



Canopy tree development and undergrowth bamboo dynamics in old-growth *Abies–Betula* forests in southwestern China: a 12-year study

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Abstract

Interactions between forest canopy characteristics and plants in the forest understory are important determinants of forest community structure and dynamics. In the highlands of southwestern, China the dwarf bamboo *Bashania fangiana* Yi is an understory dominant beneath a mixed canopy of the evergreen *Abies faxoniana* (Rheder & Wilson) and the deciduous *Betula utilis* (D. Don). The goal of this study was to better understand the role of bamboo dominance, canopy characteristics, and periodic bamboo dieback on forest development. To achieve this goal, we measured tree seedling, tree saplings, and trees, forest canopy characteristics, and bamboo cover in permanent forest ($n = 4$) and gap plots ($n = 31$) in a mixed *A. faxoniana* and *B. utilis* forest in Sichuan, China. Dwarf bamboos died off in 1983 in the gap plots, and in three of the four forest plots. Forest development was assessed for the period 1984–1996. The seedling bank in forest and gap plots increased after bamboo die-off. *A. faxoniana* seedlings increased more than *B. utilis* in forest plots; the opposite pattern characterized gap plots. The proportion of seedlings on raised micro-sites on the forest floor also changed and new seedling were more abundant on the forest floor. By 1996, bamboo seedling cover and biomass had recovered to ca. 45% or their pre-flowering values. Rates of bamboo seedling recovery were faster beneath canopy gaps and deciduous trees than beneath forest or evergreen trees. Tree mortality exceeded recruitment in plots with dense bamboo; the opposite pattern was found in the plot with little bamboo. The mortality rate for *B. utilis* trees (2.4% year⁻¹) was higher than that for *A. faxoniana* (0.8% year⁻¹) and forests with dense bamboos became more open over the census period. Tree mortality was size-dependent and intermediate sized trees had the lowest rates of mortality. Stand basal area increased mainly due to greater basal area gain than loss for *A. faxoniana*. Interactions between tree species life history, canopy type, and bamboo life-cycles create heterogeneous conditions that influence tree and bamboo regeneration and contribute to the coexistence of *A. faxoniana* and *B. utilis* in old-growth forests in southwestern China.

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1. Introduction

Interactions between forest canopy characteristics and forest understory plants are recognized as important determinants of community structure and dynamics in both tropical (e.g. Denslow et al., 1991; Griscom and Ashton, 2003) and temperate (e.g. Stewart and Veblen, 1982; Crozier and Boerner, 1984; Nakashizuka, 1987) forests. Forest canopy composition and density affect patterns of resource availability (i.e. light, precipitation, soil nutrients) on the forest floor which, in turn, influence the distribution and dominance of understory plants. In Chilean beech forests, understory bamboos (*Chusquea tenuiflora* Phil.) are taller and cover is greater beneath the broad-leaved evergreen *Nothofagus betuloides* (Mirb.) Bl. than under the deciduous *N. pumilio*. Under the evergreen canopy, snow is less persistent and growing season light penetration is higher which increases the growing season length for *C. tenuiflora* (Veblen et al., 1977, 1979). On the other hand, evergreen needle-leaved conifers in Japanese and Chinese forests inhibit dwarf bamboo growth and culms are taller and stands are denser beneath a deciduous canopy and in canopy gaps (Franklin et al., 1979; Reid et al., 1991; Taylor and Qin, 1988a, 1988b).

The distribution and dominance of understory plants may, in turn, affect long-term canopy structure and composition by influencing the establishment and growth of tree species' seedling populations (e.g. Ehrenfeld, 1980; Maguire and Forman, 1983; Taylor and Qin, 1988a; George and Bazzaz, 1999a, 1999b; Griscom and Ashton, 2003). Forest composition and structure in many forests is often determined by the pool of seedlings and saplings in the forest understory that are poised to replace canopy trees as they die (e.g. Runkle, 1981; Brokaw, 1985). In forests with dwarf bamboo, bamboos may achieve such a high degree of dominance that they impede seedling and sapling bank development. In Japanese (e.g. Franklin et al., 1979; Nakashizuka, 1987), Chilean (e.g. Veblen et al., 1981), and Chinese (Taylor and Qin, 1997) temperate forests with dwarf bamboos, small numbers of seedlings and saplings are a characteristic feature of forest stand structure. In these forests, bamboos are thought to influence tree population dynamics and stand development by suppressing tree recruitment. Yet, few studies have evaluated the effects of bamboo on stand

development by comparison of tree recruitment or mortality rates in stands with different degrees of bamboo dominance (Nakashizuka, 1991; Umeki and Kikuzawa, 1999).

The influence of dwarf bamboos on tree regeneration and hence stand development may also be temporally variable. Dwarf bamboos have a unique life history: they flower and dieback over wide areas every several decades, regenerate from seed, and grow vegetatively until the next flowering period (Numata, 1970; Veblen, 1982; Taylor and Qin, 1988c). The sudden decline of the bamboo cover after a flowering event may trigger a pulse of tree regeneration, and bamboo die-off is thought to be an important process regulating tree seedling establishment and forest stand development (Nakashizuka and Numata, 1982). Synchronized tree regeneration has been observed both beneath forest and canopy gaps after bamboo dieback (Nakashizuka, 1988; Taylor and Qin, 1992; Abe et al., 2002; González et al., 2002).

In the highlands of central Sichuan, China the dwarf bamboo *Bashania fangiana* Yi is an understory dominant on some sites where it occurs beneath a mixed canopy of the evergreen *Abies faxoniana* (Rheder & Wilson) and the deciduous *Betula utilis* (D. Don). Where *B. fangiana* is dense, seedlings and saplings of *A. faxoniana* or *B. utilis* are scarce and they often occupy raised microsites above the forest floor (i.e. logs, root plates) where the influence of bamboo is diminished (Taylor and Qin, 1988a, 1988b). The size and age structure of tree populations in old-growth stands suggest that both species can persist by periodic regeneration in tree-fall gaps (Taylor and Qin, 1988a, 1988b; Taylor et al., 1996). Tree seedling establishment immediately after a bamboo die-back has been observed (Taylor and Qin, 1992) but the effects of canopy type and canopy condition on tree seedling and bamboo seedling recovery have not been assessed. Post-flowering tree regeneration, and recruitment of seedlings and saplings into larger size-classes, may be limited by rapid development of bamboo seedlings on the forest floor.

The goal of this study was to better understand the role of bamboo dominance and bamboo dieback on tree regeneration and stand development in *A. faxoniana*–*B. utilis* forests. Specifically, we sought answers to the following questions. (1) How do tree

recruitment and mortality rates and stand development patterns vary with dwarf bamboo abundance? (2) Do tree seedling banks increase after bamboo dieback? (3) Do initial forest canopy conditions (i.e. evergreen versus deciduous; gap versus closed) influence the structure and composition of tree seedling banks that establish after bamboo dieback? (4) Do forest canopy conditions influence bamboo seedling recovery and abundance after a bamboo dieback? To help answer these questions we use repeat census data on tree seedling-sapling banks, bamboo seedling cover, and trees from gap plots and forest plots with different forest floor vegetation (i.e. dieback of dense of sparse bamboo, live bamboo) from old-growth *A. faxoniana*–*B. utilis* forests in south-western China.

1.1. Study area

Old-growth *A. faxoniana*–*B. utilis* forests were studied in the Wolong Natural Reserve (31°N, 103°10'E) in the Qionglai Mountains, central Sichuan, China. The climate is characterized by dry cold winters and wet cool summers. Mean monthly maximum temperatures, at 2960 m, are highest in August (15.3 °C) and mean monthly minimum temperatures are lowest in January (–11.2 °C). Annual precipitation is ca. 1200 mm with most falling during the May–October wet season. Snowfall is common between November and April at altitudes >2500 m. The terrain is steep, deeply dissected, and complex. Soils vary in depth from shallow (<50 cm) to deep (>100 cm) and limestone, sandstone, and phyllites are the main parent materials in our study area.

In Wolong, mixed *A. faxoniana*–*B. utilis* forest occurs between 2900 and 3200 m where large *A. faxoniana* may reach a height of 45 m and a diameter of 1.2 m dbh and large *B. utilis* are 20–25 m tall and <50 cm dbh. The understory, on many sites, is dominated by the bamboo *B. fangiana* which has culms that are ca. 1.5–2.0 m tall. On optimal sites, culm density exceeds 75 culms m⁻². In Wolong, *B. fangiana* is a key forage species for the obligate bamboo grazer the giant panda (*Ailuropoda melanoluca* David) (Schaller et al., 1985). *Bashania fangiana* is monocarpic and flowers ca. every 45 years and it flowered and died back in Wolong in 1983 over 80–90% of its range (Schaller et al., 1985).

2. Methods

2.1. Forest plots

Data on changes in seedling banks, bamboos, and trees were obtained from two types of permanent plots: forest plots and gap plots. Forest plots were selected for sampling using the following criteria: (1) accessibility (i.e. within 8 km of permanent camps); (2) presence of trees >250 years old, thus classifying them as old-growth; (3) sampled stands should include the range of observed variation in the state (live versus dieback) and density (high versus low) of understory bamboos and forest structure. Most forests below 2900 m were partially cut or clear-felled during the last 50 years (Schaller et al., 1985), so sampling was restricted to accessible sites above this elevation. Four stands (R1–R4) meeting the selection criteria were sampled and a single large plot was subjectively placed in each stand. Plots ranged in size from 2592–5832 m²; plot size varied based on stand density and areal extent of stand type (Table 1).

In each plot, we mapped and measured (dbh) all live trees (≥4.0 cm dbh), mapped saplings (stems >1.4 m tall and <4.0 cm dbh) and counted the number of small (<0.2 m tall) and large (0.2–1.4 m tall) seedlings in 3 m × 3 m contiguous quadrats. The substrate (i.e. forest floor, log, root plate) each seedling and sapling established on was also recorded. Forest canopy cover above each quadrat was classified as being open (<33% cover), intermediate (33–66%) or closed (>66%) and live bamboo cover in each quadrat was classified by cover class (<1, 1–5, 6–2, 26–50, 51–75, and 76–100%). Pre-flowering bamboo cover was also estimated by cover class in each quadrat based on the density of dead culms. Culm density and mean maximum culm height were estimated by counting and measuring the tallest culms in 50–120 restricted random 2 m × 1 m quadrats in each plot. Initial measurements in the plots were made in 1984, counts of live trees, saplings, and tree seedling were made again in two plots (R1 and R2) in 1990, and all plots were re-measured in 1996. We also measured the dbh and recorded the mode of death (i.e. stand dead, upturned, snapped) of all trees that died over the 12-year period.

In order to characterize changes in stand development post-flowering, we estimated rates of recruit-

Table 1
Plot and dwarf bamboo characteristics of old-growth *Abies–Betula* forests in the Wolong Natural Reserve sampled in 1984, 1990, and 1996

Bamboo cover (%)	Plot			
	R1	R2	R3	R4
1984	<1 (47.3) [68]	<1 (49.0) [72]	40 (24.7)	<1 (7.3) [20]
1990	16	21		
1996	34	40	46	3
Mean maximum culm height (cm)				
1984	[188.8 ± 21.2]	[203.8 ± 20.1]	135.7 ± 27.5	[123.8 ± 31.2]
1990	27.1 ± 11.9	30.5 ± 9.8		
1996	73.5 ± 24.4	77.4 ± 25.4	129.6 ± 29.4	20.7 ± 10.7
Plot size (m ²)	5832	5832	2592	2592
Plot dimensions (m)	54 × 108	54 × 108	36 × 72	36 × 72

For bamboo cover the number in parentheses is an estimate of culm density (m⁻²) and the number in brackets is an estimate of cover (%) of mature bamboo culms before flowering. The number in brackets for culm height is the estimate for mature culms before flowering. Dwarf bamboo (*B. fangiana*) died back in the understorey of R1, R2, and R4 in 1983, but it did not dieback in R3.

ment, mortality, loss or gain of basal area (BA), and changes in size structure from the repeat measurements in each plot. Recruitment and mortality were estimated for *A. faxoniana* and *B. utilis* using a logarithmic model (Condit et al., 1995; Shiel and May, 1996):

$$\text{mortality rate (\% year}^{-1}\text{)} = \ln\left(\frac{N_b/N_s}{t}\right) \times 100$$

where N_b and N_s are the number of stems alive at the beginning of the study and the number surviving to the end of the census period, respectively; t is the time interval;

$$\text{recruitment rate (\% year}^{-1}\text{)} = \ln\left(\frac{N_e/N_s}{t}\right) \times 100$$

where N_e and N_s , respectively, are the total number of the stems living at the end of the study and those surviving through the census period; t is the time interval.

The amount of basal area (BA) lost or gained in mortality and recruitment was identified using the following equations:

$$\text{loss of BA (\% year}^{-1}\text{)} = \left(\frac{BA_l}{BA_b} \times t\right) \times 100$$

where BA_l and BA_b are total BA of stems dying during the census period and stems living at the beginning of

the study, respectively;

$$\text{gain in BA (\% year}^{-1}\text{)} = \left(\frac{BA_g}{BA_e} \times t\right) \times 100$$

where BA_g and BA_e are the BA values for stems recruited during the census period and those living at the end, respectively.

Changes in the populations for stems and BA were inferred from the population growth rate (λ) (Condit et al., 1999) using data for 1984 and 1996 as:

$$\lambda_s (\% \text{ year}^{-1}) = \ln\left(\frac{N_{1996}/N_{1984}}{t}\right) \times 100;$$

$$\lambda_{BA} (\% \text{ year}^{-1}) = \left(\frac{BA_{1996} - BA_{1984}/BA_{1984}}{t}\right) \times 100;$$

where N and BA are the number of stems or the basal area of species on each census.

2.2. Gap plots

Gap plots ($n = 31$) were systematically selected for sampling along 60 m transects ($n = 17$) established in ca. a 10 ha old-growth stand near plots R1 and R2. Transects were established from a random starting point in the stand and transects ran parallel to slope contours at intervals of ca. 25 m to prevent duplicate sampling. The bamboo in the understorey of this stand died back in 1983. Each canopy gap intercepted by a transect was sampled and each gap-maker(s) was

identified, measured at breast height (dbh), and the type of gap (i.e. stem snap, uprooted, dead standing) was recorded. Gaps were considered indistinguishable from background forest when trees reached ca. 10 m in height. Gap size was estimated for canopy and expanded gaps (*sensu* Runkle, 1981) by measuring the length of a long and short axis that divided gaps into four ca. equal sized quadrants. Axes endpoints extended to the base of adjacent canopy trees and these trees were permanently tagged. Gap area was calculated using axes lengths and assuming an elliptic shape. In each gap-quarter, small and large seedlings were tallied, and pre- and post-flowering bamboo cover was estimated by cover class, in 4–8 randomly placed 1 m² quadrats. The height of the tallest culm was measured and the number of dead bamboo culms was counted in each 1 m² quadrat in the initial sample. Saplings in each gap quarter were also tallied. Gaps were sampled initially in 1985 and they were sampled again in 1990 (except for saplings) and 1996. The composition and structure of the stand was identified along the transects using the point-centered quarter method (Cottam and Curtis, 1956). Distance to the nearest tree (≥ 4.0 cm dbh) and dbh were measured and recorded by species in each quarter at 20 m intervals along each transect.

2.3. Bamboo and canopy conditions

The potential influence of evergreen (*A. faxoniana*) versus deciduous (*B. utilis*) canopy types on recovery and dominance of bamboo seedlings was examined in a mixed forest downslope from plot R1 in two ways. First, maximum culm height and bamboo cover by cover class were measured in 1 m² quadrats placed every 2 m along 8–16 m long randomly oriented transects that began at the base of large (i.e. >50 cm dbh) *A. faxoniana* trees ($n = 30$) and ended beneath a *B. utilis* canopy. Branch lengths for large *A. faxoniana* average 4.8 ± 0.7 m ($n = 30$). Second, bamboo standing crop was estimated beneath deciduous or evergreen canopies in thirty 0.1 m² plots placed every 5 m along a 150 m transect in the same stand. Bamboo cover (by cover class), maximum culm height, and forest canopy type was recorded for each plot and then bamboo culms were clipped at ground level. Above ground parts of the bamboo plant (culms, leaves, branches) were separated and weighed indivi-

dually to the nearest 0.1 g. Dry mass for each plant part was then estimated using dry weight-wet weight ratios for plant parts determined from a large sample ($n = 169$) of *B. faxoniana* culms (Taylor and Qin, 1987).

3. Results

3.1. Stand characteristics and development patterns

Mature dwarf bamboo cover, and mean maximum culm height, in the forest plots ranged from 20 to 72% and 123.8–203.8 cm, respectively (Table 1). Bamboos died back in R1, R2, and R4 in 1983, but not in R3. The cover (range 3.0–40%), and maximum culm height (20.7–77.4 cm) of bamboo seedlings in 1996 were lower than for mature bamboo. There was little change in the cover or culm height of bamboos that remained mature over the study period (R3).

At the start of the study (1984), tree density in the four plots ranged from 267 to 644 stems ha⁻¹ and the proportional abundance of *A. faxoniana* and *B. utilis* varied among plots (Table 2). In R1 and R2, the density of *A. faxoniana* and *B. utilis* were ca. equal, but in R3 and R4, *A. faxoniana* was much more abundant than *B. utilis*. Stands with the highest bamboo cover had the lowest tree density (Tables 1 and 2). There was less variation in basal area. Basal area ranged from 36.5 to 47.2 m² ha⁻¹ and *A. faxoniana* was the dominant species in each plot (Table 3).

Stand development over the census period as measured by recruitment and mortality varied with understory conditions. Tree mortality exceeded recruitment in plots with a pre-flowering bamboo cover $\geq 40\%$ (R1–R3) whereas recruitment exceeded mortality in the plot with low pre-flowering bamboo cover (R4) (Tables 1 and 2). Median annual mortality was higher for *B. utilis* (3.06% year⁻¹) than *A. faxoniana* (0.83% year⁻¹) ($P < 0.05$, Kruskal–Wallis *H*-test) in plots where both species died. There was no *B. utilis* tree recruitment in any of the plots and *A. faxoniana* recruitment was nil in two plots (R1, R2), low in another (R3), and only high in one plot (R4) (Table 2). Consequently, in the plots with higher pre-flowering bamboo cover the decline in the *B. utilis* tree population was greater than that for *A. faxoniana*. In R4, *A. faxoniana* recruitment exceeded mortality and the

Table 2

Number of living trees (stems ≥ 4.0 cm dbh) (ha^{-1}) on each census date and the rate of mortality, and recruitment over the census period

	Plot			
	R1	R2	R3	R4
<i>A. faxoniana</i>	$n = 111$	$n = 86$	$n = 80$	$n = 156$
Living 1984	190	147	308	602
Living 1996	178	130	289	775
Mortality 1984–1996	12	19	27	42
Recruitment 1984–1996	0	0	8	216
Mortality rate (% year $^{-1}$)	0.54	1.14	0.96	0.66
Recruitment rate (% year $^{-1}$)	0	0	0.24	2.97
λ_{stems} (% year $^{-1}$)	-0.54	-1.03	-0.59	2.30
<i>Betula utilis</i>	$n = 100$	$n = 70$	$n = 21$	$n = 11$
Living 1984	171	120	81	42
Living 1996	128	75	58	42
Mortality 1984–1996	46	44	23	0
Recruitment 1984–1996	0	0	0	0
Mortality rate (% year $^{-1}$)	2.62	3.87	3.06	0
Recruitment rate (% year $^{-1}$)	0	0	0	0
λ_{stems} (% year $^{-1}$)	-2.40	-3.87	-3.06	0

n : The size of the initial population in the plot.

A. faxoniana population increased while the *B. utilis* population remained constant.

Stand development as measured by total BA, in contrast, varied little among plots. Total BA increased in three of four plots (R1, R2 and R4) over the census period (Table 3). This was due mainly to higher BA

gain than loss for *A. faxoniana*. *Betula utilis* BA loss exceeded BA gain except in R4. In R4, BA for both species increased and ingrowth BA contributed more (4.4%) to BA gain than in other plots (0.4%).

There was little change in the size structure of either *A. faxoniana* or *B. utilis* over the study period

Table 3

Basal area ($\text{m}^2 \text{ha}^{-1}$) of living trees (stems ≥ 4.0 cm dbh) on each census date and the rate of basal area loss and gain over the census period

	Plot			
	R1	R2	R3	R4
<i>A. faxoniana</i>	$n = 111$	$n = 86$	$n = 80$	$n = 156$
Living BA 1984	44.50	33.00	39.00	35.10
Living BA 1996	45.40	34.80	38.60	36.30
Loss of BA 1984–1996	2.60	1.80	3.00	4.20
Gain of BA 1984–1996	3.70	4.54	4.35	5.47
BA loss rate (% year $^{-1}$)	0.48	0.46	1.15	1.08
BA gain rate (% year $^{-1}$)	0.68	0.86	1.00	1.36
$\lambda_{\text{BA}} \lambda_{\text{BA}}$ (% year $^{-1}$)	0.19	0.45	-0.09	0.30
<i>B. utilis</i>	$n = 100$	$n = 70$	$n = 21$	$n = 11$
Living BA 1984	2.70	4.30	1.90	1.40
Living BA 1996	2.40	3.10	1.50	1.60
Loss of BA 1984–1996	2.60	1.80	3.00	0
Gain of BA 1984–1996	0.23	0.24	0.21	0.21
BA loss rate (% year $^{-1}$)	7.80	2.83	2.36	0
BA gain rate (% year $^{-1}$)	0.82	0.65	0.33	0.20
λ_{BA} (% year $^{-1}$)	-1.19	-2.33	-1.91	1.29

n : The size of the initial population in the plot.

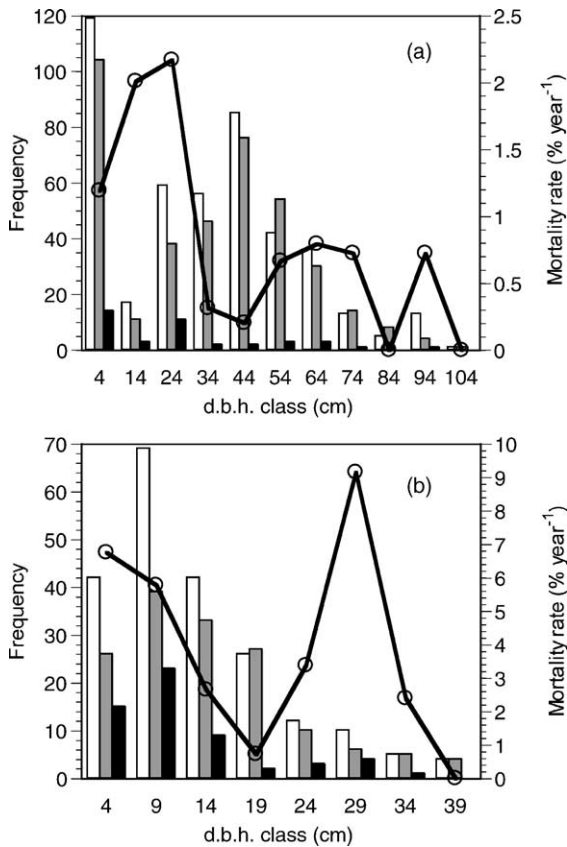


Fig. 1. Diameter (dbh) class distribution (bars) and size-specific mortality rate (line) for (a) *A. faxoniana* and (b) *B. utilis*. Open bars are trees living trees in 1984, gray bars are trees living trees in 1996 and black bars are trees that died between 1984 and 1996.

(Fig. 1), but trees of both species that died show a different pattern across dbh classes. The frequency of mortality decreased with increasing dbh, but mortality rates were lowest for intermediate sized stems and higher for both smaller and larger stems. The modes of death for *A. faxoniana* and *B. utilis* trees that died over the census period were different. Most *B. utilis* died

standing (96%), few stems were snapped (2%) or upturned (2%). In contrast, only 68% of *A. faxoniana* stems died standing while 32% were snapped or upturned.

In the gap survey stand, the cover and height of pre-flowering mature and seedling bamboos were similar to maximum values for the forest plots (Table 4). Total tree basal area ($42.8 \text{ m}^2 \text{ ha}^{-1}$) and tree density ($341 \text{ stems ha}^{-1}$) were similar to the values for plot R1 and R2 that were nearby. In the gap survey stand, *A. faxoniana* ($168 \text{ stems ha}^{-1}$) and *B. utilis* ($173 \text{ stems ha}^{-1}$) tree density were similar, but the basal area of *A. faxoniana* ($38.6 \text{ m}^2 \text{ ha}^{-1}$) was higher than that for *B. utilis* ($4.2 \text{ m}^2 \text{ ha}^{-1}$). The mean size of expanded gaps and canopy gaps was 252 m^2 (range 69–786 m^2) and 81 m^2 (range 16–404 m^2), respectively.

Modes of death for gap-makers in the gap survey were similar to the forest plots. About equal numbers of gaps were made by each species (*A. faxoniana* 46.8%, *B. utilis* 53.2%) and most *B. utilis* died standing (98%). For *A. faxoniana*, stem snap and upturned stems were more frequent (18%) and dead standing were less frequent (82%) than for *B. utilis*.

3.2. Tree seedlings and saplings patterns

3.2.1. Forest plots

Changes in the density of seedlings and saplings over the census period varied with the state of understory bamboos and by tree species (Tables 1 and 5). Seedling densities in 1984 were very low in plots R1 and R2 which had tall dense mature bamboo before die-back in 1983. Seedling density increased dramatically (28–218-fold) (except large *A. faxoniana* in R1) in these two plots over the study period and seedling density was higher in 1996 than in 1990. The density increase was greater for *A. faxoniana* than *B. utilis* and in 1996 there were more *A. faxoniana* (1.5–7.5 fold) than *B. utilis* seedlings. The proportional abundance of

Table 4

Dwarf bamboo characteristics (mean \pm S.E.) in canopy gaps ($n = 31$) in 1985, 1990, and 1996 in an old-growth *Abies-Betula* forest, Wolong Natural Reserve, Sichuan, China

	1985	1990	1996
Maximum culm height (cm)	$[195.0 \pm 2.5]^a$	$23 \text{ a} \pm 0.5$	$87^a \pm 4$
Bamboo cover (%)	$1.6 \pm 0.3 \text{ a} [80.4 \pm 1.5]^a$	$11.9 \text{ a} \pm 0.6$	$61^a \pm 4$

Bamboo in the gaps flowered and died back in 1983. The number in brackets are estimates for pre-flowering mature bamboo. Mean values in a row with the same letter were different ($P < 0.05$, Kruskal–Wallis H -test, Fischer's L.S.D.).

Table 5
Density (ha^{-1}) of small (<0.2 m tall) and large (0.2–1.4 m tall) seedlings, and saplings (>1.4 m tall and <4.0 cm dbh) of *A. faxoniana* and *B. utilis* in 1984, 1990 (R1 and R2 only) and 1996

	Plot			
	R1	R2	R3	R4
Small seedlings				
<i>Abies faxoniana</i>				
1984	82 (8)	77 (24)	4163 (3)	3295 (1)
1990	133 (10)	632 (11)		
1996	3174 (14)	6336 (17)	3005 (9)	4761 (1)
<i>Betula utilis</i>				
1984	11 (57)	14 (75)	85 (32)	4 (0)
1990	256 (26)	127 (88)		
1996	992 (22)	566 (74)	12 (33)	19 (60)
Large seedlings				
<i>Abies faxoniana</i>				
1984	12 (71)	31 (32)	1246 (5)	2272 (4)
1990	14 (13)	76 (25)		
1996	32 (5)	6778 (1)	2886 (<1)	3160 (<1)
<i>Betula utilis</i>				
1984	29 (67)	12 (55)	85 (18)	35 (33)
1990	142 (26)	197 (80)		
1996	833 (21)	566 (60)	93 (17)	85 (14)
Saplings				
<i>Abies faxoniana</i>				
1984	2 (0)	5 (50)	162 (0)	872 (2)
1990	2 (0)	5 (50)		
1996	2 (0)	5 (50)	166 (0)	930 (2)
<i>Betula utilis</i>				
1984	17 (59)	5 (0)	4 (50)	77 (0)
1990	15 (66)	5 (0)		
1996	14 (63)	5 (0)	4 (50)	81 (10)

The number in parentheses is the percentage of stems growing on a raised surfaces (e.g. logs, stumps, upturned root plates) rather than the forest floor. Bamboo flowered and died back in R1, R2, and R4, but not R3, in 1983.

the two species varied over the post flowering period, however. In 1990, there were more *B. utilis* (1.5–4.5-fold) than *A. faxoniana* seedlings.

Initial tree seedling density in plots R3 and R4, which had less bamboo and less change in bamboo abundance over the census period, was higher than in plots R1 and R2 (Tables 1 and 5). Seedling populations increased in these plots over the study period too (except small seedlings in R3), but less so (1.4–5-fold) than in R1 and R2. As in R1 and R2, the density increase was greater for *A. faxoniana* than *B. utilis*. In both 1984 and 1996, there were more *A. faxoniana* (>50-fold) than *B. utilis* seedlings.

Dwarf bamboos in the forest understory influenced the distribution of *A. faxoniana* but not *B. utilis* seedlings. In 1984, in all the forest plots, there was a negative association ($P < 0.01$, χ^2) between 3 m \times 3 m quadrats with $\pm 50\%$ mature bamboo cover and the presence of *A. faxoniana* seedlings. There was no such tendency ($P > 0.01$, χ^2) for *B. utilis*. The association between high bamboo cover and seedlings presence was the same in 1996, except in plot R4, which had very low bamboo seedling cover. In this plot, on that date, there was no association between high bamboo cover and presence of *A. faxoniana* seedlings.

The proportion of seedlings growing on raised surfaces was higher in plots with $\geq 68\%$ than $< 68\%$ bamboo cover in 1983 (i.e. R1 and R2 versus R3 and R4) (Table 5). Moreover, the proportion declined after the bamboo die-off (except small *A. faxoniana* in R1 and small and large *B. utilis* in R2). In all of the plots, *B. utilis* grew more frequently on raised surfaces than *A. faxoniana*. Sapling populations, especially of *A. faxoniana*, were larger (>30-fold) in the plots with lower (R3 and R4) than higher (R1 and R2) mature bamboo cover in 1983. This difference persisted over the study period (Table 5). In fact, there were few saplings (i.e. 10–19 ha^{-1}) in R1 and R2 on any census date. As for seedlings, saplings of *B. utilis* were proportionately more abundant than *A. faxoniana* on raised surfaces (except R2). Saplings only increased substantially over the study period in R4 and most new saplings were *A. faxoniana*. There was little change in sapling numbers in the other plots.

3.3. Gap plots

Seedling abundance in the gaps varied over the study period. In 1990, the density of small (*A. faxoniana*, *B. utilis*) and large (*B. utilis*) seedlings was higher ($P < 0.05$, Kruskal–Wallis *H*-test) than in 1985 (Table 6). Yet, by 1996, only large *B. utilis* seedlings had a higher density ($P < 0.05$, Kruskal–Wallis *H*-test) than at the beginning of the study in 1985. Overall, *B. utilis* seedling density increased more than that of *A. faxoniana* over the census period but not significantly so. In the gaps, the proportion of seedlings growing on raised surfaces was higher for *B. utilis* than for *A. faxoniana* and the proportion for both species declined between 1985 and 1996.

Table 6

Density of tree seedlings and saplings (mean \pm SE) in canopy gaps ($n = 31$) on three dates in an old-growth *Abies–Betula* forest, Wolong Natural Reserve, Sichuan, China

	1985	1990	1996
<i>Abies faxoniana</i> (m ⁻²)			
Small seedlings (<0.2 m tall)	0.01 ^a \pm 0.006 (67)	0.20 ^{ab} \pm 0.05 (11)	0.07 ^b \pm 0.02 (38)
Large seedlings (0.2–1.4 m tall)	0.01 \pm 0.006 (43)	0.07 \pm 0.03 (48)	0.07 \pm 0.02 (13)
Saplings (>1.4 m tall <4.0 cm dbh)	0.003 \pm 0.002 (52)		0.001 \pm 0.0006 (36)
<i>Betula utilis</i> (m ²)			
Small seedlings (<0.2 m tall)	0.02 ^a \pm 0.01 (100)	0.6 ^{ab} \pm 0.22 (52)	0.2 ^b \pm 0.06 (83)
Large seedlings (0.2–1.4 m tall)	0.03 ^a \pm 0.01 (94)	0.20 ^a \pm 0.07 (63)	0.24 ^a \pm 0.05 (29)
Saplings (>1.4 m tall <4.0 cm dbh)	0.004 \pm 0.001 (88)		0.006 \pm 0.002 (45)

Bamboo in the gaps flowered and died back in 1983. The number in parentheses is the % of stems growing on raised surfaces (e.g. logs, stumps, root plates). Mean values in a row with the same letter were different ($P < 0.05$, Kruskal–Wallis H -test, Fischer's L.S.D.).

Gap sapling populations also changed and the number of *B. utilis* increased and the number *A. faxoniana* declined over the census period (Table 6). The *A. faxoniana* decline was due mainly (2.5-fold greater) to sapling movement into the tree size-class rather than sapling mortality. There was no *A. faxoniana* seedling recruitment into the sapling size-class. The *B. utilis* saplings increase, in contrast, was the result of higher recruitment of seedlings into the sapling size-class (3.8-fold) than sapling mortality and sapling transitions into the tree size-class. As for seedlings, *B. utilis* saplings were proportionately more abundant than *A. faxoniana* on raised surfaces and the proportion for both species declined over the census period.

3.4. Overstorey–understorey relationships

Forest canopy density influenced pre- and post-flowering bamboo abundance in the plots with $\geq 40\%$ bamboo cover in 1983 (R1–R3). In these plots, quadrats with $\geq 50\%$ mature bamboo cover (1983), and $\geq 25\%$ bamboo seedling cover (1996), were positively associated ($P < 0.01$, χ^2) with more open forest canopy conditions. In the plot with sparse bamboo (R4) bamboo abundance and forest canopy cover were not associated ($P > 0.01$, χ^2).

Forest canopy density in the plots also influenced tree seedling distributions on the forest floor but the effect varied with understory bamboo abundance. In R4, which had low bamboo cover in 1984 and 1996, quadrats with either *A. faxoniana* or *B. utilis* seedlings were positively associated with more open forest canopy conditions ($P < 0.01$, χ^2). In the other plots,

which had higher bamboo cover, tree seedling distributions and forest canopy cover were not associated on any sampling date.

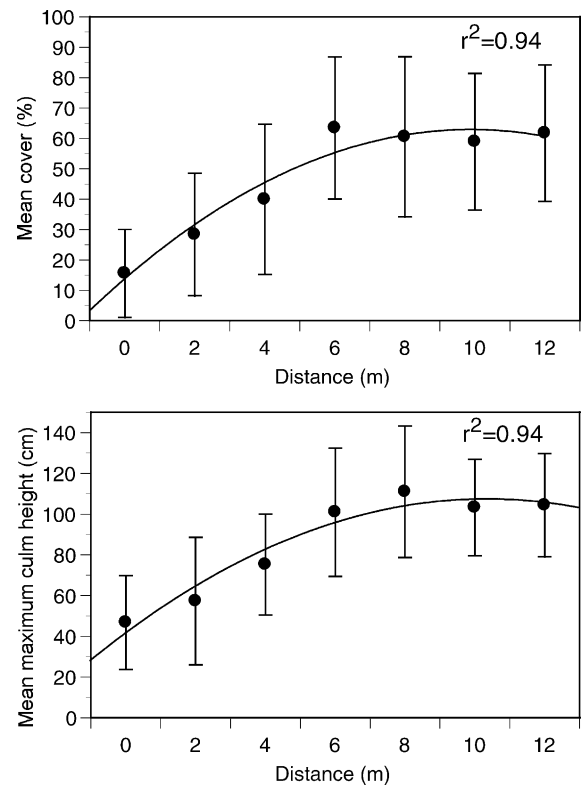


Fig. 2. Variation in mean (\pm S.D.) bamboo seedling cover and maximum culm height with distance from the bole of large (mean dbh 83.6 ± 13.0 cm) evergreen *A. faxoniana* trees ($n = 30$) into the surrounding deciduous canopy. The second order polynomial function fit to each variable was significant ($P < 0.01$).

In the gap plots, gap area influenced the density of *B. utilis* seedlings but the effect varied over the census period. In 1985, *B. utilis* seedling density was not associated with expanded gap area. In 1990 and 1996, however, expanded gap area and density of large *B. utilis* seedlings were positively associated ($r_s = 0.44$, 1990; $r_s = 0.40$, 1996, $P < 0.01$). In contrast, *A. faxoniana* seedling density was not associated with expanded gap area on any census date.

Bamboo seedling cover and height were different under evergreen and deciduous canopies. Culms were shorter (66.1 ± 5.2 cm versus 108.3 ± 7.0 cm) ($P < 0.05$, Kruskal–Wallis H -test) beneath evergreens and cover was lower ($49.8 \pm 7.8\%$ versus $64.8 \pm 8.3\%$) but not significantly so ($P > 0.05$, Kruskal–Wallis H -test). Mean above ground bamboo seedling standing crop (dry mass) (564.9 ± 81.6 g m⁻² versus 209.8 ± 29.1 g m⁻²) was also higher beneath deciduous than evergreen canopies ($P < 0.001$, Kruskal–Wallis H -test). Similarly, bamboo seedling cover ($r^2 = 0.94$, $P < 0.01$) and mean maximum culm height ($r^2 = 0.94$, $P < 0.01$) increased with distance from the bole of large (mean dbh 83.6 ± 13.0 cm) evergreen *A. faxoniana* into the surrounding deciduous canopy (Fig. 2).

4. Discussion

Forest understory plants play an important role in shaping long-term forest structure and dynamics by influencing seedling bank characteristics (Maguire and Forman, 1983; George and Bazzaz, 1999a; Abe et al., 2002). Seedlings and saplings populations in forests with dwarf bamboo understories in Japan (Franklin et al., 1979; Nakashizuka and Numata, 1982; Nakashizuka, 1989), Chile Veblen et al., 1981), Costa Rica (Widmer, 1998), and China (Taylor et al., 1996) are typically low. The lack of seedlings is probably caused by high tree seedling mortality beneath the nearly continuous bamboo canopy in the forest understory. In our study area, dwarf bamboos had a similar effect. Tree seedling and sapling were scarce in the understory of forests with $\geq 68\%$ mature bamboo cover compared to stands with less bamboo. Thus, understory bamboo abundance may influence long-term stand structure and development by suppressing tree recruitment.

The flowering and die-back of understory bamboos was an important regulator of tree seedling bank size. Bamboo die-off releases space-related resources, especially light (Taylor and Qin, 1988c), that can trigger synchronized tree regeneration. Demographic studies on tree seedlings in Japanese (Nakashizuka, 1988; Abe et al., 2001, 2002) and Chilean (González et al., 2002) forests with dwarf bamboos indicate that tree seedling establishment, survival, growth, and biomass production all increase after a bamboo die-back. Similarly, there were large increases in the size of the *A. faxoniana* and *B. utilis* seedling bank after bamboo die-back in our forests. On the other hand, where understory bamboos were sparse and died back, or mature and dense, there was less much less change in tree seedling bank size.

Forest canopy conditions at the time dwarf bamboos flowered in 1983 influenced the temporal pattern of post bamboo die-back seedling bank size. In gaps, the seedling bank was largest in 1990 and it declined by 1996. In fact, by 1996, only the density of large *B. utilis* seedlings in gaps was larger than initial seedling densities in 1985. Rapid recovery of the bamboo sward in gaps may have limited seedling establishment after 1990. In contrast, beneath forest, seedling banks were largest 12-years after bamboo die-back. Low light levels beneath forest, and additional shading from dense ranks of dead bamboo culms that persist for 3–6 years, may have delayed seedling establishment under forest compared to well lit gaps. Tree seedling emergence, establishment, and growth are stimulated by the higher soil temperatures and light levels found under dead bamboo in gaps than beneath forest (e.g. Abe et al., 2002). Higher rates of seed predation, or inter-annual variation in seed crop size, are probably not the cause of recruitment delay beneath forest. Forest and gap plots were near (< 1.0 km) each other and probably experienced similar seed rains and seed predation rates over the study period.

Forest canopy conditions also influenced post-flowering seedling bank composition. Beneath forest, the seedling bank increase was greater for *A. faxoniana* than *B. utilis* and *A. faxoniana* seedlings were several fold more abundant than those of *B. utilis* at the end of the study. The opposite was true beneath gaps. *Betula utilis* seedlings were several fold more abundant than those of *A. faxoniana*. Moreover, after bamboo die-

back, the size of the *B. utilis* seedling bank was positively correlated with gap area. There was no gap area correlation for the *A. faxoniana* seedling bank. In mixed conifer-broadleaf forests with *Betula* in east Asia (e.g. Kohyama, 1984; Nakamura, 1985; Yamamoto et al., 1995; Hiura et al., 1996), Europe (e.g. Ellenberg, 1988), and North America (e.g. White et al., 1985) *Betula* regeneration occurs mainly in gaps, and gap regeneration is an important mechanism contributing to the maintenance of species diversity in these forests. Similarly, in our study area, gap regeneration was important for the maintenance of *B. utilis*.

Dwarf bamboos seem to amplify the success of *B. utilis* regeneration in gaps. When gaps form above mature bamboos there are few seedlings or saplings in the forest understory that can fill the gap. *Betula utilis* is light seeded, establishes well on logs, root plates, and other raised substrates, and has a higher annual height growth rate in gaps than *A. faxoniana* (Taylor and Qin, 1992; Taylor et al., 1995). These life history traits favor gap capture by *B. utilis* because the dense bamboo reduces the advanced regeneration strategy used by *A. faxoniana* (Taylor and Qin, 1988b). Moreover, in gaps, the 12-year post-flowering period of lower bamboo abundance did not increase the success of *A. faxoniana* regeneration. Only *B. utilis* seedling density was higher in gaps at the end than at the beginning of the census period. On the other hand, in gaps without bamboo the seedling bank of *A. faxoniana* is well developed and mixed forests have much more *A. faxoniana* than *B. utilis* (Taylor and Qin, 1988a, 1988b; Taylor et al., 1995, 1996).

Patterns of bamboo abundance were also influenced by forest canopy conditions. Bamboo cover was higher beneath openings and these areas of higher bamboo cover, in turn, influenced tree seedling patterns. There was a negative association between areas of high bamboo cover and *A. faxoniana*, but not *B. utilis*, seedling distributions. *Betula utilis* regenerates more frequently than *A. faxoniana* on raised surfaces. Consequently, the distribution of *B. utilis* in the forest understory is strongly linked to the distribution and abundance of raised microsites on the forest floor which may be independent of bamboo abundance patterns. Microsite heterogeneity and interspecific differences in the ability of *B. utilis* and *A. faxoniana* to establish and grow on different seed beds appear to be important factors that contribute to their coexis-

tence in our forests, as they are for other tree species in dwarf bamboo forests (e.g. Nakashizuka, 1989; Takahashi, 1997; Narukawa and Yamamoto, 2002).

The time bamboos take to reach mature size after they die-back is an important factor controlling the length of the post die-back period of high tree seedling recruitment. Recovery of *Sasa* bamboos in Japanese forests takes 10–20 years (e.g. Nakashizuka, 1988; Makita et al., 1993). In our forests, culm height and bamboo cover had not yet recovered to pre-flowering levels and bamboo standing crop 12-years after die-back (mean = $387 \pm 54 \text{ g m}^{-2}$) was only 45% of that for mature stands (mean = $870 \pm 188 \text{ g m}^{-2}$) (Taylor and Qin, 1993). This suggests that *B. faxiana* takes 15–20 years to recover to full size after die-back, a period similar to *Sasa*.

The rate of bamboo recovery was spatially variable, however, and influenced by forest canopy density and composition. Recovery was faster beneath canopy gaps than beneath forest, and faster under a deciduous than evergreen canopy. In both cases, faster recovery is probably related to higher light levels that increase bamboo seedling growth rates. Annual direct and indirect sunlight is greater in canopy gaps than beneath forest (Canham et al., 1990). Light levels beneath deciduous trees are also higher in the spring, before leaf emergence, and in fall, after leaf abscission, than beneath evergreens. In Japan, *Sasa* bamboos have their period of highest carbon gain in deciduous forests during the spring and fall light phase (Lei and Koike, 1998). The greater dominance of *B. faxiana* seedlings under deciduous than evergreen canopies suggests a growth response of *B. faxiana* to variation in the light environment under deciduous trees that is similar to *Sasa*.

In our stands with dense bamboo, either seedling or mature, tree recruitment and mortality were not balanced. Over the study period, mortality exceeded recruitment, tree populations declined, and stands became more open. The population decline was greater for *B. utilis* than *A. faxoniana* because its mortality rate was two or more fold higher than *A. faxoniana*'s. The *B. utilis* BA loss rate also exceeded the gain rate, but stand level BA was static or increased slightly due to higher BA gain than loss for *A. faxoniana*. Similar tree population declines have been observed in Japanese conifer-broad-leaved forests where dwarf bamboos greatly impede tree regenera-

tion (Nakashizuka, 1991; Umeki et al., 1999). In our forests, the period needed for seedling to establish and grow to sapling size after a bamboo die-off is probably longer than the time interval covered by this study. Consequently, any influence of the post-flowering pulse of tree seedling establishment on tree recruitment and stand development is not reflected in our census data. Age-class peaks in Japanese forests that correspond with dates of bamboo flowering, however, suggest that high post-flowering tree seedling establishment and recruitment do influence forest structure and development over longer time scales (Nakashizuka and Numata, 1982; Peters et al., 1992). On the other hand, where bamboos were sparse recruitment of *A. faxoniana* seedlings into the saplings size-class and recruitment of saplings into the tree size-class more than compensated for tree mortality and both tree density and BA increased over the census period.

Tree mortality rates were also size-dependent, a pattern identified in some (e.g. Nakashizuka, 1991, Nakashizuka et al., 1992; Runkle, 2000; Miura et al., 2001) but not all (e.g. Lieberman and Lieberman, 1987; Greene et al., 1992) forests. Size-dependent mortality appears to be related to suppression and competitive effects on smaller stems, and to disturbance effects on large stems. Most small *A. faxoniana* and *B. utilis* stems died standing, a mode of death consistent with low growth and low levels of resources beneath the upper forest canopy. Larger *A. faxoniana* stems, however, were killed more often by stem snap or windthrow. Intermediate sized stems were less affected by either mortality process. At least over the study period, large stem mortality seems to be influenced by an interaction between the disturbance regime and tree size as in other temperate forests (e.g. Foster and Boose, 1992; Greene et al., 1992; Miura et al., 2001).

Understory bamboos strongly influenced patterns of tree regeneration and stand development in mixed *A. faxoniana*–*B. utilis* forests in southwestern China. Where bamboos were mature and dense, they impeded tree regeneration, especially of species with an advanced regeneration strategy. Consequently, during the mature phase of the bamboo lifecycle regeneration of species that seed in and are capable of establishing on raised surfaces are favored. This effect seems to be magnified in gaps as bamboos switch from the mature to die-off/building phase of its life cycle. Yet during

the die-off/building phase and beneath forest, tree species with advanced regeneration strategy regenerated more successfully than those that seed in. Thus, cyclic bamboo dominance, and forest canopy conditions interact with tree species' life history traits and promote tree species coexistence in old-growth forests in southwestern China.

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