

Response of plant species richness and primary productivity in shrublands along a north–south gradient in Europe to seven years of experimental warming and drought: reductions in primary productivity in the heat and drought year of 2003

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Abstract

We used a nonintrusive field experiment carried out at six sites – Wales (UK), Denmark (DK), the Netherlands (NL), Hungary (HU), Sardinia (Italy – IT), and Catalonia (Spain – SP) – along a climatic and latitudinal gradient to examine the response of plant species richness and primary productivity to warming and drought in shrubland ecosystems. The warming treatment raised the plot daily temperature by ca. 1 °C, while the drought treatment led to a reduction in soil moisture at the peak of the growing season that ranged from 26% at the SP site to 82% in the NL site. During the 7 years the experiment lasted (1999–2005), we used the pin-point method to measure the species composition of plant communities and plant biomass, litterfall, and shoot growth of the dominant plant species at each site. A significantly lower increase in the number of species pin-pointed per transect was found in the drought plots at the SP site, where the plant community was still in a process of recovering from a forest fire in 1994. No changes in species richness were found at the other sites, which were at a more mature and stable state of succession and, thus less liable to recruitment of new species. The relationship between annual biomass accumulation and temperature of the growing season was positive at the coldest site and negative at the warmest site. The warming treatment tended to increase the aboveground net primary productivity (ANPP) at the northern sites. The relationship between annual biomass accumulation and soil moisture during the growing season was not significant at the wettest sites, but was positive at the driest sites. The drought treatment tended to reduce the ANPP in the NL, HU, IT, and SP sites. The responses to warming were very strongly related to the Gausse aridity index (stronger responses the lower the aridity), whereas the responses to drought were not. Changes in the annual

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aboveground biomass accumulation, litterfall, and, thus, the ANPP, mirrored the inter-annual variation in climate conditions: the most outstanding change was a decrease in biomass accumulation and an increase in litterfall at most sites during the abnormally hot year of 2003. Species richness also tended to decrease in 2003 at all sites except the cold and wet UK site. Species-specific responses to warming were found in shoot growth: at the SP site, *Globularia alypum* was not affected, while the other dominant species, *Erica multiflora*, grew 30% more; at the UK site, *Calluna vulgaris* tended to grow more in the warming plots, while *Empetrum nigrum* tended to grow less. Drought treatment decreased plant growth in several studied species, although there were some species such as *Pinus halepensis* at the SP site or *C. vulgaris* at the UK site that were not affected. The magnitude of responses to warming and drought thus depended greatly on the differences between sites, years, and species and these multiple plant responses may be expected to have consequences at ecosystem and community level. Decreases in biodiversity and the increase in *E. multiflora* growth at the SP site as a response to warming challenge the assumption that sensitivity to warming may be less well developed at more southerly latitudes; likewise, the fact that one of the studied shrublands presented negative ANPP as a response to the 2003 heat wave also challenges the hypothesis that future climate warming will lead to an enhancement of plant growth and carbon sequestration in temperate ecosystems. Extreme events may thus change the general trend of increased productivity in response to warming in the colder sites.

Keywords: biodiversity, climate change, drought, European gradient, forest-steppe, global warming, heathland, heat wave, litterfall, net primary productivity, plant biomass, plant growth, shrubland, species richness

Received 21 March 2007; revised version received 16 August 2007 and accepted 12 September 2007

Introduction

Global air temperatures have increased by 0.7 °C during the 20th century and are predicted to increase by between 1.1 and 6.4 °C during the 21st century, with the greatest increases expected to occur at more northerly latitudes (IPCC, 2007). These increases will also be accompanied by changes in precipitation patterns that are much more difficult to forecast. However, many models predict that summer droughts in some central and southern European regions will become more prevalent (Peñuelas *et al.*, 2005; IPCC, 2007).

Over the last decade, the need for information regarding the physiological, ecological, and evolutive response of organisms and ecosystems to climate change has been addressed by a growing number of observational and temperature- and precipitation-manipulation experiments around the world. As a result, a substantial body of data now exists that demonstrates the link between changes in regional climate and alterations in biological processes in ecosystems. Arft *et al.* (1999), Shaver *et al.* (2000), Peñuelas & Filella (2001), Rustad *et al.* (2001), Walther *et al.* (2002), Parmesan & Yohe (2003), Root *et al.* (2003) and others have reviewed many of these experiments. More recently, we reported variable responses in plants and ecosystems to experimental warming and drought along a

north–south gradient in European shrublands (Beier *et al.*, 2004; Emmett *et al.*, 2004; Llorens *et al.*, 2004; Peñuelas *et al.*, 2004).

The responses of plant productivity and other ecosystem processes to climate change are quite variable and increases, decreases, or no change at all have all been reported (see references Rustad *et al.*, 2001; Peñuelas *et al.*, 2004). However, there seem to be some regularities such as a greater positive response of aboveground plant productivity to warming in colder ecosystems (Rustad *et al.*, 2001). Furthermore, Antle *et al.* (2001) assembled a database of more than 2500 studies that address climate and related physical or biological processes and found that 80% of the studied species undergoing change were shifting in response to warming in the direction expected on the basis of known physiological constraints of species, while 20% were changing in the opposite direction. There is also a large body of observational, satellite, and atmospheric data regarding plant species and ecosystems that shows clear biological responses to warming such as extended growing seasons and altitudinal and northward movement of species' distributions in both northern and southern, cold-wet and warm-dry ecosystems (Myneni *et al.*, 1997; Peñuelas & Filella, 2001; Peñuelas *et al.*, 2001, 2002; Walther *et al.*, 2002; Parmesan & Yohe, 2003; Peñuelas & Boada, 2003; Root *et al.*, 2003; Menzel

et al., 2006). Ecosystem processes and biological species may respond asymmetrically to climatic changes (Walther *et al.*, 2002) and the overall effect on ecosystem functioning and species richness is, therefore, often highly complex and determined by the relative sensitivity of the different processes to climate change.

We conducted a noninvasive field experiment (Beier *et al.*, 2004; Peñuelas *et al.*, 2004) for 7 years at six sites from northern to southern Europe (United Kingdom, Denmark, the Netherlands, Hungary, Italy, and Spain) to examine the response of plant species richness and aboveground primary productivity to warming and drought along a climatic and latitudinal gradient of shrubland ecosystems. The aim was to study the effects of the climatic changes expected to occur over the coming decades (Peñuelas *et al.*, 2005; IPCC, 2007) and, additionally, we analyzed the effects of the 2003 heat wave. Our initial hypotheses were that plant primary productivity responses to warming would be greater in colder northern latitudes and the responses to drought greater in drier southern latitudes, because higher latitude ecosystems are typically limited by temperature (Chapin *et al.*, 1995) and lower latitude Mediterranean and continental ecosystems by drought (Mitrakos, 1980; Kovács-Láng *et al.*, 2000; Peñuelas *et al.*, 2001; Terradas, 2001). We also hypothesized that effects such as species-specific responses and the reduced number of recruited seedlings in warming and, above all, in drought plots found at some sites in a previous study (Lloret *et al.*, 2004) would, thus tend to lead to decreased species richness, especially at those sites still recovering their species-richness after a severe disturbance [e.g., the serious fire that occurred 5 years before the start of the experiment at the Spanish (SP) site] by progressively recruiting new species. The experimental approach was specifically chosen to overcome some of the main drawbacks found in previous studies such as the overintrusiveness of some of the methodologies used, the constant or diurnal rather than nocturnal manipulation of warming, the predominance of studies in cold and wet temperate and Arctic ecosystems, the lack of across-the-board protocols, and temporal (our results are the fruit of 7-year study instead of the 2 years in our previous study) limitations (Beier *et al.*, 2004; Peñuelas *et al.*, 2004). To approach vegetation (and ecosystem) response at larger spatial and temporal scales, we examined local studies across a natural climatic and environmental gradient along a transect from northern to southern Europe. With this geographical approach, we aimed to take into account long-term responses of vegetation to environmental conditions (Chapin *et al.*, 1995; Shaver *et al.*, 2000; Rustad *et al.*, 2001). Long-term studies allow the natural interannual variability as a result of temporal variability

in climatic conditions to be analyzed, thereby avoiding the often initially stronger transient response to treatments (Arft *et al.*, 1999).

Material and methods

Sites and manipulations

Experimental manipulations were carried out in shrublands at six European sites, in Wales (UK), in an atlantic heathland, Denmark (DK), in an atlantic heathland/grassland, the Netherlands (NL) in an atlantic heathland, Hungary (HU), in a continental forest-steppe, Sardinia (Italy – IT), in a mediterranean shrubland and in Catalonia (SP) also in a mediterranean shrubland, spanning both a temperature and precipitation gradient, and an aridity gradient (Fig. 1) (Beier *et al.*,

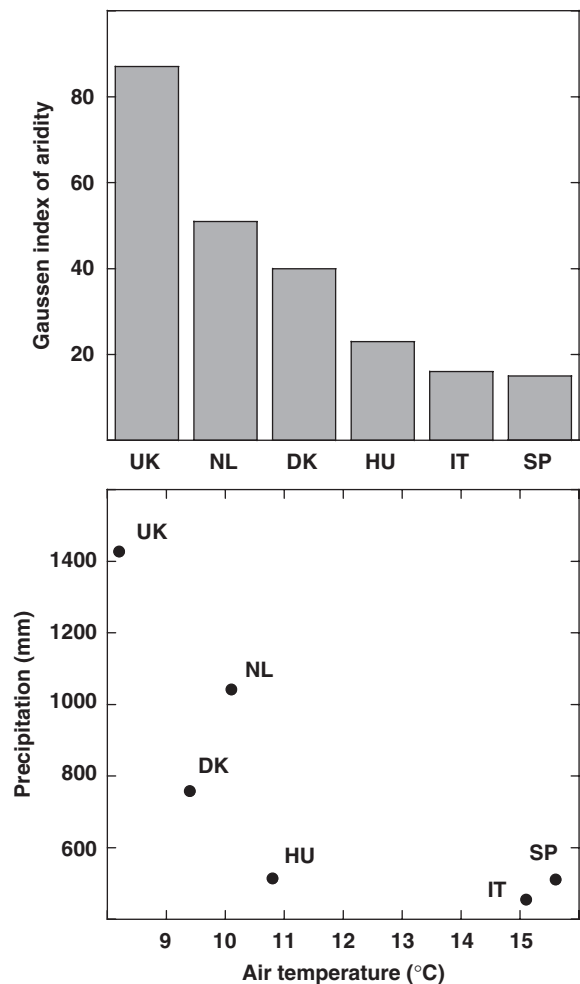


Fig. 1 Gausson index of aridity (precipitation/ $2 \times$ temperature), mean annual precipitation, and mean annual air temperature at the studied shrubland study sites in Wales (UK), the Netherlands (NL), Denmark (DK), Hungary (HU), Sardinia (Italy – IT), and Catalonia (Spain – SP).

2004). At each site, we imposed field-scale night-time warming, drought and control treatments and the response to the treatments was compared with control plots. Plots were $4 \times 5 \text{ m}^2$, allowing for a buffer strip of 0.5 m at the perimeter. Each type of manipulation was replicated three times at each site. Pretreatment measurements were conducted in order to identify variability between sites and plots.

Warming treatment

The warming treatment consisted of night-time warming provided by reflective curtains covering the vegetation at night (Beier *et al.*, 2004). Solar energy is accumulated in the ecosystem during the day and part of this energy is reradiated back to the atmosphere at night as long-wave infrared (IR) radiation. The covering of the ecosystem with reflective aluminum foil curtains (ILS ALU, AB Ludvig Svensson, Sweden) reduces the loss of IR radiation. These curtains reflect 97% of the direct and 96% of the diffuse radiation. The warming plots are 20 m^2 ($5 \times 4 \text{ m}^2$) and are framed by light scaffolding that supports the reflective aluminum curtain approximately 20 cm above the top of canopy. This curtain is activated automatically by pre-established light ($<200 \text{ lx}$), rain, and wind ($<10 \text{ m s}^{-1}$) conditions (Beier *et al.*, 2004). The curtains reduced the heat loss during night by 64%, from 33 to 12 W m^{-2} , and increased the temperature of the soil and plants by 0.5–1.5 °C (DK), 0–2 °C (UK), 0–1 °C (NL), 1–2 °C (SP), 0.3–1.3 (HU), and 0.2–0.6 °C (IT). These temperature increases are in the range predicted by the next 20–30 years by Global Circulation Models (IPCC, 2007). The magnitude of the warming effect depended on the site, time of the year, and meteorological conditions (Beier *et al.*, 2004). These moderate increases in temperature raised the average annual growth potential (growing degree days – GDD) by 3–16% at the non-Mediterranean sites. Overall at the six sites the number of days with frost was reduced by 19–44% (Beier *et al.*, 2004). In order to avoid unwanted effects on the hydrological cycle, rain sensors automatically trigger curtain removal during rainfall. This warming treatment has been applied since spring 1999 (since 2001 in HU and IT).

This method has the advantage that unintended edge effects and artifacts are minimized. Measurements of curtain movements, temperatures, precipitation, water input into the plots, radiation balance during campaigns, relative humidity, and wind speed showed that the edge effects on the temperature increase, as well as unintended effects on wind and moisture conditions, were minimal. Because night-time warming implies leaving the plots open during daytime, the effect on light conditions was negligible (Beier *et al.*, 2004).

Drought treatment

The drought treatment, which consisted of covering the vegetation with transparent waterproof covers, was put into practice for 2 months every year between 1999 and 2005 in the spring/summer growing seasons (in the SP and IT sites an additional drought period was established in the autumn growing season; Beier *et al.*, 2004). The drought plots are constructed in a similar way to the warming plots except for the fact that the curtains are made of transparent plastic and are only drawn in case of rain and wind. During the drought period the rain sensors activate the curtains whenever it rains and remove them again once the rain stops. The curtains are also removed automatically if the wind speed exceeds 10 m s^{-1} . For the part of the year without the drought treatment, the drought plots were managed in the same way as the control plots. Decreases in soil moisture during the drought treatment ranged from 82% in the NL site to 26% in the SP site; air and soil temperatures were not affected. For the rest of the year, the drought treatment was not applied and so the received precipitation was not directly affected (Beier *et al.*, 2004). Despite this soil moisture in the drought plots never completely recovered to the control levels.

Untreated control

Three untreated plots with similar light scaffolding as in the warming and drought plots but without curtains were set up as controls.

Plant response

We conducted yearly monitoring of plant responses to the above described climate manipulation treatments and measured the following variables in all the experimental plots: plant-community species richness, plant-community cover and biomass, litterfall, aboveground net primary productivity (ANPP), and individual plant growth. The objective was to assess relative changes in plant performance between treatment types for the different sites, years, and species.

Species richness, plant cover and biomass (pin-point method), litterfall, and ANPP

The pin-point method was used for measuring plant frequency and for indirectly estimating plant cover and biomass. Pin-point measurements were conducted annually at each site in July–August, although in IT measurements were taken at the end of the growing season (September–May), at the beginning of June. Vegetation response is assessed by noting species types

and calculating plant contacts and heights at a large number of points in each plot. This method enables, moreover, the assessment of changes in species composition and species-specific growth to be recorded. A sharpened pin was lowered through the vegetation with a minimum of 300 measurement points for each experimental plot. These points were arranged at 5 cm intervals along replicated five 3 m long transect lines (in SP and HU) or four 4 m long transect lines (in NL and IT) or in $0.5 \times 0.5 \text{ m}^2$ subplots (in the UK and DK). Each plant hit with the pin was counted and the plant species (or species group) recorded. At some of the sites the height above the ground was also recorded for each hit by means of 1 cm marks along the pin or along a vertical rod held behind the pin in a way that did not disturb the vegetation. We recorded the total number of hits for each species (and for each plant part of each species, if relevant) per transect and also the total number of hits as a proportion of all pin hits per transect. We also calibrated the pin-point measurements against absolute biomass using destructive sampling outside the plots. In each site biomass was regressed against hit numbers (or proportions) or, if hit heights were recorded, against heights.

In each plot, we placed litterfall collectors (between 5 and 30 – depending on the site and the traits of the corresponding vegetation – small pots with small holes allowing for drainage). These collectors ranged in diameter from 15 to 4.4 cm and were randomly placed under the plant canopy (or below *Erica multiflora*, *Globularia alypum*, and *Populus alba* plants in the scattered vegetation of SP and HU). We retrieved the litter monthly (or every 2 or 6 months, depending on the site) and then oven-dried it at 60°C until constant weight. Litterfall from grasses (DK) was estimated by harvesting the standing dead biomass once a year from a 0.5 m^2 plot since the litter is not shed from the grasses, which were a dominant part of the vegetation.

ANPP was estimated as the sum of the change in total aboveground biomass and litterfall. In DK, the ANPP is equal to the litterfall as the aboveground biomass of grasses and herbs senesce during the autumn.

Individual plant growth

The pin-point method does not provide a direct calculation of yearly plant growth at the species or individual level (although the frequency of hits is affected by plant growth and was also used to indirectly assess net aboveground biomass change). Additional direct measurement of individual plant growth was obtained in the UK, HU, IT, and SP sites by marking shoots and measuring them at intervals. A sample of 20–30 terminal shoots of the dominant site species were perma-

nently marked in each plot (in the HU site all shoots of 10 randomly selected shrubs per plot were measured). The length of each shoot was measured and plant growth estimated by using allometric relationships between biomass and shoot lengths obtained from a destructive sampling of plants from outside the plots.

Statistical analyses

We first conducted repeated measures ANOVAs and Bonferroni *post hoc* comparison tests with each measured plant variable as a dependent variable and the country and treatment as fixed factors. We used only the mean value of each variable for each plot, so that $n = 3$ per treatment, because we considered the roof/plot as the smallest independent unit. We used as many subplots/replicate samples as possible (usually three or more with a maximum of 30, depending on the variable being measured) to provide a good mean estimate for each plot.

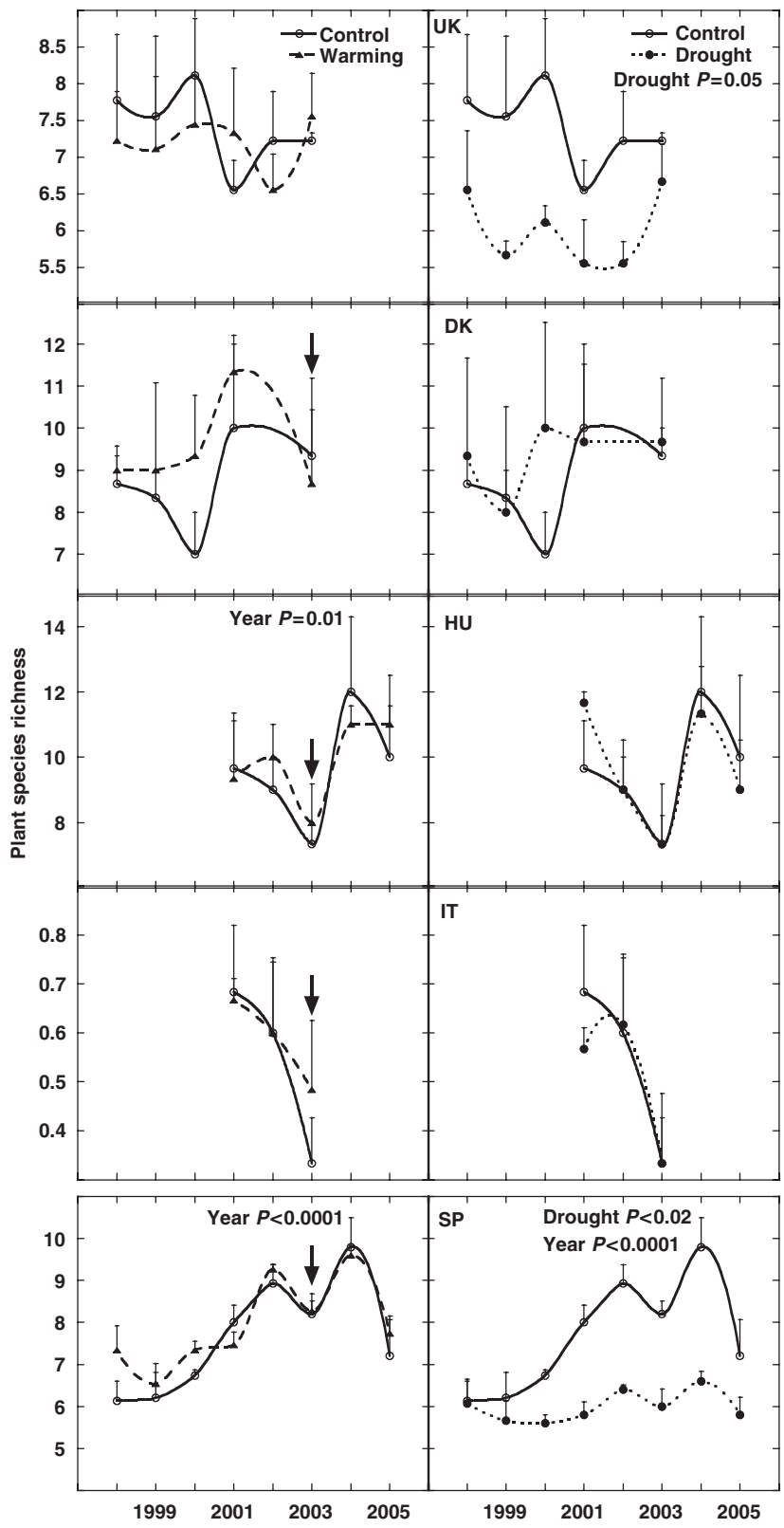
General regression models were built with plant biomass, litterfall, and individual plant growth as dependent variables, site, year, and species as fixed factors, and temperature, soil moisture, and precipitation during the growing season (i.e. the final 3 months, except in IT, where we took into account the whole growing season from September to May) as independent variables. Differences with a P -value < 0.05 were considered as statistically different. Analyses were performed with the STATVIEW software package (Abacus Concepts Inc., Cary, NC, USA) and the STATISTICA software package (StatSoft Inc., Tulsa, OK, USA).

Results

Species richness

The number of species pin-pointed per transect was lower in the drought plots than in the control plots (it was also lower in the warming plots than in the control plots although the difference was statistically not significant) at the SP site (Figs 2 and 3). At this site, the plant community was recovering from a forest fire in 1994. During the 6-year study period between 1999 and 2004, drought plots recruited less than one new species per transect and warming plots a little more than two new species, whereas control plots recruited more than three new species per transect (Figs 2 and 3). No significant changes due to warming or drought were found either at the other Mediterranean site (IT) or at the continental and northern sites (Figs 2 and 3), which were already in a more stable state of succession.

There was also a decrease in the number of species detected in 2003 at all sites apart from the UK (Fig. 2),



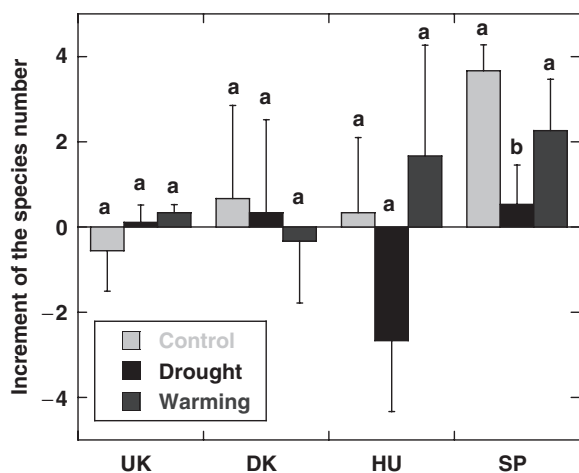


Fig. 3 Change in number of species per transect or subplot (see Fig. 2 caption), in control, drought, and warming treatments at the UK, DK, HU, and SP sites after 5–7 years of experiment in the period 1998–2005. Bars indicate the standard errors of the mean ($n = 3$ plot means). UK, Wales; DK, Denmark; HU, Hungary; SP, Catalonia (Spain).

a consequence of the especially hot and dry weather conditions of that year. A similar decrease was also noted in another very dry year in SP, 2005 (Fig. 2).

Community plant biomass

Plant biomass calculated from allometric relationships between pin-point measurements and biomass was significantly greater at the UK site (3500 g m^{-2}) than at the NL site (ca. 1000 g m^{-2}) and all the other sites (ca. 500 g m^{-2}) (Fig. 4).

The ca. 1°C experimental warming led to an increase of 69% in plant aboveground biomass accumulation during the 5 years of experimentation at the UK site and of 72% during the 3 years (2000–2002) with positive biomass accumulation at the NL site (Fig. 5). The warming treatment increased the total plant biomass at the northern sites, UK and NL, and at the continental site, HU, but when the responses during the unusually hot year of 2003 were included, the global effect of warming was not significant except slightly in HU (Fig. 5). The drought treatment tended to reduce biomass accumulation at the NL, HU, and SP sites, but again, if the whole study period is taken into account, the overall reduction was only slightly significant in HU (Fig. 5).

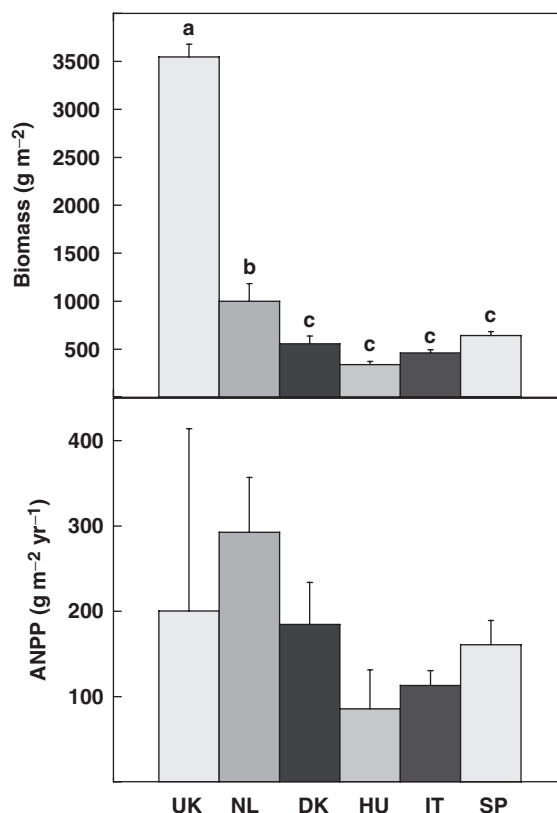
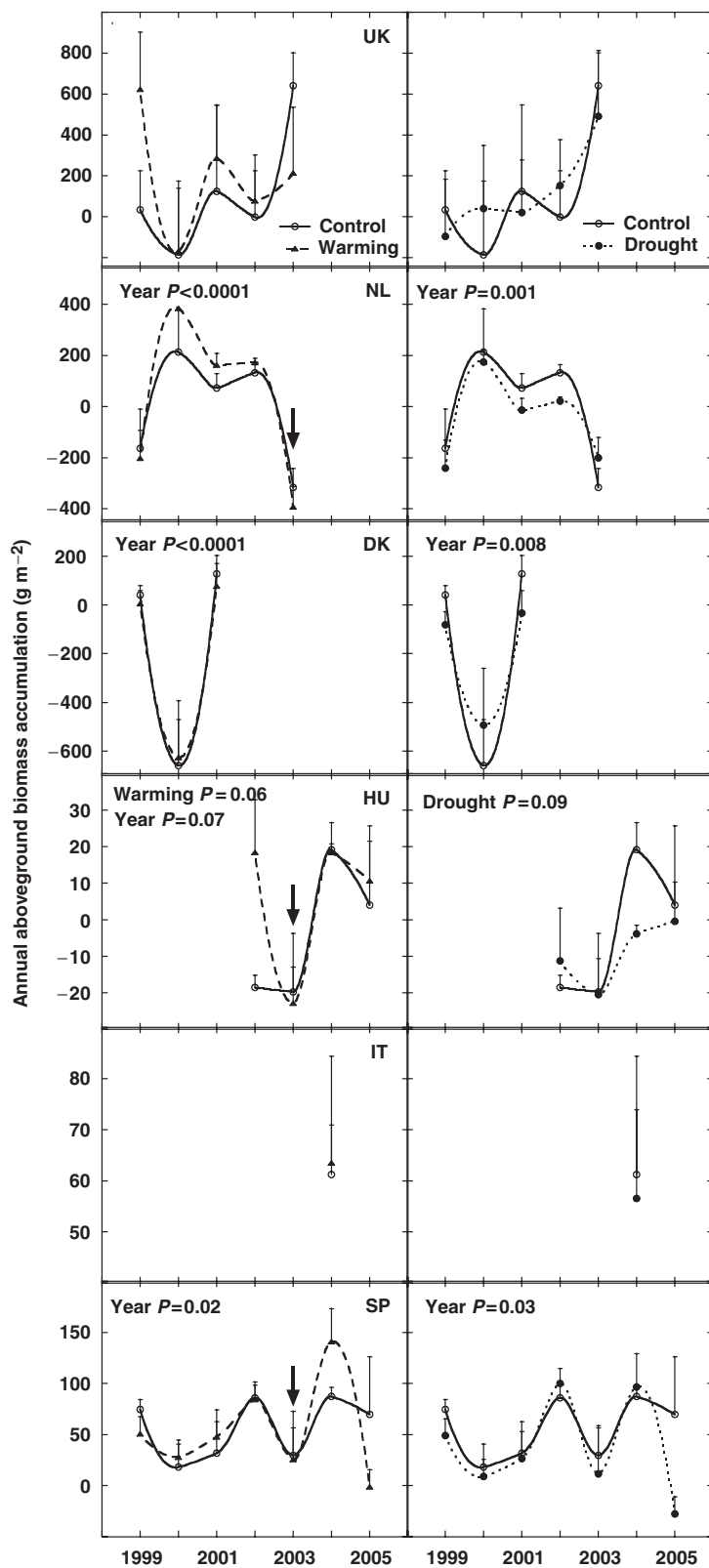


Fig. 4 Total aboveground plant biomass and annual aboveground net primary productivity in the control plots at the UK, NL, DK, SP, HU, and IT sites. Data are from control plots in 2002. Bars indicate the standard errors of the mean ($n = 3$ plots). Different letters indicate significantly different means (Bonferroni's *post-hoc* test of the ANOVA). UK, Wales; NL, the Netherlands; DK, Denmark; HU, Hungary; IT, Sardinia (Italy); SP, Catalonia (Spain).

The annual aboveground biomass accumulation (Fig. 5) followed the interannual variation in climate conditions and, moreover, presented a significant interaction for site \times year ($F = 3.89$, $P < 0.01$). However, the most outstanding change was the decrease in biomass accumulation at all sites except for the UK in the hot year of 2003, with negative accumulation values at the NL and HU sites. The UK site, on the other hand, accumulated a greater amount of biomass than usual (Fig. 7) as a likely result of increased nutrient availability as soil microbes are released from oxygen limitation caused by excess of water.

Fig. 2 Changes in plant species richness – number of species per 3 m transect (SP and HU), per m^2 (IT), or per $0.5 \times 0.5 \text{ m}^2$ subplot (UK and DK) – in response to warming and drought treatments in the period between 1998 (before the experimental treatments were applied) and the years of the experiment (1999–2005) in well-developed shrubland sites in UK, DK, HU, and IT, and in a typical shrubland recovering from 1994 fire (SP). Whenever significant (repeated measures ANOVA), the effects of the studied factor or interaction are depicted in the corresponding panel. An arrow signals the decreases in 2003 in all sites but the UK site. UK, Wales; DK, Denmark; HU, Hungary; IT, Sardinia (Italy); SP, Catalonia (Spain).



Litterfall

There was less plant litterfall at the southern sites (ca. 50 g m^{-2} at the IT site and ca. 100 g m^{-2} in the SP site) than at the northern sites (ca. 150 g m^{-2} at the NL and the UK sites) (Fig. 6), a logical consequence of their smaller plant biomass (Fig. 4).

The warming treatment tended to decrease (ca. 15%) the amount of litterfall at the northern sites, tended to increase it at the HU site, and had no effect at the Mediterranean sites (Fig. 6). The drought treatment tended to decrease litterfall at all sites by ca. 25%, the only exception being the HU site, where the drought treatment tended to increase litterfall (Fig. 6). However, the HU litter data are not comparable because of the deciduous character and the special dynamics of the clonal poplar shrubs that grow there: the amount of cover (and thus litterfall) of the poplars changed at different rates in different plots, that is, independently of the treatment type. In some plots shrub cover spread, but died back in others.

In line with the plant accumulation response, there was also an interannual variation in litterfall: an increase in the litterfall amount was recorded in the hot year of 2003 at the SP and the NL sites, whereas a decrease was recorded at the UK site (Fig. 6).

NPP

In a typical year such as 2002 the ANPP, calculated as the accumulated aboveground biomass plus litterfall, ranged between 100 and 200 g m^{-2} at the southern and continental sites and between 200 and 300 g m^{-2} at the northern sites (Fig. 4).

The warming treatment increased the ANPP, especially at the northern sites (the UK and the NL sites) and at the HU site, but when the responses to the unusually hot year of 2003 are included, the overall effect of warming throughout the whole experiment was not significant in the northern sites (see Figs 5–8). Drought treatment reduced the ANPP at the NL, HU, IT, and SP sites, but again, after taking the whole study period into account using a repeated measures analysis including all years, this reduction was nowhere significant (see Figs 5–8).

The ANPP followed the interannual variation in climate conditions and the effect was different depending on the site as indicated by the significant interaction found for site \times year ($F = 7.28$, $P < 0.001$). However, the

most outstanding change was the decrease in ANPP in 2003 in all sites except for the UK site.

Individual plant growth

Plant growth measured as shoot length was not significantly affected by the warming treatment in the studied species at the HU (*P. alba*) and IT (*Cistus monspeliensis*) sites, or in two of the three dominant species studied in SP, *G. alypum* and *Pinus halepensis*. However, at the SP site, the growth of the other dominant species, *E. multiflora*, was significantly enhanced (30%) by the warming treatment (Fig. 8). There was also a contrasting response to warming at the UK site: *Calluna vulgaris* tended to respond positively to the warming treatment, while *Empetrum nigrum* tended to respond negatively (Fig. 8).

The drought treatment decreased growth in *G. alypum* (34%) and *E. multiflora* (25%) in SP and in *C. monspeliensis* (21%) in IT, but had no significant effect either on *P. alba* at the HU site (Fig. 8) or on the two studied species in the UK (*C. vulgaris* and *E. nigrum*) that, however, also tended to grow less, especially *E. nigrum* (Fig. 8). There were also contrasting responses among the three studied species at the SP site, since the third dominant species in SP, *P. halepensis*, was not significantly affected by the drought treatment (data not shown). Drought decreased plant growth in *Deschampsia flexuosa* in DK, although in that country other more rhizomatous grasses did tend to increase growth in response to drought. Annual growth was significantly dependent not only on species and treatment, but also on the year and precipitation and soil moisture of the year (Figs 7 and 8). Most studied plant species presented significantly higher growth rates in wet years (2002 and 2004) than in dry years (2001 and 2003) (Figs 7 and 8).

Relationships between annual aboveground biomass accumulation and site temperature and soil moisture

Biomass accumulation and litterfall responses to warming and drought followed a gradient from wet/cold to dry/warm climatic environments. The responses to warming were very strongly related to the Gaussen aridity index with the maximum response occurring in the least arid site and with the minimum response in the most arid site (Fig. 9). The responses to the drought treatment were not significantly related to this aridity

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Fig. 5 Changes induced by the warming and drought treatments in the annual plant aboveground biomass accumulation throughout the study period (1999–2005). Bars indicate the standard errors of the mean ($n = 3$ plots). In DK site, there was a heather beetle attack in 1999–2000 (Peñuelas *et al.*, 2004). When significant, the effects of the studied factor or the interaction are depicted in the corresponding panel. An arrow signals the decreases in 2003 in all sites but the UK site. UK, Wales; NL, the Netherlands; DK, Denmark; HU, Hungary; IT, Sardinia (Italy); SP, Catalonia (Spain).

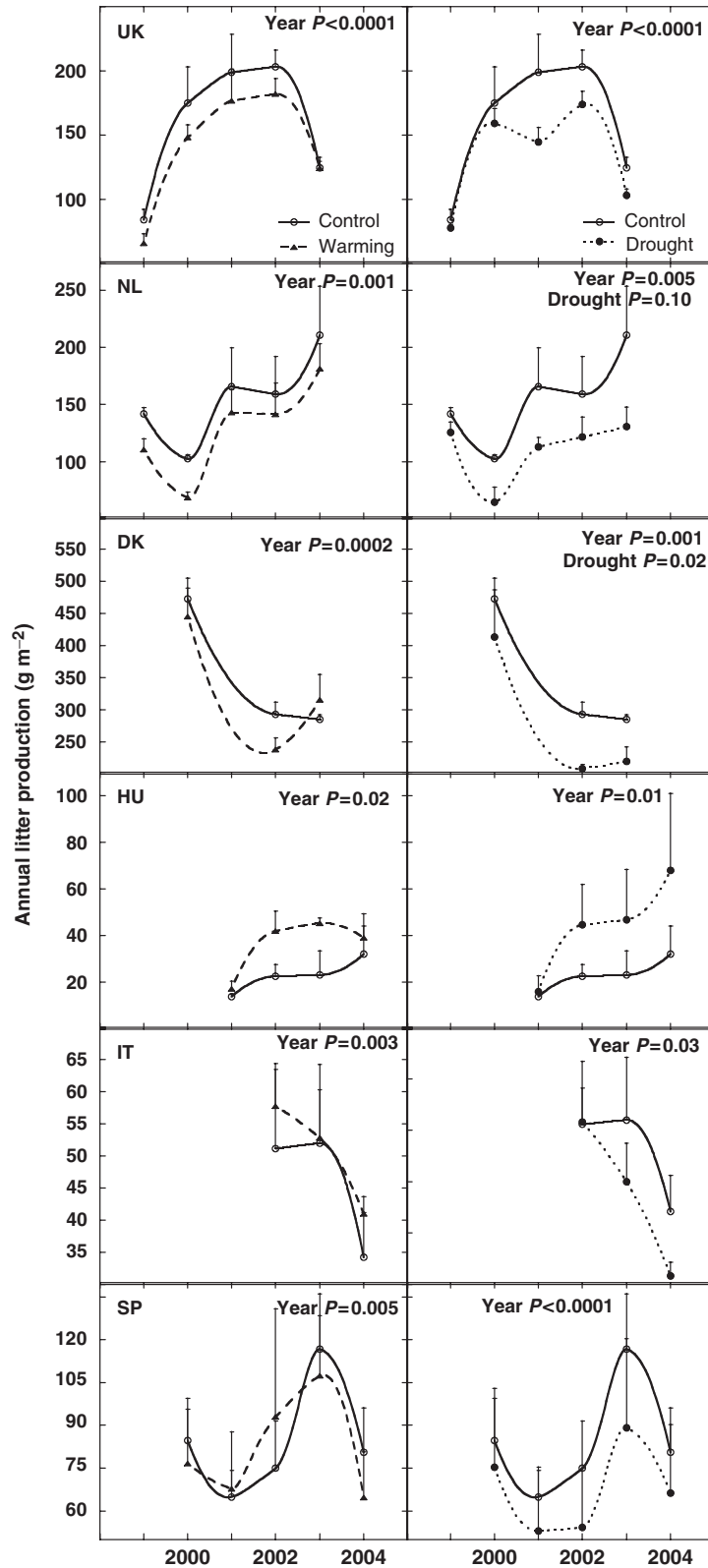


Fig. 6 Changes induced by the warming and drought treatments on amounts of annual litterfall throughout the study period (1999–2005). Bars indicate the standard errors of the mean ($n = 3$ plots). In DK site there was an attack by heather beetles in 1999–2000 (Peñuelas *et al.*, 2004). Whenever significant, the effects of the studied factor or interaction are depicted in the corresponding panel. UK, Wales; NL, the Netherlands; DK, Denmark; HU, Hungary; IT, Sardinia (Italy); SP, Catalonia (Spain).

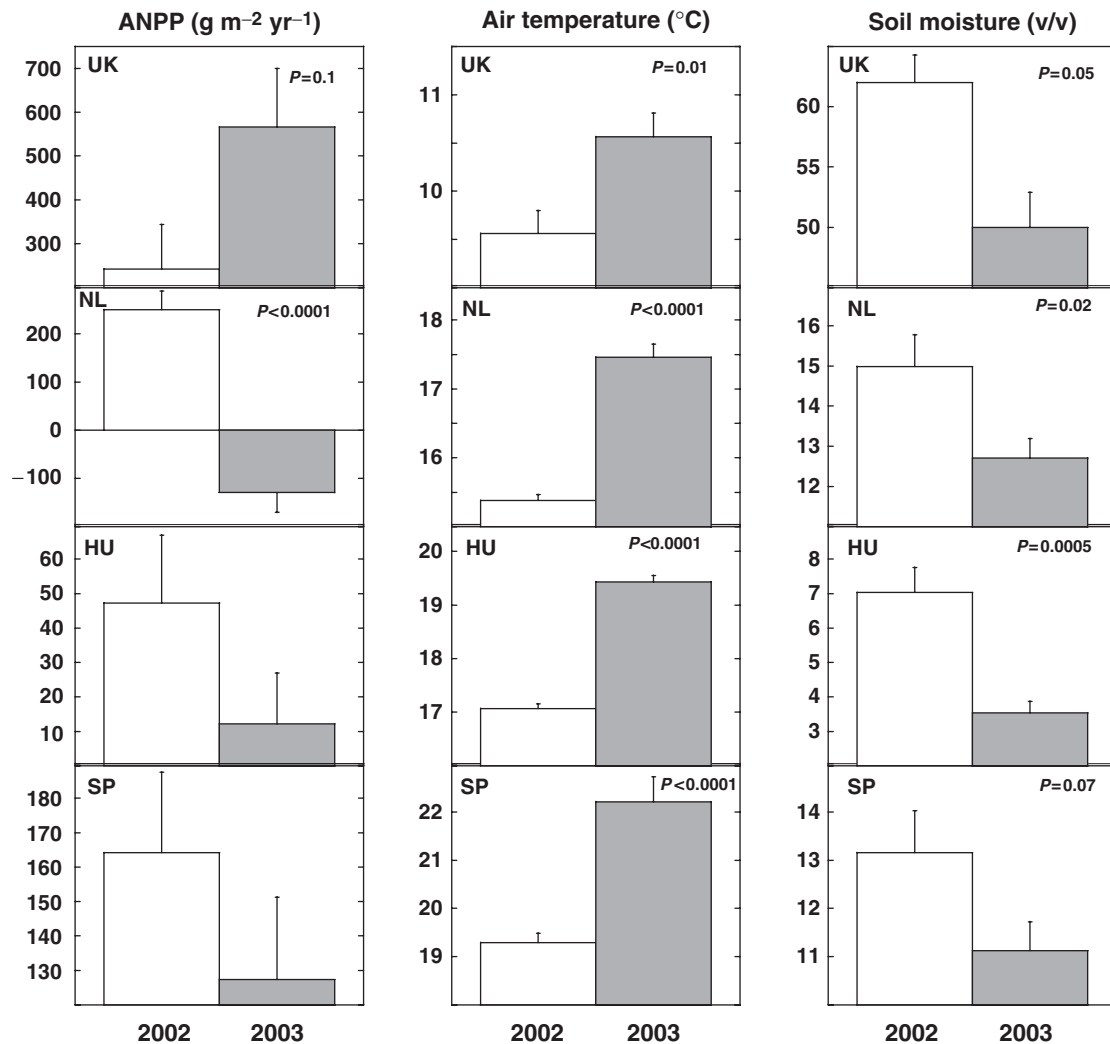


Fig. 7 Annual ANPP (g m^{-2}) and mean temperature and soil moisture during the 3 months previous to sampling (growing season) in a typical year, 2002, and in an extremely hot and dry year, 2003. The DK and IT data are not presented because of the lack of data from 2002. Whenever significant, the P -values of the differences between the 2 years are depicted in the corresponding panel. Bars indicate the standard errors of the mean ($n = 9$ plot means). UK, Wales; NL, the Netherlands; HU, Hungary; SP, Catalonia (Spain); DK, Denmark; IT, Sardinia (Italy); ANPP, aboveground net primary productivity.

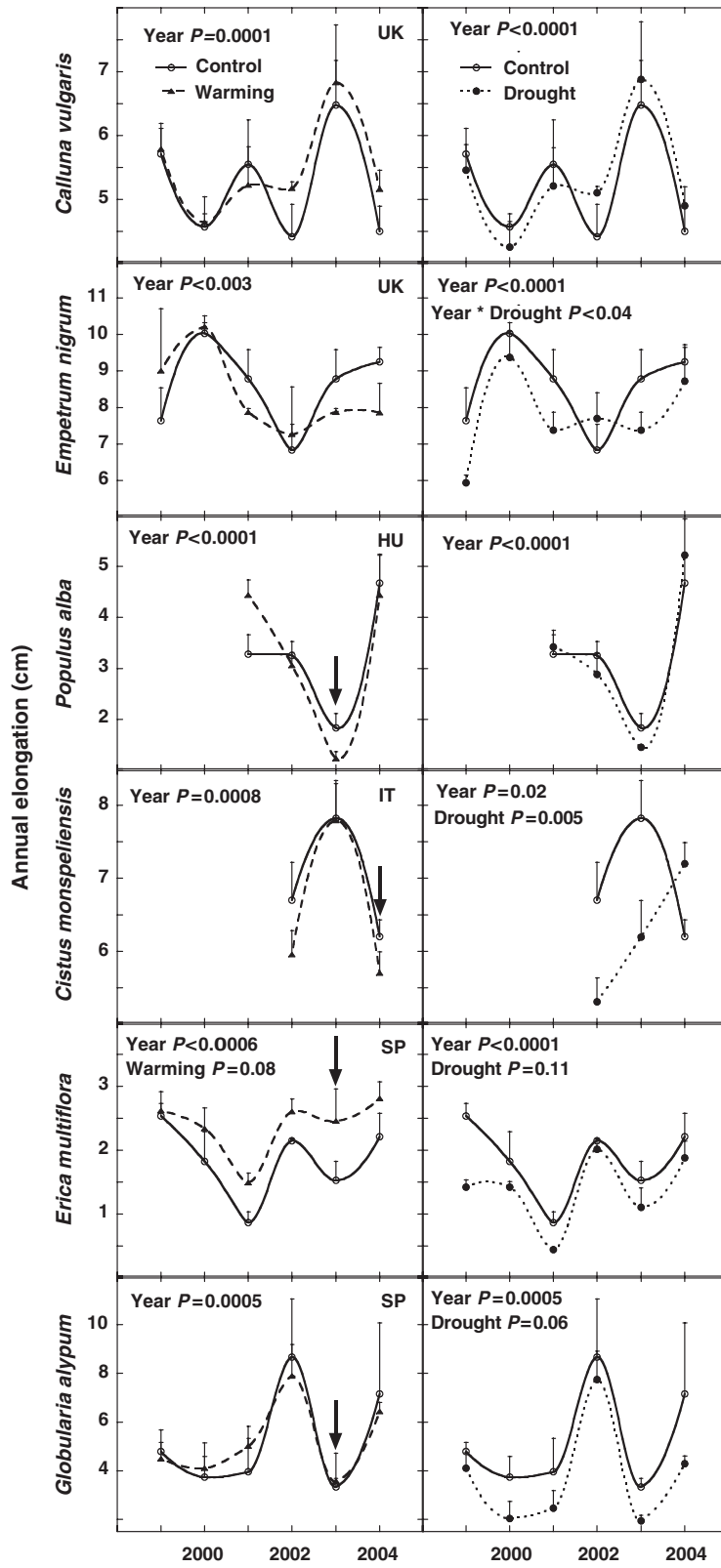
index (Fig. 9), Fig. 10 highlights this gradient by contrasting the annual aboveground biomass accumulation with the temperature and soil moisture changes at the wettest and coldest (least arid) site (the UK) with those recorded at the driest and warmest (most arid) site (SP). The relationship with temperature was positive for annual biomass accumulation at the coldest site, whereas this relationship was negative for annual biomass accumulation at the warmest site (Fig. 10). The correlation with soil moisture was not significant at the wettest site, although annual biomass accumulation was positively related to soil moisture changes at the driest site (Fig. 10). The relationship between biomass accumulation and soil moisture did not significantly differ under the drought or warming treatments. Simi-

larly, there were no significant differences between treatments in the response of biomass accumulation to temperature, except for a slight trend toward lower response of warming plots in the coldest site.

Discussion

The geographical gradient: responses in the wet/cold northern sites, but also in the dry/warm southern sites

Species richness. As a result of moderate warming (ca. 1°C) and drought (on average ca. 19% lower soil moisture) there was a lower increase in species richness in the 7 years study in treated plots than in control plots at the SP site, which had not reached a



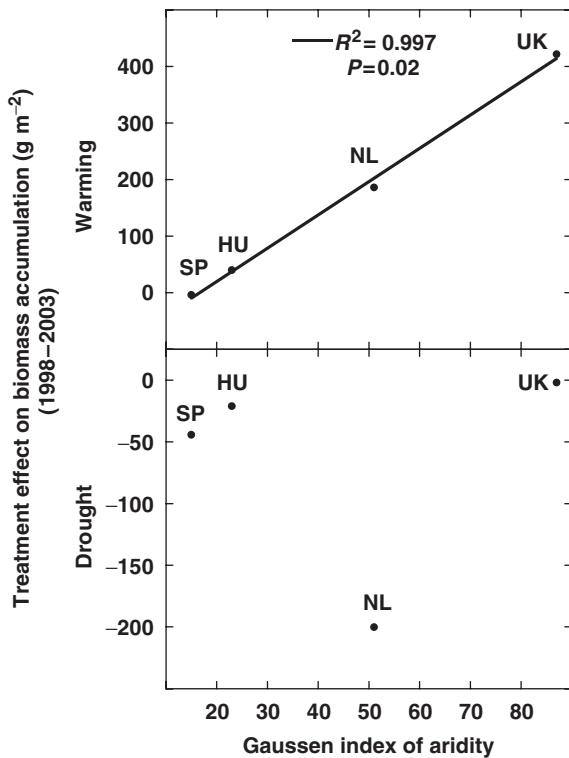


Fig. 9 Relationship between the change of annual aboveground biomass accumulation (g m^{-2}) during the period 1998–2003 in response to warming and drought treatments and the Gaussen index of aridity (precipitation/ $2 \times$ temperature) of each site. Data are from 5 years (1999–2003) for the UK, NL, and SP sites and from 4 years (2001–2004) for the HU site. (DK site was not considered here because there was a heather beetle attack in 1999–2000 (Peñuelas *et al.*, 2004); the IT site was not either considered because we only had 1 year data available). UK, Wales; NL, the Netherlands; DK, Denmark; HU, Hungary; IT, Sardinia (Italy); SP, Catalonia (Spain).

mature successional stage after the 1994 forest fire (5 years before the experiments started). The resulting decrease in species richness agrees with the decrease in seedling recruitment and seedling diversity observed at this SP site (Lloret *et al.*, 2004). This decrease in species richness shows that the climate change predicted for the coming decades will have significant implications for vegetation composition, biodiversity, and structure, especially in plant communities that have not reached a mature successional stage. Such decreases in species richness may also play an important role in

controlling the response of the overall carbon balance in these terrestrial ecosystems. In the other Mediterranean site (IT), where the state of succession was more mature and stable, no significant changes in the species richness occurred as a result of the experimental treatments. In the IT site, the previous major disturbance occurred 10 years before the beginning of the experiment and, as reported by Calvo *et al.* (2002), Mediterranean shrublands generally completely recover within 12 years of a disturbance.

Changes in species composition in response to warming and altered water availability have also been reported in colder ecosystems such as a Rocky Mountain meadow (Harte & Shaw, 1995) and temperate bogs and fens (Weltzin *et al.*, 2003). The results from our study extend species composition findings into the warm and dry Mediterranean zone, which like most warm areas is normally not considered to be temperature sensitive. On the other hand, our findings do agree with species and ecosystem changes in species composition observed in SP over the past 50 years of progressive warming and aridification (Peñuelas *et al.*, 2001; Hodar *et al.*, 2003; Peñuelas & Boada, 2003; Sanz-Elorza *et al.*, 2003; Jump & Peñuelas, 2006).

No significant changes in response to the experimental warming and drought were found in the species richness of the other sites (Fig. 2). The DK and NL sites had thick covers of grass and heather, respectively, with no bare soil available for the establishment of new species and other sites such as those in the UK, HU, and IT were in more mature successional stage as shrublands and, therefore, were less prone to new species recruitment.

This slightly greater response in species richness to warming at the SP site does not necessarily contradict our hypothesis that responses to warming would be greater at colder temperature-limited northern latitudes (Chapin *et al.*, 1995), because the SP site was at a different successional stage and its sensitive communities were still recovering from a major disturbance. However, the response of this warm site highlights the need to re-examine the assumption that sensitivity to warming will not be as great at southern latitudes, in particular wherever successional processes are still at work and where increased evapotranspiration associated to warming is significant. The

Fig. 8 Changes produced by the warming and drought treatments in the annual growth of dominant plant species measured as the increases in shoot length at the HU (*Populus alba*), IT (*Cistus monspeliensis*), and SP (*Erica multiflora* and *Globularia alypum*) sites. Bars indicate the standard errors of the mean ($n = 3$ plot means). Whenever significant, the effects of the studied factor or interaction are depicted in the corresponding panel. An arrow signals the decreases in 2003. In IT, the effects of the 2003 heat and drought were noticed in the growth measured in June 2004, at the end of the 2003–2004 growth period. UK, Wales; HU, Hungary; IT, Sardinia (Italy); SP, Catalonia (Spain).

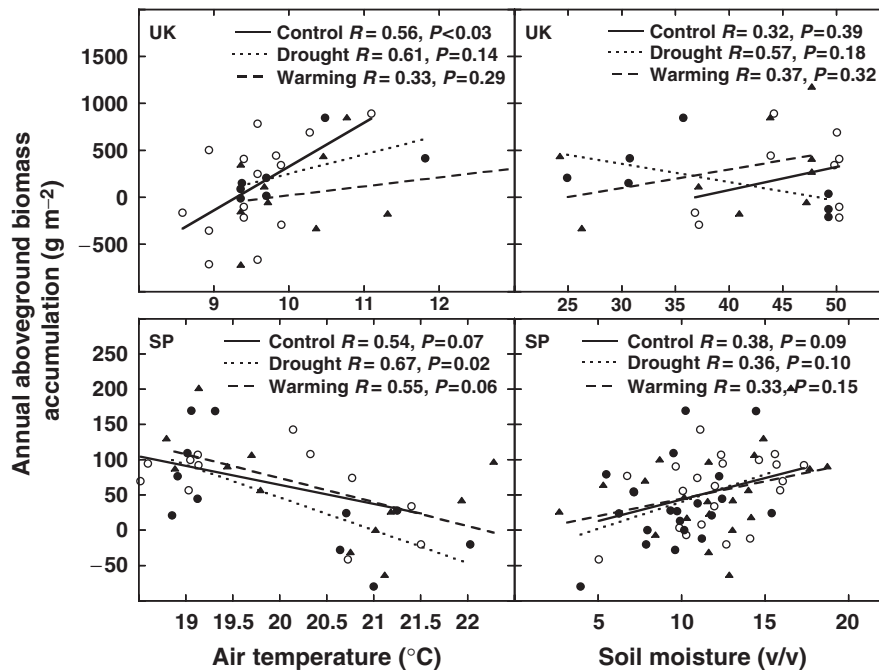


Fig. 10 Relationship between annual aboveground biomass accumulation (g m^{-2}) in each treatment and the air temperature and soil moisture during the 3 months previous to sampling (growing season). Each point represents the data for one plot for 1 year. Data are from 7 years (1999–2005) for the SP site, 5 years (1999–2003) for the UK site temperatures, and 2 years (2002–2003) for the UK site soil moistures. UK, Wales; SP, Catalonia (Spain).

expected sensitivity of these Mediterranean areas to more serious and longer droughts, which could affect natural recovery and recolonization processes, is further confirmed by the decreased species richness in the drought plots at this dry Mediterranean site.

NPP. Trends in plant productivity confirmed the hypotheses that there would be more marked responses to warming at the northern sites (Fig. 9). Plant productivity was significantly affected by interannual climatic variation as the warming treatment tended to increase the total plant biomass at the northern (UK and NL) and continental sites (HU), although overall, and including therefore the hot year of 2003, changes were mostly not statistically significant.

These increases might be a direct result of increased photosynthesis rates (Körner & Larcher, 1988), although this does not seem to be the case here (see Llorens *et al.*, 2004). The direct effect of longer growth seasons (Peñuelas & Filella, 2001; Beier *et al.*, 2004; Prieto, 2007) seems more likely since Northern sites showed greater increases in growing degree-days (Beier *et al.*, 2004). An indirect effect of increased nutrient availability resulting from increased rates of N mineralization (Robinson *et al.*, 1997; Emmett *et al.*, 2004; Schmidt *et al.*, 2004) may also be a contributory factor and has been

previously described in studies of plant growth and productivity in Arctic and sub-Arctic ecosystems that are generally limited by a low availability of N and/or P (Shaver & Chapin, 1995; Jonasson *et al.*, 1999; Schmidt *et al.*, 2002). In these ecosystems plant growth is affected by short-term temperature enhancement, partly due to the direct effects of warming and partly to the indirect effects of increased nutrient mineralization in the warmed soils (Callaghan & Jonasson, 1995). However, the lack of a very obvious and significant response in NPP to warming at the colder sites in our experiment may be related to the age of the *C. vulgaris* plants, which are in a mature phase and therefore not accumulating much new biomass (Watt, 1947). These results also show that since warming did not decrease the total aboveground biomass, there were no overall negative effects of warming on plant growth as a result of increased frost damage in early phenological stages in any of the sites, as has been suggested by other studies (Ögren, 1996).

At the southern sites that are normally water-stressed, there was no general increase in plant productivity as a result of the warming treatment, since warming increases water loss (Beier *et al.*, 2004) and temperatures in these ecosystems are already close to the optimum for photosynthesis and growth (Peñuelas *et al.*, 1998; Larcher, 2000; Shaver *et al.*, 2000). Photosynthetic rates may even decrease due to

overheating in the warmest seasons or microenvironments (Peñuelas *et al.*, 1998; Shaver *et al.*, 2000; Peñuelas & Llusà, 2002; Llorens *et al.*, 2003). Other reasons for the lack of response or a negative plant response to increasing temperature are the concomitant increases in evapotranspiration and decline in soil moisture often associated with warming, and the decreased availability of nutrient resources such as N and P (Rustad *et al.*, 2000; Sardans & Peñuelas, 2004, 2005).

The drought treatment tended to reduce biomass accumulation at the NL, HU, IT, and SP sites, although after taking into consideration the whole study period, this reduction was not significant. In fact, in most southern semiarid areas drought already limits plant productivity (Mitrakos, 1980; Larcher, 2000; Peñuelas *et al.*, 2001; Terradas, 2001), as shown by the low ^{14}C recoveries (Gorissen *et al.*, 2004), photosynthetic rates (Llorens *et al.*, 2004), and standing plant cover and biomass in Mediterranean and continental shrublands (Fig. 4). Both the direct effects due to decreased photosynthetic rates and the indirect effects due to decreased nutrient availability of the drought treatment (Sardans & Peñuelas, 2004; Sardans & Peñuelas, 2007) would tend to lead in the same direction toward decreased plant productivity.

The tendency of the warming treatment to decrease (ca. 15%) the amount of litterfall only at the northern sites may be an effect of the longer leaf life-span found at the temperature-limited northern sites (Prieto, 2007). The drought treatment litterfall decrease, or tendency to decrease, at all sites (ca. 25%) except for the HU site (where the data originating from the dynamic character of the poplar trees were not comparable) was unexpected because drought often encourages leaf fall (Harley *et al.*, 1987; Oliveira & Peñuelas, 2002; Ogaya & Peñuelas, 2006). These decreases might be related to lower precipitation levels diminishing litter production (Simmons *et al.*, 1996). Further monitoring during the coming years is needed to be able to draw reliable conclusions regarding litterfall responses to warming and drought.

Biomass accumulation responses to warming and drought lie along a gradient from wet/cold to dry/warm environments that is highlighted in Figs 9 and 10. Figure 9 shows how aridity limits the response to warming. The response to the warming treatment increased the lower the aridity of the site (it was stronger in sites with high precipitation and cold temperatures). Figure 10 shows the trend toward a positive relationship between biomass accumulation and temperature at the coldest site, a negative relationship between these two factors at the warmest site, and a positive relationship between biomass accumulation and soil moisture in the driest site. Because the relationship between biomass and soil moisture was the same under control,

drought, and warming, soil moisture alone will be a good predictor of biomass accumulation as temperatures increase due to climate change. Similarly, because the relationship between biomass accumulation and temperature was the same under all treatments, interannual temperature variation can be used to predict biomass accumulation response to warming. A slight trend toward lower response of warming plots in the coldest site can indicate a slight acclimation that deserves to be further studied.

Interannual differences. The 2003 heat wave and the decreases in species recruitment and ANPP

Interannual changes in species richness, aboveground plant biomass accumulation, and litterfall occurred at all sites and mirrored interannual variation in climate conditions. The lower number of species detected in 2003 at all sites except the UK site, in line with the especially hot and dry weather conditions that year, was especially notable. There was also a decrease in biomass accumulation at all sites except the UK site in the unusually hot year of 2003. Temperatures at the UK site did not increase as much as at most other sites and this site was the most positively sensitive to warming as was to be expected from it being the coldest site. This finding is also consistent with the fact that the UK site is limited by excess water and, thus drought can have neutral or positive effects (Fig. 7). There was also great interannual variation, with a significant increase in the amount of litterfall in 2003 at the SP and NL sites, contrasting with a decrease at the UK site, in consonance with their respective plant accumulations.

Since severe regional heat waves such as the one that occurred in 2003 may become more frequent in a changing climate (Meehl & Tebaldi, 2004; Schär *et al.*, 2004), the expected future enhancement of plant growth and carbon sequestration resulting from climate warming in temperate ecosystems may not in fact occur, as has been suggested by Ciais *et al.* (2005). In fact, our results show an even stronger decrease in NPP than the 30% reduction in gross primary productivity throughout Europe estimated by a recent study by Ciais *et al.* (2005), measuring ecosystem carbon fluxes, the remotely sensed radiation absorbed by plants, and crop yields at country level. The shrublands at the NL site even presented negative ANPP, contributing thus to positive carbon flux as previously anticipated by models (Cox *et al.*, 2000; Dufresne *et al.*, 2002).

Species-specific growth responses

Our results show different responses to warming and drought not only between years and between sites, but

also between species. Plant growth, measured as shoot length, was not significantly affected by the warming treatment in most studied species at the southern sites. On the other hand, *D. flexuosa* in DK and *C. vulgaris* in DK and UK tended to grow more in the warming plots. At the UK site *C. vulgaris* tended to grow more in the warming plots, whereas *E. nigrum* tended to grow less as expected from its more northerly distribution. Plant growth also increased in one of the dominant species at the SP site, *E. multiflora*, but not in the other dominant species, *G. alypum*. This result, apart from the previous comments on possible effects resulting from different competitive abilities, also provides further evidence of the existence of a cold temperature limitation for plants in the Mediterranean winter (Mittrakos, 1980; Oliveira & Peñuelas, 2001, 2002, 2004) and highlights again that warm southern Mediterranean ecosystems may be more sensitive to warming than expected.

The warming treatment had a significant impact on extreme and seasonal climatic conditions and led to a large reduction in the number of frost days and an extended spring growing season (Beier *et al.*, 2004). The increased growth of some of these species may therefore be a direct result of a small constant temperature increase in annual mean values and/or the indirect effects of warming such as an extended growing season (Prieto, 2007).

The drought treatment, on the other hand, decreased plant growth by 25–35% in the studied species at the SP site and by 21% in *C. monspeliensis* at the IT site. Nevertheless, no decreased plant growth was recorded in the drought resistant tree species *P. halepensis* at the SP site, in *P. alba* at the HU site (as was to be expected, since these poplar shrubs get water support from their 'mother tree' which has deep roots, and usually grows outside the plots), or at the UK site, where plenty of water was available usually in excess. In DK, the dominant grass *D. flexuosa* decreased plant growth by 30–40%, as measured by the number of hits per pin. In contrast, rhizomatous grass species at the same site increased growth.

The species-specific responses to warming at the UK and SP sites or to drought at the SP and IT sites suggest that climate change may translate into changes in the species composition of communities in the near future as a consequence of different competitive abilities.

Ecosystem and community level responses and final remarks

If plant species composition in communities change in response to climate change, ecosystem responses to warming and drought will in turn be affected (Cornelissen *et al.*, 1999), because species composition affects

ecosystem properties such as plant growth rates or litter quantity and quality (and therefore microbial dynamics and litter decomposition), frost hardiness, and drought resistance. Most of these changes are expected to occur over the coming years and decades, although our study shows that they may occur in the space of just a few years as a result of a moderate change in climate. This is shown by the sensitive SP site, still recovering from a fire and in an early stage of succession and recruitment of new species.

This study is also a relatively long-term project, a fact that has enabled us to disregard certain changes such as the often measured increase in vegetative growth after warming in the early years of most experiments (Arft *et al.*, 1999). As well, the length of the study period was sufficient for the complex interactions between environmental factors that limit plant growth to become apparent in the form of marked interannual variations. During the study period severely hot and/or dry years occurred and, given that severe regional heat waves such as those in 2003 may become more frequent in a changing climate (Meehl & Tebaldi, 2004; Schär *et al.*, 2004), the predicted enhancement of plant growth and carbon sequestration in temperate ecosystems in the future as a result of climate warming might in fact not take place, as suggested by our results and by those reported by Ciais *et al.* (2005). As commented above, these shrubs may even turn into carbon sources, contributing thus to positive carbon climate feeding.

On the other hand, the small overall differences in plant productivity in response to warming and drought treatments during the 6 years of study and the small differences between site responses along the climatic gradient suggests that the enhanced C fixation by plants induced by warming during the first 2 years of the experiment (Peñuelas *et al.*, 2004) will not be maintained in the longer term. This lack of maintenance of enhanced carbon fixation may occur as a consequence of extreme heat or drought events or due to progressive nutrient limitation (Hungate *et al.*, 2004; Luo *et al.*, 2004), as our results do not indicate any consistent increase in net N mineralization that might provide the additional inorganic-N required for continued enhanced plant growth. Limitations in other nutrients such as phosphorus (P) may become progressively more important mechanisms controlling acclimation in these areas (Peñuelas *et al.*, 2004).

An additional interesting issue raised by this study is the fact that some of the studied sites, such as those in DK and SP, experienced other disturbances apart from the experimental climate change. The attack by pests at the NL site or the earlier forest fire at the SP site represent common natural occurrences that will interact with climate change, as is also the case for the P

limitation at the NL site, where microbes are very strong competitors for P and, thereby hamper any serious response by plants (Van Meeteren, 2005).

In summary, the magnitude of the response to warming and drought was very dependent on differences between sites, years, and plant species. The differences reported here, those reported in the literature (Shaver *et al.*, 2000; Rustad *et al.*, 2001), and the fact that plant responses seem transient and changeable over time (Arft *et al.*, 1999), illustrate the multiple responses to warming and drought and the complex interactions with other environmental factors that condition plant performance. The net response is still very difficult to predict. The prediction of plant responses to climate change must account for natural variability to avoid overestimation of the importance of warming and unrealistic projections of vegetation change. The prolongation of this study in the following years will help to further clarify some of these interactions and their longer-term effects. Although the overall period responses to warming were very strongly related to the Gaussen aridity index of each site (stronger responses the lower the aridity), the decreases in biodiversity and the increased growth in *E. multiflora* in response to warming at the SP site (the most arid one) challenge the assumption that sensitivity to warming may be lower at more southerly latitudes. Finally, more frequent heat waves and droughts may further preclude predicted increases in plant productivity in response to warming and, instead, may even decrease productivity.

Acknowledgements

We would like to thank all the people involved in the extensive activities of the CLIMOOR and VULCAN projects, which include the running and maintaining of the various treatment plots and recording data. The work was financially supported by the EU (Contracts ENV4-CT97-0694 and EVK2-CT-2000-00094) and the participating research institutes. The CREAM group also received help from the Spanish Government (grants CGL2004-1402/BOS and CGL2006-04025/BOS), the Catalan Government (SGR2005-00312), the European project ALARM (Contract 506675), and the Fundación Banco Bilbao Vizcaya 2004 grant. The Hungarian team received help from the Hungarian Government (grants NKFP 3B-0008/2002) and the Hungarian Scientific Research Fund OTKA (T34790).

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