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Effects of a severe drought on water and nitrogen use by *Quercus ilex* and *Phillyrea latifolia*

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Abstract

A severe drought that took place in Spain and other Mediterranean countries in 1994 produced a dieback of *Quercus ilex* trees on south-facing conglomerates but only minor defoliations in trees on north-facing schists. The foliar $\Delta^{13}C$ of damaged trees continued to decrease in the next two wet years probably indicating increasing water use efficiency, and their $\delta^{15}N$ continued to increase indicating progressive ecosystem N saturation and/or N losses whereas there were no significant changes in undamaged trees. Pre-drought $\Delta^{13}C$ values were reached in the third year after the drought, but $\delta^{15}N$ values did not yet recover. Another co-occurring small tree, *Phillyrea latifolia*, did not show any damage and gained dominance in the most affected stands.

Additional key words: damaged trees, stable isotopes, water stress, climate change, lithologies, water use efficiency, nitrogen availability and use.

Introduction

In Spain climate has become warmer and drier during this century. Temperature and potential evapotranspiration have increased 0.10 °C and 13 mm per decade, respectively, and minimum relative humidity has decreased 0.85 % per decade (Piñol *et al.* 1998). Moreover, severe droughts occurred during 1985 and 1994. Global change effects on Mediterranean climate are likely to produce even warmer and drier conditions in the next decades and more frequent and stronger droughts (Houghton *et al.* 1996, Peñuelas 1996) with consequent effects on vegetation.

As a consequence of a very severe drought in 1994, holm oaks (*Quercus ilex*), the dominant tree species of the Mediterranean forest, were damaged (Montoya 1997) while *Phillyrea latifolia* trees were almost unaffected. We investigated the immediate and late effects of such severe drought on water and nutrient use by *Quercus ilex* and *Phillyrea latifolia* growing in different lithologies and slope aspects of central Catalonia, and therefore submitted to different water availability after the drought. As foliar $\Delta^{13}C$ and $\delta^{15}N$ measurements may be used as indicators of intrinsic long-term water use efficiency (WUE) (Farquhar *et al.* 1989) and N availability and use (Peñuelas and Estiarte 1997), we annually studied, until 1997, the leaf C and N stable isotope content in differently affected tree individuals after the 1994 drought. We used the natural leaf abundances of $\Delta^{13}C$ and $\delta^{15}N$ as indicators of long term plant responses to disturbances in availability of water, carbon and N. We also assessed tree health depending on the percentage of dry or lost leaves.

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Materials and methods

Field sites: *Quercus ilex* trees from three sites of decreasing water availability generated by different soil lithology and slopes were studied in Sant Llorenç de Munt hills park (central Catalonia). The first site presented schist and shales lithology that allows deep root penetration as we have observed in several soil profiles. The second site was on a breccia fault of silicic clastic lithology that hinders deep root penetration as we have also observed in several soil profiles. Both site slopes were oriented to the north and were at about 600 m altitude. The third site was on calcareous conglomerates and the slope was oriented to the south and was at about 800 m altitude. On this third site, *Quercus ilex* was growing together with *Phillyrea latifolia* as codominant tree species in rocky vegetation isles. These vegetation isles are about 30 - 50 m long and 5 - 10 m wide in the south-facing slopes of rocky hills. The soil is colluvial with rather important water losses through drainage, and high evaporation facilitated by high radiation and frequent and strong wind. Precipitation and temperature were recorded daily in a nearby station (2 - 5 km from the studied stands).

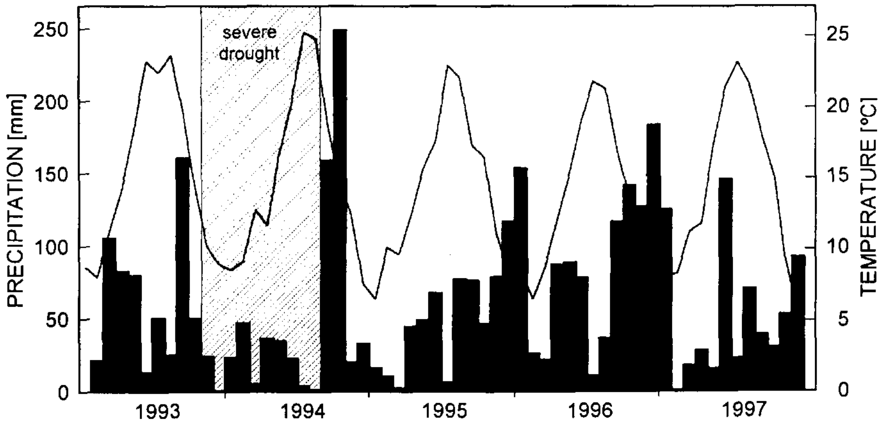


Fig. 1. Climatic diagram of monthly precipitation and monthly mean temperature of the studied area.

Climate: The year 1993 was normal compared with precipitation data from the last 25 years; on the contrary, the year 1994 and the spring of 1995 were very dry and very hot, except for the flood period of October 1994; the rest of 1995 was normal, and 1996 and 1997 were very humid (Fig. 1).

Tree status: Tree health was recorded at the end of summers 1994, 1995, 1996 and 1997 following the classification: *0* - dry with no green leaves, *1* - 5 - 25 % green leaves, *2* - 25 - 75 % green leaves, *3* - 75 - 100 % green leaves.

Isotope analyses: At the end of summer 1995, mature and apparently healthy sun leaves were collected from the terminal topmost 0.5 m of the crown of each sampled tree and dried at 60 °C until constant mass. The leaves belonged to the current-year and 1993 cohorts (5 - 6 sampled leaves for each one), while in 1994 no leaves were produced due to the extreme drought. At the end of summers 1996 and 1997, after very humid years, current-year leaves were also collected. The same 19 trees in breccia, 9 trees in schist and 12 trees in conglomerates were sampled throughout all these years.

The $\delta^{15}N$ and $\Delta^{13}C$ of the leaves were measured on a *SIRA Series II* isotope ratio mass spectrometer (*VG Isotech*, Middlewich, UK) operated in direct inlet continous flow mode after combustion of the samples in an elemental analyzer (*NA1500, Series 1, Carlo Erba Instrumentazione*, Milan, Italy). The reference CO_2, calibrated against standard Pee Dee Belemnite (PDB) was obtained from *Oztech* (Dallas, USA). A system check of analysis was achieved with interspersed working standards of cellulose, atropine and urea (*Sigma*, St. Louis, USA). The accuracy of the measurement was ± 0.001 % for $\Delta^{13}C$ and ± 0.002 % for $\delta^{15}N$. $\Delta^{13}C$ was calculated as

$$\Delta^{13}C = (\delta_{air} - \delta_{plant})/(1 + \delta_{plant})$$

where δ_{air} was assumed to be 0.008 % arround the terminal topmost 0.5 m of the crown where leaves were sampled.

Statistical analyses: Site, year, and tree status immediately after the severe drought (1994) as independent variables were used in the *ANOVA* analyses of $\Delta^{13}C$ and $\delta^{15}N$ as dependent variables. All analyses were performed using *STATVIEW 4.5* (*Abacus Concepts*, Berkeley, USA).

Results

Tree status: At the end of 1994, visible wilting and defoliation showed up to 50 % of *Quercus ilex* individuals on conglomerates of south-facing rocky vegetation isles, up to 30 % of individuals on breccia oriented to the north, and only minor number on north-facing schist lithologies.

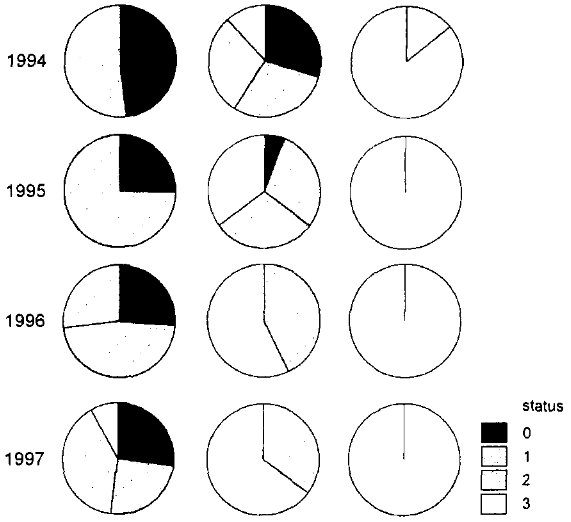


Fig. 2. *Quercus ilex* tree status in the three studied sites the years following the severe drought of 1994. *0* - no green leaves, *1* - 5 - 25 % green leaves, *2* - 25 - 75 % green leaves, *3* - 75 - 100 % green leaves (n = 30 trees in each site).

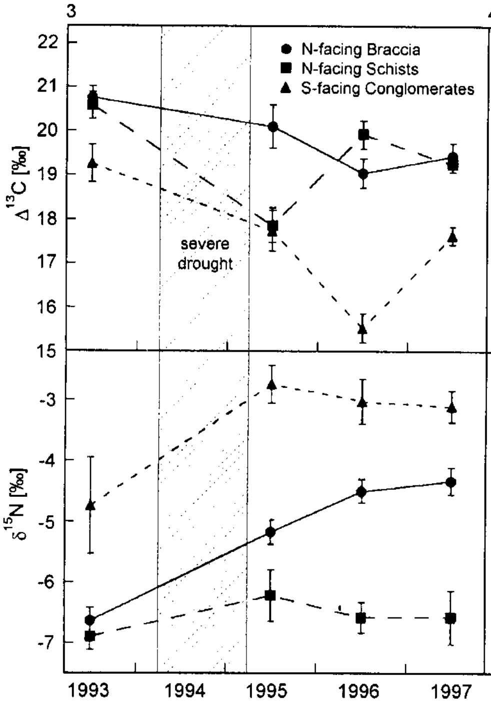
These trees progressively recovered in 1995, 1996 and 1997 through crown resprouting. However, *Q. ilex* growing on conglomerates were so strongly affected by the drought that they hardly recovered (Fig. 2). Contrary to *Q. ilex*, another co-occuring smaller tree, *Phillyrea latifolia*, that is better adapted to withstand water deficits and warm conditions (Tetriach 1993), was almost unaffected by drought (at least with respect to crown status) even in the driest of the sites.

Δ^{13}C: Site, year, and tree status immediately after the severe drought (1994) had significant effects on Δ^{13}C ($P < 0.01$). There was also a significant interaction between site and year. In 1993, foliar Δ^{13}C was lower (what generally results from higher WUE) in trees growing on south-facing conglomerate vegetation isles than in the other two north-facing sites, as expected from a drier site. In 1995, the first year after the drought, spring (time period of maximum impact of weather conditions on Δ^{13}C values, Damesin *et al.* 1997) was dry (Fig. 1) and there was a slight decrease in Δ^{13}C respective to 1993 (Fig. 3). In the wet year 1996, trees on schist almost reached their original Δ^{13}C values (Fig. 3). On the contrary, trees on breccia had lower foliar Δ^{13}C in 1996 than in 1993 showing a higher WUE, and likely a lower water use, even though it was a very wet year. The same pattern with even more accentuated decrease in Δ^{13}C was found in trees growing on the conglomerates of vegetation isles (Fig. 3). This late effect of drought was only present in those trees that were severely damaged in 1994. On breccia lithologies, the trees that were in worse status after the drought were the ones that presented a progressive decrease of foliar Δ^{13}C throughout the years of study (Fig. 4), and the same happened to trees on conglomerates, all of which were in bad status (Fig. 3). This late effect was not found on schists where there were almost no trees in bad status. On the contrary, trees in schists recovered Δ^{13}C values in 1996 (Fig. 3). In 1997, Δ^{13}C tended to recover 1993 values in the three sites.

δ^{15}N: Site, year, and tree status immediately after the severe 1994 drought had also significant effects on foliar δ^{15}N with also significant interaction between site and year ($P < 0.01$). Trees on schists did not change their δ^{15}N throughout the years. On the contrary, trees on breccia showed a progressive increase in δ^{15}N that was not even stopped in 1997. Even higher δ^{15}N values were found in trees growing on the conglomerates of vegetation isles (Fig. 3). The increase in δ^{15}N in 1996, like the decrease in Δ^{13}C, was specially strong in leaves from those trees that were most affected by the 1994 drought and that were in worse status (Figs. 2, 4).

When pooling data from the three sites and the four years, a general inverse trend between δ^{15}N and Δ^{13}C appears (Fig. 5).

***Quercus ilex* versus *Phillyrea latifolia*:** Foliar Δ^{13}C did not differ among individuals of the drought tolerant *P. latifolia* and the drought sensitive *Q. ilex* growing together on the conglomerate vegetation isles until 1996, two years after the severe drought (Fig. 6). In both species Δ^{13}C decreased in 1996 leaves with respect to 1993 leaves ($P < 0.01$) and recovered in 1997. However, the decrease was more important in *Q. ilex* than *P. latifolia*. The δ^{15}N significantly increased in *Q. ilex* the years after the drought ($P < 0.01$) but it did not significantly change in *P. latifolia* (Fig. 6).



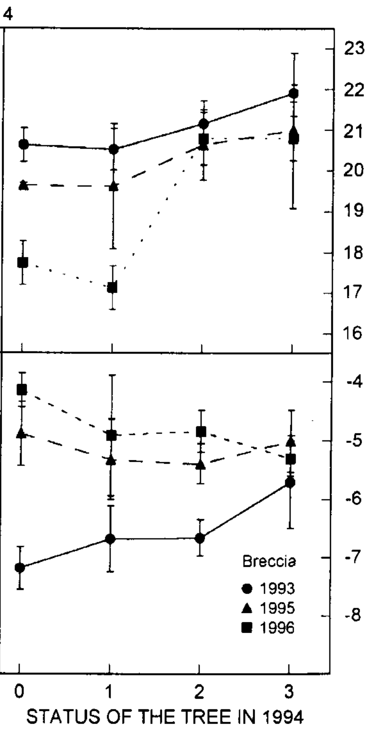


Fig. 3 (*left*). Changes in foliar $\Delta^{13}C$ and $\delta^{15}N$ of *Quercus ilex* leaves from breccia and schist north-facing lithologies and from south facing conglomerate lithologies. *Bars* are ± SE (n = 19 trees in breccia, 9 trees in schist and 12 trees in conglomerates). In 1994 no leaves were produced due to the extreme drought.

Fig. 4 (*right*). Changes in foliar $\Delta^{13}C$ and $\delta^{15}N$ as a function of the tree status on breccia lithology. For detail see Fig. 2. Means ± SE (n = 4 - 5 trees).

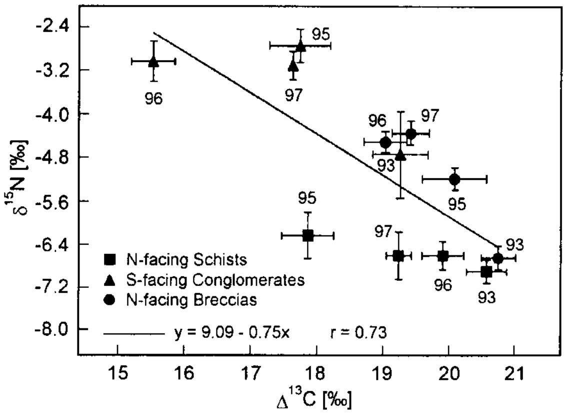


Fig. 5. Foliar $\delta^{15}N$ versus $\Delta^{13}C$ in the *Quercus ilex* trees growing on the three different lithology and slope aspect sites and in 1993, 1995, 1996 and 1997 cohorts. In 1994 no leaves were produced due to the extreme drought.

Discussion

Tree status and prolonged changes in $\Delta^{13}C$ and $\delta^{15}N$ after the drought: After the severe drought of 1994, *Q. ilex* trees had a better status on schist than on breccia. Schists allow deeper penetration of roots, which facilitates water uptake under severe drought conditions. Conglomerate south-oriented site presented the trees with worse status. Sun exposed slopes imply higher radiation and temperature, and therefore higher evaporation and water loss in south-facing slopes (conglomerates) than in north-facing slopes (schists and breccias). Moreover, in that conglomerate site there were more drainage water losses than in the other two sites.

After the severe drought, the leaf $\Delta^{13}C$ was smaller and, presumably, the water use efficiency larger in years where more water was available because of higher precipitations. Higher WUEs (in most cases due to stomata closing) are usually expected under conditions of low water availability and not under high water availability as happened in 1996 in breccia and conglomerate isles. High water use efficiency would be more beneficial on driest sites and years and less beneficial where and when water requirements of vegetation are exceeded by precipitation. High WUEs might be less beneficial on the wettest years and lithologies because it frequently comes at the expense of rapid growth (Austin *et al.* 1990), nitrogen use efficiency (Field and Mooney 1986), or competition (De Lucia and Schlesinger 1991). The prolonged late effect of severe drought may explain these $\Delta^{13}C$ results. One possibility could be that root and shoot hydraulic conductivity would have been reduced by the severe drought (Rieger 1995) and water use would have been hindered even though it was plenty available in 1996. This hypothesis should be confirmed with tree water status measurements.

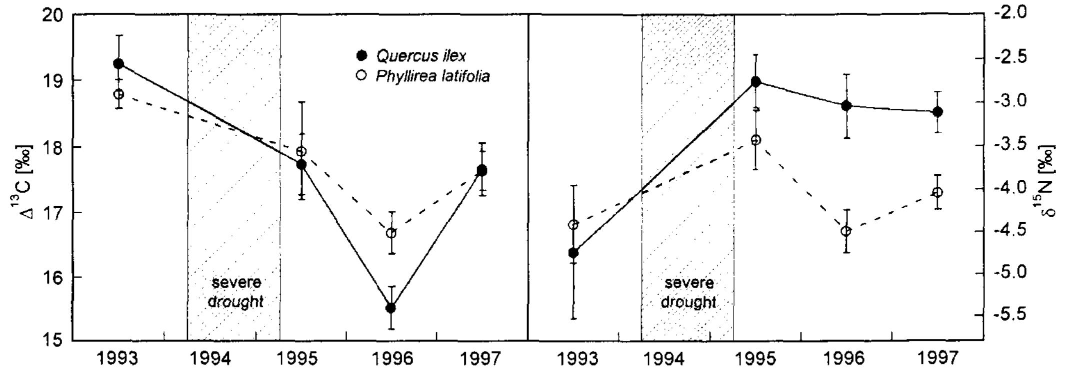


Fig. 6. Changes in foliar $\Delta^{13}C$ and $\delta^{15}N$ of *Quercus ilex* and *Phillyrea latifolia* growing on south-facing conglomerates on rocky hill vegetation isles after the severe 1994 drought. Means ± SE (n = 12 trees). In 1994 no leaves were produced due to the extreme drought.

As the $\Delta^{13}C$ of *Q. ilex* leaves remained constant after leaves were matured (Damesin *et al.* 1997) and as we did not find significant differences for 1995 leaves collected in 1995 and in 1997, we discarded possible ontogenetic effects due to leaf aging of 1993 leaves in the comparison with the values of the following years. Moreover, the temporal trends were clearly different in the different sites providing more confidence on the comparative results. A curious result was the higher $\Delta^{13}C$ of trees at the dry breccia site than at the schist site in 1995. We hypothesize a possible larger water availability for alive green trees in breccia in 1995 because of the lower competition produced by larger number of droughted non green trees. The same explanation might be valid to understand that the late effect was more pronounced two years than one year after the drought injury. Two years later there was larger green biomass and competition.

The increase in $\delta^{15}N$ after the severe drought also agrees with the hypothesis of a prolonged effect. As the $\delta^{15}N$ value of a plant sample is primarily determined by the isotope ratio of the nitrogen source (Evans *et al.* 1996), increasing leaf $\delta^{15}N$ after the drought in breccia and conglomerates could indicate a higher N saturation (*sensu* Aber *et al.* 1989) of the system (Högberg 1997), *i.e.* a lower N use. The increasing leaf $\delta^{15}N$ would indicate higher nitrogen losses in surrounding system because all major pathways of nitrogen loss (denitrification, ammonia volatilization, and nitrate leaching) are thought to cause a $\delta^{15}N$ enrichment of the remaining nitrogen (Shearer and Kohl 1986, Durka *et al.* 1994, Schulze *et al.* 1994). These nutrient losses might have been facilitated by the decreased number of living green shoots acting as a sink and by the death of fine roots which decreases N uptake. Disturbance commonly enhances N losses through soil nitrate leaching (Vitousek and Melillo 1979), and Mediterranean sclerophyllous forests have a large potential to loose nitrate when root uptake is prevented in otherwise intact soil (Bonilla and Rodà 1990). Since $\delta^{15}N$ data detected such putative N losses and/or altered N cycling patterns at the individual tree scale, this implies that these ecosystem properties show at our sites a strong patchiness linked to the presence of individual trees.

The general inverse trend between $\Delta^{13}C$ and $\delta^{15}N$ (Fig. 5) indicates higher N losses and/or higher N saturation in the surrounding system when water use efficiencies were higher (and water use likely lower), both because of site-specific characters and year-to-year responses to drought.

There is the possibility of N reallocation confounding these results, but the facts that samples were collected in similar dates and that the temporal trend of $\delta^{15}N$ differed in the three sites after the drought of 1994, provide more confidence on concluding different N use in the different water availability sites after the severe drought. However, further studies are needed to reach reliable conclusions regarding which actual processes were mainly involved.

***Quercus ilex* versus *Phillyrea latifolia*:** Since comparisons between these two species were made in identical environmental conditions, their differences in $\Delta^{13}C$ and $\delta^{15}N$ values should be a consequence of specific differences. Patterns of $\Delta^{13}C$ and $\delta^{15}N$ showed higher WUE (likely lower water use) and higher system N losses (and/or higher N saturation) in *Q. ilex* than in *P. latifolia* after two years of the severe drought. The late drought damage seemed, thus, to be stronger in *Q. ilex*, and the strong N cycling patchiness linked to the different root systems appeared again. These isotopic results, together with a lack of visual symptoms of damage, indicate a better adaptation of *P. latifolia* to drought than *Q. ilex*, which is a very competitive species only in subhumid Mediteranean areas. This is in agreement with leaf gas exchange and fluorescence measurements conducted in experimental conditions simulating severe drought and high temperature conditions (Filella *et al.* 1998). Loss of dominance by *Q. ilex* in such sclerophyllous Mediterranean forests and increasing dominance by other species such as *P. latifolia* may thus be expected in a warmer and drier climate as the one predicted in this Mediterranean region by global climate change models (Houghton *et al.* 1996, Peñuelas 1996), or even under the climatic changes already experienced during the last decades in this area (Piñol *et al.* 1998).

In summary, there were clear tree status and isotopic differences among stands on different lithologies and slopes. By comparing different temporal trends in the different stands, the data indicates an interesting late effect in drought-injured trees. In the following years they presented higher water use efficiencies (and likely lower water use) even though these following years were very wet. The different temporal trends also add a new indication that drought may influence the N cycle by decreasing plant N demand and enhancing system N saturation and/or N losses. Finally, these results provide a new evidence on *P. latifolia* better capacity to withstand drier and warmer conditions than *Q. ilex*.

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