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INVITED REVIEW

Root system adaptations represent untapped opportunities for forest tree seedling improvement

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Abstract

We reviewed approaches for combining genetic and cultural tools to solve challenges associated with the improvement of tree seedling root systems for enhanced survival and growth. Literature regarding sources of variation in root traits, relationships between root traits and seedling growth and survival, and root trait heritability estimates from published studies were used to illustrate the utility of combining myriad approaches to enhance the efficiency of tree seedling improvement programs. We found that: (1) evidence exists for genetic variation in numerous root traits, (2) root traits tend to have intermediate heritability on average, and (3) evidence supports the possibility of harnessing maternal effects to modify root traits at least temporarily. Across eight root traits from 11 studies, median family narrow-sense heritability estimates (h^2) were intermediate ($0.25 \leq h^2 \leq 0.50$) for root diameter, root count, root biomass, the ratio of root-to-stem dry biomass, and projected root area, and low ($h^2 < 0.25$) for root length, specific root length, and the ratio of total belowground-to-aboveground dry biomass. Findings from this review suggest that plant improvement pipelines can be optimized to harness root trait variation due to genetics, maternal effects, and nursery cultural regimes. However, the following related gaps in the literature emerged as fundamental obstacles to progress: What is the duration of root system responses to stress conditioning treatments? Which root traits correlate best with seedling survival and thus should be prioritized for improvement? Is it possible to reliably harness variation in root traits resulting from maternal effects?

Keywords Heritability estimates · Evolution · Genecology · Juvenile traits · Plant improvement · Survival

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Introduction

Challenges to forest regeneration globally

Declines in natural forest regeneration have been documented across the globe (Allen et al. 2010; Jakovac et al. 2015; Martínez-Ramos et al. 2016; Phillips et al. 2016; Kueppers et al. 2017; Ramírez-Valiente and Cavender-Bares 2017; Breshears et al. 2018; Petersson et al. 2019; Sáenz-Romero et al. 2020). Related shifts in ecosystem resilience are leading to landcover change across large expanses of Mediterranean shrublands (Lloret et al. 2009), North American and East Asian subalpine systems (McCaffrey and Hopkinson 2020; Xu et al. 2020), and forests across the southwestern USA (Minott and Kolb 2020), Mexico (Sáenz-Romero et al. 2020), and the Amazon basin (Silva et al. 2021). The trend of diminishing seedling establishment is expected to have major negative economic and ecological repercussions (Johnson and Yeakley 2019; Minott and Kolb 2020), yet the demand for tree seedlings capable of weathering the drying climate for reforestation and restoration remains unmet (Fargione et al. 2021). The greatest immediate challenge to tree seedling establishment following outplanting is insufficient uptake of soil-borne resources by roots, particularly water (Vyse 1981; Hau and Corlett 2003; Matzner et al. 2003; Alvarez-Aquino et al. 2004; Castro et al. 2004; Grossnickle 2005; Palma and Laurance 2015; Harvey et al. 2016; Sánchez-Romera and Aroca 2020), and strategic combinations of genetic and cultural approaches may facilitate the enhancement of belowground plant traits.

Artificial forest regeneration via planted tree seedlings has been used since at least the early nineteenth century to compensate for insufficient rates of natural forest regeneration (Huss 2004). Planting seedlings rather than relying on natural regeneration processes provides a way for land managers to modify forest species diversity, density, and genetics, but there is also an increasing risk of failed establishment of artificially regenerated forests as the climate warms (Sukhbaatar et al. 2020; Lucas-Borja et al. 2021). With increasing interest in how best to enhance the resistance and resilience of both managed and unmanaged ecosystems to undesirable landcover change (Nagel et al. 2017), and growing awareness of the importance of innovative evolutionary thinking in forestry (Lefèvre et al. 2014; Vivas et al. 2020), the time is ripe for considering untapped evolutionary opportunities that may facilitate the efficient production of climate-hardy tree seedlings.

Untapped opportunities and underexplored considerations in tree seedling improvement

Tree improvement is traditionally conducted through iterative selection of and controlled breeding among genotypes that exhibit traits expected to yield desirable aboveground characteristics at maturity (White 1987; Wheeler et al. 2015; Schreiber and Thomas 2017). However, there is growing recognition that plant traits are influenced not only by parental genetics, but also by parental environments independent of genotype and progeny environments early in development (Vivas et al. 2013, 2021; Cendán et al. 2013; Carneros et al. 2017; Sow et al. 2018; Amaral et al. 2020). This recognition suggests that genetic (as opposed to cultural) approaches to tree improvement thus implicitly selects not only for genotypes but also for gene-by-environment interactions in response to past and present environmental conditions (Herman et al. 2012; Wang et al. 2016; Zheng et al. 2017). Elucidation of the malleability and potential heritability of traits with an epigenetic basis (i.e.

altered gene expression independent of DNA mutations) has illustrated the mechanisms that underlie approaches to plant improvement based on the conditions to which plants are exposed (Moler et al. 2019; Springer and Schmitz 2017). For example, recent work has demonstrated that plant abiotic and biotic stress tolerance can be enhanced by developing genetic lines with a history of exposure of one (Fig. 1) or multiple (Fig. 2) generations to stress conditions, and this is broadly referred to as *stress memory* (Bräutigam et al. 2013; Walter et al. 2013; Crisp et al. 2016; Wibowo et al. 2016; Gonzalez et al. 2016; Carneros et al. 2017; Godwin and Farrona 2020).

Leveraging the biology of stress memories for plant conditioning (e.g. controlled exposure of parental tissue to increased temperatures to improve subsequent progeny performance under elevated thermal regimes; Yakovlev et al. 2012) appears to represent an approach to tree improvement with great potential. Research in the field of plant conditioning has, however, largely focused on mature developmental stages of agronomic species, and there is a need for clarification of the relevance of the technology to the seedling stage of tree species. Additionally, similar to improvement work focused on traits of mature plants, the improvement of tree seedling traits is achievable through genetic selection and nursery cultural regimes (Clarke and McCaig 1993; Paez-Garcia et al. 2015; Fromm 2019). But evidence suggests that the full potential of tree improvement will remain untapped until researchers leverage phenotypic variation arising from genetics, cultural regimes, and carryover effects of ancestral environments (maternal effects). Specifically, deliberate combinations of genetic and cultural tree improvement techniques hold potential for increasing the success of seedling improvement efforts if effects of cultural regimes vary appreciably across seedling genetics or maternal effects (Vivas et al. 2013, 2020; Kuijper and Hoyle 2015).

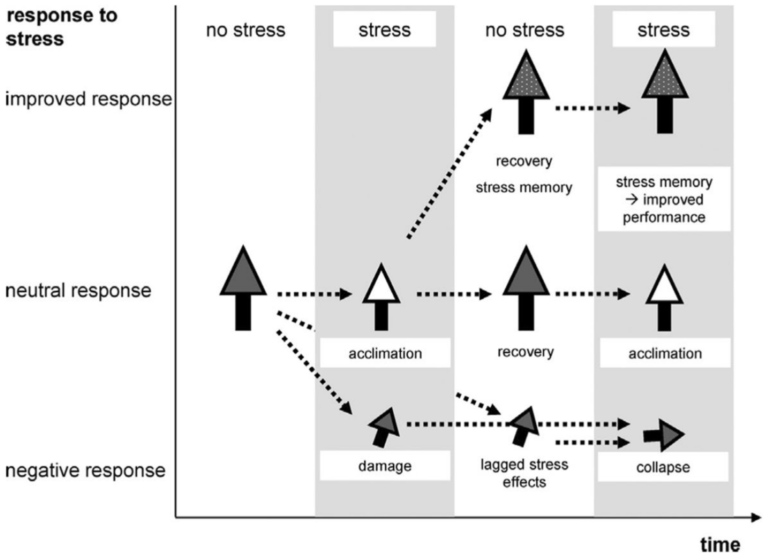

Fig. 1 Plant stress responses under an individual stress event or successive stress events with and without acclimation or an improved response (i.e. stress memory). As shown here, acclimation may aid the prevention of stress damage and recovery (albeit with corresponding depression of plant growth during a stress event). Used with permission from Walter et al. (2013)

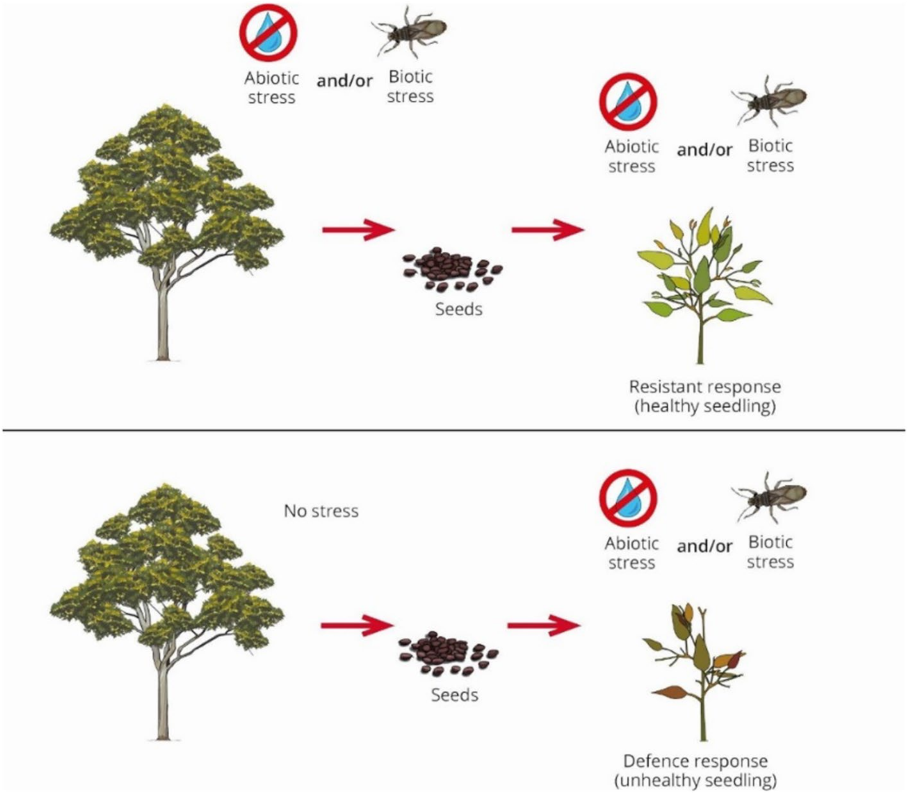

Fig. 2 Exposure of earlier generations to stress may shape subsequent progeny responses to stress exposure. Used with permission from Vivas et al. (2020)

Seedling improvement with a focus on root systems

Root system improvement is of major interest as an approach for developing plants capable of coping with the warming climate (Comas et al. 2013; Lynch 2015; Lochhead et al. 2019; Sloan et al. 2020). This follows from the fact that drought-adapted root system architecture (i.e. the spatial distribution and configuration of root systems in soil, root depth, and the opportunistic growth of plant roots to exploit soil-borne resources) are essential for tree seedling establishment (Padilla and Pugnaire 2007). Critical foundations laid for advancing root system improvement, albeit mostly concerning crop species, include precise descriptions and terminology concerning root system development (Lynch 2015), and advances in high-throughput root system imaging tools (Halter and Chanway 1993; de Dorlodot et al. 2007; Gerth et al. 2021). But it remains unknown whether seedling root system improvement may be best achieved by application of nursery cultural regimes designed to manipulate root systems of optimal genotypes or lineages with a specific pattern of stress history.

Because trees are long-lived organisms and root growth is highly responsive to the environment, improvement of tree seedling root systems implies selection for ephemeral traits rather than final yield, where the latter is the aim of most plant improvement work. Selection for short-lived traits entails unique considerations, such as how long root trait modifications can persist relative to how long they need to persist to have the intended effect. Thoughtful assessment of these considerations is necessary to guide best practices for evaluating the relevance of a root improvement program in order to enhance forest seedling establishment. Progress in root system improvement in forest tree species is further complicated by the following two obstacles: (1) there is a lack of consensus regarding which root traits correlate best with seedling survival and thus should be a target for improvement (Gravel-Grenier et al. 2011; Koevoets et al. 2016; Palta and Turner 2019), and (2) it remains unknown how best to manipulate root traits to develop seedlings with improved drought performance (Clarke and McCaig 1993).

Obstacles to progress in tree root system improvement

Obstacle 1: Which root system traits are most likely to confer increased seedling survival?

This section briefly reviews the challenges associated with selecting a root trait or suite of traits through which to enhance seedling survival. For further reading on this topic, we refer readers to reviews that elaborate on tree seedling survival as a function of root systems (Grossnickle 2005; Grossnickle and MacDonald 2018). In water-limited conditions, seedling survival depends strongly upon the extension of new roots into soil reservoirs of plant-available water (Carlson 1986; Bernier et al. 1995). But even in water-limited environments, where relationships between plant traits and survival might seem most predictable, patterns opposite of investigators' expectations have been found for carbon partitioning between roots and shoots and among compartments of root systems in the same species across precipitation gradients (Rundel and Nobel 1991; Meier et al. 2018). Furthermore, in a study of correlations between seedling survival and electrolyte leakage of fine roots, root moisture content, and root water potential after exposure to controlled desiccation, (Radoglou and Raftoyannis 2001) found different strengths (but the same direction) of correlation for sycamore maple (*Acer pseudoplatanus*), sweet chestnut (*Castanea sativa*), and South European flowering ash (*Fraxinus ornus*). Their findings suggest that the relevance of these measures of root system vitality for seedling survival can be expected to vary by species.

Root growth potential (RGP) is a measure of the ability to initiate and elongate new roots in an optimal environment within a defined period of time (Simpson and Ritchie 1997). The measure integrates the status of seedling dormancy, nutrition, moisture, and carbohydrate contents (Davis and Jacobs 2005), and some evidence exists for its utility in predicting plant hydraulic conductivity and survival during seedling establishment (Carlson 1986; McKay and Morgan 2001), but see the multi-species critical review by Binder et al. (1988), who concluded that RGP is a poor predictor of field performance. The utility of RGP as a predictor of seedling survival wanes under conditions that limit plant growth in the field, especially low soil temperature (Binder et al. 1988; Campo et al. 2007; Folk and Grossnickle 1997; Ritchie and Dunlap 1980; Simpson and Ritchie 1997). The overwhelming dependence of root growth on field conditions renders RGP mostly useful as a pre-planting indicator of plant physiological dysfunction (Simpson and Ritchie 1997).

The relevance of *root volume* and *root mass* to post-planting seedling survival tends to vary by species and thus must be used with caution. For instance, a study of root volume and performance of ponderosa pine (*Pinus ponderosa*) seedlings found that survival increased with root volume (Rose et al. 1997). In the same study, however, root volume did not correlate to survival for Douglas-fir (*Pseudotsuga menziesii*). Similarly, in a study of morphological predictors of seedling field performance using five Mediterranean tree species, Tsakaldimi et al. (2013) found that root volume correlated positively with seedling survival for Aleppo pine (*Pinus halapensis*) and the evergreen shrub *Pistacia lentiscus* with significant Pearson correlation coefficients of 0.56 and 0.90, respectively. Root volume correlated positively with hydraulic conductivity in *P. taeda*, where seedlings with root volumes of 1 mL produced a mean of 30 new roots and had a mean hydraulic conductivity of 8.9 mg/min at the end of a 28-day potted study, whereas seedlings with root volumes of 3.5 mL produced 58 new roots and had a hydraulic conductivity of 18.6 mg/min, which likely resulted from improved absorption related to a greater abundance of new unsuberized root tissue (Carlson 1986). Tsakaldimi et al. (2005) found that increased root system volume and mass, but not root surface area or length, were associated with higher survival of two species of oak (*Q. ilex* and *Q. coccifera*) both one- and two-years post-planting.

Total root length and *root surface area* were also significant predictors of *P. halapensis* seedling survival with Pearson correlation coefficients of $r = 0.62$ and $r = 0.55$, respectively (Tsakaldimi et al. 2013). But in a study of three-year-old *Acer* spp., *Q. rubra*, and *Prunus serotina* seedlings, structural biomass allocation to roots was no longer a significant predictor of seedling survival when investigators accounted for the extent of carbohydrates stored in roots (Canham et al. 1999). The Canham et al. (1999) study notes that carbohydrate reserves were, however, positively correlated with seedling survival. The findings of Canham et al. (1999) suggest that models lacking key predictor variables (e.g. root carbohydrate contents) may overestimate the importance of autocorrelated traits for seedling survival.

Root system *fibrosity*, which is usually used to describe the proportion of root systems composed of lateral roots, root tips, and root branchiness (Wilson et al. 2007), is often found to relate positively to seedling performance (see review in Davis and Jacobs 2005). But unfortunately, the measure of fibrosity is not precisely defined, and its calculation is not strictly standardized, which complicates generalizations of the utility of fibrosity as a predictor of seedling performance (Davis and Jacobs 2005). A related methodological shortcoming concerns the fact that measures of total root system volume and biomass fail to differentiate taproots from lateral roots, which may account for the species-dependent utility of these measures as predictors of postplanting performance.

Chiatante et al. (2002) demonstrated that the relevance of root traits for predicting seedling survival varies with seedling age. Specifically, in a study of indicators of survival potential for Austrian pine (*P. nigra*; Chiatante et al. 2002), total root length remained a relatively strong predictor of survival in both first- and second-year post-planting assessments ($r = 0.88$, and $r = 0.73$, respectively). Meanwhile, root electrolyte leakage was a strong predictor of second-year survival ($r = -0.91$), but not first-year survival ($r = 0.28$). In the same study, the predictive value of RGP and number of root tips for seedling survival declined from $r = 0.95$ and $r = 0.86$ in first-year assessments to $r = 0.37$ and $r = 0.52$ in second-year assessments, respectively.

In sum, experimental conditions, analytical methodology, and seedling age can be expected to influence the conclusions of studies designed to identify root system traits that are most relevant to seedling performance and survival. Additionally, identifying optimal root system traits for improvement requires consideration of variation in ecological strategies among species and among ecotypes within species, and projected conditions at outplanting sites (Grossnickle 2018). When possible, we recommend selecting root traits previously shown to correlate strongly to seedling survival for the species under study, or, if applicable, closely related species or species with similar ecological strategies.

Obstacle 2: What is the best approach for manipulating root traits to develop seedlings with improved drought performance?

The challenges associated with the second major obstacle we identified regarding the improvement of forest tree seedling root systems differ markedly from those associated with the improvement of agronomic crop species, particularly with respect to the soil environment and longevity of trees compared to annual crop plants. The physical characteristics of forest soils and terrain on which seedlings are planted are typically highly heterogeneous and far less intensively managed than crop soils. The greater homogeneity of tilled crop soils may render high phenotypic plasticity (i.e. an environmentally dependent phenotypic trait; Price et al. 2003; Schlichting and Wund 2014) a nuisance to breeders rather than a potentially useful source of trait variation, as crop breeders can more readily predict where water and nutrients are likely to occur in a well-managed agricultural field (but see Schneider and Lynch 2020).

An important idiosyncrasy of root system improvement for forest tree seedlings alluded to earlier concerns the discrepancy between the long life cycles of trees and the relatively short period of time when trees are young, during which root improvement efforts are likely to pay off due to the elevated vulnerability of seedlings to drought stress (Harper 1977; Clarke 2002; Duboscq-Carra et al. 2018; Luo et al. 2021). Evidence suggests that abiotic stress conditioning in tree seedlings, such as that achieved intentionally through stress hardening regimes (Fig. 1), or inadvertently via maternal effects (Fig. 2), may induce desirable temporary shifts in seedling growth or physiology through a stress-memory (sensu Chenard and Duckworth 2021). It may in fact be desirable for some inducible traits, such as increased root-to-shoot biomass ratio, to fade rather than persist after enhancing seedling establishment. How best to harness adaptive ephemeral phenotypic plasticity during an early developmental stage of a long-lived species is a research frontier that remains to be explored to expedite seedling root system improvement through a combination of cultural regimes, genetic selection, and control of the lineage stress history.

Genecological studies have revealed variation in seedling drought tolerance across provenances and genetic families (Bingham and Simard 2013; Barton et al. 2020; Bucholz et al. 2020). For example, Wang et al. (2015) found that provenances of white birch (*Betula platyphylla*) varied strongly in the extent of carbon concentrated in fine roots and in ratios of carbon partitioning between foliage, bole wood and bark, and fine roots. And using a rhizotron assay, Racette et al. (2019) found significant variation in root system architecture and vigor of belowground growth of peanut plants based on genotype and whether parental plants were exposed to drought. The study of Racette et al. (2019) constitutes one of the few clear examples of maternal effects influencing variation in root systems.

Current approaches to tree seedling root system improvement include nursery-based cultural techniques and genetic and genome-based selection that consider genecological patterns, but these two approaches have most often been conducted in isolation by different groups of experts rather than simultaneously and collaboratively. As depicted in Fig. 1, stress conditioning may include numerous cultural techniques that induce physiological or morphological plant characteristics that aid survival under future stressful conditions. Nursery-based cultural techniques designed to enhance seedling root systems, such as undercutting and wrenching (Rook 1971), air- and chemical-pruning of roots (Krasowski

2003; Tsakaldimi and Ganatsas 2006; Marler and Musser 2016), nutrient manipulations (Tan and Hogan 1997), and drought preconditioning by limiting water availability during seedling development (Sloan et al. 2020; Moler and Nelson 2021), have been employed to improve outplanting performance of economically and ecologically important tree species (Valliere et al. 2019; Grossnickle et al. 2020). And genome-wide association studies and other high-throughput genome-based lineage screening tools show promise for accelerating root system improvement in tree seedlings (Cobb et al. 2013; Cortés et al. 2020). For example, Jia et al. (2019) studied root system depth, root spreading angle, seminal root number, total seminal root length, and average seminal root length of spring barley and identified 55 quantitative trait loci that cumulatively explained approximately 12% of the variance in seminal root number and 48% of the variance in root system depth. Tree seedling root trait improvement may also soon be accelerated through the exploitation of maternal effects by selecting genetic material from parental environments expected to promote desirable influences on progeny phenotypes (Fig. 2). But despite extensive published work on the biology and potential applications of maternal effects in plant science, researchers have yet to articulate a robust framework for incorporating maternal effects in plant improvement (Roach and Wulff 1987; Kuijper and Hoyle 2015; Singh et al. 2017; Vivas et al. 2021).

The responsiveness of plant root traits to multiple genetic mechanisms and cultural techniques warrants exploration of the viability of combining various genetic and cultural approaches for tree root system improvement. Because phenotypic variation is the raw material by which plant populations navigate disturbance, and by which plant improvement researchers cultivate desirable traits (Ying and Yanchuk 2006; Vitt et al. 2010; Breed et al. 2013; Sork et al. 2013; Carroll et al. 2014), we now present a brief overview of the various sources of phenotypic variation, followed by a set of considerations to aid expeditious research into tree seedling root trait improvement.

Sources of root phenotypic variation

Roots of many higher plants are likely to simultaneously express both fixed and plastic qualities of quantitative traits, such as gravitropism and altered lateral root branching, respectively, to facilitate effective exploration of temporally variable physical and chemical soil conditions (Nihlgård 1971; Harper et al. 1991). Advantages could arise from the expression of increased trait plasticity during specific developmental periods when the high metabolic cost of belowground growth does not hinder critical aboveground traits such as vertical growth, leafing out, or biotic defenses. Fuchigami et al. (1982) provided a conceptual model for predicting plant phenology across dormancy and growth periods, but so far there appears to be a lack of empirical research on the ontogenetic basis of phenotypic plasticity. Intraspecific trait diversity that arises from trait plasticity can facilitate acclimation and adaptation to new or altered environments by increasing species' potential niche breadth and stress tolerance (Reusch et al. 2005; Gehring et al. 2014; Levis and Pfennig 2016). And phenotypic diversity, in turn, may arise from new or standing genetic variation (Barrett and Schluter 2008), patterns of non-genetic yet heritable mechanisms of phenotypic variation such as transposable elements and epigenomic patterns (Rando and Verstrepen 2007; Whipple and Holeski 2016), and phenotypic plasticity (Nicotra et al. 2010). Further, mechanisms responsible for enhanced phenotypic diversity are often interactive. For example, the epigenome consists of numerous environmentally and developmentally responsive molecular mechanisms that influence access of proteins to chromatin and thereby promote variable phenotypic expression (Moler et al. 2019).

Phenotypic plasticity may also buffer populations against novel environmental conditions if plasticity improves organismal tolerance of disturbance (West-Eberhard 2005). As phenotypic plasticity is considered evolutionarily expensive, however, its effect on populations, and whether it evolves in a population, strongly depends upon the conditions a population routinely encounters (Price et al. 2003). Plastic traits tend to arise mostly in heterogeneous environments where there is a lack of consistent natural selection for one optimal suite of traits (Kuijper and Hoyle 2015). Thus, increased phenotypic plasticity should increase the likelihood that at least some phenotypes yield high fitness despite a variable environment. Increasingly, trait plasticity is gaining attention as a mechanism by which populations may adapt to environmental change more rapidly than via changes in allele frequencies within populations (Nicotra et al. 2010; Bräutigam et al. 2013). And in the context of cultural approaches to plant improvement, a genetic line that responds favorably to imposed environmental stress, such as by growing longer roots in response to drought conditioning, may be highly desirable for trait improvement on the basis of expressed adaptive plasticity (Schneider and Lynch 2020).

Maternal effects enable short-term storage of recent information that is relevant to the survival of progeny, such as phenotypic responses that have proved useful in past generations and may represent carryover effects of parental environments and status on progeny performance through seed provisioning, hormones, nutrients, antibodies, small RNAs, or induced epigenomic patterns that influence gene expression (Kuijper and Hoyle 2015; Hilker et al. 2016). Maternal effects are unlikely to evolve where weak correlations exist between parental and progeny growth environments (Kuijper and Hoyle 2015). And it is important to consider that if a stress response results in a reduction instead of an increase in phenotypic plasticity, measures of plasticity will likely only be of use in predicting plant performance in the testing environment (Oleksiak and Crawford 2012); and see Valladares et al. (2002). Recent studies investigating maternal effects show that epigenetic changes affecting gene expression play a major role in stress response and adaptation in plants (Grativol et al. 2012; Yakovlev et al. 2012; Sahu et al. 2013; Kinoshita and Seki 2014; Avramova et al. 2017). Herman et al. (2012) discuss interactions between maternal effects and phenotypic plasticity of a progeny generation, which may result in the following patterns: (1) *adaptive matching* (e.g. exposing F_0 plants to stressful environmental conditions results in F_1 plants that express a genotype-dependent phenotype that would confer a selective advantage in the F_0 environment, regardless of the environment in which the F_1 plants occur), (2) *maladaptive* (e.g. exposing F_0 plants to stressful environmental conditions results in genotype-dependent F_1 plant phenotypes that perform more poorly in all environments), and (3) *preparatory* (e.g. exposing F_0 plants to stressful environmental conditions results in F_1 plants that express a genotype-dependent phenotype that confers a selective advantage *if* F_1 plants are exposed to a stress that is related to the stress imposed on the F_0 generation). If researchers can induce either preparatory or adaptive matching phenotypic patterns, it may be beneficial to operationalize maternal effects for plant improvement.

Detecting maternal effects is not straightforward, however, and will not be apparent without explicit experimental testing, as depicted in Fig. 2. Specifically, seeds must be collected from genetic families or clones from contrasting environments (left side of Fig. 2), and the performance of progeny from each maternal environment must then be evaluated in a common garden (right side of Fig. 2; Zas et al. 2013; Cendán et al. 2013; Vivas et al. 2020). Using a similar study system, Zas et al. (2013) showed that clonally propagated Maritime pine (*Pinus pinaster*) from an orchard occupying a favorable microsite produced seeds of greater mass and seedlings with increased root:shoot mass than genetic replicates occupying a harsh site. Differences in seedling phenotype were attributable to seed mass (Zas et al. 2013), but in a related study, seed mass did not explain differences in seed germination success or phenology in seeds sourced from the two orchards (Cendán et al. 2013). In addition to the challenges of detecting maternal effects, it remains poorly known how long maternal effects persist.

Operationalizing evolutionary considerations of seedling trait improvement

Whether root trait improvement programs should invest in controlling for genetics and stress history of seed sources, or can confidently disregard natural sources of trait variation and focus on single-generation cultural improvements, depends upon whether targeted traits exhibit patterns of heritability and maternal effects. Improvement programs incorporating knowledge of lineage genetics and stress history inevitably require greater investment of resources than unigenerational (cultural regime) approaches, and for some species, such as *Populus tremuloides* Michx., investment in multigenerational improvement appears unlikely to pay off (Sloan et al. 2020). But if incorporation of genetics or stress history into seedling root trait improvement programs is expected to aid improvement in a study system, pairing genotypes most amenable to improvement with appropriate cultural regimes is likely to maximize return on investment in research and development (Vivas et al. 2020). In this section, we pose three questions that investigators should explore to make an informed decision on how best to conduct plant improvement concerning root system traits of a novel species. We ask and answer the following three questions:

1. Is there evidence for genetic variation in root system traits?
2. Is there evidence for heritability of tree seedling root system traits?
3. Is there evidence for the influence of maternal effects on root system traits?

Traits that could be good candidates for root system improvement via artificial selection at the genetic or provenance level should exhibit [genetic] variation for the trait, and the trait must be heritable, as articulated by Darwin (1859) with respect to the requirements for natural selection to occur. Additionally, if traits vary due to environmental conditions of the parental generation independently of genotype, it may be advantageous to control for lineage stress history (e.g. seed source climate, edaphic features, and pest or pathogen exposure; Vivas et al. 2020). What follows is a review of evidence for each phenomenon (genetic variation, heritability, and maternal effects) to illustrate the relevance of each to root system traits of tree species.

Is there evidence for genetic variation in root system traits?

There is ample evidence for genetic variation for root system traits, and it has most often been detected across environmental clines. If species are known to or can be shown to exhibit trait variation among populations due to environmental clines, it may be possible to use knowledge of climatic variation across the species' range to expedite the improvement of target traits by focusing improvement efforts on provenances most likely to express traits of interest. For instance, improvement approaches that couple the strengths described in

Figs. 1 and 2 may be facilitated by identifying genetic material that is amenable to modification using cultural regimes.

Within and among tree populations, genetic lineages often express trait variation, which may or may not reflect varying degrees of adaptation to environmental conditions. This genetic source of trait variation facilitates evolution by natural selection as well as artificial selection. Genetic variation for root traits has been found to track environmental gradients among and within provenances. For example, among cuttings of hemlock (*Tsuga heterophylla*) taken from four source trees at different locations around the city of Seaside, OR, USA, Foster et al. (1984) reported significant variation in five root system traits, including: (1) count of rooted cuttings per five-cutting plot, (2) count of main roots, (3) count of quadrants of the cutting base with roots, (4) length of the longest main root, and (5) the sum of main root lengths. Salmela et al. (2020) measured 21 functional traits of Norway spruce (*Picea abies*) seedling root systems originating from 15 open-pollinated families from a natural stand in southern Finland. They found that the principal components describing total root length, specific root length, and the proportion of lateral roots varied significantly with genetic family, whereas two principal components (branching intensity and main root length) did not. Furthermore, they found that all traits expressed plasticity with respect to soil temperature and across three soil types, including arable soil, soil from local spruce stands, and soil from a mixed forest type. Genetic diversity for phenotypic plasticity was identified as changes in the ranking of genetic family with highest branching intensity across seedling soil environments, which was shown to result from a significant interaction between soil environment and genetic family (Salmela et al. 2020). This result illustrates that not only is branching intensity modifiable by cultural techniques, but furthermore, trait *modifiability* is amenable to genetic selection.

Seed source conditions can serve as indicators of desirable genetic resources because genetic variation for root traits is often found among provenances spanning environmental gradients (Teich and Holst 1974; Hamann et al. 2000; Rehfeldt et al. 2001; Turner et al. 2010; Rehfeldt 2014; Borgman et al. 2015; Benomar et al. 2016; Rúa et al. 2016; Yeaman et al. 2016; Boheemen et al. 2019). For instance, a study of white spruce (*Picea glauca*) seedlings from seed source trees growing on soils derived from limestone versus granitic parent materials reported that seedlings grew ~ 10% taller when grown in soil conditions in which their parents occurred than when they were planted in foreign soils (Teich and Holst 1974). Intraspecific variation was observed for fine root traits (< 2 mm diameter) of plants from the families Proteaceae, Ericaceae, Myrtaceae, Fabaceae, Restionaceae, Poaceae and Cyperaceae across a natural hydrologic gradient based on percent soil organic matter (Taseski et al. 2020). Across most families, plants were found to vary intraspecifically across the hydrologic gradient such that soil organic matter was negatively correlated with root dry matter content and tissue density, and positively correlated with root branching intensity and specific root length. A study of white spruce seedlings sourced from an orchard representing 17 provenances spanning 2° 15′ latitude and 6° 24′ longitude in eastern Canada found significant variation in root mass across genetic families during root initiation and two subsequent growing seasons (Gravel-Grenier et al. 2011). Interestingly, the authors reported low correlations of root mass measured between the root initiation stage and growing seasons, suggesting different underlying genetic mechanisms controlling root production in each growth stage. In contrast, a coupled in situ and common garden study of fine root anatomy, biomass allocation, and mycorrhizae in Scots pine (*Pinus sylvestris*) from across a 2000 km latitudinal gradient found that root traits varied significantly with mean annual temperature among provenances and with an aridity index within provenances (Zadworny et al. 2016). The authors found that for colder provenances studied in-situ and in common gardens, a larger proportion of fine-root biomass was allocated to absorptive versus transport roots. An average of 34% of fine-root biomass at the warmest sites was characterized by absorptive roots, and this percentage increased to 61% at the coldest and most northern sites. This relationship was expected to relate to the relatively shorter window of time during which trees in colder versus warmer regions can absorb soil resources, and was more apparent in the common garden experiment ($R^2 = 0.81$, $P < 0.05$) than in the *in-situ* study ($R^2 = 0.39$, $P < 0.05$).

Root growth potential was greater in southern provenances than northern provenances of nursery-grown eastern white pine (*Pinus strobus*; Johnsen 1988), and this coincided with seedling size, which was greater for southern versus northern seed sources. Container grown full- and mixed-sib genetic families of Norway spruce differing in rate of aboveground growth were harvested after 16 months of growth to investigate whether root systems of fast-growing families differed from those of slow-growing families (Hamberg et al. 2018). Fast-growing families were found to produce root systems with approximately 30% more root tips and branching points relative to slow-growing families, and this trend did not coincide with differences in seedling height or biomass, which suggests that genetic variation in biomass allocation influences the rate of root production in *P. abies*.

Finally, a growing body of literature suggests that plant genotype influences belowground symbiotic associations that may confer superior performance under drought (Gehring et al. 2017; de la Fuente Cantó et al. 2020). For instance, co-occurring seed sources of piñon pine (*Pinus edulis*) in northern Arizona (USA) were found to differ markedly in drought tolerance related to mycorrhizal fungal colonization patterns (Gehring et al. 2017). More than 60% of the drought-tolerant genotypes, characterized by roots heavily colonized by fungi in the genus *Geopora*, survived an extreme drought that killed approximately 80% of the piñon trees representing genotypes with root systems that are more dominated by fungi in the genus *Rhizopogon* (Sthultz et al. 2009; Gehring et al. 2014, 2017).

Is there evidence for heritability of tree seedling root system traits?

Heritability estimates associated with eight root traits summarized across 11 studies of woody species is shown below (Fig. 3). Further details of those 11 studies plus an additional six not included in Fig. 3, comprising 18 categories of root traits in total, are provided in Supplementary Table S1. Together, these 17 studies represented all published peer-reviewed articles we could find that clearly described calculations of heritability estimates of woody plant root traits (exclusive of studies of plant–microbe symbioses). Authors of these 17 studies variably included heritability estimates based on individuals, genetic families, provenances, or all three. Family narrow-sense heritability (h^2) was reported more frequently in the literature than broad-sense heritability (H^2), h^2 on an individual basis, and h^2 on a provenance basis. Thus, only family h^2 values are presented for comparison in Fig. 3. All four types of heritability estimates and associated details from the 17 studies summarized in this section are provided in Table S1.

It is beyond the scope of this paper to describe in detail the studies from which heritability estimates were gathered, though the estimates were undoubtedly influenced by their respective experimental conditions and the genetic diversity of the populations from which samples were drawn (Acquaah 2017). Nonetheless, comparisons of h^2 among traits and species provide useful insights into how various study systems may respond to improvement because the potential rate of adaptation to novel conditions and trait responses to artificial selection are expected to be proportional to h^2 (i.e. the extent to which phenotypic

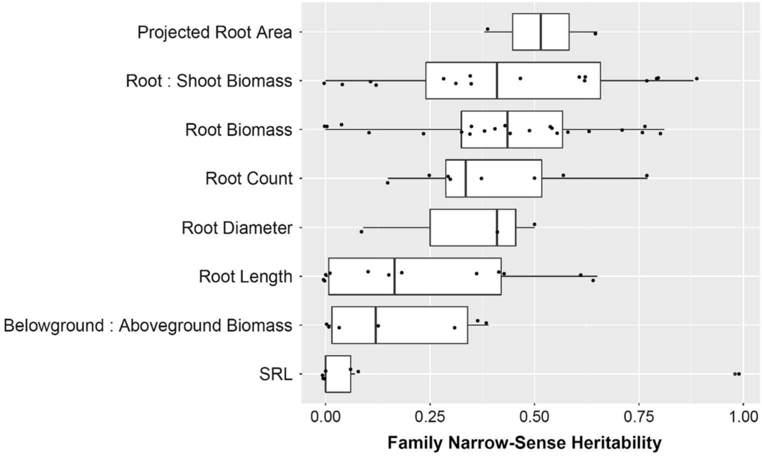

Fig. 3 Family narrow-sense heritability estimates from 11 studies representing 8 trait types. Each filled black circle represents a mean heritability estimate gathered from the literature. Metadata and references related to each mean heritability estimate are shown in Supplementary Materials Table S1, which also includes individual narrow-sense, provenance narrow-sense, and broad-sense heritability estimates not shown in this figure. SRL = specific root length. Root: Shoot Biomass is a ratio between dry root biomass and dry stem biomass without foliage, whereas Belowground: Aboveground Biomass is the ratio between total dry root biomass and total dry aboveground biomass

variation may be inherited; Bairos-Novak et al. 2021). Heritability estimates are considered low, intermediate, and high (i.e. likely to be inherited by progeny) with h^2 or H^2 values < 0.25, from 0.25 to 0.50, or > 0.5, respectively (Bennett et al. 2014; Bairos-Novak et al. 2021). We note that the magnitude of the mean of H^2 values shown in Table S1 is nearly two-fold that of h^2 values (i.e. 0.66 versus 0.36), though we acknowledge that the interpretability of comparisons of H^2 and h^2 values shown in Table S1 is limited due to the infrequent presentation of H^2 values in the literature concerning woody plant root traits. This large difference between H^2 and h^2 values indicates that non-additive sources of phenotypic variation in root traits (including dominance and epistatic effects) may strongly influence phenotypic variation of root traits (Falconer and Mackay 1996), and thus h^2 should be favored in assessments of the extent to which genetic selection may aid trait improvement.

Figure 3 and Table S1, reveal a wide range in heritability estimates for root traits. There are no immediately clear trends between heritability values and trait type. Nevertheless, median heritability estimates were intermediate for all traits except root length, specific root length, and the ratio of belowground to aboveground biomass, which were characterized by low median heritability. We caution against overinterpretation of the "high" ($h^2 > 0.50$) median heritability estimate presented for projected root area, as it was calculated from only two data points with mean h^2 values that spanned a range of 0.27 (Table S1). It is unsurprising that we detected a wide range of heritability estimates for the same trait types from different studies due to the influence of population genetic diversity and the experimental environment on heritability estimate calculations (Acquaah 2017). Nevertheless, summaries of trait heritability estimates provide a useful illustration of the extent to which a trait is likely to contribute to population adaptation to novel environmental conditions (Gunay et al. 2011; Bairos-Novak et al. 2021), and the extent to which traits may be improved via artificial selection. For example, highly heritable root traits are likely to be influenced less by nursery cultural regimes and maternal effects arising from parental environments than root traits with low heritability. Accordingly, we offer the following three speculations based on the trends shown in Fig. 3: (1) genetic selection for desirable trait characteristics may indeed be expected to yield progeny with desirable phenotypes, albeit with modest genetic gains, (2) maternal effects may be of notable importance to trait variation and thus enable novel avenues for plant improvement since traits are not strictly controlled by additive genetic variation, and (3) desirable and relatively long-lasting changes in target traits may be achievable using cultural manipulations.

Is there evidence for the influence of maternal effects on root system traits?

There is currently little empirical evidence to guide research into harnessing maternal effects for seedling root system improvement, yet the studies highlighted here suggest that the phenomenon deserves attention in the context of tree seedling research. As noted earlier, unlike in plant improvement research designed to enhance plant traits expressed after the seedling stage (e.g. tree height, seed shatter, fecundity), desirable yet ephemeral improvements of tree seedlings achieved through maternal effects may be appropriate for enhancing seedling establishment.

Potential links between maternal effects and seedling root development remain an underexplored area of research despite recent attention as an untapped source of trait variation that could aid tree improvement efforts (Vivas et al. 2020). Controlled experimental approaches to the study of maternal effects assess the traits or performance of progeny of parental genotypes replicated across multiple sites characterized by varying site conditions at the time of progeny production (Zas et al. 2013; Cendán et al. 2013). Maternal effects in seed-bearing plants are expected to be transmitted in-part through seeds (Donohue 2009; Zas et al. 2013), with larger seeds expected to produce better performing seedlings (Castro 1999). Thus, relating seed characteristics to subsequent plant traits can also illustrate potential maternal effects, provided that genotypes are replicated across maternal environments to enable partitioning of maternal effects from genetic effects (Kanaga et al. 2008). In lieu of replication of genotypes across environments, Borgman et al. (2014) assessed maternal effects on seedling performance of *Pinus flexilis* and *Pinus aristata* by collecting seed from the same maternal trees across multiple years. Maternal effects (i.e. an effect of seed collection year) was significant for seed size and seedling performance, though the influence of maternal effects on root-to-shoot mass ratio was only marginally significant ($p = 0.06$) in *P. flexilis*, and was non-significant in *P. aristata*.

Barnett (1991) described correlations between the proportion of seedcoat accounting for total seed weight and root length of *Pinus ponderosa* seedlings and found an unstable correlation between the two variables where $r = -0.96$ at 2 months of growth, but at nine months of growth $r = -0.31$. Similarly, controlling for maternal genetics in a study of *Pinus sylvestris*, Castro (1999) found a positive correlation between seed size and seedling emergence, and between seed size and shoot growth during the first growing season, but the latter correlation diminished in significance after the first growing season. Seed mass was not significantly correlated to root system mass at any point in time though root system mass varied significantly with maternal genetics (Castro 1999), further illustrating the importance of partitioning maternal genetics from variables that may be strongly correlated with maternal effects. In a study that partitioned maternal genetics from maternal effects by increasing the temperature surrounding developing cones of *Pinus strobiformis*, Moler et al. (2021) found a significant positive influence of maternal effects on seedling root length and root-to-shoot length after the first year of growth, a diminishing influence of maternal effects on root collar diameter between growth years 1–3, and a negligible influence of maternal effects on root-to-shoot mass and root mass after four years of growth in a common garden.

Conclusions and future directions

The following three findings emerged from this review: (1) evidence exists for genetic variation in a wide variety of root traits, (2) root traits tend to have intermediate heritability on average, and (3) evidence supports the possibility of harnessing maternal effects to modify root traits at least temporarily. Based on these trends, we conclude that patterns of root system adaptation, including genetics and maternal effects, offer untapped opportunities for tree seedling improvement. Combining the approaches to seedling improvement depicted in Figs. 1 and 2 will ensure that every opportunity is taken to refine seedling improvement pipelines and ensure that improvements are achieved with minimal expense. And assessment of the viability of various improvement efforts can be aided by considering the extent to which traits are heritable. The multidisciplinary tree seedling improvement approach described here suggests a need for novel collaborations among plant nursery specialists, geneticists, physiologists, and evolutionary biologists to leverage every tool available for accelerating the plant improvement pipeline.

Future investigations can engage this multidisciplinary approach by first deciding a priori the root traits to select for improvement, which, as far as possible, should consider whether the traits are strongly correlated with seedling establishment and the extent to which heritable variation in target traits exists among seed sources. Next, trials should be conducted to establish the best combination of seed sources and cultural regimes to achieve desirable trait values. Where possible, seed sources replicated across contrasting maternal environments, such as seed orchards with varying environmental conditions, should be used to capture potentially beneficial phenotypic variation due to maternal effects. Investigators should simultaneously compare the efficacy of improvement via seed source selection versus improvement via cultural regimes irrespective of seed source even if variation due to seed source does exist. Lastly, outplanting trials must be conducted to investigate links between the target trait(s) and seedling establishment.

Further important considerations include how to ensure retention of genetic diversity among outplanted seedlings, and the need to monitor for undesirable correlations between targeted traits and other traits of interest. For example, the viability of root system improvement will depend on whether selection for desirable root traits positively or negatively influences other important traits (e.g. aboveground plant growth, phenology, cold tolerance, resistance to disease and herbivory, and colonization of roots by beneficial rhizosphere microbes). The extent to which root traits covary with these and other important traits, however, also remains to be explored.

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Declarations

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