Seasonal patterns of herbivory, leaf traits and productivity consumption in dry and wet Patagonian forests

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Abstract. 1. Endemic herbivory can influence forest ecosystem function, but how annual productivity consumption relates to seasonal resource utilisation by folivore guilds remains poorly understood.

2. Monthly changes in leaf damage and foliage traits were monitored in 'dry' and 'wet' *Nothofagus pumilio* (Fagales: Nothofagaceae) deciduous forests in northern Patagonia, Argentina. Herbivore-induced leaf abscission was assessed and foliar productivity consumption was measured in the canopy and in litterfall harvests.

3. Seasonal damage ranged from 8% to 32% in dry forest, but remained below 5% in wet forest although foliar quality is higher in the latter. In dry forest, dominant guilds were temporally separated; leaf miners consumed younger foliage in spring to early summer, whereas leaf tiers prevailed in late summer to autumn. In wet forest, damage created by external chewers was concentrated in early summer.

4. Insect damage induced premature leaf abscission, especially in dry forest. Although foliar production in wet forest doubled that in dry forest, the percentage of productivity lost to folivores was higher in dry (14–20%) than in wet (1.2–1.8%) forest.

5. The overall greater impact of herbivory in dry forest canopies countered the expectation that consumption would increase with plant productivity and nutritional quality. Lower temperatures and a shorter growing season are likely to constrain folivory in wet forest stands.

Key words. Feeding guilds, leaf abscission, litterfall, *Nothofagus pumilio*, temporal niches.

Introduction

Insects are the dominant herbivores in forest canopies, consuming varying amounts of standing leaf area under endemic, non-outbreak conditions (Landsberg & Ohmart, 1989; Schowalter, 2000; Kozlov, 2008; Adams & Zhang, 2009). Chronic herbivory can influence forest ecosystem processes, although it has received little attention compared with effects of insect outbreaks (Hunter, 2001; Weisser & Siemann, 2004). Leaf area loss to insects reduces tree growth (Marquis & Whelan, 1994; Wagner *et al.*, 2008) and redirects primary production into the herbivore food chain (McNaughton *et al.*, 1989; Cebrián, 1999), altering material flows from the canopy to the forest soil (Hunter, 2001; Hartley & Jones, 2004). Yet, as consumption is often measured by 'snapshots' of leaf damage at particular time-points (Lowman, 1997; Schowalter, 2000), a full understanding of how temporal resource

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use by folivore guilds affects forest canopy processes is lacking.

Seasonal changes in foliar traits can influence insect abundance and the timing of herbivory (Feeny, 1970; Lowman, 1985; Murakami *et al.*, 2005; Forkner *et al.*, 2008; Zehnder *et al.*, 2009). In deciduous forests, leaf area loss to insects accumulates over time, although the highest damage rates occur on young, high-quality foliage. Folivory rates decline as nutritional quality (e.g. nitrogen content) decreases and leaf toughness increases in mature foliage (Feeny, 1970; Brunt *et al.*, 2006; Zehnder *et al.*, 2009). These patterns may vary depending on the synchrony between leaf flushing (Coley & Barone, 1996) and herbivore feeding guild (Andrew & Hughes, 2005). Tree species with more than one leaf flush per season provide a broader resource base for sympatric herbivores (Begon *et al.*, 2006). In addition, feeding guilds may differentially respond to seasonal shifts in leaf nutrients and defence levels (Karban & Baldwin, 1997; Peeters *et al.*, 2007), leading to predictable sequences of foliage use by different insects (Andrew & Hughes, 2005; Forkner *et al.*, 2008). Lastly, seasonal herbivory patterns may reflect either negative (Faeth, 1986; Fisher *et al.*, 1999) or positive (Nakamura *et al.*, 2003; Ohgushi, 2005) interactions between early and late feeding guilds mediated by the shared host plant (for review, see Denno & Kaplan, 2007).

Temporal partitioning of foliage resources may determine the overall impact of chronic herbivory. Herbivorous insects affect above-ground primary productivity directly by consuming photosynthetic leaf area (Schowalter, 2000). Further, insect herbivory can indirectly alter foliage production by shortening leaf area duration as a result of the premature abscission of damaged leaves (Faeth *et al.*, 1981; Nakamura *et al.*, 2003). If leaves are dropped when folivores are feeding actively, early abscission may increase insect mortality, mostly in sessile guilds (Faeth *et al.*, 1981; Stiling *et al.*, 1991). In addition, early abscission may precede a secondary leaf flush, which may either 'escape' herbivory or be exploited by late-coming insects (Nakamura *et al.*, 2003). Therefore, premature abscission will affect measures of foliage consumption (Schowalter, 2000) unless leaf area loss is assessed in both standing canopy and leaf litterfall (Adams *et al.*, 2009).

Tree folivory rates change along major environmental gradients (Coley & Barone, 1996; Andrew & Hughes, 2005; Kozlov, 2008; Adams & Zhang, 2009; Garibaldi *et al.*, 2011a,b). Habitat conditions influence leaf traits such as lifespan, specific leaf area and nutrient concentrations (Reich *et al.*, 1997; Wright *et al.*, 2004), which are relevant to plant–insect interactions (Landsberg & Ohmart, 1989; Dirzo & Boege, 2008). For instance, habitat moisture may affect the tendency to early abscission of damaged leaves (Faeth *et al.*, 1981). Herbivore consumption increases with primary productivity (McNaughton *et al.*, 1989) and plant nutritional quality (Cebrián & Lartigue, 2004) across ecosystems. Yet, within systems, regional variations in herbivory levels often reflect subtle differences in temperature and plant phenology (Dirzo & Boege, 2008; Kozlov, 2008; Garibaldi *et al.*, 2011b). A longer growing season may favour temporal separation among herbivores with different life histories or feeding

habits (van Asch & Visser, 2007; Dirzo & Boege, 2008). Thus, forest habitats that allow increased temporal packing of folivore guilds may experience higher overall consumption of productivity. By contrast, forests with a shorter foliage duration may show a greater concentration of herbivory on early-season foliage (but see Coley & Barone, 1996).

Most work on forest herbivory has focused on lowland dry versus wet tropical forests (Coley & Barone, 1996; Dirzo & Boege, 2008), broadleaved northern temperate forests (Schowalter, 2000; Kozlov, 2008), and Australian woodlands and rainforests (Lowman, 1985, 1997), whereas measures of annual productivity consumed by insects in southern temperate forests are generally lacking (McNaughton *et al.*, 1989; Cebrián & Lartigue, 2004). We report the first comprehensive assessment of productivity consumption by folivorous insects in a cool temperate forest in southern South America. We took advantage of the broad habitat range occupied by the dominant canopy tree *Nothofagus pumilio* (Fagales: Nothofagaceae) (Veblen *et al.*, 1996) to examine how seasonal patterns of herbivory and total foliar production loss to insects differ between 'dry' and 'wet' forests in the Patagonian Andes. *Nothofagus pumilio* wet forests are more productive but have a shorter growing season than their dry forest counterparts, which, in turn, exhibit higher late-season leaf damage (Mazía *et al.*, 2004; Garibaldi *et al.*, 2010). Here, we document seasonal patterns of herbivory by feeding guilds and relate them to foliage traits, leaf abscission and productivity consumption through repeated measures of leaf damage in forest canopy and litterfall.

Materials and methods

Study sites

The study was conducted during the growing seasons (October–April) of 2003–2004 and 2004–2005 in *N. pumilio* forests located at both extremes of a west–east precipitation gradient in northwestern Patagonia, Argentina. At this latitude (40–41°S), *N. pumilio* dominates the sub-alpine zone at 1000–1600 m a.s.l. (Veblen *et al.*, 1996). Soils are poorly developed Andisols derived from volcanic ashes. The climate is characterised by cold, wet winters and mild but dry summers; most precipitation falls during autumn and winter (May–September). In this region, the Andes create a pronounced rainshadow; over a distance of just 60 km, annual precipitation decreases from >3000 mm near the continental divide to ∼800 mm on the eastern foothills adjacent to the Patagonian steppe (Veblen *et al.*, 1996). Mean annual temperature for the study years (9 °C) was close to the previous 15-year average (8.5 °C), as measured at Bariloche Airport weather station (70 km south of the study sites). Total precipitation during May–April was 919 mm in 2003–2004 and 858 mm in 2004–2005 (15-year mean: 826 mm).

In October 2003, we selected four *N. pumilio* stands which had not burned for >50 years and had never been logged. Two stands were located at Paso Córdoba (40°35′S, 71°08′W; 1240 m a.s.l.), on the eastern limit of *N. pumilio* distribution, which has annual precipitation of ∼800 mm ('dry' forest).

The other two stands were located at Paso Puyehue (40°43′S, 71°54′W; 1180 m a.s.l.), on the border between Argentina and Chile, which has annual precipitation of ∼3000 mm ('wet' forest). Stand pairs were embedded in larger, continuous forest patches, were located 300 m apart, and were similar in aspect, slope and elevation. Mean monthly temperatures are ∼3 °C lower in the wet than the dry forest (Garibaldi *et al.*, 2010). Leaf flushing may be delayed by nearly 4 weeks and leaf fall may start a few weeks earlier in the wet than the drier forests. Thus, foliage duration is about 6 weeks longer in dry forest sites (Veblen *et al.*, 1996). Above-ground primary productivity estimated from satellite imagery decreases by ∼30% from wet to dry *N. pumilio* forests (Mazía *et al.*, 2004).

Foliage sampling and herbivore damage

Tree foliage was sampled at monthly intervals from mid-spring to early autumn, during November 2003 to April 2004 and October 2004 to April 2005. In the latter season, sampling was initiated 1 month earlier to include newly flushed leaves in the dry forest. In each forest stand, 10 *N. pumilio* adult trees [mean ± standard deviation (SD) tree diameter at breast height (d.b.h.): 46.3 ± 13.8 cm, *n* = 40) were randomly selected and marked with aluminium tags. Distances between tagged trees ranged from 10 m to 100 m. On each sampling date, one fully insolated branch comprising >100 leaves at a height of ∼5–6 m was harvested from each tagged tree using an extensible pole pruner. Insect damage was measured for 30 blindly chosen leaves per branch per month (13 200 leaves in total). The percentage of leaf area damaged by folivorous insects was quantified using a 1-mm² grid (Mazía *et al.*, 2004). Few leaves had >75% of the area missing, which reduced the likelihood that folivory rates would be underestimated as a result of fully eaten leaves (Coley & Barone, 1996; Schowalter, 2000). Insect defoliation was calculated at the tree level as the total percentage of leaf area damaged, which is the total area damaged divided by the total leaf area sampled × 100 (Williams & Abbott, 1991).

Foliar damage was classified into different types associated with various feeding guilds, including leaf miners, leaf folders, leaf tiers, external chewers and skeletonisers, and gall makers, which are common on *Nothofagus* species (McQuillan, 1993; Bauerle *et al.*, 1997; Mazía *et al.*, 2004; Garibaldi *et al.*, 2010). Sap suckers (mainly aphids) were not considered in this study (see Garibaldi *et al.*, 2011b). *Leaf miners* include endophagous species that feed between the layers of the leaf epidermis and produce blotched, linear or serpentine-like mines. *Leaf folders* include species that feed inside shelters constructed by folding one or two leaves attached with silk. *Leaf tiers* comprise species that feed inside and outside flat shelters made by joining two or more leaves with silk along a horizontal plane. *Leaf chewers* remove whole leaf sections by feeding from the leaf margin or by making holes on either side of the midrib. *Skeletonisers* comprise insects that consume the leaf area between veins. Lastly, *gall makers* are species whose larvae feed inside spherical galls formed beneath the leaf epidermis.

Leaf trait measurements

To characterise the quality of foliage for insect herbivores, we measured several leaf traits including leaf size (cm²), toughness (g mm⁻²), specific leaf area (SLA, mm² mg⁻¹), foliar contents (percentage of dry mass) of water, carbon (C), nitrogen (N), phosphorous (P) and total phenolics, and C : N ratio. Mean leaf size and toughness were quantified for a subsample of 30 non-senescing leaves per branch. Leaf area was visually measured using a 1-mm² grid. Toughness was recorded as the weight needed to punch a hole through the laminae between veins using a steel rod measuring 1.6 mm in diameter mounted on a hand-held penetrometer (Medio-Line Spring Scale; Pesola AG, Baar, Switzerland). Leaf water content (percentage of fresh mass) and mean dry mass (mg per leaf) were obtained from 10 leaf subsamples after drying at 60 °C for 48 h; dry mass values were then used to calculate mean SLA. Leaf subsamples (3 g) for chemical analyses were oven-dried at 60 °C and ground. Carbon content was determined after wet combustion using Tinsley's dichromate method. Leaf N content was determined by a semi-micro Kjeldhal procedure. Leaf P was extracted by humid acid digestion and measured by inductively coupled plasma atomic emission spectrometry (ICP-AES). Total phenolics were extracted with 70% acetone and assessed by spectrophotometry (720 nm) according to Folgarait and Davidson (1994); phenols were expressed as mg of gallic acid per gram of dry mass.

Leaf litterfall dynamics

Leaf abscission was evaluated in relation to insect damage at the stand scale (Faeth *et al.*, 1981) by collecting the litterfall produced during each season. In January 2004, five litter traps consisting of wooden containers measuring 0.15 m² and 0.23 m deep were placed in each forest stand. Litter material was removed at intervals of 4–6 weeks during summer and autumn in 2004 and 2005, in January (only 2005), March, April and May. Leaf litter collected on a given date comprised leaves shed during the previous month. Litterfall in winter and spring was not sampled here, but contributes < 5% of annual leaf litter in *N. pumilio* forests (Caldentey *et al.*, 2001). *Nothofagus pumilio* leaf litter was separated from other materials (twigs, flowers, bark and other leaves) and sorted into folivore-damaged and undamaged leaves. Leaves collected before peak fall in May were deemed to reflect premature abscission.

Foliage productivity and insect consumption

Leaf litterfall was dried at 60 °C for 72 h and weighed to 0.01 g. This material was used to estimate the annual net foliar production (g dry mass m⁻²) for each forest stand and study year (Austin & Sala, 2002). In deciduous trees with a highly synchronised leaf fall, as in *N. pumilio*, annual net foliar productivity (FP) can be calculated as:

$$FP = L + H \qquad (1)$$

where L represents the leaf litterfall throughout a growing season and H is herbivore consumption, or the leaf mass removed by canopy folivores (i.e. before leaves are dropped to the ground). Both parameters were estimated on a litterfall-trap basis and then averaged over replicate traps within a forest stand for each harvest date. Herbivore consumption was calculated from separate estimates of total leaf mass loss to different feeding guilds as:

$$H = \sum DA_{\mathrm{g}} \times CF_{\mathrm{g}} \qquad (2)$$

where DA is the cumulative dry mass corresponding to the leaf area damaged by feeding guild g and CF is a correction factor specific to each guild. To obtain DA_{g}, we determined the total dry mass of leaves damaged by each guild as found in the litterfall, and then used the mean leaf area damaged (%) by that guild and mean SLA ($\mathrm{mm^2\ mg^{-1}}$) in the forest canopy (as measured for the month prior to litter harvest) to calculate the mass fraction of the damaged leaf litter that was actually lost to herbivory.

Importantly, CF was added to account for the fact that the leaf area damaged by an insect herbivore may not be entirely removed from the leaf (Eqn 2). For instance, leaf miners consume cell layers within the leaf mesophyll but typically leave behind most epidermal tissue; hence, they do not consume the whole mass comprised by the damaged leaf area. We assumed a $CF = 1$ for leaf chewers and skeletonisers, and a $CF < 1$ for leaf miners and tiers. The latter was derived by weighing damaged and undamaged leaf portions of equal size, and taking the mean proportional weight difference ($n = 15$) as the actual leaf mass consumed by the insect. This procedure was repeated for each sample date within each forest stand. Notice that failing to include CF would lead to an overestimate of actual consumption, especially by leaf mining and tying insects. Finally, total herbivore consumption was expressed as a percentage of foliage production ($\%H$) per stand and year.

Data analysis

Data for insect and plant variables measured at the individual tree level were averaged ($n = 10$ trees per stand) to avoid pseudoreplication in testing for differences between dry and wet forests. We thus report means and standard errors based on two stands per forest type. Preliminary analyses showed that monthly patterns of insect damage and leaf traits were very similar between years. Therefore, statistical analyses were performed on average values obtained for each tree between study seasons. As we did not sample in October 2003, the very early season was represented by October 2004 only.

Total leaf damage, damage by feeding guild, damage diversity and measured foliar traits were analysed through repeated-measures, nested analysis of variance (ANOVA), with stands (random effect) nested within forest type and the sampling date (5 months) as the repeated measure (StatSoft, Inc., 2007). October data (dry forest) were excluded from these analyses as *N. pumilio* leaves had not yet flushed in the wet forest. The actual dates considered in the analyses depended on the phenology of each guild, and thus varied between three dates (leaf tiers) and five dates (miners, external feeders). Damage by chewers and skeletonisers was lumped into one category ('external feeders') to reduce the number of zero values. Leaf folder damage was not statistically analysed as it only occurred in the dry forest, whereas leaf galls were too infrequent to warrant analysis. Damage data were arcsine-square-root transformed to meet ANOVA assumptions (Sokal & Rohlf, 1995).

To evaluate the relationship between herbivory and leaf abscission, the frequency of damaged leaves in the litterfall was compared against that in the overstorey canopy. Damaged leaves will be more likely than undamaged leaves to drop throughout the season, except at peak leaf fall in late autumn. If folivory induced early abscission, we expected the incidence of damaged relative to undamaged leaves to be significantly higher in litterfall traps than in canopy samples prior to litterfall collection (Faeth *et al.*, 1981). To test this hypothesis, we performed separate log-linear analyses (Sokal & Rohlf, 1995) for each forest type in January, March and April. Two-way contingency tables for damaged versus undamaged leaves were constructed based on 10 litter traps and 20 tree samples, pooling over stands within forest types. The analysis was conducted for 2004–2005, when litterfall was collected from early summer to late autumn.

Annual foliar production and percentage production consumed by insects were compared between dry and wet forests using repeated-measures, mixed-model ANOVA, with the study year as repeated measure. Stands were considered as a random effect nested within forest type ($n = 5$ litter traps per stand).

Results

Seasonal pattern of herbivory

Folivory rates differed markedly between dry and wet forest stands. Total leaf area damage increased over the growing season and was nearly 10-fold higher in the dry than in the wet forest throughout (Table 1, Fig. 1). Although damage levels varied between stands (Table 1), the seasonal pattern of herbivory was consistent for both forest types. Leaf area loss peaked during mid-summer (January) in both forests (dry: ~30%; wet: ~5%), although a second peak was also apparent during early autumn in the dry forest (Fig. 1).

The identities of dominant feeding guilds differed between forests (Table 1, Fig. 2). Internal feeders, including leaf folders, miners and tiers, accounted for most damage in the dry forest (Fig. 2a), whereas external feeders, including leaf chewers and skeletonisers, prevailed in the wet forest (Fig. 2b). The main feeding guilds in each forest exhibited strong phenological patterns (Table 1). A shift in guild dominance was evident in the dry forest, whereas no clear temporal sequence occurred among guilds in the wet forest (Fig. 2). Seasonal patterns of guild dominance were consistent within forest types, despite between-stand variation in actual damage levels (Table 1).

Table 1. Results of repeated-measures, nested ANOVA (*F*-values) of monthly changes in leaf area damaged by different feeding guilds and all folivorous insects, in dry and wet *Nothofagus pumilio* forests in northern Patagonia.

Source	d.f.	All folivores	Leaf miners	Leaf tiers	External feeders
Forest type	1, 2	24.12[*]	26.37[*]	36.27[*]	0.57
Stand (forest)	2, 36	22.78[***]	19.52[***]	12.50[***]	1.97
Month[†]	4, 8	15.56[***]	10.33[**]	39.94[**]	59.54[***]
Forest × month[†]	4, 8	3.36	8.02[**]	25.76[**]	13.34[**]
Stand × month[‡]	8, 144	5.53[***]	5.69[***]	3.78[**]	1.03

[***]$P < 0.001$; [**]$P < 0.01$; [*]$P < 0.05$.
[†]Leaf tiers d.f. = 2, 4.
[‡]Leaf tiers d.f. = 4, 72.
Stands (random effect, $n = 2$) were nested within forests; each stand comprised 10 trees sampled during the 2003–2004 and 2004–2005 growing seasons (data averaged across years).
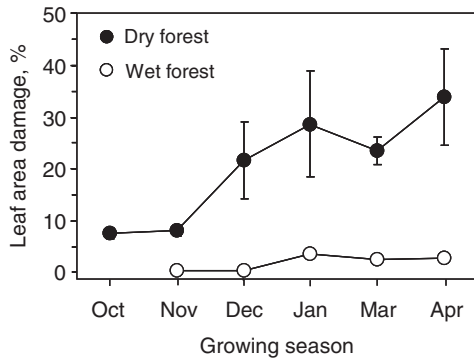

Fig. 1. Seasonal changes in leaf damage by folivorous insects in dry and wet *Nothofagus pumilio* forests in northern Patagonia. (a) Percentage of leaf area damaged, and (b) insect damage diversity (D^{-1}), where D = Simpson's diversity index. Values show means ± 1 standard error for two stands nested within each forest type. Ten trees were sampled in each stand for two growing seasons, with data averaged across years. The horizontal bar marks the extent of the austral spring (hatched), summer (white) and autumn (grey) seasons. Leaf flush was delayed by 1 month in the wet forests.

In the dry forest, most early-season damage was caused by a leaf-folding caterpillar (Lepidoptera), which attacked the apical leaves of new twigs in October and entered pupation by mid-spring. Leaf folder damage was no longer visible after November, probably because of the abscission of damaged leaves. Leaf miners colonised the dry forest canopy during October–November, as the frequency of mined leaves increased from 7% to 55%. Most miner damage was produced during late spring by sawfly larvae (Hymenoptera: Tenthredinidae) that formed blotch mines (Fig. 2a). Larval feeding was completed by mid-summer, when sawfly damage reached a seasonal peak. Based on mine morphology, we recorded two other, unidentified species of microlepidoptera, but these accounted for <5% of all mined leaves. Later in summer (February–March), dry forest trees were colonised by leaf-tying caterpillars (Lepidoptera: Gellechiidae), which
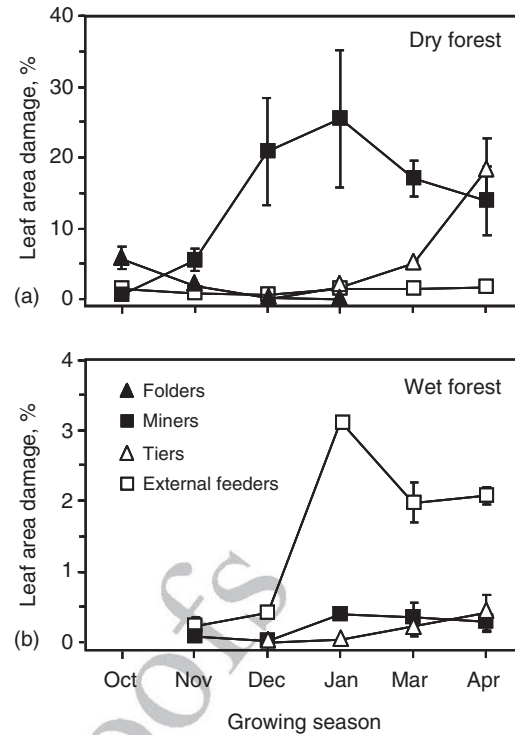

Fig. 2. Seasonal changes in leaf area damaged by different feeding guilds in (a) dry and (b) wet *Nothofagus pumilio* forests in northern Patagonia. Values show means ± 1 standard error. Note the difference in the *y*-axis scale between panels. Ten trees were sampled in each stand ($n = 2$) for two growing seasons and data were averaged across years.

became the most conspicuous folivores for the remainder of the season (Fig. 2a).

In the wet forest, external leaf chewers represented the main folivores throughout the season. Leaf area loss peaked in summer, but remained <3.5% (Fig. 2b). The most conspicuous chewers were the larvae of *Ormiscodes amphimone* (Lepidoptera: Saturniidae), which hatch in December from packs of overwintering eggs. Other chewers and leaf skeletonisers comprised several unidentified species of Lepidoptera (Geometridae, Noctuidae) and Coleoptera (Curculionidae). Gall-making insects were relatively common (3% of all leaves) at the beginning of the season but then disappeared. Leaf miners and tiers produced very low levels of damage (<0.5%) in this forest.

Seasonal changes in foliar traits

Budbreak occurred 1 month earlier in dry than in wet forest stands. In the dry forest, mean leaf size peaked as early as December (late spring), whereas leaves in the wet forest continued to expand throughout the season (Fig. 3). This resulted in wet forest trees achieving larger maximum leaf sizes than dry forest trees (Table 2). Both structural and chemical traits indicated that overall foliage quality for herbivores was higher in wet than in dry forests, although individual trait patterns depended on the time of season (Table 2).
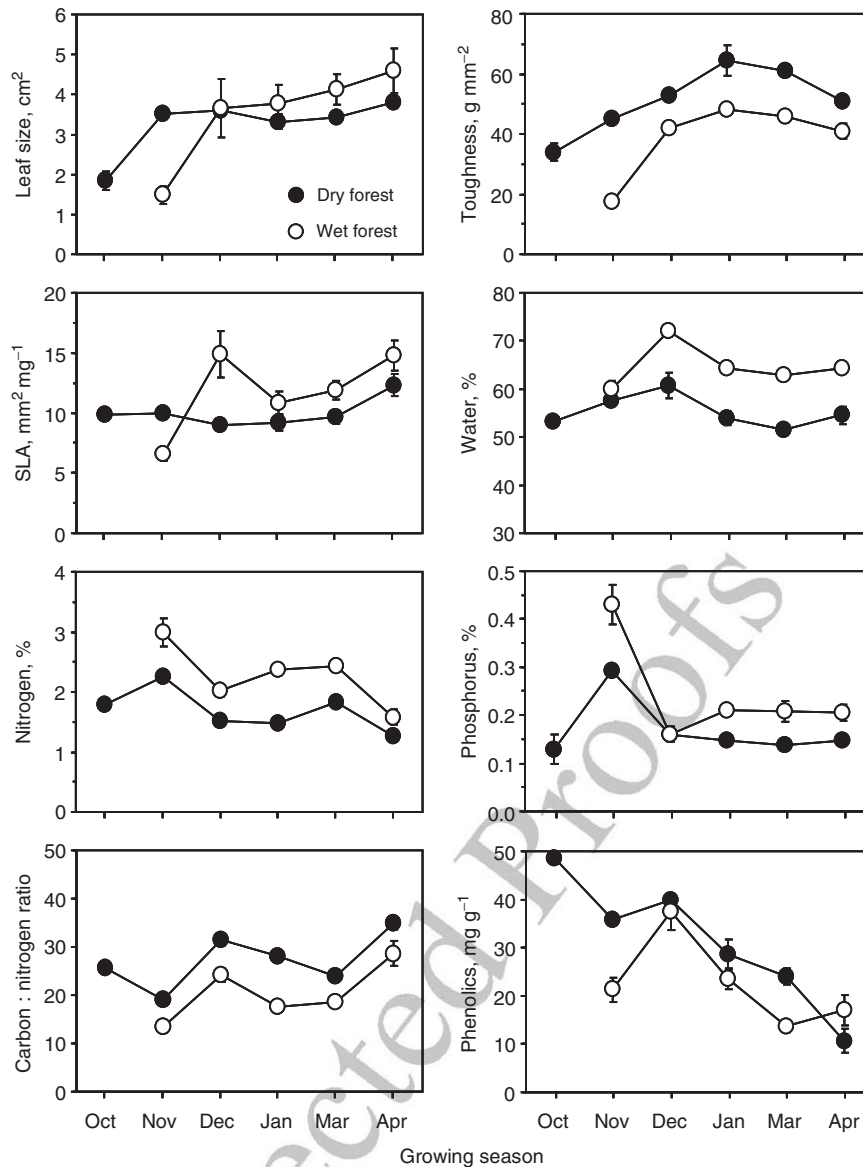
Fig. 3. Seasonal dynamics of *Nothofagus pumilio* foliage traits in dry and wet forest sites in northern Patagonia. Values show means ± 1 standard error; hidden error bars are smaller than the symbols. Ten trees were sampled in each stand ($n = 2$) for two growing seasons and data were averaged across years. SLA, specific leaf area.

Leaf toughness generally increased to mid-summer (January), but was always higher in the dry than in the wet forest. Dry forest trees had thicker leaves for most of the season, as SLA increased with leaf expansion in the wet forest (Fig. 3). By contrast, leaf water and nutrient contents were consistently higher in the wet than in the dry forest (Table 2). Foliar N and P levels tended to decrease over seasonal time. However, after an initial decline associated with leaf expansion, leaf N levels rebounded during mid- to late summer, before decreasing again with leaf senescence at the end of the season (Fig. 3). Leaf C content fluctuated (by month: $P < 0.001$), showing no definite seasonal trend, but did not differ between forests [monthly range: dry forest, 40.8–47.3%, wet forest, 39.0–48.2% ($P = 0.91$)].

Thus, changes in C : N ratios mirrored leaf N content dynamics. C : N ratios peaked in late spring (December) and autumn (April), and were generally higher in dry forest (Fig. 3). Leaf phenolics were relatively high in newly flushed leaves, but decreased through the season, and were on average slightly higher in dry than in wet forest trees (Table 2, Fig. 3).

Herbivory and leaf abscission dynamics

The frequency of damaged leaves in the canopy generally increased through the season, but was almost twice as high in the dry as in the wet forest (Fig. 3). Leaves found in

Table 2. Results of repeated-measures, nested ANOVA (*F*-values) of monthly changes in selected foliage traits, in dry and wet *Nothofagus pumilio* forests in northern Patagonia.

Source	d.f.	Leaf size, cm^2	Toughness, g mm^{-2}	SLA[†], mm^2 mg^{-1}	Water, %	N, %	P, %	C : N ratio	Phenols, mg g^{-1}
Forest type	1, 2	<0.01	117.79**	3.37	154.69**	22.09*	81.54*	23.54*	13.38
Stand (forest)[‡]	2, 36	7.53**	1.62	7.37**	2.05	7.94**	0.88	7.21**	1.46
Month	4, 8	30.55***	50.85***	20.72***	11.91**	170.29***	44.09***	152.82***	36.11***
Forest × month	4, 8	25.68***	7.08**	14.20***	3.42	10.79**	3.82*	4.22*	5.81*
Stand × month[§]	8, 144	3.30**	5.76***	1.53	4.64***	1.50	2.26*	1.87	1.86

***$P < 0.001$, **$P < 0.01$, *$P < 0.05$.
†Specific leaf area (SLA), sampled in 2004–2005 only.
‡SLA and water d.f. = 2, 29; phenols d.f. = 2, 34.
§SLA and water d.f. = 8, 116; phenols d.f. = 8, 136.
Stands (random effect, $n = 2$) were nested within forests. Each stand comprised 10 trees sampled during the 2003–2004 and 2004–2005 growing seasons (data averaged across years).

litterfall traps during summer and early autumn were highly damaged, especially in the dry forest. Litterfall damage was largely attributed to the dominant folivore guilds in each forest (dry: leaf miners and tiers; wet: leaf chewers). In the dry forest, the incidence of damaged leaves in litterfall was higher than expected from their canopy frequency (Fig. 3), a pattern most apparent in mid-summer (January, $\chi^2 = 280.5$, $P < 0.0001$; March, $\chi^2 = 23.6$, $P < 0.0001$; April, $\chi^2 = 13.8$, $P < 0.001$; all d.f. = 1). In the wet forest, the same pattern was found in January ($\chi^2 = 42.5$, $P < 0.0001$), but not in March ($\chi^2 = 0.29$, $P < 0.59$) (Fig. 3). By contrast, in early autumn (April), leaf damage frequency in wet forest litterfall was lower than that in the overstorey canopy (April, $\chi^2 = 158.3$, $P < 0.0001$).

Foliage productivity and consumption

Leaf litter production increased exponentially between January and peak leaf fall in May, from 8.1 g dry mass m^{-2} to 105.7 g dry mass m^{-2} in the dry forest, and from 6.4 g dry mass m^{-2} to 184.3 g dry mass m^{-2} in the wet forest. On average, early leaf abscission (January–March samples) accounted for ~14% and 5% of total litterfall biomass produced in the dry and wet forests, respectively. Total foliar production was nearly twice as high in wet as in dry forest stands ($F_{1,2} = 22.18$, $P = 0.042$) (Table 3). By contrast, percentage consumption of foliar production (%H) was an order of magnitude greater in the dry than the wet forest ($F_{1,2} = 79.9$, $P = 0.012$) (Table 3). Differences between forests did not vary between years ($P > 0.10$). In absolute terms, folivorous insects consumed 20.2–31.5 g m^{-2} (dry forest) and 3.1–4.4 g m^{-2} (wet forest) of foliage dry mass per year. Habitat-specific differences in consumption remained after adjusting for length of growing season (dry forest, 0.95–1.49 kg ha^{-1} day^{-1}; wet forest, 0.17–0.24 kg ha^{-1} day^{-1}).

Discussion

Patterns of forest herbivory across environmental gradients are often complicated by shifts in canopy composition and

Table 3. Total net foliage production and percentage of foliage production consumed by canopy insects in dry and wet *Nothofagus pumilio* forests, northern Patagonia, Argentina.

	Dry forest	Wet forest
Foliage production, g m^{-2} year^{-1}[*]		
2003–2004	153.6 ± 6.9	245.5 ± 16.9
2004–2005	145.3 ± 23.0	255.5 ± 14.3
Foliage consumption, %[†]		
2003–2004	20.5 ± 2.3	1.8 ± 0.1
2004–2005	13.9 ± 0.7	1.2 ± 0.1

*Measured using five litterfall traps per forest stand, including the leaf mass removed by insect herbivores.
†Calculated from leaf damage frequencies in litterfall and repeated measures of leaf area loss to canopy insects (see Materials and methods).
Values show means ± 1 standard error ($n = 2$ stands) for two growing seasons.

insect community (Andrew & Hughes, 2005; Dirzo & Boege, 2008; Kozlov, 2008; Adams & Zhang, 2009). The present study revealed habitat-specific differences in folivory on a dominant host tree in the Patagonian Andes. We found that: (i) leaf damage was higher in dry than in wet *N. pumilio* forests, although foliage quality was higher in the latter; (ii) foliage quality decreased over the growing season, with highest folivory rates affecting young, expanding leaves; (iii) temporal separation between dominant guilds was only evident in dry forest stands; (iv) herbivory was associated with premature leaf abscission, mainly in the dry forest; and (v) foliar production in the wet forest doubled that in the dry forest, whereas percentage productivity consumption was greater in the dry forest. These results contradict the expectation that herbivore consumption increases with plant productivity and nutritional quality (McNaughton *et al.*, 1989; Cebrián & Lartigue, 2004). To our knowledge, this is the first study to fully document annual foliage production consumed by forest insects in a South American temperate ecosystem.

Leaf damage levels in the wet forest were in the lower range of those previously reported for *Nothofagus* species in

cool temperate rainforests (e.g. Russell *et al.*, 2000; Altmann, 2010), but were close to a 7-year average for late season damage reported for *N. pumilio* wet forests (Mazía *et al.*, 2009). By contrast, total leaf damage in the dry forest (35–50%) was well above that reported for the region (Russell *et al.*, 2000; Mazía *et al.*, 2004; Altmann, 2010; Garibaldi *et al.*, 2011b). Working in the same dry forest, we recorded 10–14% leaf damage in late summer during 1998–2000 (Mazía *et al.*, 2004). Yet this snapshot of herbivore damage notably missed consumption peaks by leaf folders and leaf-tying caterpillars, which were responsible for half of the total folivory in the dry forest (Fig. 2). Further, published measures of defoliation in *Nothofagus* forests have generally failed to account for premature abscission of damaged leaves. Hence, differences between studies may reflect not only *Nothofagus* species and site-specific factors (Russell *et al.*, 2000), but also the fact that prior estimates were based on one-time canopy samples, which tend to underestimate folivory rates (Lowman, 1997; Schowalter, 2000).

Our folivory estimates for northern Patagonia dry and wet forests may represent upper and lower bounds for *N. pumilio* forests, respectively (see Garibaldi *et al.*, 2011a). How does endemic herbivory in this system compare with that in other forest ecosystems? Whereas total leaf damage in this study was as variable between forest sites as rates reported for broadleaved temperate forests around the world [1–20% (Schowalter, 2000); 1–10% (Kozlov, 2008); 0–21% (Adams & Zhang, 2009)], folivory in dry forest stands was higher than in most temperate forests and comparable with that reported in tropical forests (Coley & Barone, 1996; Dirzo & Boege, 2008). Taken together, these data support the growing view that herbivory in temperate forest canopies need not be lower than that in the tropics (Adams *et al.*, 2009; Moles *et al.*, 2011; cf. Coley & Barone, 1996).

Seasonal changes in leaf traits and folivore damage

On average, wet forest trees had larger leaves with high SLA, water and nutrient contents and low C : N ratios and phenolics, compared with dry forest trees (Fig. 3). Such foliar traits should favour C acquisition in the moist, shady microclimate of closed forest canopies in productive habitats (Reich *et al.*, 1997; Wright *et al.*, 2004). By contrast, the production of thick, low-nutrient (high C : N ratio) leaves by dry forest trees reflected greater allocation of C-based secondary metabolites, making for a more conservative resource strategy, as is common in drier environments (Herms & Mattson, 1992; Reich *et al.*, 1997). Such contrasting leaf economic syndromes have been predicted to determine, respectively, high and low susceptibility to herbivore damage (Coley *et al.*, 1985; Wright *et al.*, 2004). Whereas cross-habitat variation in *N. pumilio* foliar traits resulted in potential food quality to herbivores being higher in wet than in dry forests, the opposite was true for total folivory (Figs 1 and 3). It thus appears that host plant quality may not account for habitat-specific defoliation rates in these Patagonian forests.

We observed an overall decrease in leaf quality to insects associated with foliage development within forests (Coley &

Barone, 1996; Zehnder *et al.*, 2009). Seasonal variation in foliar traits was broadly synchronised between forests, which suggests the imposition of a coarse environmental control on leaf chemistry, regardless of differences in the timing of budbreak (Fig. 3). However, temporal changes in putative defences were trait-specific (Table 2). Total phenolics were high in newly flushed leaves at the onset of the season and declined steadily towards the late season. High levels of phenolics may protect young leaves from excessive damage (Feeny, 1970; Zehnder *et al.*, 2009), but would be diluted by foliar expansion (Brunt *et al.*, 2006). Conversely, leaf toughness first increased and then levelled off in mid-summer, so that later foliage was physically better defended (Coley & Barone, 1996; Peeters *et al.*, 2007). Brunt *et al.* (2006) reported similar trends in *Nothofaga moorei* from Australia, and postulated that increased toughness in mature leaves may reduce the need for investment in costly chemical defences. However, although leaf nutrients decreased in late spring, N levels rebounded during the summer, driving a decrease in C : N ratios (Fig. 3). This fluctuation was apparently associated with a secondary leaf flush (X. Xxx, personal observation, 20XX), which in the dry forest refreshed the available leaf area after heavy damage by leaf miners.

Herbivores with different feeding habits dominated the dry and wet forest canopies (Mazía *et al.*, 2004; Garibaldi *et al.*, 2010) (Fig. 2). Folivore guilds displayed distinct phenological patterns, which corresponded with a clear temporal separation in foliage use within the dry forest, but not in the wet forest. Nonetheless, the highest folivory rates in both forests were concentrated during periods of relatively high foliage quality (Lowman, 1985; Coley & Barone, 1996; Schowalter, 2000). In the wet forest, leaf damage by exophytic feeders primarily affected newly expanded leaves of high SLA during early summer (Figs 2b and 3). Larvae of *Ormiscodes* spp., the main chewers in this system (Bauerle *et al.*, 1997), hatch in early spring and feed gregariously on young leaves until they disperse in mid-summer. Other feeding guilds contributed to an increase in damage incidence later in the season (Fig. 4), but consumed little leaf area, although good quality foliage was available. It seemed that insect abundances in the high-productivity wet forest were constrained by environmental factors other than food availability (Mazía *et al.*, 2009), which is likely to reduce the potential for temporal guild separation (Lawton & Strong, 1981; Begon *et al.*, 2006).

Dry forest stands were sequentially dominated by three mostly sessile guilds occurring at different stages of a longer growing season (Fig. 2a). Early-season folivores colonised relatively soft, nutrient-rich foliage soon after budburst. Leaf folders attacked apical leaves for a brief period, and leaf miners occupied the whole canopy from spring to early summer. These endophytic guilds would be little affected by elevated phenolics in young leaves (Karban & Baldwin, 1997). Later-colonising leaf tiers encountered a heterogeneous mix of damaged and undamaged leaves. However, they would have profited from reduced phenolic levels in mature foliage, as well as from a second flush of nutrient-rich leaves (Figs 2a and 3). Temporal folivore sequences on shared host plants have been related to various mechanisms that may allow resource partitioning
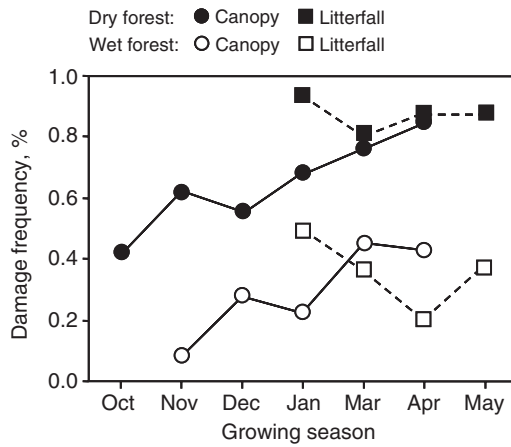
Fig. 4. Frequency of damaged leaves in the canopy (● ○) and litterfall (■ □) of dry and wet *Nothofagus pumilio* forests during the 2004–2005 growing season. Values show mean frequencies for *n* = 2 stands per forest type. Each stand comprised 10 sample trees and five litter traps. In May, litterfall samples were collected after peak leaf fall.

over time (Murakami *et al.*, 2005; Ohgushi, 2005; Denno & Kaplan, 2007). Folivorous insects may occur at different times simply because of their particular phenologies (van Asch & Visser, 2007). Herbivores may also interact via different types of indirect competition mediated by shared host plants (Lawton & Strong, 1981; Faeth, 1986; Fisher *et al.*, 1999; Denno & Kaplan, 2007). Lastly, facilitative interactions may allow the coexistence of early and late folivores (Nakamura *et al.*, 2003; Ohgushi, 2005). In the dry forest, temporal separation of mining and tying insects determined a more complete resource utilisation by the folivore community.

Impact of insect herbivory on canopy processes

Herbivory was associated with premature leaf abscission. This effect was mostly evident in the dry forest, in which early leaf drop occurred throughout the summer, reflecting intense damage by miners and tiers. In the wet forest, damage-related abscission occurred only in January, concomitant with a peak in chewer damage (Figs 2 and 4). The fact that late-season litterfall damage in the wet forest was lower than expected suggests that litter traps collected more leaves dropped from less damaged, upper canopy layers, not reached by our sampling height (see Lowman, 1997). Trees may shed partially consumed leaves as maintenance costs exceed carbon gains from remnant tissues (Faeth *et al.*, 1981), especially during abiotically stressful periods. Early leaf abscission in the dry forest became apparent only after sawfly larvae had vacated the canopy in January, and continued during February–April, when leaf-tying insects were feeding actively. Thus, premature abscission would have little impact on the demography of miners, but might affect leaf tiers (Stiling *et al.*, 1991).

Our parallel canopy and litterfall measures allowed us to estimate leaf mass loss caused by premature abscission. Leaf litterfall values were close to those reported for other *N. pumilio* forests (Caldentey *et al.*, 2001; Austin & Sala, 2002). We found that damage-related abscission accounted for a sizeable fraction of foliar production in the dry forest, reducing the total leaf area beyond direct consumption (Schowalter, 2000). Further, by measuring damage in leaf litter, we derived an estimate of folivory in the whole canopy (Adams *et al.*, 2009), which was then converted into leaf biomass consumption. When we compared our consumption estimates with those of others, we realised that few have measured the actual foliage biomass removed by insects. Most studies to date have inferred percentage consumption of forest productivity from discrete damage measures (see McNaughton *et al.*, 1989; Schowalter, 2000). The latter method overestimates consumption by assuming that the whole damaged leaf area was ingested, which is clearly not the case for leaf miners and tiers. Our results indicate that this bias can be substantial (cf. Fig. 1 vs. Table 3). Therefore, the need for more accurate measures of productivity consumption by insects in different forest ecosystems remains.

The percentage of primary production removed by herbivores gives an indication of potential consumer control over material cycling (Cebrián, 1999; Hunter, 2001; Cebrián & Lartigue, 2004). Both general theory (Oksanen & Oksanen, 2000) and global empirical relationships (McNaughton *et al.*, 1989; Cebrián & Lartigue, 2004) predict that herbivore consumption increases with foliage productivity and nutritional quality. Foliar production consumed by insects was 10-fold greater in dry than in wet forest stands, although wet forests show higher annual productivity (Table 3) and leaf N and P levels (Fig. 3). Absolute consumption in the dry forest was greater by a factor of three than that predicted from net foliage production by global regression models (McNaughton *et al.*, 1989), whereas wet forest consumption fell below model prediction by a factor of six. Similarly, levels of percentage productivity consumption in our forest sites differed from those predicted from foliar N or P concentrations (Cebrián & Lartigue, 2004). However, the inspection of such broad empirical models reveals that forests deviate considerably from predicted relationships, perhaps because herbivory is dominated by ectotherm consumers (McNaughton *et al.*, 1989; Oksanen & Oksanen, 2000).

Factors other than plant productivity and nutritional quality may influence chronic defoliation patterns in specific forest types. Top-down forces were unlikely to be responsible for folivory patterns at the present scale of study as the level of bird predation was found to be similar in dry and wet forests (Mazía *et al.*, 2004; Garibaldi *et al.*, 2010). By contrast, shifts in feeding guild dominance (Mazía *et al.*, 2004) and folivore abundance (Garibaldi *et al.*, 2010, 2011a) along environmental gradients suggest a direct role for abiotic conditions in controlling herbivore pressure (Hunter & Price, 1992). Temperature strongly affects basic insect functions (Deutsch *et al.*, 2008) and can be a major driver of plant–herbivore interactions (Bale *et al.*, 2002; Kozlov, 2008; Garibaldi *et al.*, 2011a). Wet *N. pumilio* forests provide cooler habitats, with an extended period of snow cover, which may limit the survival of insects pupating in the litter layer, such as leaf folders, miners and tiers. Heavy, frequent rainfall may

act as a physical disturbance to exophytic leaf feeders. We hypothesise that abiotically stressful conditions, coupled with a shorter growing season (Dirzo & Boege, 2008), may act to constrain total folivore activity in wet *N. pumilio* forests.

In conclusion, we have shown that the overall impact of herbivory through foliage consumption and early abscission was greater in dry than in wet *N. pumilio* forests. This pattern corresponded with a clear temporal separation in resource use by dry forest guilds, but did not reflect higher foliar quality and productivity in wet forest. Abiotic conditions and host plant phenology may differentially affect insect population dynamics between forest types (Hunter & Price, 1992; Deutsch *et al.*, 2008), and may thus contribute to habitat-specific patterns of productivity consumption in these cool temperate forests. It would be interesting to determine how differential folivory rates alter carbon and nutrient cycling via litter decomposition in wet versus dry forests (Hunter, 2001; Cebrián & Lartigue, 2004; Hartley & Jones, 2004). This is the subject of ongoing research that aims to increase understanding of the functional consequences of chronic herbivory in Patagonian forests.

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