

# Gap regeneration of shade-intolerant *Larix gmelini* in old-growth boreal forests of northeastern China

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**Abstract.** Stand mapping and vertical and oblique tree crown projections were used to study gap characteristics and gap effects on the regeneration and stand development of *Larix gmelini*. The hypothesis is that waves of advance *Larix* regeneration are recruited into the canopy layer following the creation of canopy openings. In old-growth *Larix* forests of the northern Da Xingan Ling Mts., at 52 °N, obliquely projected gaps (OPG) begin at a distance of 60 - 80 % of the canopy tree height from the southernmost stems bordering the gap and thus the OPGs may extend beyond the northern boundaries of the vertically projected gaps (VPG). Changes in the environment and resource availability in the OPG result in increased *Larix* sapling survival. Due to a greater incidence of light, 10 - 30 yr old OPG saplings were more abundant than saplings in either a near-oblique projected gap (NOPG) or in the shadow of obliquely projected crowns (SOPC). The survival of saplings more than 30-yr old was highest when they were found in the OPG of one canopy opening and the VPG of another. This means that, following recruitment into an OPG, saplings then require the space found in a VPG to permit growth into the canopy. Thus, various-sized gaps contribute to the survival of different aged saplings by increasing the complexity of stand structure. Although individuals may regenerate in an OPG, successful recruitment into the canopy requires the available growing space of a VPG. This research suggests that shade intolerant *Larix gmelini* can maintain its canopy dominance without fire via gap regeneration.

**Keywords:** Age structure; Canopy gap; Crown projection; Da Xingan Ling Mts.; Obliquely projected gap; Sapling survival; Spatial pattern; Vertically projected gap.

**Abbreviations:** OPG = Obliquely projected gap; VPG = Vertically projected gap; NOPG = Near obliquely projected gap; NVPG = near vertically projected gap; SOPC = shadow of obliquely projected crown; SVPC = shadow of vertically projected crown.

**Nomenclature:** Zhou (1996) for vascular plants.

## Introduction

Due to Watt's creative thinking (Watt 1947), the great significance of small-scale canopy disturbance in ecology is receiving increased attention (van der Maarel 1996). Most species require disturbance at some point during their life history in order to be successfully maintained in an ecosystem (Grubb 1977). Fire and canopy mortality are two commonly occurring disturbance events. In boreal regions, fire is generally regarded as the factor controlling forest dynamics (Heinselman 1973, 1981; Payette 1992; Engelmark et al. 1993), with canopy disturbances being most important in tropical and temperate regions (Whitmore 1975; Hartshorn 1978; Runkle 1982).

When a canopy tree dies, the removal of its crown from the canopy creates a gap (Watt 1947). The formation of a gap is always associated with considerable changes in local growth conditions (Vitousek & Denslow 1986), most notably due to increases in resource availability (Chazdon & Fetcher 1984; Canham 1988). Strong light regimes due to direct radiation have the greatest impact on measured understory plant growth (Veblen 1979; Canham & Marks 1985; Poulson & Platt 1989; Canham 1989; Lawton 1990) followed by temperature and soil moisture conditions (Denslow 1980; Runkle 1985; Brokaw 1985b). The creation of gaps also results in increased environmental heterogeneity (Denslow 1985). Latitude, slope, gap size, gap shape, gap orientation, and the height of the surrounding trees all affect the quantity and quality of light entering a gap (Poulson & Platt 1989; Canham 1988; Canham et al. 1990). According to Canham et al. (1990), direct light penetration as sunflecks into the understory contributes 37 - 68 % of the total seasonal photosynthetically active radiation. Chazdon (1986), in a study conducted in tropical forests, showed that seedlings of three species grown in the gap edge have higher rates of leaf production, larger leaves, and are taller than those grown in a closed-canopy understory. Light conditions along gap edges and within small gaps are ideal for these species. Incident light does not, however, arrive vertically in the canopy opening in

either temperate or tropical forests. Gap light regimes depend largely on canopy height and latitude (Canham 1988; Canham et al. 1990; Dai 1996).

The importance of treefalls in forest dynamics has been intensively studied for both tropical forests (e.g. Richards 1952; Hartshorn 1978; Brokaw 1985a, b; Brokaw & Scheiner 1989; Lawton & Putz 1988; Lawton 1990) and temperate forests (Runkle 1981, 1982, 1985; Romme & Martin 1982; Veblen 1985, 1989; Spies et al. 1989, 1990), but rarely in boreal forests (Hyttborn et al. 1991; Leemans 1991; Kuuluvainen 1994; Kneeshaw & Bergeron 1998). The characteristics and importance of small canopy gap disturbances in *Larix* forests, a widespread forest type in Northeast Asia, have not received much attention due to the emphasis placed on stand dynamics following fire.

Although fire is a controlling factor for the *Larix* forests of the Da Xingan Ling Mts. of northeastern China (Zheng et al. 1986, 1990; Uemura et al. 1990), many mature and old-growth *Larix* forests can still be found. Trees in these forests die by snapping, uprooting or while standing (Ban 1994).

*Larix* regenerates well in the forests of our study area. It produces seed every 3 - 5 yr, and a high density of 1-yr old seedlings can be found in the year following seeding. Seedling establishment among forest types varies from 120 - 250 seedlings/m<sup>2</sup> (Ban & Xu 1994) with 20 - 30 % of them still surviving 3 yr later. Regeneration success is dependent on the seed bed. Widespread moss, containing adequate moisture, is the most favourable substrate (Ban & Xu 1995). *Larix* also regenerates well on exposed mineral seed beds following surface fire (Ban et al. mscr.). *Larix* is not as shade-tolerant as other boreal trees such as *Abies* or *Picea*, and therefore the presence of saplings in forests that have not burned for long periods is dependent on changes in canopy structure, i.e. canopy gap formation (Ban et al. In press). Our objectives were therefore to document tree crown and gap characteristics, focusing particularly on such aspects as the influence of tree crown projection on effective gap area, and the ecological impact of these canopy openings on *Larix* regeneration.

## Methods

### Study area

The study area (52 °N, 121 °E) is located in a virgin *Larix gmelini* forest near Mangui in northeastern China close to the border with Russia. These forests are in the central part of the species range at an elevation of 600 - 1000 m a.s.l. The mean annual temperature in the region is - 6 °C, and the mean frost-free period is 90 days.

Mean annual precipitation is ca. 440 mm, which is mainly concentrated in July and August. The study sites are on podzolic brown forest soils ca. 20 cm in depth, under which a permafrost or seasonal frost layer is widespread.

The region's *Larix* forests include four types:

- *Larix gmelini*-*Betula fruticosa* on poorly drained flat sites;
- *Larix gmelini*-*Ledum palustre* var. *angustum* on gentle slopes at lower elevations;
- herb-rich *L. gmelini* at mid-slopes and on fertile slopes;
- *Larix gmelini*-*Alnus mandshurica* on steep slopes at high elevations.

*Larix* trees are usually found in pure stands, especially at young ages. *Pinus sylvestris* var. *mongolica*, *Betula platyphylla* and *Populus tremula* var. *duvidiana* may also be found. *P. sylvestris* occurs mainly on the upper reaches of south-facing slopes while *B. platyphylla* occurs on those sites that have been burned or disturbed by human activities, and is often mixed with *L. gmelini*.

*Larix* can grow to a maximum height of 28 - 30 m and it has a maximum life span of 300 yr in the study area. In the northern Da Xingan Ling Mts., where fire occurs every 110 - 130 yr on average (Zheng 1986; Uemura et al. 1990), fire readily kills seedlings, saplings and the thin-barked young trees. Mature and overmature *Larix* trees are more resistant because of their thick barks and the high, open branching habit of adult trees. In old-growth *Larix* forests that have escaped fire for a long period of time, large *Larix* snags and logs are abundant. The death of these trees, often more than 200 yr old, causes many small and large openings, thus leading to a patchy canopy cover.

### Data collection

Three old-growth (> 200 yr) *Larix gmelini*-*Betula fruticosa*, *Larix gmelini*-*Alnus mandshurica* and herb-rich *Larix gmelini* forest stands were selected for sampling (Table 1). Sample plots were 32 m × 32 m in size. Each plot was mapped and measured using a grid interval of 0.5 m. The crowns of all adult *Larix* trees and *Populus tremula* var. *duvidiana* trees over 6 m in height were mapped using their vertical projection onto the ground at the four cardinal points. The stem location of all trees were mapped in the 0.5 m × 0.5 m quadrats. Diameter at breast height (DBH), height (*H*) and crown length (*CL*) were also measured for each tree. In each 0.5 m × 0.5 m quadrat, the ages of seedlings (≤ 10 yr old) and the ages and heights of saplings (> 10 and ≤ 60 yr old) and young trees (> 60 and ≤ 100 yr old) were measured. Seedlings (< 10 yr old) were aged by terminal bud scar counts while ages of saplings and young trees were measured by counting tree rings on discs cut from the base of the stem.

The fire frequency and the year of fire occurrence were determined using the fire-scar methods presented by Arno & Sneek (1977) and Heinselman (1973). These

**Table 1.** Characteristics of old-growth *Larix gmelini* stands; cover data expressed as percent cover.

| Plot | Forest type                                     | Time since surface fire, yr | Aspect* | Tree characteristics                   | Understory cover  |
|------|---|-----------------------------|---------|--|---|
| 1    | <i>Larix gmelini</i> - <i>Betula fruticosa</i>  | 65, 86                      | 170     | $H = 28$ m, $DBH = 32$ cm, $CD = 0.70$ | <i>Betula fruticosa</i> 0.3, <i>Vaccinium vitis-idaea</i> 0.9, <i>Ledum palustre</i> var. <i>angustum</i> 0.9, herbs 0.5            |
| 2    | <i>Larix gmelini</i> - <i>Alnus mandshurica</i> | 80, 102                     | 182     | $H = 27$ m, $DBH = 31$ cm, $CD = 0.75$ | <i>Alnus mandshurica</i> 0.4, <i>Rhododendron dauricum</i> 0.2, herbs 0.6   |
| 3    | Herb-rich <i>Larix gmelini</i>                  | 65                          | 200     | $H = 23$ m, $DBH = 28$ cm, $CD = 0.75$ | Herbs 0.9, including <i>Deyeuxia angustifolia</i> , <i>Lathyrus humilis</i> , <i>Pyrola incarnata</i> , <i>Maianthemum bifolium</i> |

CD = crown density; \*Angle of plot orientation to geographic south in this stand which was located on a flat site.

stands have not burned for more than 65 yr. The canopy openings in these plots were formed by the death of single or multiple trees which started 30 - 40 yr ago due to senescence of the first cohort (Ban et al. 1997), but a few small openings were created by the death of small trees after the last surface fire.

### Data analysis

#### Gap assessment

Due to the high latitude and the simple vertical structure of *Larix* stands (high stature, short crown length (8 m), and narrow crown width), traditional gap measurements such as vertically projected gaps (VPGs) and the shadows of vertically projected crowns (SVPCs) do not effectively describe the gap environment of these stands. Light levels will be higher in the understory north of traditional gaps than in the VPG itself. When considering sun angle it can be shown that the shadow length of the obliquely projected crown (SOPC) is longer than the shadow cast by a vertically projected crown (SVPC). We have therefore decided to use this projection method to study the effect of small-scale canopy disturbances on *Larix* stand development. The general model used for describing crown projection is shown in Fig. 1. For the calculation of SVPC only CR is needed but for SOPC,  $H$ ,  $CL$  and  $CR$  are all needed.

Crown projection onto the ground surface depends on two factors tree height ( $H$ ) and sun angle ( $h_o$ ), such that the length of the tree's shadow,  $L$ , is

$$L = H \cdot \cotan h_o \quad (1)$$

(The same formula is used to calculate the projection of the base of the crown except that  $H$  is replaced by  $H - CL$  and the position of the tree, and thus its shadow, is moved back by  $CR$ ). This equation can be applied to trees growing on flat sites. The length of the crown projection will, however, change when the slope increases:

$$L' = H / (\cos \alpha \cdot \tan h_o - \sin \alpha), \text{ or} \quad (2)$$

$$L' = H / (\cos \alpha \cdot \tan h_o + \sin \alpha) \quad (3)$$

where  $\alpha$  is slope. Eq. (2) was used for the *Larix-Alnus* stand where the sunlight enters the stand along a slope,

and Eq. (3) for the herb-rich *Larix* stands where the sunlight enters the stand facing the slope.

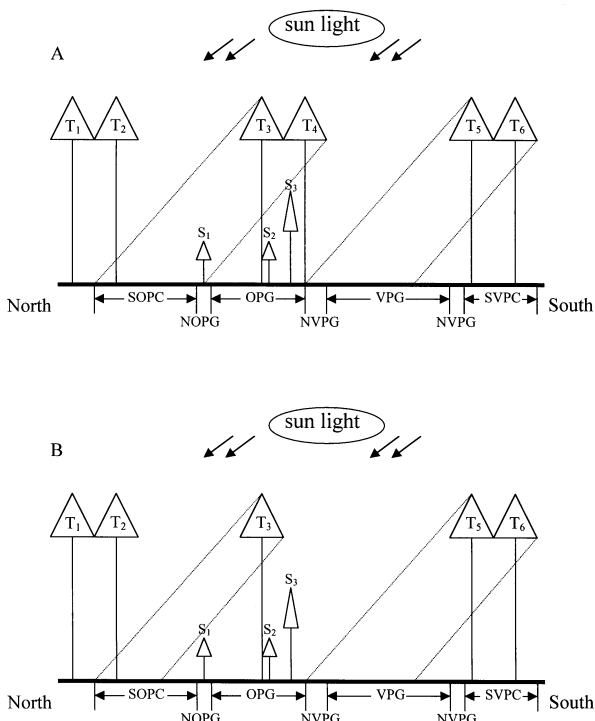
The sun angle,  $h_o$ , was calculated as follows:

$$\sin h_o = \sin \Phi \cdot \sin \delta + \cos \Phi \cdot \cos \delta \cdot \cos t_h \quad (4)$$

where  $\Phi$  is the geographic latitude of the study area ( $52^\circ\text{N}$  in our case),  $\delta$  is solar declination, and  $t_h$  is the sun hour angle. At noon, the sun is on the observer's meridian; so,  $t_h$  will be equal to 0 at solar noon. For one hour earlier or later  $15^\circ$  is added to  $t_h$ . When calculations of  $h_o$  to the nearest-degree are sufficient, the same value of  $\delta$  may be used each day because the maximum declination change in 24 h is less than  $0.5^\circ$  (Partridge & Platt 1976).

Because of a short frost-free period of 100 days, usually from late May to late August, crown projections were made for July ( $\delta = 21.5^\circ$ ) (Lu 1985) when the growth of *Larix* is fastest. We used sun hour angles of  $10^\circ$ ,  $2^\circ$ , and  $-20^\circ$  for the *Larix-Betula*, *Larix-Alnus* and herb-rich *Larix* plots, respectively, based on their respective slopes. Transects for use in subsequent calculations were placed parallel to the incident direction of solar radiation and crown projections were made around noon (at 11:00, 12:00 and 13:00). Optimal photosynthesis for woody plants occurs roughly from 10 h to 14 h, when light is most intense (Hodge 1967; Kramer & Kozłowski 1979). In the study plots, soil moisture is not limiting and photosynthesis by *Larix* saplings is at its maximum during this period. From Eq. (4), sun angles for our plots were  $59.5^\circ$ ,  $58.5^\circ$  and  $55.8^\circ$ , respectively.

In the *Larix-Betula* stand we did not have to adjust the angle of incident radiation due to the flat terrain. Although the herb-rich *Larix* stand was located on a hill, the effect of the steeper slope on crown and gap projection could be ignored because light direction was perpendicular to the slope surface when the sun hour angle was  $20^\circ$ . Crown projection – using Eq. (1) – was calculated to be  $0.59 H$  and  $0.68 H$  in *Larix-Betula* and herb-rich *Larix* stands respectively. The *Larix-Alnus* stand was located on the upper half of a northern slope. When the sun hour angle was  $10^\circ$ , the direction of incident light is parallel to a slope with an aspect of  $17^\circ$  resulting in a decrease in the angle of incidence. From Eqs. (1) to (3), the projection of tree crowns in this stand was calculated as  $0.8 H$ .



**Fig. 1.** Crown projection model. T1, T2, ..., T6 = canopy trees; S1 and S2 = younger saplings; S3 = older saplings; SOPC = shadow of obliquely projected crowns; SVPC = shadow of vertically projected crowns; OPG = obliquely projected gap; VPG = vertically projected gap. (A) Stand with tree T4 alive and standing. (B) Stand after the death of tree T4.

This approach was applied to 33 transects, 1 m wide and 32 m long, distributed over the plots. The transects were placed parallel to the direction of solar radiation. Crown projections were then made along each of these transects. The positions of crowns, gaps and saplings were transferred into the projection diagrams from plot graphs and quadrat records made in the field. The crowns of *Larix* and *Populus tremula* trees over 6 m in height were projected according to the angle of  $h_o$ .

*Larix* saplings were divided into five age groups (using 10-yr age classes) in order to compare the response of saplings to light. Seedlings < 10 yr old were excluded because they occurred in large numbers and they may persist in the understory even at low light levels (Ban & Xu 1994, 1995; Simard et al. mscr). The 60-yr old saplings we studied were released when canopy openings started to be formed 30 - 40 yr ago – after they had been suppressed for 20 - 30 yr. Older saplings have higher light requirements (Kramer & Kozlowski 1979). All saplings were put into one of three microhabitat categories for both oblique projections and vertical projections:

1. Saplings located in the gap (VPG and OPG; for OPG this also included saplings near the southern end of OPG whose crowns could receive some direct radiation).

2. Saplings located within 2 m from the projected gap edge (referred to as NOPG or NVPG). This microhabitat is regarded as a transition area from canopy gap to crown shadow and may compensate for possible errors in the measurement of tree heights.

3. Saplings located in the projected shadow far beyond the gap edge (SOPC or SVPC). Sapling distributions in 82 gaps and areas in the shade were also compared by age. There were 165 observations (33 transects  $\times$  5 age classes) for each of the six micro-habitats (three microhabitats for each of the two methods of projecting the gap): OPGs, NOPGs, SOPC, VPGs, NVPGs and SVPC.

### Statistical analysis

Data from all three plots were combined to analyze the effects of OPGs and VPGs on regeneration. In order to make comparisons among the micro-habitats (in gap, near gap or crown shadow) for both oblique and vertical crown projections, the number of saplings per quadrat was transformed into density per  $m^2$  by using the proportion of each microhabitat in each transect. The number of *Larix* saplings, stratified by age, in the six microhabitats was analysed as a function of sapling age by regression using SYSTAT's GLM procedure (Anon. 1996). Differences between the intercepts and the slopes of the regression lines for the gap, near gap and crown shadow microhabitat in each of the oblique and vertical projections were tested by an analysis of covariance (Anon. 1996). Analysis of variance and/or Bartlett's  $\chi^2$ -analysis were used to test for differences in sapling densities in 10-yr age classes under the canopy, in OPGs, in VPGs and in OPGs, in VPGs and in OPGs + VPGs using SYSTAT's ANOVA (Anon. 1996).

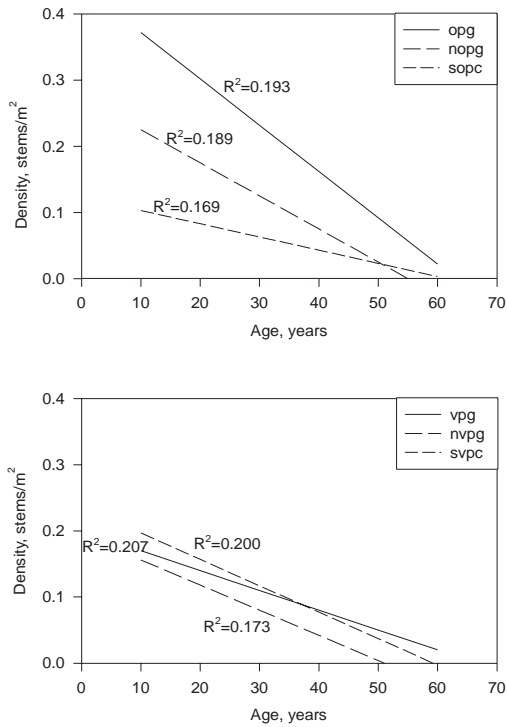
## Results

### Sapling success in OPGs

Sapling densities, pooled from the three plots, significantly decrease ( $p < 0.001$ ) with age for the three microhabitats (in OPGs, near OPGs and SOPC) (Fig. 2a). The number of differently aged saplings gradually decreases from that in OPGs, to NOPGs, to SOPCs. The differences between the intercepts ( $p = 0.001$ ) and the slopes ( $p = 0.019$ ) of the sapling density-age regressions in the three OPG microhabitats were significant ( $n = 1495$ ). The sapling density between OPGs and SOPCs also differed significantly ( $p = 0.097$ ).

### Sapling success in VPGs

Sapling densities decrease ( $p < 0.001$ ) in VPGs, near-VPGs and SVPC with age (Fig. 2). There is no significant difference ( $p = 0.836$  for intercept, 0.545 for slope,  $n = 1495$ ) for sapling densities between these micro-



**Fig. 2.** Sapling density in gaps, in near gaps and in the shadows of both obliquely and vertically projected crowns,  $p < 0.001$  for all linear regressions, sample intensity  $n = 1495$ .

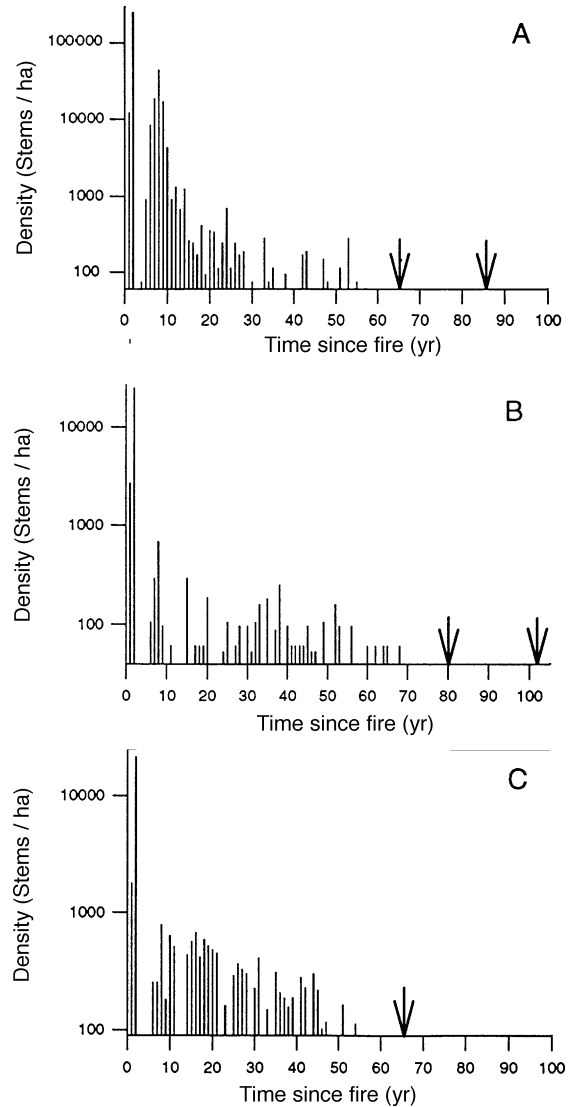
habitats. The saplings in the 11 - 40 yr classes were slightly more abundant in SVPC, but those aged 41 - 60 yr were more abundant in VPGs than in near-VPGs or SVPCs.

*Relative sapling density in both OPGs and VPGs*

$\chi^2$ -analysis ( $p < 0.001$ ) shows that the number of 31 - 60 yr-old saplings in OPGs was significantly higher ( $p < 0.1$ ) than under either the canopy or in VPG (Table 2). There was, however, no significant difference between VPGs and OPGs for the 11 - 30 yr old saplings (Table 2); there was no significant difference either when the analysis was conducted among OPGs, VPGs and overlapping OPGs and VPGs (Table 3). Saplings aged 31 - 40 yr old were more abundant in OPGs and the overlapping OPGs and VPGs than in VPGs

**Table 2.** Mean density of saplings per  $m^2$  in three microhabitats, under canopy ( $n = 155$ ), OPGs and VPGs ( $n = 165$ ), and Bartlett's  $\chi^2$ -analysis of their difference ( $p < 0.001$ ). Values followed by the same letter do not differ significantly ( $p < 0.10$ ).

| Age class (yr)         | 11 - 20 | 21 - 30 | 31 - 40 | 41 - 50 | 51 - 60 |
|------------------------|---------|---------|---------|---------|---------|
| Canopy                 | 0.218   | 0.079   | 0.093a  | 0.047a  | 0.006a  |
| VPG                    | 0.157   | 0.096   | 0.096a  | 0.082a  | 0.002a  |
| OPG                    | 0.340   | 0.222   | 0.212b  | 0.135b  | 0.017b  |
| Bonferroni probability | 0.211   | 0.108   | 0.042   | 0.071   | 0.094   |



**Fig. 3.** Age structure of seedlings and saplings of *Larix gmelini* having regenerated after surface fires in old-growth *Larix* forests. **A.** *L. gmelini*-*Betula fruticosa* forest; **B.** *L. gmelini*-*Alnus mandshurica* forest; **C.** Herb-rich *L. gmelini* forest. Sapling density as original values on a log scale. Arrows show the occurrence of surface fires.

**Table 3.** Mean number of saplings per  $m^2$  in three microhabitats, OPGs, VPGs ( $n = 165$ ) and both OPGs and VPGs ( $n = 135$ ) – in case of overlap, with an effect on sapling density (Bartlett's  $\chi^2$ :  $p < 0.001$ ). Values followed by the same letter do not differ significantly ( $p < 0.10$ ).

| Age class (yr)         | 11 - 20 | 21 - 30 | 31 - 40 | 41 - 50 | 51 - 60 |
|------------------------|---------|---------|---------|---------|---------|
| VPG                    | 0.157   | 0.096   | 0.096a  | 0.082a  | 0.002a  |
| OPG                    | 0.340   | 0.222   | 0.212b  | 0.135a  | 0.011a  |
| VPG+OPG                | 0.279   | 0.168   | 0.153b  | 0.208b  | 0.025b  |
| Bonferroni probability | 0.126   | 0.287   | 0.081   | 0.054   | 0.089   |

( $p < 0.10$ ). Saplings  $> 41$  yr old were more abundant in the overlapping OPGs and VPGs (Table 3) than in either the OPGs or the VPGs alone ( $p < 0.10$ ).

#### *Age structure of the juvenile Larix population*

Seedlings and saplings recruiting following fire have a 'reversed-J' distribution (Fig. 3), as the number of individuals decreases with age. Seedlings  $< 10$  yr old were abundant in each stand. The oldest saplings were more than 10 yr younger than the last fire date.

## Discussion

### *Gap characteristics*

Gap dimensions have traditionally been determined in two ways: for canopy gaps and expanded gaps (Runkle 1982). The former is described by the vertical projection of the crown edge onto the ground, and is thus found directly under the canopy opening, and is equivalent to VPG. The latter is the area circumscribed by the stems, rather than the crowns of trees surrounding the opening and it therefore includes the canopy gap. In dense tropical forests, the concept of canopy gap is realistic due to the high sun angle in these low latitude regions. For subtropical or temperate forests, the concept of expanded gap is more useful because the effective gap area, in terms of increased light, moves beyond the border of the VPG due to an increasing sun angle (Canham 1988). The lower structural complexity of these forests also permits a greater penetration of this lower angle light. However, for *Larix gmelini* forests situated in a boreal region with a latitude of more than  $50^\circ$ , the area affected by the gap shifts even beyond that described by the expanded gap. These gaps are also unique because of the characteristics of *Larix* trees and *Larix* forests, such as short crown lengths and narrow crown widths for relatively tall trees, as well as a simple vertical structure and an open understory. In our study, obliquely projected gaps were shown to be more useful in explaining patterns in *Larix* regeneration than vertically projected gaps. We therefore suggest the use of obliquely projected gaps, or similar gap light indexes (Canham 1988; Dai 1996), in high latitude forests because they take into account the size of trees, gap aspect and sun angle.

### *Gap regeneration*

OPGs have a strong effect on sapling recruitment success, especially for  $> 30$  yr old saplings, due to the direct sunlight that reaches the forest floor (e.g. saplings S2 and S3, see Fig. 1a). Saplings  $< 30$  yr old can survive under the canopy or in VPGs (e.g. S1, see Fig. 1a). From field observations we know that 10 % of the individuals

over 30 yr old have dead tops; this shows that these gaps do not fully meet the saplings' light needs.

When a sapling (such as sapling S3, Fig. 1) grows, it will reach a height at which most of its crown will be in the shadow. More importantly, there will not be a place for it to enter into the canopy layer until an opening is created directly above it. A sapling more than 40 yr old therefore requires an OPG to provide light and a VPG to provide a growth space to reach the canopy. For example, the snapping or uprooting of tree T4 would be necessary for sapling S3 to rapidly succeed to the canopy (see Fig. 1b). In 33 selected transects, all of the 41 - 50 yr old saplings in VPGs were also located in OPGs or in near OPGs, and 90 % of the 41 - 50 yr old saplings in near-VPGs were also in OPGs or in near-OPGs. All of the 51 - 60 yr old saplings in VPGs and 97 % of the 51 - 60 yr old ones in near-VPGs were also in OPGs or in near-VPGs. If taller saplings are, however, located only in OPGs in old-growth forests, it may be possible for them to stretch up to the canopy layer in a future growing season. Old-growth *Larix* forests are generally characterized by multi-generation stands (Xu 1991), in which old and young cohorts are composed of trees across a small age range (30 - 40 yr old for the old generation), and middle-aged or mature cohorts across a greater age range (Xu & Fan 1993). Gap formation occurs during short time periods when tree deaths are numerous. Saplings surviving in understory light conditions are then able to rapidly develop once the canopy is opened. Timing of the openings may therefore be very important (Grubb 1977).

### *Implications for stand dynamics*

Traditionally, it was thought that the boreal *Larix* forest was fire dependent (Zheng et al. 1986; Uemura et al. 1990). However, the presence of many old-growth *Larix* forests suggests that *Larix* does not require fire in order to maintain itself. The *Larix* forests of this region are multi-generation forests (Xu 1991), which are maintained through advance regeneration (Ban et al. 1997) and their successful recruitment into canopy gaps.

In 150 - 200 yr old mature *Larix* forests, no gaps have been created, and saplings  $> 30$  yr old cannot be found. Some of these stands were burned 100 yr ago by surface fire. According to a regeneration study, *Larix* seedlings are abundant following fire and they dominate the regeneration layer (Ban et al. mscr.). However, in the studied old-growth forests, where canopy openings started to be formed 30 - 40 yr ago, saplings up to 68 yr old were found, older saplings (i.e. those germinating in the first 10 yr after surface fire) were not found. These initial individuals may have died due to long periods with insufficient light. This means that surface fire alone is not able to insure successful regeneration, and that successful recruitment of older sap-

lings is dependent on gaps.

Intense fires lead to the disappearance of almost all advance regeneration while at the same time preparing the site for the establishment of a new cohort of young trees (Oliver 1981; Ban et al. mscr.). In contrast, canopy disturbances result in the death of big trees and the release of small trees (Franklin 1973; Oliver & Larson 1990). Fire cannot replace canopy disturbances in this respect. Spatially, forest regeneration after intense fires occurs in circular patterns of regeneration with radii of 1 m or 2 m around the trunk of mature trees, and can be considered 'in situ regeneration' (Ban et al. mscr.). On the other hand, regeneration following canopy disturbance can be considered 'ex situ regeneration' and will be found at a distance of 0.6-0.8 tree height north of the southern gap edge in boreal *Larix* forests.

*Larix*, therefore, appears to be successful under both disturbance regimes. The *r*-strategy characteristics of *Larix*: small seeds (Schmidt et al. 1976; Xu & Ban unpubl.), long-range wind dispersal, and short temporal seed bank (Zhang & Wu 1987; Xu & Ban 1993) are well adapted to intense forest fires. On the other hand, this species also has *K*-strategy characteristics, as it can take advantage of canopy openings by means of a sapling bank that continuously replaces itself (Ban & Xu 1996). Its ability to produce advance-growth, that may in the presence of gaps be recruited to the canopy, favours its maintenance even in long periods without fire. It can, therefore, be concluded that *Larix gmelini* has both 'invasion' and 'waiting' strategies.

**Acknowledgements.** This research was funded by the Chinese National Foundation of Natural Sciences and La Fondation de l'Université du Québec à Montréal. We particularly wish to thank Zhandong Li for assistance during the field work. We are also very grateful to Colin Kelly for his help in the editing of this paper.

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Received 14 January 1997;

Revision received 5 May 1998;

Accepted 10 May 1998.