

Changes in Ca, Fe, Mg, Mo, Na, and S content in a Mediterranean shrubland under warming and drought

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[1] In an evergreen Mediterranean shrubland we conducted a 6-year field experiment simulating the warming and drought projected by general circulation models and ecophysiological models for the next decades: 20% reduction of soil moisture and 1°C of temperature increase. We tested whether warming and drought have effects on Ca, Fe, Mg, Mo, Na and S availability, concentrations and accumulation patterns in the three dominant plant species and in soil. Warming increased concentrations of Ca and Mo in leaves in *Erica multiflora* (42% and 65%, respectively) and in *Dorycnium pentaphyllum* (38% and 60%, respectively). Warming increased Mo accumulation in leaves and aboveground biomass in *Globularia alypum* (0.07 and 0.40 g ha⁻¹) and in *E. multiflora* (0.12 and 0.4 g ha⁻¹), and increased Fe accumulation in stem biomass of *G. alypum* (600 g ha⁻¹), increasing the capacity to retain these nutrients in the ecosystem. The increase of Fe and Mo capture capacity under warming conditions was greater in *G. alypum* than in *E. multiflora* coinciding with its greater increases in photosynthetic capacity. Warming decreased soil total-Fe concentration by 24% and increased Mg accumulation in soil exchange complex by 19%. Drought increased Na leaf and stem concentrations (93% and 50%, respectively) and accumulation in leaf and aboveground biomass (780 and 800 g ha⁻¹, respectively) in *G. alypum*, allowing an increase of osmotic pressure which helps to prevent water losses and is related to its capacity to resist drought. Drought reduced S leaf and Mg leaf-litter concentrations of *G. alypum* and increased them in leaves of *E. multiflora* and also increased Mo and Na concentrations in leaves of *D. pentaphyllum*. Drought increased Fe soil solubility by 65%. The results indicate different effects of climate change on nutrient status in the ecosystem depending on whether the main change is warming or drought. The changes in concentration and biomass accumulation were different depending on the nutrient and the species, changing the stoichiometry among these nutrients and modifying the nutritional quality of plant tissues.

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1. Introduction

[2] Over the last century, temperatures in Mediterranean basin have shown a warming trend [Kutiel and Maheras, 1998; Peñuelas *et al.*, 2002]. Trends in precipitation are less clear. Whereas some authors report a long-term downward trend, principally in the dry season [Kutiel *et al.*, 1996; Esteban-Parra *et al.*, 1998], others report no significant change [Piñol *et al.*, 1998; Peñuelas *et al.*, 2002; Peñuelas and Boada, 2003], although all authors agree that the rise in potential evapotranspiration has led to more arid conditions [Palutikof *et al.*, 1994; Piñol *et al.*, 1998]. Mediterranean ecosystems are water limited [Mooney, 1989] and most climate models project even drier periods together with

more unpredictable torrential rainfalls in the Mediterranean basin for the next decades [Intergovernmental Panel on Climate Change (IPCC), 2007]. The decline in soil water availability expected for these next decades [IPCC, 2007] may turn out to be even more drastic under warmer conditions with higher potential evapotranspiration [Walker *et al.*, 1994]. The interaction of warming and/or drought with other factors critical for ecosystem functioning, such as nutrient availability, needs to be studied in order to gain knowledge on the global impacts of climate change on Mediterranean ecosystems. N and P are the most studied plant nutrients because plants need them in large quantities and they are frequently limiting for precipitation. Recent studies show drought effects on P and N cycles in Mediterranean ecosystems [Sardans and Peñuelas, 2004, 2005a, 2007] but, as far as we know, there are no reports on effects on other nutrients necessary for plant life, like Ca, Fe, Mg, Mo, Na and S. The cycle of these nutrients is being affected by climate change in boreal and temperate forest [Dixon and Wisniewski, 1995] and in tropical forest [Dixon and

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Wisniewski, 1995; Wood *et al.*, 2005]. However, there are no available experimental data on the climate change effects on the cycle of these nutrients in the Mediterranean ecosystems.

[3] Ca, Fe, Mg, Mo and S play an important role in plant nutrition and symptoms of their deficiency in plants have been described [Montès *et al.*, 2002; Shenker and Chen, 2005]. Changes in the availability of these nutrients caused by climate change can interact with direct warming and drought effects on Mediterranean plants.

[4] Although not very frequent, plant Ca deficiency has been observed in some studies [Ouimet and Camire, 1995; Gulpen and Feger, 1998; Pintro and Taylor, 2005] and can limit growth in forest ecosystems [Rodenkirchen, 1998]. In Mediterranean ecosystems, Ca can play a significant role because it is involved in the regulation of turgor pressure [Takagi and Nagai, 1992], and thus plays an important role in water losses regulation. On the other hand, Ca root content is an important factor for the capacity of plant to absorb NH_4^+ in several plants species [Fenn and Feagley, 1999]. All these properties make Ca to play an important role in water use efficiency (WUE).

[5] Fe is essential for plant growth and its deficiency occurs especially, but not only, in calcareous soils [Shenker and Chen, 2005] that are widely present in the Mediterranean Basin. Fe chlorosis is the second most important micronutrient disorder after Zn chlorosis [Rashid and Ryan, 2004]. Drastic changes in the soil $\text{Fe}^{2+}/\text{Fe}^{3+}$ ratio are common in Mediterranean areas. The Fe soil content and availability are dependent on soil water content. The $\text{Fe}^{2+}/\text{Fe}^{3+}$ ratio is higher in wet soils thus permitting greater availability of Fe for plant, whereas in drought conditions the greater presence of O_2 in soil favors a decrease of $\text{Fe}^{2+}/\text{Fe}^{3+}$ ratio and therefore a decrease of available Fe to plant absorption, as observed in a Mediterranean *Quercus suber* forest in South France [Orgeas *et al.*, 2002]. However, no data are available on the impact of sustained drought on Fe plant concentration and contents in Mediterranean ecosystems.

[6] Low Mg contents have been observed in several Mediterranean forests [Montès *et al.*, 2002], but there is also a lack of experimental data on the effects of drought on the Mg cycle in Mediterranean ecosystems. The capacity to maintain high Mg biomass contents under drought conditions is important to hold an adequate production capacity and metabolic status that allow plants to take profit of the rewetting periods. Drought can reduce the Mg accumulation in aboveground biomass in Mediterranean shrubland by reducing growth and by increasing sclerophylly and the content of defensive compounds such as tannins, and by decreasing Mg contents [Lebreton *et al.*, 1997].

[7] With some exceptions, Mo availability is not limiting in Mediterranean soils [Rashid and Ryan, 2004]. And although Mo is fundamental for plant growth [VankovaRadeva *et al.*, 1997; Kaiser *et al.*, 2005] because it is used by several enzymes (nitrate reductase, xanthine dehydrogenase, aldehyde oxidase and sulfite oxidase), it can become toxic to plants when Mo availability exceeds certain levels [Gupta, 1997] and even to most mammal herbivores [Albasel and Pratt, 1989].

[8] Na plays an important role in the control of turgor pressure [Takagi and Nagai, 1992] and in soil salinization [Lavee *et al.*, 1998]. The capacity to retain Na in plant tissues under drought as a water stress avoidance mecha-

nism [Wang *et al.*, 2008] is an interesting possibility that warrants investigation.

[9] S is essential to the growth of higher plants. S availability is also partly related to soil moisture such as observed in rainfall gradients in tropical areas of Africa. In Mediterranean ecosystems the information about S is scarce; Sardans *et al.* [2006b] observed a negative correlation between leaf sclerophylly and leaf S concentration in a Mediterranean forest. As sclerophylly is important to deal with dry conditions in Mediterranean environments [Sardans *et al.*, 2006b], reductions of S concentrations and contents in aboveground biomass are likely in response to drier conditions. Several human activities are sources of S emissions and an increase of S concentrations in plant tissues has been observed in some Mediterranean areas in the last century [Peñuelas and Filella, 2001].

[10] Climate change can affect soil nutrient availability and plant nutrient contents by affecting soil moisture, soil biological activity and plant growth. The increase of soil temperature can increase soil organic matter decomposition and mineralization rates [Rustad *et al.*, 2001; Emmett *et al.*, 2004]. However, plant nutrient concentrations or accumulation will depend on whether plant growth also increases. The increased temperatures may enhance soil microbe activity, plant photosynthetic capacity and growth, thus enhancing nutrient capture and increasing their retention in the ecosystem. Contrarily, the decrease in soil water content may reduce soil mineralization and plant nutrient uptake capacity by reducing soil water diffusion, photosynthetic capacity and transpiration, thus decreasing its accumulation in plants and increasing its accumulation in soils. The accumulation of nutrients in soil increases the risk of nutrient losses to continental waters by torrential rainfalls. On the other hand, sclerophylly, a trait typical of Mediterranean vegetation, tends to increase in drier environments [Sabaté *et al.*, 1992] resulting in enriched C/N in litter [Lebreton *et al.*, 1997] lowering decomposition rates and diminishing nutrient mineralization and plant uptake, and thus leading to nutrient accumulation in soil. All these effects on plant nutrient content can be produced asymmetrically among different plant species changing their stoichiometry which finally may affect ecosystem trophic chains [Nagai and Jefferies, 2004; Diehl *et al.*, 2005]. Additionally, warming and drought can change other soil properties, such as cation exchangeable capacity (CEC) that also affects the nutrients cycle. For example, a decrease of soil organic matter or clay formation can reduce CEC and thus the capacity of soil to retain nutrients. Furthermore, warming and drought can change soil diffusion capacity of nutrients.

[11] Significant amounts of Ca, Mg and S have been observed in the bulk deposition in Mediterranean mountain forests in Catalonia (NE Spain) [Rodrigo *et al.*, 2003], and the plant metal contents has increased throughout the last century in Spanish terrestrial ecosystems as a result of increasing pollution [Peñuelas and Filella, 2002]. In general, nutrient inputs have increased in natural ecosystems in wide areas of the Mediterranean basin in the last decades [Peñuelas and Filella, 2001; Rodrigo and Àvila, 2002]. Increasing inputs of nutrients in terrestrial ecosystems in a new climate scenario in the coming decades would also affect the future nutrient uptake by plants. The fact that warming and drought can overlap with atmospheric deposi-

tion of Ca, Mg, Fe, Mo, Na and S in Mediterranean areas in the near future increases the interest of studying the warming and drought effect on the capacity to retain these nutrients in soil and biomass, at ecosystem and species level.

[12] If climate change decreased nutrient contents and availability in these ecosystems (*it*), this would have a synergic effect that would accelerate their degradation and their substitution by more arid ecosystems. On the contrary, a possible increase of nutrient concentration in plants linked to a growth decrease or an increased pollution may have a positive effect in the capacity to respond to a decrease in soil water availability by increasing water use efficiency (WUE).

[13] We hypothesized that changes in soil moisture, soil CEC, soil pH, soil microbial activity, plant photosynthetic capacity, transpiration and plant growth produced by warming and drought would lead to changes in the concentration and the accumulation of Ca, Fe, Mg, Mo, Na and S in biomass, and total and available soil concentrations of these nutrients in a Mediterranean shrubland submitted to a 6-year field experiment, where we simulated climate changes projected by general circulation models and the ecophysiology-based model GOTILWA for the next decades [IPCC, 2007; Sabaté *et al.*, 2002; Peñuelas *et al.*, 2005]. We tested the impacts of simulated warming and drought on: (1) the Ca, Fe, Mg, Mo, Na and S concentrations and their accumulation (1999–2005) in the biomass and the losses in litter for the two dominant shrub species, (2) the total and available forms of Ca, Fe, Mg, Mo, Na and S in soil, (3) the soil exchangeable capacity, soil exchangeable cations and % of the cation exchange complex and (4) the enrichment factors of Ca, Fe, Mg, Mo, Na and S in plants with respect to bedrock.

2. Material and Methods

2.1. Study Site

[14] The study was carried out in a natural Mediterranean calcareous shrubland on a south-facing slope in the Garraf mountains in Catalonia (NE Spain) (41° 18' N, 1° 49' E). The site is located on formerly cultivated terraces-abandoned approximately a century ago-with a *Petrocalcic calcixerept* soil lying on bedrock of sedimentary limestone. During the study period (1999–2005) the average annual temperature was 15.1°C (7.4°C in January and 22.5°C in July) and the average annual rainfall was 580 mm. The summer drought is pronounced and usually lasts for three months. The total vegetation cover is 75% and consists of a calcareous shrubland with plants about 1 m high dominated by the shrubs *Globularia alypum* (L.), *Erica multiflora* (L.), *Dorycnium pentaphyllum* (Vill.), *Rosmarinus officinalis* (L.), *Ulex parviflorus* (Pourr.), and *Pistacia lentiscus* (L.). Aleppo pines *Pinus halepensis* (Mill.) were air seeded after the last forest fire in 1994 and are today gaining ground. The undergrowth is dominated by small shrubs such as *Fumana ericoides* (Cav.) and *Fumana thymifolia* (L.).

2.2. Experimental Design

[15] Treatments were established in nine plots, three plots for warming, three plots for drought and three plots for control. Plots were 4 × 5 m but 0.5 m was leaved as edge, so effective plot area was 12 m² [Beier *et al.*, 2004].

[16] The warming treatment was achieved by covering the plots during the night periods with an aluminum curtain coiled on a beam and connected to a motor. The curtain refracts long-wave infrared radiation back into the vegetation, resulting in a temperature increase in relation to untreated plots. Curtains were triggered by light sensors and roofs were automatically removed during rain events to avoid interferences with the hydrological cycle. Warming increased T an average of 0.95°C at –5 cm soil depth since the beginning of experiment.

[17] Drought treatment was achieved by automatically covering vegetation with a transparent plastic curtain during rain events by means of a rain sensor. Once the rain stopped, the curtain was automatically removed. In summer and winter, the drought treatment was not applied and drought plots were allowed to develop under the same conditions as the control plots.

[18] Since the beginning of the experiment, the drought treatment reduced soil moisture a 19% relative to control and a 17% relative to warming, mainly by reducing spring and autumn rainfall input. These reductions in soil moisture are in the range of the values predicted by Gotilwa model for the next decades [Sabaté *et al.*, 2002; Peñuelas *et al.*, 2005]. For both, warming and drought treatments, roofs were removed when wind speed exceeded 10 m s⁻¹.

[19] Environmental conditions were monitored in all plots. Soil moisture was measured weekly by three TDR (time domain reflectometry) probes installed in each plot. Air (+20 cm) and soil (–10 cm and –5 cm) temperatures were recorded from every plot by temperature sensors (RTD Pt 100 1/3 DIN, Desin Instruments, Barcelona, Spain) connected to a datalogger (Campbell Scientific, Inc. Logan, Utah, USA). Precipitation was measured by standard rain gauges.

2.3. Biomass Growth

[20] In 1999 and in 2005, the aboveground biomass was estimated by means of the pin point method [Peñuelas *et al.*, 2004, 2007]. For the details, see Sardans *et al.* [2008a].

2.4. Sampling Process

[21] Sampling process for plant biomass and litterfall was conducted as in the work of Sardans *et al.* [2008a].

[22] The Ca, Fe, Mg, Mo, Na and S content of each biomass fraction and species for each plot were calculated by multiplying their concentration in the biomass fraction by their biomass per plot. For *E. multiflora* we only used the concentration in the current-year leaves to calculate the leaf nutrient content since it represented most of the leaf biomass in this species.

[23] For soil analyses, three sample cores (30 cm deep) from each plot were taken in January 2005 and 16 rock samples were analyzed to obtain the nutrient concentrations of the bedrock.

2.5. Chemical Analyses

[24] Biomass, litterfall and soil samples were prepared previous to acid digestion before spectroscopic determination as described by Sardans *et al.* [2008a].

[25] Biomass samples were submitted to an acid digestion as described by Mateo and Sabaté [1993] before proceeding to the Ca, Fe, Mg, Mo, Na and S determination by spectroscopic methods. We used standard certified biomass

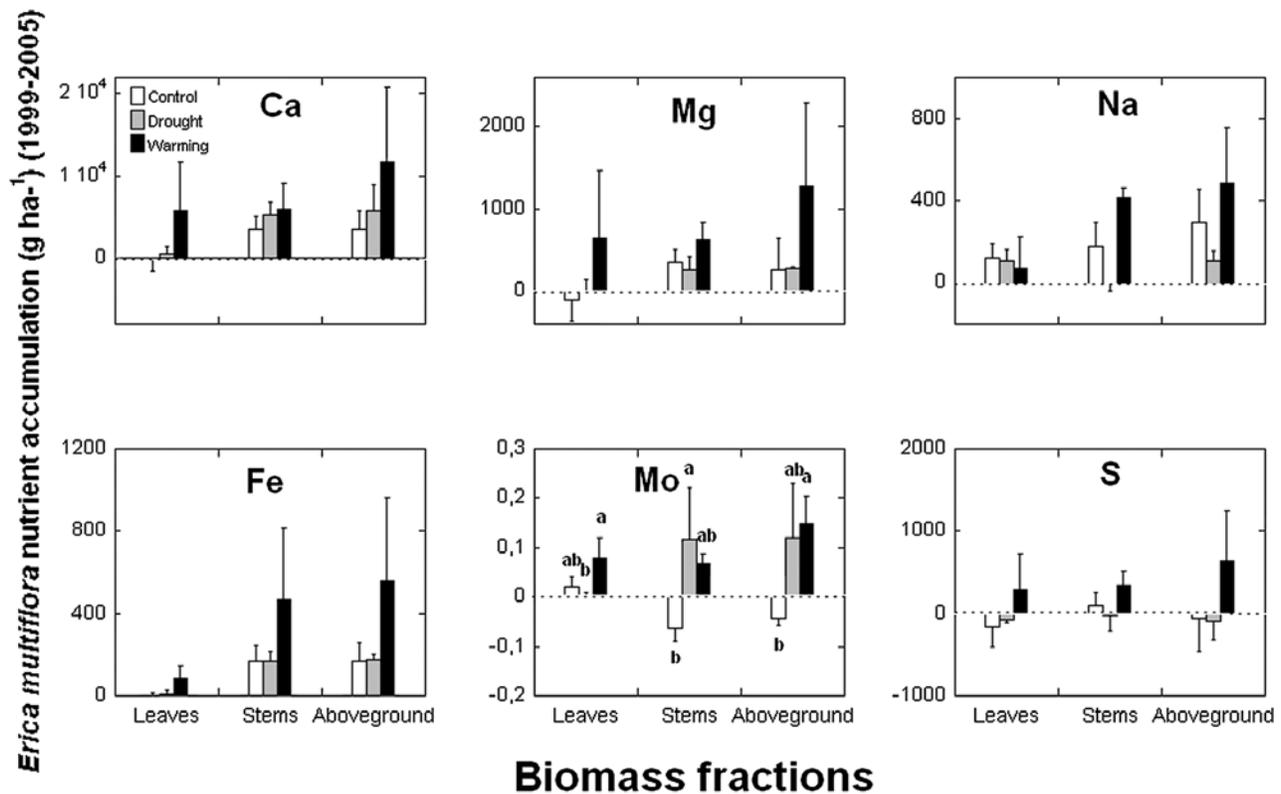


Figure 1. Nutrient accumulation (g ha^{-1}) in the different treatments in *Erica multiflora* during the period 1999–2005. Different letters indicate significant statistical differences between treatments ($P < 0.05$, post-hoc Bonferroni-Dunn test, ANOVA).

(DC73351) to assess the accuracy of digestion and analytical procedures. Soil samples were digested adding 9 ml of HNO_3 (65%) and 4 ml HF (40%) to 0.25 g of ground soil and treated for 8 h at 120°C in a microwave oven [Bargagli *et al.*, 1995]. The digested solutions were carried to 50 ml final volume, filtered through $0.45 \mu\text{m}$ and stored at 4°C until their determination. Analytical precision for soil and bedrock analyses, as verified by parallel analyses of an international (GSR-6) standard, was better than 5% for all nutrients analyzed.

[26] The soil extractable fractions of Ca, Fe, Mg, Mo and S were obtained from each soil sample. Extraction was done by shaking 2 g of soil with 10 ml of 0.01 M NaNO_3 , as in the work of van Elteren and Budic [2004] in 50-ml plastic centrifuge tubes by shaking on a reciprocal shaker at 100 strokes min^{-1} for 5 hours, a technique based on batch extraction studies by Gupta and Mackay [1966]. After equilibrium, solids were separated from the solution by centrifugation and filtration through a $0.45 \mu\text{m}$ membrane filter. Two replicates were prepared for each sample. Cation exchange capacity (CEC), total exchangeable basic cations (Na^+ , K^+ , Ca^{2+} and Mg^{2+}) and percentage of base saturation were determined by soil saturation with trietanolamine- $\text{BaCl}_2 \cdot 2\text{H}_2\text{O}$, washing of the excess of BaCl_2 with ethanol, and replacement with 1 M CaCl_2 [Mehlich, 1948], method which is adequate for CEC determination in calcareous soils.

[27] The concentrations of Ca, Fe, Mg, Na and S in all biomass and soil samples were measured by ICP-OES using a spectrophotometer model JOBIN IBON JY 38 (HORIBA Jobin Ibon S.A.S., Longjumeau, France). Mo concentration

in all biomass and soil samples was measured by using ICP-MS (Mass Spectroscopy with Inductively Coupled Plasma) with a model Elan-6000 (Perkin Elmer Corp, Inc. Norwalk, CO, USA).

[28] We measured soil pH in a 1:2.5 soil solution for all the soil samples (both in water and 1 M KCl) using a glass electrode (ORION 960 Autochemistry System).

2.6. Solubility and Soil Enrichment Factor Determination

[29] The solubility of the different nutrients was experimentally determined by the calculation of the following ratio: $[\text{Nutrient}]$ in water soil NaNO_3 extracts/ $[\text{Nutrient}]$ in soil.

[30] We calculated an enrichment factor [Sardans and Peñuelas, 2005b] of soil with respect to bedrock in order to assess the proportion of atmospheric deposition origin. To assess the soil origin fraction, we determined the concentrations of soil tracers such as Al, which are usually regarded as references for soil pollution detection, since they are amongst the most important constituents of the Earth's crust and have limited metabolic significance in plants.

$$\text{EF} = (\text{C}_x/\text{C}_{\text{Al}})_{\text{soil}}/(\text{C}_x/\text{C}_{\text{Al}})_{\text{bedrock}}$$

[31] The concentration in soil of the nutrient in question (C_x) is determined in relation to Al, and in turn is normalized with the equivalent ratio in the bedrock. The closer the EF value approaches unity, the more likely it is that the nutrient in question comes from the soil. Values above 1 are assumed to indicate atmospheric origin. The lack of past

Table 1. Concentrations of the Analyzed Nutrients (Mean \pm SE) in *Erica multiflora* Biomass Fractions^a

Year and Biomass Fraction	Treatments	Nutrients					
		Ca (mg g ⁻¹)	Fe (mg g ⁻¹)	Mg (mg g ⁻¹)	Mo* (mg kg ⁻¹)	Na (mg g ⁻¹)	S (mg g ⁻¹)
(1999) Current-year leaves	Control	10.0 \pm 1.42	0.186 \pm 0.027	2.06 \pm 0.22	0.089 \pm 0.016	0.117 \pm 0.049	1.36 \pm 0.09
	Drought	6.88 \pm 1.33	0.142 \pm 0.031	1.85 \pm 0.35	0.085 \pm 0.008	0.208 \pm 0.061	1.13 \pm 0.17
	Warming	6.81 \pm 1.85	0.113 \pm 0.044	1.43 \pm 0.38	0.079 \pm 0.010	0.096 \pm 0.026	0.935 \pm 0.21
Stems	Control	3.74 \pm 0.21	0.294 \pm 0.026	0.903 \pm 0.019	0.185 \pm 0.009	0.207 \pm 0.031	1.251 \pm 0.020
	Drought	3.59 \pm 0.36	0.254 \pm 0.039	0.774 \pm 0.080	0.164 \pm 0.013	0.311 \pm 0.039	1.077 \pm 0.079
	Warming	2.92 \pm 0.46	0.332 \pm 0.142	0.660 \pm 0.118	0.193 \pm 0.022	0.303 \pm 0.040	1.063 \pm 0.140
(2005) Current-year leaves	Control	5.33 \pm 0.44b	0.099 \pm 0.015	1.12 \pm 0.08	0.074 \pm 0.020b	0.212 \pm 0.036ab	0.699 \pm 0.055
	Drought	5.70 \pm 0.62ab	0.105 \pm 0.013	1.24 \pm 0.13	0.069 \pm 0.019b	0.318 \pm 0.072a	0.719 \pm 0.065
	Warming	7.58 \pm 1.00a	0.136 \pm 0.019	1.19 \pm 0.08	0.122 \pm 0.020a	0.170 \pm 0.042b	0.698 \pm 0.051
One-year old leaves	Control	8.00 \pm 0.63	0.166 \pm 0.016	1.38 \pm 0.11b	0.154 \pm 0.022	0.114 \pm 0.029	0.799 \pm 0.037ab
	Drought	9.06 \pm 0.96	0.161 \pm 0.010	1.85 \pm 0.15a	0.176 \pm 0.023	0.219 \pm 0.054	0.988 \pm 0.106a
	Warming	10.2 \pm 1.4	0.235 \pm 0.078	1.31 \pm 0.17b	0.212 \pm 0.047	0.190 \pm 0.054	0.765 \pm 0.086b
Stems	Control	5.27 \pm 0.80ab	0.301 \pm 0.032	0.843 \pm 0.154	0.074 \pm 0.013b	0.217 \pm 0.037	0.751 \pm 0.049
	Drought	4.53 \pm 0.35b	0.367 \pm 0.048	0.838 \pm 0.102	0.220 \pm 0.075a	0.216 \pm 0.047	0.707 \pm 0.035
	Warming	9.34 \pm 3.07a	0.336 \pm 0.030	0.729 \pm 0.049	0.139 \pm 0.012ab	0.303 \pm 0.036	0.694 \pm 0.029
Litter	Control	8.47 \pm 0.08	0.169 \pm 0.003	1.22 \pm 0.04	0.146 \pm 0.018	0.035 \pm 0.014b	0.625 \pm 0.026
	Drought	8.61 \pm 0.13	0.147 \pm 0.008	1.58 \pm 0.16	0.176 \pm 0.032	0.084 \pm 0.024a	0.691 \pm 0.059
	Warming	8.50 \pm 3.19	0.109 \pm 0.036	1.38 \pm 0.54	0.162 \pm 0.083	0.012 \pm 0.011b	0.491 \pm 0.193

^aDifferent letters indicate significant statistical differences (they are highlighted in bold type) between treatments ($P < 0.05$, post-hoc Bonferroni-Dunn test, ANOVA).

agriculture activities in this zone allowed to rule out any nutrient inputs than those of the lithosphere or atmosphere.

2.7. Statistical Analyses

[32] Treatment effects were assessed by one-way ANOVA using the treatment as factor, with Bonferroni/Dunn as post-hoc test and the plot mean values of each variable as unit of analysis. We used Stview 5.1 package (Abacus concepts, Inc. Berkeley, CA, USA).

3. Results

3.1. Plant Nutrient Concentrations

[33] Several of the studied nutrients were affected by both treatments, either increasing or decreasing their concentration. Ca leaf concentrations were increased by warming, in *E. multiflora* by 42% and in *G. alypum* by 38% (Tables 1

and 2). Drought decreased Ca concentrations in *G. alypum* stems (41%) (Table 2). Warming increased Fe concentrations in *G. alypum* stems by 101% with respect to drought plots (Table 2). Drought decreased Mg concentrations in *G. alypum* litter by 24% with respect to control. Drought increased Mg concentrations in *E. multiflora* leaves by 34% and *D. pentaphyllum* by 42% respect to control. Warming increased Mo concentrations in *G. alypum* stems by 132% with respect to drought (Table 2). Warming increased Mo concentrations in leaves of *E. multiflora* and *G. alypum* (65% and 60%, respectively) (Tables 1 and 2). Drought increased Mo concentrations in *E. multiflora* stems by 197% and increased Mo concentrations in leaves of *D. pentaphyllum* by 179% (Table 3). Drought increased Na concentration in *E. multiflora* (Figure 1) in leaf and litter (by 87% and 600%, respectively) and in *G. alypum* leaf and stems (by 92% and 75%, respectively) (Table 2). Warming

Table 2. Concentrations of the Analyzed Nutrients (Mean \pm SE) in *Globularia alypum* Biomass Fractions^a

Year and Biomass Fraction	Treatments	Nutrients					
		Ca (mg g ⁻¹)	Fe (mg g ⁻¹)	Mg (mg g ⁻¹)	Mo* (mg kg ⁻¹)	Na (mg g ⁻¹)	S (mg g ⁻¹)
(1999) Current-year leaves	Control	16.4 \pm 0.8	0.212 \pm 0.062	0.931 \pm 0.040	0.291 \pm 0.045	0.367 \pm 0.093	1.487 \pm 0.192
	Drought	16.3 \pm 1.2	0.249 \pm 0.038	0.828 \pm 0.075	0.296 \pm 0.011	0.498 \pm 0.101	1.196 \pm 0.069
	Warming	16.5 \pm 0.8	0.281 \pm 0.090	0.809 \pm 0.045	0.215 \pm 0.009	0.426 \pm 0.074	1.124 \pm 0.025
Stems	Control	5.34 \pm 0.67	0.156 \pm 0.036	0.531 \pm 0.027	0.186 \pm 0.018	0.163 \pm 0.045	1.28 \pm 0.06
	Drought	5.48 \pm 0.41	0.144 \pm 0.027	0.492 \pm 0.017	0.173 \pm 0.004	0.147 \pm 0.033	1.34 \pm 0.04
	Warming	5.31 \pm 0.35	0.164 \pm 0.025	0.545 \pm 0.024	0.171 \pm 0.022	0.151 \pm 0.046	1.26 \pm 0.08
(2005) Leaves	Control	14.6 \pm 1.2b	0.128 \pm 0.010	1.11 \pm 0.09	0.129 \pm 0.020b	0.154 \pm 0.046b	1.53 \pm 0.13a
	Drought	15.3 \pm 2.1b	0.204 \pm 0.100	1.47 \pm 0.58	0.128 \pm 0.020b	0.295 \pm 0.055a	1.13 \pm 0.13b
	Warming	20.1 \pm 1.4a	0.136 \pm 0.016	1.26 \pm 0.10	0.207 \pm 0.024a	0.154 \pm 0.040b	1.35 \pm 0.07ab
Stems	Control	11.4 \pm 3.1a	0.326 \pm 0.081ab	0.721 \pm 0.101ab	0.137 \pm 0.022ab	0.199 \pm 0.038b	0.680 \pm 0.036
	Drought	6.70 \pm 0.86b	0.175 \pm 0.017b	0.614 \pm 0.030b	0.093 \pm 0.014b	0.350 \pm 0.054a	0.701 \pm 0.056
	Warming	10.4 \pm 2.4ab	0.359 \pm 0.090a	0.865 \pm 0.110a	0.216 \pm 0.071a	0.181 \pm 0.041b	0.674 \pm 0.042
Litter	Control	20.6 \pm 0.5b	0.137 \pm 0.013	0.800 \pm 0.067a	0.187 \pm 0.020	0.054 \pm 0.055	1.37 \pm 0.05a
	Drought	20.6 \pm 1.1b	0.141 \pm 0.009	0.615 \pm 0.034b	0.226 \pm 0.023	0.051 \pm 0.027	1.30 \pm 0.04ab
	Warming	24.1 \pm 1.1a	0.144 \pm 0.005	0.724 \pm 0.037ab	0.219 \pm 0.032	0.034 \pm 0.032	1.25 \pm 0.02b
Roots	Control	14.0 \pm 2.2	0.195 \pm 0.033	1.48 \pm 0.32	0.213 \pm 0.100	0.122 \pm 0.059	1.06 \pm 0.14
	Drought	9.92 \pm 2.9	0.177 \pm 0.070	1.78 \pm 0.91	0.093 \pm 0.028	0.167 \pm 0.067	1.22 \pm 0.41
	Warming	13.3 \pm 2.6	0.176 \pm 0.025	1.49 \pm 0.26	0.183 \pm 0.033	0.051 \pm 0.035	1.15 \pm 0.18

^aDifferent letters indicate significant statistical differences (they are highlighted in bold type) between treatments ($P < 0.05$, post-hoc Bonferroni-Dunn test, ANOVA).

Table 3. Concentrations of the Analyzed Nutrients (Mean \pm SE) in *Dorycnium pentaphyllum* Biomass Fractions^a

Biomass Fractions	Treatments	Nutrients					
		Ca (mg g ⁻¹)	Fe (mg g ⁻¹)	Mg (mg g ⁻¹)	Mo* (mg kg ⁻¹)	Na (mg g ⁻¹)	S (mg g ⁻¹)
Leaves	Control	13.2 \pm 1.7	0.314 \pm 0.089	1.41 \pm 0.20b	0.118 \pm 0.026b	0.181 \pm 0.047	0.97 \pm 0.10b
	Drought	19.3 \pm 4.0	0.229 \pm 0.022	2.00 \pm 0.13a	0.329 \pm 0.082a	0.507 \pm 0.265	1.52 \pm 0.31a
	Warming	15.7 \pm 2.1	0.275 \pm 0.059	1.73 \pm 0.35ab	0.172 \pm 0.032b	0.244 \pm 0.069	1.15 \pm 0.15ab
Stems	Control	12.5 \pm 1.6	0.428 \pm 0.089	0.881 \pm 0.056	0.214 \pm 0.036	0.158 \pm 0.037	0.787 \pm 0.051a
	Drought	11.3 \pm 1.7	0.320 \pm 0.091	0.860 \pm 0.040	0.323 \pm 0.047	0.188 \pm 0.035	0.718 \pm 0.033ab
	Warming	9.6 \pm 1.0	0.316 \pm 0.064	0.871 \pm 0.036	0.343 \pm 0.184	0.127 \pm 0.040	0.667 \pm 0.018b

^aDifferent letters indicate significant statistical differences (they are highlighted in bold type) between treatments ($P < 0.05$, post-hoc Bonferroni-Dunn test, ANOVA).

decreased S concentrations in *G. alypum* litter by 26% and in *D. pentaphyllum* stems by 16% (Tables 2 and 3). Warming decreased S concentrations in *E. multiflora* one-year-old leaves with respect to drought leaves by 20% (Table 1). Drought increased S concentrations in *D. pentaphyllum* leaves by 57% and decreased S concentrations in *G. alypum* leaves by 26% (Tables 2 and 3).

3.2. Nutrient Accumulation in Plant Biomass (1999–2005)

[34] Neither warming nor drought changed significantly aboveground biomass accumulation of the two dominant shrub species (Table 4). Warming increased 0.15 g ha⁻¹ the accumulation of Mo in *E. multiflora* leaves with respect to control (Figure 1) and 0.035 g ha⁻¹ with respect to droughted plants (Figure 1). Drought increased 0.054 g ha⁻¹ the accumulation of Mo in *E. multiflora* stems and in *G. alypum* leaves and total aboveground biomass (0.07 and 0.40 g ha⁻¹, respectively) (Figure 2). Warming increased 510 g ha⁻¹ accumulation of Fe in *G. alypum* stems (Figure 2). Drought increased accumulation of Na in *G. alypum* stems and total aboveground biomass (780 and 800 g ha⁻¹, respectively) (Figure 2).

3.3. Soil Nutrient Concentrations

[35] Fe was the only nutrient affected by treatments. Warming decreased soil total-Fe concentrations by 24%, whereas drought increased Fe soil solubility by 65% (Table 5).

[36] Enrichment factors were below 1 for Ca, Mg, Mo and S (Table 5). In contrast, the EF for Fe was around 2. Warming decreased Fe EF (Table 2). Drought had not effects on soil EF of any nutrient (Table 5).

[37] Warming increased Mg accumulation in soil exchange complex by 19% with respect to control soils (Table 6). No treatment effects were observed for the rest of the exchangeable bases nor for the total exchangeable bases on the complex exchangeable capacity or the % of saturation of exchangeable complex.

[38] No significant treatments effects were observed on soil pH, nor in water (soil pH was 7.7 throughout the year and in all treatments) nor in 0.01 M KCl (soil pH was 7.5 also throughout the year in all treatments).

4. Discussion

[39] The effects of treatments on plant nutrient concentrations and accumulation depended on the nutrient and, to a lesser extent, on the species.

[40] The greater uptake capacity resulting from the autumn-winter enhancement of photosynthetic efficiency and

transpiration in warming plants [Llorens *et al.*, 2004] explains the higher Ca leaf concentrations. The decrease of Ca concentration in some biomass fractions under drought is explained by the decreased transpiration rates [Llorens *et al.*, 2004] which are highly correlated with Ca absorption [Marschner, 1995]. Ca plays a variety of roles. It is involved in the regulation of turgor pressure [Takagi and Nagai, 1992], and therefore in water losses regulation. On the other hand, Ca root content is an important factor for the capacity of plant to absorb NH₄⁺ in several plants species [Fenn and Feagley, 1999]. All these properties make Ca to play an important role in water use efficiency (WUE). Thus, drought effect decreasing Ca biomass concentration could increase the water stress in plants. However, Ca did not seem limiting since the Ca leaf concentrations we observed (4–21 mg g⁻¹) are higher than the values (0.85–1 mg g⁻¹) observed in plants with Ca deficiency [Nechwatal and Obwald, 2003]. The values of extractable Ca (0.582 mg g⁻¹ soil) are far above values for soils poor in soil extractable Ca (<0.13 mg g⁻¹) for seed development [Adams and Hartzog, 1991], and above the 0.04–0.24 mg kg⁻¹ in mineral soil layers in North-American forest with Ca availability problems [Lawrence *et al.*, 1997].

[41] The increase of Fe accumulation observed in *G. alypum* stems in warming plots may explain the decrease in soil Fe concentration. On the other hand, Fe²⁺ can precipitate forming insoluble salts with Pi. Warming decreased soil Pi by increasing P plant capture [Sardans *et al.*, 2008a]. The decrease in soil-Pi under warming may imply higher Fe²⁺ in soil solution, allowing higher plant Fe capture and decreasing Fe soil concentrations. The observed increases in Fe solubility in drought soils does not fit with the possibility of an increase in the Fe²⁺/Fe³⁺ ratio in soil, because the decrease of soil water content increases the presence of O₂ in soil decreasing Fe²⁺/Fe³⁺ ratio (in soil),

Table 4. Aboveground Biomass Accumulation (Mean \pm S.E., n = 3 Plots) of *Erica multiflora* and *Globularia alypum* in Control Plots, Drought Plots, and Warming Plots During the Period 1999–2005^a

Species	Treatments	Biomass Fractions		
		Leaves (kg ha ⁻¹)	Stem (kg ha ⁻¹)	Aboveground (kg ha ⁻¹)
<i>Erica multiflora</i>	Control	290 \pm 197	668 \pm 358	958 \pm 551
	Drought	143 \pm 47	292 \pm 87	435 \pm 129
	Warming	381 \pm 236	1066 \pm 563	1447 \pm 799
<i>Globularia alypum</i>	Control	382 \pm 249	643 \pm 153	1025 \pm 173
	Drought	263 \pm 28	1712 \pm 490	1975 \pm 477
	Warming	61 \pm 164	1023 \pm 446	1083 \pm 610

^aNo significant changes were found between treatments.

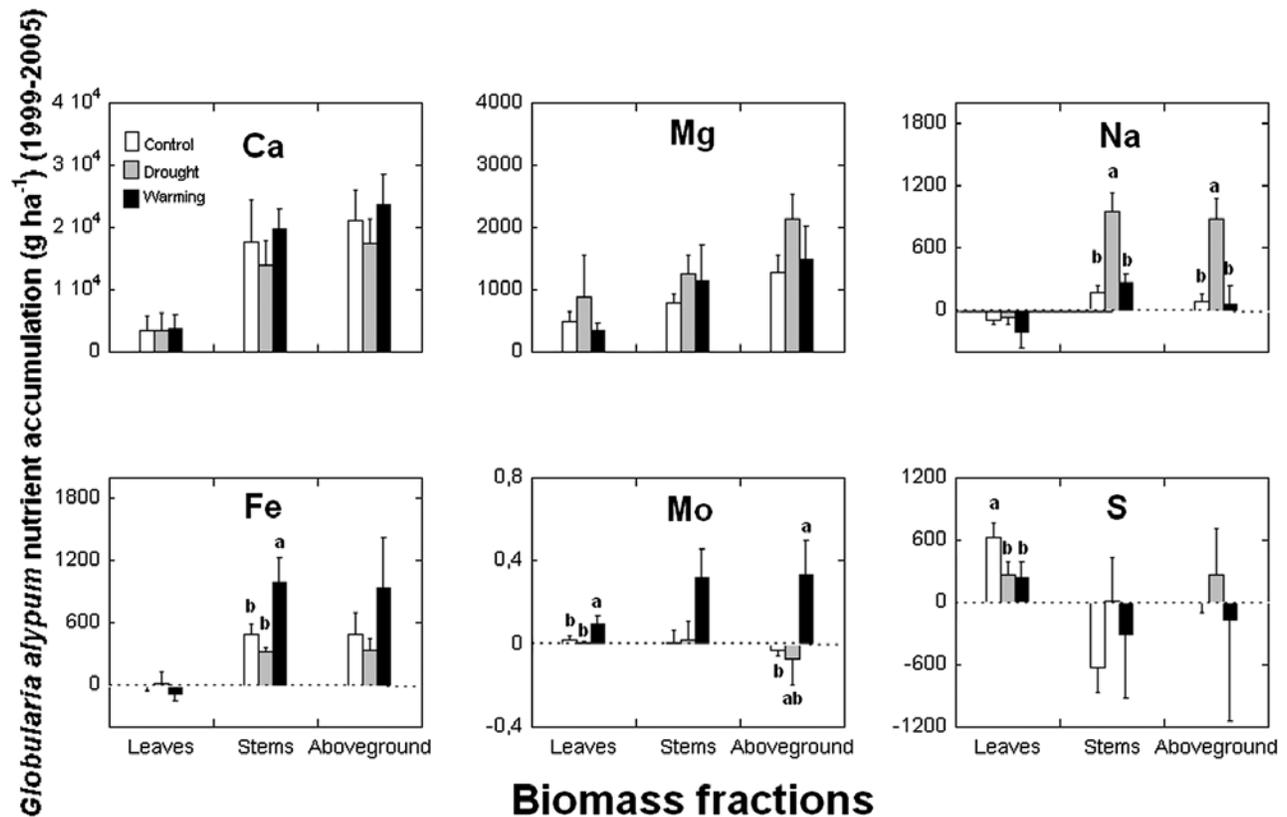


Figure 2. Nutrient accumulation (g ha⁻¹) in the different treatments in *Globularia alypum* during the period 1999–2005. Different letters indicate significant statistical differences between treatments ($P < 0.05$, post-hoc Bonferroni-Dunn test, ANOVA).

and thus increasing the more soluble chemical form of Fe (Fe²⁺) as has been described in a Mediterranean forest [Orgeas *et al.*, 2002]. The observed increase in Fe soil solubility may be due to the high mortality of microbes, which are lysed when soil is rewetted and liberate solutes to the soil [Turner and Haygarth, 2001]. A decrease of soil enzyme activity has been observed in response to drought [Sardans *et al.*, 2006a]. Thus, drought produced an increase

of soil Fe solubility without increasing the capacity of plant to accumulate it in aboveground biomass, thus opening the possibility of increasing losses of Fe to continental waters during torrential rainfalls. The total soil Fe concentrations (3.5–5 mg g⁻¹) and soil extractable Fe concentrations (0.001–0.002 mg g⁻¹) were below the range reported for unpolluted soils (22.9–67.0 mg g⁻¹, for total soil concentrations) [Abollino *et al.*, 2002; Vandecasteele *et al.*, 2005]. The low

Table 5. Concentrations (Mean ± SE) of Ca, Fe, Mg, Mo*, Na, and S (Mean ± SE) in Soils, in Soil Extracts (With 0.01 NaNO₃), the Ratio Between Concentration in Soil Extract and Concentration in Total Soil and the Enrichment Factor of Soil With Respect to Bedrock (EF = (C_x/C_{Al}) Soil/(C_x/C_{Al}) Bedrock)^a

Variable	Treatments	Nutrients					
		Ca (mg g ⁻¹)	Fe (mg g ⁻¹)	Mg (mg g ⁻¹)	Mo* (mg kg ⁻¹)	S (mg g ⁻¹)	Na (mg g ⁻¹)
Soil	Control	8.02 ± 0.57	4.68 ± 0.33a	0.414 ± 0.027	0.382 ± 0.032	0.744 ± 0.191	0.100 ± 0.099
	Drought	8.25 ± 0.71	4.79 ± 0.61ab	0.378 ± 0.015	0.377 ± 0.066	0.958 ± 0.170	0.096 ± 0.060
	Warming	8.66 ± 1.05	3.58 ± 0.34b	0.419 ± 0.027	0.348 ± 0.025	0.815 ± 0.131	0.154 ± 0.068
Soil extracts	Control	0.582 ± 0.018	1.35 ± 0.59	0.034 ± 0.002	0.013 ± 0.002	0.037 ± 0.004	
	Drought	0.601 ± 0.026	1.99 ± 1.15	0.034 ± 0.002	0.016 ± 0.002	0.040 ± 0.004	
	Warming	0.559 ± 0.020	1.16 ± 0.37	0.032 ± 0.003	0.013 ± 0.001	0.035 ± 0.003	
Ratio Soil ext./Total Soil	Control	0.075 ± 0.005	0.00035 ± 0.0002b	0.084 ± 0.008	0.038 ± 0.007	0.051 ± 0.011	
	Drought	0.075 ± 0.004	0.00058 ± 0.0004a	0.091 ± 0.007	0.041 ± 0.006	0.052 ± 0.011	
	Warming	0.072 ± 0.007	0.00039 ± 0.0001ab	0.078 ± 0.007	0.039 ± 0.004	0.043 ± 0.007	
EF	Control	0.484 ± 0.052	2.12 ± 0.17a	0.324 ± 0.047	0.164 ± 0.018	0.094 ± 0.020	
	Drought	0.478 ± 0.058	1.98 ± 0.14ab	0.300 ± 0.051	0.169 ± 0.032	0.126 ± 0.023	
	Warming	0.501 ± 0.038	1.71 ± 0.11b	0.324 ± 0.034	0.157 ± 0.020	0.127 ± 0.027	

^aDifferent letters indicate significant statistical differences (they are highlighted in bold type) between treatments ($P < 0.05$, post-hoc Bonferroni-Dunn test, ANOVA). C_x, concentration of the nutrient of concern. C_{Al}, concentration of aluminum.

Table 6. Exchangeable Cations (Ca, Mg, K, and Na) Concentrations in 1 M Ba Cl₂ Soil Extracts, Cations Exchangeable Capacity (Mean ± SE, n = 4), and Percent Base Saturation in Control Soil and in Soils Submitted to Drought and to Warming^a

Treatments	Ca (meq/100 g soil)	Mg (meq/100 g soil)	K (meq/100 g soil)	Na (meq/100 g soil)	Ca + Mg + K + Na (meq/100 g soil)	CEC (meq/100 g soil)	Percent Base Saturation (%)
Control	11.3 ± 0.7	0.43 ± 0.03ab	0.22 ± 0.01ab	0.14 ± 0.01	12.1 ± 0.9	13.8 ± 0.9	89.3 ± 4.2
Drought	10.5 ± 0.7	0.42 ± 0.03b	0.18 ± 0.01b	0.15 ± 0.01	11.3 ± 0.8	13.8 ± 0.8	83.3 ± 3.7
Warming	11.9 ± 0.6	0.50 ± 0.03a	0.23 ± 0.01a	0.13 ± 0.003	12.7 ± 0.7	14.9 ± 0.7	88.0 ± 4.6

^aDifferent letters indicate significant statistical differences (they are highlighted in bold type) between treatments ($P < 0.05$, post-hoc Bonferroni-Dunn test, ANOVA). CEC, cations exchangeable capacity.

Fe contents are aggravated by the high calcareous content of the soil, which strongly retains Fe in insoluble forms.

[42] Warming increased Mg contents in soil exchangeable complex, enhancing the capacity of the ecosystem to retain Mg. This effect can be related to the warming increase of soil enzyme activity in some seasons [Sardans *et al.*, 2006a], that permitted a high release of Mg from organic matter to exchangeable complex. The increased Mg concentration in leaves of one-year old leaves of *Erica multiflora* and the decreased Mg concentration in leaf litter and stems caused by drought indicate an increase of Mg allocation to leaves and Mg remobilization before leaf fall. The capacity to maintain high leaf concentrations under drought is important to hold an adequate photosynthetic capacity to take profit of the rewetting periods. This remobilization from senescence leaves and from stems to leaves and the low Mg leaf concentration in control leaves, point to a limiting role of Mg in this ecosystem. Leaf Mg concentrations observed in this experiment (1.1–1.6 mg g⁻¹) are in the range of values reported as limiting and/or causing chlorosis in different ecosystems (0.5–1.5 mg g⁻¹) [Laing *et al.*, 2000; Nechwatal and Obwald, 2003]. However, the total soil Mg concentrations (0.38–0.42 mg g⁻¹) are above the 0.045–0.052 mg g⁻¹ reported by Nechwatal and Obwald [2003] in a Germany Mg deficient forest. Other studies also reported that Mg is not limiting in Mediterranean ecosystems [Rashid and Ryan, 2004].

[43] Six years of warming increased the accumulation of Mo in the dominant shrubs of this community. These increases were mainly due to the increase in Mo leaf concentrations in *E. multiflora* and *G. alypum* and the increases in Mo stem concentrations in *G. alypum*. The mechanism of Mo uptake remains unclear, but an active absorption is probably involved in its absorption [Welch, 1995], and as *G. alypum* has increased its photosynthetic capacity under warming [Llorens *et al.*, 2003a, 2003b], it increases the possibility to increase its Mo uptake. Leaf Mo concentrations observed in this experiment (0.05–0.35 mg kg⁻¹) are in the range considered not limiting for the growth of most crop plants, but they are close to the values considered limiting in some reports (0.04–0.27 mg kg⁻¹) [Gupta *et al.*, 2003]. Moreover, the observed values in plant tissues fall below the limiting values that plants must reach to have sufficient Mo amounts for animal diet (about 0.5 mg kg⁻¹) and lower than the plant biomass concentrations that can be toxic for most mammals (10 mg kg⁻¹) [Albasel and Pratt, 1989; Neunhäuserer *et al.*, 2001]. The increase of Mo concentrations in some biomass fractions due to warming and drought did not affect the nutritional quality of plant tissues for herbivores because the concentration values did not reach toxic levels. Higher Mo concentration in leaves

can enhance water use efficiency (WUE) because Mo plays an important role in N assimilation and N is an important nutrient to maintain adequate water use efficiency. Soil total Mo concentrations (0.34–0.40 mg kg⁻¹) were in the low side of the normal range reported in the literature [McBride *et al.*, 2000].

[44] Drought tended to increase Na concentration in all biomass fractions analyzed, especially in leaves and stems of *G. alypum*. Na accumulation of this species increases the capacity to retain this nutrient in the ecosystem. Increases in Na concentrations in drought conditions have been observed in several species [Ottow *et al.*, 2005]. These increases provide a drought avoidance mechanism because of the increases of the osmotic pressure in the plant cells (soluble Na can contribute over 50% to total plant osmotic pressure) and the plant water uptake capacity, and water losses are prevented [Song *et al.*, 2006]. The increases of Na together with the observed increase in N concentrations in *G. alypum* stems under drought [Sardans *et al.*, 2008b] are linked to the capacity of this species to resist lower water potentials [Llorens *et al.*, 2003a, 2003b]. Since neither warming nor drought had significant effects on soil Na, they did not contribute to any salinization process. The leaf Na concentration we observed (0.1–0.5 mg kg⁻¹) are in the normal range for non saline soils [Osaki *et al.*, 1998; Tyler, 2005] and much lower than the values for saline soils [Osaki *et al.*, 1998; García *et al.*, 2002]. Thus, Na concentrations in drought plots are fairly far from toxic threshold values.

[45] Although warming decreased S litter concentration in *G. alypum*, and litter rich in S seems to be decomposed faster by soil microorganisms than litter poor in S [Ichinose *et al.*, 2002], soil enzyme activities in warming plots were not affected by the decrease in S in leaf-litter [Sardans *et al.*, 2006b] and in soil S availability. The drought effects on leaf S concentrations depended on the species, with increases in *E. multiflora* and *D. pentaphyllum* and decreases in *G. alypum*. These different drought effects in the different species may be related to the reduction in N leaf concentrations of *G. alypum* under drought [Sardans *et al.*, 2008b]. Under drought, *G. alypum* increased N contents in stems and reduced them in leaves, showing a great remobilization of proteins from leaves to stems probably as drought avoidance mechanisms [Sardans *et al.*, 2008b]. The accumulation of osmoprotectors rich in N such as nitrate, proline and other α -amino N compounds are typical of shoots in the plants adapted to drought [King and Purcell, 2006]. As S is mainly located in proteins, the protein remobilization from leaves to water transport tissues could partly account for the decrease of S leaf concentrations observed in *G. alypum* under warming. S leaf concentrations observed in this

experiment (0.65–1.65 mg g⁻¹) are in the range of the values reported in the literature [Peñuelas et al., 1997; Tyler, 2005]. The observed total soil S concentrations observed in this study (700–900 mg kg⁻¹) were higher than the values reported in the literature for most soils (188–550 mg kg⁻¹) [Tabatabai and Bremner, 1972; Wang et al., 2001].

[46] The soil enrichment factors with respect to bedrock Al contents were lower than 1 for Ca, Mg, Mo and S and higher than 1 for Fe. The presence of smelter Fe industries in the nearby Barcelona Metropolitan Area is a potential source of pollutants contributing to increase the Fe in soil. Saharan dust particles are deposited in considerable amounts (2–5 g m⁻² year⁻¹) in the Western Mediterranean region and can also contribute to the Fe enrichment of soils, since these particles have higher Fe concentrations (45 mg g⁻¹) [Guieu et al., 2002] than the soil particles (4.7 mg g⁻¹). Under warming, the increases of Fe absorption in *G. alypum* can be mostly produced from the Fe of atmospheric origin since the great plant uptake from soil coincided with the decrease in Fe soil EF. The increases of Mg and K contents in the exchangeable soil complex under warming show great liberation rates that are related to the great soil enzyme activity observed in warming plots [Sardans et al., 2006a].

[47] As previously observed with P [Sardans et al., 2008a], warming increased the leaf concentrations of Ca, Fe, Mg and Mo. Although these elements can be strongly retained in calcareous soils, the increase in soil enzyme activity and plant photosynthetic capacity have likely contributed to increase its plant capture under warming. On the other hand, drought increased Na accumulation in *Globularia alypum*. Similarly to the observed increases in N stem concentrations in this species [Sardans et al., 2008b], this effect can be related to a drought avoidance mechanism.

5. Final Remarks

[48] Warming tended to increase the accumulation of Ca, Fe and Mo. When warming is not accompanied by significant changes in soil water content it can thus increase plant photosynthetic capacity and WUE, because these nutrients are necessary for osmotic control and for the synthesis of enzymes related to photosynthesis. Warming increased the uptake of nutrients that are totally or partially dependent on active absorption, increasing the capacity to retain these nutrients in the ecosystem. These effects were observed in *G. alypum* and in *E. multiflora*. Under warming *G. alypum* presents an increase in its photosynthetic capacity whereas *E. multiflora* presents greater stem elongation. Thus, the increases in photosynthetic capacity, growth and soil enzyme activity allowed a great nutrient uptake capacity.

[49] Drought increased Na accumulation in stems of *G. alypum* and so in aboveground biomass. This accumulation is a possible mechanism of drought avoidance by increasing cell osmotic pressure, in accordance with the great capacity of this species to resist low water potentials in drier periods. Drought increased the proportion of Fe mobilized in the soil. This effect, together with the decrease of Fe accumulation in stem of one of the two dominant species, make this ecosystem more vulnerable to net losses of Fe at mid and long term under an scenario of increasing drought together with an increasing number of torrential rainfalls as projected

by several climate models for the Mediterranean basin [IPCC, 2007]. Since the effects of warming and drought depended on plant species and nutrient, there are changes in stoichiometry and nutritional quality of plant tissues that could also affect the herbivores of those plants.

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