

## Phosphorus limitation and competitive capacities of *Pinus halepensis* and *Quercus ilex* subsp. *rotundifolia* on different soils

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### Abstract

Aleppo pine (*Pinus halepensis*) and the evergreen holm oak (*Quercus ilex*) dominate forest areas of the Mediterranean Basin. Both species regenerate abundantly after fires: pine through seedlings and holm oak through resprouts. Cumulative nutrient losses caused by frequent fires may have decreased soil nutrient availability in such areas. To assess the role of nitrogen and phosphorus as limiting factors for growth of these species during post-fire recovery, a field fertilisation and competition experiment was conducted in a 5-year post-fire shrubland on calcareous soil, where naturally-regenerated saplings of Aleppo pine and resprouts of interior holm oak (*Quercus ilex* subsp. *rotundifolia*) coexist. Three years after fertilisation, relative basal area increment was 56% greater in pines fertilised with 250 kg P ha<sup>-1</sup> than in non fertilised ones. N fertilisation had small or no effects. Interactions between N and P fertilisation were not observed. Growth of Aleppo pine only increased with P fertilisation when neighbours were removed. Hence, the negative effect of neighbours on growth was greater when P availability was enhanced by fertilisation. In contrast, holm oak was able to grow more (110%) in response to increased P supply even without neighbour removal. A common garden experiment was then conducted with potted seedlings to investigate whether the suggested higher competitive capacity of holm oak for P held under a range of P amendments on different soils and competitive situations. P fertilisation increased seedling biomass yield of both species. When P availability increased, a negative effect of neighbours on growth was observed for holm oak and in 70 a lesser extent for Aleppo pine. In conclusion, in the field, holm oak resprouts showed higher competitive ability for P uptake compared to Aleppo pine saplings, but in potted seedlings in common garden conditions this trend was not observed. Therefore holm oak is not always competitively superior to Aleppo pine for P. Potted seedlings of both species had a notable plasticity in shoot/root biomass allocation, but only holm oak increased its proportional allocation to roots when neighbours were present. P availability can be a key factor in growth and competitive relations of these two species, but effects differ depending on soil type, individual age, regeneration type (i.e., seedling versus resprouts), and competitive situation.

### Introduction

Competition has been widely observed in the Mediterranean ecosystems (Vilà and Sardans 1999). Com-

petition between plant species can change with soil fertility (Bazzaz and Harper 1976; Gerdol et al. 2000; Sans et al. 2002) and on resource supply/demand by the community (Aarssen and Di Tommaso 1991). It

is not clear whether competition could be more or less intense in resource-rich or in resource-poor environments, this being a major subject of discussion and research (Grace 1991; Huisman 1994; Peltzer and Kochy 2001). In some experiments, competitive effects on growth increased when soil resource levels increased (Grime 1977; Huston and Smith 1979; Reader 1990; Fogarty and Facelli 1999; Limpens et al. 2003). However, other experiments have yielded no clear correlation between the levels of resources and competition (Newman 1973; Tilman 1982; Wilson and Tilman 1993).

Soils of Mediterranean-type ecosystems are often nutrient-poor (Di Castri 1981; Carreira et al. 1991). Nutrients are thus major determinants of plant growth and ecological patterns in many Mediterranean ecosystems (Specht 1981; Lebouggeois et al. 1997). Nutrient limitation in Mediterranean ecosystems has often been demonstrated through fertilisation (McMaster et al. 1982; Witkowski et al. 1990; Rodà et al. 1999). Frequent fires in wide areas of the Mediterranean Basin may result in cumulative nutrient losses through volatilisation, smoke particles, wind-blown ashes, soil leaching and soil erosion, hence exacerbating the possible limiting role of nutrients. N and P availability can increase in the first moments after fire (Kutiel and Shaviv 1989; Carreira et al. 1996; Thomas et al. 1999; Gimeno-Garcia et al. 2000). However, this sudden increase in P availability remains only for a short time due to the fact that such increase principally occurs in soluble P inorganic soil (Kutiel and Shaviv 1989; Thomas et al. 1999), and moreover, the P losses by volatilization can be high after fire (Soto et al. 1997). The enhanced P losses can last some years depending on rainfall intensity and periodicity (Thomas et al. 1999). Moreover, of fire, other factors such as human contamination (Peñuelas and Filella 2002) and atmospheric CO<sub>2</sub> concentration increments (Peñuelas et al. 2001) can vary the nutrient supply in the Mediterranean ecosystems.

In spite the fact that fire-reducing competition in the first regenerative phases in Mediterranean communities (Vilà and Terradas 1995a; Vilà and Lloret 2001), the competition between tree seedlings, saplings, tree resprouts and shrubs for soil resources and light can be strong (Saracino and Leone 2001). In this context, soil nutrient availability could influence growth rates and the competitive relations between trees of the same or different species growing in open, recently burned sites.

Mixed forests of Aleppo pine (*Pinus halepensis* Mill.) and the evergreen holm oak (*Quercus ilex* L.) are well represented in the northwestern Mediterranean Basin. These forests are often the result of old field succession (Aleppo pine being successional earlier than holm oak), and the dynamics of the two dominant tree species at a given site depend on light and water availabilities (Retana et al. 1999; Zavala 1999), fire regime (Rundel 1982; Fox and Fox 1987; Hester and Hobbs 1991), and grazing. Important information above the role of light and water in the mixed forest has been obtained in the last decade (Espelta et al. 1995, 1999; Retana et al. 1999), permitting the application of mechanistic models of stand dynamics (Zavala 1999), but less information is available on the role of nutrients in the growth, competitive relations and ecological succession of these mixed communities.

We conducted a fertilisation experiment in a post-fire Mediterranean shrubland to manipulate the soil nutrient availability. The aim of this experiment was to answer the following questions: (i) Do N and P limit the growth of *Pinus halepensis* and *Quercus ilex* spp *ballota* in this ecosystem?; (ii) Do the effects of competition change with N and P supply?; and (iii) do Aleppo pine and holm oak respond similarly to the increase of P and N availability? Three important effects were observed after the first three years of fertiliser applications: (1) the limiting effect of P; (2) a higher competitive ability for P capture in holm oak than in Aleppo pine; and (3) a more negative effect of competition under a higher P supply in Aleppo pine. These results led us to conduct a second experiment in a common garden to investigate: (i) variations in the competition ability of holm oak and Aleppo pine seedlings under different P availabilities, competitive situation and soil types; and (ii) the associated responses in biomass allocation to shoots and roots.

## Methods

### Field experiments

The experiment was conducted in a naturally regenerated post-fire shrubland that had burnt three times in the past twenty years. The last fire occurred in the summer of 1985, 5 years before the experiment started. The study site was located on a level hill top (slope 0-5%) at 300 m above sea level (41°37' N,

Table 1. Main soil properties (mean  $\pm$  SE,  $n = 5$ ) of the three soil types used in the common garden experiment. The calcareous soil was obtained from the field study site (– not determined).

Variable	Artificial soil	Calcareous soil	Silicate soil
P extracted with $\text{NH}_4\text{Cl}$ (ppm)	5.45 $\pm$ 2.37	1.071 $\pm$ 0.514	5.376 $\pm$ 1.44
P extracted with $\text{H}_2\text{O}$ (ppm)	8.84 $\pm$ 2.70	0.591 $\pm$ 0.270	3.83 $\pm$ 1.43
P (Olsen) (ppm)	–	4.69 $\pm$ 0.30	–
P (Bray and Kurtz) (ppm)	–	–	5.00 $\pm$ 0.23
pH ( $\text{H}_2\text{O}$ )	5.92 $\pm$ 0.01	8.51 $\pm$ 0.01	7.02 $\pm$ 0.02
pH (KCl)	5.27 $\pm$ 0.01	7.50 $\pm$ 0.02	5.76 $\pm$ 0.04
Organic matter (%)	6.51 $\pm$ 0.08	1.54 $\pm$ 0.02	1.21 $\pm$ 0.03
Total N (%)	0.052 $\pm$ 0.001	0.041 $\pm$ 0.001	0.03 $\pm$ 0.001
Fe extracted with TPA (ppm)	0.792 $\pm$ 0.144	0.286 $\pm$ 0.046	0.305 $\pm$ 0.001
S extracted with $\text{H}_2\text{O}$ (ppm)	76.2 $\pm$ 18.8	173 $\pm$ 39	35.8 $\pm$ 3.8
Ca extracted with $\text{NH}_4\text{Cl}$ (ppm)	483 $\pm$ 25	592 $\pm$ 56	301 $\pm$ 46
Mg extracted with $\text{NH}_4\text{Cl}$ (ppm)	37.8 $\pm$ 3.5	27.1 $\pm$ 1.2	21.3 $\pm$ 2.6
Particle size (coarse sand/fine sand/silt/clay)	30/32/21/17	20/18/23/39	29/19/18/34

1°50' E). Soils were *Lithic haploxerolls* associated with *Lithic xerorthents* (Soil taxonomy) developed over calcareous marls (Table 1). They had a high pH (8.5) and a high proportion of carbonates (56%) and active lime (12%). The climate is Mediterranean with a slight continental component. Mean annual rainfall is 517 mm. The vegetation type is a post-fire Mediterranean shrubland (*Erico-Thymalaeetum tinctoriae*) with young saplings of Aleppo pine and small resprouts of interior holm oak (*Quercus ilex* subsp. *rotundifolia*), a subspecies more adapted to continental conditions than the coastal holm oak (*Q. ilex* subsp. *ilex*). These two species are the dominant trees of this community with a cover that represents a 30% of total surface for holm oak and 1% for Aleppo pine at the end of the experiment (October 1993).

A field trial of N and P fertilisation was conducted at the individual target tree level. 188 pines and 52 oaks were randomly selected to establish the following experimental designs. In Aleppo pine, three factors were applied in a factorial design: P fertilisation (0, 125 and 250 kg P/ha), N fertilisation (0, 250 and 500 kg N/ha) and neighbour removal (two levels: with and without neighbours). In holm oak, a factorial design had two factors: P fertilisation (0 and 250 kg P/ha), and N fertilisation (0 and 500 kg N/ha). Solid fertilisers composed by calcareous phosphate and ammonia nitrate were applied in a single dose on 1 m<sup>2</sup> centered around each target plant in July 1990. The initial neighbour removal took place in July 1990 by cutting all aerial biomass of neighbouring plants within 1 m<sup>2</sup> centered around target plants. This vegetation removal was maintained during the three years

of the experiment. In both species, growth between July 1990 and July 1993 was evaluated by absolute and relative growth rates of stem basal area and total height. For each oak genet, the three biggest resprouts were measured and the mean of these three measurements was used as basal stem diameter and height of each genet. At the beginning of the experiment, pine heights averaged 562  $\pm$  65 (SE) mm, and basal area 208  $\pm$  12 mm<sup>2</sup>; oak resprouts averaged 304  $\pm$  10 mm for height, and 124  $\pm$  16 mm<sup>2</sup> for basal area.

#### Common garden experiments

In this follow-on experiment, we tested responses of potted seedlings of both species to different levels of soil P availability on different soil types and competitive situations. Seedlings of both species were germinated in the laboratory in January 1994 in a non-fertilised artificial soil from seeds harvested in the field study site. Two months later, seedlings were transplanted to the common garden, situated in the Barcelona Autonomous University (Bellaterra, Central Catalonia), into pots large enough (150 cm<sup>2</sup> of surface and 40-cm deep) to allow the study of root systems. The seedlings were situated under a plastic cover to exclude rainfall and allow the control of water availability during the experiment.

Two factorial experimental designs were established for each species. In the first design, two factors were included: P availability and soil type. The fertiliser was calcareous orthophosphate. It was mixed with the soil substrates before filling up the pots to homogenise P distribution throughout the soil.

Five levels of P availability were tested, equivalent to 0, 30, 60, 125 and 250 kg P/ha. Three different soil types were tested: a calcareous soil taken from the field study area, a silicate soil developed on granodiorite, and an artificial substrate made of 40% peat and 60% sand, by volume. The calcareous soil had high pH and low P content, while the silicate soil had neutral pH and a moderate P content (Table 1). The artificial soil was very poor in nutrients and it was included in the experiment as a reference for the natural soils. Texture was intermediate in all three soils (coarse sand 20%, fine sand 18%, silt 23%, clay 39% in the calcareous soil, 29-19-18-34 in the silicate soil, and 30-32-21-17 in the artificial soil). Each species had 5 levels of P availability and 3 soil types, totalling 15 treatments with 20 replicate target seedlings for each one.

The second design included 3 factors: P availability, soil type and competitive situation. P availability had three levels: 0, 125, and 250 kg P/ha. Two soil types were used: the calcareous and the silicate soils described above. The competition factor was introduced through the use of 5 different neighbourhoods for each level of P availability and soil type: pots with a holm oak, with a single Aleppo pine, with one oak and one pine, with two oaks, and with two pines. This design was established to investigate intra- and inter-specific competition. Thus, this design allowed us to conduct a factorial design for the two species. Each species had 3 levels of P availability, 2 soil types and 3 different competitive situations (without competition, with intraspecific competition and with interspecific competition), totalling 18 treatments with 20 replicated target seedlings for each species. The seedlings in the two-seedling pots were oriented East-West to minimise mutual shading.

Light availability was the same throughout the common garden and averaged 80% with respect to the light outside the plastic cover (Retana et al. 1999). Irrigation applied to each pot corresponded to the potential evapotranspiration of the zone, with a slight summer stress and with a slight excess of water supply in the cold period (September-April), in order to simulate the water availability patterns of this Mediterranean area. Seedlings of both species were on average 5-6 cm tall at the beginning of the experiment (first week of April 1994), and 18-28 cm tall at the end of the experiment. Biomass growth was measured at the end of the experiment, in October 1995, 19 months and two growth seasons after transplanting. The root, stem and leaf biomass were measured after

drying at 70° C, and weighed. Root biomass was separated in three diameter fractions (thick  $\varnothing > 3$  mm, intermediate  $3 \text{ mm} > \varnothing > 0.5 \text{ mm}$ , fine  $\varnothing < 0.5 \text{ mm}$ ). As an estimation of the effects of experimental factors on the root assimilable fraction/root structural fraction ratio, we statistically analysed the values of the fine roots/thick roots ratio through ANOVAs. Soil P contents were measured in the silicate soil by the method of Bray and Kurtz (1945), and in the calcareous soil with the method of Olsen and Sommers (1982).

### *Statistical analyses*

The effects of each studied factor were investigated through AN(C)OVA factorial analyses. We first conducted the analysis introducing the initial individual size as a cofactor in the test (ANCOVA). If the cofactor was not significant, we excluded it from the model, which became an ANOVA. Unless otherwise stated, only significant factor effects or interactions are mentioned in the text. When a factor had a significant effect at several levels, we thereafter analysed the differences among the different levels through pair-wise comparisons using the Duncan new multiple range test. The most relevant results of these pair-wise comparisons are highlighted by the Figures in the results section. Analyses were conducted with the Super ANOVA package (Abacus concepts Inc., 1989).

## **Results**

### *Field experiments*

After three years of after fertilisation, height and basal area growth rates (absolute as well as relative) were significantly higher in P-fertilised plants than in non fertilised ones for both species (Figure 1). Growth was much higher in pines ( $758 \pm 72 \text{ mm}^2$  absolute basal area growth in non P-fertilised pines and  $992 \pm 74 \text{ mm}^2$  in P-fertilised pines,  $F = 60$ ,  $P < 0.0001$ ) than in oaks ( $250 \pm 44 \text{ mm}^2$  absolute basal area growth in non P-fertilised oaks versus  $281 \pm 49 \text{ mm}^2$  in P-fertilised oaks,  $F = 8$ ,  $P = 0.003$ ), but the relative response to the increased P supply was similar in both species (Figure 1). N fertilisation had smaller effects on growth in both species. It only produced a significant positive effect ( $F = 6.6$ ,  $P = 0.014$ ) on relative basal area growth of pine ( $136 \pm 7\%$  after 3 years in non fertilised pines versus  $140 \pm$

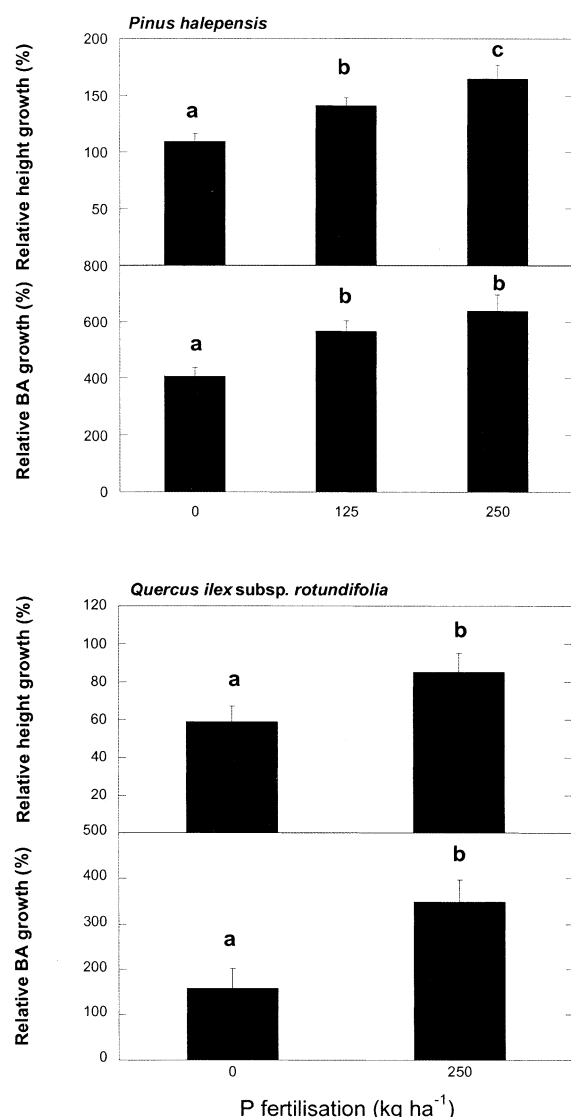


Figure 1. Mean effects ( $\pm$  SE) of P fertilisation on relative height growth and relative basal area (BA) growth of naturally-regenerated *Pinus halepensis* saplings, and of *Quercus ilex subsp. rotundifolia* resprouts 5 years after fire. The results are calculated after the first three years after fertiliser application in a field experiment. Different letters indicate significantly ( $P < 0.05$ ) different values for the different P fertilisation levels in a Duncan new multiple range post-hoc test.

8% and  $156 \pm 5\%$  after 3 years in pines that received doses of 125 and 250 kg N/ha, respectively). No interactions between N and P amendments were observed.

A significant interaction between P fertilisation and neighbour removal was observed for absolute ( $F = 3.5$ ,  $P = 0.032$ ) and relative ( $F = 8.1$ ,  $P = 0.008$ )

basal area growth of pine: P fertilisation increased basal area growth particularly when it was accompanied by neighbour removal or, conversely, neighbour removal only increased basal area growth when P fertiliser was applied (Figure 2). Thus, basal area growth revealed a significant increase in competitive intensity when P supply was increased through fertilisation. This effect was not observed for height growth. When the analysis was restricted to those pines retaining their neighbouring plants (i.e., without neighbour removal), P fertilisation lost its significant effect on basal area growth (Figure 2). On the contrary, oak resprouts were able to respond to increased P availability even in the presence of neighbours (Figure 1; notice that the experimental design for oak had no neighbour removal treatment because of lack of enough trees).

### Common garden experiments

#### Experiment 1 (P fertilisation · Soil type)

Potted oak seedlings grew faster than pine seedlings over the 19 months of the experiment on all soil types and at all levels of P availability. P fertilisation increased total biomass of seedlings of both species on the three soils (Figure 3). A significant interaction was observed between soil type and P fertilisation in oak ( $F = 2.2$ ,  $P = 0.033$ ) and was marginally significant in pine ( $F = 1.9$ ,  $P = 0.064$ ), because P fertilisation had a larger positive effects on the artificial soil than on either natural soil (Figure 3).

The ratio between aboveground and belowground biomass (shoot/root ratio) was significantly ( $F = 22$ ,  $P < 0.0001$ ) lower in oak than in pine. Seedlings of both species allocated significantly more biomass to the root fraction on the silicate soil than on the calcareous soil ( $F = 30$ ,  $P < 0.0001$  for pines,  $F = 6$ ,  $P = 0.022$  for oaks).

In pine, P fertilisation tended to increase the biomass of all diameter ( $\emptyset$ ) root fractions on all soils, but this increase was significantly ( $F = 14$ ,  $P = 0.0001$ ; Figure 4A) so only for the fine root fraction ( $\emptyset < 0.5$  mm). This effect increased the biomass ratio between fine and thick roots ( $\emptyset > 3$  mm) gradually with P fertilisation on the calcareous soil ( $F = 6.1$ ,  $P = 0.02$ ; Figure 4B). In oak, P fertilisation had a positive and significant effect on the biomass of the thick root fraction ( $F = 5.8$ ,  $P = 0.03$ ; Figure 4C).



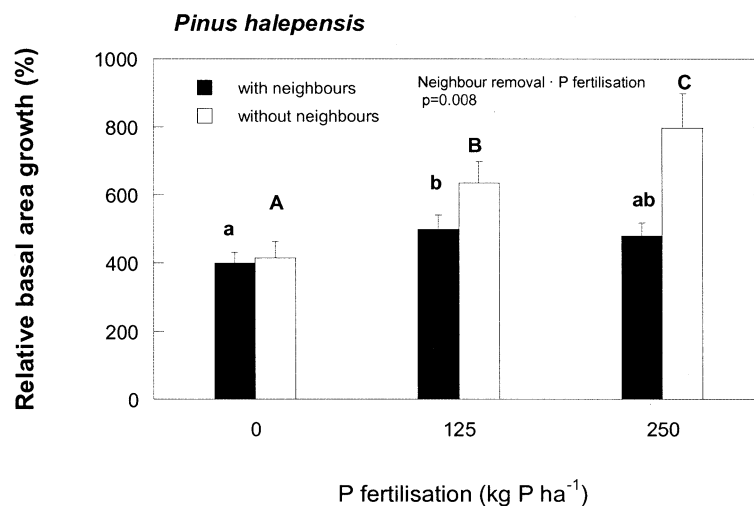


Figure 2. Relative basal area growth of *Pinus halepensis* saplings (mean  $\pm$  SE) after three years growing with and without neighbours in the field at three levels of P fertilisation. (\* = neighbour removal significant at  $P < 0.05$  in a Duncan new multiple range post-hoc test).

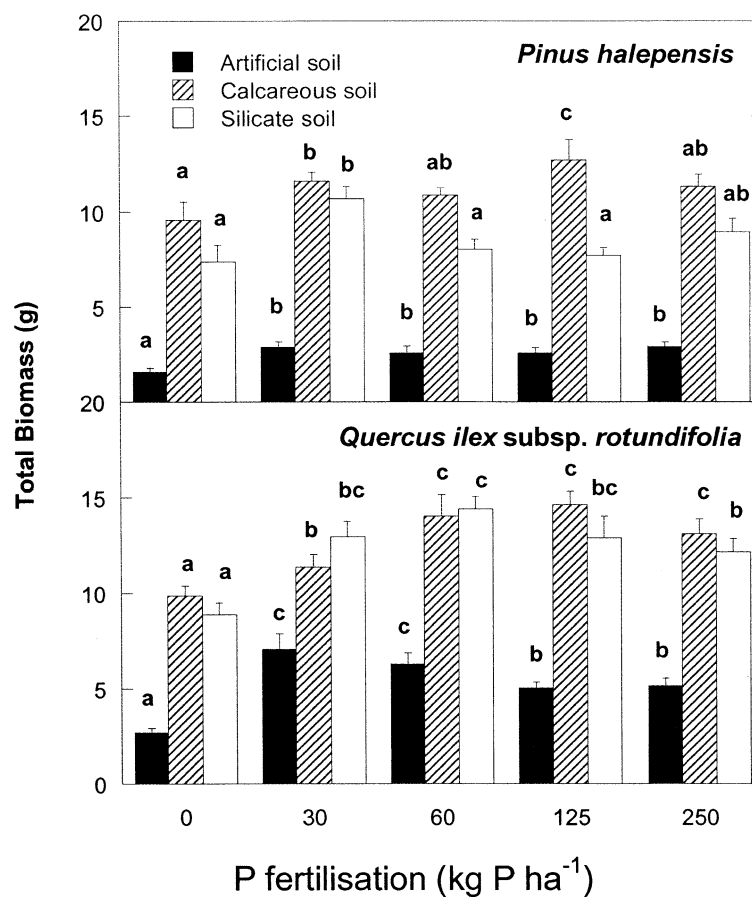


Figure 3. Total biomass (mean  $\pm$  SE) of *Pinus halepensis* and *Quercus ilex subsp. rotundifolia* seedlings grown at five levels of P fertilisation on three soil types: calcareous, siliceous and artificial in a common garden experiment. Subscripts indicate significantly ( $P < 0.05$ ) different values in response to fertilisation within each soil type in a Duncan new multiple range post-hoc test.

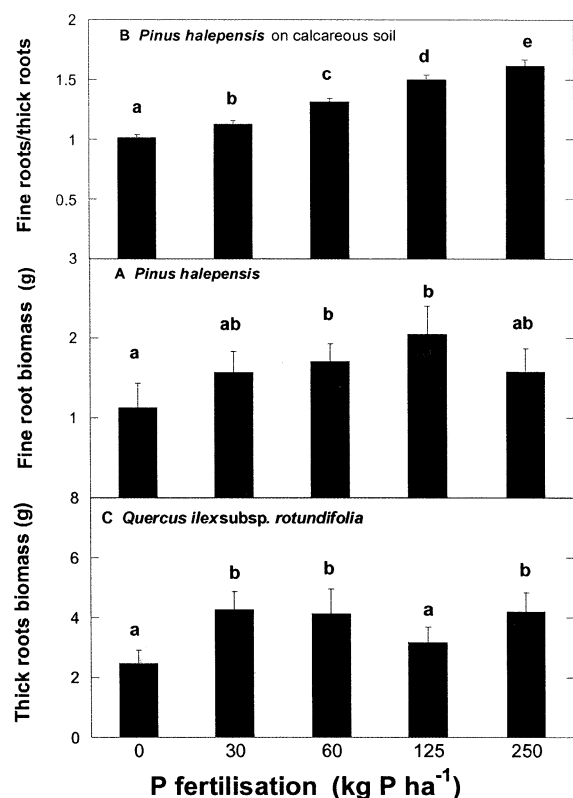


Figure 4. A. Fine root ( $\varnothing < 0.5$  mm) biomass (g) of *Pinus halepensis* seedlings grown at different levels of P fertilisation. B. Fine roots-thick roots biomass ratio in *Pinus halepensis* seedlings grown at different levels of P fertilisation on the calcareous soil. C. Thick root ( $\varnothing > 3$  mm) biomass of *Quercus ilex subsp. rotundifolia* seedlings grown at different levels of P fertilisation. Error bars are P mean  $\pm$  SE. Different letters indicate significantly ( $P < 0.05$ ) different values for the different P fertilisation levels in a Duncan new multiple range post-hoc test.

#### Experiment 2 (P fertilisation \* Soil type \* competitive situation)

Presence of a second seedling in the same pot had a negative effect on total biomass of the target seedling at the end of the experiment for both species and on the two soils (Figure 5). On the calcareous soil and for both species, the negative effect of neighbour presence was stronger when the neighbour was a pine, but this did not happen on the silicate soil. In oaks on the calcareous soil, an interaction between neighbour presence and P fertilisation was observed ( $F = 2.5$ ,  $P = 0.043$ ). The presence of a second seedling in the same pot limited the growth of oak seedlings more when P availability was increased (Figure 5). This interaction was not observed in the silicate soil (Figure 5). In contrast, in pines the pres-

ence of another seedling in the same pot had a stronger negative effect on the final biomass when P availability increased in the silicate soil ( $F = 4.5$ ,  $P = 0.004$ ) but not in the calcareous soil (Figure 5).

In oak, and independent of P supply, the presence of a seedling in the same pot increased the proportional biomass allocation to roots (except on calcareous soil when the neighbour was also an oak). However, in pine, neighbours did not affect shoot/root ratios (Figure 6).

#### Discussion

Under field conditions, P limited the growth of both pine and holm oak. Similarly P limited two dominant shrub species of the same community (*Rosmarinus officinalis* and *Erica multiflora*; Sardans 1997). In the common garden experiment, P fertilisation had a positive effect on growth in the three tested soils and for both species, although this effect was particularly high on the artificial soil. However, in the common garden the strongest differences were found between fertilised and non-fertilised seedlings, independent of fertilisation level. Even small P additions are sufficient to have a positive effect on growth. These results showing the limiting role of P agree with other experimental data from Mediterranean ecosystems (Kruger 1979; Rabinovitch-Vin 1983; Komlenovic 1997) and, in particular, in calcareous Mediterranean shrublands (Carreira et al 1991, Vilà and Terradas 1995b). The increase of P supply may have a direct impact on photosynthetic efficiency (Reich et al. 1989; Jacob and Lawlar 1992). P also often limits the Net Primary Production in many other ecosystems through the world: e.g., in tropical rainforests of South America (Raaimaker and Lambers 1996; Gehring et al. 1999), Central America (Cooperband et al. 1994) and Hawaii (Herbert et al. 1999), in evergreen sub-tropical forests in China (Zhang et al. 2000), in temperate forests of New Zealand (Mead 1990) and North America (Knox et al. 1995), and in boreal forest of Canada (Preston and Trofymow 2000).

Two factors can account for the limiting role of phosphorus in the studied Mediterranean site. First, soil extractable P (4 ppm) and P content of the bedrock are low. Second, the high soil pH (8.5) and the presence of free carbonate (12.5%) makes diphosphate ( $\text{HPO}_4^{2-}$ ) the dominant inorganic P form, leading to the precipitation of calcium monophosphate ( $\text{CaHPO}_4$ ), which reduces the amount of P available

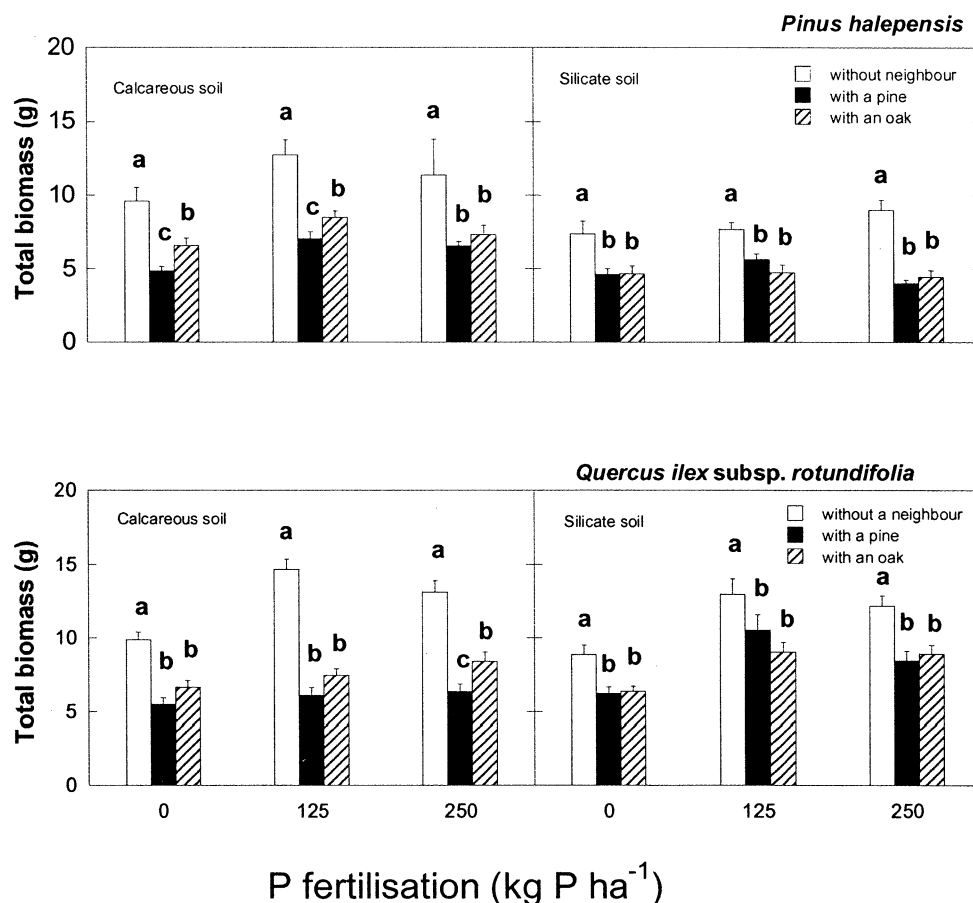


Figure 5. Total biomass (mean  $\pm$  SE) of *Pinus halepensis* and *Quercus ilex* subsp. *rotundifolia* seedlings grown in different competitive situations at different P fertilisation levels and on two different soil types in a common garden experiment. Different letters within each species, soil type and fertilisation level indicate significantly ( $P < 0.05$ ) different values for the different neighbour conditions in a Duncan new multiple range post-hoc test.

to plants. In silicate soils, aluminium and ferric oxides and hydroxides can decrease P availability (Nanzzyo et al. 1993; Crews et al. 1995). In our study, the silicate soil was also poor in naturally available P ( $5.0 \pm 0.2$  SE ppm).

In the field, few significant effects of N fertilisation on growth were observed, only a slight positive effect on stem diameter growth in pines. This low response seems to be driven by the high levels of organic matter and the high mineralisation rates of this soil that provide a good N supply. Atmospheric N deposition from the nearby Barcelona conurbation (Rodà et al. 2002) may also contribute to enriching the ecosystem with available N. Similarly, on calcareous soils in Mediterranean areas of France, the strongest response to fertilisation was also to P not to N (Bonneau 1986). The general presence of calcare-

ous soils in the western Mediterranean basin confers to P an important ecological role.

In the field, pine saplings only responded clearly to P fertilisation when neighbouring plants were removed, while coexisting oak resprouts responded significantly and positively to P fertilisation even without neighbour removal. Therefore, oak resprouts showed a higher competitive ability for P than pine saplings, as assessed through aboveground growth. Oak resprouts may probably benefit from a bigger root system than pine saplings at this site, though they were smaller than pine saplings and also sprouted from small genets. In other words; this high competitive ability of oaks with respect to pines might be due, at least in part, to their resprouting capacity.

In the second common garden experiment with potted seedlings, the interaction between P availabil-



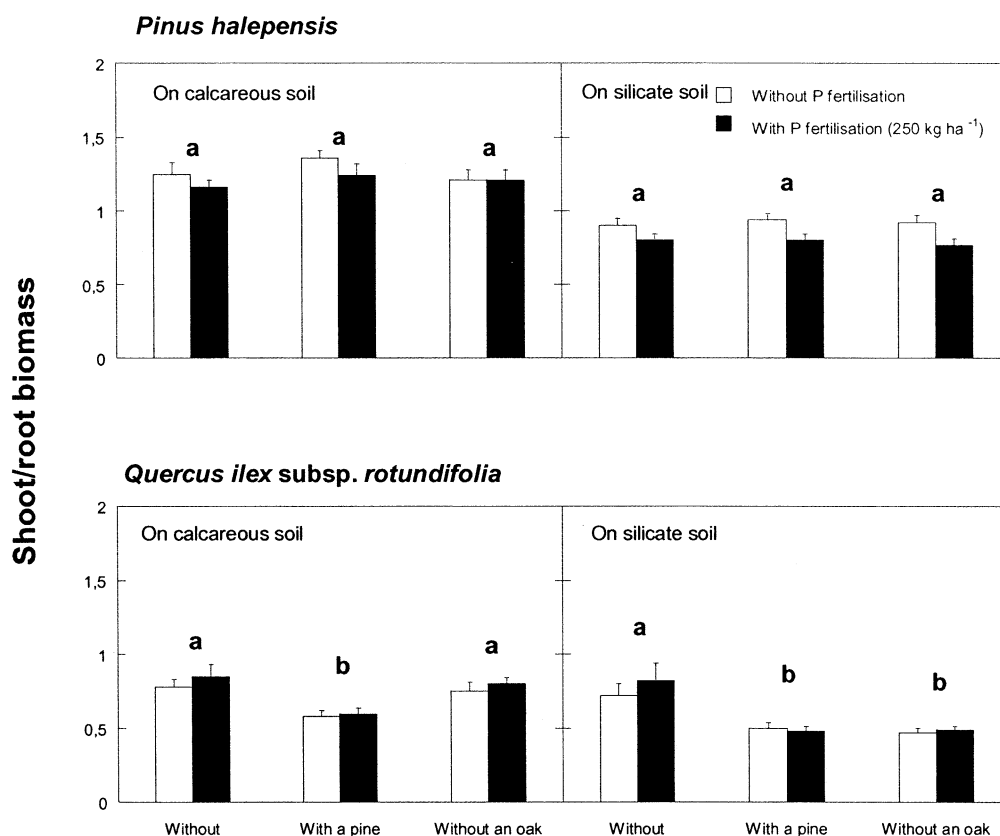


Figure 6. Effects (mean  $\pm$  SE) of competitive situations on the shoot/root biomass ratio of *Pinus halepensis* and *Quercus ilex* subsp. *rotundifolia* seedlings grown on different soil types and P fertilisation levels in a common garden experiment. Different letters within each species and soil type indicate significantly ( $P < 0.05$ ) different values for the different neighbour conditions, irrespective of P fertilisation that was not statistically significant.

ity and neighbour presence was statistically significant only for oak. The growth difference between oak seedlings growing alone or with another seedling in the same pot increased with P fertilisation. On the calcareous soil, there was a slightly more negative effect of neighbour presence on growth of both species when the neighbour seedling in the pot was a pine than when it was an oak, but this effect was not observed on the silicate soil. In general, seedlings of both species had a similar competitive ability in the common garden experiment, which is a likely consequence, at least in part, of the lack of oak big root system with respect to that in the field. The negative effect of a neighbouring seedling on total biomass of the target seedling ranged from 30% in non-fertilised pots to 55% in pots fertilised with an equivalent to 125 kg P ha<sup>-1</sup> in oak. This effect in the common garden experiment depended on soil type too. We can conclude that the negative effect of neighbour com-

petition increased with increasing P supply an effect as detected in the Aleppo pine in the field (see above). These findings agree with the conceptualisation of Grime (1977 and 1979) in the sense that the competition is stronger when the resources level is enhanced.

Potted pine seedlings show a great organ allocation plasticity depending on P availability, increasing their relative biomass allocation to roots when P availability was increased, fundamentally on the silicate soil. Also in pines, the increment in P supply significantly increased the allocation to fine roots relative to coarse ones in all soil types, thus the pines allocate more to roots, particularly to more absorbent root structures, when P availability is enhanced. These results contrast with the results obtained by other authors (Tilman 1982; Wilson and Shay 1990), who observed that the increase of soil resources allowed plants to allocate more to aerial tissues than to roots and thus

to compete better for light. In our common garden experiment, the relatively high light availability, the small size of the seedlings and the distance between them (6 cm within pots and 20 cm between pots) could have lowered the intensity of light competition. A good water supply when the soil has nutrient resources and when the light competition has not yet begun, may make a higher allocation to roots advantageous in order to secure a nutrient reserve. This response may have contributed to a better soil exploration and to improved resource capture. The presence of a pine neighbour in the same pot increased the root allocation in oak seedlings, on both the calcareous and the silicate soil. This trend could be a consequence of higher competition for soil resources (Brewster et al. 1975; Christie et al. 1975). Pine seedlings did not show such an effect.

In the common garden experiment, important growth differences were found in response to soil type. The greatest growth was observed on the calcareous soil and the lowest on the artificial soil. The changes in the relative biomass allocation to different-sized root fractions took place in contrary direction. In pines, a larger response to P availability was observed in the calcareous soil than in the two other soils. The natural P contents were similar in the two natural soils, but the total N concentration was higher in the calcareous ( $0.041 \pm 0.001$  SE, %) than in the silicate soil ( $0.03 \pm 0.001$  %). This would have allowed greater responses in growth when P fertilisation was applied in the calcareous soil than in the silicate soil.

Both Aleppo pine and holm oak have a high capacity for changing growth and biomass allocation patterns depending on soil type, P supply and neighbour presence. Such plasticity has been interpreted as a basic character in ecological plant strategies (Grime 1977; Tilman 1982; Chapin et al. 1986). Resource allocation to roots might be more intense when the competitive pressure for water and nutrients increases (Tilman 1982; Wilson and Shay 1990), a fact we observed in oak but not in pine seedlings. Pine seedlings had a higher shoot/root biomass ratio than oak seedlings and showed a higher variability in allocation to different organs on different soils. In another experiment that manipulated light and soil water levels, Aleppo pine seedlings showed a high allocation plasticity (Broncano et al. 1998). Late successional species usually have higher rates of root allocation than early successional ones (Tilman 1988; Gleeson and Tilman 1994), though in some tree species this trend

has not been observed (Kolb et al. 1990). In oaks, the allocation effort could be a function not only of an optimal resource distribution between organs but of resource accumulation in the burl as well. The evergreen holm oak is a medium- to late-successional species while Aleppo pine thrives in earlier succession stages. For some authors (Grime 1977, 1979; Coley et al. 1985) species typical of advanced succession stages would have less phenotypic plasticity to vary their resource allocation when resource supply changes. However, the results of our experiments show that Aleppo pine does not have greater phenotypic plasticity than holm oak, as would be expected from its pioneer character (Chapin and Shaver 1985; Chapin et al. 1986). Instead, our results show that the allocation capacity of different species depends strongly on environmental conditions.

In our experiments, the capacity to vary biomass allocation in response to different levels of soil nutrients was different in each species. Pine seedlings were more sensitive to P supply variations while oak seedlings were more responsive to neighbour presence. The capacity to change the shoot/root allocation in front of different levels of resource supply can be an important trait in the early live stages of the slow-growing holm oak in order to increase its survival under different resource availabilities and neighbour presence.

Our study shows that both Aleppo pine and holm oak can respond in different ways to different soil P availabilities depending on stem age (initial phases versus later phases of exponential growth in open, recently disturbed sites), stem origin (seedlings versus resprouts), soil type and neighbour competition. Recurrent fires result in cumulative P losses from soil and may reduce soil P availability to plants (Serrasolses and Vallejo 1999). On the other hand, the increases of torrential rainfalls predicted in most global circulation models (IPCC 2001) can increase the P losses in the next future. Increased P limitation to plant growth can ensue, further slowing the regeneration process of these forests, which is already compromised due to low soil water availability and scrub competition.

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