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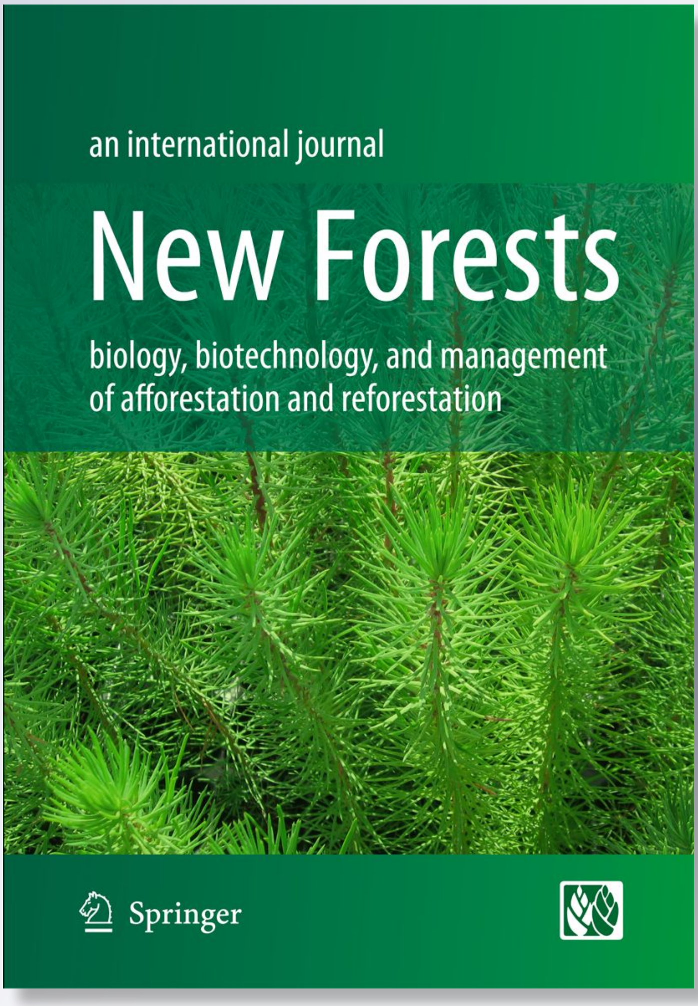

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Increase in size and nitrogen concentration enhances seedling survival in Mediterranean plantations. Insights from an ecophysiological conceptual model of plant survival

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Abstract Reduction in size and tissue nutrient concentration is widely considered to increase seedling drought resistance in dry and oligotrophic plantation sites. However, much evidence indicates that increase in size and tissue nutrient concentration improves seedling survival in Mediterranean forest plantations. This suggests that the ecophysiological processes and functional attributes relevant for early seedling survival in Mediterranean climate must be reconsidered. We propose a ecophysiological conceptual model for seedling survival in Mediterranean-climate plantations to provide a physiological explanation of the frequent positive relationship between outplanting performance and seedling size and nutrient concentration. The model considers the physiological processes outlined in the plantation establishment model of Burdett (Can J For Res 20:415–427, 1990), but incorporates other physiological processes that drive seedling survival, such as N remobilization, carbohydrate storage and plant hydraulics. The model considers that seedling survival in Mediterranean climates is linked to high growth capacity during the wet season. The model is for container plants and is based on three main principles, (1) Mediterranean climates are not dry the entire year but usually have two seasons of contrasting water availability; (2) summer drought is the main cause of seedling mortality; in this context, deep and large roots is a key trait for avoiding lethal water stress; (3) attainment of large root systems in the dry season is promoted when seedlings have high growth during the wet season. High growth is achieved when seedlings can divert large amount of resources to support new root and shoot growth. Functional traits that confer high photosynthesis, nutrient remobilization capacity, and non-structural carbohydrate storage promote high growth. Increases in seedling size and nutrient concentration strongly

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affect these physiological processes. Traits that confer high drought resistance are of low value during the wet season because hinder growth capacity. We provide specific evidence to support the model and finally we discuss its implications and the factors that may alter the frequent increase in performance with increase in seedling size and tissue nutrient concentration.

Keywords Carbohydrates · Drought stress · Fertilization · Forest plantation · Nitrogen · Nutrients · Photosynthesis · Plant quality · Remobilization · Root growth

Introduction

Water stress is a major cause of failure in forest restoration projects in Mediterranean ecosystems (Alloza and Vallejo 1999; Mendoza et al. 2009). Summer drought is the main cause of water stress and seedling mortality is concentrated during the first summer after planting (Castro et al. 2004). Plants usually do not experience water stress during the reminder of the year (Sala and Tenhunen 1994; Mediavilla and Escudero 2004), due to either low air vapor pressure deficit or high rainfall. Consequently, forest plantations in the Mediterranean basin are done in the wet season with the planting window spanning from early November to early April in most sites. Most stocktype is container plant, which is planted when seedlings are 8–12 months old in most species.

Mediterranean woody flora is mainly composed of evergreen species, which maintain appreciable photosynthesis and root elongation during the wet season (Leshem 1965; Sala and Tenhunen 1994; López et al. 2001). Plant functional attributes exert a significant influence on the carbon (C), water and mineral nutrient economy of plants and thus on their fitness. Nursery cultivation regimes strongly influence seedling morphology and physiology and, consequently, their potential outplanting performance (van den Driessche 1991a; Arnott et al. 1993; Villar-Salvador et al. 2004a, b). Shoot height and root collar diameter are the most commonly functional attributes used for operational plant quality assessment due to their measurement simplicity. European Union has regulated the shoot height and root-collar diameter standards for acceptable seedlings for forest restoration in several Mediterranean tree species (Alía et al. 2005). For instance, one-year old *Quercus ilex* L. seedlings of acceptable quality must have a shoot height ranging between 8 and 30 cm.

Seedling size is a relatively good predictor of outplanting performance in boreal and humid-temperate species when seedlings are similar in physiological quality, with survival frequently increasing with shoot size (Thompson 1985; Tuttle et al. 1988; Mexal and Landis 1990; Bayley and Kietzka 1997; South et al. 2005; Pinto et al. 2012). In the last 20 years, there has been a growing body of evidence also in Mediterranean environments that, for a given species and for plants of the same age, seedling survival increases with plant size (Guehl et al. 1989; Villar-Salvador et al. 2004a; Tsakaldimi et al. 2005; del Campo et al. 2007; Luis et al. 2009; Oliet et al. 2009 Cuesta et al. 2010b). For instance, *Q. ilex* seedlings that were 12.5 cm in height had 50 % less survival than seedlings that were 16.4 cm in height (Villar-Salvador et al. 2004a). In *Pinus canariensis* C.Sm. ex DC, 8-cm tall seedlings survived 40 % less than 20-cm tall plants (Luis et al. 2009). Similarly, differences in sapling survival across *Quercus suber* L. provenances were also positively related to the height of planted seedlings (Ramírez-Valiente et al. 2009). In this study, seedling size was closely related to acorn size, which was bigger in populations from warm and drier locations.

In their meta-analysis of 30 forest plantation studies in Mediterranean-climate areas of Spain, Navarro et al. (2006) concluded that plant size at planting significantly explained survival differences in 43 % of the case studies, whereas survival was not related to plant size in the remaining cases studies (Fig. 1). Among the former, positive relationships between survival and seedling size were three times more frequent than cases showing negative relationships. Rainfall differences among sites did not affect the outlined pattern in this meta-analysis and both positive and negative survival-plant size relationships have been reported in semiarid sites (Luis et al. 2009; Oliet et al. 2009; Trubat et al. 2011). Navarro et al. (2006) concluded that the target seedling for Mediterranean forest plantations should be larger than the conventional seedling used in most forestation programs. Many of the positive relationships between survival and plant size are supported by nursery fertilization experiments, which suggests that plant nutritional status (mainly of nitrogen) is also an important issue in explaining outplanting performance in Mediterranean environments (Villar-Salvador et al. 2004a; Luis et al. 2009; Oliet et al. 2009).

The outlined trends are in conflict with results indicating that reduction in seedling size and tissue nutrient concentration increases drought resistance and performance in oligotrophic soils located in dry environments (Tuttle et al. 1988; Tan and Hogan 1997; Leiva and Fernández-Alés 1998; Trubat et al. 2011). Therefore, we believe that the physiological processes and functional attributes underlying seedling survival in Mediterranean forest plantations must be revisited based on a different view of the Mediterranean climate.

This study proposes a physiological conceptual model of seedling survival in Mediterranean sites to explain why seedling survival frequently increases with seedling size and tissue nutrient concentration. The conceptual model considers the physiological processes outlined in Burdett's plantation establishment model (1990) but incorporates other relevant physiological processes driving seedling survival, such as nitrogen (N) remobilization, carbohydrate storage and plant hydraulics, which were not explicitly considered in Burdett's model. Additionally, our model also extends the timeframe beyond the establishment phase and considers that dry season survival is strongly linked to physiological activity in the wet season. Finally, we provide evidence for the model based either on ad hoc designed experiments to test predictions derived from an earlier version of the model (Villar-Salvador 2003) or published studies on transplanting performance of forest species.

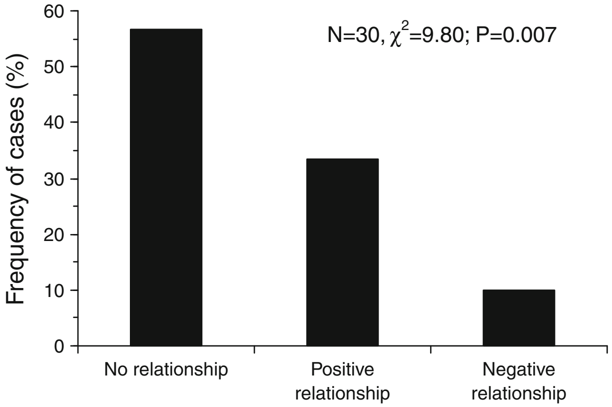

Fig. 1 Frequency of cases studies in which the relationship between seedling survival in Mediterranean-climate areas of Spain and seedling shoot size at planting was null, positive or negative. The figure has been redrawn from the meta-analysis in Navarro et al. (2006) that included 30 forest plantation studies, in which stocktype was container plant and in most cases 1 + 0 seedlings were used. The range in seedling size and other relevant information of each case study can be found in the original publication

The conceptual physiological model

The model assumes the use of container stocktypes, that selected species and provenances are appropriate for the planting site, seedlings are healthy and cold-hardy, and operational activities before, during and after planting, such as soil preparation, irrigation, weed control or herbivore exclusion, are properly implemented. It is based on three major principles:

1. Mediterranean climate has two seasons of contrasting water availability (Mitrakos 1980). Drought is usually concentrated in the summer when the combination of high temperature and lack of rainfall occurs for 1–5 months. Plants usually do not experience drought stress during the wet season, except in very dry sites or during extraordinary drought events and in sites that experience severe frost. In this scenario of variable water availability in time, correct outplanting timing (i.e., during the wet season) allows seedling establishment and growth to lessen dry season stresses.
2. Survival to summer drought is linked to the capacity of seedlings to avoid lethal water stress, which is mainly achieved by having a large, deep root system during the dry season.
3. Reallocation of large amounts of resources during the wet season is critical for high new growth prior to the onset of the dry season. The model therefore emphasizes the physiological processes that underlie root and shoot growth.

Model description

New growth depends on seedling capacity to supply C and mineral nutrients (mainly N) as long as the plant water potential does not limit cell elongation and gas-exchange (Willaume and Pages 2006; Millard and Grelet 2010). Carbon can be supplied by both current photosynthesis and carbohydrates stored during nursery cultivation (Fig. 2). Most boreal and wet temperate conifers mainly rely on current photosynthesis to support early root growth in spring (van den Driessche 1987, 1991b; Hansen et al. 1996; Millard and Grelet 2010). Some evidence also point out the importance of recently assimilated C for new growth in conifers and in evergreen broadleaf Mediterranean species (Atzmon et al. 1994; Cerasoli et al. 2004; Maillard et al. 2004). The importance of current photosynthesis and stored non-structural carbohydrates (NSC) for early root growth in deciduous species depends on whether roots resume their growth before or after shoot flush in spring. When root growth initiates after shoot flushing, shoot growth is strongly dependent on NSC but root growth is then supported by recently expanded leaves (Abod et al. 1991). When shoot and root growth initiation occurs simultaneously in spring, as in *Q. rubra* L., early root growth depends on stored NSC, but as new leaves mature current photosynthates assume a greater role (Sloan and Jacobs 2008).

The greater the contribution of photosynthesis or stored NSC, the more C there is for growth (Fig. 2). Greater shoot size usually is associated to greater foliage biomass (del Campo et al. 2010; Trubat et al. 2011) and, consequently, photosynthesis per plant (Dyckmans and Flessa 2001). Higher foliage N concentration may also increase net photosynthesis rate (A) due to higher stomatal conductance (g_s) and carboxylation capacity (Field and Mooney 1986; Clearwater and Meinzer 2001).

Variations in seedling size determine NSC content if there is not any change in NSC concentration. An increase in NSC content can enhance growth in species that chiefly rely on NSC for early growth or disturbance recovery (Puttonen 1986; McPherson and

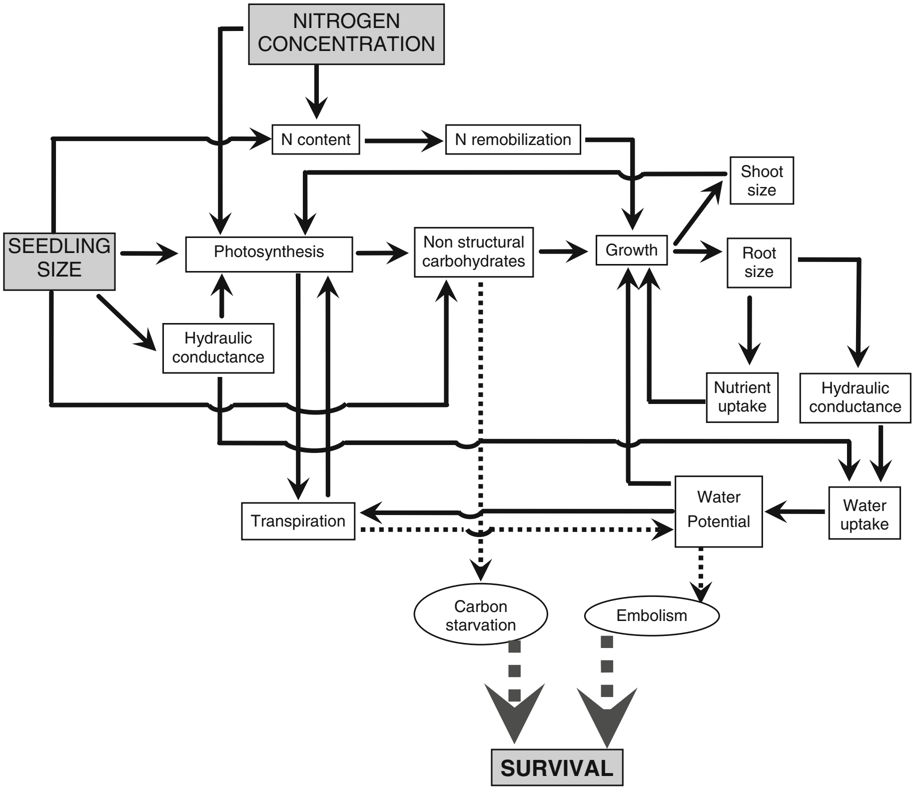

Fig. 2 Conceptual model of the physiological processes that link seedling size and tissue N concentration with seedling survival in Mediterranean forest plantations. Continuous and dotted lines indicate positive and negative relationships, respectively

Williams 1998). NSC availability also depends on the balance between photosynthesis and maintenance respiration, which will be reduced if the proportion of "heterotrophic" organs in a seedling increases. The shoot-to-root mass ratio (S/R) and the leaf mass ratio usually scale up with increased seedling size if rooting volume does not vary (Villar-Salvador et al. 2005). Therefore, it can be expected that maintenance costs will increase with reduction in seedling shoot size in container seedlings.

New organ growth depends on soil N and N remobilization from pre-existing organs (Salifu and Timmer 2003; Millard and Grelet 2010). Nitrogen remobilization is a source-driven process, i.e. the higher the N content of an organ the greater the amount of N remobilized from it (Millard and Grelet 2010). Therefore, an increase in plant size and tissue N concentration will increase N remobilization potential (Fig. 2).

Plant hydraulic conductance is the water flow rate through the plant per change in hydraulic pressure driving the flow (Sperry 2000). It is usually standardized with leaf area (leaf specific conductance, LSC), the transversal sapwood area (specific conductance, k_s) or by root surface area (k_r) when the root hydraulic conductance is studied. An increase in k enhances water flow through the plant. This effect is attributed to the link between k and g_s, which is mediated by water potential. A higher k permits the plants to maintain higher water potential at similar transpiration rate than a lower k (Bucci et al. 2006; Sperry 2000).

Increase in hydraulic conductance (k) can increase g_s and, consequently, A (Sperry 2000). k can increase with plant size (Lovelock et al. 2004) and enhance water uptake capacity (Grossnickle and Russell 1990; Sword Sayer et al. 2005) and, consequently, plant hydration. Variations in photosynthesis, mediated by changes in foliage surface and g_s, also positively affect transpiration and, therefore, negatively plant water potential.

Higher C and N availability can support higher root and shoot growth, leading to a feedback cycle where root growth supports photosynthesis and photosynthesis supports root and shoot growth (Burdett 1990) (Fig. 2). This process will ensure seedling establishment right after planting (Burdett 1990; Grossnickle 2005) and extension of the root system during the rest of the wet season. If seedlings exhibit vigorous root growth during the wet season, root systems should be large and reach deep moist soil horizons at the onset of the dry season. This increases water uptake capacity during the dry season (Padilla and Pugnaire 2007) and, consequently, gas-exchange capacity. Root elongation during the wet season should also favor soil nutrient uptake to support root and shoot growth along with nutrient remobilization. Similarly, production of high photosynthetically active new shoots in spring should foster photosynthesis in Mediterranean evergreen species, in which currently formed leaves coexist with older less photosynthetically active leaves during spring (Milla et al. 2005).

Plant water potential ultimately depends on the balance between plant water loss and uptake. If the root system is too small in relation to the plant's transpiration capacity or too shallow to reach deep moist soil layers, plant water uptake will not meet transpirational demand and will cause a reduction in water potential. This will reduce growth and gas-exchange through stomatal closure. Increased water uptake during the dry season prevents the plant from reaching lethal water potential, at which extensive embolism can cause catastrophic hydraulic failure inducing leaf shedding and, lastly, seedling death (Vilagrosa et al. 2003; Brodribb and Cochard 2009). Prolonged periods of very low photosynthesis can lead to C starvation (Adams et al. 2009), which also might be a potential cause of seedling mortality (Canham et al. 1999; McDowell et al. 2008) (Fig. 2). As high summer temperature can exacerbate C starvation by increasing seedling respiration, maintenance of a significant level of photosynthesis is critical for maintenance of plant metabolism during the dry season.

Predictions from the model and evidence of the physiological mechanisms underlying the frequent outplanting performance improvement with seedling size and N concentration increase in Mediterranean plantations.

Predictions of the model and evidence of the physiological processes

Several predictions can be established from the conceptual model. In this section we provide evidences that support main predictions and help to understand the frequent superior outplanting performance of larger and N-rich seedlings relative to smaller and poor-N plants in Mediterranean environments.

Prediction 1: Root system size and depth determine plant water status and survival in summer

Size of the root system drives drought survival of woody species in dry climate areas (Grossnickle 2005). Seedling survival differences among common woody species in the semiarid Iberian Peninsula were positively linked to the root depth achieved during summer (Padilla and Pugnaire 2007). Species that had high seedling survival produced roots that reached deeper moisture soil horizons than species that had low survival. Summer predawn water potential of *Quercus coccifera* L. seedlings that were planted within different treeshelters was positively related to the length of new roots (Bellot et al. 2002). Similarly, *Q. ilex* seedlings that differed in vigor and in planting date were also different in their midday water potential and survival by the end of the first summer, which were positively correlated with new root growth at the beginning of the summer (Fig. 3).

Prediction 2: An increase in seedling size and N content increases root growth

Many studies have shown that differences in seedling morphology and physiology status influence root growth capacity (RGC). Most RGC studies have been conducted under glasshouse or growth chamber conditions for short time periods but field studies are scarce.

RGC increases with plant size (South et al. 1989). High fertilized seedlings, which are bigger and richer in N than low fertilized plants, have greater RGC (van den Driessche 1992; Villar-Salvador et al. 2004a). Field studies rend similar results to those in controlled conditions. High N fertilized *Juniperus thurifera* L. seedlings grew deeper roots than low N fertilized plants when transplanted into 1-m long metacrylate tubes that were inserted into the soil. Deeper roots were attributed to higher root elongation rate in high fertilized plants (Fig. 4). Using the same methodology, Cuesta et al. (2010a) found that larger *Pinus halepensis* Mill. seedlings had greater root systems than smaller seedlings, but no difference in root depth could be observed. Contrary to the results for *J. thurifera*, a greater root system in larger *P. halepensis* plants was attributed to a greater number of new roots rather than a higher elongation rate of individual roots.

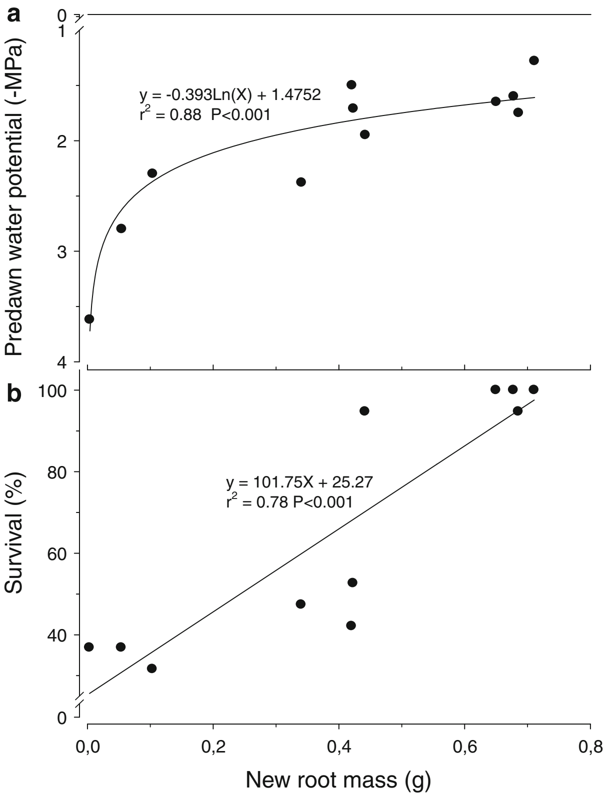

Fig. 3 Relation of **a** predawn water potential in mid summer and **b** survival at the end of the summer with new root mass as determined at the beginning of the summer in *Quercus ilex* seedlings. Each point in the graphs represents the mean of five plants for root mass and water potential and 30 plants for survival (redrawn from data in Rodríguez-García 2003)

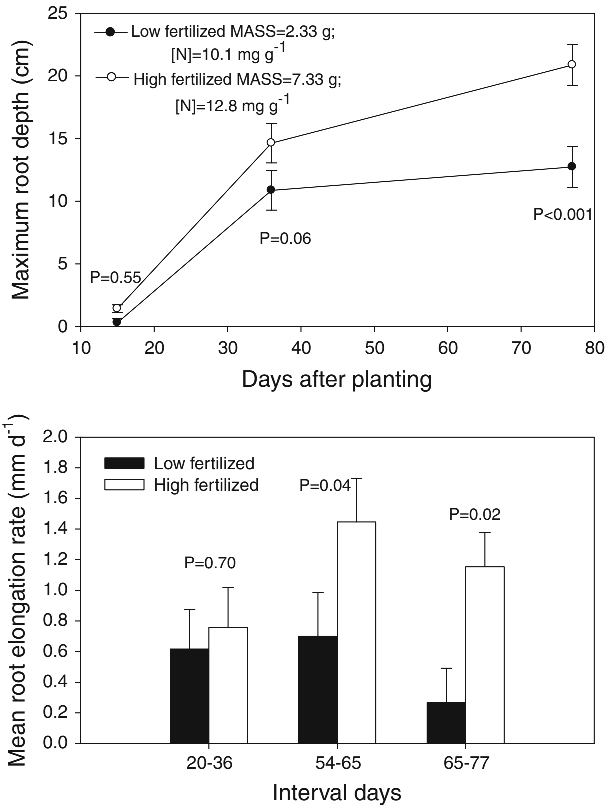

Fig. 4 Time course of root depth (*upper figure*) and mean root elongation rate (*lower figure*) in three periods of high- and low-N fertilized *Juniperus thurifera* seedlings. Measurements were made by transplanting seedlings into 1-m long metacrylate tubes filled with sand that were inserted into the field. Data are means ± 1 SE. N = 6. In the upper figure the mean plant mass and shoot N concentration of high- and low-fertilized seedlings is provided. (modified from Martínez-Sanz 2006)

Large, nutrient rich *P. canariensis* plants produced greater root systems than small, nutrient-poor seedlings 3 years after outplanting (Luis et al. 2009). Similarly, large *P. halepensis* had greater new root mass at the beginning of the dry period than small seedlings, and this difference was more pronounced in the presence rather than in the absence of weeds (Cuesta et al. 2010b).

Prediction 3: N remobilization increases with increase in plant N content

Greater plant size and tissue N concentration increases plant N content. The proportion of N remobilized to support new growth depends on species, source organ, and source/sink interactions (Silla and Escudero 2003; Millard and Grelet 2010). For instance, the proportion of new N in growing organs derived from remobilized N from old leaves and woody fractions varied from 17 to 88 % in Mediterranean oak saplings (Silla and Escudero 2003). The amount of remobilized N depends on source strength, i.e. plant N content. Using ^{15}N labeled fertilizer, Salifu and Timmer (2003) demonstrated that N-loaded *Picea mariana* (Mill.) BSP seedlings remobilized three times as much N as conventional fertilized seedlings did, which had lower N content than the former seedlings. Similar trends have also been reported for other wet temperate and boreal woody species (Millard and Neilsen 1989; Grelet et al. 2003; Millet et al. 2005).

Using a N budget approach, Cuesta et al. (2010b) found that large *P. halepensis* seedlings remobilized four to six times more N than small seedlings to support spring growth. Both seedling types did not differ in their tissue N concentration but large seedlings contained five more times N than small seedlings. El Omari et al. (2003) reported that fertilized *Q. ilex* saplings remobilized higher amounts of N than N-deprived seedlings, which was attributed to greater N reserves in high-fertilized seedlings.

Prediction 4: Increase in seedling size and nutrient concentration at planting increases water potential and photosynthesis rate in the field during the dry season

Large, nutrient-rich *P.* canariensis seedlings had higher water potential and photochemical efficiency than small, nutrient-poor seedlings 3 years after planting (Luis et al. 2009). Furthermore, large *P. halepensis* seedlings had greater field gas-exchange capacity than small plants, independent of their tissue N concentration (Cuesta et al. 2010b). These differences were apparent under moderate but not under high drought stress conditions. However, the authors did not observe differences in water potential between seedling types. Similarly, moderate and high-N fertilized *Ceratonia siliqua* L. plants had greater *A* than low-fertilized plants after planting in a site with <200 mm of annual rainfall (Planelles González 2004). High-fertilized *J. thurifera* seedlings had higher daily course of *A* in mid-summer than low-fertilized seedlings. Higher *A* was linked to significantly higher water potential in high- than in low-fertilized plants (Fig. 5). Unfertilized seedlings of the deciduous Mediterranean oak *Q. faginea* Lam. had lower mid-day water potential in mid-summer than fertilized seedlings at two inside Spain locations (Villar-Salvador, unpublished data; Fig. 6).

Prediction 5: Increase in seedling size and new root enhance hydraulic capacity

Large plants produced by high fertilization regimes have greater xylem transversal area, wider xylem conduits and, consequently, higher k_s than small plants cultivated with low fertilization (Krasowski and Owens 1999; Hacke et al. 2010). These changes in xylem structure permit high fertilized plants to meet their greater transpiring capacity. However,

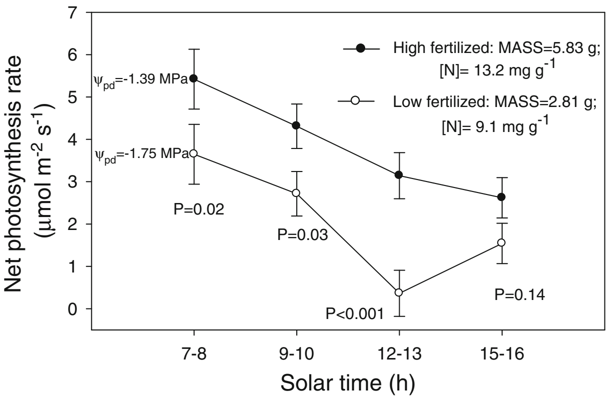

Fig. 5 Daily course of net photosynthesis rate in high- and low-fertilized two-year old *Juniperus thurifera* seedlings in late July during the first summer after transplanting into the field. The plant mass and shoot N concentration at the end of the cultivation of each seedling type is shown together with the field predawn water potential (ψ_{pd}), which was determined on the same day that gas-exchange measurements were obtained. Differences in ψ_{pd} were statistically significant ($P = 0.012$, N = 8, Villar-Salvador, unpublished data)

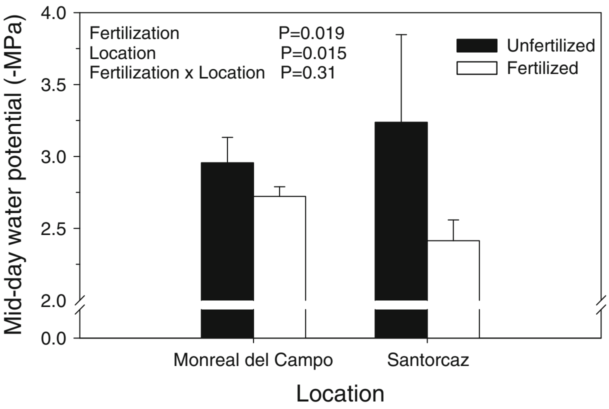

Fig. 6 Mid-day water potential of unfertilized and fertilized *Quercus faginea* seedlings transplanted at two locations inside Spain. Data are means ± 1 SE. Measurements were taken in late July. Water potential of fertilized treatments is the average data of four nitrogen fertilization rate treatments, which did not significantly differ. N > 5. Insert data show *P* values derived from ANOVA. Mean height of unfertilized and fertilized plants was 9.6 and 16.1 cm, respectively (Villar-Salvador, unpublished data)

increases in xylem conduit diameter may increase vulnerability of xylem to embolism, as reported in hybrid poplar (Hacke et al. 2010). Published studies on the effect of nursery cultivation regimes on hydraulic properties of Mediterranean plants are scarce and show varied trends. Trubat et al. (2006) found that N- and P-deficient *Pistacia lentiscus* L. seedlings had lower k_r than well fertilized seedlings, which were larger and had higher nutrient concentration than the former. On the contrary, high fertilization decreased k_r in *P. lentiscus* and *P. canariensis* but did not have any influence in *Q. suber* seedlings (Hernández et al. 2009; Luis et al. 2010). Cuesta et al. (2010b) observed higher field gas-exchange in large compared to small *P. halepensis* seedlings but no differences in their water potential, suggesting that higher gas-exchange might be attributed to k differences between plant types.

Discussion and concluding remarks

We suggest that high resource mobilization capacity to support high growth during the wet season is a key process for seedling survival during the dry season in seasonally dry climate environments such as in Mediterranean ecosystems. This ensures high growth capacity, which allows rapid seedling establishment during the wet season and drought stress avoidance during summer drought. Therefore, nursery cultivation should promote functional traits that confer seedlings high photosynthesis and nutrient remobilization capacity and low maintenance costs. Fertilization regime, container volume, cultivation density, growing media together with the length of the growing season have strong influences on these traits (van den Driessche 1991a; South et al. 2005; Oliet et al. 2009; Cuesta et al. 2010b, Verdaguer et al. 2011). In this framework, seedling size is an important attribute because it strongly determines plant photosynthesis and nutrient storage capacity and, consequently, resource mobilization and growth capacity. This explains why large seedlings frequently have higher absolute growth than small seedlings (Puértolas et al. 2003; Villar-Salvador et al. 2004a). Shoot and root elongation in small *P. halepensis* seedlings had an antagonistic pattern through time, indicating that the growth of both organs depresses each other. In contrast, large seedlings were able to simultaneously maintain high root and shoot growth without interference, evidencing that large seedlings have the capacity to divert resources to sustain two main resource sinks (Cuesta et al. 2010a).

Our model predicts that an increase in seedling size and N concentration can result in higher transpiration, which increases plant vulnerability to drought on the short-term. This is the main argument for using small seedlings in dry sites. However, seedlings with high drought resistance traits (low transpiration) have low root growth capacity resulting in a long-term survival cost. This idea is supported by results in Villar-Salvador et al. (2004b), which showed that osmotic adjustment and reduction in stomatal conductance in drought-conditioned *Q. ilex* seedlings were associated with a reduction in RGC. Plantation of seedlings in the wet season, long before summer drought onset, can minimize transpiration costs associated to increasing seedling size. This is a critical issue for two reasons. First, air vapor pressure deficit usually remains low during most of the wet season imposing low transpiration demand on seedlings. This is very important for maintaining high water potential immediately after transplanting until new root egress, especially in high transpiring seedlings. Secondly, root system size at the beginning of the dry season is directly related to the length of the wet season lasting after plantation takes place. As root growth in Mediterranean forests is inhibited during the dry season (Leshem 1965; López et al. 2001), seedling survival is not expected to occur at the expense of root growth during the dry season. In support to this reasoning, Corchero de la Torre et al. (2002) found that *P. halepensis* seedlings planted in the fall had larger roots at the beginning of the dry season than seedlings planted in early spring. This likely explains the higher mortality in late-planted plantations of *Q. ilex* as compared to those planted during the early and mid wet season (Palacios et al. 2009). Studies on natural regeneration of Mediterranean woody species also point to the importance of early seedling emergence in the wet season as a major driver for resisting drought stress during the first summer (Castro 2006; De Luis et al. 2008).

The length of the optimal root growth period determines the strength of the positive and negative feedback physiological processes of the model. Extreme climatic events, such as very low winter temperatures or very dry and warm spells during winter or lengthy delays in planting date will shorten the period of optimum growth and decrease the potential advantage of increase in seedling size and nutrient concentration. Results from an experiment performed under semi-arid condition in SE Spain on degraded soils and with a shallow soil preparation, where smaller, poor nutrient seedlings had higher survival than larger, rich nutrient plants, supports this idea (Trubat et al. 2011).

Shoot-to-root ratio scales up with above-ground seedling size when rooting volume remains constant (Villar-Salvador et al. 2005). S/R reflects the amount of roots in the plug respect to shoot size. High S/R may cause drought stress immediately after transplanting (Burdett 1990). However, seedling establishment depends on the production of new high water-uptake capacity roots, which grow out of the plug into the surrounding soil shortly after transplanting (Burdett 1990; Brissette and Chambers 1992; Sword Sayer et al. 2005). The proportion of new roots relative to shoot size (NR/S) is thus a more meaningful proxy of the balance between transpiration demand and water uptake than S/R (Grossnickle 2012). Villar-Salvador et al. (2005) reported that large seedlings in several Mediterranean species had similar or greater NR/S than small plants after RGC tests. This suggests that the "potential" vulnerability to water stress of larger seedlings due to higher S/R relative to smaller plants disappears soon after planting. This might explain the poor relationship between outplanting performance and S/R in container plants (Bernier et al. 1995).

Enhanced root growth with greater seedling size and N concentration could be reduced in soils restricting root growth, thus reducing differences in outplanting performance. Compact or low air-filled porosity soils can constrain root growth even under optimal moisture conditions (Zou et al. 2001). Shallow soils limit vertical moisture gradients and limit root extension, which can exacerbate drought vulnerability with increasing seedling size. This highlights the importance of soil preparation for the success of Mediterranean plantations (Palacios et al. 2009; Löf et al. 2012).

Most of the studies that inspired this model have been performed with Mediterranean conifers. However, Mediterranean flora has a high diversity of functional groups and it is likely that the relative importance of ecophysiological processes outlined in the model may differ among functional groups. For instance, we expect that the potential negative effect of seedling size on its water status might be lower in water-saver (e.g., *Pinus* species) than in water-spender plants (e.g., oaks and *Pistacia lentiscus*) (*sensu* Levitt 1980). Similarly, performance differences associated with seedling size are expected to be greater in pioneer rather than in late-successional species. Therefore, future studies should consider the high functional diversity of Mediterranean ecosystems and be directed to provide more solid evidence of the outlined physiological processes underpinning the proposed model. Specifically, we need information on how cultivation conditions affect seedling hydraulics and the role of plant hydraulics on seedling outplanting performance. We also need to understand better the role of current photosynthesis and stored NSC on root and shoot growth in most Mediterranean woody species. Although the model has been established from the experience gained in Mediterranean environments, we consider that it can be a suitable conceptual framework for other seasonal dry biomes, such as dry tropical forests. Finally, it can be used to understand the effect of other planting and post-planting operational works on plant performance.

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