New Forests (2022) 53:1113–1143
https://doi.org/10.1007/s11056-022-09944-8

REVIEW

Environmental conditions in the nursery regulate root system development and architecture of forest tree seedlings: a systematic review

Andrei Toca[1] · Ehren Moler[2] · Andrew Nelson[2] · Douglass F. Jacobs[1]

Received: 13 February 2022 / Accepted: 5 October 2022 / Published online: 31 October 2022

Abstract

Root system growth dynamics and architecture influence the establishment and field performance of planted forest tree seedlings. Roots display extensive phenotypic plasticity in response to changes in environmental conditions, which can be harnessed through management to produce seedlings with desirable root traits for better field performance. This systematic review synthesizes research on the effects of nutrients, light, soil temperature, water availability, and their interactions on seedling root system development and architecture in nursery production and field establishment. Major findings show that nutrient and water availability have the greatest potential for regulating root system development and architecture. High nutrient availability increases overall root growth, branching, and rooting depth until plants reach nutrient sufficiency that may cause root growth inhibition. Drought preconditioning (i.e., exposure to drought stress in the nursery) effects vary widely, but generally reduces seedling size and promotes root vs. shoot growth. Soil temperature and light availability can control seedling growth and influence stress resistance. For example, shading promotes shoot vs. root growth, while photoperiod reduction has the opposite effect. Forest tree species have an optimal temperature for root growth between 15 and 25 °C, outside of which, development is increasingly impaired. Furthermore, seedling morphology and physiology is often a result of additive or interactive effects among environmental factors. Interactions between nutrient availability and other environmental factors show the greatest potential to improve seedling root development and field performance. However, ecological differences among species and ecotypes and complex trade-offs among trait expression can entangle the identification of clear trends among interacting environmental factors.

Keywords Drought preconditioning · Nutrient availability · Root architecture · Shading · Photoperiod reduction · Soil temperature

---

✉ Andrei Toca
andrei.o.toca@gmail.com

[1] Hardwood Tree Improvement and Regeneration Center, Department of Forestry and Natural Resources, Purdue University, West Lafayette, IN 47907, USA

[2] Center for Forest Nursery and Seedling Research, College of Natural Resources, University of Idaho, Moscow, ID 83844, USA

Introduction

Importance of root development and architecture

Root system growth and architecture strongly affect seedling outplanting survival and growth (Davis and Jacobs 2005; Grossnickle 2005). Root system architecture (RSA) refers to the spatial configuration of roots in the soil and the structure of the various components constituting root systems (root segments and root topology; Lynch 1995; Hodge et al. 2009). Because plants extract water and essential minerals from soils, and those resources are heterogeneously distributed and periodically depleted and recharged, soil foraging efficiency and plant productivity depend fundamentally upon dynamic root growth and RSA (York et al. 2013). RSA is generally a product of the separation of functions among the different root components (Hutchings and de Kroon 1994; Hodge et al. 2009). The main woody roots expand the root system in depth and surface soil horizon, serving as a resource transport and storage system, and providing anchorage (Dumroese et al. 2019). Fine feeder roots, which in contrast to woody roots are not suberized and thus have lower resistance to water flow, allow plants to absorb water and solutes (Sands et al. 1982; Rüdinger et al. 1994; Wells and Eissenstat 2002; Hawkins et al. 2014).

Many RSA characteristics have been shown to increase plant growth rates and survival, which are particularly important during early stages in plant life cycles when they are the most vulnerable to environmental stress (Pulido et al. 2010; Sáenz-Romero et al. 2020). The size and proportion of plant biomass allocated to root systems influences seedling survival and the balance between seedling water uptake and evapotranspiration capacity (Grossnickle 2012; Sheridan and Davis 2021). Outplanted seedlings that rapidly grow a root system sufficiently large and deep to access stable water reserves have a greater probability of surviving dry periods (Schulze et al. 1996; Padilla and Pugnaire 2007; Villar-Salvador et al. 2012; Andivia et al. 2018). Increased root branching and a higher proportion of small roots enables foraging of greater soil volumes for required resources (Rewald et al. 2011; Hawkins et al. 2014). Plants also alter the angle of their lateral roots in order to forage different layers of the soil, which is crucial as not all nutrient or water resources are equally present across soil horizons (Forde and Lorenzo 2001; Beidler et al. 2015; Koevoets et al. 2016). Other characteristics of root systems, such as specific root length (SRL; root length divided by dry mass) and root tissue density (RTD; root dry mass divided by fresh root volume), also vary in response to a wide variety of environmental variables (Ostonen et al. 2007; Kramer-Walter et al. 2016).

Phenotypic plasticity refers to the ability of an organism to alter its phenotype depending on the environment in which it occurs (Schlichting and Pigliucci 1995). Roots show high plasticity to changes in environmental conditions, resulting in variation in RSA and growth dynamics (Lopushinsky and Max 1990; Toca et al. 2019; Moler et al. 2022). RSA is regulated by two primary, interacting mechanisms (Malamy 2005): (1) intrinsic developmental cues, and (2) responses to extrinsic environmental cues. Intrinsic drivers determine the characteristic RSA of a species such as lateral root initiation and patterning of the primordium. Intrinsic drivers explain the environmentally insensitive patterns in RSA and also define the limits for plasticity in a given species. For example, phytohormones such as abscisic acid, indoleacetic acid and cytokinins play a major role in regulating root primordia formation and growth (Casimiro et al. 2003; Lambers et al. 2008; McAdam et al. 2016). Environmental response mechanisms, on the other hand, co-ordinate environmental signals with development by regulating intrinsic pathways. For instance, water availability has a significant impact on phytohormone synthesis (Popko et al. 2010). Under limited water availability the production of abscisic acid is increased while synthesis of indoleacetic acid is suppressed, resulting in changes in root and shoot biomass allocation, root elongation rate, and lateral root formation (Popko et al. 2010; McAdam et al. 2016). Such developmental responses to environmental conditions may contribute to plant growth patterns that support the functional equilibrium hypothesis, i.e. a resource-based tradeoff between biomass allocation to above- and below-ground organs (Brouwer 1963). Generally, when development is limited by resources absorbed by roots, growth allocation is shifted toward root systems, while the opposite growth pattern is found when the limited resource is absorbed by the shoot (Brouwer 1983; Poorter et al. 2011).

Despite the advances made to increase plant production quality in forest nurseries, it is common for only 25% or less of planted seedlings to survive in areas with limited water availability or high seasonal drought stress (Davis and Frazer 1988; Engelbrecht et al. 2005; Martínez-Garza et al. 2011; Li et al. 2013; Ouzts et al. 2015). Poor seedling establishment translates to large negative economic impacts, and under current climate change projections, seedling survival is expected to decrease due to greater frequency and severity of droughts and wildfires (Seager et al. 2007; Davis et al. 2019). Therefore, advancing towards an integrated understanding of the many exogenous factors and response mechanisms that regulate plant RSA is an important goal for future reforestation efforts to design standardized nursery growth regimes that produce high quality seedlings with desirable root traits and high outplanting survival and growth.

Research advances on seedling production and field performance over the last decades allowed for extensive reviews that provide a deeper understanding of the key factors affecting survival and growth. Most reviews focus on the effects of whole seedling characteristics such as seedling size (Andivia et al. 2021), seedling quality evaluation (Grossnickle 2012; Grossnickle and MacDonald 2018), nutrition (Villar-Salvador et al. 2012, 2015), bare root and container stock type (Grossnickle and El-Kassaby 2016), and effects of container size (Poorter et al. 2012). While reviews of root systems have brought attention to the overall importance of root growth in overcoming plant stress (Grossnickle 2005) and methods of root system quality evaluation (Davis and Jacobs 2005), there has been little synthesis of the available research on how manipulation of environmental conditions affects forest seedling root system development and architecture. Therefore, the objective of this review is to synthesize the research on the effects of nutrient and water availability, light (shading and photoperiod reduction), soil temperature, and their interactions in the nursery on seedling root system development and architecture. For each of the various environmental conditions reviewed, we discuss effects in the nursery and, when available, following outplanting. Studies that evaluated the effects of environmental conditions only in the field were not included. Other metrics of outplanting performance are also discussed, such as survival and growth. We recognize that root development in the field is intimately linked with survival and aboveground growth, and most studies have focused on these metrics. Thus, studies examining post-planting root development in response to nursery treatments are more limited. Based on this synthesis we then determine the relative importance of these environmental variables for root development regulation and discuss implications of this synthesis for forest management.

Methods

For this review, we screened the literature for each environmental condition using of the following keywords in Web of Science and Google Scholar: *seedling*, *root*, and *roots*, in combination with the specific keywords for each subsection: *fertilization*, *nutrient*, *nitrogen*, *phosphorus*, *light*, *shading*, *blackout*, *short day*, *temperature*, *soil temperature*, *water*, *irrigation*, *drought preconditioning*, *drought hardening*. Because the information we were interested in is often not in article titles, keywords, or abstracts, we searched for additional articles cited in the initial list of articles to find publications that were not directly detected through our search. Searches were done with no date limits, and ranged through the end of 2021. Articles found through these combined approaches that presented results on root system development and architecture of forest tree seedlings are presented in Tables 1, 2, 3, 4 and 5.

Nutrient availability

Mineral nutrient availability helps to determine seedling growth, phenotype, and physiological status and thus, plant performance after outplanting. Fertilization increases seedling mineral nutrient content, which in turn increases remobilization capacity (Millard and Grelet 2010; Villar-Salvador et al. 2015) and photosynthesis rate (Evans 1989; Oliet et al. 2013; Zhang et al. 2018). High photosynthesis rate, nutrient storage and remobilization promote seedling growth during cultivation and after outplanting (Reich et al. 1998b; Salifu and Timmer 2001; Carles et al. 2011; Uscola et al. 2015a, b). Increasing balanced fertilizer levels increases overall seedling growth (Larigauderie et al. 1994; Villar-Salvador et al. 2004a; Luis et al. 2009; Toca et al. 2020) and promotes biomass allocation away from roots towards stems and leaves, resulting in seedlings with lower root to shoot ratios (R/S) (Driessche 1980; Proe and Millard 1994; Mackie-Dawson et al. 1995; Villar-Salvador et al. 2004a; Luis et al. 2009; Kramer-Walter and Laughlin 2017; Toca et al. 2020). Nonetheless, most studies show that an increase in nutrient availability increases root growth (Proe and Millard 1994; Mackie-Dawson et al. 1995; Salifu et al. 2008; Hernández et al. 2009; Luis et al. 2009; Adams et al. 2013; Uscola et al. 2015a, b; Toca et al. 2020), while others have reported a decrease (Wang et al. 2017) or no change (Driessche 1980; Trubat et al. 2006). The timing of nutrient application (i.e., late-season or exponential fertilization) during the year could also significantly affect seedling root development. Late-season fertilization has been shown to increase root development and root growth potential (Andivia et al. 2011; Driessche 1985). However, a review by Oliet et al. (2013) showed that the effects of late-season fertilization on seedling root development have not been consistent in Mediterranean forest species including conifers and broadleaves trees and shrubs. Responses to the timing of fertilization is likely to depend on the ecological context of each species.

Plasticity of roots in response to nutrient availability is a key process influencing plant foraging capacity and RSA. Upon encountering soil nutrients, roots increase branching density in the enriched soil patch to maximize nutrient absorption (Friend et al. 1990; Pinno and Wilson 2013). Thus, seedlings grown under high fertilization show a higher number of lateral roots with lower SRL (Larigauderie et al. 1994; Mackie-Dawson et al. 1995; Li et al. 2013; Toca et al. 2019). Because some of the most important nutrients, such as phosphorus (P) and potassium (K), are generally in greater abundance in the topsoil layers (Koevoets et al. 2016), nutrient availability also affects the depth and angle of lateral root proliferation to increase the uptake of these nutrients (Fitter and Stickland 1991; WU et al. 2005; Trubat et al. 2006). Roots growing under low nutrient availability, however, are more elongated with higher SRL and less lateral branching density, probably to increase the efficiency of soil exploration (i.e. less nutrient investment per volume of soil explored) (Larigauderie et al. 1994; Beidler et al. 2015; Toca et al. 2019). However, some studies have reported an increase in root branching in response to nutrient deficits (Trubat et al. 2012; Wang et al. 2017) to increase nutrient absorption capacity.

There are few studies that have analyzed the long-term effects of fertilization on seedling RSA following outplanting. The available results in conifer (*Pinus and Picea*) species confirm that larger seedlings with high nutrient content due to nursery fertilization developed deeper and larger root systems with higher root elongation rates and lateral branching (Folk and Grossnickle 2000; Salifu and Timmer 2001; Boivin et al. 2004; Luis et al. 2009; Cuesta et al. 2010; Toca et al. 2019). A similar effect was described for broadleaf species such as *Quercus rubra* (Salifu et al. 2008) and *Platanus occidentalis* (Luxmoore et al. 1993), which showed increased post-transplant root development in nutrient-rich seedlings. These phenotypic changes reflect growth strategies that likely improve soil foraging capacity and ensure a stable supply of water to developing seedlings. Inter- and intra-specific variation exists in how seedling RSA responds to fertilization regimes (Fitter and Stickland 1991). For example, *Pinus pinea* and *Pinus halepensis*, which are species form arid environments, show lower RSA plasticity following outplanting in response to changes in seedling nutrient content than *Pinus pinaster*, that inhabits moderate to low stress environments and prioritize root development only if resources are available (Cuesta et al. 2010; Toca et al. 2019).

Field performance of planted seedlings is greatly affected by nutrient status. Most studies report that large and nutrient-rich seedlings are linked to greater outplanting performance and survival compared to low nutrient content seedlings (Driessche 1980, 1992; Timmer and Aidelbaum 1996; Puértolas et al. 2003; Villar-Salvador et al. 2004a, 2012; Salifu et al. 2009; Oliet et al. 2009; Luis et al. 2009; Li et al. 2013; Andivia et al. 2021). The positive effects of high nutrient availability on outplanting performance, especially in dry regions, are attributed to traits such as high rates of photosynthesis, nutrient remobilization capacity and non-structural carbohydrate storage that promote rapid growth, and new root development (Timmer 1997; Luis et al. 2009; Villar-Salvador et al. 2012; Pinno and Wilson 2013). However, other studies conclude that high fertilization rates during cultivation hinder seedling outplanting performance and survival in arid environments (Trubat et al. 2008, 2011). The negative effects are mainly attributed to the imbalance between excessive water demand and uptake capacity of large nutrient-rich seedlings with lower R/S (Cortina et al. 2013). Differences in nutrient availability on plant biomass allocation between shoots and roots, root growth and architectural characteristics such as root branching and rooting depth were synthesized in Fig. 1 based on the studies listed in Table 1.

Variation in root development and RSA can also be attributed to differences in availability of specific nutrients (Friend et al. 1990; Folk and Grossnickle 2000). Next, we synthesize reports on the effects of nitrogen and phosphorus on root development, the two most well-studied macronutrients.

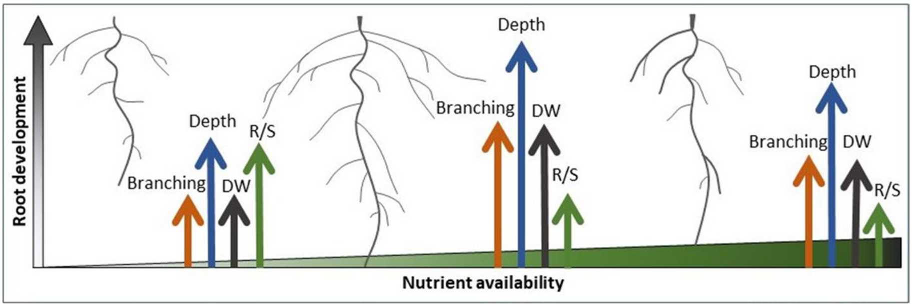

Fig. 1 Root development and architectural plasticity in response to an increasing gradient of nutrient availability. Arrow lengths indicate relative values of root system branching, depth, dry weight (DW) and root-to-shoot ratio (R/S). Increasing nutrient availability promotes overall root growth, branching, and rooting depth until plants reach nitrate sufficiency that can cause root growth inhibition. Root to shoot ratio decreases with increasing nutrient availability

Nitrogen

Nitrogen (N) is one of the main nutrients involved in root growth, which follows from the essential role of N in chloroplasts, amino acids, and nucleic acids (Schulze et al. 2005). For example, high N concentrations in leaves are frequently related to greater photosynthetic capacity of plants (Evans 1989). N generally accumulates in plant organs in the form of storage proteins that can be remobilized for new growth in spring (Salifu and Timmer 2001; Millard and Grelet 2010; Villar-Salvador et al. 2015), thus promoting high root growth (Uscola et al. 2015a, b; Fernández et al. 2007; Salifu et al. 2008). Hence, N acquisition, storage and remobilization are main processes affecting seedling root growth (Timmer 1997; Millard and Grelet 2010; Villar-Salvador et al. 2015).

Abundant soil N modulates root size but also affects RSA by increasing the number of lateral roots (Friend et al. 1990; Pregitzer et al. 1993; Mackie-Dawson et al. 1995; Li et al. 2013) and their diameter (Wang et al. 2018), reducing the ratio of fine to coarse roots (Li et al. 2015), and reducing the SRL of the root system (Ostonen et al. 2007). In addition, root lifespans of some species have been found to increase in response to the presence of N rich soil patches in order to improve resource acquisition (Adams et al. 2013). Contrary to root proliferation in nutrient rich patches of soil, high and homogeneous concentrations of N in the soil have been reported to reduce root growth, especially lateral branching (Walch-Liu et al. 2006; Wang et al. 2013). This effect of the root systems seems to be a result of nitrate (NO_3^-) sufficiency, or toxicity due to high fertilizer salt concentrations explaining root growth inhibition (Jacobs et al. 2004; Jacobs and Timmer 2005; Wang et al. 2017). Accordingly, several studies suggest that both plant-stored N and soil N may simultaneously regulate root architecture (Forde and Lorenzo 2001; Forde 2014). For instance, plant NO_3^- concentration modulates root branching in *Arabidopsis thaliana* L. (Heyn) by influencing the timing of lateral root development (Zhang et al. 1999; Walch-Liu et al. 2006). A similar effect was found in Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco), where N stressed seedlings had significantly higher root branching in nutrient rich soil patches compared to N-rich seedlings (Friend et al. 1990).

Phosphorus

After N, phosphorus (P) is the next most studied nutrient in forest tree seedling physiology. Among the essential nutrients for plant growth and development, P is a key component of nucleic acids, phospholipids, and plays a central role in energy metabolism through adenosine tri-phosphate (the energy currency of cells) (Schulze et al. 2005). P is stored mainly in the vacuole as polyphosphates or as sugar esters that can be remobilized when nutrient demand increases (Lee et al. 1990).

Seedlings show high plasticity in response to variable P availability, including significant changes in root development and architecture. Across species, the most significant effects of P on RSA were triggered by P deficiency. To cope with P deficiency, plants typically increase the length and density of lateral roots and root hairs and reduce growth of the primary root (Forde and Lorenzo 2001; Williamson et al. 2001; López-Bucio et al. 2003; Wu et al. 2005; Péret et al. 2011, 2014; Trubat et al. 2012). Low P availability has been shown to have a variable effect on total root dry weight across species. Studies of multiple conifers and broadleaf species show that low P availability reduces the total root dry weight of seedlings (Browning and Whitney 1992; Proe and Millard 1995; Oliet et al. 2005; Sardans et al. 2006). Meanwhile, low P availability had no effect on *Swietenia macrophylla* and *Eucalyptus globulus* (Fernández et al. 2007; Seabra et al. 2018), but increased the root dry weight in *Pistacia lentiscus* (Trubat et al. 2012). P deficiency also promotes lower root angles and high SRL (Trubat et al. 2006). These RSA modifications are probably an adaptive mechanism for foraging upper portions of the soil profile, where P tends to be more abundant due to the relative immobility of P in soil (Koevoets et al. 2016). Similar to N, root branching density increases upon encountering P-rich soil patches (Mickaël et al. 2007). However, most studies assessing the effects of P on RSA were done on *Arabidopsis thaliana* and other herbaceous species (e.g., Forde and Lorenzo 2001; Williamson et al. 2001; López-Bucio et al. 2003; Péret et al. 2011, 2014). Nonetheless, the same architectural responses to P availability were observed in woody species such as *Pistacia lentiscus* L. (Trubat et al. 2012) and *Fraxinus mandshurica* Rupr. (WU et al. 2005), suggesting that these effects could be prevalent in plants more broadly.

Although the RSA changes described above have been associated with greater soil foraging capacity, P deficiency may result in an undesirable tradeoff between topsoil foraging and water acquisition (Ho et al. 2005), hence impairing seedling establishment in dry regions. In addition, P deficiency is associated with lower remobilization capacity and photosynthesis rate, which can further hinder root development and seedling field performance (Driessche 1980; Proe and Millard 1995; Folk and Grossnickle 2000).

Light availability

Sunlight in the form of short-wave radiation is the main energy source for primary production on earth. To grow, trees need to adapt to local, daily and seasonal variations in photosynthetically active radiation. Even within the same plant, leaves are generally exposed to different light intensities. Thus, leaves have the capacity to morphologically and physiologically acclimate to variations in light, although species vary in their tolerance to shade, excessive light and heat (Niinemets et al. 1998; Lambers et al. 2008). Exposure to excessive light leads to photo-oxidative stress due to limited capacity to detoxify reactive oxygen species formed when absorbed light exceeds the demand for photosynthesis (Asada 2006).

If photo-oxidative stress is sustained, over time it may result in reduced photosynthesis rates, chloroplast damage, and ultimately death (Juvany et al. 2013). Exposure to low light generally results in a down-regulation of photosynthetic systems, which can significantly limit plant growth (Reich et al. 1998a; Welander and Ottosson 1998; Deng et al. 2020) and increase specific leaf area (van Hees 1997; Valladares et al. 2000; Van Noordwijk et al. 1998). Seasonal variations in photoperiod influence the life cycle of trees. Increasing length of the photoperiod stimulates seedling budbreak, leaf-out and other developmental phenomena such as flowering (Lambers et al. 2008; Zohner and Renner 2015). Photoperiod reduction plays an important role in cessation of shoot elongation, dormancy, bud formation and cold hardiness (Hawkins et al. 1996; Turner and Mitchell 2003; Wallin et al. 2017).

Light regime manipulation is used in nurseries to protect plants from excessive solar radiation through shading (Helgerson 1990) and to regulate seedling morphology and dormancy by way of photoperiod reduction (i.e. blackout treatment). While shading is effective in protecting most species, blackout is most often applied to conifers because of their responsiveness to changes in photoperiod. Both shading (Madsen 1994; Reich et al. 1998a) and blackout (Grossnickle et al. 1991; Hawkins et al. 1996) reduce seedling growth. However, the effects of shading and blackout on seedling morphology and physiology are very different and, in some cases, antagonistic.

In accordance with the theory of functional equilibrium, shading is linked to a shift in biomass allocation away from roots and towards stems and leaves (van Hees 1997; Reich et al. 1998a; Luis et al. 2009). Thus, most studies report a decrease in root development and the R/S dry mass ratio in response to shading across a wide range of conifer species (Reich et al. 1998a; Puértolas et al. 2009; Luis et al. 2010; Deng et al. 2020) and broadleaf species (Madsen 1994; van Hees 1997; Reich et al. 1998a; Welander and Ottosson 1998; Valio 2001; Puértolas et al. 2009; Villar-Salvador et al. 2004a) (Table 2). However, some studies report no effect of shading on R/S or root growth (Valladares et al. 2002; Villar-Salvador et al. 2004a; Luis et al. 2010). Shading also increases SRL and fine root length, although biomass partitioning to fine root biomass is reduced proportionally more than to coarse roots (van Hees 1997). Studies that have evaluated the long-term effects of shading during the nursery phase on seedling outplanting show that in some species root development in the field could be impaired (Puértolas et al. 2009). Ecological differences among species in response to light may account for the range of different directions and magnitudes of effects reported in the literature (Table 2), such as whether species are light-demanding or shade-tolerant during the juvenile phase (Tyree et al. 1998; Reich et al. 1998a; Welander and Ottosson 1998; Puértolas et al. 2009).

Blackout decreases shoot development due to early growth cessation. But root growth is predominantly regulated by temperature, so roots continue to grow after the application of the treatment (Grossnickle et al. 1991). Thus, most studies show no effect or an increase in overall root development as well as higher seedling R/S in response to blackout treatment (Table 3) (Immel et al. 1978; Burdett and Yamamoto 1986; Grossnickle et al. 1991; Krasowski and Owens 1991; Bigras and D'Aoust 1993; Hawkins et al. 1996; Coursolle et al. 1997; Turner and Mitchell 2003; Jacobs et al. 2008; Kostopoulou et al. 2011; Fløistad and Eldhuset 2017; Jiang et al. 2019). First order lateral roots have been shown to increase with blackout exposure in *Pinus tabuliformis* Carr. compared to seedlings grown under ambient photoperiod (Jiang et al. 2019). However, some studies show no effect of blackout treatment on seedling morphological traits such as height, shoot and root dry mass, or R/S (Table 3) (Burdett and Yamamoto 1986; Bigras and D'aoust 1992; Arnott et al. 1993; Luoranen et al. 2007; Fløistad and Eldhuset 2017).

The short- and long-term effects of blackout treatment on root development have been studied in the field (Landhäusser et al. 2012) and simulated outplanting through root growth capacity tests (Hawkins et al. 1996), and hydroponic systems (Jacobs et al. 2008). Across the different evaluation methods, most studies report no effect of blackout treatment on new root development across multiple conifer species (Grossnickle et al. 1991; Arnott et al. 1993; Hawkins et al. 1996; MacDonald and Owens 2006; Kostopoulou et al. 2011) and broadleaved species (Davis 2006; Landhäusser et al. 2012). But, cases of higher (Luoranen et al. 2007) and lower (Hawkins and Shewan 2000) new root production in response to blackout exist. Blackout was shown to increase and reduce new root growth, even for the same species, depending on the outplanting rhizosphere temperature (Jacobs et al. 2008). Seedlings exposed to blackout treatment have shown greater new root development under temperatures suboptimal for root growth, while similar or lower root growth as compared to control seedlings was observed with optimal temperatures grown under ambient photoperiod (Grossnickle et al. 1991; Hawkins and Shewan 2000; Davis 2006; Jacobs et al. 2008). Although this interaction was not observed in *Chamaecyparis nootkatensis* (D. Don) Spach. (Arnott et al. 1993) or *Picea sitchensis* (Bong.) Carrière. (Hawkins et al. 1996) where seedlings exhibited similar root development under optimal and suboptimal temperatures within a narrower range of temperatures. Additional differences among studies in the direction and magnitude of the effects of blackout could be explained by differences in the daily duration of photoperiod reduction (Bigras and D'Aoust 1993), number of days the treatment was applied (Coursolle et al. 1997), or variation in the timing of blackout application during the growing season (Krasowski and Owens 1991; Turner and Mitchell 2003). The effect of blackout treatment on plant root and shoot allometry appears to be mediated by the timing of application in relation to budset phenology. Thus, species that develop terminal buds during blackout application show greater allocation belowground than species with actively elongating shoots (Immel et al. 1978; Burdett and Yamamoto 1986; Kostopoulou et al. 2011).

Across multiple species, seedling outplanting survival and field performance was reported to be largely unaffected by shading (Madsen 1994; Valio 2001; Villar-Salvador et al. 2004a; Puértolas et al. 2009) and blackout treatment (Hawkins et al. 1996; MacDonald and Owens 2006; Kostopoulou et al. 2011). However, seedling survival was increased after exposure to blackout treatment when winter mortality due to freezing damage was considered (Mexal et al. 1979). Shading was reported to have some negative effects in *Pinus halepensis* Mill. (Puértolas et al. 2009) and *Fagus sylvatica* L. (Madsen 1994), with the most extreme shading treatments ($<5\%$ of full sunlight) resulting in higher mortality and lower growth, while a 40% shading treatment only resulted in less growth in *P. halepensis.*

Given the variability in the effects of light manipulation treatments due to ecological differences among species, implementation methods and interactions with other environmental factors (Table 2 and 3; Interactions among environmental factors section below), a graphical synthesis of the detailed changes in seedling development and RSA across gradients of light manipulation was not possible.

Soil temperature

Temperature is one of the major environmental factors affecting plant distribution. Species differ in their optimal range of temperature for growth, and are generally classified as psychrophiles, mesophiles and thermophiles in ascending order of temperature requirements (Schulze et al. 2005). The effect of temperature is different across plant organs, with roots being more responsive to variation in temperature than shoots (Grossnickle et al. 1991; Vapaavuori et al. 1992; Landhäusser et al. 2001; Domisch et al. 2002; Peng and Dang 2003; Štraus et al. 2015). Soil temperature can be an important cause of stress for root systems, especially where cold winters or high altitudes cause conditions of extreme cold or hot summers cause conditions of extreme heat. Although forest tree seedlings differ in their optimal range of temperature for root growth, most species show maximum root development between a range of 15–25 °C (Lopushinsky and Max 1990; Lyr and Garbe 1995; Lyr 1996; Peng and Dang 2003). Beyond this range of temperatures, seedlings show a gradual decrease in root development, resulting in a positive parabolic relationship between temperature and growth (Lopushinsky and Max 1990) (Fig. 2). Most species show an absence of root growth at a temperature below 5 °C (Tryon and Chapin 1983; Iivonen et al. 1999; Landhäusser et al. 2001; Alvarez-Uria and Körner 2007) and roots rapidly cease growth over 30 °C (Lopushinsky and Max 1990; Lyr 1996; Peng and Dang 2003). This response pattern is very consistent across species from different environments and phylogenetic groups (Peng and Dang 2003; Alvarez-Uria and Körner 2007) and seedling provenances within the same species (Graves and Aiello 1997; King et al. 1999). Because roots are generally very responsive to changes in temperature, studies show a decrease in the R/S of seedlings, especially with decreasing suboptimal temperatures (Kummerow and Ellis 1984; Landhäusser et al. 1996, 2001; Balisky and Burton 1997). Nonetheless, many studies report no effect of temperature on R/S ratios (King et al. 1999; Domisch et al. 2001; Peng and Dang 2003; Overdieck et al. 2007; Štraus et al. 2015), although some of these studies had a narrow range of temperatures (Table 5). Similarly, most studies show no effect of temperature on SRL (Wan et al. 2004; Alvarez-Uria and Körner 2007), with a few studies reporting lower SRL under suboptimal soil temperatures (Štraus et al. 2015). The effects of soil temperature on root development were synthesized in Fig. 2 based on the studies listed in Table 5.

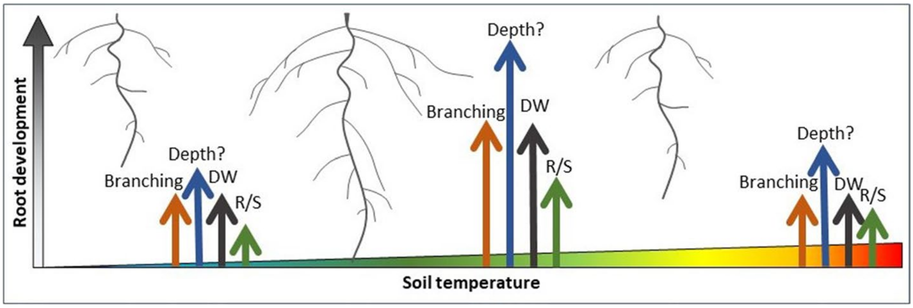

Fig. 2 Root development and architectural plasticity in response to an increasing gradient of soil temperature. Arrow lengths indicate relative values of root system branching, depth, dry weight (DW) and root-to-shoot ratio (R/S). Question marks indicates a lack of sufficient data to discern a trend. Forest tree species have an optimal temperature for root development ranging between 15 and 25 °C, beyond which, growth is increasingly impaired

Suboptimal soil temperatures reduce root development because it limits the rate of chemical, physical, and enzymatic processes (Ryyppo et al. 1998; Ostonen et al. 2007; Faget et al. 2013). Specifically, low soil temperature has been shown to increase the resistance of roots to water flow and decrease plant hydraulic conductance, thus decreasing water and nutrient uptake capacity (Lopushinsky and Max 1990; Wan et al. 1999; Pregitzer et al. 2000; Domisch et al. 2001; Sayer et al. 2005), resulting in reduced stomatal conductance and photosynthesis (Landhäusser et al. 1996, 2001; Ryyppo et al. 1998; Iivonen et al. 1999; King et al. 1999; Wan et al. 1999; Greer et al. 2006). For example, exposure of root systems to 2 °C produced a rapid and long-lasting decrease in net photosynthesis of *Juglans regia* seedlings (Lyr 1996). Accordingly, slower root elongation rates occur under suboptimal soil temperature, resulting in diminished root length and total biomass (Nambiar et al. 1979; Halter et al. 1997; King et al. 1999; Peng and Dang 2003; Sayer et al. 2005; Alvarez-Uria and Körner 2007; Jacobs et al. 2008). In addition, suboptimal temperatures reduce the formation of new root tips (Nambiar et al. 1979; Andersen et al. 1986; Lopushinsky and Max 1990; Vapaavuori et al. 1992; Balisky and Burton 1997; Halter et al. 1997; Sayer et al. 2005).

Supraoptimal soil temperature also strongly reduces root development through three mechanisms: reduction of cell elongation due to reduced seedling water potential (Grossnickle 2005), reduction of resources available for growth due to reduced net photosynthesis following limitations of stomatal conductance (Graves and Aiello 1997; Wertin et al. 2011), and increase of root respiration rates and consequent reduction of metabolizable resources available for construction of new tissues (Lyr 1996; Graves and Aiello 1997; Landhäusser et al. 2001). These effects decrease the elongation rate of root tips, resulting in lower total root length and biomass (Lopushinsky and Max 1990; Lyr 1996; Peng and Dang 2003; Wertin et al. 2011; Zhou et al. 2011; Štraus et al. 2015). Seedlings grown under supraoptimal temperatures also show increased mortality of fine roots (King et al. 1999; Pregitzer et al. 2000; Wan et al. 2004), which contributes to a decrease in fine root mass and length (Bronson et al. 2008; Zhou et al. 2011; Štraus et al. 2015).

Low soil temperature at outplanting sites is an important factor limiting seedling establishment throughout seasons and areas where temperatures are frequently suboptimal for root development (Nambiar et al. 1979; Andersen et al. 1986; Vapaavuori et al. 1992). For nursery seedlings, temperature is particularly important because container seedling production exposes the root system to a wide range of temperatures that have the potential to greatly affect root growth (Bigras and Dumais 2005). Exposure to freezing temperatures can produce damage to root systems that is not easily detectable in the short term but can significantly affect seedling survival and growth (Davis and Jacobs 2005; Toca et al. 2018). Similarly, long term exposure to supraoptimal root temperature significantly increases seedling mortality (Lyr 1996). The effects of soil temperature on outplanting seedling survival and field performance are dependent to a great extent on seedling morphology and physiological status, since processes such as water flow, water potential, photosynthesis and root elongation show a rapid recovery once seedlings are exposed to optimal temperatures (Halter et al. 1997; Iivonen et al. 1999; Lahti et al. 2005).

Water availability and drought preconditioning

Water availability is a major limiting factor for plants in many environments, and is one of the most important causes of post-transplant stress and mortality in seedlings (Haase and Rose 1993; Grossnickle 2005). Climate change projections estimate an increase in the frequency and severity of droughts in forested regions (Seager et al. 2007, Hayhoe et al. 2018). Thus, the production of seedlings able to withstand seasonal drought and post-transplant limited water availability is becoming increasingly important for reforestation. Water stress can be controlled during nursery production to manipulate seedling physiological status and morphology. While excessive water availability (waterlogging) can be a source of hydric stress for seedlings, it is generally not employed for seedling quality improvement due to its detrimental effects on development (Repo et al. 2016; Fujita et al. 2020, 2021). The effects of waterlogging on forest seedling root development were described in many broadleaved (Colin-Belgrand et al. 1991; Schmull et al. 2000; Zúñiga-feest et al. 2017; Fujita et al. 2020) and conifer (Repo et al. 2017; Fujita et al. 2020, 2021) species, and the physiological responses associated with waterlogging in trees were reviewed by Kreuzwieser et al. (2014). In contrast, controlled water limitation treatments are applied in nurseries to slow growth and promote stress resistance. There is an abundance of terminology for controlled water limitation treatments such as drought hardening, drought conditioning, or drought preconditioning. In this study, we will refer to this treatment as drought preconditioning. Drought preconditioning is practiced during seedling production to reduce transplant shock and improve seedling survival and root growth following outplanting (Guarnaschelli et al. 2003; Vilagrosa et al. 2003; Arreola et al. 2006; Moler and Nelson 2021). The technique is also frequently effective at improving frost tolerance (Villar-Salvador et al. 2013). Drought preconditioning has four objectives (Landis et al. 1998): (1) manipulate seedling morphology, (2) induce dormancy, (3) acclimate seedlings to the outplanting environment, and (4) induce stress resistance mechanisms.

The effects of drought preconditioning depend to a great extent on the intensity and duration of the water stress treatment and a species' drought tolerance or avoidance strategy (Vilagrosa et al. 2003 and 2006; Chirino et al. 2009). Several studies report higher field performance and drought resistance of seedlings grown under drought preconditioning of moderate intensity as compared to high intensity (Khan et al. 1996; Villar-Salvador et al. 1999, 2004b; Arreola et al. 2006; Shi et al. 2019). During drought preconditioning, water stress must be of sufficient intensity to induce drought resistance mechanisms, but not of such high intensity that seedlings are irreversibly damaged. Since species vary in drought tolerance, the intensity of drought preconditioning necessary to induce desirable phenotypic changes must be adjusted for each species or perhaps drought-related strategy (Vilagrosa et al. 2003). Optimal drought preconditioning increases seedling stress resistance by enhancing water uptake capacity, maintaining higher cell water content under drought conditions, and limiting water loss through morphoanatomical and physiological changes, which results in higher water use efficiency (Vilagrosa et al. 2003; Guarnaschelli et al. 2003; Sloan et al. 2020).

Drought preconditioning induces significant and varying effects on seedling physiological processes affecting development and survival. For example, net photosynthesis and stomatal conductance can increase (Landhäusser et al. 1996; Vilagrosa et al. 2003; Guarnaschelli et al. 2003; Sloan et al. 2020), decrease (Stewart et al. 1995; Landhäusser et al. 1996; Villar-Salvador et al. 2004b, 2013; Valladares and Sánchez-Gómez 2006), or remain unchanged in response to drought preconditioning (Stewart et al.

1995). Nutrient concentrations such as nitrogen, soluble sugars, and starch also show variable responses including an increase (Khan et al. 1996; Villar-Salvador et al. 1999, 2013), decrease (Sanz Pérez et al. 2007), or no change (Royo et al. 2001; Sanz Pérez et al. 2007; Sloan et al. 2020). In contrast, drought preconditioning typically reduces seedling biomass (Khan et al. 1996; van Hees 1997; Torreano and Morris 1998; Royo et al. 2001; Guarnaschelli et al. 2003; Villar-Salvador et al. 2013, 2004b; Arreola et al. 2006; Valladares and Sánchez-Gómez 2006; Sanz Pérez et al. 2007; Pritzkow et al. 2021), though some studies report no change (Villar-Salvador et al. 2004b; Sanz Pérez et al. 2007; Sloan et al. 2020). Drought preconditioning generally stimulates root growth more than shoot growth, and often reduces leaf area resulting in an increase in seedling R/S (Landhäusser et al. 1996; van Hees 1997; Arreola et al. 2006; Valladares and Sánchez-Gómez 2006; Villar-Salvador et al. 2013), though examples exist of reductions (Royo et al. 2001; Sloan et al. 2020), and neutral responses (Vilagrosa et al. 2003; Guarnaschelli et al. 2003; Villar-Salvador et al. 2004b; Padilla et al. 2007) (Table 4). Total root biomass, however, is generally unaffected (Landhäusser et al. 1996; van Hees 1997; Vilagrosa et al. 2003; Valladares and Sánchez-Gómez 2006; Padilla and Pugnaire 2007; Sloan et al. 2020) or slightly increased (Royo et al. 2001; Arreola et al. 2006; Valladares and Sánchez-Gómez 2006; Padilla and Pugnaire 2007) in response to drought preconditioning, with few examples of negative effects (Guarnaschelli et al. 2003; Arreola et al. 2006). Drought preconditioning can also increase fine root biomass (van Hees 1997). Given the variability in the effects of drought preconditioning on root development (Table 4), a graphical synthesis of the detailed changes in seedling development and RSA across a gradient of water availability was not possible.

There is little information about the effects of drought preconditioning on the development and architecture of root systems after outplanting. Nonetheless, the available results suggest that preconditioned seedlings can grow larger and deeper root systems (Arreola et al. 2006; Moler and Nelson 2021). Outplanting survival of seedlings grown under drought preconditioning treatment has been reported to increase (Driessche 1992; Guarnaschelli et al. 2003; Shi et al. 2019) or remain equal compared to well-watered control seedlings (Villar-Salvador et al. 1999, 2013; Royo et al. 2001).

Results are inconclusive on the suitability of drought preconditioning to produce seedlings with enhanced capacity to withstand arid conditions in most species, and thus debate remains concerning the applicability of the method for many species and contexts (Table 4). The morphological and physiological effects described across species and treatment levels present a tradeoff by stimulating root growth over shoot growth, but at the same time reducing growth potential since seedlings are typically smaller in size. The complexity of the interactions between species ecology, drought resistance physiology and drought preconditioning intensity calls for a more systematic study of these interactions. Specifically, there is a need to determine the optimal intensity and duration of drought preconditioning required to induce drought resistance mechanisms, to quantify effects of drought preconditioning on RSA, and to develop an understanding of species × treatment interactions.

Interactions among environmental factors

The environmental conditions discussed above have a wide range of effects on tree seedlings across their gradients. However, seedlings are often simultaneously subjected to different intensities of environmental conditions in nurseries and following outplanting. Studies have reported that seedling phenotype and outplanting performance are a result of independent effects of co-occurring environmental conditions (Krasowski and Owens 1991; Villar-Salvador et al. 2004a) or significant interactions across their gradients (Nambiar et al. 1979; Sayer et al. 2005). Among the four environmental factors considered in this study, nutrient availability shows some of the highest magnitude and consistent interactions with the potential of improving seedling RSA and field performance. For example, high nutrient availability significantly increases new root growth at low temperature (nutrients-temperature interaction, Nambiar et al. 1979; Iivonen et al. 1999), or high water availability (nutrient-water interaction, Pregitzer et al. 1993) but it does not interact with shading treatments (Villar-Salvador et al. 2004a; Hernández et al. 2009; Luis et al. 2010). Interactions between nutrient availability and water limitation have been shown to significantly influence field performance, with increased nutrient availability alongside drought preconditioning treatments yielding increased seedling outplanting growth and survival (Driessche 1992; Shi et al. 2019). Environmental conditions aside from nutrients also interact with water availability to produce biologically meaningful changes in root system development and architecture. For example, low water availability combined with shading significantly reduced root development in *Fagus sylvatica* (Madsen 1994) and *Pinus massoniana* (Deng et al. 2020). However, van Hees (1997) found no interaction in *Fagus sylvatica* and *Quercus robur*, although this study had fewer levels of water availability and shading. Similarly, drought preconditioning can significantly increase root growth under photoperiod reduction in *Tsuga heterophylla* and *Picea abies* (Grossnickle et al. 1991; Luoranen et al. 2007). However, this interaction between water availability and photoperiod was not found in *Thuja plicata* and *P. menziesii* (Krasowski and Owens 1991; MacDonald and Owens 2006). The effect of drought preconditioning also depends on soil temperature, where root growth is significantly reduced at suboptimal temperatures (Sayer et al. 2005).

Studies that simultaneously assess the effects of more than one environmental condition on seedling development often show that roots differ in their response to these environmental signals. Soil temperature has a predominant effect on root development (Nambiar et al. 1979; Sayer et al. 2005), and within a range of temperature conducive to root growth, nutrient availability appears to have the hightest impact on the control of root development (Nambiar et al. 1979), followed by water availability (Sayer et al. 2005; Villar-Salvador et al. 2013). The influence of light availability through shading and blackout is mediated by a functional equilibrium between shoot and root growth and growth cessation mechanisms, respectively, which ultimately affect biomass allocation. Light manipulation has been shown to have, overall, less influence on root systems than nutrients (Villar-Salvador et al. 2004a; Luis et al. 2010) or water availability (Madsen 1994).

Table 1 References that examined the effects of nutrient availability on seedling root to shoot ratios (R/S) and root system morphological and architectural traits. Symbols indicate a positive (+), negative (−) or neutral (=) relationship with an increase in the specific nutrient listed in the same row. Separation of symbols with a slash implies that the effect varied with treatment intensity or interaction with a different treatment in the same study

Nutrient availability							
References	Species	Nutrient	R/S	Dry mass	Length	Nr roots	Depth
Adams et al. (2013)	*Acer negundo*	N			+		
	Populus tremuloides	N			+		
	Sassafras albidum	N			+		
	Liriodendron tulipifera	N			+		
Browning and Whitney (1992)	*Pinus banksiana*	P		+			
	Piceamariana	P					
Cuesta et al. (2010)	*Pinus halepensis*	NPK	=	+	+	+	=
Fernández et al. 2007	*Eucalyptus globulus*	N	−	=/+			
Forde and Lorenzo (2001)	*Review paper*	P				−	
		N				−/+	
Friend et al. (1990)	*Pseudotsuga menziesii*	NPK				+	
Hernández et al. (2009)	*Pistacia lentiscus*	NPK	−	+	+		
	Quercus suber	NPK	−	=	=		
Kramer-Walter and Laughlin (2017)	*Agathis australis*	NPK	=			=	
	Dacrycarpus dacrydiodes	NPK	−			=	
	Knightia excelsa	NPK	−			−	
	Laurelia novae-zelandiae	NPK	−			=	
Larigauderie et al. (1994)	*Pinus taeda*	N	=/+	=/+		+	
López-Bucio et al. (2003)	Review paper	P				−	
		N				−/+	
Luis et al. (2009)	*Pinus canariensis*	NPK	−	+		+	+
Luxmoore et al. (1993)	*Platanus occidentalis*		=	+	+		
Mackie-Dawson et al. (1995)	*Acer pseudoplatanus L*	N	−	+	=	+	
	Picea sitchensis	N	−	+	=	+	
Nicodemus et al. (2008)	*Juglans nigra*	N	−	=			
Péret et al. (2011), (2014)	*Arabidopsis thaliana*	P				−	
Pinno and Wilson (2013)	*Grassland*				+	−	
	Forest				+	+	
Proe and Millard (1995)	*Picea sitchensis*	P	−	+			
Salifu and Timmer (2001)	*Picea mariana*	N		+			
Salifu et al. (2008a)	*Quercus rubra*			+			
Salifu et al. (2008b)	*Juglans nigra*	N	−	=			
Sardans et al. (2006)	*Quercus ilex*	P		+			
Seabra et al. (2018)	*Swietenia macrophylla*	P	−	=			
Toca et al. (2020)	*Pinus pinea*	NPK	−	+	+	=	=
	Pinus pinaster	NPK	−	+	+	+	+
	Pinus nigra	NPK	−	+	+	+	+
Trubat et al. (2006)	*Pistacia lentiscus*	N	−	=	=	−	
		P	=	=	−		
Trubat et al. (2012)	*Pistacia lentiscus*	N	−	=	−	−	
		P	=	=	−	−	
Uscola et al. (2015a, b)	*Quercus ilex*	NPK	−	+			

Table 1 (continued)

Nutrient availability

References	Species	Nutrient	R/S	Dry mass	Length	Nr roots	Depth
Villar-Salvador et al. (2004[a])	*Quercus ilex*		–				
Walch-Liu et al. (2006)	*Arabidopsis thaliana*	N				–/+	
Wang et al. (2013)	*Pinus tabuliformis*	N		–/=	–	–	
Wang et al. (2017)	*Pinus tabuliformis*	N		–	–	–	
Williamson et al. (2001)	*Arabidopsis thaliana*	P				–	
WU et al. (2005)	*Fraxinus mandshurica*	P				–	

Table 2 References that examined the effects of shading on seedling root to shoot ratio (R/S) and root system morphological and architectural traits. Symbols indicate a positive (+), negative (–) or neutral (=) relationship with shading treatment compared to a natural light intensity control. Separation of symbols with a slash implies that the effect varied with treatment intensity or interaction with a different treatment in the same study

Shading

Reference	Species	R/S	Dry mass	Length	Nr roots	Depth
Deng et al. (2020)	*Pinus massoniana*		–			
Luis et al. (2010)	*Pinus canariensis*	–	=	=		
Madsen (1994)	*Fagus sylvatica*	±	+			
Puértolas et al. (2009)	*Quercus ilex*	–	–/=			
	Pinus halepensis	–	–/=			
Reich et al. (1998a, b)	*Populus tremuloides*	–				
	Betula papyrifera	–				
	Betula allegheniensis	–				
	Larix laricina	–				
	Pinus banksiana	–				
	Picea glauca	–				
	Picea mariana	–				
	Pinus strobus	–				
	Thuja occidentalis	–				
Valio (2001)	*Trema micrantha*	–		–		
Valladares et al. (2002)	*Quercus ilex*	=	–			
	Quercus coccifera	=	–			
van Hees (1997)	*Quercus robur*		–		=	
	Fagus sylvatica		–		–	
Villar–Salvador et al. (2004a)	*Quercus ilex*	–	=			
Welander and Ottosson (1998)	*Fagus sylvatica*	–	–			
	Quercus robur	–	–			

Table 3 References that examined the effects of blackout treatment (photoperiod reduction) on seedling root to shoot ratio (R/S) and root system morphological and architectural traits. Symbols indicate a positive (+), negative (−) or neutral (=) relationship with reduction in photoperiod compared to a natural photoperiod control. Separation of symbols with a slash implies that the effect varied with treatment intensity or interaction with a different treatment in the same study

Blackout						
Reference	Species	R/S	Dry mass	Length	New root growth	Depth
Arnott et al. (1993)	*Chamaecyparis nootkatensis*	=	=		=	
Bigras and D'aoust (1992))	*Picea glauca*	=	=			
	Picea mariana	=	=			
Bigras and D'Aoust (1993)	*Picea glauca*	=	−			
Burdett and Yamamoto (1986)	*Pseudotsuga menziesii*	=	=			
	Pinus contorta	+	=			
Coursolle et al. (1997;)	*Picea glauca*	+	=/+	=		
Davis (2006)	*Quercus rubra*				+/=	
Fløistad and Eldhuset (2017)	*Picea abies*	+	=	=		
Grossnickle et al. (1991)	*Tsuga heterophylla*	+	=		−/+/=	
Hawkins et al. (1996;)	*Picea stichensis*	+	+		−/=	
Hawkins and Shewan (2000)	*Picea engelmannii*				−	
	Picea glauca				−	
Jacobs et al. (2008)	*Pseudotsuga menziesii*	+	=/+		−/+/=	
Jiang et al. (2019)	*Pinus tabuliformis*	=	=			
Kostopoulou et al. (2011)	Cupressus sempervirens L	+	+		=	
Krasowski and Owens (1991)	*Thuja plicata*	+	=			
Landhäusser et al. (2012)	*Populus tremuloides*	=	=		=	
Luoranen et al. (2007)	Picea abies	=	=			
MacDonald and Owens (2006)	*Pseudotsuga menziesii*	=	=		=	

Table 4 References that examined the effects of drought preconditioning on seedling root to shoot ratios (R/S) and root system morphological and architectural traits. Symbols indicate a positive (+), negative (−) or neutral (=) relationship with drought preconditioning compared to optimal water availability. Separation of symbols with a slash implies that the effect varied with treatment intensity or interaction with a different treatment in the same study

Drought preconditioning						
Reference	*Species*	R/S	Dry mass	Length	Nr roots	Depth
Arreola et al. (2006)	*Silene vulgaris*	+	±	±		+
Valladares and Sánchez-Gómez (2006)	*Quercus robur*	+/=	−			
	Quercus pyrenaica	=	−/=			
	Quercus faginea	+/=	−			
	Quercus ilex	+	−			
	Quercus coccifera	=	−			
	Pinus sylvestris	=	=			
	Pinus pinaster	+	−/=			
	Pistacia lentiscus	+	−			
	Pistacia terebinthus	=	−			
	Arbutus unedo	+	−			
	Viburnum tinus	+	=			
Guarnaschelli et al. (2003)	*Eucalyptus globulus*	=	−			+
Landhäusser et al. (1996)	*Betula papyrifera*	+	=			
	Populus balsamifera	+	=			
Padilla et al. (2007)	*Genista umbellata*	=	+	+		=
	Lycium intricatum	=	+	+		=
	Retama sphaerocarpa	=	=	+		=
Royo et al. (2001)	*Pinus halepensis*	−	+			
Sloan et al. (2020)	*Populus tremuloides*	−	=			
van Hees (1997)	*Quercus robur*	+/=	=		=	
	Fagus sylvatica	+/=	=		=	
Vilagrosa et al. (2003)	*Pistacia lentiscus,*	=				
	Quercus coccifera					
	Juniperus oxycedrus					
Villar-Salvador et al. (2004b)	*Quercus ilex*	=/−				
Villar-Salvador et al. (2013)	*Pinus pinea*	+				

Table 5 References that examined the effects of soil temperature on seedling root development, range of temperatures and species studied

Soil temperature		
Reference	Temperature range (°C)	Species
Alvarez-Uria and Körner (2007)	5, 15; heterogeneous temperature across root container	*Alnus viridis* *Alnus glutinosa* *Picea abies* *Pinus sylvestris* *Pinus cembra*
Andersen et al. (1986)	8, 12, 16, 20	*Pinus resinosa*
Balisky and Burton (1997)	18–25, 10–13	*Picea engelmannii* *Pinus contorta*
Bronson et al. (2008)	Dynamic temperature: ambient, ambient + 5	*Picea mariana* *Epilobium angustifolium*
Domisch et al. (2001)	5, 9, 13, 17	*Pinus sylvestris*
Domisch et al. (2002)	5, 13	*Pinus sylvestris*
Graves and Aiello (1997)	26, 30, 32, 34, 36	*Acer saccharinum*
Greer et al. (2006)	7, 15, 25	*Malus domestica*
Grossnickle et al. (1991)	5,22	*Tsuga heterophylla*
Halter et al. (1997)	3, 7, 13	*Eucalyptus pauciflora*
Iivonen et al. 1999	Fast and slow warming	*Pinus sylvestris*
Jacobs et al. (2008)	10, 15, 20, 25	*Pseudotsuga menziesii*
King et al. (1999)	Dynamic temperature: high and low	*Populus tremuloides*
Kummerow and Ellis (1984)	2, 7, 12	*Eriophorum vaginatum* *Carex bigelowii*
Lahti et al. (2005)	9, 13, 18, 21	*Picea abies*
Landhäusser et al. (1996)	3, 10, 15	*Betula papyrifera* *Populus balsamifera* *Picea mariana*
Landhäusser et al. (2001)	5, 15, 25	*Populus tremuloides* *Picea glauca*
Lopushinsky and Max (1990)	0.5, 5, 10, 15, 20, 25, 30	*Pseudotsuga menziesii* *Abies amabilis* *Abies procera* *Pinus contorta* *Pinus ponderosa*
Lyr and Garbe (1995)	5, 10, 15, 20, 25, 30, 35	*Pinus sylvestris* *Fagus sylvatica* *Tilia cordata* *Quercus robur*
Lyr (1996)	5, 10, 15, 20, 25, 30, 35	*Quercus robur* *Larix decidua* *Picea abies* *Pinus nigra* *Pseudotsuga menziesii*
Nambiar et al. (1979)	5, 10, 15, 20	*Pinus radiata*

Table 5 (continued)

Soil temperature		
Reference	Temperature range (°C)	Species
Overdieck et al. (2007)	4, 2, –2, –4	*Fagus sylvatica*
Peng and Dang (2003)	5, 10, 15, 20, 25, 30, 35	*Populus tremuloides* *Picea mariana* *Picea glauca* *Pinus banksiana*
Ryyppo et al. (1998)	5, 12, 20	*Pinus sylvestris*
Sayer et al. (2005)	13, 18, 23	*Pinus echinata* *Pinus palustris* *Pinus taeda*
Štraus et al. (2015)	12,15; dynamic temperature	*Fagus sylvatica*
Tryon and Chapin (1983)	5, 10, 15, 20	*Populus tremuloides* *Picea mariana* *Populus balsamifera*
Vapaavuori et al. (1992)	5, 8, 12, 16, 20	*Pinus sylvestris* *Picea abies*
Wan et al. (2004)	Dynamic temperature: ambient and high	*Acer rubrum* *Acer saccharum*
Wertin et al. (2011)	23, 26,29	*Quercus rubra*
Zhou et al. (2011)	Dynamic temperature: ambient, ambient + 5	*mixed hardwood*

Future research and conclusions

Root systems of forest tree seedlings exhibit phenotypic plasticity in response to the availability of resources and environmental conditions. Among related studies, almost all environmental factors reviewed in this paper were found to cause positive, neutral, and negative effects on seedling root development, indicating that treatments are often species-specific, the underlying mechanisms are complex, and the type, duration, and magnitude of treatments must be considered when treatments are integrated into seedling improvement programs. The neutral and moderate developmental effects described in response to environmental factors underline the important role that physiological mechanisms play in acclimation, thus conferring seedlings a certain degree of resilience to changes in environmental conditions.

Future research should more specifically focus on understanding how nursery treatments interact with major limiting factors at the outplanting site to aid in the development of treatments to improve RSA, mitigate planting stress, and improve seedling field performance. Because of the frequent interactions among factors described in this review, more studies need to be designed to improve understanding of which interactive factors most strongly affect seedling root development and architecture, as well as field performance. Future research should also link seedling post-transplant root architecture to nursery growing conditions in order to capitalize on root plasticity for improving seedling performance under stressful conditions. Furthermore, the analysis of root architecture should take into account root orders that distinguish between absorptive fine roots for resources uptake and coarse roots for transport to reduce the intrinsic limitations of assigning these functions to root diametrical classes. The new technologies being developed in agricultural research capable of visual assessment of root architecture in the soil, such as digital phenotyping based on X-ray computed tomography, can open new opportunities for studying the dynamic responses of root systems to environmental conditions in forest tree species.

Major findings synthesized in this review provide a new perspective of the importance of nursery growing conditions from the standpoint of seedling root development and architecture, which are often overlooked. Among the four environmental factors considered in this study, nutrient and water availability have the greatest potential for manipulating root development. Root growth and architecture are simultaneously regulated by soil- and plant-stored nutrient availability. High nutrient availability increases overall root development, branching, and rooting depth until plants reach nutrient sufficiency, which can cause root growth inhibition. Although water availability strongly affects root growth, results are inconclusive on the suitability of drought preconditioning to produce seedlings with enhanced capacity to withstand arid conditions in most species. Overall, drought preconditioning reduces seedling size and promotes root growth more than shoot growth, and often reduces leaf area. Nutrient availability and drought preconditioning can have opposite effects on seedling morphology and physiological status. However, high nutrient availability and strategic drought preconditioning can improve seedling outplanting stress resistance, survival and growth. Meanwhile, soil temperature and light availability manipulations can be more efficiently used to control seedling growth cessation and induce stress resistance mechanisms. Root systems respond differently to light availability, as implemented through shading or blackout treatment. While both treatments tend to reduce overall seedling growth, shading promotes shoot growth over roots and blackout treatment has the opposite effect. Due to the prominence of root system responses to interactions among growth conditions, care must be taken in interpreting studies of root systems that manipulate only one factor at a time. This synthesis shows that there is a strong potential for additive and interactive effects between environmental conditions to improve seedling RSA and outplanting performance; however, these effects need to be disentangled and tested in a variety of forest tree seedlings.

Author contributions A.T. developed the theme of the article, performed the initial literature search and produced the initial manuscript draft, figures and tables. D.F.J., A.N., and E.M. provided additional literature and contributed substantively to conceptual and organizational revisions in all subsequent drafts.

Funding This work was funded by the United States Department of Agriculture, National Institute of Food and Agriculture grant 2019–67014-29109 and the National Science Foundation awards 1916699 and 1916587.

Declarations

Conflict of interests The authors declare no conflicts of interests relevant to the content of this article.

References

Adams TS, Mccormack ML, Eissenstat DM (2013) Foraging strategies in trees of different root morphology: the role of root lifespan. Tree Physiol 33:940–948. https://doi.org/10.1093/treephys/tpt067

Alvarez-Uria P, Körner C (2007) Low temperature limits of root growth in deciduous and evergreen temperate tree species. Funct Ecol 21:211–218. https://doi.org/10.1111/j.1365-2435.2007.01231.x

Andersen CP, Sucoff EI, Dixon RK (1986) Effects of root zone temperature on root initiation and elongation in red pine seedlings. Can J for Res 16:696–700. https://doi.org/10.1139/x86-125

Andivia E, Fernández M, Vázquez-Piqué J (2011) Autumn fertilization of Quercus ilex ssp. ballota (Desf.) Samp. nursery seedlings: effects on morpho-physiology and field performance. Ann for Sci 68:543–553. https://doi.org/10.1007/s13595-011-0048-4

Andivia E, Zuccarini P, Grau B et al (2018) Rooting big and deep rapidly: the ecological roots of pine species distribution in southern Europe. Trees. https://doi.org/10.1007/s00468-018-1777-x

Andivia E, Villar-Salvador P, Oliet JA et al (2021) Climate and species stress resistance modulate the higher survival of large seedlings in forest restorations worldwide. Ecol Appl 31:1–11. https://doi.org/10.1002/eap.2394

Arnott JT, Grossnickle SC, Puttonen P et al (1993) Influence of nursery culture on growth, cold hardiness, and drought resistance of yellow cypress. Can J for Res 23:2537–2547. https://doi.org/10.1139/x93-314

Arreola J, Franco JA, Vicente MJ, MartÍnez-SÁnchez JJ (2006) Effect of nursery irrigation regimes on vegetative growth and root development of Silene vulgaris after transplantation into semi-arid conditions. J Hortic Sci Biotechnol 81:583–592. https://doi.org/10.1080/14620316.2006.11512109

Asada K (2006) Production and scavenging of reactive oxygen species in chloroplasts and their functions. Plant Physiol 141:391–396. https://doi.org/10.1104/pp.106.082040

Balisky AC, Burton PJ (1997) Planted conifer seedling growth under two soil thermal regimes in high-elevation forest openings in interior British Columbia. New For 14:63–82. https://doi.org/10.1023/A:1006592705104

Beidler KV, Taylor BN, Strand AE et al (2015) Changes in root architecture under elevated concentrations of CO2 and nitrogen reflect alternate soil exploration strategies. New Phytol 205:1153–1163. https://doi.org/10.1111/nph.13123

Bigras FJ, D'aoust AL (1992) Hardening and dehardening of shoots and roots of containerized black spruce and white spruce seedlings under short and long days. Can J for Res 22:388–396. https://doi.org/10.1139/x92-051

Bigras FJ, D'Aoust AL (1993) Influence of photoperiod on shoot and root frost tolerance and bud phenology of white spruce seedlings (Picea glauca). Can J for Res 23:219–228. https://doi.org/10.1139/x93-029

Bigras FJ, Dumais D (2005) Root-freezing damage in the containerized nursery: impact on plantation sites—a review. New For 30:167–184. https://doi.org/10.1007/s11056-005-4423-6

Boivin JR, Salifu KF, Timmer VR (2004) Late-season fertilization of Picea mariana seedlings: intensive loading and outplanting response on greenhouse bioassays. Ann For Sci 61:737–745. https://doi.org/10.1051/forest:2004073

Bronson DR, Gower ST, Tanner M et al (2008) Response of soil surface CO_2 flux in a boreal forest to ecosystem warming. Glob Chang Biol 14:856–867. https://doi.org/10.1111/j.1365-2486.2007.01508.x

Brouwer R (1963) Some aspects of the equilibrium between overground and underground plant parts. Meded Inst Biol Scheikd Onderz Landb Gewass 213:31–39

Brouwer R (1983) Functional equilibrium: sense or nonsense? Netherlands J Agric Sci 31:335–348

Browning MHR, Whitney RD (1992) The influence of phosphorus concentration and frequency of fertilization on ectomycorrhizal development in containerized black spruce and jack pine seedlings. Can J For Res 22:1263–1270. https://doi.org/10.1139/x92-168

Burdett AN, Yamamoto S (1986) Growth rate and shoot: root allometry in Pseudotsuga menziesii (Mirb.) Franco and Pinus contorta Dougl. seedlings raised under two photoperiodic regimes. Scand J For Res 1:397–402. https://doi.org/10.1080/02827588609382432

Carles S, Lamhamedi MS, Stowe DC et al (2011) Relationships between frost hardiness, root growth potential, and photosynthesis of nursery-grown white spruce seedlings. Ann For Sci 68:1303–1313. https://doi.org/10.1007/s13595-011-0138-3

Casimiro I, Beeckman T, Graham N et al (2003) Dissecting Arabidopsis lateral root development. Trends Plant Sci 8:165–171. https://doi.org/10.1016/S1360-1385(03)00051-7

Chirino E, Vilagrosa A, Cortina J et al (2009) Ecological restoration in degraded drylands: the need to improve the seedling quality and site conditions in the field. In: Grossberg Steven P (ed) Forest Management. Nova Science Publishers, New York

Colin-Belgrand M, Dreyer E, Biron P (1991) Sensitivity of seedlings from different oak species to waterlogging: effects on root growth and mineral nutrition. Ann For Sci 48:193–204. https://doi.org/10.1051/forest:19910206

Cortina J, Vilagrosa A, Trubat R (2013) The role of nutrients for improving seedling quality in drylands. New For 44:719–732. https://doi.org/10.1007/s11056-013-9379-3

Coursolle C, Bigras FJ, Margolis HA, Hébert C (1997) Dehardening and second-year growth of white spruce provenances in response to duration of long-night treatments. Can J For Res 27:1168–1175. https://doi.org/10.1139/x97-068

Cuesta B, Vega J, Villar-Salvador P, Rey-Benayas JM (2010) Root growth dynamics of Aleppo pine (Pinus halepensis Mill.) seedlings in relation to shoot elongation, plant size and tissue nitrogen concentration. Trees 24:899–908. https://doi.org/10.1007/s00468-010-0459-0

Davis SD, Frazer JM (1988) Differential survival of chaparral seedlings during the first summer drought after wildfire. Oecologia 76:215–221

Davis AS, Jacobs DF (2005) Quantifying root system quality of nursery seedlings and relationship to outplanting performance. New For 30:295–311. https://doi.org/10.1007/s11056-005-7480-y

Davis KT, Dobrowski SZ, Higuera PE et al (2019) Wildfires and climate change push low-elevation forests across a critical climate threshold for tree regeneration. Proc Natl Acad Sci 116:6193–6198. https://doi.org/10.1073/pnas.1815107116

Davis AS (2006) Photoperiod manipulation during nursery culture: effects on Quercus rubra seedling development and responses to environmental stresses following transplanting. Dissertation, Purdue University

Deng X, Xiao W, Shi Z et al (2020) Combined effects of drought and shading on growth and non-structural carbohydrates in Pinus massoniana lamb. Seedl For 11:12–14. https://doi.org/10.3390/F11010018

Domisch T, Finér L, Lehto T (2001) Effects of soil temperature on biomass and carbohydrate allocation in Scots pine (Pinus sylvestris) seedlings at the beginning of the growing season. Tree Physiol 21:465–472. https://doi.org/10.1093/treephys/21.7.465

Domisch T, Finér L, Lehto T (2002) Growth, carbohydrate and nutrient allocation of Scots pine seedlings after exposure to simulated low soil temperature in spring. Plant Soil 246:75–86. https://doi.org/10.1023/A:1021527716616

Dumroese RK, Terzaghi M, Chiatante D et al (2019) Functional traits of pinus ponderosa coarse roots in response to slope conditions. Front Plant Sci 10:1–12. https://doi.org/10.3389/fpls.2019.00947

Engelbrecht BMJ, Kursar TA, Tyree MT (2005) Drought effects on seedling survival in a tropical moist forest. Trees - Struct Funct 19:312–321. https://doi.org/10.1007/s00468-004-0393-0

Evans JR (1989) Photosynthesis and nitrogen relationships in leaves of C3 plants. Oecologia 78:9–19. https://doi.org/10.1007/BF00377192

Faget M, Blossfeld S, Jahnke S, et al (2013) Temperature effects on root growth. In: Eshel A, Beeckman T (eds) Plant Roots: The Hidden Half, 4th edn. New York, pp 31.1–31.8

Fernández M, Marcos C, Tapias R et al (2007) Nursery fertilisation affects the frost-tolerance and plant quality of Eucalyptus globulus Labill. cuttings. Ann For Sci 64:865–873. https://doi.org/10.1051/forest:2007071

Fitter AH, Stickland TR (1991) Architectural analysis of plant root systems 2. influence of nutrient supply on architecture in contrasting plant species. New Phytol 118:383–389. https://doi.org/10.1111/j.1469-8137.1991.tb00019.x

Fløistad I, Eldhuset T (2017) Effect of photoperiod and fertilization on shoot and fine root growth in Picea abies seedlings. Silva Fenn 51:1–12

Folk RS, Grossnickle SC (2000) Stock-type patterns of phosphorus uptake, retranslocation, net photosynthesis and morphological development in interior spruce seedlings. New For 19:27–49. https://doi.org/10.1023/A:1006618312161

Forde BG (2014) Nitrogen signalling pathways shaping root system architecture: an update. Curr Opin Plant Biol 21:30–36. https://doi.org/10.1016/j.pbi.2014.06.004

Forde BG, Lorenzo H (2001) The nutritional control of root development. Plant Soil 232:51–68. https://doi.org/10.1023/A:1010329902165

Friend AL, Eide MR, Hinckley TM (1990) Nitrogen stress alters root proliferation in Douglas-fir seedlings. Can J For Res 20:1524–1529. https://doi.org/10.1139/x90-202

Fujita S, Noguchi K, Tange T (2020) Root responses of five Japanese afforestation species to waterlogging. Forests 11:1–12. https://doi.org/10.3390/f11050552

Fujita S, Noguchi K, Tange T (2021) Different waterlogging depths affect spatial distribution of fine root growth for pinus thunbergii seedlings. Front Plant Sci 12:1–10. https://doi.org/10.3389/fpls.2021.614764

Graves WR, Aiello AS (1997) High root-zone temperature causes similar changes in water relations and growth of silver maples from 33° and 44°N latitude. J Am Soc Hortic Sci 122:195–199

Greer DH, Wunsche JN, Norling CL, Wiggins HN (2006) Root-zone temperatures affect phenology of bud break, flower cluster development, shoot extension growth and gas exchange of "Braeburn" (Malus domestica) apple trees. Tree Physiol 26:105–111. https://doi.org/10.1093/treephys/26.1.105

Grossnickle SC (2005) Importance of root growth in overcoming planting stress. New For 30:273–294. https://doi.org/10.1007/s11056-004-8303-2

Grossnickle SC (2012) Why seedlings survive: influence of plant attributes. New For 43:711–738. https://doi.org/10.1007/s11056-012-9336-6

Grossnickle SC, El-Kassaby YA (2016) Bareroot versus container stocktypes: a performance comparison. New For 47:1–51. https://doi.org/10.1007/s11056-015-9476-6

Grossnickle SC, MacDonald JE (2018) Seedling quality: history, application, and plant attributes. Forests 9:1–23. https://doi.org/10.3390/F9050283

Grossnickle SC, Arnott JT, Major JE, Tschaplinski TJ (1991) Influence of dormancy induction treatments on western hemlock seedlings. I. seedling development and stock quality assessment. Can J For Res 21:164–174. https://doi.org/10.1139/x91-020

Guarnaschelli AB, Lemcoff JH, Prystupa P, Basci SO (2003) Responses to drought preconditioning in Eucalyptus globulus Labill. provenances. Trees - Struct Funct 17:501–509. https://doi.org/10.1007/s00468-003-0264-0

Haase D, Rose R (1993) Soil moisture stress induces transplant shock in stored and unstored 2+ 0 Douglas-fir seedlings of varying root volumes. For Sci 39:275–294

Halter R, Sands R, Ashton DH, Nambiar EKS (1997) Root growth of subalpine and montane Eucalyptus seedlings at low soil temperatures. Trees 12:35. https://doi.org/10.1007/s004680050119

Hawkins CDB, Shewan KB (2000) Frost hardiness, height, and dormancy of 15 short-day, nursery-treated interior spruce seed lots. Can J For Res 30:1096–1105. https://doi.org/10.1139/x00-055

Hawkins CDB, Eastham AM, Story TL et al (1996) The effect of nursery blackout application on Sitka spruce seedlings. Can J For Res 26:2201–2213. https://doi.org/10.1139/x26-249

Hawkins BJ, Robbins S, Porter RB (2014) Nitrogen uptake over entire root systems of tree seedlings. Tree Physiol 34:334–342. https://doi.org/10.1093/treephys/tpu005

Hayhoe, K., D. J. Wuebbles, D. R. Easterling, D. W. Fahey, S. Doherty, J. Kossin, W. Sweet, R. Vose, and M. Wehner (2018). Our changing climate. In *Impacts, risks, and adaptation in the United States: Fourth national climate assessment*, ed. D. R. Reidmiller, C.

Helgerson OT (1990) Heat damage in tree seedlings and its prevention. New For 3:333–358. https://doi.org/10.1007/BF00030044

Hernández EI, Vilagrosa A, Luis VC et al (2009) Root hydraulic conductance, gas exchange and leaf water potential in seedlings of Pistacia lentiscus L. and Quercus suber L. grown under different fertilization and light regimes. Environ Exp Bot 67:269–276. https://doi.org/10.1016/j.envexpbot.2009.07.004

Ho MD, Rosas JC, Brown KM, Lynch JP (2005) Root architectural tradeoffs for water and phosphorus acquisition. Funct Plant Biol 32:737. https://doi.org/10.1071/FP05043

Hodge A, Berta G, Doussan C et al (2009) Plant root growth, architecture and function. Plant Soil 321:153–187. https://doi.org/10.1007/s11104-009-9929-9

Hutchings MJ, de Kroon H (1994) Foraging in plants: the role of morphological plasticity in resource acquisition. In: Advances in Ecological Research. pp 159–238

Iivonen S, Rikala R, Ryyppö A, Vapaavuori E (1999) Responses of Scots pine (Pinus sylvestris) seedlings grown in different nutrient regimes to changing root zone temperature in spring. Tree Physiol 19:951–958. https://doi.org/10.1093/treephys/19.14.951

Immel MJ, Rumsey RL, Carpenter SB (1978) Comparative growth responses of northern red oak and chestnut oak seedlings to varying photoperiods. For Sci 24:554–560

Jacobs DF, Timmer VR (2005) Fertilizer-induced changes in rhizosphere electrical conductivity: relation to forest tree seedling root system growth and function. New For 30:147–166. https://doi.org/10.1007/s11056-005-6572-z

Jacobs DF, Rose R, Haase DL, Alzugaray PO (2004) Fertilization at planting impairs root system development and drought avoidance of Douglas-fir (Pseudotsuga menziesii) seedlings. Ann For Sci 61:643–651. https://doi.org/10.1051/forest:2004065

Jacobs DF, Davis AS, Wilson BC et al (2008) Short-day treatment alters Douglas-fir seedling dehardening and transplant root proliferation at varying rhizosphere temperatures. Can J For Res 38:1526–1535. https://doi.org/10.1139/X08-020

Jiang L, Dumroese RK, Liu Y et al (2019) Short-day treatment affects growth, physiological parameters and needle proteome of Chinese pine (Pinus tabuliformis Carr.) seedlings. New For 50:469–488. https://doi.org/10.1007/s11056-018-9671-3

Juvany M, Müller M, Munné-Bosch S (2013) Photo-oxidative stress in emerging and senescing leaves: a mirror image. J Exp Bot 64:3087–3098. https://doi.org/10.1093/jxb/ert174

Khan SR, Rose R, Haase DL, Sabin TE (1996) Soil water stress: Its effects on phenology, physiology, and morphology of containerized Douglas-fir seedlings. New For 12:19–39. https://doi.org/10.1007/BF00029980

King JS, Pregitzer KS, Zak DR (1999) Clonal variation in above- and below-ground growth responses of populus tremuloides Michaux: influence of soil warming and nutrient availability. Plant Soil 217:119–130. https://doi.org/10.1023/a:1004560311563

Koevoets IT, Venema JH, Elzenga JTM, Testerink C (2016) Roots withstanding their environment: exploiting root system architecture responses to abiotic stress to improve crop tolerance. Front Plant Sci 7:1–19. https://doi.org/10.3389/fpls.2016.01335

Kostopoulou P, Radoglou K, Dini-Papanastasi O (2011) Performance and quality of Cupressus sempervirens L. mini-plug seedlings under reduced photoperiod. Eur J For Res 130:579–588. https://doi.org/10.1007/s10342-010-0447-3

Kramer-Walter KR, Laughlin DC (2017) Root nutrient concentration and biomass allocation are more plastic than morphological traits in response to nutrient limitation. Plant Soil 416:539–550. https://doi.org/10.1007/s11104-017-3234-9

Kramer-Walter KR, Bellingham PJ, Millar TR et al (2016) Root traits are multidimensional: specific root length is independent from root tissue density and the plant economic spectrum. J Ecol 104:1299–1310. https://doi.org/10.1111/1365-2745.12562

Krasowski MJ, Owens JN (1991) Growth and morphology of western red cedar seedlings as affected by photoperiod and moisture stress. Can J For Res 21:340–352. https://doi.org/10.1139/x91-042

Kummerow J, Ellis BA (1984) Temperature effect on biomass production and root/shoot biomass ratios in two arctic sedges under controlled environmental conditions. Can J Bot 62:2150–2153. https://doi.org/10.1139/b84-294

Lahti M, Aphalo PJ, Finer L et al (2005) Effects of soil temperature on shoot and root growth and nutrient uptake of 5-year-old Norway spruce seedlings. Tree Physiol 25:115–122. https://doi.org/10.1093/treephys/25.1.115

Lambers H, Chapin FS, Pons L (2008) Plant Physiological Ecology. Springer, II

Landhäusser SM, Wein RW, Lange P (1996) Gas exchange and growth of three arctic tree-line tree species under different soil temperature and drought preconditioning regimes. Can J Bot 74:686–693. https://doi.org/10.1139/b96-087

Landhäusser SM, DesRochers A, Lieffers VJ (2001) A comparison of growth and physiology in picea glauca and populus tremuloides at different soil temperatures. Can J For Res 31:1922–1929. https://doi.org/10.1139/cjfr-31-11-1922

Landhäusser SM, Pinno BD, Lieffers VJ, Chow PS (2012) Partitioning of carbon allocation to reserves or growth determines future performance of aspen seedlings. For Ecol Manage 275:43–51. https://doi.org/10.1016/j.foreco.2012.03.010

Landis TD, Tinus RW, Barnett JP (1998) Seedling propagation. In: The Container Tree Nursery Manual. USDA Forest Service, Washington, DC, p 166

Larigauderie A, Reynolds JF, Strain BR (1994) Root response to CO2 enrichment and nitrogen supply in loblolly pine. Plant Soil 165:21–32. https://doi.org/10.1007/BF00009959

Lee RB, Ratcliffe RG, Southon TE (1990) 31P NMR measurements of the cytoplasmic and vacuolar Pi con- tent of mature maize roots: relationships with phosphorus status and phosphate fluxes. J Exp Bot 41:1063–1078

Li GL, Zhu Y, Liu Y et al (2013) Effect of nursery nitrogen application of bare-root Larix olgensis seedlings on growth, nitrogen uptake and initial field performance. J Environ Biol 34:79–85

Li W, Jin C, Guan D et al (2015) The effects of simulated nitrogen deposition on plant root traits: a meta-analysis. Soil Biol Biochem 82:112–118. https://doi.org/10.1016/j.soilbio.2015.01.001

López-Bucio J, Cruz-Ramírez A, Herrera-Estrella L (2003) The role of nutrient availability in regulating root architecture. Curr Opin Plant Biol 6:280–287

Lopushinsky W, Max TA (1990) Effect of soil temperature on root and shoot growth and on budburst timing in conifer seedling transplants. New For 4:107–124. https://doi.org/10.1007/BF00119004

Luis VC, Puértolas J, Climent J et al (2009) Nursery fertilization enhances survival and physiological status in Canary Island pine (Pinus canariensis) seedlings planted in a semiarid environment. Eur J For Res 128:221–229. https://doi.org/10.1007/s10342-009-0257-7

Luis VC, Llorca M, Chirino E et al (2010) Differences in morphology, gas exchange and root hydraulic conductance before planting in Pinus canariensis seedlings growing under different fertilization and light regimes. Trees 24:1143–1150. https://doi.org/10.1007/s00468-010-0490-1

Luoranen J, Helenius P, Huttunen L, Rikala R (2007) Short-day treatment enhances root egress of summer-planted Picea abies seedlings under dry conditions. Scand J For Res 22:384–389. https://doi.org/10.1080/02827580701551382

Luxmoore RJ, Cunningham M, Mann LK, Tjoelker MG (1993) Urea fertilization effects on nutrient uptake and growth of Platanus occidentalis during plantation establishment. Trees 7:250–257. https://doi.org/10.1007/BF00202082

Lynch JP (1995) Root architecture and plant productivity. Plant Physiol 109:7–13. https://doi.org/10.1104/pp.109.1.7

Lyr H (1996) Effect of the root temperature on growth parameters of various European tree species. Ann Des Sci For 53:317–323. https://doi.org/10.1051/forest:19960214

Lyr H, Garbe V (1995) Influence of root temperature on growth of Pinus sylvestris, Fagus sylvatica, Tilia cordata and Quercus robur. Trees 9:220–223. https://doi.org/10.1007/BF00195276

MacDonald JE, Owens JN (2006) Morphology, physiology, survival, and field performance of containerized coastal Douglas fir seedlings given different dormancy-induction regimes. HortScience 41:1416–1420

Mackie-Dawson LA, Millard P, Proe MF (1995) The effect of nitrogen supply on root growth and development in sycamore and Sitka spruce trees. Forestry 68:107–114. https://doi.org/10.1093/forestry/68.2.107

Madsen P (1994) Growth and survival of fagus sylvatica seedlings in relation to light intensity and soil water content. Scand J For Res 9:316–322. https://doi.org/10.1080/02827589409382846

Malamy JE (2005) Intrinsic and environmental response pathways that regulate root system architecture. Plant, Cell Environ 28:67–77. https://doi.org/10.1111/j.1365-3040.2005.01306.x

Martínez-Garza C, Tobon W, Campo J, Howe HF (2011) Drought mortality of tree seedlings in an eroded tropical pasture. L Degrad Dev 24:287–295. https://doi.org/10.1002/ldr.1127

McAdam SAM, Brodribb TJ, Ross JJ (2016) Shoot-derived abscisic acid promotes root growth. Plant Cell Environ 39:652–659. https://doi.org/10.1111/pce.12669

Mexal JG, Timmis R, Morris WG (1979) Cold-hardiness of containerized loblolly pine seedlings: its effect on field survival and growth. South J Appl For 3:15–19. https://doi.org/10.1093/sjaf/3.1.15

Mickaël H, Michaël A, Fabrice B et al (2007) Soil detritivore macro-invertebrate assemblages throughout a managed beech rotation. Ann For Sci 64:219–228. https://doi.org/10.1051/forest

Millard P, Grelet G-a (2010) Nitrogen storage and remobilization by trees: ecophysiological relevance in a changing world. Tree Physiol 30:1083–1095. https://doi.org/10.1093/treephys/tpq042

Moler ERV, Nelson AS (2021) Perspectives on drought preconditioning treatments with a case study using western larch. Front Plant Sci 12:1–6. https://doi.org/10.3389/fpls.2021.741027

Moler ERV, Toca A, Jacobs DF, Nelson AS (2022) Root system adaptations represent untapped opportunities forforest tree seedling improvement. New For. https://doi.org/10.1007/s11056-022-09917-x

Nambiar EKS, Bowen GD, Sands R (1979) Root regeneration and plant water status of Pinus radiata D. Don seedlings transplanted to different soil temperatures. J Exp Bot 30:1119–1131. https://doi.org/10.1093/jxb/30.6.1119

Nicodemus MA, Salifu FK, Jacobs DF (2008) Growth, nutrition, and photosynthetic response of black walnut to varying nitrogen sources and rates. J Plant Nutr 31:1917–1936. https://doi.org/10.1080/01904160802402856

Niinemets Ü, Kull O, Tenhunen JD (1998) An analysis of light effects on foliar morphology, physiology, and light interception in temperate deciduous woody species of contrasting shade tolerance. Tree Physiol 18:681–696. https://doi.org/10.1093/treephys/18.10.681

Oliet JA, Planelles R, Artero F, Jacobs DF (2005) Nursery fertilization and tree shelters affect long-term field response of Acacia salicina Lindl. planted in Mediterranean semiarid conditions. For Ecol Manage 215:339–351. https://doi.org/10.1016/j.foreco.2005.05.024

Oliet J, a., Planelles R, Artero F, et al (2009) Field performance of Pinus halepensis planted in Mediterranean arid conditions: relative influence of seedling morphology and mineral nutrition. New For 37:313–331. https://doi.org/10.1007/s11056-008-9126-3

Oliet JA, Puértolas J, Planelles R, Jacobs DF (2013) Nutrient loading of forest tree seedlings to promote stress resistance and field performance: a Mediterranean perspective. New For 44:649–669. https://doi.org/10.1007/s11056-013-9382-8

Ostonen I, Püttsepp Ü, Biel C et al (2007) Specific root length as an indicator of environmental change. Plant Biosyst Int J Deal All Asp Plant Biol 141:426–442. https://doi.org/10.1080/11263500701626069

Ouzts J, Kolb T, Huffman D, Sánchez Meador A (2015) Post-fire ponderosa pine regeneration with and without planting in Arizona and New Mexico. For Ecol Manage 354:281–290. https://doi.org/10.1016/j.foreco.2015.06.001

Overdieck D, Ziche D, Bottcher-Jungclaus K (2007) Temperature responses of growth and wood anatomy in European beech saplings grown in different carbon dioxide concentrations. Tree Physiol 27:261–268. https://doi.org/10.1093/treephys/27.2.261

Padilla FM, Pugnaire FI (2007) Rooting depth and soil moisture control Mediterranean woody seedling survival during drought. Funct Ecol 21:489–495. https://doi.org/10.1111/j.1365-2435.2007.01267.x

Padilla FM, Miranda JDD, Pugnaire FI (2007) Early root growth plasticity in seedlings of three Mediterranean woody species. Plant Soil 296:103–113. https://doi.org/10.1007/s11104-007-9294-5

Peng YY, Dang QL (2003) Effects of soil temperature on biomass production and allocation in seedlings of four boreal tree species. For Ecol Manage 180:1–9. https://doi.org/10.1016/S0378-1127(02)00486-3

Péret B, Clément M, Nussaume L, Desnos T (2011) Root developmental adaptation to phosphate starvation: Better safe than sorry. Trends Plant Sci 16:442–450. https://doi.org/10.1016/j.tplants.2011.05.006

Péret B, Desnos T, Jost R et al (2014) Root architecture responses: in search of phosphate. Plant Physiol 166:1713–1723. https://doi.org/10.1104/pp.114.244541

Pinno BD, Wilson SD (2013) Fine root response to soil resource heterogeneity differs between grassland and forest. Plant Ecol 214:821–829. https://doi.org/10.1007/s11258-013-0210-1

Poorter H, Niklas KJ, Reich PB et al (2011) Biomass allocation to leaves, stems and roots: meta-analysis of interspecific variation and environmental control. New Phytol 193:30–50. https://doi.org/10.1111/j.1469-8137.2011.03952.x

Poorter H, Bühler J, van Dusschoten D et al (2012) Pot size matters: a meta-analysis of the effects of rooting volume on plant growth. Funct Plant Biol 39:839. https://doi.org/10.1071/FP12049

Popko J, Hänsch R, Mendel RR et al (2010) The role of abscisic acid and auxin in the response of poplar to abiotic stress. Plant Biol 12:242–258. https://doi.org/10.1111/j.1438-8677.2009.00305.x

Pregitzer KS, Hendrick RL, Fogel R (1993) The demography of fine roots in response to patches of water and nitrogen. New Phytol 125:575–580. https://doi.org/10.1111/j.1469-8137.1993.tb03905.x

Pregitzer KS, King JS, Burton AJ, Brown SE (2000) Responses of tree fine roots to temperature. New Phytol 147:105–115. https://doi.org/10.1046/j.1469-8137.2000.00689.x

Pritzkow C, Szota C, Williamson V, Arndt SK (2021) Previous drought exposure leads to greater drought resistance in eucalypts through changes in morphology rather than physiology. Tree Physiol. https://doi.org/10.1093/treephys/tpaa176

Proe MF, Millard P (1994) Relationships between nutrient supply, nitrogen partitioning and growth in young Sitka spruce (Picea sitchensis). Tree Physiol 14:75–88. https://doi.org/10.1093/treephys/14.1.75

Proe MF, Millard P (1995) Effect of P supply upon seasonal growth and internal cycling of P in Sitka spruce (Picea sitchensis(Bong.)Carr.) seedlings. Plant Soil 168–169:313–317. https://doi.org/10.1007/BF00029343

Puértolas J, Gil L, Pardos JA (2003) Effects of nutritional status and seedling size on field performance of Pinus halepensis planted on former arable land in the Mediterranean basin. Forestry 76:159–168. https://doi.org/10.1093/forestry/76.2.159

Puértolas J, Benito LF, Peñuelas JL (2009) Effects of nursery shading on seedling quality and post-planting performance in two Mediterranean species with contrasting shade tolerance. New For 38:295–308. https://doi.org/10.1007/s11056-009-9148-5

Pulido F, García E, Obrador JJ, Moreno G (2010) Multiple pathways for tree regeneration in anthropogenic savannas: incorporating biotic and abiotic drivers into management schemes. J Appl Ecol 47:1272–1281. https://doi.org/10.1111/j.1365-2664.2010.01865.x

Reich PB, Tjoelker MG, Walters MB et al (1998a) Close association of RGR, leaf and root morphology, seed mass and shade tolerance in seedlings of nine boreal tree species grown in high and low light. Funct Ecol 12:327–338. https://doi.org/10.1046/j.1365-2435.1998.00208.x

Reich PB, Walters MB, Tjoelker MG et al (1998b) Photosynthesis and respiration rates depend on leaf and root morphology and nitrogen concentration in nine boreal tree species differing in relative growth rate. Funct Ecol 12:395–405. https://doi.org/10.1046/j.1365-2435.1998.00209.x

Repo T, Launiainen S, Lehto T et al (2016) The responses of Scots pine seedlings to waterlogging during the growing season. Can J For Res 46:1439–1450. https://doi.org/10.1139/cjfr-2015-0447

Repo T, Heiskanen J, Sutinen M-L et al (2017) The responses of Scots pine seedlings to waterlogging in a fine-textured till soil. New for 48:51–65. https://doi.org/10.1007/s11056-016-9555-3

Rewald B, Ephrath JE, Rachmilevitch S (2011) A root is a root is a root? water uptake rates of Citrus root orders. Plant, Cell Environ 34:33–42. https://doi.org/10.1111/j.1365-3040.2010.02223.x

Royo A, Gil L, Pardos JA (2001) Effect of water stress conditioning on morphology, physiology and field performance of Pinus halepensis Mill. seedlings. New For 21:127–140. https://doi.org/10.1023/A:1011892732084

Rüdinger M, Hallgren SW, Steudle E, Schulze E-D (1994) Hydraulic and osmotic properties of spruce roots. J Exp Bot 45:1413–1425. https://doi.org/10.1093/jxb/45.10.1413

Ryyppo A, Iivonen S, Rikala R et al (1998) Responses of Scots pine seedlings to low root zone temperature in spring. Physiol Plant 102:503–512. https://doi.org/10.1034/j.1399-3054.1998.1020404.x

Sáenz-Romero C, Mendoza-Maya E, Gómez-Pineda E et al (2020) Recent evidence of Mexican temperate forest decline and the need for ex situ conservation, assisted migration, and translocation of species ensembles as adaptive management to face projected climatic change impacts in a megadiverse country. Can J For Res 50:843–854. https://doi.org/10.1139/cjfr-2019-0329

Salifu KF, Timmer VR (2001) Nutrient retranslocation response of picea mariana seedlings to nitrogen supply. Soil Sci Soc Am J 65:905–913. https://doi.org/10.2136/sssaj2001.653905x

Salifu KF, Apostol KG, Jacobs DF, Islam MA (2008) Growth, physiology, and nutrient retranslocation in nitrogen-15 fertilized Quercus rubra seedlings. Ann For Sci 65:101–101. https://doi.org/10.1051/forest:2007073

Salifu KF, Jacobs DF, Birge ZKD (2009) Nursery nitrogen loading improves field performance of bareroot oak seedlings planted on abandoned mine lands. Restor Ecol 17:339–349. https://doi.org/10.1111/j.1526-100X.2008.00373.x

Sands R, Fiscus E, Reid C (1982) Hydraulic properties of pine and bean roots with varying degrees of suberization, vascular differentiation and mycorrhizal infection. Aust J Plant Physiol 9:559. https://doi.org/10.1071/PP9820559

Sanz Pérez V, Castro Díez P, Valladares F (2007) Growth versus storage: responses of Mediterranean oak seedlings to changes in nutrient and water availabilities. Ann For Sci 64:201–210. https://doi.org/10.1051/forest:2006104

Sardans J, Peñuelas J, Rodà F (2006) Plasticity of leaf morphological traits, leaf nutrient content, and water capture in the Mediterranean evergreen oak Quercus ilex subsp. ballota in response to fertilization and changes in competitive conditions. Ecoscience 13:258–270. https://doi.org/10.2980/i1195-6860-13-2-258.1

Sayer MAS, Brissette JC, Barnett JP (2005) Root growth and hydraulic conductivity of southern pine seedlings in response to soil temperature and water availability after planting. New For 30:253–272. https://doi.org/10.1007/s11056-005-7481-x

Schlichting CD, Pigliucci M (1995) Lost in phenotypic space: environment-dependent morphology in phlox drummondii (Polemoniaceae). Int J Plant Sci 156:542–546. https://doi.org/10.1086/297277

Schmull M, Thomas FM, Göttingen U et al (2000) Morphological and physiological reactions of young deciduous trees (Quercus robur L, Q. petraea [Matt.] Liebl Fagus sylvatica L.) to waterlogging. Plant Soil. https://doi.org/10.1023/A:1026516027096

Schulze E-D, Mooney HA, Sala OE et al (1996) Rooting depth, water availability, and vegetation cover along an aridity gradient in Patagonia. Oecologia 108:503–511. https://doi.org/10.1007/BF00333727

Schulze E-D, Müller-Hohenstein K, Beck E (2005) Plant Ecology, 1st edn. Springer, Berlin

Seabra CEBC, Osiecka A, Tucci CAF et al (2018) Influence of phosphorus limitations on the growth, nutrient partitioning and physiology of mahogany (Swietenia macrophylla King) seedlings. J Plant Nutr 41:358–370. https://doi.org/10.1080/01904167.2017.1385803

Seager R, Ting M, Held I et al (2007) Model projections of an imminent transition to a more arid climate in southwestern North America. Science 80(316):1181–1184. https://doi.org/10.1126/science.1139601

Sheridan RA, Davis AS (2021) Characterizing the utility of the root-to-shoot ratio in Douglas-fir seedling production. Forests 12:1745. https://doi.org/10.3390/f12121745

Shi W, Grossnickle SC, Li G et al (2019) Fertilization and irrigation regimes influence on seedling attributes and field performance of Pinus tabuliformis Carr. Forestry 92:97–107. https://doi.org/10.1093/forestry/cpy035

Sloan JL, Burney OT, Pinto JR (2020) Drought-conditioning of quaking aspen (Populus tremuloides Michx.) seedlings during nursery production modifies seedling anatomy and physiology. Front Plant Sci 11:1–11. https://doi.org/10.3389/fpls.2020.557894

Stewart JD, Zine El Abidine A, Bernier PY (1995) Stomatal and mesophyll limitations of photosynthesis in black spruce seedlings during multiple cycles of drought. Tree Physiol 15:57–64. https://doi.org/10.1093/treephys/15.1.57

Štraus I, Mrak T, Ferlan M et al (2015) Influence of soil temperature on growth traits of European beech seedlings. Can J for Res 251:246–251. https://doi.org/10.1139/cjfr-2014-0332

Timmer VR (1997) Exponential nutrient loading: a new fertilization technique to improve seedling performance on competitive sites. New For 13:279–299. https://doi.org/10.1023/A:1006502830067

Timmer VR, Aidelbaum AS (1996) Manual for exponential nutrient loading of seedlings to improve outplanting performance on competitive forest sites. Canadian Forest Service Publications. NODA/NFP Tech Rep TR-25 1–21

Toca A, Oliet JA, Villar-Salvador P et al (2018) Species ecology determines the role of nitrogen nutrition in the frost tolerance of pine seedlings. Tree Physiol 38:96–108. https://doi.org/10.1093/treephys/tpx165

Toca A, Oliet JA, Villar-Salvador P et al (2019) Ecologically distinct pine species show differential root development after outplanting in response to nursery nutrient cultivation. For Ecol Manage 451:117562. https://doi.org/10.1016/j.foreco.2019.117562

Toca A, Villar-Salvador P, Oliet JA, Jacobs DF (2020) Normalization criteria determine the interpretation of nitrogen effects on the root hydraulics of pine seedlings. Tree Physiol 40:1381–1391. https://doi.org/10.1093/treephys/tpaa068

Torreano SJ, Morris LA (1998) Loblolly pine root growth and distribution under water stress. Soil Sci Soc Am J 62:818. https://doi.org/10.2136/sssaj1998.03615995006200030040x

Trubat R, Cortina J, Vilagrosa A (2006) Plant morphology and root hydraulics are altered by nutrient deficiency in Pistacia lentiscus (L.). Trees 20:334–339. https://doi.org/10.1007/s00468-005-0045-z

Trubat R, Cortina J, Vilagrosa A (2008) Short-term nitrogen deprivation increases field performance in nursery seedlings of Mediterranean woody species. J Arid Environ 72:879–890. https://doi.org/10.1016/j.jaridenv.2007.11.005

Trubat R, Cortina J, Vilagrosa A (2011) Nutrient deprivation improves field performance of woody seedlings in a degraded semi-arid shrubland. Ecol Eng 37:1164–1173. https://doi.org/10.1016/j.ecoleng.2011.02.015

Trubat R, Cortina J, Vilagrosa A (2012) Root architecture and hydraulic conductance in nutrient deprived Pistacia lentiscus L. seedlings. Oecologia 170:899–908. https://doi.org/10.1007/s00442-012-2380-2

Tryon PR, Chapin FS III (1983) Temperature control over root growth and root biomass in taiga forest trees. Can J for Res 13(5):827–833

Turner J, Mitchell SJ (2003) The effect of short day treatments on containerized Douglas-fir morphology, physiology and phenology. New for 26:279–295. https://doi.org/10.1023/A:1024406704381

Tyree MT, Velez V, Dalling JW (1998) Growth dynamics of root and shoot hydraulic conductance in seedlings of five neotropical tree species: scaling to show possible adaptation to differing light regimes. Oecologia 114:293. https://doi.org/10.1007/s004420050450

Uscola M, Salifu KF, Oliet JA, Jacobs DF (2015a) An exponential fertilization dose–response model to promote restoration of the Mediterranean oak Quercus ilex. New For 46:795–812. https://doi.org/10.1007/s11056-015-9493-5

Uscola M, Villar-Salvador P, Gross P, Maillard P (2015b) Fast growth involves high dependence on stored resources in seedlings of Mediterranean evergreen trees. Ann Bot 115:1001–1013. https://doi.org/10.1093/aob/mcv019

Valio IFM (2001) Effects of shading and removal of plant parts on growth of Trema micrantha seedlings. Tree Physiol 21:65–70. https://doi.org/10.1093/treephys/21.1.65

Valladares F, Sánchez-Gómez D (2006) Ecophysiological traits associated with drought in mediterranean tree seedlings: individual responses versus interspecific trends in eleven species. Plant Biol 8:688–697. https://doi.org/10.1055/s-2006-924107

Valladares F, Martinez-Ferri E, Balaguer L et al (2000) Low leaf-level response to light and nutrients in Mediterranean evergreen oaks: a conservative resource-use strategy? New Phytol 148:79–91. https://doi.org/10.1046/j.1469-8137.2000.00737.x

Valladares F, Balaguer L, Martinez-Ferri E et al (2002) Plasticity, instability and canalization: is the phenotypic variation in seedlings of sclerophyll oaks consistent with the environmental unpredictability of Mediterranean ecosystems? New Phytol 156:457–467. https://doi.org/10.1046/j.1469-8137.2002.00525.x

van den Driessche R (1980) Effects of nitrogen and phosphorus fertilization on Douglas-fir nursery growth and survival after outplanting. Can J For Res 10:65–70. https://doi.org/10.1139/x80-011

van den Driessche R (1985) Late-season fertilization, mineral nutrient reserves, and retranslocation in planted douglas-fir (Pseudotsuga Menziesii (Mirb.) Franco) seedlings. For Sci 31(2):485–496. https://doi.org/10.1093/forestscience/31.2.485

van den Driessche R (1992) Changes in drought resistance and root growth capacity of container seedlings in response to nursery drought, nitrogen, and potassium treatments. Can J For Res 22:740–749. https://doi.org/10.1139/x92-100

van Hees A (1997) Growth and morphology of pedunculate oak (Quercus robur L.) and beech (Fagus sylvatica L.) seedlings in relation to shading and drought. Ann Des Sci for 54:9–18. https://doi.org/10.1051/forest:19970102

Van Noordwijk M, Martikainen P, Bottner P et al (1998) Global change and root function. Glob Chang Biol 4:759–772. https://doi.org/10.1046/j.1365-2486.1998.00192.x

Vapaavuori EM, Rikala R, Ryyppo A (1992) Effects of root temperature on growth and photosynthesis in conifer seedlings during shoot elongation. Tree Physiol 10:217–230. https://doi.org/10.1093/treephys/10.3.217

Vilagrosa A, Cortina J, Gil-Pelegrin E, Bellot J (2003) Suitability of drought-preconditioning techniques in Mediterranean climate. Restor Ecol 11:208–216. https://doi.org/10.1046/j.1526-100X.2003.00172.x

Villar-Salvador P, Ocaña L, Peñuelas J, Carrasco I (1999) Effect of water stress conditioning on the water relations, root growth capacity, and the nitrogen and non-structural carbohydrate concentration of Pinus halepensis Mill. (Aleppo pine) seedlings. Ann For Sci 56:459–465. https://doi.org/10.1051/forest:19990602

Villar-Salvador P, Planelles R, Enríquez E, Peñuelas Rubira J, (2004a) Nursery cultivation regimes, plant functional attributes, and field performance relationships in the Mediterranean oak Quercus ilex L. For Ecol Manage 196:257–266. https://doi.org/10.1016/j.foreco.2004.02.061

Villar-Salvador P, Planelles R, Oliet J et al (2004b) Drought tolerance and transplanting performance of holm oak (Quercus ilex) seedlings after drought hardening in the nursery. Tree Physiol 24:1147–1155. https://doi.org/10.1093/treephys/24.10.1147

Villar-Salvador P, Puértolas J, Cuesta B et al (2012) Increase in size and nitrogen concentration enhances seedling survival in Mediterranean plantations. Insights from an ecophysiological conceptual model of plant survival. New For 43:755–770. https://doi.org/10.1007/s11056-012-9328-6

Villar-Salvador P, Penuelas JL, Jacobs DF (2013) Nitrogen nutrition and drought hardening exert opposite effects on the stress tolerance of Pinus pinea L. seedlings. Tree Physiol 33:221–232. https://doi.org/10.1093/treephys/tps133

Villar-Salvador P, Uscola M, Jacobs DF (2015) The role of stored carbohydrates and nitrogen in the growth and stress tolerance of planted forest trees. New For 46:813–839. https://doi.org/10.1007/s11056-015-9499-z

Walch-Liu P, Ivanov II, Filleur S et al (2006) Nitrogen regulation of root branching. Ann Bot 97:875–881. https://doi.org/10.1093/aob/mcj601

Wallin E, Gräns D, Jacobs DF et al (2017) Short-day photoperiods affect expression of genes related to dormancy and freezing tolerance in Norway spruce seedlings. Ann For Sci 74:59. https://doi.org/10.1007/s13595-017-0655-9

Wan X, Landhäusser SM, Zwiazek JJ, Lieffers VJ (1999) Root water flow and growth of aspen (Populus tremuloides) at low root temperatures. Tree Physiol 19:879–884. https://doi.org/10.1093/treephys/19.13.879

Wan S, Norby RJ, Pregitzer KS et al (2004) CO_2 enrichment and warming of the atmosphere enhance both productivity and mortality of maple tree fine roots. New Phytol 162:437–446. https://doi.org/10.1111/j.1469-8137.2004.01034.x

Wang G, Fahey TJ, Xue S, Liu F (2013) Root morphology and architecture respond to N addition in Pinus tabuliformis, west China. Oecologia 171:583–590. https://doi.org/10.1007/s00442-012-2441-6

Wang G, Liu F, Xue S (2017) Nitrogen addition enhanced water uptake by affecting fine root morphology and coarse root anatomy of Chinese pine seedlings. Plant Soil 418:177–189. https://doi.org/10.1007/s11104-017-3283-0

Wang W, Wang Y, Hoch G et al (2018) Linkage of root morphology to anatomy with increasing nitrogen availability in six temperate tree species. Plant Soil 425:189–200. https://doi.org/10.1007/s11104-018-3563-3

Welander N, Ottosson B (1998) The influence of shading on growth and morphology in seedlings of Quercus robur L. and Fagus sylvatica L. For Ecol Manage 107:117–126. https://doi.org/10.1016/S0378-1127(97)00326-5

Wells CE, Eissenstat DM (2002) Beyond the roots of young seedlings: the influence of age and order on fine root physiology. J Plant Growth Regul 21:324–334. https://doi.org/10.1007/s00344-003-0011-1

Wertin TM, McGuire MA, Teskey RO, Tissue D (2011) Higher growth temperatures decreased net carbon assimilation and biomass accumulation of northern red oak seedlings near the southern limit of the species range. Tree Physiol 31:1277–1288. https://doi.org/10.1093/treephys/tpr091

Williamson LC, Ribrioux SPCP, Fitter AH, Ottoline Leyser HM (2001) Phosphate availability regulates root system architecture in Arabidopsis. Plant Physiol 126:875–882. https://doi.org/10.1104/pp.126.2.875

Wu C, Wei X, Sun H-L, Wang Z-Q (2005) Phosphate availability alters lateral root anatomy and root architecture of fraxinus mandshurica rupr seedlings. J Integr Plant Biol 47:292–301. https://doi.org/10.1111/j.1744-7909.2005.00021.x

York LM, Nord EA, Lynch JP (2013) Integration of root phenes for soil resource acquisition. Front Plant Sci 4:1–16. https://doi.org/10.3389/fpls.2013.00355

Zhang H, Jennings A, Barlow PW, Forde BG (1999) Dual pathways for regulation of root branching by nitrate. Proc Natl Acad Sci 96:6529–6534. https://doi.org/10.1073/pnas.96.11.6529

Zhang H, Li W, Adams HD et al (2018) Responses of woody plant functional traits to nitrogen addition: a meta-analysis of leaf economics, gas exchange, and hydraulic traits. Front Plant Sci 9:1–10. https://doi.org/10.3389/fpls.2018.00683

Zhou Y, Tang J, Melillo JM et al (2011) Root standing crop and chemistry after six years of soil warming in a temperate forest. Tree Physiol 31:707–717. https://doi.org/10.1093/treephys/tpr066

Zohner CM, Renner SS (2015) Perception of photoperiod in individual buds of mature trees regulates leaf-out. New Phytol 208:1023–1030. https://doi.org/10.1111/nph.13510

Zúñiga-feest A, Bustos-salazar A, Alves F et al (2017) Physiological and morphological responses to permanent and intermittent waterlogging in seedlings of four evergreen trees of temperate swamp forests. Tree Physiol. https://doi.org/10.1093/treephys/tpx023