GLOBAL CHANGE ECOLOGY - ORIGINAL RESEARCH

Sporadic rainy events are more critical than increasing of drought intensity for woody species recruitment in a Mediterranean community

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Abstract The understanding of the impact of extreme climatic events under a global climate change scenario is crucial for the accurate forecast of future plant community dynamics. We have experimentally assessed the effect of drier and wetter summer conditions on the recruitment probabilities and the growth of seedlings from eight woody species representative of the most important functional groups in the community, pioneer shrubs, mid-successional shrubs and trees, across the main habitats in the study area (open habitat, shrubland, and forest). Our hypothesis proposes that wet summer conditions would represent a good opportunity for tree species regeneration, enhancing both forest maintenance and expansion. A drier summer scenario, on the other hand, would limit forest regeneration, and probably hinder the colonization of nearby habitats. We found a habitat effect on the emergence, survival, and final biomass, whereas different climate scenarios affected seedling survival and biomass. A wet summer boosted growth and survival, whereas greater drought reduced survival only in some cases. These results were modulated by the habitat type. Overall, shrub species presented higher survival and growth and were less affected by more severe drought, whereas some tree species proved to be extremely dependent on wet summer conditions. We conclude that the reduction in frequency of wet summers predicted for the coming decades in Mediterranean areas will have greater consequences for species recruitment than will increased drought. The different response of the species from the various functional groups has the potential to alter the composition and dominance of future plant communities.

Keywords Climate change · Rainfall variability · Recruitment · Summer drought · Vegetation dynamics

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Introduction

The way in which global climate change will affect plant community dynamics is a key topic in recent ecological research. It is increasingly clear that the alteration of rainfall patterns expected for many regions of the world during the coming decades will have far-reaching impacts on plant communities, resulting in shifts in their composition and dynamics (Peñuelas and Boada 2003; Thuiller et al. 2005; Lloret et al. 2009). Many recent papers have sought to offer insights into this complex question by adopting different approaches, ranging from ecophysiology (Linares et al. 2009; McDowell et al. 2010), community landscape concerns (Allen and Breshears 1998; Allen et al. 2010), or modeling vegetation dynamics on a broader scale (Thuiller et al. 2005; Malcolm et al. 2006). Understanding and predicting the consequences of these changes on ecosystems is emerging as one of the major challenges for scientists, and forecasting the impact on forests is of fundamental importance (Boisvenue and Running 2006; Bonan 2008).

Despite the number of studies addressing the impact of higher water availability (Cabin et al. 2002; Castro et al. 2005; Mendoza et al. 2009) or drier conditions (Holmgren

2000; Weltzin and McPherson 2000; Lloret et al. 2004; Sánchez-Gómez et al. 2006) on woody species regeneration, no available studies explicitly analyze at the same time the way in which either increasing or reducing trends expected for a given particular region will affect the recruitment bank performance at the community level. This is a key point in understanding the effect of global change on woody species regeneration at the community level, as both drier and milder years will continue to occur in many ecosystem types, even under the current scenario of growing aridity (Beniston et al. 2007). In the case of Mediterranean ecosystems, dry summers are the rule, although exceptional rainy summers occur with great irregularity (Henderson-Sellers and Robinson 1986; Esteban-Parra et al. 1998; Rodrigo 2002). These rare wet summers in terms of Mediterranean climate may represent the only windows of opportunity for the establishment (sensu Eriksson and Fröborg 1996) of some long-lived woody species, because their recruitment is otherwise hampered by drought (e.g., Traveset et al. 2003; Gómez-Aparicio et al. 2005; Urbieta et al. 2008).

From a demographic standpoint, the seedling stage is critical for recruitment (Fenner 1992; Lloret et al. 2004), and the analysis of its response to extreme climatic events under a global change scenario is crucial for the accurate forecast of future plant community dynamics for two main reasons. Firstly, because of the high sensitivity to the abiotic conditions of recruits due to their limited root system in comparison to adults (Houle 1994; Castro et al. 2005), and secondly, the quicker response to environmental changes compared to the adult phase (Lloret et al. 2009). Thus, for a proper assessment of the dynamic response of forest ecosystems to very rapid changes related to global climate change, we should pay special attention to the recruitment bank, taking into account the diverse representation of the different functional groups. This type of information on regeneration under climate change is urgently needed for modeling vegetation dynamics (Morin and Thuiller 2009).

The aim of this work has been to assess the effect of two contrasting climatic conditions that could appear during the coming decades, i.e. drier and wetter summer conditions, on the recruitment probabilities and growth of seedlings from woody species representing the entire woody community in a Mediterranean mountain environment. We followed a field experimental approach for two consecutive years, simulating: (1) sporadic wetter conditions during the growing season based on maximum historical records from the study area (Matías et al. 2011); (2) drier climatic conditions during the growing season (according to the A-2 scenario from IPCC); and (3) current climatic conditions. As targets, we considered species from the three main functional groups in Mediterranean areas: trees, mid-

successional shrubs, and pioneer shrubs. We also tested the effect of the different climate scenarios across various habitats. We chose the three principal habitat types in the Mediterranean mountains: open habitats, under shrub cover, and under tree canopies. This may result in different recruitment probabilities at the community level in different ecological templates (habitats and precipitation patterns), which would be able to alter significantly community regeneration dynamics, such as those hypothesised in Fig. 1. These changes may ultimately affect composition, relative abundance, and community dynamics. The main questions that we have sought to answer are: (1) What is the response of the species from the three functional groups to the different combination of climate scenarios and habitats in terms of survival and growth? (2) Which of the successive demographic stages involved in recruitment (emergence, growth and survival) is the most sensitive to the different climate scenarios? (3) Which is more important for plant recruitment, the expected increase in frequency of drier years or the eventual loss of wetter ones?
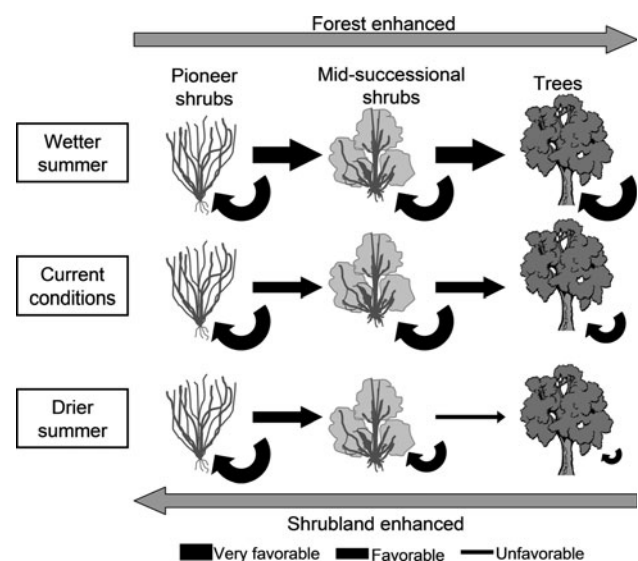

Fig. 1 Schematic diagram representing the community dynamics within the different climate scenarios predicted for the coming decades in Mediterranean areas. *Arrows* represent the hypothesized dynamics: within functional groups, they represent the self-regeneration capacity; between groups, they represent the probability of transition between stages. Arrow width is proportional to success probability—from unfavorable to very favorable. Our hypothesis proposes that: (1) wet summer conditions would represent a good opportunity for tree species regeneration, allowing forest maintenance and colonization or expansion to nearby degraded habitats; (2) a drier summer scenario, however, would limit forest regeneration and probably hinder the colonization of nearby open and shrubland habitats; (3) this drier scenario would in turn be very favorable for shrubland expansion, enhancing both shrubland maintenance and colonization and expansion, even to nearby forest environments

Materials and methods

Study area

The study was conducted from December 2006 to September 2008 in La Cortijuela area (1,650 m.a.s.l.), Sierra Nevada National Park (37°05′N, 3°28′W, Granada, SE Spain). This mountain area has a continental Mediterranean climate, with cold winters and hot, dry summers. Rainfall is 811 mm year^{-1} (mean 1990–2008), mostly during spring and autumn. The vegetation in the area is composed of patches under different successional stage, with patches of forest dominated by Scots and black pines (*Pinus sylvestris* L. and *P. nigra* Arnold.) and oaks (*Quercus ilex* L.), shrublands, and open areas. The experiment was conducted inside a natural area of 12.4 ha fenced since 1986 to prevent browsing by ungulates; see Matías et al. (2009) for further details.

Study species

We chose eight target species representative of the three main successional stages in Mediterranean mountains, all of the species native to the study area: four trees, two being deciduous (*Sorbus aria* L. and *Acer opalus* Mill.) and two evergreen (*Pinus sylvestris* and *Quercus ilex*), two mid-successional shrubs (*Crataegus monogyna* Jacq. and *Berberis hispanica* Boiss.), and two pioneer shrubs (*Salvia lavandulifolia* Vahl. and *Cytisus scoparius* L.; hereafter called by their generic names). Seeds and acorns from these species were collected from the surrounding area during the 2006 fruiting period (September–December). They were visually inspected to reject clearly aborted or depredated ones, and stored at 4°C until sowing. Seed mass and species characteristics are shown in Table 1.

Experimental design

We used a fully factorial field experiment crossing two main factors: habitat and climate scenario, each at three levels. For the habitat factor, we selected three common habitats in a Mediterranean mountain environment that differ in woody coverage: (1) open, areas of bare soil or covered with sparse herbaceous vegetation, representing the lowest canopy cover; (2) shrubland, composed of the dominant shrubs in the study area, mainly *Crataegus monogyna*, *Berberis hispanica* and *Prunus ramburii* Boiss., representing the mid-canopy cover; and (3) forest, composed of a mixed forest of *Pinus sylvestris*, *Pinus nigra*, and scattered *Quercus ilex*, representing the denser canopy cover. For the climate scenario treatment, we selected three levels differing in water availability. First, dry summer: based on the SRES A-2 model by the Intergovernmental Panel on Climate Change (IPCC 2007), according to which a reduction in summer rainfall of 30% is predicted for Mediterranean areas, as well as a longer dry period, beginning at the end of spring. For this treatment, we built rain-exclusion shelters (square shaped, 2 × 2 m) following the design of Yahdjian and Sala (2002) covering 35% of the total surface. The rainout shelters were erected from April to September in both study years to simulate longer and drier growing seasons. Second, control: natural rainy conditions during the course of the experiment. We marked out 2 × 2 m squares where water availability was not modified. And third, wet summer: increase in summer rainfall according to maximum historical data. For this, we marked out 2 × 2 m squares with a watering system composed of four sprinklers, one at each corner. We added 180 mm rainfall water from mid-June to the end of September, which is equivalent to the mean summer rainfall of the five wettest summers of the 1902–2006 series in the study

Table 1 Characteristics of eight species selected for the experiment

Species	Functional group	Distribution	Seed mass (g)	Sown per plot
Pinus sylvestris	Tr	Boreo-Alpine	0.012 ± 0.01	15
Acer opalus	Tr	Sub-Mediterranean	0.046 ± 0.011	15
Sorbus aria	Tr	Sub-Mediterranean	0.036 ± 0.038	10
Quercus ilex	Tr	Mediterranean	4.480 ± 1.25	5
Berberis hispanica	MSS	Mediterranean	0.018 ± 0.008	15
Crataegus monogyna	MSS	Mediterranean	0.079 ± 0.018	15
Cytisus scoparius	PS	Mediterranean	0.011 ± 0.002	15
Salvia lavandulifolia	PS	Mediterranean	0.005 ± 0.002	15

All species are naturally present and abundant in the study area and are representative of the different functional groups on Mediterranean mountains. Functional groups of the species are indicated as *Tr* trees, *MSS* mid-successional shrubs and *PS* pioneer shrubs. Distribution is based on the ecological requirements and actual distribution of the species (taken from Blanco et al. 2005). Seed mass is mean ± SD, $n = 100$ for all species except for *Q. ilex* ($n = 360$). The last column indicates the number of seeds sown in each plot

area (Matías et al. 2011). Summer storms were simulated by the weekly addition of 12 mm of water. If a natural storm occurred at any time, the weekly irrigation pulse was not added. The simulated precipitation regime fitted recorded data on the study area both in frequency (mean precipitation value per event 13.8 mm for the 1990–2008 series) and intensity (mean number of days between two precipitation events from June to September was 7.2 during the last two mild summers 1996 and 1997). The wet summer treatment is intended to represent sporadic mild summers in the area, and fits with the overall summer rainfall in more mesic mountain areas where the studied species are distributed (Castro et al. 2005). In each of the three habitats, we marked out 24 plots, and assigned 8 of them randomly to each of the climate scenarios, thus making a total of 72 plots (3 habitats × 3 climate scenarios × 8 replicates; see Matías et al. 2011 for additional methodological details). Precipitation during treatment applications (April to September) was 365.5 and 374.5 mm in 2007 and 2008, respectively (mean value of the 1990–2008 series: 305.9 mm). Thus, precipitation in the dry summer scenario was 237.6 and 243.4 mm in 2007 and 2008, respectively, and 545.5 and 554.5 mm in the wet summer scenario.

In each plot, the 8 species were sown inside individual 15 × 25 cm wire-mesh cages (1-cm mesh) to avoid losses due to seed predation by small mammals as well as grazing by herbivores, and keeping a 0.5-m-wide buffer area to avoid any border effect. The number of seeds sown (7,560 in all) varied for each species from 5 to 15 depending upon seed mass and germination rates (Table 1), as determined in a previous experiment (Mendoza et al. 2009). The seeds were sown in December 2006 and stayed in the soil throughout the winter, undergoing a natural cold stratification period in the field. From the beginning of May 2007, each seedling that emerged in the cages was individually tagged and its survival monitored for two complete growing seasons (May–September 2007 and May–September 2008). At the end of the experiment, in September 2008, all the surviving seedlings were harvested. We extracted the whole portion of soil containing the roots with the help of a pneumatic hammer, and then carefully removed the rest of the soil by hand and by washing. Each seedling was separated in above-ground and below-ground components, oven-dried at 70°C for at least 72 h, and weighed.

Abiotic variables

In order to describe the environmental conditions during the experiment, we measured key variables that may determine recruitment success in this Mediterranean community (Quero et al. 2008a, b). In the 72 study plots, the water content of the soil from the top 20 cm was measured monthly by the time-domain reflectometry method (TDR-100; Spectrum Technologies, Plainfield, IL, USA), sampling all study plots by two perpendicular transects and recording the volumetric water content every 0.5 m ($n = 9$ per plot). Light availability was measured in every plot ($n = 72$) by hemispherical photography (Valladares and Guzmán 2006), using a digital camera (CoolPix 5000; Nikon, Tokio, Japan) and a fish-eye lens of 180° field of view (FCE8; Nikon). The images were analyzed using Hemiview software v.2.1 (1999; delta-T Devices, Cambridge, UK), estimating the global site factor (GSF; unitless and ranging from 0 to 1). Open was the habitat with the highest radiation values (0.87 ± 0.01), followed by shrubland (0.42 ± 0.02) and then forest (0.22 ± 0.01). The wet summer increased soil volumetric water content by 2.6%, whereas the dry summer reduced it by 1.9%, compared with the control. The response to the climatic scenario varied across habitats, but was consistent in all cases (Table 2). Air and soil temperatures were recorded by two temperature probes (5 cm above and below soil surface, respectively) connected to a HOBO H8 data logger (Onset, Pocasset, MA, USA) permanently sited on half the study plots to record temperature at 30-min intervals. Mean values and differences across habitats and climate scenarios are given in Table 2.

Data analysis

The effects of the two main factors (habitat and climate scenario) on emergence and survival were analyzed using a logistic model (binomial generalized model) with emergence/survival rate (number of emerged seedlings and total number of sown seeds, or number of surviving seedlings and total number of emerged seedlings) as the response variables for each species. We used a binomial error distribution and logit as a link function for the model (Quinn and Keough 2002). Mean values per plot in above-ground and below-ground biomass were transformed by their natural logarithms and analyzed with the same model but with normal error distribution and identity as link function for each species. Due to the low number of surviving seedlings in some treatments, *Pinus* was eliminated from the biomass analysis, as were *Acer* and *Sorbus* in open habitats, and *Salvia* in forests. Differences in the biomass-allocation pattern (root-mass ratio: proportion of root mass relative to total plant mass) were also tested with the same procedure as biomass. Fisher's PLSD test was used for post hoc analyses. Sequential Bonferroni corrections (Holm 1979) were used for multiple comparisons. Values are given throughout this paper as mean ± standard error. All analyses were made using JMP v.7.0 (SAS Institute, 2007).

Table 2 Mean (±SE) of the abiotic conditions recorded during the experiment development for the three climate scenarios (D dry, C control, W wet) in the three habitats (open, shrubland, forest)

	Mean values (±SE)									Effect		
	Open			Shrubland			Forest			Habitat (H)	Scenario (S)	H × S
	D	C	W	D	C	W	D	C	W	F	F	F
Soil moisture (%)	10.5 ± 0.7	12.1 ± 0.9	14.6 ± 0.7	12.5 ± 0.8	14.4 ± 1.0	17.0 ± 0.9	12.8 ± 0.9	14.1 ± 1.0	17.6 ± 0.9	499.7**	1214.7**	2.3
Light availability (unit-less)	0.86 ± 0.01	0.88 ± 0.01	0.88 ± 0.01	0.42 ± 0.04	0.44 ± 0.04	0.41 ± 0.05	0.19 ± 0.02	0.25 ± 0.01	0.23 ± 0.02	451.5**	1.3	0.4
Air temperature (°C)	23.1 ± 0.3	24.3 ± 0.3	22.1 ± 0.3	20.0 ± 0.2	21.1 ± 0.3	23.4 ± 0.5	18.5 ± 0.3	18.3 ± 0.2	16.9 ± 0.2	12.1*	0.05	0.6
Soil temperature (°C)	23.9 ± 0.3	24.5 ± 0.4	21.4 ± 0.2	19.0 ± 0.2	20.2 ± 0.3	17.4 ± 0.2	17.2 ± 0.2	16.6 ± 0.5	14.8 ± 0.1	34.9**	8.5*	1.5

Differences in soil water content and temperatures were tested between habitats climate scenarios using repeated-measures ANOVA; differences in light availability were tested by factorial ANOVA. Significant F values: *$P \le 0.05$, **$P \le 0.0001$

Results

Seedling emergence

A total of 2,139 seedlings emerged (28%). The habitat had a significant effect on emergence for all the species studied (Table 3), with the highest values in forest for *Acer*, *Sorbus*, *Berberis*, and *Cytisus*; in shrubland for *Pinus* and *Crataegus*; and in open habitats for *Quercus* and *Salvia* (Table 4). Nevertheless, the climate scenario had no effect on emergence (Table 3).

Seedling survival

A total of 1,306 seedlings survived to the second summer at the end of the experiment (61%). We found differences in the habitat effect on the final survival for all species except *Salvia* (Table 3; data of *Pinus* were not analyzed due to the high number of zeros but survival clearly differed among habitats; Fig. 2). Overall, open was the habitat where survival was lowest for all species except for the two pioneer shrubs (*Cytisus* and *Salvia*), whereas the highest survival was in the shrubland or the forest habitats for the rest of the species (Fig. 2).

Climate scenarios showed a significant effect on the final survival for all the species except *Berberis* (Table 3; Fig. 2). Indeed, the lack of overall differences for *Berberis* was presumably related to the null survival in open habitats for both dry and wet scenarios, but climate scenarios still differed within habitats (Fig. 2). As a general trend, the wet scenario resulted in an increase in survival for most species in some of the habitats (Fig. 2). Additionally, the climate prompted the greatest differences in the open habitat for *Sorbus* and *Crataegus*, whereas in shrubland the climate scenario scarcely affected survival. Pioneer shrubs (except *Salvia* in forest) and *Quercus* were the species least susceptible to climate variations. Finally, survival was not reduced in the dry scenario compared to the control scenario, with the exception of *Acer* and *Salvia* in forest (Fig. 2). Overall, survival was 45.6 ± 3.2% in the dry summer scenario, 47.0 ± 3.1% in the control, and 75.0 ± 2.8 in the wet summer scenario (all species pooled). The effect of the dry scenario was particularly striking for *Acer* and *Pinus*, with no survivor in this scenario (Fig. 2). We also found a significant interaction between habitat and climate scenario for four of the species, caused by the different intensity of the dry summer effect on different habitats (Table 3; Fig. 2). For example, survival for *Sorbus* was lower in the dry summer scenario in open habitat and forest, but increased in shrubland.

Table 3 Summary of statistics (χ^2 or F and P values)

Species	Habitat (H)		Scenario (S)		H × S	
	χ^2/F	P	χ^2/F	P	χ^2/F	P
Seedling emergence						
Acer	11.992	**0.0025**	3.628	0.1630	2.851	0.5831
Pinus	120.701	**<0.0001**	2.635	0.2678	11.799	0.0189
Sorbus	98.315	**<0.0001**	0.274	0.8719	5.946	0.2032
Quercus	7.368	**0.0251**	0.879	0.6444	1.720	0.7870
Crataegus	100.576	**<0.0001**	1.837	0.3992	3.523	0.4744
Berberis	165.305	**<0.0001**	5.976	0.0504	1.639	0.8018
Cytisus	21.786	**<0.0001**	8.405	0.0150	9.569	0.0483
Salvia	37.428	**<0.0001**	1.667	0.4344	2.039	0.7286
Seedling survival						
Acer	19.833	**<0.0001**	12.037	**0.0024**	9.554	0.0486
Pinus	–	–	–	–	–	–
Sorbus	9.762	**0.0076**	34.339	**<0.0001**	11.298	0.0234
Quercus	11.945	**0.0043**	26.733	**<0.0001**	3.686	0.4501
Crataegus	32.212	**<0.0001**	30.314	**<0.0001**	9.578	0.0482
Berberis	23.640	**<0.0001**	0.802	0.6696	8.555	0.0732
Cytisus	9.436	**0.0089**	13.951	**0.0009**	11.647	0.0202
Salvia	0.661	0.7186	10.756	**0.0046**	7.857	0.0970
Above-ground biomass						
Acer	0.16	0.695	0.93	0.415	0.60	0.562
Sorbus	3.79	0.032	24.00	**<0.0001**	5.48	**0.001**
Quercus	13.72	**<0.0001**	2.57	0.085	0.79	0.537
Crataegus	1.76	0.184	1.26	0.295	0.24	0.914
Berberis	0.17	0.683	4.37	0.020	0.39	0.675
Cytisus	26.55	**<0.0001**	2.93	0.046	0.71	0.589
Salvia	55.06	**<0.0001**	7.91	**0.002**	0.37	0.696
Below-ground biomass						
Acer	2.16	0.161	1.74	0.207	0.85	0.446
Sorbus	5.17	**0.010**	22.99	**<0.0001**	2.70	0.045
Quercus	23.00	**<0.0001**	4.75	0.012	0.82	0.520
Crataegus	28.30	**<0.0001**	12.29	**<0.0001**	1.77	0.154
Berberis	4.19	0.048	4.15	0.024	0.08	0.926
Cytisus	56.38	**<0.0001**	3.53	0.036	0.46	0.762
Salvia	67.15	**<0.0001**	8.33	**0.002**	0.17	0.847

Emergence and survival after the second summer in different habitats and climate scenarios were analyzed by a logistic model (χ^2 values), and differences in using above-ground and below-ground biomass by the same model but with normal error distribution and identity as link function (F values). Due to high mortality, Pinus was extracted from the survival analysis, as well as the following data from the biomass analysis: Pinus: all data, Acer, and Berberis: data from open habitat, Salvia: data from forest habitat. Separate analyses were conducted for each species. Significant P values after sequential Bonferroni corrections are shown in bold

Final biomass

Plant biomass was affected by the habitat, forest being the habitat that generally showed the lowest biomass, which increased in shrubland and especially in open areas for most species (Fig. 3). The climate scenario also had an influence on seedling biomass only for some species

(Table 3; Fig. 3). Overall, the wet summer scenario had a strong effect, increasing biomass by 2.1 times with respect to the control scenario (Fig. 3). By contrast, the effect of the dry summer scenario was less pronounced, showing no differences in most cases compared to the control treatment (Fig. 3). Interactions between the two main factors appeared only in Sorbus, where the loss in biomass in the

Table 4 Mean (±SE) emergence (percentage emerged seedlings compared to the total of seeds sown) for the eight species studied for the three climate scenarios in the three habitats

Scenario	Species	Emergence		
		Forest	Shrubland	Open
Dry	*Acer*	13.3 ± 2.8	10.0 ± 2.2	8.3 ± 3.3
	Pinus	31.7 ± 6.7	25.8 ± 8.1	5.8 ± 3.4
	Sorbus	48.7 ± 11.4	47.5 ± 10.1	16.2 ± 3.7
	Quercus	85.0 ± 8.2	85.0 ± 5.0	95.0 ± 3.3
	Crataegus	45.0 ± 6.6	45.0 ± 6.9	15.0 ± 3.5
	Berberis	40.0 ± 6.0	37.5 ± 8.9	5.0 ± 1.7
	Cytisus	66.7 ± 3.6	43.3 ± 6.5	38.3 ± 5.9
	Salvia	1.6 ± 1.6	7.5 ± 2.6	10.8 ± 4.0
Control	*Acer*	15.0 ± 3.7	10.8 ± 2.8	4.2 ± 1.7
	Pinus	33.3 ± 6.5	35.8 ± 5.8	8.3 ± 3.5
	Sorbus	47.5 ± 5.9	46.2 ± 9.9	13.7 ± 7.0
	Quercus	87.5 ± 5.3	75.0 ± 12.9	92.5 ± 3.6
	Crataegus	31.7 ± 3.7	43.3 ± 8.1	14.2 ± 3.7
	Berberis	41.6 ± 6.7	34.2 ± 6.3	3.3 ± 1.7
	Cytisus	55.0 ± 5.3	45.8 ± 8.8	36.7 ± 7.4
	Salvia	0.83 ± 0.8	11.7 ± 3.0	11.7 ± 3.5
Wet	*Acer*	8.3 ± 3.3	9.1 ± 3.3	3.3 ± 1.8
	Pinus	30.8 ± 4.3	51.7 ± 5.7	5.0 ± 2.4
	Sorbus	63.7 ± 6.5	42.5 ± 9.2	11.2 ± 3.5
	Quercus	82.5 ± 8.8	82.5 ± 5.9	90.0 ± 3.8
	Crataegus	37.5 ± 5.0	49.2 ± 9.1	11.7 ± 3.7
	Berberis	28.3 ± 7.3	29.2 ± 5.3	1.7 ± 1.1
	Cytisus	40.0 ± 3.9	41.7 ± 5.7	35.0 ± 5.8
	Salvia	2.5 ± 1.7	14.2 ± 4.6	11.7 ± 4.1

drier scenario was more evident in the open habitat than in the others. Biomass allocation pattern (root-mass ratio) was not affected by the climate scenario, or was even higher in the case of *Quercus* and *Crataegus* ($F = 3.50$, $P = 0.03$, and $F = 14.21$, $P < 0.0001$ respectively) in the wet summer scenario (results not shown).

Discussion

The results show that forest recruitment depends heavily on extreme climatic events, although the species and life-stage analyzed showed different sensitivity to rainfall availability. Furthermore, the response to climatic scenarios was modulated by the type of habitat. Seedling emergence was affected mainly by the habitat type whereas the influence of the climate scenario was null, probably because we began climate scenario simulations in April 2007, after seedling germination had started (for similar results, see Castro et al. 2004a, 2005; Mendoza et al. 2009). The climate scenario may impinge upon seedling emergence only in the case of species with strong physiological seed dormancy requiring more than 1 year for germination (e.g., *Taxus baccata*; Mendoza et al. 2009), which is not a common case for

woody species in this community. Nevertheless, the effect of habitat was not the same for all species. Most emerged under a woody canopy, whether forest or shrubland, and only three of the species had comparatively high emergence in the open: the two pioneer shrubs and the Mediterranean *Quercus*. Thus, different wet/dry climate scenarios during the summer are unlikely to have a significant impact on the seedling emergence pattern, which is governed primarily by spring conditions and habitat characteristics.

Seeding survival was, by contrast, clearly altered by the climatic scenario. The wet summer scenario proved to be the most important condition, boosting seedling survival in most species except for the two pioneer shrubs (*Cytisus* and *Salvia*), in which the effect was almost null. These two species are also the most drought-tolerant, being able to survive within a wide range of water availability (Fogarty and Facelli 1999; Palacio and Monserrat-Martí 2006). Seedlings of mid-successional shrubs and especially tree species had higher rainfall requirements for survival, and thus their recruitment would likely benefit more from the existence of sporadic wet summers (Kollmann and Reiner 1996; Mendoza et al. 2009). *Quercus* and *Pinus* were the dominant tree species in the community, and any alteration

Fig. 2 Mean (±SE) percentage survivorship at the end of the experiment for the eight species in different habitats and climate scenarios as the number of surviving seedlings compared to the number of emerged seedlings per plot. *Different letters* indicate differences between climate scenarios within habitat by a Fisher's PLSD test
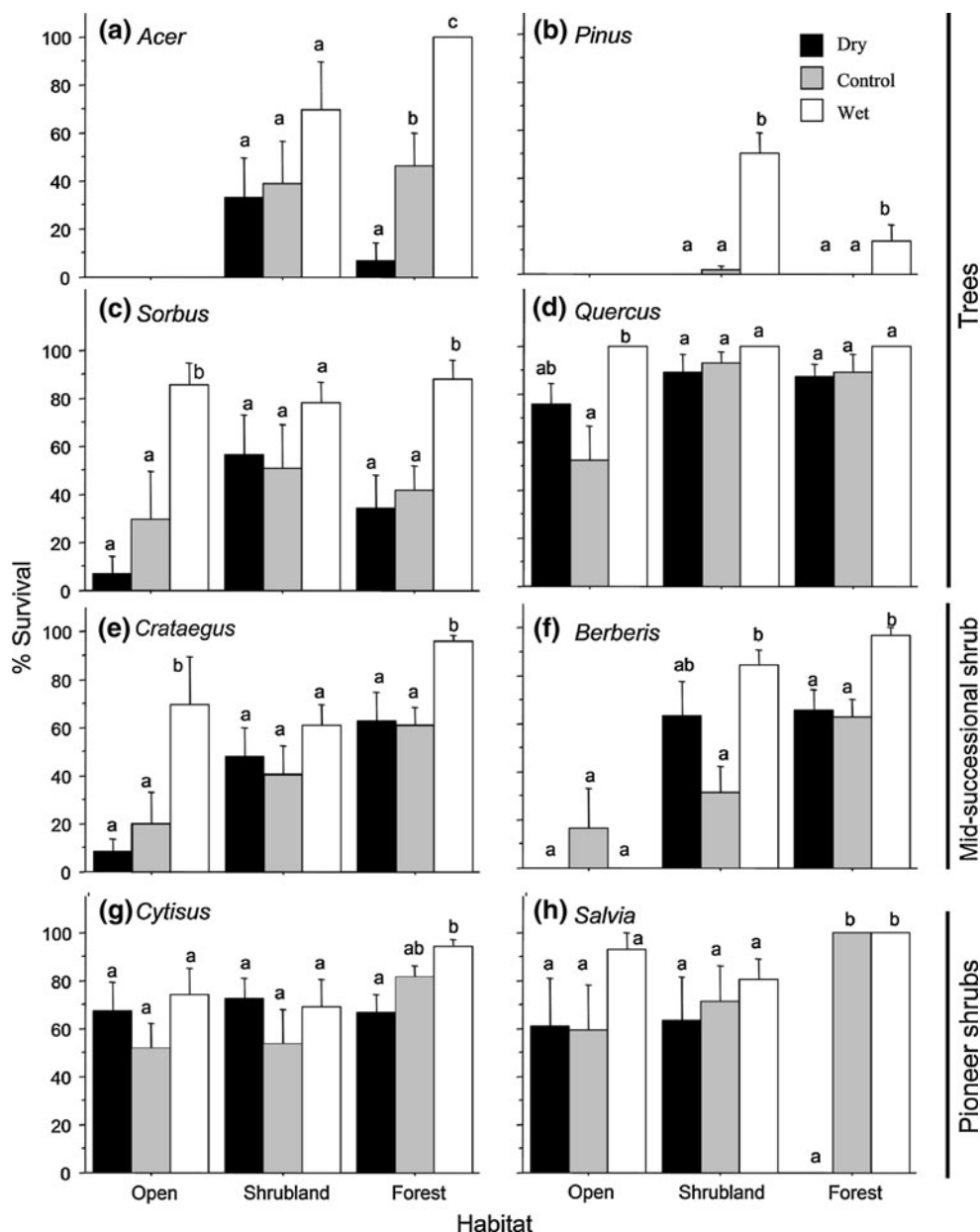

in their recruitment pattern implies major consequences for ecosystem structure and ecological interactions. In any case, besides the strong effect of climate scenarios on seedling survival, different habitats modulated survival intensity. As a general trend, plant cover (whether shrubland or forest) enhanced seedling survival, especially in the case of trees and mid-successional shrubs. The advantage of plant cover for the establishment of woody species is well known in many parts of the world (Callaway et al. 1996; Kitzberger et al. 2000), and in Mediterranean-type ecosystems in particular (Maestre et al. 2003; Gómez-Aparicio 2009), where facilitative interactions are especially important for recruitment (García et al. 2000; Castro et al. 2004a, b; Gómez-Aparicio et al. 2004). This complex

interaction among climate scenarios, habitat types, and species identity highlights the importance of taking into account the heterogeneity of habitat structure when trying to forecast accurately the eventualities of climate variation on a wider scale.

The increase in biomass, both above and below ground, induced by the wet summer scenario was consistent for most of the species and habitats studied. Wet summers were not only crucial for seedling survival in a given season but also promoted aerial growth as well as larger roots, conferring a delayed advantage for future summers and thereby improving future survival probabilities (Castro et al. 2005; Holmgren et al. 2006). A higher root-mass allocation was even promoted in the wet-summer scenario

Fig. 3 Final biomass above- and below-ground (grams) at the end of the experiment for the eight species in the three habitats. *Solid black bars* dry summers, *gray bars* controls, and *open bars* wet summers. *Bars* mean ± SE. *Error bars* are omitted in some cases due to low survival (*n* = 1). *Different letters* indicate significant differences between climate scenarios within the same habitat for total biomass (above-ground plus below-ground) according to Fisher's PLSD test
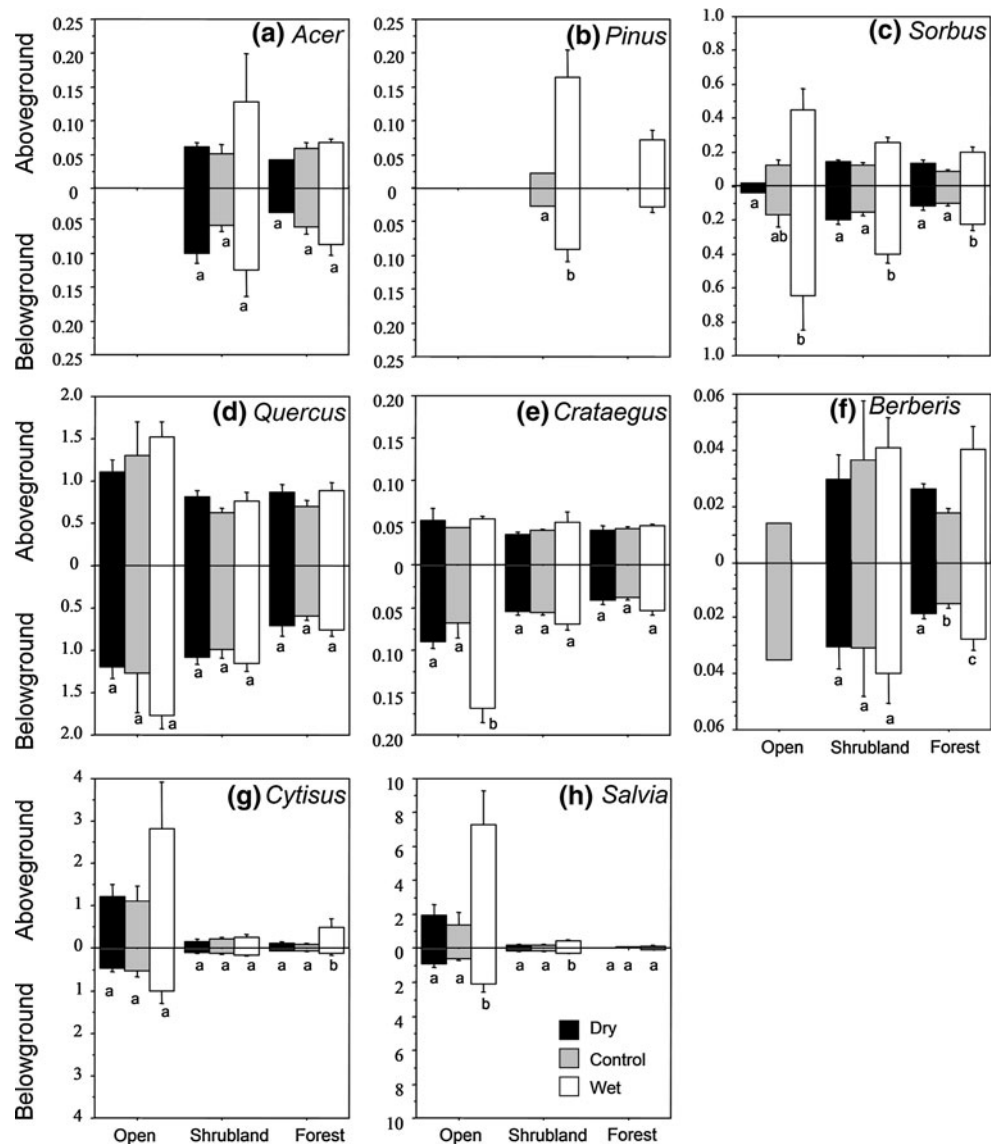
for two of the species, including *Quercus*, one of the tree species. By contrast, the dry summer scenario had a weak effect on plant growth, supporting the contention that the species in that community are growth limited by summer drought under current climatic conditions (Gómez-Aparicio et al. 2005; Mendoza et al. 2009). As with survival, the effect of climate scenarios on seedling growth was modulated by the different habitats. Overall, in the open habitat, seedlings from most species were able to take maximum advantage in terms of growth from the higher water input in the wet summer scenario.

In short, radiation and soil moisture are the most important resources determining growth and survival (Sánchez-Gómez et al. 2006; Quero et al. 2008b), and these resources could be found only under optimal conditions with the specific combination of open habitat and wet scenario. However, with the current precipitation pattern or

the drought intensity increase expected for the coming decades, recruitment is likely to be hampered by drought in open, and facilitative plant–plant interactions become essential for the community regeneration.

Consequences for community dynamics in a changing climate

Our results support the idea that increased aridity and a rarer incidence of wet summers predicted by climatic models for Mediterranean areas (Giorgi and Lionello 2008) may induce species-specific differences in recruitment, which might in the future lead to an alteration in the community structure. Thus, the recruitment of some tree species, such as *Pinus*, might be limited in drier conditions as they depend strongly on the occurrence of wet summers. Other tree species less sensitive to drought (*Acer* and

Sorbus) could maintain their populations or even extend them to shrublands thanks to the facilitation effect exerted by shrubs (Callaway et al. 1996; Castro et al. 2004b; Gómez-Aparicio et al. 2004), which overall increased emergence and survival. *Quercus*, the most drought-tolerant tree species (Quero et al. 2008b), and the only one of Mediterranean origin (Blanco et al. 2005), might be expected to recruit new individuals even during the driest years and in all the habitat types. Thus, as long as there are no differences in other demographical processes (i.e. reproduction, adult mortality), *Quercus* would have a comparative advantage relative to the other dominant tree species (*Pinus*), and its abundance in the community could be expected to increase during the coming decades. Consequently, if mild summers become less frequent, community structure is expected to change, with two main consequences: the likely decrease in dominance of drought-intolerant tree species by means of progressive recruitment reduction, resulting in some cases in a loss of biodiversity, and the growing dominance of drought-tolerant and typically Mediterranean species. Both a loss in biodiversity and shifts in species dominance support other modeled predictions (Thuiller et al. 2005; Malcolm et al. 2006) and bolster them with empirical support, although future models should take into account habitat variations on a smaller scale. As proposed in our previous hypothesis (Fig. 1), wetter summer conditions would considerably improve tree recruitment, together with the colonization of nearby degraded areas (especially shrubland, but even open areas for some species), thereby fostering forest maintenance and expansion. Shrubs (especially pioneers) will be less affected by greater summer drought, being able to expand their habitat and colonize open areas and forest gaps. This enhancement of shrubby species recruitment under the conditions predicted for the coming decades agrees with the shrub encroachment trends described for many Mediterranean ecosystems (Acácio et al. 2009; Costa et al. 2010).

Conclusions

According to our results, sporadic wet summers improve seedling regeneration in the species from the different successional stages, whereas greater drought only tends to diminish seedling growth or survival. An unusually wet summer therefore has a quantitative impact on Mediterranean communities, as the number of recruits rises for a majority of species, encouraging both forest maintenance as well as forest colonization and expansion to nearby degraded habitats. In addition, a wet summer also offers a qualitative advantage, because it might represent the only window for recruitment that boreo-alpine species may encounter at the southern limit of their distribution area (Castro et al. 2004a; Hampe and Petit 2005), enabling the maintenance of a diverse recruitment bank made up of Mediterranean and boreo-alpine species. Thus, we can affirm that the lower frequency of mild summers predicted in Mediterranean areas will have greater consequences for species recruitment than increased drought. Therefore, the expected declining frequency of wet summers, as well as the trend of steadily drier ones, may induce species loss in Mediterranean mountain environments, reducing biodiversity, changing community dominance, and limiting forest regeneration and colonization of nearby open areas. These climatic conditions may induce a regressive encroachment, as some tree species would be replaced by shrubs, since pioneer and mid-successional shrubs are less affected by both the increase of drought intensity and the reduction of mild summers. Hence, the impact of climate change on the diversity and dynamics of forest communities will depend not only on the expected increase in aridity but also on the balance between wet/dry years. In the long-term, both constraints bear the risk of converging in an overall reduction of forest diversity and an increased dominance of the most drought-tolerant species, enhancing shrubland expansion.

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