Severe Drought Effects on Mediterranean Woody Flora in Spain

Josep Peñuelas, Francisco Lloret, and Ramón Montoya

ABSTRACT. The severe drought in 1994 damaged the woody flora of central and southern Spain (80% of the 190 studied sites presented drought-damaged species). In 1996, after a wet year, 67% of the sites were still affected. Different degrees of damage and recovery were found among different functional types (trees or shrubs), and genera of different evolutionary history (Mediterranean or pre-Mediterranean). The Mediterranean genera, mostly shrubs evolved under Mediterranean climate conditions, i.e., later than 3.2 M years ago in the Pliocene, were more damaged by the drought than the earlier evolved pre-Mediterranean genera, mostly trees. However, the Mediterranean genera were more resilient and recovered much better after the following wet year. For. Sci. 47(2):214–218.

Key Words: Drought, evolutionary history, functional types, global change, Mediterranean vegetation.

VER THIS CENTURY, the climate has become warmer and drier in the Mediterranean regions of Spain. Temperature and potential evapotranspiration have increased by 0.10°C and 13 mm per decade, respectively, and minimum relative humidity has decreased 0.85% per decade (Piñol et al. 1998). Moreover, transition to a warmer and drier climate has not been gradual but punctuated by severe drought events such as in 1985 and 1994. Global change effects on Mediterranean climate are likely to produce even warmer and drier conditions in the next decades and more frequent and stronger droughts (Houghton et al. 1996, Peñuelas 1996) with consequent effects on vegetation. These effects depend on the degree of adaptation of different taxa, a characteristic that is modulated by their evolutionary history.

The contemporary flora of a region is composed of species assemblages that are transitory sets of taxa that have originated at different geological times and in different ecological scenarios. These different origins may partly explain the current ecological pattern of floras (Lechowicz 1984, Herrera 1992). The flora of central and southern Spain is well suited for an analysis of the evolutionary historical effects on contemporary patterns as it represents a complex mixture of taxa with disparate biogeographical affinities, ages of origin, and evolutionary histories (Braun-Blanquet 1937, Palamarev 1989, Herrera 1992). It is generally agreed that current Mediterranean climatic conditions with a characteristic summer drought and high interannual variability first appeared during the second half of Pliocene, 3.2 millions of years ago (Suc 1984). Genera for which early Pliocene or pre-Pliocene fossil records are available in western Mediterranean basin localities (either pollen or macrofossils) are considered descendants of lineages that certainly did not evolve under contemporary Mediterranean climatic conditions (Herrera 1992). Pre-Mediterranean genera evolved from tropical-like environments that gradually incorporated seasonal aridity (DiCastri 1981). In contrast, genera with no Pliocene fossil records more likely represent lineages appearing in the region (by in situ evolution or migration) after the establishment of current Mediterranean climatic conditions.

The summer of 1994 was extremely dry in Spain, especially in the meridional part. It was the culmination of a period of 5 dry years with an important hydric deficit (Montoya 1999). We aimed (1) to study whether there was large damage to the woody flora of central and southern Spain as a conse-

Acknowledgments: We are grateful for financial support from CICYT-CLI97-0344, CIRIT and DGCONA (Ministerio de Medio Ambiente) Spanish agencies, and the comments to the manuscript by Drs. I. Filella, J. Gamon and G. Oliveira.

Manuscript received March 23, 2000. Accepted July 27, 2000.

Josep Peñuelas, CSIC-CREAF (Center for Ecological Research and Forestry Application), Universitat Autònoma de Barcelona, 08193 Bellaterra, Spain —Phone: 34 93 5812199 (1312); Fax: 34 93 5811312; E-mail: penuelas@uab.es. Francisco Lloret, CREAF, Facultat Ciencies, Universitat Autonoma Barcelona 08193 Bellaterra, Barcelona, Spain—Phone: 34 93 5812700; Fax: 34 93 5811312; E-mail: lloret@cc.uab.es. R. Montoya, Servicio de Protección de Montes contra Agentes Nocivos. DGCONA, Ministerio de Medio Ambiente, Gran Vía de San Francisco 4, 28005 Madrid, Spain—Phone: 34-91-3476008; Fax: 34-91-3476302; E-mail: rmontoya@ctv.es.

quence of the drought, and (2) to test our hypothesis of different degrees of damage and recovery in pre-Mediterranean (pre-Pliocene) and Mediterranean (post-Pliocene) genera and in different functional types (trees versus shrubs). We monitored woody vegetation in winter 1994–1995 after the severe drought, and in autumn 1996 to follow the progression of damage after a period that included a wet year (1996).

Methods

We monitored 190 sites of 100 ha each corresponding to the sites of the Central and Southern Spain network for forest damage monitoring (a network with sampling sites located every 16x16 km in the whole European Union) (Figure 1). These network sites are being monitored annually since 1987 (Montoya and López Arias 1997). Special additional monitoring campaigns were conducted in winter 1994–1995 after the severe drought, and in autumn 1996 after a wet year (Montoya 1999, Peñuelas et al. 1998). Health status of tree and shrub species were recorded in each site.

At each 100 ha site, for each present woody species, 24 individuals chosen following the methodology of the European Union monitoring network as described in Montoya and López Arias (1997) were monitored. Four average levels of aboveground damage were established for each species based on visual examination: 0—no damage, 0.33—moderate decoloration or defoliation, 0.66—severe decoloration or defoliation, and 1—completely decolorated or

defoliated (Montoya 1999). Subsequent recovery was also assessed using this visual scale for the same individuals. The average damage for the different species of each genus was calculated in each site. Then, only the genera present in more than 10 sites (the pre-Mediterranean Pistacia, Olea, Juniperus, Pinus, and Quercus and the Mediterranean Lavandula, Erica, Genista, Cistus, and Rosmarinus) were used in the overall drought damage calculation. We studied genera instead of species as units of analysis to minimize the influence of a few genera with many species. Statistical analyses, including one-way ANOVA analyses with drought damage as dependent variable and historical group (pre-Mediterranean versus Mediterranean) or functional group (trees versus shrubs) as the independent factor, were conducted with commercial software StatView 4.5 statistical program package (Abacus Concepts, Berkeley, CA). Relative damage data were arc sin transformed to meet normality requirements.

Results

In winter 1994–1995, after the severe drought, 80% of the sites included at least one genus with some damage (Figure 1). Table 1 shows the percentage of sites with drought-damaged plants for each one of the most abundant species. In autumn 1996, 67% of the sites were still affected, thus showing the strong intensity of the drought and its persistent effects. Some of the pre-Mediterranean genera such as *Olea*



Figure 1. Natural vegetation health status in the 190 studied forest sites of Central and Southern Spain after the severe 1994 drought. Dry trees or shrubs refer to 1 (completely decolorated or defoliated), and healthy trees or shrubs refer to 0 in our genus damage scale (see Methods section in the text).

Table 1. List of the most abundant species in the 190 sites studied in central and meridional Spain together with the percentage of sites presenting drought-damaged and dry (completely decolorated or defoliated) plants in 1994, after the severe drought episode, and in 1996, after a wet year. Species are ordered by the percentage of sites in which they were dry (completely decolorated or defoliated) in 1994. Evolutionary history (Pre, Pre-Mediterranean; Med, Mediterranean; Alloc, Allocthonous).

Species	Evolutionary history	Presence (no. of sites)	Damaged 1994	Dry 1994	Damaged 1996	Dry 1996
L		/				
Total		190	80.00	11.00	67.00	6.00
Cistus monspeliensis	Med	10	70.00	60.00	30.00	10.00
Genista spp.	Med	38	60.53	55.26	15.79	13.16
Erica spp.	Med	11	81.82	54.55	0.00	0.00
Pinus sylvestris	Pre	17	70.59	35.29	35.29	5.88
Lavandula spp.	Med	13	38.46	30.77	0.00	0.00
Pinus nigra	Pre	38	73.68	28.95	26.32	15.79
Cistus albidus	Med	11	36.36	27.27	54.55	18.18
Cistus salvifolius	Med	15	33.33	26.67	0.00	0.00
Quercus coccifera	Pre	41	75.61	24.39	63.41	9.76
Juniperus communis	Pre	18	61.11	22.22	66.67	16.67
Pinus pinaster	Pre	31	45.16	19.35	32.26	19.35
Rosmarinus officinalis	Med	50	56.00	18.00	52.00	22.00
Eucalyptus spp.	Alloc	12	50.00	16.67	50.00	25.00
Quercus ilex	Pre	107	67.29	15.89	50.47	13.08
\widetilde{P} inus halepensis	Pre	46	69.57	13.04	65.22	15.22
Juniperus phoenicea	Pre	18	16.67	11.11	38.89	16.67
Quercus suber	Pre	23	91.30	8.70	56.52	0.00
Juniperus thurifera	Pre	16	12.50	6.25	25.00	6.25
Cistus ladanifer	Med	45	20.00	4.44	17.78	8.89
Juniperus oxycedrus	Pre	40	17.80	2.50	60.00	7.50
Pinus pinea	Pre	11	45.45	0.00	63.64	9.09
Olea europaea	Pre	14	35.71	0.00	50.00	0.00
Pistacia lentiscus	Pre	15	26.67	0.00	13.33	0.00
Quercus faginea	Pre	21	9.52	0.00	14.29	4.76

or *Juniperus* presented an even larger number of damaged sites in 1996 than in 1994 (Table 1). The percentage of plots that had both dry (completely decolorated or defoliated; 1 in the damage scale) trees and dry shrubs was 11% in winter 1994–1995and still 6% in autumn 1996.

Figure 2 plots the drought-damage in 1996 after the wet year versus the drought-damage in 1994 after the severe



Figure 2. Average relative drought damage (defined from 0 healthy to 1—dry, completely decolorated or defoliated) of the studied woody species in 1996 versus their average relative drought damage in 1994, immediately after the severe drought. Full squares stand for Mediterranean species and empty squares for pre-Mediterranean species.

216 Forest Science 47(2) 2001

drought for each one of the studied species. Species below the 45° line are those which recovered at least somewhat. The species that recovered better were mostly those of Mediterranean genera. Mediterranean genera (Lavandula, Erica, Genista, Cistus, and Rosmarinus) were more damaged by the 1994 drought than pre-Mediterranean genera (Pistacia, Olea, Juniperus, Pinus, and Quercus) (P < 0.01, ANOVA), but they were eventually more resilient and recovered better after the wet 1996 year (P < 0.01, ANOVA) (Figure 3). The percentage of damaged plants in the pre-Mediterranean genera did not decrease in 1996, showing a persistent drought-driven damage as confirmed by isotopic studies of holm oak (Quercus ilex) forests of NE Spain (Peñuelas et al. 2000). On the contrary, the Mediterranean genera recovered much better and had slightly healthier status than pre-Mediterranean genera in 1996. An allocthonous genus such as *Eucalyptus* was strongly affected after the drought and its damage symptoms even increased after the wet 1996 (Figures 2 and 3).

Discussion

The first conclusion of this study was that a severe drought such as that of 1994 produced severe and extensive damage to the Mediterranean vegetation of central and southern Spain (Figures 1, 2, and 3) in agreement with more local studies (Lloret and Siscart 1995). The second conclusion was that different genera responded differently to the severe drought. Mediterranean genera were more affected than the pre-Mediterranean genera, but recovered better after the wet 1996 (Figures 2 and 3). Not only



Figure 3. (a) Relative recovery after the wet year 1995–1996 versus relative drought damage after the 1994 drought for the different pre-Mediterranean and Mediterranean woody genera. Drought damage was defined from 0—healthy to 1—dry (completely decolorated or defoliated). (b) Average relative drought-damage of pre-Mediterranean genera (*Pistacia, Quercus, Olea, Pinus, and Juniperus*), Mediterranean genera (*Cistus, Rosmarinus, Lavandula, Genista, and Erica*), and allocthonous *Eucalyptus* in the 190 sites studied in central and meridional Spain. For these calculations only the genera present in more than 10 stations were considered. Bars are means \pm SE (n = 5 genera). *P < 0.01 in ANOVA of arc sin transformed data on relative damage as dependent variable and evolutionary history group as independent variable.

evolutionary history accounts for these results. Other linked factors, difficult to separate from evolutionary history, such as different functional type or generic traits, might have explained the response pattern of the different genera. For example, Mediterranean genera are mostly shrubs, whereas pre-Mediterranean genera are mostly trees. However, when all evolutionary types were combined according to functional type (trees-Olea, Juniperus, Pinus and Quercus-and shrubs-Pistacia, Lavandula, Erica, Genista, Cistus and Rosmarinus), no ANOVA significant differences between the two functional types were found either in damage or recovery. As the grouping of genera based on functional types does not differ too much from the grouping based on evolutionary history (only one pre-Mediterranean genus, Pistacia, was a shrub), it is difficult to assess the relative role of evolutionary history in comparison with the functional type. However, at least in this study, the evolutionary history appeared as a slightly better classifier of the Spanish woody flora response to the severe 1994 drought.

The two historical groups are associated with characteristic sets of life-history and functional features. The pre-Mediterranean genera mostly include large, deep rooted shrubs and trees with sclerophyllous, evergreen leaves and long life-span. The Mediterranean genera have evolved a set of characteristics that can roughly be described as small size, short lifespan, shallow root systems, and facultative drought-deciduous leaves. Some attempts to discriminate the functional response of Mediterranean sclerophyllous evergreen shrubs versus malacophyllous deciduous ones have been done in relation to water and nutrient use and in relation to drought tolerance and drought evasion (Mooney 1989). Deep-rooted systems present in most evergreen species may confer the ability to use deep water tables, while deciduous species may diminish evapotranspiration through leaf dropping. This facultative decidousness may explain the faster recovery of Mediterranean species after a severe drought period. Thus, post-Pliocene Mediterranean genera seem more adapted to respond to a highly unpredictable environment with great seasonal and interannual variability and subjected to frequent disturbances.

A long, severe drought episode followed by a rain season, as occurred along the 1994–1996 period, is an extreme case of the typical inter- and intraannual climatic variability in which new Mediterranean taxa emerged and evolved. As a result of this severe 1994 drought, there was extensive damage to the Mediterranean woody flora, and different damage and recovery responses of different genera that can be linked to their previous evolutionary history. These responses also show how changes associated with climatic change may depend on fine-scale climatic patterns (interannual variability). Understanding these responses may be important for predicting future species assemblages from the current ones, which consist of both pre-Mediterranean and Mediterranean species and provide a broad range of pre-adaptation features.

Literature Cited

- BRAUN-BLANQUET, J. 1937. Sur l'origen des eléments de la flore méditerranéenene. Communications de la Station Internationale de Géobotanique Méditerranéenene et Alpine, Montpellier 56:8–31.
- DICASTRI, F. 1981. Mediterranean-type shrublands of the world. P. 1–52 in Mediterranean-type shrublands, DiCastri, F., et al. (eds.). Elsevier Scientific Publishing, Amsterdam, The Netherlands.
- HERRERA, C.M. 1992. Historical effects and sorting processes as explanations for contemporary ecological patterns: Character syndromes in Mediterranean woody plants. Am. Natur. 140(3):421–446.
- HOUGHTON, J.T., G.J. JENKINS, AND J.J. EPHRAMUS. (EDS.) 1996. Climate change 1995. The IPCC scientific assessment. Cambridge University Press, Cambridge, UK. 572 p.
- LECHOWICZ, M.J. 1984. Why do temperate decidous trees leaf out at different times? Adaptation and ecology of forest communities. Am. Natur. 124:821–842.
- LLORET, F., AND D. SISCART. 1995. Los efectos demográficos de la sequía en poblaciones de encina. Cuadernos de la Sociedad Española de Ciencias Forestales 2:77–81.
- MONTOYA, R. 1999. The effects of the severe 1994 drought on Spanish forests. *In* Global change and temperate ecosystems, Sebastià, MT. (ed.). Centre Tecnològic i Forestal de Catalunya, Solsona, Spain, in press.

- MONTOYA, R., AND M. LÓPEZ ARIAS. 1997. La red europea de seguimiento de daños en los bosques (Nivel 1). España 1987-1996. Publicaciones del O.A. Parques Nacionales. MMA. Madrid, Spain.
- MOONEY, H.A. 1989. Chaparral physiological ecology-paradigms revisited. P. 85–90 *in* The California chaparral. Paradigms reexamined, Keeley S.C. (ed.). Natural History Museum of Los Angeles County, Los Angeles, CA.
- PALAMAREV, E. 1989. Paleobotanical evidences of the Tertiary history and origin of the Mediterranean sclerophyll dendroflora. Plant Syst. Evol. 162:93–107.
- PEÑUELAS, J. 1996. Overview on current and past global changes in the Mediterranean ecosystems. Orsis 11:165–176.
- PEÑUELAS, J., I. FILELLA, J. LLUSIÀ, D. SISCART, AND J. PIÑOL. 1998. Comparative field study of spring and summer leaf gas exchange and photobiology

of the Mediterranean trees *Quercus ilex* and *Phillyrea latifolia*. J. Exp. Bot. 49(319):229–238.

- PEÑUELAS, J., I. FILELLA, F. LLORET, J. PIÑOL, AND D. SISCART. 2000. Effects of a severe drought on water and nitrogen use by *Quercus ilex* and *Phillyrea latifolia* Biol. Plantarum 43(1):47–53.
- PIÑOL, J., J. TERRADAS, AND F. LLORET. 1998. Climate warming, wildfire hazard, and wildfire ocurrence in coastal eastern Spain. Clim. Change 38:345–357.
- Suc, J.P. 1984. Origin and evolution of the Mediterranean vegetation and climate in Europe. Nature 307:409–432.