



Is foliar flammability of woody species related to time since fire and herbivory in northwest Patagonia, Argentina?

Melisa Blackhall, Estela Raffaele & Thomas T. Veblen

Keywords

Cattle herbivory; Fire ecology; Fuel flammability; Ignitability tests; Leaf traits Plant–herbivore interactions; Resprouting species

Nomenclature

Correa (1969–1997)

Received 8 July 2011

Accepted 8 February 2012

Co-ordinating Editor: Sabine Güsewell

Blackhall, M. (corresponding author, meliblackhall@gmail.com) & **Raffaele, R.** (estelaraffaele@yahoo.com.ar): Laboratorio Ecotono, Universidad Nacional del Comahue, INIBIOMA-CONICET, Quintral 1250, 8400, Bariloche, Argentina

Veblen, T.T. (Thomas.Veblen@colorado.edu): Department of Geography, University of Colorado, Boulder, CO, 80309-0260, USA

Abstract

Question: In northwest Patagonia burning of fire-resistant forests creates a community-level positive feedback towards increased fire occurrence because of successional replacement by fire-prone shrublands. We hypothesize that variability in plant traits related to time since last fire and to herbivory by cattle may affect foliar flammability, thus providing a flammability-promoting mechanism operating at the level of individual plants. We examine how plant foliar traits affecting flammability vary across species and at sites recovering from recent fires (<15 yr) vs sites not affected by fire for > 50 yr, both in the presence and absence of cattle.

Location: Nahuel Huapi National Park, northwest Patagonia, Argentina.

Methods: We measured four foliar traits expected to affect flammability: leaf moisture, leaf size, specific leaf area and leaf strength, and conducted tests of ignitability (time to ignition and duration of combustion) on leaves of six common tall shrub and small tree species: non-palatable *Lomatia hirsuta* and *Diostea juncea*, moderately palatable *Nothofagus antarctica* and *Schinus patagonicus* and highly palatable *Maytenus boaria* and *Ribes magellanicum*. We used ANOVA and PCA to examine potential relationships among species flammability traits, time since fire and presence or absence of cattle.

Results: At plant level, variability in flammability-related foliar properties is strongly and consistently related to time since last fire, whereas effects of cattle are more variable across species and treatments. In comparison with unburned forests, the dominant woody species at shrubland sites showed reduced leaf moisture, leaf size and specific leaf area. Under pressure from cattle, *N. antarctica*, one of the most important woody species in these shrublands, showed changes in some foliar traits expected to enhance flammability (e.g. shorter time to ignition) but overall the influence of cattle on flammability was not consistent.

Conclusions: The current study demonstrates that plant foliar traits vary between recently burned and unburned sites, and that these variations may enhance foliar flammability in shrubland communities.

Introduction

Fuels, weather and ignition agents are the three factors that most directly determine fire activity (Bond & Van Wilgen 1996). Fuels in particular may determine fire intensity and other fire regime parameters (e.g. fire frequency), which in turn can determine vegetation properties, such as biomass abundance, age and species composition or fuel accumulation. Vegetation, as fuel for fire, is extremely heterogeneous, and species differences in plant properties

affecting flammability may make some plant communities more likely to burn than others (Bond & Van Wilgen 1996). The combined physical and chemical traits of all plant species that constitute the community will influence whether and how the vegetation will burn, and hence the likelihood of fire consuming the whole community (Bond & Van Wilgen 1996). Individual plant flammability has been defined as “the probability that one plant burns more readily and with greater intensity than another in the same population” (Bond & Midgley 1995). In the current study,

we apply this definition to examine variability in foliar flammability among important woody species in northwest Patagonia and potential relationships to herbivory by cattle.

Common metrics of flammability are: (1) ignitability, i.e. time until ignition once exposed to some heat source; (2) sustainability, i.e. the ability to sustain fire once ignited; and (3) combustibility, i.e. the intensity with which plant material burns (Anderson 1970). In laboratory settings, numerous techniques have been developed to study plant properties affecting these metrics, ranging from simple measures of minimum temperatures for ignition to more technically complex measures of oxygen consumption or thermal analysis (Valette 1992; White & Zipperer 2010). These flammability metrics are affected by physical and chemical plant properties.

Plant flammability is related to numerous morphological traits of plants, including canopy architecture, fine fuel biomass, surface area-to-volume ratio, standing fine litter and to a variety of chemical properties (Cornelissen et al. 2003; Schwilk 2003; Behm et al. 2004; Saura-Mas et al. 2010). Most studies agree that fuel moisture (measured as water content and drying rates of plant parts) is either the most or one of the most important properties affecting flammability at the level of both individual plants and the entire plant community (Bond & Van Wilgen 1996). Foliar traits are likely to be key indicators of plant flammability because leaves tend to have a high ratio of surface area to volume, and foliar biomass is positively correlated with total amount of fine fuels (Cornelissen et al. 2003).

Flammability is expected to be greater for species with low moisture content and high leaf dry matter content (Cornelissen et al. 2003). High leaf dry matter content is related to leaves that are more resistant to physical hazards such as wind, hail and herbivory, since this trait is positively correlated to the average density of foliar tissues (Cornelissen et al. 2003). Small leaf size and low specific leaf area also have been related to drought, high solar radiation, extreme temperature or intense herbivory (Ackerly et al. 2002; Cornelissen et al. 2003; Zinn et al. 2007). Both traits are related to the surface to volume ratio, and may be appropriate indicators of flammability. Small leaves tend to dry faster because of their higher surface to volume ratio (Gill & Moore 1996; Gill & Zylstra 2005; White & Zipperer 2010). However, when leaf area is lower in relation to dry leaf mass (low specific leaf area) leaves tend to dry more slowly (Rundel 1981; Behm 2003). Leaf thickness has been associated with foliar flammability because thicker leaves tend to experience delayed ignition after exposure to a heat source (Montgomery & Cheo 1971). Leaf strength in turn is positively correlated with foliar thickness (Choong et al. 1992), and both of these leaf properties can be influenced by a variety of abiotic factors (e.g. wind, light inten-

sity) as well as by herbivory (Cornelissen et al. 2003; Onoda et al. 2008).

In northwest Patagonia, fire and herbivory by introduced mammals are the two most pervasive disturbances affecting the landscape, and each has the potential for altering future landscape-level susceptibility to fire (Raffaele et al. 2011; Veblen et al. 2011). In this region, from dry steppe to Andean rain forests, natural and anthropogenic fires are key influences on plant community composition and structure, which in turn have been shown to control subsequent fire risk and spread (Mermoz et al. 2005). Burning of fire-resistant tall *Nothofagus* forests results in a long-lasting conversion to fire-prone tall shrublands dominated by the shrubby *N. antarctica*, many tall shrub species and the bamboo *Chusquea culeou* (Veblen et al. 2011). Tall mesic forests composed of obligate-seeding tree species often fail to regenerate to forest, and are replaced by resprouting shrub species with plant architectures that create more easily desiccated understoreys and fuel structures that are highly conducive to crown fires (Veblen et al. 2011). Risk of fire ignition as well as fire spread have been shown to be greater in these tall shrublands compared to mesic *Nothofagus* forests, which only burn under the most extreme drought conditions (Mermoz et al. 2005). Thus, initial burning of fire-resistant forests creates a positive feedback towards increased fire occurrence under less extreme drought because of forest replacement by fire-prone shrublands dominated by resprouting species.

Overlapping and often interacting with fire effects are the effects of introduced large mammals, which influence post-fire tree regeneration, species composition and vegetation structure. Native large herbivores in northern Patagonia include the huemul deer (*Hippocamelus bisulcus*) and the guanaco (*Lama guanicoe*), which prefer open habitats and are rare in areas of dense forest (Raffaele et al. 2011). Today both are absent or extremely rare in the areas included in the current study. The principal large mammalian herbivores in the forest vegetation of northern Patagonia are livestock (mainly cattle) and in some areas introduced red and fallow deer (*Cervus elaphus* and *Dama dama*; Raffaele et al. 2011). Several studies on the post-fire effects of these introduced herbivores conducted across a broad range of forest and shrubland types have shown that heavy herbivore pressure: (1) impedes regeneration of the obligate-seeding tall tree species but is less effective at inhibiting the vegetative resprouting of shrubs and bamboos (Kitzberger et al. 2005; Tercero-Bucardo et al. 2007); (2) results in reduced height growth of seedlings of tree species so that the development of a closed canopy is unlikely (Blackhall et al. 2008); (3) favours the invasion and spread of exotic forbs (Raffaele et al. 2011); and (4) increases the relative abundance and dominance of species

that are defended against herbivory by spines, chemical defences and/or low palatability (Raffaele et al. 2011).

In the current research we examine a key issue, not previously investigated: how foliar properties related to flammability of resprouting shrub and small tree species are affected by presence or absence of livestock, and if these properties differ in recently burned vs unburned communities. The current study addresses the following questions: (1) Do resprouting woody plants growing in communities originated after recent fire (i.e. within the past 15 yr) differ in foliar flammability compared to the same species growing in communities not affected by fire for at least 50 yr? (2) Do resprouting woody plants growing in areas long affected by herbivory by cattle differ in foliar flammability compared to the same species growing in areas free from large herbivores? (3) Are there interactions between cattle presence and time since last fire that would imply synergistic influences on foliar flammability? To address these questions, we considered four foliar traits assumed to affect flammability (leaf moisture, leaf size, specific leaf area and leaf strength) and conducted ignitability tests to compare species growing under different histories of fire and herbivory.

Methods

Study area and species studied

The study was carried out in Nahuel Huapi National Park, Argentina. Mean monthly temperatures range between 2.8 °C in July and 15.2 °C in January (mean 1996–2006; Bariloche Aerodrome Station, unpublished data). Study site elevations range from 766 m to 1103 m, and mean annual precipitation declines steeply from \approx 1700 mm in the west to \approx 1000 mm in the east (Barros et al. 1983). At low to mid elevations (ca. 800–1100 m a.s.l.) the tall evergreen forests are dominated by the xeric *Austrocedrus chilensis* and/or the mesic *Nothofagus dombeyi*; at high elevations (\approx 1000–1500 m a.s.l.) the deciduous subalpine forests are monospecific stands of *N. pumilio* (Mermoz & Martín 2005). All of these tall tree species are obligate seeders and generally do not resprout following fire. Tall shrublands occur on relatively dry sites juxtaposed with tall forests and replace forest following burning; they are dominated by the shrubby tree *N. antarctica*, the bamboo *Chusquea culeou* and numerous tall shrub and small tree species, all of which vigorously resprout after severe burning. Some common species accompanying the deciduous *N. antarctica* in this type of habitat are the broad-leaved evergreen species *Lomatia hirsuta*, *Schinus patagonicus*, *Maytenus boaria*, *Berberis* spp. and the deciduous *Diostea juncea* and *Ribes magellanicum* (Mermoz & Martín 2005).

The six species selected for study met the following criteria: (1) each is a native tall shrub or small tree; (2) each

is abundant in tall shrublands that develop following the burning of tall forests and in the understorey of young to moderately old post-fire forests (i.e. >50 yr old); and (3) each species vigorously resprouts after burning. The palatability of each species was classified into three classes (not palatable, moderately palatable and highly palatable) based on 3–6 yr of re-measurements of paired cattle enclosures and controls (Blackhall et al. 2008; Raffaele et al. 2011). The species studied and their palatability classes are: (1) not palatable, *Lomatia hirsuta* (Proteaceae) and *Diostea juncea* (Verbenaceae); (2) moderately palatable, *Nothofagus antarctica* (Fagaceae) and *Schinus patagonicus* (Anacardiaceae); and (3) highly palatable, *Maytenus boaria* (Celastraceae) and *Ribes magellanicum* (Saxifragaceae).

Samples sites

Seventeen sites for sampling of foliar characteristics were selected according to two principal criteria: (1) each site was classified as recently burned (i.e. within 10–15 yr) and therefore representing early post-fire vegetation, or alternatively as unburned (i.e. young to moderately old post-fire forests, not having been burned for > 50 yr); (2) each site was classified as either free of livestock or as having a history of intense and continuous presence of domestic cattle > 25 yr. Accordingly, four types of site were studied: four unburned and without cattle (-B-C), four unburned with cattle (-B+C), four recently burned without cattle (+B-C) and five recently burned with cattle (+B+C). All sites classified as recently burned had burned during extreme droughts in either January 1996 (two +B-C sites) or February 1999 (two +B-C sites and five +B+C sites). The two wildfires were anthropogenic and burned large areas including a wide range of vegetation types, from grass-dominated steppe through tall shrublands and closed canopy mesic forests. The recently burned sites were typical post-fire successional stages dominated by tall shrubs and small trees (<6-m tall). The microclimates of unburned sites were characterized as having shaded and cooler conditions beneath the closed forest canopy in contrast to high solar radiation and high temperatures at browsing heights of one to a few meters in the recently burned sites. Cattle presence or absence was derived from an assessment by National Park authorities who monitor the numbers of animals owned by local inhabitants (Lauría Sorge & Romero 1999) and was verified in our own field observations. All sites classified as having cattle present were characterized by a long history (>25 yr) of heavy browsing by free ranging cattle. In a detailed characterization of the study sites, quantification of browsing on all woody species showed that there were no significant differences in browsing intensity between -B+C and +B+C treatments and that these were similar to browse intensities in similar habitats

elsewhere in Nahuel Huapi N.P. (M. Blackhall unpublished data; Blackhall et al. 2008; Raffaele et al. 2011). Cattle faeces were observed only at sites classified as having cattle present according to Lauría Sorge & Romero (1999). All sites were characterized by rare faeces of the introduced European hare and observations of browsing effects on the vegetation indicated negligible impacts of hare. None of the sites were affected by any native large herbivores such as guanaco or the huemul deer or by introduced deer.

Leaf sampling

Samples for leaf trait measurements were collected during two summer seasons (February–March 2009 and 2010), which correspond with the season of maximum fire probability. For leaf trait measurements, 60 leaves were collected from each of ten (occasionally nine or 11) healthy individuals per species in each type of site; thus, a total of 600 leaves were collected per species per type of site. Foliar samples were collected at each site where the plant species was present (three to four individuals at each of the 17 sites). Samples generally were collected at heights of ≈ 1.2 m–2.0 m to simulate the browsing height of cattle. At sites with heavy cattle pressure, however, samples of more palatable species had to be collected from shorter plants due to the dwarfing effects of cattle browsing. From each sampled plant, we randomly harvested 60 well-developed, fully expanded non-senescent and healthy leaves (i.e. no evidence of pathogens or herbivory). Leaves were collected without removing them from twigs, enclosed in hermetic plastic bags and stored in coolers (Cornelissen et al. 2003). The same field sampling protocol was followed for collection of samples for ignitability tests, except all samples were collected in March 2010 and the number of leaves was adjusted to obtain approximately 10 g fresh leaves per plant. In the case of *D. juncea* the leaf samples for ignitability tests included the small leaf blades plus the sheaths, which are normally attached to the green thin branches.

Leaf trait measurements

In the laboratory, within 48 h of field sampling, 30 leaves from each individual were used to measure leaf moisture percentage, leaf size and specific leaf area. Fresh leaf mass was measured with a precision of 0.0001 g. Image analysis software and scans of leaves were used to measure one-sided leaf area (Sigma Scan Pro[®] 5.0 – SPSS Science, Chicago, IL, US). Afterwards, leaves were oven-dried at 60 °C for 72 h and weighed. Leaf moisture was calculated based on dry mass (Van Wilgen et al. 1990; Behm et al. 2004) as follows: Leaf Moisture = [(fresh mass – dry mass)/dry

mass] $\times 100$. After using the image analysis software, leaf size (mm^2) was directly obtained, and specific leaf area ($\text{mm}^2\text{mg}^{-1}$) was calculated by dividing the area (mm^2) by its oven-dry mass (mg; Cornelissen et al. 2003).

Thirty additional leaves from each individual were used for measuring leaf strength (g mm^{-2}) using punch-and-die tests (or penetrometer; Choong et al. 1992). Fresh leaves were clamped between two plates with a 2.7-mm diameter hole and were punched through the laminae between secondary veins with a 1.6-mm diameter steel rod at a constant angle of 90 °. The weight (g) needed to punch the hole (and penetrate leaf) per unit punched area (mm^{-2}) was measured utilizing the pressure set for Pesola[®] Medio-Line Scales.

Ignitability measurements: epiradiator tests

Samples used in the ignitability tests were first oven-dried at 30 °C for 7 d (\approx average maximum summer temperature in the study area) to a constant mass in order to account for variable atmospheric and leaf humidity associated with the time of field sampling. Thus, leaf moisture content (0% moisture) had no effect on ignitability measurements and the low oven-drying temperature prevented volatilization of potential leaf chemicals. Once dried, samples were weighed to 1.0 ± 0.01 g and stored in a hermetic recipient containing silica gel desiccant until ignitability tests were performed in June 2010. Ten 1-g samples (one per individual plant) per species per each type of site were used to perform ignitability tests using an infrared quartz-silica epiradiator (500 W), following the protocol in Valette (1992). The epiradiator consists of an electric heating resistance that reaches a standard surface temperature of 420 °C. Samples were placed on a 10-cm diameter silica disk once the electric radiator was well heated. A pilot flame was located 4 cm above the centre of the disk to initialize flames in the gas from the heated sample (Valette 1992; Hachmi et al. 2011).

All the experiments were conducted in a closed environment to prevent any draught disturbance of the ignitability tests. Using 1-g samples on the epiradiator, the following parameters were measured with a digital timer: (1) time to ignition, in seconds, measured as the time from placement of the sample on the silica disk to appearance of the first flame, and (2) duration of combustion, in seconds, determined by flame extinction. Shorter time to ignition clearly is a measure of greater ignitability. Longer duration of combustion is commonly interpreted as measure of sustainability of combustion (White & Zipperer 2010). In a recent epiradiator study, it was determined that time to ignition is strongly positively correlated with fuel moisture, whereas no strong correlation was found between humidity and duration of combustion (Hachmi et al. 2011).

Given the abundance of fine fuels (leaves and twigs) and woody fuels in the shrublands and forests included in our study, we regard time to ignition to be a more useful parameter than duration of combustion. The ignition frequency (percentage of samples that ignited) in our study was 100%.

Data analysis

Fire and herbivory effects on leaf traits and ignitability measurements

To relate foliar flammability to time since last fire and herbivory by cattle, six variables (leaf moisture, leaf size, specific leaf area, leaf strength, time to ignition and duration of combustion) were evaluated independently using 2×2 factorial ANOVAs (fire = recently burned/unburned; cattle = presence/absence; Quinn & Keough 2002). The models included a compound symmetric covariance structure for the residuals grouped by species and site to account for the correlation between plants of each species sampled at the same site (Kuehl 2001). Thus, we avoided treating these observations as being totally independent. InfoStat© software (version 2011, FCA, Univ. Nac. de Córdoba, AR) was used for running factorial ANOVAs and for modelling the error. Normality of residuals was evaluated using Shapiro-Wilk's test, and homogeneity of variances was assessed using Levene's test (Quinn & Keough 2002). When necessary, logarithmic transformations were applied to improve normality and homogeneity of variances. A mean of 30 trait measurements for each individual counted as one observation.

Species and site differences in leaf flammability

In addition to factorial ANOVAs, a principal components analysis (PCA) was performed to describe which species were more flammable and under which environmental condition (–B–C, –B+C, +B–C and +B+C). Results were organized in a single data matrix of six traits (leaf moisture, leaf size, specific leaf area, leaf strength, time to ignition and duration of combustion) \times 24 combinations of species and sites (six species \times four types of sites). Then, PCA was performed via the correlation matrix (i.e. the covariance matrix of the standardized (scaled) variables; Quinn & Keough 2002).

Results

Fire and herbivory effects on leaf traits and ignitability

Fire

All species growing in recently burned areas showed significantly different responses from unburned sites for most traits measured (Table 1). Leaf moisture of *D. juncea* and

N. antarctica was significantly lower at burned sites compared with unburned sites, regardless of the presence or absence of cattle ($P < 0.01$; Fig. 1a). The same tendency was observed for the other four species ($P \leq 0.09$). Similarly, leaf size and specific leaf area of all species were lower at recently burned sites compared to unburned sites ($P < 0.05$; Fig. 1b,c). Leaf strength was higher at recently burned sites compared to unburned sites for three of the six species: *D. juncea*, *N. antarctica* and *M. boaria* ($P < 0.05$; Fig. 1d). Leaf strength of *M. boaria* was the most affected by burn status, as leaf strength was 51% higher in recently burned sites than in sites not affected by fire. In the recently burned sites, almost all species had significantly longer time to ignition than in unburned sites ($P \leq 0.01$; Table 1). Duration of combustion was not related to burn vs unburned status for five of the six species ($P > 0.05$; Table 1, Fig. 1f).

Cattle

In contrast to time since fire, the effects of cattle were much more variable among species and across flammability variables. For five of the six species, leaf moisture and leaf strength did not vary between sites with and without cattle ($P > 0.05$; Table 1, Fig. 1a,d). For all six species, specific leaf area did not differ between –C and +C sites ($P > 0.05$). The species most affected by presence of cattle was the palatable *N. antarctica* (Table 1). Leaf size was the variable most affected by presence or absence of cattle; it had a significant effect on three of six species (Table 1, Fig. 1b). Leaves from the non-palatable *L. hirsuta* increased in leaf size at sites with cattle ($P < 0.05$), whereas leaf size of the highly palatable *M. boaria* and *R. magellanicum* decreased in the presence of cattle ($P < 0.01$).

In the presence of cattle, time to ignition decreased for the three deciduous species; it significantly decreased for *N. antarctica* ($P < 0.01$) and tended to decrease for *D. juncea* and *R. magellanicum* ($P = 0.07$; Table 1, Fig. 1f). Conversely, for *S. patagonicus* time to ignition tended to increase at sites with cattle ($P = 0.07$). *N. antarctica* and *S. patagonicus* showed a significant decrease in duration of combustion in the presence of cattle ($P < 0.05$; Fig. 1f).

Interactions of cattle and time since fire

The effects of cattle and fire generally did not interact, meaning that cattle had similar effects on leaf traits and flammability at burned and unburned sites. Only three significant interaction effects were found across all species and leaf traits (fire \times cattle: $P < 0.05$; Table 1). Leaf moisture of *N. antarctica* was higher with cattle present at unburned sites, but not at burned sites (Fig. 1a). For the highly palatable *M. boaria*, the effects of cattle on time to

Table 1. Results of 2 × 2 factorial ANOVAs (fire (F) = recently burned/unburned; cattle (C) = presence/absence) for six variables: percentage leaf moisture, leaf size, specific leaf area, leaf strength, time to ignition and duration of combustion, for all species under study.

Effect	df	<i>Lomatia hirsuta</i>		<i>Diostea juncea</i>		<i>Nothofagus antarctica</i>		<i>Schinus patagonicus</i>		<i>Maytenus boaria</i>		<i>Ribes magellanicum</i>	
		F	P	F	P	F	P	F	P	F	P	F	P
%Leaf moisture													
F	1	3.27 [†]	0.08	13.12	0.00**	29.56 [†]	0.00**	3.4 [†]	0.07	2.96	0.09	3.22 [†]	0.08
C	1	0.30	0.59	0.18	0.67	12.75	0.00**	0.01	0.91	0.93	0.34	0.94	0.34
F × C	1	0.98	0.32	0.47	0.49	5.87	0.02*	0.01	0.97	0.7	0.41	0.54	0.46
Error	36												
Leaf size													
F	1	4.7 [†]	0.04**	8.52 [†]	0.00**	8.56	0.00**	14.26 [†]	0.00**	21.45 [†]	0.00**	16.48 [†]	0.00**
C	1	5.45	0.03*	2.15	0.15	0.03	0.87	1.37	0.25	33.77	0.00**	28.42	0.00**
F × C	1	0.15	0.70	0.12	0.73	2.02	0.16	0.2	0.66	0.01	0.92	1.22	0.28
Error	36												
Specific leaf area													
F	1	9.07 [†]	0.00**	13.69 [†]	0.00**	11.74	0.00**	16.78 [†]	0.00**	11.75	0.00**	8.53 [†]	0.01*
C	1	0.01	0.97	1.06	0.31	1.8	0.19*	0.32	0.57	0.01	0.97	0.31	0.58
F × C	1	0.67	0.42	0.18	0.68	0.88	0.35	0.17	0.69	0.44	0.51	1.35	0.25
Error	36												
Leaf strength													
F	1	2.51 [†]	0.12	10.16	0.00**	5.51	0.02*	1.64	0.21	4.85 [†]	0.03*	0.23 [†]	0.63
C	1	0.43	0.52	3.8	0.06	7.49	0.01*	0.39	0.53	0.01	0.96	2.27	0.14
F × C	1	0.01	0.95	0.43	0.51	0.98	0.33	0.01	0.96	0.06	0.81	1.55	0.22
Error	36												
Time to ignition													
F	1	10.18	0.00**	0.91	0.34	6.66 [†]	0.01*	29.18 [†]	0.00**	12.17	0.00**	15.03	0.00**
C	1	2.68	0.11	3.36	0.07	10.52	0.00**	3.51	0.07	0.14	0.71	3.53	0.07
F × C	1	1.24	0.27	0.03	0.86	0.35	0.56	0.51	0.48	5.98	0.02*	0.61	0.43
Error	36												
Duration of combustion													
F	1	1.44 [†]	0.24	6.18	0.02*	1.96 [†]	0.17	0.1 [†]	0.75	0.8 [†]	0.38	1.99 [†]	0.17
C	1	2.94	0.09	2.06	0.16	6.52	0.01*	4.58	0.04*	0.58	0.45	0.86	0.36
F × C	1	0.04	0.84	1.7	0.20	0.22	0.64	0.38	0.54	8.73	0.01*	1.82	0.19
Error	36												

[†] $P < 0.05$; ** $P < 0.01$; [†]For this species and this variable a logarithmic transformation was applied.

ignition and duration of combustion were opposite at burned and unburned sites (Fig. 1e,f).

Species differences in leaf flammability

Principal components analysis (PCA) of flammability-related foliar traits of species reveals some general associations of these species with time since last fire and a weak relation with presence or absence of cattle. The first two PCA axes account for 61% of the variation in the data (Fig. 2). Axis 1 mainly represents increasing values of leaf strength and leaf size, and decreasing values of specific leaf area. Axis 2 reflects increasing values of duration of combustion, time to ignition and leaf moisture.

The PCA ordination showed that the moderately palatable *N. antarctica* and *S. patagonicus* were characterized by low values of leaf moisture and time to ignition on the second axis, which may imply enhanced foliar flammability.

N. antarctica and *S. patagonicus* on average for all sites had the lowest leaf moisture ($150.8 \pm 14\%$ and $161.4 \pm 13\%$, respectively) and moreover these values were lower for +B sites in comparison with -B sites (Fig. 1a). The highly palatable *R. magellanicum* and *M. boaria* on average also had low values for time to ignition. The non-palatable *D. juncea* showed an opposite pattern: high values for leaf moisture and time to ignition in comparison to the more palatable species. This species accounted on average for all sites, the highest values of leaf moisture ($283 \pm 9\%$) representing values 15% higher than *M. boaria* (the species with second highest leaf moisture) and 88% higher than *N. antarctica* (the species with lowest values for leaf moisture). Also in comparison to the more palatable species, the non-palatable *L. hirsuta* had high values for leaf size and leaf strength (Figs 1b,d and 2) and high values for time to ignition (Fig. 1e), implying low foliar flammability.

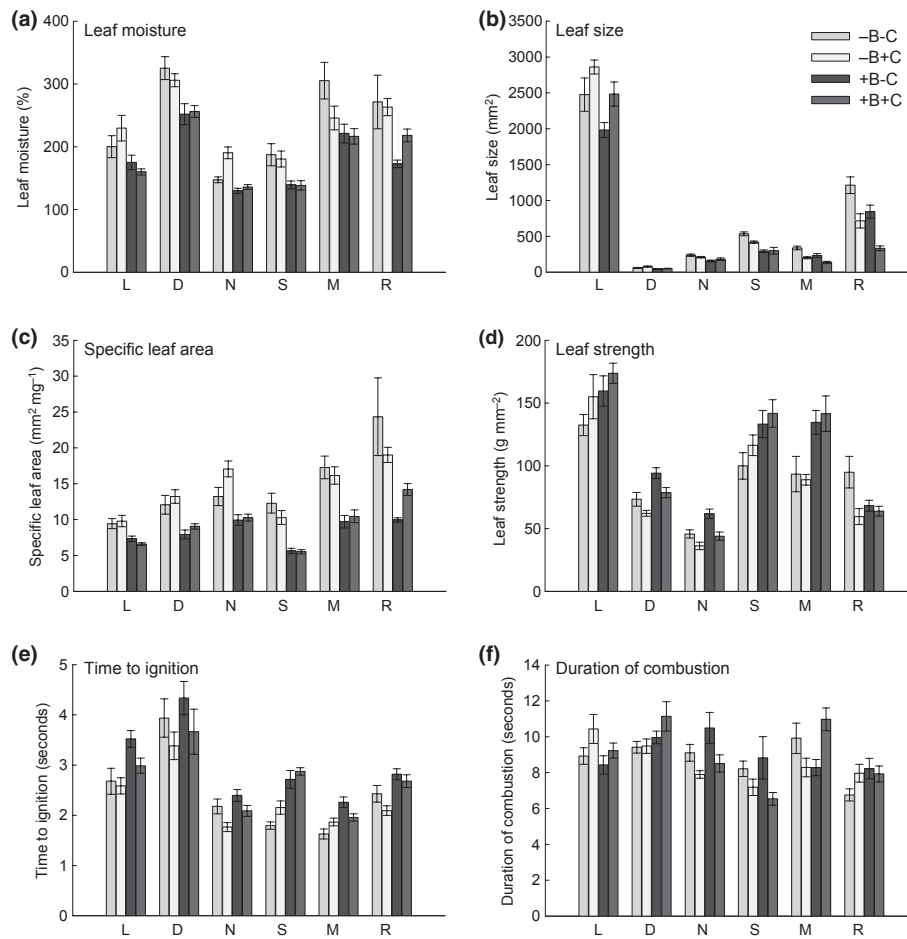


Fig. 1. Means and standard errors for *Lomatia hirsuta* (L), *Diostea juncea* (D), *Nothofagus antarctica* (N), *Schinus patagonicus* (S), *Maytenus boaria* (M) and *Ribes magellanicum* (R) for leaf traits and ignitability tests: (a) percentage leaf moisture, (b) leaf size, (c) specific leaf area, (d) leaf strength, (e) time to ignition and (f) duration of combustion. Origin of plants is indicated as follows: -B-C (unburned and without cattle); -B+C (unburned with cattle); +B-C (recently burned without cattle) and +B+C (recently burned with cattle). Species are arranged from left to right, from not palatable to highly palatable species.

PCA axis 1 appeared to be related to time since last fire as reflected by the placement of plants growing in recently burned sites towards higher values on axis 1, for each species (Fig. 2). Accordingly, recently burned sites were characterized by plants with leaves with lower specific leaf area, and higher leaf strength (Figs 1 and 2). Additionally, clusters based on leaf traits defined by PCA showed that the non-palatable species *L. hirsuta* and *D. juncea* each remain tightly grouped as individual species whereas the four moderately and highly palatable species more strongly reflect the effects of site differences.

Discussion

Fire and herbivory influences on leaf flammability

Foliar flammability of key shrubland species in northwest Patagonia is consistently associated with recent history of

fire, and for some species with herbivory by livestock. At the level of individual plants, recent fire has a strong and homogenous effect on foliar properties, whereas effects of cattle on foliar traits are species-specific. Leaf moisture is consistently lower in recent burned sites and may contribute to higher community-level flammability in comparison with sites not burned for at least 50 yr. Lower leaf moisture content means that less heat is required for ignition and fire spread (Valette 1992). At recently burned sites the two dominant and moderately palatable species *N. antarctica* and *S. patagonicus*, which provide relatively continuous fuel loads in the shrubland communities, showed large reductions in leaf moisture compared to unburned sites.

The generally decreasing values for leaf moisture, leaf size and specific leaf area, as well as the increasing values of leaf strength, probably reflect the microclimatic

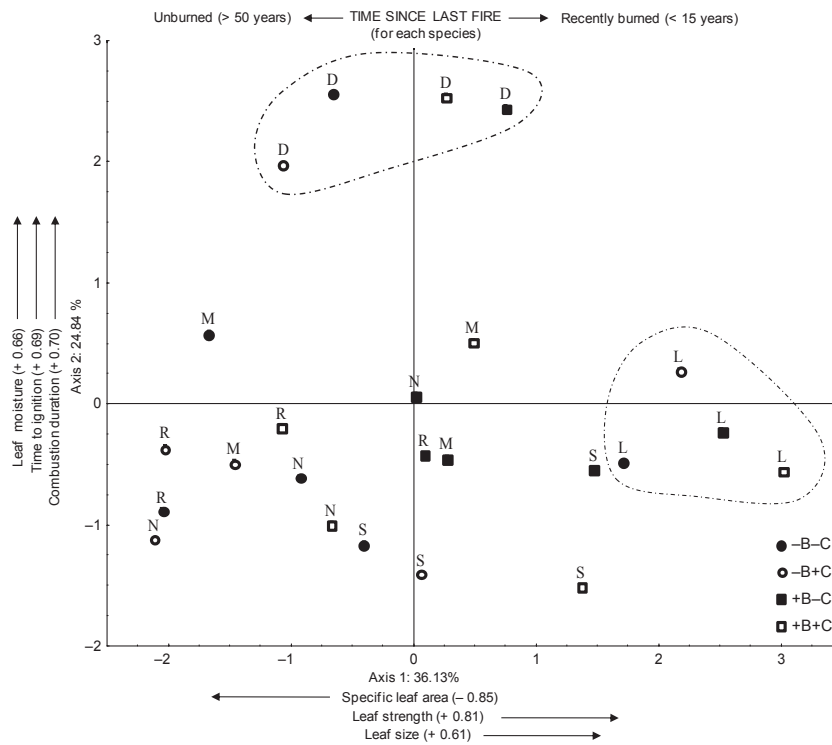


Fig. 2. Principal components analysis of leaf properties of *Lomatia hirsuta* (L), *Diostea juncea* (D), *Nothofagus antarctica* (N), *Schinus patagonicus* (S), *Maytenus boaria* (M) and *Ribes magellanicum* (R) at the four types of sites, on the basis of the following traits: percentage leaf moisture, leaf size, specific leaf area, leaf strength, time to ignition and duration of combustion. Origin of plants is indicated as follows: –B–C (unburned and without cattle); –B+C (unburned with cattle); +B–C (recently burned without cattle) and +B+C (recently burned with cattle). Labels on axis specify the traits with the highest eigenvector scores for each axis. Correlations between plant traits and PCA axis are given in parentheses and arrows indicate the direction of each correlation. Relation between data location in space, time since last fire, and axis one is specified in the figure. Dashed lines indicate clusters of non-palatable species: *L. hirsuta* and *D. juncea*.

conditions of recently burned sites. In the absence of a closed tree canopy, higher solar insolation results in warmer and drier summer conditions, and there is less sheltering from strong winds. The observed trends in foliar traits associated with the more open, xeric recently burned sites are consistent with findings in numerous other ecosystems. For example, at a global scale, lower specific leaf area is associated with more arid conditions (Reich et al. 1999). At an individual species level, leaf size and specific leaf area have been shown to decrease with increasing insolation (Ackerly et al. 2002). Analogous to our findings in recently burned sites, greater leaf strength has previously been associated with more open conditions and higher insolation (Onoda et al. 2008). In general, we observed that *D. juncea* and *N. antarctica* were the species that were most affected by time since last fire. For both species, the five foliar traits studied significantly varied depending on site conditions, implying a high sensitivity to extreme microclimate conditions.

The reduction in fresh leaf moisture at recently burned sites implies increased community flammability at these

sites (Bond & Van Wilgen 1996). However, the ignitability tests based on dried tissues generally showed that plants growing at the recently burned sites required longer time periods of exposure to a heat source in the laboratory before ignition occurred. Although other studies have shown that fuel moisture is the main factor affecting ignition times and combustion duration (Saura-Mas et al. 2010; Hachmi et al. 2011), when moisture is excluded from leaves other parameters and foliar characteristics become more determinant of how easily and rapidly they will burn. A longer time to ignition may be associated with lower specific leaf area and higher leaf strength at recently burned sites in comparison with unburned sites. Both traits are associated with herbivore resistance (Read & Stokes 2006), and they tend to reduce flammability if the effect of moisture is excluded.

In contrast to the consistent and strong association of leaf traits with more open recently burned sites in ways that would affect flammability, relationships of these traits to recent herbivory by livestock were not consistent. For the species most affected by the presence of cattle,

N. antarctica, there is some evidence that exposure to herbivory by cattle enhances foliar flammability; variations in leaf strength and time to ignition appear to enhance flammability. For this species, differences in time to ignition and duration of combustion related to the presence or absence of cattle potentially may reflect chemical defences to herbivory, which were not measured in our study.

Leaf size was the trait most affected by cattle herbivory. For the non-palatable *L. hirsuta*, larger leaf size at sites with cattle may be an indirect effect of herbivory due to the reduction of competition from more palatable species. Conversely, at sites with cattle, smaller leaf size of the highly palatable species, *M. boaria* and *R. magellanicum*, may be the consequence of reduced resources as well as defence against browsing, since smaller leaves decrease the ungulate reward per time unit (Belovsky & Schmitz 1991; Zinn et al. 2007).

The three deciduous species, the non-palatable *D. juncea*, the moderately palatable *N. antarctica* and the highly palatable *R. magellanicum*, had lower values for leaf strength in comparison to the evergreen species, independently of burning and herbivory histories (Fig. 1e). Also, *D. juncea* and *N. antarctica* experienced reduced leaf strength in the presence of cattle. In deciduous plants, high rates of photosynthesis may be necessary to accumulate reserves for foliage replacement; hence leaves may be rather thin with a high specific leaf area or leaf mass per area, allowing high rates of carbon gain per leaf mass investment (Read & Stokes 2006). In optimal environments or in situations where a short leaf life span is induced, leaves may diminish in strength (Read & Stokes 2006), and hence facilitate ignition.

Overall, the ANOVA results show that herbivory by cattle may affect foliar flammability, and in some cases may increase it in palatable species, particularly by decreasing leaf size (*M. boaria* and *R. magellanicum*) and leaf strength (*N. antarctica*) or shortening time to ignition (*N. antarctica*). Significant interactions between time since last fire and cattle presence were fewer than expected, showing almost no interaction between both effects. Leaf moisture of *N. antarctica* was higher in -B+C and lower and similar in other sites. Potentially, cattle could have reduced the abundance of competing plants that usually reduce moisture availability to *N. antarctica*, but further research is required to confirm this interpretation. For the highly palatable *M. boaria*, time to ignition decreased at sites not burned in comparison to +B-C sites, whereas duration of combustion increased in +B+C sites in comparison to sites affected by only one disturbance. Ignition and combustion traits are correlated with chemical properties (Cornelissen et al. 2003; Alessio et al. 2008) that were not measured in our study but may affect flammability.

Foliar traits and community-level flammability

Foliar traits of the most dominant species are likely to affect community-level flammability but other plant traits as well as their interactions with herbivory may also be important. The six species examined in this preliminary study of foliar flammability of woody species in northwest Patagonia account, on average, for almost 40% of the total cover of woody species of the communities studied, and their cover is only exceeded by that of the bamboo *Chusquea culeou* at some sites (M. Blackhall, unpublished data). At heavily browsed sites, the highly palatable species *M. boaria* and *R. magellanicum* are scarce and provide relatively little biomass for burning. On the other hand, *N. antarctica* and *S. patagonicus*, both moderately palatable species, are abundant at sites with intense herbivory by cattle and provide much of the fuel at these sites (Raffaele et al. 2011). Both species have a fire-prone architecture, with a high percentage of fine fuel (thin branches, high foliar biomass; M. Blackhall unpublished data). These two species on average showed the lowest percentages of leaf moisture, which are comparable to the dominants of Mediterranean type shrublands elsewhere (Countryman & Philpot 1970; Van Wilgen et al. 1990). At sites affected by recent fire and cattle, *N. antarctica* was the most flammable species, as indicated by its low leaf moisture, leaf size and foliar strength, and short time to ignition (Figs 1 and 2).

Some traits other than those measured in the current study are also important determinants of flammability. For example, retention of standing dead biomass is known to be a major influence on flammability (Schwilk 2003; Baeza et al. 2011). It is important to emphasize that low flammability for *D. juncea* was only represented by its foliage, which represents a small percentage of the total biomass of the plant (2% on average). Despite its low foliar flammability, it appears to be a highly flammable plant because almost 50% of its standing biomass can be dead tissue (M. Blackhall unpublished data).

Conclusions

In the current study we show consistent differences in the foliar traits of common shrub and small tree species at sites that were recently burned in comparison with unburned sites, which could potentially affect community flammability. In comparison with unburned forests, all of the dominant shrub and small tree species studied showed reduced leaf moisture and leaf size, both traits conducive to greater foliar flammability. Longer time to ignition for samples collected at recently burned sites may be related to the artificial removal of moisture from the samples tested.

The effects of herbivory on foliar flammability in our study are complex, and do not show a consistent pattern of enhanced foliar flammability related to cattle influences. As this study of foliar flammability is the first investigation of plant flammability in northwest Patagonia, further research is needed on the potential effects of plant architectural and chemical traits on plant-level flammability. Currently available research in our study area indicates that the primary mechanism by which cattle browsing contributes to a positive feedback enhancing community-level flammability of shrublands is through their inhibitory influence on the regeneration of forest dominants following the burning of fire-resistant tall forests (Raffaele et al. 2011; Veblen et al. 2011). The current study shows that plant foliar traits in the shrublands with high cattle pressure, originating from the burning of tall forests and dominated by the shrubby *N. antarctica*, appear to enhance the flammability of fire-prone shrublands in northwest Patagonia.

Acknowledgements

Research was supported by Universidad Nacional del Comahue (B103 and B152), UNC-PICT (Grant 01-07320) and awards No. 0117366 and 0956552 from the U.S. National Science Foundation. We thank L. Bianchi, G. Defosé and L. Garibaldi for access to laboratory equipment. For commenting on and improving the manuscript we thank A. Holz, J. Paritsis, N. Tercero-Bucardo and Dr. Sabine Güsewell. For research assistance we thank S. Polcowñuk and X. Flores. We thank the Administración de Parques Nacionales for permitting the research. M.B. is a CONICET doctoral fellow and E.R. is a researcher for Consejo Nacional de Investigaciones Científicas y Tecnológicas, Argentina.

References

- Ackerly, D.D., Knight, C.A., Weiss, S.B., Barton, K. & Starmer, K.P. 2002. Leaf size, specific leaf area and microhabitat distribution of chaparral woody plants: contrasting patterns in species level and community level analyses. *Oecologia* 130: 449–457.
- Alessio, G.A., Peñuelas, J., Llusà, J., Ogaya, R., Estiarte, M. & De Lillis, M. 2008. Influence of water and terpenes on flammability in some dominant Mediterranean species. *International Journal of Wildland Fire* 17: 274–286.
- Anderson, H.E. 1970. Forest fuel ignitability. *Fire Technology* 6: 312–319.
- Baeza, M.J., Santana, V.M., Pausas, J.G. & Vallejo, V.R. 2011. Successional trends in standing dead biomass in Mediterranean basin species. *Journal of Vegetation Science* 22: 467–474.
- Barros, V., Cordon, V., Moyano, C., Méndez, R., Forquera, J. & Pizzio, O. 1983. *Cartas de precipitación de la zona oeste del las provincias de Río Negro y Neuquén*. Facultad de Ciencias Agrarias, Universidad Nacional del Comahue., Cinco Saltos, Río Negro, AR.
- Behm, A.L. 2003. *Flammability of native understory species in Pine Flatwood and Hardwood Hammock ecosystems*. Master of Science Thesis. University of Florida, Gainesville, FL, US.
- Behm, A.L., Duryea, M.L., Long, A.J. & Zipperer, W.C. 2004. Flammability of native understory species in pine flatwood and hardwood hammock ecosystems and implications for the wildland–urban interface. *International Journal of Wildland Fire* 13: 355–365.
- Belovsky, G.E. & Schmitz, O.J. 1991. Mammalian herbivore optimal foraging and the role of plant defenses. In: Palo, R.T. & Robbins, C.T. (eds.) *Plant defences against mammalian herbivory*, pp. 1–28. CRC Press, Boca Raton, FL, US.
- Blackhall, M., Raffaele, E. & Veblen, T.T. 2008. Cattle affect early post-fire regeneration in a *Nothofagus dombeyi*–*Austrocedrus chilensis* mixed forest in northern Patagonia, Argentina. *Biological Conservation* 141: 2251–2261.
- Bond, W.J. & Midgley, J.J. 1995. Kill thy neighbour: an individualistic argument for the evolution of flammability. *Oikos* 73: 79–85.
- Bond, W.J. & Van Wilgen, B.W. 1996. *Fire and plants*, 1st ed. Chapman & Hall, London, UK.
- Choong, M.F., Lucas, P.W., Ong, J.S.Y., Pereira, B., Tan, H.T.W. & Turner, I.M. 1992. Leaf fracture toughness and sclerophylly: their correlations and ecological implications. *New Phytologist* 121: 597–610.
- Cornelissen, J.H.C., Lavorel, S., Garnier, E., Díaz, S., Buchmann, N., Gurvich, D.E., Reich, P.B., ter Steege, H., Morgan, H.D., van der Heijden, M.G.A., Pausas, J.G. & Poorter, H. 2003. A handbook of protocols for standardised and easy measurement of plant functional traits worldwide. *Australian Journal of Botany* 51: 335–380.
- Correa, M.N. 1969–1997. *Flora Patagónica (Republica Argentina)*. Colección Científica del INTA, Buenos Aires, AR.
- Countryman, C.M. & Philpot, C.W. 1970. *Physical characteristics of chamise as a wildland fuel*. Res. Paper PSW-RP-66. Pacific Southwest Forest & Range Experiment Station, Forest Service, Department of Agriculture, Berkeley, CA, US.
- Gill, A.M. & Moore, P.H.R. 1996. *Ignitibility of leaves of Australian plants*. CSIRO Plant Industry, Centre for Plant Biodiversity Research, Canberra, AU.
- Gill, A.M. & Zylstra, P. 2005. Flammability of Australian forests. *Australian Forestry* 68: 88–94.
- Hachmi, M.H., Sesbou, A., Benjelloun, H., El Handouz, N. & Bouanane, F. 2011. A simple technique to estimate the flammability index of Moroccan forest fuels. *Journal of Combustion*. doi:10.1155/2011/263531.
- Kitzberger, T., Raffaele, E., Heinemann, K. & Mazzarino, M.J. 2005. Effects of fire severity in a north Patagonian subalpine forest. *Journal of Vegetation Science* 16: 5–12.

- Kuehl, R.O. 2001. *Diseño de experimentos – principios estadísticos de diseño y análisis de investigación*, 2a. ed. Thomson Learning, México D.F., MX.
- Lauría Sorge, R.M. & Romero, C.A. 1999. *La ganadería doméstica de los pobladores con permiso de ocupación y pastaje (P.P.O.P.) en tierras fiscales del Parque Nacional Nahuel Huapi*. Administración de Parques Nacionales – Intendencia Parque Nacional Nahuel Huapi, San Carlos de Bariloche, AR.
- Mermoz, M. & Martín, C. 2005. Mapa de vegetación del Parque y la Reserva Nacional Nahuel Huapi. *Anales de Parques Nacionales* 17: 51–62.
- Mermoz, M., Kitzberger, T. & Veblen, T.T. 2005. Landscape influences on occurrence and spread of wildfires in Patagonian forests and shrublands. *Ecology* 86: 2705–2715.
- Montgomery, R.K. & Cheo, P.C. 1971. Effect of leaf thickness on ignitability. *Forest Science* 17: 475–478.
- Onoda, Y., Schieving, F. & Anten, N.P.R. 2008. Effects of light and nutrient availability on leaf mechanical properties of *Plantago major*: a conceptual approach. *Annals of Botany* 101: 727–736.
- Quinn, G.P. & Keough, M.J. 2002. *Experimental design and data analysis for biologists*. Cambridge University Press, Cambridge, UK.
- Raffaele, E., Veblen, T.T., Blackhall, M. & Tercero-Bucardo, N. 2011. Synergistic influences of introduced herbivores and fire on vegetation change in northern Patagonia, Argentina. *Journal of Vegetation Science* 22: 59–71.
- Read, J. & Stokes, A. 2006. Plant biomechanics in an ecological context. *American Journal of Botany* 93: 1546–1565.
- Reich, P.B., Ellsworth, D.S., Walters, M.B., Vose, J.M., Gresham, C., Volin, J.C. & Bowman, W.D. 1999. Generality of leaf trait relationships: a test across six biomes. *Ecology* 80: 1955–1969.
- Rundel, P.W. 1981. Structural and chemical components of flammability. In: Mooney, H.A., Bonnicksen, T.M., Christensen, N.L., Lotan, J.E. & Reiners, W.A. (eds.) *Fire regimes and ecosystem properties*. USDA Forest Service General Technical Report GTR-WO-26, pp. 183–207. USDA Forest Service, Washington, DC, US.
- Saura-Mas, S., Paula, S., Pausas, J.G. & Lloret, F. 2010. Fuel loading and flammability in the Mediterranean Basin woody species with different post-fire regenerative strategies. *International Journal of Wildland Fire* 19: 783–794.
- Schwilk, D.W. 2003. Flammability is a niche construction trait: canopy architecture affects fire intensity. *The American Naturalist* 162: 725–733.
- Tercero-Bucardo, N., Kitzberger, T., Veblen, T.T. & Raffaele, E. 2007. A field experiment on climatic and herbivore impacts on post-fire tree regeneration in north-western Patagonia. *Journal of Ecology* 95: 771–779.
- Valette, J.C. 1992. Inflammabilities of Mediterranean species. In: Balabanis, P., Eftichidir, R. & Fantechi, R. (eds.) *Forest fire risk and management: European school of climatology and natural hazard course*, pp. 51–64. General Directorate for Science, Research and Development of the European Commission, Halkidiki, GR.
- Van Wilgen, B.W., Higgins, K.B. & Bellstedt, D.U. 1990. The role of vegetation structure and fuel chemistry in excluding fire from forest patches in the fire-prone fynbos shrublands of South Africa. *Journal of Ecology* 78: 210–222.
- Veblen, T.T., Holz, A., Paritsis, J., Raffaele, E., Kitzberger, T. & Blackhall, M. 2011. Adapting to global environmental change in Patagonia: what role for disturbance ecology? *Austral Ecology* 36: 891–913.
- White, R.H. & Zipperer, W.C. 2010. Testing and classification of individual plants for fire behaviour: plant selection for the wildland urban interface. *International Journal of Wildland Fire* 19: 213–227.
- Zinn, A.D., Ward, D. & Kirkman, K. 2007. Inducible defenses in *Acacia sieberiana* in response to giraffe browsing. *African Journal of Range and Forage Science* 24: 123–129.