Moderate soil compaction: Implications on growth and architecture in seedlings of 17 woody plant species

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ABSTRACT

Generally, soil compaction is a stress factor affecting negatively the plant growth, but its effects vary between species and with the soil compaction range. The objective of this study is to know the different growth responses of 17 woody species subjected to moderate soil compaction, because most of the studies about this subject compare the effects in treatments with a wide and discrete compaction range. We explore the effects of moderate soil compaction on a continuous scale (0.1–1.0 MPa) on seedling growth. Seedlings of 17 woody species (deciduous and evergreens) mainly from Mediterranean ecosystems were grown in near optimal conditions (light, temperature and water) in a greenhouse with a sandy substrate. In general, there was a great variability of the responses depending on the species and the studied variable. About 53% of the species showed a higher total biomass with a moderate increase in soil compaction possibly being due to a greater root–soil contact. In the same way, 41% of species increase the relative growth rate and 35% the total area. Nevertheless, in spite of these positive effects on growth, for some species (23%) there was a decrease in the root proportion with soil resistance, as result of soil strength. These effects of moderate soil compaction could sum up in two general responses of woody plants: growth increment and architecture distortion. This might be relevant as a lower root investment may be a disadvantage under drought conditions. Finally, a simple conceptual model is proposed to understand the general effects of soil compaction on growth and biomass allocation.

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1. Introduction

Soil compaction is a well established corpus of investigation generating over 3000 references in the last quarter century (ISI Web of Knowledge, February 2008). Many aspects of the effects of soil compaction have been studied. Kirby (2007) in his note discussed what we know and what not about soil compaction, concentrating mainly on the effects on crops and farms and on the ways to ameliorate these effects.

Although most of the problem of soil compaction has a human origin, soils of natural areas also show a different degree of natural compaction (Pérez-Ramos, 2007; Quero et al., 2008; Gómez-Aparicio et al., 2008). A high soil compaction may have a strong effect on the first phase of establishment of wild plants (Pérez-Ramos, 2007; Gómez-Aparicio et al., 2008). Not many studies about soil compaction deals with these aspects and not much information is known about the response of wild woody species to soil compaction. In fact, Kirby (2007) appealed to re-direct compaction research on broader issues as for example natural resource management and biodiversity.

In general, at a whole plant level, it is assumed that soil compaction affects negatively root investment, due to the resistance of the substrate to be penetrated (Day and Bassuk, 1994; Kozlowski, 1999; Bassett et al., 2005). Verdú and García-Fayos (1996) found that root penetration of *Pistacia lentiscus* was negatively associated with soil compaction. Similarly, Bejarano et al. (2005) found in *Quercus pyrenaica* a decrease in root length with soil compaction. This may determine that in situations of water deficit, plants with a lower root mass proportion or shorter roots could suffer a higher water deficit which might seriously limit seedling survival. In fact, Lloret et al. (1999) stressed the importance of a greater root mass proportion (RMR, root mass ratio) in Mediterranean environments because species with a greater RMR displayed a greater survival after the period of summer drought, due to the ability to explore a greater soil surface and/or deeper soils.

Moreover of the effects on root investment, plant growth is in general negatively affected by soil compaction. Bassett et al. (2005) found in *Cordyline australis* that stem and root growth was negatively affected by soil compaction. As stated before, most of the studies on the effect of soil compaction on plants are done mainly on herbaceous species, and a minor proportion on wild woody species. Therefore, in the present study, we analysed the effects of soil compaction on the absolute growth and relative growth rate of 17 woody seedling species. Up to now, no work

exists that studies the effect of soil compaction on relative growth rate (RGR) and its underling growth components.

The relative growth rate on a biomass basis (RGR_M), which is defined as the increase of biomass per unit of biomass and time, may also be affected by soil compaction. A high RGR_M could be advantageous for a plant as it allows a greater biomass in less time (Van Andel and Biere, 1989), which would allow it to obtain more resources (light, water and nutrients) and confer a greater competitive capacity (Grime, 1977). Variation on RGR_M between different species has been found to be mainly related to a morphologic variable: the leaf area ratio (LAR; the amount of leaf area divided by the total biomass) (Poorter and Remkes, 1990). Variation in LAR is due to two components: the specific leaf area (SLA; the ratio of leaf area to leaf mass); and the leaf mass ratio (LMR, the proportion of leaf mass), being LAR = SLA × LMR. On the other hand, other morphological variables can also influence RGR_M like the proportion of biomass allocated to stem (SMR) and root (RMR), which are related to LMR.

In this comparative study, seedlings of 17 woody species, including deciduous and evergreens species, were grown for testing the influence of leaf habit on soil compaction response. These two functional groups have contrasting traits, as deciduous species usually present high photosynthetic and respiration rates, high leaf nitrogen concentration, and specific leaf area (Reich et al., 1992, 1997; Aerts, 1995; Villar et al., 1995; Wright et al., 2004; Quero et al., 2006). Consequently, deciduous species usually grow faster than evergreens ones (Reich et al., 1992; Cornelissen et al., 1996; Antúnez et al., 2001; Ruiz-Robleto and Villar, 2005). Also important differences in biomass allocation exist, as deciduous tree species invest higher proportion of biomass to roots (high RMR) than evergreens (Villar et al., 2004). As soil compaction might have an effect on root investment, the two functional groups may respond differently.

Seedlings were grown in a greenhouse with a sandy soil texture and constant water content. Therefore, the effect of a different texture or different soil moisture on soil compaction was avoided, as it has been found by Smith et al. (2001) and Souch et al. (2004). Another novel approach is that we have used a continuous range to investigate the effects of soil compaction. Most studies have analysed the effect of soil compaction using few levels of soil compaction. Only few studies have analysed the effects in a continuum soil compaction (Bassett et al., 2005). In a general ecological framework, Cottingham et al. (2005) advised the use of regressions as opposed to ANOVA for understanding the effects of different factors, because regression has a greater predictive power and the possibility to obtain predictors which can be used in ecological models.

In summary, the aims of this study are: (1) investigate the effects of moderate soil compaction on growth and other growth variables in an ample number of woody species; (2) compare the effect of soil compaction on evergreens and deciduous; and finally (3) to elaborate a general conceptual model of the effect of soil compaction on growth and biomass allocation.

2. Material and methods

2.1. Experimental design

The experiment was developed in a greenhouse with temperature control at the Campus of Rabanales (University of Córdoba, Spain) between January to July 2006. The mean ± SD of the photosynthetic active radiation measured (with EMS7, canopy transmission meter, PP-system, UK) during a clear day (May 8th, 2006) was 446 ± 89 μmol photon $m^{-2} s^{-1}$, and the total daily mean radiation throughout the experiment was 34.5 mol m^{-2} day^{-1}. Water was provided everyday by a dripping irrigation system. At 3 months of growth 1 g of slow-release fertilizer (Plantacote Pluss, NPK 14:9:15, Aglukon, Valencia, Spain) was added to avoid nutrient deficits.

The substrate was a mixture of river sand, black peat and lime in a proportion 9:6:5, having a sandy soil texture (88% sand, 8% silt and 4% clay). The soil had very similar characteristics to those found in *Q. ilex* "dehesas" (savannah-like ecosystems) of the province of Córdoba, with a 77% of sand proportion and 1.29 g cm^{-3} of bulk density (Fernández-Rebollo et al., 2004). The pots were made of PVC (4.33 L) which were 50 cm in height and 10.5 cm in diameter, to avoid limitation of space for root growth. The base of the pots (a square of 12 × 12 cm) was perforated with 5 orifices of 2 mm diameter to allow a good drainage.

Eight treatments of soil compaction were made in order to obtain a continuous soil compaction range using bulk density increment as reference. The first level (null compaction) was made filling the whole volume of the pot with soil without compacting it. The following compaction levels (from 2 to 8) were made increasing the pot weight by 265 g dry mass in average for each level by adding more substrate. Therefore, pots of level 8 weighted about 1900 g dry mass more than level 1. The substrate was manually compacted with a metallic rod (10 cm diameter). Initially, all pots were filled up with substrate about 49 cm of height. However, in the lower compaction treatments the substrate height was reduced after few days of watering and therefore its soil volume decrease in these treatments. Soil compaction levels were related to soil penetration resistance and bulk density increment (Table 1).

The total number of pots was 408, distributed in 8 levels of soil compaction with 3 replicates by each soil compaction level for each of the 17 species studied.

2.2. Growth

Woody species were chosen from families representative of the Mediterranean forest with deciduous and evergreen species. Most species were autochthonous, but some were naturalised (*Ceratonia siliqua*), ornamentals (*Cercis siliquastrum*) or invaders (*Ailanthus altissima*). In general, 40–50 seedlings of each species were selected when seedlings had a pair of expanded leaves or had a root length of 3–4 cm (for *Quercus* species). For each species, individuals with a similar size were selected to avoid a high variability between

Table 1
Mean values (±SD) of soil characteristics of compaction treatments.

Treatment	Mean penetration resistance (MPa)	Maximum penetration resistance (MPa)	Bulk density (g cm^{-3})	VWC (%)	MWC (%)
1	0.13 ± 0.08	0.42 ± 0.54	1.12 ± 0.12	21.57 ± 7.19	18.96 ± 5.64
2	0.12 ± 0.06	0.44 ± 0.26	1.09 ± 0.08	20.86 ± 5.41	18.99 ± 5.03
3	0.16 ± 0.08	0.51 ± 0.40	1.10 ± 0.08	23.22 ± 6.33	20.09 ± 5.24
4	0.16 ± 0.06	0.47 ± 0.24	1.19 ± 0.07	21.55 ± 5.29	17.65 ± 3.55
5	0.17 ± 0.06	0.50 ± 0.23	1.19 ± 0.10	23.11 ± 5.68	18.30 ± 6.69
6	0.25 ± 0.07	0.57 ± 0.23	1.23 ± 0.09	24.59 ± 6.00	18.3 ± 4.47
7	0.35 ± 0.16	0.75 ± 0.45	1.26 ± 0.07	24.23 ± 7.21	17.17 ± 4.82
8	0.58 ± 0.18	1.16 ± 0.51	1.28 ± 0.10	28.61 ± 7.05	18.7 ± 5.32

VWC is the volumetric water content measured with a TDR. MWC is the mass water content.

individuals and have a more precise RGR_M estimate (Poorter and Garnier, 1996). An initial harvest was done to have an initial biomass estimate for each species. For that, between 10 and 15 seedlings of each species were fresh weighed and dried at 70 °C for at least two days, then the dry mass was weighed. As *Quercus* seedlings had only a small root, we measured fresh and dry root mass and root length, to build a predictor for root biomass. With these data we have an estimate of the initial mass and the dry matter content (ratio of dry mass to fresh mass) for each species. The remaining plants were weighed individually (obtaining the plant fresh mass) and then planted in the pots. Each seedling was planted making a small hole of a few centimetres in the substrate to place the root. The mean initial root length for all the 17 species was 5.3 ± 3.4 cm.

Approximately, after 137 days of growth plants were harvested. Previously for each plant three measures of soil penetration resistance were taken each 0.5 cm using a penetrometer (developed by the Department of Agroforesty Engineering, University of Córdoba) with a cone of 12.6 mm diameter and 30° of angle. For each pot, we use the average value of the three measurements of soil penetration resistance for the whole soil profile (approximately 45 cm) as a representative value of soil compaction. Additionally, three measures of water volumetric percentage in the upper and in the lower 20 cm of the substrate were taken with a TDR (FieldScout TDR 100, Spectrum Inc. Technologies). The mean value of water volumetric percentage of the soil was $18 \pm 5\%$ (for the upper 20 cm) and $30 \pm 8\%$ (for the down 20 cm). We did not find any significant correlation between soil water volumetric percentage and plant biomass for any of the studied species (data not shown). The harvest of each plant was made by extracting carefully the plant from the pot and roots were washed in a container with water. Roots were gently dried out, maximum root length and plant fresh mass were measured. Then fresh leaves, stems and roots were weighed. Fresh leaves were stored in plastic bags with humidified paper and placed in a cool box. A sub sample of fresh leaves was scanned and the area measured with an image analyzer software (Image Pro, v4.5; Average Cybernetic, Inc., Silver Spring, Md, USA). After these measurements, leaves, stems and roots were dried at 70 °C for at least two days to obtain the dry biomass.

2.3. Analysis of growth

The relative growth rate on a biomass basis was calculated following the classical approach (Hunt, 1990) as: $(LnM_2-LnM_1)/(t_2-t_1)$, being M_2 and M_1 the final and initial dry mass of the seedling, respectively and $t_2 - t_1$ the growth period. Final dry mass for each plant was obtained at the harvest after the period of growth. Initial dry mass for each plant was obtained as: initial fresh mass × dry matter content. The initial fresh mass for each plant was obtained weighing each seedling at the time of planting. The dry matter content (dry mass/fresh mass) was obtained from a sub sample of plants (10–15 seedlings per species) at the beginning of the experiment (see above). For *Quercus* species, most of the initial fresh mass was due to the seed and only a minor amount to the root, therefore we calculate the biomass of the root using a predictor for each species. For that, a regression between fresh root mass and root length was made, giving acceptable predictions (R^2 average of 0.62 ± 0.15) for the six species of *Quercus*. Then, the initial fresh mass was transformed to initial dry mass using the dry matter content of the roots.

The growth variables were calculated following Hunt (1990). Specifically, the proportion of leaves (leaf mass ratio), stems (SMR, stem mass ratio) and roots (root mass ratio) were calculated as the ratio of dry biomass of leaves, stems and roots, respectively and total dry biomass. Specific leaf area was calculated as the ratio of leaf area and leaf dry mass. The leaf area ratio (LAR, the total leaf area per unit of total plant dry mass) was calculated as the product of SLA and the proportion of leaves (LMR). In May and July two stem height measurements were taken for each plant. RGR height (RGR_H) was calculated as $(LnH_2-LnH_1)/(t_2 - t_1)$, being H_2 and H_1 the stem height at the different times (t_2 and t_1).

2.4. Statistical analysis

In order to see the influence of soil compaction on the different variables measured, multiple regressions were performed for each species. Because the soil compaction treatments showed a continuous range in soil penetration resistance (from 0.1 to 1 MPa), the regressions were the most appropriate test to determine the influence of soil compaction on growth variables. Multiple regression models used as independent variables: soil penetration resistance (SPR) and SPR^2. Therefore, three types of results could be obtained: non-significant effect, a linear regression or a polynomic regression. The polynomic regression could be of three forms ($x + x^2$; $x - x^2$ or x^2). We use the procedure of multiple stepwise regression for each dependent variable and species and those models with a higher R were chosen.

To evaluate soil compaction influence on species with a different leaf habit (evergreens versus deciduous) a covariance analysis was carried out (ANCOVA). For that, we chose leaf habit as the covariate, the growth variable as the dependent variable and soil penetration resistance as the continuous predictor. All statistical tests were made with Statistica 7.1 (StatSoft, Inc.).

3. Results

3.1. Biomass, relative growth rate and total leaf area

In general, we obtained three types of responses of the effects of moderate soil compaction on growth variables: non-effect, linear positive effect and a polynomic response ($x + x^2$) effect with parabolic dynamic (Table 2, Fig. 1). For brevity only six species have been choosen to show the different effects of a moderate soil compaction (Fig. 1).

Ten out of 17 species (53%) showed a significant increase of total biomass with soil penetration resistance (Table 2). For five species the relationship had a bell shape (Fig. 1), having an increase in total biomass of up to about 0.4 MPa of soil resistance, afterwards showing a decrease in total biomass.

Seven out of 17 species (41%) also showed a significant increase of relative growth rate on a biomass basis (RGR_M) with soil penetration resistance (Table 2). Similarly, as for biomass, for some species the relationship had a bell shape (Table 2). In relation to the relative growth rate on a height basis (RGR_H), we also found for four species a significant increase with soil compaction (Table 2).

However, the results on RGR_H were very different of those to RGR_M (on biomass basis), because for both variables (RGR_H and RGR_M) none of the species with a significant effect of soil compaction were the same (Table 2). For many species RGR_M was not correlated ($P > 0.05$) with RGR_H, only five out of 17 species (*Q. canariensis, C. siliquastrum, P. sylvestris, P. lusitanica* and *P. lentiscus*) showed a positive and significant correlation between RGR_M and RGR_H, but these showed a low percentage of variance explained (mean R^2 of 0.24).

Total leaf area showed a similar trend to that found for total biomass, for seven species (35%) there was a significant increase with soil compaction. Four out seven species showed a linear increase with soil compaction and three species had a bell shape (Table 2 and Fig. 1).

The percentage of variance of these growth variables explained by the effect of soil compaction was between 29 and 37% ($R^2 \times 100$; Table 2).

Table 2
Species studied and correlation coefficients between different variables and soil compaction.

Family	Species	Leaf habit	N	Growth variables				Architecture variables			
				Total dry biomass	RGR$_M$	RGR$_H$	Total area	R/S	RMR	SLA	LAR
Fagaceae	Quercus ilex subsp. ballota (Desf.) Samp.	E	32	–	–	0.41[*]	–	–	–	–	–
	Quercus coccifera L.	E	32	–	–	0.65[***]	–	–0.38[*]	–0.40[*]	–	–
	Quercus suber L.	E	23	0.54[*](2)	0.54[*](2)	–	–	0.48[a](3)	0.51[*](3)	–	–
	Quercus faginea Lam.	D	31	–	–	0.77[***]	0.52[**]	–0.41[*]	0.50[*](3)	–	0.43[*]
	Quercus canariensis Willd.	D	30	–	–	–	–	0.40[a](3)	–	–	–
	Quercus pyrenaica Willd.	D	24	–	–	–	–	–	–	–	–
Simaroubaceae	Ailanthus altissima (Mill). Swingle	D	22	0.45[*]	–	–	0.48[*]	–	–	0.53[*](4)	–
Rhamnaceae	Rhamnus alaternus L.	E	22	0.49[*]	0.48[*]	–	0.58[*](2)	0.54[*](3)	0.53[*](3)	–	–
	Frangula alnus Mill.	D	24	0.42[*]	0.46[*]	–	0.35[a]	–	–	–	–
Pinaceae	Pinus sylvestris var. nevadensis H. Christ.	E	24	–	–	–	–	–	–	–0.57[**]	–
Anacardiaceae	Pistacia lentiscus L.	E	24	0.45[a](2)	0.54[*](2)	–	0.45[a](2)	–	–	–	–
	Pistacia terebinthus L.	D	24	0.56[**]	0.44[*]	–	0.50[*]	–	–	0.56[*](3)	–0.41[*]
Rosaceae	Prunus lusitanica L.	E	24	–	–	0.37[a](4)	–	–	–	–	–
Caesalpinaceae	Ceratonia siliqua L.	E	24	0.61[**](2)	–	0.56[*]	–	–	–	0.56[*](3)	0.57[*](3)
	Cercis siliquastrum L.	D	23	0.46[*]	–	–	–	–	–	–0.42[*]	–
Oleaceae	Olea europaea var. sylvestris (Mill.) Lehr	E	24	0.57[*](2)	0.67[**](2)	-0.36 a	0.52[*](2)	–	–	0.44[a](3)	–
	Fraxinus angustifolia Vahl.	D	22	0.70[**](2)	0.64[**](2)	–	0.68[**]	–	–	–	–
	%Significative effects			53	41	23	35	17	23	30	17
	Mean R^2 (×100)			29	34	37	30	20	24	28	23

Leaf habit: evergreen (E) and deciduous (D). N is the number of replicates for each species. Significant correlations are displayed: $0.05 < {}^aP < 0.10$; $^*P < 0.05$; $^{**}P < 0.01$; $^{***}P < 0.001$. RGR$_M$: relative growth rate in a biomass basis; RGR$_H$: relative growth rate in a stem height basis; Total area: plant total area; R/S: root-shoot mass ratio; RMR: root mass ratio; SLA: specific leaf area; LAR: leaf area ratio. Nomenclature follows Lopez-Lillo and Sanchez-Lorenzo (2001). Subscripts indicate the type of polynomial regression: (2) $x - x^2$; (3) $-x + x^2$; (4) $-x^2$. Those numbers with no subscripts mean a lineal regression. % Significative effects are the number of species with a statistically significant effect of soil compaction divided by the total number of species (17).

3.2. Biomass allocation and SLA

For 17% of species Root/Shoot ratio (R/S) had a negative relationship with soil compaction, that is, a decrease of root biomass respect to shoot biomass. Similarly, four out of 17 species (23%) showed a decrease of root biomass ratio with soil resistance (Table 2 and Fig. 1). In both variables, apart from a linear negative response there was a polynomic response ($-x + x^2$), showing a decrease at low soil resistance and reaching an asymptote on high values of penetration resistance (Fig. 1, see Q. suber and R. alaternus).

Five out of 17 species (30%) showed a significant effect of soil resistance to SLA (Table 2), having a negative linear response or a polynomic response of type $-x + x^2$. Also, three out of 17 species (17%) showed a significant effect of soil resistance to LAR but some species showed a linear decrease (P. terebinthus) and other species a positive relationship (Q. faginea) (Table 2).

3.3. Leaf habit

In general, the two functional groups respond differently to soil compaction for many of the variables measured. The ANCOVA showed a significant Leaf habit × Soil Resistance interaction (data not shown) for leaf, root and total biomass, total area and Shoot/Root ratio. Deciduous species showed a higher and positive effect of soil resistance on leaf, root and total biomass, total area and Shoot/Root ratio than evergreen species.

4. Discussion

Soil compaction is one of the stress factors that can affect the development of plants (Kozlowski, 1999), nevertheless, little has been studied from an ecological point of view. Most of the studies have been made with herbaceous or woody species of agricultural, forest or ornamental interest. Very few studies have been focused on wild woody species (e.g. Mósena and Dillenburg, 2004; Bassett et al., 2005; Pérez-Ramos, 2007). The present work has several novel points: the study of the effect of soil compaction on an ample number of wild woody species (17), the comparison of two different plant strategies (deciduous and evergreens) and the study of the effects of moderate soil compaction on biomass, relative growth rates and their growth components. Most of the studies on biomass and relative growth rate have been focused on the effects of other conditions and resources (light, water, nutrients, temperature) (see for example Lambers et al., 1990, 1998), but very few on the effects of soil compaction.

In the present work, the seedling phase has been studied since it can be the most sensitive stage, as found by Souch et al. (2004), since the young roots, of slight thickness, are those that have to colonize the soil and have to overcome the soil resistance. On the other hand, the sandy texture used, slightly compactable, has allowed us to create moderate levels of compaction (from 0.1 to 1.0 MPa), but very similar to the levels found in soils from "dehesas" (savannah-like ecosystems) (Fernández-Rebollo et al., 2004) in the Iberian Peninsula. Also, other studies (Godefroid and Koedam, 2004; Souch et al., 2004; Bassett et al., 2005) have maximum values of soil compaction around 1.2–1.4 MPa.

In general, the results of our study show that moderate soil compaction affects differently to woody species. Different responses have been found, from null effect, positive or negative linear effects or a bell shape response on growth and growth components. Similarly, Godefroid and Koedam (2004), found a very diverse influence of soil compaction on the plant cover of 107 herbaceous species. In that study, most of the species showed a bell
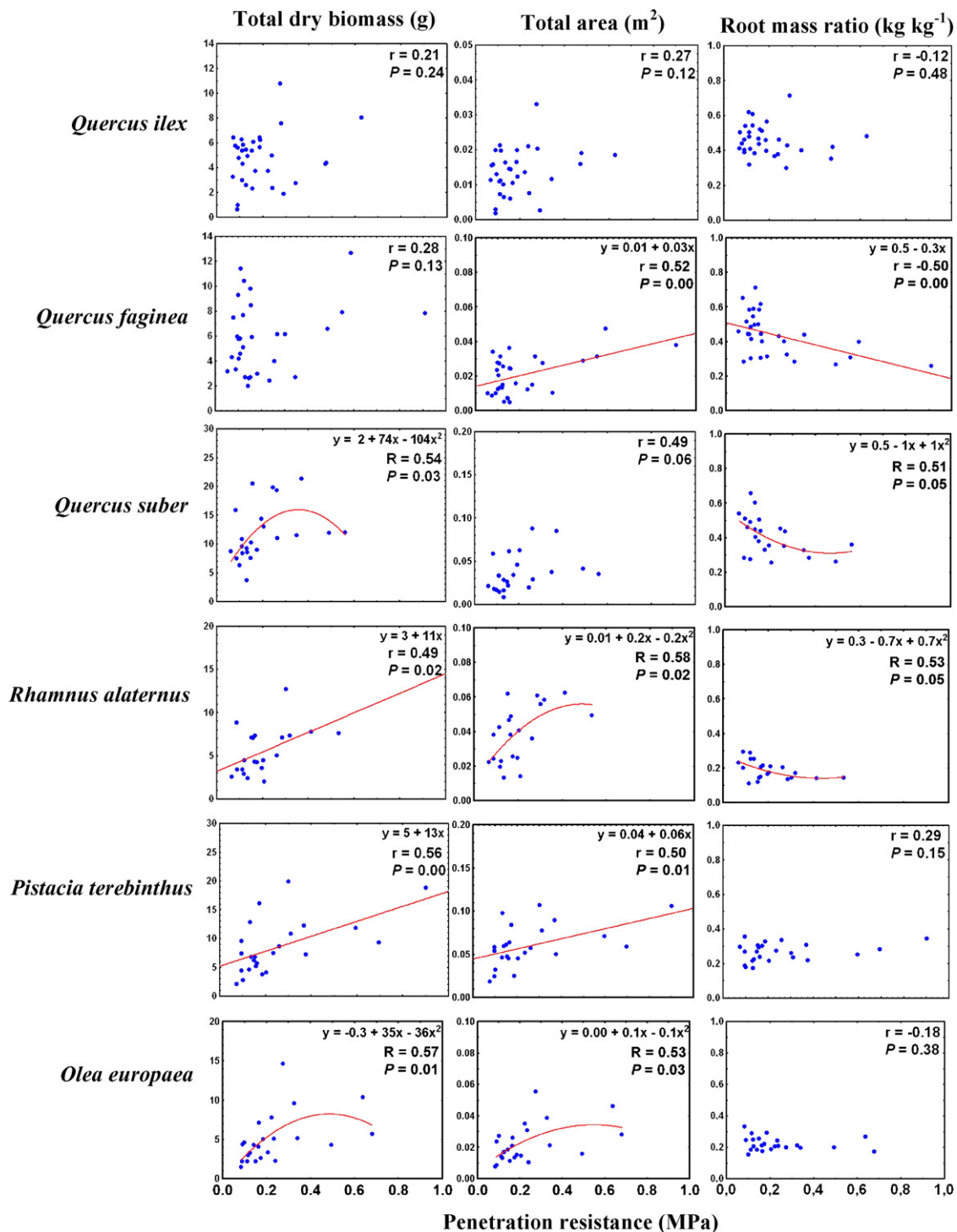
Fig. 1. Relationships between soil penetration resistance and some growth variables [total biomass, total leaf area and root mass ratio (RMR)] in 6 woody species. Species with a different response were selected. For each graph, the correlation coefficient (r) or in cases of a polynomial regression the multiple R and P are indicated.

shape response with respect to soil compaction, with a maximum plant cover between 0.2 and 0.6 MPa, decreasing it at higher soil compaction values.

In our study, 53% of the species showed a significant increase of total biomass with soil resistance. Similarly, RGR_M for some species was also increased with a moderate increase in soil resistance. In general, the results found in the literature have been a negative effect on total biomass and growth. However, most of the studies have higher soil compaction ranges and they use a discrete approach. Few studies have found similar results to ours.

For example, Mósena and Dillenburg (2004) found also for *Araucaria angustifolia* an increase in biomass with higher soil compaction. These results would be coherent with some agro-forestry practices directed to increase plant growth and to facilitate the contact of root with soil, consisting of the induction of a moderate compaction at sowing or planting. In fact, some studies (Arvidsson, 1999; Gomez et al., 2002b) have found that a moderate soil compaction can determine a greater contact between the root and the substrate and allow for a greater water and nutrient absorption.

However, in spite of the positive effect of a moderate soil resistance on the total biomass for some species, the architecture of the plants was negatively affected, concretely the root mass ratio. A general result found in the literature is a negative effect of the soil resistance on the root, measured as a decrease in root penetration (Verdú and García-Fayos, 1996), root growth (Conlin and van den Driessche, 1996; Bassett et al., 2005) or root investment (Kozlowski, 1999). This can determine that in situations of water deficit, plants with a lower root development may suffer drought more severely, and therefore it could seriously limit seedling survival (Lloret et al., 1999). Studies to test this hypothesis are lacking.

However, although the effect is statistically significant for few species, the percentage of variation of the root growth explained by soil compaction is usually very low. For example, Bassett et al. (2005) using regressions, found that soil resistance explained a very small percentage of the variation (between 16 and 22%) of the root growth. This agrees with our results since in the cases in which there is a significant effect, the explanatory percentage of soil compaction on plant traits ($R^2 \times 100$) is between 20 and 37% (Table 2). It is expected that higher soil compaction levels (>1.5 MPa) may have a higher effect on plants.

In relation to the differences between deciduous and evergreens species, our hypothesis was that soil compaction could have a different effect in these two functional groups, since in general deciduous invest more biomass to roots (higher RMR and largest root pattern) (Antúnez et al., 2001; Villar et al., 2004; Ruiz-Robleto and Villar, 2005). We have found that evergreens responded less to the soil compaction than deciduous, which could be interpreted that evergreens have therefore a smaller level of plasticity. Similarly, results of other studies (Valladares et al., 2000) suggest that evergreens species are less plastic to changes in conditions and resources.

As in other studies about soil compaction, the obtained results are subject to the experimental conditions, concretely to a sandy texture, optimal conditions of water and moderate levels of compaction. It is well known that soil penetration resistance is very dependent on the soil texture and water content (Smith et al., 2001; Souch et al., 2004). Gomez et al. (2002a) found that the effect of soil compaction on the growth of saplings of *Pinus ponderosa* could be negative, insignificant or positive, depending on the texture or water content of the soil. Therefore, it is very difficult to extrapolate the results to other soil conditions. Overall, the fact that all the plants were in the same conditions is an important advantage, since it allowed the study of the effect of soil compaction, without other interacting variables, such as soil texture or soil water content.

4.1. A conceptual model

The general trends in our results, allow us to propose a general conceptual model where most of the tendencies found can be synthesized. Two fundamental aspects are of interest: a) the biomass or growth and b) the plant architecture.

On one hand, we have found that growth measured like total dry biomass, displays two types of response (Fig. 2A). *Species type I* are those in which we found an increase of biomass (or another variable of growth) with an increase of soil compaction until moderate levels. At greater values of soil compaction some species started to decrease growth (as has been found in our study and by other authors). Arvidsson (1999) found a bell response in *Hordeum vulgare*, with low yield in the lowest and highest soil compaction. The other type of response are the *species type II*, which showed no effect on growth (at the measured levels of compaction), but that would show a reduction of growth at greater levels of compaction, as has been suggested in the literature.
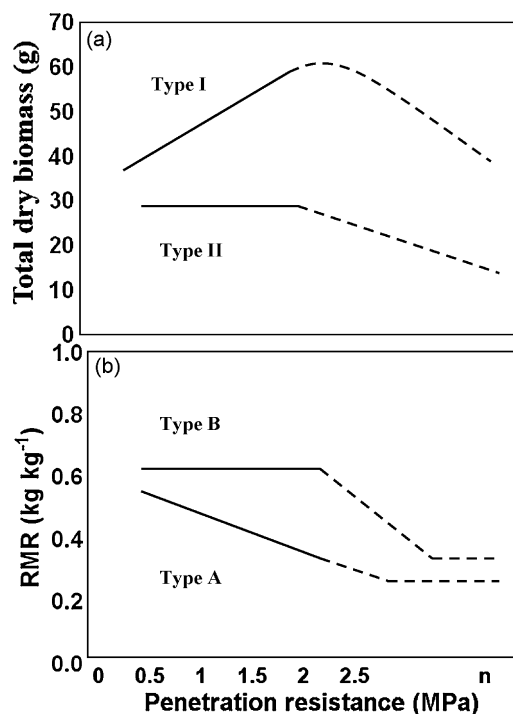

Fig. 2. Conceptual model summarising the effects of soil penetration resistance on total dry biomass (a) and root mass ratio (RMR; b). Solid lines indicate the response found in this study under moderate levels of soil compaction (<1 MPa) and slash lines indicate the possible response under higher levels of soil compaction (found in literature).

In relation to the plant architecture (e.g. the root proportion), we have found two main types of response (Fig. 2B). *Species type A* which showed a reduction of RMR with an increase in soil compaction, and at much greater levels of compaction they would reach a minimum RMR. *Species type B* where those that did not show any effect of moderate soil compaction on RMR, but they probably change RMR at higher levels of soil compaction. Within this general scheme, we could find species showing all the possible combinations of these responses. For example, *Rhamnus alaternus* follows type I-A, *Pistacea terebinthus* follows I-B, *Quercus faginea* II-A and *Quercus ilex* follows II-B.

5. Conclusion

In summary, in this work we have found a great variability of responses to soil compaction which is dependent on the variable and the species studied. The effects of a moderate soil compaction on the studied variables vary from positive or null effects on growth and biomass but null or negative on plant architecture, concretely a decrease of the root proportion, that it could have great consequences for survival. In general, it is proposed that soil compaction would have a bell effect for growth, where we would have values of non-effect, a central range of positive effect (on the growth) and a negative effect for high values of soil compaction.

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