TRANSPLANTING SHOCK IN BAREROOT CONIFER SEEDLINGS

W. J. Rietveld, Research Plant Physiologist
North Central Forest Experiment Station
Forestry Sciences Laboratory, Rhinelander, Wi 54501

ABSTRACT

Transplanting shock of bareroot conifer seedlings is a condition of distress from injuries, depletion of energy reserves, and impaired functions; a process of recovery; and a process of adaptation to a new environment. Some degree of transplanting stress is unavoidable, even when stock with high performance potential is planted in a favorable environment, but the degree and duration of stress can be minimized. Pre-plant handling and exposure and post-plant drought aggravate transplanting shock. New root growth into surrounding undisturbed soil is critically important to renew the root-to-soil contact necessary for efficient water and nutrient absorption and to alleviate plant water stress. Root growth is very sensitive to plant moisture stress. The severity and duration of transplanting shock depend on the interactions of seedling performance potential and site environment. If transplanting shock is protracted, reserve carbohydrates may be exhausted before replenishment from photosynthesis, and the seedlings will starve to death. Minimizing transplant shock involves prescribing appropriate quality planting stock conditioned to resist stress, preserving seedling performance potential to the planting site, preparing a favorable planting site environment, and planting the seedlings properly.

Additional keywords: Planting stock quality, performance potential, stress physiology, field performance, seedling establishment.

INTRODUCTION

Many foresters view transplanting shock as a "black box" that outplanted seedlings enter and survivors exit. It is actually quite explainable. The severity of stress, the duration, and the outcome depend on a number of interacting factors. Some degree of transplanting stress is unavoidable, even under ideal planting conditions. The dictionary[1] defines "shock" as: (1) a blow, impact, collision, or violent shake or jar; (2) a sudden agitation of the mental or emotional sensibilities; and (3) a state of profound depression of the vital processes resulting from wounds, hemorrhage, crushing injuries, blows, etc. These definitions may seem amusing and exaggerated when applied to seedlings, but they describe transplanting shock surprisingly well (although a bit anthropomorphically).

This paper describes the processes involved in the development and progression of transplanting shock in bareroot conifer seedlings and discusses how it can be minimized. After you understand the principal processes involved, you will be impressed with the seedlings' inherent ability to overcome such stressful setbacks, and how we can help lessen the impacts and speed recovery.

---

[1]Webster's New Collegiate Dictionary. 1959. G and C Merriam Co., Springfield, MA, USA.

TERMINOLOGY

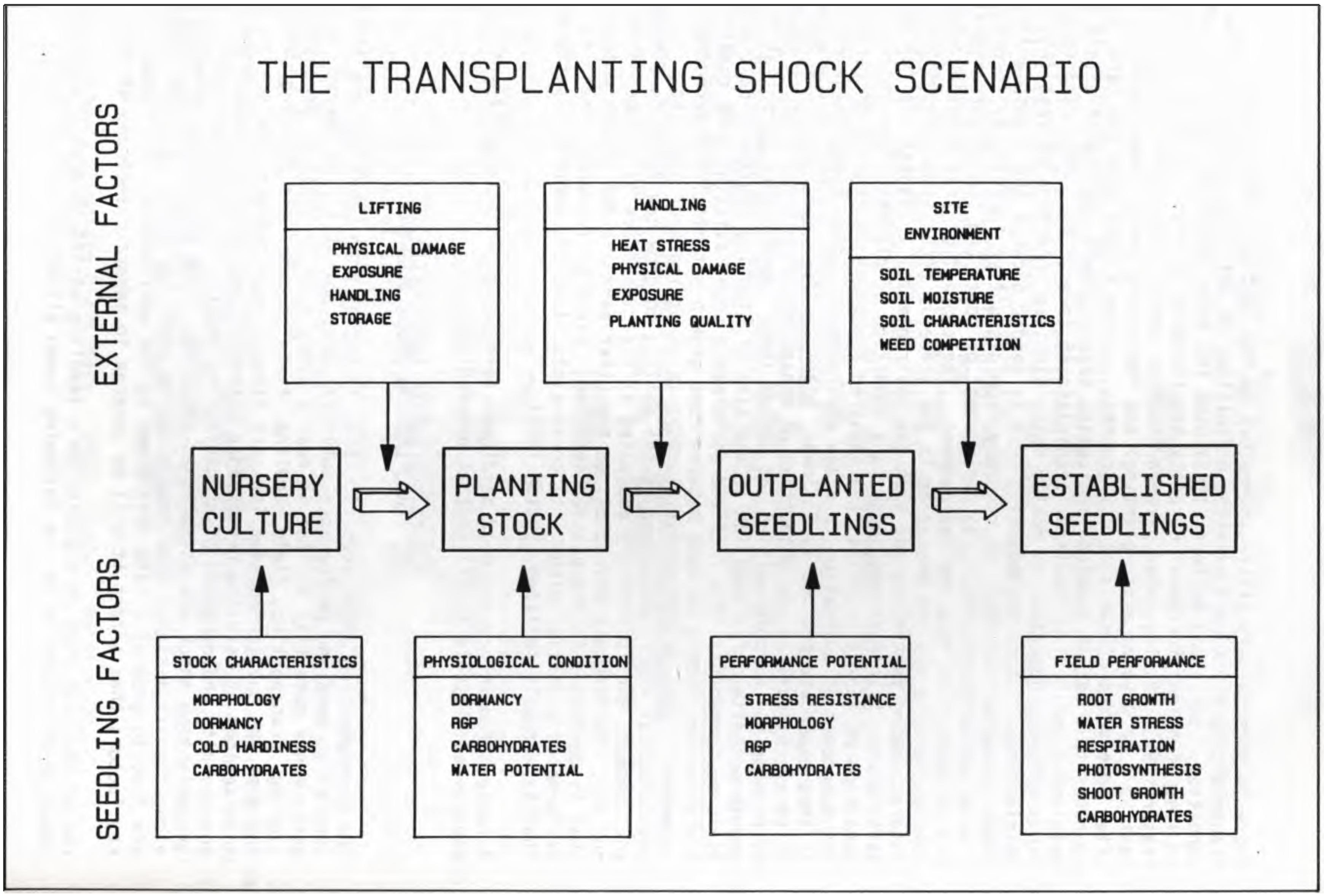
There is surprisingly little literature on the specific subject of transplanting shock, and existing definitions do not clearly describe the condition. Smith and Walters (1963) used the term "planting check" to refer to loss of height increment directly attributable to outplanting disturbance. Fraser (1933) distinguished between "initial check" (unsatisfactory growth lasting 1 or 2 years after planting) and "secondary check" (developing only after some years of satisfactory growth). Sutton (1968) used the term "check" to refer to a set of symptoms indicating severe growth constraint within newly outplanted conifers. The term "transplanting stress" is often used (e.g. Sands 1984) to describe the mostly water-stressed condition of seedlings after outplanting. A more encompassing term is needed because the transplanting shock scenario includes: 1) recovery from disruptive impacts, 2) recovery from plant moisture stress, 3) replacement of roots and stored carbohydrates, and 4) adaptation to a new environment. The concept of transplanting shock is complex because all the processes in the scenario occur simultaneously and interact among themselves and with the environment. I suggest the following definition: transplanting shock is a condition of distress from injuries, depletion of energy reserves, and impaired functions; a process of recovery; and a process of adaptation to a new environment. Other terms frequently used in this paper are defined as follows: planting stock quality is the degree to which stock realizes the objectives of management at minimum cost. . .quality is fitness for purpose (Willen and Sutton 1980); performance potential is the growth potential of a seedling at the time of planting (Sutton 1982); and field performance is the realized performance under existing site conditions. A distinction should be made between root growth potential and performance potential. Root growth potential (RGP) is an estimate of seedling physiological vigor, expressed as the ability to grow new roots in a favorable environment, and is commonly evaluated at the time stock is shipped from the nursery. Performance potential, on the other hand, is the growth potential that is contained in the planted seedling. Field performance, then, is performance potential minus site constraints, i.e. the amount of performance that is actually realized (Sutton 1982).

A review of dormancy and cold hardiness terminology is also pertinent to this paper; see Rietveld (1987) in this proceedings.

THE TRANSPLANTING SHOCK SCENARIO

The transplanting shock scenario (fig. 1) begins when seedlings are lifted. Generally, seedling performance potential goes downhill from there. Some performance potential is lost in nearly every step -- lifting, processing, storing, transporting, field handling, field storage, and planting -- up to the time the outplanted seedlings are finally reunited with the soil. The interactions of seedling performance potential and site environment determine the severity and duration of transplanting shock. The survivors of transplanting shock are established seedlings. The occurrence of rapid shoot elongation is a signal that transplanting shock has ended, and the seedlings are free to grow at a rate determined by the environment. Each stage and the key factors that affect it will be covered in separate sections of this paper.

One of the best ways to explain how a seedling passes through transplanting shock is to relate it to the following human situation:



factors and internal processes involved in the progression from lifting of nursery seedlings to establishment of outplanted trees.

A person working in a job with good pay, few concerns, and a good savings account suddenly becomes unemployed and must relocate. The new location offers some good job prospects and good growth potential, but those seem unimportant compared to the immediate concern -- survival. To survive in this more hostile environment, he must quickly overcome the traumas from being suddenly uprooted and relocated, sustain himself, and adapt to living under less than ideal conditions. The situation could be worsened by physical abuse during the move and aggressive coworkers in the new location. Success depends on his recovering quickly, surmounting the obstacles, and asserting his ability to perform. There is no welfare, so if he runs out of food or water, he dies. On the other hand, if he succeeds, his wealth increases in direct proportion with his performance and the constraints of his job.

Following a similar scenario, a seedling first grows in a nursery, then is lifted, processed, and outplanted in a new location. To survive transplanting shock, the seedling must: (1) recover from the injuries and stresses resulting from lifting and handling, (2) grow new roots to avoid plant moisture stress, (3) continue maintenance and growth respiration, and (4) adapt physiologically to a more hostile environment -- and do all that before stored carbohydrates run out. Promptness is important because the obstacles and depletion of reserve carbohydrates compound with time, and the probability of either extended stress or death increases. If stored carbohydrates are exhausted, the seedling literally starves to death. A successful seedling is able to avoid plant moisture stress and produce sufficient new photosynthate to support root and shoot growth and restore carbohydrate reserves. Once a seedling has survived transplanting shock, subsequent performance is governed by its growth potential and constraints of the site. In the following sections, I will discuss the principal factors contributing to each stage of the scenario.

PLANTING STOCK - SEEDLING CHARACTERISTICS AND CONDITION

The final product of nursery culture - planting stock - is a composite of the influences of weather during the culture period, a well as nursery cultural practices, resulting in specific morphological and physiological attributes shown in the following tabulation:

Nursery Culture	Planting Stock	
	Morphology	Physiology
stock type	height	carbohydrates
seedbed density	caliper	mineral nutrients
fertilization	root area	root growth pot.
irrigation	shoot:root	bud development
transplanting	dry weight	plant moisture str.
root pruning	bud size	cold hardiness
shoot pruning		stress resistance
wrenching		
dorm. induction		
lifting time		
lifting method		
processing		
storage		

A detailed discussion of the effects of nursery culture on the quality of planting stock is beyond the scope of this paper; see Duryea 1985 and Duryea and Landis 1984 for specific information. In this paper I will focus on the quality attributes of finished planting stock that play key roles in initial seedling performance. Dozens of morphological and physiological factors contribute to the quality and performance potential of planting stock (Duryea 1985), and an aberrant level of any one factor could jeopardize field performance. Assuming that all planting stock attributes are adequate, the attributes that relate most to the degree of transplanting shock are seedling size, shoot:root ratio, root fibrosity, carbohydrate reserves, dormancy, cold hardiness, stress resistance, and root growth potential. The latter four factors are closely interdependent, as will be explained shortly.

Seedling Morphological Factors

Seedling diameter is probably the best overall predictor of subsequent survival and growth (Thompson 1985). Several other morphological attributes are also related to performance, but are either harder to measure (e.g. dry weight) or more variable (e.g. height). These factors are also highly related to diameter. Beyond a certain seedling size, survival declines as diameter increases, presumably because of the larger seedlings' lack of balance.

Shoot:root ratio corrected for seedling size is another good indicator of survival potential (Thompson 1985). Shoot:root ratio increases as seedling height increases (Ledig and Perry 1970). By plotting seedling shoot:root ratio against seedling height for data from several wrenching studies reported in the literature, Thompson (1985) found that the "acceptable" shoot:root ratio increases as seedling height increases.

Seedling root fibrosity is closely related to seedling size and shoot:root ratio, and plays an important role in sustaining the seedling until new root growth occurs (Carlson 1986). Seedling hydraulic conductivity is directly related to root system size, i.e. seedlings with larger root systems absorb more water. After new root growth, the relation is even stronger because new roots extract soil moisture more efficiently than suberized roots, and larger root systems have more sites for root growth and tend to produce more new roots (Carlson 1986).

Although the size and shape of the plant do not guarantee performance, optimizing seedling size, balance, and root system fibrosity can contribute significantly to reducing the intensity and duration of transplanting stress.

Seedling Physiological Factors

Survival and growth of transplanted bareroot seedlings are critically dependent on the seedlings' ability to resist stresses and grow new roots. Root growth potential is a particularly important attribute of planting stock quality because it integrates numerous morphological and physiological factors into a single biologically meaningful estimate of performance -- the ability of seedlings to grow new roots. Basically, if there is anything physiologically wrong with a seedling, it will show up as a decrease in the ability to produce new roots in a favorable environment.

The effectiveness of RGP as an estimate of seedling performance potential, and its relationship with field survival and growth are well documented in the scientific literature (Feret and Kreh 1985, Larsen et al. 1986, Ritchie and Dunlap 1980, Ritchie 1985). In addition to measuring the ability of seedlings to grow new roots, RGP may also estimate seedling hardiness. Periods of high RGP apparently coincide with periods of high cold hardiness and stress resistance (Richie 1986, Ritchie and Shula 1984, Tinus et al. 1986). Thus, when we measure RGP, we may also be obtaining an estimate of the relative stress resistance of the seedlings.

Factors that affect the development and/or maintenance of root growth potential include genetics, seedbed density, fertilization, shoot pruning, undercutting and wrenching, soil moisture management, dormancy and cold hardiness status at lifting, and storage conditions and length (Rietveld 1987). Cultural treatments may increase root fibrosity, increase stored carbohydrates, or speed dormancy and hardiness development, and thus indirectly increase RGP.

There has been some debate over the relation of stored carbohydrates to RGP. The conclusion seems to be that while root activity may require carbohydrates, the level of food reserves does not alone control root growth (Zaerr and Lavender 1974). Ritchie (1982) found that the levels of RGP and stored carbohydrates varied independently during overwinter storage of Douglas-fir seedlings.

Evidence is accumulating that the pattern of RGP in planting stock is closely related to its dormancy and cold hardiness status. The following general pattern is interpreted from research reports on Douglas-fir: RGP rises after deep dormancy has been attained, intensifies in winter coincident with the accumulation of chilling hours and release of dormancy, peaks with the fulfillment of the chilling requirement and the development of maximum cold hardiness, and falls abruptly at approximately the time of bud break and concurrent loss of cold hardiness (Ritchie and Dunlap 1980, Richie 1986, Stone et al. 1963, Tinus et al. 1986). The actual pattern of RGP can vary widely depending on species and seed zone, weather, and nursery (Jenkinson 1980). For a review of the interrelations among dormancy, cold hardiness, stress resistance, lifting time, and RGP, see Rietveld (1987) in this proceedings.

AGGRAVATORS OF TRANSPLANTING SHOCK

Two factors that aggravate the natural stresses that constitute transplanting shock are: (1) pre-plant handling and exposure, and (2) post-plant drought. These factors are always detrimental to some degree, and they intensify and/or prolong transplanting shock. Although it is nearly impossible to eliminate these factors, their effects can be minimized.

Pre-plant Handling and Exposure

During lifting, grading, storing, shipping, and field handling, seedlings may lose many of their fine roots and may be exposed to damaging root drying, leading to severe internal water deficits even before they are planted. The principal causal factors are loss of fine roots, exposure, physical damage, handling, heat stress, and improper planting. By its very nature, the process of bare-rooting seedlings will entail some degree of root loss, exposure, and handling. But most of the component factors are controllable, and their influence can be minimized through proper care and handling.

Exposure of roots of bareroot seedlings results in delayed bud burst, reduced survival, and reduced growth (Feret et al. 1985, Hermann 1967, Mullin 1974). In addition Hermann (1967) found that exposure of roots was much more damaging to Douglas-fir (Pseudotsuga menziesii (Mirb.) Franco.) seedlings lifted in November or March and those that had been cool-stored. Seedlings lifted in midwinter and not stored were least affected. Feret et al. (1985) found that each 10 minutes of root exposure diminished first-year survival of loblolly pine seedlings 6.97, and 35 minutes of root exposure decreased RGP 507. Mullin (1974) found that fourth-and fifth-year survival of red pine (Pinus resinosa Lit.) and white spruce (Picea glauca (moench) Voss) seedlings root exposed for 1 hour was decreased 347 and 397, respectively. The potential severity of any period of exposure will depend on the timing and nature of the lifting practice, the environmental conditions, seedling size, species, and physiological state of the plants. Any amount of seedling desiccation should be considered detrimental and should be minimized if seedling performance potential is to be maintained at the planting site.

Physical damage includes the loss of fine roots and any damage to the seedlings caused by rough handling. Most root losses occur during lifting and grading, but fine roots may be lost at any stage of handling. Fine roots are important for water absorption and carbohydrate storage, and care should be exercised to retain them.

The simple act of handling seedlings can retard their growth. New Zealand nurserymen found a surprising increase in growth of monterey pine (Pinus radiata D. Don) seedlings moved directly from the nursery bed to the field (Tinus 1980). Tabbush (1986) recently reported that dropping bundles of sitka spruce (Picea sitchensis (Bong.) Carr.) and Douglas-fir seedlings from a height of 3 meters to a hard floor severely depressed seedling root growth potential, ectomycorrhizal development, and predawn water potential. Growth was temporarily slowed, not permanently stopped. These responses to handling are similar to the physiological responses to mechanical stimuli reported by Jaffe (1980), which he calls thigmomorphogenesis. The mechanical stimulus apparently causes the production of "stress metabolites" that interact with ethylene to produce the growth retardation, usually shortening and thickening of the stem (Takahashi and Jaffe 1984).

Seedlings in exposed packing bags may accumulate heat from two sources, radiation from the sun and release from accelerated respiration (DeYoe et al. 1986). Allowing moist planting stock to heat up inside bags or boxes is a good way to convert perfectly good planting stock to ensilage. When the temperature of seedlings in package rises above 40°F for longer than a few hours, the risk to seedlings is increased because of respiratory expenditure of food reserves (Ritchie 1982), potential for mold, initiation of stress metabolism (Haard 1983), and loss of cold hardiness (Levitt 1980). DeYoe et al. (1986) found that covering packaged seedlings with Mylar tarps maintains internal temperature at approximately the same level as that of seedlings stored in the shade. This is a very temporary measure; planting stock should be kept in cool storage, and no more than 1 day's supply should be kept on the planting site.

Post-plant Drought

The occurrence of drought (lack of precipitation) immediately after outplanting is a common event over which we have no control, and the degree of drying is influenced by the presence of competing vegetation, over which we have some control. The transplanted seedling usually develops some degree of plant moisture stress because of the inability of the planted root system to keep up with water losses. Post-plant drought intensifies that condition. Stoneham and Thoday (1985) found that the effects of preplant root exposure and post-plant drought on shoot growth were additive and strongly affected by lifting and planting dates. Late winter lifting and planting conferred an advantage because the seedlings were more dormant and stress tolerant, and prolonged the time available for root regeneration.

DEVELOPMENT OF TRANSPLANTING SHOCK

Some degree of transplanting shock is unavoidable because seedlings have been barerooted and outplanted into a different, usually less favorable environment. Seedling recovery and adaptation involve several interactive concurrent processes. The intensity of these processes is governed by a large number of variables, which contributes to the complexity. These processes are discussed separately in the following sections.

New Root Growth

Seedling survival and growth are critically dependent on new root growth because new roots are necessary to: 1) re-establish the root-to-soil contact, 2) absorb water and nutrients, 3) avoid plant moisture stress, and 4) produce phytohormones to support new growth. Sands (1984) described the mechanism of transplanting stress: 1) an air gap is present at the root-soil interface; 2) this presents a high resistance to liquid water flow, even in wet soil because water must move to the roots in the vapor phase, which is very inefficient; and 3) recovery from such stress occurs in direct proportion to the rate that new roots grow into the surrounding soil and have good root-soil contact. Carkett (1982, cited by Stoneham and Thoday 1985) found that seedlings given even a short period in soil at field capacity were far more resistant to subsequent desiccation by drought conditions than seedlings planted into dry soil. Apparently regeneration of a few new roots is much better than no new root growth. Transplanted dormant seedlings have mostly suberized roots, which are much less efficient in water and nutrient uptake than unsuberized (new) roots. Chung and Kramer (1975) found that water absorption by loblolly pine (*Pinus taeda* L.) seedlings through suberized roots was only 11% of uptake through unsuberized roots. Before new root growth, root system size and the degree of root/soil contact determine the potential for water uptake, but after new root growth, the potential for water uptake is proportional to the number of new roots produced (Carlson 1986). This suggests that nursery practices that favor the production of seedlings with high root volume and high RGP will maximize both water uptake and sites for new root growth after transplanting.

Soil Temperatures

Soil temperature has a dramatic influence on root growth. Root growth of most species is minimal at soil temperatures below 10°C (Carlson 1986, Nambiar et al. 1979) and is optimal between 18 and 25°C (Ritchie and Dunlap 1980). Species, seed sources, and families vary in their minimum and optimum temperatures for root growth (Carlson 1986, Nambiar et al. 1979, DeWald and Feret 1985). Thus, when seedlings are planted early in the spring, new root growth is often delayed until soil temperature rises to a favorable level. Several patterns of spring soil warming may occur: (1) loosened and exposed mineral soil results in earlier warming than undisturbed or mulched soil, (2) wet soils are slow to warm, (3) south and west slopes warm faster than north and east slopes, (4) without precipitation, soils warm faster as they dry, and (5) warm spring rains both warm and moisten the soil. Thus the period of favorable soil temperatures (and moisture) for root growth, before shoot growth begins, may vary greatly in time, duration, and location.

Plant Moisture Stress

A "catch-22" factor in the transplanting shock scenario is plant moisture stress because of its profound effects on root growth. As discussed above, new root growth into surrounding soil to reestablish an intimate root/soil contact is extremely important if seedlings are to avoid plant moisture stress and to establish quickly. However, even low levels of stress severely retard the ability of plants to regenerate roots. Thus, new root growth is needed to avoid plant moisture stress, but if plant moisture stress develops, the seedlings cannot grow new roots. Transplanting stress is intensified and/or prolonged until adequate moisture becomes available. Day and MacGillivray (1975) found that RGP of white spruce seedlings was significantly reduced in soil at -0.6 bar, and was non-existent at soil matric potentials below-1.5 bars. Similarly, Larson and Whitmore (1970) observed excellent RGP expression of transplanted red oak (*Quercus rubra* L.) seedlings at -0.3 bar (field capacity), substantially reduced root growth at -2.0 bars, and virtually no root growth at -6.0 bars.

Rapid production of abscisic acid (ABA) is a common response to moisture stress in higher plants. It is thought that stomatal closure in response to rising plant moisture stress is mediated by a rise in endogenous ABA level (Quarrie 1983). Drought resistant varieties of corn, sorghum, and millet produce larger amounts of ABA during stress than nonresistant varieties (Larque'-Saavedra and Wain 1976, Hewnson et al. 1981). Roberts and Dumbroff (1986) found that ABA content of jack pine, black spruce (*Picea mariana* (Mill.) BSP), and white spruce shoots increased during a period of drought as water potentials decreased. The increase in ABA levels was closely associated with a decrease in rates of transpiration. The three species differed in their basal ABA levels, the proportional increase during drought, and the rate of return to prestress levels. Thus, a rise in ABA level in conifers may be a controlling factor in stomatal closure, thereby contributing to the conservation of a seedling's water supply during periods of drought.

Carbohydrate Reserves

Seedlings depend on reserve carbohydrates from the time they are lifted until photosynthesis in outplanted seedlings is sufficient to meet the demands of growth and respiration. Carbohydrates are the stored fuel and respiration is the process whereby the fuel is converted to energy for maintenance and growth. Maintenance respiration continues in seedlings overwintering outside or in storage, so the normal trend is a gradual consumption of stored carbohydrates (Marshall 1985, Rietveld et al. 1983, Ritchie 1982, 1987). The depletion rate during storage depends on seedling physiological condition when they entered storage, storage temperature, and storage duration. Storage temperatures within the range of -2 to +5°C are most beneficial to chilling and maintenance of stored carbohydrates.

After planting, carbohydrates are consumed at an accelerated rate because of higher temperatures and demands from growth processes. Carbohydrate reserves may be reduced to critically low levels by the time photosynthesis exceeds respiration in the spring. The goal is to maximize carbohydrate reserves in lifted seedlings, preserve carbohydrates during storage, and minimize unnecessary losses during shipping and handling, so that adequate carbohydrate reserves remain to sustain the seedlings through the period of transplanting shock. If carbohydrate reserves are too low at time of planting to sustain the seedling until photosynthesis begins, or if transplant shock is severe and prolonged, the seedlings will literally run out of energy and starve to death.

As stored carbohydrates are consumed, many fine roots are lost (Marshall 1986), which results in impaired water uptake, buildup of plant moisture stress, and retarded new root growth. Elevated respiration from heat stress may further increase the consumption of carbohydrates (DeYoe et al. 1986). Fine root mortality appears to be more related to the inability of roots to continue to respire (Marshall 1986) than to drought or heat stress. When stored carbohydrates in fine roots are depleted, maintenance respiration can no longer continue, and the roots die.

Under relatively favorable planting site conditions the amount of new root growth in transplanted conifers is primarily dependent on currently assimilated photosynthates (van den Diessche 1987). As conditions become less favorable, the level of stored carbohydrates becomes more important to production of new roots (Marshall 1985, van den Driessche 1987). This assumes that the seedlings have been adequately preconditioned (chilled) to produce new roots (Krugmann and Stone 1966). There is evidence that disruption of the phgotosynthetic apparatus from frosts and storage may delay photosynthesis after transplanting (McCracken 1978). Thus it may be several weeks before photosynthesis exceeds respiration requirements for maintenance and growth and a positive carbon balance is achieved. The implication is that there may be an additional period of heavy demand on carbohydrate reserves to support higher levels of maintenance and growth respiration before photosynthesis can supply these needs.

Once root growth has been triggered and is proceeding in a favorable environment, its rate seems to come under the influence of an internal carbohydrate source-sink regime. Before budbreak, roots are the major metabolic sink in the plant and are actively drawing upon currently assimilated carbohydrates. Resumption of shoot growth is accompanied by a rapid decline in root growth, suggesting a sink strength reversal favoring the shoot.

The net amount of photosynthate available for root growth depends on light intensity, soil moisture, temperature, nutrition, and competition from shoot growth. In general, mild moisture stress has a greater effect on growth than on photosynthesis, so carbohydrates will tend to build up during mild moisture stress (Hsiao 1973).

Factor Interactions

The severity and duration of transplanting shock will depend on the interactions of seedling performance potential and environmental factors. Early planting is desirable from the standpoint of maximizing seedling performance potential, i.e. the ability of seedlings to resist stresses and grow new roots. Initially low soil temperatures may limit water absorption and root growth, so planting too early may result in dehydration and further depletion before root growth can occur. Feret et al. (1986) suggested that the reason for inconsistent correlation between RGP and survival in some experiments is that low soil temperatures may inhibit new root growth for several weeks, allowing RGP to decline before conditions become favorable.

Seedlings with a low shoot:root ratio, high root fibrosity, and good root/soil contact are more capable of extracting soil moisture and avoiding plant moisture stress under conditions of soil drying. Relatively little is known about the relation between seedling dormancy/cold hardiness status and the ability to tolerate stresses after planting. Larsen et al. (1986) found that loblolly pine seedlings with a high proportion of quiescent buds had higher RGP and better survival than seedlings with dormant buds. To some extent, early planted seedlings are being "stored" in the field, but the conditions are less than ideal because of the difference between air and soil temperatures.

Seedlings planted late may have lower RGP and are more likely to be confronted with higher air temperatures, higher evaporative demand, more competition from other vegetation, a higher possibility of post-planting drought, and competition with shoot growth for available substrates. The fate of these seedlings depends on sustained adequate soil moisture. If soil moisture remains high, the seedlings may survive well and grow modestly; but if soil moisture becomes limiting, the seedlings are vulnerable to severe stress and may die.

Ideally, seedlings with high performance potential should be in place before the optimum period for root growth so that their potential can be realized, and plant moisture stress can be kept to a minimum. In reality, we are forced to work within the constraints of weather and the size of the planting operation, which usually means that all seedlings are not planted at the ideal time.

ESTABLISHMENT

A newly planted seedling has a diminished and dysfunctional root system that provides access to only a limited volume of soil, and thus is highly vulnerable to soil drying. The ability of seedlings to become established depends on their ability to expand their root system into the surrounding soil to obtain adequate water and nutrients (Sands 1984, Sands and Nambiar 1984).

The rate at which this occurs depends on a number of seedling and environmental factors. Seedling establishment can be separated into three phases (Carlson 1986): 1) postplanting but pre-root-elongation, 2) rapid root development, and 3) rapid shoot elongation and leaf area expansion (fig. 2).

Successful passage through the first phase is directly related to seedling stress resistance, i.e. the capacity of the seedling to maintain performance potential, avoid stresses, and minimize depletion until conditions are favorable for growth. Seedlings depend on the planted root system to extract water and nutrients from the soil. Plant moisture stress will build up if water losses significantly exceed uptake. Seedlings with a larger root system in relation to shoot size are better able to balance water absorption with water loss and avoid plant moisture stress during this phase. Water and nutrient uptake are reduced at low soil temperatures because of the increased viscosity of water.

Passage through the second phase depends on the successful completion of phase one, on expression of seedling performance potential, and on environmental constraints. As the air and soil warm, the progress of establishment becomes increasingly dependent on new root growth and avoidance of the retarding effects of plant moisture stress. The rate of progression of phase two will vary with air and soil temperatures, soil moisture availability, and photosynthetic rate. If plant and environmental conditions are favorable, the seedling will grow new roots into the surrounding soil and quickly move through phase two. Success in promptly growing new roots into the surrounding soil (reducing the likelihood of plant moisture stress) followed by the replacement of lost roots and carbohydrates seem to be the key to successful establishment.

Entry into the rapid shoot elongation phase is a signal that the seedling has become successfully established. Although survival is more at issue in phases one and two, seedling growth rate is the dependent variable in phase three.

The time span of the three phases may be weeks under favorable conditions or months or years under unfavorable conditions. The possible interactions of seedling performance potential and site constraints, and their projected outcomes are listed in fig. 3. Planting stock with high performance potential, combined with good site preparation, will result in prompt and consistent establishment in most years. Stock with high performance potential planted on poorly prepared sites may give acceptable but inconsistent survival and fair to good growth. Planting stock with low performance potential may survive and grow sluggishly (the seedlings that do survive may grow well) on well prepared sites in favorable years, but will fail under more difficult site and weather conditions.

MINIMIZING TRANSPLANT SHOCK

There are five ways to approach the task of minimizing transplanting shock: 1) prescribe planting stock of appropriate quality, 2) condition stock in the nursery to increase stress resistance, 3) preserve performance potential from lifting to planting, 4) prepare a favorable planting site environment, and 5) plant the seedlings properly. To keep the cost of planting stock and site preparation within reasonable limits and still obtain successful plantations, the emphasis has been to match planting stock quality and site preparation to individual situations, with the goals of completely stocking and realizing the full growing potential of each site.

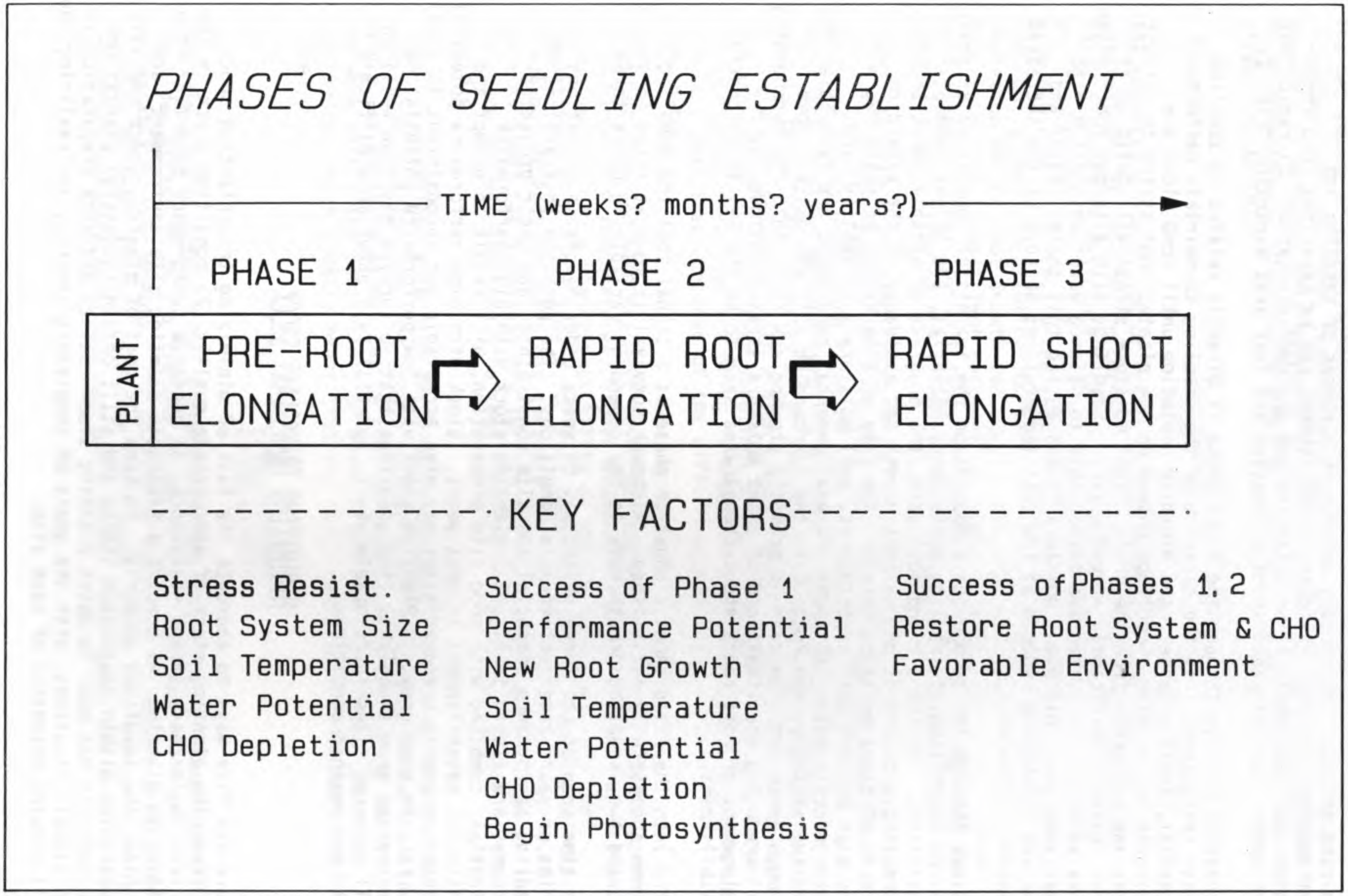


Figure 2. Establishment phases of outplanted bareroot seedlings and key factors effecting the duration of each phase. Entry into phase 3 is a signal that the seedling is successfully established and free to grow.

PERFORMANCE POTENTIAL	−	SITE CONSTRAINTS	=	FIELD PERFORMANCE: SURVIVAL	FIELD PERFORMANCE: GROWTH
HIGH		FAVORABLE		EXCELLENT	EXCELLENT
HIGH		UNFAVORABLE		VERY GOOD	FAIR-GOOD
LOW		FAVORABLE		FAIR-GOOD	POOR
LOW		UNFAVORABLE		POOR	POOR

Figure 3. Expected field performance of outplanted seedlings in relation to performance potential of the planting stock and constraints of the planting site.

Prescribe Planting Stock of Appropriate Quality

The accepted definition of planting stock quality ("fitness for purpose ... the degree to which stock realizes the objectives of management at minimum cost") (Sutton 1979), defines a reflexive condition, i.e., if the stock prescribed exactly met our performance standards (no more, no less), than we conclude that stock quality was 100%. If performance expectations were not attained or were exceeded, then planting stock quality was less than or more than 100%. For example, if our performance standards require a minimum of 85% survival in 9 out of 10 plantations and trees averaging 1 m in height at the end of the second growing season, then we would prescribe a specific stock type for each individual site that we expect will attain that objective. If our expected performance was exceeded on the average, we would cut back on the quality of the planting stock prescribed, and presumably cost. Similarly, we would prescribe a higher stock quality if our performance objectives were not being met on the average. Note that regeneration success can also be improved by increasing performance potential of the existing stock through prudent care and handling. More often than not, performance expectations are not being met and a higher grade of planting stock is warranted. If field performance is highly inconsistent, then it may be necessary to add a "safety factor" to the quality of the planting stock prescribed. All other factors being adequate, key quality factors that increase seedling performance potential include: moderate size (25-30 cm shoot), large root system in relation to shoot size, large stem caliper, high nutrient and carbohydrate concentrations, and high RGP. Standards, and the ability to attain them, will vary for different species. One of the best ways to obtain the desired attributes is to reduce seedbed density (Carlson 1986).

Condition Seedlings to Increase Stress Resistance

Various cultural treatments have been tried to increase stress resistance, but few have been consistently successful, mainly because there is a lack of information on the physiology and longevity of such treatments. Although transplanting is a common practice in Ontario nurseries, it is rarely done in the U.S because of its expense. For some species, wrenching has been found to be an effective cultural treatment to reduce excessive shoot growth, increase root fibrosity, and increase stress resistance (Bacon and Bachelard 1978, Rook 1969), but results have been variable for other species (Tanaka et al. 1976, van den Driessche 1983). Blake (1983) found that cold storage, but not root-pruning, was effective in pre-conditioning white spruce stomata to reduce water loss when water was limiting. Abod and Sandi (1983) found that restricted watering before lifting Caribbean pine (*Pinus caribaea* var *hondurensis* (Morelet) Loock.) seedlings was the most effective way to precondition them to survive bareroot planting. Hennessey and Dougherty (1984) found that loblolly pine seedlings that were moderately water-stressed in late summer showed a better degree of osmotic adjustment, a capacity for greater turgor maintenance over a range of water potentials, and significantly greater root regeneration the following spring compared to unstressed seedlings.

It is important to note that conditioning treatments that stress the seedlings should not be starvation nursery practices. Conditioning treatments should be combined with adequate fertilization, so that the conditioned seedlings also have good mineral nutrient status (Duryea and McClain 1984). Fall fertilization may be a successful method to increase seedling nitrogen concentration without interfering with dormancy induction and deepening. Margolis and Waring (1986) found that outplanted Douglas-fir seedlings that had been fertilized with nitrogen in October broke buds 9 to 10 days earlier, produced more shoot growth, and had higher relative growth rates than unfertilized seedlings.

Lifting seedlings and planting them when cold hardiness and stress resistance are greatest appears to be an effective approach to minimizing transplanting shock (Jenkinson and Nelson 1984, Ritchie et al. 1985, Stoneham and Thoday 1985). However, for many species in northern nurseries, it is not possible to lift and plant seedlings in midwinter when cold hardiness and stress resistance are greatest. The alternatives, fall lifting and overwinter storage and late winter lifting and temporary storage, involve many variables and tradeoffs. Research needs to be concentrated on the interrelations among dormancy, cold hardiness, stress resistance, and storage, and how these factors may be optimized or manipulated to increase seedling performance potential. Jenkinson (1980) has developed time windows for lifting several major species and specific seed sources at individual nurseries. Lifting seedlings outside these windows results in reduced survival and growth, and possibly plantation failure. Weyerhauser Company' has led the way in growing seedlings by family (seed collected from a clone in a seed orchard), observing growth response to cultural treatments, and grouping families with similar growth into "response groups". Cultural treatments are then tailored to each "response group" to grow seedlings to desired specifications.

Physiological responses to drought stress may be moderated by mycorrhizal associations. Inoculation of planting stock with ectomycorrhizae appears to be most important in clearcuts where the population of host plants is not adequate to maintain fungal populations, on trees growing in poor soils, and in environments where seedlings must establish quickly to survive (Perry et al. 1987). Ectomycorrhizae may be beneficial under droughty conditions by providing some resistance to soil water deficits and improving phosphorus absorption (Parke et al. 1983). Because maximal stress resistance is needed immediately after outplanting, ectomycorrhizae need to be well adapted to the planting site environment and in place at the time of planting if their benefits are to be realized. Research is needed to determine the extent to which ectomycorrhizal colonization of planting stock can be exploited to increase the drought tolerance of planted seedlings.

One approach to explore further is the utilization of species, seed source, and family differences in seedling root growth potential and drought resistance to improve reforestation success. Some genetic strains of a species possess inherently greater innate levels of RGP (DeWald and Feret 1985, Jenkinson 1980, Larsen and Boyer 1986), and more capable of growing roots at lower soil temperatures (Carlson 1986, Nambiar et al. 1979), or are more drought tolerant because of their morphology or phenology (White 1987), or possess mechanisms to maintain growth at lower water potentials

---

'Personal communication with Dr. William C. Carlson, Tree Physiologist, Weyerhauser Co., Southern Forestry Center, Hot Springs, AR 71902

(Newton et al. 1985). Although we may not always think of it this way, choosing the proper species to plant on a given site is the most powerful genetic method we now have of managing moisture stress. For example, jack pine (Pinus banksiana Lamb.) avoids drought better than red pine because it can maintain a higher needle water potential through drying cycles (Pereira and Kozlowski 1977). Thus, jack pine is a better choice for droughty sites than red pine. Selection or breeding for root growth at lower temperatures or maintenance of growth at lower soil matric potentials would contribute significantly to planting stock quality and performance potential. Because 80 to 907 of the variation in tree growth is attributable to drought stress (Zahner 1968), the potential gains from breeding trees for drought resistance are enormous.

Preserve Seedling Performance Potential from Lifting to Planting

The principal factors that result in loss of performance potential include root exposure, handling, storage conditions and length, shipping, temporary storage in the field, and planting. The effects of storage on RGP and carbohydrate reserves are perhaps the most complex. For the most part, all these factors have the net effect of losing fine roots and reducing levels of RGP and stored carbohydrates. Storage may actually extend dormancy and RGP (Ritchie 1986, Carlson 1985). This is an area that deserves more monitoring and research to determine the extent of the losses and how much they can be minimized. The goal should be to identify and utilize the best practices to preserve the quality of the seedlings that nurserymen have labored hard to produce.

Prepare a Favorable Planting Site Environment

Site preparation practices, and success, differ greatly by region and agency. Site alterations include removing competing vegetation, loosening the soil, and incorporating surface organic materials. The benefits are increased availability of soil moisture for the tree seedlings, reduced soil compaction, improved soil aeration, reduced resistance to root penetration, earlier warming of the soil (Hansen et al. 1984), increased light, and reduced pest populations'. These are the manageable aspects of the planting site environment. We have no control over weather, and only partial control over pests. To a very large extent, site preparation is actually moisture management, i.e. assuming there is a limited amount of soil moisture available on the site and excluding evaporative losses, the site preparation prescription amounts to a decision of how much of the available moisture will be reserved for the planted seedlings, and how much will be given up to competing vegetation. To some extent, higher grade stock will compensate for incomplete site preparation and vice-versa, but to obtain consistent success the planting stock quality and site preparation need to be matched.

Plant the Seedlings Properly

Planting quality is measured in terms of returning the seedlings to the soil in as near the natural position as possible. Seedlings may be planted slightly deeper than the root collar, with the roots spread out and in good contact with the surrounding soil. Quality planting involves making sure the planting stock is well cared for and not planted into dry soil.

Abod, A. S. and S. Sandi. 1983. Effect of restricted watering and its combination with root pruning on root growth capacity, water status and food reserves of Pinus caribaea var. hondurensis seedlings. Plant and Soil 71:123-129.

Bacon, G. J. and E. P. Bachelard. 1978. The influence of nursery conditioning treatments on some physiological responses of recently transplanted seedlings of Pinus caribaea Mor. var. hondurensis B. & G. Aust. For. Res. 8:171-183.

Blake, R. J. 1983. Transplanting shock in white spruce: effect of cold-storage and root pruning on water relations and stomatal conditioning. Physiol. Plant. 57:210-216.

Carlson, W. C. 1985. Effects of natural chilling and cold storage on budbreak and root growth potential of loblolly pine (Pinus taeda L.). Can. J. For. Res. 15:651-656.

Carlson, W. C. 1986. Root system considerations in the quality of loblolly pine seedlings. Southern J. Appl. For. 10:87-92.

Chung, H. and P. J. Kramer. 1975. Absorption of water and ^{32}P through suberized and unsuberized roots of loblolly pine. Can. J. For. Res. 5:229-235.

Day, R. J. and G. R. MacGillivray. 1975. Root regeneration of fall-lifted white spruce nursery stock in relation to soil moisture content. For. Chron. 51:196-199.

DeWald, L. E. and P. P. Feret. 1985. Genetic variation in loblolly pine root growth potential. Pages 155-162 In Proc 18th Southern Forest Tree Improvement Conf. [Long Beach, MS. May 21-23, 1985]. Southern Forest Tree Improvement Committee Publ. No. 40.

DeYoe, D., H. R. Holbo, and K. Waddell. 1986. Seedling protection from heat stress between lifting and planting. West. J. Appl. For. 1:124-126.

Duryea, M. L. (ed.). 1985. Evaluating seedling quality: principles, procedures, and predictive abilities of major tests. For. Res. Lab., Oregon State Univ., Corvallis, 143 pp.

Duryea, M. L. and T. D. Landis (eds.) 1984. Forest nursery manual: production of bareroot seedlings. College of For., Oregon State Univ., Corvallis, 385 pp.

Duryea, M. L. and K. M. McClain. 1984. Altering seedling physiology to improve reforestation success. Pages 78-114 In Duryea, M. L. and G. N. Brown (eds.) Seedling physiology and reforestation success. Martinus Nijhoff/Dr. W. Junk Publishers, Dordrecht/Boston/London. 325 p.

Feret, P. P. and R. E. Kreh. 1985. Seedling root growth potential as an indicator of loblolly pine field performance. For. Sci. 31:1005-1011.

Feret, P. P., R. E. Kreh, and C. Mulligan. 1985. Effects of air drying on survival, height, and root growth potential of loblolly pine seedlings. South. J. Appl. For. 9:125-128.

Feret, P. P., R. C. Freyman, and R. E. Kreh. 1986. Variation in root growth potential of loblolly pine from seven nurseries. Pages 317-328 In D. B. South (ed.) Proc. Internatl. Symp. on Nursery Management Practices for the Southern Pines. [Birmingham, AL Aug. 4-7, 1985] Auburn Univ., Alabama.

Fraser, G. K. 1933. Studies of certain Scottish moorlands in relation to tree growth. U. K. For. Comm. Bull. 15, 112 p.

Haard, N. F. 1983. Stress metabolites. Pages 299-314 In M. Lieberman (ed.) Post-harvest physiology and crop preservation. Plenum Publishing Co., New York.

Hansen, E., D. Netzer, and W. J. Rietveld. 1984. Site preparation for intensively cultured hybrid poplar plantations. USDA For. Serv. Res. Note NC-320, 4 p., North Central Forest Exp. Stn., St. Paul, MN.

Hennessey, T. C. and P. M. Dougherty. 1984. Characterization of the internal water relations of loblolly pine seedlings in response to nursery cultural treatments: implications for reforestation success. Pages 225-243 In M. L. Duryea and G. N. Brown (eds.) Seedling physiology and reforestation success. Martinus Nijhoff/Dr. W. Junk Publishers, Dordrecht/Boston/London. 325 p.

Hensen, I. E., V. Mahalakshmi, F. R. Bidinger, and G. Alagarswamy. 1981. Genotypic variation in pearl millet (Pennisetum americanum (L.) Leeke) in the ability to accumulate abscisic acid in response to water stress. J. Expl. Bot. 32:899-910.

Hermann, R. K. 1967. Seasonal variation in sensitivity of Douglas-fir seedlings to exposure of roots. For. Sci. 13:40-149.

Hsiao, T. C. 1973. Plant responses to water stress. Ann. Rev. Pl. Phys. 24:519-570.

Jaffe, M. J. 1980. Morphogenic responses of plants to mechanical stimuli or stress. BioSci. 30:239-243.

Jenkinson, J. L. 1980. Improving plantation establishment by optimizing growth capacity and planting time of western yellow pines. USDA For. Serv. Res. Pap. PSW-154, 22 p. Pacific Northwest For. and Range Exp. Stn., Portland, OR.

Jenkinson, J. L. and J. A. Nelson. 1984. Cold storage increases resistance to dehydration stress in pacific Douglas-fir. Pages 38-44 In Thomas D. Landis (ed.), Proc. Western Forest Nursery Council and Intermountain Nurserymen's Assoc. Combined Meeting [Coeur d'Alene, ID, August 14-16, 1984]

Krugmann, S. L. and E. C. Stone. 1966. The effect of cold nights on the root regenerating potential of ponderosa pine seedlings. For. Sci. 12:451-459.

Larque'-Saavedra, A. and R. L. Wain. 1976. Studies in plant growth-regulating substances. XLII. Abscisic acid as a genetic character related to drought tolerance. Ann. Appl. Biol. 83:291-297.

Larsen, H. S. and J. N. Boyer. 1986. Root growth potential of loblolly pine (Pinus taeda L.) seedlings from twenty southern nurseries. Circ. 286, Alabama Agric. Expt. Stn., Auburn Univ. Auburn, AL.

Larsen, H. S., D. B. South, and J. N. Boyer. 1986. Root growth potential, seedling morphology and bud dormancy correlate with survival of loblolly pine seedlings planted in December in Alabama. Tree Phys. 1:253-263.

Larson, M. M. and F. W. Whitmore. 1970. Moisture stress affects root regeneration and early growth of red oak seedlings. For. Sci. 16:495-498.

Ledig, F. T. and T. O. Perry. 1970. Physiological genetics of the shoot-root ratio. Pages 39-43 In Proc. Soc. Am. For. [Detroit, MI, 1960]. Society of American Foresters, 5400 Grosvenor Lane, Bethesda, MD 20814.

Levitt, J. 1980. Responses of plants to environmental stress. I. Chilling, freezing, and high temperatures. Academic Press, New York.

Margolis, H. A. and R. H. Waring. 1986. Carbon and nitrogen allocation patterns of Douglas-fir seedlings fertilized with nitrogen in autumn. II. Field performance. Can. J. For. Res. 16:903-909.

Marshall, J. D. 1985. Carbohydrate status as a measure of seedling quality. Pages 49-58 In M. L. Duryea (ed.) Proc. Evaluating seedling quality: principles, procedures, and predictive abilities of major tests. [Corvallis, OR Oct. 16-18, 1984] For. Res. Lab., Oregon State Univ., Corvallis.

Marshall, J. D. 1986. Drought and shade interact to cause fine-root mortality in Douglas-fir seedlings. Plant and Soil 91:51-60.

McCracken, I. J. 1978. Carbon dioxide uptake of pine seedlings after cool storage. For. Sci. 24:17-25

Mullin, R. E. 1974. Effects of root exposure on establishment and growth of outplanted trees. Pages 229-242 In G. Hoffman (ed.) Second International Symp. on Ecol. and Physiol. of Root Growth. Akademie-Verlag, Berlin.

Nambiar, E.K.S., G. D. Bowen, and R. Sands. 1979. Root regeneration and plant water status of Pinus radiata D. Don seedlings transplanted to different soil temperatures. J. Expl. Bot. 30:1119-1131.

Newton, R. K., V. E. Meier, J. P. van Buijtenen, and C. R. McKinley. 1985. Cultural and genetic management of drought stress. Pages 215-219 In Proc. 1985 SAF National Convention. [Fort Collins, CO July 28-31, 1985] Society of American Foresters, 5400 Grosvenor Lane, Bethesda, MD 20814.

Parke, J. L., R. G. Linderman, and C. H. Black. 1983. The role of ectomycorrhizae in drought tolerance of Douglas-fir seedlings. New Phytol. 95:83-95.

Pereira, J. S. and T. T. Kozlowski. 1977. Water relation and drought resistance of young Pinus banksiana and P. resinosa plantation trees. Can. J. For. Res. 7:132-137.

Perry, D. A., R. Molina, and M. P. Amaranthus. 1987. Mycorrhizae, mycorrhizospheres, and reforestation: current knowledge and research needs. Can. J. For. Res. 17:929-940.

Quarrie, S. A. 1983. Genetic differences in abscisic acid physiology and their potential uses in agriculture. Pages 365-419 In F. T. Addicott (ed.) Abscisic acid. Praeger Scientific, New York.

Rietveld, W. J. 1987. Production of conifer planting stock with high root growth potential. In Proc. Northeastern Nurserymen's Conference [Cable, WI, August 18-20, 1987] WI. Dept. of Nat. Res., Madison. (in press)

Rietveld, W. J., R. D. Williams, and F. D. McBride. 1983. Starch levels in fall-lifted hardwood seedlings and their relation to field survival and growth. Pages 86-97 In Proc. Northeastern Area Nurserymen's Conf. [Halifax, Nova Scotia, July 26-30, 1982] Nova Scotia Dept. of Lands and Forests, Box 68, Truro, Nova Scotia.

Ritchie, G. A. 1982. Carbohydrate reserves and root growth potential in Douglas-fir seedlings before and after cold storage. Can. J. For. Res. 12:905-912.

Ritchie, G. A. 1985. Root growth potential: principles, procedures, and predictive ability. Pages 93-104 In Duryea, M. L. (ed.) Proc. Evaluating seedling quality: principles, procedures, and predictive abilities of major tests. [Corvallis, OR Oct. 16-18, 1984] For. Res. Lab., Oregon State Univ., Corvallis.

Richie, G. A. 1986. Relationships among bud dormancy status, cold hardiness, and stress resistance in 2+0 Douglas-fir. New For. 1:29-42.

Ritchie, G. A. 1987. Some effects of cold storage on seedling physiology. Tree Planters' Notes 38(2):11-15.

Ritchie, G. A. and J. R. Dunlap. 1980. Root growth potential: its development and expression in forest tree seedlings. New Zealand J. For. Sci. 10:218-248.

Ritchie, G. A. and R. G. Shula. 1984. Seasonal changes in tissue-water relations in shoots and root systems of Douglas-fir seedlings. For. Sci 30:536-546.

Ritchie, G. A., J. R. Roden, and N. Kleyn. 1985. Physiological quality of lodgepole pine and interior spruce seedlings: effects of lift date and duration of freezer storage. Can. J. For. Res. 15:636-645.

Roberts, D. R. and E. B. Dumbroff. 1986. Relationships among drought resistance, transpiration rates, and abscisic acid levels in three northern conifers. Tree Phys. 1:161-167.

Rook, D. A. 1969. Water relations of wrenched and unwrenched Pinus radiata seedlings on being transplanted into conditions of water stress. New Zealand J. For. 14:50-58.

Sands, R. 1984. Transplanting stress in radiata pine. Aust. For. Res. 14:67-72.

Sands, R. and E. K. S. Nambiar. 1984. Water relations of Pinus radiata in competition with weeds. Can. J. For. Res. 14:233-237.

Smith, J. H. G. and J. Walters. 1963. Planting check (reduction in height growth) of planted Douglas-fir seedlings. Univ. B. C., For. Fac., Res. Note 42, 4p.

Stone, E. C., G. H. Schubert, R. W. Bensler, F. J. Baron, and S. L. Krugman. 1963. Variation in the root regenerating potentials of ponderosa pine from four California nurseries. For. Sci. 9:217-225.

Stoneham, J. and P. Thoday., 1985. Some physiological stresses associated with tree transplanting. Sci. Hort. 36:83-91

Sutton, R. F. 1968. Ecology of young white spruce (Picea glauca (Moench) Voss.). Ph.D. thesis, Cornell Univ., Ithaca, N.Y., 500 p.

Sutton, R. F. 1982. Plantation establishment in the boreal forest: planting season extension. Canadian Forestry Serv, Dept. of the Environment Rpt. 0-X-344, Great Lakes Forest Res. Centre, Sault Ste. Marie, Ontario.

Sutton, R. F. 1979. Planting stock quality and grading. For. Ecol. Manage. 2:123-132.

Tabbush, P. M. 1986. Rough handling, soil temperature, and root development in outplanted sitka spruce and Douglas-fir. Can. J. For. Res. 16:1385-1388.

Takahashi, H. and M. J. Jaffe. 1984. Thigmomorphogenesis: the relationship of mechanical perturbation to elicitor-like activity and ethylene production. Physiol. Plant. 61:405-411.

Tanaka, Y., J. D. Walstad, and J. E. Borrecco. 1976. The effect of wrenching on morphology and field performance of Douglas-fir and loblolly pine seedlings. Can. J. For. Res. 6:453-458.

Thompson, B. E. 1985. Seedling morphological evaluation -- what you can tell by looking. Pages 59-71 In M. L. Duryea (ed.) Proc. Evaluating seedling quality: principles, procedures, and predictive abilities of major tests. [Corvallis, OR Oct. 16-18, 1984]. For. Res. Lab., Oregon State Univ., Corvallis.

Tinus, R. W. 1980. Forestation concepts and practices developing in New Zealand. Pages 11-16 In Proc. Intermountain Nurserymen's Assoc. and Western Forest Nursery Assoc. Combined Meeting [Boise, ID Aug. 12-14, 1980] USDA For. Serv. Gen. Tech. Rpt. INT-109, March, 1981. Intermountain Forest and Range Experiment Station, Ogden, UT.

Tinus, R. W., K. E. Burr, S. J. Wallner, and R. M. King. 1986. Relation between cold hardiness, root growth capacity, and bud dormancy in three western conifers. Pages 80-86 In Thomas D. Landis (ed.), Proc. Western Forest Nursery Council and Intermountain Nursery Association Combined Meeting. [Tumwater, WA, August 12-15, 1986] USDA Forest Service General Technical Report RM-137. Rocky Mountain Forest and Range Experiment Station, Fort Collins, CO.

van den Driessche, R. 1983. Growth, survival, and physiology of Douglas-fir seedlings following root wrenching and fertilization. Can. J. For. Res. 13:270-278.

van den Driessche, R. 1987. Importance of current photonysthate to new root growth in planted conifer seedlings. Can. J. For. Res. 17:776-782.

White, T. L. 1987. Drought tolerance of southwestern Oregon Douglas-fir. For. Sci. 33:283-293.

Willen, P. and R. F. Sutton . 1980. Evaluation of stock after planting. New Zealand J. For. Sci. 10:297-299.

Zaerr, J. B. and D. P. Lavender. 1974. The effects of certain cultural and environmental treatments upon the growth of roots of Douglas-fir (Pseudotsuqa menziesii (Mirb.) Franco) seedlings. Pages 27-32 In Proc. 2nd Int. Symp. on Ecol. and Phys. of Root Growth. Potsdam. Academie-Verlag, Berlin.

Zahner, R. 1968. Water deficits and growth of trees. Pages 191-254 In Kozlowski, T. T. (ed.) Water deficits and plant growth, vol II. Academic Press, New York. 333 p.