Drought changes phosphorus and potassium accumulation patterns in an evergreen Mediterranean forest

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Summary

1. Climate models predict more extreme weather in Mediterranean ecosystems, with more frequent drought periods and torrential rainfall. These expected changes may affect major processes in ecosystems such as nutrient cycling. However, there is a lack of experimental data regarding the effects of prolonged drought on nutrient cycling and content in Mediterranean ecosystems.

2. A 6-year drought manipulation experiment was conducted in a Quercus ilex Mediterranean forest. The aim was to investigate the effects of drought conditions expected to occur over the coming decades, on the contents and concentrations of phosphorus (P) and potassium (K) in stand biomass, and P and K content and availability in soils.

3. Drought (an average reduction of 15% in soil moisture) increased P leaf concentration by 18.2% and reduced P wood and root concentrations (30.9% and 39.8%, respectively) in the dominant tree species Quercus ilex, suggesting a process of mobilization of P from wood towards leaves. The decrease in P wood concentrations in Quercus ilex, together with a decrease in forest biomass growth, led to an overall decrease (by approximately one-third) of the total P content in above-ground biomass. In control plots, the total P content in the above-ground biomass increased 54 kg ha⁻¹ from 1999 to 2005, whereas in drought plots there was no increase in P levels in above-ground biomass. Drought had no effects on either K above-ground contents or concentrations.

4. Drought increased total soil soluble P by increasing soil soluble organic P, which is the soil soluble P not directly available to plant capture. Drought reduced the ratio of soil soluble inorganic P : soil soluble organic P by 50% showing a decrease of inorganic P release from P bound to organic matter. Drought increased by 10% the total K content in the soil, but reduced the soil soluble K by 20.4%.

5. Drought led to diminished plant uptake of mineral nutrients and to greater recalcitrance of minerals in soil. This will lead to a reduction in P and K in the ecosystem, due to losses in P and K through leaching and erosion, if the heavy rainfalls predicted by IPCC (Intergovernmental Panel on Climate Change) models occur. As P is currently a limiting factor in many Mediterranean terrestrial ecosystems, and given that P and K are necessary for high water-use efficiency and stomata control, the negative effects of drought on P and K content in the ecosystem may well have additional indirect negative effects on plant fitness.

Key-words: Arbutus unedo, biomass, climate change, drought, nutrient content, Phillyrea latifolia, phosphorus, potassium, Quercus ilex, soil

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Introduction

Water is the most important limiting factor in Mediterranean ecosystems. In these ecosystems, aridity has increased in recent decades (Piñol, Terradas & Lloret 1998; Peñuelas, Filella & Comas 2002) and both Global Circulation (Houghton et al. 2001) and ecophysiological models predict greater levels of drought in the near future: for example, GOTILWA (Growth Of Trees Is Limited by Water) predicts a decrease of 25% in soil moisture between 2000 and 2040 (Sabaté, Gracia & Sánchez 2002; Peñuelas et al. 2005). Furthermore, more intense and more frequent dry periods are expected...
dynamic patterns in an evergreen Mediterranean forest, the Mediterranean Basin has ever studied the effects of drought. Nevertheless, to our knowledge, no field experiment in such a forest in the Mediterranean Basin has ever been investigated further in order to fully understand the indirect effects of drought on P and K availability and its role in stomata control and leaf water loss. These nutrients are particularly important in dry environments due to their very important roles in plant biology (Sundareshwar et al. 1994; Sardans, Rodà & Peñuelas 2005b) and their availability has been reported to be inversely correlated with water availability (Kemp & Moody 1984; Díaz & Roldan 2000).

A decrease in soil moisture may have a negative effect on soil microbial activity (Sardans & Peñuelas 2005) and as sclerophyll usually increases when the environment evolves towards drier conditions (Sabaté, Calvet & Gracia 1992; Oliveira et al. 1994; Sardans, Peñuelas & Rodà 2006b), the resulting accumulation of recalcitrant organic matter in soil may slow down organic matter decomposition (Pastor et al. 1984; Coïteaux, Aloui & Kurz-Besson 2002). Previous work has shown a decrease in soil soluble P as a consequence of drought in Mediterranean forests (Sardans & Peñuelas 2004).

Drought can reduce the P and/or K contents in stand biomass by reducing soil mineralization rates (Sardans & Peñuelas 2005) and plant absorption capacity and/or growth, resulting in an accumulation of P and K nonavailable forms, in soil and plant litter. If plant P and K contents are reduced and soil P and K contents are increased, the risk of P and K losses given that IPCC (Intergovernmental Panel on Climate Change) models predict an increase in torrential rainfall in the Mediterranean Basin (Houghton et al. 2001) and thus greater soil erosion (De Luis, González-Hidalgo & Raventós 2003). If drought affects P and K cycling and availability, a strong synergic effect will result as P availability has a positive effect on water-use efficiency (Sing et al. 2000; Ruiz-Lozano et al. 2001; Mohammad & Zuraiga 2003; Sardans, Peñuelas & Rodà 2005b) and K is particularly important in dry environments due to its role in stomata control and leaf water loss. These indirect effects of drought on P and K availability and content in different ecosystems compartments, in the mid- and long-term (the coming decades), still need to be investigated further in order to fully understand the overall effect of the drought predicted by IPCC models. Nevertheless, to our knowledge, no field experiment in the Mediterranean Basin has ever studied the effects of drought on P and/or K contents at a ecosystem level.

To investigate the effects of drought on P and K dynamic patterns in an evergreen Mediterranean forest, a 6-year field experiment was conducted in a holm oak Quercus ilex forest by means of a simulation of the drought levels predicted by GCM and ecophysiological models for the next decades (Houghton et al. 2001; Sabaté et al. 2002; Peñuelas et al. 2005). We investigated the impacts of this experimental decrease of soil moisture on: (1) P and K concentrations and contents in the biomass (leaf, wood, root and litter) of the three dominant species in the ecosystem, and (2) on the concentrations of total and available forms of soil P and K.

Materials and methods

FIELD SITE

The study was carried out in a natural Quercus ilex oak forest in the Prades mountains in southern Catalonia (north-east Spain) (41°13' N, 0°55' E) on a south-facing slope (25%). The soil is a stony Dystric Xerochrept (Soil Survey Staff 1999) lying on a bedrock of metamorphic sandstone. Its depth ranges between 35 and 100 cm, with the depth of Horizon A ranging between 25 and 30 cm. The average annual temperature is 12 °C and an average rainfall of 658 mm, with a period between September to November experiencing the maximum of rainfall. Summer drought is pronounced and usually lasts for 3 months. The vegetation consists of a dense forest with a canopy height average of 8–10 m dominated by Quercus ilex L. (20–8 m ha⁻¹ of trunk basal area at 50 cm of height) accompanied by abundant Phillyrea latifolia (7–7 m ha⁻¹ of trunk basal area at 50 cm of height and Arbutus unedo L. A number of other evergreen species well-adapted to drought conditions such as Erica arborea L., Juniperus oxycedrus L., Cistus albidus L., and occasional individuals of deciduous species such as Sorbus torminalis L. Crantz and Acer monspessulanum L. are also present. In winter 1999, the above-ground biomass (AB) of Quercus ilex represented 77·1% of the total biomass, while Phillyrea latifolia represented 12·6% and Arbutus unedo 7·8%; the sum of the aerial biomass of these three species thus represented 97·6% of the whole ecosystem AB. In the winter of 2005, the biomass for the same three species were 75·6%, 13·3% and 8·7%, respectively, representing in total a 97·6% of the total AB.

EXPERIMENTAL DESIGN

Eight 15 × 10 m plots were established at the same altitude (930 m above sea level) on a slope. Four of the plots received the drought treatment and four plots left as controls. All the plots were established in an area with the same aspect and altitudinal level, with a minimum distance between plots of 15 m. The treatments were randomly assigned to different plots. The drought treatment consisted of partial rainfall exclusion by suspending transparent PVC strips at a height of 0·5–0·8 m above soil level and covered approximately 30% of the total soil surface. Four plastic strips 14 m long and 1 m wide were placed along the drought treatment
plots and a 0·8–1 m deep ditch was dug along the entire top edge of the upper part of the treatment plots to intercept runoff water. The water intercepted by the strips and ditches was channelled to the bottom edge of the plots. The drought treatment began in March 1999 (Ogaya et al. 2003). Soil moisture content was measured every 2 weeks throughout the experiment period by time domain reflectometry (Tektronix 1502 C, Beaverton, OR, USA; Zegelin, White & Jenkins 1989). Three stainless steel cylindrical rods, 25-cm long, were driven into the soil at four randomly selected places in each drought plot. The time domain reflectometer was connected to the ends of the rods to determine the soil moisture content.

**BIOMASS AND LITTER DETERMINATION**

Just before the treatment was begun, all living stems of the three dominant species with a diameter of over 2 cm at 0·5 m height above the ground were tagged and their circumferences measured at 50 cm height with a metric tape. In January 2005, the circumferences of the stems were measured again to calculate the annual stem diameter increment.

Allometric relationships between above-ground tree biomass and the diameter at 50 cm (D50) were calculated for *Quercus ilex* and *Phillyrea latifolia* in the studied area (outside the plots). Total AB, leaf biomass (LB) and stem biomass were measured by weighing plant material after it had reached a constant weight in an oven at 70 °C. The allometric relationships in *Quercus ilex* (ln AB = 4·9 + 2·277 ln D50, r² = 0·98, n = 12) and in *Phillyrea latifolia* (ln AB = 4·251 + 2·463 ln D50, r² = 0·97, n = 13) were used thereafter to estimate the above-ground standing biomass of these two species in the studied area (see Ogaya et al. 2003). To estimate *Arbutus unedo* biomass, we used the allometric relationship (ln AB = 3·830 + 2·563 ln D50, r² = 0·99, n = 10) previously calculated in the same area by Lledó (1990).

LB was calculated by the following allometric relationships for *Quercus ilex*: In LB = 1·43 + 2·43 ln D50, r² = 0·94, and for *Arbutus unedo*: In LB = 1·887 + 2·157 ln D50, r² = 0·95. Stem biomass was calculated by the difference between total AB and total LB.

Litterfall was collected in 20 circular baskets (27 cm diameter with 1·5 mm mesh diameter) randomly distributed on the ground of each of the eight plots. The fallen litter was collected every 15 days during 1999 and every 2 months during 2004. Total litterfall was estimated by the proportion of the surface area of the plots covered by the collecting baskets.

**BIOMASS AND SOIL SAMPLING PROCESS**

Prior to the start of the experiment (March 1999), eight soil samples (four control plots and four drought plots) were analysed to test the spatial variability of the soils. There were no significant differences in P and K availability and contents between control and drought plots. In January 2005, just 6 years after the experiment was initiated, all the soil and biomass samples were collected, in order to evaluate the total contents in soil and in stand biomass, at the same time. Eight samples of leaf and stems from the three dominant species (*Quercus ilex*, *Phillyrea latifolia* and *Arbutus unedo*) were randomly sampled in each plot (four samples in the sun and four samples in the shade). The leaves were sampled from between 1·5 and 6 m where most foliar biomass was located. Sample collection was standardized in order to avoid bias due to differences in the age of tissues and their position with respect to sunlight. The leaves sampled were those from current year leaves of 1998 and 2004 and represented the majority of the leaves of the plants of these three species. Stems were collected separately and stems of 0·3–2 cm and more than 2 cm in diameter were differentiated. We collected four samples of each stem diameter class per plot. We only sampled the trees and shrubs of the diameter class between 2 and 12 cm of BD (at 5 cm), that represents most of the community biomass (Ogaya et al. 2003; Ogaya & Peñuelas 2007). The concentrations in the stems of diameter 0·3–2 cm did not differ from those with a diameter greater than 2 cm and thus only one stem concentration was calculated for all stem diameters, which was taken as the wood concentration. All leaves and stems were collected from different plants in each plot. In 1999 and in 2005, five leaf litter samples from each species (*Quercus ilex*, *Phillyrea latifolia* and *Arbutus unedo*) from each plot, were analysed separately. The leaf litter that represented 87% of the total litter mass, was analysed in the same way as the biomass.

We conducted the soil sampling in January 2005, i.e. following 6 years of drought treatment. We randomly sampled five cores from the first 30 cm of soil profile (Horizon A) in control plots and 10 in each drought plot. In the drought plots, we distinguished two levels of drought: that of the soil between the strips (D) (runoff exclusion) and that under the strips (DD) (runoff exclusion plus rainfall exclusion). We analysed these two soil fractions separately because we had previously observed that soil moisture decreased more under plastic strips than between plastic strips, being the soil moisture 27% lower under plastic strips than between plastic strips in winter. Five soil cores were taken between strips and five from under the strips, at a minimum distance of 1 m from the nearest tree or shrub; in each control plot only five soil cores were randomly sampled. We collected and analysed separately the 0–15 cm deep soil and the 15–30 cm deep soil in each soil core, as horizon A had an A subhorizon (first 15 cm) rich in organic matter (7·25% W/W) and an A2 subhorizon (15–30 cm) with only moderate amounts of organic matter (1·3% W/W). However, as extractable soil P and K can have great variations through the year, we conducted a seasonal study with additional samplings in spring, summer and autumn in order to investigate possible fluctuations in these variables.
Additionally five soil holes per plot under *Quercus ilex* trees were dug and roots of this species were sampled (Ø > 5 mm) in order to study the effects of drought on root P and K concentration.

All the samples were taken to the laboratory and stored at 4 °C until the analyses were carried out. In order to analyse P and K in foliar tissues, leaves were washed with distilled water as in Porter (1986).

For the analyses of total P and K, biomass and soil samples were washed and dried in an oven at 60 °C until constant weight was obtained. Then, they were ground up in a CYCLOTEC 1093 (Foss Tecator, Höganäs, Sweden) – in the case of the biomass samples – or in a FRITSCH Pulverisette (Rudolstadt, Germany) – in the case of the soils and bedrock samples.

P and K concentrations in all biomass and soil samples were measured using ICP-AES (Atomic Emission Spectroscopy with Inductively Coupled Plasma) in a JOBIN IBON JY 38 (Longjumeau, HORIBA Jobin Iken, Seoul, South Korea). Two millilitres of the mixed acid solution were added to 100 mg of dry biomass for each sample. The digested solutions were brought to 10 mL of final volume (HClO$_4$ 3%). During the acid digestion process, two blank solutions (2 mL of acid mixture without any sample biomass) were also analysed. In order to assess the accuracy of digestion and analytical procedures of biomasses, a standard certified biomass (DC73351) was used.

For the determination of total P and K soil samples, digestion was carried out in a microwave oven at 120 °C for 8 h with 0.25 g of ground sample in 9 mL of HNO$_3$ (65%) and 4 mL HF (40%) (Bargagli, Brown & Nelli 1995). The digested solutions were adjusted to 50 mL final volume of HClO$_4$ (3%), filtered with a Millex 0.45 μm pore-size membrane filter. The concentrations of K in the filtrates were determined as described above for biomass and soil digests. In order to detect possible annual variations in K concentrations in soil extracts an additional soil sampling and K concentrations in soil extracts was conducted in April 2005.

### STATISTICAL ANALYSES

The effects of drought treatment on plant P and K concentrations and contents were investigated by t-test using plot mean values of each variable. In the case of soil P and K contents, we differentiated between soils under plastic strips (runoff plus partial rainfall exclusion) and soils without plastic strips (runoff exclusion). Thus, for soil analyses we used an ANOVA post-hoc test (Bonferroni/Dunn) to compare the three levels of water availability (Control, D and DD). These analyses were conducted with the STATVIEW 5.01 program (Abacus Concepts, SAS Institute Inc., Berkeley, CA, USA).

### Results

#### SOIL MOISTURE

Between 1999 and 2005 the soil in drought treatment plots submitted to runoff exclusion (D) had an average soil moisture of 17.5% (SE = 0.5%, n = 100), 9% lower than the soil from control plots, which had an average soil moisture of 19.2% (SE = 0.5, n = 100) (ANOVA, F$_{1,9}$ = 5.3, P = 0.03). The soil submitted to both runoff and partial rainfall exclusion (DD) had an average soil moisture of 15.4% (SE = 1.0, n = 100), 20% lower than the soil from control plots (ANOVA, F$_{1,9}$ = 15.2, P = 0.002). In the sampling data (January 2005), the decrease of soil moisture was also more noticeable below plastic strips (DD) than between plastic strips (D).


Drought conditions had a tendency to reduce *Quercus ilex* biomass accumulation (Table 1), while had no effects on *Phillyrea latifolia* biomass accumulation (Table 1). In *Arbutus unedo*, drought decreased the
absolute biomass accumulation of leaves (75%), wood (77%) and total above-ground growth (77%).

**BIOMASS CONCENTRATIONS**

The P and K concentrations in 1999 were very similar to those from 2005 for all species and biomass fractions (Table 2).

In *Quercus ilex*, drought increased P concentrations in leaves (18.2%) and decreased P concentrations in wood (30.9%) and roots (39.8%) (Fig. 1). Drought had no effect on P concentrations in *Phillyrea latifolia* or *Arbutus unedo* leaves, wood or litter. Drought had no effects either on K concentrations in the different fractions of the three studied species (Table 2).

**P AND K CONTENTS**

P contents in wood and in total AB of *Quercus ilex* decreased 15.9 kg P ha⁻¹ (SE = 18.6, n = 4) (−21%, SE = 15.5) and 14.5 kg P ha⁻¹ (SE = 17.5, n = 4) (−19.0%, SE = 14.2) after 6 years of drought; however, P contents increased by 45.4 kg P ha⁻¹ (SE = 15.125, n = 4) (33.7%, SE = 6.5%) and 46.7 kg P ha⁻¹ (SE = 14.069, n = 4) (33.1%, SE = 6.3) in the control plots (Fig. 2). Drought had no effects on the P contents in leaves and litter of *Quercus ilex* (Fig. 2). This negative effect of drought on P biomass contents was due to both its negative effects on biomass growth and on P concentrations.

Drought had no significant effects on P contents in *Phillyrea latifolia* biomasses. Drought decreased P...
Table 2. Phosphorus (P) and potassium (K) concentrations (mg g\(^{-1}\), mean ± SE, \(n = 4\) plots) in different biomass fractions of the three species studied in control and in drought plots

<table>
<thead>
<tr>
<th>Species</th>
<th>Element</th>
<th>Treatment</th>
<th>1999 (before treatment)</th>
<th>2005 (6 years treatment)</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td></td>
<td>Leaves</td>
<td>Wood</td>
</tr>
<tr>
<td>Quercus ilex</td>
<td>K</td>
<td>Control</td>
<td>5.99 ± 0.50</td>
<td>3.89 ± 0.28</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Drought</td>
<td>5.63 ± 0.60</td>
<td>3.55 ± 0.41</td>
</tr>
<tr>
<td></td>
<td>P</td>
<td>Control</td>
<td>1.00 ± 0.08</td>
<td>1.28 ± 0.08</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Drought</td>
<td>1.17 ± 0.09</td>
<td>1.18 ± 0.12</td>
</tr>
<tr>
<td>Phillyrea latifolia</td>
<td>K</td>
<td>Control</td>
<td>6.40 ± 0.37</td>
<td>4.02 ± 0.22</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Drought</td>
<td>6.17 ± 0.34</td>
<td>3.96 ± 0.31</td>
</tr>
<tr>
<td></td>
<td>P</td>
<td>Control</td>
<td>1.21 ± 0.05</td>
<td>1.81 ± 0.13</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Drought</td>
<td>1.43 ± 0.10</td>
<td>1.25 ± 0.10</td>
</tr>
</tbody>
</table>

Different letters indicate statistically significant differences between control and drought plots at *t*-test, \(P < 0.05\) (a and b between brackets when *t*-test, \(P < 0.1\)). Significant differences are highlighted in bold type.
Drought changes
P and K accumulation patterns

Drought had no significant effects on the K content in any species or fractions analysed (Figs 2 and 3), although trends towards an increase in the K above-ground content in *Quercus ilex* and *Phillyrea latifolia* and towards a reduction in *Arbutus unedo*, were observed as a response to drought (Fig. 2).

The amounts of P and K loss in litterfall (kg ha$^{-1}$) for these three species together during 2004 were greater in drought plots 1.97 (SE = 0.20, n = 4) and 6.05 (SE = 0.20, n = 4), respectively, than in control plots 1.59 (SE = 0.20, n = 4) and 5.05 (SE = 1.45, n = 4), respectively, but these differences were not statistically significant.

Soil Concentrations

Drought had no effects on the total P soil concentrations, although it did increase the K in the soil at depths of 0–15 cm (10%) and at 15–30 cm (8.6%) (Table 3).

Drought conditions increased the total soil soluble P (Olsen-P) and soil organic soluble P (Olsen-P$_{org}$) (Fig. 4), but not soil inorganic soluble P (Olsen-P$_{inorg}$) in the January 2005 sample. In addition, a decrease in the ratio of inorganic : organic soil soluble P fractions (Olsen-P$_{i}$ : P$_{o}$) by 50% in the first 15 cm of the soil layer (Fig. 4) and by 183% between 15 and 30 cm in the soils, under transparent plastic strips. Drought produced similar effects on P soil fractions in the soil sample collected in April 2005.

Drought decreased soil available K (NaNO$_3$ extractable K) both at 0–15 cm (Fig. 5) and at 15–30 cm depths (20% and 19%, respectively) in the soil sampled in January 2005; drought thus decreased the ratio between available K : total soil K (NaNO$_3$ extractable K and total K) at 0–15 cm (20%) (Fig. 5) and 15–30 cm (14%) depths. Similarly, drought decreased soil available K (NaNO$_3$ extractable K) both at 0–15 cm depths and at 15–30 cm depths (37% and 44%, respectively) in the soil sampled in April.

Discussion

Phosphorus in above-ground biomass and soil

Total P content in AB decreased by approximately one-third after 6 years of moderate drought. Although drought increased the P concentration in leaves, a drought-induced reduction in LB means that there was no increase in the leaf P contents at ecosystem level. In fact, after 6 years of drought, there was a decrease in above-ground P contents in *Quercus ilex* due to both the decrease in P wood concentrations and the decrease in wood biomass (Ogaya & Peñuelas 2007). The observed tendency of drought to decrease P contents in wood and total AB in *Arbutus unedo* was mainly due to the negative effect of drought on stem growth.

Drought increased the soil soluble P$_{org}$, but not the soil soluble P$_{inorg}$, that is the directly available P source for plants, thereby decreasing the soil soluble P$_{inorg}$ : P$_{org}$ ratio. Drought slowed down the release of soluble orthophosphate from organic to inorganic forms, leading thus to an accumulation of soluble
organic forms in the soil and consequently an increase in total soluble P. The decrease in the soil soluble P_inorganic : soil soluble P_organic ratio produced by drought is related to the decrease in soil enzyme activity induced in these soils by drought (Sardans & Peñuelas 2005) and agrees with previous studies in the same forest (Sardans & Peñuelas 2004). The reduction in mineralization rates as a result of drought has also been observed in other Mediterranean ecosystems (Gorissen et al. 2004). All these results indicate that drought leads to diminished plant P uptake of nutrients and greater recalcitrance in the soil.

POTASSIUM IN ABOVE-GROUND BIOMASS AND SOIL

The 6 years of drought reduced the soil K-extractable content but increased the soil total K content, indicating a slowdown in meteorization and/or mineralization rates. Several studies have shown that drought reduces soil K release capacity (Ruan et al. 1997; Oliveira, Rosolem & Trigueiro 2004; Kaya, Higgs & Kirnak 2005) and can thus increase K accumulation in the soil. In this case, the most likely explanation for K accumulation in the soil is the decrease in meteorization rates and to a lesser extent the decrease in soil enzyme activity (Sardans & Peñuelas 2005), which generates a reduction in the soluble forms in the soil and an accumulation of unavailable forms. Another possible cause of the reduction in the concentrations of soluble K forms in the soil and the increase in the total soil K, is a change in humus quality as a result of decreased microbial activity, which can reduce the soil K-soluble retention capacity. Drought frequently increases sclerophyll (Bussotti et al. 2002; Bacelar et al. 2004) and sclerophyll can often decrease the nutritional quality of plant tissues owing to the higher concentrations of structural compounds such as lignin (Pérez 1994; Fell et al. 1999). A significant presence of structural compounds hinders the mineralization processes. However, in the present study, the negative effect of drought on mineralization rates could not be imputed to an increase in LMA (Leaf Mass Area), which remained unchanged (Ogaya & Peñuelas 2006).

DIFFERENCES BETWEEN PHOSPHORUS AND POTASSIUM RESPONSES

P foliar concentrations were changed by the drought treatment but K foliar concentrations were not. The increases in P concentrations as a response to drought conditions have been widely reported (Utrillas, Alegre & Simon 1995; Díaz & Roldan 2000; Samarah, Mullen & Cianzio 2004) and have been related variously to an increase in water-use efficiency (Díaz & Roldan 2000; Graciano, Guiamé & Goya 2005), to a drought-resistance mechanism (Egilla, Davies & Drew; Egilla et al. 2005; Samarah et al. 2004) and/or to a decrease in the dilution effect (Sabaté & Gracia 1994; Peñuelas & Estiarte 1998). The increase in P leaf concentrations and the decrease in root and stem concentrations suggest a mobilization of P from wood towards leaves in order to improve the water-use efficiency.

The 6 years of drought generated different responses of P and K also at the ecosystem level. Whereas drought decreased P contents in AB and increased total soil soluble P without affecting soil soluble inorganic P, drought did not change K contents in AB, reduced soil-soluble K in the soil, and increased total soil K.

Two differences in the geochemical traits of these two nutrients account for the different results obtained. First, K is more mobile than P and therefore P absorption is more dependent on the capacity of roots to explore new soil volumes (given the low mobility of P in soil when compared with K). Secondly, soil K is in mineral form and only a minimal proportion of K resides in organic matter and litter, whereas in P the proportion of P in organic forms and litter with respect to total P soil is greater. Drought decreases soil enzyme activity (Sardans & Peñuelas 2005), thereby decreasing soil soluble inorganic P and the capacity of soil to supply P to plants. This effect together with the decrease in growth in AB accounted for the reduction of P accumulation in AB in the plants subject to drought conditions. K soil contents were greater in drought plots because K mostly resides in silicates and both solubility and meteorization is reduced if soil moisture decreases, which in turn will lead to an increase in total K and decrease in soluble K in soils of drought plots. K contents in AB did not change in drought soils probably because...
Drought changes in K plant capture. In this context, the rewetting effect assures significant K capture, even in drought plots.

DIFFERENCES IN PLANT RESPONSES

Drought changed P concentrations and accumulation patterns in Quercus ilex and Arbutus unedo more than in Phillyrea latifolia. This different response may lead to changes in competitive ability and eventually changes in the species composition of the plant community in favour of shrub species. This different response in nutrient status as a result of drought coincides partially with these species’ different growth responses (Ogaya et al. 2003; Ogaya & Peñuelas 2007), mortality (Ogaya et al. 2003; Ogaya & Peñuelas 2007) and reproductive effort and seed recruitment (Lloret, Peñuelas & Ogaya 2004; Ogaya & Peñuelas 2004). The effect of drought on AB accumulation in the period 1999–2005 was also different between species: in Arbutus unedo the AB accumulation fell significantly, in Quercus ilex there was a tendency for AB accumulation to drop, and in Phillyrea latifolia there were no effects at all on AB accumulation (Ogaya & Peñuelas 2007).

POSSIBLE IMPLICATIONS: NUTRIENT LOSSES AND STOICHIOMETRIC CHANGES

As torrential rainfall is typical of the Mediterranean region (Ramos & Porta 1994) and it is predicted to become more extreme and frequent in the near future (Houghton et al. 2001; Peñuelas et al. 2005), and as P and K losses during a single sudden rainstorm may be very high (Ramos & Martinez-Casanovas 2004), greater losses of P and K are thus likely to occur over the coming decades in these Mediterranean ecosystems. The rewetting effect during rainfall should increase the amounts of mobilized P and K, thereby increasing the possibility of P and K ecosystem losses during torrential rainfall.

Another possible implication of lower P and/or K content and availability in soil may be an enhancement of the usual increase in the below-ground : AB ratio observed in Mediterranean forests (Keith, Raison & Jacobsen 1997). As drought can also directly increase the above-ground : AB ratio (Noordwijk et al. 1988; Jose, Merritt & Ramsey 2003; Chiatante, Di Iorio & Scippa 2005), a reduction in AB more than in below-ground biomass can be expected under future arid conditions in those ecosystems.

The differing effects of drought on the accumulation of P and K in the biomass changes the stoichiometry between these two nutrients in this ecosystem and affects the proportional availability of these two nutrients to trophic chains. Changes in nutrient concentration ratios in plants, affect trophic chains and are likely to produce shifts in the composition of herbivore communities and in the specific selection of plants by herbivores as food sources (Makino et al. 2003; Ngai & Jefferies 2004; Diehl, Berger & Wohrl 2005). If drought increases as fast as climate models predict, a period with rapid changes in nutrient ratios will favour species with more flexible body compositions. This could negatively affect the resistance of the ecosystem to drought in Mediterranean ecosystems, as species of some taxonomic groups such as invertebrates (Drosophila sp., Daphnia sp.) with flexible body compositions have low physiological functioning efficiencies (Jaenike & Markow 2003) and their capacity to respond to water availability reduction may be hampered. Furthermore, although it has been suggested that terrestrial plants have limited capacity of changing their body composition (Zhang, Bai & Han 2004), some recent experiments have shown that Mediterranean plants change their nutrient composition under different environmental conditions but in different proportions depending on the species, e.g. Pinus halepensis and Quercus ilex saplings and on the elements (Sardans, Rodà & Peñuelas 2006c).

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