Contrasting Growth Changes in Two Dominant Species of a Mediterranean Shrubland Submitted to Experimental Drought and Warming

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● *Background and Aims* Climate projections predict drier and warmer conditions in the Mediterranean basin in the next decades. The possibility of such climatic changes modifying the growth of two Mediterranean species, *Erica multiflora* and *Globularia alypum*, which are common components of Mediterranean shrublands, was assessed.
● *Methods* A field experiment was performed from March 1999 to March 2002 to prolong the drought period and to increase the night-time temperature in a Mediterranean shrubland, where *E. multiflora* and *G. alypum* are the dominant species. Annual growth in stem diameter and length of both species was measured and annual stem biomass production was estimated for 1999, 2000 and 2001. Plant seasonal growth was also assessed.
● *Key Results* On average, drought treatment reduced soil moisture 22 %, and warming increased temperature by 0·7–1·6 °C. *Erica multiflora* plants in the drought treatment showed a 46 % lower annual stem elongation than controls. The decrease in water availability also reduced by 31 % the annual stem diameter increment and by 43 % the annual stem elongation of *G. alypum* plants. New shoot growth of *G. alypum* was also strongly reduced. Allometrically estimated biomass production was decreased by drought in both species. Warming treatment produced contrasting effects on the growth patterns of these species. Warmer conditions increased, on average, the stem basal diameter growth of *E. multiflora* plants by 35 %, raising also their estimated stem biomass production. On the contrary, plants of *G. alypum* in the warming treatment showed a 14 % lower annual stem growth in basal diameter and shorter new shoots in spring compared with controls.
● *Conclusions* The results indicate changes in the annual productivity of these Mediterranean shrubs under near future drier and warmer conditions. They also point to alterations in their competitive abilities, which could lead to changes in the species composition of these ecosystems in the long term.   © 2004 Annals of Botany Company

Key words: Biomass, climate change, drought, *Erica multiflora*, *Globularia alypum*, growth, Mediterranean species, warming.

INTRODUCTION

Climate projections predict drier and warmer conditions in the Mediterranean basin in the next decades (Houghton *et al.*, 2001). Responses to such climatic changes may differ among species and cannot be readily generalized, since contrasting effects of simulated climate changes on the ecophysiology of co-occurring species have often been reported (Chapin and Shaver, 1985; Chapin *et al.*, 1995; Day *et al.*, 1999). Hence, it is essential to improve our knowledge on the response of the different Mediterranean species to drier and warmer conditions to be able to predict the impact of climate change on Mediterranean ecosystems. Specifically, a proper understanding of how decreases in water availability and increases in temperature might affect the growth patterns of Mediterranean species will allow more reliable climate change scenarios of ecosystem functioning to be developed.

Water is the resource most often limiting plant growth in the Mediterranean-climate ecosystems (e.g. Mayor and Rodà, 1994; Borghetti *et al.*, 1998; Royce and Barbour, 2001; Ogaya *et al.*, 2003). Water scarcity may affect plant growth through effects on photosynthetic rates that can be direct, mostly as a consequence of stomatal closure

(for reviews, see Chaves, 1991; Yordanov *et al.*, 2000), or indirect, mostly because of reduced nutrient supply to the roots (Chapin, 1980). In addition, water stress may result in accelerated leaf senescence and, in consequence, after a period of water stress, even if gas exchange rates are re-established, whole-plant growth may be reduced due to a decrease in the leaf area per unit of dry weight (leaf area ratio, LAR) (Pereira, 1995).

Temperature may influence plant growth through direct effects on metabolic rates, including photosynthesis, respiration, nutrient and water uptake, and resource utilization. Temperature is also a key modifier of ontogenetic development rate (Morison and Lawlor, 1999) and thus, it has been found that warmer conditions accelerate organ initiation and expansion rates (Yoshie and Fukuda, 1994; Chapin and Shaver, 1996; Morison and Lawlor, 1999). Moreover, since temperature is an important factor controlling the phenology of plants, climatic warming is likely to affect the timing of the onset and cessation of growth (Kramer, 1995). Indeed, studies of phenological time series have showed a lengthening of the growing season over the last century in North America and Europe (e.g. Menzel and Fabian, 1999; Menzel, 2000; Schwartz and Reiter, 2000; Peñuelas and Filella, 2001), and particularly in the Mediterranean basin (Peñuelas *et al.*, 2002), as spring events have advanced and autumn events have been delayed

(Menzel, 2000; Peñuelas *et al*., 2002). In addition, plant growth might be affected indirectly by temperature effects on decomposition of soil organic matter, mineralization of soil nutrients and soil moisture (Chapin *et al*., 1995; Jarvis and Linder, 2000; Kirschbaum, 2000). Because evapotranspiration rates are positively related to temperature, increased temperatures are likely to be associated with increased rates of water loss (Kirschbaum, 2000; Lloyd and Fastie, 2002). Therefore, if temperature warms without a compensating increase in precipitation, plants may become increasingly water-stressed, which could lead to decreases in growth rate in water-limited ecosystems (Kirschbaum, 2000; Lloyd and Fastie, 2002).

Different responses of co-occurring species to climate change may alter their competitive interactions and lead to changes in the species composition of ecosystems. Hence, the present study deals with the effects of extended summer drought or night-time warming on the annual and seasonal growth of two co-occurring shrubs, *Erica multiflora* and *Globularia alypum*, which are common species of the Mediterranean shrublands. Evergreen shrubland is an important and widespread vegetation type throughout the Mediterranean region. The shrubs do provide substantial cover in these otherwise sparsely vegetated landscapes, thus controlling runoff and soil erosion, and have become important grazing grounds for local pastoral animals. Climatic changes may have particular strong effects on these ecosystems, which are already subjected to other stresses such as drought, intensive grazing or frequent fires. A previous study suggested a differential effect of drier conditions on the growth of these two Mediterranean species, since, although both species showed lower shoot water potentials, transpiration rates and stomatal conductances under our drought treatment, only *E. multiflora* plants had lower leaf net photosynthetic rates (Llorens *et al*., 2003*b*). Even though no significant effect of warmer conditions on the photosynthetic performance of these two species was found, this does not preclude an effect of warming on growth. It has been established that processes that are integrated at annual time steps (as is growth) provide insight into longer term responses of vegetation to environmental changes and thus, are more useful than instantaneous physiological measurements (e.g. gas exchange rates) in predicting decadal vegetation changes (Chapin and Shaver, 1996).

In the present study the aim was to assess whether near future drier or warmer conditions could (*a*) modify the annual or seasonal growth patterns of the two studied species, and (*b*) affect differently each species which, thus, could lead to a change in their competitive balance in these ecosystems. To address these issues, a field experiment was performed using a new non-intrusive technique to experimentally dry or warm a Mediterranean shrubland (Beier *et al*., 2004).

MATERIALS AND METHODS

The study site and species description

The study was carried out in a dry shrubland (Rosmarino-Ericion) at the Garraf Natural Park, Barcelona, noth-east Spain (41°18′N, 1°49′E), at 210 m a.s.l. and on a south-south-east slope (13°). The climate is typically Mediterranean. The site, which is located on terraces of abandoned vineyards, suffered big fires in the summers of 1982 and 1994. The soil is a petrocalcic calcixerept (Soil Survey Staff, 1998), thin (12–37 cm), with a loamy texture and abundant calcareous nodules. Currently the regenerating vegetation covers 50–60 % with a maximum height of 70 cm. The dominant species at the study site, *Erica multiflora* L. (Ericaceae) and *Globularia alypum* L. (Globulariaceae), are evergreen, sclerophyllous shrubs that typically occur on basic soils of the western Mediterranean Basin, where they are common components of the coastal shrubland. Both species resprout from underground organs after above-ground biomass removal. Vegetative growth occurs twice a year: in spring (from March to June) and autumn (from September to November). Flowering starts in August–September.

Experimental system

Two types of climatic manipulations were carried out on the study site, using automatically sliding curtains (approx. 20 cm above vegetation maximum height) (Beier *et al*., 2004):

(1) Extended summer drought was induced by covering the natural vegetation and soil with transparent and water-proof plastic curtains during all rain events over the two growing seasons, from March–April to July–August and from September–October to December–January. During the period when the drought treatment was working, the rain sensors activated the curtains to cover plants and soil whenever it rained and removed the curtains when the rain stopped.

(2) Passive night-time warming was achieved by covering the vegetation and soil during the night by aluminium curtains. Solar energy is accumulated in the ecosystem during the day and a fraction of the energy is re-radiated back to the atmosphere at night as long-wave infrared radiation. The covering of the ecosystem with the curtains at night reduced the loss of infrared radiation, simulating the mechanism of global warming due to the accumulation of greenhouse gases. The coverage of the study plots was activated automatically according to preset light (<5 μmol m^{-2} s^{-1}). This treatment was started on 16 March 1999 and continued throughout the study, except during three periods (August 1999, January 2000 and September–October 2001), when the treatment was stopped for calibration of system effects or due to mechanical problems. The curtains were automatically removed during night-time rain events to avoid excluding precipitation.

Nine plots of 20 m^2 (4 × 5 m) were established in the study site: three untreated controls, three warming and three drought plots. Plots were organized in three blocks (each block with one control, one drought and one warming plot). Control plots had similar scaffolding to warming and drought plots, but with no curtain. All the study plots were open around the edges. The outer 0·5 m of each study plot

was considered a buffer zone and all the measurements were conducted in the central 12 m² area.

Environmental data

Precipitation was registered at the study site with a standard rain gauge. Soil moisture was measured every 1–2 weeks throughout the study period using Time Domain Reflectometry. At each sampling date, volumetric water content at 0–15 cm was estimated on three fixed sampling points per plot using a cable tester (1502B, Tektronix, Beaverton, OR, USA). Air (20 cm above ground) and soil temperatures (2 and 10 cm depth) were obtained by means of temperature sensors RTD Pt100 1/3 DIN (Desin Instruments, Barcelona, Spain) located in open areas of the three plots (control, drought and warming) of one block. Sensors were always protected against solar radiation. Temperatures were measured every 10 min, the average of three measurements of each sensor being recorded.

Plant annual growth

Before treatment applications, five to seven living stems on each of four or five plants of *E. multiflora* and *G. alypum* were tagged in each plot. In total, 235 stems of *E. multiflora* and 268 of *G. alypum* were labelled. Basal diameters and maximum lengths of the tagged stems were measured in winter each year from 1999 to 2002. To minimize the impact of noncircular stem cross-sections, stem diameter was calculated as the mean of two perpendicular measurements taken at the stem base with a digital caliper to the nearest 0·01 mm. To allow re-measuring, a line was painted with a permanent marker on the exact point of the stem where the diameter was measured. Maximum stem length was assessed by measuring the distance from the stem base to the more distant point at the end of the longest branch. Annual stem growth was calculated as the difference between consecutive winter measurements.

Plant seasonal growth

Whereas stem growth of *E. multiflora* is mainly apical, lateral shoot growth may account for a large proportion of stem growth of *G. alypum*. For this reason, different parameters were used to assess the seasonal stem growth of these two species. In *E. multiflora*, the maximum stem length was used to evaluate seasonal growth, whereas in *G. alypum* the number and length of all the new shoots of each tagged stem were measured. The total shoot growth per stem of *G. alypum* was calculated as the sum of the length of all the new shoots. Seasonal growth was calculated as the difference between consecutive non-growing season (winter and summer) measurements.

Shoot elongation rates

At the beginning of the experiment three shoots from three different stems of five plants of each species in each plot were labelled. Thus, 15 shoots of each species

were tagged in each plot, 135 in total per species. At the beginning of May 2000 the spring length of these shoots was measured and the measurements after 1 month were repeated. The shoot elongation rate was calculated as: (final length – initial length)/number of days.

Biomass allometric relationships

Allometric relationships between stem biomass (dry weight) and stem diameter or length were calculated for both species, using plants collected from the surrounding area outside the plots. Total stem biomass was measured after drying the plant material in an oven at 70 °C until constant weight. Since multiple stepwise regression analysis showed that both stem diameter and stem length explained a significant part of the variability in stem biomass, allometric equations including both variables were used to estimate the annual stem biomass increments of the tagged stems of each species for 1999, 2000 and 2001.

Environmental influence on plant growth

The influence of soil moisture on annual stem diameter growth of both species in the different treatments was analysed by means of Pearson correlations using the annual means per plot of 2000 and 2001 (*n* = 6 for each treatment). Data from 1999 were not used because no soil moisture records were available until mid-March.

Leaf fall

The leaf fall of four to eight plants of *E. multiflora* and nine to 12 plants of *G. alypum* per plot was monitored during 2000. Plant litterfall was collected bimonthly by means of open collectors (4·4 cm of diameter) located under each selected plant. Samples were dried to constant weight and afterwards leaves were separated and weighted.

Statistical analyses

Statistical analyses were performed by means of repeated-measures analysis of variance (ANOVAR, GLM procedures in SPSS 10·0·6) with the initial stem diameter, length or biomass as a covariate. To compare annual stem growth between the two species or between years or seasons for each species, only control plants were used. In the analyses of treatment effects, the factor 'block' was included to assess whether treatment effects were homogeneous among the blocks. However, neither the effect of block nor the interaction between block and treatment were significant. To test the effect of treatments on seasonal growth parameters, ANOVARs were performed for each species for spring and autumn separately. Data on stem length and biomass of both species and on length, number and total growth of *G. alypum* shoots were log transformed to achieve normality. To analyse the effect of treatments on shoot relative growth rates and leaf fall of each species, ANOVAs with treatment and block as factors were performed. Drought and warming treatments were always compared with control treatment separately. In all the analyses, means per plant were used.
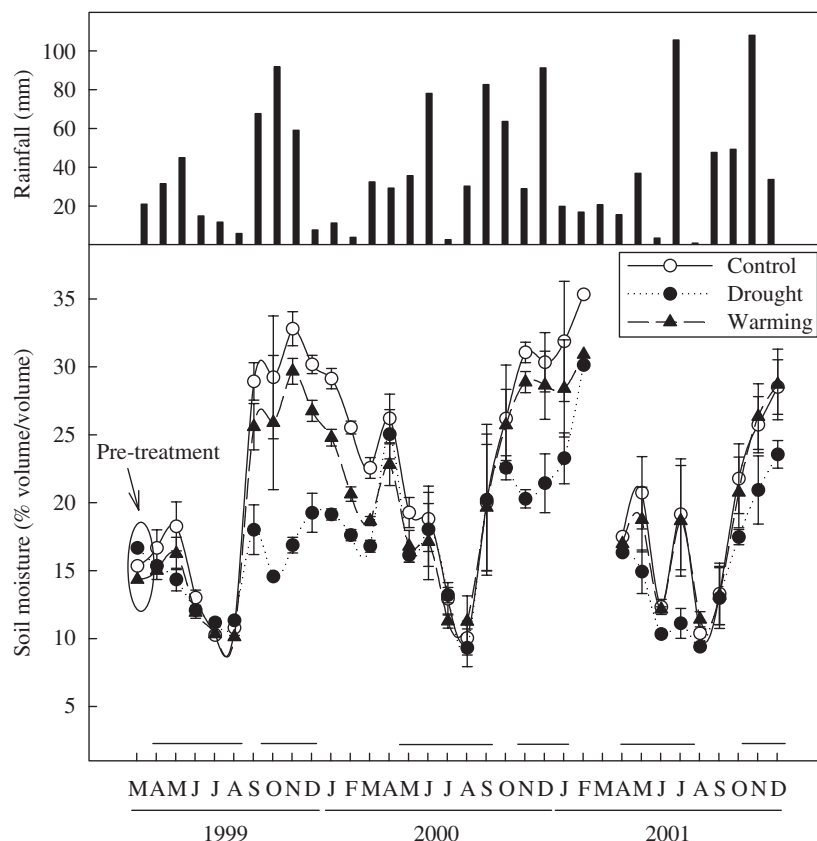
FIG. 1. Monthly rainfall (mm) and mean soil moisture (% volume/volume) of control, drought and warming treatments throughout the study period. Error bars indicate the standard error of the mean ($n = 2–5$ d; values are averages of three plots). Lines above the months indicate the periods when drought treatment was acting. Data partly derived from Llorens *et al.* (2003*b*).

RESULTS

Environmental data

Total annual rainfall was 420, 489 and 458 mm in 1999, 2000 and 2001, respectively. Drought treatment reduced the soil moisture 22 % on average throughout the study period (Fig. 1). The maximum reductions occurred in autumn (up to 50 % in October and November 1999). Warming treatment had a slight effect on soil moisture, reducing it on average 8 % throughout the study period (Fig. 1).

Mean annual air temperatures were slightly lower in 1999 and 2000 (13·8 °C both years) than in 2001 (14·0 °C). Warming treatment increased minimum temperatures on average 0·7 °C in the air, 1·6 °C at 2 cm depth and 1·1 °C at 10 cm depth. The reduced heat loss in the warming plots at night also increased the diurnal air and soil temperatures, with a maximum after sunrise and a minimum in the late afternoon (Fig. 2).

Annual stem growth in basal diameter and length

Control plants of *E. multiflora* showed significantly lower annual stem growth in basal diameter ($F_{1,21} = 11·1$, $P = 0·003$) and length ($F_{1,22} = 15·8$, $P = 0·001$) than control plants of *G. alypum* throughout the study period (Fig. 3).

Although drought did not affect significantly the overall annual stem diameter growth of *E. multiflora,* plants of this species had a 46 % lower annual stem elongation in the drought plots compared with controls throughout the study period ($F_{1,22} = 13·5$, $P = 0·001$). *Globularia alypum* plants showed overall reductions of 31 % and 43 % in their annual stem diameter growth ($F_{1,21} = 9·7$, $P = 0·005$) and elongation ($F_{1,23} = 9·2$, $P = 0·006$), respectively, under drier conditions (Fig. 3).

In the warming treatment, annual stem diameter growth was 35 % higher overall in *E. multiflora* plants ($F_{1,22} = 7·1$, $P = 0·01$) and a 14 % lower in *G. alypum* plants ($F_{1,22} = 6·7$, $P = 0·02$) compared with controls. Warming did not affect significantly the annual stem elongation of these species (Fig. 3).

Seasonal stem elongation of E. multiflora plants

Control plants of *E. multiflora* showed higher stem elongation in spring than in autumn ($F_{1,25} = 46·3$, $P < 0·001$) (Fig. 4). Drought reduced significantly the stem elongation of *E. multiflora* plants in spring ($F_{1,22} = 9·9$, $P = 0·005$), but not in autumn. Warming had no significant effect on the seasonal stem elongation of *E. multiflora* (Fig. 4).

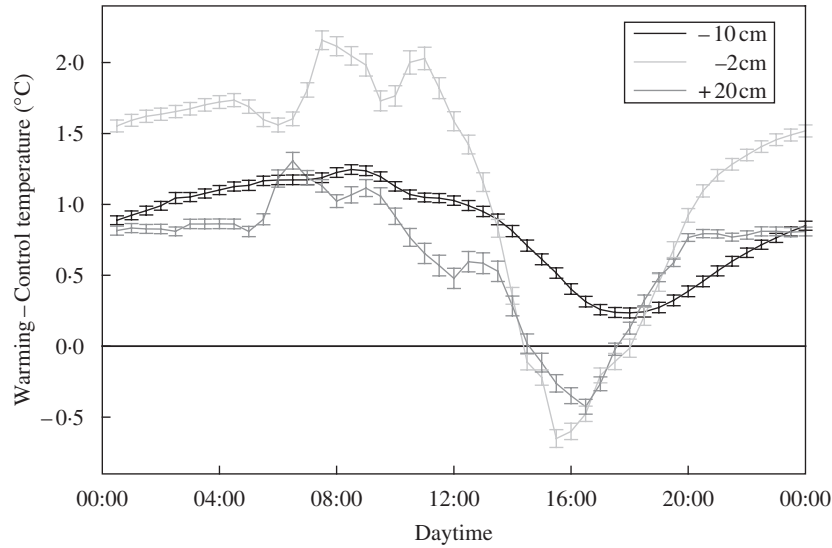F I G . 2. Annual averages of air (20 cm above ground) and soil (2 and 10 cm depth) temperature (°C) differences between warming and control plots (measured in one of the blocks from April 2000 to April 2001). Error bars indicate the standard error of the mean ($n = 365$). Data partly derived from Llorens *et al.* (2003*b*).
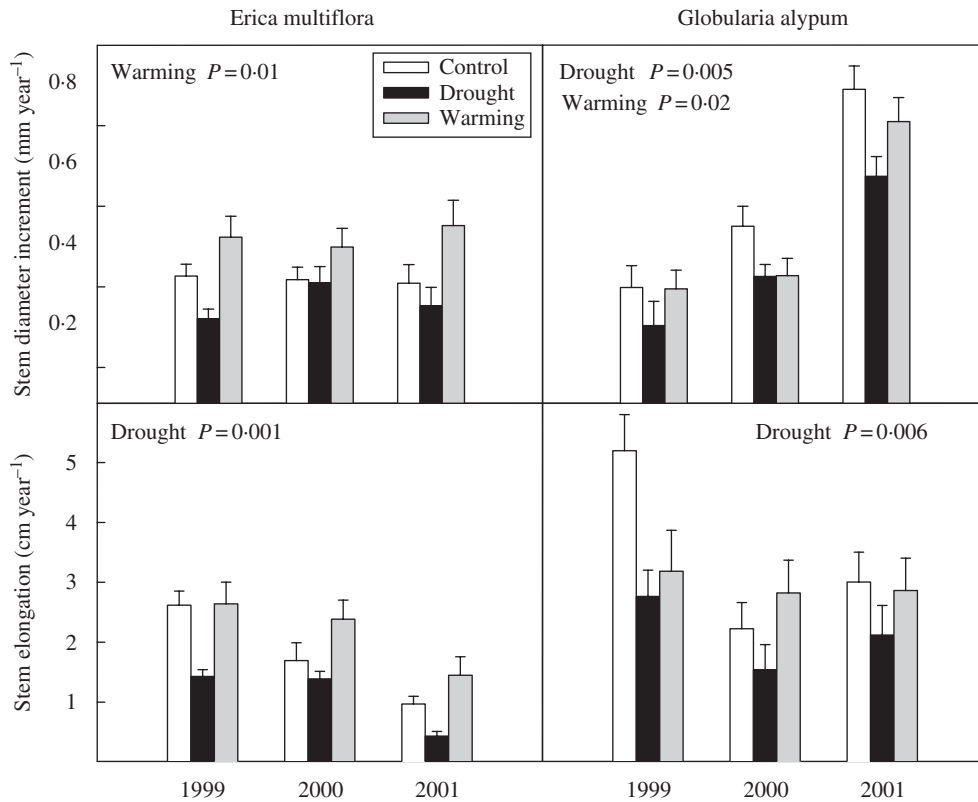

F I G . 3. Diameter and length increment of *E. multiflora* and *G. alypum* stems in 1999, 2000 and 2001 for control, drought and warming plants. Overall treatment effects are depicted when significant. Error bars indicate the standard error of the mean ($n = 14$–16).

Seasonal shoot growth of G. alypum *plants*

Mean length and number of new shoots per stem and, thus, total new shoot growth of *G. alypum* was also higher in spring than in autumn ($P < 0.001$ in all the analyses) (Fig. 5).

Drought significantly reduced the mean length ($F_{1,22}$ = 46·6, $P < 0.001$) and number ($F_{1,22}$ = 14·9, $P = 0.001$) of *G. alypum* new shoots throughout the study period. However, whereas drought effects on the length of the new
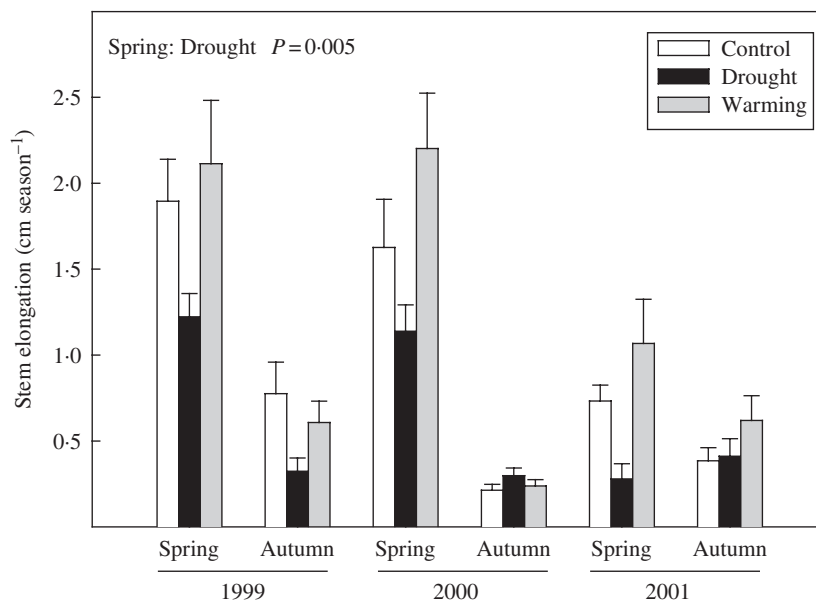
FIG. 4. Stem elongation of *E. multiflora* in spring and autumn of 1999, 2000 and 2001 for control, drought and warming plants. Effects of treatments in spring and/or autumn are depicted when significant. Error bars indicate the standard error of the mean ($n = 14$–15).

shoots of *G. alypum* were significant both in spring ($F_{1,23} = 12\cdot6$, $P = 0\cdot002$) and autumn ($F_{1,22} = 28\cdot4$, $P < 0\cdot001$), drought effects on the number of new shoots were significant only in autumn ($F_{1,22} = 41\cdot1$, $P < 0\cdot001$). Overall, this species showed a lower shoot growth per stem under drier conditions compared with controls ($F_{1,22} = 33\cdot4$, $P < 0\cdot001$), with significant effects in spring ($F_{1,23} = 9\cdot4$, $P = 0\cdot006$) and autumn ($F_{1,22} = 43\cdot7$, $P < 0\cdot001$) (Fig. 5).

In spring, shoots of *G. alypum* were shorter in the warming plots than in controls ($F_{1,22} = 7\cdot0$, $P = 0\cdot01$) (Fig. 5).

Shoot elongation rates in spring 2000

Drought did not affect significantly the elongation rates of *E. multiflora* and *G. alypum* new shoots. In contrast, shoot elongation rates of *E. multiflora* were slightly higher under warming treatment compared with controls ($F_{1,24} = 3\cdot2$, $P = 0\cdot08$) (Fig. 6).

Annual stem biomass increments

Allometric relationships between stem biomass and stem diameter or length were highly significant; the correlation between stem biomass and diameter being stronger than between stem biomass and length (Table 1). As the allometric equations including both variables, stem diameter and length, had slightly stronger correlation coefficients, both variables were used to estimate stem biomass.

Plants of both species showed a lower production of annual stem biomass in the drought plots than in controls throughout the study period ($F_{1,22} = 5\cdot7$, $P = 0\cdot03$ and $F_{1,22} = 5\cdot3$, $P = 0\cdot03$ for *E. multiflora* and *G. alypum*, respectively; Fig. 7). Conversely, warming enhanced the annual stem biomass production of *E. multiflora* plants ($F_{1,22} = 4\cdot1$, $P = 0\cdot05$), whereas it did not significantly affect the estimated annual stem biomass production of *G. alypum* (Fig. 7).

Environmental influence on annual stem diameter growth

Annual stem diameter increments of *E. multiflora* did not significantly correlate with soil moisture. Conversely, annual stem diameter increments of *G. alypum* plants showed positive significant correlations with mean soil moisture throughout the first six months of the year, and mainly with the mean soil moisture of February and March (Fig. 8).

Leaf fall

The treatments did not significantly affect the leaf fall of the two species studied (Table 2).

DISCUSSION

Species comparison

The lower annual stem growth found in control plants of *E. multiflora* compared with control plants of *G. alypum* (Fig. 3) is in accordance with the lower photosynthetic rates found in the former compared with the latter species in a previous study (Llorens *et al.*, 2003*a*). In this earlier study, *E. multiflora* was described as a water conservative species and *G. alypum* as a water spender species. Accordingly, in the present study, no significant dependence on soil moisture of annual stem diameter growth of *E. multiflora* was found, whereas stem diameter increments of *G. alypum* were significantly correlated with volumetric soil water content, the strongest correlations being with the average soil moisture of February and March (Fig. 8). This result suggests that *E. multiflora* probably relies more on the reserves stored during winter to supply seasonal growth in spring, whereas *G. alypum* depends more on concurrent carbon and nutrient uptake.

FIG. 6. Shoot elongation rate (mm day^{-1}) of *E. multiflora* and *G. alypum* in spring 2000 for control, drought and warming plants. (*) indicates marginally significant ($P < 0.1$) differences between treatment and control plants. Error bars indicate the standard error of the mean ($n = 15$).

days or might be due to reserve depletion in summer (Larcher and Thomaser-Thin, 1988), since these shrubs show null or very low net photosynthesis during the hottest season (Llorens *et al.*, 2003*a*). In contrast, mild temperatures allow net photosynthesis and probably accumulation of carbon reserves during winter (Larcher and Thomaser-Thin, 1988; Llorens *et al.*, 2003*a*) and these reserves are likely to support the comparatively strong stem and shoot development observed in spring, as it has also been suggested for other Mediterranean sclerophylls (Oliveira *et al.*, 1994). Resource competition between growth and reproduction in autumn might also contribute to the higher growth observed in spring, since reproductive organs are usually strong sinks for carbohydrate and nitrogen reserves (Bloom *et al.*, 1985).

Drought treatment effects

Drier conditions reduced the annual and seasonal growth of *G. alypum*, as it has been reported for other Mediterranean species (e.g. Borghetti *et al.*, 1998; Lebourgeois *et al.*, 1998; Ogaya *et al.*, 2003). The imposed drought also reduced the annual stem elongation of *E. multiflora* plants, as a consequence of spring rather than autumn decreases (Figs 3 and 4). However, drought did not significantly affect the annual stem diameter growth of *E. multiflora* (Fig. 3), in accordance with the lower dependence on soil moisture of this species compared with *G. alypum* (Fig. 8; Llorens *et al.*, 2003*a*). The observed reductions in stem growth in both species would have decreased their annual stem biomass production (Fig. 7), assuming that drier conditions did not modify the allometric relationship between stem biometry and biomass.

Reductions in growth under the imposed drier conditions might be explained by decreases in leaf net photosynthetic rates. Indeed, leaf net photosynthetic rates of *E. multiflora* plants were 34 % lower in the drought plots than in controls (Llorens *et al.*, 2003*b*). In contrast, drier conditions did not affect significantly the leaf net photosynthetic rates
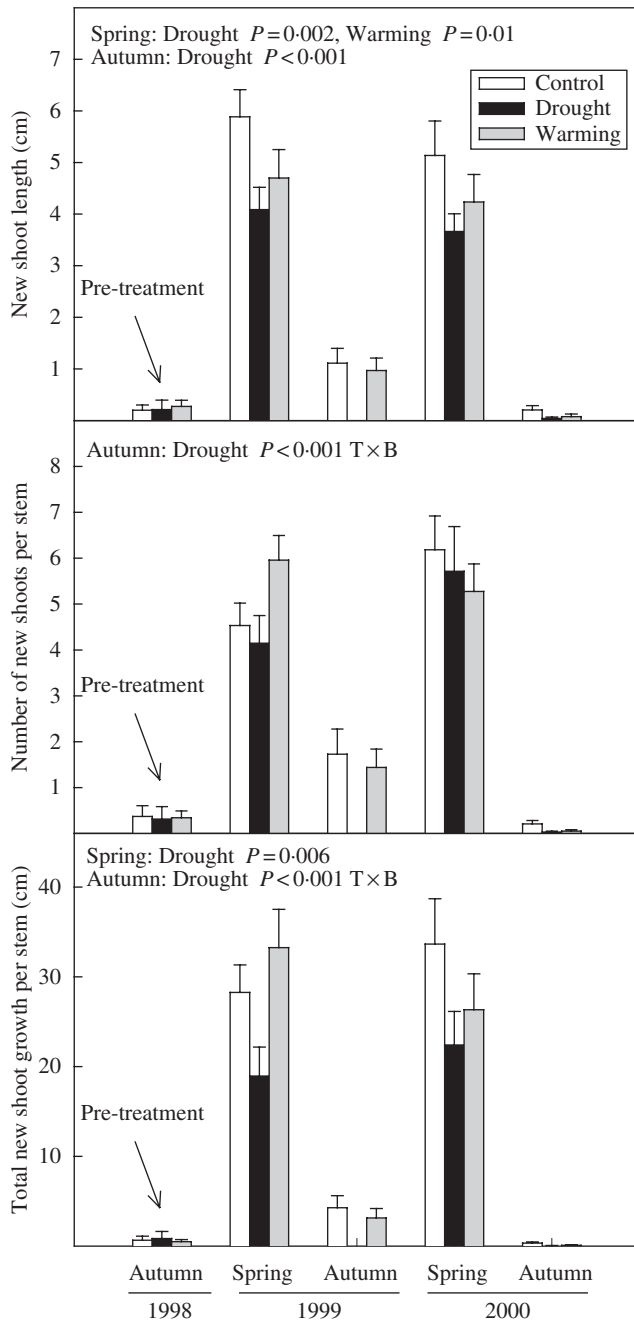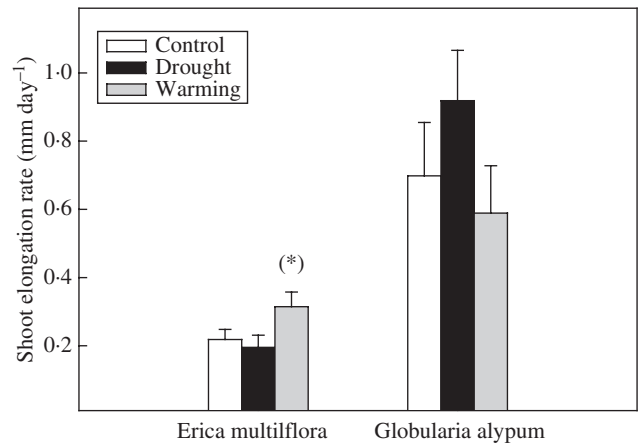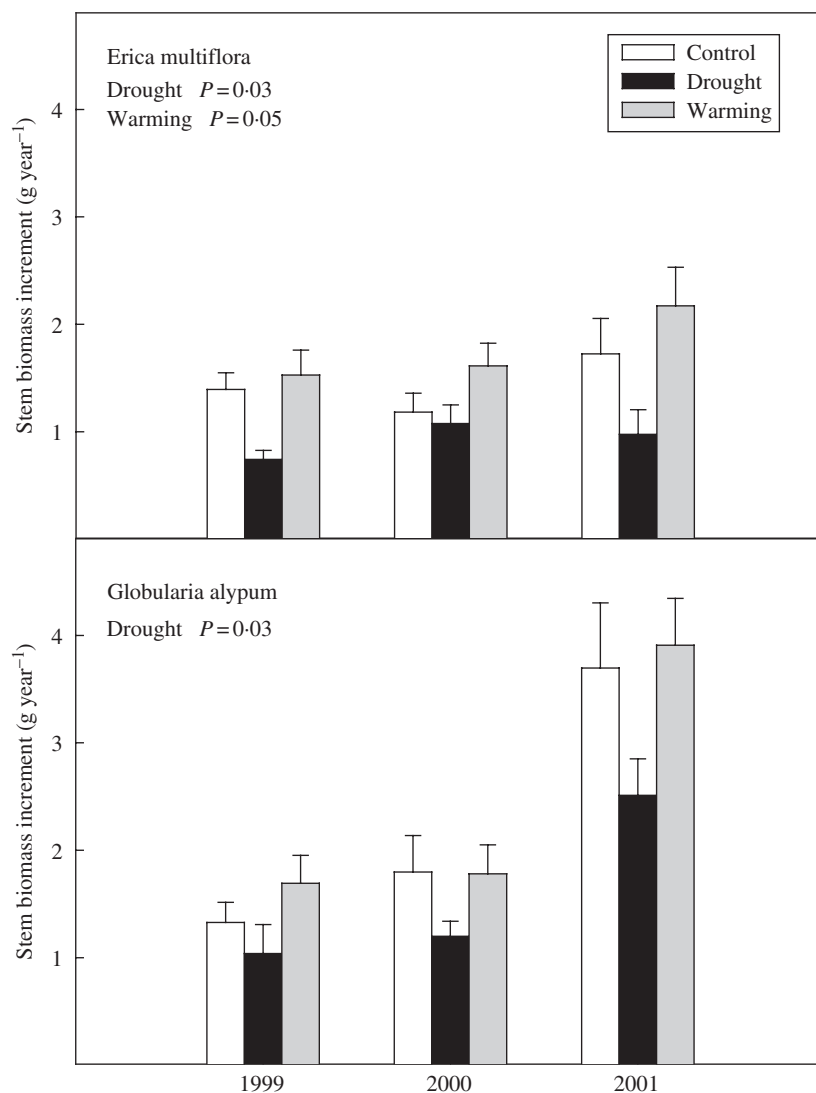

FIG. 5. Mean shoot length, number of shoots and total shoot growth of *G. alypum* in autumn 1998 and spring and autumn of 1999 and 2000 for control, drought and warming plants. Effects of treatments in spring and autumn are depicted when significant. T×B indicates that the interaction between treatment and block was significant. Error bars indicate the standard error of the mean ($n = 14$–15).

Seasonal growth comparison

Seasonal stem growth of the two studied species was higher in spring than in autumn (Figs 4 and 5), despite precipitation and photosynthetic rates of these species being lower in spring (Fig. 1; Llorens *et al.*, 2003*a*). Lower growth in autumn might be a consequence of shorter

TABLE 1. *Allometric relationships between stem biomass (B) and stem diameter (D) and length (L) in* E. multiflora *(n = 40) and* G. alypum *(n = 100)*

	Species	Allometric relationship	r^2	P
Stem diameter	*E. multiflora*	log B = −0·506 + 2·324 log D	0·947	<0·001
	G. alypum	log B = −0·897 + 2·619 log D	0·926	<0·001
Stem length	*E. multiflora*	log B = −4·738 + 2·086 log L	0·839	<0·001
	G. alypum	log B = −5·408 + 2·280 log L	0·640	<0·001
Stem diameter + length	*E. multiflora*	log B = −1·73 + 1·79 log D + 0·57 log L	0·961	<0·001
	G. alypum	log B = −2·11 + 2·23 log D + 0·54 log L	0·942	<0·001

FIG. 7. Stem biomass increment of *E. multiflora* and *G. alypum* in 1999, 2000 and 2001 for control, drought and warming plants. Overall treatment effects are depicted when significant. Error bars indicate the standard error of the mean (*n* = 14–16).

of *G. alypum* plants (Llorens *et al*., 2003*b*). This apparent discrepancy between photosynthesis and growth reflects a complex relationship between these two processes. Besides the large difference in the time scales between instantaneous photosynthetic measurements and long-term growth, growth is controlled by several other processes in addition to carbon acquisition (Xiong *et al*., 2000). For instance, differences in plant leaf area may
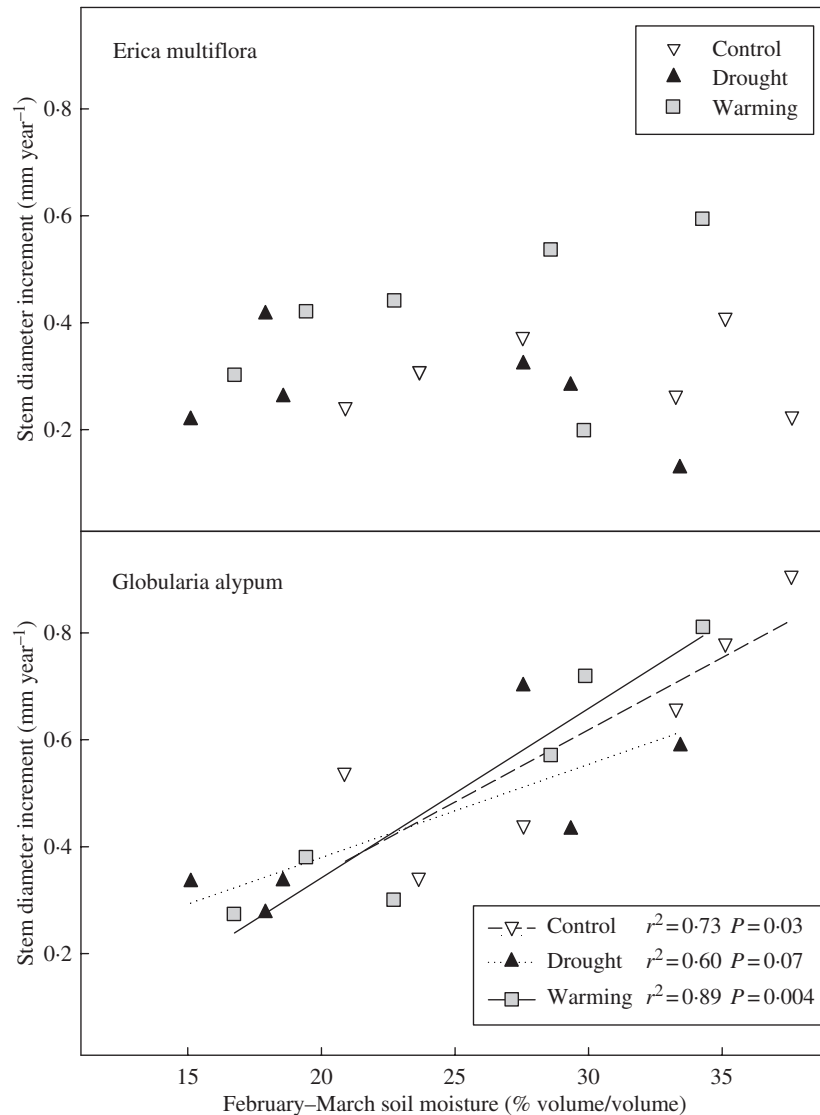
FIG. 8. Annual diameter increment *vs.* mean soil moisture of February and March for control, drought and warming plots in 2000 and 2001 (*n* = 6 for each treatment).

TABLE 2. *Annual leaf litter production (g m^{-2} year^{-1}) below* E. multiflora *and* G. alypum *plants in 2000 for control, drought and warming treatments*

	Control	Drought	Warming
E. multiflora (*n* = 19–23)	141·8 ± 11·4	145·7 ± 14·6	118·6 ± 12·3
G. alypum (*n* = 30–33)	94·4 ± 8·6	93·7 ± 9·4	92·0 ± 5·1

Values are means ± standard errors.

change growth rates without important changes in photosynthetic rates (Pereira, 1995). Since it has been reported that water stress may result in accelerated leaf senescence (Pereira, 1995), a greater leaf fall in *G. alypum* plants in the drought treatment, might result in a lower total leaf area and, thus, might explain the observed reduction in growth without any change in leaf net photosynthetic rates. However, no significant effect of the present drought treatment was found on the annual leaf fall of *G. alypum* plants in 2000 (Table 2). Drought-induced limitation in growth of *G. alypum* does not either seem to be due to reduced N or P acquisition associated with water shortage, since it had previously been found that N and P foliar concentrations tended to increase in *G. alypum* plants under drought treatment (Peñuelas *et al.*, 2004). Alternately, a greater carbon allocation to roots in droughted plants of *G. alypum* might explain a lower carbon investment on above-ground growth in this species. Further more detailed studies on gas exchange, growth patterns and carbon allocation are warranted to disentangle this apparent contradiction between growth decrease and unchanged photosynthetic rates.

Warming treatment effects

Warming produced contrasting effects on the annual stem diameter growth of these species. While warming increased the annual stem diameter growth of *E. multiflora* by 35 % on average, it decreased the annual stem diameter growth of *G. alypum* by 14 % over the whole study period (Fig. 3). Assuming no changes in carbon allocation patterns, an approx. 1 °C increase in temperature would enhance annual stem biomass production of *E. multiflora*, but it would not affect *G. alypum* (Fig. 7). Other studies have also reported contrasting effects of warming on the growth patterns of co-occurring species (e.g. Chapin and Shaver, 1985, 1996; Day *et al.*, 1999; Weltzin *et al.*, 2000).

Positive growth responses to temperature increases have often been reported (e.g. Coleman and Bazzaz, 1992; Graglia *et al.*, 1997; Arft *et al.*, 1999; Jarvis and Linder, 2000; Ro *et al.*, 2001; Theurillat and Guisan, 2001), although most of warming experiments have been performed in cool and moist regions. Enhanced diameter growth of *E. multiflora* plants in warming plots might result from higher relative growth rates (RGR) or a longer growing season. Indeed, it was found that plants of *E. multiflora* in the warming treatment showed slightly higher shoot elongation rates than controls (Fig. 6), as has also been reported for other shrub species in experimentally heated plots in a Rocky Mountain meadow (Harte and Shaw, 1995). Since there were no significant differences in leaf net photosynthetic rates or specific leaf area (SLA) between warming and control plants of *E. multiflora* (Llorens *et al.*, 2003*b*), the observed higher shoot elongation rates in warming plants compared with controls could be the result of a greater biomass allocation to leaves (Xiong *et al.*, 2000). However, warming did not modify significantly the relationship between stem length and diameter of this species (data not shown), which suggests that there were no significant changes in biomass allocation between leaves and woody tissues. A lengthening of the growing season might also have contributed to the observed higher annual stem growth of *E. multiflora* plants under warmer conditions. In fact, it is predicted that the onset of the spring growing season will advance by up to 6 d per 1 °C increase in winter air temperature (Menzel and Fabian, 1999), which is similar to the temperature rise achieved in the present warming treatment. Peñuelas *et al.* (2002) reported that leaves of deciduous species unfold on average 16 d earlier and fall 13 d later in a nearby area after a temperature increase of 1·4 °C over 49 years.

The reduction by warming of the annual diameter growth of *G. alypum* plants cannot be explained by changes in leaf gas exchange rates, SLA or leaf fall, since no significant effect of our warming treatment was found on these parameters (Llorens *et al.*, 2003*b*; Table 2). Decreases in growth with increasing temperature have been related to increased heat damage or temperature-induced drought stress (Barber *et al.*, 2000; Kirschbaum, 2000; Lloyd and Fastie, 2002). In our study, warming treatment reduced the soil moisture on average 8 % compared with control treatment. Particularly, soil moisture was significantly lower in the warming plots compared with controls during February and March 2000.

Accordingly, the highest reduction in diameter increment of *G. alypum* plants under warming was observed in 2000. Thus, it is suggested that the higher sensitivity to soil moisture found in *G. alypum* compared to *E. multiflora* might explain the reduction in basal diameter growth of *G. alypum* in the warming plots. Although increases in dark respiration of *G. alypum* plants in the warming treatment might have contributed to their reduction in growth (Pereira, 1995), several studies have concluded that the ratio of respiration to photosynthesis does not deviate significantly from constancy over a broad range of temperatures (e.g. Gifford, 1994, 1995; Waring *et al.*, 1998).

The present warming treatment also reduced the mean length of new shoots of *G. alypum* plants in spring (Fig. 5). Shoot length of *G. alypum* plants was, in general, more sensitive to our experimental changes of climatic conditions than the number of shoots. Pre-formation of buds in the previous spring could explain why the effect of treatments on the number of shoots was not evident until autumn 1999 or even spring 2000. The likely dependence of the number of shoots in a particular growing season on the biomass of shoots in the preceding growing seasons, would act as an important buffer against exceptionally severe growing seasons, as it was found for the number of leaves in *Cassiope tetragona* (Callaghan *et al.*, 1989). Thus, similar shoot growth can be attained in different years by small numbers of long shoots or large numbers of short shoots, according to weather conditions. Such a mechanism, which buffers annual variation in growth, could be of considerable importance in the Mediterranean-climate areas, where there is a large unpredictability in the precipitation patterns. Thus, significant decreases in the number of shoots and in the total shoot growth per stem of *G. alypum* plants can be expected from consecutive adverse growing seasons.

Concluding remarks

The results of the present study point to changes in the annual productivity of these Mediterranean shrubs under near future drier and warmer conditions. Drier conditions would decrease the annual productivity of both species, but, in *E. multiflora*, the stimulation of growth by warmer conditions might compensate, at least partially, such a decrease. Thus, future drier and warmer conditions would probably have a stronger negative impact on the annual productivity of *G. alypum* than of *E. multiflora*. Alterations in the competitive interactions of these two species in response to the predicted climatic changes could lead, in the long-term, to variations in the species composition of these Mediterranean ecosystems.

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