Chapter 8

Seedling Quality of Southern Pines

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Abstract

Seedling quality is related to a seedling's ability to survive prolonged environmental stresses and produce vigorous growth following outplanting. This complex concept includes both a seedling's "physiological readiness" to grow and suitable morphological features that will allow the seedling to overcome site limitations. Seedling ontogeny (genetically coded course of development) and phenology (response to environment) alter seedling physiology (processes), and fluctuations in physiology are, in turn, manifested in seedling morphology (structure). Morphological criteria for assessing seedling quality — shoot height, root-collar diameter, and root and shoot architecture — can be manipulated by nursery cultural practices. However, to implement these practices, nursery personnel must understand seedling growth dynamics and allometry (interrelationship of shoot and root growth over time). Physiological criteria for assessing quality include water relations, nutrition, carbohydrates, and dormancy and cold hardiness. Water and nutritional status, responsive to environmental changes, also can be influenced by nursery practices and, in turn, affect carbohydrate production and storage and, in part, dormancy and cold hardiness. Inappropriate or ill-timed cultural practices can produce seedlings of inferior morphological grade that perform poorly in the field. Moreover, careless handling during lifting, packaging, storing, and planting can degrade high-quality seedlings such that field survival and growth suffer. To predict quality before planting, nursery managers and foresters can subject seedlings to morphological, physiological, and/or performance tests. The better morphological tests are based on diameter, alone or in combination with height. Physiological tests include mitotic index, carbohydrate concentration, and cold hardiness, and performance tests include root-growth potential and budbreak with or without stressing. Future tests may rely on infrared thermography and spectroradiometry, chlorophyll *a* fluorescence, volatile-compound emissions, and biochemical markers.

8.1 Introduction

A high-quality seedling can generally be defined as a seedling that can survive prolonged environmental stresses and produce vigorous growth following outplanting. Although this definition identifies the goal, it has little practical value to those responsible for rearing or planting quality seedlings.

South and Mexal [72] suggest that what constitutes a high-quality seedling will vary with the management objectives of the buyer. Some might argue, however, that the primary objective of rearing commercial planting stock is to produce seedlings that will exhibit high growth and survival regardless of the buyer's objectives. Willen and Sutton [88] proposed that planting-stock quality is "fitness for purpose," a concept that includes the degree to which it achieves end-of-rotation goals at a minimum cost. Implicit in "fitness for purpose" are realistic management objectives concerning site factors, cultural practices, and species characteristics.

In any case, the term "high quality" assumes new dimensions once logistical and economic realities are considered. Then, the best seedling is one that can be produced at low cost, conforms to the existing site preparation and planting system, and survives and grows well after outplanting. In this chapter, we focus on morphological and physiological aspects of seedling quality, considering the practical limitations facing nursery operators today.

8.2 Relation of Morphology and Physiology to Seedling Quality

Seedling quality is a complex concept that requires consideration of both morphology — a seedling's shape and structure — and physiology — a seedling's functions and vital processes — which are not mutually exclusive. Table 8.1 presents a number of seedling characteristics and advantages that they may confer to planting stock. The "physiological readiness" of a seedling to grow following outplanting must be matched with morphological features

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Table 8.1. Seedling characteristics and their potential advantages for survival and growth upon outplanting.

Characteristic	Advantage
Well-developed terminal bud	Dormant stock; greater shoot growth
Large root-collar diameter	Greater survival and volume growth; resistant to animal and heat damage
Tall	Better competitor with weeds and brush
Low height:diameter ratio	Better resistance to wind desiccation; greater survival and growth on droughty sites
Numerous secondary needles	Greater regulation of water loss; better light interception and utilization in photosynthesis
Fibrous root system	Greater exploitation of soil; more root-initiation points
High root-growth potential	More rapid proliferation of roots; greater survival
Cold hardy	Better resistance to cold damage and other environmental stresses

that allow the seedling to overcome site limitations (e.g., insects, competing vegetation). For example, the appropriate morphological and physiological characteristics of a quality seedling destined for a droughty site will not be the same as those of a seedling destined for a mesic site.

Attempts to quantify morphological attributes of quality seedlings have resulted in the development of grades characterizing seedling vigor. Wakeley [81] proposed grades for loblolly *(Pinus taeda* L.) and slash *(P. elliottii* Engelm.) pine field performance (Table 8.2). Although such grades provide guidelines for morphological characteristics and a method for comparing past research results, other morphological measures may provide valuable information that can be used to predict seedling field performance. In this chapter, past work on seedling morphology is reviewed and possible refinement of current techniques for assessing quality discussed. All quality assessments based solely upon morphology assume that seedling physiology and stage of development are optimal for outplanting success.

In most cases, however, morphology offers little information as to physiological status of nursery seedlings. Foliage color may give a crude indication of nutrient status, and the presence of secondary needles, bark, and apical buds may signal that a particular developmental stage has been attained. But from physical appearance little can be said definitively about a seedling's readiness to grow when outplanted. In this chapter, the physiology of seedlings as influenced by plant carbohydrate levels, moisture status, nutrient content, dormancy, and cold hardiness is addressed relative to planting-stock quality. Techniques for assessing physiological grade of seedlings before outplanting are also discussed.

8.3 Relation of Morphology and Physiology to Seedling Phenology

To produce a high-quality seedling at lifting, growers must understand the interaction of ontogeny and phenology in both seedling morphology and physiology. The ontogeny, or course of development, of a pine seedling is genetically encoded in its nuclei, but development varies because of phenology, or response of a seedling to recurring annual climate changes or other environmental factors, including those manipulated in a nursery or glasshouse. Phenological changes alter seedling physiology, and fluctuations in physiology are, in turn, manifested in seedling morphology.

The relation between physiology and morphology, especially causal aspects, is not well understood. Many

Table 8.2. Criteria for morphological seedling grades, as established by Wakeley [81], for two southern pine species.

Pine species, by grade	Height, in.	Stem diameter, in.	Nature of stem	Bark on stem	Needles	Winter bud
Slash						
1	6–14	> 3/16	Stiff; woody	Entire stem	Nearly all in 3s and 2s	Usually present
2	5–8; some up to 12	at least 1/8	Moderately stiff	Lower stem	Part at least in 3s and 2s	Occasionally present
3	Usually < 6	< 1/8	Weak; succulent	Lacking	All single; bluish	Almost never present
Loblolly						
1	5–12	> 3/16	Stiff; woody	Entire stem	Nearly all in 3s	Usually present
2	4–7; some up to 10	at least 1/8	Moderately stiff	Lower stem	Part at least in 3s	Occasionally present
3	Usually < 5	< 1/8	Weak; succulent	Lacking	All single; bluish	Almost never present

NOTE: 1 in. = 2.54 cm.

physiological processes are elastic with respect to ontogeny; that is, physiology can vary significantly without changing morphology. For example, short-term variations in photosynthesis in response to environmental fluctuations have little impact on root development. However, prolonged depression of photosynthesis will affect root development. Likewise, there is usually a time lag between physiological response to an environmental change and morphological manifestation of that physiological response. The primary effect of this elasticity, or adaptability, is the development of a pine seedling that is recognizable as such with only slight variations in morphology.

However, some physiological processes — those related to survival mechanisms — are plastic, or invariant. Such plasticity is associated with switching from normal ontogeny to another developmental path. For example, the triggering of budset and associated dormancy in response to shortening photoperiod in the fall protects shoot meristems from damage due to low temperatures, which would impair the seedling's ability to compete and survive.

8.3.1 Morphology

Morphology during the early ontogeny of a pine seedling is greatly influenced by phenology and is manifested by traits that can be quantified. Here, the effects of phenology on three morphological traits — shoot height, root weight, and stem diameter — and their interrelationships are discussed (Fig. 8.1A). Other morphological traits important to seedling quality are discussed later in 8.4.

The most observable morphological trait of a pine seedling is shoot height. Once the epicotyl pushes through the soil surface and the cotyledons unfold, height can increase 10-fold or more over the growing season. Height growth begins at a slow rate after seedlings emerge, then accelerates during early to mid-summer, and slows again in fall (Fig. 8.1A). Height growth during the first growing season is due exclusively to free growth [49], that is, the simultaneous differentiation and elongation of leaf primordia, and therefore is controlled by environmental factors. In spring, soil and air temperatures play an important role, stimulating shoots to elongate; in fall, both temperature and photoperiod contribute to slow height growth, culminating with the development of a resting bud. The environmental conditions during bud development determine the potential for initial height growth the following spring (cf. [9]).

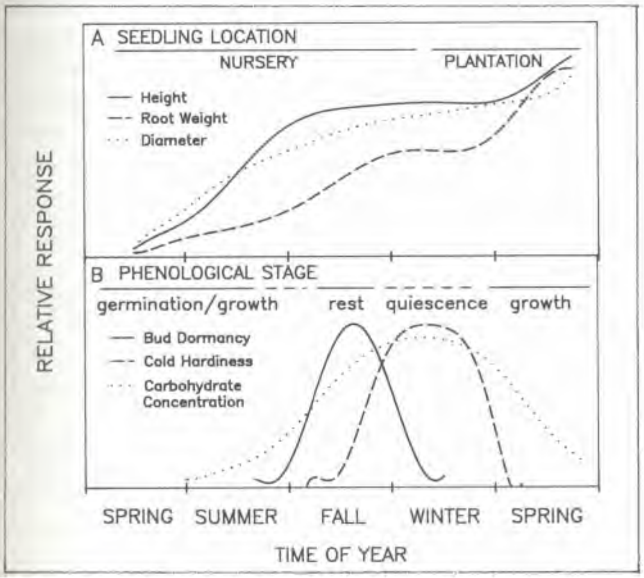

Figure 8.1. Idealized changes in seedling morphology (A) and physiology (B) over time.

Belowground changes in seedlings are not so easily observed, but are equally important to proper seedling development. Although root morphology is typically complex and not well understood in its relation to function, root weight provides a measure of photosynthate accumulation in belowground portions of the seedling. Root weight increases significantly during the first year of development (Fig. 8.1A). Root growth begins immediately after seeds germinate, continuing well into mid-summer, but slows when height growth accelerates, then surges in fall when height growth has slowed [46]. Apparently, only low soil temperature restricts root growth in late fall and winter. As soil temperature begins rising the following spring, root growth accelerates, usually slightly before height growth resumes.

Associated with height growth is an increase in stem diameter in response to mechanical stress produced by the elongating shoot and a need to supply the expanding foliage with water and nutrients (Fig. 8.1A). Concurrent with the expansion of the cotyledons, the epicotyl begins increasing in girth, perhaps in response to high soil-surface temperatures. Diameter growth continues at the same rate for most of the summer and then begins to slow, again in association with budset. Some evidence suggests, however, that diameter growth may continue through winter at a slow rate and is controlled by air temperature [91]. In the subsequent growing season, diameter growth lags behind both root and height growth.

Huberman [38] documented the first-year phenology of four southern pine species — longleaf *(Pines palustris* Mill.), shortleaf *(P. echinata* Mill.), slash, and loblolly — over 3 years in a central Louisiana nursery. Stages of seedling development varied from year to year by up to 1 month and were affected by sowing date. Root growth, as measured by length, was more rapid early in the season, showed two distinct peaks of activity (alternating with shoot growth as previously discussed), and was more variable year to year than shoot growth. In addition, there was significant genetic variation with respect to final height and root length. Slash pine height averaged 24 cm, compared to 10 cm for both shortleaf and loblolly pine. Longleaf pine height, measured to the tip of secondary needles, averaged 30 cm. Root length ranged broadly: 68 cm for longleaf, 45 cm for shortleaf, 43 cm for loblolly, and 38 cm for slash.

8.3.2 Physiology

As with morphology, physiology during the early ontogeny of a pine seedling is influenced by phenology, but, unlike morphology, is not readily manifested by observable traits. The importance of diurnal and annual changes in seedling physiology in response to environmental cues, however, cannot be understated. Certain physiological changes must occur in order for the development of a quality seedling. Three physiological processes — dormancy, cold hardiness, and accumulation of carbohydrate reserves — are important with respect to stress resistance during lifting, handling, and planting, and to root and shoot growth after outplanting. Other physiological processes important to seedling quality are discussed later in 8.5.

Dormancy and cold hardiness are difficult to separate under field conditions because both appear to respond to similar environmental cues. They are, however, separated both spatially, in terms of organs and tissues, and temporally (Fig. 8.1B). Dormancy, typically initiated before cold hardiness, pertains specifically to shoot meristematic regions (i.e., apical buds). Cold hardiness, in contrast, is tissue dependent and is predicated on the cessation of growth, but not necessarily on the development of bud dormancy [85]. Bud dormancy in southern pines occurs in phases similar to those in other woody species [7]. Slowing of shoot growth coincides with a shift from the active growth phase during late spring and summer to the quiescence phase, typically characterized by the formation of buds. Quiescence is initiated primarily by decreasing temperatures in early September or October, though shortening photoperiod may be important in some northern provenances. Under favorable environmental conditions (warm temperatures and adequate soil moisture), quiescence is reversible [46]. The next phase, rest or true dormancy, begins sometime in October or November and continues into December. It is characterized by the seedling's inability to rapidly grow under warm temperatures without first experiencing some period of low temperatures (i.e., meeting a chilling requirement). During rest, the chilling requirement is met and the seedling reenters quiescence, which usually lasts into late winter and early spring. During this time, only low temperatures are inhibiting the resumption of shoot growth.

Cold hardiness develops once shoot growth ceases and is associated with cellular changes in ultrastructure and membrane permeability [7]. The development of cold hardiness in loblolly pine correlated with decreasing temperatures in the fall [60] and was undoubtedly related to cessation of shoot growth. However, the development of cold hardiness requires time, 42 days for loblolly pine [60]. Thus, cold hardiness lags behind bud dormancy, reaching a maximum mid-winter when the probability of freezing temperatures is highest (Fig. 8.1B). As air temperatures begin rising in late winter and early spring, the degree of cold hardiness lessens until it is at a minimum when buds begin elongating. As will be discussed later, tissues and organs achieve varying degrees of cold hardiness.

Carbohydrates in various forms begin accumulating as photosynthesis achieves its maximum rate in mid-summer and growth processes begin slowing (Fig. 8.1B). Carbohydrates continue to accumulate throughout winter primarily due to photosynthesis on warm days and depressed metabolic levels. In late winter and early spring, carbohydrate reserves begin to be depleted as seedling metabolism accelerates in preparation for the resumption of root and shoot growth.

8.3.3 Special Considerations

The previous discussion on pine seedling morphology and physiology in relation to phenology has addressed ontogeny under natural conditions. With increasing interest in container seedlings and the use of glasshouses for their production, additional comments are necessary (see chapter 7, this volume).

The use of glasshouses allows essentially all environmental factors that impact seedling ontogeny to be manipulated; hence, both seedling morphology and physiology can be controlled. The active growth phase can be extended by artificially lengthening photoperiod and thermoperiod, and changing light intensity and quality. However, such morphological manipulations are not without problems, especially if seedlings are to develop proper physiological conditions of bud dormancy and cold hardiness. Typically, glasshouse-grown seedlings are "out of phase" with the natural environment. Therefore, care must be exercised to ensure against producing seedlings unsuited for the immediate, short-term environmental conditions of the planting site. A number of cultural techniques are available for hardening seedlings before transplanting them (see chapter 7).

8.4 Morphological Criteria for Assessing Seedling Quality

Development of seedling grades based on morphology (e.g., Table 8.2) has defined a target for the external appearance of planting stock with the greatest potential for successful plantation establishment. Seedling morphology has also been explored as an indicator of physiological status because morphological features such as bud condition, foliage color, or secondary needles, which correlate with different stages of physiological development, are relatively easy to observe or measure.

Assessing seedling morphological features could include an endless range of potential measurements, from height and biomass to stomatal number and needle serrations. In developing morphological criteria for high-quality seedlings, several characteristics — seedling height, root-collar diameter, root and shoot architecture, and shoot-root relationships — may impart durability and enhance growth.

8.4.1 Shoot Height

As previously noted, the most obvious and easily determined seedling attribute is shoot height. Considered in isolation, it may be of little value as a morphological indicator of seedling quality. However, combined with root-collar diameter (see 8.4.2) and shoot architecture (see 8.4.5), it becomes an important indicator.

Armson and Sadreika [1] suggested that shoot height relates to photosynthetic capacity and transpirational surface area. This may hold true for some situations, but for southern pines, nursery bed position and ratio of secondary to primary needles may weaken any such correlation. Distribution of foliage along the stem must also be considered. Nienstaedt [62] proposed that the taller seedlings in the nursery bed may be genetically superior to neighboring seedlings. Nevertheless, other factors, such as timing of germination and microsite bed differences, may also influence shoot growth in the nursery.

Tall seedlings are more difficult to lift, handle, and plant properly; often, seedlings that are too tall or too short are culled. Wakeley [79] called for shoot lengths of 12 to 36 cm for southern pines; more recent guidelines specify shoots 20 to 25 cm tall with many secondary needles to ensure an adequate supply of both reserve carbohydrate and current photosynthate [13].

Top pruning has become a common practice for making shoot height and weight more uniform [59], thereby increasing the percentage of plantable seedlings from nursery beds. Proper top pruning removes only a small portion of the stem, but many secondary needles may be lost. Although field performance of top pruned stock may be enhanced [59], the loss of seedling foliage with the highest potential for current photosynthesis cannot occur without at least some short-term compromise in growth.

Unpruned loblolly pine of plantable size were more than twice as tall and had nearly twice the root-collar diameter of top-pruned seedlings at lifting [27], but the unpruned plots had more cull seedlings. Top pruning increased the number of plantable seedlings from nursery beds; however, it did so at the expense of producing fewer grade 1 seedlings (see Table 8.2). Thus, nursery managers should consider alternatives for controlling shoot growth, e.g., presowing seed treatments, seedbed density, fertilization, and irrigation, other than simply removing seedling tops.

8.4.2 Root-Collar Diameter

Probably the single most useful morphological measure of seedling quality is diameter [87], although other good indicators include height:diameter ratio [14] and sturdiness quotient [67]. Diameter often reflects seedling durability and root-system size [45]. Seedlings with large diameters are better supported, resist bending better, tolerate more insect and animal damage, and are better insulated from heat than those with smaller diameters.

Reviewing the relationship of southern pine seedling diameter to field survival, South et al. [73] reported a strong correlation between planting-stock diameter and initial survival after outplanting. They also reported 17.5% greater volume after 13 years for grade 1 than grade 2 loblolly pine seedlings planted in blocks. Greater volume production of grade 1 seedlings may result from enhanced survival; however, grade 1 seedlings may also be larger on an individual-tree basis [2, 32, 33].

In east Texas, loblolly pine at age 2 years displayed a strong positive curvilinear relationship between initial seedling diameter and survival, and a positive relationship between seedling diameter at planting and average tree volume [74]. At ages 0 to 30 years, average volumes of l- and 3-mm-diameter seedlings were lower than those of 4-, 5-, 6-, and 7-mm-diameter seedlings. According to the resulting regression equations, the absolute volume differences between seedlings of different diameters increased with time [74]. In work by Zobel et al. [93], the superior survival of larger over smaller diameter loblolly pine seedlings was accentuated under severe drought.

Gains from planting higher grade seedlings are often reported as a percentage volume increase at a particular age. With increased plantation age, the percentage volume gains decrease, although the absolute volume differences may increase. To determine whether absolute volume differences between seedling grades increase with age because (1) larger diameter seedlings have higher growth rates than smaller diameter seedlings or (2) larger diameter seedlings maintain their lead on the same growth curve, South et al. [74] examined relative volume growth of loblolly pine over 30 years. Results indicated that, regardless of age, all trees were following the same growth curve and that larger trees simply maintained their advantage over time. An average seedling diameter difference of 2 mm could result in a 6.5% difference in tree volume at age 30 years.

Wakeley [82] examined slash and loblolly pine plantations established in the 1920s and reported that grade 1 seedlings consistently outperformed grade 3 seedlings in survival, height and diameter growth, and pulpwood and sawtimber yields per acre. With minor exceptions, grade 2 seedlings were intermediate between grades 1 and 3. Environmental and genetic differences were found to be large and economically important to survival and growth.

Large loblolly pine seedlings planted in Georgia produced 20% more volume than average size seedlings after 15 years [71]. Hatchell et al. [36] examined the growth of "select" (root-collar diameters > 4.7 mm) and "average" (diameter = approx. 3.5 mm) slash and loblolly pine after 10 years and reported 80 and 240% greater volume for select seedlings, respectively.

Large-diameter grade 1 seedlings may not always produce better survival on all sites [2, 77], but the bulk of the literature suggests that survival and productivity can be enhanced with higher grade seedlings in most cases.

8.4.3 Height-Diameter Considerations

Standards based on a combination of seedling shoot height and diameter appear to offer a good rule-of-thumb guide to morphological seedling quality. Roller [67] devised the "sturdiness quotient" as a means of determining the stockiness of seedlings. The sturdiness quotient is obtained by dividing seedling height (in centimeters) by root-collar diameter (in millimeters); an acceptable value depends on landowner specifications. Although such testing is appropriate to both bareroot and container stock, most applications have been to container stock.

Dickson et al. [20] developed the "quality index," which involves seedling biomass in addition to height and diameter:

$$\text{Quality index} = \frac{\text{Total seedling dry weight (g)}}{\underset{\text{(cm/mm)}}{\text{(Height/diameter)}} + \underset{\text{(g/g)}}{\text{(Shoot dry weight/root dry weight)}}}$$

Seedling-quality assessments involving combinations of morphological characteristics appear to be useful indicators of field performance so long as the physiological condition of different planting stock is the same. In addition, they offer an easy method for quality assessment that can be used throughout the growing season to judge seedling crop development.

8.4.4 Root Architecture

Root architecture refers to the spatial orientation of the root system — the extent and configuration of the various components. Even though roots are less conspicuous than shoots and therefore more difficult to study, an extensive, fibrous root system that taps multiple soil layers upon planting has long been considered an attribute of high-quality planting stock. Huberman [37] recognized the importance of root architecture to seedling quality and developed an index of root extent by adding together lengths of all roots over 2 cm long as measured from root collar to root tip. Other measures of root condition include number of roots > 0.3 mm, fibrosity, taproot morphology, mycorrhiza development, soil adhering to roots, root damage and loss, root mass, root volume, root length, root area, shoot:root ratio, and moisture status of roots [14]. Hatchell [34, 35] demonstrated that longleaf pine seedlings with fibrous root systems survived better after outplanting than those seedlings with less fibrous roots.

Although it is difficult to significantly alter the growth rates of various plant parts relative to one another, i.e., the allometric relationships, the configuration or expression of growth can be controlled to some extent. Undercutting, wrenching, and lateral or box pruning of nursery beds has become common practice to modify root architecture such that laterals are concentrated at a set depth, near and around the taproot. Undercutting significantly increases the percentage of secondary and tertiary lateral roots and improves root fibrosity [58, 76]. Work by Carlson [13] indicates that root systems with greater fibrosity have higher hydraulic conductivity, which should be advantageous to seedling survival.

Root systems of container seedlings have been similarly modified by treating inside container walls with a root-inhibiting chemical such as cupric carbonate [4, 5, 56]. The chemical arrests root elongation at the soil/wall interface, promoting branching of higher order laterals within the soil "plug." Untreated containers produce seedlings with a number of first-order laterals that grow along the interface to the bottom drain hole where they are air pruned. Chemical root pruning distributes active apical meristems throughout the soil plug rather than concentrating them at the bottom of the container [15].

The amount and distribution of seedling roots are key to the quality of planting stock. Assuming careful lifting, handling, and planting of seedlings, nursery cultural practices that produce seedlings with extensive, yet compact, fibrous root systems have great potential benefits for plantation establishment.

8.4.5 Shoot Architecture

Shoot architecture reflects the manner in which a seedling's stem and branches develop and the way in which foliage is displayed. Old grading criteria of planting stock were based on the presence of secondary needles, winter buds, and stem bark, and little attention was paid to shoot architecture. However, in the 1930s, root-collar diameter and minimum shoot and root lengths became part of the basis for classification [80].

Shoot architecture of a quality seedling should be appropriate for the size of the root system, and needle arrangement should maximize sunlit leaf area but minimize transpirational demands. For any tree, the growth characteristics of the central shoot define the basic structure and, in combination with the features of the lateral shoots, determine leaf-area distribution [25]. As such, shoot architecture is largely controlled by genetics. Nursery operators must grow the genotypes selected on the basis of their productivity over the course of a rotation, not their performance in the seedbed.

Differences in shoot architecture are responsible for the light- interception attributes of isolated plants and crop canopies and have been described as important components of ideotypes [21]. An ideotype is a biological model that is expected to perform or behave in a predictable manner within a defined environment (see chapters 6 and 7, this volume, for discussion of bareroot and container ideotypes, respectively). "Competitive" ideotypes have tall, dense, broad crowns with high branching frequency, low apical dominance, and slow branch ageing [6]. In contrast, "crop" ideotypes have dense, narrow, pointed crowns with high branch frequency, strong apical dominance, and rapid branch ageing, yielding high stemwood volumes per year in proportion to crown size. Crop ideotypes use space efficiently, possibly because they have more effective shoot architecture, or perhaps also because they partition more assimilates to stemwood [6].

The same ideotypic features expressed by a genotype in a forest stand may be expressed to some degree in the nursery bed. That is, some trees that have competitive ideotypes become large at the expense of surrounding trees that they overtop [6, 19, 21]. Others that have crop ideotypes, though not strong competitors, make efficient use of the resources accessible to them. Whereas seedlings tending toward the crop ideotype might be produced at relatively high nursery-bed densities, those tending toward the competitive ideotype may require lower densities. When planted together, competitive ideotypes will dominate crop ideotypes; however, when segregated, crop ideotypes may have the highest per-area productivity [6]. Family block planting in the nursery tends to minimize these potential differences in seedling form.

Top pruning can obviously have a significant effect on shoot architecture that can be further influenced by the frequency and timing of application. Although top pruning may control height growth and increase crop uniformity, it is not typically used to develop a particular shoot configuration.

8.4.6 Shoot-Root Relationships

One of the most widely reported parameters in seedling-quality research is shoot:root ratio (dry weight of shoot divided by dry weight of root), but alone it is of limited usefulness. Because shoot:root ratios change over time and with plant size, it is difficult to compare and interpret shoot:root data [52]. Indeed, comparison of the relative growth rates of the shoot and root is a more dynamic measure of plant carbon partitioning than of shoot:root ratio [54]. However, since a plant's roots and shoot grow at different relative rates, most environmental manipulations that alter total plant weight will also alter shoot:root ratio because of the correlation of growth between plant parts. The difference in relative growth rates of roots and shoots can best be compared with allometric growth analysis by contrasting allometric coefficients (k) [39]; values > 1.0 indicate greater allocation of carbon to shoots, values < 1.0 greater allocation of carbon to roots (Fig. 8.2). Shoot and root growth are logarithmic in seedling stages of many plants, and the ratio of the relative growth rates (allometric coefficient) is constant [52].

Ledig and Perry [54] reported decreased shoot:root ratio with increasing size of loblolly pine seedlings during the first growing season and substantiated results in later work [52]. However, most work on southern pines suggests that shoot:root ratios increase as seedlings grow larger [16, 38, 42, 61]. Allometric coefficients calculated for loblolly pine indicated that root growth was more rapid than shoot growth during the first 60 days of development, but that after 60 days and for the following two growing seasons the opposite was true [16]. K values for shoot:root ratios during the first year of growth in the nursery were approximately 1.07 for loblolly pine and 1.04 for slash pine (Table 8.3), demonstrating a higher relative growth rate of shoots over roots (determined from Huberman [38]).

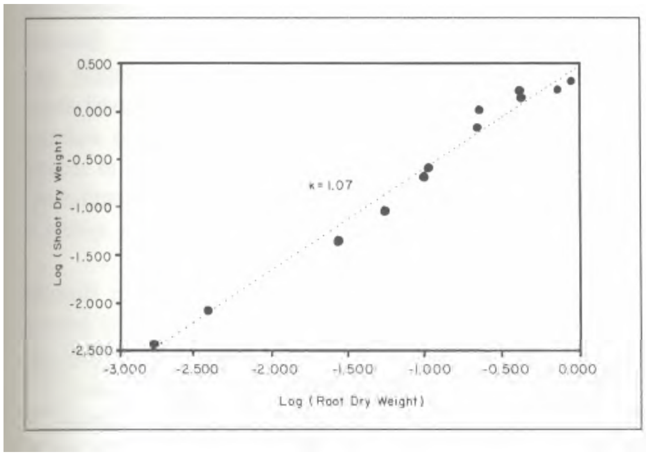

Figure 8.2. Allometric relationship between shoot and root for loblolly pine (adapted from Huberman, [381). Note allometric coefficient, *k*.

Allometric coefficients of young loblolly pine have been found to be relatively insensitive to environmental perturbations including variation in light and soil moisture, as well as stage of development, e.g., transition from primary to secondary needle initiation [52, 83]. The use of allometry in seedling growth studies has been primarily applied to demonstrate differences in assimilate partitioning among provenances [10] and families [8, 23, 52] of conifers. According to Ledig and Perry [54], only drastic treatments, such as exceeding optimal nutrient concentrations for growth, can alter a seedling's allometric coefficient.

However, Johnson [42] demonstrated that loblolly and slash pine shifted the rate of carbon allocation from roots to shoots in response to fertilization and irrigation during their third growing season. These results suggest that nursery operators may be able to cultivate planting stock that truly has lower shoot:root ratios by adjusting irrigation and fertilization regimes. Work is needed to determine the plasticity of the allometric coefficient relative to nursery cultural practices and the impact of potential changes on seedling quality.

Evidence of endogenous rhythms, or episodic growth (distinct periods of enhanced root or shoot growth), has been reported in loblolly and other pine species [22, 53]. Large short-term variability in dry-matter partitioning to roots and foliage was found in red (*Pinus resinosa* Ait.) and pitch (*P. rigida* Mill.) pine [22, 53]; loblolly pine was less variable, although episodic growth was evident [23]. Nevertheless, allometric coefficients of six full-sibling loblolly pine families remained constant over 2 years [8, 23, 54]. Allometry tends to smooth out some of the minor fluctuations (episodic growth) in carbon allocation over the course of the growing season that may be particularly important to nursery management.

Table 8.3. Allometric coefficients (k values) for commercially important southern pine species grown in a bareroot nursery (from Huberman [38]).

Pine species	Allometric coefficient	R^2
Loblolly	1.065	0.98
Longleaf	0.885	0.98
Shortleaf	0.987	0.97
Slash	1.037	0.98

Feedback mechanisms appear to operate to correct seasonal imbalances in shoot-root relationships in pine so that, over several years, the allometric coefficient is maintained [10, 23]. Late-fall and winter root growth may cause rapid changes in allometry that are readjusted when shoots elongate in spring (see Fig. 8.1).

Nursery managers should be able to use this episodic growth pattern to determine a "lifting window" when seasonal partitioning of carbon to shoots or roots is optimal for best field performance. Episodic growth should be further examined in relation to root-growth potential and chilling requirements (see later in this chapter) to determine correlations with field performance and best nursery cultural practices. A clear understanding of partitioning patterns in nursery seedlings, seasonal changes, and the manner in which cultural practices may affect patterns is essential if the highest quality planting stock is to be produced.

8.5 Physiological Criteria for Assessing Seedling Quality

Seedling morphology, as previously discussed, provides an integrated measure of past growing conditions and, in some instances, can be used as a qualitative predictor of future performance. In contrast, seedling physiology is indicative of both past and present conditions which, for selected parameters, can be related directly to short-term, and in some cases long-term, future performance. Although many physiological parameters could be used as quality indicators, only a few — water relations, nutrition, carbohydrates, dormancy and cold hardiness — have received sufficient study with respect to pine seedlings.

8.5.1 Water Relations

Water is one of the most important environmental factors affecting seedling physiology. It is a constituent of cells; a solvent for gases and nutrients, allowing their movement among cells and organs; and a reagent in many biochemical processes. It provides the turgor pressure that drives cell elongation [46]. The primary cause of seedling mortality after outplanting can be traced to water; seedlings may die either from desiccation due to the lack of soil water or the inability to take up water, or from oversaturation leading to anaerobiosis (oxygen depletion and a change to anaerobic respiration) and root dysfunction, especially where improper species are planted.

The watering regime during seedling culture in the nursery or glasshouse influences germination, seedling size, shoot:root ratio, and duration of fall growth (see chapters 6 and 7, this volume). Too little water can cause irreversible physiological dysfunction that will impair seedling survival and growth. During the growing season, too much water limits oxygen in the soil and inhibits root growth; during fall, it can delay cessation of shoot growth, dormancy induction, and initiation of the stages of cold hardiness, depressing overall seedling resistance to stress. In contrast, controlled wetting and drying cycles in later summer and early fall that impose repeated, moderate water stress on seedlings can favor their physiology through a hardening process that promotes bud development, budset, dormancy, and cold hardiness, generally increasing resistance to subsequent stresses (see 8.5.4). An associated benefit of hardening is osmotic adjustment in cells of seedlings, imparting an ability to withstand subsequent water stress typically associated with transplanting [70].

Maintaining adequate water immediately before and during lifting is also important for sustaining seedling quality. The possibility of desiccation after lifting is very real and can lead to rapid reduction in quality that will be reflected in both impaired survival and performance after planting. Watering seedlings after lifting, especially those that will be stored for extended periods, can offset potential reduction in quality. Since pine seedlings have a xylem water potential of near -1.0 MPa at lifting, the presence of free water on seedling surfaces will allow for some uptake.

8.5.2 Nutrition

Adequate, properly balanced nutrition is paramount to the production and maintenance of quality seedlings. Although severe nutrient deficiencies have been eliminated from most nurseries through improved diagnostic and application technology, there are occasions when improper fertilization timing or rate can cause nutritional stress. Such stress leads to reduced growth and, if prolonged, can affect morphology.

Nitrogen (N) is probably the most limiting nutrient and, therefore, has received much attention with respect to seedling growth and development. Nitrogen supply influences all components of seedling growth including carbon partitioning and phenology. Increasing nitrogen levels shifts carbon allocation from roots to shoots. Pharis and Kramer [64] found that loblolly pine seedlings grown under suboptimal levels of N allocated 50% of fixed carbon to shoots and 50% to roots. When seedlings were given near optimal levels, 66% of fixed carbon was allocated to shoots, the remaining 34% to roots. Similar responses have been reported for other conifer species [40]. However, when seedlings grown under differing N supply were subjected to water stress, those that had received above-optimal concentrations of N were less able to withstand desiccation [64]; this response was attributed to reduced root production (because of shifts in carbon partitioning) and the resultant inability of the smaller root system to provide adequate water for the larger shoots.

Fertilization late in the growing season can stimulate seedling growth beyond the normal phenology by delaying budset or even causing buds to elongate. Such improper timing postpones the development of cold hardiness, which protects succulent tissues from freezing temperatures. On the other hand, fertilization after budset and during periods of relatively low temperatures may enhance photosynthesis, improving carbohydrate levels [47].

Other than increasing seedling size at lifting, fertilization rates in the nursery apparently had little effect on performance of loblolly pine in the field [75]. Therefore, as long as nursery seedlings are fertilized above critical levels and in proper proportions, their nutritional status should not hamper field survival and performance.

8.5.3 Carbohydrates

Carbohydrates — direct products of photosynthesis — constitute the primary energy storage compounds for seedlings, provide the basic carbon skeleton for the synthesis of essentially all other organic compounds, and constitute up to 75% of total dry mass [46]. In discussions of seedling quality, however, the term "carbohydrate" is often used imprecisely. By strict definition, a carbohydrate is any compound that has the empirical formula $(CH_2O)_n$, though a compound may contain additional elements such as nitrogen or phosphorus. In more recent literature, the term total nonstructural carbohydrate (TNC) has been used to refer to ethanol-soluble sugars, primarily sucrose, plus starch which is enzymatically degraded into sucrose for colorimetric assay. Carbohydrates, when referred to in this chapter, are synonymous with sucrose and starch.

Sucrose and starch are the carbohydrates most important to seedling quality and are what most people imply by the term carbohydrate. Sucrose is the primary form in which carbohydrates are translocated throughout the plant; up to 95% of translocated dry mass is sucrose [46]. In contrast, starch is the primary form in which carbohydrates are stored and can be found in virtually all seedling tissue. Sucrose and starch are enzymatically interconvertible, and conversion appears to be controlled by sucrose concentration; high sucrose concentration favors the synthesis of starch, whereas low concentration favors starch breakdown. Such substrate control helps ensure adequate sucrose levels for both maintenance (cellular respiration) and growth metabolism.

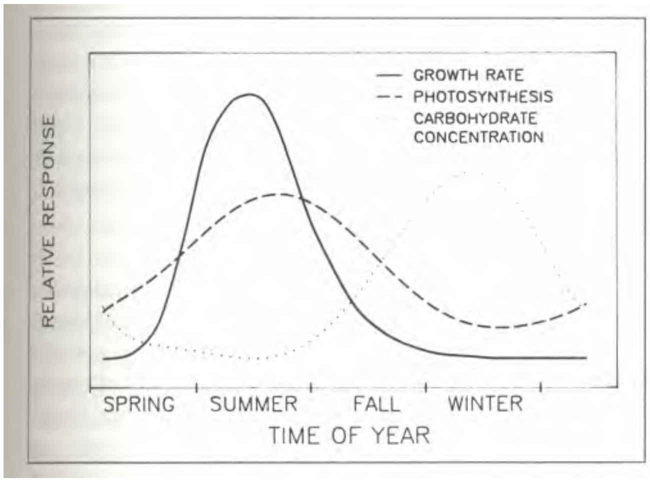

Figure 8.3. Idealized changes in growth rate, photosynthesis, and carbohydrate concentration in southern pine seedlings over time.

Interpretating carbohydrate changes in seedlings requires an understanding of the relationship seedling carbohydrate economy to photosynthesis and growth (Fig. 8.3). In summer, when growth rate is maximum, most of the photosynthate (sugars produced by photosynthesis) goes directly into the production of cellulose. As growth slows in early fall but rate of photosynthesis is still relatively high, photosynthate is allocated to roots (see Fig. 8.1) and starch production. Once root growth slows, photosynthate is almost exclusively converted into starch for storage, though a small percentage is used for maintenance metabolism. In colder climates where photosynthesis is inhibited by low temperatures, seedlings must rely exclusively on carbohydrate reserves for maintenance metabolism throughout winter.

In evergreen species such as pine, starch is stored in the needles as well as in the stem and roots. Many attempts have been made to correlate root starch, sugar, and TNC with field performance, but few have had consistent success. This, in part, may be due to the omission of the needle starch component from these correlations.

Growth resumption in spring coincides with mobilization of starch as sucrose. The relative importance of starch and sucrose to new seedling growth, however, is not well understood [47]. It is not clear whether the photosynthate used for growth comes from starch or current photosynthesis.

Environmental factors during fall can affect total carbohydrate reserves. Water stress, then, if severe enough, can diminish photosynthate production and subsequent growth the next spring. McNabb [57] found in slash pine that limiting irrigation to only 2.5 cm in fall decreased total carbohydrate concentration at lifting by 13% and reduced subsequent height growth by 82%, compared to keeping seedlings well watered. In addition, he found that the more water supplied to the seedlings, the greater the proportion of carbohydrates in the form of starch, even though the total concentration of sucrose and starch remained relatively constant.

Carbohydrate concentrations are also important after planting when photosynthesis is depressed. During this period when photosynthesis is recovering, seedlings must rely on carbohydrate reserves. This recovery time lasted up to 4 weeks in slash pine planted into soil with adequate moisture [57].

8.5.4 Dormancy and Cold Hardiness

The physiological processes of dormancy and cold hardiness are complex and not well understood, especially in the southern pines. As discussed earlier (see 8.3.2), dormancy is a physiological state attained by one tissue type, specifically the shoot apical meristem (bud), whereas cold hardiness is a state achieved in all tissues, at least to some degree. The two processes normally occur sequentially, beginning in mid-fall with the onset of dormancy and followed in late fall and early winter by the development of cold hardiness (see Fig. 8.1B).

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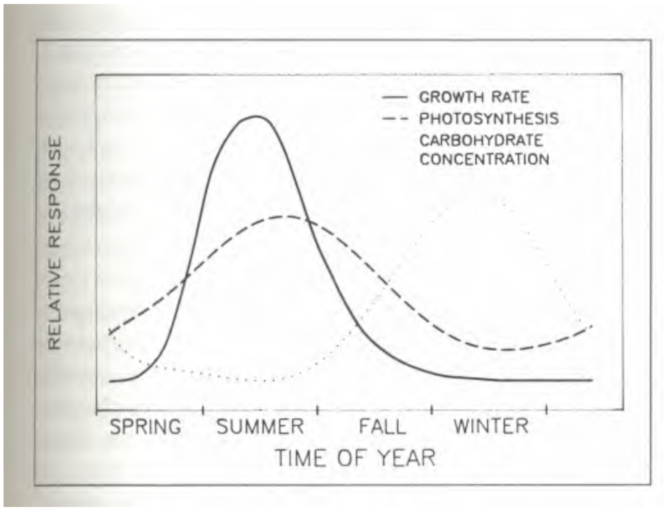

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Dormancy is defined as all instances in which a tissue pre-disposed to elongate does not do so [68]. Although various phases of dormancy are recognized (see Fig. 8.1B and text in 8.3.2), in reality dormancy is a continuum of changing physiological state. Meristems shift from actively growing into quiescence, which is defined as dormancy imposed by external environment [68]. Quiescence can occur any time during active growth in response to stressful conditions such as drought, high or low temperature, or nutrient limitation or excess. Moreover, quiescence is reversible; amelioration of the limiting environmental factor will cause the meristem to become active again, which can lead to problems in southern pines that are over watered or fertilized in fall. Rest, the next phase, is defined as dormancy maintained by agents within the meristem itself [68]. Regardless of how favorable the environment may be for growth, resting buds will not elongate. Rest is overcome by exposure to a certain period of low temperatures (chilling requirement). Once this requirement is met, buds become quiescent again and remain so until temperatures increase, when they become active and resume growth.

For the southern pines, the role of bud dormancy with respect to seedling quality is as unclear as is the question of the presence of rest [68]. Little is known about the acquisition of bud dormancy in southern pines [7] other than that it appears to be related to changing photoperiod and temperature, though nutrition and water availability can influence the timing of bud development. Onset of dormancy also seems to be related to plastochron age (a quantitative measure of a seedling's phenological development); that is, there appears to be a minimum seedling age (size) for the development of resting buds [7]. Late-sown seeds will not attain the proper plastochron age to respond to the environmental cues for normal bud development and dormancy, and will instead produce apical meristems surrounded by underdeveloped needles and needle primordia lacking bud scales [68]. Slash and loblolly pine seedlings exhibiting such meristems began elongating sooner than those with true resting buds, but grew less the first year after planting [30]. The greater growth of seedlings with true resting buds can be attributed, at least in part, to the production of more stem units (node plus subjacent internode) during the normal dormancy cycle [8].

Buds break dormancy in response to exposure to a period of low temperatures. Northern species dormant in winter must fulfill a chilling requirement before buds can elongate [11]. In contrast, southern pines appear to respond to chilling quantitatively; the more chilling received, the faster the rate of budbreak up to a maximum. The cumulative number of hours of exposure to temperatures between 0 and 8°C (arbitrarily chosen) is referred to as chilling hours; loblolly pine requires between 200 and 400 chilling hours to overcome dormancy, depending on geographic origin of the trees [11]. Chilling requirements are typically met by early to mid-December for southern pines. Increased photoperiod was found to partially substitute for chilling temperatures [29]. Furthermore, exposure to low (but above freezing) temperatures once the chilling requirement had been fulfilled enhanced height growth in the subsequent growing season [29].

Cold hardiness involves physiological changes throughout the tissues of a seedling after rapid cell expansion has ceased. The primary changes affect ultrastructure and membrane permeability and depend on a sufficient photosynthate supply [7]. Cold hardening or acclimation begins in southern pine when air temperatures decrease. Further hardening is accelerated by short photoperiods (< 10.5 hours) [7]. Mexal et al. [60] reported that loblolly pine required 42 days of cool temperatures or 8-hour photoperiods to cold harden to -12°C. Seedlings deharden in response to increasing temperatures.

The tissues of southern pines acclimate to different degrees; needles and stems, exposed to the air, tend to acclimate more readily than roots, which are insulated by the soil. It is of interest that most of the seedling injury and associated mortality from the freezes of 1983 and 1984 were due to damage to cambial tissue located 3 to 5 cm below the soil surface [50].

The importance of cold hardiness to seedling quality may in fact reside in the increased resistance to stress conferred upon seedlings by the hardening process. It is more than coincidence that nursery managers over the years have found that southern pine seedlings can withstand the stresses associated with lifting, packaging, storage, transporting, and planting during the period between early December and late March (cf. Fig. 8.1). In contrast, dormancy is not well correlated with stress resistance because it involves only the apical meristems of seedlings.

8.6 Critical Factors That Reduce Quality

There are numerous points during which seedling rearing and plantation establishment at which improper care of planting stock can degrade quality. It is possible, using inappropriate cultural practices, to produce seedlings of inferior morphological grade that ultimately perform poorly in the field. It is also possible, through careless handling, to degrade high-quality seedlings during lifting, packaging, storing, transporting, and outplanting such that survival and growth suffer (see also chapters 16 and 17, this volume).

8.6.1 Cultural Management

Producing high-quality seedlings is an integrated process that relies upon consistency in cultural treatments based on historical performance in the nursery. Seedling growth in the nursery depends upon the level and timing of cultural practices. Common growth-limiting factors in the nursery are too much or too little soil moisture or light, and improper levels of soil fertility. Early in the growing season, managers seek to eliminate these limiting factors in order to produce a rapidly growing seedling crop that will attain desired size specifications. Later in the growing season, managers may control these same limiting factors to reduce height growth or induce seedling dormancy.

High levels of fertilization early in the growing season may result in rapid development of seedlings from early germinating seeds to the detriment of seedlings emerging later on. Therefore, managers may need to top prune later in the season to develop a more uniform seedling crop and greater yield. Fertilizing seedlings later in the growing season or at levels resulting in high residual concentrations in the soil can stimulate fall seedling growth and postpone dormancy induction (see Fig. 8.1). Ideally, fertilization (and irrigation) might eventually be used to control seedling growth such that morphological specifications are achieved without top pruning.

Although top pruning might be viewed by some individuals as a measure of last resort, root pruning (lateral or undercutting) produces desirable, compact, fibrous root systems and can be employed to slow seedling growth. However, the success of both top- and root-pruning treatments depends upon the amount of material removed and the time of application during the growing season. Pruning too much plant material, too often, or too late in the season can stunt seedling growth, resulting in undersized stock or seedlings subject to shock from which they will not recover before lifting.

A working knowledge of soil management and plant science is absolutely necessary to avoid management mistakes in the nursery. However, equally important is an understanding of equipment limitations and historical documentation of soil conditions and nursery performance of the crop. Thus, building an accurate database of the effects of past cultural practices on seedling quality is fundamental to consistently producing high-quality seedlings (Table 8.4). Nursery crops developed in response to the manager's "gut feeling" will seldom be high-quality planting stock.

In southeastern nurseries, seedling quality can be jeopardized by inadequate soil organic matter content, nutrient deficiencies (especially nitrogen and phosphorus), poor control of pH, soil compaction, and/or lack of suitable mycorrhizal fungus populations. Whereas compaction problems can be ameliorated by frequent subsoil cultivation, many other soil-management problems can only be addressed effectively by careful, long-term monitoring of prescribed cultural treatments. Most of these problems are interrelated and nursery specific, and therefore must be treated holistically.

Preparing and sowing nursery beds cannot be divorced entirely from soil management, but other considerations or activities not directly related to soil can reduce seedling quality if not handled carefully. Genetically improved seed commands a premium price and must be used efficiently by ensuring the highest seedling-to-seed conversion ratio [92]. Seed sizing, stratification, and sowing in the nursery by family are necessary to raise the ratio. Others suggest that separation of seed on the basis of size may not enhance uniformity or vigor and may actually degrade the gene pool [31]. Regardless, information that describes seed collection date and source, storage conditions, presowing treatment schedule, and current vigor should be obtained for each seedlot.

Table 8.4. Information required to develop records of nursery cultural practices useful for future prescriptions and trouble-shooting.

Information	Frequency of monitoring
Nursery	
Meteorological data	Continuously
Soil Analysis	At least annually
Cover crop	Annually
Cultivation	Each application
Fumigation	Each application
Organic matter amendments	Annually
Sowing density and method	Annually
Fertilization	Each application
Irrigation	Each application
Top pruning	Each application
Root pruning	Each application
Pesticides	Each application
Seedling	
Seedlots; germination	Annually
Seedling size	Minimum, every 2 weeks
Tissue nutrient analysis	Annually or as needed
Disease incidence	Each occurrence
Mycorrhiza population	Annually or as needed
Secondary needles	First occurrence
Dormant terminal bud	First occurrence

Because of the great variation from nursery to nursery, it is impossible to list specific cultural practices that should always be adopted or avoided, but careful monitoring and recordkeeping can improve nursery success. One important step is the development of "life history" graphs, based on height, diameter, and biomass measurements, to determine whether seedlings are "on target" for any time in the growing season. Such documentation will not only form the basis for increased quality, it will also permit managers to make informed "trouble-shooting" decisions about fertilization and pathogen problems [89].

8.6.2 Seedling Harvest

When seedling harvest begins, nursery operations become a handling challenge (see also chapters 16 and 17, this volume). Planning and coordination among nursery manager, forester, and planting crew *before lifting* can make the difference between high- and low-quality planting stock.

The lifting operation always somewhat damages seedling tops but can be especially hard on roots. Producing seedlings with desirable root architecture will do little to enhance seedling quality unless root loss is minimized during lifting and handling. The removal of roots, either by pruning or inadvertent stripping during and following lifting, can adversely affect survival [69, 81]. Lifting can result in the loss of 50% of all roots [82] and as much as 75% of the small roots [69]; the loss of small mycorrhizal roots has been correlated with reduced survival of outplanted loblolly and longleaf pine [55]. However, managers can minimize the impact of lifting damage by matching the proper machine with the stock and soil type and by performing the task under the proper weather and soil-moisture conditions. Excessive tension on lifting-machine belts can damage stems, inappropriate soil-moisture conditions can result in excessive root stripping, and poor control of root-wrenching depth can cause large losses of root biomass.

Managers can further ensure success by paying close attention to seedling physiological status during lifting. Only fully dormant seedlings should be lifted.

8.6.3 Post-Harvest Handling

8.6.3.1 Post-lifting care and packaging

The months of hard work producing high-quality planting stock in the nursery can be in vain if seedlings are mishandled following lifting from nursery beds, when they are either bagged on site or placed in tubs or canvas slings for transfer to packing sheds. In both cases, lifting trailers must be shaded and water available for moistening seedlings before packing.

If seedlings are to be packaged in the packing shed, cool temperatures should be maintained in that room and the amount of time between lifting and packing minimized. The risk of desiccation associated with exposure can be reduced by keeping seedlings moistened in the shed. If seedlings are to be culled or graded, the increased exposure and potential for root loss should be recognized and crews properly advised.

8.6.3.2 Storage

Storage success largely depends upon the packaging method, storage temperature, humidity, air circulation, and length of time in storage (see also chapter 16, this volume). Most bareroot nursery stock is packaged in kraft-polyethylene (KP) bags, although some nurseries use bundles or boxes. Bundles are preferred if seedlings are to be stored without refrigeration because water can be applied easily; however, even under the best conditions, storing bundles for more than a week can degrade stock quality. If bags are used, care must be exercised to avoid crushing stock during packing, stacking, and sewing of bags.

Storage temperatures that drop below freezing or rise substantially above 3°C can adversely influence seedling quality. Freezing temperatures damage roots, whereas warmer temperatures encourage seedling respiration, ethylene production, and fungus growth. Moreover, because cold storage can also affect seedling physiology by partially satisfying the chilling requirement necessary to break dormancy [13], managers should know the seed source of the crop, its performance history, and the chilling received in the nursery.

High relative humidity and good air circulation are required in cold storage to prevent rapid desiccation of seedling tissues and reduce problems associated with fungus growth. Prolonged periods of cold storage should be avoided, as these can increase respiration rates, thereby depleting seedling carbohydrate reserves crucial after outplanting. In sum, constancy of environmental conditions in cold storage should be continuously monitored and any malfunctions documented.

8.6.3.3 Transportation

Moving seedlings from cold storage to the planting site or refrigerated "satellite" facilities in open, uninsulated vehicles can desiccate or otherwise damage seedlings. Only enough seedlings required for 1 day should be transported to the planting site. At the site, packaged seedlings must be kept out of direct sun on cool, dry ground. If no natural shade is available, temporary shelters should be constructed.

8.6.3.4 Planting

Preserving stock quality should drive the planting process, as well as all other aspects of seedling culture and handling. For example, the planting technique should ensure a hole or slit in the mineral soil that is adequately large to accommodate seedling roots. Root systems poorly positioned in the planting hole may expose seedlings to greater desiccation; those that are crammed will later be deformed and provide poor stability. Anecdotal accounts of root pruning essentially all roots to make seedlings easier to plant or placing exposed seedling bags in the middle of a clearcut to reduce travel time are, unfortunately, based on fact. However, all the resources brought to bear on growing and processing high-quality stock will be for nought if planting techniques are careless or faulty (see chapter 17, this volume, for a detailed discussion of planting).

8.7 Methods for Testing Seedling Quality

Implicit in "fitness of purpose" for nursery-grown seedlings is their ability to survive and grow once planted. Thus, when testing for seedling quality, managers hope to be able to predict seedling performance. To be useful, predictability of the test should be consistently high despite varying conditions of nursery environments and planting sites.

A review of the testing methods for southern pines and other conifers [3, 24, 41, 66] indicates that no single method is best and that, until some technological breakthrough occurs, a battery of tests is required to consistently predict seedling quality [66] for the following three reasons: (1) the nature of lifting and planting techniques necessitates that the tests be rapid, easy to conduct, and readily interpreted; (2) the constraints imposed by reason (1) limit the test response variables to those that are influenced by numerous physiological processes subject to variations in past and present environmental factors; and (3) the relationships between test

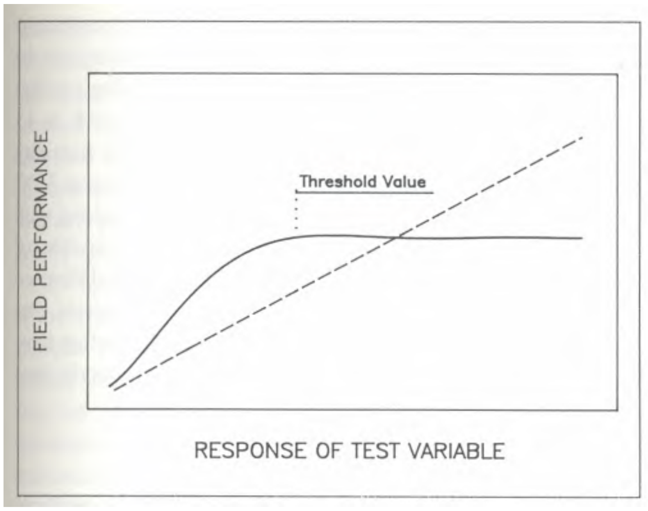

Figure 8.4. Hypothetical linear (dashed) and saturating-type (solid) relationship between seedling test variable and field performance.

variables and field performance are rarely linear over the entire range of test variables, typically exhibiting some threshold value beyond which field performance does not change (Fig. 8.4). The problem of testing becomes more clouded with respect to reasons (2) and (3) above because of mitigation and compensation by other seedling processes and environmental factors. Thus, testing for seedling quality distills to looking for performance-limiting test variable(s) both in terms of magnitude and number.

For purposes of discussion here, test methods currently used for southern pine seedling quality have been grouped into the broad categories of morphological, physiological, and performance tests. New emerging technologies also are briefly described, to suggest future trends.

8.7.1 Morphological Tests

Seedling morphology, as mentioned previously, is the manifestation of past environmental factors affecting physiological processes. Ritchie [66] pointed out that the use of morphological traits for comparing and predicting seedling performance is valid only when seedlings are in the same physiological condition — a test condition that is rarely achieved. Hence, the numerous seedling studies based upon morphological traits alone are suspect and should be viewed as biased and qualitative. Because morphological traits have been used historically for grading and culling, however, a short discussion is warranted.

Wakeley [81] provides the most comprehensive review of relating morphological traits with field performance. The single most important morphological trait is root-collar diameter because it is related to both shoot biomass and leaf area as well as to root volume [45, 66]. A further refinement, the sturdiness quotient [67], a function of stem diameter and height, provides information on how spindly a seedling is in relation to leaf area, that is, leaf-area distribution (see also 8.4.3). Shoot:root ratio is probably the most commonly employed morphological variable and the least useful. Because the value is a ratio, it tells nothing about actual seedling size. It is well known that larger seedlings tend to outperform smaller ones; thus, shoot:root ratio can be misleading. The quality index [20], an integrated morphological measure based on total seedling dry weight, height, diameter, shoot weight and root weight (see also 8.4.3), seemed promising; Ritchie [66] found good correspondence between quality index and Douglas-fir *[Pseudotsuga menziesii* (Mirb.) Franco] stock types.

In addition to the limitations of morphological traits discussed above, the fact that seedling morphology can be significantly manipulated and altered by normal nursery cultural practices further nullifies any possible correlations among morphology, physiology, and field performance.

8.7.2 Physiological Tests

A number of methods for testing the physiological state of seedlings have been proposed and evaluated. However, most have limitations that preclude their routine use. Three tests with potential — mitotic index, carbohydrate concentration, and stress resistance as measured by cold hardiness — need further validation for application to southern pines.

Mitotic index (MI), a measure of the activity of cell division within the shoot apical meristem, is expressed as a ratio of the number of dividing cells to the total number of cells counted. Carlson [12] found that the MI of loblolly pine seedlings corresponded well with seedling phenology, stages of bud dormancy, and accumulation of chilling hours. Because several factors appeared to be controlling MI, further validation of MI is required on loblolly and the other southern pines. Of particular importance is determining the MI value suitable for lifting and planting and evaluating the effects of higher air temperatures during the winter at lower latitudes. The advantage of MI as a physiological test is that it is one of the few direct measures of a physiological process (i.e., bud dormancy) that can be conducted rapidly, at least relative to the other available tests.

Carbohydrate concentration (carbohydrates defined here as ethanol-soluble sugars plus starch; see also 8.5.3) has good potential as a test for determining past and present physiological status and for predicting future performance, though several factors can influence the amount and form of carbohydrates in a seedling. For this test to be useful, tissue sampling must be standardized (roots and shoots analyzed separately) and validated by field performance. Recently, Puttonen [65] reported that needle carbohydrate concentration in Scots pine *(Film sylvestris* L.) seedlings was related to field survival and performance; trees died when the concentration dropped below 2%. Unfortunately, such a clear relationship does not appear in southern pines [57]; the best single variable for predicting slash pine seedling performance was root-starch concentration. It may be that in the geographical range of the southern pines, winter photosynthesis is sufficient to maintain needle carbohydrate concentrations, whereas root carbohydrate concentration is more closely related to root growth [48].

Stress resistance can be estimated by a seedling's response to subfreezing temperatures, that is, by its level of cold hardiness [51]. To assess cold hardiness, whole seedlings or shoots are exposed to a range of freezing temperatures and then evaluated for damage. Evaluation can be visual (damage-rating index) or more quantitative (electrolyte leakage from selected tissue). The former approach takes about 2 weeks and requires a heated holding chamber or greenhouse, whereas the latter takes only 3 days. Recently, freezing damage in slash and loblolly pine was evaluated by measuring ethane production from needles [30, 44]; freezing damage was linearly related to ethane production. This method requires only small amounts of tissue, allows repeated sampling from the same seedlings if desired, and takes only 2 days. In adapting any of these freezing tests to southern pines, LT_{50} values (the temperature at which 50% of the seedlings die) must be calibrated to field survival and performance. Once the value is determined, testing is needed only until that value is achieved in the fall and then checked periodically in the spring during dehardening.

8.7.3 Performance Tests

Performance tests are predicated on the assumption that seedling growth response under favorable conditions is related to field performance. Only two tests will be discussed here: root-growth potential and budbreak. The drawbacks to these tests are the time needed to conduct them (7 to 30 days), the involved nature of data acquisition, and the variability in their correlation with field performance.

The root-growth potential (RGP) test determines the number of new roots produced in a given period while the seedling is exposed to an environment favorable for growth. At the end of that period, seedlings are uprooted and the number and/or length of new roots determined. The higher the RGP value, the better the chances for survival and growth. Numerous problems exist with this test, however. Environmental factors before, during, and after the test can affect both the absolute RGP value and its ability to predict field performance (see [26]). Seedlings lifted early in the season may exhibit a low RGP (suggesting a low survival potential) but, once planted and exposed to low winter temperatures, may survive and perform very well.

The budbreak test determines the number of days buds take to elongate under favorable conditions. It suffers from most of the same drawbacks as the RGP test, though assessing bud elongation is much faster than measuring roots. Typically, the time required for buds to elongate decreases as the chilling requirement for bud dormancy is met. For example, buds of slash pine took 60 days to elongate in November-lifted seedlings but only 17 days in February-lifted seedlings [28, 30]. Here again, field validation is necessary in order to correlate days to bud elongation with field survival and performance.

Stress testing has been used for assessing seedling quality in the Pacific Northwest for 10 years and appears to have potential for southern pines [43]. Stress testing can be added to either RGP or budbreak tests by exposing a paired sample of seedlings to a drying environment, such as 15 minutes in an enclosed cabinet at 30% relative humidity and 32°C [66] or a forced-air oven for 30 minutes at 35°C [43]. The stressed seedlings are then processed along with the unstressed seedlings, and the response variable of interest for paired samples is compared. A large difference between stressed and unstressed samples suggests that seedlings are not very resistant to stress and therefore have a higher probability of dying or of performing poorly once outplanted.

8.7.4 Rapid, Nondestructive Tests

To be useful for operational application, any seedling-quality test must be rapid to conduct and interpret. Several new technologies are emerging that may, in the near future, provide rapid, nondestructive tests.

One of these tests, which has been used on a limited basis for about 10 years, is infrared thermography [63, 84]. The technique is based on measuring the temperature of a seedling or its parts and relating temperature with survival or performance. Further development of this technique has led to the use of spectroradiometry to measure wavelengths of radiation emitted or reflected from the seedling crop [86]. Not only is the infrared band scanned but also numerous bands in the visible and near-visible radiation spectrum, which have been related to plant nutritional status, photosynthesis, and leaf anatomy.

Another rapid, nondestructive measure of seedling physiological state is variable chlorophyll *a* fluorescence [78]. Seedling foliage is placed into an integrating light sphere and illuminated. Of the incident light impinging on the leaf surface, about 90% is absorbed; this may be used in the photochemical reactions of photosynthesis, dissipated as heat, or given off as fluorescence. The change in fluorescence of dark-acclimated seedlings (usually darkened 10 to 20 minutes before measurement) over about 5 minutes is representative of chloroplast activity, which has been demonstrated to vary consistently with water and nutrient status, temperature, and light and was highly correlated to RGP in cold-stored white spruce [*Picea glauca* (Moench) Voss] seedlings [78]. Further validation of fluorescence response to environmental factors could provide a useful test for seedling quality.

Analysis of volatile chemicals emitted from Douglas-fir seedlings subjected to environmental stresses common to nurseries has been reported recently [17, 18]. Stress-induced volatile emissions (SIVE) are collected from the air of either individual seedlings or racks of seedlings enclosed in an airtight container and are analyzed using existing gas-chromatography technology. The volatile chemicals analyzed include ethylene, ethane, ethanol, and acetaldehyde, though an unidentified terpene was found to decrease with increasing stress. The utility of such a test is that, with one sample, several compounds can be neously quantified, providing a "fingerprint" of the physiological state of the seedling or seedling lot. As with the other new testing methods, further validation is required. Moreover, the effects of temperature on the emission rate of the volatile compounds must be fully characterized; this is especially important for application in southern pine nurseries, where temperatures can fluctuate greatly during winter.

New techniques for assessing biochemical processes may be useful for evaluating seedling quality [90]. For example, absolute concentrations of important biochemical compounds such as starch and glucose or activity of important enzymes might be quantified by colorimetric or spectrophotometric techniques. Recent application of immunological techniques to plants may provide a fast, quantitative measure of important compounds or enzyme activity as well.

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