Variable community responses to herbivory in fire-altered landscapes of northern Patagonia, Argentina

T Kitzberger1*, E Raffaele1 and T Veblen2

1 Laboratorio Ecotono, Universidad Nacional del Comahue, Quintral 1250, 8400 Bariloche, Argentina
2 Department of Geography, University of Colorado, Campus Box 260, Boulder, CO 80309, USA
* Corresponding author, e-mail: tkitzber@crub.uncoma.edu.ar

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Landscapes in northern Patagonia have undergone dramatic changes in fire regimes over the last century. Superimposed on this changing vegetation mosaic are impacts from introduced herbivores. In this paper we identify synergistic interactions developing into positive fire-herbivory feedbacks that maximise vegetation change. Analyses of vegetation changes over 30 years at low altitude (c. 800m) montane forest indicates that fire-fragmented forest has coalesced despite relatively heavy grazing pressure. During recent fire suppression, vegetation shifted in dominance from short-lived resprouting species (mostly shrubs) to obligate seed-dispersed trees, some of them requiring initial facilitation by shrubs. Transitions from shrubland and grassland to forest were restricted to c. 20–30m from the nearest forested patches. Beyond this distance, shrublands and grassland are stable in time. In contrast, post-fire responses of high altitude (>1 000m) subalpine forests show a much higher sensitivity to herbivory. Experimental evidence suggests strong fire severity x herbivory interactions affect tree seedling mortality. Severe fires and/or repeated fire create conditions where trees are unable to establish due to unfavorable microenvironments and because fire-opened forests are more heavily used by herbivores. These patterns are consistent with century-long trends of increase in montane forest at the expense of shrublands and increase in shrublands over former subalpine forests.

Keywords: fire-herbivory, fire regime, survivorship, synergism, tree seedling

Introduction

Fire has played a major role in controlling changes in vegetation structure and composition of many ecosystems (Bond and Van Wilgen 1996). At broad scales, fire exclusion often results in increases in patch size and connectivity of vegetation types that are most affected by fire (Gardner et al. 1999), usually dominated by fire-sensitive obligate seed-dispersed species at the expense of shorter-lived, resprouting or fire-tolerant species (Keeley 1977). Consequences of these shifts in dominance range from changes in habitat configuration for wildlife and socioeconomic consequences of land use to feedbacks into future fire regimes. Thus, knowledge and prediction of the response of communities and landscapes to altered fire regimes is of crucial ecological and economic importance.

Herbivores often interact with fire (Mills 1986, Hobbs and Gimingham 1987), modifying vegetation trajectories. However, synergistic relationships between fire and herbivores are complex and rather system-dependent. Herbivores may retard or even completely impede the effects of fire suppression if the fire-sensitive community is negatively affected by herbivores. In contrast, other fire-sensitive communities may be more resistant or even benefited by herbivores (e.g. dispersal, compensatory growth, etc.), in which case herbivores may accompany or even accelerate fire-induced rates of community and landscape change.

Clearly, herbivore pressure is an important factor that may determine the concurrent effects of herbivory and post-fire succession. Within a given landscape, differential habitat use by herbivores as determined by pre-existing landscape configuration (generally a consequence of fire severity) can lead to spatial gradients in herbivore pressure and, thus, community consequences may become habitat and space-specific.

In the long-term, herbivore-fire interactions are crucial in determining feedbacks into future fire regimes. However, again, synergistic effects may be highly variable and complex. If herbivores promote shorter-lived species and prevent establishment and growth of species with slower fuel buildup rates, overall fire frequency may increase and fire intensity may decrease. If, in contrast, herbivores do not affect or even accelerate rates of afforestation, the system may enter a regime of less frequent but intense crown fires. If herbivore effects are space or habitat specific, fuel spatial discontinuities may create regimes of smaller fires, whereas if herbivores affect landscapes in a homogeneous fashion, regimes dominated by large fires may result.

In this paper, we present two case studies from northern Patagonia conducted in systems with contrasting herbivore...
responses after fire or when fire was excluded. Based on empirical evidence from multiple approaches, we attempt to understand how herbivores affect vegetation processes such as tree establishment and changes in vegetation cover types over time. Finally, we produced a conceptual model that incorporates variable herbivory synergism into the vegetation-fire regime interrelationship.

**Recent vegetation changes in northern Patagonia**

Vegetation patterns in northern Patagonia, Argentina (c. 37°–43°S) are the result of dominant disturbances such as naturally ignited and anthropogenic fire, climatic variability and impacts from introduced herbivores superimposed on the main W-E rainfall and altitudinal gradients (Veblen et al. 1992a, Veblen et al. 1992b). Major decadal- to century-scale vegetation changes at local and landscape scales have been attributed to changes in precipitation regimes, fire frequency and livestock numbers (Kitzberger and Veblen 1999, Kitzberger et al. 1997, Veblen and Lorenz 1987, Villalba and Veblen 1997).

Twentieth century fire exclusion after periods of extensive burning by either Euro-Argentinean settlers or by aboriginals has had major impacts on tree demography and present patterns of forest structure and distribution (Veblen and Lorenz 1988). Towards the dry eastern foothills, Austrocedrus chilensis woodlands have dramatically increased in dominance at the expense of Patagonian grasslands and shrublands (Veblen and Lorenz 1988), whereas in wetter areas, entire regions formerly opened by repeated burning have become large, continuous, even-aged A. chilensis or Nothofagus dombyei dominated forests or shrublands that are now c. 100 years old (Burns 1993, Dezzotti 1996, Kitzberger 1994, Veblen and Lorenz 1987, 1988). At higher elevations, landscapes have developed in a more erratic fashion, locally displaying even-aged Nothofagus pumilio forests or, alternatively, sharp boundaries of old-growth N. pumilio with post-fire shrublands, suggesting post-fire tree regeneration failure (Veblen et al. 1996).

The interactive effects of fire suppression and herbivory by introduced cattle, horses, sheep, cervids and European hares is less clear. Despite high livestock populations, which peaked in the 1930s–1940s (Eriksen 1971), extensive forests developed after fires. Nevertheless, locally high herbivore pressure probably impeded tree regeneration at some sites. Exceptionally heavy cattle load in post-fire areas can lead to turfs of exotic species, spiny shrubs and sparse dwarfed trees (De Pietri 1992, Veblen et al. 1992b). Resprouting spiny shrubs may, however, both facilitate tree seedling establishment and protect tree saplings from browsing (Kitzberger et al 2000). Thus, shrubland that is more resilient to browsing may change in dominance towards woodlands or even forests in the long term (Kitzberger and Veblen 1999). The role of herbivores in preventing subalpine N. pumilio post-fire regeneration is not clear because many confounding variables such as climatic variation, remnant tree configuration as potential seed sources, and canopy retention as a modifier of microhabitat for tree establishment and of habitats of herbivores may be interacting (Veblen et al. 1996).

**Methods**

**Study sites**

Two sites reflecting contrasting communities were selected within northern Nahuel Huapi National Park, Argentina: West Trafal (WT) representing submesic montane landscapes and Chall Huaco (CH) representing xeric (north-facing) subalpine forested landscapes. WT is located on a north-facing slope located at the eastern end of Lago Trafal at c. 900m asl. With mean annual precipitation of c. 2 000mm, forests are dominated by c. 30m high evergreen N. dombyei and codominated by c. 25–30m tall A. chilensis conifers. Forest patches are intermingled with shrublands dominated by xerophyllous small trees and shrubs such as Lobaria hirsuta, Schinus patagonicus, Dioctea juncea, Berberis darwinii, N. antarctica and the bamboo Chusquea culeou. Small patches of anthropogenic grasslands are dominated by Acaena splendens, Mulinum spinosum and exotics such as Rumex sp. and Plantago sp. (Figure 1).

Fire frequency at WT peaked during the late 19th century coincident with massive clearing of forests for pastures (Willis 1914). During the early 20th century, fire frequency declined sharply as burning practices were abandoned and the area was given protected status (Kitzberger 1994, Kitzberger and Veblen 1999, Veblen et al. 1992a). The region of Lago Trafal where WT is located has long supported one of the densest cattle populations for this habitat type within Nahuel Huapi National Park (Veblen et al. 1992a). Cattle were not eradicated from the region after the creation of north Patagonian national parks, and only in recent decades have efforts been made to reduce cattle populations in regions of highest protection value.

CH is located in the lower Chall Huaco valley in central Nahuel Huapi National Park in one of the easternmost outskirts of the subalpine N. pumilio forests where mean annual precipitation is 800mm. Nothofagus pumilio forests extend altitudinally from c. 1 000–1 600m. Lower slopes and xeric slopes are shrublands dominated by N. antarctica, Dioctea juncea, Schinus patagonicus and Mulinum spinosum. In the undisturbed N. pumilio forest, the herbaceous stratum is dominated by Alstroemeria aurea, a rhizomatous forb that forms dense thickets up to 1.2m tall, and in lower proportion by Osmorhiza chilensis and Perezia prenanthoides. Other species present include shrubs such as Ribes magellanicum, Berberis seradentata and vines such as Vicia nigricans. In contrast, in recently burned forests dominance shifts towards resprouting shrubs such as Schinus patagonicus, native herbs such as Phacelia secunda, Oxlalis valdiviensis and Geranium sp. and exotics such as Epilobium glaucum and Rumex acetosella.

Chall Huaco valley has a rich history of fire occurrence, but most fires occurred in the late 19th and early 20th centuries. Recently, the area witnessed large fires in 1956, 1996 and 1999 (Bruno and Martin 1982). During January 1996, an extensive fire burned for 45 days in the valley. Fire affected mostly shrublands and pine plantations at the lower valley bottom (c. 680ha), but fire spread also into the N. pumilio-forested slopes and upper valley, affecting c. 400ha of subalpine forests.
Changes in montane landscapes 1940–1970

Aerial photographs (1:24 000) taken in 1940 and 1970 over WT were scanned at 300dpi corresponding to 2m ground resolution, entered into a GIS (IDRISI), and an area of 21ha was co-registered by identifying 15 common ground control points. The procedure resulted in Root Mean Square (RMS) errors of 1.3m. Three main cover types were classified a priori: forests, shrublands and grasslands. For each cover type, training areas were digitised into 1940 and 1970 images. The distributions of digital numbers were fitted to normal distributions and cutoff values were determined based on 95% critical values. Due to differences in the tone of photographs this procedure was performed separately for the 1940 and 1970 images. Thematic accuracy of the 1970 image was 84.4% (Overall Accuracy Index) based on 45 stratified, random ground control points collected in the field.

Change detection was performed by cross-tabulating cover class images with IDRISI CROSSTAB routine. A 3 x 3 cross-classified image was obtained with all 1940–1970 cover class transitions. To test the hypothesis that transitions occurred independently of the distance from 1940 forest patches, a distance image was generated in which each pixel represented the distance to the nearest 1940 forest patch.

Figure 1: Landscape changes in the montane areas. Air photographs (A and B) and cover classes (F: forests, S: shrublands, and G: grasslands; C and D) of western Lago Trafal (Nahuel Huapi National Park) for 1940 and 1970. Cross-classified image that represent the nine possible transitions between 1940 and 1970 cover classes (E and F). From black to light gray are represented: F-F, S-F, G-F, F-S, S-S, G-S, F-G, S-G and G-G.
Post-fire tree seedling establishment in subalpine forests

To determine factors related to fire severity that affect tree establishment in subalpine forests, we performed a manipulative experiment at CH. Factors that were considered were: canopy mortality (hereafter CMORT), fire effects on soils (SOIL) and effects of herbivores (mostly horses and introduced hares: HERB).

Along a boundary caused by the 1996 Chall Huaco fire, three sites located on a south-facing slope were selected, each of them covering an area of approximately 1ha, and c. 200m apart from each other, representing three levels of fire severity. Site S1 had the highest severity, with extensive (>90%) canopy mortality, site S2 showed intermediate severity with 25–75% dead standing trees, and site S3 was only slightly affected by scattered small fire spots that affected <10% of the trees.

In each of the three sites, 30 plots (50 x 50cm) were randomly established. Soil of each of the three sites was reciprocally transplanted to the other two, resulting in 10 plots with each type of soil burning severity within each study site. Soil transplants were made by removing a 40 x 40 x 20cm volume of top soil in each plot and placing it randomly in a pre-assigned excavated plot of a different site. To homogenise changes in soil properties due to the excavation, plots with an equal degree of canopy mortality class and soil burning severity class were excavated and placed back into their own excavation. In each site, five plots of each soil burning severity class were excluded from herbivores with a 50 x 50 x 50cm, 1cm mesh. This led to a completely randomised design where factors were: CMORT (high, intermediate and low severity), SOIL (high and intermediate burned, and unburned) and HERB (fenced and unfenced treatments).

In mid-spring (October) 2000, 25–30 *N. pumilio* seedlings were transplanted to each of the 90 plots. Seedlings were collected from the forest floor from a nearby site and belonged to the same cohort of spring 1999, a mast year in the *N. pumilio* forest. During two growing seasons, from November 2000 to March 2002, plots were monitored every 15 days during the first year and monthly during the second year. In each plot, we recorded the number of live seedlings and measured gravimetric soil water content (SWC) of the top 10cm at three random points in the plot using a hand-held three-rod ML2x Theta Probe (Delta-T Devices). Values from the three points were averaged to represent the moisture availability in the plot. The main and combined effects of the factors over time (CMORT X SOIL X HERB) on soil moisture availability and seedling survival were tested using repeated measures ANOVA incorporating five time classes. Time was incorporated into the analyses to detect possible effects on soil water changes and seedling survivorship trajectories (i.e. differences in water status or survival of seedlings in different seasons between treatments).

Results

**Montane landscape changes under heavy herbivory**

Montane landscapes of northern Nahuel Huapi have changed dramatically during the 30 years analysed. Despite the fact that the 1940–1970 period covers the period of highest regional cattle pressure of the 20th century, forest area has increased by a factor of 260% (from 22.2 to 66.3% of the study area). Shrublands decreased in extent by a similar factor (from 67.5 to 26.2% of the study area) and grassland proportions remained stable (10.3% in 1940 to 7.5% in 1970: Figure 1). The most important transitions during the analysed period were shrublands that converted into forests (S-F transition probability 0.43), whereas transitions of grasslands to forest and grasslands to shrublands were an order of magnitude lower (0.03 and 0.04, respectively). Transition probabilities into cover types of lower physiognomic stature (i.e. F-S, F-G and S-G) were <0.03. Cover types that remained stable (did not show changes in the 1940–1970 comparison) were mostly shrublands (S-S transition probability 0.2) and forests (F-F transition probability 0.19) and, less extensively, grasslands (G-G transition probability 0.03: Figure 1).

When we cross-classified the transition image with distances from 1940 forest patches (Figure 2) important associations emerged (Figure 3). Based on deviations from the pattern expected from a distance-independent hypothesis, most land-cover transitions were associated with proximity to 1940 forest patches. The most frequent transition from shrubland to forests was highly restricted to the closest 7.5m. However, forests also developed up until 25m from forest patches on former grassland areas. Shrublands developed on former grasslands only along a belt from 10–30m, whereas stable grasslands were restricted to the outer 20–45m.

**Figure 2:** Image representing the distance between each cell and the nearest 1940 forest patch. Black: 1940 forests, increasingly lighter gray tones: longer distances. Longest recorded distance was 43m.
Herbivores and seedling establishment in post-fire subalpine forests

The main factor that negatively influenced soil water status and changes in soil water was canopy mortality class (CMORT and CMORT x TIME, P < 0.00001, respectively: Table 1), while soil burning (SOIL x TIME, P > 0.41) and herbivory (HERB x TIME, P > 0.54) had no significant effects. Overall seedling survival (CMORT, P < 0.00001) and survivorship patterns were negatively influenced by canopy mortality classes over time (CMORT x TIME, P < 0.0002: Table 1). In correspondence with the lack of effect on water content, soil burning had no significant effect on overall survival (SOIL, P > 0.06) or on seedling survivorship patterns (SOIL x TIME, P > 0.46: Table 2).

Herbivory significantly affected seedling survival (HERB, P < 0.006) and survivorship patterns (HERB x TIME, P < 0.05: Table 1). In general, plots exposed to browsing and mechanical damage by herbivores had lower seedling survival; this trend intensified towards the second growing season. Interestingly, the interaction CMORT x HERB was significant (P < 0.038), indicating that herbivory-mediated seedling mortality varies with canopy mortality class. Differences in survival between protected and unprotected plots were maximal in the severely fire-opened forest.

Discussion

Despite the differences in approach presented in these two case studies, it is clear that the post-fire responses of montane and subalpine ecosystems to the interaction with introduced herbivores as well as to other direct factors related to fire severity are rather different. In the montane systems, despite very high cattle pressure, *N. dombeyi* and *A. chilensis* were able to colonise shrublands and open grassland areas. Neither water shortages in the soil nor heavy browsing prevented the forest from dominating during a period when fire frequency declined. Causes of this response are related to life history and physiology of the dominant species of these communities. *N. dombeyi* is a very efficient coloniser of substrates opened by large-scale disturbances (Veblen et al. 1996). Large amounts of small seeds may produce carpets of light-demanding, fast-growing seedlings, some of which may escape from herbivores. On the other hand, the other dominant tree, *A. chilensis*, is less prone to regenerate in open areas but does successfully establish under the partial shade of nurse shrubs which, under heavy herbivore pressure, may also act as mechanical defense against browsing if spiny or unpalatable (Veblen et al. 1992a, 1992b, Kitzberger et al. 2000). Typically, *A. chilensis* overtops shrubs after c. 10–20y of establishment (Kitzberger et al. 2000) and accelerates its growth, thus efficiently escaping from large herbivores.

This study suggests that, in montane habitats, herbivores were not able to counteract natural afforestation trends induced by a reduction in fire frequency. Grasslands remained stable for 30y only at sites where seed sources for tree species are too distant for seedling recruitment. Alternatively, microsite conditions farther away from forest edges may become too dry for seedling establishment. Other possible explanations could be edaphic factors, e.g.
shallow or waterlogged soils. Contrasting with the active trend towards coalescence of montane forests are the subalpine *Nothofagus pumilio* which show a highly variable post-fire development (Rusch 1989, Veblen et al. 1996). The experimental data presented here suggest that the primary factor that limits forest re-establishment after fire in the subalpine zone is the lack of surviving adult trees. Remnant trees improve microenvironmental conditions (radiation, soil moisture) for establishment of *Nothofagus pumilio* seedlings. Due to a relatively high sensitivity to temperature, severe stand-devastating crown fires may not leave a single remnant tree over hundreds of hectares and thus entire forests may convert into shrublands, bamboo thickets or grasslands. Given sufficient remnant trees for propagules, herbivores may severely limit seedling establishment. Herivores select open habitats Herbivores do not disperse trees

Table 1: Seedling post-fire survival experiment in subalpine forest of Chall Huaco. Summary statistics of three-way repeated-measures ANOVA for the effect of canopy mortality (CMORT: three levels), (soil burning severity (SOIL: three levels), and herbivory (two levels) on top soil water content and *Nothofagus pumilio* seedling survival recordings over two growing seasons (November 2000 to March 2002). Note: percent seedling survival was arcsine transformed

<table>
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<tr>
<th>Effect</th>
<th>df effect</th>
<th>df error</th>
<th>F</th>
<th>P</th>
<th>df error</th>
<th>F</th>
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<td>TIME</td>
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<td>276</td>
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Table 2: Sets of species/community characteristics that may promote or retard afforestation trends induced by fire exclusion

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<th>Factors Retarding Afforestation</th>
<th>Factors Promoting Afforestation</th>
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<td>Low/variable seed output</td>
<td>High seed output</td>
</tr>
<tr>
<td>Low seed viability</td>
<td>High seed viability</td>
</tr>
<tr>
<td>Higher shade tolerance</td>
<td>Lower shade tolerance</td>
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<tr>
<td>Slow growth</td>
<td>Fast growth</td>
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<tr>
<td>High fire sensitivity</td>
<td>Low fire sensitivity</td>
</tr>
<tr>
<td>Lack of adaptations to fire</td>
<td>Adaptations to fire (eg. serotiny)</td>
</tr>
<tr>
<td>Lack of nurse plant syndromes</td>
<td>Use nurse plants</td>
</tr>
<tr>
<td>Lack of resprouting shrubs</td>
<td>Association with resprouting shrubs</td>
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<tr>
<td>Herbivores select open habitats</td>
<td>Herbivores are less selective</td>
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<tr>
<td>Lack of alternative food</td>
<td>Other food items (grass, bamboo)</td>
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<tr>
<td>Herbivores do not disperse trees</td>
<td>Herbivores disperse trees</td>
</tr>
</tbody>
</table>

shallow or waterlogged soils. Contrasting with the active trend towards coalescence of montane forests are the subalpine *Nothofagus pumilio* which show a highly variable post-fire development (Rusch 1989, Veblen et al. 1996). The experimental data presented here suggest that the primary factor that limits forest re-establishment after fire in the subalpine zone is the lack of surviving adult trees. Remnant trees improve microenvironmental conditions (radiation, soil moisture) for establishment of *Nothofagus pumilio* seedlings. Due to a relatively high sensitivity to temperature, severe stand-devastating crown fires may not leave a single remnant tree over hundreds of hectares and thus entire forests may convert into shrublands, bamboo thickets or grasslands. Given sufficient remnant trees for propagules, herbivores may severely limit seedling establishment. Interestly, this study found that the effect of herbivores on seedling mortality was only present in forests with high canopy mortality. Spatial variations in fire severity may have produced a heterogeneous matrix differentially used by grazers. Results of the present study document a substantial preference of herbivores in selecting burned patches for grazing at a local scale. Small herbivores are generally faced with the tradeoff between browsing on more palatable open patches at the cost of being more exposed to predators (Wright and Bailey 1982, Bond and van Wilgen 1996). In our case, hares concentrated in open patches even at the risk of higher predation. Hares may find important refuges from predators in burned patches under the dense isolated canopies of resprouting shrubs. Larger herbivores clearly select for more open patches and are well known to spend more time grazing in burned than in unburned patches due to higher abundance of grasses in comparison to woody plants in the former. Herbivores and their synergism with fire are extensively credited in the literature for inducing and maintaining savannas and grasslands (e.g. McNaughton et al. 1988). In the long term, positive feed-backs between fire-induced change in habitat and grazing may gradually shift forest ecosystems towards more open structured communities such as shrublands or grasslands.

**A model of variable herbivore effects in fire-excluded landscapes**

The case studies presented here depict only two points or degrees of a range of possible synergistic effects that
herbivores may have on fire-altered landscapes. Fire exclusion in temperate forest ecosystems is generally assumed to be a process in which landscapes quickly restock their lost forests, increase forest continuity and reach high fuel loads. Little attention has been paid to interacting forces that may accelerate or retard effects such as herbivory. Table 2 lists species/community characteristics that may promote or retard afforestation trends induced by fire exclusion. Rangers and park managers should attempt to identify and consider differences in synergistic effects of herbivores among communities that are undergoing processes related to fire suppression.

References