Growth of bamboo *Fargesia qinlingensis* and regeneration of trees in a mixed hardwood-conifer forest in the Qinling Mountains, China

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Abstract

Gap characteristics and effects of gaps on plasticity of *Fargesia qinlingensis* and tree regeneration were studied under canopy, and in small, medium, and large gaps in a mixed hardwood-conifer forest in the Qinling Mountains, China. Gap formation was mainly tree snipping (40%). Gapmakers were dominated by *Betula albosinensis* and *Abies fargesii* (85%). Gap area ranged from 23.8 to 594.2 m² and averaged 178.4 m². In the canopy layer, 148 adult trees and 13 species were recorded. Gaps had an obvious effect on population parameters and morphological plasticity of *F. qinlingensis*. Large gaps had higher densities of dead culms, lower shoot percentages, and higher dead culm percentages, suggesting that intraspecific competition for resources was stronger in large gaps. Bamboo branch angle was larger under closed canopy, indicating a lower degree of self-shading, which may facilitate light acquisition and thus enhance plant growth. Tree composition in understory was different than in canopy. Shade-tolerant species (*Malus baccata*, *Acer maximowiczii*, and *Prunus pilosiuscula*) dominated the understory, while *B. albosinensis*, *A. fargesii*, and *Betula utilis* dominated the canopy. Tree species dominating under canopy were the same as in gaps, consisting of shade-tolerant canopy species and a few sub-canopy species. Tree seedling density and diversity were low in understory, implying an inhibitory effect (ecological filter) of dense culms on seedling establishment. Further, gap sizes occurring in the mixed hardwood zone were generally small and regeneration of shade-intolerant species was limited to the few larger gaps. Seedling density was higher in medium gaps than in large gaps and under canopy, largely due to two sub-canopy species (*M. baccata* and *P. pilosiuscula*). Density of *A. maximowiczii* was similar under canopy and in various sized gaps. Age structure showed that most saplings ≥14 years old were shade-tolerant *A. maximowiczii*. Results suggest that current dominance of *B. albosinensis*, *A. fargesii*, and *B. utilis* may be replaced by shade-tolerant species such as *A. maximowiczii*.

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1. Introduction

Bamboos have an extremely wide range of distribution, and grow in different habitats, from open environments to shaded forests (Soderstrom and Calderon, 1979). Relationships of gaps and bamboo understories have been studied in both tropical and temperate forests (Agata et al., 1985; Franklin et al., 1979; Nakashizuka and Numata, 1982a,b; Oshima, 1961; Schnitzer et al., 2000; Shidei, 1974; Taylor and Qin, 1988, 1989; Veblen, 1982; Veblen et al., 1977, 1981; Widmer, 1998) to understand the competition between bamboo taxa and forest taxa regeneration. Studies of the influence of canopy cover on pattern and performance of dominant understory bamboo species often show divergent, and sometimes contradictory, results, mainly due to differing habitat conditions (Veblen et al., 1977, 1979; Widmer, 1998). If water and nutrients in soil are in adequate supply, then light is probably the limiting factor controlling rate of growth and production of dry matter (Widmer, 1998). Due to their clonal life history, bamboos may optimize the efficiency of light use in their growth either by spreading (Whitmore, 1989) or by morphological plasticity (Widmer, 1998). In an effort to understand the regeneration of bamboo for giant panda habitat (*Ailuropoda melanoleuca* David), we were interested in the response of bamboo and tree seedlings to gaps in mixed hardwood-conifer forests in the Qinling Mountains, China.

It has been proposed that in forests where large-scale disturbances are rare, plant community composition is controlled by the creation of gaps and gap-phase regeneration
(Brokaw, 1985; Kneeshaw and Bergeron, 1998; Phillips and Gentry, 1994; Wright et al., 2003). In conventional tree-dominated gaps, advanced regeneration of long-lived species are present and are subsequently released. Pioneer species only establish in large gaps. Therefore, gap dynamics play an important role in the determination of floristic composition (Runkle, 1981, 1982; Whitmore, 1989). Regeneration in forest canopy gaps is thought to lead invariably to the rapid recruitment and growth of trees and the redevelopment of the canopy. However, in bamboo or liana-dominated gaps, tree seedling establishment and regeneration are inhibited due to the dominance of bamboo or lianas in the understory (Franklin et al., 1979; Nakashizuka and Numata, 1982a,b; Oshima, 1961; Schnitzer et al., 2000; Shidei, 1974; Taylor and Qin, 1988, 1989; Veblen, 1982; Veblen et al., 1977, 1981), a successional stalled-gap pathway (sensu Schnitzer et al., 2000). Reversion of gaps back to tall forest can be delayed for decades or longer by vigorous growth of understory plants (Taylor and Qin, 1988, 1989; Schnitzer et al., 2000).

Bamboos in temperate and tropical forests appear particularly effective in reducing tree seedling establishment and development, or inhibiting tree regeneration entirely, because of their rapid growth and high degree of dominance (Franklin et al., 1979; Nakashizuka and Numata, 1982a,b; Oshima, 1961; Shidei, 1974; Taylor and Qin, 1988, 1989; Veblen, 1982; Veblen et al., 1977, 1981; Widmer, 1998; Lusk, 2001). For example, Nakashizuka (1989) suggests that gap formation itself does not contribute substantially to the maintenance of pioneer tree populations in mixed hardwood-conifer forest in Japan due to the dominance of bamboo Sasa borealis that retards the establishment of pioneer species. Understory Chusquea bamboos often suppress the establishment of trees in Nothofagus forests in Chile (Veblen, 1982, 1989; Veblen et al., 1977, 1979, 1981) and in Costa Rican Quercus forests (Widmer, 1998). Taylor and Qin (1988, 1989) studied the regeneration patterns in old-growth Abies–Betula forests in Wolong giant panda reserve, China, and found that seedlings, saplings and young trees are scarce in stands where bamboo (Sinarundinaria fangiana) impedes tree regeneration. Tree regeneration can be improved by the death of bamboos after bamboo mass flowering in gaps (Abe et al., 2001; Holz and Veblen, 2006; Nakashizuka, 1987; Taylor and Qin, 1992; Taylor et al., 1995).

To date, canopy gap formation and subsequent regeneration have not been studied in the Qinling Mountains, although such successional knowledge is vital to the management of forests and giant panda habitat. Dependence between endangered giant pandas and the bamboo forests that provide both habitat and 99% of the panda’s diet is well documented (Liu, 2001; Long et al., 2004). Giant pandas are herbivorous carnivores that evolved as obligate bamboo grazers (Wei et al., 1999). Thus, the life history of the giant panda is directly related to the life histories of the bamboos it feeds upon, and the regeneration of bamboo is linked directly to the panda’s survival and conservation (Taylor and Qin, 1988). In this study, we examined response of Fargesia qinlingensis Yi and J.X. Shao and tree diversity and establishment under canopy and different sizes of gaps. We tested the hypothesis that tree density and biodiversity are higher in larger gaps, and we asked the following questions: (1) what are the characteristics of a natural gap? (2) do bamboo culms show morphological plasticity in their response to gap formation; (3) how does canopy and gap size affect tree seedling establishment and development to saplings? (4) what is the relationship between tree regeneration and bamboo growth?

2. Methods

2.1. Study site

The mixed hardwood-conifer forest we studied is in Foping National Natural Reserve (FNNR, 33°33′–33°46′N, 107°40′–107°55′E), located in the Qinling Mountains of Shaanxi Province, China. FNNR was built to protect endangered giant pandas. FNNR is in the northern edge of a subtropical area. Mean annual temperature is 11.5 °C; −0.3 °C in January and 21.9 °C in July. Precipitation averages 924 mm year −1 with 91% of annual rainfall occurring between April and October. Frost free days average 220.

The vegetation is diverse due to coexistence of both northern and southern Chinese taxa. Forest communities cover about 80% of FNNR, made up of generally four vegetation types along an elevation gradient: deciduous broad-leaved forests (<1500 m), mixed hardwood-conifer forests (1700–2800 m), coniferous forests (2400–2900 m), and interspersed shrublands and meadows (>2900 m).

Three bamboo species are distributed in FNNR. F. qinlingensis dominates at higher elevations (1700–3000 m) and Bashania fargesii (Camus) Keng and Yi dominates at lower elevations (900–1900 m). Fargesia dracocephala Yi (Masman) is restricted to a small area in southeastern FNNR. F. qinlingensis is giant panda’s only food resource during the summer season, and B. fargesii is giant panda’s main food resource in spring and winter seasons.

Like most other bamboos in tropical and temperate regions (Janzen, 1976; Gadgil and Prasad, 1984), F. qinlingensis is also a perennial monocarpic species which is known for its long period of vegetative growth followed by mast seeding; it has a flowering period of ca. 50 years (Tian, 1987). F. qinlingensis is a clump-forming bamboo with a robust pachymorph rhizome. Rhizome growth is the only way to spread ramets during flowering period. New shoots regenerate from rhizomes in May and June. F. qinlingensis can grow up to 3.6 m in height and 11 mm in basal diameter. F. qinlingensis is dominant in understory of mixed hardwood-conifer forests, giant panda’s summer habitat in FNNR.

2.2. Field methods

Eight parallel 100 m transects were located 80 m apart crossing perpendicular to slope contours in a mixed hardwood-conifer forest. Natural canopy gaps encountered along transects were recorded. A total of 28 gaps were encountered in the eight transects (800 m). In this study, canopy gap was defined as an
area >10 m² without any tree crown >15 m high, a definition following Nakashizuka (1989). At each canopy gap, gap-forming species (gapmakers, sensu Runkle, 1982) were identified to species and diameter at breast height (dbh) was measured to the nearest 0.1 cm. Gapmakers were then categorized as: tree standing dead, tree snapped, tree uprooted, branch fallen, or any combination of these modes following Dalling et al. (1998) and Nakashizuka (1989). Canopy height was estimated for each gap.

Areas of canopy gaps were measured as expanded gaps which are commonly used in literature (e.g., Runkle, 1981, 1982; Clinton et al., 1993; Kneeshaw and Bergeron, 1998; Shen, 2002). Expanded gap consists of the canopy gap and the area extending to the stems of canopy trees that circumscribe the canopy gap (Runkle, 1982). One benefit of expanded gap is that it includes area directly and indirectly influenced by the canopy opening (Runkle, 1982). Most gaps were roughly elliptical; therefore, gap area was estimated by using an elliptical formula. Percentage of the forest in canopy opening was calculated following Runkle (1985) as the proportion of the total distance of the transect in canopy opening divided by the length of the transect (see Kneeshaw and Bergeron, 1998). Besides gaps encountered in transects, seven understory sites were randomly laid out under intact canopy along transects. A total of 26 gaps in the first seven transects and seven canopy sites were sampled. The 33 sites were divided into four groups: seven canopy sites, nine small gaps (78.18 ± 10.90 m²), nine medium gaps (142.10 ± 3.77 m²), and eight large gaps (331.95 ± 55.20 m²) based on gap size. Canopy density in each gap and canopy site was measured by using forest spherical densitometer (O’Brien, 1989).

Two 1 m wide transect belts were established across each gap and canopy site. Each transect was then divided into 1 m × 1 m quadrats. In 20 quadrats in every single gap and canopy site, all bamboo culms (ramets) were counted. In five randomly chosen quadrates in each gap and site, height of each bamboo ramet was measured to the nearest 1 cm and basal diameter of each ramet was measured to nearest 0.01 mm. We also measured several other morphological parameters of mature ramets, including number of nodes, number of branches, clear length (i.e., the distance between the ramet base and the first branch, defined by Widmer, 1998). Bamboo ramets were divided into four categories: dead, senescent/diseased, mature (ramet stem > 1 year old), and shoot (ramet stem < 1 year old) based on criteria of Widmer (1998). Within the 20 quadrats in each gap and canopy site, all tree seedlings and samplings were identified to species and ages were estimated by counting bud scars.

We used a plotless method to investigate forest composition. Five points were located at 25 m intervals along each transect (except transect 1 where only two points were located), resulting in a total of 37 points. In each quadrant with transect as one axis, adult tree (dbh > 5.5 cm and height > 4 m) nearest to the point was identified to species, and dbh was measured to the nearest 0.1 cm. A total of 148 trees were measured. All field work was performed between 5 and 20 August 2004.

2.3. Statistical analysis

We used one-way ANOVAs to test for effect of gap size (canopy, small gap, medium gap, and large gap) on bamboo culm density, culm percentage, culm growth parameters, and tree seedling diversity and density. If there was a significant effect, a multiple comparison Tukey test was used to determine significant differences among the four treatments. Percentage data were arcsin square root transformed prior to analysis to meet the assumptions of normality and homogeneity of variance. Analysis was performed using the GLM procedure in SAS/STAT (SAS, 2004). In addition, effect of gap size on species frequencies and tree age structure were tested by using chi-square tests, performed by using the FREQ procedure in SAS/STAT (SAS, 2004). Differences were considered significant at $P < 0.05$ level.

3. Results

3.1. Gap formation and characteristics

The percentage of forest in canopy opening (the proportion of the total distance of transect in canopy opening divided by the length of transect) was 37.75%. Among the 25 gaps with gapmakers, the mechanism of gap formation was mainly tree snapping which accounted for 40% of total gap formation, followed by tree uprooting (20%), uprooting + snapping (16%), and standing dead + snapping (16%). Few standing dead tree (4%) and branch falling + snapping (4%) occurred (Table 1). Of the 47 gapmakers found, 85% were Betula albosinensis Burk. or Abies fargesii Van Tieghem. Five other gap-forming species accounted for only 15% of the makers (Fig. 1a).

Expanded gap area averaged 178.4 ± 26.9 m², ranging from 23.8 to 594.2 m² with median 139.2 m². Of the 26 gaps, 77% were > 200 m² and 85% were < 300 m². Canopy density ranged from 94 to 57% under closed canopy and in the three sizes of gaps (Table 2). Gap size was highly associated with canopy density (Pearson correlation coefficient, $N = 28, r = 0.85, P < 0.0001$). In addition, gap area and canopy density were significantly different among the four types of gaps (Table 2).

3.2. Bamboo growth

Total bamboo density tended to increase from canopy to large gaps, but the difference was not significant (Table 2).

<table>
<thead>
<tr>
<th>Gap formation</th>
<th>Number</th>
<th>Percent (%)</th>
</tr>
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<tbody>
<tr>
<td>Standing dead tree</td>
<td>1</td>
<td>4</td>
</tr>
<tr>
<td>Tree snapped</td>
<td>10</td>
<td>40</td>
</tr>
<tr>
<td>Tree uprooted</td>
<td>5</td>
<td>20</td>
</tr>
<tr>
<td>Uprooted + snapped</td>
<td>4</td>
<td>16</td>
</tr>
<tr>
<td>Standing dead + snapped</td>
<td>4</td>
<td>16</td>
</tr>
<tr>
<td>Branch fallen + snapped</td>
<td>1</td>
<td>4</td>
</tr>
</tbody>
</table>

Table 1
Mechanisms of gap formation in a mixed hardwood-conifer forest in the Qinling Mountains, Shaanxi Province, China
Mature culm density had the same trend, but again the difference was not significant. Dead culm density was highest in large gaps, and smallest in medium gaps (Table 2). Shoot basal diameter had a significant trend of increase from canopy to large gaps (Table 2). Among the six ramet morphological parameters, branch angle was significantly different among gaps types, with canopy sites having the highest branch angle (Table 2).

3.3. Forest canopy composition

In the canopy layer, 148 adult trees (from the 37 points of eight transects) and 13 species were recorded. Among them, three species, B. albosinensis, A. fargesii, and Betula utilis D. Don., dominated the canopy community, accounting for 71% of total canopy trees. Another 10 species accounted for the remaining 29% of canopy tree species (Fig. 1b). The three main canopy trees accounted for 88.6% of total basal area (Fig. 1c).

3.4. Tree regeneration

Eight tree species were found in the understory, and among them six were canopy trees. The understory was dominated by Malus baccata (Linn.) Borkh., Acer maximowiczii Pax., and Prunus pilosiuscula (Schneid.) Koehne. They accounted for 81.8, 91.0, 95.7, and 84.0% under canopy, in small gaps, medium gaps, and large gaps, respectively. However, these three species only accounted for 16.2% of main canopy trees. The three main canopy tree species B. albosinensis, A. fargesii, and B. utilis accounted for 0, 1.25, 1.96, and 3.45% of the tree species in understory under canopy, in small gaps, medium gaps, and large gaps, respectively (Fig. 2).

Although seedling richness varied from 1.75 to 3.11 species gap⁻¹, it was not significantly different among four gap sizes (Table 2). Seedling density ranged from 0.17 to 0.49 seedlings m⁻². Gap size significantly affected tree seedling density, with medium gaps having highest seedling density (Table 2). Density of seedlings of M. baccata + A. maximowiczii + P. pilosiuscula was significantly different among four gap types, with medium gaps having greatest density, mainly due to the significant difference of M. baccata + P. pilosiuscula. Gap size had no significant effect on density of A. maximowiczii (Table 2). Density of three main canopy tree species (B. albosinensis, A. fargesii, and B. utilis) was extremely low; 0, 0.0062, 0.0110, 0.0063 seedling m⁻² under canopy, in small gaps, medium gaps and large gaps, respectively.

Gap size had a significant effect on tree species frequencies in understory (chi-square test, $X^2_{21} = 235.3$, $P < 0.0001$, Fig. 2). Only five tree species established seedlings in understory of canopy. Canopy understory had fewer M. baccata + A. maximowiczii + P. pilosiuscula (81.8%) than gaps (92.5, 97.1, and 89.7% in small gap, medium gap, and large gap, respectively), and more Acer erianthum Schuer. + Sorbus hupehensis Schneid. (18.2%) than gaps (2.5, 1.0, and 6.9% in small gap, medium gaps, and large gaps, respectively, Fig. 2).

Gap size had a significant effect on age structure of tree species in understory (chi-square test, $X^2_{39} = 62.2$, $P = 0.01$, Fig. 3). Age class distribution of seedlings and saplings showed that 0, 2.67, 1.98, and 20.69% seedlings were ≥14 years old.

Fig. 1. Percentage of gap-forming species from 25 gaps (a) and percentage of species (b) and percentage of basal area (c) of canopy tree composition in a mixed hardwood-conifer forest in the Qinling Mountains, Shaanxi Province, China.
under canopy, in small gaps, medium gaps, and large gaps, respectively. Tree saplings >14 years old included *M. baccata*, *Am = Acer maximowiczii*, *Pp = Prunus pilosiuscula*, and *S. hupehensis*. None of these species were a component of the forest canopy.

4. Discussion

In this study, 22 out of 26 (84.6%) natural gaps in mixed hardwood-conifer forest were <300 m², which supports other research showing smaller gaps (<300 m²) dominate natural disturbance regimes in many temperate and tropical broad-leaved forests (Brokaw, 1985; Clinton et al., 1993; Runkule, 1985; Sipe and Bazzaz, 1994). Expanded gap area ranged from 23.8 to 594.2 m² in this study and averaged 178.4 m², slightly smaller than mixed-oak forests in southern Appalachians where gap areas range from 40 to 850 m² and average 239 m² (Clinton et al., 1993) and coniferous forests in another giant panda habitat in Wanglang Reserve in China, which range from 86 to 675 m² and average 232 m² (Shen, 2002). Percentage of the forest in canopy opening was 37.8%, which fell within the range (22.1–47.0%) in Great Smoky Mountains National Park of North Carolina and Tennessee (Runkule, 1982).

Of the canopy gaps in this study, 76% were snaps or snap-related types, inconsistent with the mechanism of canopy gap formation in mixed-oak forests in southern Appalachians where 74% are standing dead types (Clinton et al., 1993). Uprooting accounted for 20% of canopy gaps, consistent with *Abies-* *Picea* forests (24%) in Wanglang Reserve in China (Shen, 2002).

In the mixed hardwood-conifer forest in the present study, *Betula* (56%) and *Abies* (25%) dominated the canopy. Among gapmakers, *B. alboinensis* and *A. fargesii* accounted for 60 and 26%, while *A. maximowiczii* only accounted for 4% (currently 8% of the canopy density), suggesting a strong successional trend from the second-growth *Abies–Betula* dominated forest to shade-tolerant *Acer*-dominated forest. Trees of the *Betula* genus regenerate best following large-scale, exogenous disturbances (Hibbs, 1983; Peterson and Pickett, 1995; Walters and Reich, 1996), regenerating from the seed bank (White, 1991). While *Betula* species can serve as gap fillers, their ability for regeneration in gaps decreases as the forest ages (Kneeshaw and Bergeron, 1998). Thus, current forest composition suggests historical-large-scale disturbance.

The effect of gaps on bamboo population and plasticity has been studied in other bamboo species, such as *Chusquea culeou* (Schlegel, 1991), *Chusquea talamancensis*, *Chusquea tomentosa*, and *Chusquea foliosa* (Widmer, 1998), and *Sasa* species (Kawahara, 1987). Morphological responses of bamboos to gaps are variable, depending on taxa and site conditions. In this study, gaps had an obvious effect on both population parameters and morphological plasticity of *F. qinlingensis*. Population parameters showed that large gaps had higher densities and percentages of dead culms and lower percentages of shoots, with larger shoot diameters. One explanation is that increased...
Fig. 2. Percentage of tree seedlings and saplings in understory under canopy (a), in small gap (b), medium gap (c), and large gap (d) in a mixed hardwood-conifer forest in the Qinling Mountains, Shaanxi Province, China.

Fig. 3. Tree seedling (<13 years old) and sapling (>14 years old) age structure under canopy (a), in small gap (b), medium gap (c), and large gap (d) in a mixed hardwood-conifer forest in the Qinling Mountains, Shaanxi Province, China.
light led to maturation and self-thinning of the bamboo stand, resulting in fewer individuals of greater size. However, density of all culms, albeit not significant, showed an increasing trend with increasing gap size. Another possible explanation is that intraspecific competition for resources was stronger in large gaps, which was the case for two bamboos, C. talamancensis and C. tomentosa, in oak forests in Costa Rica (Widmer, 1998). Percentage of dead culms was also high under canopy, likely due to lower levels of light created by dense bamboo ramets, tree seedlings and saplings in the understory, and closed canopy (i.e., interspecific competition). Most bamboos do not tolerate full shade, resulting in this study with the lowest density of new shoots having the smallest diameters under canopy.

Plants often respond plastically to light differences in gap and shade environments (Osada et al., 2003). Species capable of Architectural plasticity are considered more successful across varying environmental conditions (Sipe and Bazzaz, 1994), an especially important trait for bamboo that is monocarpic and flowers at long intervals (e.g., 50 years for F. qinlingensis, Tian, 1987). Bamboos optimize the efficiency of light use in their clonal growth by spreading (Whitmore, 1989) or by morphological plasticity (Rao et al., 1990; Widmer, 1998). Our study showed that the phenotypic plasticity of F. qinlingensis was reflected in culm branch angle and new shoot diameter. Branch angle appeared larger under closed canopy, yielding a lower degree of self-shading, which is also observed in Elatierospermum tapos under shading conditions (Osada et al., 2003). Larger branch angle facilitates light acquisition and thus enhances plant fitness (De Kroon and Hutchings, 1995; Hutchings, 1998). A gap effect on culm branching pattern is also shown in C. tomentosa, which develops more branches in closed canopy than in gaps in order to exploit favorable light patches (Widmer, 1998). F. qinlingensis shoot diameter was larger in medium gaps and large gaps. Size of new shoots is determined by light when there is an adequate supply of water and nutrients (Widmer, 1998). The above data suggest light is a limiting factor on bamboo growth in the Qinling Mountains, and gaps favor bamboo growth. However, competition from tree species in the understory must also be considered.

Density and diversity of tree seedlings were low in closed canopy and all gap sizes in mixed hardwood-conifer forests in FNNR, implying the inhibitory effect of dense bamboo culms on seedling establishment. Similar inhibitory effects of bamboos on tree regeneration have been reported in other forests in Chilí (Veblen, 1982; Veblen et al., 1977, 1981), Japan (Oshima, 1961; Shidei, 1974; Franklin et al., 1979; Nakashizuka and Numata, 1982a,b), and Sichuan Province of China (Taylor and Qin, 1988, 1989). The inhibitory effect results from the rapid growth and large biomass of bamboos. For example, Taylor and Qin (1988, 1989) report that lack of Abies faxoniana regeneration over the last 50 years is due to dense S. fangiana understory (as high as 70%) which reduces seedling establishment. Veblen (1982) reports that, in the forests of south-central Chile, dense bamboos C. culeou and Chusquea tenuiflora suppress establishment and development of Nothofagus seedlings, due to low light intensities beneath bamboo and competition for other resources. Sasa bamboos form dense undergrowth in the deciduous beech and coniferous forests in Japan, which also retard tree regeneration (Oshima, 1961; Shidei, 1974). Different to the traditional belief that woody species diversity increases with gap size (Runke, 1981, 1982), gap size had no effect on tree diversity in the understory of gaps in this study, and density appeared greatest in small and medium gaps. Stronger inhibitory effects in large gaps should not be surprising in consideration of the greater density of culms in large gaps, as described above.

The inhibitory effect of bamboo culms was more obvious for seedlings and saplings of canopy trees. Three main canopy tree species (B. albosinensis, A. fargesii, and B. utilis) were lacking in understory in all gap types and under canopy. Instead, the understory seedling composition was dominated by three shade-tolerant species (M. baccata, P. pilosiuscula, and A. maximowiczii). Seedling and sapling densities were higher in medium gaps than in large gaps and under canopy. Two sub-canopy species (M. baccata and P. pilosiuscula) largely attributed to the difference, while density of canopy tree species A. maximowiczii remained stable among four gap types. Our results were consistent with those of Nakashizuka (1989), who finds seedling communities under dense bamboo in gaps consist of a low diversity of shade-tolerant species in a mixed hardwood-conifer forest in Japan. Our data support the premise that understory communities act as ecological filters of canopy tree regeneration (George and Bazzaz, 1999). The bamboo understory favors shade-tolerant taxa (e.g., Acer) and filters out shade-intolerant taxa (e.g., Betula), leaving mostly shade-tolerant species able to respond to gaps in the canopy.

The gap partitioning hypothesis suggests that species differ in their aecological responses along the gap-understory microenvironmental gradient such that species will show distinct preferences for gaps of different size (Ricklefs, 1977; Sipe and Bazzaz, 1994). Indeed, gradients of gap size have been proposed as important elements in determining the composition of gap-filling species (Kneeshaw and Bergeron, 1998; Whitmore, 1989). The partitioning of gaps and their maintenance of tree diversity may function in bamboo forests too (e.g., Abe et al., 2002; Taylor and Qin, 1988), but we found no evidence in FNNR. Contrarily, species dominating under canopy were the same as in gaps, consisting of shade-tolerant canopy species and a few sub-canopy species, with gaps only releasing their growth and hastening succession. Age structure showed that most seedlings ≥14 years old were shade-tolerant A. maximowiczii, a result of the bamboo understory acting as an ecological filter. Closed canopy forests in FNNR had almost no advanced regeneration of shade-intolerant species. Saplings of shade-tolerant species grow to maturity through repeated experience of release from shade by canopy openings (Osada et al., 2003). Further, gap sizes occurring in the mixed hardwood zone were generally small, with 62% falling below the minimum estimated 150 m² necessary for establishment of pioneer species (Brokaw, 1985; Runke, 1981; Whitmore, 1982). Thus, regeneration of shade-intolerant species was limited to the few larger gaps, and, as we have already discussed, seedlings attempting to establish in the larger gaps were under strong competition from bamboo, already
established in the understory and released by the canopy gap. This scenario was similar to liana-dominated gaps (Schnitzer et al., 2000). Results suggest the current overstory dominance of *B. albosinensis*, *A. fargesii*, and *B. utilis* may be replaced by shade-tolerant species such as *A. maximowiczi*.

Canopy tree seedlings may be enhanced by larger scale disturbances such as fire and bamboo die-off following mass flowering that increase space-related resources, especially light, and initiate a period of regeneration (Franklin et al., 1979; Makita, 1992, 1996; Taylor et al., 1995; Veblen, 1982). For example, regeneration of *Fagus crenata*, a canopy dominant in Japanese temperate forests, seems to occur only after *Sasa palmate* flowers and dies in the understory (Nakashizuka and Numata, 1982a,b). Abe et al. (2002) report that the dominance and died back cycle of *Sasa* contributes to species diversity in an old-growth forest dominated by dwarf bamboo *Sasa kurilensis*. Without such large scale disturbances in FNNR, forests will likely succeed to dominance by *Acer* species.

5. Implication for giant panda habitat management

In this study, we showed that tree regeneration was lacking in the understory of mixed hardwood-conifer forests in the Qinling Mountains due to the inhibitory effects of dense bamboo *F. qinlingensis* in the understory and closed canopy forest, which may have significant effects on giant panda habitat. Mixed hardwood-conifer forests are giant panda’s summer habitat in the Qinling Mountains, where they spend about half the year from May to October (Pan et al., 1988). Large conifers, typical of older stands, provide cover and critical habitat (e.g., maternity dens) for panda (Taylor and Qin, 1989). Panda abundance in subalpine forest habitats may therefore be linked to forests with certain structural characteristics (e.g., bamboo and large hollow conifers). Thus, preservation of current panda populations may require maintenance of forests with these structural characteristics (Taylor and Qin, 1989), and the management of mixed hardwood-conifer forests should focus on the regeneration of main canopy tree species, especially *Abies*. A practical method could coordinate artificial gap formation and clearing of bamboo in medium gaps which improve tree seedling establishment and regeneration in mixed hardwood-conifer forests.

6. Conclusions

Of the canopy gaps in the mixed hardwood-conifer forest, 85% were smaller than 300 m² and 76% were snaps or snap-related types. *Betula* and *Abies* dominated the canopy layer, and were also the main gapmakers. Current forest composition suggests historical large-scale disturbance.

Population parameters of *F. qinlingensis* showed that large gaps had higher densities and percentages of dead culms and lower percentages of shoots. The phenotypic plasticity of *F. qinlingensis* was reflected in culm branch angle and new shoot diameter. Branch angle appeared larger under closed canopy, yielding a lower degree of self-shading; shoot diameter was larger in medium gaps and large gaps, suggesting a light determination.

Density and diversity of tree seedlings were low in closed canopy and all gap sizes, implying the inhibitory effect of dense bamboo culms on seedling establishment. The inhibitory effect was more obvious for seedlings and saplings of canopy trees. The bamboo understory favored shade-tolerant taxa (e.g., *Acer*) and filtered out shade-intolerant taxa (e.g., *Betula*), leaving mostly shade-tolerant species able to respond to gaps in the canopy. We found no evidence of gap partitioning by species. In summary, without large scale disturbances such as fire or bamboo mast-flowering in FNNR, forests will likely succeed from the second-growth *Abies-Betula* dominated forest to shade-tolerant *Acer*-dominated forest.

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