the plants) match the changing (S-shaped) demand of the seedlings. Usually, this will mean using repeated applications of fertilizers, or granules of different sizes, or granules coated with diffusion barriers, or inhibitors to delay enzymatic hydrolysis to nitrate. These methods are costly, but they may become increasingly cost effective as fertilizers become more expensive.
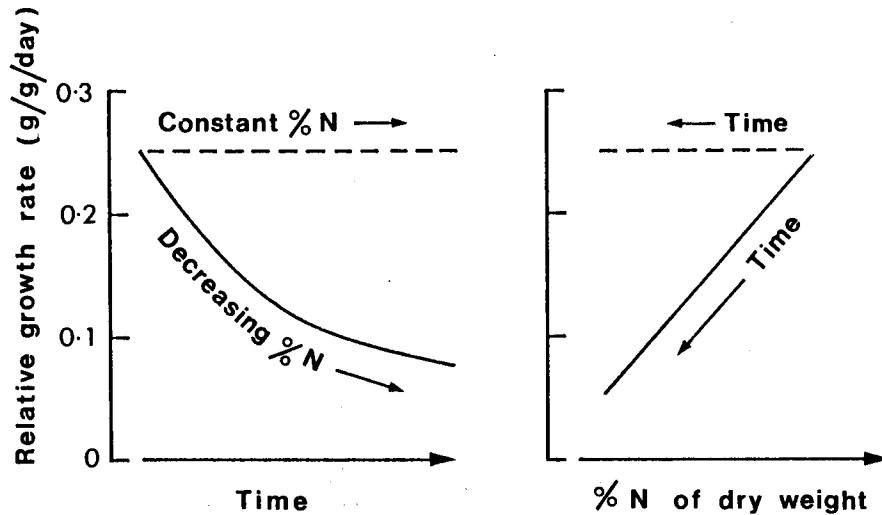
Figure 4. Theoretical changes in the relative growth rates and tissue nitrogen concentrations of __Betula pendula__ seedlings with exponentially increasing rates of N supply (---), and constant rates of N supply (——). After Linder and Rook (1984), based on Ingestad (1982).

__Effective rooting intensity__. Compared with grasses, most trees, including southern pines, produce relatively poorly-branched thick roots. The rooting 'abundance' of trees in the surface soil is about 0.2 to 5.0 cm root/cm^3 soil, compared with up to 50 cm/cm^3 for grasses (Bowen, 1984). According to Fowkes and Landsberg (1981) coarse root systems may have a higher conductance to water and nutrient transfer than finelybranched root systems once the soil is fully exploited and there is interference between roots. But at seedling and sapling stages, the low rooting abundance of trees will limit the potential nutrient flux densities to the plants, especially of poorly mobile ions in dry or coarse sandy soils, even though the suberized parts of the roots have a high absorptive ability (Chung and Kramer, 1975).

The major benefit claimed for ectomycorrhizas is that they extend the volume of soil exploited by roots, sometimes by promoting root branching, but most of all by extending hyphae into the soil, perhaps up to 12 cm from the roots and into soil that may be harmful to root growth (Bowen, 1984). Mycorrhizas can also store P, may increase the 'sink strength' of the roots, and the water use efficiency of the seedlings (Ford, pers. comm.).

Clearly, a barerooted transplant must rely initially on absorption through its roots and mycorrhizas, rather than through a hyphal web, and this may be one reason why undercutting and wrenching to produce a more fibrous root system can increase the survival of seedlings after planting - especially tap-rooted pines. These treatments may also hasten the onset of shoot dormancy, and so prolong the autumn period of root growth, thereby increasing root/shoot ratios (e.g. Tanaka __et al__., 1976).

Responses to water stress

It is evident from Figure 1 that water is potentially the most limiting environmental resource for seedling growth during the summer months in the southeastern USA. In the forest, water deficits have almost continual influence over the summer growth of southern pines, even in humid areas of the southeast (e.g. Bassett, 1964; Zahner, 1968). We may therefore expect southern pines to have developed a number of mechanisms to avoid or tolerate water stress. In terms of nursery management, the existence of such mechanisms may be both (a) disadvantageous, in that seedling growth may be sensitive to moderate levels of water stess, and (b) beneficial, in that some mechanisms may be exploited to enhance survival after planting on dry sites.

Disadvantageous responses. There is some evidence that loblolly, and perhaps other southern pines (depending on the provenance), can close their stomata, stop growing and even undergo some sort of stress dormancy when subjected to mild levels of water stress. Thus, loblolly restricts transpiration more than many other tree species at similar water potentials (Lopushinsky and Klock, 1974), and loblolly seedlings can take many hours or days to begin growing again after experiencing pre-dawn leaf water potentials of only -0.5 MPa, whereas Pseudotsuga menziessii (Mirb.) Franco seedlings recover from -1.3 MPa in 1-3 hours (Brix, 1962; Elfing et al., 1974; Zaerr and Holbo, 1976; Cannell et al., 1978). Such responses may greatly restrict seedling growth in poorly irrigated nurseries.
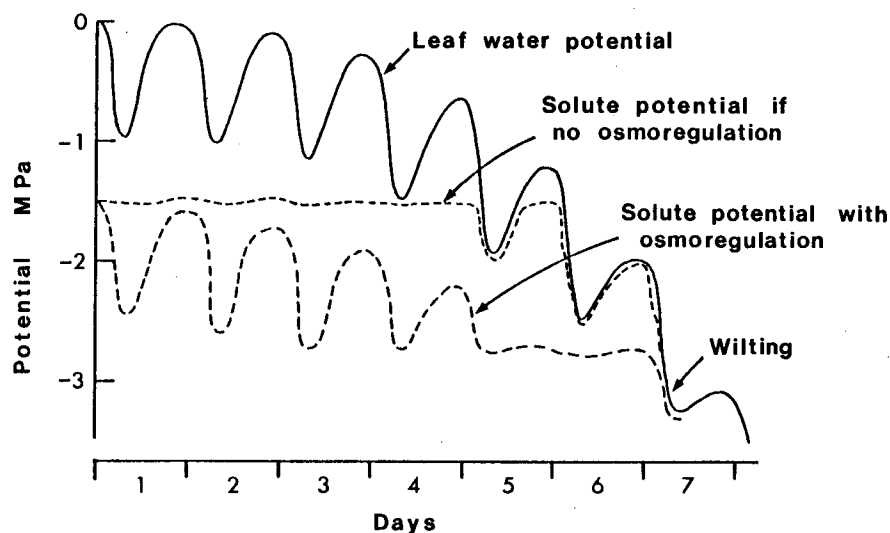

Figure 5. The possible magnitude of changes in leaf water potential and solute potential (osmotic potential) in plant leaves during a 7-day period of increasing water stess. The low solute potential in leaves which osmoregulate can persist, enabling the leaves to main turgor at lower water potentials during subsequent periods of stress.

Advantageous responses. Two related responses to water stress that may be advantageous in nurseries are (i) an increase in carbon partitioning to roots relative to shoots, and (ii) osmoregulation. The latter is the ability of plant tissues to develop low osmotic potentials (by accumulating solutes) in response to water stress, which enables them to maintain turgor and hence to continue growing at relatively low water potentials (Hsiao et al., 1976; Morgan, 1984). Figure 5 illustrates the likely magnitude of the decrease in leaf osmotic potential within plants that osmoregulate.

High solute levels following water stress may persist, so that plants previously subjected to water stress can show an improved capacity to tolerate subsequent periods of water stress. Most importantly, roots seem to have a high capacity to osmoregulate, which may be one mechanism for the common increase in root/shoot partitioning during periods of water stress. In the nursery, water stress induced by with-holding irrigation in late summer, or by root wrenching, may precondition seedlings (i) to grow at relatively low water potentials after planting, and (ii) to maintain positive turgor in their roots and so to extract more soil water at low soil water potentials.

Hennessey and Dougherty (1984) found that loblolly pine seedlings that were subjected to moderate levels of water stress (-0.75 MPa pre-dawn) in an Oklahoman nursery in September-October, showed an apparent 0.4 MPa osmotic adjustment, which increased their ability to maintain turgor at low water potentials in January and increased their root growth potential when transplanted in February. Also, downward osmotic adjustment has been observed following mild pre-stressing in seedlings of Tsuga heterophylla (Rafn.) Sarg. (Kandiko et al., 1980) and Quercus robur L. (Davies and Lakso, 1979). It is possible that inherent differences in osmoregulation were partly responsible for family differences in responses to water stress in loblolly pine observed by Cannell et al. (1978).

Responses to competition (density stress)

Although seedling size is no reliable measure of the potential to survive and grow after planting, it is generally agreed that large seedlings (loblolly with root collar diameters over 3.2 mm or 1/8 inch) often survive and grow best in dry planting years. The reasons may be simply that large seedlings have large root systems and are capable of having large reserves. Reserves of nutrients may be especially important. The needle percent N in P. menziesii and Picea sitchensis (Bong.) Carr. seedlings was positively correlated with survival and growth after outplanting in British Columbia (van den Driessche, 1984), and the foliar N content of loblolly pine seedlings was closely correlated ($r^2 = 0.84$) with their heights 3 years after planting in Mississippi (Switzer and Nelson, 1963).

The relationships between southern pine seedling dimensions and plant population (nursery bed density) seem to conform closely to the general responses found for trees and other plants (e.g. Perry, 1985), as shown by the following analyses of data published by Shoulders (1961) on loblolly and slash pine and by Benson and Shepherd (1976) on Pinus radiata.
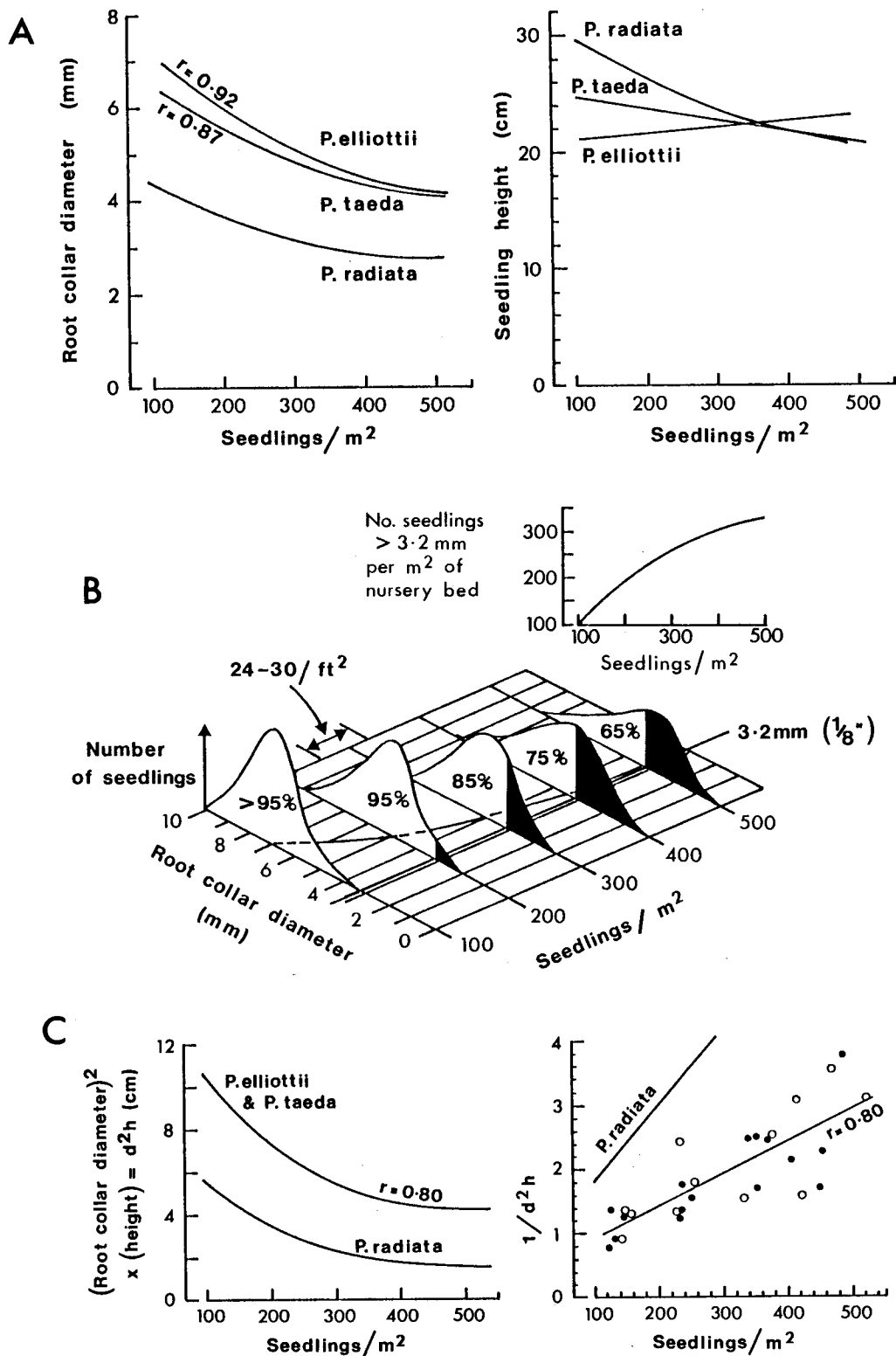
Figure 6. Responses of loblolly, slash and radiata pine seedlings to density stress (data derived from Shoulders, 1961, and Benson and Shepherd, 1976). A. and C. Loblolly and slash pine data refer to seedlings with root collar diameters over 3.2 mm (grades 1 and 2). B. Frequency distributions estimated from Shoulders (1961). C. The 'reciprocal yield law', assuming seedling weights are linearly related to d^2h; closed circles = slash, open circles = loblolly.

i. Mean seedling height can increase or decrease with increase in density (experiments and replicates can differ), but the magnitude of the effect is small compared with a large decrease in mean stem diameter (Fig. 6A).

ii. The frequency distributions of seedling diameters become negatively kurtotic (i.e. the seedlings become more variable) and perhaps positively skewed (with a high proportion of small seedlings) with increase in density (Fig. 6B).

iii. Shoulder's (1961) data suggest that about 85% of loblolly and slash pine seedlings are 'plantable' (with root collar diameters over 3.2 mm) at the common seedbed density of 258-323 seedlings/m^2 (24-30 seedlings/ft^2), but the number of plantable seedlings per m^2 of nursery bed increases to much greater densities (Fig. 6B).

iv. Assuming that seedling dry weights are linearly related to diameter^2 x height, (d^2h), pine seedlings seem to conform to the 'reciprocal yield law' (see Harper, 1977) in that there is a linear relationship between mean d^2h and density (Fig. 6C).

PHASE II. GROWTH CESSATION AND AUTUMN HARDENING

During the period July to November, southern pine seedlings grow more slowly in height and undergo developmental and physiological changes which prepare them to withstand freezing temperatures during the winter. The main environment cues for these changes are decreasing temperatures and daylengths (Fig. 1), to which the nursery manager may add water stress and nutrient shortage, perhaps induced by undercutting or wrenching.

Shoot growth cessation

A distinction must be made between the elongation of the shoots, and the development of the buds. In Arkansas, loblolly pine seedlings germinated in April, May and June stop elongating, and start developing terminal buds, in July, August and September, respectively, while seedlings germinated in July-August stop elongating in September-October, without developing distinct terminal buds.

For the first 1-2 months after germination it appears that loblolly pine seedlings will grow in height in warm temperatures, even in short days (9-11 hr). If temperatures fall, these young seedlings stop growing and become frost hardy without forming winter buds (e.g. Mexal et al., 1979). But, unlike northern spruces and P. menziesii, once loblolly pine seedlings reach a critical size, or plastochron age, they stop elongating and set buds, even in long days (12-14 hr) and at high temperatures. However, in aritificial conditions, the onset of budset can be hastened by shortening photoperiods and falling temperatures (e.g. Kramer, 1936; Zahner, 1955; Downs and Piringer, 1958), and it is possible that the critical daylengths and temperatures for budset change with increase in plastochron age. Of course, elongation can also be curtailed by inducing water or nutrient stress (by withholding irrigation or root wrenching), and there are provenance and family differences in the proportion of late season growth, reflecting differences in response to photoperiod, temperature and perhaps plastochron age (e.g. Perry et al., 1966; Bengston et al., 1967; Krall, 1969).

After height growth ceases, bud development continues until terminal meristem activity ceases in response to low temperatures and perhaps short photoperiods. Again, provenances and families will differ, and some southern pines may continue bud development throughout the winter.

It might be of advantage (i) to promote seedling growth in early summer so that the seedlings reach the required root collar diameter as soon as possible, (ii) to curtail further height growth, and hence (iii) to promote a prolonged period of bud development and autumn root growth, without unduly delaying frost hardening. The seedlings might then have large root/shoot ratios (see Cannell and Willett, 1976) and possess buds with large numbers of stem units ready for rapid expansion after outplanting (see Thompson, 1981).

Dormancy onset

Sometime during the period September–November the buds and shoot apices of many southern pines develop a true dormancy, in that they become unable to grow rapidly at warm temperatures without previous chilling (see below). Although much is known about the loss of winter dormancy in conifers, very little is known about its acquisition. It might be important to know, for instance, whether dormancy acquisition occurs independently from frost hardening, and the cessation of shoot meristematic acitivity (within the buds), particularly as bud dormancy status has been linked to seedling root growth potential (see below; Ritchie and Dunlap, 1980). Dormancy development is affected by shortening photoperiods, cool night temperatures and nutritional and water stress conditions that also induce frost hardening and slow down meristematic activity (Perry, 1971), but do these physiological changes always occur together? Work on deciduous species (Cornus sericea L.) suggests that frost hardening and dormancy acquisition begin at the stage of 'vegetative maturity', when defoliation no longer stimulates resting buds to break (see Kobayashi et al., 1982).

Frost hardening

Although the average daily minimum temperatures rarely fall below freezing in the southern pine region, the absolute minimum temperatures have reached -20 °C at Montgomery (Fig. 1, within the period 1872–1948) and -11 °C even on the Gulf Coast at Pensacola (Fig. 7, 1880–1949). Thus, loblolly pine, for instance, is likely to harden to between -15 °C and -25 °C throughout most of its natural range, northerly provenances becoming more frost hardy than southerly ones (Fig. 7). By contrast, absolute minimum temperatures rarely fall below -6 °C at Rotorua, New Zealand (1886–1950), so P. radiata seedlings, which harden to only about -11 °C at Palmerston North, are likely to be sufficiently hardy to escape winter frost damage in most plantation regions of north island New Zealand (Menzies and Holden, 1981; Greer, 1983; Fig. 7).

Frost hardening is a photosynthate-dependent metabolic process that begins after rapid cell expansion has ceased and involves changes in protoplasm ultrastructure and membrane permeability. As such, it can be delayed by treatments that promote late-season growth, or inhibited by debilitating water stress or nutrient imbalances (e.g. van den Driessche, 1969; Timmis, 1975). Also, it takes time; thus it takes about 42 days in cool temperatures or short daylengths (8hr) for loblolly pine seedlings to harden to about -12 °C (Mexal et al., 1979).
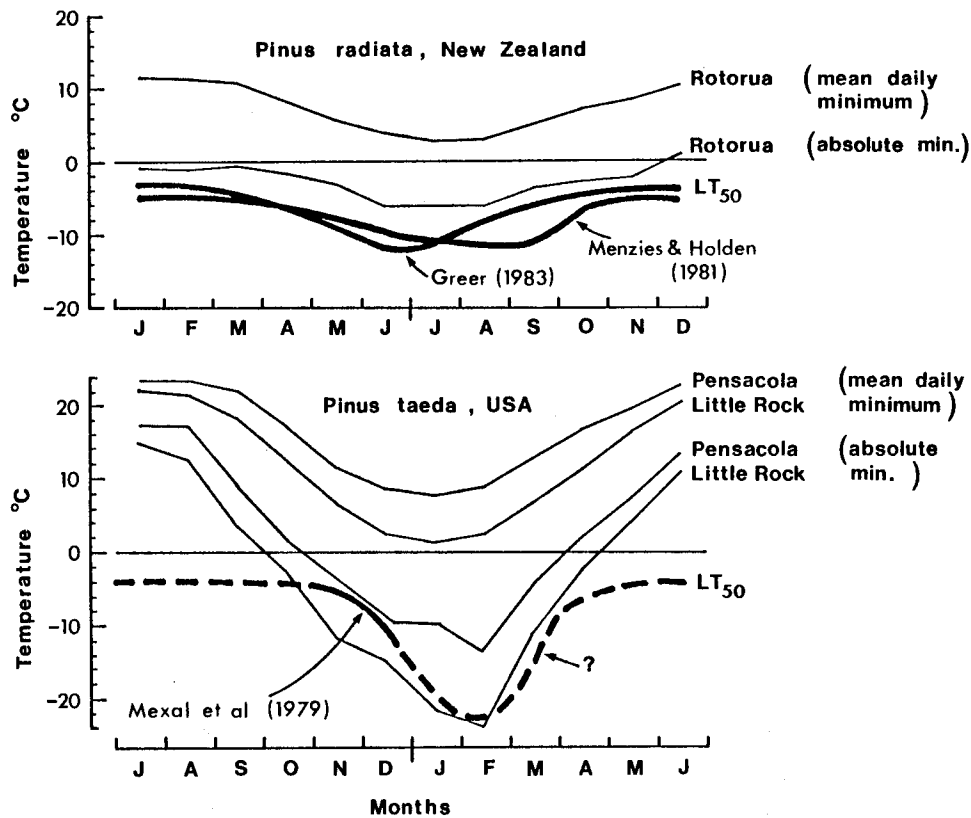
Figure 7.   Changes during the winter months in the daily minimum and
            absolute minimum air temperatures, and in the frost hardiness
            of the shoots (lethal temperature killing 50% of seedlings,
            LT_{50}) of Pinus radiata in New Zealand (LT_{50} at Palmerston
            North, from Menzies and Holden, 1981; Greer, 1983) and of
            Pinus taeda in USA (LT_{50} of N. Carolina piedmont families at
            Hot Springs, Arkansas, from Mexal et al., 1979). The
            temperature data were taken from Anon (1958), based on the
            period about 1880-1950.

    In natural conditions the initial stages of hardening of loblolly
pine seem to parallel the downward trend in daily minimum temperatures
(Mexal et al., 1979) and, indeed, this is the case for most north
temperate conifers (see Cannell et al., 1985). Later hardening, during
December-January, may be triggered or accelarated by short photoperiods
(below about 10.5 hr) and can certainly be promoted in artificial
conditions by 8 hr photoperiods (Mexal et al., 1979). However, little is
known, for southern pines, about the role, if any, of sequencing warm,
long days → warm, shorter days → cool, short days → frosts, which seems
to be important for more northern conifers to achieve prompt and full
hardening (see Cannell et al., 1985). Also, little seems to be known
about the extent to which southern pines can deharden if exposed to warm
temperatures during the winter, or the potential for root hardening of,
for instance, container seedlings placed outside during the winter (see
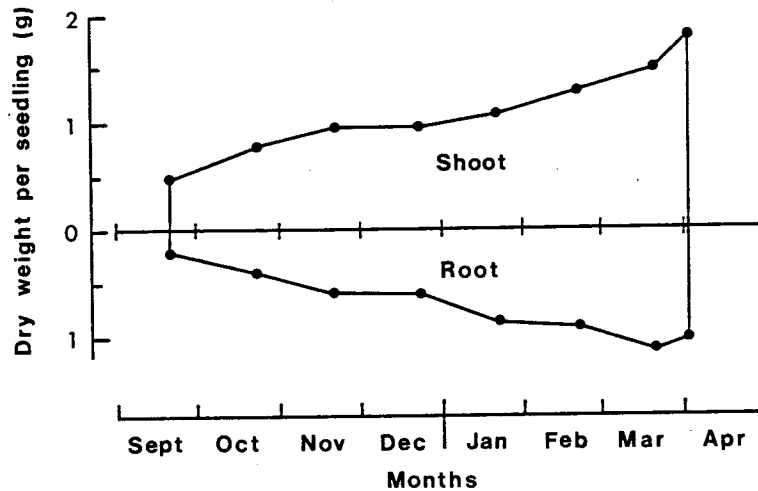Havis, 1976).

Figure 8. Changes in the dry weight of _Pinus taeda_ seedlings during the
winter at Raleigh, North Carolina. The seedlings did not
increase in weight significantly in the period 20 November to
20 December.

PHASE III. OVERWINTERING AND REGROWTH IN SPRING

During the winter period of November to March, Montgomery receives
about 28% of its total annual solar radiation, and mean daily maximum
temperatures commonly reach 15 °C (Fig. 1). Consequently, there is
considerable potential for photosynthesis, carbohydrate storage and
growth during this period. Strain et al. (1976) found that the foliage
on loblolly pine seedlings, and on young trees, acclimated in response to
cool temperatures (17/11 °C day/night for seedlings), shifting the
optimum temperature for photosynthesis from 25 °C to 10 °C. Indeed, the
photosynthetic rates of loblolly pine needles in mid-November and
mid-January were as great as those in September. It is well-known that
some root, cambial and even shoot growth can occur during the winter
months; indeed Perry (1971) reported a 68% increase in the dry weight of
loblolly pine seedlings growing at Raleigh between 20 December and 1
April (Fig. 8).

However, there is a risk of killing frosts of below -10 °C until
late February even at Pensacola (Fig. 7). Consequently, although some
shoot growth can occur in winter, in nature, rapid bud elongation and
associated dehardening in warm weather is prevented by a gradual loss of
dormancy. Similarly, rapid root growth may be prevented indirectly or
directly by shoot dormancy mechanisms, or by low soil temperatures.

It is helpful to distinguish between actual shoot and root growth -
limited by both the internal status of the seedlings and external
conditions - and their potential growth - limited by the internal status

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of the seedlings alone. Both actual and potential growth rates change
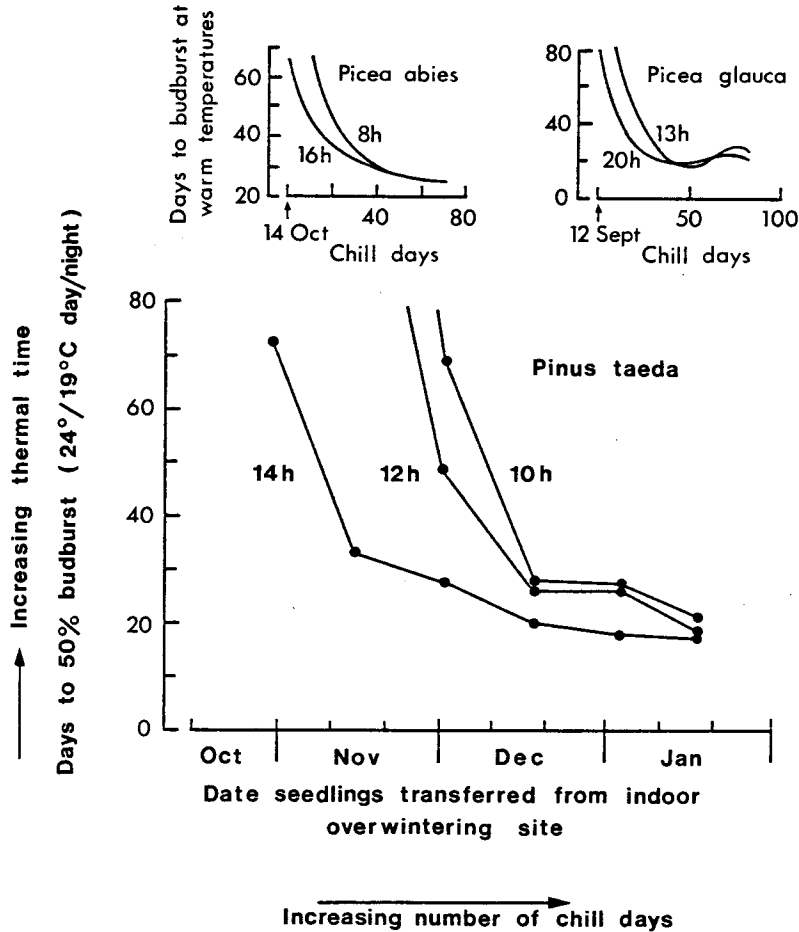greatly during the winter months.

Figure 9. Decreased thermal time (heat sum) to budburst on seedlings
with increased chilling (loss in dormancy). Long photoperiods
seem to replace chilling in decreasing dormancy. P. abies
data from Worrall and Mergen (1967), P. glauca from Nienstaedt
(1966) (see Cannell and Smith, 1983).
P. taeda data derived from Garber (1983, his Fig. 1) for an
Arkansas seed source grown at Hot springs, Arkansas, sown in
containers in June.

Actual and potential shoot growth

The rates at which winter buds grow may be regarded as functions of
their temperatures throughout the winter. In early winter, when the buds
are dormant, the slope of the bud growth rate/temperature relationship is
very shallow (and possibly zero). During the winter, exposure to 'chill'
temperatures (0-8 °C for loblolly pine) increases the slope of this

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relationship, and hence the potential shoot growth rate, to some inherent maximum (which may, itself, change with increase in ambient temperatures, Koboyashi and Fuchigami, 1983). Bud dormancy is not suddenly 'broken' by chilling, it is progressively decreased.

If a unit of bud growth (in length or weight) is equivalent to a unit of thermal time (in day degress 'heat sum'), then the effect of chilling will be to decrease the thermal time that the buds take to reach the critical size we call budburst. For many trees, the form of the relationship between chill days and thermal time to budburst tends towards a decreasing exponential (Fig. 9; Cannell and Smith, 1983). That is, the loss in dormancy per unit of chilling is rapid in early winter, and then diminishes.

In many temperate tree species the effects of chilling can be partly replaced by long photoperiods. Consequently, if the buds are poorly chilled, following exceptionally mild winters, the long days in late spring will increase the slope of the bud growth rate/temperature relationship and prevent unduly delayed budburst. However, if the buds are well-chilled, following normal winters, the long days in late spring may have little added effect, because the buds are already capable of their maximum potential growth rate.
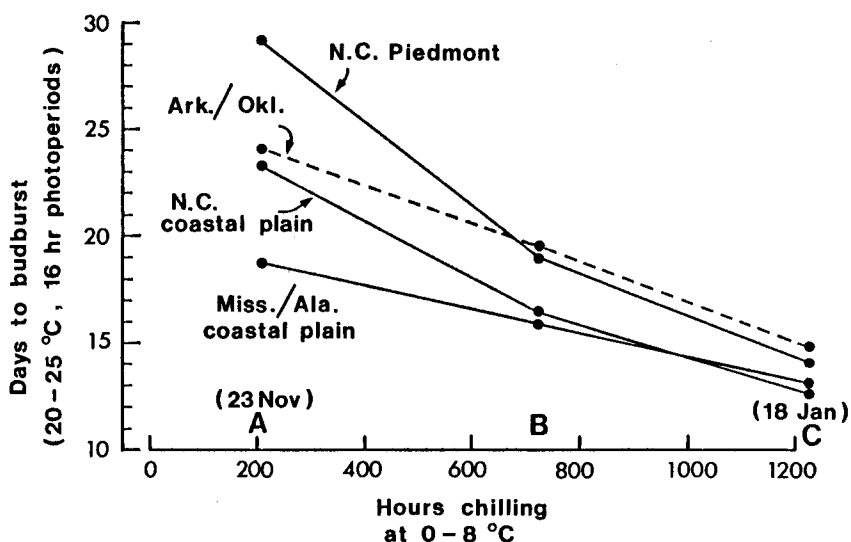

Figure 10. Decreased thermal time (heat sum) to budburst with increased chilling (loss in dormancy) of seedlings of four Pinus taeda provenances (means of 3-6 families per provenance) grown in a nursery in southeastern Oklahoma. A = 207 hr of natural chilling; B = mean of 734 hr natural chilling and 207 hr natural plus 500 hr cold store chilling; C = 734 hr natural plus 500 hr cold store chilling. Data derived from Carlson (1985).

Cannell and Smith (1983) showed that the above model of loss in bud dormancy (elaborated by Campbell, 1978) applied to the vegetative and floral buds of several temperate tree species. Figure 9 illustrates the thermal time-chilling curves for _Picea abies_ (L.) Karst and _Picea glauca_ (Moench) Voss, including the effects of long photoperiods on poorly chilled seedlings. The work of Garber (1983) suggests that this model also applies to loblolly pine, assuming that the period his seedlings spend in an overwintering site was equivalent to a period of chilling (Fig. 9). Note that the effect of photoperiods over 12 hours fell to near zero by January, so, in natural conditions, photoperiods over 12 hours after 21 March will have little effect on promoting budburst – unless the seedlings are very poorly chilled (e.g. in the study of Hellmers and Hesketh, 1974).

The thermal times and chilling 'requirements' for budburst are difficult to define. The optimum and base temperatures may change, and chill days alternating with warm days can be less (Timmis and Worrall, 1974), equally (Carlson, 1985), or more effective (Garber, 1983) than the same number of continuous chill days. Also, chilling requirements differ between provenances, families and cultivars. As expected, loblolly pine families from the Mississippi/Alabama coastal plain tend to be less winter-dormant – and so respond less to chilling – than families from Arkansas/Oklahoma or the North Carolina piedmont (Carlson, 1985; Fig. 10).

It is worth noting that any future CO_2-induced climatic warming will increase the necessity to keep winter dormant families of southern pines in cold stores, or alternatively to give long photoperiods to seedlings in containers, or conceivably in the nursery. Conversely, it may sometimes be desirable for southern pine seedling dormancy to be prolonged, if potential shoot growth rates are large enough to permit actual growth on warm days in January-February, as in Perry's study (Fig. 8).

Actual and potential root growth

Figure 11 describes possible changes in three aspects of southern pine seedling root growth, which often seem to be confused. However, the lines in Fig. 11 are no more than guesses, based on work reviewed by Ritchie and Dunlap (1980) and on recent work on loblolly pine by Carlson (1985).

Figure 11A shows the potential ability of undisturbed roots to grow _in situ_, in response to warm temperatures. Here it is assumed that the changes in potential growth of roots parallel those of the winter buds, as partly described in Fig. 9. Although the roots themselves may not undergo any true dormancy, there is considerable evidence for many tree species (Ritchie and Dunlap, 1980) including loblolly pine (Carlson, 1985), that the roots are unable to grow while the shoot buds are dormant
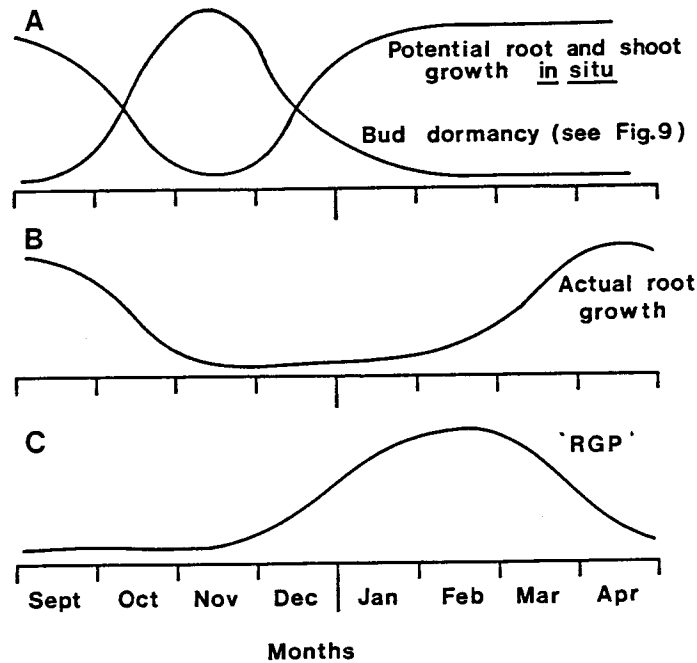
Figure 11. Possible changes in potential and actual rates of root growth
of southern pines during the winter.
A. Potential root (and shoot) growth rates of undisturbed
    seedlings in situ is assumed to be directly related to the
    level of bud dormancy.
B. Actual root growth rate is perhaps limited by shoot
    dormancy in November, and by low soil temperatures in
    December–February. Root growth will slow down in May as
    shoot elongation accelerates.
C. The 'root growth potential' (RGP) of uprooted seedlings is
    limited by damage to growing roots in September–October
    and March–April, and by low potential growth in November–
    December.

Figure 11B shows possible changes in the actual growth rate of
southern pine seedling roots. In November, growth is limited by dormancy
mechanisms, while in December–February growth is limited by low soil
temperatures. The optimum temperature for root growth in non-dormant
seedlings of P. taeda and P. radiata is about 25 °C, but some growth
occurs at 5 °C (Fig. 12), and it is possible that the roots acclimate to
grow at lower temperatures in the winter. Some root growth probably
occurs in all months, but there is clearly a surge in September–October
and in early spring prior to rapid shoot elongation.

Figure 11C shows changes in the ability of uprooted seedlings to
produce new roots at warm temperatures. This is the 'root growth
potential' (RGP) discussed by Ritchie and Dunlap (1980), which is often
directly related to survival and/or growth rate after planting. Here, I

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have assumed that the potential to produce new roots is inversely related
to actual root growth rate before lifting: that is, seedlings which have
actively growing roots in the nursery are less likely to be able to
regenerate new roots than seedlings with slowly growing roots. If this
is true, then RGP will be low in September-October and in late spring, as
well as in November. Several authors have suggested that actively
growing roots are easily damaged by the act of lifting or by short
periods of drying (e.g. Coutts, 1981).

Factors other than bud dormancy and actual root growth rates will
affect RGP, such as the nutrient and carbohydrate reserve status of the
seedlings, their morphology (as affected by wrenching), their water and
solute potential and so on. Also, I have not speculated on the many
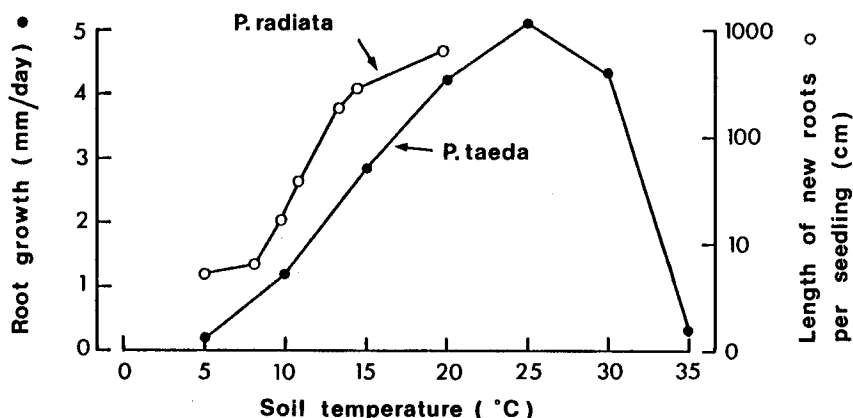factors that may alter RGP in cold storage.

Figure 12. Effect of soil temperature on the growth of (non-dormant)
roots of P. radiata and P. taeda seedlings.
0 = root length on 8-month-old P. radiata seedlings 32 days
after planting in a sandy forest soil (from Nambiar et
al., 1983).
● = growth of roots of P. taeda seedlings grown in glass tubes
of loam, placed at an angle of 40° and maintained at given
temperatures in water baths (from Barney, 1951).

CONCLUSIONS

The ability of southern pine barerooted seedlings to produce new
roots and shoots after planting in the forest is related to their
morphology and physiological status at the time of planting.
Considerable efforts have been made to try to characterize the desirable
dimensions and to measure the physiological status of seedlings, and so

to obtain an instant assessment of their potential to survive and grow (see Timmis, 1980). An alternative approach would be to model the shoot and root growth, dormancy status, frost hardiness, nutrient and carbohydrate status, and root growth potential of seedlings as functions of their physical environment and nutrition. It might be difficult to obtain sufficient information to build all-purpose models, covering all possible artificial environments, but general-purpose models, restricted to given species, growing in particular areas of the southeastern USA, might be more easily constructed. Such models would immediately focus research on critical relationships and environmental responses, and might soon serve as models for nursery managers to predict the future outcome of treatments or to assess the current status of their planting stock. Garber's (1983) work on the chilling requirements of loblolly pine, and the studies that are reported in these proceedings, form a good basis for a modelling approach.

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