

Why seedlings grow: influence of plant attributes

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Abstract Successful forest restoration requires planting quality seedlings with optimal growth potential. Thus, nurseries need to produce seedlings with plant attributes that favor the best chance of successful establishment once they are field planted. From the mid-twentieth century on, research foresters have critically examined plant attributes that confer improved seedling growth under various restoration site conditions. This review examines the value of commonly measured seedling quality attributes (i.e., height, diameter, root mass, shoot-to-root ratio, drought resistance, freezing tolerance, nutrient status, root growth potential, and root electrolyte leakage) that have been recognized as important in explaining why seedlings with improved attributes have better growth after planting. Seedlings with plant attributes that fall within the appropriate range of values can increase the speed with which they overcome planting stress, initiate growth, and become “coupled” to the forest restoration site, thereby ensuring successful seedling establishment. Although planting high quality seedlings does not guarantee successful seedling establishment, it increases chances for successful establishment and growth.

Keywords Forest restoration · Morphological attributes · Physiological attributes · Seedling growth

Introduction

Many factors contribute to successful forest restoration. During the initial stages of forest restoration, a series of intensive nursery and silviculture practices are implemented to ensure successful seedling establishment (Gladstone and Ledig 1990; Grossnickle 2000).

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These practices include choosing suitable tree species and provenance, applying nursery culture practices to produce quality seedlings, ensuring proper seedling handling practices, and making site modifications to improve the physical environment of the restoration site. This review focuses on the role of seedling quality in ensuring successful forest restoration.

Central to any successful forest restoration program is the quality of seedlings used in the program. In the mid-twentieth century, researchers started to examine plant attributes that improved seedling performance after planting, marking the start of seedling quality programs. By the late twentieth century, seedling quality assessment had evolved to include measurement procedures for numerous morphological and physiological attributes that defined seedling field performance (i.e., survival and growth) (Burdett 1983; Ritchie 1984; Mattsson 1997; Grossnickle 2000). Subsequently, a wealth of information has been published on plant attributes that improve seedling field performance after planting.

There are many proposed plant attributes for measuring seedling quality in relation to field performance. Burdett (1983) was the first to propose a comprehensive list of morphological and physiological parameters that, if present in seedlings within the appropriate range of values for a given parameter, would “enhance” seedling performance after planting. The evaluation of seedling quality can occur at various stages of nursery production to provide either crop monitoring for the nursery practitioner or end-product description, as it relates to the expression of future growth, for the forester (Ritchie 1984; Duryea 1985). This expression of field growth is a basic tenet of the “target seedling concept,” which advocated that cultural practices can be improved to meet defined standards for morphological and physiological attributes that define field performance (Rose 1990). By the late 1990s, an extensive array of over 30 potential seedling quality tests was available to practitioners, ranging from morphological through whole plant physiology to biochemical or molecular (Mohammed 1997). However, only a limited number of these attributes are now measured in operational programs; namely, the few that are rapid, simple, cheap, reliable, nondestructive, quantitative, and diagnostic (Zaerr 1985). Some of the most common operational procedures to assess seedling quality at lifting are the morphological attributes of shoot height, stem diameter, root systems, and morphological ratios together with the physiological attributes of drought resistance, freezing tolerance, mineral nutrient status, root growth potential, and root electrolyte leakage (Mohammed 1997; Haase 2008; Ritchie et al. 2010).

Seedling field performance is affected by both seedling quality and reforestation site conditions. 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), then mortality can occur. This is why seedling growth just after planting is critical to seedling survival (Burdett 1990). Once seedlings are established, their inherent growth potential is related to their morphological and physiological attributes and their ecophysiological response to site environmental conditions (Grossnickle 2000), which ultimately determines seedling field performance.

Implicit within a forest restoration program is that the most suitable species and only the highest quality genetic material adapted to the forest restoration site are used (Zobel and Talbert 1984). This is becoming increasingly critical as some jurisdictions are considering genetic material for assisted migration to address climate change (Spittlehouse and Stewart 2003; Gray and Hamann 2011; Pedlar et al. 2011; Dumroese et al. 2015). Historic discussions of seedling quality have proposed that phenotypic traits created during nursery culture can be as important as genetic traits in determining initial field performance (Burdett 1983). This view was confirmed in studies showing that initial field performance of seedlings from improved genetic sources was limited because nursery culture resulted in

poor phenotypic traits (Grossnickle and Major 1994a, b). Furthermore, nursery culture that created desirable phenotypic traits (Grossnickle and Folk 2005, 2007) was essential for seedlings from improved genetic sources to initially grow better (Grossnickle and Pait 2008; Grossnickle 2011). Thus, an understanding of what plant attributes are important in ensuring that seedlings have the ability to withstand environmental stress and grow well after planting is crucial in future assisted-migration programs.

A recent review examined the above mentioned, commonly assessed plant attributes and examined their effects on seedling survival after planting on forest restoration sites (Grossnickle 2012). The objective of the review that follows is to discuss the value of these same plant attributes in explaining why seedlings grow after planting on forest restoration sites across all stocktypes.

Methods

Several approaches were used to search the literature for this review. First, Forest Nursery Notes (USDA Forest Service 1995–2015) was examined for articles. Second, after reading these articles, a list of additional articles became apparent. Third, during the peer-review process, we continued to survey the literature and included pertinent articles in the revised manuscript. Thus, a comprehensive, although not exhaustive, examination of the literature on plant attributes used in seedling quality programs to define field performance was completed. These combined approaches resulted in over 350 articles related to this review, with the final list of references including only those judged relevant to meeting the objective of this review. A detailed examination of these plant attributes comparing bareroot and container-grown stocktypes is discussed elsewhere, so only minor comments on stocktype differences are provided (Grossnickle and El-Kassaby 2016). For each attribute, this review presents a summary of previous reviews to provide background information followed by current findings published between 1991 and 2016.

Morphological attributes

Background

Acknowledgment of the importance of seedling morphological attributes dates back a century to Toumey (1916). Extensive research from the 1930s to the 1950s by Wakeley (1954) began to delineate morphological attributes that described seedling field performance. These attributes were used to define “high-quality” seedlings for forest practitioners (Cossitt et al. 1949). Morphological attributes are considered reliable measures of seedling quality because they are retained for extended timeframes after seedlings are outplanted (Puttonen 1997). Various reviews have defined the importance of morphological attributes (Table 1) stating that seedlings should have a height within a defined range so they are not too tall or too short, a sturdy stem with at least a minimum diameter, a large fibrous root system, and a well-balanced shoot-to-root system for good seedling field performance (Thompson 1985; Mexal and Landis 1990). Various reviews concluded that initial stem diameter, a very easily measured morphological attribute, was the best morphological attribute to forecast future growth (Chavasse 1980; Johnson and Cline 1991; Mexal and Landis 1990; Omi 1993) because it often correlates with seedling weight and

Table 1 References that reviewed seedling quality issues and discussed the ability of these defined morphological or physiological attribute(s) to forecast field performance

Author(s)	Morphological attribute				Physiological attribute				
	Height	Diameter	Root system ^b	S:R ^c	Drought resistance	Freezing tolerance	Nutrient status	RGP ^d	REL ^e
Toumey (1916)	≠ ^a	≠	↑	↑					
Wakeley (1954)	≠	↑	↑		↑		↑		
Lavender (1976)	≠		↑	↔	↑		↔	↔	
van den Driessche (1976)	↔	↔			↔	↔		↔	
Cleary et al. (1978)	↑	↑		↓	↑		↑	↑	
Sutton (1979)	≠	≠	↔	↔		↔	↔	↔	
Sutton (1980)					↔	↔	↔	↔	
Timmis (1980)	↔	↔	↔	↑	↑	↑	↔	↔	
Chavassee (1980)	↔	↑	↔	↔	↔		↔		
Schmidt-Vogt (1981)	≠	↑	↑		↑				
Burdett (1983)	↑	↑	↑	↑	↑	↑	↑	↑	
Ritchie (1984)	↑	↑	↔	↑	↑	↑	↓	↑	
Kramer and Rose (1986)	≠	≠	↑	↔	↔	↔		↔	
Glerum (1988)	↔	↑	↑	↓	↑	↑	↔	↑	
Lavender (1988)	↔	↑	↔	↔	↔	↓	↔	↔	
Puttonen (1989)	≠	≠		↑	↑	↑	↑	↑	
Hawkins and Binder (1990)	↔	↔	↔			↔		↔	
Rose (1990)	≠	≠	≠	≠	↑	↔			
Johnson and Cline (1991)	≠	↑	↑	↓	↑	↑	↔	↑	
Omi (1993)	≠	↑	↑	↑	↔	↑		↔	
Grossnickle and Folk (1993)	↑	↑	↑	↑	↑	↑		↑	↑
Mattsson (1997)	↔	↑	↑	↑	↔	↑	↔	↑	↑
Puttonen (1997)	↑	↑	↑	↑	↔	↔		↔	↔
Mohammed (1997)	↔	↔	↔	↔	↔	↔	↔	↔	↔
Grossnickle (2000)	↑	↑	↑	↑	↑	↑	↑	↑	↑

Table 1 continued

Author(s)	Morphological attribute				Physiological attribute				
	Height	Diameter	Root system ^b	S:R ^c	Drought resistance	Freezing tolerance	Nutrient status	RGP ^d	REL ^e
Wilson and Jacobs (2006)	≠	↑	↑	↑	↑	↔	↔	↔	↑
Ritchie et al. (2010)	≠	↑	↔	≠	↑	↑	↑	↔	↑

^a Symbols summarize the reference author(s)' view on an attribute's potential to affect seedling performance after planting on forest restoration as follows: ↑ was positive; ↓ was negative; ≠ defined an acceptable attribute range, but outside this range the attribute was considered unacceptable; or ↔ no conclusion was drawn by the author(s)

^b Root system is defined as root system quality

^c S:R is shoot-to-root ratio

^d RGP is root growth potential

^e REL is root electrolyte leakage

root system size (Thompson 1985; Mexal and South 1991). The root system was considered important because greater root system size provides a greater root absorptive surface (Thompson 1985) for water uptake (Carlson and Miller 1990). Although the conclusions from previous reviews were mixed on the benefits of this attribute to improve growth (Table 1), correct proportionality between shoot and root systems is a desirable plant attribute because water status is directly tied to the shoot-to-root ratio of bareroot (Baldwin and Barney 1976) and container-grown (Grossnickle and Reid 1984) seedlings.

Morphological attributes have been inconsistent in describing seedling field performance (Wakeley 1954; Thompson 1985; Mexal and Landis 1990). Morphological parameters only measure overall size and shoot-to-root balance, not physiological quality. As such, they are only a subset of plant attributes required for defining successful seedling establishment (Wakeley 1948, 1954; Tinus 1974; Ritchie 1984; Mexal and Landis 1990). Seedlings must also have “optimum physiology and vigor” for morphological attributes to forecast field performance (Wakeley 1948, 1954; Tinus 1974; Schmidt-Vogt 1981; Ritchie 1984; Mexal and Landis 1990).

Current findings

Morphological attributes are the most common measures relating seedling quality to field performance (Pinto 2011). The ease of measuring morphological attributes in operational settings worldwide ensures their use in small-scale nurseries in developing countries (Takoutsing et al. 2013) and large, commercial nurseries in operational forestry programs in first-world countries (Grossnickle 2000; South 2000).

Stock quality assessment shows that bareroot seedlings have larger shoot-to-root ratios than container-grown seedlings because they are grown at lower densities and for longer timeframes (Grossnickle and El-Kassaby 2016). In contrast, container-grown seedlings have smaller shoot-to-root ratios that confer drought avoidance (Grossnickle and El-Kassaby 2016). Field trials have found that this attribute together with greater root growth potential confers container-grown seedlings with greater field performance potential compared with bareroot seedlings (Grossnickle and El-Kassaby 2016).

Height

Seedling height at planting can forecast growth because taller seedlings keep their height advantage over time (Grossnickle 2005b; Pinto 2011; Pinto et al. 2015). On sites with competing vegetation, this height advantage is beneficial (Rose and Ketchum 2003; Grossnickle 2005b; Haase et al. 2006; Morrissey et al. 2010; Thiffault et al. 2014) in part because they outgrow competitors (South et al. 2005b). However, the positive growth response of tall seedlings diminishes as they become established (South et al. 2001; Oliet et al. 2005; Pinto et al. 2011). Furthermore, seedlings with greater initial height can subsequently have greater shoot-system development, due to a greater number of branches, buds, and foliage in conifers (Fig. 1a) and hardwoods (del Campo et al. 2010). As a result, such seedlings have a greater photosynthetically active surface area (Grossnickle 2000; Luis et al. 2009). A positive relationship between initial seedling height and subsequent height growth has been reported in 70% of studies (Table 2). These findings validate research showing larger stocktypes have improved growth (Thiffault 2004; Grossnickle 2005b; Villar-Salvador et al. 2012; Pinto et al. 2012; Aghai et al. 2014). However, 20% of studies report no relationship and 10% of studies report a negative relationship (Table 2). This negative relationship is attributed to taller seedlings being exposed to greater water stress than smaller seedlings under harsh conditions (Grossnickle 2005b; Grossnickle and El-Kassaby 2016) because root systems cannot supply enough water to transpiring foliage to maintain a proper water balance (Grossnickle 2005a). Thus, shorter seedlings of both stocktypes can have an advantage on stressful sites (Mexal and Landis 1990; Stewart and Bernier 1995; Jurásek et al. 2009; Grossnickle 2012).

Fig. 1 **a** Relationship between percentage increase in shoot-system length (i.e., all fully elongated current-year shoots on seedling) and seedling height at planting for clonal populations of *Picea glauca* (Moench) Voss \times *Picea engelmannii* Parry ex Engelm. seedlings (adapted from Grossnickle 2005b). Data represent shoot growth potential, i.e., seedlings were grown for 13 weeks under ideal conditions until budset. Symbols represent means \pm SEs. **b** Relationship between initial shoot-to-root ratio and the incremental increase in shoot volume (D^2H) of *Pinus nigra* J.F. Arnold ssp. *nigra* var. *nigra* J.F. Arnold seedlings after 2 years on deep or shallow soil sites (adapted from Ivetic et al. 2016a, b). Symbols represent means

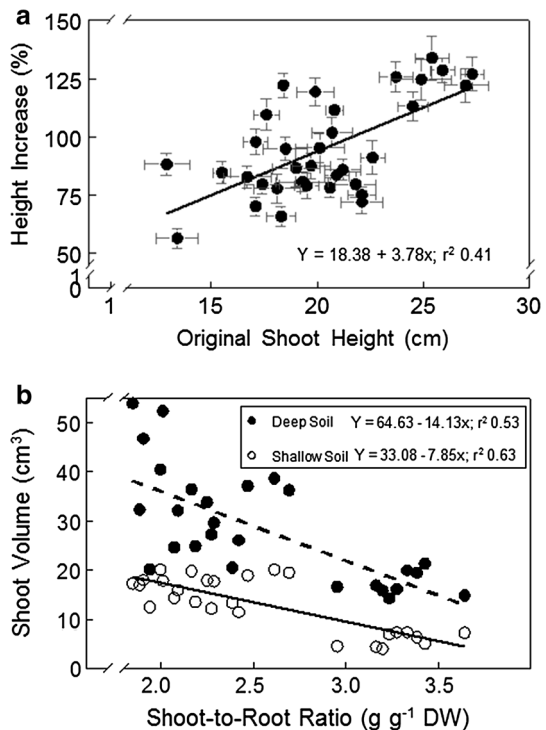


Table 2 General findings on the effects of plant attributes on seedling root or shoot growth reported in papers published between 1991 and 2016

Attribute	Response (%)	References
Height (20)	Positive	70 <i>Shoot</i> —Grossnickle (2005b), Jacobs et al. (2005), Cicek et al. (2007), Oliet et al. (2009a), del Campo et al. (2010), Maltoni et al. (2010), Li et al. (2011), Pinto et al. (2011, 2015), Deligöz et al. (2013), Regan et al. (2015) Akpo et al. (2014), Clark et al. (2016) and Ivetić et al. (2016a)
	Neutral	20 <i>Shoot</i> —Dey and Parker (1997), Rawat and Singh (2000), Aphalo and Rikala (2003) and Close et al. (2006)
	Negative	10 <i>Shoot</i> —Thompson and Schultz (1995) and Ivetić et al. (2016b)
Diameter (22)	Positive	91 <i>Shoot</i> —Dey and Parker (1997), South and Mitchell (1999), Ward et al. (2000), South et al. (2001, 2005a, b), Mexal et al. (2002), Aphalo and Rikala (2003), Rose and Ketchum (2003), Howell and Harrington (2004), Jacobs et al. (2005), Semerci (2005), Mexal et al. (2008), Bayala et al. (2009), Li et al. (2011), Clark et al. (2015, 2016) and Ivetić et al. (2016a, b)
	Neutral	9 <i>Shoot</i> —Zida et al. (2008) and Maltoni et al. (2010)
Root system (23)	Positive	78 <i>Shoot</i> —Kormanik et al. (1995), Thompson and Schultz (1995), Dey and Parker (1997), Rose et al. (1997), Schultz and Thompson (1997), Kormanik et al. (1998), Clark et al. (2000, 2015), Ponder (2000), Rawat and Singh (2000), Jacobs et al. (2005), Dominguez-Lerena et al. (2006), Cicek et al. (2007), Bayala et al. (2009), del Campo et al. (2010), Li et al. (2011), Ivetić et al. (2016b) and Sambeek et al. (2016)
	Neutral	22 <i>Shoot</i> —Krasowski and Owens (2000), Ponder (2000), Ward et al. (2000), Jacobs et al. (2005) and Maltoni et al. (2010)
Low shoot to root ratio; field—normal to dry (11)	Positive	82 <i>Shoot</i> —Génére and Garriou (1999), Andersen and Bentsen (2004), Villar-Salvador et al. (2004a), del Campo et al. (2010), Maltoni et al. (2010), Landhäusser et al. (2012), Pinto et al. (2015), Ivetić et al. (2016b) and Yamashita et al. (2016)
	Neutral	18 <i>Shoot</i> —Bernier et al. (1995) and Aphalo and Rikala (2003)
Drought resistance—tolerance (6)	Positive	50 <i>Shoot</i> —Grossnickle and Folk (2007), del Campo et al. (2010) and Liu et al. (2012)
	Neutral	50 <i>Shoot</i> —Royo et al. (2001), Villar-Salvador et al. (2004b) and Guarnaschelli et al. (2006)
Drought resistance—shoot water potential (15)	Positive	100 <i>Root</i> —Tinus (1996), Girard et al. (1997b), Grossnickle (2000), Mena-Petite et al. (2001) and Helenius et al. (2005)
		<i>Shoot</i> —Tinus (1996), Bigras (1997), Bigras and Margolis (1997), Girard et al. (1997a), McKay and White (1997), Génére and Garriou (1999), Garriou et al. (2000), Joustra et al. (2000b), O'Reilly et al. (2002), Brønnum (2005) and Helenius et al. (2005)

Table 2 continued

Attribute	Response (%)		References
Freezing tolerance (9)	Positive	100	<i>Root</i> —Lindström and Stattin (1994), Perks et al. (2001), Lindström et al. (2014), Malmqvist et al. (2016) and Haase et al. (2016) <i>Shoot</i> —Bigras (1998), Brønnum (2005), L'Hirondelle et al. (2006), Fernández et al. (2007), Lindström et al. (2014) and Haase et al. (2016)
Nutrient status (36)	Positive	100	<i>Root</i> —Malik and Timmer (1996), Puértolas et al. (2003), Boivin et al. (2004), Rikala et al. (2004), Villar-Salvador et al. (2004a), Way et al. (2007), Heiskanen et al. (2009), Luis et al. (2009), Oliet et al. (2009b, 2011), Cuesta et al. (2010a) and Andivia et al. (2011, 2012)
	Positive	78	<i>Shoot</i> —Malik and Timmer (1996), Fraysse and Crémière (1998), Irwin et al. (1998), Qureshi and Timmer (2000), Puértolas et al. (2003), Boivin et al. (2004), Rikala et al. (2004), Close et al. (2005a), Jackson et al. (2007, 2012), Way et al. (2007), Heiskanen et al. (2009), Oliet et al. (2009b, 2011), Oskarsson and Brynleyfsdottir (2009), Salifu et al. (2009), Barker (2010), Cuesta et al. (2010a), Luoranen and Rikala (2011), Jonsdottir et al. (2013), Hu et al. (2015), Li et al. (2016), Ovalle et al. (2016), Schott et al. (2016) and Wang et al. (2016)
	Neutral	22	<i>Shoot</i> —Birchler et al. (2001), South and Donald (2002), VanderSchaaf and McNabb (2004), Hawkins et al. (2005), Everett et al. (2007), Andivia et al. (2011), Hu et al. (2015) and Wang et al. (2015)
Root growth potential (10)	Positive	50	<i>Shoot</i> —O'Reilly et al. (2002), Luoranen et al. (2003), Villar-Salvador et al. (2004a), Brønnum (2005) and L'Hirondelle et al. (2007)
	Neutral	50	<i>Shoot</i> —Simpson and Vyse (1995), McKay (1998), Garriou et al. (2000), McKay and Morgan (2001) and O'Reilly et al. (2003)
Root electrolyte leakage (19)	Positive	58	<i>Root</i> —McKay et al. (1993), Lindström and Mattsson (1994), Folk et al. (1999), Grossnickle (2000), O'Reilly et al. (2002) and Brønnum (2005) <i>Shoot</i> —McKay and Mason (1991), McKay (1992, 1998), Bigras (1997), McKay and White (1997)
	Neutral	42	<i>Root</i> —McKay and Morgan (2001) and Chiatante et al. (2002) <i>Shoot</i> —McKay and Mason (1991), McKay and White (1997), McKay (1998), Généré and Garriou (1999), Joustra et al. (2000b) and O'Reilly et al. (2002)

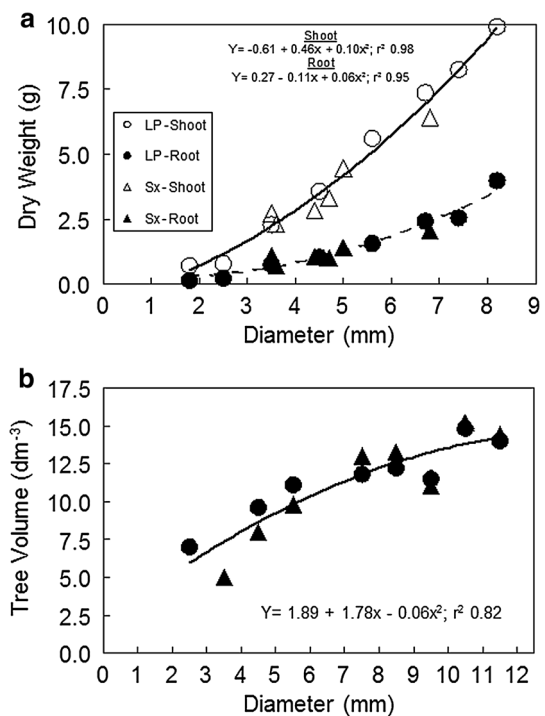
Number in parentheses below each attribute is the number of studies reporting either shoot and/or root growth. In some cases, an article is recorded under two responses when multiple tree species were assessed and the responses were different

Diameter

Initial stem diameter is considered the best morphological attribute to forecast future growth because it correlates with seedling weight and root system size (see “[Background](#)” in “Morphological attribute”). Specifically, stem diameter has been positively correlated with seedling weight (i.e., overall seedling size) at the end of nursery development (Rose

et al. 1997; Jinks and Mason 1998; Rawat and Singh 2000; Binotto et al. 2010), and across species and stocktypes (Fig. 2a). Modeling studies, examining various plant attributes, confirmed stem diameter to be the most reliable indicator of field performance (Mason et al. 1996; Levy and McKay 2003), with initial seedling biomass having the highest correlation with first-year growth (Levy and McKay 2003). A conceptual model considered seedling size (i.e., shoot biomass) a crucial attribute because it integrates nutrient reserves, assimilation size (i.e., leaf area and cambial area), and competitive ability in relation to field performance (Villar-Salvador et al. 2012). Shoot system size can be important on sites where soil water and nutrients are not limiting because competition for light between planted seedlings and other vegetation is a main factor limiting growth (Grossnickle 2000). Finally, stem diameter describes seedling sturdiness and thus helps reduce damage from drought and heat (Tsakalimi et al. 2005; Grossnickle 2012), as well as competing vegetation (Mason 2001). A positive relationship between initial stem diameter and growth after planting was reported in 91% of studies, with only 9% of studies reporting no relationship (Table 2). This positive response has been documented for 4 (Fig. 2b), 5 (Aphalo and Rikala 2003; Howell and Harrington 2004; Semerci 2005), and 17 years (Dierauf and Garner 1996) after planting. An increase in initial seedling diameter resulted in increased volume gains in southern pine plantations older than 9 years of age (South and Rakestraw 2002), thereby showing the long-term effects of this attribute on field growth. Initial seedling size can have a long-lasting effect on field growth. For example, seedlings that were larger at planting had greater height and diameter 32–37 years after planting (Jäghagen and Albrektson 1996). When initial stem diameter is not related to field growth it is often due to stressful site conditions (McKay and Morgan 2001; Renou-Wilson et al. 2008).

Fig. 2 **a** Relationship between shoot and root dry weight and stem diameter at time of lifting for bareroot, clonal *Pinus taeda* L. seedlings (LP) (adapted from South et al. 2015) and container-grown *Picea glauca* (Moench) Voss × *Picea engelmannii* Parry ex Engelm. seedlings (Sx) (adapted from Grossnickle 2000). Symbols represent means. **b** Relationship between root collar diameter of bareroot *Pinus taeda* seedlings at planting and stem volume after 4 years on two intensively managed field sites (adapted from South et al. 2001). Symbols represent means



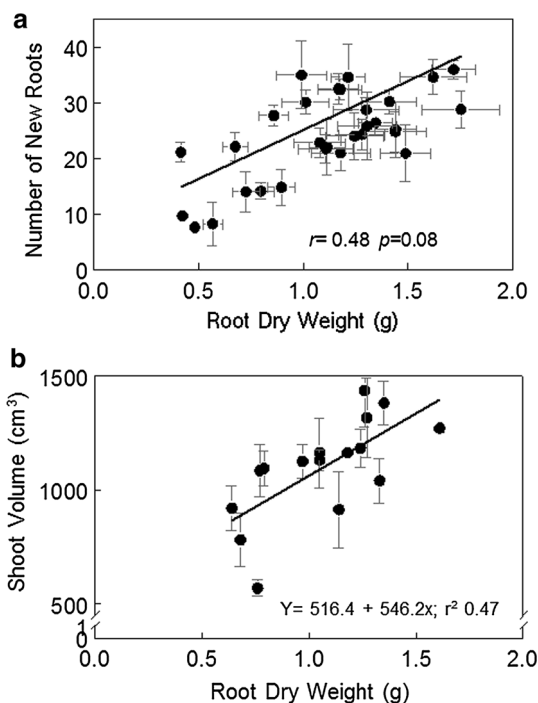
Root system

Seedlings with root systems that meet high morphological standards (i.e., root mass, fibrosity, volume, first-order laterals, area, and length) and physiological standards (i.e., root growth potential) have a higher capability to rapidly grow roots after planting (Davis and Jacobs 2005; Haase 2011). This is why there is a positive relationship between root mass and root growth potential (Fig. 3a). Greater root system size provides seedlings with the capacity to overcome planting stress and become established after planting (Grossnickle 2005a). A positive relationship between root system quality and growth is reported in 78% of studies (Table 2). For example, *Pinus pinea* L. seedlings with initially greater root dry weight had greater shoot growth 3 years after planting (Fig. 3b). Root system quality is important, but 22% of studies found that there was no growth response (Table 2), showing that this attribute does not always forecast seedling growth.

Shoot-to-root ratio

Shoot-to-root ratio (S:R) forecasts seedling growth on dry or normal sites in 82% of studies (Table 2). For example, a low initial S:R resulted in positive growth over 2 years in *Pinus nigra* J.F. Arnold ssp. *nigra* var. *nigra* J.F. seedlings (Fig. 1b). Low S:R together with high root growth capability are considered desirable attributes for maximizing seedling growth (Close et al. 2005b). In certain instances, a high S:R is beneficial to seedling growth. For example, under conditions where a wet season precedes a dry summer, seedlings defined as productive phenotypes (i.e., large seedlings with both high S:R and fertility) have higher growth capability (Oliet et al. 2005; Cuesta et al. 2010b) with larger seedlings becoming better established during the wet season (Villar-Salvador et al. 2012, 2015).

Fig. 3 **a** Relationship between number of new roots >0.5 cm (i.e., root growth potential) and root dry weight at summer lifting for clonal populations of *Picea glauca* (Moench) Voss \times *Picea engelmannii* Parry ex Engelm. seedlings (adapted from Grossnickle 2000). Symbols represent means \pm SEs. Note Pearson product-moment correlation coefficient was used to measure the relationship, with the line drawn for visual purposes. **b** Relationship between root dry weight of container-grown *Pinus pinea* L. seedlings at planting and stem volume after 3 years on a field site (adapted from Dominguez-Lerena et al. 2006). Symbols represent means \pm SEs



Drought resistance

Background

It was recognized early on (e.g., Wakeley 1954) and reinforced several decades later (e.g., van den Driessche 1976; Timmis 1980; Schmidt-Vogt 1981; Burdett 1983; Ritchie 1984) that drought resistance was important for seedling field performance (Table 1). The application of drought hardening (process of plant adaptation) in the nursery is reported to improve seedling survival (Grossnickle 2012) and field performance (Kozłowski et al. 1991). Drought resistance takes on many forms of seedling quality attributes [e.g., drought tolerance including osmotic and cell wall elasticity adjustment (e.g., Timmis 1980; Ritchie 1984; Joly 1985; Lopushinsky 1990), chloroplast drought resistance (e.g., Timmis 1980; Colombo et al. 2001b) together with drought avoidance including cuticular development (e.g., Grossnickle 2000), stomatal sensitivity (e.g., Timmis 1980; Folk and Grossnickle 1997; Colombo et al. 2001b), morphological balance (e.g., Thompson 1985; Mexal and Landis 1990), and increased root water absorption (e.g., Carlson and Miller 1990; Colombo et al. 2001b)].

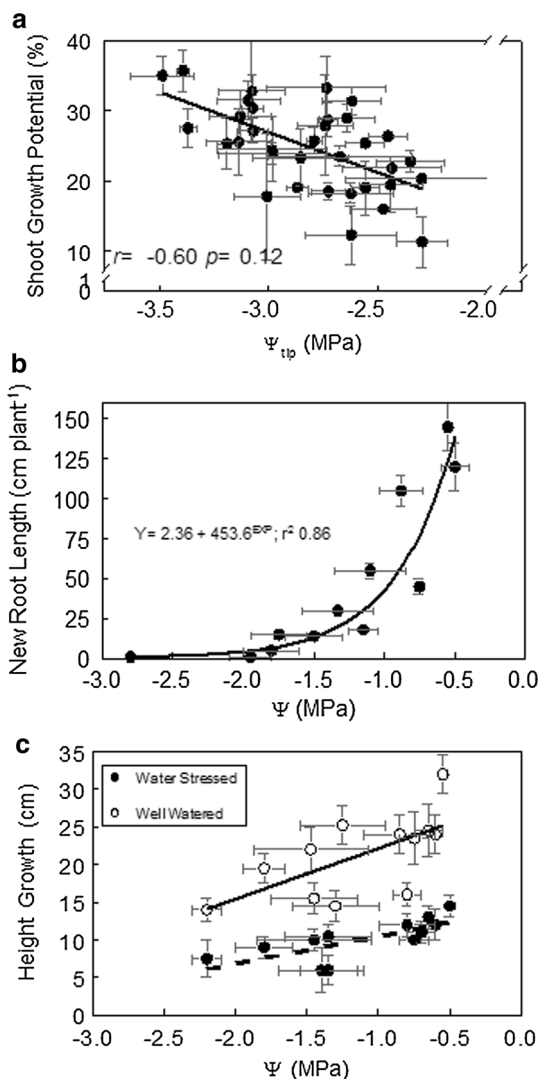
Seedling water potential is considered to best reflect instantaneous seedling water status because it integrates seedling response in relation to its drought resistance status relative to the surrounding environment (Joly 1985). This is why early reviews identified this attribute as a good measure of seedling quality (Schmidt-Vogt 1981; Glerum 1988). However, one author suggested seedling water potential may not always be a true reflection of seedling physiological response to water stress because of its instantaneous nature (Lavender 1988) and because it can vary among species or phenotypes under similar stress conditions according to their functional traits. This is why Ritchie (1984) recommended using this attribute in relation to a species' critical water potential [i.e., osmotic potential at the turgor loss point (Ψ_{tlp})], which shifts in relation to seasonal changes in drought tolerance (Teskey and Hinckley 1986; Abrams 1988). Drought tolerance values (e.g., Ψ_{tlp}) have long been considered a desirable attribute for field performance, especially in relation to summer droughts (Hennessey and Dougherty 1984; Newton et al. 1986; Abrams 1988). Several reviews defined ranges of water potential for assessing seedling physiological state during nursery development and just before planting (Cleary et al. 1978; Landis et al. 1989), suggesting that greater water stress possibly affects field performance. Finally, monitoring seedling water status during nursery cultural activities can determine whether seedlings have been exposed to harsh conditions that may limit their subsequent field performance (Schmidt-Vogt 1981).

Benefits of drought resistance are ephemeral because seedlings rapidly lose drought tolerance once shoot elongation begins (Teskey and Hinckley 1986; Abrams 1988; Grossnickle 2000, 2012). Thus, a seedling's ability to use improved drought tolerance to overcome planting stress and become established has a very narrow phenological window, making it difficult to use this attribute to forecast growth.

Current findings

Only a few trials have measured drought tolerance for forecasting seedling growth (Table 2). Hardening seedlings with periodic water stress during nursery culture can increase stress resistance and improves root growth after planting, resulting in improved field performance (Liu et al. 2012). However, when drought tolerance was measured preplanting, only 50% of studies found it to forecast first-year field growth (Table 2). In a

Fig. 4 **a** Relationship between shoot growth potential (i.e., current-year shoot length at budset in relation to seedling height at planting) and seedling osmotic potential at turgor loss point (Ψ_{tlp}) at planting of *Picea glauca* (Moench) Voss \times *Picea engelmannii* Parry ex Engelm. clonal seedlings after exposure to planting stress (stress was a preplanting exposure to -4.0 MPa of water stress through shoot transpiration, with roots protected) (adapted from Grossnickle and Folk 2007). Symbols represent means \pm SEs. *Note* Pearson product-moment correlation coefficient was used to measure the relationship, with the line drawn for visual purpose. **b** Relationship between new root length and leaf water potential at planting of *Pinus radiata* D. Don seedlings (adapted from Mena-Petite et al. 2001). Symbols represent means \pm SEs. **c** Relationship between height growth (mean \pm SE) after one growing season and shoot water potential (Ψ) just prior to planting for bareroot *Pseudotsuga menziesii* (Mirb.) Franco seedlings planted under well-watered and water-stressed field conditions (adapted from Généré and Garriou 1999). Symbols represent means \pm SEs. *Note* Lines are drawn for visual purpose



controlled assessment of seedling growth to planting stress, *Picea glauca* (Moench) Voss \times *Picea engelmannii* Parry ex Engelm. seedlings with greater drought tolerance before planting overcame planting stress and had somewhat better shoot growth (Fig. 4a). In contrast, other work (Villar-Salvador et al. 2004b; Guarnaschelli et al. 2006) did not find drought tolerance attributes related to field performance under either mesic or xeric conditions. Villar-Salvador et al. (2004b) speculated that any potential field performance advantage for seedlings with improved drought tolerance attributes was probably limited to harsh conditions.

Seedling water potential is another measured attribute used to forecast growth. Where shoot water potential (Ψ) was measured just before planting there was a positive relationship with growth (root and shoot) in 100% of reported studies (Table 2). For example, root growth potential measured at planting was related to the level of seedling water stress

just before planting (Fig. 4b). The measurement of Ψ just before planting was also related to seedling shoot growth in the field. For example, shoot growth measured under well-watered or water-stressed field conditions during the first season after planting was related to preplanting seedling Ψ , with shoot growth reductions occurring if seedlings were initially exposed to greater water stress (Fig. 4c). In these cases, measurement of Ψ just before planting defined a seedling's functional integrity (i.e., indication of seedling stress, although no description of the reason for this stress). Functional integrity indicates whether seedlings are, or are not, damaged to the point of limiting primary physiological processes (Grossnickle and Folk 1993). Measurement of Ψ is also used as an indirect measure of root system capability to absorb water (McCreary and Duryea 1985; McKay and White 1997). In many cases, measurement of Ψ was comparable to the measurement of alternative attributes, such as root electrolyte leakage (McKay and White 1997; Folk et al. 1999; Garriou et al. 2000; Grossnickle 2000; O'Reilly et al. 2002; Brønnum 2005), photosynthesis (Folk et al. 1999; Grossnickle 2000), and root growth potential (Folk et al. 1999; Grossnickle 2000; Brønnum 2005) in its forecasting ability. Measurement of Ψ at lifting, in the first step of handling practices, can define seedlings with (McKay and White 1997; Girard et al. 1997a, b; Folk et al. 1999) or without (O'Reilly et al. 2003) root damage, with the forecasting ability limited to low quality seedlings. This is why root damage levels detected with measurement of Ψ can define field performance of newly planted seedlings (Bigras 1996).

Freezing tolerance

Background

Freezing tolerance is a physiological parameter that changes in response to seasonal environmental conditions (Fuchigami and Nee 1987; Burr 1990). It is at its highest level in winter (Burr 1990; Bigras et al. 2001) and has been related to budset or cessation of shoot growth, leaf maturation, and seasonal temperature shifts (Lavender 1985; Grossnickle 2000). Colombo (1997) reviewed a large (i.e., >200 stock lots) database of operational nursery seedlings of high latitude species and found the transition from shoot growth to endodormancy required the completion of terminal bud development before freezing tolerance increased. In contrast, freezing tolerance develops in the mid-latitude species *Pinus taeda* L. after shoot growth cessation, but without a terminal bud (Grossnickle and South 2014). This interspecific variability is why there are a number of testing procedures that are used in seedling quality assessment programs [e.g., whole plant freezing, electrolyte leakage of plant tissues, or needle chlorophyll fluorescence (Glerum 1985; Burr et al. 2001)] to define freezing tolerance.

A number of reviews suggested measuring freezing tolerance at lifting was beneficial to defining field performance (Table 1). In contrast, Lavender (1988) felt that freezing tolerance was not related to seedling vigor, and its use as an assessment procedure “may not be justified.” Freezing tolerance has been discussed from two perspectives. Some reviews considered freezing tolerance to be related to increased seedling stress resistance, thereby maintaining their quality during handling/storage practices, resulting in greater growth potential after planting (Timmis 1980; Burdett 1983; Johnson and Cline 1991; Mattsson 1997). Other reviews considered freezing tolerance an important indicator of survivability

to determine timing of fall lifting and winter storage before spring planting (Ritchie 1984; Glerum 1988; Puttonen 1989; Omi 1993).

Current findings

Freezing tolerance testing is now applied to provide flexibility to nursery lifting/store operations and to meet planting schedules (Colombo et al. 2001a; L'Hirondelle et al. 2006; Landis et al. 2010; Grossnickle and South 2014). In addition, recent gene expression analysis techniques have found several genes to be highly correlated with freezing tolerance in *Picea abies* (Stattin et al. 2012), *Pinus sylvestris* (Joosen et al. 2006), and *Pseudotsuga menziesii* (Balk et al. 2008) seedlings, making them candidate marker genes for rapid molecular tests of freezing tolerance relative to lifting and storability of sufficiently hardened seedlings.

The robustness of freezing tolerance makes it useful in defining subsequent seedling growth. When freezing tolerance was measured just before lifting/store there was a positive relationship with growth (root and shoot) in 100% of reported studies (Table 2). Lifting seedlings at the correct time avoids damage to root systems from fall freeze events, thereby minimizing reductions in subsequent root growth potential (RGP) (Lindström and Stattin 1994; Lindström et al. 2014; Malmqvist et al. 2016). In an assessment of five conifer species, as the level of freezing tolerance increased at lifting, shoot dry weight after one growing season increased (Fig. 5). The extent of root system damage from fall freeze events has been directly related to subsequent shoot growth (Bigras 1998), indicating that root system integrity is important for good root and shoot growth. Nursery practices that affect fall acclimation, lifting, and storage are critical to seedling field performance (Grossnickle and South 2014). This is why recent reviews considered both changes in stress resistance and lifting/store decisions as important reasons for including freezing tolerance within a seedling quality assessment program (Ritchie et al. 2010; Haase 2011).

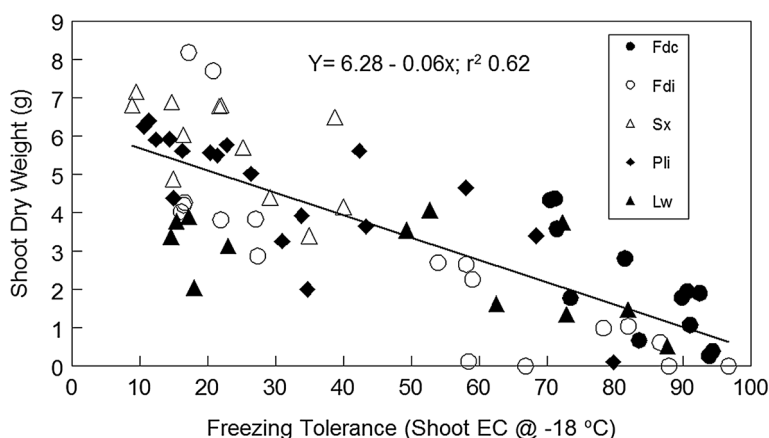


Fig. 5 Relationship between shoot dry weight after one field growing season and prestorage freezing tolerance (shoot relative electrical conductivity measured after a -18°C freeze event) in conifer seedlings. Fdc: *Pseudotsuga menziesii* (Mirb.) Franco var. *menziesii*; Fdi: *Pseudotsuga menziesii* (Mirb.) Franco var. *glauca* (Beissn.) Franco; Sx: *Picea glauca* (Moench) Voss \times *P. engelmannii* Parry ex Engelm.; Pli: *Pinus contorta* Dougl. ex Loud. var. *latifolia* Engelm.; Lw: *Larix occidentalis* Nutt. (adapted from L'Hirondelle et al. 2006). Symbols represent means

Freezing tolerance has been related to other seedling attributes. In *Eucalyptus globulus* Labill., freezing tolerance at lifting was positively related to first-year diameter growth because seedlings with higher nitrogen (N) levels ($>1.3\%$) also had greater freezing tolerance than those with lower N levels ($<1.0\%$) (Fernández et al. 2007). Other studies have also reported that higher N levels in ecodormant seedlings can benefit the development of freezing tolerance and also subsequent seedling growth (see “Nutrient status” section).

Nutrient status

Background

Nutrient status was considered an important seedling attribute in relation to field performance in just a few early reviews (Table 1). Early on, Wakeley (1954) stated that mineral nutrition was important in the “physiological condition” of southern pine seedlings. Several reviewers in the 1980s felt that high mineral content was important for promoting growth (Burdett 1983; Puttonen 1989). Numerous reviews recognized the importance of seedling nutrition, but drew no conclusions as to benefits (Table 1). Possible reasons are that few studies reported a relationship between nutrient levels and field performance (Jaramillo 1980), or there were contradictory findings (Mattsson 1997). Also, nutritional requirements for optimizing various attributes (e.g., shoot development, freezing tolerance, root growth potential, and hardening) require different fertilization regimes, making it difficult to find the balance among all desired attributes (Bigg and Schalaus 1990).

Nutrition is considered an important attribute when viewed through the concept that accumulating nutrient reserves, regardless of the fertilization regime, is potentially beneficial for seedling field performance. This is why nutrition is considered an important attribute in recent seedling quality discussions (Ritchie et al. 2010; Hawkins 2011). Typical fall fertilization regimes that shift to lower rates as the season progresses provide sufficient nutrient levels for growth after planting (Landis 1985; Dumroese 2003; Hawkins 2011), whereas fall nutrient loading is a cultural practice designed to increase seedling nutrient reserves, thus increasing field performance potential (Timmer 1997; Dumroese 2003; Hawkins 2011). Using fertilization to increase seedling nutrient reserves has long been considered a beneficial nursery practice (Benzian et al. 1974; Brix and van den Driessche 1974), providing seedlings with greater reserves that can be rapidly remobilized to support nutrient demands of shoot and root growth once seedlings are planted (Ingstad and Lund 1986). Moreover, increasing nutrient reserves through nursery fertilization is considered very efficient, compared with nutrient acquisition on the planting site (Tinus 1974; Binkley 1986). Thus, the growing season or fall fertilization regimes are intended to create seedlings with nutrient reserves that can be remobilized to support new growth after planting.

Current findings

Since nitrogen (N) is the most abundant mineral element in plants, seedling quality research has focused on how seedlings respond to its availability in relation to field performance. In conifer seedlings, foliar N concentration ranges from 0.8 to 3.5%, with 1.5–2.5% were historically considered optimal (Landis et al. 1989), but the optimal N level has more recently been defined as $>2.5\%$ (i.e., luxury consumption) (Dumroese 2003). Nitrogen reserves are predominantly held in needles and roots of evergreen conifer species

(Millard and Grelet 2010; Villar-Salvador et al. 2015), whereas deciduous hardwood (Millard and Grelet 2010; Villar-Salvador et al. 2015) and deciduous conifer species (Zhu et al. 2013) accumulate N in their stems and roots prior to leaf abscission. These species differences make it important to define the proper N concentration within defined plant tissue and timing of its application to optimize this attribute.

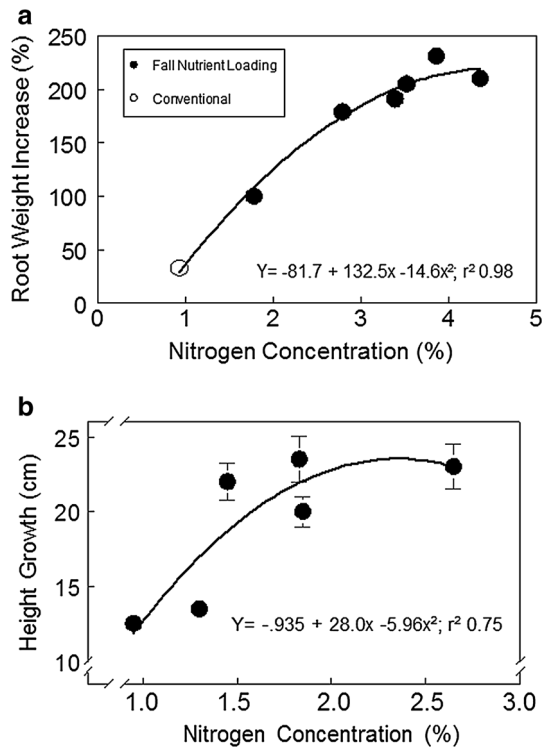
Optimal nutrient reserves can have a positive effect on various seedling attributes before planting. They are reported to produce more morphologically balanced seedlings (under an exponential fertilization regime—Timmer and Aidelbaum 1996) with greater shoot growth potential (i.e., more needle primordia in buds) (Colombo et al. 2003; Islam et al. 2009). Optimal fall nutrient reserves are reported to increase (Timmer 1997; Andivia et al. 2011, 2012, 2014) or have no effect (Heredia-Guerrero et al. 2014) on drought resistance (i.e., morphological balance, osmotic adjustment). Freezing tolerance is reported to be improved with optimal nutrient reserves typically through faster development in the fall or with acclimation to lower freezing temperatures (Rikala and Repo 1997; Islam et al. 2009; Davis et al. 2011; Andivia et al. 2012; Li et al. 2012; Oliet et al. 2013), although studies also found no effect on freezing tolerance (Puértolas et al. 2005; Luoranen et al. 2008; Heredia-Guerrero et al. 2014). Thus, nutrient status is important because it is, in many cases, related to various plant attributes contributing to positive seedling field performance (del Campo et al. 2010).

In early spring, remobilization from nutrient reserves is the main N source for new, fine-root growth in both evergreen hardwood and conifer species (Uscola et al. 2015). Increased root egress after planting is reported for all studies where seedlings had optimal nutrient reserves (Table 2). For example, in *Picea mariana* (Mill. B.S.P.) seedlings new root weight increased after planting in relation to initial N concentration (Fig. 6a). Reviews of seedling field performance in harsh Mediterranean environments (Oliet et al. 2013) and temperate zone eucalyptus plantations (Close 2012) found that N-rich seedlings had improved establishment, due to their ability to grow new roots rapidly and outcompete other vegetation. Seedlings with optimal nutrient reserves also have the ability to absorb more nutrients after planting (Malik and Timmer 1996, 1998; Wang et al. 2016), which was attributed, in part, to greater root system development (Malik and Timmer 1996, 1998). This is important because, by mid-spring, soils at the planting site supply most of the N required for new root growth in both evergreen hardwood and conifer species (Uscola et al. 2015). Root egress into the surrounding soil establishes a favorable morphological balance for water and nutrient uptake, which reduces planting stress (Grossnickle 2005a) and ultimately enhances shoot growth (Margolis and Brand 1990).

Optimal nutrient reserves can increase shoot growth during the field establishment phase. Seedlings with optimum nutrient reserves before planting had a positive relationship with shoot growth in 78% of reported studies (Table 2). For example, shoot growth after one growing season was positively related to preplanting N concentration for *Pinus halepensis* Mill. seedlings (Fig. 6b). In *Pinus palustris* Mill., which has a unique “grass stage” before height growth begins, optimal nutrient reserves increased diameter growth during the grass stage (Jackson et al. 2007) and, in turn, faster initiation of shoot development (Jackson et al. 2012). These two examples show that species with differing growth strategies both had higher shoot growth rates when seedlings had optimal nutrient reserves at planting.

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 when nutrient stress was most severe (McAlister and Timmer 1998; Xu and Timmer 1999; Imo and Timmer 2001; Salifu and Timmer 2003). Nutrient remobilization occurs

Fig. 6 **a** Relationship between percentage increase in root weight 18 weeks after planting and nitrogen (N) concentration at planting after conventional growing season fertilization or optimal fall nutrient reserves for *Picea mariana* (Mill. B.S.P.) seedlings (adapted from Boivin et al. 2004). Symbols represent means. **b** Relationship between shoot growth after one growing season and preplanting N concentration for *Pinus halepensis* Mill. seedlings (adapted from Puértolas et al. 2003). Symbols represent means \pm SEs



when seedlings are not fully coupled to the restoration site (Villar-Salvador et al. 2015), thereby providing a capability to overcome planting stress and become established. This is why seedlings with optimal nutrient reserves quickly couple to the site, enabling them to withstand subsequent harsh summer environmental conditions (Timmer and Aidelbaum 1996; Luoranen and Rikala 2011).

Optimal seedling nutrient reserves, in certain instances, have a minimal effect on subsequent seedling growth; with 22% of reported studies showing no benefit (Table 2). In a process-based model, simulations found that N content had a low correlation with initial seedling growth across a range of climatic conditions (Levy and McKay 2003). The lack of a positive response to optimal nutrient reserves has been attributed to sufficient nutrient availability at the planting site (Andivia et al. 2011) or other site factors that are limiting growth (e.g., water stress) (Wang et al. 2015). Cortina et al. (2013) hypothesized that nutrient-limited small seedlings may be better adapted to arid conditions and water-limited microsites, suggesting a conservative water-use strategy. This strategy was also reported for *Quillaja saponaria* (Mol.) seedlings exposed to droughty site conditions (Ovalle et al. 2016). In British Columbia, where conifer seedlings typically have initial optimal N (Hawkins 2011), fall nutrient loading had no beneficial effect on growth after planting in *Tsuga heterophylla* (Raf.) Sarg. (Hawkins et al. 2005) or *Pseudotsuga menziesii* (Mirb.) Franco (Everett et al. 2007) seedlings. Everett et al. (2007) speculated that it is not the method of nursery fertilization that is important, rather the nutrient status at planting.

Any benefit from optimal nutrient reserves in relation to improved field performance is short term. Nutrient reserves decline after planting, due to dilution of nutrient concentrations if nutrient sources on the planting site cannot meet demands of new growth

(Munson and Bernier 1993; Kim et al. 1999; Villar-Salvador et al. 2015). For example, black spruce seedlings with optimal fall nutrient reserves lost 26% of their initial N concentration just after bud flush and had a N concentration comparable to that of control seedlings by the end of the growing season (Malik and Timmer 1998). This is why improved growth that comes directly from optimal nutrient reserves lasts only for the first season after planting (Rikala et al. 2004; Heiskanen et al. 2009; Luoranen and Rikala 2011).

The long-term effect of optimal nutrient reserves is the stimulation of rapid seedling growth after planting, thereby creating increased seedling size and a competitive advantage on sites with competing vegetation (van den Driessche 1991; Timmer 1997; Malik and Timmer 1998). This positive growth response in seedlings with optimal nutrient reserves can be maintained for up to 6 years because they can outcompete other vegetation at an earlier stage than control seedlings (Way et al. 2007). Larger seedlings produce greater absolute amounts of new shoot biomass, thereby capturing more incoming solar radiation (Grossnickle 2000) (see “Height” section).

Nitrogen content, rather than N concentration, has been reported to better forecast long-term seedling growth. For example, N content was the attribute most strongly related to third-year shoot growth in a survey of *Pinus taeda* seedlings produced in 20 nurseries (Larsen et al. 1988). There are reports of a close relationship between seedling N content at planting and field height growth (Quoreshi and Timmer 2000; Puértolas et al. 2003). Cuesta et al. (2010b) found that large *Pinus halepensis* Mill. seedlings remobilized four to six times more N to support growth than small seedlings. Some have postulated that N content is more useful in forecasting seedling field performance because it reflects differences in both initial seedling size and nutrient status (Quoreshi and Timmer 2000; Puértolas et al. 2003; Cuesta et al. 2010b).

Optimal nutrient reserves are reported to occasionally result in poor seedling field performance. Studies show optimal nutrient reserves can cause earlier bud flush after planting (Fløistad and Kohmann 2004; Luoranen and Rikala 2011; Oliet et al. 2011). Although rapid shoot elongation can be beneficial on sites with competing vegetation (Grossnickle 2000), caution is recommended on frost-prone sites because freezing tolerance is rapidly lost during shoot elongation, and frost damage to shoots could occur (Burr 1990; Bigras et al. 2001). Another potential drawback with optimal nutrient reserves is grazing from herbivores because seedlings with optimal nutrient reserves can have a higher frequency of browsing, thereby reducing their shoot growth potential (Grossnickle 2012; Burney and Jacobs 2013).

Root growth potential

Background

New root growth in recently planted seedlings has long been recognized as important in enhancing establishment and growth (Toumey 1916; Rudolf 1939; Wakeley 1948, 1954; Stone 1955; Tinus 1974) (Table 1). Seedlings with rapidly expanding root systems can mitigate water stress (Stone 1955) as they quickly establish a proper water balance, thus becoming coupled with the hydrologic cycle at the planting site (Grossnickle 2005a). If sufficient root development does not occur just after planting, seedlings can be exposed to water stress, reducing survival (Grossnickle 2012). This view that initial root growth is

critical for seedling survival and growth is why root growth capability is measured in operational programs to define seedling quality (Simpson and Ritchie 1997). This attribute is assessed in a root growth capacity or potential (RGP) test, where seedlings are grown under controlled environmental conditions and root growth is measured after a defined length of time. Root growth potential is considered a direct indicator of a seedling's ability to grow roots and that all plant systems are functioning properly (Ritchie 1984; Ritchie and Tanaka 1990). Thus, RGP is an indicator of seedling functional integrity (Grossnickle and Folk 1993) and it provides a measure of seedling field performance potential (Burdett 1987; Grossnickle 2000).

Numerous reviews have discussed the merits of measuring RGP within a quality assessment program for determining seedling field performance (Ritchie and Dunlap 1980; Ritchie 1985; Burdett 1987; Landis and Skakel 1988; Ritchie and Tanaka 1990; Sutton 1990). Cleary et al. (1978) stated that “early, vigorous root growth is important for seedling establishment.” Burdett (1983) indicated that high RGP was important for water and nutrient uptake to minimize growth check. Johnson and Cline (1991) pointed out that seedlings with high RGP had improved “chances for survival and growth.” This is why previous reviews found that 75–85% of 38 articles reported a positive relationship between RGP and field performance (Ritchie and Dunlap 1980; Ritchie and Tanaka 1990). These same reviews also note that RGP may not forecast field performance under all field site conditions. Upon a review of the literature, Simpson and Ritchie (1997) concluded that RGP predictions are reliable for harsh sites, but not for mild sites. It is the variability of environmental conditions at the planting site that makes it difficult for RGP to consistently forecast field performance (Binder et al. 1988; Landis and Skakel 1988; Grossnickle and Folk 1993). Moreover, RGP values can be variable due to differences in test practices (e.g., sample collection, handling, storage, test environment, root growth rating system) or species differences (Landis and Skakel 1988), seasonal phenological changes (Ritchie and Tanaka 1990), seedling (Grossnickle 2000) and root system size (Fig. 3a), and stocktype differences (Grossnickle and El-Kassaby 2016). This is why caution is needed when using RGP to “predict” field performance and why many of the reviews questioned the ability of this attribute to consistently forecast field performance (Table 1). Nevertheless, RGP is a useful measure of vigor (Burdett 1983; Ritchie 1984; Glerum 1988; Johnson and Cline 1991; Mattsson 1997; Davis and Jacobs 2005; Grossnickle 2012) and remains a standard attribute in many seedling quality assessment programs (Ritchie et al. 2010; Landis 2011).

Current findings

There has not been a substantial body of work on RGP and field growth in recent years. A synthesis of trials across multiple European sites assessing 20 tree species reported RGP to be a good (40%), promising (30%), or poor indicator (30%) of field performance (Joustra et al. 2000a). A review of stocktype trials found RGP was consistently greater for container-grown seedlings compared with bareroot seedlings (Grossnickle and El-Kassaby 2016). Further, the greater RGP together with better morphological balance conferred greater survival and growth of container-grown seedlings under field conditions causing planting stress (Grossnickle and El-Kassaby 2016). Root growth potential was reported to effectively forecast shoot growth in 50% of the reported studies (Table 2). In a comprehensive study of four conifer species, RGP provided a good forecast of subsequent first-year shoot growth (Fig. 7a). A process-based model comparing forecasting ability of various attributes to field growth found RGP had a high correlation with first-year seedling growth across a range of climatic conditions, suggesting that RGP was a reliable indicator

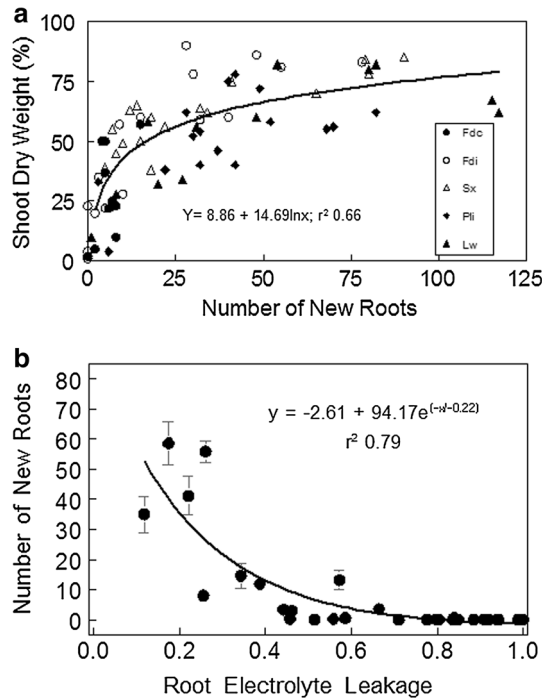


Fig. 7 **a** Relationship between shoot dry weight after one growing season and number of new roots (root growth potential) at planting in container-grown conifer seedlings. Fdc: *Pseudotsuga menziesii* (Mirb.) Franco var. *menziesii*; Fdi: *Pseudotsuga menziesii* (Mirb.) Franco var. *glauca* (Beissn.) Franco; Sx: *Picea glauca* (Moench) Voss \times *P. engelmannii* Parry ex Engelm.; Pli: *Pinus contorta* Dougl. ex Loud. var. *latifolia* Engelm.; Lw: *Larix occidentalis* Nutt.) (adapted from L'Hirondelle et al. 2007). Symbols represent means. **b** Relationship between number of new roots (root growth potential) (measured 2 weeks after a stress event) and root electrolyte leakage (measured 1 day after a stress event) of *Picea glauca* (Moench) Voss \times *P. engelmannii* Parry ex Engelm. seedlings (adapted from Grossnickle 2000). Symbols represent means \pm SEs

of field performance (Levy and McKay 2003). L'Hirondelle et al. (2007) found that a RGP value of up to 20 (new roots) was related to a rapid increase in shoot dry weight and was a threshold above which seedlings had good shoot growth regardless of increasing RGP value. Other studies similarly reported a critical RGP value for improved field performance of conifer species [e.g., 5 (Simpson et al. 1994), 10 (Simpson and Vyse 1995), or 30 (Deans et al. 1990) new roots]. Earlier, Landis and Skakel (1988) proposed that the relationship between increased RGP and field performance might not be a direct one, but rather there may be a “threshold point” when growth (as shown in Fig. 7a) changes and higher RGP values are no longer related to field performance.

Alternatively, RGP was reported as ineffective in forecasting field growth in 50% of reported studies (Table 2). For example, in three conifer species, RGP at planting was not related to either height growth or mean annual stem-volume relative-growth rate during the first 5 years (Simpson and Vyse 1995). This lack of RGP forecasting ability could be due to a number of factors. First, there is a seasonal periodicity of root growth in healthy seedlings during which roots do not grow even under ideal environmental conditions (Ritchie and Tanaka 1990; Grossnickle 2000). Thus, false assumptions can be made that

seedlings are of poor quality. Second, studies have found RGP changes because of the following parameters: inter- and intraspecific variation, seedling size (Fig. 3), nursery cultural practice, and RGP testing procedures (Simpson and Ritchie 1997; Grossnickle 2000; Ritchie et al. 2010). Third, RGP does not always forecast seedling growth because one cannot always determine whether newly planted seedlings will initially require new root growth for good field performance (i.e., planting stress vs. optimum field site conditions) (Simpson and Ritchie 1997). Thus, RGP is a measure of the functional integrity of the seedling (Grossnickle and Folk 1993), and it is a useful stock quality test that can determine seedling growth, although only under certain conditions.

Root electrolyte leakage

Background

Work on root system quality has expanded to include root electrolyte leakage (REL), which defines the ability of cell membranes to control the rate of ion movement in and out of cells. As such, REL is a measure of root damage and an indirect measure of root system integrity (McKay and Mason 1991; McKay 1992, 1993, 1994, 1998; Bigras and Calmé 1994; Bigras 1997; McKay and White 1997). Bigras and Calmé (1994) concluded that REL estimated root-system damage in a short timeframe, thereby making it a desirable attribute to measure. Also, the measure of REL characterizes live roots and has been correlated to root water loss, root freezing tolerance, as well as root and shoot water potentials (Bigras 1997). O'Reilly et al. (2001, 2003) found comparable seasonal shifts in RGP and REL, which were considered a reflection of root quality. Early reviews did not discuss the merits of measuring REL within a quality assessment program for determining seedling field performance (Table 1). It wasn't until the mid-1990s (Grossnickle and Folk 1993; Mattsson 1997) and more recently (Wilson and Jacobs 2006; Ritchie et al. 2010) that measuring REL was considered a useful measure of seedling field performance potential. This is because REL testing, like RGP, is a measure of root system viability (i.e., functional integrity) that determines whether the root system can efficiently take up water and avoid planting stress.

Current findings

There was a positive relationship between REL and shoot and/or root growth in 58% of reported studies (Table 2). For example, REL was correlated to RGP (Fig. 7b), allowing one to consider measuring REL as an alternative to RGP. Both RGP and REL were correlated with conifer seedling growth over 2 years, although neither forecast growth under all conditions (McKay 1998). In a review of REL as a measure of root system integrity, Radoglou et al. (2007) found that REL correlates with field performance in some cases, although not under all situations. As with all attributes, REL has limitations to consistently forecast field performance because it is not just related to root quality, but also to species, genetic make-up, dormancy status, and test population age (Radoglou et al. 2007; Ritchie et al. 2010). These are the same issues that have been identified as limitations to RGP testing. Also, because REL does not predict root growth in the field or whether there is the need for a fully functional root system under all field site conditions, this test can have limited forecasting capability for subsequent seedling field growth. The lack of a

positive relationship between REL and growth in all studies could also be because it only measures a small part of the root system, thus it may not detect damage due to root sampling procedures. Nevertheless, REL is an attribute with an ability to forecast field performance, which is why it is considered a viable measure of seedling quality for forest restoration programs (Radoglou et al. 2007; Ritchie et al. 2010).

Conclusions

Morphological attributes influence seedling growth after planting on forest restoration sites because they retain their mark on seedling characteristics for extended timeframes. In particular, morphological attributes that limit susceptibility to planting stress and enhance growth are important for seedling establishment. This is why studies measuring morphological attributes typically reported a positive response between measured attributes and subsequent seedling growth. Greater root-system size and stem diameter, which enhance water uptake and transport to foliage, respectively, confer a higher chance of avoiding planting stress and enhancing seedling growth. Greater shoot height is beneficial on sites with competing vegetation because of improved competitive ability, whereas the balance between the shoot and root systems together with overall size need to be adjusted in relation to potential site environmental conditions. A smaller shoot system or lower S:R are critical attributes where dry soils and high evaporative demand are limiting factors. Taken as a whole, this synthesis of information shows that it is critical for forest practitioners to define standards for morphological attributes of their crop and to avoid planting seedlings that do not meet these standards. However, morphological attributes only define overall seedling size, growth potential, and balance, whereas seedling physiological attributes also influence subsequent growth after planting.

Measures of seedling functional integrity (i.e., shoot water potential and freezing tolerance) showed how critical it is to plant seedlings that are not damaged to the point of limiting primary physiological processes; specifically, planting undamaged seedlings improves their subsequent growth. Interestingly, REL, which measures root functional integrity, did not show a consistent relationship with subsequent seedling growth. This could be because REL is related only to those sections of the root system that are assessed and not to the overall root system. This could affect whether this attribute is always an accurate measure of potential seedling growth. Measures of functional integrity need to be considered when the nursery practitioner or forester perceives that the crop has been damaged. Further, such testing is recommended within a defined seedling quality program (developed jointly by the nursery and the client) well before shipping so if these tests detect a level of damage that could potentially limit field performance, then an additional test for seedling growth (e.g., RGP) can be conducted before seedlings are field planted.

Greater drought tolerance and optimal nutrient reserves increase the speed with which seedlings can overcome planting stress and become established. Improved shoot growth can also be attributed to greater root growth immediately after planting. However, direct benefits from improved physiological attributes are ephemeral. This is why measures of these attributes did not always show a consistent positive response with subsequent shoot growth. Thus, their primary purpose is in overcoming stress or nutrient limitations, thereby supporting root and shoot system growth and improving seedling establishment within months of planting. Ultimately, a well-established seedling having a combination of desirable shoot and root development is what ensures rapid subsequent growth.

This review reiterates long-held beliefs within the forest restoration community that desirable morphological and physiological attributes improve chances for increased seedling growth. These conclusions are similar to the review of these attributes, which were found to be critical for seedling survival (Grossnickle 2012) and for selection of bareroot or container-grown stocktypes (Grossnickle and El-Kassaby 2016). Furthermore, evidence from work conducted during the past 25 years confirms these long-held beliefs, with individual studies defining species-specific ranges for these plant attributes. Finally, planting seedlings with desirable attributes does not guarantee superior growth. This is because the expression of seedling field performance is controlled by both seedling quality and reforestation site conditions. The forester can only partially control field conditions through silvicultural practices and timing of planting. The one facet of the restoration program under the forester's complete control is what stocktype is planted. Thus, planting seedlings with desirable attributes increases chances for improved growth on forest restoration sites.

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Compliance with ethical standards

Conflict of interest The authors declare that they have no conflict of interest.

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