

Mexical plant phenology: is it similar to Mediterranean communities?

MIGUEL VERDÚ^{1,2*}, JUAN A. BARRÓN-SEVILLA¹, ALFONSO VALIENTE-BANUET³, NOE FLORES-HERNÁNDEZ³ and PATRICIO GARCÍA-FAYOS²

¹UBIPRO-ENEP Iztacala. Universidad Nacional Autónoma de México. Apartado Postal 310, C. P. 54090, Tlalnepantla, México

²Centro de Investigaciones sobre Desertificación (CSIC-UV), Apdo Oficial. Albal (Valencia), E-46470 Spain

³Instituto de Ecología. Universidad Nacional Autónoma de México, Apartado Postal 70–275, C.P. 04510, D.F., México

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The sclerophyllous, evergreen vegetation found in Mexico under tropical climate is named 'Mexical' (MEX) and presents many traits that have been thought to converge under a Mediterranean climate. Flowering phenology is strongly similar across Mediterranean-type ecosystems (MTEs) and this paper investigates MEX plant phenology in this context. The common history of the vegetation and the differences in the climatic conditions experienced by MEX and MTE taxa provide an ideal scenario to infer the relative importance of natural selection and historical constraints in the phenological response of plants to climatic conditions. This study has involved collecting field and bibliographic data on flowering phenology of MEX communities to detect (1) similarities at the community level between MTEs and MEX, (2) similarities between Tertiary and Quaternary taxa in MTEs and MEX, and (3) similarities between congeneric taxa from MEX and MTEs (taxa sharing a common ancestor but having evolved under different climates). Flowering in MEX does not occur mainly in spring, as in MTEs, but in summer, suggesting a response that maximizes water use in the rainy season. Flowering phenology of MEX species differed from their MTE congeneric species, suggesting that even though a common ancestor is shared, environmental pressures have led to different phenological responses in MEX and MTE plants. The flowering season for species that originated in the Tertiary and Quaternary did not differ in MEX, as expected, because of climatic uniformity along the whole time line. In MTEs, flowering differences between Tertiary and Quaternary species were not congruent, suggesting that the balance between the historical constraints and the selective force of the Mediterranean climate is different among the three MTEs, and a particular explanation is needed for each. © 2002 The Linnean Society of London, *Botanical Journal of the Linnean Society*, 2002, 138, 297–303.

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INTRODUCTION

Mediterranean floras originated from subhumid plant communities that were widely distributed in the world since the Cretaceous (Raven, 1973). The increase of aridity due to climatic change during the Tertiary period reduced the distribution range of the subhumid vegetation not only to Mediterranean-type ecosystems (MTEs) but also to summer-rain tropical areas like

'Mexical' communities (Axelrod, 1975; Pons, 1981; Suc, 1984; Valiente-Banuet *et al.*, 1998). Mexical (MEX) is mainly composed of sclerophyllous, evergreen shrubs developed under a non-mediterranean, tropical climate (Valiente-Banuet *et al.*, 1998) and it is distributed at 1700–2800 m along rain-shadowed slopes of the mountain chains of México, including Sierra Madre Oriental, Sierra Madre Occidental, Neovolcanic belt, and Oaxaca mountains. This community presents the same characters that have been thought to converge under a Mediterranean climate (Barbour &

*Corresponding author. E-mail: Miguel.Verdu@uv.es

Minnich, 1990). Such characters consist of a one-layered vegetation formed by woody vegetation (woody cover > 40%), sclerophyllous and evergreen subshrubs, and herbs located in the canopy breaks. As in Mediterranean communities, Mexical plants respond to fire by resprouting or germinating (Lloret *et al.*, 1999). The climate at MEX communities has never been mediterranean-type (Raven, 1973) and seasonality changes in the Tertiary-Quaternary transition were not so marked as occurred in Mediterranean communities (Rzedowski, 1978).

After climatic changes at the end of the Tertiary, two groups of plants coexist in MTEs (at least in the Mediterranean Basin and California). The first contains ancient taxa evolved in the Tertiary under non-mediterranean, tropical-like climate; the second contains taxa evolved in the Quaternary under mediterranean climate (Keeley, 1991; Herrera, 1992; Bond, 1997). The age of the lineage (Tertiary *vs* Quaternary) explains many differences between the two groups of plants regarding life-history traits and associated syndromes (Herrera, 1987; Herrera, 1992; Aronne & Wilcock, 1994; Verdú, 2000). In MEX, Tertiary and Quaternary taxa coexist, and differences between their life-history traits remain unknown (but see Lloret *et al.*, 1999 for differences in resprouting ability after fire).

Plant phenology in MTEs is one of the traits that have been thought to converge (Mooney *et al.*, 1974). Phenological convergence may be the result of similar adaptations in all MTEs to summer drought (Mooney & Kummerow, 1981). The response of plants to these factors is supposed to be modelled by natural selection (Rathcke & Lacey, 1985). However, some authors have considered that natural selection has nothing to do with phenology because genetic constraints (phylogenetic inertia) may explain the current phenological patterns (Kochmer & Handel, 1986; Primack, 1987; Ollerton & Lack, 1992). It is probable that the optimal time to flower is determined by several factors, both intrinsic (e.g. constrained by phylogeny) and extrinsic (pollinator and seed disperser availability, interspecific competition, climatic and microclimatic conditions) (Petanidou *et al.*, 1995 and references therein).

In the Mediterranean Basin, historical effects on flowering phenology have been detected because Tertiary species which evolved under a tropical climate present different phenologies from Quaternary species which evolved under a 'typical' Mediterranean climate (Herrera, 1986; Cabezudo *et al.*, 1993; Aronne & Wilcock, 1997). Because the current Mexical conditions approximate those under which the pre-Mediterranean flora lived during the Tertiary period (Axelrod, 1973), knowledge of the phenological patterns of Tertiary and Quaternary taxa

occurring in MEX compared to those of MTEs may permit us to infer the relative importance of the Mediterranean climate as a selective pressure *vs* phylogenetic inertia. In particular, if Mediterranean climate has been a strong selective pressure towards spring flowering, then phenological differences between Tertiary and Quaternary species from MTEs would not be expected. In contrast, if phylogenetical and historical constraints are limiting natural selection, Tertiary species would be expected to retain a tropical (Mexical)-like phenology whereas Quaternary species would show spring (mediterranean) flowering.

This paper compares the flowering phenology of MEX communities with that of MTEs (California, Chile, and Mediterranean Basin) in order to detect: (1) similarities at the community level between MTEs and MEX; (2) similarities between Tertiary and Quaternary taxa in MTEs and MEX; and (3) similarities between congeneric taxa from MEX and MTEs (taxa sharing a common ancestor but evolved under different climates).

MATERIAL AND METHODS

Data on flowering phenology from MTEs woody species were obtained from Munz & Keck (1973), and from Wiggins (1980) for California, Hoffman (1978) for Chile, and Mateo & Crespo (1998) for the Mediterranean Basin. All the species included in the analysis live in areas with mediterranean climate. Data on MEX flowering phenology were obtained from the MEXU herbarium and field visits during one year to the semiarid Tehuacán-Cuicatlán valley, in the states of Puebla and Oaxaca, México (see Valiente-Banuet *et al.*, 1998 for a description of the area).

The age of the lineage of species from Mediterranean Basin, California, Chile and Mexical was determined as Tertiary or Quaternary on the basis of the presence/absence of pre-Pliocene fossils of the genus, and/or the presence/absence of geographical disjunction (Herrera, 1992). Fossil data was obtained from Axelrod (1975, 1979), Herrera (1992), Vilagrán & Hinojosa (1997), Zhilin (1989), and from palaeobotanical databases on the web (Plant Fossil Record Database from the International Organisation of Palaeobotany at <http://ibs.uel.ac.uk/palaeo/pfr2/pfr.htm>; The Museum of Palaeontology from University of California at <http://annie.ucmp.berkeley.edu/tutor/pbcSpC.hei>; The Yale Peabody Museum collections at <http://www.peabody.yale.edu/collections/pb/SEARCH.html>). Associations between the age of the lineage and the flowering season of 576 species from California, Chile, Mediterranean Basin and Mexico were analysed in a $4 \times 2 \times 4$ saturated log-linear model (4 areas \times 2 lineage

ages × 4 seasons). Our database is available upon request to the senior author.

A more detailed flowering phenology for common genera in MEX and MTEs was obtained in the literature and from the field in order to compare the response of congeneric species under different climates and geography. The genera and the number of species considered in this analysis were *Amelanchier* (4), *Arctostaphylos* (= *Comarostaphylis*) (14), *Dodonaea* (1), *Gochnatia* (2), *Krameria* (3), *Rhus* (10), *Quercus* (15), *Salvia* (28), *Satureja* (7) and *Sophora* (= *Calia*) (2).

RESULTS

Flowering seasonality followed a very similar phenological pattern in California, Chile and the Mediterranean Basin, consisting of a peak in spring (Fig. 1). In contrast, phenology of MEX had a flowering peak in summer, not spring, reflecting the fact that summer was the wet season (Fig. 1).

The log-linear model showed a significant three-way interaction (L.R. $\chi^2 = 46.2$; d.f. = 9; $P < 0.0001$), indicating that the age of the lineage was associated with the flowering season in a different way for each of the geographical areas (Table 1). In the Mediterranean

Basin, Quaternary species flowered mainly in spring whilst Tertiary species flowered less frequently than expected at this time. In contrast, Californian Quaternary species flowered less frequently in spring and winter, and more frequently in summer and autumn. Flowering seasonality was not associated with the age of lineage in Chile and Mexico.

Flowering phenology of the MEX species differed from their congeneric species in MTEs (Table 2). The general pattern found in MEX species was that they had several flowering periods in the year, whereas MTE species flowered in one period. Only *Krameria cytisoides* Cav. in MEX had a continuous flowering period over the whole year. None of the comparisons revealed a similar phenology between a MEX species and their MTE congeners.

DISCUSSION

MEX vegetation presents characteristics very similar to those of MTEs in spite of living under a summer-rain, tropical climate. Valiente-Banuet *et al.* (1998) and Lloret *et al.* (1999) have documented a strong similarity in both communities in physiographic structure and also at the species level in terms of sclerophylly, leaf architectural mechanisms of water stress avoidance, response to fire, and shrub dominance.

The origin of MTEs is geologically and ecologically marked by a progressive transition from summer-wet to summer-drought (Roy *et al.*, 1995). Dry summer and cool winter conditions limit plant activity, and for this reason flowering in spring is a widespread character of MTE plants (Mooney & Kummerow, 1981; Rundel, 1995). The climatic scenario in MEX has summer rains, and here summer is the most favourable season to grow and flower. As expected, plants from MEX have their main flowering peak in summer. This difference between MEX and MTEs flowering phenologies supports the hypothesis that plants are responding to climatic factors. The response of plants to climate is supposed to be driven by natural

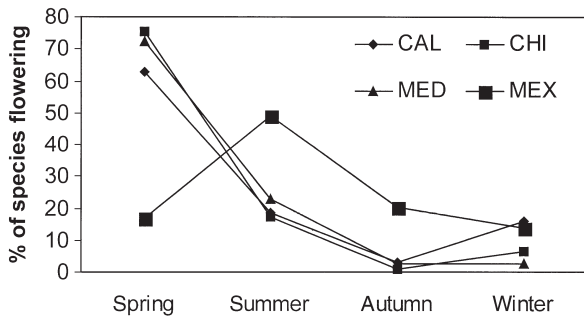


Figure 1. Seasonal variation in the percentage of species flowering in Mediterranean and Mexical communities.

Table 1. Number of species of different lineage age flowering at each season in the communities studied. Signs in brackets are shown if the observed frequencies are significantly greater (>) or lower (<) than expected by chance in the saturated log-linear model

	California				Chile				Mediterranean				Mexical			
	SP	SU	AU	WI	SP	SU	AU	WI	SP	SU	AU	WI	SP	SU	AU	WI
Tertiary	89 (>)	9 (<)	1 (<)	27 (>)	46	10	1	4	109 (<)	40	6	6	8	21	9	7
Quaternary	23 (<)	24 (>)	4 (>)	1 (<)	24	6	0	2	68 (>)	16	0	0	3	7	3	2

Table 2. Flowering phenology of congeneric species shared between Mexical and Mediterranean climate zones

Species	Location	Ref.*	Climate†	J	F	M	A	M	J	J	A	S	O	N	D
<i>Amelanchier denticulata</i> C. Koch	Mexical	1	T						—			—	—	—	
<i>A. ovalis</i> Medic.	Spain	4	M				—	—							
<i>A. utahensis</i> Koehne	California	3	M				—	—							
<i>A. pallida</i> Greene	California	3	M				—	—							
<i>Arctostaphylos polifolia</i> Torr.	Mexical	1	T						—				—		
<i>A. uva-ursi</i> Spreng	Spain	4	M		—	—	—	—							
<i>A. pumila</i> Nutt	California	3	M		—	—	—	—							
<i>A. morroensis</i> Wiesl. & Schreiber	California	3	M	—	—	—	—	—							
<i>A. nummularia</i> A. Gray	California	3	M			—	—	—							
<i>A. tomentosa</i> Lindl.	California	3	M	—	—	—	—	—							—
<i>A. canescens</i> Eastw.	California	3	M	—	—	—	—	—							
<i>A. auriculata</i> Eastw.	California	3	M		—	—	—	—							
<i>A. densiflora</i> M.S. Baker	California	3	M			—	—	—							
<i>A. manzanita</i> Parry	California	3	M		—	—	—	—							
<i>A. pajaroensis</i> J. E. Adams	California	3	M	—	—	—	—	—							—
<i>A. pringlei</i> Parry	California	3	M		—	—	—	—							—
<i>A. hookeri</i> G. Don	California	3	M		—	—	—	—							—
<i>A. virgata</i> Eastw.	California	3	M	—	—	—	—	—							—
<i>Dodonaea viscosa</i> Jacq.	Mexical	1	T			—	?		—	?					
<i>D. viscosa</i> Jacq	Baja California	2	M			—	—	—	—	—					
<i>Gochnatia hipoleuca</i> A. Gray	Mexical	1	T	—	—	—	—	—						—	
<i>G. foliolosa</i> D. Don ex Hook. & Arn.	Chile	5	M	—	—	—	—	—							
<i>Krameria cytisiodes</i> Cav.	Mexical	1	T	—	—	—	?	—	—	?	—	—	—	—	
<i>K. paucifolia</i> Rose	Baja California	2	M				—	—	—	—					
<i>K. grayi</i> Rose & Painter	Baja California	2	M				—	—	—	—					
<i>Rhus standleyi</i> F. A. Barkley	Mexical	1	T	—	—	?				?	—				—
<i>R. virens</i> Lindheim. Ex A. Gray	Mexical	1	T		—	?				?					
<i>R. chondroloma</i> Standley	Mexical	1	T		—	?			—	?					—
<i>R. lentii</i> Kellogg	Baja California	2	M		—	—	—	—							
<i>R. ovata</i> S. Wats.	Baja California	2	M		—	—	—	—							
<i>R. microphylla</i> Engelm.	Baja California	2	M		—	—	—	—							
<i>R. diversiloba</i> Torr. & A. Gray	Baja California	2	M		—	—	—	—							
<i>R. integrifolia</i> Engl.	California	3	M	—	—	—	—	—						—	
<i>R. ovata</i> S. Wats.	California	3	M		—	—	—	—							
<i>R. trilobata</i> Nutt.	California	3	M		—	—	—	—							
<i>R. coriaria</i> Linn.	Spain	4	M				—	—	—	—					
<i>Quercus sebifera</i> Trelease	Mexical	1	T		—	?				?	—				
<i>Q. dunnii</i> Kellogg	Baja California	2	M		—	—	—	—							
<i>Q. cedrosensis</i> C.H. Muller	Baja California	2	M		—	—	—	—							
<i>Q. ajoensis</i> C.H. Muller	Baja California	2	M		—	—	—	—							
<i>Q. turbinella</i> Greene	Baja California	2	M				—	—							
<i>Q. peninsularis</i> Trelease	Baja California	2	M				—	—							
<i>Q. engelmannii</i> Greene	Baja California	2	M				—	—							
<i>Q. chrysolepis</i> Liebm.	Baja California	2	M				—	—							
<i>Q. tomentella</i> Engelm.	Baja California	2	M				—	—							
<i>Q. agrifolia</i> Nee	Baja California	2	M				—	—							
<i>Q. coccifera</i> Linn.	Spain	4	M		—	—	—	—							
<i>Q. ilex</i> Linn.	Spain	4	M				—	—	—	—					
<i>Q. suber</i> Linn.	Spain	4	M				—	—	—	—					
<i>Q. faginea</i> Lam.	Spain	4	M				—	—	—	—					
<i>Q. pyrenaica</i> Stev.	Spain	4	M				—	—	—	—					
<i>Salvia candicans</i> Mart. & Gal.	Mexical	1	T	—		?				?					
<i>S. aspera</i> Mart. & Gal.	Mexical	1	T	—		?		—	—	?	—				

Table 2. Continued

Species	Location	Ref.*	Climate†	J	F	M	A	M	J	J	A	S	O	N	D
<i>S. similis</i> T. S. Brandegee	Baja California	2	T, M	_____											_____
<i>S. carduacea</i> Benth	Baja California	2	M			_____									
<i>S. columbariae</i> Benth	Baja California	2	M			_____									
<i>S. peninsularis</i> T. S. Brandegee	Baja California	2	M												_____
<i>S. marci</i> Epling	Baja California	2	M												_____
<i>S. cedrosensis</i> Greene	Baja California	2	M	_____											
<i>S. munzii</i> Epling	California	3	M		_____										
<i>S. brandegei</i> Munz	California	3	M				_____								
<i>S. eremostachya</i> Jepson	Baja California	2	M					_____	_____						
<i>S. pachyphylla</i> Epling	Baja California	2	M							_____					
<i>S. chionoeplica</i> Epling	Baja California	2	M			_____									
<i>S. clevelandi</i> Greene	Baja California	2	M			_____									
<i>S. mohavensis</i> Greene	Baja California	2	M					_____							
<i>S. platycheila</i> A. Gray	Baja California	2	M	_____									_____		
<i>S. californica</i> Jepson	Baja California	2	M					_____	_____						
<i>S. mellifera</i> Greene	California	3	M				_____								
<i>S. apiana</i> Jepson	California	3	M				_____								
<i>S. clevelandi</i> Greene	California	3	M				_____								
<i>S. lavandulifolia</i> (Pau) R. Figuerola	Spain	4	M					_____							
<i>S. blancoana</i> Webb & Heldr. ex Walp	Spain	4	M					_____							
<i>S. sclarea</i> Linn.	Spain	4	M					_____							
<i>S. phlomooides</i> Asso	Spain	4	M					_____							
<i>S. aethiopis</i> Linn.	Spain	4	M					_____							
<i>S. verbenaca verbenaca</i> Linn.	Spain	4	M	_____											
<i>S. verbenaca clandestina</i> Linn.	Spain	4	M		_____										
<i>S. pratensis</i> Linn.	Spain	4	M					_____							
<i>S. valentina</i> Vahl	Spain	4	M					_____							
<i>Satureja oaxacana</i> (Fernald) Standleyi	Mexical	1	T	_____			?	_____			?				_____
<i>S. chandleri</i> (Brandegee) Druce	Baja California	2	M					_____							
<i>S. ganderi</i> Epling	Baja California	2	M			_____									
<i>S. montana</i> Linn.	Spain	4	M						_____						
<i>S. obovata</i> (G.López) M.B.Crespo	Spain	4	M						_____	_____					
<i>S. intricata</i> (Willk.) Rivas-Martinez ex G.López González	Spain	4	M							_____					
<i>S. gilliesi</i> Benth	Chile	5	M	_____											_____
<i>Sophora secundiflora</i> Lag. ex DC	Mexical	1	T	_____											
<i>S. macrocarpa</i> Sm.	Chile	5	M										_____		

*References: 1, Present study; 2, Wiggins (1980); 3, Munz & Keck (1973); 4, Mateo & Crespo (1998); 5, Hoffman (1978).

†T, Tropical climate; M, Mediterranean climate.

selection (Rathcke & Lacey, 1985). Some authors have stated that natural selection cannot shape flowering phenology because of phylogenetic constraints (Kochmer & Handel, 1986; Primack, 1987; Ollerton & Lack, 1992). In this study, congeneric species living in both MEX and MTEs displayed different flowering patterns, suggesting that even though a common ancestor is shared, environmental pressures have led to different phenologies. Similar results have been

found by Petanidou *et al.* (1995) who show that flowering phenology of a Mediterranean Basin plant community is not set by phylogenetic constraints because of the overriding influence of the mediterranean climate.

Some studies in the Mediterranean Basin have shown that flowering phenology is related to the age of the lineage, because Tertiary species originated under a tropical-like climate (very similar to the

current Mexical climate), whereas Quaternary species evolved under the Mediterranean climate (Herrera, 1986; Cabezudo *et al.*, 1993; Aronne & Wilcock, 1997). For this reason, phenology in Tertiary species may be a relictual behaviour while phenology in Quaternary species may be a derived behaviour. The Mexical phenology approximates the conditions under which the pre-Mediterranean flora lived during the Tertiary (Axelrod, 1973). Tertiary and Quaternary species from MEX do not differ in their flowering seasonality, as expected, because the climate has not changed (Rzedowski, 1978). In MTEs, however, flowering of species originating in Tertiary and Quaternary periods is different. The main difference between Californian and Mediterranean Basin phenologies was that Quaternary taxa flower in spring more frequently than expected in the Mediterranean Basin but less than expected in California. These differences suggest that the balance between the historical constraints and the selective force of the mediterranean climate is different among the three MTEs, and a particular explanation is needed for each. Further research is needed to explore the different responses of Tertiary and Quaternary species across the MTEs and assess the relative importance of the mediterranean climate as a selective pressure *vs* the historical constraints.

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REFERENCES

- Aronne G, Wilcock CC. 1994.** Reproductive characteristics and breeding system of shrubs of the Mediterranean region. *Functional Ecology* **8**: 69–76.
- Aronne G, Wilcock CC. 1997.** Reproductive phenology in Mediterranean macchia vegetation. *Lagascalia* **19**: 445–454.
- Axelrod DI. 1973.** History of the Mediterranean ecosystem in California. In: di Castri F, Mooney H A, eds. *Mediterranean-type ecosystems. Origin and structure*. New York: Springer-Verlag. 225–277.
- Axelrod DI. 1975.** Evolution and biogeography of Madrean-Tethyan sclerophyll vegetation. *Annals of the Missouri Botanical Garden* **62**: 280–334.
- Axelrod DI. 1979.** Desert vegetation, its age and origin. In: Goodin JR, Northington DK, eds. *Arid land plant resources*. Texas: Institute Center for Arid and Semiarid Land Studies 1–72.
- Barbour MG, Minnich RA. 1990.** The myth of chaparral convergence. *Israel Journal of Botany* **39**: 453–463.
- Bond WJ. 1997.** Fire and the evolutionary origins of chaparral. *Abstracts of the MEDECOS VIII San Diego*, California, pp. 17.
- Cabezudo B, Pérez-Latorre AV, Navarro T, Nieto-Caldera JM. 1993.** Estudios fenomorfológicos en la vegetación del sur de España. II. Alcornocales mesomediterráneos (Montes de Málaga, Málaga). *Acta Botanica Malacitana* **18**: 179–188.
- Herrera CM. 1992.** Historical effects and sorting processes as explanations for contemporary ecological patterns: character syndromes in mediterranean woody plants. *American Naturalist* **140**: 421–446.
- Herrera J. 1986.** Flowering and fruiting phenology in the coastal shrublands of Doñana, South Spain. *Vegetatio* **68**: 91–98.
- Herrera J. 1987.** Flower and fruit biology in southern Spanish Mediterranean shrublands. *Annals of the Missouri Botanical Garden* **74**: 69–78.
- Hoffman A. 1978.** *Flora silvestre de Chile: zona central*. Santiago: Fundación Claudio Gay.
- Keeley JE. 1991.** Seed germination and life history syndromes in the California chaparral. *Botanical Review* **57**: 81–116.
- Kochmer JP, Handel SN. 1986.** Constraints and competition in the evolution of flowering phenology. *Ecological Monographs* **56**: 303–325.
- Lloret F, Verdú M, Flores-Hernández N, Valiente-Banuet A. 1999.** Fire and resprouting in Mediterranean ecosystems: insights from an external biogeographical region, the Mexical shrubland. *American Journal of Botany* **86**: 1655–1661.
- Mateo G, Crespo MB. 1998.** *Manual para la determinación de la flora Valenciana*. Valencia: Monografías de la flora montibérica 3.
- Mooney HA, Kummerow JK. 1981.** Phenological development of plants in Mediterranean-climate regions. In: di Castri F, Goodall DW, Specht RL, eds. *Mediterranean-type shrublands*. Amsterdam: Elsevier. 303–307.
- Mooney HADJ, Parsons Kummerow J. 1974.** Plant development in mediterranean climates. In: Lieth H, ed. *Phenology and seasonality modeling*. New York: Springer. 255–267.
- Munz PA, Keck DD. 1973.** *A California flora and supplement*. California: University of California Press.
- Ollerton J, Lack AJ. 1992.** Flowering phenology: an example of relaxation of natural selection? *Trends in Ecology and Evolution* **7**: 274–276.
- Petanidou T, Ellis WN, Margaris NS, Vokou D. 1995.** Constraints of flowering phenology in a phryganic (East Mediterranean shrub) community. *American Journal of Botany* **82**: 607–620.
- Pons A. 1981.** The history of the Mediterranean shrublands. In: di Castri F, Goodall DW, Specht RL, eds. *Mediterranean-type shrublands*. Amsterdam: Elsevier. 131–138.
- Primack RB. 1987.** Relationships among flowers, fruits, and seeds. *Annual Review of Ecology and Systematics* **18**: 409–430.
- Rathcke B, Lacey EP. 1985.** Phenological patterns of terres-

- trial plants. *Annual Review of Ecology and Systematics* **16**: 179–214.
- Raven P. 1973.** The evolution of Mediterranean floras. In: Di Castri F, Mooney HA, eds. *Mediterranean-type ecosystems. Origin and structure*. New York: Springer-Verlag. 213–224.
- Roy J, Aronson J, di Castri F. 1995.** Water constraints and mediterranean biota response: towards an integrated multi-scale picture. In: Roy J, Aronson J, di Castri F, eds. *Time scales of biological responses to water constraints. The case of Mediterranean biota*. Amsterdam: SPB Academic Publishing bv. 1–4.
- Rundel PW. 1995.** Adaptive significance of some morphological and physiological characteristics in Mediterranean plants: facts and fallacies. In: Roy J, Aronson J, di Castri F, eds. *Time scales of biological responses to water constraints. The case of Mediterranean biota*. Amsterdam: SPB Academic Publishing bv. 119–139.
- Rzedowski J. 1978.** *Vegetación de México*. México D.F: Limusa.
- Suc JP. 1984.** Origin and evolution of the mediterranean vegetation and climate in Europe. *Nature* **307**: 429–432.
- Valiente-Banuet A, Flores-Hernández N, Verdú M, Dávila P. 1998.** The chaparral vegetation in México under non-mediterranean climate: convergence and Madrean-Tethyan hypotheses reconsidered. *American Journal of Botany* **85**: 1398–1408.
- Verdú M. 2000.** Ecological and evolutionary differences between Mediterranean seeders and resprouters. *Journal of Vegetation Science* **11**: 265–268.
- Vilagrán C, Hinojosa LF. 1997.** Historia de los bosques del sur de Sudamérica, II: Análisis fitogeográfico. *Revista Chilena de Historia Natural* **70**: 241–267.
- Wiggins IL. 1980.** *Flora of Baja California*. California: Stanford University Press.
- Zhilin SG. 1989.** History of the development of the temperate forest flora in Kazakhstan, USSR from the Oligocene to the early Miocene. *Botanical Review* **55**: 205–332.