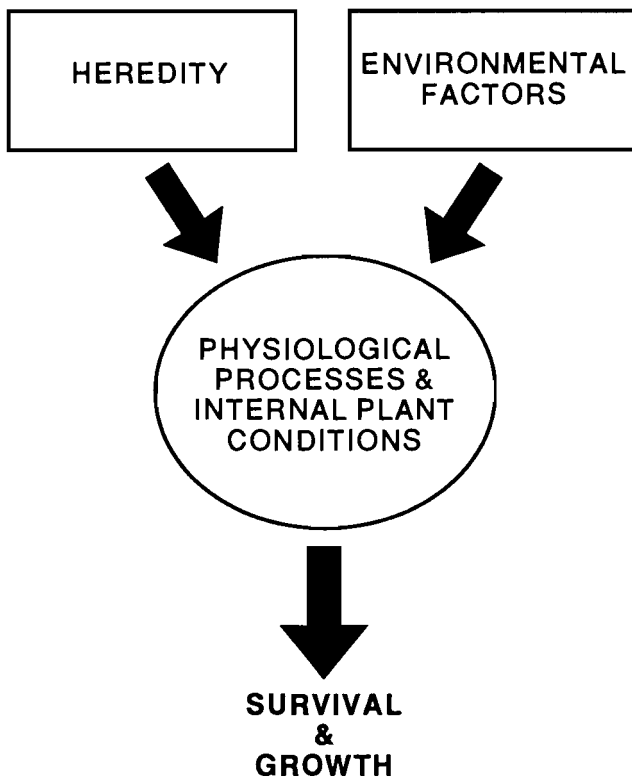


# **6** *Seedling and Site Interactions*

*Stephen D. Hobbs*

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## INTRODUCTION



*Figure 6-1. Klebs' concept. Heredity and environmental factors combine to influence physiological processes and internal plant conditions, and hence, plant survival and growth.*

Understanding how seedlings are likely to react to site conditions is essential before formulating reforestation objectives. This requires a general knowledge of plant physiology, and more specifically, an appreciation of how the tree seedling as a complex system responds to environmental change. Physiology acts as the integrator of heredity and environmental factors that determine seedling survival and growth or field performance. The idea that heredity and environmental factors influence the plant by affecting physiological processes—Klebs' concept—was first advanced by the German plant physiologist Klebs in the early 1900s (Figure 6-1). Because we are able to manipulate some aspects of the seedling environment and to a limited extent seedling genetics (e.g., through tree improvement programs, genetic engineering), we can exercise considerable control over seedling physiology and thus field performance and wood characteristics.

The intent of this chapter is to provide a clear understanding of what is meant by the operational environment as a framework for understanding the interaction between the seedling and its surroundings. In addition we will explore how changing environmental conditions affect various physiological processes and hence seedling response. Inherent in this presentation is the need for a brief review of several important physiological processes and conditions as they pertain to tree seedlings. This chapter emphasizes seedling ecophysiology, or seedling-site interactions from the physiological perspective. The effects of different types of stress, particularly water stress, on seedling physiology and subsequently field performance, will be discussed. A brief overview of seedling growth and stock quality will also be presented.

## THE SEEDLING ENVIRONMENT

From a reforestation perspective, the word "environment" is generally used to mean a seedling's total surroundings—the abiotic (nonliving) and biotic (living) components both above and below ground with spatial and temporal dimensions. However, in the preceding chapters and in the introduction to this chapter, the term "operational environment" was used. It is important to distinguish "environment" from "operational environment" because successfully explaining or predicting seedling response to environmental change is contingent on understanding what is meant by the latter term.

Building on the concept first advanced by Mason and Langenheim (1957), Spomer (1973) states that the operational environment is that portion of an organism's total environment composed of operational factors (Table 6-1) or

Table 6-1. Generalized list of operational factors or factor groups.<sup>1</sup> Adapted from Spomer (1973); used by permission of the Ecological Society of America.

### *Energy factors*

- Ionizing radiation
- Light
- Heat
- Mechanical energy
- Miscellaneous energy (chemical, electrical, gravitational, etc.)

### *Inorganic (mass) factors*

- Gases
- Liquids and solutes (including water, dissolved salts, etc.)
- Solids

### *Organic (mass) factors*

- Nutrients
- Toxins

<sup>1</sup> Groupings are somewhat arbitrary and are intended only to display the various types of operational factors possible for any organism.

("real") entities, either energy or material, which can be exchanged between an organism and its environment." A critical part of Spomer's definition is that in order to be operational, a factor must be exchangeable, or "interact" between the environment and the organism. This means that the internal concentration of an operational factor changes as the factor is transferred either into or out of the seedling. In the case of energy, one form may be converted to another form in the exchange (e.g., light energy to chemical energy). It is only through this exchange process, and the subsequent change of the internal concentration, that physiology, and consequently seedling survival and growth, can be affected.

The exchange process of an operational factor between a seedling and its environment is also referred to as a flux. Fluxes have sources and sinks: the operational factor moves from the source to the sink. For example, when soil water is absorbed from the soil matrix into the root in response to the water vapor pressure deficit at the leaf-atmosphere interface, the soil matrix serves as the source and the conducting tissue of the root as the sink. However, soil as an entity does not interact with the seedling or affect its physiology *per se*. Instead, various soil components, such as water, heat, nutrients, and soil oxygen, are exchanged with the seedling and affect its physiology. Similarly, aspect or slope direction is a commonly used site variable; yet aspect does not interact nor is it exchangeable with the seedling. What is important is the effect aspect has on light and heat energy, operational factors that do affect seedling physiology.

By understanding the operational environment, we can identify factors affecting seedling response and use appropriate treatments to either optimize or minimize their effect on seedling physiology. In the nursery the manager exercises considerable control over the operational environment, particularly in container facilities. Somewhat less control is obtainable in the field, but control of surrounding vegetation can significantly alter the operational environment both spatially and temporally to better achieve reforestation goals. Failure to understand and correctly identify the operational factors most limiting to seedling survival and growth can have long-lasting biological and economic consequences.

## SEEDLING PHYSIOLOGY

A detailed knowledge of seedling physiology is not a prerequisite for successful reforestation, but foresters should have a general understanding of important physiological processes and conditions and how these relate to seedling response to changes in the operational environment. This section provides an overview of some of the more important physiological processes that affect seedling performance.

### Water Movement and Transpiration

All things considered, water is probably the single most important operational factor limiting seedling survival and growth in southwestern Oregon and northern California. Indeed, "biological function is completely dependent upon water" (Salisbury and Ross 1969). Consider water's impact on tree growth. Zahner (1968, as summarized by Kramer and Kozlowski 1979) "reported that up to 80 percent of the variation in diameter growth of trees in humid areas (and up to 90 percent in arid areas) can be attributed to variations in rainfall and water stress."

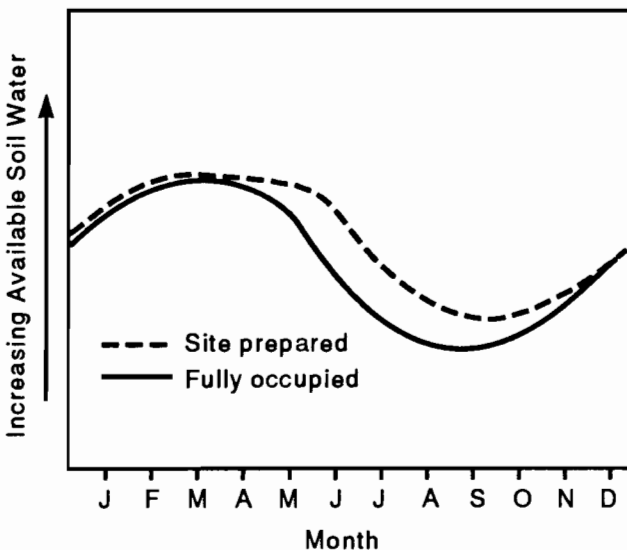


Figure 6-2. A generalized illustration of available soil water depletion and recharge over a 12-month period on a site fully occupied by vegetation and one site recently prepared and planted.

The Mediterranean-like climate of the region, with its hot, dry summers, sets the stage for a prolonged period of high evapotranspirational demand. This period, generally extending from May through September, is characterized by high daytime temperatures, low relative humidity, and very little precipitation. During summer, the combined effect of these atmospheric factors and competition from associated vegetation results in plant moisture deficits in seedlings.

Starting in fall and ending in spring, available soil water levels are restored to field capacity. As air and soil temperatures warm and photoperiod lengthens, vegetative growth resumes. The result is a marked decline in available soil water, which generally starts in June and levels off in late July or early August depending on site conditions (Figure 6-2). The decline in available soil water is the result of evaporation from the soil surface and transpiration from vegetation. Transpiration is the evaporation of plant water from the leaf surface primarily through the stomata. Although direct evaporation from the soil surface is a source of water loss, transpiration has the greatest effect on both the extent and rate of available soil water depletion.

The amount of plant water loss due to transpiration is largely a function of the vapor pressure deficit at the leaf-air interface. This deficit is simply the difference between water vapor pressure in the leaf stomata (usually considered to be saturated, or 100 percent) and that of the surrounding air (Figure 6-3). Atmospheric water vapor pressure is largely influenced by temperature and relative humidity (Figure 6-4). As temperature increases and relative humidity declines, the vapor pressure deficit increases. We know that water vapor will always move from areas of higher to areas of lower concentration. When transpiration occurs, the vapor pressure of water in the stomata is greater than that of the surrounding air. It is this difference that drives the energy (water potential) gradient, causing water to move from the soil into the plant and eventually to the atmosphere through the process of transpiration. This is known as the soil-plant-atmosphere continuum of water movement (Philip 1966).

The soil-plant-atmosphere continuum of water movement is characterized by water movement along a free energy gradient of increasing water

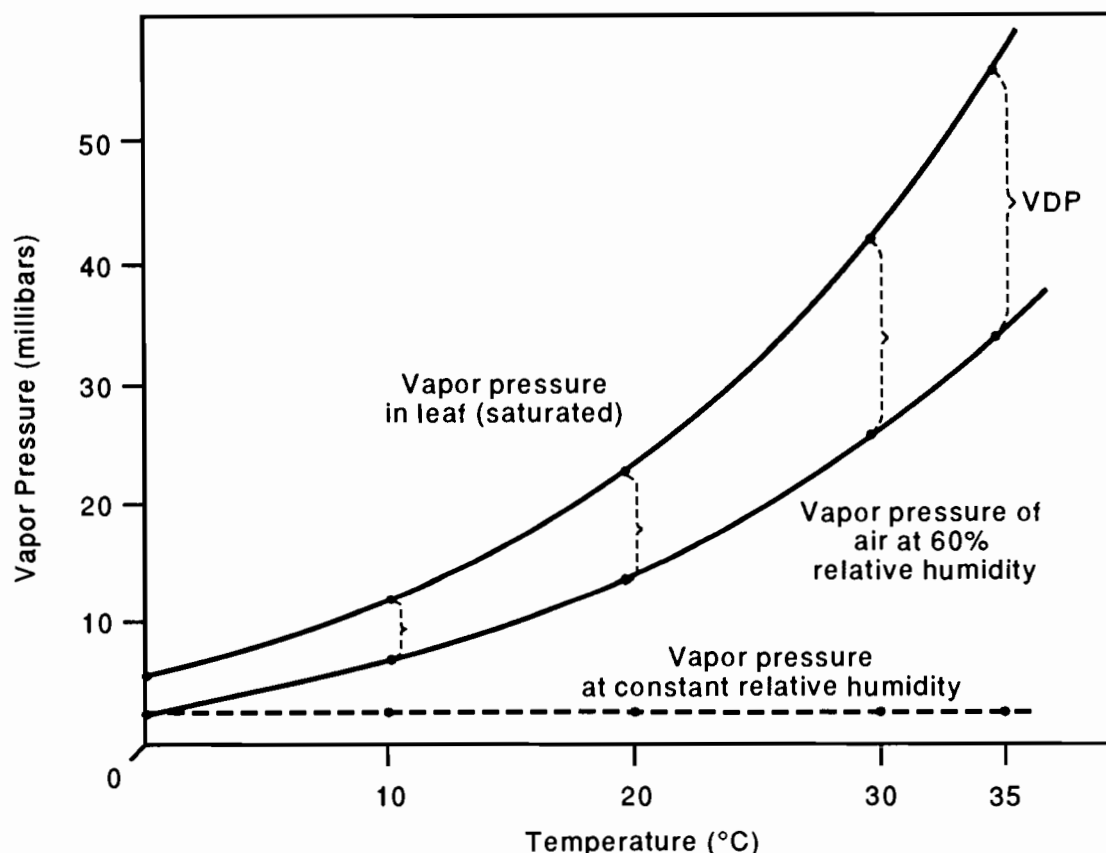


Figure 6-3. The relationship between water vapor pressure and air temperature with relative humidity held constant at the evaporative leaf surface (saturated) and the surrounding air (60 percent). As temperature increases, corresponding increases in the vapor pressure deficit (VDP) occur, thus increasing atmospheric evaporative demand. From Kramer and Kozlowski (1979); used by permission of Academic Press.

potential. This starts in the soil and is completed as water evaporates into the atmosphere through the leaf stomata. In general, the atmospheric demand for moisture (vapor pressure deficit) acts as the pumping force that moves water from the soil through the plant and into the atmosphere. This relationship is important and explains why competing vegetation can have such a negative effect on conifer seedlings when available soil water is limited. Water potential, expressed as negative bars, atmospheres, or mega-Pascals, is indicative of the tension on the water column in the plant. The more negative the number, the less the water potential and the greater the stress. Another term more commonly used to represent water potential is plant moisture stress, or PMS (Waring and Cleary 1967). This term is often used

by foresters when describing the amount of stress a seedling is under when it experiences water deficits. Plant moisture stress is typically measured with a pressure chamber (Waring and Cleary 1967), but in actuality what is measured is xylem pressure potential. This is the tension with which water is held in the xylem and is only one component of plant water potential.

Seedlings generally have characteristic patterns of annual and diurnal plant moisture stress. For example, in late spring or early summer, as available soil water declines and evapotranspirational demand increases, predawn moisture stress in seedlings increases as the summer progresses (Figure 6-5A). As conditions moderate in late summer and early fall, moisture stress declines. Depending upon site, seedling, and cli-

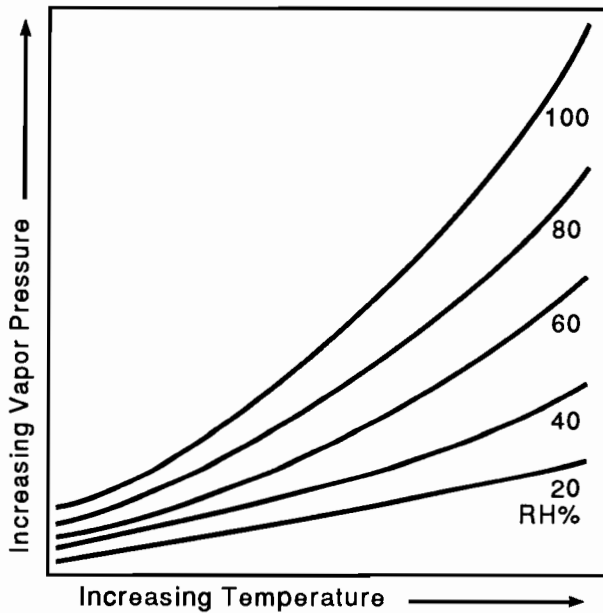


Figure 6-4. The effect of temperature and relative humidity (RH) on water vapor pressure. Adapted from Lowry (1969); used by permission of Academic Press.

matic conditions, this pattern will vary from year to year, but the general shape of the curve remains the same. There is a notable exception, however. For some higher-elevation sites in the region, seedlings may experience winter desiccation when there is little or no snow and when soils are either frozen or very cold and seedlings are exposed to dry, upslope winds. With little or no water movement from the roots, moisture stress increases as tops lose water.

The diurnal pattern of plant moisture stress is similar to the annual pattern (Figure 6-5B). For example, during mid-summer in the early morning as light increases and temperature rises, stomata open and transpiration begins. As this process intensifies, moisture stress increases through the afternoon and then decreases again as atmospheric evaporative demand declines or stomata close when guard cells lose turgor pressure in response to increased moisture stress. In the region, the moisture stress threshold that causes stomatal closure usually reflects the combined effect of low available soil water and high evaporative demand. This example is, of course, a generalization; the pattern of diurnal moisture stress is affected by heredity and the many different components of the soil-plant-atmosphere continuum. The pattern of diurnal moisture

Table 6-2. Factors affecting the internal water status of seedlings.

External	Plant
Soil	Leaf
Available water <sup>1</sup>	Dimensions (area, size, shape)
Temperature	Orientation
Physiographic	Temperature
Elevation	Stomata
Aspect	Root absorptive area
Slope steepness	
Atmospheric	
Precipitation	
Air temperature	
Relative humidity	
Water vapor pressure of the air	
Wind	
Light	

<sup>1</sup> Available soil water is affected by soil texture, organic matter, macro- and micropore space, soil depth, rock fragments, soil structure, and evapotranspirational demand.

stress will also change with the seasons as the environmental factors that control it change (Hinckley et al. 1978).

Although water movement in seedlings is driven by the vapor pressure deficit at the leaf-air interface, numerous other factors influence the internal water status of the seedling (Table 6-2). Clearly, the combined influence of many factors in the soil, plant, and atmosphere, acting in concert, affect seedling water.

## Mineral Nutrition

Thirteen minerals are considered essential to the growth of woody plants (Kramer and Kozlowski 1979). Six of them—nitrogen, potassium, phosphorus, calcium, magnesium, and sulfur—are macronutrients because they are required in larger amounts than are the others. The micronutrients are iron, boron, manganese, zinc, copper, molybdenum, and chlorine. Carbon, hydrogen, and oxygen are not considered mineral nutrients, but are obviously essential and in fact are found in seedlings in much greater quantities than are any of the other elements. The amounts of each nutrient required by seedlings vary among and within species, by time of year and by the

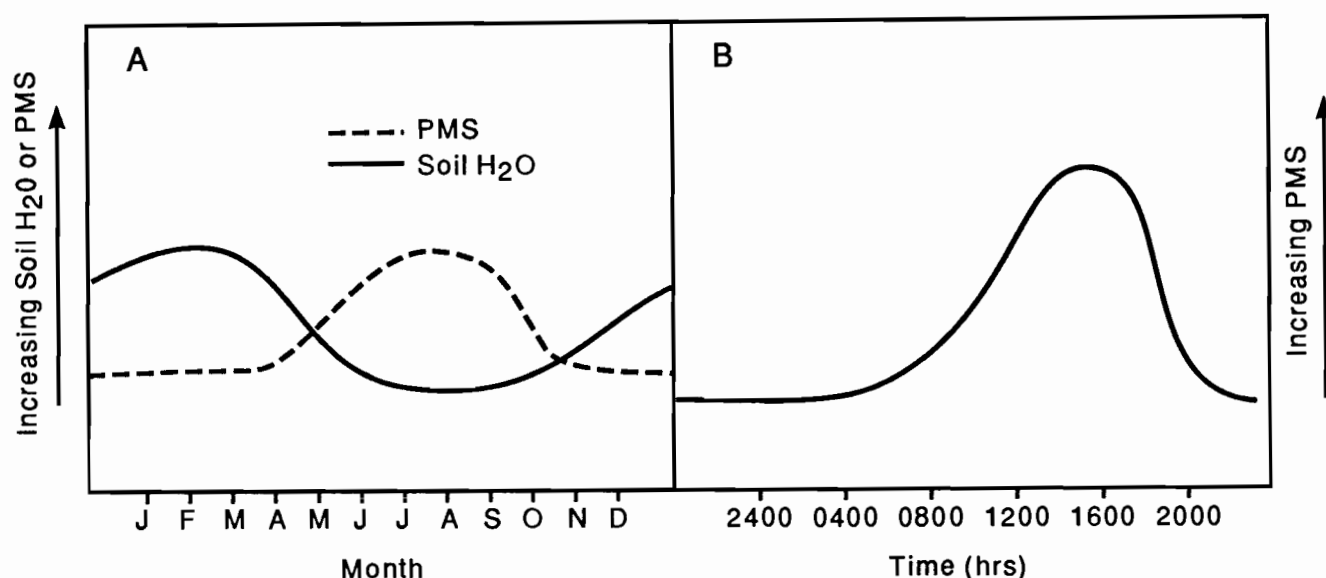


Figure 6-5. (A) The generalized annual pattern of soil moisture depletion and recharge and corresponding changes in plant moisture stress (PMS). (B) Diurnal pattern of PMS during mid-summer.

operational environment in which the seedlings are grown.

Both macro- and micronutrients are involved in the synthesis of a wide array of organic and inorganic compounds necessary to seedling physiology. For example, nitrogen is an essential element in amino acids, the building blocks of protein, whereas phosphorus is critical to the formation of energy-transfer compounds such as adenosine triphosphate (ATP). Almost all essential nutrients play important roles in enzyme synthesis.

When nursery-grown seedlings arrive at the planting site, their nutritional status should be very good. Bareroot and container nursery facilities provide an environment where the nursery manager can carefully control and monitor seedling nutrition and take quick corrective action if problems develop. This ability is built on a solid information base, much of which is discussed by van den Driessche (1984) and Youngberg (1984).

Naturally regenerated seedlings must cope with the nutrient regime of the site, which is never opti-

mal. Usually nitrogen is the nutrient most limiting to seedling growth in the region. However, natural seedlings are genetically well adapted to site conditions and quickly develop mycorrhizae (Chapters 3, 5, and 13) that increase nutrient uptake.

Nutrients move along an energy gradient from higher to lower concentrations. Nutrient uptake is largely the result of seedling transpiration, which causes the movement of water containing dissolved nutrients through the soil-plant-atmosphere continuum. Nutrients actually move through mass flow or diffusion and are absorbed by the root in ionized form as either cations (e.g.,  $\text{Ca}^{++}$ ,  $\text{K}^+$ ,  $\text{NH}_4^+$ ) or anions (e.g.,  $\text{SO}_4^-$ ,  $\text{H}_2\text{PO}_4^-$ ,  $\text{NO}_3^-$ ). Seedling roots or mycorrhizae can seek out sites where nutrient ions are held by soil organic matter or clay minerals. This may be particularly important for the uptake of relatively immobile ions such as those of phosphorus (Newman and Andrews 1973).

The absorption of nutrients is affected by the physiological condition or health of the seedling and by numerous influences in the soil, such as

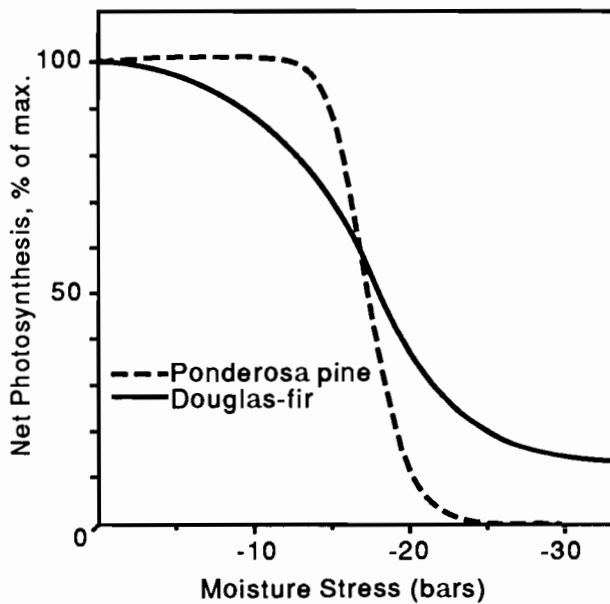
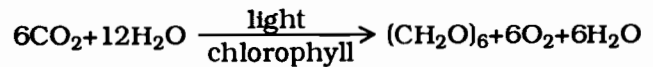


Figure 6-6. The effect of increasing moisture stress on net photosynthesis of Douglas-fir and ponderosa pine seedlings. Adapted from Cleary (1971).

the amount of water and heat, texture and clay mineralogy, cation exchange capacity (CEC), the amounts and types of organic materials, fauna, flora, and mycorrhizae. These interact and vary in importance from one site to another.

## Photosynthesis

Photosynthesis is the major photochemical energy transformation of ecosystems (Jensen and Salisbury 1972). Essentially, it is the conversion of light energy to chemical energy in the presence of chlorophyll, a process that involves the production of carbohydrates, oxygen, and water from carbon dioxide and water. It is fundamentally the fixation of atmospheric carbon which is taken into the plant as carbon dioxide through the leaf stomata. This inward diffusion of carbon dioxide is driven by the same laws as the outward diffusion of water vapor.



Operational environmental factors that influence the rate and duration of photosynthesis are water, carbon dioxide, light (intensity, duration, quality), heat, macro- and micronutrients, and air pollutants.

The effects of increasing moisture stress on photosynthesis in forest trees have been widely studied, and it is a well-established fact that at some point increasing levels of moisture stress cause a decline in net photosynthesis. This obviously varies by species and other conditions, as previously noted. In work often cited and of particular relevance to the region, Cleary (1971) showed the effect of increasing moisture stress on the net photosynthesis of Douglas-fir and ponderosa pine

Table 6-3. The four phases of dormancy in Douglas-fir. From Lavender (1984); used by permission of Martinus Nijhoff/Dr W. Junk Publishers.

Phase	Period of year	Physiology	Environment
Initiation of dormancy	July-late September	Cessation of growth, increased desiccation, lignification of tissue	Mild to hot days, shortening photoperiod, mild to strong moisture stress
Deep dormancy	Late September-early December	Accumulation of growth inhibitors, increased cold resistance	Mild temperatures, shortening days
Dormancy lifting	Early December-late February	Breakdown of inhibitors, virtual cessation of metabolic activity	Short days, low temperatures
Postdormancy	Late February-bud break	Accumulation of growth promoters, gradual conversion of carbohydrate substrates	Lengthening days, mild temperatures, low moisture stress



seedlings (Figure 6-6). The decline in net photosynthesis, as a percent of maximum photosynthesis, starts at a greater level of moisture stress for ponderosa pine than for Douglas-fir but drops off dramatically with only a relatively small increase of stress. Regardless of species, the important relationship to understand is that at a certain threshold of moisture stress, leaf stomata will start to close to conserve moisture. As this progresses, seedling water loss declines, but as a consequence of stomatal closure,  $\text{CO}_2$  absorption into the leaf also decreases. This results in less photosynthesis, or less fixation of atmospheric carbon. Interestingly, Teskey and Hinckley (1986) summarize research from other studies which indicates that photosynthesis may be inhibited in the leaf mesophyll at lower moisture stress levels (less negative) than those required for stomatal closure.

### *Respiration*

Respiration is the process of energy production in the plant through the metabolism of carbohydrates and other organic compounds. The resulting energy drives other important processes, such as assimilation or conversion of food materials (principally carbohydrates) into such things as plant tissue. Whereas photosynthesis produces food materials, the process of respiration consumes them. A simplification of this relationship is "input" versus "output." When photosynthesis equals respiration little growth occurs, but when photosynthesis exceeds respiration (net photosynthesis) then food materials are available for conversion into new plant tissue. However, if respiration exceeds photosynthesis for a prolonged period, overall seedling health will decline, eventually resulting in death. A classic example involves seedlings stored in bags. As the temperature inside the bags rises, respiration increases, carbohydrate reserves are depleted, and seedling physiological vigor or general health declines. In general, the degree to which respiration is less than photosynthesis will have a profound effect on growth.

### *Dormancy and Cold Hardiness*

Dormancy is "a general term of all instances in which a tissue predisposed to elongate (or grow in

some other manner) does not do so" (Lavender 1984, after Doorenbos 1953). An annual period of rest is required by seedlings in order for normal growth to be resumed in the spring. This rest requirement is confined to apical meristems (Lavender 1990). The dormancy cycle has four phases, each of which occurs at a different time of the year (Lavender 1984) (Table 6-3). Dormancy requirements may vary among species, but for species found in the region the physiological characteristics unique to each phase of dormancy and the types of environmental conditions that produce them are the same. A major difference, however, is the time of year the different phases occur. For example, interior valley Douglas-fir initiates dormancy earlier because of greater moisture stress than does Douglas-fir grown at mid-elevation.

Dormancy is promoted by increasing moisture stress, decreasing photoperiod, and cooler temperatures. Loss of dormancy is induced by opposite trends during the winter and early spring. An important precondition for dormancy loss and the normal resumption of growth is that seedlings must fulfill their "chilling" requirement, or experience a period of low ( $<5^\circ\text{C}$ ) temperatures. The amount of time required varies within and among species. The exact biochemical mechanisms that induce and release seedlings from dormancy are poorly understood, but changes in plant growth regulators in response to changes in the operational environment are thought to play a major role.

Cold hardiness (sometimes called frost hardiness) is the ability of a seedling to withstand subfreezing temperatures without suffering irreversible damage (Lavender 1984). The degree of cold hardiness varies among and perhaps within species. However, relatively little is known about the physiology of cold hardiness and its development. Seedlings enter the dormancy cycle before they start to develop cold hardiness. In general the development of both conditions is parallel, although there is only slight evidence to indicate a physiological relationship. Once deep dormancy is achieved, apical growth cannot be induced by favorable conditions, but cold hardiness can be lost by a brief period of thawing. Also, low temperatures that induce cold hardiness do not necessarily facilitate dormancy (Weiser 1970).

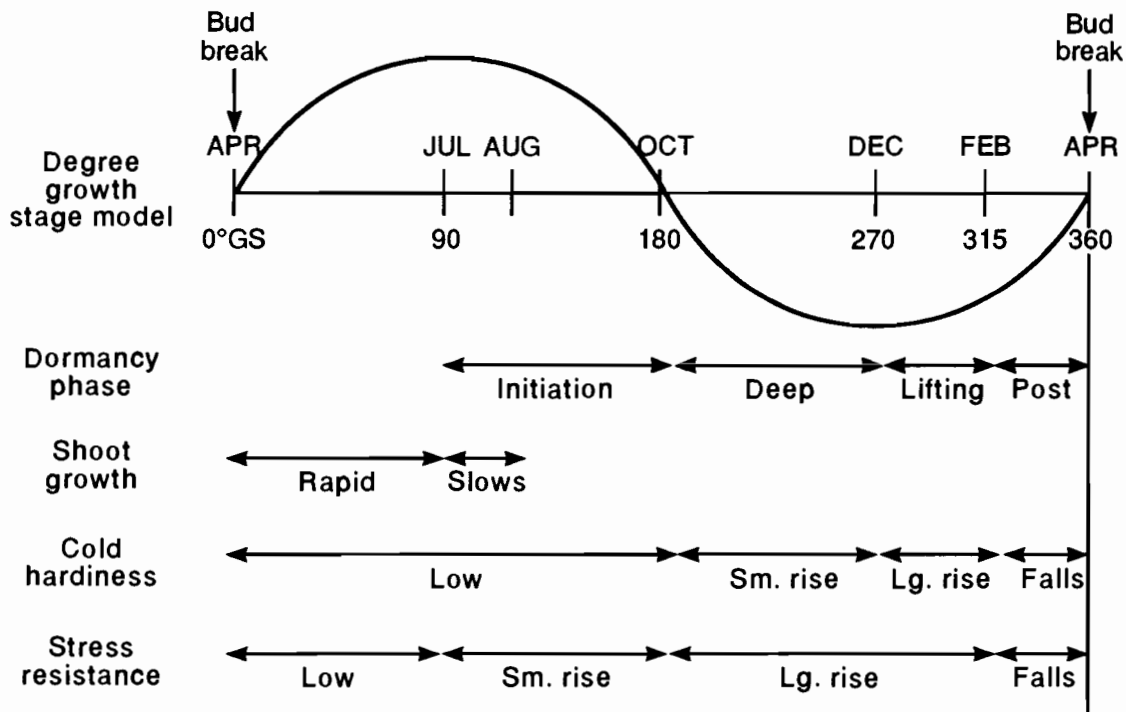


Figure 6-7. A generalized model of the relationship between growth, dormancy, cold hardiness, and stress resistance on an annual basis. Adapted from Burr (1990); based on the degree growth stage model by Fuchigami et al. (1982) and Fuchigami and Nee (1987).

Fuchigami et al. (1982) developed the degree growth stage model to explain the annual relationship between growth and bud dormancy. A sine wave function from 0 to 360° was used because this pattern more accurately reflects the nonlinear character of physiological processes and conditions over time. Using the model, Burr (1990) showed its relationship to other seedling attributes. We have modified Burr's original figure to show how the degree growth stage model relates to the four phases of dormancy (Lavender 1984) and to reflect regional patterns (Figure 6-7). As photoperiod lengthens and temperatures rise, growth increases. This is a period when seedling stress resistance is at a minimum. However, by mid-summer, moisture stress has increased to the point where budset is induced and dormancy ini-

tiation begins. As the season progresses, photoperiod decreases and temperatures become cooler, causing the seedling to enter deep dormancy and assume a modest level of cold hardiness. Usually by December, seedlings are well into deep dormancy, have adequate cold hardiness, and are relatively resistant to stress. In February, chilling requirements have been met, dormancy lifting is well underway, and cold hardiness is at its peak. As spring approaches, moderating temperatures and ever-increasing photoperiod are associated with postdormancy and declines in cold hardiness and stress resistance.

It is important to understand that this is a simplification. Spatial and temporal variations occur across the landscape as operational environments change. For example, apical growth will be initi-

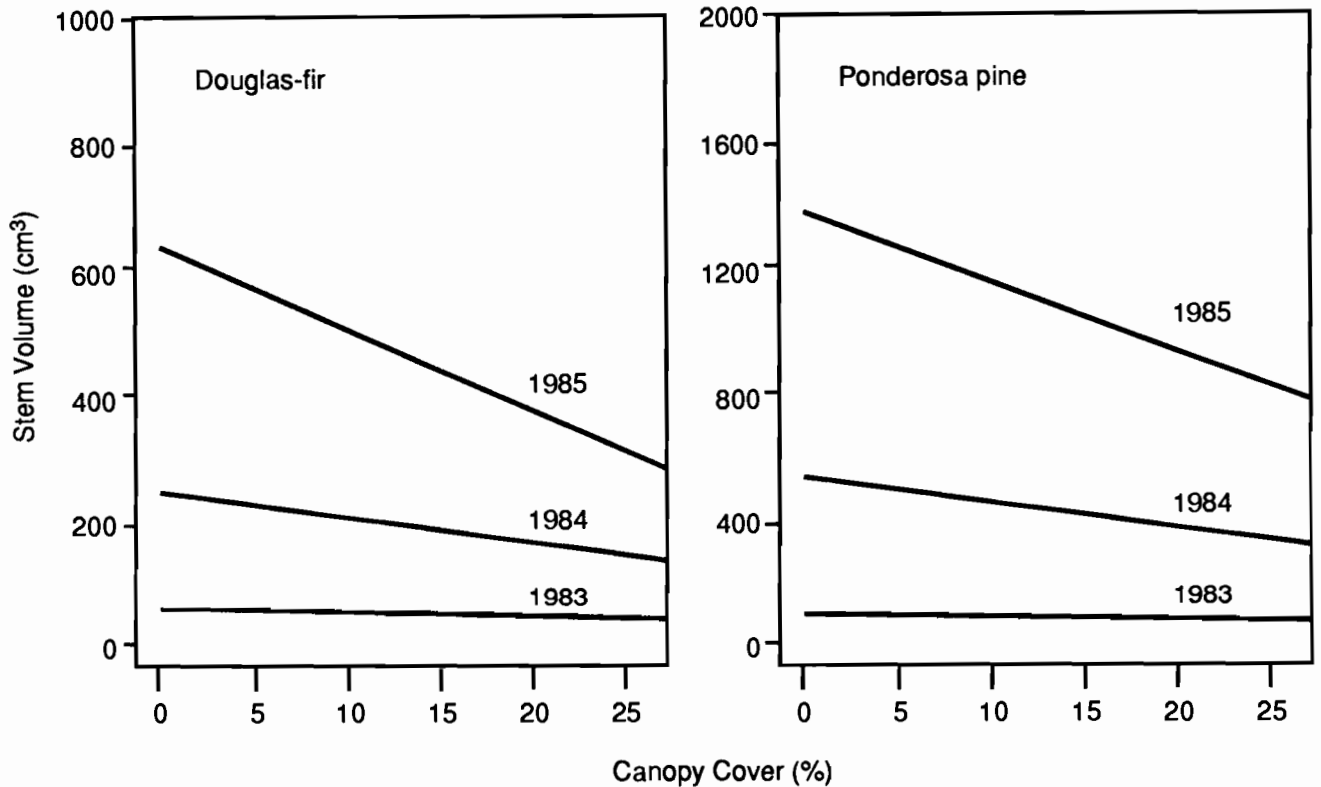


Figure 6-8. The relationship between Douglas-fir and ponderosa pine stem volume and percent cover of white-leaf manzanita over 3 years. Increasing steepness of regression lines from 1983 to 1985 reflects the increasing competitive effect of whiteleaf manzanita on conifer seedling growth. Adapted from White and Newton (1989); used by permission of the National Research Council of Canada.

ed earlier in spring on a south-facing, low-elevation site than on a north-facing, mid-elevation site. Awareness of these differences is important because they have practical implications (e.g., sites where growth begins earliest should be planted first).

### *An Integrated System*

The seedling is a complex, integrated system of physical and chemical processes that are controlled by heredity and operational factors in the surrounding environment. Each is linked to the other, and changes in the status of one affect the entire system.

For example, unusually high seedling moisture stress because of competition causes premature stomatal closure, decreased photosynthesis, decreased nutrient uptake, and most likely increased respiration. This will result in poor

growth during the current year and probably in the next year as well, because buds will be small and relatively few in number. Foresters should understand that these physiological processes do not function independently and that silvicultural activities that either degrade or enhance a particular process affect the entire seedling and its field performance.

## **RESPONSE TO ENVIRONMENTAL STRESS**

Seedlings experience stress when factors in the operational environment become deleterious to seedling general health. Levitt (1980) defines stress as "any environmental factor capable of inducing a potentially injurious strain in living organisms." He goes on to suggest that organisms have an elas-

tic strain capability from which they can recover as the operational factor inducing the strain moderates. However, when the limit to the elastic strain capability ("yield point") is reached, the damage caused may be permanent and irreversible. To quote Pallardy (1986), from a practical sense our intent is "to work toward maintaining stands under minimal elastic strain." This idea certainly applies to reforestation.

Clearly, any of the operational factors important to plant distribution can affect seedling field performance and reforestation success. Significant stress factors in southwestern Oregon and northern California are moisture, temperature, light, nutritional, and mechanical. How seedlings respond to these stresses depends upon their physiological vigor, "adaptational stage" (i.e., dormant, cold hardy), the magnitude and duration of the stress, and genetic influences.

### Moisture Stress

Moisture stress is the most common and important cause of reforestation failure in the region. When available soil water decreases, physiological functions important to growth are affected. For example, as moisture stress increases or is prolonged, cell division is inhibited (Kramer 1969), leaf size is diminished (Kozlowski 1971), photosynthesis decreases (Cleary 1971), root development is slowed (Zahner 1968), and fewer bud primordia form for the next year's growth. If moisture deficits become severe enough, seedlings die. However, the first effects are expressed in reduced growth, particularly in diameter, which is more sensitive to moisture stress than is height growth.

The negative impact of increasing moisture stress on seedling survival and growth is well documented (e.g., Cleary 1971, Conard and Radosevich 1982, Lanini and Radosevich 1986, Shainsky and Radosevich 1986, Flint and Childs 1987, White 1987, Tesch and Hobbs 1989). The effect over time of increasing competition for moisture is particularly well illustrated by work conducted in Jackson County, Oregon (White 1987, White and Newton 1989). On sites where soil moisture was particularly limiting, the competitive effect of whiteleaf manzanita on Douglas-fir and ponderosa pine seedlings increased with

time (Figure 6-8). On a nearby site, but 2,500 ft higher in elevation, Tesch and Hobbs (1989) found that increasing cover of canyon live oak and greenleaf manzanita caused increased moisture stress and decreased growth of Douglas-fir seedlings. The study by White and Newton (1989) showed that when herbaceous vegetation was also present with whiteleaf manzanita, Douglas-fir and ponderosa pine mean stem volumes were reduced on average from 311 to 134 cm<sup>3</sup> (57 percent) and from 668 to 438 cm<sup>3</sup> (34 percent), respectively. Interestingly, the herbaceous vegetation also substantially reduced whiteleaf manzanita growth.

Diurnally, stress levels start to increase from a predawn minimum soon after sunrise. As air and foliage temperatures increase, light activates stomata, and transpiration increases, water stress levels increase rapidly to a maximum usually reached in early to mid-afternoon depending upon site factors (e.g., aspect, shading from adjacent vegetation). As the sun angle declines and air temperatures moderate, transpirational flow decreases with an accompanying decrease in water stress.

Both the diurnal and annual fluctuations in seedling stress are predictable, as is the effect on field performance. Clearly, the single most important action that can be taken to increase available soil water to seedlings is to minimize competition from surrounding vegetation.

As previously discussed, moisture stress may also occur in the winter and early spring if seedlings are exposed to warm daytime air temperatures or to dry winds while soils are cold. Soils do not have to be frozen for winter desiccation to occur, because at temperatures just above freezing, soil water movement and root absorption activity are relatively slow. As foliage and stems warm and lose moisture, a serious moisture deficit can develop in seedlings when roots are unable to supply adequate moisture. We should note, however, that high-elevation reforestation failures due to cold soil may not always be the result of winter desiccation. Lopushinsky and Kaufmann (1984) suggest that when seedlings are planted in cold soils shortly after snowmelt, low soil temperature prevents adequate new root development before shoot growth begins. Once shoot growth has started, root growth stops.

Consequently, as the summer progresses, seedlings may experience growth-reducing or lethal moisture deficits because of inadequate root development.

## *Temperature Stress*

Temperature stress is the result of either too little or too much heat. Mortality due to high temperatures is unusual, but it does occasionally happen on some sites in southwestern Oregon and northern California. It is difficult to predict when and where this will happen, but site factors such as percent slope, aspect exposure, soil heat capacity, surface albedo, and shading from adjacent vegetation all play a part (Chapter 16). The single most important factor, however, is soil surface temperature. Heat damage occurs as lesions on the stem at the soil surface/seedling interface. Stems usually are damaged when soil surface temperatures reach anywhere from 54 to 66°C (Helgerson 1990), depending on species, seedling morphology, and duration of the exposure. Surprisingly, leaf temperatures have been found to exceed air temperature by only 3°C (Vanderwaal and Holbo 1984). As the soil immediately surrounding the seedling reaches and maintains a critical temperature for an adequate period, proteins denature (Levitt 1980), destroying meristematic and conducting tissues. Although soil surface temperatures may reach lethal levels during mid-summer, the duration is usually not sufficient to cause serious damage.

High temperatures can also indirectly affect seedling field performance by decreasing photosynthesis while respiration rates stay high, depleting carbohydrate reserves (Kramer and Kozlowski 1979). As previously discussed in the chapter, increasing temperatures also increase the vapor pressure deficit and seedling water loss. More-detailed discussions of heat damage can be found in Levitt (1980) and Helgerson (1990).

Low temperatures present a serious problem on many sites above 4,000 ft, such as in areas of eastern Jackson County, Oregon. Except as previously noted, low-temperature damage usually takes the form of frost damage either in late summer before seedlings have reached an adequate level of cold hardiness or in spring after cold hardiness has been lost and growth has resumed. When tem-

peratures are unseasonably cold, ice crystals form in the intercellular spaces. As crystals form, water is hydrated from the protoplasm (Glerum 1976) and is not rehydrated when temperatures moderate. Stathers and Spittlehouse (1990) reported that actively growing seedlings can be killed by a low temperature of only -3°C. Susceptibility to frost damage largely depends on species, but Melton (1989) found that seedlings growing in areas with good control of competing vegetation suffered less frost damage than did those grown in areas without vegetation control. This suggests that conservation of available soil moisture may help mitigate mild frosts.

Minimizing radiative heat loss at night by using shelterwoods or an uneven-aged stand structure in areas historically prone to frost damage (frost pockets) can also decrease damage. Mitigating treatments are discussed in Chapters 1, 8, and 16.

Under some conditions, low temperatures can also cause frost heaving, which usually occurs in three distinct phases (Heidmann and Thorud 1976). First, as the soil freezes, it grips the seedling stem. Next, ice lenses form in the soil and force the seedling and surrounding soil upward. Finally, the soil thaws and drops back into place, leaving the upper part of the seedling root system exposed to desiccation. On some sites, mortality can be serious. In a study of ponderosa pine seedlings, over half were killed from desiccation as a result of frost heaving (Larson 1961). However, large seedlings are less susceptible to frost heaving (Heidmann 1976). Additional information on frost heaving is offered by Cochran (1975).

Potential reforestation problems associated with temperature extremes can be largely avoided through species selection and the choice of appropriate silvicultural practices that ameliorate the operational environment (Chapters 8 and 16).

## *Light-induced Stress*

As an operational factor, light has three components: quality, intensity, and duration (photoperiod length). All influence seedling physiology and growth (Brown 1971, Daniel et al. 1979). Light quality is rarely a limiting factor except under very dense canopies, and the duration of light exposure primarily exerts its influence by contributing to

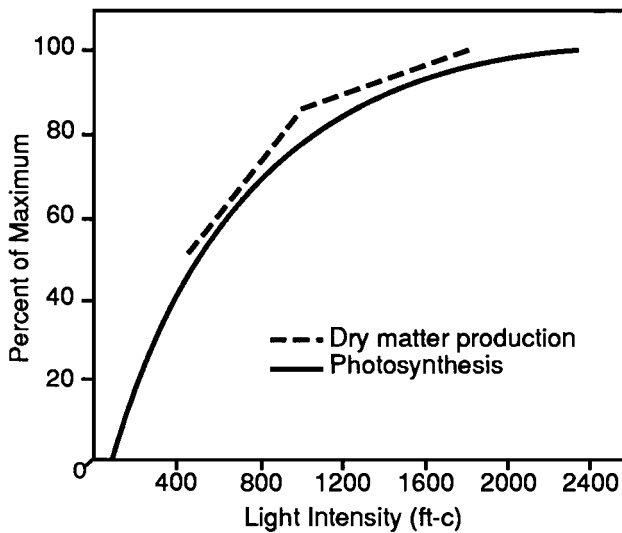


Figure 6-9. The effect of light intensity (foot-candles) on dry-matter production and rate of net photosynthesis of Douglas-fir seedlings at 18°C expressed as percent of maximum observed. From Brix (1967); used by permission of the National Research Council of Canada.

dormancy induction, development of cold hardiness, and resumption of growth in spring. From a reforestation perspective, light intensity is by far the most important characteristic affecting seedling field performance. The effect of light intensity is species-specific in that different species have different shade tolerance levels. Most species regenerated in southwestern Oregon and northern California can tolerate full sun provided other factors, such as moisture or temperature, are not limiting. However, for young seedlings (less than 1 year old), light saturation may occur at intensities less than that of full sunlight.

When seedlings that are not shade tolerant are exposed to light intensities below optimum levels, photosynthesis is reduced (Figure 6-9). This results in reduced root growth, decreased leaf area and diameter growth, and increased height growth. Overall, seedling physiological vigor declines, causing the seedlings to become more susceptible to other types of stress.

When seedlings are suppressed and overtopped by surrounding vegetation, the foliage gradually adjusts to lower light intensities. Seedlings that have existed under such conditions for several years and then are suddenly exposed to full sun-

light as the result of release may experience "thinning shock." These seedlings may develop chlorotic foliage and have reduced growth and, in some cases, needle drop. This is generally a temporary condition, however, and the effects can be moderated by the use of release treatments that produce a more gradual increase of light intensity. For example, if the release is accomplished with herbicides, dead plants can provide some shade for several years after foliage drop.

### Nutritional Stress

Nutritional stress refers to deficiencies or excessive (toxic) levels of macro- or micronutrients in the forest environment that adversely affect seedling growth. In general, nutrient stress affects all physiological processes and conditions, but in particular it results in reduced photosynthesis. Lack of nitrogen is often responsible for reduced seedling growth. Nitrogen is critical to photosynthesis because it is an essential part of the chlorophyll molecule and is also important in the formation of amino and nucleic acids and proteins, as well as many other compounds (Kramer and Kozlowski 1979).

Nutrient-caused stress is difficult to identify in the field and is usually first reflected in reduced growth followed by foliage discoloration. However, nutrient-related stress disorders are unusual in the region unless planting stock is genetically poorly matched to the planting site or the nutrient pool has been degraded by severe disturbance (e.g., excessive displacement of nutrient-rich topsoil or intensive fires that consume all surface organic matter). Aside from severely disturbed sites, areas dominated by ultrabasic parent materials (peridotites and serpentines) have relatively low productivity. Such soils are high in magnesium, chromium, and nickel, but low in molybdenum and calcium (Walker 1954), and only those species adapted to this unusual nutrient regime do well. Among coniferous species, only Jeffrey pine is relatively well adapted to these sites.

### Mechanical Stress

Mechanical stress usually entails the application of a force to the seedling that results in readily apparent physical damage such as breakage,



uprooting, debarking, or defoliation. Mechanical stress can come from either biotic or abiotic sources. Biotic sources include animal and insect pests that damage various parts of the plant through consumption. Abiotic sources include toppling and sometimes uprooting from the downslope movement of rock fragments, logging debris, and snow. In such cases, conducting tissues may be damaged by stem abrasions, bud damage, or the burial of foliage by moving material. Seedlings can also be damaged by ice storms and heavy snowfall, but this is unusual. Chapter 16 provides information on ways to prevent or minimize damage from mechanical stress.

### *Stress from Atmospheric and Soil Gases*

Except for atmospheric pollutants in topographic depressions with large populations, atmospheric gases are not a significant stress factor in reforestation operations. On the other hand, soil oxygen deficiency may occur in areas subjected to periodic flooding. In such circumstances, physiological functions of the roots are impaired. The most important of these is water absorption. Although the surrounding soil may be saturated, seedlings not adapted to flooding conditions have reduced growth, and in many cases die, because roots are unable to absorb adequate water due to an oxygen deficiency.

### *Stress Factor Interaction*

Although a single operational factor can be identified as the primary one limiting reforestation success on most sites (Hobbs 1984), other factors often contribute to problems in seedling establishment. In the region these frequently involve various combinations of moisture, heat, light, and mechanically induced stress.

Consider the case in which a south-facing unit has been harvested and planted without adequate site preparation. During the first growing season, newly planted seedlings experience transplant shock as they adjust to site conditions. Consequently, little root and shoot growth occurs, whereas the well-established residual vegetation responds vigorously to greater light intensity, thus

increasing in size and water use. Conifer seedlings, as yet unable to compete successfully, experience increased moisture stress, which in turn causes a decrease in net photosynthesis. This sets the stage for poor seedling growth in the coming year. Depending upon the competing species involved, conifer seedlings become more shaded by adjacent vegetation with each succeeding year. Subsequently, there is not only increasing competition for moisture, but competition for light as well, further reducing photosynthesis. This annual cycle of intensifying competition for moisture and light places the seedling at greater risk as its competitive ability erodes. This particular combination of stress factors is one of the major forms of factor interaction that slows seedling growth and significantly delays site domination by the desired species.

It is important to recognize that stress, regardless of its type, generally affects whole-seedling physiology because the seedling is a system in which all physical and chemical processes are interdependent. One part of the system cannot change substantially without affecting the others. These changes are almost always reflected in field performance.

## *SEEDLING GROWTH*

### *Overview*

The growth component of seedling field performance is often overlooked when new plantations are evaluated for reforestation success, which is unfortunate because it can lead to a false sense of security that may be short-lived. Rapid seedling growth during the first few years following planting is essential if site domination by the desired species is to be achieved in a specified period. This is particularly crucial if followup treatments to control competing vegetation during the first 2 or 3 years after planting cannot be conducted. Although competing vegetation may be controlled during site preparation, recovery can be rapid depending upon species, degree of initial control, and site conditions. Conifer seedlings that do not achieve significant growth increases during the first few years will likely suffer increasing water and light stress from the encroachment of com-

peting vegetation. From the stand management perspective, a clear objective is to obtain closure of the conifer canopy as quickly as possible.

Seedling growth is a complex process influenced by heredity and a wide array of physiological processes and conditions (e.g., cold hardiness, dormancy) that interact with the changing operational environment. For example, we have already seen how changes in the seedling's internal water balance and different levels of photosynthesis affect growth. Another dimension to seedling growth is the role of plant hormones or plant growth regulators such as gibberellins, auxins, cytokinins, ethylene, and abscisic acid. The biochemistry of these compounds is complex, but it has been established that patterns of increasing and decreasing levels of these hormones contribute to the regulation of seedling growth.

### Transplant Stress

Typically during the first year following planting, seedling growth is slow. This is often attributed to transplant stress, which is also referred to as transplant shock or planting check. Until recently, the term has been loosely defined as a period following planting when growth is minimal and the seedling is susceptible to permanent injury from various stresses while it adjusts to its new environment and establishes a solid soil-root contact. Rietveld (1989) summarized existing knowledge on transplant stress and offered the following defini-

tion: "Transplanting stress is a temporary condition of distress from injuries, depletion, and impaired functions; a process of recovery; and a period of adaptation to a new environment." The duration and extent of transplant stress can vary tremendously depending upon both seedling and site conditions.

Very little research has been done on ways to lessen transplant stress. A logical approach is to take appropriate steps to minimize physical damage and degradation of seedling physiological vigor up to and through the planting process. Seedling recovery from transplant stress may be further delayed by additional stress, such as that associated with the rapid encroachment of competing vegetation, although the relationship is not clear. The primary goal should be to place the seedling into conditions where its full growth potential can be realized as quickly as possible.

Rietveld (1989) suggested that for seedlings to recover from transplant stress they must: "(1) recover from injuries and stresses that result from lifting and handling; (2) resist desiccation stresses and grow new roots to avoid plant moisture stress; (3) continue maintenance and growth respiration; and (4) adapt to a more hostile environment." To meet these requirements, seedlings must be in good physiological condition before transplanting, lifted and stored appropriately, carefully handled and protected from physical damage and desiccation, and properly planted in an environment conducive to rapid root and shoot development.

### Growth Patterns

The duration, magnitude, and timing of seedling growth vary within and among species and by site conditions (i.e., the operational environment). However, all species have characteristic annual patterns of growth. In Douglas-fir and ponderosa pine, root growth starts in late winter and continues into spring, ceasing roughly at bud break (Figure 6-10). Stem and foliage development continues into mid-summer and then stops with bud set as moisture stress increases and photoperiod shortens. Root growth resumes in fall as soils are remoistened and temperatures moderate. This second period of root growth is of shorter duration and of less magnitude than that in spring. The alternating pattern of root, shoot, and root growth

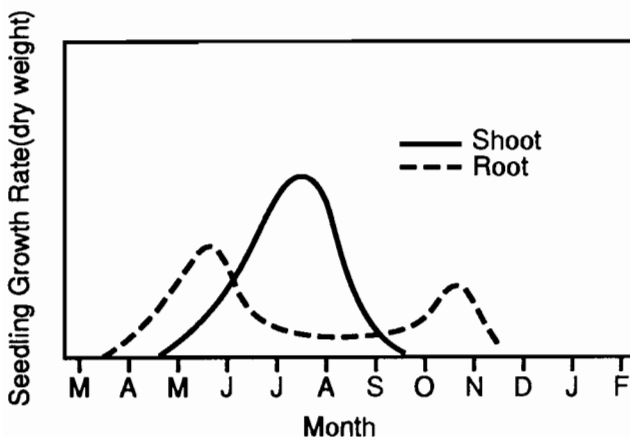


Figure 6-10. Generalized annual cycle of root and shoot growth of Douglas-fir and ponderosa pine seedlings. From Cleary et al. (1978).



reflects seedling sensitivity to changing conditions in the operational environment and the selective allocation of photosynthate (carbohydrates) to the assimilation process in roots and shoots.

Following planting, the growth of roots and shoots when plotted over 4 or 5 years should exhibit a pattern of rapidly increasing (exponential) growth. During the first year or two, shoot growth is relatively small as the seedling overcomes transplant stress, but by the third year growth should be significantly greater with even more substantial increases through the fourth and fifth years (Figure 6-11). Similar but less dramatic growth patterns have also been identified in roots (Tesch and Hobbs 1989). High stress levels, such as water stress induced by competing vegetation, decrease the slope of the growth curve for both roots and shoots. If stress is severe enough, these growth curves can even have negligible slope. As already pointed out, other operational factors can adversely affect the extent of seedling growth. For example, low light intensities promote shoot elongation at the expense of foliage, diameter, and root growth in moderately shade-tolerant and -intolerant species.

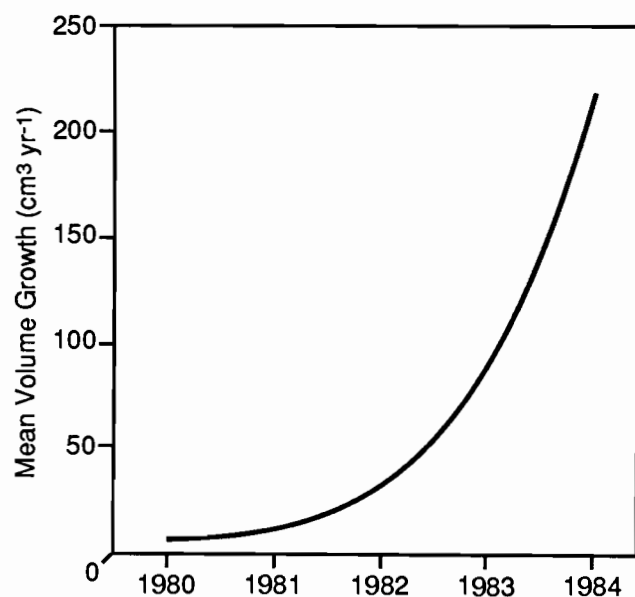


Figure 6-11. Exponential growth of Douglas-fir seedling stems with minimum competition. Developed from data from Hobbs et al. (1989).

## Seedling Quality

High seedling quality is a prerequisite to reforestation success. If seedlings are of poor quality or low physiological vigor, they suffer more severe transplant stress, produce less growth, and are less able to withstand various types of stress without sustaining permanent injury.

There are various definitions of seedling quality, but generally all refer to the seedling's overall health or physiological condition. Hobbs (1982) defines high seedling quality as the "ability to initiate and maintain growth under favorable circumstances, and adjust to changing environmental conditions." Duryea (1985b) defines high-quality seedlings as "those that meet defined levels of survival and growth on a particular planting site." Seedling quality can be easily degraded, particularly from the time the seedling is lifted from the nursery bed or leaves the greenhouse until it is planted.

Numerous tests have been developed to measure seedling quality (Duryea 1985a). Although some have proven useful, many fail to consistently predict field performance. More recently, Ritchie and Tanaka (1990) summarized the usefulness of root growth potential (RGP) tests as a measure of seedling quality and potential field performance. They point out that although RGP is a reasonably good indicator of stock quality, its usefulness as a predictor of field performance is only fair because it does not account for the effects of planting quality or site conditions. New methods of assessing stock quality, such as variable chlorophyll fluorescence and stress-induced volatile emissions, are also being investigated (Hawkins and Binder 1990). These investigators present the case for using a number of different tests integrated to produce better predictions of field performance.

## SUMMARY

Understanding the term "operational environment" is essential to successfully explaining and predicting seedling response to environmental change. The operational environment consists of materials and forms of energy exchanged between the seedling and its environment that affect the physiological processes and conditions of the

seedling. Key among these are water movement and transpiration, mineral nutrition, photosynthesis, respiration, dormancy, and cold hardiness. If foresters are to prepare and implement appropriate reforestation prescriptions, they must have a general knowledge of how seedlings respond physiologically and phenologically to changes in the operational environment. Physiological processes of the seedling are affected either positively or negatively by such changes. The most common adverse effect is high moisture stress, which in turn influences such critical processes as photosynthesis. Over time these changes manifest themselves in impairments in survival and growth of the seedling. On a site where the operational environment is relatively unconstrained during the growing season, seedlings will typically exhibit exponential growth during the first few years following planting. As factors in the operational environment become limiting—light or water, for example—stress increases and growth declines.

It is important to understand that seedlings placed in an operational environment where stress increases from one year to the next have little chance of meeting management objectives. Although some stresses, such as transplant stress, cannot be avoided, they can be minimized in many cases. Through careful planning, selection of species, utilization of improved seed, and appropriate manipulation of the operational environment, foresters can exert considerable influence over seedling survival and growth. Correctly interpreting what the operational environment will be at the time of planting and during the first few years afterward is critical to establishing a stand. Of equal importance is understanding how the seedling will respond to adverse effects in the operational environment, and how the resulting stresses can be modified.



## LITERATURE CITED

- BRIX, H. 1967. An analysis of dry matter production of Douglas-fir seedlings in relation to temperature and light intensity. *Canadian Journal of Botany* 45:2063-2072.
- BROWN, C.L. 1971. Growth and form. P. 125-167 in M.H. Zimmermann and C.L. Brown, eds. *Trees: Structure and Function*. Springer-Verlag, New York.
- BURR, K.E. 1990. The target seedling concept: bud dormancy and cold-hardiness. P. 79-90 in R. Rose, S.J. Campbell, and T.D. Landis, eds. *Target Seedling Symposium: Proceedings of a Combined Meeting of the Western Forest Nursery Associations*. USDA Forest Service, Rocky Mountain Forest and Range Experiment Station, Ft. Collins, Colorado. General Technical Report RM-200.
- CLEARY, B.D. 1971. The effect of plant moisture stress on the physiology and establishment of planted Douglas-fir and ponderosa pine seedlings. Ph.D. thesis, Oregon State University, Corvallis. 85 p.
- CLEARY, B.D., R.D. GREAVES, and P.W. OWSTON. 1978. Seedlings. P. 63-97 in B.D. Cleary, R.D. Greaves, and R.K. Hermann, eds. *Regenerating Oregon's Forests*. Oregon State University Extension Service, Corvallis.
- COCHRAN, P.H. 1975. Soil temperatures and natural forest regeneration in south-central Oregon. P. 37-52 in B. Bernier and C.H. Winget, eds. *Forest Soils and Forest Land Management, Proceedings, Fourth North American Forest Soils Conference*. Les Presses de l'Université Laval, Quebec.
- CONARD, S.G., and S.R. RADOSEVICH. 1982. Growth response of white fir to decreased shading and root competition by montane chaparral species. *Forest Science* 28:309-320.
- DANIEL, T.W., J.A. HELMS, and F.S. BAKER. 1979. *Principles of Silviculture*. McGraw-Hill, New York. 500 p.
- DOORENBOS, J. 1953. Review of the literature on dormancy in buds of woody plants. *Mededelingen Lanbouwhogeschool Wageningen* 53:1-23.
- DURYEA, M.L., editor. 1985a. *Evaluating Seedling Quality: Principles, Procedures and Predictive Abilities of Major Tests*. Forest Research Laboratory, Oregon State University, Corvallis. 143 p.
- DURYEA, M.L. 1985b. Evaluating seedling quality: importance to reforestation. P. 1-4 in M.L. Duryea, ed. *Evaluating Seedling Quality: Principles, Procedures, and Predictive Abilities of Major Tests*. Forest Research Laboratory, Oregon State University, Corvallis.

- FLINT, L.E., and S.W. CHILDS. 1987. Effect of shading, mulching and vegetation control on Douglas-fir seedling growth and soil water supply. *Forest Ecology and Management* 18:189-203.
- FUCHIGAMI, L.H., and C.C. NEE. 1987. Degree growth stage model and rest-breaking mechanisms in temperate woody perennials. *Horticultural Science* 22:836-845.
- FUCHIGAMI, L.H., C.J. WEISER, K. KOBOYASKI, R. TIMMIS, and L.V. GUSTA. 1982. A degree growth stage (°GS) model and cold acclimation in temperate woody plants. P. 93-115 in P.H. Li and A. Saki, eds. *Plant Cold Hardiness and Freezing Stress*. Academic Press, New York.
- GLERUM, C. 1976. Frost hardiness of forest trees. P. 403-420 in M.G.R. Cannell and F.T. Last, eds. *Tree Physiology and Yield Improvement*. Academic Press, New York.
- HAWKINS, C.D.B., and W.D. BINDER. 1990. State of the art seedling stock quality tests based on seedling physiology. P. 91-121 in R. Rose, S.J. Campbell, and T.D. Landis, eds. *Target Seedling Symposium: Proceedings of a Combined Meeting of the Western Forest Nursery Associations*. USDA Forest Service, Rocky Mountain Forest and Range Experiment Station, Ft. Collins, Colorado. General Technical Report RM-200.
- HEIDMANN, L.J. 1976. Frost heaving of tree seedlings: a literature review of causes and possible controls. USDA Forest Service, Rocky Mountain Forest and Range Experiment Station, Ft. Collins, Colorado. General Technical Report RM-21. 10 p.
- HEIDMANN, L.J., and D.B. THORUD. 1976. Controlling frost heaving of ponderosa pine seedlings in Arizona. USDA Forest Service, Rocky Mountain Forest and Range Experiment Station, Ft. Collins, Colorado. Research Paper RM-172. 10 p.
- HELGERSON, O.T. 1990. Heat damage in tree seedlings and its prevention. *New Forests* 3:333-358.
- HINCKLEY, T.M., J.P. LASSOIE, and S.W. RUNNING. 1978. Temporal and spatial variations in the water status of forest trees. *Forest Science Monograph* 20. 72 p.
- HOBBS, S.D. 1982. Stocktype selection and planting techniques for Douglas-fir on skeletal soils in southwest Oregon. P. 92-96 in S.D. Hobbs and O.T. Helgersson eds. *Reforestation of Skeletal Soils, Proceedings of a Workshop*. Forest Research Laboratory, Oregon State University, Corvallis.
- HOBBS, S.D. 1984. The influence of species and stocktype selection on stand establishment: an ecophysiological perspective. P. 179-224 in M.L. Duryea and G.N. Brown, eds. *Seedling Physiology and Reforestation Success*. Martinus Nijhoff/Dr W. Junk Publishers, Dordrecht/Boston/Lancaster.
- HOBBS, S.D., M.S. CRAWFORD, and B.A. YELCZYN. 1989. Early development of three Douglas-fir stocktypes on a droughty skeletal soil. *Western Journal of Applied Forestry* 4(1):21-24.
- JENSEN, W.A., and F.B. SALISBURY. 1972. *Botany: An Ecological Approach*. Wadsworth Publishing Company, Belmont, California. 748p.
- KOZLOWSKI, T.T. 1971. *Growth and Development of Trees. Volume 1, Seed Germination, Ontogeny, and Shoot Growth*. Academic Press, New York. 443 p.
- KRAMER, P.J. 1969. *Plant and Soil Water Relationships: A Modern Synthesis*. McGraw-Hill, New York. 482 p.
- KRAMER, P.J., and T.T. KOZLOWSKI. 1979. *Physiology of Woody Plants*. Academic Press, Orlando, Florida. 811 p.
- LANINI, W.T., and S.R. RADOSEVICH. 1986. Response of three conifer species to site preparation and shrub control. *Forest Science* 32(1):61-77.
- LARSON, M.M. 1961. Seed size, germination dates, and survival relationships of ponderosa pine in the Southwest. USDA Forest Service, Rocky Mountain Forest and Range Experiment Station, Ft. Collins, Colorado. Research Note 66. 4 p.
- LAVENDER, D.P. 1984. Plant physiology and nursery environment: interactions affecting seedling growth. P. 133-141 in M.L. Duryea and T.D. Landis, eds. *Forest Nursery Manual: Production of Bareroot Seedlings*. Martinus Nijhoff/Dr W. Junk Publishers, The Hague/Boston/Lancaster for Forest Research Laboratory, Oregon State University, Corvallis.
- LAVENDER, D.P. 1990. Physiological principles of regeneration. P. 30-44 in D.P. Lavender, R. Parish, C.M. Johnson, G. Montgomery, A. Vyse,

- R.A. Willis, and D. Winston, eds. Regenerating British Columbia's Forests. University of British Columbia Press, Vancouver.
- LEVITT, J. 1980. Responses of Plants to Environmental Stresses. Volume 1, Chilling, Freezing, and High Temperature Stresses. Academic Press, New York. 497 p.
- LOPUSHINSKY, W., and M.R. KAUFMANN. 1984. Effects of cold soil on water relations and spring growth of Douglas-fir seedlings. *Forest Science* 30(3):628-634.
- LOWRY, W.P. 1969. Weather and life: an introduction to biometeorology. Academic Press, New York, New York. 305 p.
- MASON, H.L., and J.H. LANGENHEIM. 1957. Language analysis and the concept environment. *Ecology* 38:325-340.
- MELTON, L. 1989. Soil surface effects on soil water, soil temperature, and Douglas-fir seedling injury following radiation frost damage events. M.S. thesis, Department of Soil Science, Oregon State University, Corvallis. 83 p.
- NEWMAN, E.I., and R.E. ANDREWS. 1973. Uptake of phosphorous and potassium in relation to root growth and root density. *Plant and Soil* 38:49-69.
- PALLARDY, S.G. 1986. Introductory overview. P. 1-8 in T.C. Hennessey, P.M. Dougherty, S.V. Kossuth, and J.D. Johnson, eds. *Stress Physiology and Forest Productivity*. Martinus Nijhoff Publishers, Dordrecht, The Netherlands.
- PHILIP, J.R. 1966. Plant water relations: some physical aspects. *Annual Review of Plant Physiology* 17:245-268.
- RIETVELD, W.J. 1989. Transplanting stress in bareroot conifer seedlings: its development and progression to establishment. *Northern Journal of Applied Forestry* 6(3):99-107.
- RITCHIE, G.A., and Y. TANAKA. 1990. Root growth potential and the target seedling. P. 37-51 in R. Rose, S.J. Campbell, and T.D. Landis, eds. *Target Seedling Symposium: Proceedings of a Combined Meeting of the Western Forest Nursery Associations*. USDA Forest Service, Rocky Mountain Forest and Range Experiment Station, Ft. Collins, Colorado. General Technical Report RM-200.
- SALISBURY, F.B., and C. ROSS. 1969. *Plant Physiology*. Wadsworth Publishing Company, Belmont, California. 848 p.
- SHAINSKY, L.J., and S.R. RADOSEVICH. 1986. Growth and water relationships of *Pinus ponderosa* seedlings in competitive regimes with *Arctostaphylos patula* seedlings. *Journal of Applied Ecology* 23:957-966.
- SPOMER, G.G. 1973. The concept of "interaction" and "operational environment" in environmental analyses. *Ecology* 54(1):200-204.
- STATHERS, R.J., and D.L. SPITTLEHOUSE. 1990. *Forest Soil Temperature Manual*. British Columbia Ministry of Forests, Victoria. FRDA Report 130. 47 p.
- TESCH, S.D., and S.D. HOBBS. 1989. Impact of shrub sprout competition on Douglas-fir seedling development. *Western Journal of Applied Forestry* 4(3):89-92.
- TESKEY, R.O., and T.M. HINCKLEY. 1986. Moisture: effects of water stress on trees. P. 9-33 in T.C. Hennessey, P.M. Dougherty, S.V. Kossuth, and J.D. Johnson, eds. *Stress Physiology and Forest Productivity*. Martinus Nijhoff Publishers, Dordrecht, The Netherlands. 239 p.
- van den DRIESSCHE, R. 1984. Soil fertility in forest nurseries. P. 63-74 in M.L. Duryea and T.D. Landis, eds. *Forest Nursery Manual: Production of Bareroot Seedlings*. Martinus Nijhoff/Dr W. Junk Publishers, The Hague/Boston/Lancaster for Forest Research Laboratory, Oregon State University, Corvallis.
- VANDERWAAL, J.A., and H.R. HOLBO. 1984. Needle-air temperature differences of Douglas-fir seedlings and relation to microclimate. *Forest Science* 30(3):635-644.
- WALKER, R.B. 1954. The ecology of serpentine soils. Factors affecting plant growth on serpentine soils. *Ecology* 35:259-266.
- WARING, R.H., and B.D. CLEARY. 1967. Plant moisture stress: evaluation by pressure bomb. *Science* 155(3767):1248-1254.
- WEISER, C.J. 1970. Cold resistance and injury in woody plants. *Science* 169:1269-1278.
- WHITE, D.E. 1987. Competitive effects between Douglas-fir or ponderosa pine and whiteleaf manzanita. Ph.D. thesis, Oregon State University, Corvallis. 132 p.
- WHITE, D.E., and M. NEWTON. 1989. Competitive interactions of whiteleaf manzanita, herbs, Douglas-fir, and ponderosa pine in southwest

Oregon. Canadian Journal of Forest Research  
19:232-238.

YOUNGBERG, C.T. 1984. Soil and tissue analysis:  
tools for maintaining soil fertility. P. 75-80 in  
M.L. Duryea and T.D. Landis, eds. Forest  
Nursery Manual: Production of Bareroot  
Seedlings. Martinus Nijhoff/Dr W. Junk  
Publishers, The Hague/Boston/Lancaster for  
Forest Research Laboratory, Oregon State  
University, Corvallis.

ZAHNER, R. 1968. Water deficits and growth of  
trees. P. 191-254 in T.T.Kozlowski, ed. Water  
Deficits and Plant Growth. Volume 2. Academic  
Press, New York.