

The role of nutrients for improving seedling quality in drylands

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Abstract Forest plantations have been extensively used to combat desertification. In drylands, harsh climate conditions and unfertile soils often preclude seedling establishment. The improvement in seedling quality by manipulating nutrient availability could contribute to increase planting success. However, morpho-functional traits defining optimum seedling quality in drylands, and the fertilization schemes to achieve them, are still under discussion. Several studies suggest that well fertilized seedlings may perform better than nutrient limited seedlings in these environments. However, recent works have shown opposite results. In this review, we discuss the concept of seedling quality in drylands based on an evaluation of the effects of nutrient manipulation on seedling morpho-functional traits and field performance. According to existing data, we hypothesize that nutrient-limited small seedlings may be better adapted to arid environments and unfavorable microsites, where access to water is uncertain and a conservative water use strategy may be advantageous. In contrast, in dry sub-humid areas, areas with deep soils, protected from excess radiation, and areas where irrigation is feasible, well-fertilized big seedlings with high root growth potential may have more chances of success. We discuss this theory in the context of the multiple objectives of dryland restoration and the environmental constraints posed by these areas, and identify knowledge gaps that should be targeted to test our hypothesis.

Keywords Nursery fertilization · Forest plantation · Ecological restoration · Nutrient deficiency · Morpho-functional traits

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Introduction

Drylands cover 41 % of the Earth emerged surface and host 36 % of the global population (Millennium Ecosystem Assessment 2005). Population density is highly heterogeneous in these areas. Similarly, human impact on dryland ecosystems can be very low to extremely high. Semi-arid areas are particularly prone to degradation because of the combination of harsh abiotic conditions and high population density. Indeed, human actions favored the formation of large drylands. The combination of limiting environmental conditions and a long history of human use explain why vast areas of drylands are currently degraded or under high risk of desertification (Dregne and Chou 1992).

For a long time, humans have combated desertification using a wide diversity of approaches and techniques. Among the most common actions to combat desertification is forest plantation (Requier-Desjardins et al. 2009; Oliet and Jacobs 2012), as woody species contribute to ecological restoration and to the provision of a wide variety of ecosystem services (Cortina et al. 2011). The various aims of forest plantations have traditionally driven species selection and plantation techniques. However, this diversity of aims has hardly been considered in seedling production.

Seedling establishment in drylands is strongly limited by abiotic and biotic factors. As in other harsh environments, soon after planting, seedlings must cope with unfavorable conditions compromising their survival and growth. Morpho-functional traits conferring resistance and resilience against stress, and increasing seedling competitive ability, can critically affect the outcomes of plantations (Navarro et al. 2006; del Campo et al. 2010). However, there is a lack of consensus on the traits defining high quality woody seedlings in drylands, which may be related to differences in species strategies, spatial and temporal heterogeneity in soil and climatic conditions, and nursery cultivation techniques.

In this work we first review the concept of seedling quality in drylands, considering the diversity of aims that forest and shrubland establishment have in these areas, and the spatial and temporal variability in environmental conditions characterizing them. Later, we review the ecophysiological basis for nutrient limitation and multiple stresses in drylands, and we present examples on how nutrient management affect seedling morpho-functional traits and field performance. Then, we discuss the importance of seedling quality and nutritional regime in determining plantation success compared to other aspects of nursery production and plantation management. Finally, we propose a conceptual framework relating seedling quality in drylands with the timing and intensity of drought.

Objectives of ecological restoration and seedling quality

Forest plantations have been carried out for a wider variety of purposes, not necessarily related to commercial products (Birch et al. 2010). These include soil protection and improvement, carbon sequestration, and ecological restoration. Such objectives are more prominent in drylands, as in these areas productivity is low, whereas the risk of degradation and the need for recovering damaged, degraded and destroyed areas is high. Woody species contribute to improving ecosystem processes by reducing the kinetic energy of rain drops, building up the litter layer, increasing water infiltration, reducing runoff generation, transferring nutrients from the atmosphere and deep soil horizons to the soil surface, producing edible fruits, storing carbon or modulating climate oscillations (Viles 1988; Rey Benayas et al. 2009; Allen et al. 2010).

The production of high quality woody seedlings has traditionally focused on improving short-term survival and growth in the field. These aspects are particularly relevant in drylands, as economic incomes are frequently low, and plantations are commonly carried out on tight budgets (Requier-Desjardins et al. 2009). In addition, the production of high quality seedlings has prioritized seedling traits that generate high quality wood (e.g., straight unbranched logs and low taper; Jozsa and Middleton 1994). Surprisingly, scarce attention has been given to seedling traits that are related to other features than wood production and quality. For example, the production of high quality seedlings for soil protection should prioritize morpho-functional traits related to lateral canopy expansion, early formation of a litter layer, multiple branching, resprouting ability, surface rooting, plasticity and genetic diversity (Cortina et al. 2006).

In some cases, seedling traits promoting early survival and growth also enhance seedling capacity for ecological engineering (*sensu* Jones et al. 1994). Thus, fast development of a tap root colonizing deep soil horizons may reduce the intensity of competition with neighboring vegetation, facilitating the establishment of other plants (Chirino et al. 2008; Oliet et al. 2012, Vallejo et al. 2012b). Similarly, leaf shedding in drought stressed plants may attenuate stress and reduce the risk of hydraulic failure, while protecting soil from erosion (García Cano et al. 2000). High rates of nitrogen fixation may contribute both to the establishment of N-fixers in N-poor soils and to the increase in soil fertility (Derbel et al. 2009; Jeddi et al. 2009). Finally, high growth capacity may contribute to high resprouting ability. But in other cases, traits associated with early seedling performance are negatively related to soil protection and facilitation. For example, low growth rates and slow canopy deployment may increase seedling ability to withstand stress, but may hamper its ability to facilitate the establishment of other plants by habitat modification (Jones et al. 1994). Trade-offs represent a challenge for the definition of seedling quality in drylands. Additional complexity resides in the fact that ecological strategies may change over the lifespan of woody plants (Mediavilla and Escudero 2004). Failure to identify morpho-functional traits fitted to the objectives of dryland restoration may decrease our efficiency to reach restoration targets.

Multiple stresses in drylands

Nutrient limitation of plant productivity is common in dryland soils (Lal 2009). Low levels of nutrient availability may result from natural factors, including low productivity and scarce capacity to concentrate nutrients in the topsoil, dominance of alkaline soils with high phosphorus and micronutrient binding capacity, and high erodibility. Furthermore, human pressure, and particularly tillage, fire, erosion and crop harvest have contributed to nutrient depletion and decline in soil fertility (García Cano et al. 2000; Lal 2009). Thus, it is not surprising that fertilization exerts a strong effect on the productivity of agricultural crops and forest plantations (Valdecantos et al. 2006; Fuentes et al. 2010). In this context, high levels of nutrient reserves and ability to capture nutrients may improve seedling performance in the field.

On the other hand, multiple resource limitation probably represents the rule, rather than the exception, particularly in drylands, where water is scarce. Understanding multiple resource limitation has been a major challenge in ecological research (Bloom et al. 1985; Vitousek et al. 2010). In some cases, morpho-physiological responses to different sources of stress converge. For example, an increased shift in biomass allocation from leaves to roots is common in water- and nutrient-deficient plants (Poorter and Nagel 2000). Indeed,

both sources of stress are difficult to disentangle, as water scarcity directly affects nutrient uptake and translocation (Hu and Schmidhalter 2005). However, in other cases, morpho-physiological responses are specific of the source of stress. Thus, deep rooted genotypes are favored in water-limited environments, whereas shallow-rooting represent an advantage for genotypes living in P-limited areas (Ho et al. 2005; Zhu et al. 2011). Antagonistic effects of different sources of stress on a particular morpho-physiological trait hamper the definition of high quality seedlings for drylands. In these cases, access to water should be prioritized, as this is the major limiting factor for seedling performance in these areas.

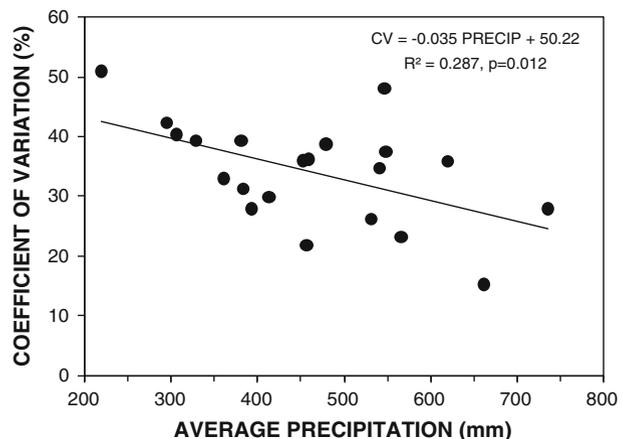
Spatial and temporal variability and seedling quality

Drylands show high spatial variability in soil and microclimate properties (Maestre and Cortina 2002). This is the result of differences in exposition, the presence of precipitated caliche, past sediment export favoring the presence of decapitated and polycyclic soils, stone mulches, stone lines, rock outcrops, surface and sub-surface resource transport, soil faunal activity and heterogeneous distribution of plant cover (Yaalon 1997; Maestre and Cortina 2002, Maestre et al. 2003). Soil heterogeneity strongly affects seedling establishment (Gómez-Aparicio et al. 2008), even when differences in soil properties are relatively small and operate at small spatial scales (Maestre et al. 2003).

Similarly, intra- and inter-annual variability in rainfall distribution in drylands is high, particularly in the driest extremes of the precipitation gradient (Fig. 1). With some notable exceptions, as drylands under El Niño-Southern Oscillation (ENSO) and (North Atlantic Oscillation (NAO) cycles, forecasting annual and seasonal rainfall in these areas is currently unfeasible (Holmgren and Scheffer 2001). As a consequence, plantation management can only mitigate but not anticipate the effects of drought, and plantation success is still highly dependent on the amount and timing of precipitation (Squeo et al. 2007; Vallejo et al. 2012a).

Spatial and temporal heterogeneity complicates the identification of high quality seedlings, as best suited seedlings for a particular site and planting time may not be optimum when conditions change. Given these limitations, we would recommend using a range of morpho-physiological types that may be suited to the different landscape units and precipitation regimes. In parallel, we should improve our capacity to identify suitable sites

Fig. 1 Relationship between average precipitation and the corrected coefficient of variation in annual precipitation in 21 stations from E Spain (data from AEMET, Ministerio de Agricultura, Alimentación y Medio Ambiente)



for planting particular morpho-physiological types, refine methods to forecast rainfall, and use existing and new technology to maximize available water.

Nutrient manipulation and seedling traits

Fertilization has a strong potential to alter plant morpho-physiological traits (see below). In some cases, changes may increase water uptake and contribute to preserve water balance. In others, changes resulting from increased nutrient availability may reduce seedling ability to withstand drought. Seedling production in drylands should distinguish both groups of traits and identify suitable growing conditions, including fertilization regimes, to promote the former.

Fertilization promotes changes in leaf nutrient content and leaf morphological and physiological traits (Meziane and Shipley 1999, 2001). Indeed, leaf size, leaf mass to plant biomass ratio, specific leaf area (SLA), photosynthetic capacity, leaf life span and leaf dry matter content are related to leaf nutrient concentration and content (Meziane and Shipley 1999; Wright et al. 2004; Poorter et al. 2009; Domínguez et al. 2012). In addition, some traits as SLA, leaf nitrogen content and maximum photosynthetic capacity are correlated on the basis of the leaf economics spectrum (Wright et al. 2004; Donovan et al. 2010), and other functional traits as light response curves can be predicted from them (Marino et al. 2010).

Increase in photosynthetic rates resulting from improved nutrient status may have a positive effect on seedling performance as water use efficiency is increased (Medrano et al. 2008). Conversely, high nitrogen content in leaves may unbalance carbon gain due to higher carbon losses via respiration, and increase the risk of carbon starvation under drought (Walters and Reich 2000, McDowell et al. 2008). High SLA could negatively affect seedling performance under drought, as increased SLA may result from lower leaf thickness (Meziane and Shipley 2001) and less efficient control of water loss (Salleo and Lo Gullo 1990; Corcuera et al. 2002). Finally, fertilization may increase the number of leaves and average leaf size (Hernández et al. 2009), promoting passive water losses (Vilagrosa et al. 2003a; Aranda et al. 2005).

Fertilization may affect biomass accumulation and allocation patterns, enhancing biomass allocation aboveground (Poorter and Nagel 2000; Hernández et al. 2009). This may reduce root system ability to supply water and nutrient, and hamper carbon and nutrient storage capacity (Vilela et al. 2003). Fertilized seedlings may be more vulnerable to drought than unfertilized seedlings because of the increase in aboveground biomass accumulation and allocation, and the increase in transpiration rates (Harvey and van den Driessche 1997). It is worth emphasizing that the increase in belowground biomass allocation when nutrients are limiting is stronger than the increase observed when water is limiting (Poorter et al. 2012). However, fertilization may also induce morpho-physiological changes favoring water uptake. For example, root growth potential commonly increase with the increase in phosphorus and nitrogen availability (Larigauderie and Richards 1994; Singh and Sale 2000; Trubat et al. 2006), and thus the ability to capture water may be enhanced in fertilized seedlings (Reinbott and Blevins 1999).

Nitrogen and phosphorus limitation also affects plant morpho-functional traits related to fine root structure and architecture. Phosphorus deficiency increases average link length, specific root length, root system magnitude and length, lateral root dispersion, the number of root hairs and root surface area (Lynch and Brown 2001, Trubat et al. 2006; Lynch 2011). In addition, specific root length increases in response to N limitation (Ostonen et al.

2007). These changes have been associated with an increase in plant capacity for capturing soil resources, particularly immobile resources as phosphorus, and may not represent an improvement in the uptake capacity of mobile resources as water (Comas and Eissenstat 2002; Lambers et al. 2006). Similarly, changes in root lifespan, root respiration, N:C ratio and other root traits induced by increased nutrient availability affect resource capture strategies and seedling functions, and may compromise their capacity to withstand stress (McCormack et al. 2012; Mommer and Weemstra 2012).

High nutrient availability reduces biomass allocation belowground and fosters changes in root architecture, affecting root capacity to supply water aboveground (Wu et al. 2005; Trubat et al. 2012). However, the relationship between nutrient status, and root and shoot capacity for water transport is still under discussion (Table 1). These apparently conflicting results may reflect differences in species strategy, the specific nutrients involved and the degree of nutrient limitation, and is in agreement with studies emphasizing the plasticity of traits related to hydraulic architecture in response to changing environmental conditions (Nardini and Tyree 1999; Barigah et al. 2006).

Reductions in the capacity for water transport may increase water use efficiency, but also decrease water potential and increase the risk of xylem cavitation (Vilagrosa et al. 2003b; Hernández et al. 2009). The close relationship between hydraulic conductivity of whole plants and rooting systems, and conductivity to water vapor at the leaf level suggests that stomatal response is controlled by hydraulic restrictions (Hubbard et al. 2001). Similarly, leaf gas exchange, root hydraulic conductance and specific root length may be related (Hernández et al. 2010). Higher specific root length is commonly associated with higher exploitation efficiency (Nicotra et al. 2002, Trubat et al. 2006). Root hydraulic conductance and root specific hydraulic conductance may be lower in N and P deficient seedlings than in well fertilized seedlings (Radin and Matthews 1989; Trubat et al. 2006). The reduction in seedling capacity to transport water may be mostly related to the increase in the number of branchings in roots of nutrient-deficient seedlings (Trubat et al. 2012). However, other studies have shown neutral to positive effects of fertilization on hydraulic conductance (Table 1). All these studies suggest a close relationship between nutritional status, root system morphology and architecture, root capacity for resource uptake and transport, and leaf gas exchange.

Fertilization may also promote changes in xylem resistance to cavitation. Thus, stem vulnerability may increase with N fertilization (Harvey and van den Driessche 1997; Hacke et al. 2010). In contrast, other studies have found higher resistance to cavitation in well fertilized plants (Ewers et al. 2000). Opposite results are not surprising as fertilization commonly affects morpho-functional traits as biomass allocation patterns, foliar surface and water demand, hydraulic architecture, and cation concentration in the xylem sap.

Nutrient deficiency may enhance the accumulation of non structural carbohydrates (Oliet et al. 2006), which may function as energy reserves as well as osmolites, increasing seedling ability to face transplant shock (Burdett 1990). However, there are exceptions to this rule (Trubat et al. 2010). For example, we found that late season fertilization had no effect on soluble carbohydrate concentration of *Quercus ilex* L. seedlings, whereas, it decreased and increased starch concentration in leaves and roots, respectively (Fig. 2).

The relative importance of seedling quality and performance

Growth and field survival usually increase with the improvement in nutrient status (Oliet et al. 1997; Luis et al. 2009; Oliet et al. 2009, Villar-Salvador et al. 2012b). But some

Table 1 A synthesis of studies evaluating the effect of fertilization on hydraulic conductance of woody species published between 2000 and 2012

Species	Fraction analyzed	Response	Reference
<i>Avicennia germinans</i>	Stem, branches	No effect	Lovelock et al. (2006)
<i>Blepharocalyx salicifolius</i>	Branches	No effect	Bucci et al. (2006)
<i>Caryocar brasiliense</i>	Branches	Decreased	Bucci et al. (2006)
<i>Eucaliptus grandis</i>	Stem	Enhanced	Clearwater and Meinzer (2001)
<i>Fraxinus pennsylvanica</i>	Roots	Enhanced	Andersen et al. (1989)
<i>Laurus nobilis</i>	Stem	Enhanced	Oddo et al. (2011)
<i>Ouratea hexasperma</i>	Branches	No effect	Bucci et al. (2006)
<i>Picea abies</i>	Whole tree	Decreased	Ward et al. (2008)
<i>Pinus canariensis</i>	Whole root system	Decreased	Luis et al. (2010)
<i>Pinus contorta</i> var. <i>latifolia</i>	Stem	Enhanced	Amponsah et al. (2004)
<i>Pinus taeda</i>	Root and branches	Decreased	Ewers et al. (2000)
<i>Pinus taeda</i>	Branches	Decreased	Domec et al. (2009)
<i>Pinus taeda</i>	Root to leaf	Enhanced	Samuelson et al. (2008)
<i>Pistacia lentiscus</i>	Whole root system	Decreased	Trubat et al. (2006)
<i>Pistacia lentiscus</i>	Whole root system	Decreased	Hernández et al. (2009)
<i>Populus deltoides</i>	Whole tree	Enhanced	Samuelson et al. (2007)
<i>Populus trichocarpa</i> × <i>deltoides</i>	Stem segments	Enhanced	Hacke et al. (2010)
<i>Populus trichocarpa</i> × <i>deltoides</i> clones	Stem	Enhanced with P Decreased with N	Harvey and Van Den Driessche (1997)
<i>Qualea parviflora</i>	Branches	Decreased	Bucci et al. (2006)
<i>Quercus suber</i>	Whole root system	No effect	Hernández et al. (2009)
<i>Rhizophora mangle</i>	Stem	Enhanced	Lovelock et al. (2004)
<i>Schefflera macrocarpa</i>	Branches	No effect	Bucci et al. (2006)

studies have shown opposite results (Oliet et al. 2006; Trubat et al. 2008; Trubat et al. 2011; Villar-Salvador et al. 2012a, Fig. 3). Disagreements are not related to differences in average precipitation in a simple manner (Navarro et al. 2006), but the interaction between the type of drought, site conditions and species response to resource limitations may explain them (Valdecantos et al. 2006; Villar-Salvador et al. 2012a).

Over the last decades, improvements in seedling quality have substantially increased seedling survival rates and early growth. Similarly, there have been significant improvements in species selection, identification of suitable planting sites, and use of low-impact soil preparation techniques. Deeper understanding of ecological interactions and assembly rules has also contributed to a general improvement in plantation success. Still, high seedling mortality and stunted growth are common in dryland plantations.

Plantation success in drylands is obviously related to climatic conditions after plantation. Whereas plantations are commonly carried out during the rainy season, a few dry

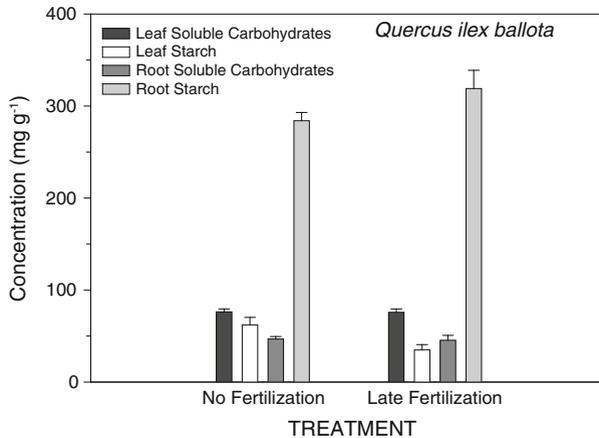


Fig. 2 Foliar and root concentration of soluble carbohydrates and starch in *Q. ilex* subsp. *rotundifolia* seedlings receiving no fertilization, or receiving complete fertilization after the onset of autumn arrested growth (November 2007; Late Fertilization). Leaves were analyzed in February 2008 (J. Moneris, University of Alicante, unpubl. data). Data are means and standard error of $n = 10$ seedlings per treatment. Only starch showed a significant or marginally significant effect of treatment (oneway ANOVA: $F = 7.46$, $p = 0.013$, and $F = 2.49$, $p = 0.132$ for leaves and roots, respectively)

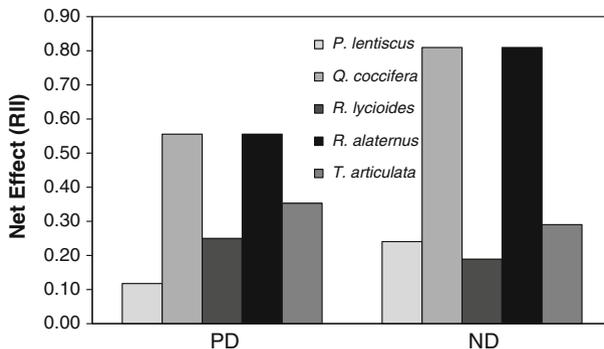


Fig. 3 Net effect (RII; Armas et al. 2004) of phosphorus deficiency (PD) and nitrogen deficiency (NP) on the 3-year survival of five Mediterranean woody species planted in a semiarid degraded area (Albatera, southeastern Spain). RII is calculated as the difference in survival between PD or ND seedlings and seedlings receiving optimum fertilization divided by their summation, and thus, positive values reflect increases in seedling survival. Further details in Trubat et al. (2011)

warm weeks after planting or a long summer may compromise seedling establishment. For example, Vallejo et al. (2012a) found a strong relation between the mortality of planted seedlings and the length of dry spells in eastern Spain (i.e., periods with no rain above 5 mm). Failure to establish forest plantations in drylands may also result from poor planting practices, particularly inadequate seedling management and delayed planting. Thus, in Vallejo et al. (2012a) study, survival of seedlings produced and planted with low technological inputs could not increase above 30 % when summer drought lasted for more than 5 months. Still, plantations performed using higher technological inputs may not

guarantee success (Vallejo et al. 2012a). Our ability to predict seedling survival on average years is still poor, and surprises arise too often.

An analysis of short-term survival of seedlings planted simultaneously on replicated plots showed a high degree of spatial variability (Cortina et al. 2011). Whereas nursery and field treatments, albeit significant, explained from 0 to 53 % of the variability in seedling survival, site and planting conditions explained an average of 79 % of this variability. Reasons for this are not obvious. Planting sites were selected as replicates because they showed similar soil properties, exposition, altitude, plant cover and community composition. In a detailed analysis of soil properties explaining the survival of *Pistacia lentiscus* L., Maestre et al. (2003) showed that seedling survival in a semi-arid plantation was related to small changes in bare soil cover, sand content, and soil compaction. These results suggest that even weak differences in soil properties may put a strong burden on seedling survival. Unfortunately, our knowledge on the effects of stone content or soil depth on seedling performance is still limited. Our inability to understand the interactions between seedling quality and soil properties hampers progress towards the identification of traits defining high seedling quality in drylands.

Concluding remarks: towards a unifying theory of nutrient status and seedling performance

The production of quality seedlings for dryland restoration should pay attention to its multiple objectives, and should consider spatial and temporal variability in site conditions. Fertilization has a strong potential to manipulate seedling morpho-functional traits, and promote those traits that may confer higher potential to establish in drought-prone and nutrient-depleted sites.

The net effect of fertilization on seedling traits and water balance may depend on the relative importance of changes in biomass allocation versus changes in foliar accumulation and leaf structure, root architecture and growth potential. We hypothesize that the net outcome of fertilization may largely depend on the timing and intensity of drought. When drought occurs shortly after planting, water conservation strategies (i.e., high biomass allocation belowground, low foliar surface area and specific leaf area) may prevail, and nutrient limited plants may be better fitted to withstand drought and establish in the field. On the contrary, when the onset of drought is delayed, naturally or by irrigation, plants with higher growth rates and particularly with higher root growth capacity may quickly reach deep soil horizons and be in a better position to endure ensuing drought. Similarly, nutrient limited seedlings may be more suitable for the driest end of an aridity gradient

Table 2 Recommendations for target seedling traits and nursery practices under harsh and mild environmental conditions

Harsh conditions, exposed microsite or early drought	Mild conditions, protected microsite or delayed drought
Control aboveground biomass → Restrict nutrient inputs if necessary	Large, well fertilized seedlings, with high growth potential above and belowground
Promote belowground biomass and rooting depth → Containers +20 cm depth	
Ensure that nutrient status is good → Fertilization immediately pre-planting	

than well fertilized seedlings, whereas the opposite may be true at the milder end of this gradient.

Accordingly, we suggest that seedlings prepared for harsh sites (i.e., sunny slopes, shallow soils) should be grown in the open air, under nutrient limiting conditions, favoring root development (Table 2). Containers should promote rapid and deep root growth. Finally, seedlings should be preconditioned to drought by reducing watering frequency by the end of the nursery period, and allowed to reach optimum nutritional status by fertilizing some weeks before planting. These general recommendations should be further tested taking site conditions and species requirements and strategy into account.

Finally, studies showing the potential for increase in plantation success derived from improved seedling quality versus understanding local drivers of seedling performance suggest that research should focus on the later, as the degree of uncertainty in the outcomes of plantations is still very high and probably driven by subtle differences in soil properties.

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