

Chapter 14

Plant Physiology and Nursery Environment: Interactions Affecting Seedling Growth

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Abstract

Environmental factors (such as light, moisture, nutrients, density, and temperature) and plant physiological factors (such as carbohydrate reserves, hormone levels, frost hardiness, and dormancy) interact to shape growth and survival of coniferous seedlings in nursery fields and after outplanting. Nursery managers can manipulate moisture, nutrients, and density to achieve desired seedling morphology and vigor. However, the annual growth cycle of perennial plants has evolved in response to environmental pressures. When the environment is modified, as with heavy irrigation in a nursery, to permit growth at a time when natural seedlings are dormant, the ensuing phases of the growth cycle will not be properly synchronized with their environments. Seedlings so cultivated lack vigor after outplanting. Nursery managers should aim at keying their cultivation schedules to both environmental conditions and endogenous seedling physiology to ensure production of high-quality seedlings.

14.1 Introduction

The annual growth cycle of most temperate-zone plants seems regulated by endogenous, or internal, rhythms. But these rhythms may be overridden by exogenous, or environ-

mental, factors which can, either collectively or individually, strongly limit or stimulate active growth [38]. Because the details of endogenous activity or of response to exogenous stresses or stimulation vary widely among temperate-zone plant species, botanists, horticulturists, foresters, and nursery personnel should be thoroughly familiar with the physiology of their plant populations and the environmental sequences necessary to produce plants of uniformly high vigor.

Cultivation according to physiological guidelines is essential to produce plants with maximum survival and growth potential. Such cultivation includes proper manipulation of seeds to assure a stand of well-spaced young seedlings by early June of the first year, irrigation schedules designed to promote growth in the spring and early summer and dormancy thereafter, and fertilizer applications which will provide the proper balance of the essential nutrients for optimum seedling growth and vigor.

14.2 Seedling Growth

14.2.1 The shoot

The first-year coniferous seedling commonly has an indeterminate growth habit; that is, shoot elongation results from production of cells by the apical meristem during the growth season. The significance of this habit to the nursery manager is that seedlings will often continue to grow as long as their environment favors growth [10, 42]. For example, it is not at all uncommon to observe first-year Douglas-fir [*Pseudotsuga menziesii* (Mirb.) Franco] seedlings in a nursery actively growing in October.

Research on the annual growth cycle of coastal Douglas-fir (var. *menziesii*) [5, 40, 41] suggests that, in nature, seedlings germinate in early spring and complete shoot elongation by midsummer, when increasing drought stimulates dormancy. Hermann and Lavender [25] demonstrated that seedlings grown from high-elevation seed sources entered dormancy earlier than those from low-elevation sources, whereas Rehfeldt [64] and Lavender and Overton [42] showed that Douglas-fir seedlings of the Rocky Mountain form (var. *glauca*) enter dormancy without appreciable environmental stress. Other western conifers have not been investigated as thoroughly as Douglas-fir. Nonetheless, the available data suggest that western hemlock [*Tsuga heterophylla* (Raf.) Sarg.] [36, 56, 57], true firs (*Abies* spp.) [39], and ponderosa pine (*Pinus ponderosa* Dougl. ex Laws) [37, 79] all have annual growth cycles comparable to that of the associated Douglas-fir and that these species respond to environmental stimuli in a similar manner.

After their first growing season, temperate-zone conifers generally demonstrate a determinant growth habit; that is, shoot elongation results from expansion of primordia laid

down in buds produced the previous growing season. Under natural conditions, this period of shoot elongation is typically brief [38], seldom more than 3 months. Normally, most western species complete their season's height growth in a single flush; but if the environment in midsummer favors growth (particularly after a heavy rain), these species can produce lammas shoots (one or more additional flushes of terminal growth on the terminal shoot) or prolepsis growth (elongation of lateral buds at the base of the terminal bud or on lateral shoots) [37, 69]. Such growth is undesirable in western nurseries because it generally does not develop frost hardiness early and hence may be killed by fall frosts. More importantly, it indicates that the seedling is not proceeding through the dormancy sequence properly (see 14.4.4) and therefore will not have high resistance to the stresses inherent in the harvest-storage-outplanting sequence and will not grow vigorously after outplanting.

14.2.2 The root

The roots and, generally, the fungi which form symbiotic structures with the roots or rhizomes of higher plants absorb most of a plant's nutrient and moisture requirements and support the aerial part of the plant. The obvious importance of the woody plant root system has stimulated research for at least a century, but work has suffered from the following weaknesses. First, the opaque nature of soil has made direct observation of root growth almost impossible; unfortunately, the glass-soil interface of glass-fronted boxes or underground containers creates an atypical rooting environment that is exacerbated by the fight used for observation. Second, growth and physiology of individual roots are extremely variable; the erratic growth rhythms of temperate-zone plant roots are more similar to the uncoordinated shoot-growth patterns of tropical plants than they are to the more regulated shoot-growth patterns of temperate-zone plants. Third, attempts to use environmental controls to study root growth and physiology have largely been frustrated by the extreme difficulty of maintaining or manipulating endogenous moisture and temperature gradients in soil isolated in discrete containers.

Notwithstanding the above, Sutton [80] reviewed extensive research demonstrating that a number of environmental factors may affect the growth, form, and physiology of roots. Such factors, however, seem to more heavily influence growth of second-year and older seedlings; the root form of first-year seedlings is often controlled more by genetics than environment [84].

Although Stone and his colleagues have repeatedly stressed the importance of the nursery environment in producing seedlings with a high potential for early root growth after outplanting [35, 76, 77, 78], there is no such consensus on the effects of planting techniques upon survival and growth of properly conditioned seedlings in plantations [22, 45, 60, 61, 62, 68, 91, 93, 94]. However, the results obtained with 1+0 Monterey pine (*Pinus radiata* D. Don) seedlings in New Zealand [86]—where careful nursery procedures preserved an intact root system and permitted twice the growth after outplanting of project-harvested seedlings—and the vigorous growth reported for 1+0 bareroot and container-grown Douglas-fir [21, 31] seem to support Tourney's [84] observation that roots of older seedlings are more affected by the environment (i.e., planting technique) and that the adverse impact of present planting techniques is reflected in the postplanting growth of older seedlings. Perhaps if planting techniques more compatible with maintaining seedling vigor were developed, the effects of nursery practice upon growth of second-year and older planting stock would be more evident. Conflicting evidence suggests both that well-developed root systems are associated with high seedling survival [23, 47] and that plantation growth

and root form are not correlated [46]; certainly, until such conflict is resolved, the more subtle effects of nursery practice upon seedling growth will be difficult to assess.

14.2.3 Shoot:root ratio

Wakeley [93] concluded that measurements of seedling morphology were poor indicators of future field performance. However, subsequent reports equivocate on this point. Some workers [6, 7, 18, 47, 75, 92] suggest that seedling shoot:root ratios at the time of planting do predict seedling performance—a low shoot:root ratio would indicate good survival and growth potential—but others [1, 2, 53, 54, 55, 70, 99] disagree.

Several probable reasons underlie this sharp divergence of opinion. First, shoot:root ratio may vary as a result of:

- **Seedling age or size:** Older, larger plants generally have higher shoot:root ratios than smaller, younger ones [32, 87].
- **Seedling genetics:** Plants grown from seed collected in dry regions have lower shoot:root ratios than similar plants grown from seed collected in moist areas [42].
- **Environment:** Plants grown with high levels of water, nutrients, or both or with less than full sunlight often have higher shoot:root ratios than similar plants grown with relatively limiting levels of water and nutrients under full light [106].
- **Cultural practices:** Root or shoot pruning or wrenching, for example, may stimulate either high or low shoot:root ratios, but this effect is generally transitory [51]. Wareing [96] has shown, for example, that shoot growth may be quantified in terms of root growth according to the formula $S = cRk$, where S is shoot growth, R is root growth, and c and k are constants specific for a given species and environment. Ledig and Perry [44] suggest that the constants are stable over a range of environments. Obviously, unless both c and k equal 1, the shoot:root ratio will change with time.

Second, stresses present at the planting site vary widely with climate and vegetation type. A plantation established on a relatively dry site in eastern Oregon and Washington, for example, may well have higher survival if the seedlings have a low shoot:root ratio. But the major stress on a typical Oregon Coast Range plantation will be competition for light [29], in which case seedling survival is more heavily dependent on shoot size than on shoot:root ratio.

Third, there is no standardized methodology for determining shoot:root ratios. Some workers use the dry weights of roots and shoots [32, 44, 47]; others use the relative volumes of these seedling parts [53, 54]; and still others use the relationship of foliage weight to root-surface area [18] as a "drought resistance index." Edgren and Iyer [18] note that shoot:root ratios calculated by the volumetric technique may be transformed to the drought index by dividing by 0.04.

Finally, reports frequently neither cite the probable cause for shoot:root differences nor demonstrate the probable effects of planting-site environment on the physiological parameters determining shoot:root ratio.

14.3 Exogenous Factors Affecting Growth

14.3.1 Light

Light profoundly affects the growth and development of temperate-zone plants in two ways. First, it is the energy source that drives photosynthesis, the process by which plants create the organic substrates necessary for growth. Second,

light-or, more properly, the absence of light—regulates seedling development through a phenomenon termed photoperiodism; that is, daily dark periods of less than 10 hours stimulate active shoot elongation, whereas daily uninterrupted dark periods longer than 14 hours stimulate dormancy.

In spite of the extreme importance of light, however, the bareroot nursery manager can affect the light environment of seedlings by (1) reducing light intensity with shading materials; (2) manipulating density of both crop and weed species; and (3) controlling the photoperiod by installing either artificial light sources or blackout devices designed to shorten seedlings' daily exposure to light. Shading seedlings or manipulating their density, which may significantly affect morphology and carbohydrate reserves, will be discussed more fully in 14.3.4. Controlling the photoperiod, which has been done occasionally in eastern U.S. nurseries and in research trials, is not a technique used by Northwest nurseries and therefore will not be discussed in this chapter.

14.3.2 Moisture

Like light, moisture influences seedling growth and development by its presence or absence. The rate of photosynthesis, one major key to total seedling growth, may be sharply reduced by soil moisture deficits that are relatively small (-1 to -3 bars) [105]; but it may also be slowed by saturated soils, which produce an anaerobic environment [102]. In addition, excess moisture may promote growth of plant pathogens such as *Phytophthora*, *Pythium*, and *Fusarium* [19].

The regulatory role of moisture in the annual growth cycle of Northwest conifers, especially in initiating dormancy (see 14.4.4), reflects the region's climate, which is characterized by dry summers and wet winters. Such a precipitation pattern is similar to that of California and the Mediterranean area, but is sharply different from that of most land areas, which receive the majority of their annual precipitation during summer. Dormancy in perennial, temperate-zone plants indigenous to areas with moist summers is initiated primarily by shortening photoperiods in late summer and only secondarily by plant moisture stress [38]. Therefore, timing and intensity of irrigation in eastern U.S. nurseries do not impact the annual growth cycle. But in the Northwest, most species grown in coniferous forest nurseries have evolved to initiate dormancy primarily in response to midsummer drought [9].¹

Nursery personnel can effectively manipulate plant moisture. For example, they can help protect seedlings from moisture stress by carefully noting both seedling and environmental conditions during nursery operations. Not infrequently, weather during the lifting and packing period may be sufficiently desiccating to cause severe moisture stress. Seedlings should be moistened thoroughly when dry days occur during harvest because even brief periods of moisture stress at that time will reduce subsequent seedling growth [15]. Furthermore, seedlings that are stressed when packed must endure many days in storage before such stress can be alleviated [15](see chapters 21 and 22, this volume). Conversely, however, irrigating at the wrong times-physiologically-can do damage. Frequent irrigation of nursery stock to relieve moisture stress due to late-summer drought can cause dormancy to be initiated too late to permit the sequence of physiological changes necessary for vigorous seedling growth [41](see chapter 15).

14.3.3 Nutrients

Seventeen elements have been shown to be essential to plant growth. Three of these-carbon, hydrogen, and oxygen—are absorbed from the atmosphere or from water. The remain-

ing 14 are taken up from the soil. Several of these—nitrogen, phosphorus, potassium, calcium, sulfur, and magnesium—are termed macronutrients because harvesting an acre of coniferous seedlings commonly removes from 1 to more than 100 pounds of each of these elements [90]. The remaining elements—boron, chlorine, copper, zinc, iron, manganese, molybdenum, and cobalt—are required in much smaller quantities and, hence, are termed micronutrients. A healthy seedling, however, must be well supplied with **all** nutrients in proper proportions [28]. Any environmental or cultural factor that affects growth will, of course, affect seedling nutrient requirements. Though it is not possible to specify absolute soil-fertility standards, ranges within which vigorous seedlings may be grown can be specified (see chapters 7 and 8, this volume).

If a given nutrient is deficient, seedlings may compensate to some extent by increasing their capacity to take up the deficient ion [26]. More commonly, such stress is reflected by reduced growth and by distinct changes in the plant's habit. Plants require nitrogen, for example, to synthesize chlorophyll; nitrogen-deficient plants, therefore, often appear chlorotic. Low levels of phosphorus, which is essential to seedling metabolism, result in reddish-purple foliage. Boron is required for lignification; deficiency causes terminal dieback and necrotic buds. Other symptoms characteristic of malfunctioning physiology are exhibited by seedlings deficient in other nutrients [43].

van den Driessche [89, 90] reviewed reports that indicate both positive and negative effects of nursery fertilizer applications on subsequent seedling growth and survival. Both van den Driessche's trials with Douglas-fir [89] and those of Smith et al. [73] showed positive growth responses after outplanting for Douglas-fir seedlings fertilized with various levels of nitrogen in the nursery. Radwan et al. [63], however, suggest that the form of nitrogen fertilizer strongly affects response; in their trials, nitrate and urea fertilizers produced greater seedling response than did ammonia salts.

Several reports have suggested that cold hardiness in conifer seedlings may be affected by adding mineral nutrients to the nursery seedbed in late summer [90]. For example, potassium has been shown to increase drought resistance when soils are frozen in winter, and both potassium and nitrogen, applied too late to affect the dormancy cycle, have increased seedling frost hardiness in both Sitka spruce [*Picea sitchensis* (Bong.) Carr.] and western hemlock seedlings.

The above studies as well as others not mentioned here suffer from lack of positive control of nursery environmental factors other than nutrients and from lack of uniformity and control of physical and biological factors in the outplanting area. Although the results of such research may provide empirical guidelines for the moment, they fail to elucidate the physiological role of nutrients in seedling vigor. A range of carefully controlled, designed studies—such as those conducted by Ingstad [27], wherein all environmental factors including nutrients are fully controlled—is needed to answer questions about species, quantities, and timing of nursery nutrient applications.

Given the above caveats, the following points, discussed by van den Driessche [90] in his comprehensive review of nursery soil fertility, are valid, useful guides:

- Nutrient availability may be affected by soil pH and organic matter content.
- Harvest of 2+0 seedlings removes significant quantities of nutrients. Continual cropping of nursery soils, then, requires adding nutrients to maintain fertility.
- Adding nutrients, especially nitrogen or phosphorus, affects the growth of soil microorganisms and may stimulate pathogens.

¹With the probable exception of ecotypes or species native to either the fog belt or to the *Abies amabilis* and *Tsuga mertensiana* zones in the Cascade Mountains [20].

- Frequent, light additions of nutrients will provide more constant levels of seedling nutrition than less frequent, heavy applications.
- Evaluating the effects of individual nutrients on certain aspects of seedling physiology is difficult because of the possible interactions of those particular nutrients with other aspects of seedling physiology. A comprehensive study relating nursery fertilization practices with seedling growth and survival after outplanting has not yet been made.

14.3.4 Density

Reports on a wide range of forest types throughout the world suggest that the density of coniferous seedlings in seedbeds dramatically affects seedling development [4](see chapters 5 and 15, this volume). A study from New Zealand [8] suggests that the optimum spacing between 1+0 Monterey pine seedlings is about 1/8 of their height. However, age of planting stock at the time of harvest and variations in seeding method and densities make it impossible to generalize about an optimum density for all nurseries.

For example, Mullin and Bowdery [52] demonstrated that white pine (*Pinus strobus* L.) and red pine (*Pinus resinosa* Ait.) seedlings grown at 15 seedlings/ft² survive and grow better than similar plants grown at 30 seedlings/ft². However, Shoulters [72] and Shipman [71] reported that loblolly pine (*Pinus taeda* L.) and slash pine (*Pinus elliottii* Engelm.) seedlings generally have equivalent survival whether grown at 20 or 40 seedlings/ft². The greater size and growth of the lower density stock in Shipman's [71] trials find support from the unpublished data of Meal [50] who argues that 18 seedlings/ft² is the optimum density for 1-year-old loblolly pine.

In the Northwest, unpublished data from Weyerhaeuser Company reforestation projects [30] suggest that in the state of Washington, 25 2+0 Douglas-fir seedlings/ft² is the optimum spacing when costs of both nursery cultivation and plantation establishment are related to seedling survival. In British Columbia, Revel [65] proposes that 30 to 50 seedlings/ft² will produce the highest yield of plantable 2+0 Douglas-fir, but Edgren [17] argues that a spacing of no more than 20 seedlings/ft² is necessary to produce 2+0 seedlings with a 4-mm caliper. The foregoing data demonstrate that spacing in the seedbed affects seedling caliper. Lopushinsky and Beebe [47] note that seedling stem caliper is correlated with root development and that seedling survival on droughty sites is improved if plants have well-developed roots. Very probably, wide spacing in the seedbed permits increased photosynthesis, hence the increased food reserves necessary for vigorous growth after cold storage. It should be emphasized, however, that the densities referenced in this and the preceding paragraphs are **means**, which can vary significantly within treatments.

In summary, density itself affects seedlings indirectly—by impacting available light, moisture, and nutrients. Generally, wide spacing (lower density) promotes greater root development and higher levels of carbohydrate reserves, which are essential for development of cold hardiness [97], and reduces losses to insects and disease [74].

14.3.5 Temperature

Temperature is a measure of the heat energy available to plants. Higher plants, under normal growth conditions, are poikilothermic—that is, they assume the temperature of their environment. Further, the rates of most metabolic processes are strongly regulated by temperature: for example, a 10°C increase in temperature may cause a plant's respiratory rate to double [98]. The temperature at which maximum plant growth occurs is not necessarily that which permits maximum gross photosynthesis—it is the temperature at which the rates of the

plant's synthetic processes exceed those of its catabolic processes by the greatest margin.

Controlled-environment trials with Douglas-fir seedlings suggest that the optimum temperature for growth of this species is 24°C [42]; similar results are reported for seedlings of other coniferous species [83]. But findings from trials with other plants suggest that the optimum temperature for growth may drop slightly as plants increase in size and age ([13] for Monterey pine, [95] for agricultural crops).

The preceding data are largely concerned with the effect of air temperature, primarily during the day, on active plant growth. However, Lavender and Overton [42] demonstrated that warm, not cool, nights stimulated Douglas-fir seedling dormancy under short photoperiods, and Lavender [38] reviewed data which indicate that soil, as well as air, temperatures may greatly influence the growth of plant shoots.

The optimum growth period for nursery stock in the Northwest seems to occur—not during the hot days of summer—but during the relatively mild days of spring. However, when daytime temperatures exceed 20°C, a decided moisture stress, which will limit photosynthesis, may develop by 10 a.m. even in seedlings growing in moist soil. Seedling growth in spring may be maximized by applying intermittent, light irrigation during bright spring days to reduce seedling moisture stress and subsequent stomatal closure [105].

Although nursery managers can do little to regulate the temperature of nursery seedbeds, they can produce superior seedlings by scheduling annual growth cycles so that seed and seedling physiology is compatible with environmental conditions. For example: (1) seed germination in the relatively cool soils of April or early May is facilitated by presowing stratification periods of 3 months; (2) seedling quiescence (summer dormancy), initiated by midsummer drought, is associated with hot summer days; (3) early rest (winter dormancy) is stimulated by the mild temperatures of early fall. Failure to match seedling physiological states with the temperature regimes occurring naturally during those states may have a profound negative impact on seedling quality [38].

Temperature extremes may damage seedlings (see chapter 12, this volume). However, effects of high temperatures may be minimized by proper seedling spacing and cultural regimes supplemented by occasional, light, cooling irrigation on hot days. Frost damage may be avoided by initiating dormancy in midsummer and by seedling spacing which permits maximum photosynthesis and production of carbohydrate reserves.

14.4 Physiological Factors Affecting Growth

14.4.1 Carbohydrates

The heterogeneous group of compounds termed carbohydrates provides the principal substrates for producing the energy necessary for plant metabolism. Simple sugars may be converted to amino acids, the basic compounds of the proteins essential to cell structure.

Although carbohydrate levels in plant tissues have been studied for decades, the literature contains little really definitive data for several reasons. First, "carbohydrate" is an imprecise term. It includes monosaccharides, oligosaccharides, and polysaccharides and should include sugar derivatives such as alcohols, cyclitols, their methylated derivatives, and even such compounds as gluconic acid. Second, carbohydrate levels may change after sample harvesting as seedling metabolism continues until tissue is killed: enzyme activity may interconvert various carbohydrate species. Probably the best harvest procedure is immediately placing sample tissues into liquid nitrogen, followed by freeze-drying and dry storage at about

0°F (-17°C) [unpubl. data, 101]. Third, before the development of sophisticated gas-liquid chromatography [12], the methodology used to analyze carbohydrates was not sufficiently precise to provide accurate estimates of many species of interest.

Carbohydrate levels have been related to: (1) development of cold hardiness [97], based on the hypothesis that relatively high levels of substrate are necessary if a plant is to cold-harden fully; (2) nursery cultural practice, in which the effects of box pruning and wrenching on carbohydrate content of Monterey pine seedlings were shown to increase the level of substrate [11]; (3) growth of seedling roots [103]; and (4) duration of cold storage [66]. In the last case, carbohydrate reserves of Douglas-fir seedlings decreased as length of storage increased; concurrently, root-growth potential declined for storage periods longer than 6 months. But Krueger and Trappe [34] reported little correlation between root activity and seedling carbohydrate reserves.

14.4.2 Hormones

A hormone, or plant-growth regulator, is a substance synthesized (usually in minute quantities) in one location (i.e., the plant root) but transferred to another location (i.e., the plant leaf), where it exerts an effect upon growth and differentiation. This concept is not without controversy [85] because, unfortunately, methodologies for isolating and identifying hormones have lacked the precision necessary for obtaining unequivocal data. Nevertheless, a substantial volume of literature has appeared in the past 50 years relating plant hormones to such a bewildering array of metabolic and differentiation processes that even a summary is beyond the scope of this chapter. The following are the major, accepted hormones and the growth parameters most characteristic of each [81]:

Auxins: Stimulate cell enlargement, rooting of cuttings, and apical dominance; inhibit abscission of leaves, fruits, and root elongation.

Gibberellins: Stimulate cell division, seed germination, and reproductive growth.

Cytokinins: Retard senescence; promote bud growth as well as cell division, expansion, and differentiation.

Ethylene: Stimulates fruit ripening, breaking of dormancy, and epinasty (downward twisting of leaves or other organs); inhibits elongation of shoots and roots.

Inhibitors (e.g., abscisic acid): Reduce growth; may inhibit seed germination; may control stomatal physiology.

Plant growth and differentiation are generally believed to be controlled by interactions of the above compounds, in the manner suggested by Khan [33] for seeds, such that high concentrations of promoters favor germination, high concentrations of inhibitors favor dormancy, and cytokinins facilitate the action of promoters.

Reviewing a wide range of literature investigating the role of plant-growth regulators in woody-plant seedling physiology, Zaerr and Lavender [104] concluded that limitations in analytical methods have prohibited satisfactory understanding of the relationship, if any, between levels and species of plant-growth regulators and seedling vigor. Current work at Oregon State University, Corvallis, is concerned with developing more efficient, definitive analysis procedures for plant regulatory compounds, especially gibberellins and cytokinins, and with describing the role of such substances in the growth of coniferous seedlings [3, 14,49].

14.4.3 Frost hardiness

Frost or cold hardiness is the ability of plant cells to withstand temperatures below freezing without suffering irreversible physical damage. The nature of the changes that occur in

plant cells during the hardening process is not fully known or understood, but the hardening process apparently involves changes (1) in cell membranes, to allow movement of water to extracellular ice crystals, and (2) in the protoplasm, to resist effects of desiccation [97].

Significant frost hardiness is developed in coniferous seedlings only if the plants have an adequate carbohydrate reserve and if active growth has ceased [97]. The weather sequence that best promotes frost hardiness is warm, dry days and nights to favor growth cessation: mild, short days and mild nights to initiate hardening; cool, short days and cool nights to develop moderate hardiness; and, finally, cool days and freezing nights to develop maximum cold hardiness [82]. If this sequence is begun in mid-July and completed by late November, seedlings should be frost hardy to from -20 to -30°C by early December.

Frost hardiness in plants is quite labile. A few days of mild temperatures during winter may greatly reduce a seedling's cold resistance so that at least part of the foregoing sequence must be repeated before maximum cold hardiness is restored. However, frost damage to buds or foliage (at least after mid-November) does not affect seedling survival significantly [24].

14.4.4 Dormancy

The growth habit of perennial, temperate-zone plants is generally characterized by a relatively short period (about 3 months) of active shoot elongation followed by a lengthy "dormancy." Dormancy is a general term for all instances in which a tissue predisposed to elongate (or grow in some other manner) does not do so (after [16]). Romberger [67, p. 74] describes the nomenclature of dormancy, which still tends to be vague and confusing. Although dormancy is an adoption to permit plant survival during periods of stress (e.g., drought or frost), a plant is not equally resistant to all environmental factors during the entire dormant period, nor are the phases of dormancy normally defined in relation to stress resistance.

14.4.4.1 Growth patterns during dormancy

Only the apical meristems demonstrate true, endogenous dormancy. This is in sharp contrast to the phenomenon of cold hardiness, a parallel, associated physiological state which affects, at least in some degree, the **entire** plant.

Lateral meristems of Douglas-fir seedlings grow from about budbreak until midfall [34]. Root meristems of Douglas-fir seedlings grow mainly during two peak periods. The first and larger peak extends from late winter until shortly after budbreak; the second and smaller peak occurs from late summer until midfall. During the rest of the year, either adverse environment or competition with the shoot for substrates results in relatively little root activity [34].

Lyr and Hoffman [48] present data generally confirming the above root-growth pattern for other temperate-zone woody perennials, whereas Sutton [80] suggests that root growth is controlled by environment rather than endogenous rhythms; he notes that both dry soils in summer and cold soils in winter may strongly limit root growth. Given the above general patterns, transplanting seedlings in late summer allows plants so handled to develop strong root systems by utilizing the period of root growth in both fall and early spring.

Even the buds of dormant seedlings are not inactive for the entire dormant period. Internals that will develop into the following year's shoots are laid down from July until November, the rate decreasing with time [58, 59].

14.4.4.2 Phases of dormancy

Although the sequence of physiological changes occurring during dormancy is not clearly understood, recent data [9, 38, 41] describe the environments necessary to permit proper

Table 1. Dormancy sequence In Douglas-fir (adapted from [41]).

Phase of dormancy	Period of year	Physiology	Environment
1: Initiation of dormancy	July-late September	Cessation of growth, increased desiccation, Jig-nification of tissues	Mild to hot days, shortening photoperiod, mild to strong moisture stress
2: Deep dormancy	Late September-early December	Accumulation of growth inhibitors, increased cold resistance	Mild temperatures, shortening days
3: Dormancy lifting	Early December-late February	Breakdown of inhibitors, virtual cessation of metabolic activity	Short days, low temperatures
4: Postdormancy	Late February-budbreak	Accumulation of growth promoters (gibberel-lins, cytokinins, auxins), gradual conversion of carbohydrate substrates	Lengthening days, mild temperatures, low moisture stress

progression through dormancy from early budset in summer until budbreak the following spring. It cannot be emphasized too strongly that any major deviations from the endogenous pattern of dormancy will greatly diminish seedling vigor and reduce the survival potential of affected seedlings when outplanted. The environments necessary to permit normal development of dormancy in Douglas-fir are presented in Table 1; the phases of dormancy—and the consequences of deviation from the proper progression—are described in detail below, by phase. Bear in mind, however, that the dates, conditions, and processes in Table 1 are approximations—all these can vary from one year to the next—and that the transitions between phases are gradual rather than sharp.

Phase 1—Initiation of dormancy: Shortening photoperiods stimulate many temperate-zone plants to initiate dormancy during late August and September. However, the Northwest is relatively unique in that most of its annual precipitation falls during winter rather than summer, as it does for the majority of agricultural regions throughout the world. Accordingly, the prime impetus for initiation of dormancy in Douglas-fir is drought.

In nature, seedlings commonly set a resting terminal bud no later than mid-July. However, because nurseries can irrigate seedbeds during the entire summer, the natural chronology can be altered. Seeds are commonly sown in May or early June, resulting in germination and early seedling growth no earlier than early June (as opposed to early April under most natural environments). Nurseries irrigate seedlings until mid-August to achieve the growth most foresters want. As a result, plants are actively growing in late August, when fall rains start, and continue to grow until late September or early October before initiating a bud. Obviously, the environment in October is not that of July. Bud development is slowed, and the seedling remains out of phase with the environment through the winter and following spring, with a corresponding reduction in field-survival potential.

Phase 2—Deep dormancy: This is the critical phase for nursery operations. If resting buds are not well formed by mid-August, the requirements of buds for shortening days and mild temperatures, which occur during September and October, will not be met. A seedling that sets bud in late September will experience the cold temperatures of late October and subsequent months before its physiology has progressed sufficiently to benefit from the chilling, and phase 3 of dormancy will not be completed satisfactorily. As a result, the seedling will have a delayed budbreak the following spring and lower field-survival potential.

Phase 3—Dormancy lifting: Virtually all perennial, temperate-zone plants have a strong requirement for exposure to temperatures between 0 and 5°C during winter. Some horticultural varieties are characterized by the number of hours of

such chilling they require. Douglas-fir has been shown to require from 8 to 12 weeks of chilling at temperatures around 5°C [88, 100]. However, these data are based on laboratory trials in which the temperature was continually maintained at that level.

In nature, warm periods during winter are frequent. During those times, the chilling process is disrupted, and the warmth actually reverses part of what the previous cold had accomplished. (It is generally believed that low temperatures facilitate destruction of the hormones that inhibit plant growth.) Winter weather normally just satisfies the seedling's requirement for low temperatures. However, if the environments during phases 1 and 2 were not conducive to bud formation and development, the seedling will require a much longer period of chilling to complete phase 3 satisfactorily. Seedlings lacking the necessary chilling will begin to grow later than normal in the spring, and their field-survival potential will be correspondingly reduced.

Phase 4—Postdormancy: If seedlings have progressed properly through the first three phases of dormancy, they should enter phase 4 no later than early March. In this phase, the plant is ready to grow and remains dormant only so long as temperatures are unfavorable for growth. If seedlings have not progressed through the first three phases of dormancy properly, they will fail to grow in response to the warming temperatures of early spring. Lack of root growth will greatly reduce the plant's ability to take up necessary moisture from the soil, and it will probably die of drought before mid-June.

By definition, dormancy is related to the ability of the apical meristem to grow. However, the concepts in Table 1 are based more on the resistance of seedlings to the stress inherent in the reforestation process than they are on the classical definition of dormancy. For example, the period from early October until early November usually corresponds with the time when the apical meristem is least likely to resume growth under favorable conditions. However, the period from late September until early December corresponds with the time when seedlings are most easily injured by the transplanting process. Accordingly, that period (late September to early December) has been identified as phase 2 so that nursery personnel can better interpret seedling physiology in terms of nursery operations.

To complicate the role of dormancy in seedling physiology still further, Owens and Molder [59] demonstrated that there is no strong correlation between the phases of dormancy and initiation and development of primordia in buds. It is clear, then, that the phases outlined in Table 1 cannot be identified with anatomical or morphological changes in seedlings but must result from changing hormonal levels. Until analytical techniques are sufficiently precise to accurately determine species and quantities of these compounds, the true nature of the physiology of dormancy will remain unknown.

14.5 Conclusions

This chapter has described the effects of a range of environmental factors and cultural treatments upon the physiology of coniferous seedlings. Most of this discussion has been based upon empirical trials, which generally suffer in that they are not sufficiently precise to permit uncritical extrapolation.

The nursery manager, then, should use the relationships presented here as general guides, realizing that specific nursery environments and specific genetic stock may produce results which deviate, at least in detail, from those outlined in this chapter. A thorough knowledge of the meteorological and edaphic characteristics of the nursery and of the genetic composition of the major stock types is necessary if nurseries are to consistently produce high-quality seedlings.

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