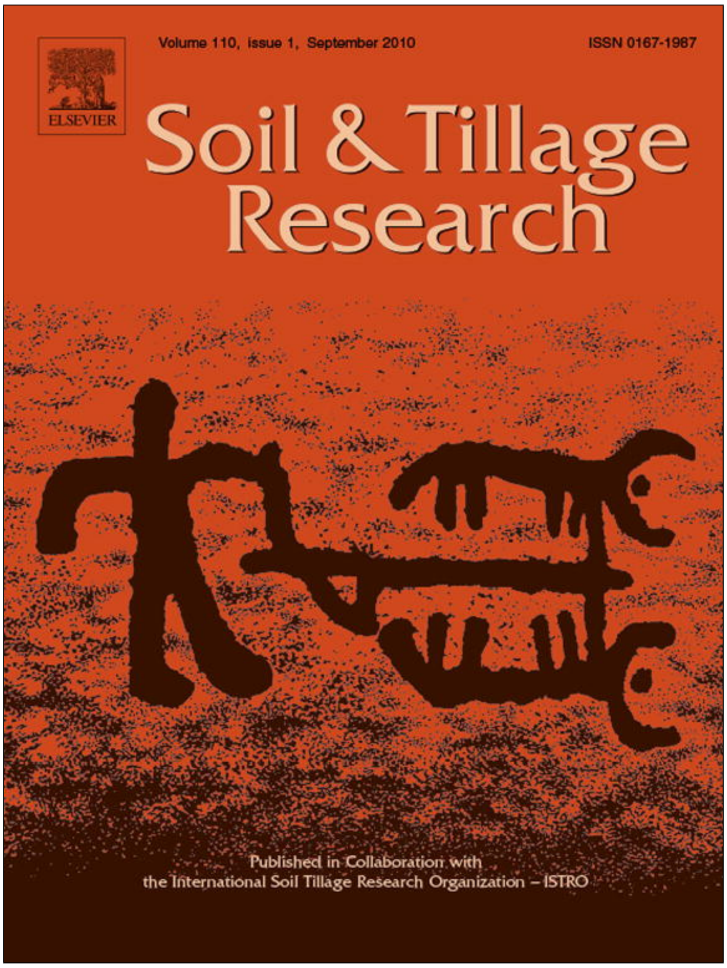
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# Effects of soil compaction and light on growth of *Quercus pyrenaica* Willd. (Fagaceae) seedlings

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ABSTRACT

Soil compaction and light availability influence plant growth via different mechanisms. In general, soil compaction has a direct effect on roots, whereas light affects leaves and stems. Although plants in nature are exposed to variable levels of soil compaction and light, no study on the potential mutual interactions of these limiting factors in woody plants has to the authors' knowledge been reported to date. The aim of this work was therefore to elucidate the effects of soil compaction and light availability on growth and biomass allocation in the deciduous oak *Quercus pyrenaica*. To this end, a study was conducted at two light levels (*viz.* 3% and 100% of incident light, designated as low-light and high-light, respectively) under a wide range of soil compaction (0.02–3 MPa as penetration resistance) in a greenhouse. Total biomass was found to be positively affected by both light and soil compaction. There was marginally significant interaction between the effects of the two factors on total biomass, which was positively affected by soil compaction only under high-light conditions. Soil compaction had a strong, negative effect on the length of the main root; thus, at maximum soil compaction, such a length was roughly one-half that observed at lower compaction levels. Also, the specific root length of main root (root length to root mass ratio) was reduced by roughly one-half in highly compacted soils. These results suggest that an unfavourable combination of soil compaction and light availability may have severely adverse effects on woody plant performance in drought periods since plants with short roots can hardly access water at deep soil levels. The strength of this effect may be modulated by light availability.

## 1. Introduction

Tree seedling performance is affected by various abiotic factors, but particularly light, temperature and nutrient and water availability (Canham et al., 1996; Holmgren, 2000; Sack, 2004). In addition, seedling growth may be influenced by various physical properties of soil including compaction (Kozlowski, 1999, 2002; Mósena and Dillenburg, 2004; Alameda and Villar, 2009; Pérez-Ramos et al., 2010). In fact, compaction increases the bulk density and penetration resistance of soil, and decreases the size and proportion of voids in it, which in turn reduces soil permeability, and water and air diffusivity (Gayoso and Iroumé, 1991; Verpraskas, 1994). A soil with an increased bulk density and penetration resistance may require greater energy investments for root development, thus raising energy costs for plants and potentially reducing their growth rate and performance. In this way, soil compaction may diminish root development (Verdú and García-Fayos, 1996; Passioura, 2002) and stem growth (Wolfe et al., 1995; Ferree and Streeter, 2004). However, compaction may also have favourable effects on plant growth (Brais, 2001; Fleming et al., 2006), especially in coarse-textured soils with a low water retention capacity. Alameda and Villar (2009) found growth and biomass allocation in woody species to respond differently to changes in soil compaction. Also, they found the response to depend on the particular soil compaction range; thus, the effects on plant growth were generally positive in the low to medium compaction range, but negative at high compaction levels.

The seedling stage is usually a critical phase in the regeneration of woody species under natural conditions (Pulido and Díaz, 2005; Acácio et al., 2007); thus, the risk of environmental stress during this stage is very high, and so is the likelihood of seedlings dying as a result (Acácio et al., 2007). Because early seedlings must develop effective roots to obtain water and nutrients, soil compaction may have a strong effect on the earliest development stages of woody

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plants. Reduced seedling root growth by effect of a high soil compaction under natural conditions may thus diminish plant survival (Lloret et al., 1999; Verdú and García-Fayos, 1996).

A number of studies have used experimentally set compaction levels to explore the effects of soil compaction on plant performance under controlled conditions. Most only examined the effect of this factor, see for example, Bassett et al. (2005) and Tubeileh et al. (2003). Recently, however, the effect of soil compaction has been examined simultaneously with other factors including drought (Ferree et al., 2004; Mósena and Dillenburg, 2004; Maganti et al., 2005), waterlogging (Maganti et al., 2005), soil texture (Gómez et al., 2002), forest litter amendment (Tan and Chang, 2007) and nutrient addition (Williamson and Neilsen, 2003; Cubera et al., 2009). These studies are more realistic since plants in nature are exposed to a wide array of variables affecting performance in addition to soil compaction.

One of the abiotic factors most strongly influencing plant growth and development is light availability (Sánchez-Gómez et al., 2006; Quero et al., 2008). In general, a low-light level usually reduces plant growth (Sack and Grubb, 2002; Sánchez-Gómez et al., 2006; Quero et al., 2008) and increases the proportion of biomass allocated to leaves and stems at the expense of roots (Holmgren, 2000; Antúnez et al., 2001; Ruíz-Robleto and Villar, 2005; Villar et al., 2008).

Although it may be interesting to establish the specific effects of individual factors, plant responses to a specific factor may be influenced by other factors (Woodward and Slater, 2006). For example, the effects of soil compaction may depend on other factors such as water and nutrient availability or soil texture (Gómez et al., 2002; Cubera et al., 2009; Ferree et al., 2004). This has aroused increasing interest in examining potential interactions between the effects of soil compaction and other factors. Although plants in nature are exposed to variable levels of light and soil compaction, whether the effect of the latter factor on woody plants is affected by available light levels has never seemingly been studied to date (Web of Science, January 2010). The only exception is a study by Small and McCarthy (2002) where they examined the joint effects of soil compaction and light on herbaceous species and found certain species to respond differently to changes in soil compaction depending on the particular light level.

The structure of leaves, stems and roots can be altered by some environmental factors. Thus, roots are usually modified by soil compaction, which can decrease their specific length (length to biomass ratio) (Simojoki, 2001; Mósena and Dillenburg, 2004). The specific root length is a key plant trait related to growth and ecological attributes (Comas and Eissenstat, 2004). Leaves and stems can also be structurally altered by light; thus, both leaves (Poorter et al., 2009) and stems tend to be thinner (*i.e.* to possess a higher specific stem length, SSL, which represents the stem length to stem biomass ratio) under low-light conditions (Pérez-Ramos et al., 2010). No study on the joint effects of soil compaction and light on the structure of leaves, stems and roots appears to have been reported, however.

The starting hypothesis for this work was that soil compaction effects depend on light availability. Thus, plants growing under low-light conditions should exhibit a decreased photosynthesis rate (Niinemets et al., 2004; Quero et al., 2006) and should have a lower energy input to overcome soil penetration resistance by its roots. Likewise, we expected soil compaction to affect root growth mainly and light availability to influence seedling shoot growth primarily.

Our main specific objective was to assess the effect of light availability and soil compaction on absolute growth, biomass allocation and morphologic traits of stems and roots in seedlings of *Quercus pyrenaica* Willd. (Fagaceae), which is a resprouting deciduous oak distributing from south-western France to northern Morocco. This oak is a late-successional species exhibiting shade tolerance (Baraza et al., 2004) and abundant production of root biomass at the seedling stage (Quero et al., 2007, 2008). Also, it is on the Red List of Threatened Vascular Plants of Andalusia (Blanca et al., 2000). Although soil compaction is deemed a major influential factor for early performance in *Q. pyrenaica* (Urbieta et al., 2008), little is known about the specific effects of soil compaction on this endangered tree species.

Apart from the basic knowledge that understanding the effect of soil compaction and light availability on this species may provide, the present study was thought interesting inasmuch as forest management practices alter soil compaction and light availability by effect of tree harvesting or forest floor removal (Fleming et al., 2006; Ampoorter et al., 2007). Similarly, successful forest management (*e.g.* reforestation practices) requires an accurate knowledge of species-specific requirements.

The primary objectives of this study were thus as follows: (1) to establish the effect of soil compaction and light availability on absolute growth, biomass allocation and structural traits of stems and roots in *Q. pyrenaica* seedlings and (2) to determine whether the effect of soil compaction on the previous variables depends on the available light level.

## 2. Materials and methods

### 2.1. Experimental design

*Q. pyrenaica* acorns were supplied by “Semillas Silvestres” (http://www.semillassilvestres.com; Córdoba, Spain) and collected during the winter of 2003 from various trees in the Sierra de Cardeña y Montoro Natural Park (southern Spain, 38°15′N, 4°22′W, 700 m a.s.l.). The deciduous oak *Q. pyrenaica* is mainly distributed in the northwest of the Iberian Peninsula, in areas with a climate sharing Atlantic and Mediterranean characteristics, having acid or neutral soils and shady orientations, and lying in valley heads above 1000–1200 m (Blanco-Castro et al., 1998). This species is relatively rare in southern Spain, where it forms forests stands in areas with a summer precipitation exceeding 730 mm (Castillo and Castillo, 2004).

The acorns were stored at 4 °C until February 2004, when they were placed in water for 1 day and then kept at 5 °C in a moisture-saturated atmosphere. In March 2004, 30 freshly germinated acorns with roots *ca.* 1–2 cm long were randomly selected for sowing in PVC cylindrical pots 50 cm high and 10.5 cm in diameter (volume, 4.3 L). A large pot size was used to allow for extensive root growth. The base of each pot (a square of 12 cm × 12 cm) was drilled with 5 holes 2 mm wide in order to ensure efficient draining. The pots were filled with a mixture of 2/3 sand and 1/3 peat. The soil was very similar to that present in *Q. ilex* dehesas (savannah-like ecosystems) in the province of Córdoba (Spain), contained 77% sand and had a bulk density of 1.29 g $cm^{-3}$ (Fernández-Rebollo et al., 2004).

The experiment was conducted in a greenhouse at the University of Córdoba, Spain (37°51′N, 4°48′W, 100 m a.s.l.).

Several soil subsamples were taken for measurement of fresh mass and dry mass (following heating at 75 °C for 3 days) in order to calculate the proportion of water in the soil and its bulk density. We did seven soil compaction levels in order to span a continuous range, using the bulk density increment as reference. The first level (no compaction) was obtained by filling up the pots with uncompacted soil; the others (second to seventh), by increasing the pot weight with 360 g dry mass (in the form of additional substrate) on average per level. The substrate was compacted by hand, using a metal rod 10 cm in diameter. Initially, all pots were filled up with substrate to a height about 49 cm. At the lower compaction levels, however, the substrate height – and the

**Table 1**
Mean (±SD) initial and final bulk density, and soil penetration resistance, at variable soil compaction levels.

| Soil compaction level | Initial bulk density (g cm$^{-3}$) | Final bulk density (g cm$^{-3}$) | Penetration resistance (MPa) |
|---|---|---|---|
| 1 | 0.95 ± 0.04 a | 1.18 ± 0.03 a | 0.16 ± 0.01 a |
| 2 | 1.02 ± 0.04 b | 1.19 ± 0.02 a | 0.20 ± 0.05 a |
| 3 | 1.07 ± 0.02 b | 1.18 ± 0.01 a | 0.19 ± 0.01 a |
| 4 | 1.18 ± 0.01 c | 1.27 ± 0.01 b | 0.33 ± 0.02 b |
| 5 | 1.22 ± 0.02 c | 1.29 ± 0.01 b | 0.62 ± 0.08 c |
| 6 | 1.27 ± 0.02 d | 1.34 ± 0.03 c | 1.13 ± 0.35 d |
| 7 | 1.34 ± 0.01 d,e | 1.37 ± 0.01 c,d | 2.38 ± 0.72 e |

The soil penetration resistance values shown are the means for the whole soil profile. The initial and final bulk density were measured at the beginning and end of the experiment, respectively. Different letters in each column indicate significant differences between soil compaction levels ($P < 0.05$, Tukey's HSD test).

effective soil volume as a result – was reduced after few days of watering. The content in fresh soil of each pot was taken to be the weight difference between the empty and soil-filled pot, and the initial volume of soil was calculated from substrate height. Soil bulk density was calculated as the ratio of soil dry mass (determined from the soil water content and fresh soil mass) to soil volume.

We used an experimental design involving two light level treatments, namely: (a) high-light (HL), under full light (no shade frame, 100% light intensity) and (b) low-light (LL, 3% light intensity, obtained by using a shade frame covered by with a 1.5 m × 1.2 m × 2 m green cloth); plants from each of the seven soil compaction groups were randomly selected for subjection to each light treatment. The mean ± SE of photosynthetic active radiation (PAR) as quantified with a light PAR sensor (with EMS7, canopy transmission meter, PP-system, UK) at midday on a sunny day (May 28, 2003) for each light treatment was 760 ± 150 μmol photons m$^{-2}$ s$^{-1}$ with the high–light treatment and 23 ± 2 μmol photons m$^{-2}$ s$^{-1}$ with the low-light treatment. Light quality (red:far red ratio, R:FR) was measured with a SKR 110 sensor (Skye Instruments, Llandrindod Wells, UK). R:FR was 1 (the expected value in an open habitat) for the high-light treatment and different from 1 (0.25 ± 0.004) for the low-light treatment – as expected from the presence of the green cloth, but similar to the typical values for a dense forest microhabitat (0.28 ± 0.03, *t*-test, $P = 0.31$). A drip-irrigation system was inserted in the pots to ensure that water would be no limiting factor. Also, an amount of 10 g of slow-release fertilizer (Plantacote, Pluss, 14:9:15 NPK, Aglukon, Valencia, Spain) was added to each pot at the start of the experiment.

### 2.2. Data collection

In September 2004, after 7 months of growth, the soil penetration resistance (a surrogate of soil compaction) of the soil in each pot was measured with a penetrometer (Penetrologger, Eijkelkamp Agrisearch Equipment, Giesbeek, The Netherlands). This model affords measurements at 1 cm depth intervals. Soil compaction was expressed in terms of penetration resistance (specifically, as the pressure required to insert a 60 cm long cylindrical probe with a 1 cm$^2$, 30° angle cone into the soil) (Passioura, 2002). The data thus obtained were used to calculate the mean and maximum soil resistance for the whole soil profile in each pot (Table 1).

Once soil resistance was measured, individual seedlings were carefully withdrawn from each pot and rinsed gently to remove soil from their roots. Plants were then split into acorn remnant, leaves, stem and roots. The lengths of the stem and main root of each seedling were then measured. The dry mass of the plant organs was determined following oven-drying at 75 °C for at least 48 h. The fractions of biomass allocated to leaves (LMR), stem (SMR) and roots (RMR) were calculated as the ratio of biomass in each organ to total biomass (Hunt, 1990). Then, the roots were split into two fractions, namely: coarse roots (more than 2 mm thick) and fine roots (less than 2 mm thick) (Cubera et al., 2009). The dry mass of each fraction, and the total length of the coarse root fraction, were then calculated. The specific root length (SRL) of the main root was calculated as the root length/mass ratio. The mass ratio of coarse roots to fine roots ($R_{\text{coarse}}/R_{\text{fine}}$) was also calculated. Finally, the specific stem length (SSL) was obtained as the stem length/stem mass ratio.

The initial and final soil bulk density of soil in each pot was calculated as the ratio of substrate dry mass to volume occupied at the beginning and end of the experiment, respectively (Table 1). Substrate height was found to have diminished after 7 months as a result of natural clodding (Alameda and Villar, 2009).

### 2.3. Statistical analyses

The influence of light availability (categorical factor) and soil penetration resistance (continuous factor) on plant variables (dependent variables) was assessed by analysis of covariance, using the General Lineal Models (GLM) procedure as implemented in Statistica v. 7.1. The specific plant variables studied were total biomass, biomass allocation, stem and root length, specific stem length, specific root length and coarse root/fine root mass ratio. The mean soil penetration resistance for the whole profile was used as a proxy of soil compaction in the statistical tests. Cottingham et al. (2005) recommend using regression methodology instead of ANOVA in order to obtain a better understanding of the effects of each factor; in fact, regression methods have an increased predictive power and facilitate the obtainment of useful predictors for ecological models. Data were log- or arcsine-transformed in order to ensure fulfilment of normality and homoscedasticity requirements (Zar, 1996). Linear regressions between different plant variables and soil penetration resistance were established at each light level. The relationship between soil density and soil resistance was fitted to a non-linear regression equation. All statistical analyses were done with Statistica v. 7.1 (Statsoft, Inc., Tulsa, OK, USA).

## 3. Results

### 3.1. Soil density and compaction

An increase in soil compaction was found to significantly increase bulk density, and also the mean resistance to penetration as measured with a penetrometer (Table 1, Fig. 1).

The final soil bulk density (after 7 months) was greater than the initial value by effect of clodding, reducing the substrate volume. In any case, the initial and final soil bulk density were very highly correlated ($r = 0.94$; $P < 0.0001$). Also, the final soil bulk density was positively correlated, in an exponential manner, with the penetration resistance (Fig. 2).

### 3.2. Absolute growth and biomass allocation

Absolute growth (total biomass) was significantly affected by soil compaction and light availability, with a marginally significant

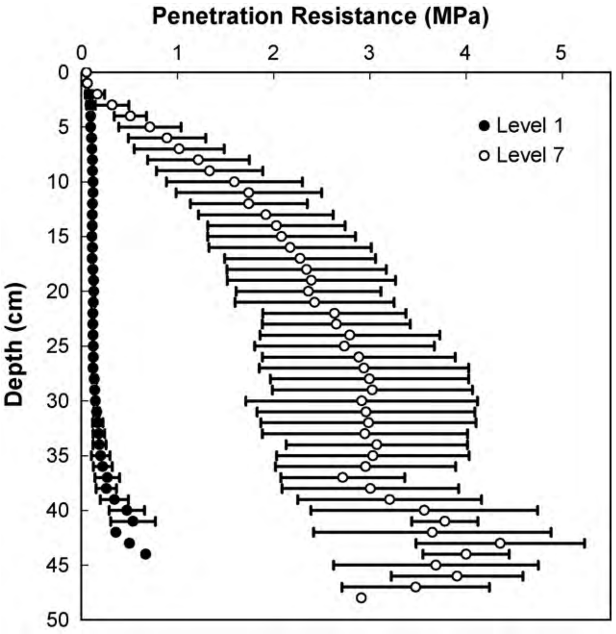

**Fig. 1.** Variation of the soil penetration resistance with depth averaged among pots. The mean values (±SD) for the highest (1) and lowest compaction level (7) are shown.

(0.10 > $P$ > 0.05) interaction between the effects of light and soil resistance on total biomass (Table 2). This suggests that the effect of soil resistance may vary with the particular light level. In fact, soil compaction had a positive effect on total biomass under high-light conditions ($P < 0.05$), but not under low-light conditions ($P = 0.17$) (Fig. 3a). Total biomass was also strongly dependent on light availability; thus, it was much greater with the high-light treatment than with the low-light treatment (Table 2; Fig. 3a).

Unexpectedly, biomass allocation to leaves, stems and roots was unaffected by soil compaction, but affected by light availability (Table 2). Plants subjected to the high-light treatment exhibited higher proportions of leaves (0.23 ± 0.05) than did those under the low-light treatment (0.05 ± 0.06). However, the plants grown under high-light conditions exhibited lower root proportions (0.65 ± 0.06) than did those under low-light conditions (0.79 ± 0.20). By contrast, light availability had no effect on stem biomass allocation ($P > 0.80$).

### 3.3. *Stem and root traits*

Stem length was affected by neither soil compaction nor light availability (Table 2). However, the specific stem length (SSL) was influenced by both factors. Thus, SSL decreased with increasing soil compaction, especially under high-light conditions (Fig. 3b). On the other hand, the low-light treatment increased SSL (Fig. 3b).

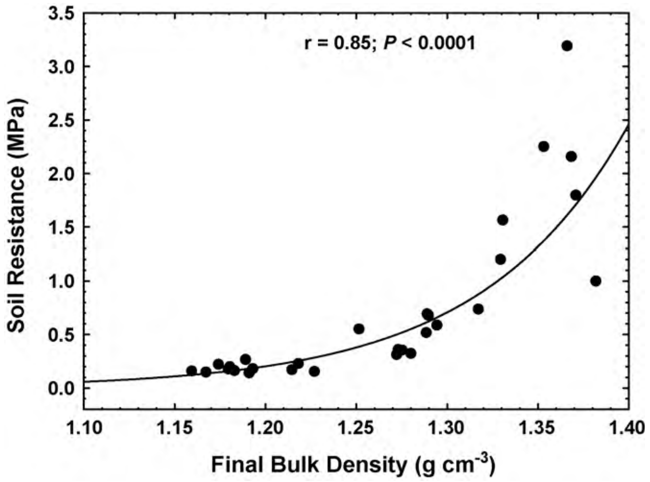

**Fig. 2.** Relationship between final bulk density (after 7 months) and penetration resistance as measured with a penetrometer. The curve represents an exponential regression fitted to the experimental data.

Interestingly, the length of the main root was strongly affected by soil penetration resistance (Table 2). A negative correlation between this variable and soil penetration resistance was found irrespective of the available light level (Fig. 3c). On the other hand, root length was unaffected by light availability (Table 2).

The specific root length (SRL) of the main root was influenced by both soil penetration resistance and light availability (Table 2). Thus, SRL decreased with increasing soil compaction, especially under low-light conditions (Fig. 3d). However, the coarse root mass/fine root mass ratio ($R_{\text{coarse}}/R_{\text{fine}}$) was influenced by neither soil compaction nor light availability (Table 2).

## 4. Discussion

In general, we found the effects of soil compaction on some variables (*e.g.* plant biomass) to vary with light availability. However, most of the studied variables exhibited no significant interaction between soil compaction and light. On the other hand, based on our starting hypothesis that both factors affect root and shoot traits differently, we found the length of the main root to be influenced by soil compaction and the proportion of leaves to be affected by light availability (*i.e.* soil compaction influences roots, whereas light affects shoot). However, this hypothesis failed with other shoot and root traits.

The working levels of the factors involved in a controlled experiment should be similar to those prevailing in nature.

**Table 2**
Effects of soil compaction, light availability and their interaction on various plant characteristics.

| | Biomass | LMR | SMR | RMR | Stem length | SSL | Root length | SRL | $R_{\text{coarse}}/R_{\text{fine}}$ |
|---|---|---|---|---|---|---|---|---|---|
| Soil resistance ($R$) | **6.0*** | 0.1 | 0.1 | 0.1 | 0.5 | **12.3**** | **49.9***** | **15.9**** | 9.9 |
| Light ($L$) | **72.3***** | **64.1***** | 1.2 | **18.1*** | 6.2 | **62.7***** | 3.3 | **54.3***** | 0.2 |
| $R \times L$ | **2.8**[a] | 1.9 | 0.1 | 0.9 | 2.1 | 0 | 4.1 | 0.0 | 2.1 |
| $R^2$ | **0.84***** | **0.71***** | 0.00 | **0.14**[a] | 0.00 | **0.83***** | **0.56***** | **0.81***** | 0.0 |

Results of the general linear model (GLM) for the different variables measured as dependent variables, light availability ($L$) as a categorical factor and soil resistance to penetration ($R$) as a continuous predictor. Values represent the percent variance absorbed by $L$, $R$ and the interaction $L \times R$, calculated as $(SS_{\text{factor}}/SS_{\text{total}}) \times 100$ and the $R^2$ value for the model. Variables: biomass (total seedling dry mass); LMR (leaf mass ratio, leaf mass/total biomass); SMR (stem mass ratio, stem mass/total biomass); RMR (root mass ratio, root mass/total biomass); stem length and root length (maximum length of stems and main root); SSL (specific stem length, stem length/stem mass); SRL (specific root length, root length/mass ratio for main root); $R_{\text{coarse}}/R_{\text{fine}}$ (coarse root/fine root mass ratio). Numbers in boldface indicate significant differences.

[a] 0.10 > $P$ > 0.05. *$P < 0.05$; **$P > 0.01$; ***$P < 0.001$.

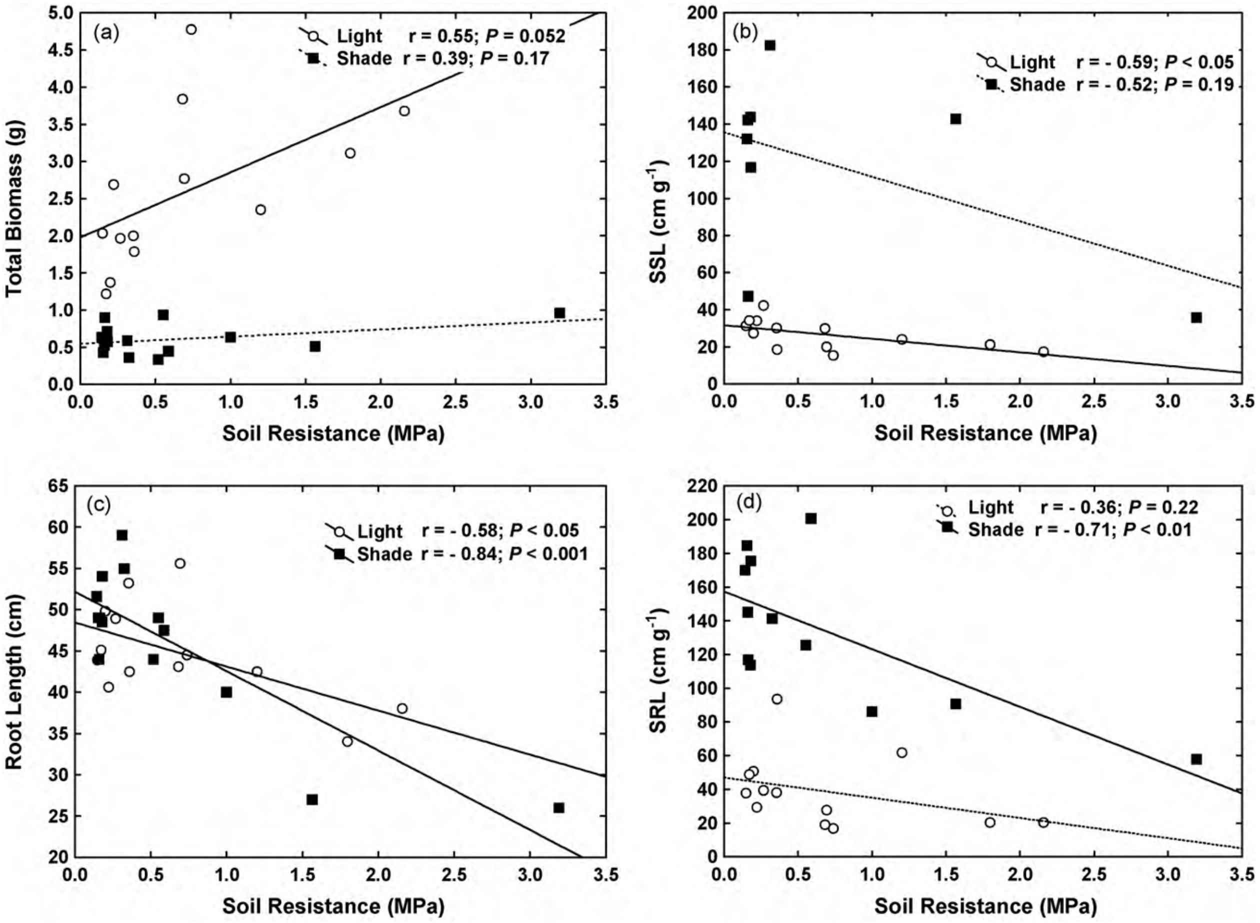

**Fig. 3.** Relationship of (a) total biomass, (b) specific stem length (SSL), (c) length of the main root and (d) specific root length (SRL) with soil penetration resistance in *Quercus pyrenaica* seedlings grown under full light (100%) and in the shade (3% light intensity). Solid lines represent significant regression ($P < 0.05$) and dotted lines non-significant regression ($P > 0.05$).

Regarding soil compaction, we established different levels by using a simple, effective method. Previous studies on Mediterranean ecosystems provided soil compaction values similar to those found for *Q. pyrenaica* seedlings in this work. Thus, Pérez-Ramos et al. (2010) found soil compaction levels from 0.9 to 3.4 MPa in a *Quercus* forest in SW Spain, and Quero et al. (2008) levels from 0.14 to 4.2 MPa in a Mediterranean forest in Granada (southern Spain). As regards light availability, the levels under low-light conditions were low, but realistic, as they were similar to those previously found in an understory of oak forests in SW Spain (Marañón et al., 2004).

Our final soil bulk density values were strongly correlated with soil penetration resistance (Fig. 2). However, the relationship was exponential rather than linear at densities in the region above 1.3 g $cm^{-3}$. Similar results were previously obtained by Ampoorter et al. (2007) in sandy soils. An increase in soil bulk density above a certain level apparently leads to a more marked change in penetration resistance.

Unlike the results of previous studies, ours suggest that the effects of soil compaction on plant may vary with the available light level. Thus, under high-light conditions, soil compaction appears to have a positive effect on total biomass (Fig. 3a). Although, in general, soil compaction has a negative effect on plant biomass, other studies (Atwell, 1993; Jordan et al., 2003; Tubeileh et al., 2003; Alameda and Villar, 2009) have found a positive effect on plant growth. This has been ascribed to soil compaction facilitating root–soil contact, and favouring nutrient and water absorption as a result (Arvidsson, 1999). However, the positive relationship between soil penetration resistance and total biomass under high-light conditions is unlikely to hold at increased compaction levels. Also, under low-light conditions, total biomass was unaffected by soil compaction (Fig. 3a). This can be ascribed to shady seedlings already being subject to strong light restrictions and a concomitant increase in soil compaction would have a less marked effect on seedling growth (Canham et al., 1996). Whether the effect of soil compaction invariably depends on the particular light conditions is uncertain; therefore, it would be interesting to know how other species respond to the combined effects of compaction and light availability.

As expected, biomass production by *Q. pyrenaica* seedlings was substantially greater under high-light conditions (100%) than under low-light conditions (3%). An extreme reduction in light availability generally results in lower growth (77% less here). For instance, Sack and Grubb (2002) found plants under deep shade to grow 50–70% less than similar plants under high-light conditions.

Surprisingly, soil compaction had no effect on biomass allocation here. In many previous studies, soil compaction was found to influence root growth, and hence the proportion of roots (Kozlowski, 1999; Ferree et al., 2004). Like us, however, Cubera et al. (2009) found the root/shoot ratio of another *Quercus* species (*Q. ilex*) not to change with soil compaction. Therefore, plant response seemingly varies between species and depends on the particular range of soil compaction (Alameda and Villar, 2009). On the other hand, light restrictions affect biomass allocation to leaves and roots. Surprisingly, the proportion of leaves was lower under low-light conditions than under high-light conditions, which departs from the results of other studies (Sack, 2004). However, in response to restricted light conditions, *Q. pyrenaica* seedlings allocate an increased fraction of resources from the acorns to roots at the expense of leaves (Quero et al., 2007).

The structural traits of stems and roots also changed with soil compaction and light availability. Thus, an increased soil compaction had a negative effect on SSL and SRL (Fig. 3b and d). Whalley et al. (1995) and Mósena and Dillenburg (2004), obtained similar results for roots and found plants to develop shorter, coarser roots in highly compacted soils. To our knowledge, however, no other authors have found soil compaction to affect stem structure (in the form of decreased SSL values). It would be interesting to ascertain whether this is a general response and, if so, establish the underlying mechanism. Most of the change (50–60%) in specific length of stems and roots (SSL and SRL) was due to light (Table 2), with higher SSL and SRL values under low-light conditions (Fig. 3b and d). One typical response of stems to shade is to elongate and have a higher SSL as a result (Poorter, 1999). However, we found the effect of light availability on specific root length to contradict that observed in previous studies. Thus, Reich et al. (1998) and Curt et al. (2005), found decreased SRL values under low-light conditions, possibly as a result of different species responding in a different manner to shading. Based on our results, light had a similar effect on the structure of stems and roots: specific length increased with decreasing light availability.

As in several previous studies (Whalley et al., 1995; Mósena and Dillenburg, 2004; Bassett et al., 2005; Cubera et al., 2009), the length of the main root was constrained by soil compaction (Fig. 3c). Thus, the length of the main root in seedlings grown in a soil compacted to about 3 MPa was roughly 50% smaller than in less compacted soil. Whalley et al. (1995) showed root growth in many plants to be restricted above a soil penetration resistance of 2 MPa. It would be interesting to identify the exact soil compaction threshold above which root growth is diminished in different species. In any case, an increased soil compaction had no negative effect on aerial growth in *Q. pyrenaica* (neither on biomass allocated to leaves and stems, nor on stem length); therefore, the water and nutrient requirements for appropriate development of aerial structures must have been met despite the reduced root length observed. As noted in the Introduction, a moderate increase in soil bulk density leads to an increase in cohesion between particles and better adhesion to root surfaces, thereby facilitating water and nutrient absorption. Previous studies revealed that the number of small pores decreases, and so does the amount of plant-available oxygen as a result, as soil density increases (Mósena and Dillenburg, 2004). This, however, seemingly has no effect on growth of *Q. pyrenaica* since neither total biomass nor above-ground biomass was negatively affected over the studied soil compaction range. As a result, the decreased length of the main root at high soil compaction levels posed no constraint on nutrient or water uptake under our experimental conditions.

Under Mediterranean conditions, seedlings lacking deep roots will be at a clear disadvantage during the summer, when soil water is scant and can only be obtained at much greater depths (Lloret et al., 1999). This is even more important in new emerged seedlings during spring, which have to develop a pivoting root before the summer drought arrives, which considerably hinders plant regeneration in Mediterranean areas (Pulido and Díaz, 2005; Acácio et al., 2007). Having a deep root system at an early stage is therefore crucial for plant survival. Also, the role of roots in providing physical support for plants is as important as their role in water and nutrient uptake. The better the root system develops, the better an adult plant will anchor to the ground. Therefore, a reduced length of the main root in adult plants can compromise survival by limiting not only their ability to reach water in dry periods, but also that to remain erect and anchored to the substrate.

## 5. Conclusions

The effect of soil compaction on total biomass in *Q. pyrenaica* was found to depend on light availability. Thus, total biomass was positively affected by soil compaction only under high-light conditions. Soil compaction had a strong, negative effect on the length of the main root, which was reduced by 50% relative to less compacted soil. Also, roots and stems had lower specific lengths in highly compacted soils. These results suggest that the combined effects of soil compaction and light availability may have adverse consequences for plant survival in drought periods since plants with short roots may be unable to access water at deep soil levels. Further research is therefore needed in order to establish the response of other woody species to the combined effects of soil compaction and light.

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