Vegetation disturbance by fire affects plant reproductive phenology in a shrubland community in northwestern Patagonia, Argentina.

Juan Paritsis,[1,2*] Estela Raffaele [1], and Thomas T. Veblen [2]
[1]Laboratorio Ecotono, Universidad Nacional del Comahue, Quintral 1250, 8400 Bariloche, Argentina
[2] Department of Geography, University of Colorado, Campus Box 260, Boulder, CO 80309-0260, USA
*Author for correspondence (E-mail: paritsis@colorado.edu)

Abstract: Reproductive phenology is likely to vary spatially with environmental conditions that alter microclimate, in particular temperature. We hypothesized that within the same plant community type, environmental changes produced by recent burning would alter plant phenological patterns and temporal structure of the plant community. Specifically, we predicted accelerated flowering and fruiting dates in the burned, open environment compared with the unburned, intact community. We tested this hypothesis in a post-fire tall shrubland (*matorral*) in northwestern Patagonia, Argentina. During the reproductive season, phenological stages of seven vascular plant species were monitored weekly. Temperature, humidity, soil nutrients and photosynthetically-active radiation were also recorded. At the burned site, flowering began earlier in all species and the success rate of fruiting was higher. These patterns correlated with significant environmental differences, including higher mean temperatures at the burned site.

Keywords: flowering; fruit set; *matorral*; microclimate; nutrient availability; phenology

Introduction

Plant reproductive phenology plays a key role in the dynamics of plant and animal communities in many ways. The reproductive success of individual plant populations often depends in part on flowering phenology allowing plants to take advantage of temporally varying periods of favorable conditions (Zimmerman, 1988; Kearns and Inouye, 1993; Mahoro, 2002). Temporal patterns of plant reproduction have major impacts on other trophic levels and the temporal structure of the entire community (Herrera, 1986). Many animals depend, directly or indirectly, on the phenological patterns of plants (Smith-Ramírez and Armesto, 1994). For example, the survival and behavior of many pollinators depend directly on the timing of flowering in relation to their life cycles (e.g. Petit, 1997), and timing of fruiting plays a key role in controlling the abundance and variety of obligate frugivores (Fenner, 1998). Given the critical roles played by reproductive plant phenology in plant and animal communities, it is important to know how coarse-scale disturbances might affect phenological patterns through alteration of the environmental cues.

The primary environmental factors that influence plant phenological patterns are temperature, photoperiod and soil moisture (Rathcke and Lacey, 1985; Smith-Ramírez and Armesto, 1994). Other variables such as soil chemistry (Warembourg and Estelrich, 2001) may also affect plant phenological patterns but such effects are less clear. In temperate environments most woody species flower in response to temperature, and consequently cumulative heat sums often predict flowering (Rathcke and Lacey, 1985). Higher temperatures result in heat sums exceeding some required threshold level in the flowering season and may trigger earlier onset of flowering. Except for photoperiod, all the environmental factors mentioned above may potentially be modified by severe fire (Hassan and West, 1986; Certini, 2005). For example, sites where a forest or shrubland has been recently and severely burned, thus creating a more open environment, can present higher light and nutrient availability and higher maximum temperatures during the growing season (White *et al.*, 1991; Bond and van Wilgen, 1996). It is likely that if fire alters the vegetation structure in a way that results in higher temperatures, then plant reproductive phenology will be accelerated.

Environmental changes generated by fire can also affect time and/or amount of fruit set. This mainly occurs through increased solar radiation, temperature, and nutrient availability in a recently burned environment. The buildup of reproductive structures such as flowers and fruits demands high amounts of N and P to synthesize proteins and other essential substances (Sardans *et al.*, 2001). In addition, in temperate regions higher than average solar radiation and temperature usually have positive effects on fruit formation (Rathcke and Lacey, 1985). Therefore, increases in nutrients and solar radiation following a severe fire might be expected to result in early or more fruit set in a recently burned environment.

Numerous studies have focused on the effects of fire on successional development of plant communities (e.g. Hanes, 1971; Turner *et al*., 1997; Raffaele and Veblen, 2001; Ghermandi *et al*., 2004), but few have addressed the effects of fire on plant reproductive phenology (but see White *et al*., 1991). Fire, both natural and anthropogenic, is an important determinant of vegetation patterns near the ecotone of the Patagonian steppe and forests of the Andean foothills of southwestern Argentina (Veblen *et al*., 1992; Kitzberger and Veblen, 1999). Fire occurs more frequently in tall shrublands than in adjacent tall forests, and repeated fire results in the expansion of shrublands at the expense of forests (Kitzberger and Veblen, 1999). Given the widespread importance of fire in these shrublands and the effects of microenvironment on plant phenology, it seems likely that fire will have some influences on the reproductive phenology of the common plant species. Thus, the primary aim of this work is to determine if there are any differences in the flowering and fruiting phenology of the dominant woody species between a recently burned and an unburned shrubland community in northwestern Patagonia. Furthermore, key environmental variables are measured and compared between burned and unburned shrublands to explore possible environmental explanations for any differences in plant phenology.

We examine two hypotheses. First, in recently burned areas, flowering and fruiting will initiate earlier in comparison with unburned sites because of fire-induced changes in environmental variables such as increased light and temperature. Second, fruit set will be higher in burned areas than in the unburned environment because of the higher availability of light, nutrients and the higher temperatures.

Methods

Study area and plant species

The study was conducted in a shrubland plant community located in Nahuel Huapi National Park in Patagonia, Argentina (41° 21′ S, 71° 37′ W; c. 850 m above sea level) during the austral spring and summer 2002-2003. Mean annual precipitation is approximately 1600 mm (Barros *et al.*, 1983). Soils are medium-textured udands (INTA, 1990) and the area is located on a north-facing slope of generally < 10°. An extensive (3212 ha) and severe wildfire affected part of the shrubland in February 1999 (Administración de Parques Nacionales, unpublished report "PN Nahuel Huapi Argentina: Incendios Temporada 1998-1999"). Common plant species in this post-fire community (four years after the fire) are the small trees *Diostea juncea* (Gillies ex Hook.) Miers, *Lomatia hirsuta* (Lam.) Diels ex J. F. Macbr. and *Nothofagus antarctica* (G. Forst) Oerst., the shrub *Schinus patagonicus* (Phil.) I. M. Johnst., the semi-woody climber *Vicia nigricans* Hook. and Arn., and a variety of herbaceous species.

An unburned control area was established in an unburned portion of the shrubland seven kilometers west from the burned site (41° 20′ S, 71° 40′; c. 800 m above sea level). The control and burned site are both mapped as the same shrubland vegetation type in the Argentine National Parks map of the area (Mermoz and Martín, 1986) and our field observations did not reveal any significant differences in species composition or structure of the vegetation in the control and burned site. Precipitation, soil texture and aspect are similar at both sites (Barros *et al.*, 1983; INTA, 1990). At the unburned site the canopy is dominated by 8–9 m tall *Nothofagus antarctica*, accompanied by isolated individuals 5–6 m tall of *Diostea juncea*. The most abundant understory species are the shrubs *Maytenus chubutensis* (Speg.) Lourt. and O'Don. and Sleum., *Schinus patagonicus*, *Berberis buxifolia* Lam., the semi-woody climber *Mutisia spinosa* Ruiz and Pav., and the tree *Maytenus boaria* Molina.

Flowering and fruiting phenology of seven species was monitored in the burned and unburned sites. The selected species were: the small trees *Diostea juncea* and *Lomatia hirsuta*; the shrubs *Berberis buxifolia*, *B. darwinii* Hook. and *Schinus patagonicus*; and the climbers *Vicia nigricans* and *Mutisia spinosa*. These species collectively account for approximately 30% of plant cover and 30% of total richness in the unburned shrubland and are characteristic of this vegetation type elsewhere in the region (Raffaele and Veblen, 1998). All the studied species are entomophilous, and, with the exception of the annual *Vicia nigricans*, all can regenerate by resprouting. Little is known about the pollinator guild in these shrublands, and what is known is derived from observations of the pollinators in nearby *Nothofagus* forests (Aizen *et al*., 2002). Common pollinators of the monitored species are the native and generalist bumble bee *Bombus dahlbomii*, the bees *Ruizantheda mutabilis* and *Cadeguala albopilosa*, and the dipteran *Trichophthalma amoena* (Aizen *et al*., 2002).

Environmental variables

Air temperature and relative humidity (RH) were recorded at one hour and half intervals from December 2002 to the end of the study period (April 2003), using two sensors with data loggers (HOBO®). One was placed in the recently burned environment and the other in the unburned environment. Both were located one meter above the ground and in shade.

Volumetric soil moisture (volume water/total volume) was measured with a Theta Probe type ML2X (Delta-T devices), at 13 cm depth, below each marked plant. We took soil moisture measurements at each individual plant at the beginning, middle and end of the sampling period (October–March), and averaged the three values for each plant. Photosynthetic photon flux density (PPFD) was measured at each individual plant by using a sensor. We placed the sensor at the top of the crown of each plant, except for the small trees *Diostea juncea* and *Lomatia hirsuta*, in which case we placed it as high as practical (c. 2.5 m). Measurements of PPFD were initiated at noon and there was a maximum of two hours of difference in recording time between sites. Both types of data were transformed to percentages; the maximum value for soil humidity corresponds to pure water, and the maximum value for light corresponds to the PPFD recorded in a large open area.

Soil samples were taken in each environment two years after fire. We collected 0.5 kg of the top 10 cm of soil in five randomly located points in each environment. Soils were air dried, sieved through a 2-mm mesh, and analyzed for extractable P in 0.5 M $NaHCO_3$ by the molybdate ascorbic acid method (Olsen and Sommers, 1982). Organic C and total N were analyzed by Walkley-Black wet digestion and semi-micro Kjeldahl, respectively, in samples ground to pass a 0.5-mm mesh (Nelson and Sommers, 1982; Bremner and Mulvaney, 1982).

Phenology

From 23 September 2002 to late March 2003, we made three types of observations to assess the reproductive phenology of the seven species. All these observations were carried out the same day at weekly intervals.

For the first type of observation, we marked and monitored five to ten mature individuals of each selected species in each environment. Individuals of the same species were of similar size in both environments. For each individual we chose and marked three ramets, and counted the total number of flowers or fruits throughout the reproductive period. Phenological stages were classified as flower bud, open flower, senescent flower, unripe fruit, and ripe fruit.

The second type of observation was made to obtain a more complete phenological record at the community level. In this case we monitored unmarked individuals of the seven selected species by walking and recording phenological stage in 5-m wide transects. At each sampling date, we located new transects separated by c. 15 m from previous locations to capture possible within-habitat variability in phenology. The most advanced phenological stage observed for each individual was recorded as its current phenological stage. We moved along the belt transect until the phenological stages of at least 20 individuals of each species were observed.

The third type of observation consisted of recording dates of flowering initiation at a broad spatial scale. We recorded the date at which the first individual of each species was seen bearing open flowers in each environment based on observing the marked individuals and belt transects as well as a general search of each study site. Additionally, we calculated the fruit set for each species in the two environments as the percentage of open flowers that developed ripe fruits. The fruit set was the average for all the marked individuals of each species' population.

Data analysis

To evaluate the differences between mean values of all the environmental variables (i.e. PPFD, air temperature, air humidity, soil moisture, and soil nutrients) between burned and unburned environments we computed bootstrapped 95% confidence intervals of the differences between means. Confidence intervals were estimated from 1000 Monte Carlo simulations (Manly, 1997).

Dates of phenological events were converted to a single number by setting the first day of sampling as day one, numbering the subsequent days sequentially. We used only marked individuals to compare average date of flowering and fruiting onset, average duration of these phenological stages, and fruit set for each species. To evaluate effects of recent fire disturbance on the reproductive phenology of each species separately, we calculated the difference in the mean flowering and fruiting onset between unburned and burned sites for each species. We also calculated the difference between sites for the mean flowering and fruiting duration for each species. To test statistical significance of differences between means we computed bootstrapped 95% confidence intervals of the differences between means based on 1000 Monte Carlo simulations (Manly, 1997) and compared these with the actual differences.

Percentage differences in fruit set between environments were calculated for each species. Bootstrapped 95% confidence intervals of the differences in fruit set between sites were calculated using 1000 Monte Carlo simulations to evaluate the statistical significance of the differences of means between environments (Manly, 1997).

Results

Environmental variables

All environmental variables (except soil C) showed significant differences between the two sites (Table 1). The unburned area had higher mean air temperatures

Table 1. Means ± SE and differences between means of the burned and the unburned sites of all the measured environmental variables. The asterisk (*) indicates significant differences based on bootstrapped 95% confidence intervals computed for the difference s between means derived from 1,000 Monte Carlo simulations (P < 0.05).

Environmental variables	Unburned site	Burned site	Difference between sites	Sample size
Solar radiation (%)	25.3 ± 3.4	49.5 ± 5.2	24.2*	7
Air temperature (°C)	10.1 ± 0.1	12.0 ± 0.2	1.9*	135
Air humidity (%)	80.9 ± 0.9	72.5 ± 0.9	8.4*	135
Soil moisture (%)	23.3 ± 0.6	17.9 ± 0.7	5.4*	7
Soil phosphorus (mg kg^{-1})	0.4 ± 0.1	4.3 ± 0.8	3.9*	5
Soil nitrogen (mg kg^{-1})	3.2 ± 0.1	3.9 ± 0.1	0.7*	5
Soil carbon (mg kg^{-1})	54.2 ± 1.2	52.9 ± 1.8	1.3	5

and solar radiation than the unburned site ($P < 0.05$). Thermal amplitude was also wider at the burned site (-5 to 38 °C) than in undisturbed vegetation (-3.5 to 30 °C). Soil moisture at the unburned site was higher than at the burned site ($P < 0.05$). Soil phosphorus concentration was ten times higher at the burned site than in the unburned shrubland ($P < 0.05$). Soil nitrogen was also significantly more abundant at the burned site than in the unburned shrubland ($P < 0.05$). On the other hand, organic Carbon concentrations showed no significant differences between burned and unburned environments ($P > 0.05$).

Phenology

For individual species there was an advance in flowering onset in the burned environment compared to the unburned environment (Fig. 1). Comparing the first date of flowering (flowering onset) of all the marked individuals, we found a significant advance ($P < 0.05$) in the burned area in five of the seven species (*Berberis darwinii, B. buxifolia*, *Lomatia hirsuta*, *Vicia nigricans*, and *Diostea juncea*; Fig. 1). These species flowered 12 ± 2 days earlier on average in the burned environments than in the unburned one. At the community level, flowering onset (based on observing both marked and

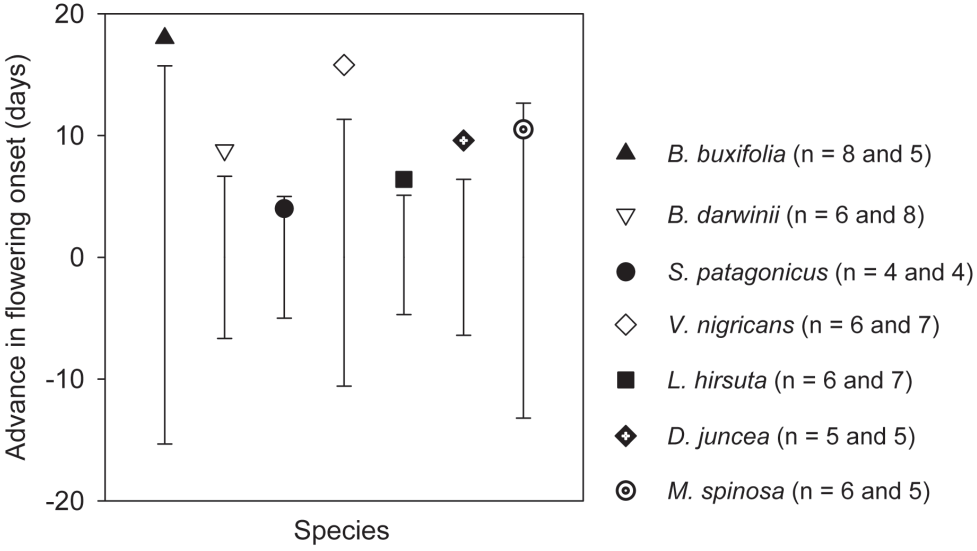

Figure 1. Differences in flowering onset for each species between the burned and the unburned environments expressed in days from the beginning of the observation period. Bars are bootstrapped 95% confidence intervals of the differences between means, estimated from 1000 Monte Carlo simulations, for each species. Only marked individuals are included in the analysis. Sample size (n) shows the number of marked individuals at the unburned and burned sites, respectively.

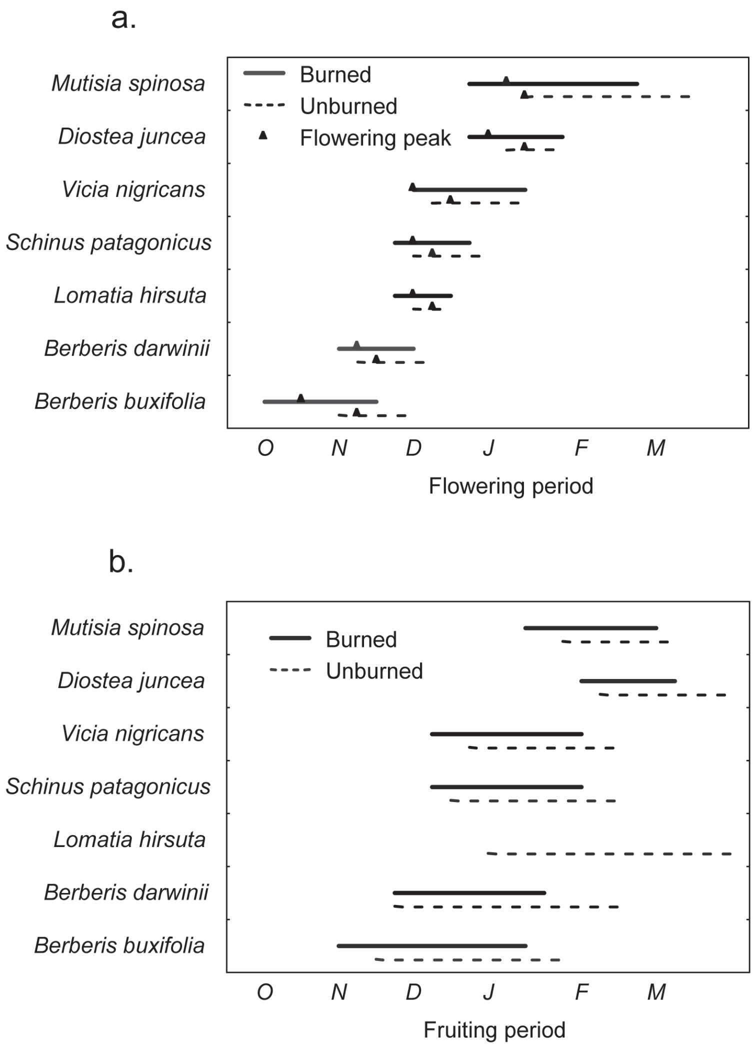

Figure 2. Timing of flowering (a) and fruiting (b) of the studied species in the burned and unburned environments based on marked individuals and belt-transects phenological data. Species' flowering peak corresponds to the date in which the highest percentage of open flowers was recorded (ranging from 30% to 70% for different species). In (b), there is no value for *L. hirsuta* in the burned environment because there was no fruit formation (all senescent flowers were abscised).

unmarked plants) started 18 ± 2 days earlier (total species average) in the burned environment than in the unburned area.

The lengths of flowering and fruit-ripening span were similar between environments. Only *Berberis buxifolia* and *Schinus patagonicus* exhibited a significant longer flowering span in the burned shrubland compared with the unburned one (based on marked individuals only; $P < 0.05$, $n = 3$ to 8, depending on the species). *B. buxifolia* was one of the first species in the community to bear open flowers, and *Mutisia spinosa* was the last one to maintain opened flowers (Fig. 2a). The first open flowers of *B. buxifolia* appeared in late September in the burned environment and the last flowers of *M. spinosa* remained opened until early March in the unburned shrubland. Together, these two species almost encompass the entire flowering span of the whole community (including the species not included in this study). The flowering span lasted approximately five months in both environments, with an average duration of flowering of 22 ± 3 days per species (at individual level) and 45 ± 4 days (at population level). Plants in the recently burned shrubland tended to develop their fruits earlier than their counterparts in the unburned shrubland (Fig. 2b). However, we found significant differences in the initiation dates of fruit formation between environments only for three of the seven species (*Vicia nigricans*, *Diostea juncea*, and *Mutisia spinosa*; $P < 0.05$).

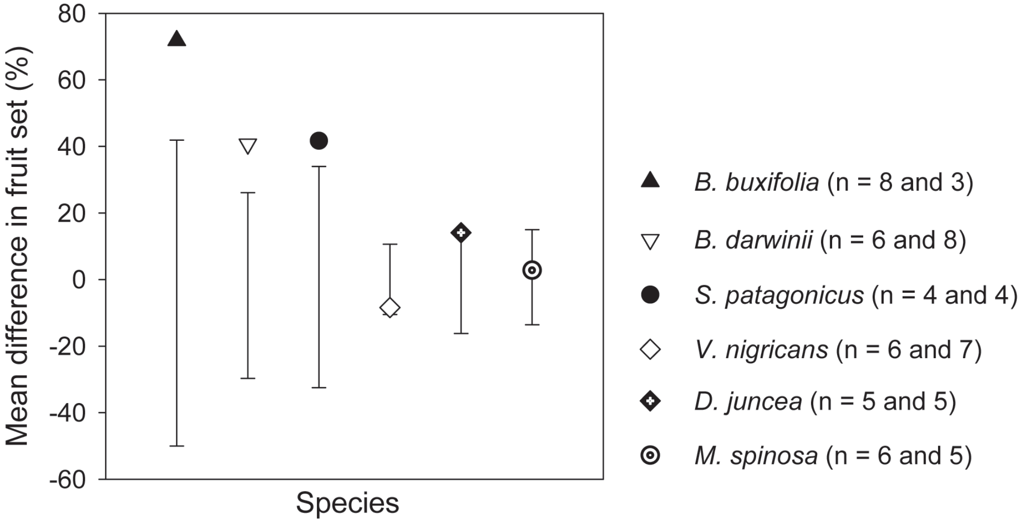

Figure 3. Fruit set (%) differences between burned and unburned environments and lower and upper 95% confidence intervals of the differences between means for each species, determined from 1,000 Monte Carlo simulations. Significant differences in fruit set between environments are noted with an asterisk. The sample size column shows the number of individuals at the unburned and burned sites, respectively. No values are given for *L. hirsuta* because of its failure to form fruits

In most species, fruit set (measured as percentage of open flowers that developed into ripe fruits) was greater in the recently-burned environment than in the unburned one (Fig. 3). These differences were significant ($P < 0.05$) only in the three shrub species (*Berberis buxifolia*, *B. darwinii*, and *Schinus patagonicus*). Two more species (*Diostea juncea* and *Mutisia spinosa*) showed the same tendency but without significant differences.

Discussion

Flowering was initiated earlier on the burned site than on the unburned one, supporting our first hypothesis (Figs. 1 and 2a). Similar results were found in studies of ponderosa pine forest in Arizona, U.S.A. (White *et al.*, 1991) and in big sagebrush communities in Oregon, U.S.A. (Wrobleski and Kauffman, 2003). Both of those studies analyzed the effects of prescribed burning on the phenology of herbaceous species. In the first study, the phenology of four grasses was recorded during the first and second growing seasons after fire. During the second season there was an advance in reproductive phenology in two of the four species. The second study analyzed the phenological response to fire of nine forbs during the first growing season after fire and found an advance in flowering in only two species. The advance in flowering we recorded in our study is somewhat greater than those recorded in the cited studies. An important difference with previous studies is that we analysed the phenology of woody plants, instead of herbaceous plants (with the exception of *V. nigricans*). Because of their longer lifespan, woody species can be assumed to have more plastic responses than herbaceous species and thus may be better able to respond to the increase in resource availability generated by fire.

We detected significant differences between the burned and unburned sites for most of the monitored environmental variables (i.e. temperature, solar radiation, moisture, and soil nutrients; Table 1). All of these variables can potentially contribute to the advance in the reproductive phenology observed in the burned shrubland (Rathcke and Lacey, 1985; Smith-Ramírez and Armesto, 1994; Warembourg and Estelrich, 2001). Nevertheless, some factors are considered more likely to influence plant phenology and may have more explanatory weight than others.

The time of flowering onset of most temperate woody species depends primarily on certain temperature thresholds (Rathcke and Lacey, 1985; Larcher, 1995). The higher mean and maximum temperatures recorded in the burned shrubland compared to the unburned one may have generated the more rapid attainment of the flowering threshold in the former. Environmental cues have less influence on fruiting onset than on flowering onset. Fruiting is primarily determined by internal factors that control the rate of fruit development (Rathcke and Lacey, 1985). Thus, the relatively weak effect of the environmental differences on fruiting onset between the burned and unburned shrublands (Fig. 2b) is consistent with the literature.

The higher N and P soil concentrations at the burned site might be surprising because intense fires can cause considerable loss of nutrients through volatilization, leaching and erosion (Agee, 1993). However, the pre-fire nutrient concentration can be recovered and even enhanced after a certain period of time (Certini, 2005). In a meta-analysis of fire effects on soil N, Johnson and Curtis (2001) found that N levels often show an increase in years following fire, but the authors did not distinguish between total and available N. Specifically, they found that among those studies carried out 10 years after fire, a significantly higher number of them recorded an increase in soil N. Fires do not have the same effect on N as they do on P. In fact, P tends to increase right after fire (Serrasolsas and Khanna, 1995) and starts to decline soon after. However, the timing of these trends in P concentration is extremely variable (Certini, 2005). In other studies of the effects of fire on soil nutrients in similar ecosystems in northern Patagonia, in some cases, the concentration of nutrients, particularly Nitrogen (measured as total N) was shown to be variable after fire (Alauzis *et al.* 2004, Kitzberger *et al.* 2005). In one study (Urretavizcaya, 2005) the concentration of nitrogen was higher in the burned sites.

The combination of higher solar radiation, higher temperatures and greater availability of soil nutrients at the recently burned site could explain the more abundant fruit set in this environment than at the unburned site (Fig. 3). Both N and P are key elements for flower and fruit formation (Alva *et al.*, 2001; Sardans *et al.*, 2005). In addition, Chapin *et al.* (1995) found that the major effect of increased temperature was to accelerate plant response to changes in soil nutrient concentrations, suggesting an interactive effect of these two factors. Thus, the higher solar radiation and temperatures of the recently burned site could favor the assimilation of the greater nutrient availability.

Because pollinator activity was not monitored in the current study, we could not determine if greater fruit set at the recently burned site was due to physiological conditions of the plants related to environmental differences among the two areas, or if it was due to greater abundances or activity of pollinators in one of the environments. Potentially, both explanations contribute to the recorded fruit set differences, but further studies are required to assess the effects of pollinators on the observed variations in plant phenology.

We presume that the differences we found in flowering onset have ecological implications on other taxa, mainly pollinators. All of the studied plant species share the same pollinator syndrome, entomophily, and had a relatively short flowering span (45 days on average). Consequently, the average advance of 12 days found in more than half of the species in the recently burned shrubland represents a significant modification of flowering onset and flower senescence, which could influence pollinator activity. Future research on this topic should consider the effects of the changes in plant reproductive phenology on the associated mutualistic organisms of the community.

Acknowledgments

This research was funded by the National Science Foundation of the U.S.A. (Award No. 0117366) and Foncyt PICT 01-07320. We thank Norlan Tercero Bucardo, Carolina Quintero and María Clara Paritsis for field assistance. Comments from three anonymous referees, C.H. Lusk and D. Peltzer significantly helped to improve this manuscript and are greatly appreciated.

References

Aizen, M.A.; Vázquez, D. P.; Smith-Ramírez, C. 2002. Natural history and conservation of plant-animal mutualisms in the temperate forest of southern South America. *Revista Chilena de Historia Natural 75*: 79-97.

Agee, J.K. 1993. *Fire ecology of Pacific Northwest forests*. Island Press, Washington, D.C.

Alauzis, M.V.; Mazzarino, M.J.; Raffaele, E.; Roselli, L. 2004. Wildfires in NW Patagonia: long-term effects on a *Nothofagus* forest soil. *Forest Ecology and Management 192*: 131-142.

Alva, A.K.; Paramasivam, S.; Hostler, K.H.; Easterwood, G.W.; Southwell, J.E. 2001. Effects of nitrogen rates on matter and nitrogen accumulation in *Citrus* fruit yield. *Journal of Plant Nutrition 24:* 561-572.

Barros, V.; Cordón, V.; Moyano, C.; Méndez, R.; Forquera, J.; Picio, O. 1983. *Cartas de precipitación de la zona oeste de las provincias de Río Negro y Neuquén*. Informe de la Facultad de Ciencias Agrarias, Universidad Nacional del Comahue, Neuquén, Argentina.

Bond, W.J.; van Wilgen, B.W. 1996. *Fire and plants*. Chapman and Hall, London.

Bremner, J.M.; Mulvaney, C.S. 1982. Nitrogen-total. *In:* Page, A. L.; Miller, R. H.; Keeney, D. R. (Editors), *Methods of soil analysis. Part 2*, pp 595-624. Second Edition. Series Agronomy American Society of Agronomy-Soil Science Society of America, Madison, Wisconsin, USA.

Certini, G. 2005. Effects of fire on properties of forest soils: a review. *Oecologia 143:* 1-10.

Chapin, F.S.III, Shaver, G.R., Giblin, A.E., Nadelhoffer, K.J.; Laundre, J.A. 1995. Responses of Artic tundra to experimental and observed changes in climate. *Ecology 76:* 694-711.

Fenner, M. 1998. The phenology of growth and reproduction in plants. *Perspectives in Plant Ecology, Evolution and Systematics 1:* 78-91.

Ghermandi, L.; Guthmann, N.; Bran, D. 2004. Early post-fire succession in northwestern Patagonia grasslands. *Journal of Vegetation Science 15*: 67-76.

Hanes, T.L. 1971. Succession after fire in chaparral of southern California. *Ecological Monographs 41:* 27-52.

Herrera, J. 1986. Flower and fruiting phenology in the coastal shrublands of Doñana, South Spain. *Vegetatio 68:* 91-98.

Hassan, M.A.; West, N.E. 1986. Dynamics of soil seeds pools in burned and unburned sagebrush semi-deserts. *Ecology 67:* 269-273.

INTA. 1990. *Atlas de suelos de la República Argentina*. Secretaria de Agricultura, Ganadería y Pesca. Proyecto P.N.U.D. 85/019.

Johnson, D.W.; Curtis, P.S. 2001. Effects of forest management on soil C and N storage: meta analysis. *Forest Ecology and Management 140:* 227-238.

Kearns, C.A.; Inouye, D.W. 1993. *Techniques for pollination biologists*. University Press of Colorado. Niwot, Colorado.

Kitzberger, T.; Veblen, T.T. 1999. Fire-induced changes in northern Patagonian landscapes. *Landscape Ecology 14:* 1-15**.**

Kitzberger, T.; Raffaele, E.; Heinemann, K.; Mazzarino, M.J. 2005. Direct and indirect effects of fire severity in north patagonian subalpine forests. *Journal of Vegetation Science 16*: 5-12.

Larcher, W. 1995. *Physiological plant ecology*. Springer-Verlag, Berlin.

Mahoro, S. 2002. Individual flowering schedule, fruit set, and flower and seed predation in *Vaccinium hirtum* Thunb. (Ericaceae). *Canadian Journal of Botany 80:* 82-92.

Manly, B. F. 1997. *Randomization, Bootstrap and Monte Carlo methods in biology*. 2nd Edition. Chapman and Hall, London.

Mermoz, M.; Martín, C. 1986. *Mapa de la vegetación del Parque y Reserva Nacional Nahuel Huapi*. Unpublished report. Administración de Parques Nacionales, Buenos Aires.

Nelson, D.W; Sommers, L.E. 1982. Total carbon, organic carbon and organic matter. *In:* Page, A. L.; Miller, R. H.; Keeney, D. R. (Editors), *Methods of soil analysis. Part 2*, pp 403-430. Second Edition. Series Agronomy American Society of Agronomy-Soil Science Society of America, Madison, Wisconsin, USA.

Olsen, S. R.; Sommers, I. E. 1982. Phosphorus. *In:* Page, A. L.; Miller, R. H.; Keeney, D. R. (Editors), *Methods of soil analysis. Part 2*, pp 403-430. Second Edition. Series Agronomy American Society of Agronomy-Soil Science Society of America, Madison, Wisconsin, USA.

Petit, S. 1997. The diet and reproductive schedules of *Leptonycteris curasoae* and *Glossophaga longuirostris elongata* (Chiroptera: Glossophaginae) on Curacao. *Biotropica 29:* 214-223.

Raffaele, E.; Veblen, T.T. 1998. Facilitation by nurse shrubs of resprouting behavior in a post-fire shrubland in northern Patagonia, Argentina. *Journal of Vegetation Science 9:* 693-698.

Rathcke, B.; Lacey, E.P. 1985. Phenological patterns of terrestrial plants. *Annual Review of Ecology and Systematics 16:* 179-214.

Sardans, J.; Rodà, F.; Peñuelas, J. 2005. Effects of water and a nutrient pulse supply on *Rosmarinus officinalis* growth, nutrient content and flowering in the field. *Environmental and Experimental Botany 53:* 1-11.

Serrasolsas, I.; Khanna, P.K. 1995. Changes in heated and autoclaved forest soils of S.E. Australia. II. Phosphorus and phosphatase activity. *Biogeochemistry 29:* 25-41.

Smith-Ramirez, C.; Armesto, J.J. 1994. Flowering and fruiting patterns in the temperate rain forest of Chiloe, Chile – ecologies and climatic constraints. *Journal of Ecology 82:* 353-365.

Turner, M.G.; Romme, W.H.; Gardner, R.H.; Hargrove, W.W. 1997. Effects of fire size and pattern on early succession in Yellowstone National Park. *Ecological Monographs 67:* 411-433.

Urretavizcaya M. F. 2005. Cambios ambientales y restauración ecológica post-incendio en bosques de *Austrocedrus chilensis*. Doctoral thesis, Universidad Nacional del Comahue, Bariloche, Argentina.

Veblen, T.T., Kitzberger, T.; Lara, A. 1992. Disturbance and forest dynamics along a transect from Andean rain forest to Patagonian shrublands. *Journal of Vegetation Science 3:* 507-520.

Warembourg, F.R.; Estelrich, H.D. 2001. Plant phenology and soil fertility effects on below-ground carbon allocation for annual (*Bromus madritensis*) and a perennial (*Bromus erectus*). *Soil Biology and Biochemistry 33:* 1291-1303.

Wrobleski, D.W.; Kauffman, J.B. 2003. Initial effects of prescribed fire on morphology, abundance and phenology of forbs in big sagebrush communities in Southeastern Oregon. *Restoration Ecology 11:* 82-90.

White, A.S.; Cook, J.E.; Vose, J.M. 1991. Effects of fire and stand structure on grass phenology in a ponderosa pine forest. *American Midland Naturalist 126:* 269-278.

Zimmerman, M. 1988. Nectar production, flowering phenology, and strategies for pollination. *In:* Lovett Doust, J.; Lovett Doust, L. (Editors), *Plant reproductive ecology: Patterns and strategies*, pp 157-178. Oxford University Press, New York.

Editorial Board member: Chris Lusk