

# Regeneration patterns and tree species coexistence in old-growth *Abies–Picea* forests in southwestern China

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## Abstract

We analyzed the population structure (size, age, spatial patterns) and radial growth patterns of *Abies faxoniana* Rehder & Wilson, *Picea purpurea* Mast., and *Betula* sp. to investigate the role of dwarf bamboo abundance, gap disturbance, and species life history on the coexistence of canopy dominants in old-growth forests in the Wang Lang Natural Reserve in southwestern China. Four stands were sampled with a single large plot (0.4–0.5 ha). There were fewer tree seedlings and saplings in the two plots with a dense bamboo understory, and *A. faxoniana* seedlings and saplings were much more abundant than those of *P. purpurea*. *Picea purpurea* and *Betula* sp. seedlings established more frequently on raised surfaces than those of *A. faxoniana*. Seedling density of *A. faxoniana*, and *B. utilis* was also higher beneath open than closed canopy conditions in the plots with little bamboo. Young *A. faxoniana* and *Betula* sp. trees were clumped at small to intermediate scales (25–900 m<sup>2</sup>), which are scales of clumping consistent with past regeneration in canopy gaps. Frequent peaks in radial growth releases in the canopy trees in the plots suggest a prevailing regime of small-scale gap disturbances. In each plot, *A. faxoniana* tree density and basal area was greater than that of *P. purpurea*. *Picea purpurea* trees were present in a wide range of age-classes in each plot indicating a pattern of intermittent regeneration in each stand for at least 500 years. In contrast, *Abies faxoniana* were abundant in age-classes <250 years, and few *A. faxoniana* were >350 years old. *Betula* sp. were mainly <120 years old. *Betula* sp. and *P. purpurea* preferred different seed-beds than *A. faxoniana* for establishment and regeneration of *A. faxoniana*, and especially *Betula*, is associated with gaps. Longevity and high survivorship are key life history traits of *P. purpurea* that prevent its replacement by *A. faxoniana*. In Wang Lang, stable coexistence is maintained by differences in species regeneration niche, species demographic characteristics, and species responses to the gap disturbance regime.

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## 1. Introduction

In a heterogeneous forest environment differences in species life histories play an important role in promoting species coexistence (Schmida and Ellner, 1984; Nakashizuka, 2001). For example, the establishment, growth, and survival of different species of tree seedlings are known to vary with forest floor microsite heterogeneity caused by disturbance or the influence of overstory or understory plants (Beatty and Stone,

1986; Nakashizuka, 1989; George and Bazzaz, 1999a, 1999b; Mori and Takeda, 2004). In turn, the differential success of species to establish on the forest floor, on logs, or in patches of understory plants is thought to play a key role in maintaining tree species diversity in old-growth temperate forests (Duncan, 1991; Takahashi, 1994; Umeki and Kikuzawa, 1999; Mori et al., 2004; Taylor et al., 2004). Development of seedlings and saplings into adult trees is subsequently influenced by tree-fall gaps that create further environmental heterogeneity (Canham et al., 1990) and a variable response among species that fill the gap (Runkle, 1981; Canham, 1988, 1989). Gaps localize formation of tree patches that develop from seedlings already established on the forest floor (re-organization) or from new arrivals (new establishment) (Marks, 1974). Species that fill gaps by seeding in, or from seed buried in the soil, often have

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different height growth rates, shade tolerances, seed weights, dispersal vectors, and demographic parameters than those species that fill gaps from a pool of tree seedlings or saplings on the forest floor at the time of gap formation (Canham, 1988, 1989; Nakashizuka, 1989, 2001; Abe et al., 2002; Mori et al., 2004). Furthermore, conditions for tree growth and survival in the understory change continuously as patches of regeneration form, develop, and eventually fill canopy openings. Consequently, temporal and spatial patterns of regeneration are influenced by heterogeneous conditions in both the forest canopy and on the forest floor (Veblen et al., 1977; Mori and Takeda, 2004; Taylor et al., 2004).

In some forests, understory plants are thought to play an important role in shaping forest structure and canopy composition by differentially influencing tree seedling establishment and growth (Ehrenfeld, 1980; Taylor and Qin, 1988a; George and Bazzaz, 1999a, 1999b; Takahashi and Kohyama, 1999; Gonzalez et al., 2002). In Japanese (Franklin et al., 1979; Nakashizuka, 1987), Chilean (Veblen et al., 1981), and Chinese (Taylor and Qin, 1988a, 1988b; Tang and Oshawa, 2002) forests where understory bamboos achieve a high degree of dominance, bamboos impede tree seedling establishment—especially of species that prefer to establish on the forest floor (Taylor and Qin, 1988a, 1989, 1992; Takahashi, 1994, 1997). Seedlings, saplings, and small trees in these forests are often scarce and concentrated on raised microsites (logs, buttresses, root plates) above the forest floor where competition between seedlings and bamboos is diminished (Suzuki et al., 1987; Taylor and Qin, 1988a; Nakashizuka, 1989; Takahashi, 1994, 1997; Hiura et al., 1996). Thus, understory bamboos can influence canopy diversity by regulating the proportional abundance of species that fill gaps from a pool of advanced regeneration on the forest floor or from species that regenerate on raised microsites (Taylor and Qin, 1988a, 1988b, 1992; Takahashi, 1994, 1997; Abe et al., 2002; Taylor et al., 2004).

In northern Japan, subalpine forests have a mixed canopy of evergreen *Abies* and *Picea*, and deciduous *Betula* (Oshima et al., 1958; Suzuki et al., 1987; Hiura et al., 1996; Takahashi, 1997; Narukawa and Yamamoto, 2001). Dwarf bamboos (*Sasa* sp.) dominate the forest understory on some sites and they are thought to play a key role in maintaining the mixed forest canopy of *Abies sachalinensis* (Fr. Schm) and *Picea glehnii* (Fr. Schm) Masters. *Picea glehnii* seedlings and saplings are present in the forest understory but in low numbers and they occur almost exclusively on elevated microsites (logs, mounds, root buttresses) above the forest floor. *Abies sachalinensis* seedlings and saplings, in contrast, are abundant and they occur both on the forest floor and on raised surfaces, preferring the latter (Takahashi, 1994, 1997; Hiura et al., 1996). In Japanese subalpine forests *Picea* are longer lived than *Abies* (Suzuki et al., 1987; Hiura et al., 1996; Miyadokoro et al., 2004), as they are in *Abies–Picea* forests in North America (White et al., 1985; Aplet et al., 1988). *Picea* are also thought to have a lower mortality rate than *Abies* and this is supported by short-term (<10 years) observations on marked populations in Japanese forests (Mori et al., 2004). Thus, in stands where bamboos

occupy the forest floor, regeneration is mainly restricted to elevated surfaces and the greater longevity and lower mortality for *P. glehnii* is thought to promote stable coexistence despite higher fecundity for *A. sachalinensis* (Suzuki et al., 1987; Hiura et al., 1996; Takahashi, 1997; Miyadokoro et al., 2004). In stands where understory bamboos are sparse or absent, the more fecund *A. sachalinensis* is thought to eventually exclude *P. glehnii* because *A. sachalinensis* regeneration on the forest floor is abundant and is more successful than it is on elevated surfaces (Takahashi, 1997). On the other hand, deciduous *Betula* is maintained by regeneration in gaps made by small-scale canopy disturbances such as tree-falls (Kohyama, 1984; Nakamura, 1985; Yamamoto et al., 1995; Hiura et al., 1996).

In northern Sichuan, China, dwarf bamboos (*Fargesia denudata*) (species authorities are given in Table 4) dominate the understory of old-growth mixed *Abies faxoniana–Picea purpurea* forests (Wang, 1961; Taylor et al., 1996). Where dwarf bamboo cover is high, tree seedlings and saplings are scarce and they occupy raised surfaces where tree seedling competition with bamboos would be reduced. Aggregations of saplings and small trees are common in the forest understory and suggest that regeneration in old-growth stands occurs in canopy gaps produced by the periodic death of one or a few canopy trees. Standing dead, snapped, and uprooted trees are common structural features of old-growth *Abies–Betula* and *Abies–Picea* stands in southwestern China (Taylor and Qin, 1988a, 1988b; Taylor et al., 1995, 1996). The structural and compositional features of *Abies–Picea* forests in Sichuan are similar to those reported for *Abies–Picea* forests in northern Japan (Suzuki et al., 1987; Hiura et al., 1996; Takahashi, 1994, 1997; Takahashi and Kohyama, 1999) and dwarf bamboos may interact with the life history traits of *Abies* and *Picea* to promote their coexistence in old-growth forests in southwestern China. In this study, we investigate the role of bamboo dominance and canopy gaps on forest structure and composition to determine if regeneration patterns and mechanisms of species coexistence in *Abies–Picea* forests in southwestern China are similar to those in Japanese forests. We identified regeneration patterns by analyzing the age structure, size structure, and spatial pattern of tree populations in old-growth stands.

## 2. Study area

Old-growth *P. purpurea–A. faxoniana* forests were studied in the Min Mountains in the Wang Lang Natural Reserve (31°N, 103°10'E), on the eastern edge of the Tibetan Plateau in north-central Sichuan, China. Elevations in the reserve range from 2300 to 5089 m. The terrain is steep, deeply dissected, and complex. Limestone is the most common parent material in the reserve. Soils vary in depth from shallow (<30 cm) to deep (>100 cm) and limestone is the main parent material in our study area. Soils that support subalpine forest are classified (Chinese system) as mountain brown dark coniferous forest soils. Soils beneath forest similar to those sampled in Wang Lang, 200 km south in the Qionglai Mountains, have the following properties: pH (3.9), NO<sub>3</sub> (20.6 ppm), P (58.5 ppm), K (183.5 ppm) (Taylor and Qin, 1988c). Scars on mountain

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