Functional Ecology

British Ecological Society

Functional Ecology 2012, **26**, 265–273 doi: 10.1111/j.1365-2435.2011.01910.x

Gregarious flowering and death of understorey bamboo slow litter decomposition and nitrogen turnover in a southern temperate forest in Patagonia, Argentina

Amy T. Austin* and Victoria A. Marchesini

IFEVA-CONICET, Facultad de Agronomía, Universidad de Buenos Aires, Av. San Martín 4453, Buenos Aires C1417DSE, Argentina

Summary

1. The massive synchronized flowering and subsequent mortality of understorey bamboo species occur in infrequent and unpredictable intervals in temperate and subtropical forests around the world. Because of the sporadic occurrence of these flowering episodes and the long intervals between events, very little is known about their consequences on biogeochemical cycling in natural ecosystems.

2. In 2001, a synchronized flowering and dieback of the native bamboo, *Chusquea culeou* E. Desv., occurred, covering more than 200 000 ha in the north-west region of Patagonia, Argentina. We explored the impacts of this gregarious flowering event on litter decomposition and nitrogen turnover in an old-growth southern beech forest for 3 years after the flowering event.

3. Bamboo litter decomposed significantly slower than overstorey tree litter, and decomposition in flowered patches overall was significantly reduced compared to remnant live understorey patches. In addition, soil mineral nitrogen was reduced in flowered patches, and nitrogen transformations were altered, most notably in the third year after the flowering event.

4. This infrequent phenomenon of gregarious flowering could have consequences for carbon and nutrient cycling, as low-quality standing dead biomass is gradually incorporated into soil organic matter pools. This study demonstrates that large biotically mediated perturbations of understorey vegetation can impact biogeochemical cycles in temperate forest ecosystems by reducing carbon turnover and altering nitrogen availability and transformations, even in the absence of physical disturbance.

Key-words: bamboo flowering, biotic disturbance, carbon cycling, litter decomposition, nitrogen cycling, *Nothofagus* forest, southern beech, South America

Introduction

Understorey vegetation can have considerable impacts on biogeochemical cycles in forest ecosystems, affecting carbon and nutrient mineralization through the characteristics of the senescent material entering the soil organic matter pools (Lorenz *et al.* 2000; Prescott *et al.* 2000; Wardle, Bonner & Barker 2002), through environmental control on moisture and temperature conditions (Xiong *et al.* 2008) or because of overstorey litterfall interception (Dearden & Wardle 2008). In addition, alterations in dominant understorey vegetation through natural or human-induced physical perturbations can impact forest biogeochemical cycles. The destruction of understorey vegetation by hurricanes, for example, can cause major increases in soil nitrogen losses (Wright & Coleman 2002), although rapid understory regeneration can provide for high resilience for nutrient cycling (Cooper-Ellis *et al.* 1999). In addition, human-caused alterations in understorey species composition had larger effects on decomposition as opposed to direct effects resulting from land-use changes (Quested *et al.* 2007).

Biotically mediated disturbances affecting understorey vegetation have the potential to affect biogeochemical cycles. One of the most studied of these impacts is the effect of species invasions that result in alteration of the dominance in understorey vegetation. These invasions generally increasing litter decomposition and nutrient pools, retention and turnover (Ehrenfeld, Kourtev & Huang 2001; Allison & Vitousek 2004; Harner *et al.* 2009; Sharma & Raghubanshi 2009). Other biotic disturbances such as large-scale insect

---

*Correspondence author. E-mail: austin@ifeva.edu.ar

defoliation can also impact carbon and nutrient cycling in forest ecosystems and the functioning of soil organisms (Yang 2006). Plant responses of understorey and overstorey vegetation with gypsy moth infestation can dramatically affect carbon fluxes, for example, with a general reduction in plant growth and carbon fixation in the wake of these events (Kosola *et al.* 2001; Clark, Skowronski & Hom 2010), as well as reduced input of senescent material to soil organic pools.

In some temperate and subtropical forests, bamboo grasses dominate the understorey (Janzen 1976; Pearson, Pearson & Gomez 1994; Judziewics *et al.* 1999) and can substantially affect ecosystem characteristics and processes. Because of their fast growth and considerable biomass (Veblen 1982; Christanty, Mailly & Kimmins 1997; Singh, Singh & Tripathi 1999), it has been suggested that live bamboos can affect competitive interactions (Young & Peffer 2010; Tomimatsu *et al.* 2011) and, in particular, overstorey tree regeneration, because of light limitation imposed by the dense understorey cover (Veblen 1982; Taylor *et al.* 2006; Tang, Li & Zhu 2007). In addition, litter quality of bamboo can affect rates of decomposition (Tripathi & Singh 1992b; Arunachalam, Upadhyaya & Arunachalam 2005; Fujimaki, Takeda & Wiwatiwitaya 2008), with a general trend for reduced rates of mass loss in litter compared with dominant tree species in temperate forests (Liu, Fox & Xu 2000; Tripathi *et al.* 2006; Fujimaki, Takeda & Wiwatiwitaya 2008). Finally, carbon fixation by bamboo can contribute substantially to soil organic matter and nutrient pools, accounting for up to one-third of the net primary productivity in forests with dense bamboo understorey (González & Donoso 1999; Singh & Singh 1999; Tripathi *et al.* 2006) and for the maintenance of soil fertility, particularly nitrogen pools (Christanty, Mailly & Kimmins 1997, Singh & Singh 1999).

An unusual characteristic of nearly all bamboo species is a single reproductive event that leads to massive flowering, seed production and senescence (Janzen 1976; Keeley & Bond 1999; Jaksic & Lima 2003), with the period between flowering episodes ranging from 3 to 120 years (Campbell 1985; McClure 1993). The intervals between flowering events are then entirely dominated by vegetative growth and clonal reproduction. Bamboo flowering events have been recorded for centuries in Asia (Numata 1970; Gadgil & Prasad 1984) and the Americas (Seifriz 1950; Filgueiras 1988; Jaksic & Lima 2003), but the unpredictable nature of these flowering episodes and the long intervals between events complicate the assessment of ecological consequences of these events in natural ecosystems. The physiological mechanisms controlling these sporadic events are not understood (Janzen 1976; Lin *et al.* 2009, 2010), although various hypotheses regarding the evolutionary value of this semelparous flowering behaviour have been postulated (Keeley & Bond 1999; Franklin & Bowman 2003; Franklin 2004).

Variable conditions in both space and time created by gregarious bamboo flowering could alter ecosystem processes in forests. Typically, in the years following these flowering events, bamboo seedlings regenerate directly from seeds (Marchesini, Sala & Austin 2009), and the return to the pre-flowering vegetative condition can take up to 15 years, depending on the climate and species (Janzen 1976; Pearson, Pearson & Gomez 1994). Dramatic changes in light availability in this post-flowering period can favour overstorey tree regeneration (Taylor, Jinyan & ShiQiang 2004; Holz & Veblen 2006; Giordano, Sánchez & Austin 2009; Marchesini, Sala & Austin 2009), alter species diversity and composition (Budke *et al.* 2010) and affect trophic interactions, particularly with respect to predation and herbivory (Kitzberger, Chaneton & Caccia 2007; Raffaele, Kitzberger & Veblen 2007). Flowering events have been shown to affect nutrient availability, with reduced soil mineral nitrogen pools observed after a large-scale flowering event in Japan (Takahashi *et al.* 2007). Carbon turnover, and particularly litter decomposition, has yet to be evaluated following a gregarious flowering event of understorey bamboo in temperate forest ecosystems.

A massive flowering event of the understorey bamboo, *Chusquea culeou* E. Desv., occurred in the north-west Patagonian region of Argentina in 2001, which affected more than 200 000 ha of native forest ecosystems (Fig. 1). We hypothesized that this infrequent event could have substantial effects on carbon and nutrient mineralization because of large changes in live and senescent biomass pools and the disruption of plant nutrient uptake. We predicted that the flowering event would have two major consequences for biogeochemical cycling: (i) the death of the understorey would initially cause an increase in soil mineral nitrogen because of reduced plant uptake by understorey vegetation, and (ii) the input of large amounts of low-quality litter would reduce litter decomposition of both understorey bamboo and overstorey canopy species and provoke immobilization of nutrients by soil microbial communities. As these two effects could be

Fig. 1. *Chusquea culeou* in the understorey of a temperature Patagonian forest. The two photographs show the different understorey conditions 2 years after the 2001 flowering event, with the left panel showing the remnant green live bamboo patches, and the right hand panel with the senescent bamboo understorey. Photographs courtesy of V. Marchesini.

compensatory, it is the net effect of mineralization–immobilization and plant uptake that would determine the impact on nitrogen dynamics in this ecosystem. We compared rates of litter decomposition and soil N availability in areas where bamboo had flowered and senesced with that in remnant patches of live bamboo in the 3 years following this massive flowering bamboo event in an old-growth forest in Patagonia.

Materials and methods

STUDY SITE

The study site is in the Neuquén Province of Argentina, in an old-growth temperate forest (40°S 71°W) within the boundaries of Lanín National Park. The site is located at an elevation of 800 m with mean annual precipitation of 2200 mm and with minimum and maximum temperatures that range from 3 (July) to 18 °C (January). Soils are Andisols, derived from volcanic ash, with a high content of silt, clay and organic matter (Dezzotti *et al*. 2003). The forest canopy is co-dominated by three *Nothofagus* species: the deciduous *Nothofagus obliqua* (Mirb.) Blume and *Nothofagus nervosa* (Phil.) Dim. *et* Mil. and the evergreen *Nothofagus dombeyi* (Mirb.) Blume (Vivanco & Austin 2008). The understorey vegetation is entirely dominated by the bamboo species *C. culeou*, which is dense and monospecific, with above-ground biomass *c*. 3·5 kg m^{-2} (Marchesini, Sala & Austin 2009). *Chusquea culeou* synchronously flowered and senesced in early 2001 in the region covering an expanse of over 200 000 ha, resulting in the death of 95% of the above-ground bamboo biomass (Sanguinetti & García 2001; Marchesini, Sala & Austin 2009). Small (< 200 m^2) remnant patches of understorey bamboo interspersed throughout the study site did not flower and remained green. Although it is not understood why these small patches did not flower, there were no obvious differences in terms of understorey and overstorey biomass, slope or aspect as compared to the areas that did flower.

EXPERIMENTAL DESIGN

To compare the effects of bamboo flowering on litter decomposition and nutrient cycling, two patch types were established, representing live understorey (LU) and senescent understorey (SU) conditions. Remnant green bamboo patches (LU) that had not flowered were used as control microsites, representing forest conditions prior to the flowering event. Flowered bamboo patches (SU) consisted of areas where *C. culeou* flowered and subsequently died in 2001 and contained all standing dead material. Eight plots of 25 m^2 in each understorey condition were established, with similar overstorey canopy conditions and homogeneous bamboo cover. None of the plots were located in gaps or open areas, and as the three *Nothofagus* spp. coexist throughout the site (Vivanco & Austin 2008), there was no species-specific bias associated with the plots. Soil sampling and litter decomposition experiments were conducted over a 2-year period from 2003 to 2005, with various sampling dates in all seasons except winter.

LITTER DECOMPOSITION

Senescent material of the overstorey *Nothofagus* species and the bamboo species, *C. culeou*, was collected in fall of 2002 for litter decomposition experiments. We collected recently senesced leaves of the three *Nothofagus* species (*N. dombeyi, N. obliqua and N. nervosa*) using nets suspended 1 m from the soil surface. *C. culeou* leaves, stems and petioles were collected from standing dead culms and from fresh senescent litter on the forest floor. In the laboratory, litter was separated in intact, undamaged senescent leaves (*Nothofagus* spp. and *C. culeou*), petioles and culms (*C. culeou*); 1·500 g of senescent plant material was placed in 2-mm mesh fibreglass litterbags of 15 × 15 cm. In the case of the overstorey *Nothofagus* species, 0·500 g of each *Nothofagus* was mixed and put together in a single litterbag. Litterbags of the four litter types (*C. culeou* leaves, petioles and stems, and *Nothofagus* spp.) were placed on the soil surface at the study site after removing the litter layer in late February 2003 in plots of both flowered and unflowered understorey conditions ($N = 5$ for each patch, litter type and date). Litterbags were placed in the centre of the 5 × 5 m plot and collected after 78, 137, 365, 553 and 739 days. Once retrieved from the field, litterbags were carefully cleaned; extraneous debris was removed, and after 2 days of drying in a 65 °C oven, remaining litter was weighed for determination of mass loss. All samples were also corrected for soil contamination by calculating ash-free dry mass (AFDM). A ground subsample of each litterbag was combusted in a muffle furnace at 450 °C for four hours to determine inorganic matter content (Robertson & Paul 2000). The decomposition rate was estimated assuming an exponential decay rate, where $\ln(M_t/M_0) = -k_t$, where M_0 is the initial AFDM, M_t is the AFDM at time *t*, and *k* is the decomposition constant (Swift, Heal & Anderson 1979). In all cases, the single exponential function with a zero intercept had a better fit than a simple linear regression and also allowed for direct comparison among litter types and treatments (Vivanco & Austin 2008). Initial litter quality measurements for per cent nitrogen, per cent phosphorus and lignin were conducted with subsamples of the initial litter pool for each species ($N = 5$ for each litter type). Subsamples of litter material were ground to pass a 20-μm mesh, and nitrogen (%N) and phosphorus (%P) were determined using a Kjeldahl acid digestion procedure (Florence & Milner 1979) with digestion extracts measured colorimetrically using an Alpkem® autoanalyser (O-I Corporation, College Station, Texas, USA). Lignin concentrations were determined using a standard fibre acid detergent method (Van Soest 1963). Carbon content (%C) was calculated as 50% of AFDM. Statistics for differences in litter quality were conducted using a one-way ANOVA and differences in organic mass loss of decomposition constants (*k*) using two-way ANOVA with litter type and understorey condition (LU and SU) as the main factors.

CARBON AND NUTRIENT LITTER INPUT

Cover of understorey bamboo was monitored over 3 years from 2003 to 2006 (for more details on methodology, see Marchesini, Sala & Austin 2009). A calibration was completed in these plots to correlate basal cover of bamboo stems with the total biomass in LU and SU plots (Marchesini, Sala & Austin 2009). In addition, the relative contribution of stem, leaf and petiole biomass was determined with harvests of understorey bamboo in 12 secondary adjacent plots of 1·5 m^2 ($N = 6$ of each patch type). A subsample of this biomass (*c*. 20%) was taken to the laboratory in Buenos Aires, and stems of diameters ranging from 1 to 4 cm ($N = 38$) were separated to determine the proportions of leaf and petiole biomass to stem biomass. Average values of leaf and petiole biomass per stem were 5·7 (± 0·6)% and 7·6 (± 0·7)%, respectively.

The estimations from standing live and dead biomass and relative proportions of leaf and petiole biomass to stem biomass were used to calculate the total input of material in live and SU plots based on the aerial stem cover at each sampling date. Estimates for leaf litterfall from LU patches were derived from live stem biomass (Marchesini, Sala & Austin 2009) and assumed a turnover time of 1 year. Biomass input from SU biomass was calculated as the difference with the measurements for remnant standing dead biomass values over consecutive years from Marchesini, Sala & Austin (2009). Overstorey litterfall from *Nothofagus* spp. are average values from the study site used for all years (Vivanco 2008). Estimations of nitrogen content and C/N ratios of litter input were then calculated based on litter quality determinations described previously together with total biomass litterfall estimations. Finally, average site decomposition rates for each understorey condition were determined as an average of decomposition for each litter type weighted by its relative contribution to overall litter input in each year, in both understorey conditions.

SOIL NITROGEN DYNAMICS

For determination of inorganic soil nitrogen (NH_4-N and NO_3-N), soil samples of 0–10 cm of mineral soil were extracted at a randomly selected point in each plot ($N = 8$ for each patch type) using a 5-cm-diameter PVC tube. Soils were kept in airtight plastic bags and were processed the same day of extraction. Soils were initially sieved through a 2-mm mesh, and a subsample of 10 g of soil was added to 50 mL 2N KCl (Robertson *et al.* 1999). Once in the laboratory, soil extracts were filtered using Whatman® No. 42 filters; extracts were then analysed colorimetrically using an Alpkem® autoanalyzer (O-I Corporation). Water content was estimated gravimetrically, where a subsample of humid soil was weighed and dried in a 105 °C oven for 48 h. Soil N concentrations were corrected for soil water content. Daily values for NH_4-N and NO_3-N were calculated based on interpolations of the values from each sampling date, and average annual values were then calculated based on the average values across the entire year. Differences in soil mineral N were evaluated using a two-way ANOVA, with year and understorey condition as the two main factors. Data for nitrate were log-transformed to meet assumptions for homogeneity of variance. Post hoc comparisons were completed using a Tukey's HSD test.

Soil net N mineralization was estimated using the buried bag technique (Stark 2000). We used as the initial sample (T0) the soil cores that were sampled for inorganic N determination, and a second sample of similar size (0–10 cm depth) was incubated in a polyethylene bag (40 μm) until the following sampling date. At this point, soil within the bag was removed from the plastic bag and processed as described earlier for the determination of inorganic N concentrations. Net nitrification was calculated as the difference in ammonium and nitrate concentration between the initial and the sample incubated in the buried bag, and net mineralization as the difference of the sum of both ammonium and nitrate, divided by the days of incubation. Differences for nitrogen transformation rates were evaluated using two-way ANOVA with time and understorey condition (LU or SU) as the main factors. In all cases for statistical tests, an alpha of 0·05 was used to establish significant differences among means for both one-way and two-way ANOVAS.

Results

LITTER QUALITY AND DECOMPOSITION

Litter quality varied with litter type (Table 1), with significant differences between bamboo litter and overstorey *Nothofagus* spp. for almost all evaluated characteristics. Bamboo leaf litter had significantly less %N and %P and lignin than overstorey *Nothofagus* spp. leaf litter (Table 1). The C/N ratio (> 600) of the bamboo stem material deviated strongly from all other litter types and was more similar to litter quality from coarse and fine woody debris.

Litter decomposition in both understorey conditions and for all litter types followed an expected exponential decline in organic mass remaining over time, with large differences between litter types (Fig. 2). Most notably, stem bamboo litter decomposed very slowly, with less than 10% of organic matter loss at the end of the 2-year incubation period. When decomposition was considered as the slope of organic matter loss over time [*k* constants (Vivanco & Austin 2008)], both litter type and patch type demonstrated significant effects on decomposition (Fig. 3; $P < 0{\cdot}001$, and $P < 0{\cdot}05$ for litter type and understorey condition, respectively). There were large differences among the *k* constants of litter types (Fig. 3a), with the litter mixture of overstorey tree species, *Nothofagus* spp., decomposing significantly faster than the bamboo litter and stem material decomposing slowest, with the leaf and petiole bamboo litter demonstrating intermediate values of decomposition. Decomposition correlated positively with initial per cent N, P and lignin (correlation coefficients of 0·81, 0·41 and 0·41 for N, P and lignin, respectively) and negatively with C/N and C/P ratios (correlation coefficients of −0·85 and −0·63 for C/N and C/P, respectively).

Beyond the litter quality effects on decomposition, there was a direct microsite effect between the LU and SU patches, which resulted in a significant reduction of decomposition in

Table 1. Nutrient content, organic matter and lignin concentrations, and carbon/nutrient ratios of senescent material of *Chusquea culeou* and *Nothofagus* spp. in a temperate forest in Patagonia, Argentina

		Litter quality variable				
	%N	%P	C/N	C/P	%OM	%Lignin
Chusquea culeou						
Leaf	0·51 (0·022)^{a}	0·042 (0·004)^{a}	43·5 (2·12)^{a}	559 (73)^{a}	66·2 (1·07)^{a}	8·1 (0·82)^{a}
Petiole	0·46 (0·027)^{a}	0·028 (0·008)^{a}	90·9 (6·51)^{a}	1858 (367)^{b}	90·0 (0·29)^{b}	12·9 (1·20)^{a}
Stem	0·09 (0·016)^{b}	0·039 (0·013)^{a}	609 (113)^{b}	2273 (817)^{b}	99·0 (0·52)^{c}	11·9 (2·12)^{a}
Nothofagus spp.	0·89 (0·078)^{c}	0·093 (0·003)^{b}	49·5 (4·56)^{a}	462 (25)^{a}	92·7 (1·02)^{b}	23·2 (0·84)^{b}

Values are means of litter samples ($N = 5$, SE in parentheses). The litter of overstorey for *Nothofagus* spp. was an equivalent mixture of the three co-dominant *Nothofagus* species in the site (Vivanco & Austin 2008). Different letters indicate significant differences between litter types at $P < 0{\cdot}001$.

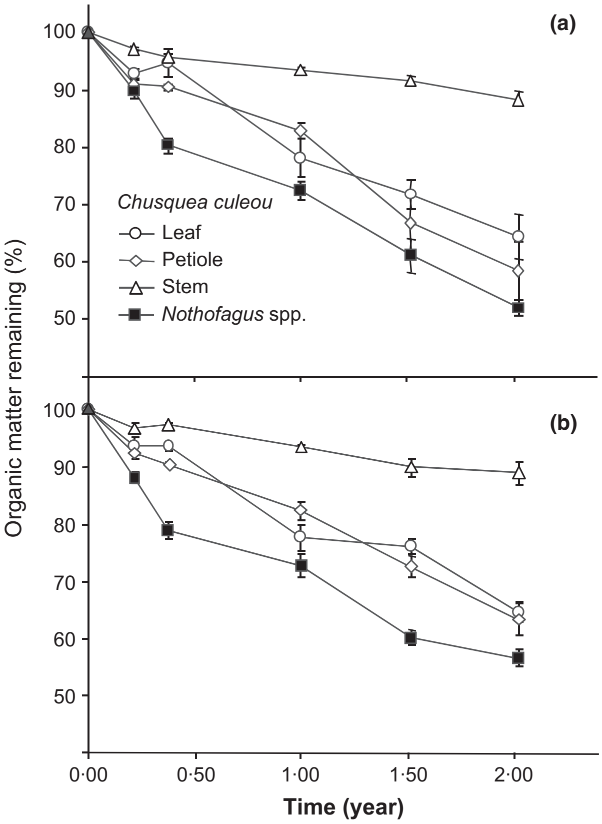

Fig. 2. Organic matter loss from litter over time after a massive bamboo flowering event in (a) live understorey and (b) senescent understorey patches in a Patagonian temperate forest. Symbols are mean values (±SE) for each sampling date and indicate different litter types of *Chusquea culeou* and a mixture of the dominant overstorey *Nothofagus* species.

SU patches (Fig. 3b, $P < 0·05$). As the interaction between litter type and understorey condition was not significant, we could not evaluate the relative effect of understorey condition on each litter type statistically, but those most affected by the understorey condition were *Nothofagus* spp. (15% slower) and *C. culeou* petiole litter (32% slower) in the SU patches (Fig. 2).

INORGANIC SOIL NITROGEN AND NET MINERALIZATION

Flowering understorey condition had significant effects on soil mineral N (Fig. 4) and N transformations of net nitrification and net mineralization (Fig. 5). Ammonium was significantly lower in SU patches in both 2003–2004 and 2004–2005 (Fig. 4, $P < 0·05$). Soil nitrate demonstrated a significant interaction with understorey conditions and time, with a significant decrease in SU patches 2003–2004, but with a return to pre-flowering conditions in the 2004–2005 period (Fig. 4b, interaction understorey × year $P < 0·05$). Differences in mineralization between LU and SU patches followed a different pattern from inorganic soil N, although both net mineralization (Fig. 5a) and net nitrification (Fig. 5b) had a significant understorey × time interaction ($P < 0·05$ in both cases). No detectable differences for net mineralization and nitrification were observed in 2003–2004, but significant differences were observed in 2004–2005, with higher net nitrification in LU plots in mid-summer (December) and fall (March). Net mineralization was significantly higher in LU plots in mid-summer (December) and was significantly lower in the fall sampling point (May).

LITTER AND NUTRIENT INPUT AT THE ECOSYSTEM SCALE

Estimations for total litter input from SU and LU patches showed substantial differences in inputs between understorey conditions (Table 2). In addition, there was a shift in the type and quantity of senescent material over time in the two patch types, which did not alter the total amount of nitrogen in the litter input, but substantially changed the C/N ratio (Table 2). As time passed after flowering, the continued lack of leaf litter inputs from bamboo and the large increase in standing dead culms falling to the soil surface almost doubled total litter input in the third year of the study, accompanied with a substantial increase in the C/N ratios (Table 2).

Discussion

The ecological consequences of biotically mediated disturbances on ecosystem processes can be considerable and

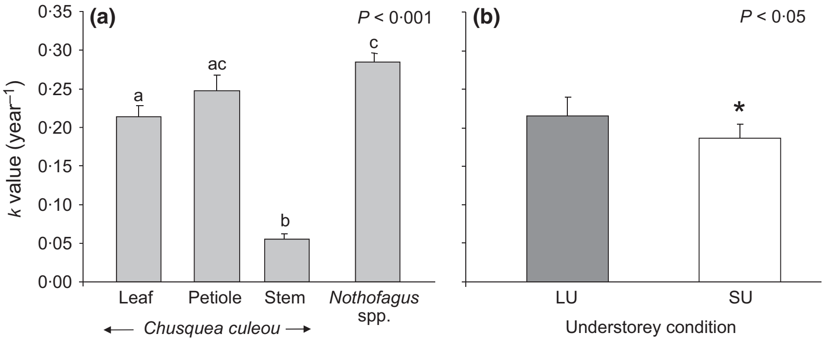

Fig. 3. Decomposition constants (k, per year) for (a) different litter types and (b) all litter types in live understory and senescent understorey conditions. Bars indicate mean values + SE. Both litter type ($P < 0.001$) and understorey condition ($P < 0.05$) were significantly different for decomposition rates; different letters or asterisks indicate significant differences for post hoc comparisons with a Tukey's HSD test.

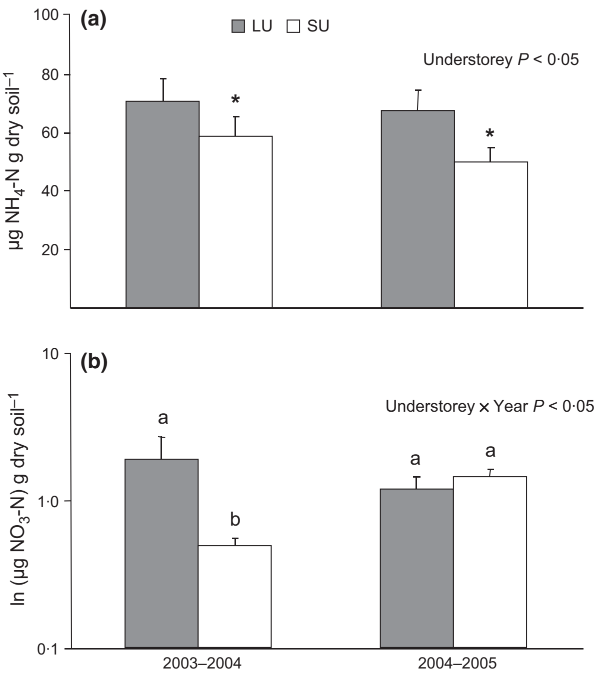

Fig. 4. Inorganic mineral nitrogen of (a) ammonium and (b) nitrate in surface soils (0–10 cm) for 2003–2005 in live understory and senescent understorey conditions. Bars indicate daily weighted annual means (+SE) for different understorey conditions (live or senescent), and different letters or asterisks indicate significant differences for post hoc comparisons with Tukey's HSD test.

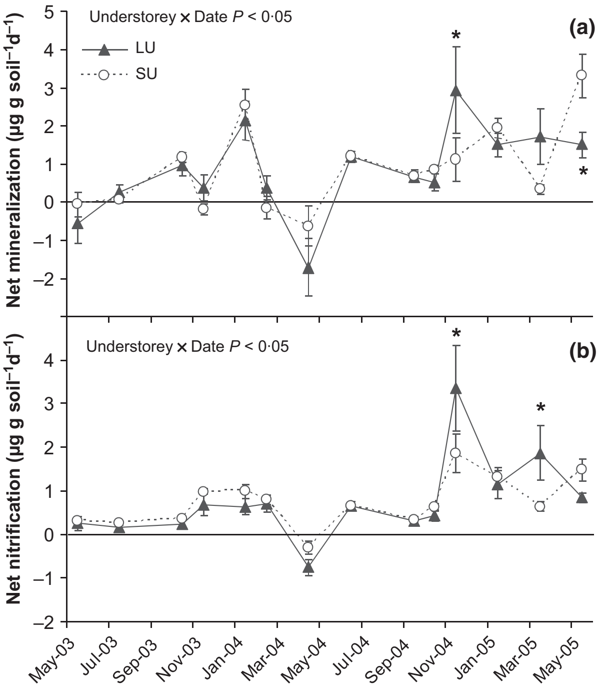

Fig. 5. Nitrogen transformations in surface soils from 2003 to 2005 in live understory and senescent understorey conditions for (a) net nitrogen mineralization and (b) net nitrification. Symbols indicate mean values ($N = 8, \pm$SE). In both cases, the interaction between understorey condition and date was significant ($P < 0.05$), and asterisks indicate significant differences between patch types at the given sampling date.

lasting in terrestrial ecosystems. We demonstrate in this study that gregarious flowering and death of the bamboo understorey impacted both carbon and nutrient turnover in this Patagonian temperate forest. The extensive death of the dense monospecific understorey had marked effects on the light environment in this forest (Giordano, Sánchez & Austin 2009, Marchesini, Sala & Austin 2009), but without strong effects on soil temperature or soil moisture (Marchesini, Sala & Austin 2009). As such, the main impacts on biogeochemical cycling appear to stem primarily from the quality and quantity of senescent material on the forest floor and the subsequent plant–soil interactions affecting carbon and nutrient turnover.

IMPACTS OF BAMBOO FLOWERING ON LITTER INPUTS AND DECOMPOSITION

Understorey bamboo can be an important component of forest litterfall, with one-third of litterfall from bamboo leaf litter in some temperate forests (González & Donoso 1999; Tripathi *et al.* 2006). In addition, gregarious bamboo flowering events have been shown to markedly increase the input of leaf litterfall, as much as doubling the contribution from non-flowering years (González & Donoso 1999), which is consistent with the results from this study (Table 2). In this study, we also demonstrated that the large increase in standing dead culms, which greatly exceeded leaf litterfall and decomposed more slowly, was an important consequence of the flowering event. (Figs. 2 and 3). The dieback of the *C. culeou* understorey resulted in an input of nearly 4·4 kg m^{-2} of organic matter over a 4-year period (leaf litter and standing dead culms combined), more than doubling average overstorey litter production (Marchesini, Sala & Austin 2009). However, because this senescent material was gradually incorporated into soil organic matter pools over several years following the flowering event, the effects on soil organic matter accumulation and dynamics were attenuated, unlike a single physical disturbance that would result in an immediate large pulse of organic input (Table 2, Marchesini, Sala & Austin 2009).

The increase in low-quality litter resulted in direct (litter quality) and indirect (site) inhibition of decomposition, which was consistent with our original hypothesis. The chemical composition of the litter types from bamboo leaves, petioles and culms (Table 1) and their respective decomposition (Fig. 2) suggest that the low quality of material from the bamboo flowering event could be responsible for the reduction in decomposition observed in the SU patches. Although a single study in a subtropical forest showed no site-specific effects of a sporadic bamboo flowering event on litter decomposition (Montti *et al.* 2011), litter quality of bamboo and agricultural activity have been shown to be factors affecting decomposition in ecosystems where bamboo species are an important component of the vegetation (Deka & Mischra 1982; Tripathi & Singh 1992b; Arunachalam, Upadhyaya & Arunachalam 2005, Fujimaki, Takeda & Wiwatiwitaya 2008). A study in a tropical savannah showed similar trends, with leaf and sheath

Table 2. Estimations of litter input, nutrient content, C/N ratios and site-level decomposition for 2003–2006 after a gregarious bamboo flowering event in a temperate forest in Patagonia, Argentina. For details on calculations, please see Methods section

	Live understorey (LU)			Senescent understorey (SU)		
	2003–2004	2004–2005	2005–2006	2003–2004	2004–2005	2005–2006
Chusquea culeou						
Leaf (g m^{-2})	240	273	167	339	–	–
Petiole (g m^{-2})	321	366	480	459	–	–
Stem (g m^{-2})	–	–	–	418	1497	2440
Nothofagus spp.						
(g m^{-2})	478	478	478	478	478	478
C/N of litter input	75	76	77	100	176	226
Decomposition (k, per year)	0·22	0·23	0·23	0·21	0·13	0·14
Total N (g m^{-2})	6·9	7·3	7·3	8·4	5·6	6·4
Total (g m^{-2})	1039	1117	1125	1694	1975	2918

litter decomposing substantially faster than stem tissue (Tripathi & Singh 1992a). In addition, bamboo litter decomposed more slowly than overstorey tree litter in several studies in Asian temperate forests (Liu, Fox & Xu 2000, Tripathi *et al.* 2006; Fujimaki, Takeda & Wiwatiwitaya 2008), similar to the patterns observed in this study. Thus, one of the direct effects of this gregarious flowering event stems from changes in the quality of senescent material entering the soil organic matter pool.

Slowed decomposition in SU microsites supports this litter quality influence, and additionally, the increased input in the amount of low-quality litter reduced decomposition at the ecosystem scale in this temperate forest ecosystem (Table 2, Fig. 3b). There were no detected differences in microclimatic conditions of air temperature and surface soil water content (0–5 cm) in these two understorey conditions (Marchesini, Sala & Austin 2009), but it cannot be ruled out entirely that other environmental conditions caused the observed changes in litter decomposition in the two understorey conditions. Over time, the absence of high litter quality inputs from the understorey combined with the gradual incorporation of standing dead material from fallen culms created distinctive conditions that differ from the normal live bamboo understorey, which could persist for some years following the flowering event. In addition, pulsed inputs of heterogeneous litter quality and quantity could also affect resilience and stability of the decomposer food webs (Moore *et al.* 2004), although the evaluation of trophic dynamics was beyond the scope of the present study.

IMPACTS OF BAMBOO FLOWERING ON NITROGEN CYCLING

There were observed changes in inorganic nitrogen pools and nitrogen mineralization because of the gregarious flowering event. Our original hypothesis was that an initial increase in soil nitrogen would occur because of reduced understorey plant uptake. However, we observed no initial increase in mineral soil nitrogen. As such, the responses in N cycling appear to reflect a changing importance of possible leaching losses and microbial immobilization over time (Figs. 4 and 5). A single study that evaluated flowering effects in a seasonal tropical forest in Thailand demonstrated an overall decrease in soil nutrient status after flowering, including nitrogen and calcium concentrations. These authors suggest that the alterations in N cycling were attributed to strong immobilization by microbial biomass because of the large input of low-quality plant litter (Takahashi *et al.* 2007), which is consistent with the patterns observed in this study for both carbon and nitrogen mineralization. The combination of decreased ammonium pools in both years (Fig. 4) and reduced net nitrogen mineralization (Fig. 5) suggests that low-quality litter inputs could have enhanced microbial immobilization in spite of presumed lower plant uptake. It should be noted that while changes in uptake and retention of nitrogen in the ecosystem by plants were very likely to have been reduced, it was not possible to quantify the importance of nutrient absorption by live bamboo, which can be substantial in some bamboo-dominated forests (Christanty, Mailly & Kimmins 1997; Tripathi *et al.* 2005). In addition, while increased leaching losses cannot be ruled out to explain the reduction in soil mineral nitrogen, the impact of an increase in low-quality litter may actually have reduced nitrogen losses from the ecosystem through the stimulation of microbial immobilization in areas where bamboo flowering occurred.

Further insights regarding the impacts of bamboo flowering on nutrient cycling can be gained from removal experiments of understorey bamboo, which mimic to a certain degree the active condition of the understorey after bamboo flowering but without the effect of increased litter inputs (Table 2). Complete removal of all understorey biomass in a forest dominated by dwarf bamboo demonstrated higher levels of soil nitrate, which the authors attribute to increased N inputs from root biomass and decreased N uptake by bamboo (Tripathi *et al.* 2005). This result is not consistent with the results of our study, which demonstrated a significant reduction in soil nitrate in the first year of measurement (Fig. 4). This evidence supports the conclusion that one of the principal causes of the slowed decomposition and reduction in soil mineral nitrogen is owing to the incorporation of large quantities of low-quality senescent material resulting from the gregarious flowering and death of the understorey.

ECOLOGICAL IMPLICATIONS

Infrequent ecological events can profoundly affect ecosystem processes as they reset the successional and biogeochemical clock in natural ecosystems (Aber *et al.* 2002; Kitzberger, Chaneton & Caccia 2007). The biotically mediated disturbance evaluated in this study is more similar to an abiotic disturbance (e.g. Cooper-Ellis *et al.* 1999; Wright & Coleman 2002) than a biotic disruption because of invasion or defoliation (e.g. Ehrenfeld, Kourtev & Huang 2001; Clark, Skowronski & Hom 2010), in large part because of the synchronized mortality of the above-ground biomass at a large spatial scale. At the same time, the biological significance of this flowering event for this old-growth forest, which has demonstrated importance for early-stage overstorey regeneration (Giordano, Sánchez & Austin 2009) and plant-animal interactions (Kitzberger, Chaneton & Caccia 2007), is particularly relevant considering the demonstration of an affinity of the soil decomposer community for particular litter types ('home-field advantage') where overstorey litter always decomposed faster when placed in sites with its own litter (Vivanco & Austin 2008). The demonstration that this delicate plant–soil interaction is eliminated due to changes in nitrogen availability (Vivanco & Austin 2011) highlights the potential importance of this flowering event for its impact on plant–soil interactions due to alterations in nutrient cycling. At present, the trigger that elicits gregarious flowering events is currently unknown (Janzen 1976; Lin *et al.* 2009, 2010), but the return to the pre-flowering vegetative state could take more than 15 years (Pearson, Pearson & Gomez 1994), followed by an estimated future 60 years of vegetative growth. It seems clear that these large, unpredictable events create fluctuating biogeochemical conditions with significant consequences for soil organic matter quality and ecosystem functioning in this Patagonian forest. Potential future work examining longer-term effects on carbon and nutrient pools as the understorey returns would be important to understand how these changes could affect tree regeneration, plant competitive interactions and the maintenance of overstorey and understorey diversity in this temperate forest ecosystem.

Acknowledgements

This work was funded principally by a National Science Foundation Small Grant in Ecological Research (SGER 02134174). Additional funding came from an early career grant to ATA from the Fundación Antorchas of Argentina, the Inter-American Institute for Global Change Research (CRN-012) and ANPCyT (PICT 21247/4 and PICT 31970/5) of Argentina. We are grateful to the staff of Parque Nacional Lanín for permission to work in the park; we thank J. Sanguinetti and M. Sosa for local information regarding the flowering event. L. Vivanco, M. Gonzalez-Polo, A. Fernández Souto, A. González Arzac, P. Araujo, F. Biganzoli, M. Moore, M. Dosantos, I. Miranda, M. Plumífero and P. Rojas Machado provided invaluable field and laboratory assistance. We appreciate the input of O. E. Sala and G. H. Goldstein for support during the initial part of this project, and we thank three anonymous reviewers for comments on an earlier version of this manuscript.

References

Aber, J.D., Ollinger, S.V., Driscoll, C.T., Likens, G.E., Holmes, R.T., Freuder, R.J. & Goodale, C.L. (2002) Inorganic nitrogen losses from a forested ecosystem in response to physical, chemical, biotic, and climatic perturbations. *Ecosystems*, **5**, 648–658.

Allison, S.D. & Vitousek, P.M. (2004) Rapid nutrient cycling in leaf litter from invasive plants in Hawai'i. *Oecologia*, **141**, 612–619.

Arunachalam, K., Upadhyaya, K. & Arunachalam, A. (2005) Foliage decomposition and nutrient release dynamics of *Bambusa balcooa* and *Bambusa pallida* in a 9-year-old jhum fallow. *Journal of Bamboo and Rattan*, **4**, 41–54.

Budke, J.C., Alberti, M.S., Zanardi, C., Baratto, C. & Zanin, E.M. (2010) Bamboo dieback and tree regeneration responses in a subtropical forest of South America. *Forest Ecology and Management*, **260**, 1345–1349.

Campbell, J.J.N. (1985) Bamboo flowering patterns: a global view with special reference to East Asia. *Journal of the American Bamboo Society*, **6**, 17–36.

Christanty, L., Mailly, D. & Kimmins, J.P. (1997) 'Without bamboo, the land dies': a conceptual model of the biogeochemical role of bamboo in an Indonesian agroforestry system. *Forest Ecology and Management*, **91**, 83–91.

Clark, K.L., Skowronski, N. & Hom, J. (2010) Invasive insects impact forest carbon dynamics. *Global Change Biology*, **16**, 88–101.

Cooper-Ellis, S., Foster, D.R., Carlton, G. & Lezberg, A. (1999) Forest response to catastrophic wind: results from an experimental hurricane. *Ecology*, **80**, 2683–2696.

Dearden, F.M. & Wardle, D.A. (2008) The potential for forest canopy litterfall interception by a dense fern understorey, and the consequences for litter decomposition. *Oikos*, **117**, 83–92.

Deka, H. & Mischra, R. (1982) Decomposition of bamboo (*Dendrocalamus hamiltonii* Nees.) leaf litter in relation to age of jhum fallows in Northeast India. *Plant and Soil*, **68**, 151–159.

Dezzotti, A., Sbrancia, R., Rodríguez-Arias, M., Roat, D. & Parisi, A. (2003) Regeneración de un bosque mixto de *Nothofagus* (Nothofagaceae) después de una corta selectiva. *Revista Chilena de Historia Natural*, **76**, 591–602.

Ehrenfeld, J.G., Kourtev, P. & Huang, W. (2001) Changes in soil functions following invasions of exotic understory plants in deciduous forests. *Ecological Applications*, **11**, 1287–1300.

Filgueiras, T.S. (1988) A floração dos bambus eu seu impacto ecolôgico. *Eugeniana*, **15**, 1–8.

Florence, E. & Milner, D.F. (1979) Routine determination of nitrogen by Kjeldahl digestion without use of catalyst. *Analyst*, **104**, 378–381.

Franklin, D.C. (2004) Synchrony and asynchrony: observations and hypotheses for the flowering wave in a long-lived semelparous bamboo. *Journal of Biogeography*, **31**, 773–786.

Franklin, D.C. & Bowman, D.J.M.S. (2003) Bamboo, fire and flood: regeneration of *Bambusa arnhemica* (Bambuseae: Poaceae) after mass-flowering and die-off at contrasting sites in monsoonal northern Australia. *Australian Journal of Botany*, **51**, 529–542.

Fujimaki, R., Takeda, H. & Wiwatiwitaya, D. (2008) Fine root decomposition in tropical dry evergreen and dry deciduous forests in Thailand. *Journal of Forest Research*, **13**, 338–346.

Gadgil, M. & Prasad, S.N. (1984) Ecological determinants of life history evolution of two Indian bamboo species. *Biotropica*, **16**, 161–172.

Giordano, C.V., Sánchez, R.A. & Austin, A.T. (2009) Gregarious bamboo flowering opens a window of opportunity for regeneration in a temperate forest of Patagonia. *New Phytologist*, **181**, 880–889.

González, M. & Donoso, C. (1999) Seed and litter fall in *Chusquea quila* (Poaceae: Bambusoideae), after synchronous flowering in south-central Chile. *Revista Chilena de Historia Natural*, **72**, 169–180.

Harner, M.J., Crenshaw, C.L., Abelho, M., Stursova, M., Shah, J.J.F. & Sinsabaugh, R.L. (2009) Decomposition of leaf litter from a native tree and an actinorhizal invasive across riparian habitats. *Ecological Applications*, **19**, 1135–1146.

Holz, C.A. & Veblen, T.T. (2006) Tree regeneration response to *Chusquea montana* bamboo die-off in a subalpine *Nothofagus* forest in the southern Andes. *Journal of Vegetation Science*, **17**, 19–28.

Jaksic, F.M. & Lima, M. (2003) Myths and facts on ratadas: bamboo blooms, rainfall peaks and rodent outbreaks in South America. *Austral Ecology*, **28**, 237–251.

Janzen, D. (1976) Why bamboos take so long to flower. *Annual Review of Ecology and Systematics*, **7**, 347–391.

Judziewics, E.J., Clark, L.G., Londoño, J. & Stern, M.J. (1999) *American Bamboos*. Smithsonian Institution Press, Washington.

Keeley, J.E. & Bond, W.J. (1999) Mast flowering and semelparity in bamboos: the bamboo fire cycle hypothesis. *American Naturalist*, **154**, 383–391.

Kitzberger, T., Chaneton, E.J. & Caccia, F. (2007) Indirect effects of prey swamping: differential seed predation during a bamboo masting event. *Ecology*, **88**, 2541–2554.

Kosola, K.R., Dickmann, D.I., Paul, E.A. & Parry, D. (2001) Repeated insect defoliation effects on growth, nitrogen acquisition, carbohydrates, and root demography of poplars. *Oecologia*, **129**, 65–74.

Lin, E.P., Peng, H.Z., Jin, Q.Y., Deng, M.J., Li, T., Xiao, X.C., Hua, X.Q., Wang, K.H., Bian, H.W., Han, N. & Zhu, M.Y. (2009) Identification and characterization of two Bamboo (Phyllostachys praecox) AP1/SQUA-like MADS-box genes during floral transition. *Planta*, **231**, 109–120.

Lin, X.C., Chow, T.Y., Chen, H.H., Liu, C.C., Chou, S.J., Huang, B.L., Kuo, C.I., Wen, C.K., Huang, L.C. & Fang, W. (2010) Understanding bamboo flowering based on large-scale analysis of expressed sequence tags. *Genetics and Molecular Research*, **9**, 1085–1093.

Liu, W., Fox, J.E.D. & Xu, Z. (2000) Leaf litter decomposition of canopy trees, bamboo and moss in a montane moist evergreen broad-leaved forest on Ailao Mountain, Yunnan, south-west China. *Ecological Research*, **15**, 435–441.

Lorenz, K., Preston, C.M., Raspe, S., Morrison, I.K. & Feger, K.H. (2000) Litter decomposition and humus characteristics in Canadian and German spruce ecosystems: information from tannin analysis and ^{13}C CPMAS NMR. *Soil Biology and Biochemistry*, **32**, 779–792.

Marchesini, V.M., Sala, O.E. & Austin, A.T. (2009) Ecological consequences of a massive flowering event of bamboo (*Chusquea culeou*) in a temperate forest of Patagonia, Argentina. *Journal of Vegetation Science*, **20**, 424–432.

McClure, F.A. (1993) *The Bamboos*. Smithsonian Institution Press, Washington.

Montti, L., Campanello, P.I., Gatti, M.G., Blundo, C., Austin, A.T., Sala, O.E. & Goldstein, G.H. (2011) Understory bamboo flowering provides a very narrow light window of opportunity for canopy-tree recruitment in a neotropical forest of Misiones, Argentina. *Forest Ecology and Management*, **262**, 1360–1369.

Moore, J.C., Below, E.L., Coleman, D.C., de Ruiter, P.C., Dong, Q., Hastings, A., Johnson, N.C., McCann, K.S., Melville, K., Morin, P.J., Nadelhoffer, K., Rosemond, A.D., Post, D.M., Sabo, J.L., Scow, K.M., Vanni, M.J. & Wall, D.H. (2004) Detritus, trophic dynamics and biodiversity. *Ecology Letters*, **7**, 584–600.

Numata, M. (1970) Conservation implications of bamboo flowering and death in Japan. *Biological Conservation*, **2**, 227–229.

Pearson, A.K., Pearson, O.P. & Gomez, I.A. (1994) Biology of the bamboo *Chusquea culeou* (Poaceae: Bambusoideae) in southern Argentina. *Vegetatio*, **111**, 93–126.

Prescott, C.E., Vesterdal, L., Pratt, J., Venner, K.H., De Montigny, L.M. & Trofymow, J.A. (2000) Nutrient concentrations and nitrogen mineralization in forest floors of single species conifer plantations in coastal British Columbia. *Canadian Journal of Forest Research*, **30**, 1341–1352.

Quested, H., Eriksson, O., Fortunel, C. & Garnier, E. (2007) Plant traits relate to whole-community litter quality and decomposition following land use change. *Functional Ecology*, **21**, 1016–1026.

Raffaele, E., Kitzberger, T. & Veblen, T.T. (2007) Interactive effects of introduced herbivores and post-flowering die-off of bamboos in Patagonia *Nothofagus* forests. *Journal of Vegetation Science*, **18**, 371–378.

Robertson, G.P. & Paul, E.A. (2000) Decomposition and soil organic matter dynamics. *Methods in Ecosystem Science* (eds O.E. Sala, R.B. Jackson, H.A. Mooney & R.W. Howarth), pp. 104–116. Springer, New York.

Robertson, G.P., Sollins, P., Ellis, B.G. & Lajtha, K. (1999) Exchangeable ions, pH and cation exchange capacity. *Standard Soil Methods in Long-Term Ecological Research* (eds G.P. Robertson, D.C. Coleman, C.S. Bledsoe & P. Sollins), pp. 106–114. Oxford University Press, Oxford.

Sanguinetti, J. & García, L. (2001) Floración masiva de *Chusquea culeou* en el Parque Nacional Lanín. Eventuales consecuencias ecológicas, su vinculación con las actividades humanas y necesidades de manejo y monitoreo. pp. 21. Parque Nacional Lanín, San Martín de los Andes, Argentina.

Seifriz, W. (1950) Gregarious flowering of *Chusquea*. *Nature*, **4199**, 635–636.

Sharma, G.P. & Raghubanshi, A.S. (2009) Lantana invasion alters soil nitrogen pools and processes in the tropical dry deciduous forest of India. *Applied Soil Ecology*, **42**, 134–140.

Singh, A.N. & Singh, J.S. (1999) Biomass, net primary production and impact of bamboo plantation on soil redevelopment in a dry tropical region. *Forest Ecology and Management*, **119**, 195–207.

Singh, K.P., Singh, P.K. & Tripathi, S.K. (1999) Litterfall, litter decomposition and nutrient release patterns in four native tree species raised on coal mine spoil at Singrauli, India. *Biology and Fertility of Soils*, **29**, 371–378.

Stark, J.M. (2000) Nutrient transformations. *Methods in Ecosystem Science* (eds O.E. Sala, R.B. Jackson, H.A. Mooney & R.W. Howarth), pp. 215–234. Springer, New York.

Swift, M.J., Heal, O.W. & Anderson, J.M. (1979) *Decomposition in Terrestrial Ecosystems*. University of California Press, Berkeley.

Takahashi, M., Furusawa, H., Limtong, P., Sunanthapongsuk, V., Marod, D. & Panuthai, S. (2007) Soil nutrient status after bamboo flowering and death in a seasonal tropical forest in western Thailand. *Ecological Research*, **22**, 160–164.

Tang, C.Q., Li, T. & Zhu, X. (2007) Structure and regeneration dynamics of three subtropical midmontane moist evergreen broad-leaved forests in southwestern China, with special reference to bamboo in the forest understories. *Canadian Journal of Forest Research-Revue Canadienne De Recherche Forestiere*, **37**, 2701–2714.

Taylor, A.H., Jinyan, H. & ShiQiang, Z. (2004) Canopy tree development and undergrowth bamboo dynamics in old-growth *Abies-Betula* forests in southwestern China: a 12 year study. *Forest Ecology and Management*, **200**, 347–360.

Taylor, A.H., Jang, S.W., Zhao, L.J., Liang, C.P. & Huang, J. (2006) Regeneration patterns and tree species coexistence in old-growth *Abies-Picea* forests in southwestern China. *Forest Ecology and Management*, **223**, 303–317.

Tomimatsu, H., Yamagishi, H., Tanaka, I., Sato, M., Kondo, R. & Konno, Y. (2011) Consequences of forest fragmentation in an understory plant community: extensive range expansion of native dwarf bamboo. *Plant Species Biology*, **26**, 3–12.

Tripathi, S. & Singh, K. (1992a) Abiotic and litter quality control during the decomposition of different plant parts in dry tropical bamboo savanna in India. *Pedobiologia*, **36**, 241–256.

Tripathi, S. & Singh, K. (1992b) Nutrient immobilization and release patterns during plant decomposition in a dry tropical bamboo savanna, India. *Biology and Fertility of Soils*, **14**, 191–199.

Tripathi, S.K., Sumida, A., Shibata, H., Uemura, S., Ono, K. & Hara, T. (2005) Growth and substrate quality of fine root and soil nitrogen availability in a young *Betula ermanii* forest of northern Japan: effects of the removal of the understorey dwarf bamboo. *Forest Ecology and Management*, **212**, 278–290.

Tripathi, S., Sumida, A., Shibata, H., Ono, K., Uemura, S., Kodama, Y. & Hara, T. (2006) Leaf litterfall and decomposition of different above- and belowground parts of birch (*Betula ermanii*) trees and dwarf bamboo (*Sasa kurilensis*) shrubs in a young secondary forest in Northern Japan. *Biology and Fertility of Soils*, **43**, 237–246.

Van Soest, P.J. (1963) Use of detergents in analysis of fibrous feeds II: a rapid method for the determination of fiber and lignin. *Association of Official Analytical Chemists*, **46**, 829–835.

Veblen, T.T. (1982) Growth patterns of *Chusquea* bamboos in the understory of Chilean *Nothofagus* forests and their influences in forest dynamics. *Bulletin of the Torrey Botanical Club*, **109**, 474–487.

Vivanco, L. (2008) *Efectos de la identidad y diversidad de especies de plantas sobre el reciclado de carbono y nutrientes en bosques templados en Patagonia, Argentina*. Ph.D Thesis, University of Buenos Aires, Buenos Aires.

Vivanco, L. & Austin, A.T. (2008) Tree species identity alters litter decomposition through long-term plant and soil interactions in a natural forest ecosystem in Patagonia, Argentina. *Journal of Ecology*, **96**, 727–736.

Vivanco, L. & Austin, A.T. (2011) Nitrogen addition stimulates forest litter decomposition and disrupts species interactions in Patagonia, Argentina. *Global Change Biology*, **17**, 1963–1974.

Wardle, D.A., Bonner, K.I. & Barker, G.M. (2002) Linkages between plant litter decomposition, litter quality, and vegetation responses to herbivores. *Functional Ecology*, **16**, 585–595.

Wright, C.J. & Coleman, D.C. (2002) Responses of soil microbial biomass, nematode trophic groups, N-mineralization, and litter decomposition to disturbance events in the southern Appalachians. *Soil Biology and Biochemistry*, **34**, 13–25.

Xiong, Y.M., Xia, H.X., Li, Z.A., Cai, X.A. & Fu, S.L. (2008) Impacts of litter and understory removal on soil properties in a subtropical *Acacia mangium* plantation in China. *Plant and Soil*, **304**, 179–188.

Yang, L.H. (2006) Interactions between a detrital resource pulse and a detritivore community. *Oecologia*, **147**, 522–532.

Young, T.P. & Peffer, E. (2010) ''Recalcitrant understory layers'' revisited: arrested succession and the long life-spans of clonal mid-successional species. *Canadian Journal of Forest Research*, **40**, 1184–1188.

Received 25 January 2011; accepted 15 August 2011
Handling Editor: Edith Allen