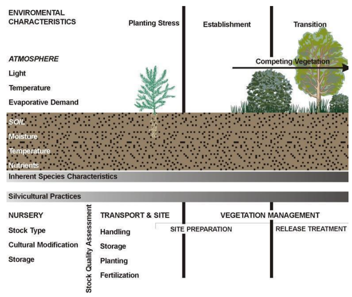

Restoration Silviculture: An ecophysiological perspective - Lessons learned across 40 years

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Abstract

Involvement in forest restoration programs across North America for the past 40 years, dealing with nursery cultural practices, operational seedling quality programs and defining seedling performance on restoration sites has given me a unique perspective, which I have used to examine programs from both a research and operational perspective. Certain biological patterns and themes continually appeared across these programs and this paper discusses five of the most common themes.

Learning To Think Like a Tree – It is important for practitioners to develop an understanding of the ecophysiological performance of tree species in a nursery or forest restoration program in order to understand how seedlings grow. This understanding leads to sound biologically based cultural decisions to improve seedling performance.

Stress and the Cyclical Nature of Stress Resistance – Seedlings are exposed to stress when environmental conditions limit their performance. Plants develop physiological resistance attributes to mitigate stress and these attributes change throughout the seasonal cycle. Practitioners have developed hardening cultural practices that enhance seedling stress resistance, thereby improving seedling quality and site restoration success.

Seedling Quality: Product versus Process – Seedling quality is an important component of successful restoration. Typically seedling quality is examined from a product perspective, thus defining functional integrity, operational grading or sometimes performance potential. An alternative approach monitors the process, with product quality the final output.

Planting Stress and Seedling Establishment – Planting stress is prevalent in forest restoration. The act of planting can result in a seedling that does not have proper connections for water movement through the soil-plant-atmosphere continuum (SPAC). Seedling water stress, reduced growth performance and potentially death can occur if this SPAC connection is not restored.

Seedling Death: Sometimes Simple and Sometimes Complicated – Seedling death can occur in restoration programs as a result of environmental extremes or incorrect management practices. Some problems can be easy to diagnose and correct practices can be implemented to rectify the problem. Other times, issues are complicated and it can be a challenge to define the potential factors causing seedling death.

Keywords

Ecophysiology, Stress Resistance, Seedling Quality, Planting Stress, Seedling Death

Contents

1 Introduction

***"In the direction from which we had come the slopes were covered with trees twenty to twenty-five feet tall. I remembered how the land had looked… a desert….* [The]*...serenity of spirit had endowed this old man with awe-inspiring health….* [And] *I wondered how many more acres he was going to cover with trees."* From: "The Man Who Planted Trees", Giono (1954)**

Programs I was involved with to restore disturbed forest ecosystems generally dealt with two aspects of the restoration process. First, proper nursery cultural practices are needed in order to improve seedling quality. Developing nursery cultural practices for growing miniplug and finished seedlings, plus creating and operating industrial seedling quality programs all speak to the issue of improving seedling quality. Second, field-related programs need to focus on improving practices of restoring disturbed ecosystems, by either site rehabilitation (i.e. restoring the forest of an existing but degraded ecosystem) or site reclamation (i.e. restoring severely degraded land devoid of vegetation) (as defined by Stanturf et al. 2014). These programs applied reclamation and silvicultural practices to improve outplanted seedling performance.

This body of work examined issues around nursery operations and stand restoration from both a research and operational perspective in programs that spanned North America. Typical biological patterns and themes continually appeared across these programs. In no way is it possible to describe all combinations of factors that affect seedling performance through various stages of nursery and forest restoration programs. Also, it not possible to provide examples of all published work conducted by the many researchers and practitioners on various aspects of forest restoration. Instead, this paper focuses on my observations and some of the major lessons learned during my years in the field of forest restoration. Five of the most common themes observed during these programs will be discussed. By highlighting, and providing examples, nursery personnel and foresters can begin to understand the complexity of the process required for successful forest stand restoration.

2 Learning to think like a tree

*"...**forestry problems are recognized first in the field at the whole plant level…*** **[and]*…remedies are usually found at the whole plant level in terms of silvicultural treatments…"*** **Kramer (1986)**

During the initial stages of restoration, a series of intensive nursery and silviculture practices are required to ensure successful stand establishment (Gladstone and Ledig 1990; Grossnickle 2000). First, a forester must choose the appropriate crop species. Second, tree improvement programs are required to define genetic sources suitable to site conditions. Third, nursery personnel must apply culture practices to optimize morphological and physiological conditions of seedlings prior to and at planting. Fourth, site modification may be required to improve the physical environment of the restoration site. These practices are essential in enhancing seedlings physiological performance and morphological development during field establishment.

Foresters and nursery personnel must understand the ecophysiological capability of the crop species and its performance in relation to restoration practices and have the means to effectively apply intensive cultural practices to increase chances to successfully re-establish a forest stand. Foresters and nursery personnel are trained to grow trees, but do not typically know how trees grow. Therefore, operational restoration programs do not always meet the objective of producing quality seedlings and having successful stand establishment. Developing an understanding of the ecophysiological performance of the crop species is required to provide the knowledge of how seedlings grow. Making the proper selection of genetic sources and silvicultural decisions are only effective when they improve the physiological performance of the desired tree species (Kramer 1986). If foresters and nursery personnel have a good understanding of plant ecophysiological performance, they can improve their ability to grow seedlings within restoration programs.

Whether talking about the nursery or forest site environment the energy, hydrologic, and nutrient cycles have a direct bearing upon seedling performance. It is not possible to describe the myriad of environmental conditions and physiological responses seedlings undergo in the nursery and after being planted in the field. Thus, the following are just a few examples of ecophysiological performance in response to these cycles. These examples are drawn from Grossnickle (2000) and are intended to show how seedling performance is tied to ecophysiological processes, which are directly influenced by the nursery or forest site environment cycles. Readers seeking further information on the ecophysiological processes related to plant performance should examine suggested publications in the Information Sources section.

2.1 Energy cycle

Solar radiation as a general term refers to energy transmitted to the earth by the sun. A seedling growing in the nursery or planted on a restoration site, the surrounding vegetation complex, and the soil absorb the downward flux of shortwave radiation from the sun (i.e. light) and long-wave radiation (i.e. heat) from the atmosphere (Fig. 1). They exchange energy amongst themselves and emit energy to the atmosphere as long-wave radiation. The difference between this absorption, temporary storage, and reradiation of energy throughout the season, or on any individual day, is a measure of the energy available to drive the site environmental processes.

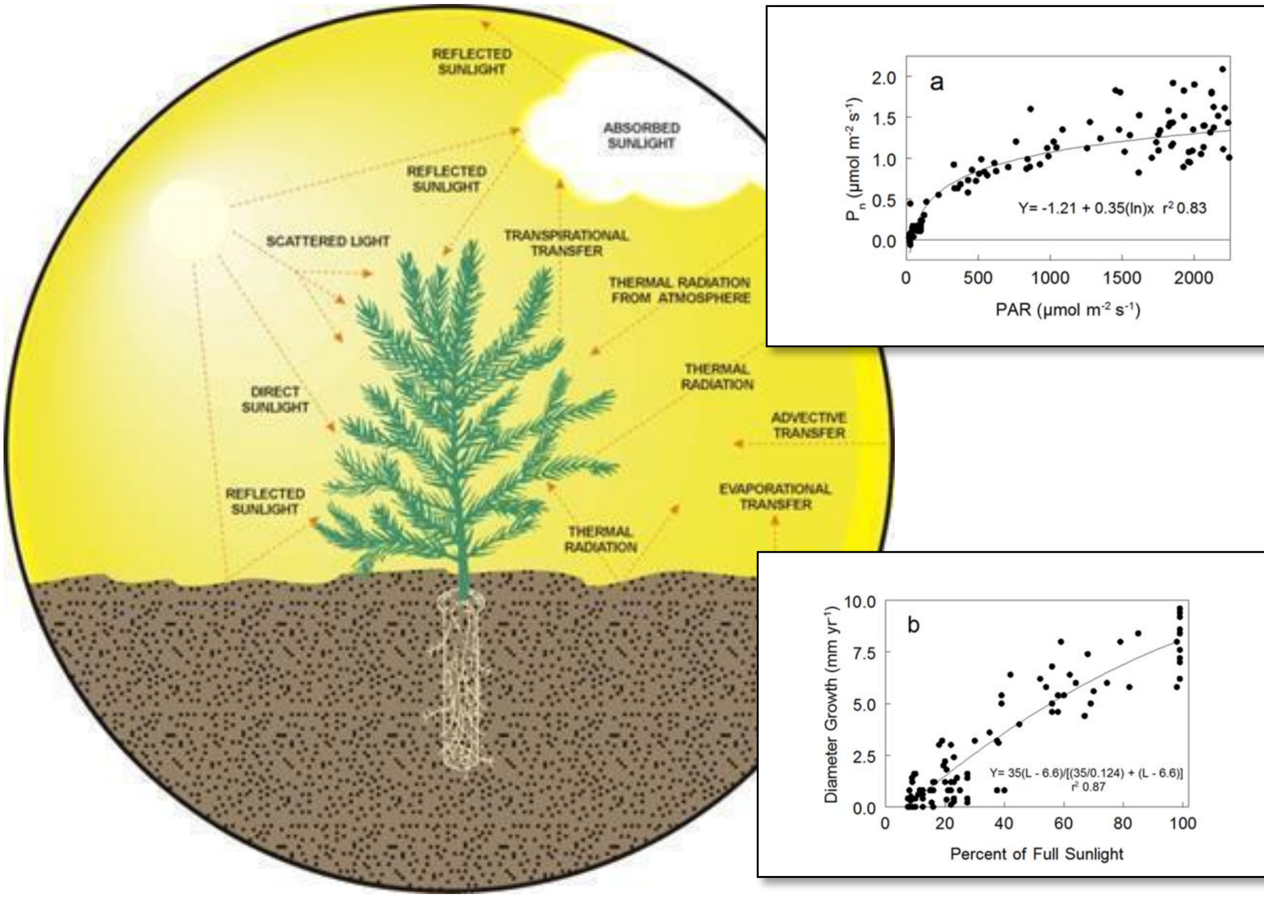

Figure 1. Representation of the energy cycle between a seedling and the environment (Grossnickle 2000). Insert top figure (a): The pattern of net photosynthesis (P_n) for interior spruce (*Picea glauca* (Moench) Voss x *P. engelmannii* Parry ex Engelm.) seedlings over a range of photosynthetically active radiation (PAR) (adapted from Grossnickle and Fan 1998). Insert bottom figure (b): Diameter growth rates (average increment per year over 3, 4, and 5 years after field planting) for interior spruce seedlings in relation to percent of full sunlight reaching the site (adapted from Coates and Burton 1999).

Of the light absorbed by seedling foliage, approximately 75–97% is lost as heat (i.e., transpiration, sensible heat, and thermal radiation) and 3–5% goes into fluorescence emission, while only up to 5% of light absorbed by plant chlorophyll is actually used in the light-activated processes of photosynthesis (Nobel 1991). Net photosynthesis (P_n) of a seedling increases as light intensity increases from dark conditions past what is called the light compensation point (i.e. where the photosynthetic uptake of CO_2 equals its release due to respiration), with P_n then rising rapidly up to 25–33% full sunlight and increasing only gradually after that point (Fig. 1a). Depending upon the species, the foliage reaches the photosynthetic light saturation point between 33% and 50% of full sunlight (reviewed by Kozlowski and Pallardy 1997). Thereafter, increasing light results in only a slight increase in P_n depending upon foliage distribution (i.e. mutual shading) around twigs of shoot systems. This is why there is still a gradual increase in P_n as light levels increase above what is normally considered the light saturation level.

The amount of solar radiation reaching a seedling has a direct effect on growth. In general, seedling growth increases at greater levels of sunlight on a field site (Fig. 1b). Thus under nursery conditions or productive restoration sites (i.e., high availability of water and nutrients), the amount of light transmittance to the shoot system has a direct effect on growth. Any condition where neighbouring vegetation reduces light reaching the seedling causes a reduction in growth. This is why growing density in the nursery (reviewed by Grossnickle and El-Kassaby 2015) or plant competition on a restoration site (reviewed by Grossnickle 2000) can have a direct effect on seedling performance.

2.2 Hydrologic cycle

The hydrologic cycle surrounding seedlings growing in the nursery or planted on a restoration site is made up of water inputs and losses from the soil profile (Fig. 2). Inputs occur through precipitation and, in the field, downslope seepage. Losses occur through interception of rainfall or irrigation, runoff, redistribution within the soil profile, and site drainage. Site factors that affect the soil energy balance (i.e., incoming solar radiation that affects air temperature and relative humidity) also affect water losses that occur through soil evaporation, plus water uptake by vegetation and the transpirational transfer to the atmosphere driven by the vapor pressure deficit. The flow of water through the hydrologic cycle affects many physiological processes. The following are examples showing the effect of the hydrologic cycle on seedling performance.

Seedlings are continually exposed to a wide range of atmospheric conditions in the field. This occurs because temperature and relative humidity of the air are continually changing, and they determine the atmospheric evaporative demand, or the vapor pressure deficit (VPD). Atmospheric VPD has been defined as the drying power of air (Grossnickle 2000). Under adequate soil water, fluctuations in VPD cause changes in seedling stomatal conductance and P_n capability (Fig. 2a). This is a typical gas exchange response to VPD for tree species (reviewed by Hinckley et al. 1981; Whitehead and Jarvis 1981). In addition, the plant water status (i.e. water potential (Ψ)) has a direct effect on gas exchange processes (reviewed by Ritchie and Hinckley 1975). When soil water availability changes, seedling gas exchange processes change in response to the combination of VPD and plant Ψ. This combination of atmospheric evaporative demand and plant Ψ has been found to affect the performance of seedlings on restoration sites (e.g. subalpine forest of the Rocky Mountains (Grossnickle and Reid 1985), boreal forest (Grossnickle and Blake 1986), and the Pacific Northwest coastal forest Grossnickle 1993)). This is why daily changes in VPD, with or without the availability of soil water, have a direct influence on plant Ψ and gas exchange processes, which in turn affect restoration site seedling performance (Grossnickle 2000).

Limited soil water can cause plant water stress and reduce gas exchange processes. For example, P_n decreases as soil water availability (i.e. defined by predawn plant water potential; Ψ_{pd} - Ritchie and Hinckley 1975) declines (Fig. 2b). A decrease in P_n occurs with declining plant Ψ_{pd}, with P_n typically decreasing to the compensation point for most tree species between a plant Ψ_{pd} of -2.0 to -3.0 MPa, though for some tree species it is as high as -1.0 MPa or as low as -7.0 MPa; depending on species adaptation to mesic or xeric conditions (reviewed by Ritchie and Hinckley 1975; Kozlowski 1982). Stomatal closure occurs during low to moderate drought (Fan and Grossnickle 1998; Grossnickle and Fan 1999) and is considered the primary factor limiting photosynthesis (Brodribb 1996). Under severe drought, nonstomatal limitations to P_n (i.e., mesophyll limitations) become increasingly more important than stomatal limitations (Beadle et al. 1981; Stewart et al. 1995), as further drought stress limits the transfer and fixation of CO_2 in chloroplasts.

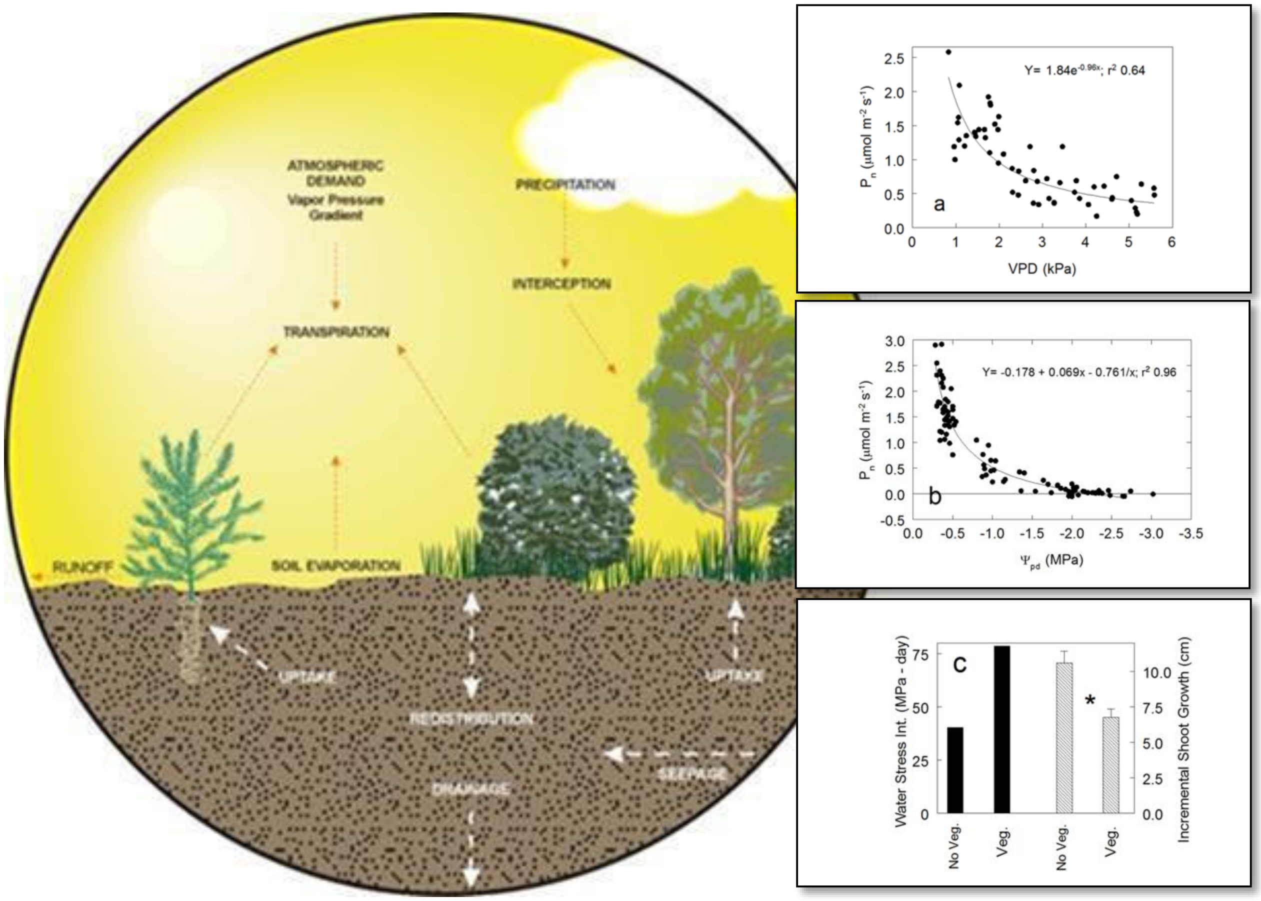

Figure 2. Representation of the hydrologic cycle between a seedling and the environment (Grossnickle 2000). Insert top figure (a): Net photosynthesis (P_n) of interior spruce seedlings in response to a range of summertime vapor pressure deficit (VPD) conditions on a boreal restoration site (adapted from Grossnickle and Major 1994b). Insert middle figure (b): Response of P_n to changes in predawn plant water potential (Ψ_{pd}) for interior spruce seedlings (adapted from Grossnickle and Fan 1999). Insert bottom figure (c):Water stress integrals (i.e. a measure of cumulative seasonal water status) and shoot growth (* indicates TRT difference at p= 0.05) of white spruce (*Picea glauca* (Moench Voss)) seedlings planted on a northern latitude restoration site, with and without low lying competing vegetation over a 125-day growing season (adapted from Grossnickle and Heikurinen 1989).

Any condition in the nursery or restoration site that reduces soil water availability has a direct influence on seedlings morphological response. For example, a reduction in soil water due to low lying vegetation cover on a restoration site caused an increase in the level of seasonal water stress in newly planted white spruce seedlings (Fig. 2c). This increased seasonal water stress caused a reduction in their gas exchange processes over the first growing season (Grossnickle and Heikurinen 1989) and a reduction in subsequent growth (Fig. 2c). Any condition where water availability is limited to the plant ultimately causes a reduction in growth (reviewed by Kozlowski 1982).

2.3 Nutrient cycle

The circulation of nutrients through the nursery or restoration site is an important ecosystem component. All nutrients have three major cycles (shown for N in Fig. 3): geochemical, biogeochemical, and internal. The geochemical cycle involves atmospheric and soil weathering inputs (and fertilizer inputs in a nursery) or nutrient losses. The biogeochemical cycle involves nutrient uptake by seedlings from the soil and its return to the soil via litterfall, death, or foliar leaching. Internal cycling is the movement of nutrients within plants. These three nutrient cycles affect where and in what amounts various nutrients are available for seedling performance.

Nutrient concentration of needle tissue has been related to many ecophysiological processes in tree species, with greater nutrient concentrations attributed to improved gas exchange capability, drought resistance (i.e., avoidance and tolerance) and freezing tolerance (reviewed by van den Driessche 1991). For example, an increase in P_n with increasing needle N concentrations occurs in Norway spruce seedlings (Fig. 3a). An increase in P_n with increasing N concentration is attributed to greater chlorophyll and carotenoid concentrations (Chandler and Dale 1995), thereby improving both the light-harvesting activity (Centritto and Jarvis 1999) and dark reaction (Tan and Hogan 1995; Brown et al. 1996a; Centritto and Jarvis 1999) of the photosynthetic process. Thus, many tree species have a strong positive relationship between P_n and increased leaf N concentration (reviewed by Kozlowski et al. 1991).

Increased N is important because it can increase the capability of seedlings to quickly become established after being outplanted, with the availability of nutrient ions affecting growth after being outplanted (van den Driessche 1991). Recently planted seedlings are more likely to have a lower nutrient status as they begin to grow during the establishment stage. This occurs because a seedling’s nutrient status and subsequent growth are tied to its internal mobilization of nutrients to sites of active growth and the external uptake of soil nutrients (Kozlowski et al. 1991). Recently planted seedlings’ lack of proper root development can cause a low level of nutrient uptake from the soil (reviewed by Villar-Salvador et al. 2015). As a result, seedlings can have a lower N status during the first growing season after field planting, indicating the occurrence of nutrient stress (Grossnickle 2000).

Seedling performance after outplanting in terms of nutrient availability is addressed from a number of silvicultural perspectives. First, the application of fertilization treatments in the nursery can be used to “nutrient-load” seedlings (i.e. fall fertilization practices after budset or the cessation of shoot growth to increase nutrient concentration) (Timmer 1997). Second, fertilization treatments can be applied around seedlings at the time of, or after planting to maintain site productivity (Binkley 1986). Third, site preparation and vegetation management practices can reduce competition but leave organic layers of the forest site available for the gradual release of nutrients for planted seedlings (Chapin 1983). For example, improved growth for white spruce seedlings was still evident four years after application of vegetation control treatments, and this was, in part, attributable to greater levels of N in the current foliage receiving this treatment (Fig. 3b). These nursery and site silvicultural practices are approaches intended to improve the internal seedling nutrient status and their subsequent field performance.

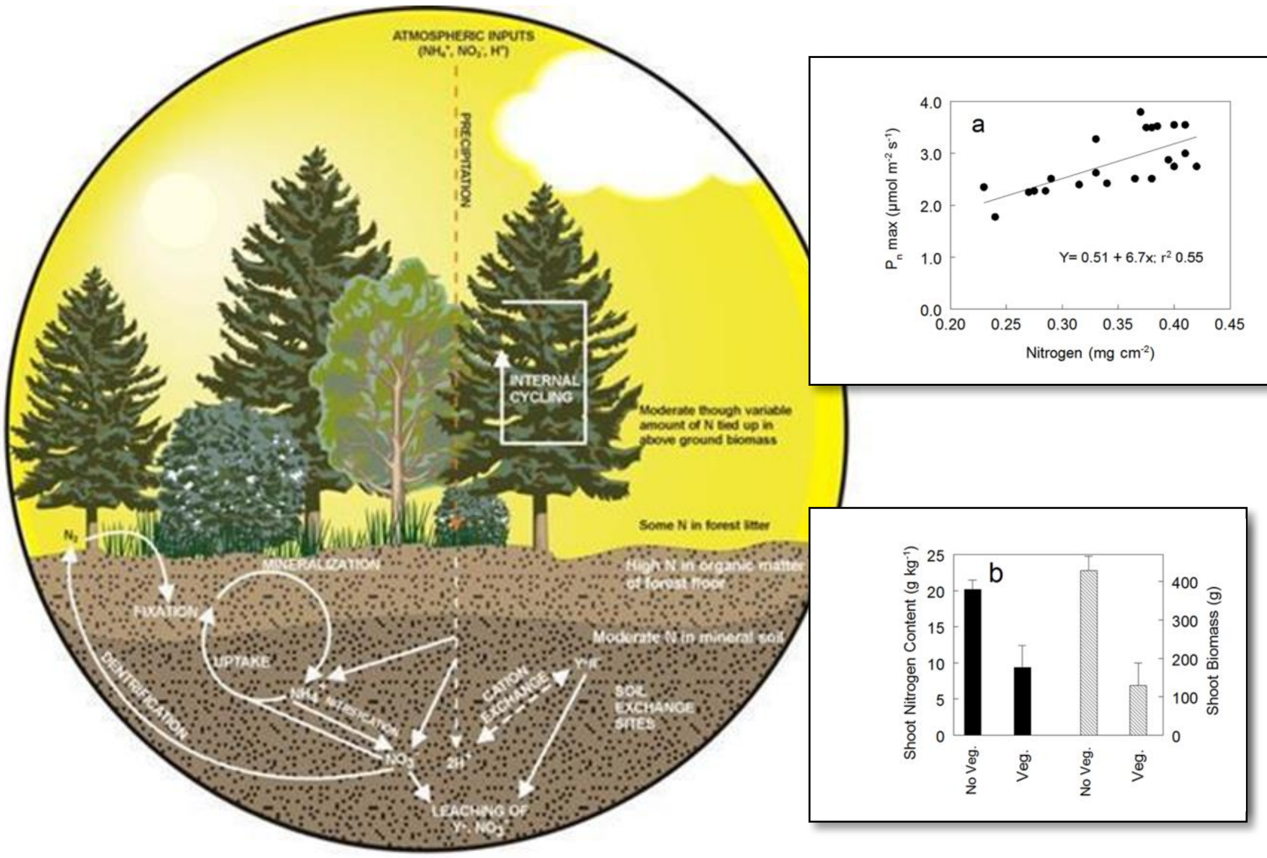

Figure 3. Representation of the nitrogen cycle and the boreal site environment (Grossnickle 2000). Insert top figure (a): The relationship between light-saturated net photosynthesis (P_n) (Note: Adapted one sided needle surface area measurements to total surface area) and N concentration for shoots of field-grown Norway spruce (*Picea abies* L.) trees (adapted from Roberntz and Stockfors 1998). Insert bottom figure (b): Impact of vegetation control (i.e., No Veg. - herbicide each spring in each of the four years following planting to remove vegetation) or control treatment on (i.e., Veg. – vegetation present) nitrogen content and shoot biomass of white spruce seedlings after four years of growth on a boreal restoration site (adapted from Munson et al. 1993).

2.4 Interaction of cycles

Seedling response to the energy, hydrologic, and nutrient cycles does not occur in isolation, rather as a complex interplay of hourly, daily and seasonal environmental conditions. This makes it difficult for practitioners to clearly define why seedlings are performing in a certain manner. One needs to recognize this environmental dynamism when trying to understand seedling performance in relation to cultural practices.

When considering interactions between these environmental cycles, and in trying to describe seedling performance, practitioners should think of Liebig's Law of the Minimum. This law states that the productivity and ultimately the survival of a complex system (e.g. seedlings in the nursery or on a field site) that is dependent on a number of essential inputs (i.e. environmental variables) are limited by the single variable in least supply. Time and again, whether observing seedling performance in a nursery where environmental conditions are semi-controlled or on a wide range of restoration sites, this law has been an underlying truism when trying to define their performance. However, sometimes seedling performance is limited not only by one primary limiting variable, but also by secondary environmental variables which may also contribute to a reduction in performance. Therefore, it has been stated that "Usually no one environmental factor limits the growth of evergreen [and hardwood] trees." (Waring 1991). By defining all potential limiting variables in descending order of importance, practitioners can focus on cultural practices that alleviate, or mitigate the most limiting environmental condition(s) and, thereby, improve seedling performance. Nursery personnel and foresters need to recognize this when defining cultural practices providing the best environmental conditions to optimize seedling performance.

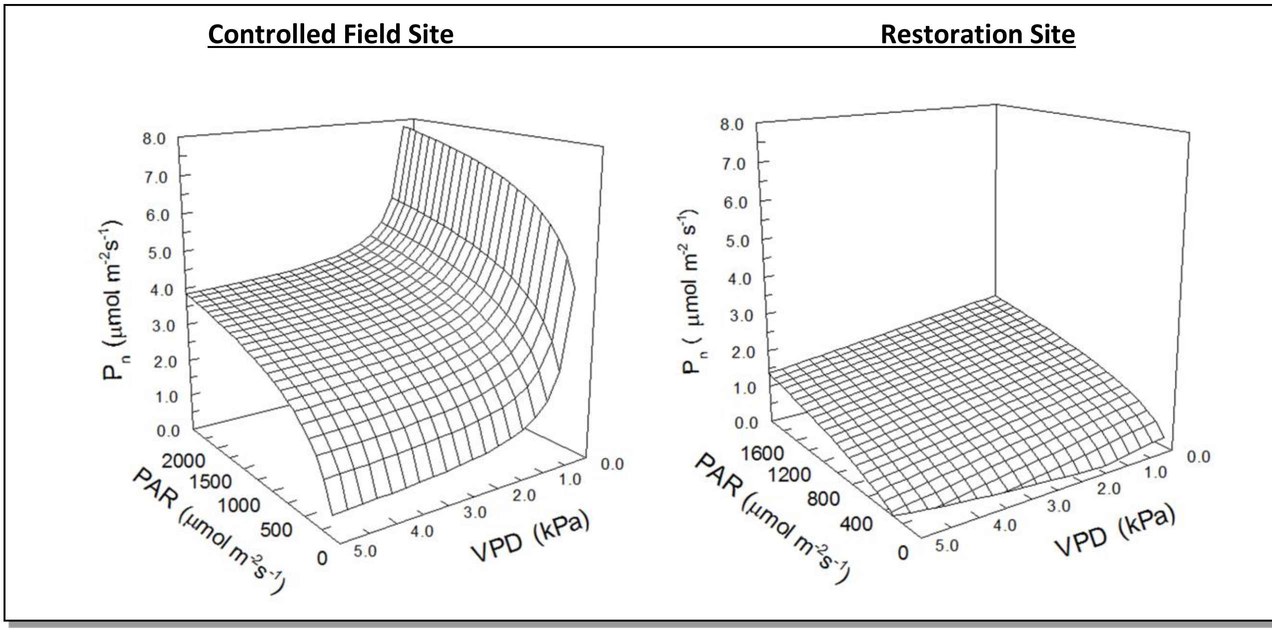

Figure 4. Net photosynthesis (P_n) of interior spruce seedlings in response to photosynthetically active radiation (PAR) and vapor pressure deficit (VPD) under optimum (i.e. well-watered, soil temperatures between 15 and 20°C, and adequate fertility to ensure optimum tissue nutrient concentrations), or restoration site edaphic conditions (i.e., midday plant Ψ of -1.2 to -1.4 MPa, soil temperatures ranged between 12 and 18°C, and fertility levels in the hidden hunger nutrient deficiency range). The controlled field site is adapted from Grossnickle and Fan 1998; with the restoration site adapted from Grossnickle and Major 1994b. Note: seedlings used in these trials were the same genotype and stocktype.

The above example demonstrates how multiple environmental variables can affect seedling performance. A combination of environmental variables cause changes in gas exchange processes in spruce seedlings. Evaporative demand and light are the primary environmental variables affecting gas exchange under optimum edaphic conditions (Fig. 4). In the field, light and VPD continually change in an interrelated fashion, with the relationship of daily P_n related to both variables. When edaphic conditions are limiting, the gas exchange response of tree species to light and VPD is altered (reviewed by Hinckley et al. 1981). Under restoration site conditions exhibiting mild edaphic stress, the P_n response of spruce seedlings was reduced to ~25% of values recorded under optimum conditions. In this restoration site example, five different environmental variables (i.e. light, VPD, soil water, soil temperature, nutrition) were influencing the gas exchange process. This example shows how seedling gas exchange response is altered depending upon which environmental variable, or variables, are most limiting.

This above example shows the dynamic nature of how multiple environment factors can affect seedling performance. Generally, it is some combination of light, temperature, humidity, water, and nutrient supply that limits growth of woody plants (Kozlowski et al. 1991; Mooney et al. 1991; Larcher 2003). It is important to define the combination of environmental conditions that limit successful seedling performance (e.g. nursery conditions, bareroot: Lavender 1984 and container-grown Landis et al. 1989 & 1992; or restoration site conditions - Gjerstad et al. 1984; Sutton 1985; Grossnickle 2000) and to implement cultural practices that can improve environmental conditions.

2.5 Information Sources

These examples have demonstrated how plant ecophysiological processes are directly influenced by the environment cycles and that they are important to seedling performance in restoration programs. Similar seedling ecophysiological response patterns to the site environment, as those described above, were observed in restoration programs conducted in subalpine forest of the Rocky Mountains (Grossnickle and Reid 1985), boreal forest (Grossnickle and Blake 1986, 1987, Grossnickle 1988b), or Pacific Northwest coastal forest (Grossnickle and Russell 1991; Grossnickle 1993) ecosystems. Also, studies showed that field silvicultural practices affect ecophysiological response and this information can be used to improve field performance (Grossnickle and Reid 1984 a&b; Grossnickle and Heikurinen 1989; Folk et al. 1996). These environmental cycles universally affect seedling performance and it is the variation in species specific response to site environmental conditions that defines their performance on restoration sites across North America.

Further information on ecophysiological processes of plants can be found in a number of publications (Landsberg 1986; Kozlowski et al. 1991; Larcher 2003; Smith and Hinckley 1995a, 1995b; Kozlowski and Pallardy 1997; Bigras and Colombo 2001; Lambers et al. 2008; Lange et al. 2011a&b; Osmond et al. 2011a&b). Publications in the form of books (Duryea and Brown 1984; Duryea and Landis 1984; Lavender et al. 1990; Duryea and Dougherty 1990; Hobbs et al. 1992; Grossnickle 2000; Landis et al. 1989, 1990, 1992, 1999 & 2010; Wagner and Colombo 2001) or reviews (Burdett 1990; Margolis and Brand 1990; Lamhamedi and Bernier 1994; Grossnickle et al. 2001; Grossnickle 2005 & 2012; Grossnickle and South 2014) specifically related to nursery practices and forest restoration programs are available with an ecophysiological perspective.

3 Stress and the cyclical nature of stress resistance

"A biological stress may be defined as any environmental factor capable of inducing a potentially injurious strain in living organisms." **Levitt (1980)**

Seedlings are exposed to stress when environmental conditions limit their performance. Levitt (1980) considers there to be two main types of stress: biotic (i.e. infection or competition from other organisms) and physiochemical (i.e. temperature [low – chilling & freezing, heat], water [drought & flooding], radiation [type &

amount], chemical [salts, herbicides & insecticides], and physical [wind, pressure & sound]) affecting plant performance. In addition, the duration, timing and intensity of stress events can add multiple layers to these types of stress (Kozlowski 1991). The combination of various types of stress along with the multiple layers of stress makes it a complex process for practitioners to avoid or moderate their effects on seedling performance. Plants have developed various physiological attributes to alleviate impacts of stress. In addition, the capability of seedlings to minimize impacts of stress on performance changes throughout the year. The following discussion examines how seedlings respond to frost and drought, cyclical changes in stress resistance throughout the year and how these cyclical changes can be used to develop cultural practices to harden seedlings and, thereby improve field performance.

Freezing tolerance is defined as the lowest temperature below the freezing point that a tissue can be exposed to without damage (Sakai and Larcher 1987). Up until the point that cells are damaged by frost they retain their functional integrity. Plants have a combination of physiological mechanisms that act to develop a tolerance to freezing temperatures (i.e. changes in tissue water content, cell solute concentration, and membrane permeability – Levitt 1980) as they go through the fall acclimation process. Morphological structures of tree species have varying degrees of freezing tolerance, with foliage, branches, and stems having the greatest level; the shoot structure and buds having usually a moderate level; root systems the lowest level of freezing tolerance (Sakai and Larcher 1987). Thus seedling exposure to a frost event can be lethal or not, depending on what plant parts are exposed to the event, exemplifying the multi-faceted nature of stress.

Water stress occurs in trees "...when a decrease in water content, or an increase in water deficit, reaches a level which negatively affects a physiological process..." (Teskey and Hinckley 1986). Each plant species responds to water stress through a combination of avoidance and tolerance physiological mechanisms (Jones et al. 1981; Kramer and Boyer 1995; Ludlow 1989). Drought avoidance is the postponement of dehydration by the reduction of water loss from foliage (cuticular development, stomatal control, total leaf area), a very efficient water transport system (xylem conducting capability), or through the maintenance of water uptake (increased rooting) (Teskey and Hinckley 1986). Drought tolerance is the capacity of the plant protoplasm to undergo dehydration without irreversible injury and is primarily determined by the maintenance of turgor (tissue elasticity and solute accumulation) or desiccation tolerance (protoplasmic and chloroplast tolerance to drought) (Teskey and Hinckley 1986). Drought resistance is the combination of avoidance and tolerance mechanisms (Levitt 1980). Tree species are considered to be under water stress when exposed to values of plant Ψ that decline below -1.0 to -1.25 MPa (Cleary and Zaerr 1980). Different plant physiological activities cease to function (e.g., growth, stomatal closure, reduction in P_n) at different levels of moderate water stress (-0.5 to -2.0 MPa), while other activities occur to enhance drought resistance (e.g. osmotic adjustment, ABA accumulation) (Hsaio 1973), with plant Ψ values below -2.0 MPa causing a shutdown in physiological processes (e.g. P_n in Fig. 2b) and potentially severe physiological damage (Hsaio 1973). Seedlings regularly undergo a range of plant Ψ values on any given day (e.g. Fig.7a) with certain physiological processes ceasing to function while exposed to a specific plant Ψ (reviewed by Hsaio 1973), with a continuous exposure to water stress limiting seedling growth (Fig. 2c). Forest tree species can seasonally reach plant Ψ levels as low as -2.5 to -3.0 MPa and desert tree species can decline to levels as low as -8.0 MPa (Scholander et al. 1965) and are still able to recover and grow under less stressful water deficits. Thus when seedlings recharge from water in the soil, low plant Ψ is relieved and physiological activities resume, though if drought was severe enough it might take an extended timeframe for the recovery of normal physiological activities (e.g. gas exchange response can take weeks to recover – Fan and Grossnickle 1998; Grossnickle and Fan 1999).

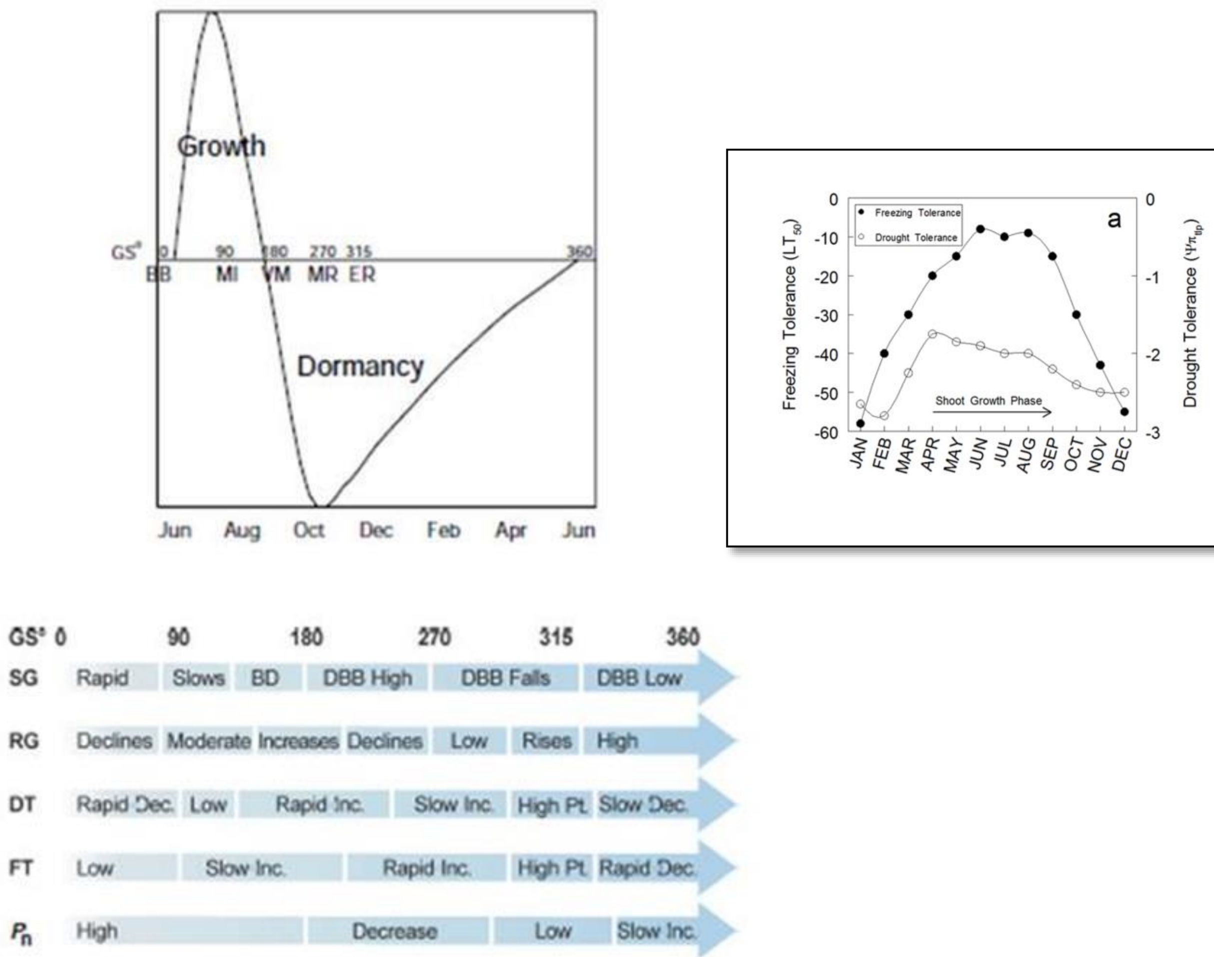

Figure 5. Degree growth stage model for spruce, depicting the seasonal cycle of morphological development and physiological processes (Grossnickle 2000). Abbreviations for the growth stage model are as follows: (BB) budbreak, (MI) maturity induction, with (VM) vegetative maturity to (MR) maximum rest (i.e. endodormant), (ER) end of rest (i.e. ecodormant). Abbreviations for morphological development are (SG) shoot growth, (BD) bud development, (DBB) days to budbreak, and (RG) root growth. Abbreviations for physiological processes are (DT) drought tolerance, (FT) freezing tolerance, and (P_n) net photosynthesis. Insert figure (a): Seasonal change in the freezing tolerance (LT_{50} - temperature causing 50% foliage electrolyte leakage) and drought tolerance ($\Psi_{\pi tlp}$ - osmotic potential at turgor loss point - MPa) of spruce seedlings (adapted from Grossnickle 2000 and Grossnickle 1989, respectively).

Timing of stress throughout a plant's seasonal cycle can influence the stress intensity required for environmental conditions to limit seedling performance. Tree species undergo many morphological and physiological changes during an annual cycle in response to seasonal environmental conditions. The dynamic nature of these changes is illustrated by a degree growth stage model (Fuchigami et al. 1982;

Fuchigami and Nee 1987), with this model used to define seasonal physiological cycles of stress resistance (e.g. drought and freezing tolerance – reviewed by Burr 1990; Bigras 1996), as well as shoot (reviewed by Lang et al. 1985; Lavender 1985) and root (reviewed by Ritchie and Tanaka 1990) growth patterns for tree species. Similar seasonal cycles, as those described above, were observed in programs whether these conifer species originated from the northern latitude boreal forest (spruce species – Fig. 5), the Pacific Northwest coastal forest (western red cedar – Grossnickle 1992; Grossnickle and Russell 2006), or to a lesser extent the mid-latitude forest (loblolly pine – Grossnickle and South 2014). Seasonal changes in phenological, physiological, and morphological parameters occur in parallel and are not always directly linked throughout the yearly cycle (Bigras 1996). However, their parallel nature allows one to draw general observations on the timing of stress events and their effects on plant performance. For example, spruce seedlings have minimal drought and freezing tolerance during the growing season (Fig. 5a); which is why timing of planting programs and silvicultural practices is important to minimize effects of potential stress events on seedling performance (Grossnickle 2000). As spruce seedlings go through fall acclimation, tolerance to both drought and frost increases (Fig. 5a) and a point of maximum stress tolerance occurs in the winter when they are ecodormant (Fig. 5).This means that stress intensity that can limit performance shifts as a tree species tolerance to stress shifts seasonally. One has to take into consideration both seasonal timing, along with stress intensity, when trying to define whether environmental conditions are limiting seedling performance.

Cultural practices that provide an enhanced “physiological quality” to seedlings have long been considered important in increasing their chances for improved field performance (Wakeley 1948 & 1954), as nonhardened seedlings lack the physiological capability to become rapidly established after planting on forest restoration sites (Rowe 1964; Tinus 1974; Hobbs 1984). Levitt (1980) describes plants as adaptable, meaning they are capable of gradually developing physiological resistance when exposed to moderate stress, which provides them with capabilities to handle environmental stress events. Since acclimation of seedlings is based on the concept of “slowly increasing stresses to induce physiological adjustments in plants” (Kozlowski and Pallardy 2002) one can create cultural practices to enhance tolerance or avoidance to stress (e.g. frost and drought), thereby developing protection from potentially stressful field site conditions. Nursery practitioners have come to understand this phenomenon and have created practices that either moderate the potential stress event on their crop or enhance the development of seedling stress resistance (Wakeley 1954; Lavender and Cleary 1974; Landis et al. 1999).

This knowledge of plant acclimation can be applied to improve seedling quality and resulting field performance. For example, understanding that seedlings in the fall require exposure to shortening photoperiods and cold temperatures to stop shoot growth and develop stress resistant is important for proper lift/store practices (Grossnickle and South 2014). Knowing this pattern of fall acclimation also allows for the application of nursery practices to protect root systems, because frost events can expose tree species lacking sufficient root freezing tolerance to crop damage (Colombo et al. 2001; Landis et al. 2010). Also, the late growing season application of nursery cultural practices such as moderate water stress and reduced fertilization, along with this understanding of seasonal shift in stress resistance, can be used as a means to stop growth and ‘harden’ seedlings with nursery cultural practices (e.g.

bareroot – Duryea 1984; Mexal and South 1991 or container-grown – Landis et al. 1989; Wenny and Dumroese 1999) for improved field performance. As an example, this principal was applied to create hardening nursery cultural practices for growing seedlings used in restoration programs in the boreal forest (Binnie et al. 1994; Grossnickle et al. 1994; Grossnickle and Folk 2003), mid-latitude forests (Grossnickle and South 2014) and Pacific Northwest coastal forests (Grossnickle et al. 1991a; Arnott et al. 1994; Major et al 1994a). These hardening nursery cultural practices enhanced seedling performance on restoration sites in the Pacific Northwest coastal forests (Grossnickle et al.1991b; Grossnickle and Arnott 1992; Major et al 1994b; Folk et al. 1994; Folk et al. 1995) and the boreal forest (Grossnickle and Major 1994b; Grossnickle and Folk 2003). This demonstrates that the seasonal cycle of stress resistance broadly affects seedling quality and field performance of many tree species.

Since plant resistance to drought and freeze events can be tied to their normal phenological cycle, hardening benefits are ephemeral in nature. As tree species initiate shoot growth in the spring, drought tolerance (Teskey and Hinckley 1986; Abrams 1988; Grossnickle 2000) and freezing tolerance (Burr 1990; Bigras et al. 2001) can be lost in rapid fashion. For example, interior spruce seedlings lost a good portion of their stress resistance to drought and frost within weeks of initiating growth (Fig. 5a). In addition, seedling nutrient reserves (e.g. from standard or nutrient loading cultural practices) decline after planting, due to dilution in tissue nutrient concentrations where external nutrient sources cannot meet demands of new growth (Munson and Bernier 1993; Malik and Timmer 1998; Kim et al. 1999). By knowing how tree species respond to stress, nursery practices can be applied as a means to improve seedling quality prior to outplanting and their subsequent field performance. However, a seedling's ability to utilize improved physiological plant attributes to overcome planting stress and become established is a narrow window, making it very difficult to quantify long term field performance solely on these hardening or nutrient loading practices. For this reason, seedling survival and successful establishment is not only predicated on hardiness and nutrient status, but also on morphological attributes and capability to grow roots after planting (Grossnickle 2012).

4 Seedling quality: Product versus Process

"The whole concept of nursery stock grades is based upon seedling capacities for survival and growth after planting." **Wakeley (1954)**

Seedling quality programs have evolved over the past 60 years because of the need for a better understanding of nursery-grown seedling performance capabilities on restoration sites. Wakeley (1954) is usually recognized as the first person to identify the importance of morphological and physiological grading of seedlings prior to planting onto restoration sites. Seedling quality is now defined as the seedlings' "fitness for purpose" (Sutton 1980), as it relates to achieving specific silvicultural objectives. Clear and comprehensive seedling quality information is necessary to make effective stocktype selection and field planting choices. Worldwide, seedling quality programs are used by nursery personnel and foresters to ensure quality control, enhance consumer confidence, avoid planting damaged stock, and improve nursery cultural practices (Dunsworth 1997). The following discussion examines seedling quality from two approaches. From a product approach, one can define functional integrity, operational grading and sometimes performance potential. An alternative approach is to monitor the process. Thus, there are a number of conceptual approaches that can be applied in conducting a seedling quality program.

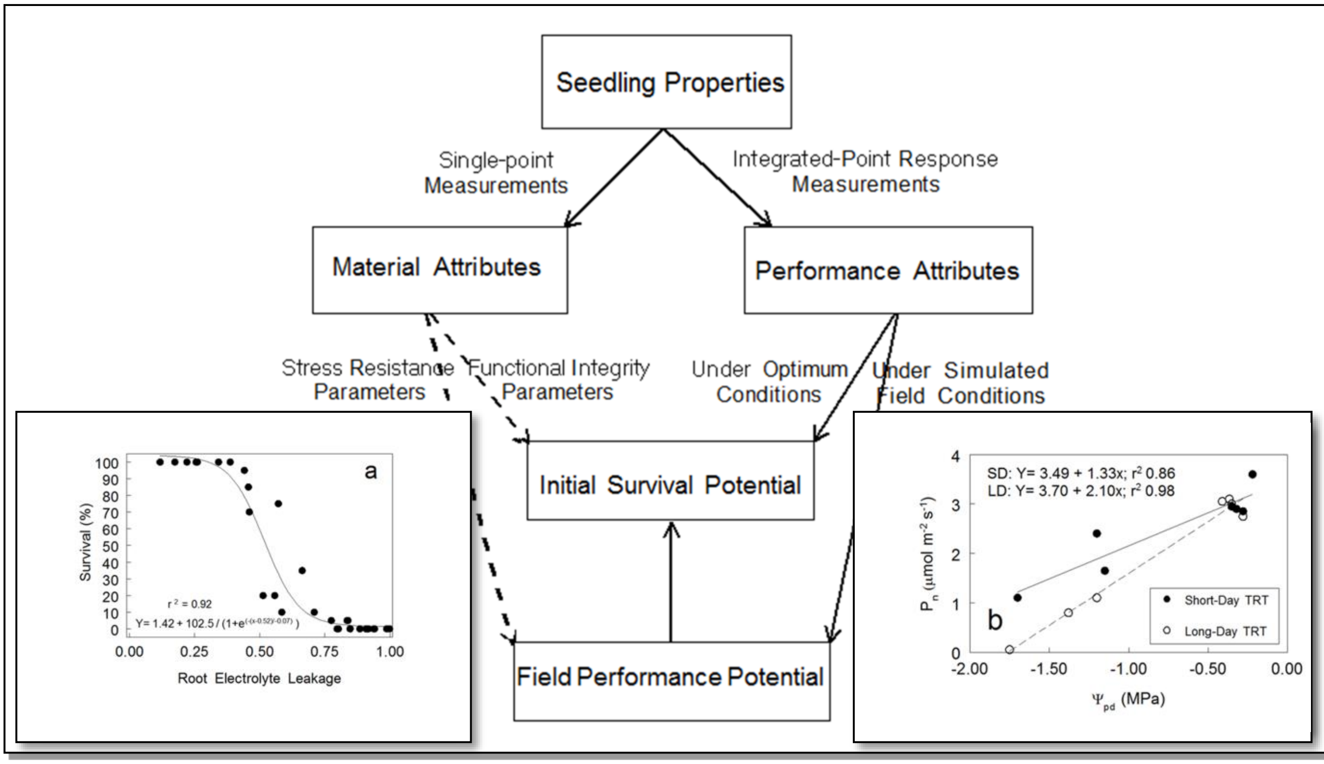

Figure 6. A conceptual seedling quality model describing the relationship between material attributes and performance attributes in relation to initial survival potential or field performance potential in an assessment program (adapted from Folk and Grossnickle 1997). Insert left figure (a) Functional integrity assessment of interior spruce seedlings with damaged root systems measured by root electrolyte leakage (1 day after stress) (subpopulation of N = 8) and survival (N = 25) (8 weeks after stress) (Grossnickle 2000). Insert right figure (b) Performance potential assessment of western hemlock (*Tsuga heterophylla* (Raf.) Sarg.) seedlings defined by changes in net photosynthesis (P_n) during simulated planting stress for seedlings with a number of defined drought resistant material attributes (i.e. Short-day treated seedlings had an osmotic potential at turgor loss point (Ψ_{tlp}) of -2.7 MPa and a shoot to root ratio (S/R) of 2.6, while long-day treated seedlings had a Ψ_{tlp} of -2.3 MPa and a S/R of 4.2 (adapted from Grossnickle et al. 1991a).

Seedling quality has evolved to include both morphological and physiological tests (see Information Sources section below for references on specific tests). The wide array of testing procedures now available has sometimes led to confusion in defining the specific purpose of an assessment program. Part of this confusion stems from the fact that measuring seedling quality encompasses both nursery development (nursery growth phase, determination of lifting for storage, quality during/after storage) and testing immediately before planting to forecast survival and/or field performance (Duryea 1985b). With a clear definition of purpose for using specific testing techniques, nursery personnel and foresters can focus on obtaining detailed information needed to make effective decisions.

When nursery personnel and foresters consider using a quality program to assess their seedlings, a commonly expressed concern is how to select tests that are useful in providing information needed to make effective cultural decisions, stock selection and field planting choices. A conceptual model provides a means of understanding the importance of plant attribute types when defining their usefulness within a seedling quality program having a specific silvicultural objective (Fig. 6). Seedling quality combines measurements of plant properties defined as material or performance attributes (Ritchie 1984). Material attributes are single-point measures of individual parameters representing specific plant subsystems (e.g., morphology, osmotic potential, root electrolyte leakage, nutrient content/concentration, and individual gas exchange measurements). In contrast, performance attributes reflect an integration of many material attributes, are environmentally sensitive plant properties, and are measured under specific testing conditions (e.g., root growth potential, freezing tolerance, 14-day gas exchange integrals). Both attribute types provide information on initial survival and field performance potential. Nursery personnel and foresters need to define specific objectives before selection of various testing procedures within a seedling quality program.

4.1 Product - Functional integrity

Initial survival potential is a measure of seedling "functional integrity" (Grossnickle and Folk 1993). Functional integrity indicates whether stock is, or is not, damaged to the point of limiting primary physiological processes. This testing approach removes seedlings that do not meet certain minimum physiological performance standards (i.e. "bad apple concept"). For example, root electrolyte leakage (REL) is a good measure of root system integrity (McKay 1992; Bigras and Calmé 1994) and is an assessment procedure that can be used to cull damaged crops. An example of this assessment procedure shows how it was able to detect root damage, with survival of spruce seedlings related to measured REL values (Fig. 6a). Seedlings meeting minimum standards typically have a greater capability to survive in all but the most severe of field site conditions (Sutton 1988). There are a number of plant attributes that effectively forecast survival after outplanting (reviewed by Grossnickle 2012). However, there is no guarantee that testing for initial survival potential provides information on field performance potential under limiting environmental conditions.

4.2 Product - Performance potential

Seedling performance on a restoration site depends on inherent growth potential and the degree to which field site environmental conditions limit or enhances that potential. Thus, the degree to which seedlings are suited to site conditions has the greatest influence on their performance immediately after planting (Burdett 1983). Plant attributes forecasting field growth need to define the intrinsic performance potential of planting stock to site conditions (Sutton 1982 & 1988). There are a number of operational grading criteria that can be used to forecast field performance (e.g. height, diameter, various shoot to root ratios, root growth potential, nutrient status, stress resistance); references describing specific attributes and testing procedures are found in the Information Sources section. However, when looking at more detailed assessment of seedling performance potential, plant attributes should be selected that characterize performance in relation to anticipated field site environmental conditions (Duryea 1985b; Sutton 1988; Puttonen 1989a; Grossnickle et al. 1988; Hawkins and Binder 1990; Grossnickle and Folk 1993; Folk and Grossnickle 1997). For example, in a controlled assessment of seedling performance, western hemlock (*Tsuga heterophylla* (Raf.) Sarg.) seedlings with a desirable pre-plant drought tolerance and avoidance attributes were able to withstand simulated planting stress (Fig. 6b). In the field, these same seedlings had more rapid initial root growth resulting in a better field shoot/root ratio (Grossnickle et al. 1991b), thereby resulting in a higher P_n and water use efficiency during the growing season (Grossnickle and Arnott 1992). One caveat to this approach is that attempting to forecast seedling field performance can only simulate anticipated field environmental conditions and it is just a "snap-shot" of a single point along their seasonal performance pattern (Grossnickle and Folk 1993), which changes as they go through their normal phenological cycle (see Stress and the Cyclical Nature of Stress Resistance section). Therefore, this approach of measuring seedling quality should be considered as a method to forecast, but not predict, field performance. With this caveat in mind a number of approaches have been developed to combine testing procedures to characterize seedling performance to stress events they are typically exposed to on restoration sites (e.g. performance potential index (Grossnickle et al. 1991c), covariate morphological attributes (Kaczmarek and Pope 1993), multiple variable models (Jacobs et al. 2005)). These approaches provide forecasting models to help define new stocktypes and cultural practices.

Specifically, the approach taken by Grossnickle et al. (1991a) was designed as a means to characterize new stocktypes (Grossnickle and Major 1994a), cultural products (Grossnickle et al. 1996) and cultural practices (Grossnickle et al. 1991b; Arnott et al. 1994; Major et al. 1994). The long term planned use of this assessment procedure was to characterize somatic stocktypes whereby genotypes could be reproduced as needed for forest restoration. This assessment procedure was a companion program to scaling the somatic embryogenesis tissue culture procedures for use in forest regeneration (Grossnickle et al. 1996; Sutton et al. 2004). Once the nursery production system could produce comparable operational quality somatic and zygotic seedlings (Grossnickle and Folk 2005), performance potential testing enabled the characterization of every genotype within a somatic seedlot (Grossnickle and Folk 2007). This information allowed for the selection of genotypes best suited to forest site conditions, thereby creating tailored seedlots to aid foresters in applying benefits of clonal forestry.

One must recognize that no single test is available for all seedling quality issues (Mattsson 1997; Puttonen 1997). Morphological attributes should not be used solely to assess seedling quality, because morphology does not describe their physiological vigor (Mexal and Landis 1990). Also, seedling quality cannot be determined by individual physiological attributes in isolation from other physiological and morphological attributes (Lavender 1988). A proper program should use a combination of morphological and physiological attributes to provide information to make sound seedling-related nursery cultural and forest restoration decisions.

4.3 Monitor the process

To develop an effective seedling quality program that monitors the process, one needs to understand how the crop responds to nursery cultural conditions. A crop's physiological response to the environment ultimately determines its performance in relation to nursery conditions (see Learning to Think Like a Tree section). If nursery personnel understand a species' physiological capability in relation to environmental conditions, then one can create cultural guidelines, or standard operating procedures, that guarantee a quality crop. Guidelines define the cultural process in detail and ensure the repeat growing of a quality crop within each production season. This approach fits into concepts put forward by the ISO Quality Assurance program that is built on the principle of a controlled and consistent approach for the production of a product to ensure effective program operation (Anon 2002).

Every crop has its own unique identity. Thus, one needs to select the correct cultural guidelines for application to a crop that is started at a specific time, resulting in the exposure to certain seasonal environmental conditions, with a delivery date meeting the customer's requirements. Guidelines need to be integrated into a crop plan to satisfy specific objectives for producing each crop of high quality seedlings (e.g. bareroot - May 1985; container-grown - Landis et al. 1999).

Once the plan has been developed, a tracking system is important to ensure that the agreed-upon cultural guidelines are being followed. The process needs to be consistently monitored to ensure the crop is growing according to the plan. The process of monitoring crop production falls into three major activities (Grossnickle 2011). First, tracking the environment to define both optimum and limiting conditions for crop performance. Second, tracking crop performance is done by defining important points in the plant development process. This is accomplished by selecting critical morphological and physiological parameters that describe crop performance. Third, there needs to be a crop diary to describe operational and cultural adjustments to the crop plan. Deviations to the plan are recorded so that during a crop review and after crop completion, one can understand where adjustments to cultural practices (i.e. guidelines) need to be refined to improve performance in future production cycles. All of this information does not help in producing a quality crop unless there is a system to respond when the crop starts to deviate from the plan. To ensure continued improvement with each production cycle the quality system needs to track crop cycles, and define good, bad and ugly patterns of performance. This information then needs to be synthesized across crops and seasons to define cultural practices to eliminate, as well as to integrate beneficial practices into guidelines. In this way the quality assurance program becomes a positive system of change and continued improvement in crop cultural practices.

This approach fits into concepts put forward by the ISO Quality Assurance program; to apply suitable methods for monitoring the production process to ensure achievement of the planned results (Anon 2002). At CellFor Inc., this form of quality monitoring system was designed and operated for a nursery program that scaled to tens of millions of seedlings (i.e. miniplug and finished) at ten nurseries across North America. This program enabled CellFor Inc. to produce high quality somatic loblolly pine (*Pinus taeda* L.) seedlings used in forest restoration throughout the Southeastern United States. The conclusion drawn from creating and running this operational quality program demonstrated that when designed to monitor the process, quality seedlings were the final output.

4.4 Information sources

This discussion focused on conceptual approaches used in conducting a seedling quality program. Further information on seedling quality testing approaches and detailed descriptions on measuring specific plant attributes can be found in the following references (see reviews by Sutton 1979; Chavasse 1980; Jaramillo 1980; Schmidt-Vogt 1981; Ritchie 1984; Duryea 1985; Glerum 1988; Lavender 1988; Puttonen 1989; Hawkins and Binder 1990; Johnson and Cline 1991; Omi 1991; Mattsson 1997; Mohammed 1997; Puttonen 1997; Grossnickle 2000; Colombo et al. 2001; Landis et al 2010; Riley et al. 2011).

5 Planting Stress and Seedling Establishment

"The most important cause of death of transplanted seedlings is desiccation." **Kozlowski and Davies (1975)**

Planting stress is prevalent in all forest restoration programs. Since hundreds of millions of seedlings are planted world-wide every year, planting operations are consistently challenged by planting stress. A number of surveys evaluating reasons for poor plantation establishment have determined that the greatest mortality on restoration sites occurs from planting stress (Vyse 1981; Waters et al. 1991; Grossnickle and El-Kassaby 2015). Therefore, planting stress has been identified as a detrimental phenomenon to the establishment of newly planted seedlings (Kozlowski and Davies 1975; Grossnickle 1988a; Rietveld 1989; Burdett 1990). Planting stress occurs when seedlings are not fully coupled into the hydrologic cycle whereby water flows from the soil to plant roots, through the plant and into the atmosphere through the soil-plant-atmosphere continuum (SPAC) (Grossnickle 2005). There are a number of factors restricting this SPAC water movement which can result in planting stress (Fig. 7) and they are discussed below.

The environment around newly planted seedlings has a direct bearing on exposure to planting stress. Restoration sites present extreme environmental conditions that alter site heat exchange processes and soil water relations (Miller 1983). The availability of soil water within the root-zone of a newly planted seedling is restricted under drought or low temperature edaphic conditions. These limiting edaphic conditions cause increased resistance to water flow through the SPAC, thereby limiting water uptake and resulting in plant water stress (reviewed by Grossnickle 2005). In addition, VPD of air is the driving force within the hydrologic cycle causing transpiration (Fig. 2). As VPD increases, plant Ψ declines (Ritchie and Hinckley 1975; Hinckley et al. 1978) creating conditions where seedling water stress can reach a level causing reduced growth and establishment capability. In a number of studies, seedlings exposed to planting stress had plant Ψ levels as low as -2.0 to -3.0 MPa (e.g. Dixon et al. 1983; Hobbs and Wearstler 1983; Grossnickle and Heikurinen 1989) (Fig. 7a) indicating that water stress levels were severe enough to cause a shutdown in physiological processes (e.g. P_n in Fig. 2b) and cause potentially severe physiological damage (Hsaio 1973).

Planting stress does not occur when newly planted seedlings have abundant soil water and low atmospheric evaporative demand. Under these conditions, minimal new root growth is required because the existing root system of a newly planted seedling adequately supplies water to the shoot system to meet transpirational demands (Simpson and Ritchie 1997).

During the planting process, soil is placed around the seedling root system and firmly packed in by the planter. Due to the irregular nature of soil particles, air gaps may occur at the root-soil interface. These air gaps can result in planting stress (Sands

1984), as water can cross this air gap only in the vapor phase, which is considerably less efficient than liquid water movement (Kramer 1983). These air gaps can result in a greater resistance to water flow (e.g. 25 to 50% greater plant resistance) from the soil to the root system of a newly planted seedling (Grossnickle 1988a; Wilson and Clark 1998) due to the failure of freshly disturbed soil to pack properly around roots (Stirzaker and Passioura 1996). As soil particles start to settle and pack around the root system and with an initiation of new root growth there is a decline in resistance to water movement through the SPAC (Wilson and Clark 1998).

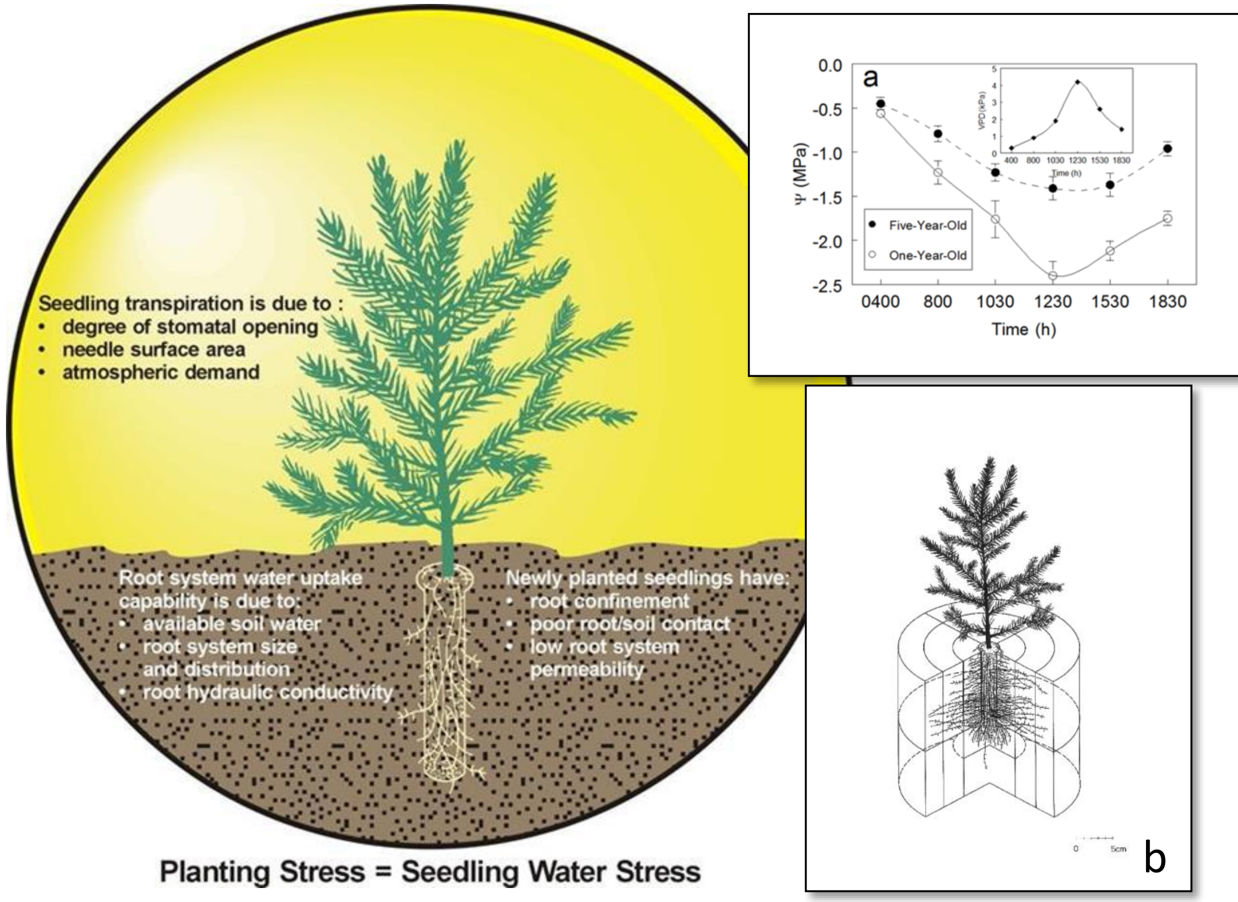

Figure 7. Descriptive representation of planting stress in a recently planted seedling (adapted from Grossnickle 2000). Insert top figure (a): Mid-summer diurnal water status (shoot water potential - Ψ) of newly planted and established (i.e. planted five years earlier) container-grown Lodgepole pine (*Pinus contorta* Dougl.) seedlings planted on a restoration site in Colorado (Grossnickle 1983). Insert figure represents vapor pressure deficit (VPD) measured during the day. Insert bottom figure (b): Diagrammatic representation of root development for established interior spruce seedlings (n= 25 – averaging 108 (+/- 12) new roots resulting in 365 cm (+/- 30) of new roots out of the container plug) four months after planting on a restoration site (Grossnickle and Major 1994b).

Root resistance to water uptake is variable, depending upon the amount of new root development that occurs just after planting. New unsuberized roots allow for a more efficient uptake of water (i.e., lower resistance to water flow) than suberized roots (reviewed by Grossnickle 2005). This ability of newly developed roots to have high water uptake capability allows recently planted seedlings with new root growth to maintain a proper water balance, thereby decreasing the chance of water stress (Nambiar et al. 1979).

Root confinement due to the lack of new root growth in newly planted seedlings can result in increased water stress (Baldwin and Barney 1976; Sands 1984; Draper et al. 1985; Kaushal and Aussenac 1989; Bernier 1993). Newly planted seedlings have a higher resistance to water movement through the SPAC than older seedlings with root systems that have developed outward into the surrounding soil (Grossnickle 1983). Thus, under the same environmental conditions newly planted seedlings can have greater water stress compared to older seedlings with well-developed root systems (Fig. 7a). Minimal root development into the surrounding soil limits newly planted seedlings access to soil water and can result in water stress. Therefore, planting stress can lead to root growth being limited by the lack of water and photosynthates, and in turn photosynthesis being limited by water stress due to a lack of root growth (Burdett 1990; Grossnickle 2000).

Recently planted seedlings that have sufficient new root development become coupled to the field site resulting in improved water status, allowing them to enter the establishment phase (reviewed by Grossnickle 2005). For example, recently outplanted interior spruce seedlings with minimal water stress during the first month after planting (i.e. -0.52 MPaΨ_{pd} & -1.20 MPaΨ_{min} – minimum daytime water potential) had rapid root development during this timeframe (i.e. 25 new roots resulting in 60 cm of new roots out of the container plug) (Grossnickle and Major 1994b). These seedlings had a water balance throughout the remainder of the summer (i.e. -0.62 MPa Ψ_{pd} & -1.26 MPaΨ_{min}) that was a typical pattern for established trees (Ritchie and Hinckley 1975). The result was seedlings with a well-developed root system (Fig. 7b) and very high survival (96%) (Grossnickle and Major 1994b) at the end of the first field season. Therefore, root growth out into the surrounding soil has been defined as the most critical step in overcoming planting stress (Grossnickle 2005). This positive feedback loop of better plant water balance and root growth allows recently planted seedlings to become established on the restoration site (Burdett 1990; Carlson and Miller 1990; Margolis and Brand 1990; Grossnickle 2000).

6 Seedling death: Sometimes simple and sometimes complicated

"Trees die when they cannot acquire or mobilize sufficient resources to heal injuries or otherwise sustain life." **Waring (1987)**

Tree death can sometimes seem very abrupt, though it is typically a complex and gradual process (Franklin et al. 1987; Waring 1987). Franklin et al. (1987) defined very similar abiotic and biotic (i.e. physiochemical) factors to those of Levitt (1980) (see Stress and the Cyclical Nature of Stress Resistance section) as the common contributors or causes of tree death. These factors in combination with their duration, timing and intensity are the source of stress (Kozlowski 1991), which can be severe enough to cause seedling death. In addition, the final cause of death might not actually be the factor that initiated the "mortality spiral", because typically there can be a cumulative series of stress factors that contribute to tree death (Franklin et al. 1987). For example, many times tree death occurs due to disease causing agents, though previous factors may have predisposed trees to death by disease (Shigo 1985). It is difficult to always define the specific factor(s) that cause death. If seedling death is to be avoided, it is critical to ameliorate environmental stress and to reestablish normal plant physiological processes (Waring 1987). The following discussion describes reasons for seedling death and how to institute practices to moderate conditions that cause stress, thereby improving chances for successful forest restoration.

6.1 Sometimes simple

Within operational nursery and forestry programs environmental conditions can occasionally become extreme or management practices can fail and seedling death occurs. Sometimes issues surrounding seedling death are easy to diagnose. This typically occurs when there is an easily identifiable operational event that is not conducted correctly (e.g. equipment malfunction, improper timing of a cultural practice, or miscommunication between personnel). In these cases there is a rapid identification of the problem, with nursery personnel or foresters able to apply correct cultural practices or revised management decisions to rectify the problem.

Ambient nursery or field site condition can cause an identifiable environmental event, such as frost (Bigras et al. 2001) or drought (McDowell et al. 2008), that is severe enough to cause death. Both frost (reviewed by Sakai and Larcher 1987) and drought (reviewed by Allen et al. 2015) are considered predominant environmental factors that cause tree death. Cultural practices can be applied to minimize the potential of severe environmental site conditions causing further losses, though sometimes it is unavoidable that seedlings are exposed to stressful frost or drought events in the field that can cause death. The following are examples of seedling death in response to these environmental factors.

Spring and fall frost events are common on restoration sites in the northern latitude forests with the greater frequency of frost events increasing as silvicultural systems remove the vegetation cover and exposes the site to more open sky (Grossnickle 2000). Damage and seedling losses due to frost typically occur when shoot growth initiates in the spring, because tree species normally have a low level of frost resistance as they enter the shoot growth phase (see Stress and the Cyclical Nature of Stress Resistance section). These spring frost events can causing instantaneous cellular damage (i.e. cellular damage occurs within minutes of exposure to an overnight frost event) and depending on their shoot developmental stage the potential for tissue damage or death can be high at frost temperatures ranging from -2 to -10°C (Fig. 8a). Most conifer species have minimum levels of frost tolerance from 0 to -10°C during their active growing phase (reviewed by Bigras et al. 2001). As a result, frosts during the growing season are considered a principal problem in establishing tree plantations in northern latitude forests (Sakai and Larcher 1987).

When seedlings are exposed to drought the response causing death can either be very rapid in recently planted seedlings (see Planting Stress and Seedling Establishment section), or it can be long and drawn–out. Extended periods of drought (i.e. months to years) are typically required for water stress to become extreme enough to cause death in established trees (Allen et al. 2015). However, the combination of warmer air temperatures and lower humidity create higher VPD conditions (Grossnickle 2000) which reduces the time required to reach water stress conditions that can cause mortality (Adams et al. 2009). These more extreme atmospheric conditions increase the potential for greater tree mortality in drought-prone forests (Eamus et al. 2013). Open forest restoration sites can create summer conditions (i.e. high atmospheric evaporative demand and low available soil water) which can cause seedling mortality (Grossnickle 2000). Depending on the tree species and state of development and ecosystem setting, death occurs when plant Ψ for forest tree species exceeds -2.5 to -6.0 MPa (McDonald and Running 1979; McDowell et al. 2008; Adams et al. 2009; Duan et al. 2015) while for some desert tree species a plant Ψ as low as –7.0 to -8.0 MPa is required (McDowell et al. 2008; Duan et al. 2015). For example, established western red cedar (*Thuja plicata* Donn ex D. Don) seedlings died after three months of drought that became severe enough (i.e. plant Ψ < -3.3MPa) to cause death (Fig. 8b). This species typically grows in the Pacific Northwest coastal forests where precipitation is abundant, though it can be exposed to summer drought conditions, thus it is a tree species that can only withstand moderate drought conditions (Lassoie et al. 1985). Established seedlings can withstand a wide range of plant Ψ for long periods of water stress and still recover, if rewatered, before water stress becomes extreme and causes death. Alternatively, the combination of dry summer atmospheric conditions and a reduction in available soil water due to vegetation cover can cause drought to become severe enough to increase mortality of seedlings during their initial years on restoration sites (Grossnickle 2000) and in established trees (Birdsey and Pan 2011) in northern latitude forests.

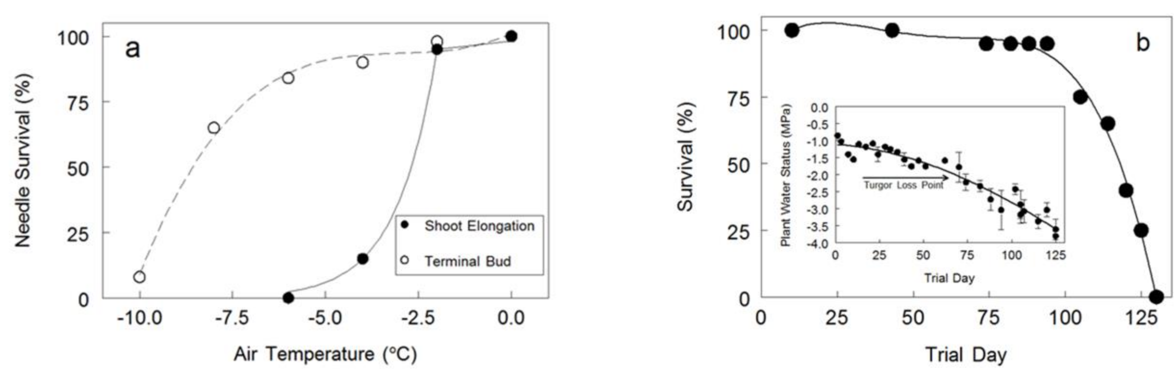

Figure 8. (a) Needle survival of black spruce seedlings in response to springtime frost events for shoots undergoing elongation or with non-swollen terminal buds (adapted from Bigras and Herbert 1996). (b): Change in the survival and plant water status (measured as plant Ψ) of established western redcedar (*Thuja plicata* Donn ex D. Don) seedlings in relation to drought over time (Note: $\Psi_{\pi tlp}$from Grossnickle 1993, with survival and plant water status from Grossnickle unpublished data).

6.2 Sometimes complicated

Other times the issues around seedling death are complicated, because reasons are not readily apparent. What makes the restoration process unique is that not only are abiotic and biotic factors part of the equation, but the restoration process itself is a situation where a practitioner is involved in the process of growing seedlings in the nursery, handling them as they move from the nursery to the field and then applying silvicultural practices on the restoration site. These practices are intended to mitigate potential environmental stress events and enhance seedling performance as they go through various phases of development in the field (Fig. 9). Thus, it is difficult to discern the cause of seedling death due to all of these possible interactions between the environment and various practices that can create abiotic stress related to multiple factors. Experience has shown that sometimes forest restoration operations break down due to the biology of hundreds of thousands to millions of seedlings, interacting with a multi-faceted operational nursery and regeneration silviculture programs that are driven by deliverables and timelines. A successful restoration program requires personnel from many disciplines to work as an integrated team handing-off seedlings through a series of operational steps. As a result, sometimes seedlings are exposed to environmental stress, which can limit their physiological performance causing reduced growth (Kozlowski 1991; Waring 1991) and sometimes death (Waring 1987). The result can be seedling losses without a true understanding of where the program did not meet the planned outcome. Many times it is a combination of factors, each done slightly outside of the defined standard practice, across the entire restoration process resulting in a cumulative number a stress events that leads to seedling losses in the field. Unfortunately, in most cases for operational programs, fully detailed information is not recorded to help identify potential issues that caused seedling death.

A Quality Assurance program (i.e. systematic process of checking to see whether practices used to ensure positive crop performance are meeting specified requirements) can identify and define reasons for seedling loss. This program monitors the production process and environmental conditions, identifies performance issues and defines plans to rectify any deviations (see Seedling Quality – Monitor the Process section and Grossnickle 2010). When a Quality Assurance program is not in place, forensic investigations are typically required to try and sort out which factor(s) caused seedling losses. Relying on the involved participants to have sufficient ‘program memory’ to identify environmental conditions or practices that did not meet defined standards is not ideal and ultimately leads to incident reports trying to define all parameters that ‘could’ have contributed to these losses. This information can then be used to define steps to avoid operational practices that can cause stress on seedlings and lead to their death.

The forest restoration process is complex because successful stand regeneration requires combining an understanding of physiological performance and morphological development characteristics of the crop species in relation to proper nursery and silvicultural practices. Thus, a conceptual model effectively describes all steps within a forest restoration program (Fig. 9). Ultimately, seedling performance depends on inherent growth potential and the degree to which environmental conditions limit or enhances this potential (Grossnickle 2000). Cultural practices applied are intended to enhance this growth potential, minimize environmental stress, while avoiding seedling losses. There are a number of places along this restoration pathway where practices need to be addressed to enhance seedling survival.

Nursery operations have a strong influence on seedling performance. First, cultural hardening practices (see Stress and the Cyclical Nature of Stress Resistance section), plus lift and store operations (Grossnickle and South 2014) can all affect seedling survival after outplanting. During operations from lifting to planting, stress typically occurs through a combination of handling activities, making it difficult to define what combination caused resulting poor seedling performance or death (reviewed by McKay 1997). Seedling quality programs can apply assessment procedures to identify if they are physiologically ready for lifting and whether they are damaged just prior to outplanting (see Seedling Quality - Product - Functional Integrity subsection). Seedlings that are physiologically sound have a good chance at survival once they are outplanted (Sutton 1988; Grossnickle and Folk 1993). Thus, the application of a seedling quality program can remove damaged seedlings and minimize the impact of handling issues on field survival (Further information found in publications identified in Seedling Quality – Information Sources subsection). Second, cultural practices can produce seedlings with material and performance attributes that enhance their survival. Findings show morphological and physiological attributes that increase the speed with which seedlings can overcome planting stress and become 'coupled' to the restoration site are critical for their survival (reviewed by Grossnickle 2012). This review found diameter and root system size were morphological attributes that conferred a greater chance of seedling survival. Also, seedling balance between the shoot and root systems, and their overall size need to be adjusted in relation to potential site environmental conditions; whether competition for light within the vegetation complex (i.e. higher shoot to root ratio) or dry soils and high evaporative demand (i.e. lower shoot to root ratio) are potential site limiting factors. Factors affecting physiological quality also have a major influence on survival. Improved root growth after planting is attributed to greater root system size, fibrosity, proper timing within the phenological cycle. Greater stress resistance (i.e. through hardening practices) and improved nutrition at planting (i.e. through fall nutrient loading) increase the speed with which seedlings can overcome planting stress and become established. Stocktype selection can also influence field performance, especially on droughty sites, because container-grown, compared to bareroot seedlings, can have higher survival that is related to factors (i.e. lower shoot to root ratio, greater root growth capability) reducing planting stress (reviewed by Grossnickle and El-Kassaby 2015). Findings also show that planting seedlings with desirable plant attributes does not guarantee high survival; rather planting seedlings with desirable plant attributes increases chances for field survival.

The restoration site is a unique ecosystem, as a forested stand subjected to a disturbance such as harvesting alters the basic structure and function. This altered stand structure influences many processes of the future ecosystem by affecting environmental cycles and thus the microsite environment into which seedlings are planted (Grossnickle 2000). The previous discussion (see Learning to Think Like a Tree section) briefly examines the dynamic nature of these environmental cycles. Silvicultural practices (e.g. harvesting systems, site preparation, planting window, fertilization, vegetation management) are applied to modify the site environment to enhance seedling performance. However, these practices only modify, but do not control, the site environment. Thus, any restoration operation only partially controls site variables and how seedlings respond to site conditions. Further details on this topic are found in Grossnickle (2000) and in identified references (see Learning to Think Like a Tree - Additional References subsection).

Newly planted seedlings undergo a series of developmental phases (planting stress, establishment, and transition) on restoration sites (Grossnickle 2000) (Fig. 9). The length of each phase is dependent upon inherent seedling quality and their response to site environmental conditions. Phases may overlap, depending on seedling development and competing vegetation. Whether seedlings survive and grow within each of these forest development phases is dependent upon how they respond to potential site limiting conditions and silvicultural practices designed to mitigate environmental constraints.

Planting stress is a critical phase that seedlings need to overcome so death does not occur immediately after field planting (see Planting Stress and Seedling Establishment section). The length of this phase is dependent on how long it takes a seedling to become coupled to the field site (Fig. 9). Producing seedlings with high levels of stress resistance and root growth potential, proper planting practices and correct timing of the planting window to avoid limiting environmental factors (i.e. hydrologic cycle conditions of inadequate soil water and high VPD) dictate whether planting stress conditions are avoided that could cause death.

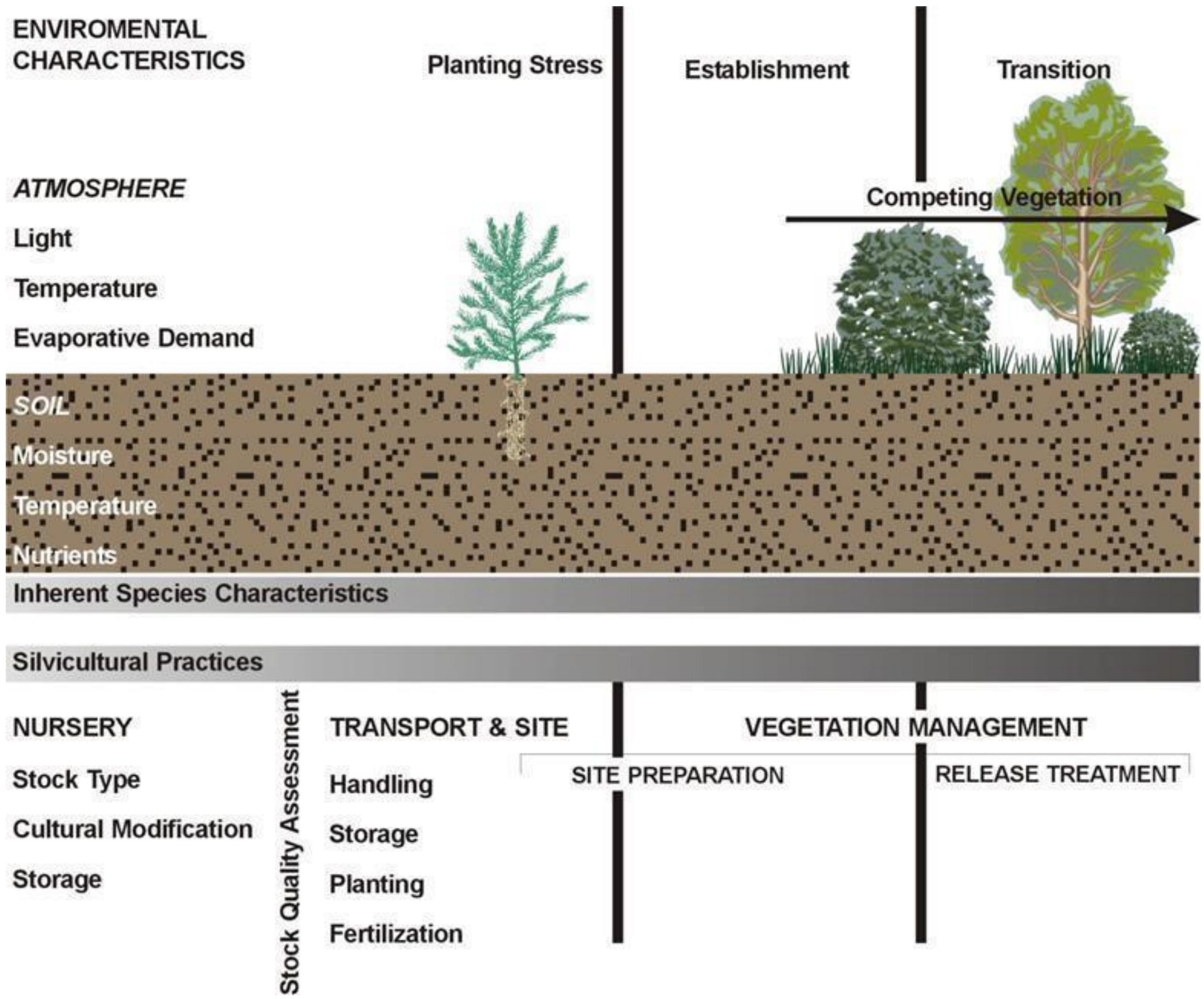

Figure 9. The forest restoration process is described in relation to site environmental characteristics, and nursery, handling and field silvicultural practices that can affect seedling performance (Grossnickle 2000). Newly planted seedlings undergo a series of developmental phases (planting stress, establishment, and transition) on restoration sites. The length of each phase and whether these phases overlap is dependent upon the seedling response to site environmental conditions. It is the combination of these various components of the forest restoration process that affect seedling survival and performance.

Seedlings enter the establishment phase when they start to develop root systems into the surrounding soil (Grossnickle 2000) which allows them to establish a proper water balance and respond to field site atmospheric conditions without exposure to planting stress. During the establishment phase seedlings are exposed to the local climate, which broadly reflects regional climate with microclimatic conditions varying considerably, depending upon elevation, topography and aspect (Fig. 9). At the microclimate scale, forest canopy removal has a major effect on the site environment. The regeneration niche for reforestation sites proposed by Margolis and Brand (1990) provides a generalization of environmental conditions seedlings are exposed to on an open site. These include: (i) high light intensity, (ii) high or low soil water availability, (iii) low to medium soil temperatures, (iv) high soil surface temperatures, (v) high vapor pressure deficits, (vi) high incidence of frost, (vii) high wind speeds, and (viii) high nutrient availability in the soil solution. Franklin et al. (1987) considered environmental stress the major cause of seedling death during the pre-vegetative closure successional stage, though predation and pathogens can also cause death. To avoid death in the establishment phase, seedlings require a) a certain level of quality (i.e. specific stocktypes or treated with certain nursery cultural practices) to respond to site conditions with rapid growth, and b) silvicultural practices that mitigate limiting environmental conditions, described above, within the regeneration niche.

Competing vegetation on restoration sites can affect seedling performance during the transition phase of stand development (Fig. 9). The transition phase is defined as a period when competing vegetation begins to reinvade the site and impose limitations on seedling performance (Grossnickle 2000). Site environmental conditions continually change due to the development of competing vegetation and management practices applied to mitigate their influence on seedling performance. If seedlings are not able to grow and occupy the site, there is a good possibility that the site vegetation complex will out-compete planted seedlings resulting in death (Grossnickle 2000). Plant competition for site resources is one of the major factors attributed to tree death (Franklin et al. 1987) and is considered a factor in limiting successful seedling establishment and growth (reviewed by Dobbs 1972; Gjerstad et al. 1984; Sutton 1985; Radosevich and Osteryoung 1987; Coates et al. 1994). Producing seedlings with high growth potential and using silvicultural practices that control the site vegetation will dictate whether or not seedlings survive as they transition into a forested stand.

Seedling ecophysiological response during these restoration phases determines their survival and subsequent growth. Successful seedling growth is affected by not only past nursery cultural and silvicultural practices, but by future silvicultural activities, along with past, current and future site environmental conditions. This dynamic and complex nature of the entire restoration process makes it challenging for nursery and forest personnel to define practices to ensure seedlings survive and grow into a forested stand.

7 Conclusions

"…forest regeneration decisions based on a sound knowledge of ecophysiological principles can improve the success of … seedling survival and growth." **Grossnickle (2000)**

Presented were five of the most common themes personally observed in programs designed to restore disturbed forest ecosystems. Typical biological patterns and themes continually appeared across these programs. Themes one and two dealt with learning to think like a tree and the complex nature of stress and the capability of plants to respond to environmental stress. They provided an ecophysiological perspective to forest restoration and pointed to the fact that seedling performance is a complex process integrating cultural practices with environmental conditions, and the seedling biological response to these practices and conditions. Theme three considered seedling quality and its importance in successful restoration. Seedling quality programs need to be designed to meet restoration program objectives. Practitioners must consider whether they want to measure the seedling product through measurement of functional integrity, operational grading or performance potential testing. Alternatively, a seedling quality program can monitor the process with the end result being a quality product. Theme four examined planting stress, which is a real and constant presence within forest restoration programs. Planting stress needs to be recognized as the major limiting factor in restoration, and practices should be implemented to mitigate its effect. Theme five defined issues around seedling death and their occurrence in nursery and restoration programs. Reasons for seedling loss can be simple or complicated. In the case of the former, cultural practices can be applied to minimize the potential of defined severe environmental conditions to cause further losses. In the case of the latter, it is usually a combination of small things (i.e. a combination of past and current cultural practices and/or environmental conditions) that when added together, affect seedling performance. In this case, the correct diagnosis of seedling losses can be accurate only when all variables are considered, by leaving 'no stone unturned'.

It was not possible to discuss all combinations of factors affecting the performance of seedlings through various stages of their nursery development and performance on the forest restoration site. Highlighted were some of the most common themes that occurred across programs I was involved with during my 40 years of working in this field. This discussion was intended to educate nursery personnel and foresters to think about the complexity of an operational program that must incorporate biological indices with operational objectives, so as to be better equipped to achieve successful forest restoration.

8 References

Abrams MD (1988) Sources of variation in osmotic potentials with special reference to North American tree species. For Sci 34:1030-1046.

Adams, HD, Guardiola-Claramonte M, Barron-Gifford GA, Villegas JC, Breshears DD, Zou CB, Troch PA, Huxman TE (2009) Temperature sensitivity of drought-induced tree mortality portends increased regional die-off under global-change-type drought. Proc Nat AcadSci 106:7036-7066.

Allen CD, Breshears DD, McDowell NG (2015) On underestimation of global vulnerability to tree mortality and forest die-off from hotter drought in the Anthropocene. Ecoshpere 6:129 http://dx.doi.org/10.1890/ES15-00203.1

Anonymous (2002) ISO9000:2000 Series Foundation. Ashbrooke Quality Assurance, Issue 2 Rev. 2 1.8.05

Arnott JT, Grossnickle SC, Puttonen P, Mitchell AK, Folk RS (1994) Influence of nursery culture on growth, cold hardiness and drought resistance of yellow cypress. Can J For Res 23:2537-2547.
Baldwin VC, Barney CW (1976) Leaf water potential in planted Ponderosa and lodgepole pines. For Sci 22:344-350.
Beadle CL, Neilson RE, Jarvis PG, Talbot H (1981) Photosynthesis as related to xylem water potential and carbon dioxide concentration in Sitka spruce. Physiol Plant 52: 391-400.
Bernier PY (1993) Comparing natural and planted black spruce seedlings. Can J For Res 23: 2427-2434.
Bigras FJ (1996) Conifer bud dormancy and stress resistance: a forestry perspective. In: Lang GE (ed) Plant dormancy, CAB Int, pp 171-192.
Bigras FJ, Calmé S (1994) Viability tests for estimating root cold tolerance of black spruce seedlings. Can J For Res 24:1039-1048.
Bigras FJ, Colombo SJ (eds) (2001) Conifer cold hardiness. Kluwer Academic Publ, Dordrecht, The Netherlands
Bigras FJ, Hébert C (1996) Freezing temperatures and exposure times during bud break and shoot elongation influence survival and growth of containerized black spruce (*Picea mariana*) seedlings. Can J For Res 26:1481-1489.
Bigras FJ, Ryyppo A, Linderstrom A, Stattin E (2001) Cold acclimation and deacclimation of shoots and roots of conifer seedlings. In: Bigras FJ, Colombo SJ (eds) Conifer cold hardiness. Kluwer Academic Publ, Dordrecht, The Netherlands, pp 57-88.
Binkley D (1986) Forest nutrition management. John Wiley & Sons, NY
Binnie SC, Grossnickle SC, Roberts DR (1994) Fall acclimation patterns of interior spruce seedlings and their relationship to changes in vegetative storage proteins. Tree Physiol 14:1107-1120.
Birdsey R, Pan Y (2011) Ecology: Drought and dead trees. Nature Climate Change, 1: 444-445.
Brodribb T (1996) Dynamic changes in intercellular CO_2 concentration (c_i) during drought and determination of minimum functional c_i. Plant Physiol 111:179-185.
Brown KR, Thompson WA, Camm EL, Hawkins BJ, Guy RD (1996). Effects of N addition rates on the productivity of *Piceasitchensis*, *Thujaplicata*, and *Tsugaheterophylla* seedlings. II. Photosynthesis, ^{13}C discrimination and N partitioning in foliage. Trees 10:198-205.
Burdett AN (1983) Quality control in the production of forest planting stock. For Chron 59:132-138.
Burdett AN (1990) Physiological processes in plantation establishment and the development of specifications for forest planting stock. Can J For Res 20:415-427.
Burr KE (1990) The target seedling concept: bud dormancy and cold-hardiness. In: Rose R, Campbell SJ, Landis TD (eds) Target Seedling Symposium: Proceedings of the Western Forest Nursery Associations. USDA For Serv Gen Tech Rep RM-200. pp 79-90.
Carlson WC, Miller DE (1990) Target seedling root system size, hydraulic conductivity, and water use during seedling establishment. In: Rose R, Campbell SJ, Landis TD (eds) Target Seedling Symposium: Proceedings of the Western Forest Nursery Associations. USDA For Serv Gen Tech Rep RM-200. pp 53-66.
Centritto M, Jarvis PG (1999) Long-term effects of elevated carbon dioxide concentration and provenance on four clones of Sitka spruce (*Picea sitchensis*). II. Photosynthetic capacity and nitrogen use efficiency. Tree Physiol 19:807-814.
Chandler JW, Dale JE (1995) Nitrogen deficiency and fertilization effects on needle growth and photosynthesis in Sitka spruce (*Picea sitchensis*). Tree Physiol 15:813-817.
Chapin FS, III.(1983) Patterns of nutrient absorption and use by plants from natural and man-modified environments. In: Mooney HA, M. Godron M (eds) Disturbance and ecosystems, components of response. Springer Berlin pp. 175-187.
Chavasse CGR (1980) Planting stock quality: a review of factors affecting performance. NZ J For Sci 25:144-171.
Cleary BD, Zaerr JB (1980) Pressure chamber techniques for monitoring and evaluating seedling water status. NZ J For Sci 10: 133-141.
Coates KD, Burton PJ (1999) Growth of planted tree seedlings in response to ambient light levels in northwestern interior cedar-hemlock forests of British Columbia. Can J For Res 29:1374-1382.

Coates KD, Haeussler S, Lindeburgh S, Pojar R, Stock AJ (1994) Ecology and silviculture of interior spruce in British Columbia. FRDA Rep. 220. For Can and BC Min of For, Victoria, BC.

Colombo SJ, Sampson PH, Grossnickle SC, Templeton CWG, McDonough TC, Menes PA, DeYeoe D (2001) Nursery stock quality assessment in Ontario. In Wagner B, Colombo SJ (eds) Regenerating Ontario's Forests. Fitzhenry & Whiteside Ltd., Markham, Ont. pp 307-324.

Dixon RK, Pallardy SG, Garrett HE, Cox GS, Sander IL (1983) Comparative water relations of container-grown and bare-root ectomycorrhizal and nonmycorrhizal *Quercus velutina* seedlings. Can J Bot 61: 1559-1565.

Dobbs RC (1972) Regeneration of white and Engelmann spruce: a literature review with special reference to the British Columbia interior. Can For Serv Inf Rep BC-X-69.

Draper D, Binder W, Fahlman R, Spittlehouse D (1985) Post-planting ecophysiology of interior spruce. In Interior spruce seedling performance. N Silviculture Com, BC Min For, Res Br, Victoria, BC. 18 pp

Duan H, O'Grady AP, Duursma RA, Choat B, Huang G, Smith RA, Jiang Y, Tissue DT (2015) Drought responses of two gymnosperm species with contrasting stomatal regulation strategies under elevated [CO_2] and temperature. Tree Physiol 35:756-770.

Dunsworth GB (1997) Plant quality assessment: an industrial perspective. New For 13:439-448.

Duryea ML (1984) Nursery cultural practices: impacts on seedling quality.In: Duryea ML, Landis TD (eds) Forest nursery manual: production of bareroot seedlings. Martinus Nijhoff / Dr W Junk Publishers, Boston, pp 143-164.

Duryea, ML (ed) (1985a) Evaluating seedling quality: principles, procedures, and predictive abilities of major tests. For Res Lab, OR St Univ, Corvallis, OR.

Duryea, ML (1985b) Evaluating seedling quality; importance to reforestation. In: Duryea, ML (ed) Evaluating seedling quality: principles, procedures and predictive abilities of major tests. For Res Lab, OR St Univ, Corvallis, OR pp 1-4.

Duryea ML, Brown GH (1984) Seedling Physiology and Reforestation Success: Proceedings of the Physiology Working Group Technical Session. Martinus Nijhoff / Dr W Junk Publishers, Boston

Duryea ML, Dougherty PM (eds) (1991) Forest regeneration manual. Kluwer Academic Publ, Dordrecht, The Netherlands.

Duryea ML, Landis TD (eds). 1984. Forest nursery manual: production of bareroot seedlings. Martinus Nijhoff / Dr W Junk Publishers, Boston.

Eamus D, Boulain N, Cleverly J, Breshears DD (2013) Global change-type drought-induced tree mortality: vapor pressure deficit is more important than temperature per se in causing decline in tree health. Ecol Evol 3:2711-2729.

Fan S, Grossnickle SC (1998) Comparison of gas exchange parameters and shoot water relations of interior spruce (*Picea glauca* (Moench) Voss x *P. engelmannii* Parry ex engelm.) clones under repeated soil drought. Can J For Res 28:820-830.

Folk RS, Grossnickle SC (1997) Determining field performance potential with the use of limiting environmental conditions. New For 13:121-138.

Folk RS, Grossnickle SC, Russell JH (1995) Gas exchange, water relations and morphology of yellow-cedar seedlings and stecklings before planting and during field establishment. New For 9:1-20.

Folk RS, Grossnickle SC, Major JE, Arnott JT (1994) Influence of nursery culture on western red cedar. II. Freezing tolerance of fall-planted seedlings and morphological development of fall- and spring-planted seedlings. New For 8:231-247.

Folk RS, Grossnickle SC, Arnott JT, Mitchell AK, Puttonen P (1996) Water relations, gas exchange and morphological development of fall- and spring-planted yellow cypress stecklings. For Ecol Manage 81:197-213.

Franklin JF, Shugart HH, Harmon ME (1987) Tree death as an ecological process. BioSci 37:550-556

Fuchigami LH, Nee CC (1987) Degree growth stage model and rest-breaking mechanisms in temperate woody perennials. HorticSci 22: 836-845.

Fuchigami LH, Weiser CJ, Kobayashi K, Timmis R, Gusta LV (1982) A degree growth stage (°GS) model and cold acclimation in temperate woody plants. In: Li PH, Sakai A (eds) Plant cold hardiness and freezing stress. Academic Press, NY pp 93-116.

Giono J (1954) The man who planted trees. Vogue, Copyright by Chelsa Green Publ Co 1985.

Gjerstad DH, Nelson LR, Dukes JH, Ratzlaff SA (1984) Growth response and physiology of tree species as affected by weed control. In: Duryea ML, Brown GN (eds) Seedling physiology and reforestation success. Martinus Nijhoff / Dr W Junk Publishers, Boston, pp 247-257.

Gladstone WT, Ledig FT (1990) Reducing pressure on natural forests through high-yield forestry. For Ecol Manage 35: 69-78.

Glerum C (1988) Evaluation of planting stock quality. In: Smith CR, Reffle RJ (eds) Taking stock: the role of nursery practice in forest renewal. OFRC Symp.Proc. O-P-16.CdnForServ, pp 44-49.

Grossnickle SC (1983) Growth, development and water relation patterns of conifer seedlings on a high-elevation mine site. CO State Univ. PhD Thesis. 252 pp.

Grossnickle SC (1988a) Planting stress of bare-root jack pine and white spruce seedlings. I. Factors influencing seedling water uptake. Tree Physiol 4:71-84.

Grossnickle SC (1988b) Planting stress of bare-root jack pine and white spruce seedlings. II. Changes in tissue water potential components. Tree Physiol 4:85-97.

Grossnickle SC (1989) Shoot phenology and water relations of *Picea glauca*. Can J For Res 19:1287-1290.

Grossnickle SC (1992) Relationship between freezing tolerance and shoot water relations of western red cedar. Tree Physiol 11:229-240.

Grossnickle SC (1993) Shoot water relations and gas exchange of western hemlock and western red cedar seedlings during establishment on a reforestation site. Trees 7:148-155.

Grossnickle SC (2000) Ecophysiology of northern spruce species: the performance of planted seedlings. NRC Research Press.

Grossnickle SC (2005) Importance of root growth in overcoming planting stress. New For 30:273-294.

Grossnickle SC (2011) Tissue culture of conifer seedlings - Twenty years on: Viewed through the lens of seedling quality. USDA For Serv Gen Tech Rep RMRS-P-65. pp 139-146.

Grossnickle SC (2012) Why seedlings survive: importance of plant attributes. New For 43:711-738.

Grossnickle SC, Arnott JT (1992) Gas exchange response of western hemlock seedlings from various dormancy induction treatments to reforestation site environmental conditions. For Ecol Manage 49:177-193.

Grossnickle SC, Blake TJ (1986) Environmental and physiological control of needle conductance for bare-root black spruce, white spruce and jack pine seedlings on boreal cut-over sites. Can J Bot 74:943-949.

Grossnickle SC, Blake TJ (1987) Water relations and morphological development of bare-root jack pine and white spruce seedlings: Seedling establishment on boreal cut-over site. For Ecol Manage 18:299-318.

Grossnickle SC, Fan S (1998) Genetic variation in summer gas exchange patterns of interior spruce (*Picea glauca* (Moench) Voss × *Picea engelmannii* Parry ex Engelm.). Can J For Res 28:831-840.

Grossnickle SC, Fan S (1999) Genetic variation in response to drought of interior spruce (*Picea glauca* (Moench) Voss × *P. engelmannii* Parry ex Engelm.). Scand J For Res 14: 251-261.

Grossnickle SC, Folk RS (1993) Stock quality assessment: Forecasting survival or performance on a reforestation site. Tree Planter's Notes 44:113-121.

Grossnickle SC, Folk RS (2003) Spring versus summer spruce stocktypes of western Canada: Nursery development and field performance. W J Appl For 18:267-275.

Grossnickle SC, Folk RS (2005) Stock quality assessment of a somatic interior spruce seedlot. N J Appl For 22:197-206.

Grossnickle SC, Folk RS (2007) Field Performance Potential of a Somatic Interior Spruce Seedlot. New For 34:51-72.

Grossnickle SC, Heikurinen J (1989) Site preparation: water relations and growth of outplanted jack pine and white spruce. New For 3:99-123.

Grossnickle SC, El-Kassaby YA (2015) Bareroot versus container stocktypes: a performance comparison. New For DOI 10.1007/s11056-015-9476-6.

Grossnickle SC, Major JE (1994a) Interior spruce seedlings compared to emblings produced from somatic embryogenesis. II. Stock quality assessment prior to field planting. Can J For Res 24:1385-1396.

Grossnickle SC, Major JE (1994b) Interior spruce seedlings compared to emblings produced from somatic embryogenesis. III. Physiological response and morphological development on a reforestation site. Can J For Res 24:1397-1407.

Grossnickle SC, Reid CPP (1984a) Water relations of Engelmann spruce on a high elevation mine site: An example of how reclamation techniques can alter micro-climate and edaphic conditions. Reclam Reveg Res 3:199-221.

Grossnickle SC, Reid CPP (1984b) The influence of reclamation practices on the micro-climate of a high elevation mine site, and their effect on water relation patterns of *Pinus contorta* seedlings. Reclam Reveg Res 3:31-48.

Grossnickle SC, Reid CPP (1985) Environmental and physiological control of stomatal response of *Picea engelmannii* seedlings on a high elevation mine site. Acta OEcol OEcol Plant 6:111-123.

Grossnickle SC, Russell JH (1991) Gas exchange processes of yellow-cedar (*Chamaecyparis nootkatensis* (D. Don) Spach) in response to environmental variables. Can J Bot 69:2684-2691.

Grossnickle SC, Russell JH (2006) Yellow-cedar and western redcedar ecophysiological response to fall, winter and early spring temperature conditions. Ann For Sci 63:1-8.

Grossnickle SC, South DB (2014) Fall acclimation and the lift/store pathway: Effect on reforestation. The Open For Sci J 7:1-20.

Grossnickle SC, Arnott JT, Major JE (1988) A stock quality assessment procedure for characterizing nursery-grown seedlings. USDA For Serv Gen Tech Rep RM-167. pp 77-88. Also published as FRDA Res. Rep. ISSN 0835-0752; 069.

Grossnickle SC, Cyr D, Polonenko DR (1996) Somatic embryogenesis tissue culture for the propagation of conifer seedlings: A technology comes of age. Tree Planters' Notes 47:48-57.

Grossnickle SC, Major JE, Arnott JT (1991b) Influence of dormancy induction treatments on western hemlock seedlings. 2) Physiological and morphological response during the first growing season on a reforestation site. Can J For Res 21:175-185.

Grossnickle SC, Major JE, Folk RS (1994) Interior spruce seedlings compared to emblings produced from somatic embryogenesis. I) Nursery development, fall acclimation and over-winter storage. Can J For Res 24:1376-1384.

Grossnickle SC, Major JE, Arnott JT, LeMay VM (1991c) Stock quality assessment through an integrated approach. New For 5:77-91

Grossnickle SC, Major JE, Arnott JT, Tschaplinski TJ (1991a) Influence of dormancy induction treatment on western hemlock seedlings. 1) Seedling development and stock quality assessment. Can J For Res 21:164-174.

Grossnickle SC, Parker BC, Blake TJ, Sutton RF (2001) Ecophysiological Principles. In: Wagner B Colombo SJ (eds) Regenerating Ontario's Forests. Fitzhenry & Whiteside Ltd., Markham, Ont. pp 91-118.

Grossnickle SC, Folk RS, Abrams SR, Dunstan DI, Rose PA (1996) Performance of interior spruce seedlings treated with abscisic acid analogs. Can J For Res 26:2061-2070.

Hawkins CDB, Binder WD (1990) State of the art stock quality tests based on seedling physiology. USDA For Serv Gen Tech Rep RM-200 pp 91-122.

Hinckley TM, Lassoie JP, Running SW (1978) Temporal and spatial variations in the water status of forest trees. For Sci Monogr No 20.

Hinckley TM, Teskey RO, Duhme F, Richter H (1981) Temperate hardwood forests. In: Kozlowski TT (ed) Water deficit and Plant Growth Vol VI, Woody Plant Communities. Academic Press, NY, pp 154-208.

Hobbs SD (1984) The influence of species and stocktype selection on stand establishment: An ecophysiological perspective. In: Duryea ML, Brown GH (eds) Seedling Physiology and Reforestation Success: Proceedings of the Physiology Working Group Technical Session. MartinusNijhoff / Dr W Junk Publishers, Boston, pp 180-224.

Hobbs SD (1992) Seedling and site interactions. In: Hobbs SD, Tesch SD, Owston PW, Stewart RE, Tappeiner JC, Wells GE (eds) Reforestation practices in southwestern Oregon and northern California. For Res Lab OR St Univ, Corvallis, OR. pp 114-135.

Hobbs SD, Wearstler KA Jr (1983) Performance of three Douglas-fir stocktypes on a skeletal soil. Tree Planters' Notes 34:11-14.

Hsiao TC (1973) Plant response to water stress. Annu Rev Plant Physiol 24:519-570.
Jacobs DF, Salifu KF, Seifert JR (2005). Relative contribution of initial root and shoot morphology in predicting field performance of hardwood seedlings. New For 30: 235-251.
Jaramillo A (1980) Review of techniques used to evaluate seedling quality. USDA For Serv Gen Tech Rep INT-109. pp 84-95.
Johnson JD, Cline ML (1991) Seedling quality of southern pines. In: Duryea ML, Dougherty PM (eds) Forest regeneration manual. Kluwer Academic Publ, Dordrecht, The Netherlands, pp 143-162.
Jones MM, Turner NC, Osmond CB (1981) Mechanisms of drought resistance. In: Paleg LG, Aspinall D (eds) Physiology and biochemistry of drought resistance. Academic Press, Australia pp 15-37.
Kaczmarek DJ, Pope PE (1993).Covariate analysis of northern red oak seedling growth. In: Proceedings of 7th biennial southern silvicultural research conference. USDA For Serv Gen Tech Rep SO-93. pp 351-356.
Kaushal P, Aussenac G (1989) Transplanting shock in Corsican Pine and Cedar of Atlas Seedlings: internal water deficits, growth and root regeneration. For Ecol Manage 27:29-40.
Kim YT, Colombo SJ, Hickie DF, Noland TD (1999) Amino acid, carbohydrate, glutathione, mineral nutrient and water potential changes in non-water-stressed *Picea mariana* seedlings after transplanting. Scand J For Res 14:416-424.
Kozlowski TT (1982) Water supply and tree growth. Part I. Water deficits. For Abstr 43: 57-95.
Kozlowski TT (1991) Effects of environmental stress on deciduous trees. In: Mooney HA, Winner WE, Pell EJ, Chu E (eds) Responses of plants to multiple stresses. Academic Press, San Diego, CA. pp 391-411.
Kozlowski TT, Davies WJ (1975) Control of water balance in transplanted trees. Arboriculture 1:1-10.
Kozlowski TT, Pallardy SG (1997) Physiology of woody plants.2nd edition. Acedemic Press, New York.
Kozlowski TT, Pallardy SG (2002) Acclimation and adaptive response of woody plants to environmental stress. Bot Rev 68:270-334.
Kozlowski TT, Kramer PJ, Pallardy SG (1991) The physiological ecology of woody plants. Academic Press, NY.
Kramer PJ (1983) Plant and soil water relationships, Academic Press, NY.
Kramer PJ (1986) The role of physiology in forestry. Tree Physiol 2: 1-16.
Kramer PJ, Boyer JS (1995) Water relations of plants and soils. Academic Press, NY.
Lambers H, Chapin III FS, Pons TL (2008) Plant Physiological Ecology. Springer, Berlin.
Lamhamedi MS, Bernier PY (1994) Ecophysiology and field performance of black spruce (*Picea mariana*): a review. Ann For Sci 51:529-551.
Landis TD, Dumroese RK, Haase DL (2010) Seedling processing, storage, and outplanting. The container tree nursery manual. Vol 7. USDA For Serv Agric Handb 674, 199 pp.
Landis TD, Tinus RW, Barnett JP (1999) Seedling propagation. The container tree nursery manual, Vol 6. USDA For ServAgricHandb 674, 167 pp.
Landis TD, Tinus RW, McDonald SE, Barnett JP (1989) Seedling nutrition and irrigation. The container tree nursery manual. Vol 4.USDA For Serv Agric Handb 674, 87 pp.
Landis TD, Tinus RW, McDonald SE, Barnett JP (1990) Containers and growing media. The container tree nursery manual.Vol. 2.USDA For Serv Agric Handb 674.88 pp.
Landis TD, Tinus RW, McDonald SE, Barnett JP (1992) Atmospheric environment.The container tree nursery manual. Vol. 3.USDA For Serv Agric Handb 674.145 pp.
Landsberg JJ (1986) Physiological ecology of forest production. Academic Press, NY.
Lang GA, Early JD, Arroyave NJ, Darnell RL, Martin GC, Stutte GW (1985) Dormancy: toward a reduced, universal terminology. HortSci 20:809-812.
Lange OL, Nobel PS, Osmond CB, Ziegler H. (2011a) Physiological Plant Ecology II: Water Relations and Carbon Assimilation. Springer, Berlin.
Lange OL, Nobel PS, Osmond CB, Ziegler H. (2011b) Physiological Plant Ecology III: Responses to the Chemical and Biological Environment. Springer, Berlin.
Larcher (2003) Physiological plant ecology: Ecophysiology and stress physiology of functional groups. 4th Edition, Springer, Berlin.

Lassoie JP, Hinckley TM, Grier CC (1985) Coniferous forests of the Pacific Northwest. In: Chabot BF, Mooney HA (eds) Physiological ecology of North American plant communities. Chapman and Hall, NY, pp. 127-161.

Lavender DP (1984) Plant physiology and nursery environment: Interactions affecting seedling growth. In: Duryea ML, Landis TD (eds) Forest nursery manual: production of bareroot seedlings. MartinusNijhoff / Dr W Junk Publishers, The Hague, pp 133-142.

Lavender DP (1985) Bud dormancy. In: Duryea ML (ed) Evaluating seedling quality: principles, procedures, and predictive ability of major tests. For Res Lab, OR St Univ, Corvallis, OR. pp 7-15

Lavender DP (1988) Characterization and manipulation of the physiological quality of planting stock. In: Worrall J, Loo-Dinkins J, Lester D (eds) Proceedings, 10th NA For Biol Wrkshp, Physiology and Genetics of Reforestation. Univ BC Press, Vancouver, BC. pp 32-57.

Lavender, D.P. 1990. Physiological principles of regeneration. In: Lavender DP, Parish R, Johnson CM, Montgomery G, Vyse A, Willis RA, Winston D (eds) Regenerating British Columbia's forests. Univ BC Press, Vancouver, BC. pp. 30-44.

Lavender DP, Cleary BD (1974) Coniferous seedling production techniques to improve seedling establishment. In: Tinus RW, Stein WI, Balmer WE (eds) Proceedings of the North American Containerized Forest Tree Seedling Symposium. Great Plains Ag Coun Publ No. 68, pp 177-180.

Lavender DP, Parish R, Johnson CM, Montgomery G, Vyse A, Willis RA, Winston D (eds) (1990) Regenerating British Columbia's forests. Univ BC Press, Vancouver, BC .

Levitt J (1980) Response of plants to environmental stress. Vol. I. Chilling, freezing and high temperature stress. Academic Press, NY.

Ludlow MM (1989) Strategies of response to water stress. In: Kreeb KH, Richter H, Hinckley TM (eds) Structural and functional responses to environmental stresses. Academic Publishing, The Hague pp 269-281.

Major JE, Grossnickle SC, Arnott JT (1994) Influence of dormancy induction treatments on the photosynthetic response of field planted western hemlock seedlings. For Ecol Manage 63:235-246.

Major JE, Grossnickle SC, Folk RS, Arnott JT (1994) Influence of nursery culture on western red cedar. I. Measurement of seedling attributes before fall and spring planting. New For 8:211-229.

Malik V, Timmer VR, (1998) Biomass partitioning and nitrogen retrains location in black spruce seedlings on competitive mixed wood sites: a bioassay study. Can J For Res 28:206-215.

Margolis HA, Brand DG (1990) An ecophysiological basis for understanding plantation establishment. Can J For Res 20:375-390.

Mattsson A (1997) Predicting field performance using seedling quality assessment. New For 13:227-252

May JT (1985) Administration, accounting and records. In: Lantz CW (ed) Southern Pine Nursery Handbook. USDA For Serv Coop For, Southern Region, 17-13.

McDonald SE, Running SW (1979) Monitoring irrigation in western forest tree nurseries. USDA For Serv Gen Tech Rep RM-61.

McDowell N, Pockman WT, Allen CD, Bershears DD, Cobb N, Kolb T, Plaut J, Sperry J, West A, Williams DG, Yepez EA (2008) Mechanisms of plant survival and mortality during drought: why do some plants survive while others succumb to drought? New Phytol 178:719-739.

McKay HM (1992) Electrolyte leakage from fine roots of conifer seedlings: a rapid index for plant vitality following cold storage. Can J For Res 22:1371-1377.

McKay HM (1997) A review of the effects of stresses between lifting and planting on nursery stock quality and performance. New For 13:369-399.

Mexal JG, Landis TD (1990) Target seedling concepts: height and diameter. In: Rose R, Campbell SJ, Landis TD (eds) Target Seedling Symposium: Proceedings of the Western Forest Nursery Associations. USDA For Serv Gen Tech Rep RM-200, pp 17-36.

Mexal JG, South DB (1991) Bareroot seedling culture. In: Duryea ML, Dougherty PM (eds) Forest regeneration manual. Kluwer Academic Publ, Dordrecht, The Netherlands pp 89-115.

Miller PC (1983) Comparison of water balance characteristics of plant species in "natural" versus modified ecosystems. In: Mooney HA, Godron M (eds) Disturbance and ecosystems. Components of response.Springer, Berlinpp 188-212.

Mohammed GH (1997) The status and future of stock quality testing. New For 13: 491-514.
Mooney HA, Winner WE, Pell EJ (1991) Response of plants to multiple stresses. Academic Press, NY.
Munson AD, Bernier PY (1993) Comparing natural and planted black spruce seedlings. II. Nutrient uptake and efficiency of use. Can J For Res 23:2435-2442.
Munson AD, Margolis HA, Brand DG (1993) Intensive silviculture treatment: impacts on soil fertility and planted conifer response. Soil Sci Soc Am J 57:246-255.
Nambiar EKS, Bowen GD, Sands R (1979) Root regeneration and plant water status of *Pinus radiata* D. Don seedlings transplanted to different soil temperatures. J Exp Bot 30:1119-1131.
Nobel PS (1991) Physiochemical and environmental plant physiology. Academic Press, San Diego, CA.
Omi SK (1991) The target seedling and how to produce it. In: van Buijtenen JP, Simms T (eds) Nursery management workshop. Publ. 148. Texas For Serv College Station, TX. pp 88-118.
Osmond CB, Lange OL, Nobel PS (2011a) Physiological Plant Ecology I: Responses to the Physical Environment. Springer, Berlin.
Osmond CB, Lange OL, Nobel PS (2011b) Physiological Plant Ecology IV: Ecosystem Processes: Mineral Cycling, Productivity and Man's Influence. Springer, Berlin.
Puttonen P (1989a) Criteria for using seedling performance potential tests. New For 3:67-87.
Puttonen P (1989b) Variation of root growth capacity and triphenyl-tetrazolium chloride in *Pinus sylvestris* and *Picea abies* planting stock. For 62:229-240.
Puttonen P (1997) Looking for the "silver" bullet — can one test do it all? New For 13:9-2.
Radosevich SR, Osteryoung K (1987) Principles governing plant-environment interactions. In: Walstad JD, Kuch PJ (eds) Forest vegetation management for conifer production. John Wiley & Sons, NY pp 105-156.
Rietveld WJ (1989) Transplanting stress in bareroot conifer seedlings: its development and progression to establishment. North J Appl For 6:99-107.
Riley LE, Haase DL, Pinto JR (Tech Coord) (2011)Joint Meeting of the Western Forest and Conservation Nursery Association and Forest Nursery Association of British Columbia Target Seedling Symposium USDA For Serv Gen Tech Rep RMRS-P-65.
Ritchie GA (1984) Assessing seedling quality. In: Duryea ML, Landis TD (eds) Forest Nursery Manual: Production of Bareroot Seedlings. Martinus Nijhoff / Dr. W. Junk Publishers, The Hague, pp 243-266.
Ritchie GA, Hinckley TM (1975) The pressure chamber as an instrument for ecological research. Adv Ecol Res 9:165-254.
Ritchie GA, Tanaka Y (1990) Root growth potential and the target seedling. In: Rose R, Campbell SJ, Landis TD (eds) Target Seedling Symposium: Proceedings of the Western Forest Nursery Associations. USDA For Serv Gen Tech Rep RM-200, pp 37-51.
Roberntz P, Stockfors J (1998) Effects of elevated CO_2 concentration and nutrition on net photosynthesis, stomatal conductance and needle respiration of field-grown Norway spruce trees. Tree Physiol 18:233-241.
Rowe SJ (1964) Environmental preconditioning with special reference to forestry. Ecology 45:399-403
Sakai A, Larcher W (1987) Frost survival of plants. Ecological studies Vol. 62. Springer, Berlin.
Sands R (1984) Transplanting stress in radiata pine. Aust For Res 14:67-72.
Schmidt-Vogt H (1981) Morphological and physiological characteristics of planting stock: present state of research and research tasks for the future. In: Proceedings, IUFRO 17th World Congress, Tokyo
Scholander PF, Hammel HT, Hemmingsen EA, Bradstreet ED (1965) Sap pressure in vascular plants. Sci 148:339-346.
Shigo AL (1985) Wounded forests, starving trees. J For 83:668-673.
Simpson DG, Ritchie GA (1997) Does RGP predict field performance? A debate. New For 13:253-277.
Smith WK, Hinckley TM (1995a) Ecophysiology of coniferous forests. Academic Press, NY.
Smith WK, Hinckley TM (1995b) Resource physiology of conifers: acquisition, allocation, and utilization. Academic Press, NY.
Stanturf JA, Palik BJ, Dumroese RK (2014) Contemporary forest restoration: A review emphasizing function. For Ecol Manage 331: 292-323.

Stewart JD, Zine El Abindine A, Bernier PY (1995) Stomatal and mesophyll limitations of photosynthesis in black spruce seedlings during multiple cycles of drought. Tree Physiol 15:7-64.

Stirzaker RJ Passioura JB (1996) The water relations of the root interface. Plant Cell Environ 19:201-208.

Sutton BCS, Attree SA, El-Kassaby YA, Grossnickle SC, Polonenko DR (2004) Commercialization of somatic embryogenesis for plantation forestry. In: Walter C, Carson M (eds) Plantation Forest Biotechnology for the 21st Century. Research Signpost, pp. 275-301.

Sutton, R.F. 1979. Plantation establishment in the boreal forest: nutrient redistribution during mechanized planting. Rep. 0-X-303.Can For Serv, Great Lakes For Center, Sault Ste. Marie, ON

Sutton R (1980) Evaluation of planting stock quality. N Z J For Sci 10: 293-300.

Sutton RF (1982) Plantation establishment in the boreal forest: planting season extension Can For Serv, Great Lakes For Center, Sault Ste. Marie, ON.

Sutton RF (1985) Vegetation management in Canadian forestry. Inf. Rep. 0-X-369. Environ Can, Can For, Great Lakes Forestry Center, Serv, Sault Ste. Marie, ON.

Sutton RF (1988) Planting stock quality is fitness for purpose. In Proceedings, Symposium on Taking Stock: The Role of Nursery Practice in Forest Renewal. Ontario Forest Research Committee O-P-16, Can ForServ, Great Lakes For Center, Sault Ste. Marie, ON, pp 39-43.

Tan W, Hogan GD (1995) Limitations to net photosynthesis as affected by nitrogen status in jack pine (*Pinus banksiana* Lamb.) seedlings. J Expt Bot 46:407-413.

Teskey RO, Hinckley TM (1986) Moisture: effects of water stress on trees. In: Hennessey TC, Dougherty PM, Kossuth SV, Johnson JD (eds) Proceedings of the physiology working group technical session. SAF National Convention: Stress Physiology and Forest Productivity. Martinus Nijhoff Publishers, Dordrecht, The Netherlands. pp 9-33.

Timmer VR (1997) Exponential nutrient loading: a new fertilization technique to improve seedling performance on competitive sites. New For 13:279-299.

Tinus RW (1974) Characteristics of seedlings with high survival potential.In: Tinus RW, Stein WI, Balmer WE (eds) Proceedings of the North American Containerized Forest Tree Seedling Symposium. Great Plains Ag. Council Publ. No. 68, pp 276-282.

van den Driessche R (1991) Mineral nutrition of conifer seedlings. CRC Press, Boca Raton, FL.

Villar-Salvador P, Uscola M, Jacobs DF (2015) The role of stored carbohydrates and nitrogen in the growth and stress tolerance of planted forest trees. New For 46:813-839.

Vyse A (1981) Growth of young spruce plantations in interior British Columbia. For Chron 57:174-180.

Wagner B, Colombo SJ (Eds) (2001) Regenerating Ontario's Forests. Fitzhenry & Whiteside Ltd., Markham, Ont.

Wakeley PC (1948) Physiological grades of southern pine nursery stock. SocAmerFor Proc 1948:311-322.

Wakeley PC (1954) Planting the southern pines. Agric. Monogr. No. 18. USDA For Serv WA, DC, pp 233.

Waring RH (1987) Characteristics of trees predisposed to die. BioSci 37: 569-574.

Waring RH (1991) Responses of evergreen trees to multiple stresses. In: Mooney HA, Winner WE, Pell EJ, Chu E (eds) Responses of plants to multiple stresses. Academic Press San Diego CA, pp 371-390.

Waters WE, DeMars CJ, Cobb FW (1991) Analysis of early mortality of Douglas-fir seedlings in postharvest plantings in northwestern California. For Sci 37:802-826.

Wenny D, Dumroese K (1999) Seedling development: the establishment, rapid growth, and hardening phases. In: Landis TD, Tinus RW, Barnett JP (eds) Seedling propagation. The container tree nursery manual, Vol 6.USDA For Serv Agric. Handb. 674, pp 123-163.

Whitehead D, Jarvis PG (1981) Coniferous forests and plantations. In: Kozlowskii TT (ed) Water deficits and plant growth. Volume VI. Woody plant communities. Academic Press, NY, pp 49-152.

Wilson SJ, Clark RJ (1998) Changes in water relations of *Eucalyptus nitens* nursery stock during and after lifting and transplanting. New For 16:199-211.