

(This is a sample cover image for this issue. The actual cover is not yet available at this time.)

This article appeared in a journal published by Elsevier. The attached copy is furnished to the author for internal non-commercial research and education use, including for instruction at the authors institution and sharing with colleagues.

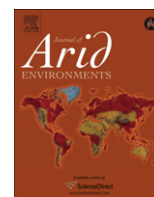
Other uses, including reproduction and distribution, or selling or licensing copies, or posting to personal, institutional or third party websites are prohibited.

In most cases authors are permitted to post their version of the article (e.g. in Word or Tex form) to their personal website or institutional repository. Authors requiring further information regarding Elsevier's archiving and manuscript policies are encouraged to visit:

<http://www.elsevier.com/copyright>

Contents lists available at [SciVerse ScienceDirect](http://www.sciencedirect.com)

## Journal of Arid Environments

journal homepage: [www.elsevier.com/locate/jaridenv](http://www.elsevier.com/locate/jaridenv)

# Plant phenology as affected by land degradation in the arid Patagonian Monte, Argentina: A multivariate approach

A.J. Bisigato<sup>a,b,\*</sup>, M.V. Campanella<sup>a</sup>, G.E. Pazos<sup>a,b</sup><sup>a</sup> Centro Nacional Patagónico/CONICET, Blvd. Brown 2825, 9120 Puerto Madryn, Chubut, Argentina<sup>b</sup> Universidad Nacional de la Patagonia San Juan Bosco, Blvd. Brown 3700, 9120 Puerto Madryn, Argentina

## ARTICLE INFO

## Article history:

Received 15 June 2011

Received in revised form

29 November 2012

Accepted 12 December 2012

Available online

## Keywords:

Global change

Grazing

Growing season

Plant cover

Plant size

## ABSTRACT

In recent years, there has been an increasing interest in the study of climate change effects on plant phenology. However, the effects of other more localized components of global change such as land degradation have been almost completely ignored. In this paper we evaluate the phenological patterns of 10 plant species at three sites with contrasting levels of land degradation due to overgrazing in the Patagonian Monte, Argentina, and their relationship with plant morphology, browsing intensity, and plant competition.

Plant phenology differed among sites in eight species, but plant responses were species-specific. In six species the dormancy and senescence periods were shorter indicating longer growing cycles at high degradation than at low degradation site. Generally, plants growing at high degradation site present longer and frequently incomplete vegetative periods and shorter and less dominant reproductive periods than those at low degradation site. However, in some species the duration of reproductive periods was greater in the high degradation site. Plant size (i.e. height, area, and/or internal cover) affected plant phenology in seven species. In contrast, browsing and neighbor's cover were rarely related to plant phenology. Our results suggest that other global change components such as land degradation may affect plant phenology.

© 2012 Elsevier Ltd. All rights reserved.

## 1. Introduction

Plant phenology and its relationship with environmental drivers such as temperature, precipitation or CO<sub>2</sub> concentration has received increasing attention in recent years (e.g. Archibald and Scholes, 2007; Vitasse et al., 2009). This interest is motivated by our need for understanding the consequences of climate change on both natural (Cleland et al., 2006; Peñuelas et al., 2002; Sherry et al., 2007) and agricultural ecosystems (Tubiello et al., 2007). Although the consequences of some components of global change such as climate change on plant phenology have been tackled, the effects of other less widespread components of global change (Vitousek, 1994), such as land degradation (e.g. desertification), have been almost completely ignored. In the few articles where the relationships between land degradation and phenology were

studied, this was mostly done at community or ecosystem level through remote sensing, evaluating changes in the length and timing of the growing season (e.g. Asner et al., 2003).

Analysis of plant phenology provides information regarding the abiotic and biotic variables that determine the seasonal development of plant organs (Shackleton, 1999). Temperature, soil moisture and photoperiod have been identified as the main factors triggering foliage, flower and fruit production in different plant communities (Rathcke and Lacey, 1985). For arid zones, the accepted belief is that phenological patterns are intimately related to water availability (Abd El-Ghani, 1997). Beyond these studies highlighting the importance of precipitation, there are also evidence of the influence of temperature and photoperiod on leafing, flowering and fruiting in desert plants (Abd El-Ghani, 1997; Archibald and Scholes, 2007). This is especially true in the case of deep-rooted species reaching deep soil water, which is less variable and more predictable than surface water (Pavón and Briones, 2001).

Besides these factors, plant size also affects phenology. It is well known that plants should reach a threshold size before reproduction (Rathcke and Lacey, 1985). However, plant size not only affects the magnitude and occurrence of reproductive growth but also

\* Corresponding author. Centro Nacional Patagónico/CONICET, Blvd. Brown 2825, 9120 Puerto Madryn, Chubut, Argentina. Tel.: +54 280 4451024x1321; fax: +54 280 4451543.

E-mail addresses: [bisigato@cenpat.edu.ar](mailto:bisigato@cenpat.edu.ar) (A.J. Bisigato), [campanella@cenpat.edu.ar](mailto:campanella@cenpat.edu.ar) (M.V. Campanella), [gpazos@cenpat.edu.ar](mailto:gpazos@cenpat.edu.ar) (G.E. Pazos).

influences leaf initiation (Otieno et al., 2005). Moreover, competition, through its effects on resource availability, can also affect plant phenology (Marco et al., 2000).

Grazing has a negative direct effect on reproduction of plants through consumption (Noy-Meir and Briske, 2002). Indirect effects of grazing are also common. For instance, Nötzold et al. (1998) showed that herbivory reduced plant height and biomass, delaying and shortening the flowering period. The effects of defoliation might last several years when reserve carbohydrates are depleted after foliage regeneration, affecting vegetative and/or reproductive growth in the following years (Goheen et al., 2007).

Patagonian Monte ecosystems have been grazed by sheep since early 20th century (Ares et al., 1990). As in other arid ecosystems, this disturbance has triggered changes in vegetation (Bisigato and Bertiller, 1997; Bisigato et al., 2005) and soils (Bisigato et al., 2008) consistent with land degradation (Ares et al., 2003). Under high grazing intensity, plant cover decreases by 62% (Bisigato et al., 2005), grasses are partially replaced by shrubs (Bisigato and Bertiller, 1997) and 17% of organic matter and nitrogen are lost from top soil by wind erosion (Bisigato et al., 2008). In addition, Bisigato and Lopez Laphitz (2009) found that grazing-induced degradation in the Patagonian Monte have a profound impact on soil water; soil water content in the whole profile was higher in degraded areas than in more conserved areas. These ecohydrological consequences of grazing affected the phenology of a perennial species: *Nassella tenuis* (ex-*Stipa tenuis*) had longer growth cycles both at degraded sites, where water availability was greater, and in the second growing season, when total rainfall was higher (Bisigato and Lopez Laphitz, 2009). However, it should be mentioned here that extended growth periods do not compensate the strong reduction in plant cover, and that ecosystem transpiration (i.e. productivity) is reduced as a consequence of land degradation.

The above mentioned results suggest that land degradation may affect phenological patterns at the community level. To test this, it is necessary to know whether similar changes in plant phenology as a consequence of grazing-induced degradation occur in other species belonging to different life forms, and whether they are related to direct (i.e. browsing) or indirect effects of grazing (i.e. through changes in plant size, plant density, and soil water). In this paper we compare the phenological patterns of the 10 dominant plant species at three sites with contrasting levels of land degradation due to overgrazing in the Patagonian Monte, Argentina, and their relationship with plant morphology, browsing intensity, and plant competition. In accordance with a previous study in *N. tenuis*, we hypothesize that plant phenology will be affected by land degradation; more specifically, growing periods will be extended with degradation. To our knowledge, this is the first report of phenological changes induced by land degradation that includes field observations of several dominant species in an arid plant community.

## 2. Materials and methods

### 2.1. Study site

The study area is representative of the Patagonian Monte located in north-eastern Chubut Province, Argentina (42° 39' S, 65° 23' W, 115 m.a.s.l.). The mean annual temperature is 13.4 °C and the average precipitation is 235.9 mm with high mean interannual variation and even seasonal distribution across the year (Anon, 2011). A seasonal pattern of wet (winter) and dry (summer) periods in surface soil moisture was observed (Bisigato and Lopez Laphitz, 2009). Soils are a complex of Typic Petrocalcids-Typic Haplocalcids (Soil Survey Staff, 1999). Soil mounds associated with shrub patches present higher sand, organic matter, and total nitrogen contents than bare soil areas (Bisigato et al., 2008;

Rostagno et al., 1991). Organic matter and nitrogen are accumulated in top soil (0–30 cm in depth), whereas deep soil layers present low concentration of these variables (Rostagno et al., 1991). Vegetation is representative of the shrubland of *Larrea divaricata* Cav. and *Stipa* spp., and it is arranged in patches of varying size and species richness surrounded by bare soil areas (Bisigato and Bertiller, 1997).

Few authors have studied the phenology of Patagonian Monte species and their relationships with climatic and/or edaphic variables (Bertiller et al., 1991; Campanella and Bertiller, 2008). Two main groups of species were identified by Campanella and Bertiller (2008) based on the season of phenological activity. In one group, evergreen shrubs (*Larrea* spp., *Chuquiraga* spp., and *Atriplex lampa*) and some deep-rooted deciduous shrubs (*Prosopis alpataco* and *Prosopidastrum globosum*) showed vegetative or reproductive growth during the dry season (summer). In the other group, a deep-rooted deciduous shrub (*Bougainvillea spinosa*), a shallow-rooted deciduous shrub (*Lycium chilense*) and perennial grasses (*N. tenuis* and *Poa ligularis*) concentrated vegetative activity during the wet winter–spring period.

### 2.2. Field sampling

Sampling was performed in three sites of about one ha each, located in a plain area at <4 km from each other. Based on previous studies, where the plant cover, the arrangement and development of plant patches and the density of faeces and sheep paths were reported (Bisigato and Lopez Laphitz, 2009; Bisigato et al., 2005, 2008; Pazos et al., 2007), these sites can be arranged along a degradation gradient (see Appendix 1, supplementary material). Such sites are ideal to study the relationships between land degradation and plant phenology since 1) dominant species are present in all sites, although their cover strongly vary among them (Bisigato et al., 2005), 2) the sites have a homogeneous soil (Bisigato and Lopez Laphitz, 2009), and 3) the short distance among them precludes any difference in climate (i.e. temperature, precipitation, and/or photoperiod). Henceforth, the sites will be called “low degradation”, “intermediate degradation”, and “high degradation”. Due to logistical constraints, we included in this study only one set of three contrasting land degradation sites. The three sites represent a degradation gradient found in previous studies (Ares et al., 2003; Bisigato and Bertiller, 1997; Bisigato and Lopez Laphitz, 2009; Bisigato et al., 2005, 2008; Pazos et al., 2007). In each site we randomly selected 20 mature individuals of the ten commonest species in terms of plant cover (Bisigato et al., 2005). We included four evergreen shrubs (*A. lampa*, *C. avellanadae*, *Chuquiraga erinacea* ssp. *hystrix*, *L. divaricata*), a dwarf-shrub (*Nassauvia fuegiana*), three deciduous shrubs (*B. spinosa*, *P. alpataco*, *P. globosum*), and two perennial grasses (*Pappostipa speciosa* (ex-*Stipa speciosa*) and *N. tenuis*). Due to sheep preference for perennial grasses, they were protected by individual exclosures. Nevertheless, the inflorescences of some individuals were eaten because they grown out of the exclosures. Likewise, a few shrubs were severely browsed. We considered that an individual was severely browsed when, as a consequence of browsing, it was impossible to follow its subsequent phenological development (e.g. when all reproductive structures in one individual were consumed). Finally, some shrubs and grasses died during the study. Both, severely browsed and dead individuals were not included in the analyses.

During fourteen months (April 2008–June 2009), we registered the phenophases (Table 1) of every plant at each site at intervals of fifteen/thirty days. Longer intervals were employed during summer and winter, when phenological development was slow in most species due to dryness and low temperatures, respectively. When a plant exhibited more than one phenophase, we registered all of them in order of importance based on the proportion of the plant

**Table 1**  
Phases describing phenological development (phenophases), based on Bertiller et al. (1991).

<b>Vegetative growth</b>	
le	Leaf emergence: first immature leaves visible.
ev	Early vegetative: shoots or tillers with green leaves not expanded.
iv	Intermediate vegetative: shoots or tillers with green leaves both expanded and not expanded.
lv	Late vegetative: internode elongation in shoots or tillers.
<b>Reproductive growth</b>	
<b>Flowering</b>	
ee	Ear emergence (grasses only): ears pre-formed but not visible.
sb	Swelling buds (shrubs only).
bu	Buds: flower buds visible. In grasses ears visible.
f	Flowers.
<b>Fruiting</b>	
gf	Green fruits.
mf	Mature fruits and seed dispersal.
<b>Non-growing, senescence and dormancy</b>	
vi	Vegetative inactivity: no growth but shoots or tillers still green.
s	Senescence: Senescence of green tissues.
d	Dormancy: Total vegetative inactivity, no green tissues present.

displaying each phenophase. Likewise, some morphological attributes were registered: every plant was measured (*height*, *area*) and their internal cover (*covi*, i.e. the percentage of the plant area effectively covered by plant tissues) was visually estimated. The proportion of browsed branches was also registered (*browsing*), but only in shrubs, as grasses were protected against grazers. Similarly, competitive effects of any neighboring plants were evaluated estimating their cover (*N-cover*) around the focal plant in the area encompassed by a circle of two focal plant diameters.

### 2.3. Climate during the study

At each site, we registered daily precipitation and air temperature with an automatic weather station. At one of the sites we also registered solar radiation. On the basis of these data, we estimated soil water content at each site using the soil water balance model of Bisigato and Lopez Laphitz (2009), developed and validated in these study sites.

### 2.4. Data analysis

#### 2.4.1. Calculation of phenological indices

For each individual plant and date, we calculated the following phenological index, *Phen*, for each phenophase *i*:

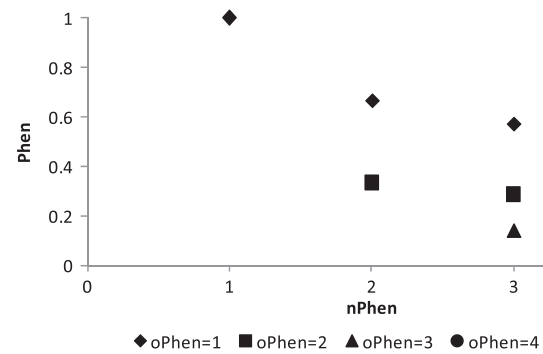
$$Phen_i = 0 \text{ when } i \text{ was absent, and}$$

$$Phen_i = \frac{2^{nPhen-1} / 2^{oPhen_i-1}}{2^{nPhen-1}} \text{ when } i \text{ was present}$$

where *nPhen*: number of phenophases present, and *oPhen*: order of importance of the phenophase *i*. Thus, for each individual and date, this index monotonically decreases from 1 (if *i* was the only phenophase present) to 0 (if *i* was absent) with increasing order of importance and number of phenophases present (Fig. 1). When more than one phenophase was present, the sum of *Phen* across them equals 1.

#### 2.4.2. Ordination of phenological data

For each species, *Phen* values were organized in a matrix of *p* combinations of dates and phenophases by *n* individuals and sites. After removing any combination of dates and phenophases without variance (both when *Phen<sub>i</sub>* = 0 and *Phen<sub>i</sub>* = 1 for all individuals), we submitted the matrix to a Principal Component Analysis (PCA) based on the correlation matrix of *Phen* values. Afterward, we



**Fig. 1.** Relationship between Phenological Index (*Phen*), the number of phenophases (*nPhen*) and the order of importance (*oPhen*) of the phenophase of interest.

calculated the mean scores on the first two PCA axes for each site. For simplicity, we only considered the first two principal components because the inclusion of additional axis changed the results only marginally (the analysis including a third axis is included on the Appendix 2, supplementary material). This method is similar to that used by Seghier and Simier (2002).

#### 2.4.3. Relationship between degradation and commonly used phenological variables

For every plant we also calculated the following phenological variables, which are commonly used in more descriptive approaches to plant phenology: duration (in days) of vegetative (DURVEG), reproductive (DURREP), senescence (DURSEN), and dormancy (DURDORM) periods; number of vegetative (#VEG) and reproductive (#REP) periods; and the period of dominance of each phenophase in days (D-phenophase). We considered a phenophase as dominant when it was the first in order of importance. To help interpret PCA results, we then assessed the relationship among the eigenvector scores on PCA axes 1 and 2 and phenological variables by means of Pearson's correlation coefficients.

#### 2.4.4. Land degradation and plant phenology

To separate the effects of site (i.e. land degradation) from those of plant morphology, browsing and N-cover on plant phenology, the ordination scores of plants on the first two principal components were then compared by ANCOVA, including site as a fixed factor and morphological variables, browsing and N-cover as covariates. In each case, the non significant terms were dropped from the models, and the simpler models were used for the analysis. If ANCOVA revealed a significant interaction site × covariate, additional analysis were conducted for each site.

## 3. Results

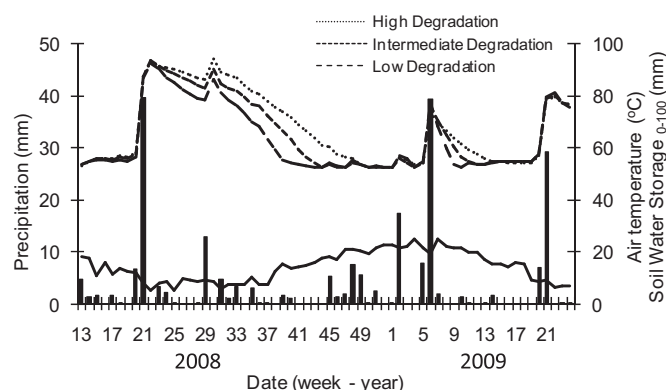
### 3.1. Climate during the study

The precipitation during the study period was lower than the long-term average, limiting the availability of water in the soil profile. However, a few precipitation events greater than 20 mm partially wetted the soil profile. After these events, water was more slowly lost from the high degradation site. As a consequence, mean water availability in the soil throughout the study increased with degradation (Fig. 2). Mean daily air temperatures and precipitation did not differ among sites.

### 3.2. Ordination of phenological data

The first 2 components of the principal component analyses explained between 23 and 35% of the total variability in phenology





**Fig. 2.** Weekly precipitation (bars), mean weekly air temperature (solid line), and estimated soil water storage in the soil profile (0–100 cm) during the study period in each site. Since there were not differences among sites, precipitation and air temperature are the means across sites.

across this 10-species dataset (Fig. 3, Appendix 3 supplementary material). In all species and axes (except PCA2 in *P. globosum*), plant scores were related with at least 3 commonly used phenological variables (Table 2, Fig. 3). In addition, in all species plant scores in at least one PCA axis were related to the duration of vegetative (DURVEG) and reproductive (DURREP) periods, and to the dominance of late vegetative growth (D-lv) (Table 2).

### 3.3. Relationship between degradation and commonly used phenological variables

The relationship between degradation and phenological variables can be analyzed in those PCA axes where sites displayed significantly different mean scores (Table 3b, Fig. 3). In half of the cases (*B. spinosa*, *C. avellanadae*, *C. erinacea* ssp. *hystrix*, *N. fuegiana*, and *P. globosum*) degradation was positively associated with the duration (DURVEG) and number (#VEG) of vegetative periods, and/or with higher dominance of late vegetative phenophases (D-iv and D-lv) (coefficients in bold and italics in Table 2). Among these species, *C. avellanadae*, *C. erinacea* ssp. *hystrix*, and *N. fuegiana* also exhibited shorter reproductive periods as a consequence of degradation. In contrast, three species (*B. spinosa*, *N. tenuis* and *P. globosum*) showed longer (DURREP) or more numerous (#REP) reproductive periods, and higher dominance in some reproductive phenophases (D-bu, D-ee, D-f, D-gf) with increasing degradation. Finally, *A. lampa* exhibited longer dormancy periods (DURDOR) and more dominant vegetative inactivity (D-vi) at high degradation. In contrast to this, *B. spinosa*, *C. avellanadae*, *C. erinacea* ssp. *hystrix*, *N. fuegiana*, *N. tenuis*, and *P. globosum* showed shorter dormancy (DURDOR) periods in the high degradation site (bold plain coefficients in Table 2), suggesting longer growing seasons as expected.

### 3.4. Degradation effects on plant phenology

In general, the effect of the covariates was not significant and in consequence they were dropped from the final models (Table 3a). Browsing only affected plant phenology in *B. spinosa* and *C. erinacea* ssp. *hystrix*, although it should be mentioned here that this relationship was only evaluated in 5 species and that severely browsed plants were excluded from the analysis. Plant size (i.e. height and/or area) affected plant phenology in 7 species, only *A. lampa*, *B. spinosa* and *C. avellanadae* remained unaffected. Plant internal cover influenced plant phenology in 3 species (*C. avellanadae*, *C. erinacea*, and *N. fuegiana*) whereas N-cover affected plant phenology in *A. lampa*, *N. fuegiana* and *P. speciosa*. Usually, when

a covariate was retained in a model, its inclusion did not affect the significance of the fixed effect site. Finally, eight combinations of species, axis and covariate showed significant site  $\times$  covariate interaction, indicating that the effect of the covariate depended on the site (Appendix 4, supplementary material). Although these results highlight the influence of plant morphology, browsing and N-cover on plant phenology, in most cases covariates were significantly related to PCA axes where sites did not differ in mean plant scores (Table 3a). When the effect of plant morphology, browsing and neighbor's cover was accounted for, plant scores differed among sites in eight species (Table 3b). Plant phenology in the high degradation site significantly differed from that in the low degradation site, whereas plant phenology in the intermediate degradation site was similar to that of either extreme of the degradation gradient.

### 3.5. Plant morphology, browsing and neighbor's cover effects on plant phenology

The relationship of morphological variables, browsing and N-cover with plant phenology can be evaluated by comparing the sign of the correlation coefficient between plant scores and covariates (Table 3) with PCA results (Fig. 3). Browsing was negatively related to PCA2 in *B. spinosa* and *C. erinacea* ssp. *hystrix*. In the first case, browsed plants exhibited higher dominance of late vegetative growth (D-lv), whereas in *C. erinacea* ssp. *hystrix* browsed plants exhibited longer and more numerous vegetative periods. Plant size (i.e. area, height) was negatively related to PCA1 in *N. tenuis*, *P. speciosa* and *P. globosum*, but positively in *L. divaricata*. Likewise, plant size was positively related to PCA2 in *P. alpataco*. In the cases of *L. divaricata*, *P. speciosa*, and *P. alpataco*, bigger plants showed more and/or longer reproductive periods. In contrast, taller plants in *N. tenuis* showed greater dominance of late vegetative growth, and bigger plants in *P. globosum* exhibited longer and more dominant dormancy periods. Finally, N-cover was positively related to PCA in *A. lampa* and negatively in *N. fuegiana*. In both cases, higher neighbor cover was related to number and/or duration of vegetative and reproductive growth.

## 4. Discussion

Plant phenology differed among sites in eight out of ten species (Table 3). With the exception of *A. lampa* and *P. alpataco*, the remaining six species showed shorter dormancy (DURDOR) periods with increasing degradation, indicating longer growing cycles as previously reported in *N. tenuis* (Bisigato and Lopez Laphitz, 2009). However, not only the duration of senescence and dormancy periods differed among sites showing contrasting degradation. In some species (*C. avellanadae*, *C. erinacea* ssp. *hystrix*, and *N. fuegiana*), degradation conducts to longer and frequently incomplete vegetative periods (i.e. absence of late vegetative growth) and shorter and less dominant reproductive periods. However, in other species (*B. spinosa*, *P. globosum* and *N. tenuis*) the duration of reproductive periods was longer in the high degradation site. In contrast, plant phenology in *L. divaricata* and *P. speciosa* did not differ among sites. Consequently, plant phenology responses were species-specific; and they were not related to plant life form, since evergreen shrubs, deciduous shrubs, and perennial grasses include species showing opposite changes as well as species exhibiting no changes in phenology as a consequence of degradation. These results indicate that phenological changes induced by land degradation such as those previously found in *N. tenuis* (Bisigato and Lopez Laphitz, 2009) are not restricted to that species, as plant phenology differed among sites in eight out of the ten commonest species in this community, although plant responses were species-

**Fig. 3.** Principal component analysis (PCA) of phenological data. Eigenvalues of each PCA axis are in parenthesis. Circles indicate individual plant scores. Squares and bars indicate mean  $\pm 1$  standard error of PCA scores in each site. White, gray and black filled symbols indicate low, intermediate and high degradation, respectively. Direction and length of arrows indicate Pearson's correlation coefficients between commonly used phenological variables and the axes ( $r_{PCA1}$  and  $r_{PCA2}$ ). Commonly used phenological variables = DURVEG: duration of vegetative growth, DURREP: duration of reproductive growth, DURDOR: duration of dormancy period, DURCS: duration of senescence period, #VEG: number of vegetative periods during the study, #REP: number of reproductive periods during the study, D-ev: Dominance of early vegetative growth, D-iv: Dominance of intermediate growth, D-lv: Dominance of late vegetative growth, D-ee: Dominance of ear emergence, D-bu: Dominance of buds, D-sb: Dominance of swelling buds, D-f: Dominance of flowers, D-gf: Dominance of green fruits, D-mf: Dominance of mature fruits and seed dispersal, D-s: Dominance of senescence, D-vi: Dominance of vegetative inactivity. Only variables with significant Pearson's correlation coefficient with either or both PCA axes are shown.

**Table 2**  
Pearson's correlation coefficients between commonly used phenological variables and the first two PCA axes. Commonly used phenological variables = DURVEG: duration of vegetative growth, DURREP: duration of reproductive growth, DURDOR: duration of dormancy period, DURS: duration of senescence period, #VEG: number of vegetative periods during the study, #REP: number of reproductive periods during the study, D-ev: Dominance of early vegetative growth, D-iv: Dominance of intermediate growth, D-lv: Dominance of late vegetative growth, D-ee: Dominance of ear emergence, D-bu: Dominance of buds, D-sb: Dominance of swelling buds, D-f: Dominance of flowers, D-gf: Dominance of green fruits, D-mf: Dominance of mature fruits and seed dispersal, D-s: Dominance of senescence, D-vi: Dominance of vegetative inactivity. Bold letters indicate significant ( $p < 0.05$ ) coefficients, italics indicate those variables which increases with degradation (See Fig. 3 for graphic representations of principal component analyses).

	<i>Atriplex lampa</i>		<i>Bougainvillea spinosa</i>		<i>Chiquiraga avellanadae</i>		<i>Chiquiraga erinacea ssp. hystrix</i>		<i>Larrea divaricata</i>		<i>Nassauvia fuegiana</i>		<i>Nassella tenuis</i>		<i>Pappostipa speciosa</i>		<i>Prosopis alpataco</i>		<i>Prosopidastrum globosum</i>	
	PCA1	PCA2	PCA1	PCA2	PCA1	PCA2	PCA1	PCA2	PCA1	PCA2	PCA1	PCA2	PCA1	PCA2	PCA1	PCA2	PCA1	PCA2	PCA1	PCA2
DURVEG	<b>-0.643</b>	<b>0.645</b>	<b>0.839</b>	0.042	<b>-0.784</b>	<b>0.329</b>	0.032	<b>-0.597</b>	<b>0.255</b>	-0.110	<b>-0.641</b>	<b>-0.490</b>	0.097	<b>0.351</b>	<b>0.321</b>	0.194	<b>-0.287</b>	0.067	<b>0.841</b>	0.021
DURREP	<b>0.511</b>	<b>0.421</b>	<b>0.267</b>	0.084	<b>0.647</b>	<b>0.422</b>	0.059	<b>0.822</b>	<b>0.847</b>	-0.007	<b>0.457</b>	<b>-0.563</b>	-0.206	<b>-0.588</b>	<b>-0.517</b>	-0.146	<b>0.439</b>	<b>0.756</b>	<b>0.848</b>	-0.041
DURSEN	<b>0.657</b>	0.177	<b>0.406</b>	0.049	-0.196	<b>-0.682</b>	0.190	<b>0.377</b>	0.089	0.073	-0.093	0.185	-0.136	-0.295	0.186	<b>0.633</b>	-0.193	0.120	0.014	0.183
DURDORM	<b>0.630</b>	<b>-0.658</b>	<b>-0.498</b>	<b>0.312</b>	<b>0.785</b>	<b>-0.413</b>	0.086	<b>0.277</b>	-0.197	<b>0.346</b>	<b>0.630</b>	<b>0.476</b>	0.175	<b>0.470</b>	<b>0.401</b>	-0.048	0.187	-0.079	<b>-0.917</b>	0.042
#VEG	0.197	-0.064	<b>0.352</b>	-0.115	-0.143	-0.074	0.064	<b>-0.498</b>	-0.082	<b>0.418</b>	0.248	<b>0.349</b>	0.164	<b>-0.397</b>	-0.145	-0.051	-0.203	-0.109	0.120	0.221
#REP	<b>0.398</b>	<b>0.606</b>	0.247	-0.062	0.128	0.166	0.184	0.201	<b>0.563</b>	-0.097	0.033	<b>-0.694</b>	-0.120	<b>-0.482</b>	<b>-0.501</b>	-0.150	-0.008	<b>0.613</b>	<b>0.374</b>	0.145
D-ev	<b>-0.295</b>	<b>-0.434</b>	<b>-0.305</b>	0.067	-0.180	<b>0.589</b>	-0.046	-0.121	-0.031	0.169	<b>0.491</b>	<b>0.272</b>	<b>0.665</b>	0.156	0.239	<b>-0.551</b>	0.159	<b>-0.306</b>	<b>0.553</b>	-0.089
D-iv	0.231	0.069	<b>-0.513</b>	<b>0.658</b>	<b>-0.286</b>	0.246	0.181	-0.110	-0.061	<b>0.599</b>	-0.195	<b>0.403</b>	<b>0.729</b>	-0.184	<b>0.889</b>	0.076	<b>0.625</b>	<b>-0.451</b>	&	&
D-lv	<b>-0.563</b>	<b>0.754</b>	<b>0.660</b>	<b>-0.676</b>	<b>-0.845</b>	0.142	<b>-0.726</b>	-0.098	<b>0.262</b>	<b>-0.651</b>	<b>-0.624</b>	<b>-0.576</b>	<b>-0.768</b>	<b>0.497</b>	<b>-0.880</b>	0.145	<b>-0.685</b>	<b>0.297</b>	<b>0.776</b>	-0.022
D-sb	&	&	&	&	-0.011	0.031	&	&	&	&	&	&	%	%	%	%	&	&	&	&
D-bu	&	&	-0.005	-0.031	<b>0.285</b>	-0.175	&	&	&	&	&	&	-0.116	-0.258	<b>-0.353</b>	-0.088	-0.096	<b>0.292</b>	<b>0.492</b>	-0.023
D-ee	*	*	*	*	*	*	*	*	*	*	*	*	-0.179	<b>-0.498</b>	<b>-0.313</b>	-0.110	*	*	*	*
D-f	&	&	0.012	-0.034	<b>0.729</b>	-0.141	&	&	&	&	<b>0.334</b>	-0.202	&	&	<b>-0.291</b>	-0.022	&	&	<b>0.454</b>	-0.169
D-gf	&	&	0.028	-0.024	<b>0.683</b>	0.112	-0.089	<b>0.441</b>	&	&	<b>0.330</b>	-0.172	0.038	<b>-0.335</b>	-0.175	-0.030	&	&	&	&
D-mf	&	&	-0.056	0.012	<b>0.550</b>	-0.204	-0.076	<b>0.399</b>	<b>0.484</b>	-0.141	<b>0.583</b>	<b>-0.313</b>	-0.184	-0.028	<b>-0.469</b>	-0.129	&	&	&	&
D-d	&	&	<b>-0.528</b>	<b>0.421</b>	&	&	&	&	&	&	<b>0.564</b>	0.039	0.162	<b>0.634</b>	<b>0.390</b>	<b>0.553</b>	<b>0.271</b>	-0.083	<b>-0.915</b>	0.060
D-vi	<b>0.613</b>	<b>-0.670</b>	&	&	<b>0.516</b>	-0.137	<b>-0.903</b>	-0.168	<b>-0.339</b>	<b>0.362</b>	-0.251	<b>0.389</b>	-0.054	<b>-0.549</b>	-0.038	<b>-0.545</b>	-0.023	0.023	&	&
D-s	<b>0.405</b>	0.064	<b>-0.261</b>	0.201	<b>-0.407</b>	-0.204	<b>0.940</b>	0.144	-0.135	-0.186	0.182	<b>0.301</b>	-0.131	<b>-0.332</b>	0.198	<b>0.472</b>	0.018	<b>0.272</b>	&	&

& = Not calculated because the variable was constant (zero).

% = Not calculated because this phenophase is only present on shrubs.

\* = Not calculated because this phenophase is only present on grasses.

Table 3

a). Significant *P*-values for fixed effect (Site), covariates (browsing, height, area, Covi, and N-cover) and their interaction. . = not included in the final model because lack of significance. – = no measured and/or not browsed. Bold, italics, and plain *P*-values indicate that covariates were positively, negatively, and unrelated to land degradation. Plus and minus signs indicate positive and negative slopes. b) Relationship between the loadings of each site (*L* = low degradation, *I* = intermediate degradation, *H* = high degradation) and first (PCA1) and second (PCA2) principal components. Differences among mean scores were evaluated by ANCOVA.

Covariate	Effect	Atriplex lampa		Bougainvillea spinosa		Chiquiraga avellaneda		Chiquiraga erinacea ssp. hystrix		Larrea divaricata		Nassauvia fuegiana		Nassella tenuis		Pappostipa speciosa		Prosopis alataco		Prosopidactrum globosum	
		PCA1	PCA2	PCA1	PCA2	PCA1	PCA2	PCA1	PCA2	PCA1	PCA2	PCA1	PCA2	PCA1	PCA2	PCA1	PCA2	PCA1	PCA2	PCA1	PCA2
a)	Browsing																				
	Site		<0.001																		
	Cov.				0.007(–)																
	S × C																				
Height	Site		<0.001		<0.001																
	Cov.																				
	S × C																				
	S × C																				
Area	Site		<0.001		<0.001																
	Cov.																				
	S × C																				
	S × C																				
Covi	Site		<0.001		<0.001																
	Cov.																				
	S × C																				
	S × C																				
N-cover	Site		<0.001		<0.001																
	Cov.																				
	S × C																				
	S × C																				
b)	Site																				
	Loadings																				

specific. What is more important, our results suggest that other global change components besides climate change can be affecting plant phenology. Commonly, recent changes in plant phenology are unanimously attributed to global warming, ignoring the importance of other components such as elevated CO<sub>2</sub> and nitrogen deposition (Cleland et al., 2006). Our results indeed confirm that not only climate but also human pressure (i.e. land degradation) significantly affects plant phenology in the arid Patagonian Monte.

Commonly, bigger or denser plants showed longer and/or more intense reproductive periods, in accordance with previous studies (Naito et al., 2008; Zeiter and Stampfli, 2008). Likewise, browsing was related to plant phenology in *B. spinosa* and *C. erinacea* ssp. *hystrix*. However, it should be recognized here that we can be underestimating browsing effects on plant phenology because this relationship was not evaluated in grasses given that they were protected against grazers by individual enclosures, and that severely browsed plants were excluded from the analysis. In *B. spinosa* and *C. erinacea* ssp. *hystrix* browsing was positively related to variables relative to vegetative growth. Examples of negative effects of herbivory on plant reproduction are common in literature, both as a consequence of direct consumption of reproductive structures (Noy-Meir and Briske, 1996) as well as reduced vigor in consumed plants (Nötzold et al., 1998). Commonly, those plants whose reproductive development is reduced by herbivores remain in a vegetative stage due to the time invested in regrowth (e.g. Freeman et al., 2003). Surprisingly, only *A. lampa*, *N. fuegiana* and *P. speciosa* phenologies were related to neighbor's cover, suggesting that neighbors' competition is not enough to affect the phenology of most plant species. Probably, low plant cover in Patagonian Monte ecosystems (Bisigato and Bertiller, 1997) forming vegetation patches where soil resources are accumulated (Bisigato et al., 2008) reduces competition among plants.

Because only two species (*B. spinosa*, *C. erinacea* ssp. *hystrix*) showed a relationship between browsing and plant phenology, the differences among sites found in phenology of the remaining six species can be attributed to degradation and not to direct consumption of plant tissues. Because morphological covariates were mostly retained in models for PCA axes where sites did not differ, we can discard indirect effects of grazing such as those mediated by plant size. Thus, in these cases we have no evidences of morphology-mediated effects of grazing on plant phenology. However, as previously stated, we recognize that we can be underestimating browsing/grazing effects on plant phenology because severely browsed plants were excluded from the analysis and this variable was not evaluated in grasses.

Previous studies carried out in other water-limited ecosystems around the world have highlighted the temporal (i.e. interannual) and spatial variation in plant phenology, and have related these differences with climatic differences among areas, mainly precipitation (e.g. Ghazanfar, 1997). Our study, which was carried out in three sites with similar soil and located at less than 4 km in a plain area, did not show differences in precipitation and temperature which could be responsible for phenological differences among sites (Fig. 2). Similarly, as a consequence of proximity among sites, photoperiod differences among sites can be excluded. However, due to reduced plant cover, both our modeling approach (Fig. 2) and previous field samplings carried out in our study sites (Bisigato and Lopez Laphitz, 2009) showed that water lasts more time in the soil after the biggest precipitation events in degraded sites. Thus, it could be that phenology is responding to enhanced water availability as previously reported in *N. tenuis* (Bisigato and Lopez Laphitz, 2009). In that article, Bisigato and Lopez Laphitz found increased water availability in degraded areas in years varying in precipitation from 87 to 410 mm (37%–174% long-term average) and extended growing periods in *N. tenuis* in all years. This



evidence suggests that our results are not restricted to years with below-average precipitation.

Variability among species in phenological responses to grazing-induced land degradation is likely to result in highly unpredictable community-level impacts, as previously found as a consequence of climate change (Peñuelas et al., 2002). The diverse responses of the dominant species in Patagonian Monte communities to land degradation may progressively change their competitive ability, altering the structure and functioning of these ecosystems as formerly reported by Bisigato and Bertiller (1997) and Ares et al. (2003).

The reduction in the dominance and duration of reproductive periods found in three species could affect seed production. Previous studies carried out in grazed Patagonian Monte areas have reported strong reductions in the size of the soil seed bank of grasses and shrubs (Bisigato, 2000; Pazos and Bertiller, 2008), and have proposed that this reduction can explain, at least in part, the changes in species cover and density characteristic of land degradation (Bisigato and Bertiller, 1997). Although we did not evaluate seed production in this study, some of the species whose cover is more strongly reduced in grazed areas (e.g. *C. erinacea* ssp. *hystrix*) (Bisigato, 2000) are among the species with decreased length and/or dominance of reproductive periods. In addition, the reduction in dominance and duration of reproductive periods combined with variable responses among species could affect pollinators because the plant assemblage in the Patagonian Monte is characterized by insect pollination syndromes (Tadey et al., 2009). In that sense, Tadey (2008) found reduced pollination levels in two Patagonian Monte shrubs as a consequence of increased grazing pressure.

Phenological data are frequently descriptive. In most cases, they are displayed in graphs and the relationships between environmental factors and plant phenology are not statistically tested (but see Menzel et al., 2006). Although sometimes quantitative variables are calculated, they are restricted to single phenophases, hindering the comparison of the whole growing cycle of different individuals or populations at the same time. However, other authors (Pavón and Briones, 2001; Seghieri and Simier, 2002) have employed a multivariate approach which allows the inclusion of all the phenological data in the same analysis, synthesizing the information contained in them into a few factor scores. Our results indicate that this approach is appropriate to evaluate intra-species differences in plant phenology and their relationship with commonly used phenological variables and morphological variables.

The present study, despite the fact that it is limited by a lack of degradation level replication, supports the idea that land degradation may affect plant phenology in water-limited ecosystems. Future studies should employ a replicated design to evaluate whether land degradation effects on plant phenology vary across communities and/or among years.

## 5. Conclusions

Our results suggest that other global change components may affect plant phenology in water-limited ecosystems. Recent changes in plant phenology have been commonly attributed to global warming, ignoring the importance of other less widespread components such as land degradation. Our results indicate that in the Patagonian Monte land degradation affects plant phenology, but the responses are species-specific.

## Author contributions

AJB conceived, designed and performed most of field sampling. MVC and GEP collaborated in the field work. MVC constructed the

data matrix. All authors participated in data analysis and wrote the manuscript.

## Acknowledgments

This research was supported by PICT 05-32596, National Agency for Scientific and Technological Promotion. MV Campanella and GE Pazos fellowships were supported by CONICET (National Research Council of Argentina). Recognition is also given to Mr Fermín Sarasa who allowed the access to the study area in Estancia “San Luis”.

## Appendix A. Supplementary data

Supplementary data related to this article can be found at <http://dx.doi.org/10.1016/j.jaridenv.2012.12.003>.

## References

- Abd El-Ghani, M.M., 1997. Phenology of ten common plant species in western Saudi Arabia. *Journal of Arid Environments* 35, 673–683.
- Anon, 2011. Estación meteorológica. Área de física ambiental. CENPAT-CONICET. URL: <http://www.cenpat.edu.ar>.
- Archibald, S., Scholes, R.J., 2007. Leaf green-up in a semi-arid African savanna-separating tree and grass responses to environmental cues. *Journal of Vegetation Science* 18, 583–594.
- Ares, J., del Valle, H., Bisigato, A., 2003. Detection of process-related changes in plant patterns at extended spatial scales during early dryland desertification. *Global Change Biology* 9, 1643–1659.
- Ares, J., Beeskow, A.M., Bertiller, M., Rostagno, M., Irisarri, M., Anchorena, J., Defosse, G., Merino, C., 1990. Structural and dynamic characteristics of overgrazed lands of northern Patagonia, Argentina. In: Breymer, A. (Ed.), *Managed Grasslands*. Elsevier Science, Amsterdam, pp. 149–175.
- Asner, G.P., Archer, S., Hughes, R.F., Ansley, R.J., Wessman, C.A., 2003. Net changes in regional woody vegetation cover and carbon storage in Texas Drylands, 1937–1999. *Global Change Biology* 9, 316–335.
- Bertiller, M.B., Beeskow, A.M., Coronato, F., 1991. Seasonal environmental variation and plant phenology in arid Patagonia (Argentina). *Journal of Arid Environments* 21, 1–11.
- Bisigato, A.J., 2000. Dinámica de la vegetación en áreas pastoreadas del extremo austral de la Provincia Fitogeográfica del Monte. PhD thesis, University of Buenos Aires, Buenos Aires, Argentina.
- Bisigato, A.J., Bertiller, M.B., 1997. Grazing effects on patchy dryland vegetation in northern Patagonia. *Journal of Arid Environments* 36, 639–653.
- Bisigato, A.J., Lopez Laphitz, R.M., 2009. Ecohydrological effects of grazing-induced degradation in the Patagonian Monte, Argentina. *Austral Ecology* 34, 545–557.
- Bisigato, A.J., Bertiller, M.B., Ares, J.O., Pazos, G.E., 2005. Effect of grazing on plant patterns in arid ecosystems of Patagonian Monte. *Ecography* 28, 561–572.
- Bisigato, A.J., Lopez Laphitz, R.M., Carrera, A.L., 2008. Non-linear relationships between grazing pressure and conservation of soil resources in Patagonian Monte shrublands. *Journal of Arid Environments* 72, 1464–1475.
- Campanella, M.V., Bertiller, M.B., 2008. Plant phenology, leaf traits and leaf litterfall of contrasting life forms in the arid Patagonian Monte, Argentina. *Journal of Vegetation Science* 19, 75–85.
- Cleland, E.E., Chiariello, N.R., Loarie, S.R., Mooney, H.A., Field, C.B., 2006. Diverse responses of phenology to global changes in a grassland ecosystem. *Proceedings of the National Academy of Sciences USA* 103, 13740–13744.
- Freeman, R.S., Brody, A.K., Neefus, C.D., 2003. Flowering phenology and compensation for herbivory in *Ipomopsis aggregata*. *Oecologia* 136, 394–401.
- Ghazanfar, S.A., 1997. The phenology of desert plants: a 3-year study in a gravel desert wadi in northern Oman. *Journal of Arid Environments* 35, 407–417.
- Goheen, J.E., Young, T.P., Keesing, F., Palmer, T.M., 2007. Consequences of herbivory by native ungulates for the reproduction of a savanna tree. *Journal of Ecology* 95, 129–138.
- Marco, D.E., Calviño, A.A., Páez, S.A., 2000. Patterns of flowering and fruiting in populations of *Larrea divaricata* in dry Chaco (Argentina). *Journal of Arid Environments* 44, 327–346.
- Menzel, A., Sparks, T.H., Estrella, N., Koch, E., Aasa, A., Ahas, R., Alm-Kubler, K., Bissolli, P., Braslavská, O., Briede, A., Chmielewski, F.M., Crepinsek, Z., Curnel, Y., Dahl, A., Jactzak, K., Máge, F., Mestre, A., Nordli, Ø., Peñuelas, J., Pirinen, P., Remisová, V., Scheffinger, H., Striz, M., Susnik, A., van Vliet, A.J.H., Wielgolask, F.E., Zach, S., Züst, A., 2006. European phenological response to climate change matches the warming pattern. *Global Change Biology* 12, 1969–1976.
- Naito, Y., Kanzaki, M., Numata, S., Obayashi, K., Konuma, A., Nishimura, S., Ohta, S., Tsumura, Y., Okuda, T., Lee, S.L., Muhammad, L., 2008. Size-related flowering and fecundity in the tropical canopy tree species, *Shorea acuminata* (Dipterocarpaceae) during two consecutive general flowerings. *Journal of Plant Research* 121, 33–42.

- Nötzold, R., Blossey, B., Newton, E., 1998. The influence of below ground herbivory and plant competition on growth and biomass allocation of purple loosestrife. *Oecologia* 113, 82–93.
- Noy-Meir, I., Briske, D.D., 1996. Fitness components of grazing-induced population reduction in a dominant annual, *Triticum dicoccoides* (wild wheat). *Journal of Ecology* 84, 439–448.
- Noy-Meir, I., Briske, D.D., 2002. Response of wild wheat populations to grazing in Mediterranean grasslands: the relative influence of defoliation, competition, mulch and genotype. *Journal of Applied Ecology* 39, 259–278.
- Otieno, O., Schmidt, M.W.T., Kinyamario, J.I., Tenhunen, J., 2005. Responses of *Acacia tortilis* and *Acacia xanthophloea* to seasonal changes in soil water availability in the savanna region of Kenya. *Journal of Arid Environments* 62, 377–400.
- Pavón, N.P., Briones, O., 2001. Phenological patterns of nine perennial plants in an intertropical semi-arid Mexican scrub. *Journal of Arid Environments* 49, 265–277.
- Pazos, G.E., Bertiller, M.B., 2008. Spatial patterns of the germinable soil seed bank of coexisting perennial-grass species in grazed shrublands of the Patagonian Monte. *Plant Ecology* 198, 111–120.
- Pazos, G.E., Bisigato, A.J., Bertiller, M.B., 2007. Abundance and spatial patterning of coexisting perennial grasses in grazed shrublands of the Patagonian Monte. *Journal of Arid Environments* 70, 316–328.
- Peñuelas, J., Filella, I., Comas, P., 2002. Changed plant and animal life cycles from 1952 to 2000 in the Mediterranean region. *Global Change Biology* 8, 531–544.
- Rathcke, B., Lacey, E.P., 1985. Phenological patterns of terrestrial plants. *Annual Review of Ecology and Systematics* 16, 179–214.
- Rostagno, C.M., del Valle, H.F., Videla, L., 1991. The influence of shrubs on some chemical and physical properties of an aridic soil in north-eastern Patagonia, Argentina. *Journal of Arid Environments* 20, 179–188.
- Seghieri, J., Simier, M., 2002. Variations in phenology of a residual invasive shrub species in Sahelian fallow savannas, south-west Niger. *Journal of Tropical Ecology* 18, 897–912.
- Shackleton, C.M., 1999. Rainfall and topo-edaphic influences on woody community phenology in South African savannas. *Global Ecology and Biogeography Letters* 8, 125–136.
- Sherry, R.A., Zhou, X., Gu, S., Arnone III, J.A., Schimel, D.S., Verburg, P.S., Wallace, L.L., Luo, Y., 2007. Divergence of reproductive phenology under climate warming. *Proceedings of the National Academy of Sciences USA* 104, 198–202.
- Soil Survey Staff, 1999. Soil Taxonomy, a Basic System of Soil Classification for Making and Interpreting Soil Surveys, second ed.. In: Agricultural Handbook 436 National Resources Conservation Service, USDA, Washington DC.
- Tadey, M., 2008. Efecto del ganado sobre los niveles de polinización en especies vegetales del monte patagónico. *Ecología Austral* 18, 89–100.
- Tadey, M., Tadey, J.C., Tadey, N., 2009. Reproductive biology of five native plant species from the Monte Desert of Argentina. *Botanical Journal of the Linnean Society* 161, 190–201.
- Tubiello, F.N., Soussana, J.F., Howden, S.M., 2007. Crop and pasture response to climate change. *Proceedings of the National Academy of Sciences USA* 104, 19686–19690.
- Vitasse, Y., Porté, A.J., Kremer, A., Michalet, R., Delzon, S., 2009. Responses of canopy duration to temperature changes in four temperate tree species: relative contributions of spring and autumn leaf phenology. *Oecologia* 161, 187–198.
- Vitousek, P.M., 1994. Beyond global warming: ecology and global change. *Ecology* 75, 1861–1876.
- Zeiter, M., Stampfli, A., 2008. Long-term assessment of seed provenance effect on the establishment of the perennial grass *Bromus erectus*. *Journal of Vegetation Science* 19, 821–830.