Root Physiology and Phenology: the Key to Transplanting Success

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Ritchie G.A. 2003. Root physiology and phenology: the key to transplanting success. In: Riley L.E., Dumroese R.K., Landis T.D., technical coordinators. National Proceedings: Forest and Conservation Nursery Associations—2002. Ogden, UT: USDA Forest Service, Rocky Mountain Research Station. Proceedings RMRS-P-28: 98–104. Available at: http://www.fcnanet.org/proceedings/2002/ritchie.pdf

Abstract

This paper presents a summary of several key aspects of root physiology that directly affect success of nursery transplanting. Three transplanting systems are considered: container to container (C:C), container to bareroot (C:BR), and bareroot to bareroot (BR:BR). While differing in detail, each of these systems involves growing a starter plant, transplanting it, and growing it longer in a transplant bed or larger container.

The aspects of root physiology discussed are: root system hydraulic conductance, phenology and growth, stress resistance, root cold hardiness, shoot/root interconnectedness, and root pathogens. The paper discusses each of these aspects of root physiology and explores where they might be affected by, or limiting to, the process of growing transplants.

Key Words

Root hydraulic conductance, root cold hardiness, stress resistance, root pathogens, seedling storage

Introduction

I wish to thank the organizers of this conference for inviting me out of retirement to, once again, probe the mysteries of roots—this time as they relate to the operation of producing nursery transplants. As you know, production of transplants for reforestation is rapidly eclipsing production of 1+0 or 2+0 bareroot stock throughout much of the Pacific Northwest US and western Canada. This is because, in spite of their higher production costs, transplants have consistently delivered better field performance across a wide range of sites. It is in concert with this development that a major portion of this meeting has been devoted to a review of nursery transplanting: its history, equipment and culturing methods, and related aspects of seedling physiology.

Root physiology cannot be considered in a vacuum. As this paper develops it will become clear that roots are intimately connected to, and utterly dependant upon, other parts of the plant. To attempt to address root physiology without these important connections would be misleading and inappropriate.

I will not burden you with an exhaustive review of the literature on root physiology. Rather, I intend to share with you an on-the-ground account of how an understanding of certain key aspects of root function can directly affect the success of your transplant production operations. This summary is drawn largely from my nearly 30 years' experience as a researcher in the field of seedling physiology and seedling production. As such, it reflects both personal biases and interests.

This paper will address the subject of root physiology and phenology as it relates directly to the operation of nursery transplanting. It will not address root system morphology, plant culture, or nursery equipment, as these topics will be reviewed by other speakers.

Transplanting Systems

We will focus on 3 transplanting systems.

Container to Container Systems

In container to container (C:C) systems, seeds for starter plants are sown into small containers and cultured in a greenhouse or cover house where the seedlings are protected from the elements (stage 1). Following a prescribed period of time, often 1

growing season, the starter plants are removed from these small containers and transplanted into larger containers where they are grown on to outplantable size (stage 2). This can be done either indoors or outdoors.

Throughout the C:C process, plants are grown in sterile, artificial growing medium in containers made of Styrofoam, plastic or other materials. Stage 1 is almost always conducted indoors in a greenhouse or coverhouse where light intensity is well below ambient and where the grower can exert precise control over container volume, soil moisture, soil temperature, nutrition and other factors. In stage 2, if conducted outdoors, some loss of control over some factors (for example, soil temperature) is experienced. In the C:C system the seedlings are not intentionally bare rooted. The process of transplanting from small to large containers may or may not be automated.

Container to Bareroot Nursery Bed Systems

In container to bareroot nursery bed (C:BR) systems, starter plants are sown and cultured in the same manner as described above. However, they are then transplanted into an outdoor bareroot nursery where they undergo the second stage of development. Such systems produce stock often referred to as "Plug+1s", or "Mini-plugs".

Again, stage 1 is done in containers in a greenhouse in sterile medium under very tight environmental control. Light intensity is normally considerably lower than ambient. In stage 2, plants are grown in natural soil under natural environmental conditions and natural light intensities. There is still the opportunity to control some conditions such as soil moisture. But many other important factors, such as temperature and light, are not controllable. Sometimes the transition from stage 1 to stage 2 in the C:BR system can cause considerable transplant shock (Haase and Rose 1993) and even photodamage (Demmig-Adams and Adams 1992). In the C:BR system, roots are generally not intentionally bare rooted.

Bareroot to Bareroot System

In the bareroot to bareroot (BR:BR) system, stages 1 and 2 are both carried out in an outdoor bareroot nursery. Seed is sown in spring in intensively prepared seedbeds at relatively high densities, where starter plants are grown for one or more years under intensive culture. In winter or early spring, they are lifted, graded and generally stored in a cooler at slightly above freezing, or a freezer at slightly below freezing. In spring, following storage, they are transplanted back into the nursery at a much lower growing density. Here they are cultured for an additional year or two before being lifted for field planting. These are often referred to as 1+1 or 2+1 stock.

In the BR:BR system, both stages of growth are conducted under semi-natural outdoor conditions under full sun. There is only minimal control of root volume, no control of soil temperature, and some control of soil moisture (water can be added to the system, but not removed). Seedlings are always bare rooted between stages 1 and 2.

Despite many differences, these three systems all involve two stages. In stage 1, a starter plant is produced. This is lifted but may or may not be graded or stored. In stage 2, the starter plant is transplanted and cultured into a field-plantable seedling. It is then lifted, graded and packed for field planting.

Root Physiology And Phenology

In this section we will visit several key physiological and phenological attributes of seedling roots and indicate where and when they might be affected by, or limiting to, various stages in the process of growing transplants. The factors we will consider are: hydraulic conductance; phenology, dormancy and growth; cold hardiness; stress resistance; shoot/root interconnectedness; and root pathogens.

Hydraulic Conductance

Hydraulic conductance expresses the ability of a root system to extract water from the growing medium. Water uptake also includes nutrient uptake; hence, this is a critical function of roots. Hydraulic conductance is affected by 3 main factors (Carlson and Miller 1990). First is the temperature of the soil and root system. As temperature decreases, the viscosity of water increases and root activity decreases. Second, is the volume of the root system. All other things equal, greater root volume leads to greater hydraulic conductance. The developmental state of the root system is also critical. This is because unsuberized (white) roots have greater conductance than suberized (brown) roots. As growth rate increases, the ratio of unsuberized to suberized root surface area increases and so does hydraulic conductance.

To maximize hydraulic conductance after planting, it is important that the roots begin growing rapidly.

This improves root to soil contact, gives a higher proportion of unsuberized (growing) roots, and allows roots to probe new moisture reserves in the soil. So, in transplanting, achieving good hydraulic conductance requires that starter plants be grown with adequate root volume to support its foliage area. For starter plants to begin growing new roots soon after transplanting, planting should be done when soil conditions favor root growth. These conditions are outlined below.

Dormancy, Phenology, And Growth

In seedling shoots, phenology is under control of the dormancy cycle (Romberger 1963; Perry 1971). Briefly, the dormancy cycle comprises 4 stages. In spring and early summer, active growth is occurring in the shoot tips and cambium. By late summer, a period called "quiescence" develops during which growth is impeded by external conditions. This is followed in fall by the induction of dormancy, or winter "rest". During rest, growth will not resume until after the shoot has been exposed to a prolonged period of low temperature—a phenomenon called the chilling requirement. Once this period has elapsed, usually by late winter, dormancy weakens and quiescence returns. Growth resumes as a response to rising spring temperatures.

The important point here is that roots do not adhere to this schedule. Roots exhibit no innate cycle of growth and dormancy as do shoots. Rather, they are opportunistic growers, growing and stopping in response to environmental conditions. For example, if the temperature suddenly rises to 68 °F (20 °C) during November, when shoots are dormant, roots would suddenly begin to grow. (This can be confirmed at the nursery by lifting seedlings in November, bringing them into a warm greenhouse and potting them. Remove the seedlings after 2 or 3 weeks and observe the proliferation of new, white root tips).

The most important environmental factor controlling root growth may be soil temperature. As a general rule, for tree seedlings native to this region, no root growth occurs when soils are below about 46 °F (8 °C) (fig. 1). Above 46 °F, roots begin to develop white tips and some elongation may be apparent. Between about 54 °F (12 °C) and 68 °F (20 °C), root growth increases linearly with temperature then plateaus or even declines in some species above 68 °F. The second most important factor is probably soil moisture content or soil water potential, which interacts strongly with soil temperature (fig. 2).

When soil moisture becomes limiting, not only does the root growth temperature response tend to flatten out, but the optimum temperature for root growth can fall (Teskey and Hinckley 1981; Kuhns and others 1985). Root growth of container crops is very strongly controlled by container volume up to a point (Endean and Carlson 1975) (fig. 3). In a bareroot nursery, this effect is much weaker, but root growth can be manipulated somewhat by managing sowing or transplanting density. Aeration of the soil or growing medium is also very important to root growth. Poor aeration leads to root deformities, root thickening, reduced fibrosity, and increased risk of pathogens.

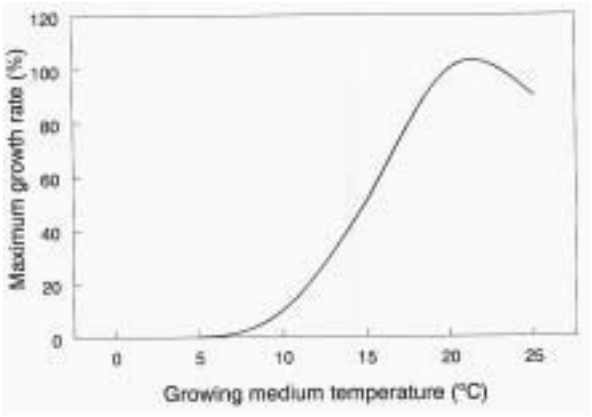

Figure 1. Generalized diagram illustrating how root growth is affected by the temperature of the growing medium for seedlings of many tree species.

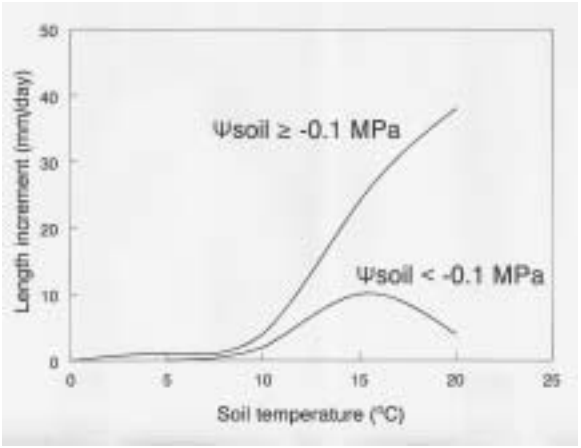

Figure 2. The dependence of root growth on soil temperature is strongly mediated by soil water potential (redrawn from Kuhns and others 1985).

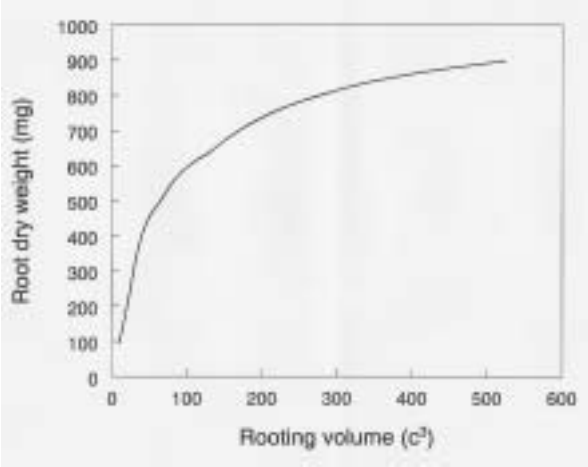

Figure 3. Effect of container rooting volume on root dry weight of lodgepole pine seedlings after 20 weeks (Endean and Carlson 1975).

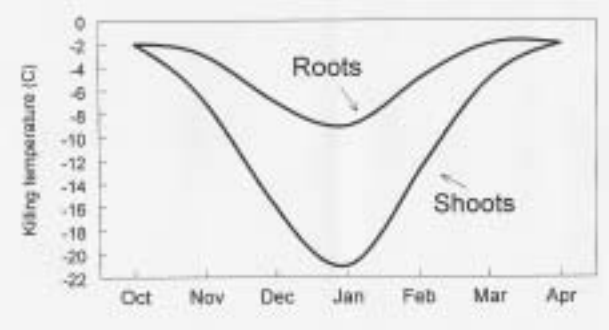

Figure 4. Generalized plot of root and shoot cold hardiness for Douglas-fir seedlings.

The above physiological responses have many practical implications. Soil temperature, while generally well controlled in container systems, is not controllable in the bareroot nursery. Therefore, if transplanting occurs before soil has warmed, little or no root growth can be expected. Similarly, soil moisture is under good control in container systems. In the bareroot nursery, it is possible to add water through irrigation, but it is generally not possible to remove it. During rainy periods this can lead to water logging of nursery soils and poor aeration for root systems. In container systems, poor container design, poorly draining medium, and over watering can have the same negative effect on root development. Limited soil volume in container systems can lead to inadequate root fibrosity and "pot binding" of starter plants. Both of these situations can lead to poor performance following transplanting.

Cold Hardiness

Cold hardiness can be defined as the ability of a plant to resist sub-freezing temperatures. Cold hardiness is a trait normally associated with seedling tops. However, root systems also display a seasonal rhythm of hardening and de-hardening (Lindström and Nyström 1987; Colombo and others 1995). This rhythm reflects temperature conditions within the soil, which are far more stable and less extreme than those above ground. As might be expected, roots do not attain the same level of cold hardiness as shoots, but both reach peak hardiness at roughly the same time (fig. 4).

When roots are exposed to temperatures approaching their hardiness limits, several negative impacts can occur. First, root growth potential (RGP) and top growth can be substantially reduced. Stomatal conductance decreases, leading to a reduction in photosynthesis, which can further impact root growth (see below). Furthermore, the susceptibility to root pathogens, particularly in storage, can be increased when roots are suffering from cold injury.

These phenomena can have major implications in transplant production. While it would be unusual for seedlings growing in the bareroot nursery to suffer from cold damage, container stock that is exposed to cold weather, or that is over-wintered outdoors, can be killed by cold injury to roots (Lindström 1986; Lindström and Stattin 1994). It has also been suggested that lifting for freezer storage, if done too early, can predispose seedlings to root damage in storage (GA Ritchie, unpublished data).

Stress Resistance

Stress resistance is similar to cold hardiness. It can be defined as the ability of a root system to resist stresses associated with lifting, handling, drying, and other nursery operations. Interestingly, stress resistance in roots has a very strong seasonal periodicity (Hermann 1967; Ritchie 2000), reaching a peak in mid-winter (fig. 5). During times when roots are active, their stress resistance is very low, so that a slight disturbance can have serious consequences.

This phenomenon has important implications in BR:BR operations during the time that seedlings are being lifted, handled, packed, and stored (Ritchie 1986). It's probably not an exaggeration to say that this phenomenon, more than any other, defines the

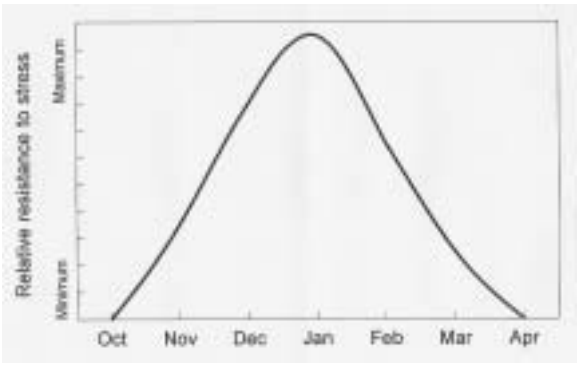

Figure 5. Seasonal changes in root system stress resistance for Douglas-fir seedlings.

biological "lifting window" for bareroot stock. It is much less important in container stock, however, because the roots remain protected by a plug of soil (assuming that the plug remains on the roots) and suffer much less direct exposure to stress. This is one of the key advantages of container stock and is the main reason that fall planting and late spring planting are often more successful with this stock type than with bareroot stock. In northern regions where the BR lifting window (nominally late November through March) is closed owing to frozen ground, containers are often the preferred stock type.

Root/Shoot Interconnectedness

Roots depend on shoots and shoots depend on roots. Neither can be considered without the other. This point will be illustrated with 2 examples. The first involves production and transport of photosynthate. Figure 6 summarizes results of a series of experiments done with Douglas-fir seedlings (Zaerr and Lavender 1974; Ritchie and Dunlap 1980; Philipson 1988). The seedlings were planted into pots containing moist growing medium, then placed into an environment conducive to rapid root growth. Controls behaved as expected, initiating and elongating numerous new roots. Seedlings that were girdled (ring of bark and phloem removed from around the lower stem) produced few or no roots in the same environment. An interpretation of this result was that some factor that is transported from the crown to the roots through the phloem is necessary for root growth. In a second treatment, seedlings were defoliated before potting. These seedlings also failed to produce roots, suggesting that this "factor", or some component of it, originated in the foliage. If the seedlings were held in darkness during the rooting period they also failed to produce new roots. These results taken together strongly implied that new root production in these seedlings depends on photosynthate that is being produced in the foliage and transported through the phloem to the roots. This was tested in an experiment (van den Driesshe 1990) in which Douglas-fir seedlings were grown in an atmosphere that was scrubbed of CO_2. Since plants are constantly producing CO_2 through respiration, it was impossible to remove all of it from the air. Scrubbing most of it resulted in a near complete cessation of root growth in these seedlings.

The conclusion is that Douglas-fir seedlings rely strongly on current photosynthate for new root growth. Therefore, anything that interferes with photosynthesis, or transport of photosynthate, will reduce root growth. Such factors may include cold damage, photodamage, inadequate nutrition, leaf pathogens and mechanical or insect-related damage to stems. It should also be noted that similar experiments with Sitka spruce gave different results (Philipson 1988), so all conifers may not respond in the above manner.

The second example involves carbon source:sink dynamics within the plant (see Kramer and Kozlowski, p 380-389). Carbon sources include the photosynthesizing foliage, as well as stored starch and sugar contained in the foliage, stem, and roots. Carbon sinks are located in the meristematic tissues—the developing buds and cambium, and the growing roots. Carbon sinks compete with each other. Generally, the more actively a tissue is growing, the stronger a sink for carbon it becomes.

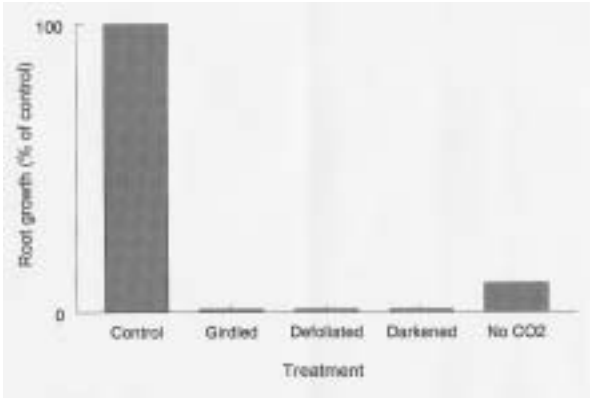

Figure 6. Summary of several experiments with Douglas-fir seedlings in which root growth was measured following various treatments to the tops of the seedlings (after Zaerr and Lavender 1974; Ritchie and Dunlap 1980; Philipson 1988; van den Driessche 1990).

After transplanting, carbon sinks in the developing buds and emerging shoots will overpower the root sinks, causing a temporary reduction in root growth below its potential. However, soon the emerging foliage will begin to photosynthesize and become a net carbon source exporting to the roots. Then, with warming soil and an abundant source of currently produced photosynthate, root growth will resume at a near-optimum rate.

Root Pathogens

No matter how well the transplant production processes are managed, root pathogens can trump success at nearly every point (Hamm and others 1990). Some important root pathogens encountered in this area are *Fusarium* sp., *Pythium* sp., *Phytopthora* sp., and *Cylindrocarpon* sp. The main points of vulnerability in C:C are non-sterile container media, equipment, trays, and greenhouses. In BR, ineffective nursery fumigation procedures are very important, as is cleanliness of equipment and facilities. Improper storage can have serious pathogenic consequences in both BR and C systems. In general, when stock is carrying a root pathogen load, cold storage (storage above 32 °F [0 °C]) promotes the colonization of stock by the pathogen during storage. Given time, the pathogen can completely destroy cold stored seedlings. In contrast, frozen storage (below 32 °F), while it does not kill pathogens, will arrest their development. A useful rule of thumb is: cooler for short term storage (less than one month); freezer for long term storage.

Summary

Transplanting systems discussed here involve container to container (C:C), container to bareroot (C:BR) and bareroot to bareroot (BR:BR). All three systems involve two growing stages interrupted by a transplanting step. Root physiology and phenology can be affected by, or limiting to, each of these.

Root hydraulic conductance, the root system's ability to extract water and nutrients, is affected by soil temperature, root system surface area/volume ratio and developmental state. Achieving good conductance requires that the plant commence root growth soon after planting. Roots have no internal dormancy cycle, as do shoots, but respond to environmental conditions. Soil temperature, moisture content, rooting volume and aeration are key variables controlling root growth. Roots attain some degree of cold hardiness in winter, but do not harden as much as shoots. Lack of root hardiness can limit C:C and C:BR production and control the date of lifting for freezer storage. Root system stress resistance varies seasonally, being greatest in mid winter. The degree of stress resistance largely defines the "lifting window" for BR stock, but is less important in container stock where roots are protected by an intact plug. Pathogens such as *Pythium*, *Phytopthora*, and others can derail success at any step in transplant production. Main points of vulnerability to pathogens include un-sterile growing medium and trays, inadequate nursery bed fumigation, and improper storage temperatures.

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