ENVIRONMENTAL CONTROL OF SEEDLING PHYSIOLOGY

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Abstract.--The greenhouse container nursery offers a degree of control of seedling physiology that the outdoor bare-root nursery cannot match, but this potential can be realized only by a thorough understanding of seedling environmental requirements and the procedures for providing them.

Résumé.--Une pépinière de plants en mottes emballées permet de bien mieux contrôler la physiologie des semis qu'une pépinière en plein air de plants à racines nues, mais il faut pour cela une connaissance parfaite des exigences écologiques des semis et les moyens d'y satisfaire.

The principal difference between the outdoor bare-root nursery and the greenhouse container nursery is in the degree to which the environment can be manipulated to control seedling growth. Seedling genetics are fixed by seed source and cannot be manipulated in the nursery.

In nature, trees receive signals from the environment that tell them when to germinate, grow vigorously, set bud and become dormant, become cold hardened, and break bud. In the greenhouse, we use these same signals to grow the seedlings according to our schedule, not nature's. In this way we can optimize conditions to minimize growing time, thereby achieving a desired seedling size much more quickly than if the seedling were exposed to less controlled conditions (Tinus 1971).

SEED PREPARATION

Seed for the container nursery should be the finest available. Ideally, germination should be prompt and 100% complete, but no seed lot is that good. As germination decreases, an increasing proportion of containers remain empty, unless they are multiple seeded. It is usually worth recleaning the seed to raise germination above 75% rather than wasting a lot of seed and accepting large numbers of multiple seedlings, as these must be thinned to one anyway (Belcher 1978).

Transplanting is feasible during the short period after germination before lateral roots have developed, but it is laborious and often results in stunted seedlings with root deformities. Transplanting should not be adopted in preference to the use of high-quality seed.

Some seedlots can be used dry as they come from the freezer, but in many instances, seed pretreatment is necessary to insure prompt germination (Anon. 1974). In order to germinate, dry seed needs first to imbibe water and, second, to have a supply of oxygen for aerobic respiration. Soaking for 12-48 hours in aerated warm water is usually beneficial and may be all that is required. If not, the next stage is usually cold stratification in which the seed is stored at 1-5 °C and kept moist and well aerated for anywhere between 7 and 150 days, depending on species and seed origin. For instance, jack pine *(Pines banksiana* Lamb.) generally requires no stratification. Lodgepole pine *(P. contorta* Dougl.), red pine *(P. resinosa* Ait.) and ponderosa pine *(P. ponderosa* Laws.) require 30-60 days' stratification only if the seed has been stored for a year or more. Stratification of spruce seed generally does not increase germination capacity but frequently increases germination energy. Alternating day and night temperatures and light at 500 lux or more often enhance spruce germination. During stratification, the necessary processes for breaking seed dormancy are completed; these include completion of embryo development, decrease in germination inhibitors, increase in germination promotors, and activation of enzymes. Sometimes stratifica-

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tion can be shortened or eliminated by treatment with hormones such as gibberellic acid or cytokinin (Bonner 1972, Webb and Wareing 1972). In other cases special treatments are required, such as warm stratification before cold stratification, or chemical or abrasive treatment to render the seed coat permeable. However it is done, adequate time must be allowed for presowing treatments so that germination is prompt and complete.

SEED GERMINATION

The seed is sown in a container filled with growing medium and covered with a coarse-textured material that is usually different from the growing medium. The covering should protect the seed from drying and excessively high temperatures, inhibit weed and moss growth, prevent the seed from being dislodged by water or wind, and not interfere with seedling emergence. The two most commonly used materials are granite grit and perlite. Although both serve the purpose well, grit is preferred wherever the containers will be exposed to wind or heavy rain. Many hardwoods can be covered with growing medium, because they grow rapidly and their broad leaves quickly shade out weeds. Some preformed blocks of growing medium are intended to be used without the seed being covered, which is feasible if humidity can be kept sufficiently high.

During germination, the most critical variables are temperature and availability of moisture. Temperature optima for germination vary considerably. Temperature should be maintained at or slightly below optimum. The slightly lower temperature is often preferable because it decreases hypocotyl elongation and results in a sturdier seedling. A high light intensity (50% full sunlight) also helps. A light-colored seed covering is preferred, because it helps keep surface temperatures down. Additional shading may also be necessary.

Standard conditions for germination tests are usually 30°C (daytime) at 500 lux for 8-16 hours, and 20°C for the remainder of the 24-hour period. These conditions are not necessarily optimal for germination. Germination of coastal Douglas-fir *(Pseudotsuga menziesii* [Mirb.] Franco) may be predicted from heat sums over a wide temperature range from 4° to 28°C. The higher the temperature, the faster the germination (Bloomberg 1978). *Betula nana*, a Scandinavian birch, germinated well between 15° and 24°C constant day/night temperatures. Temperature fluctuation of 3°C improved germination at 12-15°C but made no difference at higher temperatures (Junttila 1970). Fraser (1971) found that white spruce *(Picea glauca* [Moench] Voss) germinated best at constant temperatures of 18-22°C, with some variation between seed origins. Fluctuating temperatures were not tested. Godman and Mattson (1980) found temperatures just above freezing optimum for germination of northern red oak *(Quercus rubra* L.).

Until it has developed a fairly deep root system, the seedling is very susceptible to surface drying; therefore, humidity must be kept high and waterings must be frequent. At this stage seedlings are very susceptible to damping-off, although the use of a sterile medium and good greenhouse sanitation generally help to prevent any problem. The need to maintain low water stress must be balanced against the need to let the surface dry as soon as possible to reduce the risk of damping-off. Fungicides are sometimes used routinely as prophylactic measures, but unless disaster is fairly certain without fungicides being applied, I recommend against using them except when a specific need arises. In addition to the risks of reducing root growth and killing mycorrhizal fungi, there is the danger of creating fungicide-resistant strains of pathogens. This has already happened with *Botrytis* spp. (Gillman and James 1980).

During germination, the seedling is supplied with food and mineral nutrients stored in the seed. Hence, mineral nutrients do not need to be supplied by the medium; in fact, keeping such nutrients low, particularly nitrogen, helps minimize pathogen growth. High light intensity and supplemental carbon dioxide are not beneficial at this time. However, total darkness is not recommended either. Some seeds germinate better in light (Smith 1975). In addition, light helps to dry the foliage and pot surface, and this further reduces the chance of fungal infections and keeps the hypocotyl short and sturdy.

JUVENILE GROWTH

Light Requirements

As soon as the food reserves in the seed are used up, the environmental needs of the seedling change. Adequate but not excessive light becomes paramount, because the seedling must now provide its own photosynthate. Inadequate light, which may occur at low sun angles in winter, during extended periods of cloudy weather, or with dirty or discolored greenhouse covering, slows growth. Stem diameter and foliage area are reduced more than height. Excessive light results in unnecessary moisture stress and, in extreme cases, may cause chlorosis by solarization (Ronco 1970).

Shading to reduce excess light is cheap and easy. Adding high-intensity light to increase photosynthesis is expensive and generally not cost effective. It is usually better to plan the growing schedule to avoid the need to add high-intensity supplementary light.

Light required for photosynthesis should not be confused with the low-intensity light used to lengthen the photoperiod, which is one of the most important tools the greenhouse grower has to control growth. When daylength is longer than a critical number of hours, woody plants will continue height growth or may be induced to break bud. When daylength is shorter than a critical number of hours, the plants will set bud. For a given species, the farther north or higher the elevation of its origin, the stronger its reaction to photoperiod, and the longer the daylength required to prevent dormancy (Junttila 1980). The longer a seedling has been growing without a dormant period, the longer the critical daylength. Since the critical daylength is usually not known for a given group of seedlings, the safest and surest way to prevent bud dormancy is to give them the equivalent of a 24-hour day (Tinus and McDonald 1979).

There are several important differences between the quality of light required for photosynthesis and that required for dormancy prevention. For the latter, wavelengths shorter than 550 nm are of no value, and wavelengths between 700 and 770 nm reverse the effect of red light (600-700 nm). As red light intensity increases from zero, there is a threshold below which there is no photoperiodic growth response. Above the threshold, height growth increases rapidly with light intensity and then tapers off at an upper intensity limit above which there is no further response. For the majority of species, full response can be obtained with 400 lux (even less for some species [Arnott 1974, 1976, 19791), which is two orders of magnitude less than what is required for maximum photosynthesis.

The light required for photosynthesis provides energy for synthesizing carbohydrates, and this is why the light intensity must be high and continuous. In contrast, light for dormancy control acts as a trigger; it requires very little energy and may be intermittent (Cathey and Campbell 1977). The photoperiod control lights can be on as little as 3% of the time, provided that no single dark period is longer than 30 minutes. Since the intensity and duration of light required for dormancy control are minimal, it is not only economically feasible to provide this amount of light but, under most conditions, it is important to do so (Tinus and McDonald 1979).

Temperature

Temperature is also important in determining growth rate, bud set, and bud break. Optimum growing temperatures for many species have been determined (Tinus and McDonald 1979). Many species e.g., lodgepole pine[2], will continue height growth over a wide range of temperatures provided that the photoperiod is sufficiently long. Others, such as bur oak *(Quercus macrocarpa* Michx.), may set bud in response to cool nights regardless of photoperiod.

Species differ in the minimum age or size at which they can set bud. Engelmann spruce *(Picea engeZmannii* Parry) and white spruce are capable of setting bud in the cotyledon stage, and they should be started on extended photoperiod as soon as they germinate. On the other hand, pines will generally not set bud until they have made substantial epicotyl growth.

Nutrients

After the seed coat is shed, the seedling must be provided with mineral nutrients, particularly nitrogen. The best way to provide them is "according to need", which is easier said than done (Mills and Jones 1979, Brown 1980). Each element needed has a specific role to play in plant metabolism, and the quantity available to the plant must not only be adequate, but must also be in balance with the other mineral nutrients. The provision of a balanced and adequate supply of nutrients is an important function of the growing medium. Nutrient ions may be present in three forms: in the soil solution, adsorbed on the exchange complex, or as a slightly soluble solid. The plant takes up nutrient ions from the soil solution, but exchangeable and solid forms provide a reservoir that can greatly increase the available supply without raising the salt concentra-

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[2] Tinus, R.W. 1976. Growth of white spruce and lodgepole pine under various temperature and light conditions. Unpubl. Rep. to Alberta Dep. Energy and Nat. Resour., Edmonton. 19 p. (Under coop. agreement 16-573-CA with USDA For. Serv.)

tion. Some ions also act as buffers to keep the pH in a favorable range. Control of pH is important for maintaining nutrient ion availability, promoting the development of mycorrhizae, and suppressing pathogens. Detailed recipes for preparation of nutrient solutions are available in Tinus and McDonald (1979) and Carlson (1979).

Growth Medium

As the seedling root grows downward, the texture and composition of the growing medium become important. Roots must be able to penetrate the medium easily. Both adequate water supply and good aeration are necessary. High cation-exchange capacity is desirable, and addition of solid mineral nutrients and inoculation with mycorrhizal fungi may also be desirable. The medium should contain no toxic materials or pathogens.

To date, peat alone or mixed with vermiculite has been the overwhelming favorite, because it meets the above criteria well. Nevertheless, the search for other materials goes on, either for manufacturing convenience or because of an abundance of a cheap local material.

Containers

Sooner or later, the seedling roots strike the container wall. The container itself is an important component of the seedling environment, because it determines the size and shape of the root system (Hiatt and Tinus 1974, Biran and Eliassaf 1980). Container volume determines the size of tree that can be grown in the container; container shape is important for the production of an unentangled root system that will promote rapid field establishment and windfirmness. The container and its support structures also determine bed density. Here, there is a direct conflict between production economics, which dictates maximum number of trees per unit area, and seedling biology, which requires ample growing room to produce seedlings of adequate diameter. High density seedlings may be sufficiently tall, but they will be spindly and their photosynthetic area will be inadequate. Tightly packed crowns also promote foliar disease.

In rigid, impermeable-walled containers, vertical ribs or grooves, lack of sharp horizontal corners, and an egress hole at the bottom for air pruning, are almost universally used to produce a vertical root system without spiralling roots. The container is removed before outplanting, leaving the roots free to grow into the surrounding soil. Unfortunately, most of the new roots develop from growing points at the very bottom of the plug, leaving the seedling with an inadequate surface lateral root system that may lead to twizzling and toppling of older trees (Tinus 1978). A new technique to increase the number of surface lateral roots by treating the container walls with latex paint containing copper carbonate appears promising (Burdett 1978, McDonald et al. 1980).

Containers with walls permeable to roots prevent root spiralling in a manner different from impermeable-walled containers. Where it is possible for roots to grow from one container into the next, the roots must be broken cleanly at the container wall to separate the containers for planting. Therefore, seedlings must generally be limited to a small size to ensure that the roots broken are not very strong and only a small portion of the root system is lost. Containers may also be separated by an air space which the roots do not cross. The seedlings are ready to plant when the roots emerge from the containers, and they should not be held longer.

EXPONENTIAL GROWTH

After the seedling is firmly established, provided that growing conditions are near optimum, it begins growing exponentially, i.e., the bigger it gets the faster it grows. This takes place either continuously or in a series of sequential flushes. The key to growing a large seedling in a short time is to keep it growing exponentially until it is as tall as desired. If the seedling sets bud and becomes dormant prematurely, it may be impossible to meet height specifications on schedule. If it is necessary to meet bud chilling requirements to obtain another flush of height growth, the crop will likely be an economic disaster.

The environmental requirements for exponential growth are usually much the same as for juvenile growth, except that optimum temperatures are often a few degrees higher, and as the crowns close, the seedlings can use higher light intensity. Elevated CO2 levels increase growth, especially in cold weather when the greenhouse can be kept closed, provided that nothing else limits growth. For maximum growth rate, it is important that as many environmental factors as possible be optimized, since a number of factors often act synergistically (Tinus 1977).

HARDENING

Before a seedling can be moved out of the greenhouse to the holding area or planting site, it must be in proper condition to withstand a less favorable environment. In maritime climates and sometimes in continental climates as well, it is possible to transplant an actively growing succulent tree seedling directly to the field; however, survival is usually better if dormant seedlings are planted.

There are two stages in the hardening process: dormancy induction and cold hardening (Alexander and Havis 1980). The first stage is induced by shortening the daylength and reducing temperature about 5-10 °C below optimum for growth. For some species this is all that is required, whereas others also require drought stress. The seedlings are first leached to remove nitrogen. Then water is withheld until moisture stress reaches 15 bars or higher, depending on ecotype. The seedlings may be rewatered with a low N nutrient solution as needed. If they show signs of breaking bud again, they may need another drought stress. Induction of dormancy in some species such as Siberian larch *(Larix sibirica* Ledeb.) is difficult, and drought stress must start up to 3 weeks before the seedlings have reached the desired height.

During the first stage of hardening, buds are set. It is important that the buds be given enough time to develop adequately, because in many species the primordia laid down in the bud constitute most if not all of the cells for the next flush of growth (Owens and Molder 1973, 1976a, 1976b, 1979; Young and Hanover 1977). At the same time stem diameter and lignification increase, greatly increasing the sturdiness of the seedling and its chances of survival in a hostile environment. A flush of root growth commonly occurs at this time, thereby reducing the shoot:root ratio. It has also been my experience that during rapid height growth few if any mycorrhizae appear on the roots, even though the growing medium was inoculated before seeding, and the seedlings show increased vigor and freedom from pathogens because of the inoculation. However, with the reduced stem growth and increased root activity, mycorrhizal structures appear.

High CO2 can be beneficially maintained during the first stage of hardening of most conifers, but it must be shut off to begin hardening of deciduous species, as high CO_2 retards leaf abscission.

At this point, seedlings are "summer dormant" and prepared to withstand full sunlight, drought stress, wind, and even a light frost. They are ready to be outplanted during the summer or early fall. Many species in this condition should not be spring planted, because they will not break bud until the following year. They should be planted not later than 4 weeks before the soil temperature falls below the minimum for root growth (about 5 °C).

The only additional change to initiate the second stage of hardening is to lower the temperature to just above freezing and shut off supplemental CO2, if that has not already been done. The seedlings should be on short days, but they must have light because, during hardening, metabolic changes occur that require photosynthate. Under these conditions the seedlings will develop cold hardiness and become resistant to hard frosts, but to develop full hardiness, they must experience subfreezing temperatures. Seedlings should be subjected to frost only after being held for at least 2 weeks at temperatures just above freezing. Depending on how they will be overwintered and where and when they will be planted, they may not need to be fully cold-hardened.

The other function of low temperature is to meet bud chilling requirements. After the bud becomes fully dormant, it frequently will not break dormancy when the seedling is returned to favorable growing conditions. Prolonged chilling releases bud dormancy. After the necessary chilling period, it is only low temperatures, sometimes aided by a short photoperiod, that keep the buds from breaking (Litzow and Pellett 1980).

OVERWINTERING

Once fully hardened, seedlings can be stored in the dark if necessary, but light is usually beneficial. In cold climates container nurserymen have frequently raised beautiful seedlings only to have them damaged during overwinter storage (Desjardins and Chong 1980).

There are three principal causes of overwinter damage, the most obvious of which is low temperature. Containerized seedlings are more susceptible to low temperature damage because the roots, the most sensitive part of a hardened seedling, are above ground. To avoid damage, the seedlings must have had adequate time under proper conditions to harden sufficiently and be adequately protected against lethal temperatures.

The second cause of winter damage is desiccation. When the rootball is frozen, seedlings may not be able to replace moisture as fast as it is lost. Desiccation can be avoided by preventing the rootball from freezing. If freezing is unavoidable, moisture loss can be retarded by using moisture barriers and minimizing temperature fluctuations, or perhaps by supplying moisture to the tops as well as the roots.

Finally, rodents and diseases may damage seedlings. Mouse damage may be eliminated by preventing mice from gaining access to the crop. The second best approach is to minimize suitable pest habitat, and to bait and trap. Foliage molds are more likely to develop if the seedlings are in the dark, too wet, or much above freezing. Disease during the winter is insidious, because the rot and mold fungi responsible can grow at low temperatures, but the seedling cannot, and its internal defenses are minimal. The crop generally receives less attention and supervision over winter, and the damage is often not quickly evident.

SPRING CARE

If the crop is overwintered in a greenhouse, it must be watched carefully in late winter for signs of bud swell. In late winter it becomes difficult to keep day temperatures in a greenhouse below 10 °C, and the seedlings begin to deharden. Before the first sign of dehardening, the trees must be moved to alternative storage, either in a cooler or in a lathhouse outdoors. Under most circumstances the seedlings should not be allowed to break dormancy before they are outplanted. Even if budbreak does occur in the nursery, often the seedlings are still plantable, but more care in transit is needed to avoid damaging the new growth. Often it is better to hold the seedlings until the new flush of growth is complete and the new growth hardened. Full sunlight, drought stress, and low N can be used to keep the seedlings from outgrowing their containers.

PITFALLS

A decade ago, the number of container-grown seedlings in North America was negligible. Today, containerized seedlings account for about 12% or 150 million of all forest tree seedlings produced. Such an achievement would be impossible without the extensive information we now have on seedling biology. However, certain problems resulting from the conflict between the needs of seedling biology and production economics or from poor management practices tend to recur frequently (Tinus 1982).

The selection of too small a container may keep nursery and planting costs low, but what really counts is the cost of an established seedling free to grow. It is better to start with a large enough container, even if it looks too expensive. After the planting system succeeds, then see if a smaller one will do. Frequently, a variety of sizes will be needed to handle different species and different planting sites.

There is often a great temptation to cut short the hardening process to save operating costs, because during hardening there is often little change in the appearance of evergreen seedlings, and there are no quick, readily available tests for monitoring the degree of hardening. Currently, the best assurance is adequate time under proper hardening conditions.

Every nursery should keep careful and detailed records of all cultural operations and seedling growth. If anything goes wrong, these records are invaluable for determining the cause quickly and prescribing corrections.

If the system works, don't tamper with it. Any proposed change should be tested in a small way before it is applied to the entire nursery. Unfortunately, it is not uncommon that after two successful crops a nurseryman may think he is an expert and entitled to remold the growing regime at will. Frequently, when called upon to help, I find the nursery is no longer doing the things that originally made it successful.

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