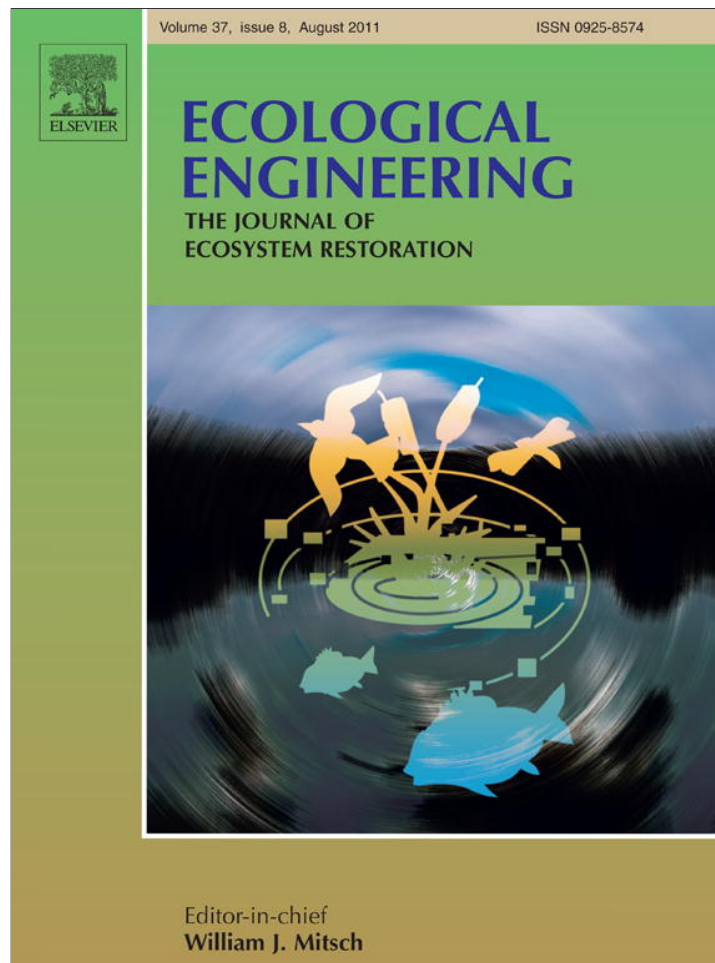


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Nutrient deprivation improves field performance of woody seedlings in a degraded semi-arid shrubland

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ABSTRACT

The performance of planted seedlings in drylands is affected by seedling morphological and physiological traits. Recent studies support a positive relationship between seedling size and field performance. However, exceptions to this paradigm suggest that this relationship may be dependent on species and degree of stress. To test the hypothesis that small seedlings would be favored under harsh semi-arid conditions over large seedlings, we produced seedlings of five Mediterranean woody species (*Pistacia lentiscus*, *Quercus coccifera*, *Rhamnus lycioides*, *Rhamnus alaternus* and *Tetraclinis articulata*) under contrasted fertilization regimes, and evaluated their performance after planting in a semi-arid area. Seedlings were cultivated under full sunlight and received either slow release fertilizer or bi-weekly applications of complete nutrient solution, diluted fertirrigation, or nutrient solutions containing no nitrogen or no phosphorus. Fertilization had a strong effect on nutrient status, above and belowground biomass accumulation, and biomass allocation patterns. Root: shoot ratio was higher in nitrogen- and phosphorus-deficient seedlings than in seedlings receiving complete nutrient solution or slow-release fertilizer. One year after planting, seedling survival was negatively correlated with plant size for all species. The effect of nutritional regime on field survival decreased over the 2 following years. Our results show that nutrient-deprived seedlings are more likely to establish under semi-arid conditions than well-fertilized seedlings, suggesting that morphological and functional characteristics associated with nutrient deficiency may outbalance the scarcity of nutrient reserves in seedling tissues.

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1. Introduction

In arid and semi-arid areas, woody species frequently act as keystone species (*sensu* Hulbert, 1997), because they are positively associated with ecosystem functioning and community diversity whereas their cover is scarce (Whitford, 2002; Maestre and Cortina, 2004). Woody species have been intensely harvested, grazed and cleared in drylands worldwide, resulting in an overall reduction in cover (Le Houérou, 1986; Maestre and Cortina, 2003). Seedling recruitment, once anthropogenic pressure has stopped, is frequently too slow or absent (Martínez-Mena et al., 2002; Bonet and Pausas, 2004), increasing the risk of further land degradation. In degraded environments, planting seedlings of sprouting woody species represents a suitable alternative to foster succession and restore ecosystem integrity (Whisenant, 1999; Cortina et al., 2004).

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The performance of planted seedlings is affected by various factors, such as environmental conditions, biotic interactions, and morpho-physiological traits (South and Smith, 2000; Palacios et al., 2009). These factors are particularly important in drylands, as adverse environmental conditions exert a strong filter for seedling establishment (Maestre et al., 2003; Cortina et al., 2006). Morpho-physiological traits are partly controlled by genetic origin (Van Andel, 1998), but they can be modified by cultural practices such as sowing density, container size, irrigation and fertilization regimes (Vilagrosa et al., 2003a; Luis et al., 2004; Chirino et al., 2008). Nevertheless, there is currently no consensus on the optimum traits defining seedling quality in drylands (Cortina et al., 2006). In mesic environments, larger plants frequently show higher survival and growth in the field than smaller plants (Kormanik et al., 1997). The pattern may be similar in drylands (Oliet et al., 2005; Luis et al., 2009), but the literature shows several examples of neutral and negative relationships between seedling size and field performance, particularly under semi-arid conditions (Tuttle et al., 1988; Rose et al., 1993; Seva et al., 2000; Trubat et al., 2008).

Fertilization is a common nursery technique that strongly influences plant growth and modifies seedling morphological and

physiological traits (Lambers and Poorter, 2004; Grossnickle, 2005; Oliet et al., 2006). Several studies have shown a positive relationship between nutritional status at planting and field performance (Pueirtolas et al., 2003; Milla et al., 2005; Luis et al., 2009). However, seedlings cultivated with low nutrient availability may be better prepared to drought because of their reduced size and leaf area, greater biomass allocation belowground, increased water-use efficiency and changes in xylem hydraulic architecture (Liu and Dickmann, 1993; Forde and Lorenzo, 2001; Hernández et al., 2009). In fact, low growth rates are common in plants growing under nutrient and water stress (Chapin, 1991). On the other hand, soil nitrogen availability is frequently low in degraded Mediterranean soils, and may limit seedling establishment (Martínez-Mena et al., 2002; Navarro et al., 2006a). Depletion of seedling N reserves could compromise seedling performance in the field (Cortina et al., 2009). But a reduction in N supply may increase the concentration of other nutrients in leaves, as potassium (Lee and Rudge, 1986). Nutrient hardening (i.e., the suppression of N inputs in late stages of seedling production) has shown promising results in semi-arid areas (Trubat et al., 2008). Effects of late-nitrogen deprivation, such as a reduction in water transport capacity (Ewers et al., 2000; Trubat et al., 2006), may also play a role in the water economy of N-limited plants by promoting a conservative use of water (Sperry, 2003).

Mediterranean species show contrasted strategies to cope with drought (Larcher, 1995; Vilagrosa et al., 2003b) and contrasted sensitivity to nutrient availability (Valdecantos et al., 2006). Some species and genotypes are less responsive to changes in resource supply than others (Coleman, 2007). Thus, the ability of seedlings receiving contrasted nutrient supply to withstand drought and establish under harsh field conditions will likely be species-specific (Cuesta et al., 2010).

The objective of the present work is to evaluate the effect of nutrient deficiency on the functional traits of seedlings of five Mediterranean woody species widely used in reforestation programs (Cortina et al., 2004; Vallejo et al., 2006), and to compare the performance of nutrient-deficient seedlings with well fertilized seedlings after planting in a semi-arid degraded area. Our underlying hypothesis is that functional adjustments to nutrient stress outbalance the negative effect of nutrient deficiency, improving seedling capacity to withstand drought and their ability to establish under field conditions. To achieve the objectives, we grew seedlings of *Pistacia lentiscus*, *Quercus coccifera*, *Rhamnus alaternus*, *Rhamnus lyciodes* and *Tetraclinis articulata* under contrasted fertilization regimes, and evaluated their morpho-physiological features and field performance 1 and 2 years after planting.

2. Materials and methods

2.1. Experimental design

Seedlings of *P. lentiscus* L. (Anacardiaceae), *Q. coccifera* L. (Fagaceae), *Rhamnus lyciodes* L., *R. alaternus* L. (Rhamnaceae), and *T. articulata* (Valh) Masters Cupressaceae were grown in a nursery (Santa Faz, Alicante, SE Spain; 38°23'N, 0°26'E, 50 m elevation), under semi-arid climate, with a 30-year average annual precipitation and temperature of 353 mm and 18 °C, respectively (Fig. 1). The first four species are sprouting shrubs widespread in the western Mediterranean. In semi-arid steppes, they are considered keystone species affecting community composition and ecosystem function (Maestre and Cortina, 2003). *T. articulata* is one of the few tree species that thrives in semi-arid SE Spain, where only a few small populations remain. They are all common species in the Mediterranean basin and they are widely used in reforestation projects in SE Spain (Cortina et al., 2004; Vallejo et al., 2006;

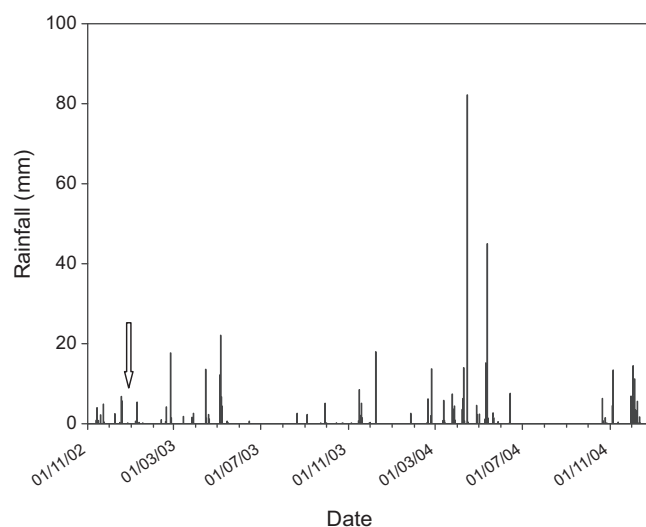


Fig. 1. Rainfall events between November 2002 and December 2004 at the weather station nearest to the experimental area (Albatera, SE Spain). The arrow indicates the planting date.

F. Gil, Regional Government of Valencia, personal communication).

Seedlings were cultivated in the open air from February 2002 to January 2003 in 305 cm³ forest containers (Super-leach®) filled with a mixture of peat (Kekkilä) and coco-peat (1:1, v/v). A total of 175 seedlings per species and treatment were grown on 5 separate trays randomly distributed in 12 blocks. Seeds of the five species were collected from local provenances (Region of Valencia, Eastern Spain) by the Forest Service (Regional Forest Seed Bank, Generalitat Valenciana). Seedlings were cultivated under full sunlight and received a modified Hoagland's solution containing 150 mg N L⁻¹ (as Ca (NO₃)₂ and KNO₃), 80 mg P L⁻¹ (as KH₂PO₄) and 100 mg K L⁻¹ (Control, hereafter CON), similar solutions containing no N (Nitrogen-deficient seedlings, hereafter NDF), no P (Phosphorus-deficient seedlings, hereafter PDF), or half of the concentration of the CON solution (hereafter DEF) (Table 1). In NDF and PDF seedlings, the osmolarity of the nutrient solution was adjusted with KCl (Radin, 1984). Nutrient solutions were applied every two weeks during the whole nursery period by saturating the growing media. The fertilizer dose applied to CON seedlings has been recommended for forest species and is widely used in forest nurseries (Landis, 1985). An additional set of seedlings was grown by adding 1.8 g of a commercial 14–9–15 (N:P:K) slow-release fertilizer (Plantacote®) per L of growing substrate (hereafter SRF). These seedlings received no further fertilization during the nursery period.

Table 1

Composition of the nutrient solutions and the slow release fertilizer used in this study. Concentrations are in mg L⁻¹ and %, respectively.

	CON	NDF	PDF
KNO ₃	258		258
Ca(NO ₃) ₂ ·4H ₂ O	689		698
NaH ₂ PO ₄ ·H ₂ O	356	356	
MgSO ₄ ·7H ₂ O	570	570	570
KCl		191	
CaCO ₃		420	
SRF			
N total	14		
P ₂ O ₅	9		
K ₂ O	15		
MgO	2		

2.2. Morphological and physiological traits

We measured stem height, root collar diameter (RCD), leaf area, biomass accumulation, and foliar nutrient concentration at the end of the nursery period (February 2003). Measurements were taken in 10 randomly selected seedlings per species and treatment. Leaf area was measured by scanning the leaves (EPSON Expression 1680 Pro scanner with transparency adapter) and images were analyzed by means of specific software (WinRhizo, Régent Instruments Inc., Quebec, Canada). Biomass fractions were measured after drying at 65 °C for 48 h. The root:shoot ratio (g g^{-1}) was calculated as the ratio between the root and the shoot dry weight. Specific leaf area (SLA, $\text{cm}^2 \text{g}^{-1}$) was calculated as the ratio between total leaf area and foliar dry weight. Dry leaves were ground in a ring mill and digested in a heating block at 250 °C with a mixture of H_2SO_4 and H_2O_2 (1:1, v/v). Total N concentration was determined by using semi-micro Kjeldahl distillation (Tecator Kjeltac Auto 1030 Analyzer, Hogana, Sweden), and P and K concentration by ICP spectrometry (Perkin Elmer Optima 3000, Perkin Elmer Corp., Norwalk, CT, USA).

Root growth potential (RGP) was measured in another 10 seedlings per species and treatment. *T. articulata* was excluded from this analysis because of the lack of seedlings. Seedlings were transplanted to 3 L PVC pots filled with vermiculite and watered with CON solution every two days. The growth chamber provided day conditions of 22 °C for 16 h with a photosynthetic photon flux density of $400 \mu\text{mol m}^{-2} \text{s}^{-1}$ and 18 °C night temperature. The number of newly elongated white roots longer than 5 mm was recorded at the end of a 21-day period.

2.3. Field performance

On January 31st 2003, one 50 m × 50 m plot was established in a degraded area close to Albaterra (Alicante, SE Spain; 38°14'N, 0°56'E, 350 m a.s.l.; 24° slope; 240° SW aspect). The area is covered with sparse vegetation and showed evidence of soil compaction and erosion. Thirty-five randomly selected seedlings per species and treatment were planted in 40 cm × 40 cm × 40 cm planting holes dug with a backhoe mounted on a spider tractor. Species and treatment distribution were also random. The climate of the experimental area is Mediterranean semi-arid, with a 30-year average annual precipitation and temperature of 277 mm and 18.2 °C, respectively. Average annual rainfall and temperature in 2003 were 151 mm and 17.2 °C, respectively. Soils are loam to silty loam, Lithic Calciorthiss (Soil Survey Staff, 1990). Seedling survival, stem height and root collar diameter (RCD) were monitored in all seedlings before and after the summer of 2003, in winter 2004, and after summer 2004.

2.4. Statistical analyses

We used analysis of variance (ANOVA) to evaluate the effect of nutritional regime (fixed factor with five levels) on seedling traits and Student–Newman–Keuls test at $P < 0.05$ for pair-wise comparisons when results of the ANOVA were significant. All variables fulfilled ANOVA requirements of normality and homoscedasticity. The relationships between RGP and seedling survival, and RGP and RCD, were assessed by Pearson correlation analysis. Relationships between seedling size and seedling survival were analyzed using logistic regression. The regression coefficient (B) was transformed into the odds ratio to facilitate interpretation. Odds ratios were calculated as the probability of the event occurrence divided by the probability that the event would not occur: $(p_n)/(1 - p_n)$, where p_n is the probability of seedling survival. In this study, the odds ratio corresponds to the multiplicative factor

that describes the increase in the probability of seedling survival when the independent variable (stem height) increases by one unit. The statistical significance of this parameter was evaluated with Wald's test (Hosmer and Lemeshow, 1989). Finally, comparisons of survival between CON seedlings and treated seedlings were performed using logistic regression analysis. All analyses were carried out with SPSS v.15.0 statistical package (SPSS Inc., Chicago, IL, USA).

3. Results

3.1. Nutrient status

Leaf N concentration ranged from 5 to 32 mg g^{-1} (Table 2). *R. lycioides* and *T. articulata*, showed lower variability in N concentration in response to fertilization than the other species, as the differences between minimum and maximum concentration were slightly higher than 100% in the former 2 species, and above 300% in the other species. *R. lycioides* showed the smallest relative changes in P concentration in response to fertilization, and *T. articulata* showed the highest variability. Foliar N and P concentration were strongly reduced in NDF and PDF seedlings, respectively. Foliar P concentration in NDF seedlings was significantly lower than in CON seedlings in *P. lentiscus*, *R. alaternus*, and *Q. coccifera*. The same trend was observed for the other two species, but the difference was not statistically significant. NDF seedlings showed an increase in foliar K which was statistically significant in *P. lentiscus*, *R. alaternus*, *Q. coccifera* and *R. lycioides*, and marginally significant in *T. articulata*. Seedlings receiving slow release fertilizer showed the highest N concentration in *P. lentiscus* and *Q. coccifera* but not in the other species. Slow release fertilizer decreased foliar P concentration as compared to CON seedlings in all species.

3.2. Seedling growth

Nutrient deprivation had a strong negative effect on seedling size (Table 3). Reductions in stem height in NDF seedlings ranged from 22% (*R. lycioides*) to 44% (*R. alaternus*) relative to CON seedlings. Seedlings receiving slow release fertilizer increased stem height compared to CON seedlings in all species but *Q. coccifera*. Root collar diameter showed a similar trend. *R. alaternus* showed the highest reduction in root collar diameter when N was removed from the nutrient solution (Table 3).

Fertilization showed a significant effect on the aboveground biomass, and biomass allocation patterns of the five species (Table 3). Changes in leaf area paralleled those in aboveground biomass. SLA decreased in NDF seedlings as compared to CON seedlings in *Q. coccifera*, *R. lycioides*, and *T. articulata*, but not in *P. lentiscus* where we observed the opposite trend. *R. alaternus* responded to SRF fertilization by increasing SLA. SRF application significantly enhanced aboveground and belowground biomass in all species but *R. alaternus*, compared to the application of complete nutrient solution.

Despite the increase in root: shoot in NDF and PDF seedlings in all species but *R. alaternus*, root growth potential decreased in nutrient-deficient seedlings as compared to seedlings receiving standard fertilization (Fig. 2). A decrease in RGP was observed in NDF and PDF seedlings compared to CON seedlings in *P. lentiscus*, *R. alaternus*, *Q. coccifera*, and *R. lycioides*. SRF promoted RGP in all species but *R. alaternus* and *R. lycioides*. The correlation between RGP and seedling size was highly significant for all species (*P. lentiscus* $r^2 = 0.788$; *R. alaternus* $r^2 = 0.629$; *Q. coccifera* $r^2 = 0.753$; *R. lycioides* $r^2 = 0.614$; $N = 10$ and $P < 0.05$ in all cases). The relationship between RGP and RCD showed a similar pattern (data not shown).

Table 2

Foliar nutrient concentration in seedlings of woody species growing in the nursery under a standard fertilization regime (CON), 50% reduction in nutrient supply (DEF), application of slow release fertilizer (SRF), and phosphorus (PDF) and nitrogen (NDF) deprivation. Data are means ± S.E. (n = 10 plants). Different letters indicate significant differences for a given species and nutrient at P < 0.05.

Treatment	Nutrient	<i>P. lentiscus</i>	<i>R. alaternus</i>	<i>Q. coccifera</i>	<i>R. lycioides</i>	<i>T. articulata</i>
CON	N (mg g ⁻¹)	19 ± 1.2a	32 ± 2.0a	19 ± 1.5b	17 ± 1.3a	16 ± 1.1a
	P (mg g ⁻¹)	6.4 ± 0.5a	4.4 ± 0.8a	3.8 ± 0.5a	3.1 ± 0.5a	6.1 ± 0.9ab
	K (mg g ⁻¹)	8.3 ± 0.5a	6.9 ± 0.9a	5.4 ± 0.3b	5.7 ± 0.6a	8.1 ± 1.4ab
DEF	N (mg g ⁻¹)	16 ± 1.5a	12 ± 1.2c	14 ± 1.1b	13 ± 1.2a	13 ± 1.4b
	P (mg g ⁻¹)	3.8 ± 0.3b	2.1 ± 0.4b	3.4 ± 0.3a	2.1 ± 0.2a	3.2 ± 1.4a
	K (mg g ⁻¹)	5.7 ± 0.6b	3.9 ± 0.4b	4.5 ± 0.5c	4.1 ± 0.3a	5.3 ± 1.1a
SRF	N (mg g ⁻¹)	25 ± 1.3a	24 ± 2.1b	26 ± 1.3a	13 ± 1.0a	14 ± 1.1b
	P (mg g ⁻¹)	2.7 ± 0.3b	2.1 ± 0.1b	2.5 ± 0.1b	2.3 ± 0.3a	3.3 ± 0.2a
	K (mg g ⁻¹)	7.5 ± 0.7ab	6.1 ± 0.8c	7.5 ± 0.7a	4.1 ± 0.3a	7.3 ± 0.7a
PDF	N (mg g ⁻¹)	22 ± 1.6a	21 ± 1.4b	12 ± 1.2b	19 ± 1.7a	16 ± 1.3a
	P (mg g ⁻¹)	2.1 ± 0.5c	1.6 ± 0.1c	1.8 ± 0.2b	1.6 ± 0.8b	1.8 ± 0.4c
	K (mg g ⁻¹)	6.1 ± 0.9ab	5.20 ± 4bc	4.2 ± 0.5c	2.5 ± 0.5b	6.7 ± 0.6a
NDF	N (mg g ⁻¹)	6 ± 1.0b	8 ± 1.1c	5 ± 1.0c	9 ± 1.1b	7 ± 2.1c
	P (mg g ⁻¹)	3.5 ± 0.4b	2.8 ± 0.4b	2.2 ± 0.1b	2.6 ± 0.1a	5.9 ± 1.1b
	K (mg g ⁻¹)	7.8 ± 0.5ab	3.9 ± 0.5b	4.4 ± 0.6c	5.6 ± 0.2a	10.1 ± 2.4b
F	N	4.8***	33.8***	33.6***	7.1***	7.1***
	P	25.7***	15.1***	12.2***	9.3***	8.9***
	K	3.1*	13.7***	4.32**	7.5***	6.2**

* Asterisk indicates the statistical significance of ANOVA, 0.05 > P > 0.01.

** Asterisk indicates the statistical significance of ANOVA, 0.01 > P > 0.001

*** Asterisk indicates the statistical significance of ANOVA, P < 0.001.

Table 3

Morphological traits of seedlings of Mediterranean woody species growing under various fertilization regimes. See Table 1 for a description of the treatments. Data are means ± S.E. (n = 10 plants). Different letters indicate significant differences for a given response variable and species at P < 0.05.

	Leaf dry weight (g)	Root dry weight (g)	Leaf area (cm ²)	Root:shoot	SLA (cm ² g ⁻¹)	Height (cm)	RCD (mm)
<i>Pistacia lentiscus</i>							
CON	1.14 ± 0.06b	1.18 ± 0.10b	37.55 ± 2.35ab	0.72 ± 0.08b	32.88 ± 2.29ab	19.5 ± 1.3	4.2 ± 0.3c
DEF	1.09 ± 0.10b	1.02 ± 0.10b	29.96 ± 4.58b	0.67 ± 0.10b	28.17 ± 1.58b	13.5 ± 0.8c	3.4 ± 0.2b
SRF	2.40 ± 0.40a	2.57 ± 0.29a	49.81 ± 4.17a	0.76 ± 0.07b	28.17 ± 1.58b	24.8 ± 0.9e	5.8 ± 0.2d
PDF	0.25 ± 0.10c	0.40 ± 0.02c	8.63 ± 1.13c	0.90 ± 0.09a	34.03 ± 1.76ab	7.7 ± 0.5b	3.0 ± 0.2b
NDF	0.10 ± 0.01d	0.18 ± 0.01d	4.78 ± 0.85d	0.89 ± 0.15a	57.05 ± 11.68a	4.7 ± 0.2a	1.6 ± 0.1a
F	66.78***	151.29***	76.49***	5.44**	3.56*	145.87***	97.93***
<i>Rhamnus alaternus</i>							
CON	0.92 ± 0.07a	0.86 ± 0.10ab	81.30 ± 7.60a	0.60 ± 0.07c	90.56 ± 9.25b	13.3 ± 1.3c	3.0 ± 0.2d
DEF	0.67 ± 0.08b	0.66 ± 0.08b	35.10 ± 3.70b	0.65 ± 0.07c	53.71 ± 1.76c	11.0 ± 1.0c	2.6 ± 0.1c
SRF	0.94 ± 0.07a	1.05 ± 0.11a	97.80 ± 4.74a	0.68 ± 0.03c	107.20 ± 5.43a	19.3 ± 1.3d	3.8 ± 0.2e
PDF	0.52 ± 0.06b	0.13 ± 0.01d	8.57 ± 1.08c	0.81 ± 0.03b	17.21 ± 1.78d	4.2 ± 0.3b	1.9 ± 0.1b
NDF	0.11 ± 0.01c	0.15 ± 0.01d	5.61 ± 0.40d	0.95 ± 0.15a	50.43 ± 1.76c	3.0 ± 0.1a	1.2 ± 0.1a
F	57.57***	53.67***	173.09***	18.07***	104.75***	84.43***	46.02***
<i>Quercus coccifera</i>							
CON	1.30 ± 0.12b	4.52 ± 0.66b	62.9 ± 9.98b	2.08 ± 0.21b	51.41 ± 11.72a	17.3 ± 1.3c	3.5 ± 0.2bc
DEF	0.87 ± 0.10b	3.44 ± 0.36c	49.6 ± 4.50b	0.67 ± 0.30a	59.15 ± 4.52a	11.7 ± 1.1b	3.2 ± 0.2a
SRF	2.05 ± 0.16a	7.30 ± 0.49a	100.20 ± 4.22a	0.42 ± 0.08ab	50.63 ± 2.74a	17.8 ± 1.4c	3.7 ± 0.2c
PDF	0.82 ± 0.05b	4.10 ± 0.26b	37.90 ± 1.70c	0.64 ± 0.15a	46.24 ± 1.46ab	13.7 ± 1.2b	3.4 ± 0.1ab
NDF	0.48 ± 0.17c	1.93 ± 0.17d	13.10 ± 2.05c	0.75 ± 0.52a	35.17 ± 7.20b	8.2 ± 0.7a	3.0 ± 0.2a
F	20.29***	20.99***	70.76***	4.38***	4.01***	13.18***	7.01***
<i>Rhamnus lycioides</i>							
CON	1.19 ± 0.13b	0.92 ± 0.12b	62.36 ± 8.26cb	0.56 ± 0.07b	54.11 ± 17.11a	10.3 ± 0.8b	2.3 ± 0.1b
DEF	0.58 ± 0.04c	0.89 ± 0.07b	28.53 ± 3.20c	0.71 ± 0.08a	48.70 ± 15.40a	9.1 ± 0.6b	2.3 ± 0.1b
SRF	2.65 ± 0.20a	2.54 ± 0.16a	97.30 ± 4.79a	0.54 ± 0.01b	37.81 ± 11.96ab	21.5 ± 1.7c	3.4 ± 0.2c
PDF	0.15 ± 0.05d	0.25 ± 0.06c	5.38 ± 0.75d	0.69 ± 0.72a	48.70 ± 15.40a	6.1 ± 0.5a	1.4 ± 0.1a
NDF	0.22 ± 0.03d	0.26 ± 0.03c	5.13 ± 0.96d	0.75 ± 0.03a	27.93 ± 8.83b	4.5 ± 0.3a	1.2 ± 0.1a
F	84.09***	85.04***	135.21***	44.46***	4.05***	60.78***	51.95***
<i>Tetraclinis articulata</i>							
CON	0.31 ± 0.06bc	0.22 ± 0.05c	14.10 ± 1.80b	0.66 ± 0.16c	50.71 ± 4.88a	9.8 ± 0.6c	2.2 ± 0.2b
DEF	0.50 ± 0.05bc	0.28 ± 0.05c	18.61 ± 1.74b	0.44 ± 0.13c	31.12 ± 0.84b	7.8 ± 0.4b	2.1 ± 0.1b
SRF	3.12 ± 0.30a	3.30 ± 0.19a	96.21 ± 7.87a	0.84 ± 0.05b	31.12 ± 0.84b	16.1 ± 1.1d	4.1 ± 0.2c
PDF	0.29 ± 0.03b	0.34 ± 0.04b	9.13 ± 1.20c	0.81 ± 0.07b	31.30 ± 1.44b	7.0 ± 0.6b	1.7 ± 0.1ab
NDF	0.10 ± 0.01c	0.14 ± 0.01ad	3.05 ± 0.40d	0.93 ± 0.09a	28.32 ± 1.80b	3.8 ± 0.2a	1.4 ± 0.1a
F	181.02***	113.87***	134.84***	13.81***	7.14***	58.24***	36.33***

* Asterisk indicates the statistical significance of ANOVA, 0.05 > P > 0.01.

** Asterisk indicates the statistical significance of ANOVA, 0.01 > P > 0.001

*** Asterisk indicates the statistical significance of ANOVA, P < 0.001.

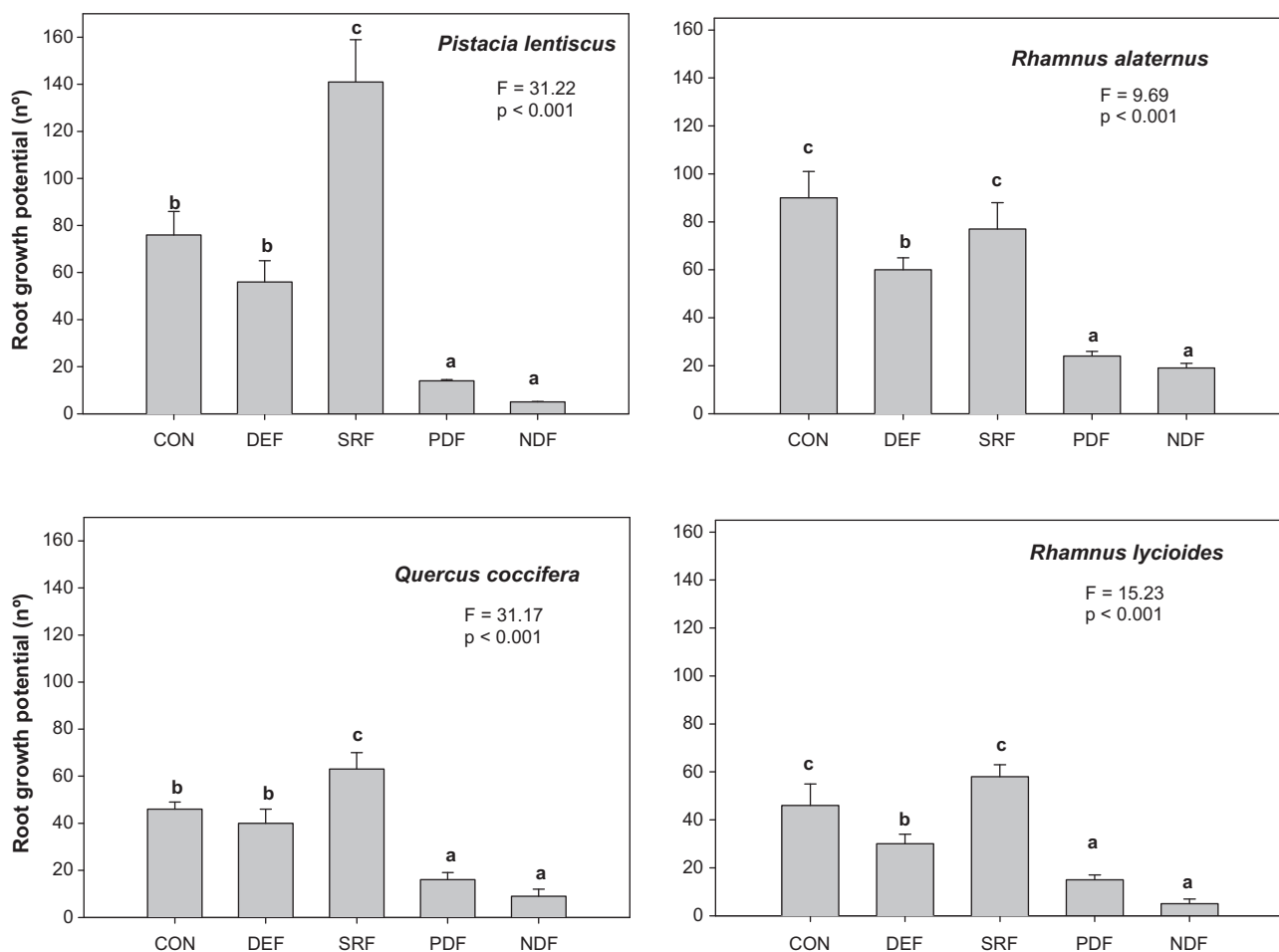


Fig. 2. Root growth potential of *Pistacia lentiscus*, *Rhamnus alaternus*, *Quercus coccifera* and *Rhamnus lycioides* seedlings grown under a standard fertilization regime (CON), 50% reduction in nutrient supply (DEF), application of slow release fertilizer (SRF), and phosphorus (PDF) and nitrogen (NDF) deprivation. Data are means \pm S.E. ($N = 10$ plants). Different letters indicate significant differences at $P < 0.05$.

3.3. Field performance

Four months after planting seedling survival ranged between 60% and 100% (Fig. 3). Survival decreased to 18–79% after the first summer and to 2–54% after the second summer. The effect of nitrogen deficiency on seedling survival was evident after the first summer (October 2003) compared with other treatments in all species (Table 4). After the third summer (October 2005) only *P. lentiscus* showed a significant difference in survival rate between NDF and CON seedlings.

Logistic regressions showed a significant increase in seedling mortality with plant size. There was a highly significant odds-ratio for all species (Fig. 4). *T. articulata* showed the highest increases in mortality with seedling size, as denoted by the high value of the odds ratio. Logistic regressions also showed significant odds-ratios when each treatment was analyzed separately (data not shown).

4. Discussion

4.1. Fertilization and seedling traits

We found a strong effect of N and P deprivation on foliar nutrient concentration. Nitrogen concentration in NDF seedlings was close to levels of N deficiency described in Mediterranean species (Fernández-Escobar et al., 1999). All species showed similarities

in the way they responded to contrasting nutrient availability, but there were substantial differences in the magnitude of such responses. Nitrogen and phosphorus deprivation resulted in an overall decrease in shoot and root biomass. The effect was stronger for aboveground biomass accumulation, as all species showed a significant increase in root: shoot ratio when N and P were removed from the nutrient solution. A shift in biomass allocation from shoots to roots is a well-documented response to nutrient limitation (Ingestad and Ågren, 1991; Poorter and Nagel, 2000), and may promote plant ability to access soil resources (Ingestad and Ågren, 1991) and improve water supply aboveground (Hernández et al., 2009). In contrast, changes in specific leaf area were highly dependent on species. The significant reduction in SLA with PDF in *R. alaternus*, *Q. coccifera*, *R. lycioides* and *T. articulata* may be a consequence of anatomical changes, such as reductions in cell diameter, increases in cell wall thickness and increases in the proportion of dense tissues (Castro-Díez et al., 1997). Increased biomass allocation belowground and decreased specific leaf area have been associated with a greater ability to withstand drought (Corcuera et al., 2002), as they may reduce water losses and increase seedling capacity to access soil water (Gratani and Bombelli, 2001).

4.2. Species-specific responses

R. alaternus and *P. lentiscus* showed the highest variability in stem height and RCD in response to changes in nutrient supply,

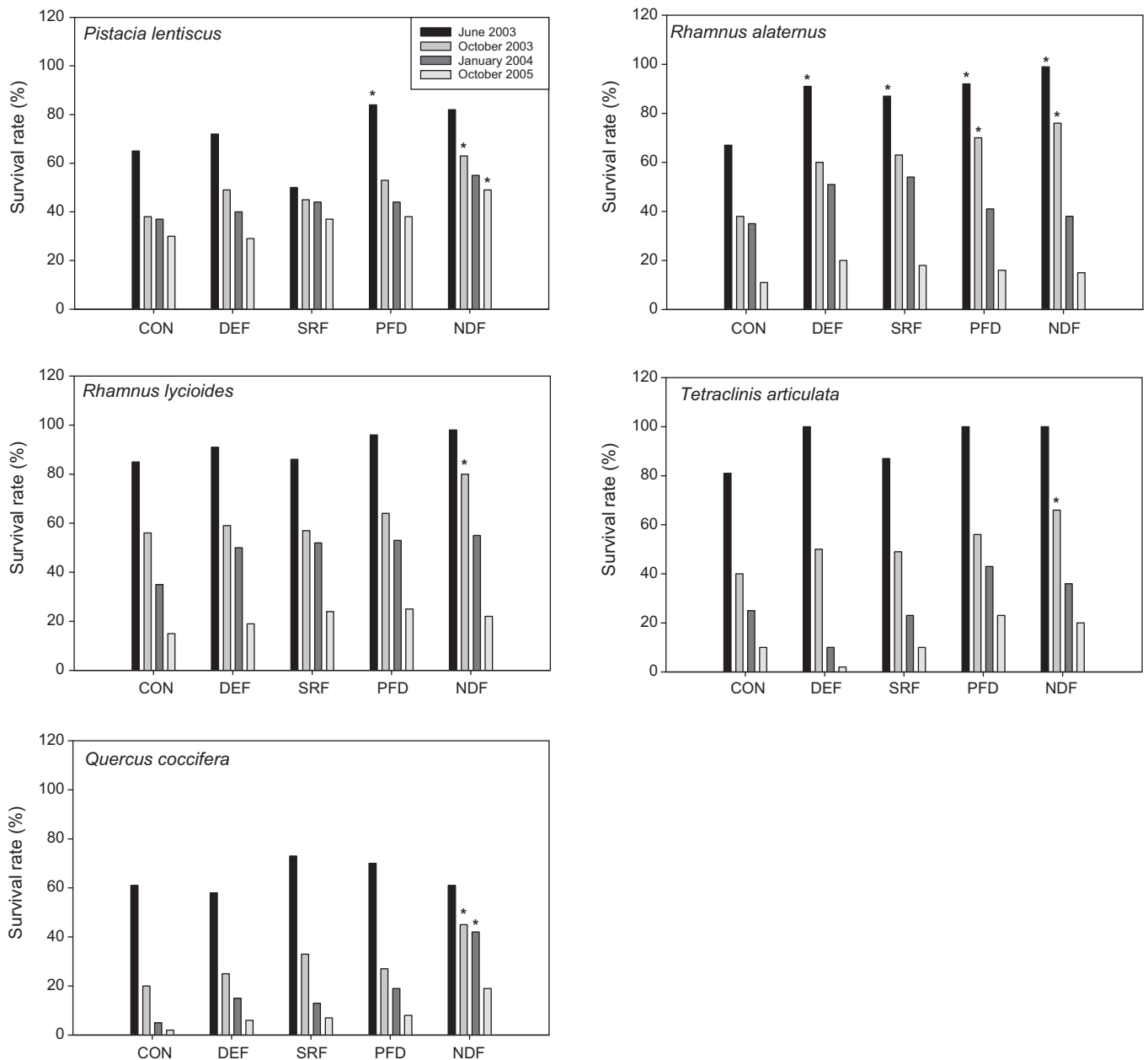


Fig. 3. Field survival of seedlings of Mediterranean woody species grown under various fertilization regimes. Bars correspond to consecutive sampling dates. Asterisks indicate the statistical significance of logistic regression.

whereas *Q. coccifera* was the least responsive species. Different responses to fertilization may be a result of interspecific dissimilarities in nutrient transport and partitioning (Van de Dijk et al., 2006), morphological and anatomical structure (Mediavilla and Escudero, 2003), and nutrient resorption efficiency (Aerts and Chapin, 2000).

In addition, differences in species response to contrasted nutrient availability may be the result of differences in the amount of nutrients supplied by the seeds (Fenner, 1983; Jurado and Westoby, 1992; Wu et al., 2006). *Q. coccifera* acorns were bigger than seeds from the other species tested (García-Fayos et al., 2001). Observations from another Mediterranean oak, *Quercus ilex*, suggest that nutrient reserves may supply seedling demands until the end of the first spring after germination (Villar-Salvador et al., 2010).

4.3. Root growth potential

New roots are critical for the establishment of woody seedlings in the field (Grossnickle, 2005) and there is a general consensus on the benefits of a high rooting capacity for seedling establishment in drylands (Lloret et al., 1999; Padilla and Pugnaire, 2007). Root growth potential tests (RGP) have been widely used to evaluate the effect of environmental stress on plant performance, and they have been recommended as an indicator of seedling vitality and stock quality (Simpson and Ritchie, 1997). Simpson and Ritchie (1997) suggested that the predictive ability of RGP increases with environmental stress, particularly in species with low resistance to stress. However, the use of RGP to predict seedling growth and survival in the field has been debated (Mohammed et al., 1997; L'Hirondelle et al., 2007) as several studies suggest that RGP does

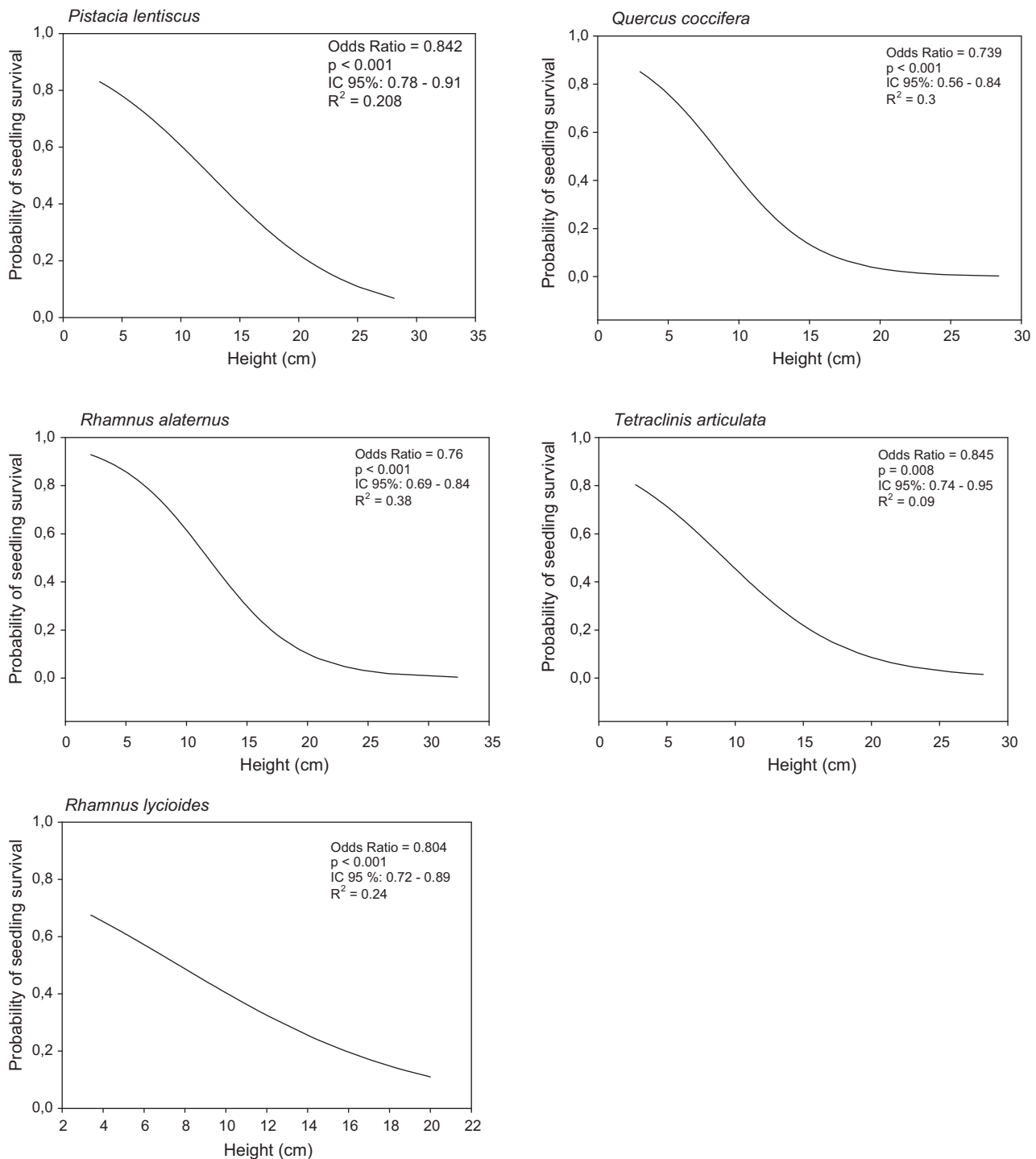


Fig. 4. Logistic regression between seedling size and field survival of Mediterranean woody species four months after planting ($N=150$ for each species). Data from all fertilization regimes were pooled for these analyses. Parameters of the logistic regression, including the Odds ratio, probability, confidence interval and Nagelkerke R^2 are included in each graph.

not necessarily reflect seedling ability to establish under harsh field conditions (Davis and Jacobs, 2005; Trubat et al., 2006). In the present study, RGP was positively correlated with shoot size in all species but *Q. coccifera*, suggesting that RGP could be a suitable indicator of seedling vitality under favorable environmental conditions. In contrast, the relationship between RGP and seedling performance in the field was opposite to what was expected. We

did not expect a direct negative effect of RGP on seedling performance in the field. As high RGP may be positive for seedling establishment, other traits covarying with RGP were probably responsible for the observed decrease in survival. Regardless of the causal relationship, our results show that RGP is a poor indicator of seedling performance under field conditions in semi-arid lands when other morpho-physiological traits are not taken into account.

Table 4
Results of logistic regression analyses to compare the survival of CON seedlings and seedlings subjected to various nutritional regimes. See Table 1 for a description of the treatments.

DEF	Wald	Exp (b)	<i>P. lentiscus</i>															
			<i>R. alaternus</i>				<i>Q. coccifera</i>				<i>R. lycioides</i>				<i>T. articulata</i>			
			June 03	October 03	January 04	October 05	October 03	June 03	October 03	January 04	October 05	October 03	June 03	October 03	January 04	October 05		
	0.42	0.72	0.26	0.36	3.37	1.58	0.58	0.07	0.43	0.08	1.44	0.19	1.01	0.13	0.87	0.21		
	0.70	0.65	0.76	0.71	0.36	0.50	0.53	0.75	0.60	0.86	0.54	0.74	0.31	0.778	2.27	1.75		
SRF	1.54	0.24	0.53	1.39	3.72	2.80	0.19	1.46	0.01	0.04	1.71	0.88	0.26	0.34	0.005	0.02		
	1.84	0.78	0.69	0.53	0.35	0.40	0.69	0.34	0.92	0.89	0.51	0.54	0.62	0.68	1.05	0.85		
PDF	3.00	1.94	0.70	1.61	5.52	6.42	0.28	1.17	2.26	2.41	2.47	0.95	0.62	1.01	0.95	1.173		
	0.35	0.5	0.65	0.51	0.14	0.24	0.75	0.38	2.52	0.72	0.45	0.53	0.40	0.49	0.49	0.37		
NDF	1.81	4.53	2.62	5.33	6.03	0.64	6.95	2.37	0.01	3.72	2.46	0.88	2.12	3.34	0.78	0.88		
	0.47	0.34	0.45	0.30	0.07	0.24	0.15	0.26	0.92	0.33	0.44	0.54	0.19	0.34	0.58	0.47		

4.4. Seedling traits and field performance

In Mediterranean areas, bigger seedlings commonly show higher survival and growth when planted in the field (Villar-Salvador et al., 2004; Oliet et al., 2005). But this relationship may be different in semiarid areas, where several studies have failed to find a positive relationship between seedling size and field survival (Cortina et al., 1997). The reasons for this may be related to the balance between root and foliar surface area (Trubat et al., 2006), and to the ability of seedlings to produce deep root systems before the onset of summer drought (Padilla and Pugnaire, 2007). Conceptual models describing the mechanisms that relate seedling size and N concentration with seedling survival in the field have been extensively discussed (Tan and Hogan, 1995; Villar-Salvador, 2003; Luis et al., 2009; Cuesta et al., 2010). But the increase in transpiration resulting from the increase in foliar surface area has received scarce attention. Decreases in leaf area commonly enhance convective heat loss and facilitate the maintenance of leaf energy balance. A reduction in leaf area may reduce transpiration rate in leaves exposed to high radiation, improving water use efficiency under drought (Miller and Stoner, 1979). Mediterranean plants may withstand drought by decreasing water losses and increasing water uptake and transport capacity to aboveground parts (Larcher, 1995). In the present study, both N and P deficiencies resulted in substantial decreases in leaf area, which probably lowered transpiration rates and reduced water demands. We may note, however, that the lack of a positive relationship between seedling size and field performance may have been favored by the lack of significant rainfall events between the planting date and the onset of summer.

In our study, biomass allocation belowground was reduced by N and P deprivation, but the proportional decrease was lower than the decrease observed in aboveground biomass. As a result, the root: shoot ratio increased in NDF and PDF seedlings as compared to CON and SRF seedlings in all species but *Q. coccifera*. Increased biomass allocation belowground may have enlarged root capacity to supply water per unit of leaf area, provided that changes in hydraulic conductivity did not outbalance changes in biomass allocation patterns. Studies of the effect of nutrient availability on seedling ability to transport water are scarce (but see Harvey and van den Driessche, 1999, for an example from mesic environments). Previous works on *P. lentiscus* have shown that N and P deficiency decreases specific hydraulic conductivity on a root area basis, but does not significantly affect seedling capacity to transport water per unit of leaf area (Trubat et al., 2006). A decrease in hydraulic conductivity can be associated to reduced vulnerability to cavitation (Sperry, 2000) and thus higher resistance to drought. Similar results were presented by Syvertsen and Graham (1985) in citrus. In contrast, Hernández et al. (2009) found a decrease in root hydraulic conductance with increasing fertilization in *P. lentiscus*, suggesting that the response of hydraulic conductivity to the direct and indirect effects of increased nutrient availability may not be linear.

Nutrient concentration in seedlings deprived of N and P was substantially lower than the values shown by well-fertilized seedlings. Nutrient deficiency has been associated with lower establishment success in Mediterranean species, probably as a result of impaired carbon assimilation (Cortina et al., 2008). On the other hand, we observed no significant increase in P concentration in NDF seedlings, N concentration in PDF seedlings and K concentration in NDF and PDF seedlings of most species compared to CON seedlings. These results suggest that the overall positive effect of N and P deficiency on field performance was not a result of luxury consumption or promoted storage of limiting nutrients.

4.5. Management implications

Several studies have shown a positive relationship between seedling size at planting and field performance (Cortina et al., 1997; Villar-Salvador et al., 2004; Luis et al., 2009). But the number of studies showing no significant or negative relationships is substantial (Navarro et al., 2006b). In our study, five species showed a negative relationship between size and survival which persisted for 1 year in the field. We should note that the improvement in seedling performance occurred despite that seedlings were severely nutrient-deficient. Results of late-season fertilization experiments with seedlings of the species used in the current experiment suggest that improving nutrient status with small changes in seedling morphology increase seedling performance after planting (Trubat et al., 2008). Studies with *Q. ilex* and *Quercus suber* suggest that late-season fertilization may also be suitable to improve plantation success under dry sub-humid conditions (Trubat et al., 2010). However, small seedlings can be hard to handle, particularly if container size is large and the rooting system cannot hold the growing substrate. This limitation should be solved before the use of small seedlings can be recommended for the restoration of semi-arid lands.

Logistic regression models developed for *P. lentiscus*, *R. alaternus*, *Q. coccifera*, *R. lycioides* and *T. articulata* showed significant odds ratios, indicating that stem height was significantly related to seedling survival and that seedling size could be used to predict short-term field mortality under the conditions of the study. In addition, the odds ratio was lower than one in all species, indicating a negative relationship between size and survival. From the regression equation, we were able to determine the height of the different species at planting for a 50% probability of survival (P_{50}). The values obtained (7.6 cm for *R. lycioides*, 8.8 cm for *Q. coccifera*, 9.0 cm for *T. articulata*, 11.7 cm for *R. alaternus* and 12.0 cm for *P. lentiscus*), are lower than those recommended by current regulations for tree species (Generalitat Valenciana, DOGV 2780 16/05/1996; RD 1356/1998; BOE 153 27/05/1998). These regulations are applied in a wide range of environmental conditions, and should be reviewed for semiarid lands in the light of the results obtained in this study.

5. Conclusions

Since resistance to drought is crucial for seedling establishment in drylands, our results highlight the importance of nutrition management during stock production in the nursery. Defining optimum morpho-physiological traits for the establishment of woody seedlings is a major step towards improving the efficiency of forest plantations in dryland restoration. Our results show that nutrient supply has a strong potential to modify the morphology of Mediterranean woody seedlings in the nursery. We have shown that nutrient-deficient plants of 5 different species may be more likely to establish under harsh semi-arid conditions than well fertilized plants, suggesting that morphological and physiological traits associated with nutrient deficiency may outbalance the scarcity of nutrient reserves, supporting our first hypothesis. Despite small differences in species sensitivity to nutrient supply, the five species tested showed a consistent response to fertilization in the nursery and in the field. Thus, contrasting ecological strategies do not seem to separate from this general pattern. Our results stress the need to refine the concept of seedling quality in drylands, and to explore the interactions between seedling quality and site conditions. These results emphasize the difficulty in establishing strict regulations on the quality of seedling stocks and the need to focus on nursery techniques promoting rooting ability rather than aboveground traits.

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