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Why seedlings survive: influence of plant attributes

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Abstract Seedling survival and successful forest restoration involves many silvicultural practices. One important aspect of a successful forest restoration program is planting quality seedlings with high survival capability. Thus the nursery needs to create seedlings with plant attributes that allow for the best chance of success once a seedling is field planted. Since the mid-twentieth century, research foresters have critically examined plant attributes that confer improved seedling survival to field site conditions. This review describes the value of commonly measured seedling quality material (i.e. shoot height, stem diameter, root mass, shoot to root ratio, drought resistance, mineral nutrient status) and performance (i.e. freezing tolerance and root growth) plant attributes defined as important in answering the question of why seedlings survive after planting. Desirable levels of these plant attributes can increase the speed with which seedlings overcome planting stress, become 'coupled' to the forest restoration site, thereby ensuring successful seedling establishment. Although planting seedlings with these desirable plant attributes does not guarantee high survival rates; planting seedlings with desirable plant attributes increases chances for survival after field planting.

Keywords Seedling survival · Forest restoration · Morphological attributes · Drought resistance · Freezing tolerance · Seedling nutrition · Root growth capability

Introduction

Why seedlings survive after planting has long been debated because seedling survival is pivotal in the initial success of a forest restoration program. During the early part of the twentieth century, programs planting nursery-grown seedlings in North America reached an annual size of 10–20 million (Toumey 1916). Due to this silvicultural investment, foresters began examining plantation failures and tried to discern reasons for seedling mortality (e.g. Tillotson 1915; Young 1921; Kittredge 1929; Rudolf 1939). Often seedling

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losses were attributed to environmental stress, animal grazing, disease, or insects. However, in many cases poor quality planting stock (Kittredge 1929) or the inability of planted seedlings to grow roots (Rudolf 1939) was defined as the cause of plantation failure. The work of Toumey (1916) and studies initiated on southern pines in the 1920s (reported by Wakeley 1954) were some of the initial attempts to grade nursery stock using morphological parameters to improve seedling establishment. Thus, early in the twentieth century researchers began to ask the question of how plant attributes influence seedling survival after field planting.

Nursery cultural and silvicultural practices have a strong influence on seedling performance immediately after planting. Effects of these practices on seedling performance need to be understood to make sound forest restoration decisions. Regeneration silviculture is a complex process and many factors go into making a successful forest restoration program. Implicit within a seedling production program is recognition of the inherent species characteristics when making the proper selection of the genetic source that is adapted to forest restoration site conditions (Zobel and Talbert 1984). Also silvicultural practices related to the regeneration process (e.g. storage, handling, planting date, planting practices, site preparation, and vegetation management) all have an effect on the success of a forest restoration program. Readers interested in understanding effects of these factors can examine a number of excellent texts on silvicultural practices and forest regeneration site performance of planted seedlings (e.g. Cleary et al. 1978a; Lavender et al. 1990; Duryea and Dougherty 1991; Hobbs et al. 1992; Grossnickle 2000; Wagner and Colombo 2001).

How recently planted seedlings initiate growth and become “coupled” into the forest ecosystem (Grossnickle 2005a), thereby avoiding water stress, are critical factors for success of a forest restoration program. It is the lack of coupling (i.e. due to a restricted rooting volume limiting access to soil water) that increases the possibility of excessive water stress in seedlings which can result in either carbon starvation or hydraulic failure, and subsequently seedling death (McDowell et al. 2008). Thus, seedling survival is related to their inherent growth potential and the degree to which field site environmental conditions limits or enhances this potential for seedlings to become established or coupled into the forest ecosystem (Grossnickle 2000).

In the mid-twentieth century, researchers started to critically examine plant attributes that conferred improved survival for bareroot (Wakeley 1948, 1954; Stone 1955) and container-grown (Tinus 1974) seedlings. This was the start of seedling quality programs based on the need for a better understanding of performance capabilities of nursery-grown seedlings in relation to the forest restoration site. Seedling quality assessment has evolved to include numerous morphological and physiological measurement procedures for defining field performance (Mattsson 1996; Grossnickle 2000). Subsequently, a wealth of information has been published on plant attributes that improve the odds of survival once a seedling is field planted.

Defining seedling quality comes from measurements of seedling properties that describe material (i.e. single point measures of individual plant parameters) and performance (i.e. plant measurements reflecting an integrated response of many material attributes to defined environmental conditions) attributes (Ritchie 1984). This review examines the seedling through commonly measured material (i.e. shoot height, stem diameter, root mass, shoot to root ratio, drought resistance, mineral nutrient status) and performance (i.e. freezing tolerance and root growth) plant attributes used to define seedling quality. The objective of this review is to conduct a comprehensive, though not exhaustive, examination of work describing the value of primary plant attributes that are important in answering the question of why seedlings survive after planting on forest restoration sites.

Material morphological attributes

> …serve their purpose only so far as they actually separate seedlings with a high capacity for survival and growth after planting from those with a low capacity. (Wakeley 1948)

Extensive work since the 1950s shows desirable morphological attributes contribute to seedling survival after transplanting on to forest restoration sites. To summarize this work, a well-balanced shoot to root system, with a sturdy stem and a large fibrous root system provides the best chance for seedling survival (e.g. southern pines—Lantz 1985; South 2000, radiata pine (*Pinus radiata* D. Don)—Menzies et al. 1985, Pacific Northwest and Northern British Columbia tree species—Scagel et al. 1993, temperate zone deciduous hardwoods—Wilson and Jacobs 2006). Morphological attributes are considered a reliable measure of seedling quality (Puttonen 1997) because they retain their mark on the seedling identity for extended timeframes after seedlings are field planted and start to grow. These plant structural features play a key role in defining their hydraulic architecture (i.e. potential water balance), thus helping to determine whether plants live or die during exposure to drought (McDowell et al. 2008).

Even so, historical work has found morphological attributes to be an inconsistent measure of seedling survival (Wakeley 1954; Thompson 1985; Mexal and Landis 1990). This stems from the fact that morphological parameters only measure overall seedling size, growth potential and shoot to root balance, not seedling physiological quality. Thus measures of morphological parameters are only part of the equation of plant attributes required for successful seedling survival (Wakeley 1948, 1954; Tinus 1974; Ritchie 1984; Mexal and Landis 1990). With this caveat in mind, the following discussion focuses on the influence morphological parameters have on seedling survival.

Shoot height

Large seedlings have been recommended for planting on sites where there is little environmental stress but there is the potential for excessive competition (Toumey 1916). As black spruce (*Picea mariana* (Mill.) B.S.P.) seedlings increased in shoot size they had a greater exposure to growing season available light on sites with high competition, resulting in greater survival and shoot growth (Jobidon et al. 1997, 2003). Taller bareroot loblolly pine (*Pinus taeda* L.) seedlings at planting confer higher survival on sites with little environmental stress (Fig. 1). Numerous studies show large stock on sites where competition is prevalent can improve survival and growth (Newton et al. 1993; Mason et al. 1996; Mohammed et al. 1998; South and Mitchell 1999; Puértolas et al. 2003; Villar-Salvador et al. 2004a).

Shoot height is a general measure of photosynthetic and transpirational capacity and also a reflection of potential height growth (Armson and Sadreika 1979; Cleary et al. 1978b; Mexal and Landis 1990). As the shoot system initiates growth, larger seedlings produce greater absolute amounts of new shoot biomass (Thiffault 2004; Grossnickle 2005b) and occupy a greater area within the planting spot than smaller seedlings, thereby capturing more incoming solar radiation. This is critical because the effect of competition

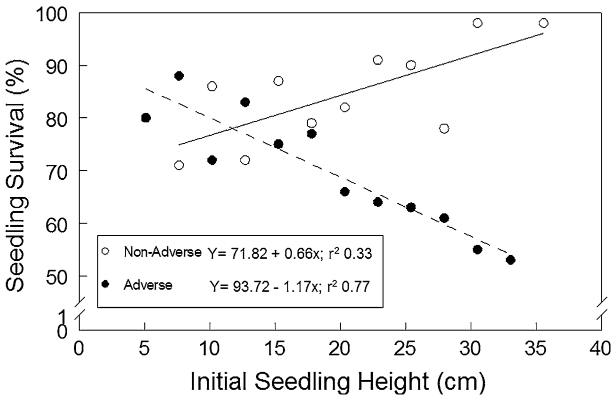

Fig. 1 The relationship between survival (year 2) and initial seedling height for bareroot loblolly pine (*Pinus taeda* L.) seedlings on adverse and non-adverse sites (Tuttle et al. 1987)

on limiting sunlight, thus seedlings net photosynthetic carbon gain, is related to survival (Johnson and Smith 2005). Shoot system size is important because on sites with available soil water and nutrients, competition for light between planted seedlings and the site vegetation complex is a main factor limiting seedling performance (Grossnickle 2000).

In contrast, planting seedlings with greater height can result in lower survival on droughty sites (Larsen et al. 1986; Boyer and South 1987; Tuttle et al. 1988; McTague and Tinus 1996). For example, shorter bareroot loblolly pine seedlings had higher survival on sites with limited soil water and greater environmental stress (Fig. 1). Under dry soil conditions, larger, compared to smaller, conifer seedlings can have greater water stress (Rose et al. 1993; Stewart and Bernier 1995), lower photosynthesis (Lamhamedi et al. 1997) and reduced growth (Baer et al. 1977; Hahn and Smith 1983). As the shoot system reaches a certain size, increased foliar mass can increase the seedling's susceptibility to planting stress because a newly planted seedling's root system cannot supply enough water to transpiring foliage to maintain a proper water balance (Grossnickle 2005a). The susceptibility of larger seedlings being exposed to water stress at planting is mitigated if they have the capability to quickly develop new roots (see Root Growth).

Stem diameter and root mass

Seedling stem diameter is a general measure of seedling sturdiness, root system size, and protection against drought and heat damage (Cleary et al. 1978b; Mexal and Landis 1990). Thus, it is difficult to separate the relationship between these two parameters, with a greater root system size occurring as stem diameter increases in both bareroot (Ritchie 1984) and container-grown (Grossnickle 2000) seedlings. Greater root mass is an indicator of root absorptive surface (Thompson 1985) conferring a greater seedling drought avoidance capability after field planting.

Johnson and Cline (1991) considered stem diameter the single most useful morphological measure of seedling quality. Numerous studies show larger stem diameter seedlings tend to survive better than small stem diameter seedlings (e.g. bareroot; van den Driessche 1980, 1984; South and Mexal 1984; Long and Carrier 1993; McGrath and Duryea 1994; South 1993; Zwolinski et al. 1996; South and Mitchell 1999; South et al. 2001, 2005; Rose and Ketchum 2003; Morrissey et al. 2010) (e.g. container-grown; Hines and Long 1986;

Bayley and Kietzka 1997; Mexal et al. 2008; South et al. 2005; Oliet et al. 2009b; Morrissey et al. 2010). This is why Mexal and Landis (1990) felt stem diameter can best forecast field survival because it indirectly confers a number of desirable plant attributes (i.e. water absorption—roots, water transport—stem) that are considered important parameters of the plant hydraulic architecture that play a role in plant survival during drought (McDowell et al. 2008).

The relationship of larger seedling stem diameter, and by extension root development, and survival is not universal. In a review of bareroot pine seedlings spanning many trial sites in the southeastern US, survival was related to initial stem diameter at planting in most, but not all cases (Fig. 2). As seedling stem diameter increased in size the probability that a plantation would have survival at <75 % declined from a high of 88 % for seedlings with a small stem diameter (i.e. <2.4 mm) to only 9 % for seedlings with a very large stem diameter (i.e. >6.3 mm). Seedlings with a larger stem diameter had a greater probability of high survival, but not in all field situations.

Seedlings with more roots have better survival potential (Toumey 1916) and seedlings with a good quality root system have better establishment capability after field planting (Davis and Jacobs 2005). Greater root system size at planting can result in greater seedling survival (Larsen et al. 1986; Rose et al. 1997). Seedlings with a larger stem diameter and more roots exhibit fewer symptoms of planting stress (Haase and Rose 1993) and have better survival than seedlings with a smaller stem diameter and fewer roots (South et al. 1985; Carlson 1986; Blake et al. 1989; Hobbs et al. 1989; Long and Carrier 1993). Greater root system size can confer greater root growth capability (see Root Growth). On harsh sites, a greater capability for absorption and transport of water from roots through the stem to the transpiring shoot system gives seedlings a better chance of overcoming planting stress (Grossnickle 2005a).

Shoot to root ratio

Measures of shoot to root (S:R) balance define seedlings drought avoidance potential (Thompson 1985). The need for seedlings to have root systems in proper proportion to the

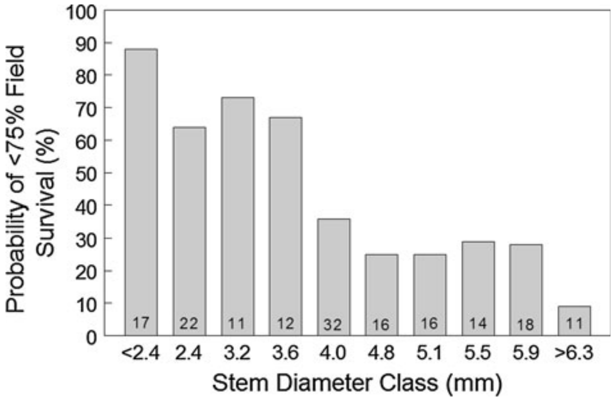

Fig. 2 The probability of seedling survival in the field <75 % for bareroot loblolly pine (*Pinus taeda* L.) and slash pine (*Pinus elliottii* Engelm.) seedlings graded into stem diameter classes (adapted from South et al. 1985). *Note*: Number within a bar for a stem diameter class defines the number of field sites from where data was collected

shoot system has long been recognized as a desirable seedling attribute (Toumey 1916) because seedling water status is directly tied to their S:R (Parker 1949). An imbalance in the shoot transpirational surface to the root absorbing surface (i.e. S:R > 3.0) can result in water stress for bareroot seedlings (Baldwin and Barney 1976). A S:R between 1.0 and 3.0 gave bareroot seedlings a better chance of survival (Hermann 1964; Foiles and Curtis 1973; Hobbs 1982), with survival increasing as S:R decreases (Tanaka et al. 1976; Lopushinsky and Beebe 1976; Larsen et al. 1986; Boyer and South 1987; Chamshama and Hall 1987; Kainer and Duryea 1990; Haase and Rose 1993; Généré and Garriou 1999) (Fig. 3a). Thompson (1985) found bareroot seedlings with lower S:R on average had a 29 % higher level of survival. The bareroot nursery cultural practices of undercutting (reviewed by South and Donald 2002) and top pruning (South and Blake 1994) are commonly used to decrease the S:R and produce seedlings with better survival capability. Even though data showing the importance of S:R for bareroot seedling survival is compelling, Hobbs (1984) warns that assessing potential survival based on the S:R without also judging the quality of the root system (i.e. fibrous root system with many growing tips) can limit its reliability to forecast survival.

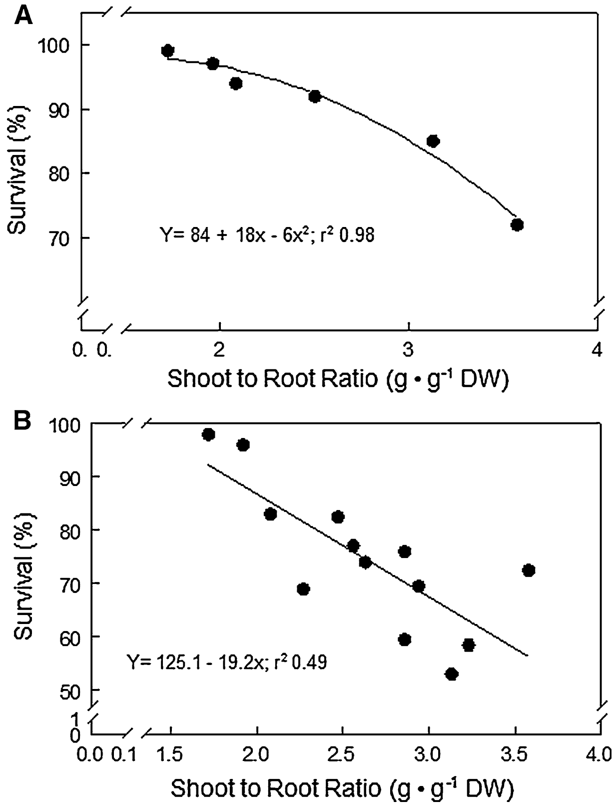

Fig. 3 **a** The effect of shoot to root ratio of bareroot loblolly pine (*Pinus taeda* L.) seedlings on the survival under a simulated drought environment (adapted from Mexal and Dougherty 1983). **b** The effect of shoot to root ratio of container-grown Patula pine (*Pinus patula* Schiede ex Schltdl. & Cham.) seedlings on survival 1 month after field planting (adapted from Bayley and Kietzka 1997)

Studies have also found the survival of container-grown seedlings to be greater with lower S:R under droughty field conditions (Zida et al. 2008; del Campo et al. 2010) (Fig. 3b). While these reports show the importance of initial S:R to enhance survival for container-grown seedlings, S:R based on total shoot and root weights may be limited in forecasting survival except under harsh field conditions. Bernier et al. (1995a) found little evidence that the S:R based on total shoot and root weights forecast survival for container-grown seedlings on sites lacking severe environmental stress. Bernier et al. (1995a) argued that the root plug-soil interface is the primary limiting factor rather than the overall root system in affecting seedling performance. Container-grown seedlings are typically grown in a medium that has desirable characteristics for root growth in the nursery (i.e. increased aeration and water holding capacity, low bulk density) (Tinus and McDonald 1979). These media characteristics limit movement of water into the root plug, after field planting, due to physical constraints of low density peat plugs (Bernier 1992; Bernier et al. 1995b) causing an imbalance of soil matric potential between plug media and field site soil (Day and Skoupy 1971). The ratio of root development outside of the container plug to total shoot dry weight best represented container-grown seedling drought avoidance potential; seedlings with minimal root development outside the plug having the greatest level of water stress (Grossnickle and Reid 1984). This is because the root plug-soil interface is the point of greatest resistance to water flow for newly planted container-grown seedlings (Örlander and Due 1986). A measure of root development out of the plug and into the soil in relation to shoot mass is a logical description of S:R balance of container-grown seedlings that better reflects their drought avoidance, thus survival potential.

Material and performance physiological attributes

> …seedlings must be produced in such a way as to be physiologically ready to outplant into the field environment. (Lavender and Cleary 1974)

Survival is determined, in part, by the ability of seedlings to respond to environmentally stressful conditions that can occur after being planted. The most dramatic of these site conditions are alterations in the heat exchange processes and site-water relations limiting seedling performance (Miller 1983), while site nutrient dynamics are also considered rate limiting to young forest stands (Troth et al. 1986). The following discussion focuses on physiological attributes that allow seedlings to survive conditions of drought, frost and nutrient dynamics just after planting on a forest restoration site.

Cultural practices that provide an improved "physiological quality" to seedlings have long been considered important in increasing their chances for survival just after field planting (Wakeley 1948, 1954). This is because nonhardened seedlings (Rowe 1964; Tinus 1974; Hobbs 1984) or seedlings lacking the proper nutrient balance (see Nutrient Status) lack the physiological capability to become rapidly established after planting on forest restoration sites. Acclimation of seedlings is based on the concept of "slowly increasing stresses to induce physiological adjustments in plants" (Kozlowski and Pallardy 2002) thereby developing protection from potentially stressful field site conditions. Thus, plant acclimation or nursery cultural hardening practices (Wakeley 1954; Lavender and Cleary 1974; Landis et al. 1999) are applied to increase the odds in favor of seedling survival to field site conditions. Nursery practitioners have used cultural practices of reduced day-length, temperature, watering and fertilization regime modification to harden container-grown seedlings (Tinus and McDonald 1979; Landis et al. 1999), with watering and fertilization regime, plus shoot and root culturing modification used to harden (also improve S:R) bareroot seedlings (Duryea 1984; Mexal and South 1991). These treaties provide a detailed explanation of cultural practices used to harden seedlings. The following sections discuss physiological attributes, adjusted by hardening practices, which can improve seedlings chances of survival after transplanting to forest restoration sites.

Drought resistance

Drought stress causes tree species to develop drought resistance (Abrams 1988). Nurseries apply cultural practices that create water stress events at the end of the growing season to trigger budset or the cessation of shoot growth, and initiate stress resistance in seedlings. Periodic moderate water stress is used as a nursery cultural practice to induce bud formation (Lavender and Cleary 1974; Timmis and Tanaka 1976; Young and Hanover 1978; Macey and Arnott 1986; Calmé et al. 1993) as well as improve drought resistance (i.e. tolerance and avoidance) through osmotic adjustment (Kandiko et al. 1980; Hennessey and Dougherty 1984; Buxton et al. 1985; Ritchie and Roden 1985; Seiler and Johnson 1985; Grossnickle et al. 1991a; Major et al. 1994; Villar-Salvador et al. 2004b), stomatal sensitivity to drought (Unterschuetz et al. 1974; Roberts and Dumbroff 1986; Zwiazek and Blake 1989; Villar-Salvador et al. 1999), reduce susceptibility to xylem cavitation in some species (Beikircher et al. 2010), but not all species (Harvey and van den Driessche 1999; Beikircher et al. 2010), and create seedlings with lower S:R (Timmer and Miller 1991; Bayley and Kietzka 1997; Biel et al. 2004; Thomas 2009; Verdauger et al. 2011). Adjustment of the fertilization regime (i.e. from a high to lower N concentration plus improving the P and K status) in combination with drought hardening can improve drought resistance in hybrid poplars (*Populus* spp.) (Harvey and van den Driessche 1997, 1999). Short-day treatments that initiate budset can enhance drought resistance in the summer (Grossnickle and Folk 2003; Tan 2007) and fall (Colombo 1987; Grossnickle et al. 1991a; Major et al. 1994) crops of temperate zone tree species, though an extended short-day regime can be counterproductive causing increased mortality of summer-planted white spruce (*Picea glauca* (Moench) Voss) seedlings (Tan et al. 2008).

The use of hardening practices can improve the performance of field planted seedlings (Kozlowski et al. 1991). For example, drought hardening allowed seedlings to have a faster recovery of photosynthetic capability after transplanting (Kaushal and Aussenec 1989), better control of water loss (Christersson 1972; Clemens and Jones 1978; Johnson et al. 1985; Timmer and Miller 1991; Villar-Salvador et al. 1999, 2004b), and greater root regeneration after planting into soils having limiting edaphic conditions (i.e. droughted soils—Kaushal and Aussenec 1989, and cold soils—Hennessey and Dougherty 1984; Arnott et al. 1994). This improved performance has, in some cases, resulted in drought hardened seedlings having increased survival (Blake et al. 1979; van den Driessche 1991a, 1992) (Fig. 4) and growth when planted in xeric soil conditions (Johnson et al. 1985).

Drought hardening cultural practices does not always have beneficial effects on seedling field survival. This cultural practice can have either no effect (Grossnickle et al. 1991b; Folk et al. 1994; Royo et al. 2001; Biel et al. 2004; Villar-Salvador et al. 2004b) or a negative effect (Jospon and Paul 1985; O'Reilly et al. 1994) on survival in the field. This discrepancy probably stems from stress intensity during nursery application (Kozlowski and Pallardy 2002), timing of hardening practices (Duryea and McClain 1984; Landis et al. 1999), or the fact that stress resistance is not required to ensure seedling survival when exposed to optimum field conditions.

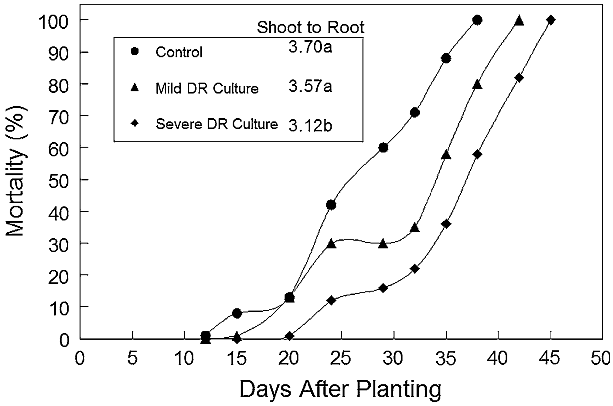

Fig. 4 Drought avoidance response of control and drought hardened (mild and severe drought (DR) culture) *Eucalyptus pilularis* Sm. seedlings to drought conditions in a glasshouse (adapted from Thomas 2009) (Insert data shows the shoot to root ratio of seedlings after drought hardening cultural conditions with different letters indicating treatment differences ($p = 0.05$))

Freezing tolerance

Drought hardening practices can improve freezing tolerance in some conifer species (Timmis and Tanaka 1976; Blake et al. 1979; Grossnickle et al. 1991a). However, this phenomenon has not been observed in other conifers (van den Driessche 1969; D'Aoust and Cameron 1982; Menzies et al. 1981; Arnott et al. 1994). Drought hardening can improve seedling survival after field planting into frost prone conditions (Mexal et al. 1979).

Most tree species undergo many morphological and physiological changes during an annual phenological cycle in response to seasonal environmental conditions (Fuchigami and Nee 1987; Ritchie and Tanaka 1990; Burr 1990) with freezing tolerance (Burr 1990; Bigras et al. 2001) shifting to its highest level in the winter in many tree species. This phenomenon has been related to budset or the cessation of shoot growth, leaf maturation and seasonal shifts in temperature (Grossnickle 2000). Short-day treatments are an effective means to initiate budset (Vaartaja 1960; Lavender and Wareing 1972; Williams et al. 1972), control dormancy patterns (Lavender and Cleary 1974; Lavender 1985) and enhance freezing tolerance in the fall (Colombo et al. 2001) for temperate zone tree species. Proper fall hardening of temperate zone tree species ensures they can be lifted and stored for extended periods to maintain a high level of seedling quality (Colombo et al. 2001) without a depletion of carbohydrate reserves below a critical level that can affect survival (Ritchie 1982; Marshall 1985). These practices result in increased seedling survival (McKay and Mason 1991) (Fig. 5), improved capability to overcome planting stress (Grossnickle 2000) and become established when planted into the spring planting window (Grossnickle et al. 1991a, b, c; Jacobs et al. 2008).

However, short-day treated spruce (*Picea* spp.) seedlings can show earlier budbreak setting up the potential for damage of actively growing seedlings by early-spring frost (Grossnickle 2000). Terminal bud damage of short-day treated spruce seedlings is attributed to early growing season frost, although this only occurs on frost-prone sites (Krasowski et al. 1993). This is a possible limitation of this cultural practice to maintain desired

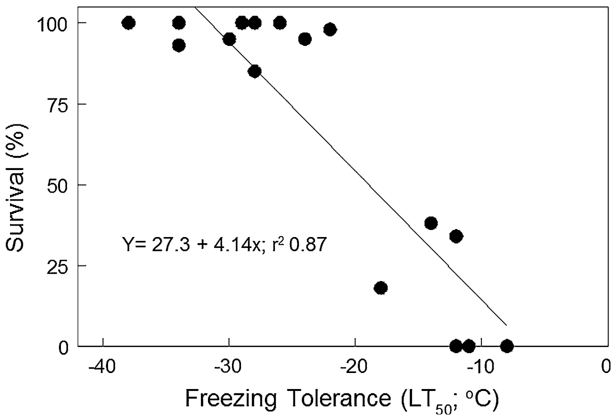

Fig. 5 Relationship between first year field survival and pre-storage freezing tolerance (measured as the temperature at which 50 % needle electrolyte leakage occurred: LT_{50}) for lodgepole pine (*Pinus contorta* Dougl.) seedlings (Simpson 1990)

freezing tolerance levels, thereby limiting damage or mortality when planting seedlings into frost prone conditions.

Nutrient status

Proper nutrient balance

During the nursery acclimation process, fertilization practices are shifted in concert with other cultural parameters to slow and then cause growth cessation in container-grown (Landis et al. 1989) and bareroot (Duryea 1984; Lantz 1985) seedlings. This approach was developed under long held fertilization adjustment practices (bareroot seedlings—Wakeley 1954, container-grown seedlings—Lavender and Cleary 1974) to ensure seedlings had budset or the cessation of shoot growth at the proper time to develop hardiness and still go to the field with sufficient nutrient levels for good survival and growth. Sufficient nutrient levels at planting are critical because seedlings have a limited ability to access required nutrients from the field site during the establishment process (Tinus 1974).

Nursery fertilization can affect seedling survival after planting. In a review of 22 trials van den Driessche (1991b) found that "suitable nursery fertilization" resulted in 57 % of trials showing an increase in survival, 30 % of trials showing no effect and 13 % reported a decrease in seedling survival in the field. In a series of trials, survival of Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco) seedlings was related to N concentration at planting, with a 2 % (±0.5 %) N concentration resulting in the highest rate of survival 1 and 2 (Fig. 6), and 3 years (van den Driessche 1984, 1988) after planting.

Nutrient loading

The shift of fertilization practices after budset or the cessation of shoot growth to increase nutrient concentration (i.e. fall nutrient loading) with little effect on seedling development has long been considered a beneficial nursery cultural practice (Benzian et al. 1974; Brix and van den Driessche 1974). Fall fertilization after seedlings have ceased growth, can

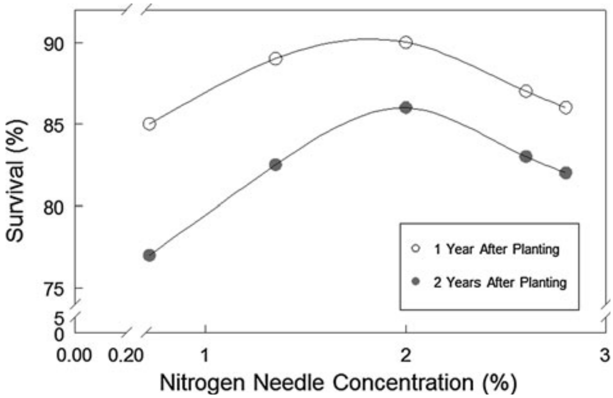

Fig. 6 Seedling survival at 1 and 2 years after field planting in relation nitrogen concentration for Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco)) seedlings at planting (van den Driessche 1980)

increase the nutrient status without delaying progression of the bud dormancy cycle (Williams and South 1992), while not affecting (Luoranen et al. 2008) or even improving (Islam et al. 2009; Andivia et al. 2012) the fall development of freezing tolerance. Ingestad and Lund (1986) theorized that nutrient loading in the nursery provided seedlings with greater nutrient reserves to utilize after field planting, while Binkley (1986) considered increasing nutrient reserves through nursery fertilization a very energy-efficient approach to nutrient acquisition for recently planted seedlings, compared to the uptake of nutrients from the soil. Fall nutrient loading can also contribute to enhanced stress resistance (Timmer 1997), shoot growth potential (i.e. increased needle primordial in buds) (Colombo et al. 2003; Islam et al. 2009) and a lower S:R at planting (Timmer et al. 1991). Fall nutrient loading increases the availability of nutrient reserves that are rapidly remobilized to support nutrient demand of new growth once seedlings are planted.

Application of fall nutrient loading has a number of effects on the physiological response of seedlings after field planting. Reports show fall nutrient loading results in earlier shoot flush (Margolis and Waring 1986; Floistad and Kohmann 2004; Oliet et al. 2011), increased new root growth (van den Driessche 1985, 1988, 1992; Malik and Timmer 1996, 1998; Boivin et al. 2004; Villar-Salvador et al. 2004a; Oliet et al. 2009a, 2011; Andivia et al. 2011, 2012), increased nutrient uptake (Timmer and Aidelbaum 1996) and shoot growth (van den Driessche 1985, 1992; Margolis and Waring 1986; Malik and Timmer 1996; VanderSchaaf and McNabb 2004; Puértolas et al. 2003; Boivin et al. 2004; Close et al. 2005; Salifu et al. 2009; Oliet et al. 2009a, 2011). Nutrient loaded seedlings can have a greater capability to overcome planting stress on harsh sites and they can be an effective stocktype on forest restoration sites with high levels of competition (van den Driessche 1991b; Timmer 1997).

In some instances, fall nutrient loading improves seedling survival in the field (van den Driessche 1980, 1984, 1992; Irwin et al. 1998; Oliet et al. 2009b; del Campo et al. 2010), while in other field trials minimal survival benefits were noted (Benzian et al. 1974; van den Driessche 1988; Gleason et al. 1990; Birchler et al. 2001; South and Donald 2002; VanderSchaaf and McNabb 2004; Salifu et al. 2009; Andivia et al. 2011). In a few instances nutrient loading reduced seedling survival in the field (Benzian et al. 1974; South and Donald 2002; Boivin et al. 2004) and Boivin et al. (2004) attributed this phenomenon to excessive nutrient loading causing toxic nutrient concentrations. Variability in the response to nutrient loading indicates that this practice may only be beneficial when site nutrient restrictions are limiting seedling establishment.

Seedlings loaded with nutrient reserves can have unintended consequences to forest restoration programs. Higher mortality for nursery-grown spruce seedlings by grazing from snowshoe hares (*Lepus americanus* Erxleben) was attributed to preferential feeding on nursery-grown than naturally regenerated seedlings (Sullivan and Moses 1986; Rodgers et al. 1993). A similar phenomenon of herbivores feeding occurs in conifers (Bergquist and Örlander 1998; Burney and Jacobs 2011) and hardwoods (Close et al. 2004; Paul et al. 2012) where the frequency of browsing by herbivores was greater with higher N concentration. However, increased browsing was not always associated with N levels (Burney and Jacobs 2011; Paul et al. 2012) and on sites with high browse pressure seedlings with both high and low N levels were browsed (Close et al. 2004). Increasing nutrient reserves, through nursery fertilization, may decrease seedling field survival due to browsing damage of herbivorous animals.

Shift in physiological attributes

Since effects of drought and cold hardening can be tied to a plants normal phenological cycle, these 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 (*Picea glauca* (Moench) Voss × *Picea engelmannii* Parry) seedlings lost a good portion of their stress resistance within weeks of initiating growth (Fig. 7).

Any potential benefit of increased fertility in the nursery in terms of improved seedling performance in the field is also short-lived. Seedling nutrient reserves decline after planting, due to dilution in tissue nutrient concentrations if external nutrient sources cannot

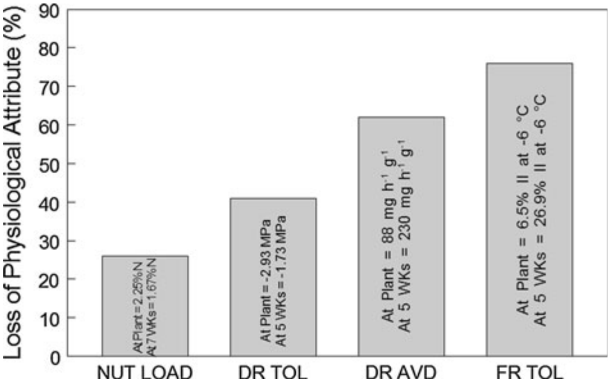

Fig. 7 Shift in physiological attribute status of nutrient loaded spring planted black spruce (*Picea mariana* (Mill.) B.S.P.) seedlings (NUT Load; adapted from Malik and Timmer 1998), and drought tolerance (DR TOL—osmotic potential at turgor loss point), drought avoidance (DR AVD—cuticular transpiration) and freezing tolerance (FR TOL—Index of Injury at −6 °C), of spring planted interior spruce (*Picea glauca* (Moench) Voss × *Picea engelmannii* Parry) seedlings (adapted from Grossnickle and Folk 2007) at time of planting and 5–7 weeks after planting. *Note*: Seedlings had budbreak 2–3 weeks after planting

meet demands of new growth (Munson and Bernier 1993; Kim et al. 1999). Nutrient loaded black spruce seedlings lost 26 % of their N concentration 7 weeks after they resumed growth (Fig. 7) and N concentration of nutrient loaded and control seedlings were comparable by the end of the growing season (Malik and Timmer 1998).

Seedlings ability to utilize improved physiological plant attributes to overcome planting stress and become established is a very narrow window, making it very difficult to quantify benefits of these hardening and nutrient loading practices on survival. For this reason, seedling survival and successful establishment is not only predicated on their hardiness and nutrient status, but also on their morphological attributes (see above discussion) and capability to grow roots (see below discussion) after planting.

Performance attribute: root growth

> If the root system did not increase in size at a fairly rapid rate…the seedling would die of drought…. (Stone 1955)

Seedlings that develop a root system after planting establish a proper water balance because they are coupled into the hydrologic cycle whereby water flows from the soil to plant roots, through the plant and into the atmosphere (Grossnickle 2005a). If sufficient root development does not occur just after field planting, seedlings can be exposed to stress because they do not have access to soil water. This planting stress can lead to a cycle of 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). Alternatively, seedlings that establish roots quickly after planting develop a favorable water status which continues the cycle of root growth supported by photosynthesis (Guehl et al. 1989) and photosynthesis supported by root growth (Burdett 1990). This is why survival is predicated on sufficient root growth coupling the newly planted seedling to the site, thereby maintaining a proper plant water balance (Margolis and Brand 1990; Grossnickle 2005a).

This view that root growth is critical for seedling survival is why root growth capability is reported to be a common measurement tool used in operational programs worldwide to define seedling quality (Simpson and Ritchie 1997). This assessment approach is determined through a testing procedure called root growth capacity or root growth potential. Numerous reviews have discussed merits of measuring root growth within a seedling quality assessment approach for determining seedling performance (Ritchie and Dunlap 1980; Ritchie 1985; Burdett 1987; Ritchie and Tanaka 1990; Sutton 1990). This assessment approach is considered a direct indicator of a seedlings ability to grow roots and is a general indicator that all physiological systems are functioning properly and thus provides a measure of seedling performance potential (Ritchie 1984; Burdett 1987). This is why root growth in newly planted seedlings has long been recognized as important to ensure successful survival and establishment (Toumey 1916; Rudolf 1939; Wakeley 1948, 1954; Stone 1955; Tinus 1974).

Due to the necessity of root growth in successful seedling establishment, a critical aspect of nursery cultural programs is to produce seedlings with the capability to rapidly grow roots after field planting. Factors of seedling size, root system fibrosity and stocktype affect their capability to grow roots.

Seedling size

Seedling size affects a seedling's ability to grow roots. Greater initial root mass is related to greater root growth (Brissette and Roberts 1984; Johnsen et al. 1988; Williams et al. 1988; van den Driessche 1992; Grossnickle and Major 1994; Villar-Salvador et al. 2004a; Grossnickle 2005b; Chirino et al. 2008; Cuesta et al. 2010a, b). Greater root growth in larger seedlings after planting can reduce plant water stress and increase survival (Hines and Long 1986; Luis et al. 2009).

Root system fibrosity

Greater root system fibrosity (i.e. branchiness) in bareroot seedlings (i.e. through undercutting—Faulkner 1953; Tanaka et al. 1976; Stupendick and Shepherd 1980; Schultz and Thompson 1996) has been related to increased root growth capability (Rook 1969; Bacon and Bachelard 1978; Hallgren and Tauer 1989) and in certain instances increased survival (Shoulders 1959; Tanaka et al. 1976; Kormanik 1986; Hallgren and Tauer 1989; Muse and Hatchell 1992; Schultz and Thompson 1996; Li et al. 2011). Greater root system fibrosity can lead to greater water movement capability through the root system (Carlson 1986) thereby reducing seedling water stress (Nambiar 1984). Conversely, stripping lateral roots during the lifting of bareroot seedlings, thus reducing root system fibrosity and root growth capability (South and Stumpff 1990), can reduce survival after field planting (Dierauf et al. 1992).

Manipulation of the container surface can increase root system fibrosity of container-grown seedlings (i.e. copper treatment on container walls; Burdett and Martin 1982; McDonald et al. 1984 and side slit containers for air pruning; Whitcomb 1984). These container treatments redistribute primary roots more evenly along the plug length (Wenny et al. 1988; Jones et al. 2002; Sword Sayer et al. 2011) and increase the number of first order lateral roots (McDonald et al. 1982; Smith and Mccubbin 1992; Nelson 1999). This can result in greater root growth capability (Arnold and Struve 1989; Dumroese 2000; Moore 2002; Tsakaldimi and Ganatsas 2006) and increased seedling survival (Barnett and McGilvray 1974).

Stocktype influence

Stocktype selection can influence survival because bareroot and container-grown seedlings can have differing root growth capabilities. Extensive comparisons between container and bareroot stocktypes across a range of sites lack no clear consensus favouring survivability of one particular stocktype (Hobbs 1984; Owston 1990; Grossnickle 2000). Trials that detected any survival differences, found container-grown, compared to bareroot, seedlings had greater initial survival on droughty sites (Arnott 1981; Dixon et al. 1981; Hahn and Smith 1983; Hobbs and Wearstler 1983; Burdett et al. 1984; South and Barnett 1986; Becker et al. 1987; Barnett and McGilvray 1993; Nilsson and Örlander 1995; Wilson et al. 2007).

Container-grown, compared to bareroot, seedlings can have greater root growth during the first field growing season (Dixon et al. 1981; Burdett et al. 1984; Johnson et al. 1984; Becker et al. 1987; Wilson et al. 2007). This improved root growth for container-grown seedlings reduces their resistance to water flow through the soil–plant-atmosphere-continuum (Dixon et al. 1983; Grossnickle and Blake 1987) thereby minimizing plant water stress (Burdett et al. 1984; Becker et al. 1987; Blake and Sutton 1987). Increased survival of container-grown, compared to bareroot, seedlings on drought prone sites has been related to lower plant water stress (Hobbs and Wearstler 1983; Nilsson and Örlander 1995).

Superior survival capability of container-grown, over bareroot, seedlings has also been attributed to their intact, undisturbed and multidimensional root systems that minimizes stress and leads to a quick root growth response (Tinus 1974). A growing media based plug surrounding the root system can improve seedling water status, compared to bareroot seedlings, independent from soil water availability (Jutras et al. 2007). Encasing roots of container-grown seedlings in a plug acts as a protective barrier against root desiccation, thereby creating a favorable plant water status to support photosynthesis and root growth (Burdett 1990; Mena-Petite et al. 2001).

Restoration site performance

Root growth, though critical for survival and (or) growth of seedlings is not a perfect predictor of seedling performance on forest restoration sites (Simpson and Ritchie 1997). The relationship between root growth capability and field performance varies. Many studies have shown that when seedlings grow roots they survive in the field (Stone 1955; Sutton 1980; Burdett et al. 1983, 1984; Feret and Kreh 1985; Hines and Long 1986; Larsen et al. 1988; Simpson 1990; Simpson and Vyse 1995; McTague and Tinus 1996; Mena-Petite et al. 2001; del Campo et al. 2007). Reviews on this issue (Ritchie and Dunlap 1980—26 trials, Ritchie and Tanaka 1990—12 trials) found ~80 % of trials reported a positive relationship between root growth capability and seedling survival. Though most work has found a positive relationship between root growth and survival, the lack of consistent trend has led to operational assessments questioning the importance of root growth to seedling survival (South and Hallgren 1997). An extensive assessment of operational plantings in British Columbia Canada, found that root growth potential failed to display a strong relationship with field survival (Binder et al. 1988).

A reassessment of the Binder et al. (1988) data base using boundary line analysis might reveal how root growth relates to seedling survival capability across a range of forest restoration sites. Field data collected across a range of environmental conditions tends to have a scatter of biological response to these conditions. On careful examination, normally a series of biological response points occur within an upper boundary of response to the dependent variable. Jarvis (1976) stated that this upper boundary is a maximum biological response one can expect in the way of plant performance, while Webb (1972) credited the scatter of biological response points below the boundary line to errors in measurement, variability of biological data and the interaction with other site environmental factors. Several researchers (Chambers et al. 1985; Grossnickle and Arnott 1992) used this premise to create upper boundary biological response data sets (i.e. systematic selection of 20–25 % of data from across the dependent variable range) to quantify the maximum biological response expected with a given dependent variable. When used on the Binder et al. (1988) data, the boundary line shows that low root growth capability equates with the chance of low survival, while high root growth capability equates with the chance of high survival when these seedlings were field planted (Fig. 8). A further examination of this data showed that if seedlings had low root growth capability (i.e. Index of Root Growth or IRG < 1) the probability was 52 % that the field plantation had <75 % survival, while some seedling populations with low root growth capability had high field survival rates. As the root growth capability of sample seedlings increased there was a greater chance of survival. Seedlings with very high root growth capability (i.e. IRG > 4) had <10 % chance of a plantation having <75 % survival.

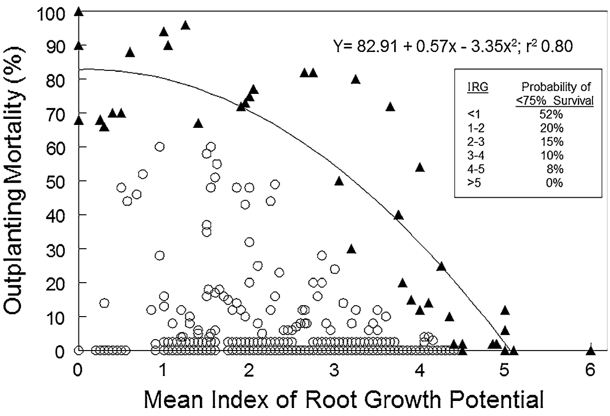

Fig. 8 Second year seedling survival of field planted seedlings to mean index of root growth potential (adapted from Binder et al. 1988). Data is from operational testing of 540 samples of seedlings. Data includes 12 species and numerous stocktypes tested by the British Columbia Ministry of Forests. Mean index root growth potential (IRG) classes are: *0* no new root growth, *1* some new roots, but none over 2 cm, *2* 1–3 new roots over 1 cm long, *3* 4–10 new roots over 1 cm long, *4* 11–30 new roots over 1 cm long, *5* and *6* >35 new roots over 1 cm long. Boundary layer analysis (data defined by *solid triangles*) and the regression equation were determined by analysis procedures of Grossnickle and Arnott (1992)

Whether or not newly planted seedlings initially require new root growth for proper field performance is related to the planting stress phenomenon. One way planting stress is relieved is when root growth occurs and seedling water stress is reduced (Grossnickle 2005a). Simpson and Ritchie (1997) believe that root growth is strongly related to field performance when seedlings have an inherently low level of stress resistance and/or when site environmental conditions become more severe. These are conditions that lead to planting stress. However, if seedlings are not exposed to planting stress, then initial root growth is not essential for good field performance (Simpson and Ritchie 1997). This view is exemplified by Stone et al. (2003), where critical root growth capacity (i.e. the minimum root growth required for seedling survival on a given planting site) was twice as high for harsh sites compared to gentle sites. Thus, survival of newly planted seedlings improves when they can extend new roots into the soil, ensuring that water intake equals or exceeds water loss (Wakeley 1948, 1954) and forest restoration site conditions dictate the amount of root growth required to overcome planting stress and ensure survival.

Conclusions

Morphological plant attributes influence a seedlings ability to survive after being planted on to a forest restoration site because a plants susceptibility to drought induced mortality can be due to their hydraulic architecture (McDowell et al. 2008). Thus, nursery cultural practices that alter seedling morphological characteristics (i.e. hydraulic architecture) can limit their susceptibility to planting stress (i.e. water stress). This is why morphological attributes such as greater seedling stem diameter and root system size confer a higher chance of survival. Seedling balance between the shoot and root systems, and seedling overall size need to be adjusted in relation to potential forest restoration site environmental conditions. Greater shoot system height is important if competition for light within the vegetation complex is the potential site limiting factor. A somewhat smaller shoot system and/or lower S:R are critical attributes if dry soils and high evaporative demand are potential site limiting factors. However, morphological parameters are only measures that help define overall seedling size, growth potential and balance, while seedling physiological quality and root growth capability also have a major influence on survival.

Factors affecting seedling physiological quality such as stress resistance and nutritional status have a major influence on survival. Improved survival is attributed to greater stress resistance (i.e. through nursery cultural hardening practices that enhance drought resistance and freezing tolerance) and improved seedling nutrition at planting (i.e. through fall nutrient loading) that increases the speed with which seedlings can overcome planting stress and become established on the forest restoration site. However, direct benefits from improved seedling physiological attributes are ephemeral. Thus the primary purpose of these improved physiological attributes is in aiding root growth, displaying a shoot system of sufficient size within the forest restoration site complex and conferring improved seedling establishment within months of planting. Ultimately the combination of a well-established seedling having desirable shoot and root development is what ensures high survival.

Improved survival can be attributed to greater root growth immediately after seedlings are field planted. Greater root growth is the result of greater root system size, fibrosity, plus greater seedling stress resistance and improved nutrient status. Stocktype selection can also influence survival, especially on droughty sites, because container-grown, compared to bareroot, seedlings can have better root growth that is related to plug protection of roots against desiccation and greater root growth capability that reduces potential planting stress.

These conclusions reiterate long held beliefs within the forest restoration community that desirable morphological attributes (Toumey 1916), root growth (Stone 1955) and physiological attributes (Wakeley 1948, 1954; Tinus 1974) improve chances for increased seedling survival. Work conducted during the past half century has confirmed that these historical beliefs were correct, while defining species specific ranges for these plant attributes. Planting seedlings with these desirable plant attributes does not guarantee high survival; rather planting seedlings with desirable attributes increases chances for survival within a forest restoration program.

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