# Seedling establishment on a forest restoration site – An ecophysiological perspective

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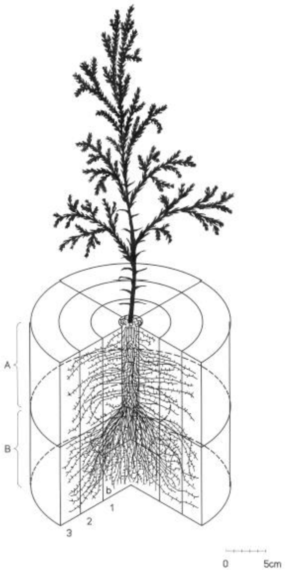
## Abstract

Seedling field performance is affected by both their quality and restoration site conditions. Seedlings enter the establishment phase when they start to develop root systems into the surrounding soil and are coupled to the restoration site. Once seedlings are established, their inherent growth potential is related to morphological and physiological attributes and their ecophysiological response to site environmental conditions, which ultimately determines field performance. This establishment phase is a time when seedlings developed with certain nursery cultural practices begin to respond to site conditions. This phase is also a period when silvicultural practices have created microsites intended to benefit established seedlings field performance. Seedlings can be exposed to a wide range of environmental conditions during the establishment phase, some of which may be extreme enough to exceed their ability to physiologically tolerate environmental stress. When this occurs, seedling growth on the restoration site is reduced. On the other hand, this phase can provide planted seedlings with ideal environmental conditions that allow for an optimum physiological response and maximization of their growth potential. An understanding of the ecophysiological capability of planted seedlings can ensure their best chance at rapid stand establishment.

## Keywords

Establishment phase; Ecophysiological capabilities; Seedling performance

## Contents



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## 1 Introduction

Forest restoration sites are unique ecosystems, because disturbance of the site alters the basic forested stand structure and function. This altered stand structure influences many processes of the future ecosystem and microsite environment in which seedlings are planted. Newly planted seedlings undergo a series of developmental phases (planting stress, establishment, and transition) on reforestation sites (Grossnickle 2000). Seedlings may undergo various transplanting stresses before they can initiate growth and become ‘‘coupled’’ into the forest ecosystem (Grossnickle 2005a). Furthermore, if these environmental stresses are excessive (Grossnickle 2005a) or seedlings are of poor quality (Grossnickle 2012; Grossnickle and MacDonald 2018), then poor field performance can occur. This is why seedling performance just after planting is critical to their survival and growth (Burdett 1990). The establishment phase is a period when silvicultural practices have reduced the vegetation, thereby creating sites free from competition of established plants (Spies 1997; Grossnickle 2000). Once seedlings enter the establishment phase, their inherent growth potential is related to morphological and physiological attributes (Burdett 1990) and their ecophysiological response to site environmental conditions (Margolis and Brand 1990), which ultimately determines seedling field performance. These post disturbance forest restoration sites are the only period when tree canopies do not dominate the forest site, and so this stage can have a high level of prolific of plant species (e.g. grasses, herbs and shrubs) due to large nutrient fluxes, resulting in high structural and spatial complexity (Keenan and Kimmins 1993; Swanson et al. 2011). Thus, the transition phase is defined as a period when competing vegetation begins to reinvade the reforestation site and impose limitations on seedling performance (Grossnickle 2000). These developmental phases are conceptual in nature because their timeframe varies inversely with rapidity of seedling growth versus the field site vegetation complex. Thus they are used to identify and examine specific processes that can occur after planting seedlings on restoration sites.

Developing an understanding of the ecophysiological performance of tree species planted on a forest restoration site is required to provide practitioners with the knowledge of how seedlings grow. From an anthropocentric perspective, this understanding can provide a seedling’s view of restoration practices effect on their performance. This provides an understanding of how silvicultural practices directly affect seedling physiological response to specific environmental conditions (Margolis and Brand 1990; Colombo and Parker 1999) and is reflected in their actual growth on reforestation sites (Grossnickle 2000).

During the establishment phase seedlings have an opportunity to develop under a range of site conditions; from an open site to partial forest retention silviculture systems. Thus, site disturbance has a direct effect upon the site microclimate, thereby affecting site energy hydrologic and nutrient cycles (Swanson et al. 2011) and this directly influences the physiological response of seedlings during the establishment phase (Margolis and Brand 1990; Grossnickle 2000). The concept of an “operational environment” defined by Spomer (1973) is appropriate to a discussion of the seedling environment, as it includes only those biotic and abiotic factors directly interacting with or capable of being exchanged with seedlings during their establishment phase. Seedlings can be exposed to a wide range of environmental conditions, some of which may be extreme enough to exceed their ability to physiologically withstand environmental stress (Grossnickle 2000; Dumais and Prévost 2008). When this occurs, growth of seedlings is reduced. On the other hand, this phase can also provide seedlings with ideal environmental conditions that allow for an optimum physiological response and a maximization of their growth.

Following examples provide ecophysiological response patterns of conifer species within restoration programs in the boreal forests (Spruce species, *Picea* spp.) and the Pacific Northwest (western redcedar *Thuja plicata* Donn). It is recognized there is species variation, and within species genetic variation (Zobel and Talbert 1984), that dictates the specific range of physiological responses that can occur to site environmental conditions (e.g. Mitton 1995). It is also recognized that restoration sites in forest ecosystems throughout the world are exposed to a differing array of microsite environmental conditions. All combinations of restoration site conditions are not discussed. The intent of examples presented are to show that growing season site conditions affect plant ecophysiological responses and subsequent seedling performance during the establishment phase. By understanding tree species ecophysiological response patterns to growing season site conditions, one can apply best silvicultural practices to ensure that planted seedlings survive and respond with rapid growth.

## 2 Response to the energy cycle

### 2.1 Seedling environment

Full sunlight (i.e. radiant energy) falls on the restoration site during the establishment phase when the site vegetation complex is removed. This means that energy distribution can result in the soil surface receiving 10–20 times more shortwave radiation on a clear, summer day (Fowler and Anderson 1987; Spittlehouse and Stathers 1990) because what was previously captured within the forest canopy is now intercepted at or near the soil surface. This means that photosynthetically active radiation received at a site at sea level under full sunlight conditions is $450 Wm^{-2}$ or $2000\ \mu mol\ m^{-2}\ s^{-1}$. Thus, seedlings receive solar energy as direct light from the sun, or as light that has been modified as it passes through the atmosphere, or is reflected off objects. Light levels and energy balance in the atmosphere near the soil surface and upper portions of the soil profile are of great importance to forest restoration efforts because these regions determine the daily seedling environment.

Alternatively, if a partial stand retention silvicultural system is applied the amount of sunlight reaching the ground is dependent on percent retention of the original forest stand structure. Structure and species composition of the canopy, stand density, variation in sun position, sky conditions, and proportion of direct to diffuse solar irradiance determines the amount of soil surface radiation (Federer and Tanner 1966; Reifsnyder et al. 1971; Jarvis et al. 1976). For example, the presence of a continuous forest overstory results in ~80% of light absorbed by conifer (Larcher 1995) and hardwood (Groot et al. 1997; Messier et al. 1998) forests, though there is a dynamic seasonal pattern in the range of light transmission (i.e. low during the growing season) through a deciduous forest canopy. Height, density, and leaf orientation of vegetation cover has a direct influence on the interception of light reaching seedlings (Spittlehouse and Stathers 1990; Shainsky and Radosevich 1992).

On open forest restoration sites, daytime air temperatures at seedling height are greater and nighttime air temperatures lower than those found in a forested stand, with soil having their highest yearly temperatures and stored heat during the growing season (Grossnickle 2000). Growing season temperature conditions go through a daily cycle with positive net radiation during the daytime causing morning temperatures to rise in regions near the soil surface, with this positive input continuing until early afternoon, when air and soil surface temperatures reach their maximum daily values. This concentration of solar energy near the ground means that maximum daily air temperature at seedling height can be 10°C higher than air temperatures at 2 m, with soil or litter surfaces up to 30°C higher (Geiger 1980; Spittlehouse and Stathers 1990). At night under clear skies, heat is lost from ground to sky as thermal radiation, with heat stored in soil transferred to the soil surface and then to the sky, with soil acting as a source of atmospheric heat resulting in the soil profile being slightly warmer than the atmosphere just before dawn (Geiger 1980). As a result, air temperatures at seedling height on open restoration sites site are greater during the daytime and lower during the nighttime than those found in a forested stand.

Forest canopy removal also causes an increase in seasonal soil temperatures (Hungerford 1979; Childs et al. 1985; Viereck et al. 1993) with heat sums during the summer in boreal forest stands 25% less than occur on an open restoration site (Viereck et al. 1993). The capacity of a soil to store or transfer heat and maintain a specific soil temperature is determined by their thermal properties (i.e. composition, bulk density, and water content) (Geiger 1980). Extreme diurnal soil surface temperatures can occur, especially in dry organic soils having very low thermal conductivity. Soil surface temperatures of open restoration sites can normally be 2.5–3.0 times greater than soil surfaces under a heavy vegetation cover (Spittlehouse and Stathers 1990), with soil surface temperatures on open sites sometimes reaching 40–50°C, and in certain instances exceeding 55°C (e.g., Day 1963; Ballard 1972; Nobel and Alexander 1977; Tranquillini 1979) and 60°C (Kolb and Robberecht 1996). In addition, light vegetation cover that allows sunlight to reach the soil surface can create conditions where temperatures around the seedling are 20°C higher than similar site conditions without vegetation cover (Grossnickle and Reid 1984a). This is because partially open vegetation cover can trap heat absorbed by the soil and not let wind currents or thermal transfer of radiation effectively dissipate a heat buildup, thereby causing soil surface temperatures to rise to extremely high levels (Geiger 1980).

In northern latitude and high elevation forests, canopy removal can increase frost events during the growing season (i.e. inflow of a cold air mass and radiative frost). Radiative frosts occur during the summer on calm and clear nights when the ground surface cools due to thermal energy transfer into the air. As a result, clear sky conditions can result in a 4–5°C decrease in minimum air temperature at seedling height (Geiger 1980; Stathers 1989) with temperatures 2–6°C lower than air temperatures found under a forest canopy (Stathers 1989; Örlander et al. 1990; Groot and Carlson 1996; Groot et al. 1997). Temperature near the soil surface can decreases rapidly, and frost occurs at 5–15 cm even though air temperature above the ground (at 1.3 m) is well above the freezing point (Grossnickle 2000).

Site exposure to high light conditions can create microsites where established seedlings are exposed to up to a 50 to 60°C temperature range on any given day during the growing season. Thus, open restoration sites can create microsites with a range of light and temperature conditions. Seedlings ability to endure a wide range of growing season light and temperature conditions determines their ability to grow on open restoration sites.

## 2.2 Seedling response

### Light

Spruce species have a two-phase net photosynthesis ($P_n$) response to growing season light level conditions. As light intensity increases from dark conditions, a point is reached where the photosynthetic uptake of $CO_2$ equals its release due to respiration (i.e. light compensation point at <5% full sunlight) (Figure 1a). The light compensation point varies because of many factors: species, needle type, needle age, $CO_2$ concentration in the air, and air temperature (Pallardy 2008). As light levels increase up to 25–33% full sunlight, $P_n$ rises rapidly and then increases only gradually after that point; independent of changes in vapor pressure deficit (VPD) (Figure 1a). Between 25 and 50% full sunlight $P_n$ reaches light saturation of photosynthetic processes; which is a comparable across spruce species (Grossnickle 2000). Thereafter, increasing light results in only a slight increase in $P_n$. Spruce species shoot system needle distribution can cause $P_n$ not to reach complete light saturation of all foliage because of mutual needle shading (Leverenz and Jarvis 1979). This is why there is still a gradual increase in $P_n$ at light that is normally considered above spruce species light saturation level (Figure 1a).

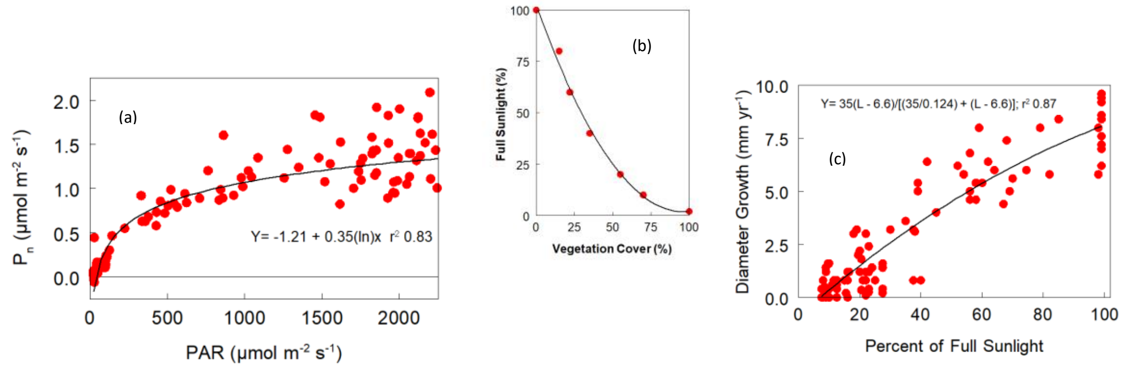

Figure 1. Growing season light response for interior spruce ((*Picea glauca* (Moench) Voss x *Picea engelmannii* Parry ex Engelm.)); (a) Net photosynthesis ($P_n$) response to increasing photosynthetically active radiation (PAR) (adapted from Grossnickle and Fan 1998); (b) percent vegetation cover effect on light at seedling height (adapted Spittlehouse and Stathers 1990; Stathers et al. 1990); (c) diameter growth rates (average increment per year over 3, 4, and 5 years after field planting) in relation to percent of full sunlight on sites with a range overstory canopy structure (adapted from Coates and Burton 1999).

From the establishment into the transition phase, light level received by seedlings is determined by the degree of forest canopy retention and how rapidly fast-growing early seral stage species occupy the site. Thus, the amount of solar radiation reaching a seedling is directly related to vegetation cover (Figure 1b) and developmental stage of competing vegetation (Draper et al. 1988; Comeau et al. 1993). Solar radiation reaching seedlings has a direct influence on their shoot growth. Height growth typically increases to 40-60% of full sunlight, and thereafter shows no further growth improvement, while diameter growth of spruce seedlings continues to increase at greater light levels (Figure 1c) (Grossnickle 2000).

Within partial forest canopy retention systems, spruce seedlings in some cases have improved growth (Tanner et al. 1996; Man and Lieffers 1999), while numerous studies have found limited growth (Hagner 1962; Youngblood and Zasada 1991; Kabzems and Lousier 1992; Groot 1999) when compared to seedlings planted in adjacent open sites. Meta-analysis found that this variability in seedling performance is related to degree to which partial forest canopy retention, or gaps, alters energy and hydrologic cycles (Zhu et al. 2014). Recent work on spruce seedlings planted in overstory mixed wood covers found they had better ecophysiological response and greater growth in openings that maximized light transmission (Dumais and Prévost 2014; Dumais et al. 2018; Rutenbeck et al. 2018). Historical (Gustafson 1943; Eis 1967) and recent (Dumais et al. 2018; Lu et al 2018) findings report that spruce seedlings growth is suppressed when the overstory results in <25% full sunlight reaching the forest floor. This need to exceed 30% of full sunlight in these forest retention systems compares with the rapid rise to 40-50% of maximum $P_n$ in spruce seedlings with an increase of up to 25–33% full sunlight (Figure 1a).

Stocktype selection in relation to potential site conditions can ensure planting of seedlings that have a growth advantage over competing vegetation (Grossnickle and MacDonald 2018). For example, height at planting can forecast growth on sites with competing vegetation because taller seedlings keep their height advantage over time (Grossnickle 2005b; Pinto et al. 2011; Pinto et al. 2015), and this advantage (Jobidon et al 2003; Rose and Ketchum 2003; Grossnickle 2005b; Haase et al. 2006; Morrissey et al. 2010; Thiffault et al. 2014; Devetaković et al. 2017) allows them to outgrow competitors (South et al. 2005; Youngblood et al. 2011). Seedling diameter is considered the most reliable indicator of field performance (Mason et al. 1996; Levy and McKay 2003), with a positive relationship between initial stem diameter and growth after planting (i.e. reported in 91% of studies, Grossnickle and MacDonald 2018). This is because seedlings with a large stem diameter have a greater shoot system size resulting in superior shoot-system development, due to a greater number of branches, buds, and foliage in conifers (Grossnickle 2005b) and hardwoods (del Campo et al. 2010). This greater shoot system size can be important on sites where soil water and nutrients are not limiting with competition for light between planted seedlings and other vegetation the main factor limiting growth.

As seedlings move from the establishment to transition phase, growth can be reduced when neighboring vegetation reaches a sufficient height and density to reduce light (Grossnickle 2000). Removal of vegetation through various site preparation treatments can increase incoming light (Draper et al. 1988; Brand 1991), thereby increase spruce seedling growth (Comeau et al. 1993). After openings are created, the degree of new vegetation cover within the opening is dependent upon original opening size and ingress of competing vegetation. These factors change over time in a dynamic pattern between seedlings and competing vegetation (Örlander et al. 1990). The pattern of incoming light can be manipulated through site preparation and vegetation management techniques, to temporarily allow planted seedlings access to incoming light.

### Temperature

Seedlings have a series of physiological responses across the growing season temperature range they can be exposed on restoration sites. Temperatures can range from freezing to as high as 60 °C. Spruce species have an ecophysiological profile to this range of growing season temperature conditions (Figure 2). This profile provides examples of how temperature conditions influence seedling development.

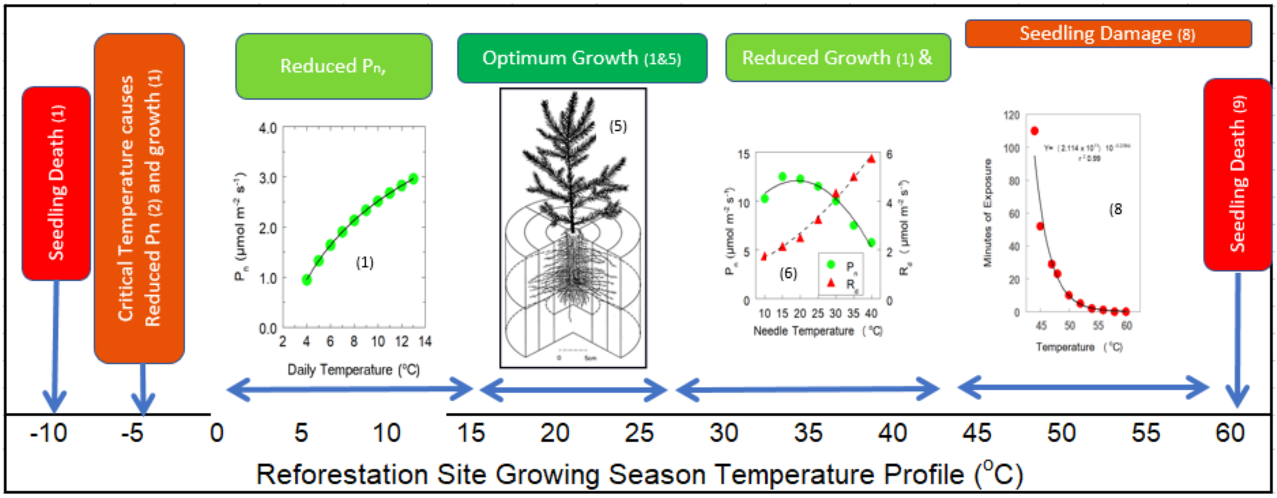

Figure 2. Growing season temperature profile for spruce (*Picea* spp.) seedlings. This temperature profile shows how spruce species physiological processes change along the following temperature gradient: at temperatures -10°C death occurs due to freezing (1; Grossnickle 2000); at - 5 °C is a critical temperature that causes reduced net photosynthesis ($P_n$) (2; Dang et al. 1992) and growth (1); from 0 to 15 °C there is reduced growth (1) and at these low soil temperatures there is reduced water uptake (3; Kaufman 1975 & 4; Grossnickle 1988), with $P_n$ increasing as the air and soil temperatures increase (1); at a range from 15 to 25 °C there is optimum growth, shown as a diagrammatic representation of an established seedling (5; Grossnickle and Major 1994 – from morphological data n= 25) & $P_n$ (1); from 25 to 40 °C there is reduced growth (1), and increasing respiration ($R_d$) and decreasing $P_n$ (6; Benomar et al. 2018 & 7; Weger & Guy 1991); from 40 to 55 °C damage occurs based on exposure time at a given temperature (8; Colombo & Timmer 1992); from 55 to 60 °C death occurs (9; Seidel 1986).

On open northern latitude restoration sites where the forest canopy has been removed, seedlings can be exposed to frost events during the growing season. These frost events are considered a chief problem in establishing tree plantations in northern latitude forests (Sakai and Larcher 1987) because frosts occur when spruce species have low freezing tolerance during shoot elongation (Figure 2). Freezing during the growing season can also reduce spruce species stomatal conductance ($g_{wv}$) (Kaufmann 1982; Smith et al. 1984), with $P_n$ depressed for days after exposure to a freeze event (DeLucia 1987; DeLucia and Smith 1987; Dang et al. 1992; Welander et al. 1994). As a result, summer frosts can have long-term effects on stand development by causing seedling damage (Luoranen et al. 2018) and reducing growth (Glerum and Paterson 1989; Stathers 1989; Krasowski et al. 1993). On sites subjected to frequent summer frosts, reductions in cover may be more detrimental than beneficial to initial performance of spruce seedlings. For example, vegetation cover reduced exposure to freezing temperatures and allowed white spruce (*Picea glauca* Moench) seedlings to have higher spring and fall seasonal $P_n$ compared to open-grown seedlings (Man and Lieffers 1997). Optimum regeneration niche on northern latitude restoration sites would protect from both radiative frosts and intense sunlight, as this combination of environmental conditions causes damage to the photosynthetic system (Ball 1994). On sites with no vegetation cover site preparation (e.g. burning, scalping, trenching, and mounding) (Stathers 1989; Steen et al. 1990; Örlander et al. 1990) or planting seedlings near stumps and downed logs (Spittlehouse and Stathers 1990) can decrease the risk of radiation frost damage. This microsite effect can cause enough of a temperature increase above the critical freezing point to prevent seedling damage during the growing season.

Low air and soil temperatures can reduce gas exchange processes of spruce species during the growing season. The $P_n$ declines at air temperatures that are just below and above freezing (Figure 2). Seedlings can have restricted water uptake in cold soils even when there is available soil water (Kaufmann 1975; Grossnickle 1988). At root temperatures below 10 °C there is a decrease in $P_n$, with very little effect at root temperatures above 10 °C (DeLucia 1987).

Rooting zone soil temperatures in northern latitude restoration sites normally range between 6 and 12 °C during the growing season when vegetation has not been removed (Grossnickle 2000). Site preparation treatments that remove shading vegetation (Spittlehouse and Childs 1990) or raise the soil surface (i.e. mechanical site preparation creating mound or berm planting spots) (Spittlehouse and Stathers 1990; Örlander et al. 1990; Kubin and Kemppainen 1994; Hansson et al. 2018) cause an increase in soil temperature. Reoccupation of the site by competing vegetation results in a decrease in soil temperature (Youngblood et al. 2011). Site preparation treatments need to create a window of open site conditions on cold soil sites to improve soil temperatures to ensure seedling growth.

Optimal temperature range for both photosynthesis and dry matter production, as a rule, is no wider than 10 °C and is related to the species natural thermal climate (Larcher 1995). Spruce species reach maximum $P_n$ at air temperatures between 15 and 25 °C and this temperature range is also where optimum growth occurs (Figure 2).

Spruce species have a decrease in $P_n$ above ~25°C, with very low or no $P_n$ at temperatures >35–40 °C (Figure 2). This shows that photosynthetic capacity of spruce can be adversely affected by air temperatures higher than ~25 °C. Warm temperatures increase photosynthates use for maintenance respiration in tree species (Pallardy 2008). Actively growing spruce species have a continual increase in respiration rates as temperature increases up to 40 °C (Figure 2). Interaction of these gas exchange conditions can limit seedling growth on sites exposed to warm growing season temperatures.

Heat damage can occur through direct plant exposure to high air temperatures or through heat stress accumulation over a period of time (Levitt 1980). Spruce seedlings are damaged at a temperature of 36 °C after 3 h of exposure (Koppenaal et al. 1990), with damage occurring after less exposure time as temperatures increase up to 55 °C (Figure 2). Constriction of the root collar at ground level (“heat girdling”) occurs in field-planted seedlings at soil surface temperatures >46 °C (Tranquilini 1979). Seedlings with a large stem diameter at planting is a measure of their sturdiness and helps reduce heat damage (Cleary et al. 1978; Mexal and Landis 1990; Tsakaldimi et al. 2005); thus, this plant attributes can mitigate heat stress (Grossnickle 2012; Grossnickle and MacDonald 2018). Seedlings that have developed root systems to access soil water can move water through their stems and transpire under high heat conditions (i.e. cooling effect), thereby improve their survival capability (Kolb and Robberchet 1996). However, when temperatures exceed 55 °C for short durations it can cause irreversible tissue damage and plant death (Seidel 1986; Larcher 1995; Kolb and Robberchet 1996).

Application of silvicultural practices to alter the soil surface structure or constituency, or reduce the amount of incoming solar radiation received at the soil surface, mitigates potential heat damage (Helgerson 1990) and seedlings water balance and gas exchange response (Grossnickle and Reid 1984a&b; Montague et al. 2000) during the establishment phase. Practices can be applied to reduce seedling exposure to extreme heat (e.g. removing surface litter or dark organic matter, planting on north-facing side of trenches or furrows created through mechanical site preparation treatments, shading from natural site features or shade cards, or by leaving an adequate overstory vegetation cover) (Grossnickle 2000).

Silvicultural practices can create microsites with a range of soil temperatures. These practices will result in a spruce seedling ecophysiological response which affects their field performance. Before applying these practices to recently planted seedlings, foresters need to identify whether growing season frosts, low or high microsite temperatures are likely to be a site environmental factor limiting their performance.

## 3 Response to the hydrological cycle

### 3.1 Seedling environment

Water inputs into the hydrologic cycle come primarily through precipitation and secondarily through downslope drainage. Losses occur through many sources, including interception of rainfall by vegetation, evaporation from plant and soil surfaces, soil drainage, and vegetation transpiration. Restoration sites where the site vegetation complex has been reduced through forest canopy removal can lower total stand transpiration rates (Hornung and Newson 1986) and site evapotranspiration (Miller 1983) resulting in potentially readily available soil water. However, at the effective rooting depth of established seedlings, other vegetation cover can compete for soil water (Sutton and Tinus 1983), resulting in localized conditions of soil water deficit (Newton and Comeau 1990). Alternatively, forest canopy removal can cause the water table to rise into surface layers where it can come in contact with root systems of recently planted seedlings (Williams and Lipscomb 1977; Dubé et al. 1995). Restoration sites can present conditions where seedlings are exposed to either low or excessive soil water at the effective rooting depth during the growing season.

Amount of plant available soil water in unsaturated soils is dictated largely by size distribution of individual soil particles, or soil texture. Relative amount of water retained in the upper soil layers as capillary water and the portion that sinks through as gravitational water depends upon the soil type. Soils with small pore size (i.e. 10 mm diameter) hold water, while coarser soils (pores >60 mm) allow water to rapidly pass through (Hillel 1971). As a result, water drains rapidly from coarse-textured soils, resulting in a lower soil water potential than mineral soils under unsaturated conditions. As soil dries, there is an attraction of water to soil particles resulting in lower or more negative soil water potentials (Kohnke 1968). Soil texture also affects soil water availability through its influence on hydraulic conductivity. Soil hydraulic conductivity is higher in very porous soils under saturated conditions, while conductivity under unsaturated soil conditions is higher in soils with smaller soil pores (Kohnke 1968). Consequently, effective rooting zone soil texture can create stressful conditions (e.g. coarse textured soils below saturated conditions), requiring seedlings to tolerate low plant water potentials necessary for water uptake (Dosskey and Ballard 1980; Bernier 1992).

Forest soils can also become anaerobic whenever there is an elevated water table or when an impermeable subsoil or flooding reduces soil aeration (Kozlowski 1982a). Water itself is not damaging, and trees can grow in aerated, nutrient-rich water. Roots are damaged in flooded soils from the lack of oxygen, which causes roots to produce ethylene and toxic substances (Kozlowski 1982a), and this effects seedling performance. However, an increased soil water table on restoration sites is usually short-lived as competing vegetation starts to occupy the site.

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 their transpirational transfer to the atmosphere. Atmospheric humidity has a strong effect on the site hydrologic cycle through its effect on evapotranspiration processes. Vapor pressure deficit (VPD) is the difference between saturated water vapor pressure and ambient vapor pressure at a given temperature. VPD can be viewed as an indicator of the drying power of air. VPD is the driving force that cycles water back into the atmosphere through evaporation of water from the soil and transpiration from plants. VPD fluctuates in an interdependent fashion with changes in both air temperature and relative humidity. Forest canopy removal can cause a reduction in the relative humidity (Reynolds et al. 1997) and an increase in VPD (Marsden et al. 1996; Groot et al. 1997), thereby increasing growing season site evapotranspiration (Viereck et al. 1993).

## 3.2 Seedling response

Soil water availability is one of the most critical environmental parameters required for successful seedling establishment (Grossnickle 2000). Water is essential for normal functioning of trees; with either too little or too much water limiting their physiological processes and subsequent morphological development (Pallardy 2008).

Flooding causes limited soil aeration, with this limitation dependent on soil temperature and season (i.e. flooded soils have a greater effect on seedling performance during the active growth phase and under warmer soil temperatures) (Kozlowski et al. 1991). Under conditions of excessive soil water, total anoxia can occur and plant tissues are unable to sustain metabolic processes. Flooding causes reduced $g_{wv}$ and $P_n$ because poor aeration impedes water uptake by roots, causing a drying of needles (Kozlowski 1982a). For example, spruce seedlings planted into flooded soils showed reduced $g_{wv}$ and lower predawn water potential ($\Psi_{pd}$) (Grossnickle 1987) and reduced $P_n$ (Dang et al. 1991) under flooded soil conditions. In addition, spruce seedlings have reduced root regeneration due to low soil aeration, and this results in limited shoot growth (Grossnickle 2000). Silvicultural practices that raise the planting spot elevation, or increase water drainage can create favorable edaphic conditions for conifer seedlings to develop roots into the soil (Adams et al. 1972; Söderstöm 1981; Lieffers and Rothwell 1986; von der Gönna 1989), resulting in enhanced shoot growth (Söderstöm 1981; Lieffers and Rothwell 1986; Schaible and Dickson 1990; Hånell 1992; Wells and Warren 1997).

Water stress occurs in trees when their water deficit reaches a level which negatively affects their physiological process (Teskey and Hinckley 1986). Different physiological activities in a plant cease to function at different values of plant $\Psi_{pd}$, (i.e. a measure of plant water status in relation to available soil water; Ritchie and Hinckley 1975) with Figure 3 providing a profile of how western red cedar responds to a range of water status conditions. Under high levels of available soil water, stomata are open (Lassoie et al. 1985), there is the potential for high levels of $P_n$ (Kozlowski et al. 1991), and there is optimum growth (Figure 3). Plant $\Psi$ levels that are >-0.5 MPa are considered optimum water status levels for growth (Hsiao 1973). Western redcedar seedlings have a continuous increase in shoot growth and can develop a well-formed root system when soil water is available (Figure 3).

As soil water becomes slightly restricted in western redcedar (i.e. $\Psi_{pd}$ declines from -0.5 to -1.0 MPa), shoot growth decreases by 33% (Figure 3). Studies show root growth in tree species declines and then stops over this range of soil water status (Kozlowski et al. 1991). These moderate levels of plant water stress can reduce seedling growth and cause complete growth cessation between -0.5 and -1.5 MPa in conifer species (Kozlowski 1982b; Grossnickle 2000). For example, a recent paper on piñon pine (*Pinus edulis*) found zero growth when $\Psi_{pd}$ declined to -1.3 MPa (Manrique-Alba et al. 2018).

As soils dry the rate of soil water movement to the seedling root system is restricted, limiting access to soil water. As a result, relative resistance in the soil-plant-atmosphere continuum (SPAC) increases because the root system is unable to take up sufficient water from surrounding soil to meet evaporative demands placed upon the shoot system by the atmosphere (Elfving et al. 1972; Hinckley et al. 1978). This causes water stress and reduces gas exchange processes. For example, as available soil water declines, causing a decrease in $\Psi_{pd}$, western redcedar maximum daytime $g_{wv}$ declines and $P_n$ decreases (Figure 3). This same response pattern occurs across all tree species (e.g. Jarvis and Jarvis 1963; Hinckley et al 1981; Kozlowski 1982b; Lassoie et al. 1985; Kozlowski et al. 1991; Grossnickle 2000; Pallardy 2008). Interestingly, western redcedar was able to maintain a high level of $g_{wv}$ as $\Psi_{pd}$ declined over the summer on a restoration site (Grossnickle 1993) and this response pattern is comparable to jack pine (*Pinus banksiana* Lamb.) seedlings on a boreal reforestation sites (Grossnickle and Blake 1986, 1987). In contrast, restoration site observations found western hemlock (*Tsuga heterophylla* (Raf.) Sarg.) (Grossnickle 1993) and spruce species (Grossnickle 2000) stomata to be very sensitive to drought; resulting in a rapid decline in $g_{wv}$ and $P_n$ as $\Psi_{pd}$ decreases. Western redcedar and jack pine show characteristics of an anisohydric plant species (i.e. maintain higher $g_{wv}$ for a given $\Psi_{pd}$ to sustain photosynthetic capability), while western hemlock and spruce species behave more like isohydric plants (i.e. respond quickly to declining $\Psi_{pd}$ by reducing $g_{wv}$ in order to avoid excessively low $\Psi$) (McDowell et al. 2008). It has been hypothesized that anisohydric type plants, such as western redcedar, have a greater risk of hydraulic failure because they have less strict stomatal regulation in response to drought (McDowell et al. 2008). Species differences in gas exchange response patterns to their water status need to be considered when applying silviculture practices to mitigate potentially stressful field site environmental conditions.

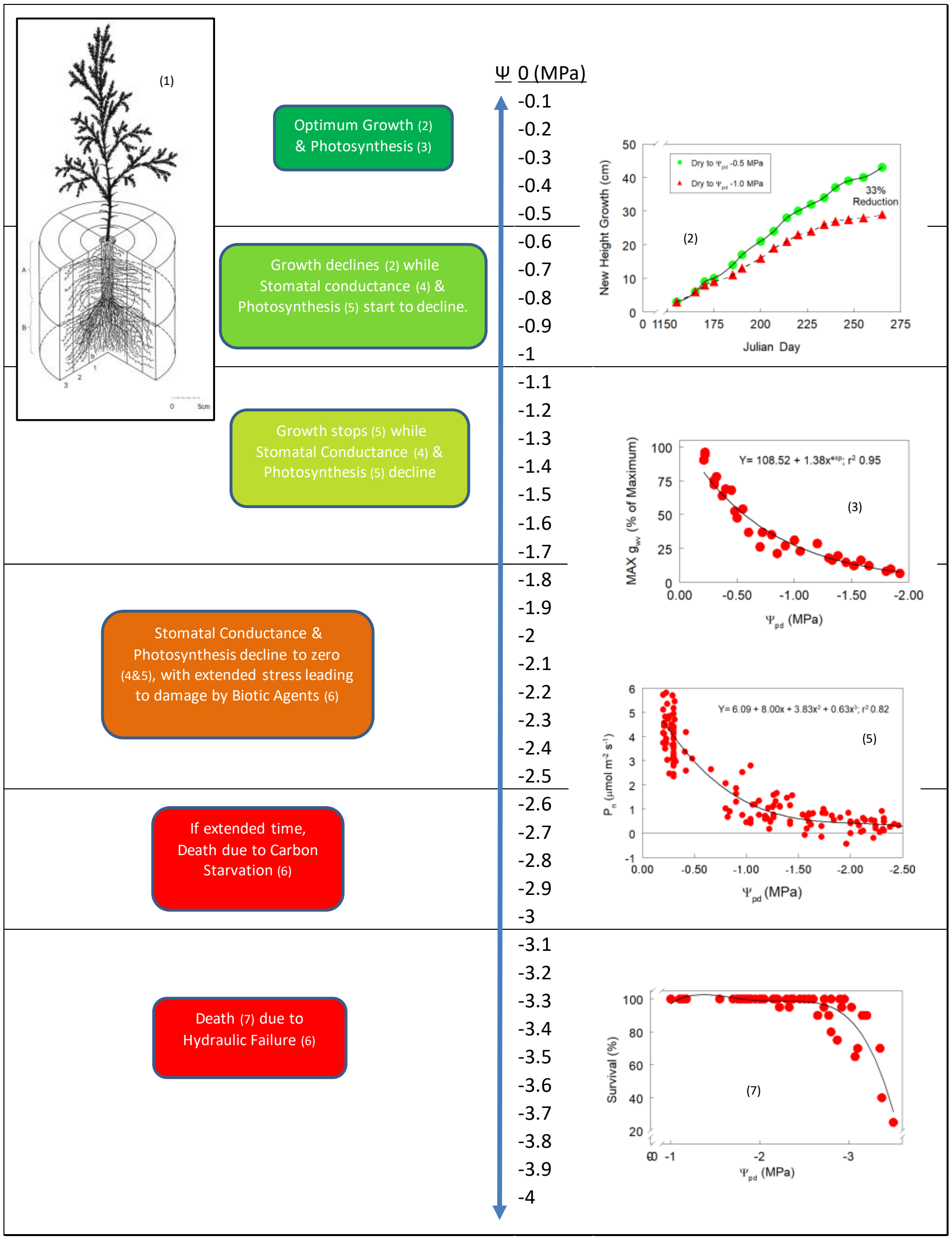

Figure 3. Growing season seedling water balance profile for western redcedar (*Thjua plicata*). This profile shows how established western redcedar seedlings (1; adapted data from Folk et al. 1994 showing optimum growth due to readily available soil water [a diagrammatic morphological representation; n= 20]) respond to changing water status. Physiological processes change along the following predawn water potential ($\Psi_{pd}$) gradient: from a $\Psi_{pd}$ 0 to -0.5 MPa optimum growth (2; Fan et al. 2008) & Net photosynthesis ($P_n$) (3; Grossnickle et al. 2005); from $\Psi_{pd}$ -0.5 to -1.0 MPa growth declines (2), while there is an initial decline in maximum stomatal conductance ($MAX_{gwv}$) (4; Grossnickle 1993) and $P_n$ (5; Grossnickle and Russell 2010); from $\Psi_{pd}$ -1.1 to -1.7 MPa growth stops (5); from $\Psi_{pd}$ -1.1 to -2.5 MPa $MAX_{gwv}$ (4) and $P_n$ (5) decline to zero; from $\Psi_{pd}$ -2.5 to -3.0 MPa $MAX_{gwv}$ (4) and $P_n$ (5) are at zero, with an extended timeframe possibly resulting in carbon starvation (6; McDowell et al. 2008); at $\Psi_{pd}$ <-3.0 MPa death occurs (7; Grossnickle unpublished data) attributed to hydraulic failure (6).

As drought conditions become more severe, excessive water stress can result in either carbon starvation or hydraulic failure, and subsequently plant death (McDowell et al. 2008). Western redcedar can be exposed to either severe drought pathway (Figure 3). For example, as $\Psi_{pd}$ declines to <-2.0 MPa, $P_n$ declines to nearly zero. Most Pacific Northwest coastal forest conifer species have complete stomatal closure between -1.5 and -2.5 MPa (Lassoie et al. 1985). Spruce species show a similar pattern with $P_n$ decreasing to the compensation point between a $\Psi_{pd}$ of –2.0 to –3.0 MPa (Grossnickle 2000). Thus, carbon starvation could occur if these tree species are exposed to drought long enough to limit photosynthesis longer than plant usage of stored carbon reserves. Alternatively, as $\Psi_{pd}$ declines to <-3.0 MPa, seedling death occurs in western redcedar (Figure 3). This is an expression of hydraulic failure because the drought intensity was sufficient to push them past their threshold for irreversible desiccation before carbon starvation occurs. Each species has a different level where drought stress becomes severe enough to cause death. For example, spruce seedlings start to die when shoot Ψ exceeds –4.0 MPa (McDonald and Running 1979) and this indicates that they can withstand very low Ψ before water stress causes death.

Daytime change in Ψ of trees is typically driven by VPD influencing transpiration, when soil water is not limiting (Ritchie and Hinckley 1975). This occurs because water loss from open stomata, in the form of water vapor, is controlled by the VPD gradient between water evaporating from internal stomata leaf surfaces and the outside air, and an increased resistance to water flow along the SPAC pathway to meet these evaporation demands. Thus, Ψ declines as VPD increases in spruce seedlings on restoration sites even when they have adequate soil water (Figure 4a). Stomata are sensitive to daily changes in VPD; typically having a high $g_{wv}$ when evaporative demand is low with a reduction in $g_{wv}$ as VPD increases, with this pattern occurring in both spruce species (Grossnickle 2000) and western red cedar (Grossnickle 1993; Grossnickle et al. 2005). Dramatic decrease in $g_{wv}$ to increasing VPD is due to lower shoot Ψ causing greater stomatal sensitivity (Pallardy 2008). For example, stomata of Engelmann spruce (*Picea engelmannii* Parry ex Engelm.) seedlings on a restoration site respond to the interaction between daytime changes in Ψ and VPD, thereby causing $g_{wv}$ to decline as Ψ decreases and VPD increases (Figure 4b).

A decline in $P_n$ as VPD increases is a typical pattern for conifer species (Kozlowski et al 1991). For example, western redcedar seedlings have a decrease in $P_n$ as VPD increases (Figure 4c) even when they have sufficient soil water (i.e. $\Psi_{pd}$, was >-0.85 MPa), with this same pattern found across spruce species (Grossnickle 2000). Increasing VPD is thought to cause either $g_{wv}$ to decline, as a guard against excessive plant water loss as $P_n$ declines (Sharkey 1984), or $P_n$ to decline, as a consequence of stomatal closure (Schulze et al. 1987).

It needs to be recognized that restoration site 'dryness' is dictated by the combination of low available soil water and VPD (Larcher 1995) and is a major limiting factor in achieving successful seedling establishment in ecosystems with a defined dry summer season (Mucina et al. 2017). Typically, exposure of plants to just one of these hydrologic parameters is insufficient to cause site aridity, but the combination of dry soils and high VPD conditions create stressful restoration site conditions (Larcher 1995). For example, $P_n$ of western redcedar is suppressed across all restoration site VPD conditions when $\Psi_{pd}$, was <-0.75 MPa, with $P_n$ decreasing to zero as VPD increased (Figure 4c). An increase in restoration site aridity causes a suppression in growth, either through its effect on lowering Ψ or reduced $P_n$ (Kozlowski et al. 1991; Grossnickle 2000). In addition, a rise in VPD can increase tree water use and potentially hasten mortality during severe drought (Will et al. 2013). Seedling exposure to high VPD and limited soil water availability are a main cause of reduce field performance.

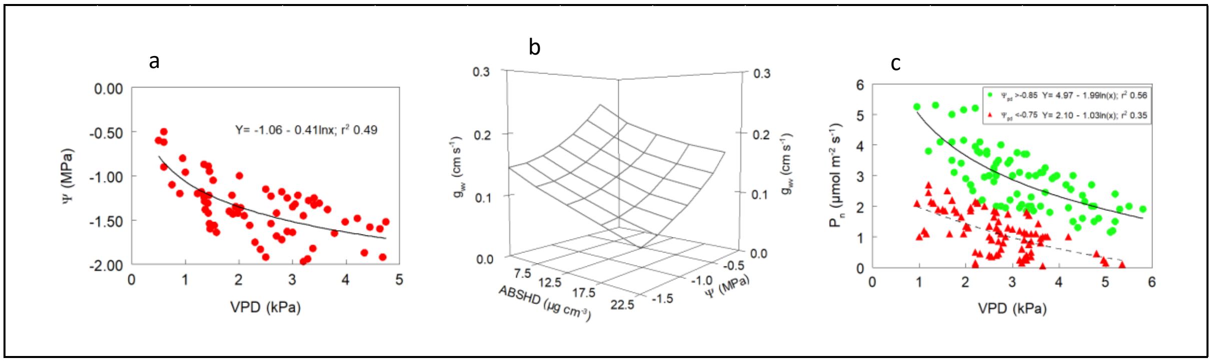

Figure 4. Response of seedlings on restoration sites to vapor pressure deficit (VPD) conditions. (a) White spruce (*Picea glauca*) water potential (Ψ) in response to VPD and on boreal reforestation site (Grossnickle and Blake 1986); (b) Engelmann spruce (*Picea engelmannii*) stomatal conductance ($g_{wv}$) in response to both Ψ and absolute humidity deficit (ABSHD) (Y= 0.315 – 0.205x -0.0139y + 0.096$x^2$ – 0.005$y^2$-(0.002x X y); $r^2$ 0.72) on a high elevation Rocky Mountain restoration site (Grossnickle and Read 1985); (c) Western redcedar (*Thjua plicata*) net photosynthesis ($P_n$) response to VPD on Pacific Northwest restoration sites under either low water stress (predawn water potential $\Psi_{pd}$ >-0.85 MPa) (Grossnickle et al 2005), or high water stress ($\Psi_{pd}$ <-0.75 MPa) (Grossnickle 1993) conditions.

A critical factor for successful stand establishment, thereby limiting effects of field site aridity is planting suitable species (Raftoyannis et al. 2006) and producing seedlings with desirable plant attributes (Pinto et al. 2011) that provide a capability to withstand drought stress and grow well after planting. There are morphological attributes that provide a measure of drought avoidance. Seedlings with smaller shoot systems perform better under harsh conditions (Grossnickle 2005b) because root systems can supply enough water to transpiring foliage to maintain a proper water balance (Grossnickle 2005a). Thus, shorter seedlings of both bareroot and container-grown stocktypes can have an advantage on stressful sites (Mexal and Landis 1990; Stewart and Bernier 1995; Jurásek et al. 2009; Grossnickle 2012), though overall container-grown stocktypes are better suited to dry sites (Grossnickle and El-Kassaby 2016). Stem diameter is a general measure of sturdiness, root system size, and protection against drought (Cleary et al. 1978; Mexal and Landis 1990); with numerous studies showing larger versus small stem diameter seedlings having better survival on dry sites (Grossnickle 2005a; Grossnickle 2012; Khanal et al. 2018). Seedlings with root systems that meet high morphological standards (i.e. increased root mass, fibrosity, volume, first-order laterals, area, and length) and physiological standards (i.e. greater root growth potential) have a capability to rapidly develop their root system after planting (Davis and Jacobs 2005; Haase 2011). This capacity to grow a sufficient root system helps overcome planting stress (Grossnickle 2005a) and survive (Grossnickle 2012), thereby become established after planting (Figures 3 & 4). This is why there is a positive relationship between root system quality and growth in many reported studies (Grossnickle and MacDonald 2018). Shoot-to-root ratio has also been found to forecast growth on dry or normal sites because it defines their drought avoidance potential (Thompson 1985). Root systems in proper proportion to the shoot system has long been recognized as a desirable attribute (Toumey 1916) because their water status is directly tied to their shoot-to-root balance (Parker 1949); which can result in improved seedling survival (Grossnickle 2012) and growth (Grossnickle and MacDonald 2018) under dry site conditions.

Application of drought hardening (process of plant physiological adaptation) in the nursery to increase stress tolerance (Kozlowski and Pallardy 2002) is reported, in some cases, to improve seedling survival (Grossnickle 2012) and growth (Grossnickle and MacDonald 2018). Spruce species (Grossnickle 2000) and western redcedar (Major et al. 1994; Grossnickle and Russell 2010) develop drought tolerance when exposed to drought hardening. However, benefits of drought hardening are ephemeral because seedlings rapidly lose drought tolerance once shoot elongation begins (Teskey and Hinckley 1986; Abrams 1988). Improved drought tolerance to allow seedlings to overcome planting stress and become established has a very narrow phenological window, making it difficult for this attribute to consistently result in good field performance.

Seedling quality can mitigate but not overcome severe field site drought conditions. Pinto et al. (2016) found that longer-rooted, larger stocktype provided no advantages in survival, growth, or carbon allocation compared with smaller stocktypes when seasonal drought occurred soon after planting and was severe enough to inhibit root growth to access soil water. Recently planted seedlings need to initiate growth and become ‘‘coupled’’ into the forest ecosystem (Grossnickle 2005a), thereby avoiding water stress. It is the lack of coupling (i.e. restricted rooting into the soil profile limiting soil water access) that increases the possibility of water stress which can result in death. Simpson and Ritchie (1997) believe that root growth is critical to seedling field performance under severe site environmental conditions. Thus, seedling survival is related to their inherent root growth potential (Grossnickle 2012) and the degree to which field site environmental conditions limits or enhances this potential to become established or coupled into the forest ecosystem (Margolis and Brand 1990; Grossnickle 2000).

Competition for reforestation site resources is a major factor limiting successful seedling growth (Dobbs 1972; Gjerstad et al. 1984; Sutton 1985; Radosevich and Osteryoung 1987; Coates et al. 1994) because competition can remove soil water from the soil root zone via transpiration (Sutton and Tinus 1983; Newton and Comeau 1990). There are numerous studies describing how an increase in plant cover resulted in a reduction in seedling seasonal Ψ (Eissenstat and Mitchell 1983; Grossnickle and Reid 1984a; Elliot and White 1987; Petersen et al. 1988; Pabst et al. 1990; Shainsky and Radosevich 1992; Perry et al. 1994), with this greater water stress causing a reduction in $g_{wv}$ (Grossnickle and Heikurinen 1989) and $P_n$ (Pinto et al. 2018), and growth of recently planted seedlings (Nambiar and Zed 1980; Carter et al. 1984; Sands and Nambiar 1984; South and Barnett 1986; Margolis and Waring 1986; Grossnickle and Heikurinen 1989; Wood and von Althen 1993; Wagner et al. 1999; Dinger and Rose 2009; Gonzalez-Benecke and Dinger 2018). Removal of competing vegetation and keeping it in check allows planted seedlings better access to site resources, thereby improving their field performance.

Site preparation can modify soil properties to affect site water status (Prévost 1992; Sutton 1993). For example, site preparation practices that raise planting spot elevation to increase soil temperatures (Grossnickle 2000; Luoranen et al. 2018) can also dry out quickly when water table is low (Örlander et al. 1990; Luoranen et al. 2018), causing water stress and reduced growth (Bassman 1989). Alternatively, site preparation treatments on arid sites (e.g. trenching and ripping to lower the planting spot) are considered one of the best options to improve seedling water status (Cortina et al. 2011) because it increases access to soil water (Querejeta et al. 2001), which reduces water stress and improves their gas exchange response (Fleming et al. 1996; Ruthrof et al. 2016), and subsequent field performance (Palacios et al. 2009). When applying site preparation treatments, one must consider whether low soil water availability is the primary field site limiting environmental factor to ensure proper treatment selection to enhance seedling growth.

Plant facilitation has been proposed to benefit plant establishment on sites with increasing environmental severity (i.e. stress gradient hypothesis) (Bertness and Callaway 1994). Proposed benefits of facilitation within dryland ecosystems are primarily through shading causing a reduction in incident radiation and ameliorating microclimatic conditions (Callaway 2007; Holmgren et al. 2012). This effect can directly or indirectly enhance soil water status under plant cover compared to sites without competition, thereby by improving seedling water status (Nuñez et al 2009) and photosynthetic response (Yang et al. 2009). Model simulations for *Pinus pinea* L. under arid conditions found the best planting spot to be mid-shade locations because it provides enough shade to improve survival while allowing $P_n$ to reach maximum values (Calama et al. 2015). Benefits of facilitation are mixed based on meta-analyses at the individual plant response level (Soliveres et al. 2014), with it considered to have the greatest benefit when seedling establishment occurs in communities dominated by shrubs and trees (Gómez-Aparicio 2009) and on arid sites (Gómez-Aparicio et al. 2004; Butterfield et al 2016). Alternatively, artificial shading on arid sites can reduce incoming solar radiation and increase soil water, thereby improving seedling performance (Benyas et al. 2005). Shading can be an option to alter energy and hydrologic cycles to ameliorate severe environmental conditions on arid sites.

Under some conditions site preparation treatments to remove vegetative competition can improve water availability in the soil profile, while under other conditions leaving plant cover might create facilitation and ameliorate potentially stressful microsite conditions. One needs to consider site microclimatic conditions to determine what environmental variables are limiting seedling ecophysiological performance. Then one can define silvicultural treatments to enhance microclimate conditions, thereby improve growth of planted seedlings.

## 4 Response to the nutrient cycle

### 4.1 Seedling environment

All nutrients have three major cycles; geochemical, biogeochemical, and internal cycling. Geochemical cycle involves atmospheric and soil weathering inputs or losses of nutrients through forest stand removal, leaching, or erosion. Biogeochemical cycle involves nutrient uptake by trees from the soil and their return to the soil via litterfall, tree 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 accumulate within the forest ecosystem. Nutrients within the forest ecosystem are located in four main nutrient pools: (*i*) aboveground tree layer, (*ii*) ground cover vegetation, (*iii*) forest floor and organic soil layers, and (*iv*) mineral soil. In most forest ecosystems, forest floor and organic soil layers and mineral soil are the main storage components of nutrient reserves (e.g. Pacific Northwest coastal forests Johnsen et al. 1982; boreal forests, Grossnickle 2000; Southeastern pine forests, Fox et al. 2007). If the restoration site soil system is retained then the nutrient budget comes primarily from forest floor organic matter, and is more rapidly cycled within the ecosystem through decomposition and mineralization. If the site has a readily available source of carbon, this in combination with an increased soil energy balance can stimulate site microbial populations to cause decomposition of organic matter and release nutrients into the available soil pool (Vitousek et al. 1979; Chapin 1983; Staaf and Olsson 1994).

### 4.2 Seedling response

Forest restoration sites initial abundance of available nutrients can be utilized by both established seedlings and competing vegetation (Grossnickle 2000; Fox et al. 2007). For example, soil N availability is high after harvesting; which is why nutrient limitations are not considered a factor on most forest restoration sites just after site disturbance (Grossnickle 2000; Fox et al. 2007). Nutrient limitations become a factor as vegetative competition starts to reoccupy the site because weed species can have soil profile root densities 50-100 times those of planted seedlings (Nambiar 1990) and these rapidly growing competitive species respond to site available nutrients with an accelerated growth rate (Chapin 1983) which can negatively affect seedling growth (Pernot et al. 2019).

Nutrient concentration of needle tissue has been related to many ecophysiological processes in tree species, with greater nutrient concentration attributed to improved gas exchange capability, drought resistance (i.e. avoidance and tolerance), freezing tolerance, and growth (van den Driessche 1991a; Pallardy 2008). Optimal nutrient reserves can have a positive effect on various seedling attributes before planting. For example, N concentration can alter the $P_n$ rate and subsequent growth of spruce seedlings (Grossnickle 2000) and, in certain instances, improve conifer seedling drought resistance and freezing tolerance (Grossnickle and MacDonald 2018). Thus, seedling nutrient status is important because it is, in many cases, related to various plant attributes contributing to positive field performance (del Campo et al. 2010).

Recently planted seedlings are more likely to have a lower nutrient status as they begin to grow during the establishment phase. This occurs because their nutrient status and subsequent growth are tied to internal mobilization of nutrients to sites of active growth and external uptake of nutrients from the soil. Recently planted seedlings are likely to have a low level of nutrient uptake from the soil until new root and mycorrhizal development can balance nutrient demand that occurs due to active growth. As a result, newly planted seedlings can have a lower nutrient status during the first growing season after field planting, indicating limited access to site nutrients (Munson and Bernier 1993; Kim et al. 1999; Villar-Salvador et al. 2015). Improved nutrient status can occur during the second field growing season, which indicates that planted seedlings are better able to acquire soil nutrient resources as root systems develop out into the surrounding soil (Munson and Bernier 1993; Kim et al. 1999). This is confirmed in recent work showing that new root growth in recently planted seedlings improves their uptake of nutrients on a forest restoration site (Pernot et al. 2019).

Nutrient needs of recently planted seedlings can be addressed through field site fertilization. However, reviews have found variable field performance of conifer seedlings in response to field site fertilization (Sutton 1982; Brockley 1988; van den Driessche 1991b). Field site fertilization can cause rapid development of vegetative competition during early stages of stand establishment because early successional species extensive root development creates a competitive advantage over recently planted seedlings. This imbalance in root site occupancy can result in very little field site fertilization actually being utilized by planted seedlings (Staples et al. 1999). However, there are instances where site nutrient limitations are an issue and field site fertilization has benefited seedling establishment (e.g. Grossnickle 2000; Koňasová 2012; Ruthrof et al. 2016). Due to the variability of success in past field fertilization programs to consistently enhance performance on restoration sites, this silvicultural practice is considered an expensive and an inefficient approach to supplying nutrients to seedlings under all but sites with defined nutrient limitations (Brockley 1988).

The physiological phenomenon of a lower internal nutrient status, due to a dilution of existing internal nutrient pool as young seedlings begin to grow, is the reason why their nutrient status at planting can be important for their establishment. Increasing nutrient reserves through nursery fertilization is considered very efficient, compared with planting site nutrient acquisition (i.e. field fertilization) (Tinus 1974; Binkley 1986). Planting seedlings with optimum nutrient reserves had a positive relationship with shoot and root growth after outplanting in most reported studies (Grossnickle and MacDonald 2018). Positive growth responses to optimal nutrient reserves in newly planted seedlings have been attributed to increased remobilization of nutrients from old tissue to actively growing tissue to satisfy growth needs (McAlister and Timmer 1998; Xu and Timmer 1999; Imo and Timmer 2001; Salifu and Timmer 2003; Pokharel et al. 2017). Benefits of nutrient remobilization occur when seedlings are not fully coupled to the restoration site (Villar-Salvador et al. 2015), thereby providing a capability to grow roots, overcome planting stress (Grossnickle 2005a) and become established. Seedlings with optimal nutrient reserves can quickly couple to the site, enabling them to withstand subsequent harsh summer environmental conditions (Timmer and Aidelbaum 1996; Luoranen and Rikala 2011). In certain instances, there is a lack of a positive response to optimal nutrient reserves which can be attributed to other limiting site factors (Grossnickle and MacDonald 2018). One must also recognize improved growth that comes directly from optimal seedling nutrient reserves at planting only lasts for the first season (Rikala et al. 2004; Heiskanen et al. 2009; Luoranen and Rikala 2011). The effect of optimal nutrient reserves is a stimulation of rapid growth after planting, thereby creating a seedling size advantage on sites with competing vegetation (van den Driessche 1991b; Timmer 1997; Malik and Timmer 1998).

Site preparation treatments that reduce vegetative competition but leave organic layers on the forest site cause a gradual release of nutrients (Chapin 1983; Nilsson et al. 1996). Treatments that mix organic and mineral soil layers (e.g., berms or mounds) increase mineralization within the soil profile and can improve nutrient availability with the effective duration dependent upon climate and soil conditions (Örlander et al. 1990). In contrast, site preparation that removes much of the biologically active, nutrient-rich organic layers can reduce site nutrients (Grossnickle 2000). Availability of site nutrient reserves during the establishment phase can be altered by site preparation treatments, with the magnitude of growth response also tied to how these treatments influence other environmental parameters known to affect seedling performance.

## 5 Conclusions

The establishment phase is a period during stand development when seedlings have an opportunity to express their inherent growth potential. This expression of growth is related to their morphological and physiological attributes and their ecophysiological response to site environmental conditions. By understanding how seedlings respond to site conditions, practitioners can apply proper cultural practices to maximize their growth potential. It is this interaction between seedling ecophysiological capabilities and restoration site environmental conditions that ultimately determines their field performance.

## 6 Tribute

This article is dedicated to John H. Russell, who passed away on December 21, 2018. John collaborated on the research related to western redcedar reported on in this paper. John was a colleague and friend. He will be missed.

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