

Edge effects on recruitment of *Trillium camschatcense* in small forest fragments

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Abstract

To evaluate edge effects on recruitment of the understory perennial herb *Trillium camschatcense*, spatial distribution and stage-class structure based on four life-history stages were investigated within a small forest fragment in eastern Hokkaido, Japan. Seedlings were most affected by edge effects. The density of seedlings was considerably lower in the forest edges than in the interiors and was higher on the northern side of the forest. Although three stages suffered edge and orientation effects, flowering plants experienced much more moderate edge effects than juvenile stages and showed relatively uniform distribution. The results suggest that the recruitment of juvenile stages was strongly limited near forest edges. Seedling density was correlated with microclimatic conditions, not with seed production. The edge and orientation effects on stage-class structures were also observed in two other small populations, emphasizing the role of edge-related decreases in seed germination and subsequent survival for limiting the recruitment of small, fragmented populations of *T. camschatcense*.

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1. Introduction

Forest fragmentation yields a large number of small forest remnants. One of its important consequences is a dramatic increase in edges (reviews by Lovejoy et al., 1986; Saunders et al., 1991; Murcia, 1995), where many physical conditions are often altered. Forest edges, for example, are characterized by higher air and soil temperatures; and lower relative humidity and soil moisture than forest interiors (Kapos, 1989; Matlack, 1993; Young and Mitchell, 1994; Chen et al., 1995). Therefore, small forest fragments are exposed to great changes in microclimatic conditions (Kapos, 1989; Didham and Lawton, 1999) because they have high proportions of edges.

An altered microclimatic environment around forest edges could directly influence plant reproduction and recruitment (Powell and Powell, 1987; Ferreira and Laurance, 1997; Laurance et al., 1998a,b; Jules and Rathcke, 1999; Mesquita et al., 1999; Restrepo and Vargas, 1999; Sizer and Tanner, 1999; Meiners et al., 2002). For

instance, in Amazonian rain forests, the rate of tree mortality was sharply elevated especially within 100 m of forest edges, which was assumed to result from abrupt shifts in microclimatic conditions (Ferreira and Laurance, 1997; Laurance et al., 1998a; Mesquita et al., 1999). Instead, the recruitment of pioneers and secondary species increased (Laurance et al., 1998a,b; Sizer and Tanner, 1999), indicating that edge effect is a major factor that changes the composition of tree communities in this region (Laurance et al., 1998a). The recruitment of plants around the edges can also be affected indirectly through the modifications of biological interactions such as pollination (Powell and Powell, 1987), seed predation (Jules and Rathcke, 1999), and herbivory (Restrepo and Vargas, 1999).

Plant responses to anthropogenic forest edges, however, are not fully understood. The net effects on recruitment through the direct and indirect processes can be either positive or negative, and therefore vary among species (Harris, 1988). Moreover, in the temperate zone, the situation could be more complex than that in the tropics because microclimatic edge effects are strongly influenced by edge orientation (Matlack, 1993; Young and Mitchell, 1994; Chen et al., 1995). At

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mid- to high-latitudes in the northern hemisphere, north-facing edges receive low solar radiation. Thus, microclimatic edge effects at north-facing edges are weaker than at edges facing other directions (Matlack, 1993; Chen et al., 1995). However, despite the many concerns over forest fragmentation and edge formation, few studies have addressed how plant species are influenced by edge orientation, as well as distance from the forest edge (Wales, 1972; Matlack, 1994; Gehlhausen et al., 2000). More vigorous investigations on edge effects including the orientation perspective are required to understand plant responses to fragmentation in the temperate zone.

Trillium camschatcense Ker Gawler (Trilliaceae) is a long-lived herbaceous perennial common to the understory of the mesic, broad-leaved deciduous forests throughout Hokkaido, Japan. In the Tokachi plain of eastern Hokkaido, *T. camschatcense* has recently experienced extensive habitat loss because of large-scale agricultural development, and is now often found in the understory of small remnant forests surrounded by pastureland or agricultural fields. In a previous study (Tomimatsu and Ohara, 2002), we demonstrated using 14 populations that small populations produced fewer seeds than large populations, although the relationship between population size and seed production was significant only in one of two study years. We also showed that seed production was related to some landscape conditions that surround a focal population. While many factors affected the level of seed production in fragmented populations as such, demographic structures based on life-history stages had strong correlations with population size but not with the number of seeds produced; that is, seedling recruitment was more limited in smaller populations. We then inferred that seed production was unlikely to contribute much to subsequent demography (Tomimatsu and Ohara, 2002). Because small populations, which typically grow in small forest remnants, have high proportions of edges, edge-related changes in abiotic and biotic environments may provide better explanations for low seedling recruitment in small populations.

Here we investigate edge effects on recruitment of *T. camschatcense* in small fragments of cool-temperate deciduous forest. (1) We assessed the spatial distribution of *T. camschatcense* individuals from different life-history stages along six transects established within a small forest fragment to see if the distribution of each stage shows edge effects, and if the extent of effects depends on edge orientation. (2) We also quantified seed production and microclimatic conditions that might affect recruitment of *T. camschatcense* to see if they show edge effects, and if they show any spatial patterns associated with the distribution of *T. camschatcense*. (3) To examine the importance of edge effects in determining demographic structure (especially seedling recruitment)

in small populations, we further compared the stage-class structures in forest edges and interiors with those of other small fragments.

2. Methods

2.1. Study species

Trillium camschatcense, correct name for *T. kamtschaticum* Pall. (Fukuda et al., 1996), is an understory perennial herb commonly found throughout Hokkaido, Japan. This plant has four growth stages: seedling, one-leaf sterile, three-leaved sterile, and flowering (Ohara and Kawano, 1986b). It takes more than 10 years for a seedling to become a flowering plant with a gradual yearly increase in leaf size, and after reaching flowering, the plants can live for at least 20 years. A flowering plant sometimes returns to its three-leaved sterile stage the following year, possibly because of impaired photosynthesis (Ohara and Kawano, 1986b). Stems and leaves emerge annually in late April to early May from the underground rhizome. In the Tokachi plain, *T. camschatcense* flowers during mid- to late May before the leaf expansion of canopy trees and has mature fruit by the end of July. No clonal reproduction occurs in this species (Ohara and Kawano, 1986a). Populations in the region are self-incompatible and seed production results from obligatory outcrossing by insect pollination (Ohara et al., 1996). Most reproductive plants have one or two flowers. The showy white flowers are visited by a wide range of insects, primarily by Coleoptera (e.g. *Epuraea* spp.) and Diptera (e.g. *Scatophaga stercoraria*) species (Ohara et al., 1991; Tomimatsu and Ohara, in press). A mature fruit produces ~80 seeds on average (Tomimatsu and Ohara, 2002). Each seed produced has an elaiosome, which is twice the size of the seed. Therefore, the seeds are attractive to ants, which consequently contribute to seed dispersal (Ohara and Higashi, 1987).

2.2. Study populations

The study was conducted in the Tokachi plain of eastern Hokkaido, Japan. Out of the 14 populations investigated in this series of studies (Tomimatsu and Ohara, 2002, 2003), the Kiyokawa population (42°45'22"N, 143°6'52"E; elev. 149 m) was selected for this study. Unless otherwise noted, the experiments were conducted using this forest fragment. The population grows in a small (approximately 0.8 ha, a size typical in this region), cool-temperate deciduous forest, which is 350 m apart from other large forest remnants. The size of this population, defined as the estimated number of flowering plants, was 10,200, while the size of the other 13 populations used in our series of studies ranged from 4 to 153,600. The site is bordered on the northwest by a

10-m wide paved road followed by pastureland and on the other directions by agricultural fields (Fig. 1). The area over ~ 10 m from the southwest-facing edge into the forest was ploughed up for the adjacent field, resulting in an artificial mound where no *T. camschatcense* individuals were found. However, the topography within the forest is generally gentle and no treefall gap was found during the course of this study. The vegetation was cool-temperate deciduous forest, dominated by *Ulmus davidiana* var. *japonica* and *Fraxinus mandshurica* var. *japonica*. To investigate abiotic and biotic environmental gradients within the forest, six transects (A–F) that cross at right angles were established (Fig. 1).

In this region, intensive agricultural development began in the 1880s and has resulted in a large number of forest remnants, many of which are smaller than 1 ha. Although the detailed history of the forest remnant is unavailable, a series of recent aerial photographs has revealed that the southwestern side of the study forest was logged 20–30 years ago. The other edges were most likely created 60–100 years ago, according to the development history of the region. The edges could be clearly defined as the location where the environment abruptly changes due to the creation of the road or the fields.

2.3. Spatial distribution and stage-class structure

In May 2000, data sampling was carried out every 10 m along six transects (0, 10, 20 m, ...). Additionally, data were collected at 85 m points for transects C and F (i.e., edges; Fig. 1). Six 1×1 m quadrats were randomly established around each sample point and all *T. camschatcense* individuals were classified into one of the four stage-classes (i.e., seedling, one-leaf sterile, three-leaved sterile, and

flowering). We excluded sample points on the southwest-facing edge because no *T. camschatcense* individual was found there due to the artificial mound mentioned previously. In total, we examined 55 sample points and 330 quadrats. The stage-class structure was determined for each sample point as the relative frequency of each stage-class.

2.4. Seed production

In 1999, seed production was evaluated for individuals found on two transects (B and E; Fig. 1), intersecting at almost the center of the forest. Not to interfere with the survey of spatial distribution, measurements were made every 10 m along these transects, starting from a sample point at 5 m (5, 15, ..., 85 m). At each point, we established a 5×5 m quadrat. Flowers (7–27; total $N=285$) within the quadrat were randomly selected, marked before anthesis in early May, and left in an open-pollinated condition. Individuals with single-flowering stems were sampled for this study; however, the number of seeds produced per flower showed no significant difference between plants with different numbers of flowering stems (H. Tomimatsu and M. Ohara, unpublished data). All fruits were collected from the marked individuals in July, and the number of seeds was counted for each fruit under a stereomicroscope. For each quadrat, fruit set and the number of seeds per flower were calculated.

2.5. Microclimatic conditions

Three variables—air temperature, soil temperature, and soil moisture—were measured for all six transects in 2000. Air and soil temperatures were measured at 5-m intervals along the transects and soil moisture was measured at 10-m intervals. All measurements were made before (late May; flowering period) and after (mid July; fruiting period) the canopy closure. Air and soil temperatures were measured with digital thermometers (NT-220, NT Corporation, Japan; precision 0.1°C) 1.3 m above the ground and 10 cm into the soil. We selected three sunny days for each of the two sample periods and measured successively during the daytime [10.30–15.30 hours JST (Japanese Standard Time)]. Soil moisture was gravimetrically measured by collecting soil samples (with two replicates) with a soil-core sampler (5 cm in diameter \times 5 cm in depth) from the soil surface. For each sample period, samples were collected in a single day at least 2 days after rainfall.

2.6. Statistical analysis

The following analyses of spatial distribution of *T. camschatcense* were conducted based on the means of six quadrats per sample point. For the analysis of edge effects, the distance from the nearest forest edge was determined for each sample point. The distance was measured directly to the nearest edge, not along a

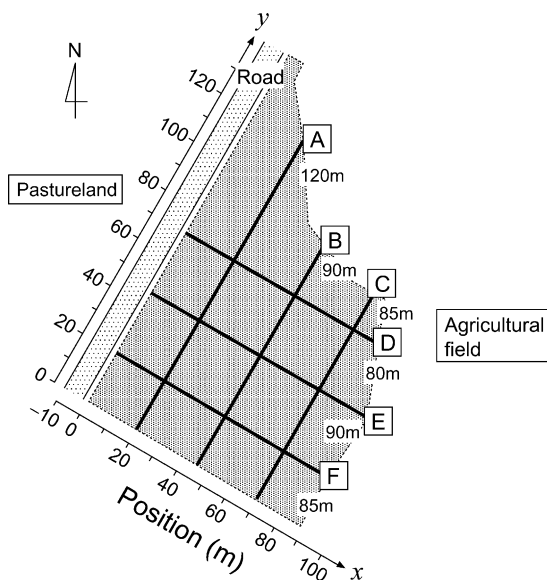


Fig. 1. Map showing the Kiyokawa population in the Tokachi plain of eastern Hokkaido, Japan, and the six transects (A–F) within the site for edge effects experiment.

transect. The significance of edge effects on the number of *T. camschatcense* individuals in each stage-class was tested by regressing the number of individuals to the distance from the nearest forest edge. In addition, response surface regression (SAS Institute, 2000) was performed on the number of individuals in each stage-class. Every sample point is indexed by its spatial coordinates (x , y ; Fig. 1) and a regression model is quadratic: $z = a + bx + cx^2 + dy + ey^2 + fxy$, where z is the number of individuals. The resulting response surfaces visually characterized the patterns of edge effects. The effects of edge orientation were evaluated by comparing observed values between points around edges facing different orientations and by response surfaces.

Edge effects on stage-class structures were analyzed as follows. Tests of relative frequencies of all four stage-classes would not allow for statistical independence, as frequencies of any three stage-classes determine frequency of the fourth. We therefore employed a log-linear analysis for frequency tables, where the frequencies are the number of individuals involved (Caswell, 2001). First we placed all sample points into four discrete categories based on the distance from the nearest forest edge ($0 \leq x < 10$, $10 \leq x < 20$, $20 \leq x < 30$, $x \geq 30$ m) and then produced a three-way contingency table classified by life-history stage (four stage-classes), transect (A–F), and distance from the edge (four categories). We added 0.5 to all cells to avoid estimation problems of cells with zero observations. The null hypothesis is that the number of individuals in each life-history stages (S) are independent of transect (T) and distance from the edge (D). The complete, saturated model is

$$\log m_{ijk} = u + u_{T(i)} + u_{D(j)} + u_{S(k)} + u_{TD(ij)} + u_{TS(ik)} \\ + u_{DS(jk)} + u_{TDS(ijk)}$$

where m_{ijk} is the count in the three-way contingency table. Each effect was examined by comparing the goodness-of-fit G^2 of two models that differ in the terms corresponding to the effect under consideration (Proc CATMOD; SAS Institute, 1999). The effects of transect and distance from the edge can be tested in two different ways. For example, the effect of transect was tested with models including or excluding the effect of distance from the edge. The effects of edge orientation were also analyzed by the log-linear analysis (see below).

The significance of edge effects on seed production and microclimatic variables were analyzed by regressing each variable to the distance from the nearest forest edge. To examine the relationships between microclimatic conditions and the spatial distributions of *T. camschatcense*, we calculated Pearson's correlations between microclimatic variables and the number of individuals in each stage-class. Where necessary, the data were log-transformed to meet the assumptions of analyses.

2.7. Comparison of stage-class structures with other fragments

We further compared the stage-class structures in forest edges and interiors with those of two other small fragmented populations, Toyonishi ($42^\circ 48' 11''$ N, $143^\circ 9' 9''$ E; elev. 114 m; population size 2200) and Motoimatsu ($42^\circ 48' 18''$ N, $143^\circ 6' 43''$ E; elev. 120 m; population size 18,000), of which the shape and orientation are similar to those of the Kiyokawa population. On the basis of the aerial photographs and development history, the edges of these fragments were most likely created 60–100 years ago [see Tomimatsu and Ohara (2002) for further details of these populations]. In each population, nine 1×1 m quadrats were established for three categories of plot type: forest interiors (>20 m from forest edges), southern edges (≤ 10 m from south-facing edges), and northern edges (≤ 10 m from north-facing edges). All *T. camschatcense* individuals within the quadrats were counted and the stage-class structure was determined for each plot type as the relative frequency of each stage-class. The differences in relative frequencies of stage-classes among plot types and populations were tested by the log-linear analysis. The data of the Kiyokawa population were also extracted, categorized into the three plot types, and included in this analysis.

3. Results

3.1. Spatial distribution and stage-class structure

We counted 6586 *T. camschatcense* individuals for all 330 quadrats of 1 m² (Fig. 2). The number of seedlings, one-leaf steriles, and flowerings were positively related to distance from the nearest forest edge (least-square linear regressions; $df=1$, $t=4.86$, $P < 0.001$ for seedling; $df=1$, $t=2.14$, $P < 0.05$ for one-leaf sterile; $df=1$, $t=3.12$, $P < 0.01$ for flowering), indicating that these growth stages were reduced in the forest edges. Response surface models were also significant in these three stages (Table 1). By contrast, the number of three-leaved steriles did not show significant relation to distance from the nearest forest edge ($df=1$, $t=0.10$, $P=0.92$). The response surface model also did not significantly differ from the null model (Table 1).

The resulting response surfaces comprehensively showed the patterns of edge and orientation effects and also the differences of those effects among the three stages (Fig. 3). The number of seedlings was predicted to be highest on the northern side of the forest ($x=36$, $y=58$; Fig. 3) rather than the center, and reduced toward the edges. This reflects the fact that the number of seedlings in almost all the transects (except F) were highest on the northern side of the forest (approximately 70 m from the southwest- or southeast-facing edges), not in the

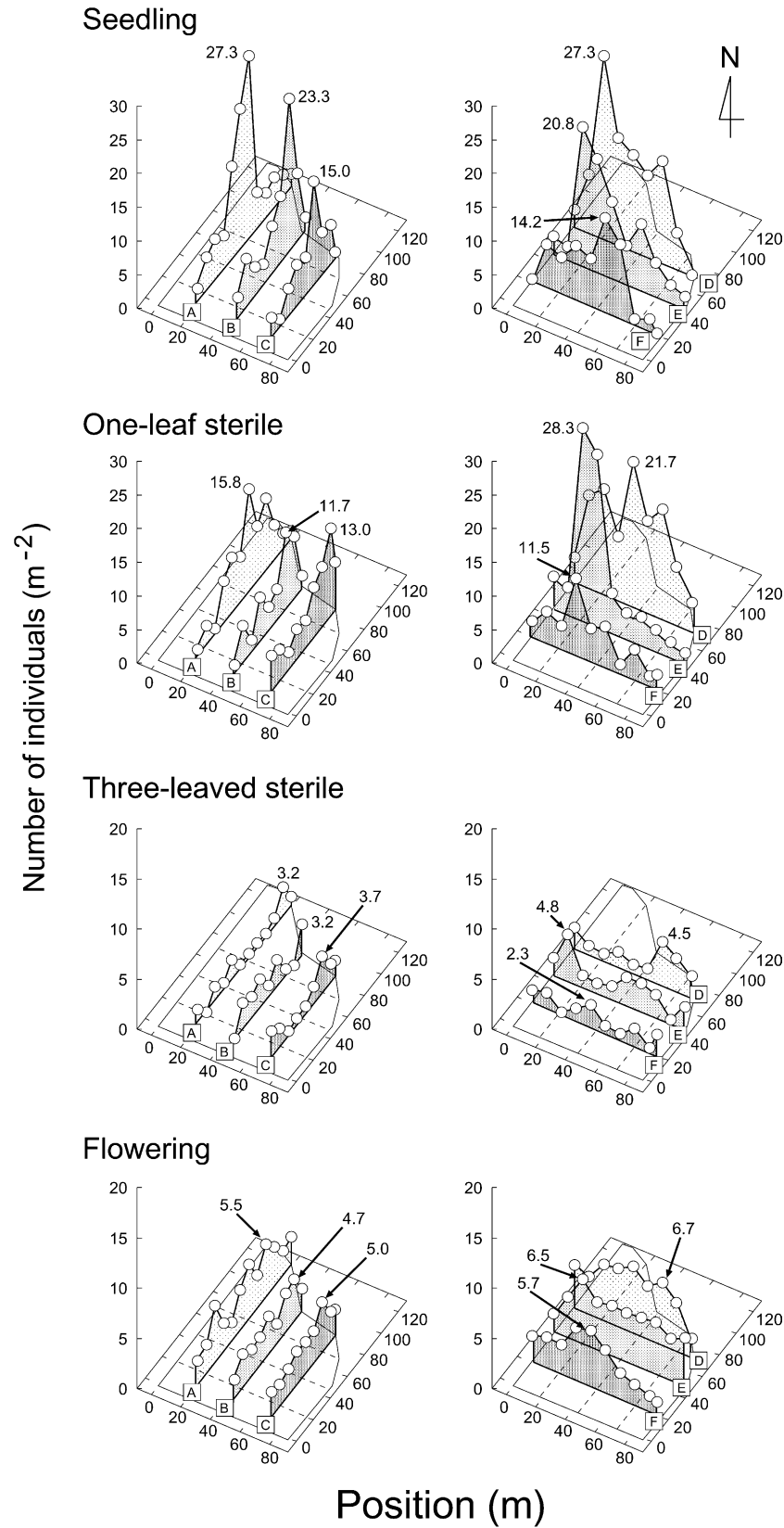


Fig. 2. Number of *Trillium camschatcense* individuals from four life-history stages (seedling, one-leaf sterile, three-leaved sterile, and flowering) per 1 m^2 along six transects (A–F) established within the Kiyokawa population. The data for transects A–C and D–F are separately drawn and the peak of the number of individuals is indicated for each transect. For transects A–C, the data for the sample points at 0 m could not be obtained because of the artificial mound (see text).

Table 1
Results of response surface analyses for the number of *Trillium camschatcense* in each stage-class

Parameter	df	t	P
<i>Seedling</i> ($R^2=0.45$)			
x	1	-2.00	0.05
y	1	1.80	0.08
x ²	1	-4.34	<0.001
y ²	1	-4.35	<0.001
xy	1	-1.26	0.21
<i>One-leaf sterile</i> ($R^2=0.25$)			
x	1	-1.52	0.14
y	1	2.37	<0.05
x ²	1	-1.78	0.08
y ²	1	-2.72	<0.01
xy	1	0.03	0.97
<i>Three-leaved sterile</i> ($R^2=0.04$)			
x	1	0.69	0.49
y	1	0.91	0.37
x ²	1	0.36	0.72
y ²	1	-0.24	0.81
xy	1	0.92	0.36
<i>Flowering</i> ($R^2=0.29$)			
x	1	-1.24	0.22
y	1	2.25	<0.05
x ²	1	-2.64	<0.05
y ²	1	-3.12	<0.01
xy	1	-0.39	0.70

The quadratic models using spatial coordinates (x, y; Fig. 1) were fitted. Estimated response surfaces are shown in Fig. 3. Analyses were conducted for the data obtained in the Kiyokawa population.

middle of the transect (Fig. 2). Fig. 2 also shows that the transects established on the northern side (A and D) had higher peaks than those established on the southern side (C and F). At edges, the number of seedlings was much less (≤ 3 individuals/m²).

Although the results for one-leaf steriles showed the same trend, the edge effects were somewhat weaker than those for seedlings (Fig. 3). Instead, the effect of edge orientation was more emphasized in the response surface than the effect of forest edges. As with the seedlings, the number of one-leaf steriles was predicted to be highest on the northern side of the forest ($x=33$, $y=64$; Fig. 3). Edge effects experienced by flowerings were rather weak (Fig. 3). The differences in the number of flowerings between the forest edges and interiors were not as large as those of seedlings and one-leaf steriles (Figs. 2 and 3). However, the number of flowerings was also predicted to be highest on the northern side of the forest ($x=36$, $y=62$; Fig. 3).

Stage-class structure defined as the relative frequency of each stage-class was related to the distance from the nearest forest edge (Fig. 4). The relative frequency of seedlings was low in the forest edges and increased with the distance from the edge. Conversely, the frequency of three-leaved steriles was high in the forest edges. These changes in stage-class structures with distance from the edge were corroborated by the log-linear analysis (Table 2). The number of individuals in each stage-class was not independent of transect and distance from the nearest forest edge (df = 69, $G^2 = 555.73$, $P < 0.001$). The effect of distance from the edge was significant both when the effect was evaluated independently and when the effect of transect was included in the model (Table 2). The effect of transect was significant when the effect was evaluated independently and when the effect of distance from the edge was included in the model. The results showed that the relative frequencies of four stage-classes were significantly affected by those factors. The differences among transects may reflect the orientation effects. In fact, the frequency of seedlings were lower and the frequency of three-leaved steriles were higher in the southern edges than in the northern edges (Fig. 5A).

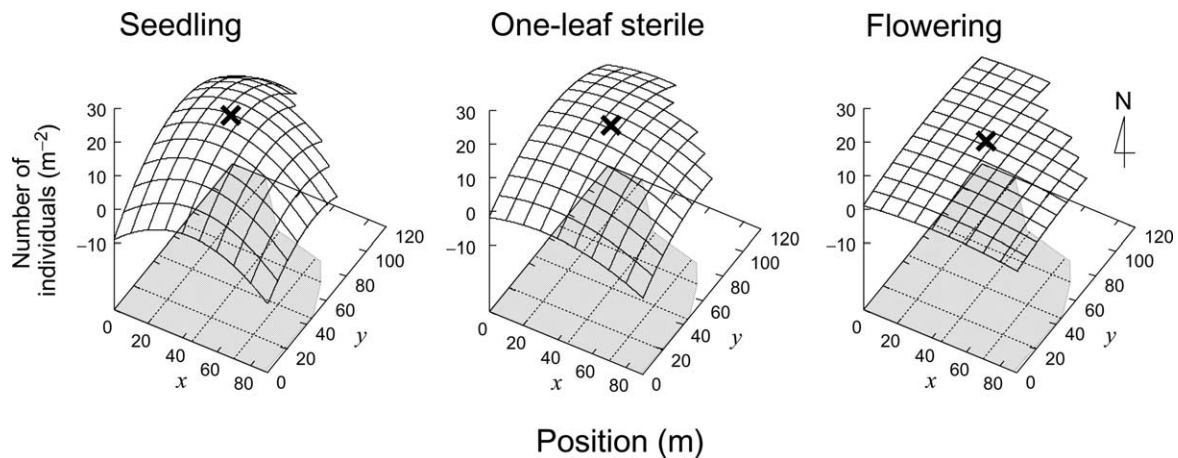


Fig. 3. Response surfaces of the number of *Trillium camschatcense* in each stage-class. The model for the three-leaved sterile stage did not differ from the null model (Table 1), so that the response surface was not shown. An interval between grids of response surfaces is 10 m. The point where the number of individuals was predicted to be highest by the model is indicated by a cross (x). Shaded areas indicate the forest fragment (Kiyokawa population).

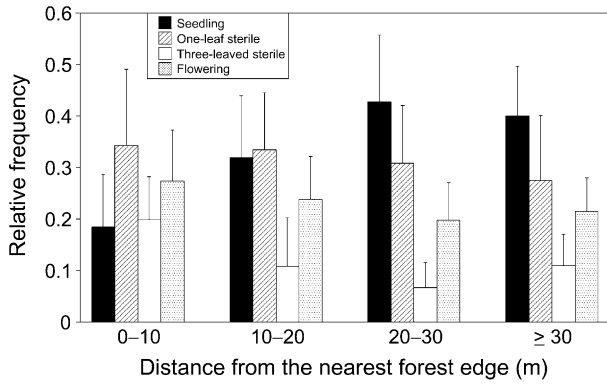


Fig. 4. Relative frequency (mean of sample points + 1 S.D.) of each stage-class of *Trillium camschatcense* found in each of four categories of distance from the nearest forest edge.

Table 2

Log-linear analysis testing the effects of transect (T), distance from the nearest forest edge (D), and their interaction (T×D) on the number of *Trillium camschatcense* in each stage-class (S)

Effect	Contrast of models ^a	Δdf	ΔG ²	P
Transect (T)	TD, S vs. TD, TS	15	83.77	<0.001
Distance (D)	TD, S vs. TD, DS	9	279.96	<0.001
Transect (T), given distance	TD, DS vs. TD, TS, DS	15	52.37	<0.001
Distance (D), given transect	TD, TS vs. TD, TS, DS	9	248.56	<0.001
T×D	TD, TS, DS vs. TDS	45	223.40	<0.001

Analysis was conducted for the data obtained in the Kiyokawa population.

^a Notation denotes hierarchical models in which the presence of an interaction means the presence of all lower-order interactions involving those variables (Caswell, 2001, Chapter 3). Thus, TDS means the saturated model which includes all possible terms.

These analyses of stage-class structure showed that the forest edges were characterized by the low frequency of seedlings and high frequency of three-leaved steriles.

3.2. Seed production

Fruit set and the number of seeds per flower of *T. camschatcense* varied among the sample points on the two transects, B and E. The number of seeds per flower, which was employed as an index of total seed production, varied from 10.7 ± 5.4 (mean ± S.E.) (B, 75 m) to 109.2 ± 12.5 (B, 25 m). In spite of the microsite variability, neither indices of seed production showed any systematic relationship with distance from the nearest forest edge (least-square linear regressions; df = 1, $t = 0.14$, $P = 0.89$ for fruit set; df = 1, $t = 0.25$, $P = 0.81$ for number of seeds per flower).

3.3. Microclimatic condition

All microclimatic variables exhibited significant edge effects. Air and soil temperatures were high on the forest

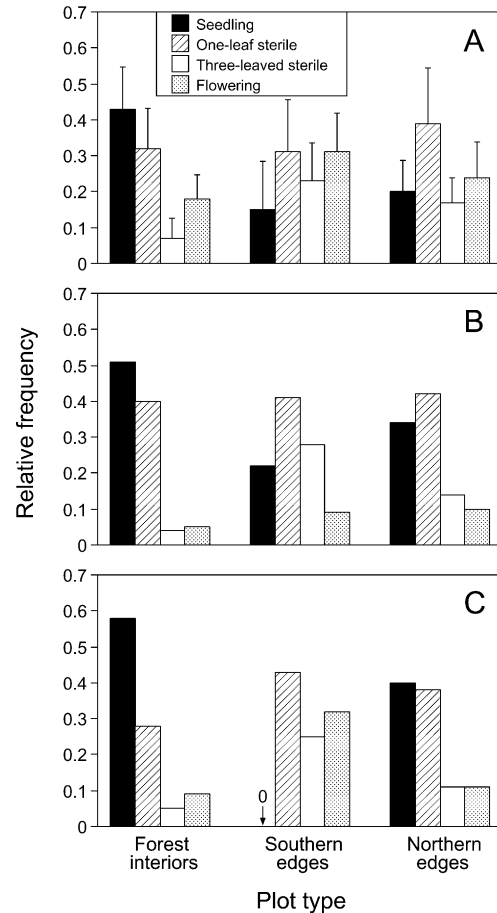


Fig. 5. Comparison of stage-class structures in the Kiyokawa population (A) with those of two other populations, Toyonishi (B) and Motoimatsu (C). Stage-class structure was shown for each plot type: forest interiors (> 20 m from forest edges), southern edges (≤ 10 m from south-facing edges), and northern edges (≤ 10 m from north-facing edges). For the Kiyokawa population (A), relative frequency was shown as the mean of sample points (+ 1 S.D.).

edges, and significantly decreased with the distance from the edge (least-square linear regressions, $P < 0.001$). A significant positive relation was observed between soil moisture and the distance from the nearest forest edge in May ($P < 0.05$), but not in July ($P = 0.58$). However, all microclimatic conditions in the two sample periods were strongly positively correlated with each other (Pearson's correlations, $P < 0.05$). In general, air temperature was most affected by edge effects and the extent of effects was larger in July when the canopy had fully developed. Air temperature also experienced the effects of orientation; it was lowest on the northern side of the forest. Soil moisture was less affected.

3.4. Relationship between microclimatic conditions and spatial distribution

Because there was no evidence that seed production had reduced at edges, we further examined the relation of the abundance of *T. camschatcense* with microclimatic

conditions as a candidate that might affect seedling recruitment and survival. As microclimatic conditions in the two sample periods were strongly correlated with each other, we used only the data in July where the edge effects were more exacerbated. The number of seedlings was significantly negatively correlated with air and soil temperatures (Table 3), while the numbers of the other stages showed no correlation with any microclimatic variables.

3.5. Comparison of stage-class structures with two other fragments

Although stage-class structures significantly differed among the three populations examined, the structures in the Toyonishi and Motoimatsu populations consistently showed the edge and orientation effects (Table 4; Fig. 5). In both populations, the frequencies of seedlings were highest in the forest interiors and lowest in the southern edges. The frequencies of three-leaved steriles were highest in the southern edges and lowest in the forest interiors. These changes in the stage-class structures were highly significant in the log-linear analysis (Table 4).

Table 3
Correlation coefficients between microclimatic variables measured in the fruiting period (July) and the number of *Trillium camschatcense* in each stage-class ($n = 55$)

	Seedling	One-leaf sterile	Three-leaved sterile	Flowering
Air temperature	-0.42	-0.34	0.10	-0.28
Soil temperature	-0.38	-0.19	0.13	-0.22
Soil moisture	-0.05	0.00	0.00	0.05

Analyses were conducted for the data obtained in the Kiyokawa population. Numbers in boldface significantly differ from zero. The table-wide significance was assessed using α -levels calculated according to the sequential Bonferroni technique (Rice, 1989).

Table 4
Log-linear analysis testing the effects of population (P), plot type (T), and their interaction (P×T) on the number of *Trillium camschatcense* in each stage-class (S)

Effect	Contrast of models ^a	Δdf	ΔG^2	P
Population (P)	PT, S vs. PT, PS	6	240.96	<0.001
Plot type (T)	PT, S vs. PT, TS	6	446.54	<0.001
Population (P), given plot type	PT, TS vs. PT, PS, TS	6	325.55	<0.001
Plot type (T), given population	PT, PS vs. PT, PS, TS	6	534.13	<0.001
P×T	PT, PS, TS vs. PTS	12	50.21	<0.001

Analysis was conducted for the data obtained for three populations examined (Kiyokawa, Toyonishi, and Motoimatsu).

^a Notation denotes hierarchical models in which the presence of an interaction means the presence of all lower-order interactions involving those variables (Caswell, 2001, Chapter 3). Thus, PTS means the saturated model which includes all possible terms.

4. Discussion

4.1. Edge and orientation effects on recruitment

T. camschatcense showed different responses to the forest edges among the four life-history stages (Figs. 2 and 3). The density of seedlings and one-leaf steriles was considerably lower in the forest edges (especially in the edges with southerly orientation) than in the interiors, whereas the edge effects experienced by flowering plants were much more moderate. The results suggest that seedling recruitment is strongly limited around the forest edges. Because seed production did not differ between the forest edges and interiors, the distribution of seeds may not be edge-related. Although the seeds that fell on the ground could be dispersed by ants, the dispersal distance has been reported to be short (0.60 m on the average), up to only 3.3 m (Ohara and Higashi, 1987). We also did not observe significant seed predation. Intensive seed predation was unlikely to occur, because large mammals such as deer, supposedly predominant predators in this region, did not have access to the small forest isolated by large fields. Thus, it is suggested that seed germination and establishment are strongly limited by edge effects.

The density of seedlings was negatively related to some microclimatic variables; that is, the density was low at the sample points where air and soil temperatures were high (Table 3). The edge environment was characterized by these microclimatic conditions, which may be deleterious for seed germination and the establishment of *T. camschatcense* that normally occurs in the stable and mesic forest floor. After the fruit of *T. camschatcense* matures in July, the seeds require two cold periods (normally two winter seasons) to become seedlings (Samejima and Samejima, 1962). Only the root emerges underground after the first cold period. Another cold period is required for the emergence of the shoot ('complete double dormancy'; Barton, 1944). Thus, seedlings experienced microclimatic conditions throughout the year including the fruiting season, when microclimatic conditions may be more exacerbated. Various microclimatic changes in response to forest fragmentation can affect the cues required for germination (Bruna, 1999).

The analyses of spatial distribution and population structure made it appear that forest edges were characterized by the low frequency of seedlings and high frequency of three-leaved steriles (Figs. 2–5). As was discussed, low seed germination could reduce seedling frequency. Then, why did the frequency of three-leaved steriles increase near edges? One possible explanation is step-back change of flowerings to the three-leaved sterile stage (Tomimatsu and Ohara, 2002). Flowering plants that suffer accidental damage to their stems or leaves sometimes return to the three-leaved sterile stage the following year (Ohara and Kawano, 1986b). Thus,

the step-back change may have also occurred due to environmental deterioration such as edge effects. If this is the case, the step-back change would also contribute to the slight decrease in flowering plant density near edges (Figs. 2 and 3).

As expected, this study demonstrated that edge orientation plays a significant role in the demography of *T. camschatcense*. In particular, the recruitment of young stages was clearly associated with edge orientation and was higher on the northern side of the forests (Figs. 2, 3 and 5). Although microclimatic edge effects have often been found to interact with orientation in the temperate zone (Matlack, 1993; Young and Mitchell, 1994; Chen et al., 1995), only a few studies have addressed how plants respond to the forest edges facing different orientations (Wales, 1972; Matlack, 1994; Gehlhausen et al., 2000). For example, Wales (1972) showed that the effects on species composition differed between edges with northerly and southerly orientations. The present study shows evidence that the recruitment of *T. camschatcense* is affected by edge orientation. Because the south-facing edge of the Kiyokawa population was formed more recently than the other edges, the differences in the ages of edge formation could affect the results. Some studies showed that older edges experience milder edge effects because of the development of side vegetation (Matlack, 1993, 1994). In this study, however, it was unlikely to be responsible because the age of the south-facing edge is >20 years and its side canopy closes in summer as well as in the other edges. Also, we consistently observed the effects of edge orientation in the other fragments (Fig. 5).

Two possible scenarios are proposed for the fate of these remnant populations, which suffer from strong edge effects on the young life-history stages. One scenario is that density-dependent mortality buffers the edge effects on seedling recruitment with the progress of the stage. Because the spatial distribution of *T. camschatcense* changes successively from aggregated to random with growth from seedling to flowering (Ohara and Kawano, 1986b), the mortality may be density-dependent. This density-dependent mortality can regulate the number of flowering plants (Silvertown, 1987) and therefore buffer the edge effects on seedling recruitment. An alternative scenario is that reduced seedling recruitment drives this population into decline. Because of its long life span (at least 30 years) and the high survival rates of flowering plants (Ohara et al., 2001; H. Tomimatsu and M. Ohara, unpublished data), it is probable that many flowering plants may still have survived fragmentation. This may be the reason why flowering plants suffered moderate edge effects. If so, there is the possibility that this plant species will undergo considerable losses in the next several generations. Further demographic analyses including population projections will be able to test these possibilities.

4.2. Importance of edge effects in limiting recruitment and implications for conservation

The stage-class structure in the forest edges (Figs. 4 and 5) well corresponded to that of small, fragmented populations observed in a previous study (Tomimatsu and Ohara, 2002). Using 14 populations with various sizes, we previously found that seed production was reduced in fragmented populations although stage-class population structures were not significantly correlated with seed production but with population size (Tomimatsu and Ohara, 2002). Specifically, smaller populations had a lower frequency of seedlings and a higher frequency of three-leaved steriles. Because small populations were expected to have high proportions of edges, the correspondence in the stage-class structures between small populations and forest edges points to the importance of edge effects in determining population structures (especially in limiting seedling recruitment) of small, fragmented *T. camschatcense* populations. The magnitude of edge effects may be related to population size, as the distance from the center of the population to the nearest forest edge was highly correlated with the size of the 14 study populations (Kendall's correlation $\tau = 0.729$, $P < 0.001$; H. Tomimatsu and M. Ohara, unpublished data). Although fragmented populations also experienced reduced seed production (Tomimatsu and Ohara, 2002), edge-related decreases in seed germination and subsequent survival, which was related to some microclimatic variables, had higher relative importance. The disruptions of pollination and seed production have been emphasized as particularly important for population persistence especially in self-incompatible species (Rathcke and Jules, 1993; Kearns et al., 1998); though, some recent studies (Bruna, 1999, 2002; Jules and Rathcke, 1999) and the present study demonstrated that survival processes after seed production can also be crucial.

On the other hand, site effects were also observed across the three populations. The Toyonishi population had higher frequency of seedlings than the Kiyokawa population irrespective of its small size. This may be partly explained by an annual fluctuation of seedling abundance and/or by inbreeding depression. Using allozyme analysis of flowering plants, we also previously observed significant excess of homozygotes in some small populations including the Kiyokawa population, which infers significant biparental inbreeding (Tomimatsu and Ohara, 2003). Thus, inbreeding depression may also have reduced seed germination and subsequent survival (Oostermeijer et al., 1995; Luijten et al., 2002).

The distributions of young life-history stages (i.e., seedling and one-leaf sterile) in the Kiyokawa population were highest on the northern side of the forest and decreased toward the edges (Figs. 2 and 3). The result

obviously indicates that the small forest fragment has no core area that is unaffected by edge effects. Even the highest seedling density within this fragment (27.3 individuals/m²; Fig. 2) was much lower than the mean seedling density in a large population of 5 ha (59.2 individuals/m²; Tomimatsu and Ohara, 2002). Accordingly, seedling recruitment was limited everywhere within the forest. It seems that edge effects extended >70 m from the southwest- or southeast-facing edges (Fig. 2). However, because this forest fragment is small, each sample point may be influenced by not only the nearest edge but also by more distant edges (Malcolm, 1994). The extent of edge effects would be more or less complicated by these effects, especially in the sample points that are close to more than one edge. Thus the present study may give only limited information on how large the distance of edge influence was.

We can at least conclude that the size of fragment of the Kiyokawa population (0.8 ha), which is typical in this region, is insufficient to avoid significant edge effects. The size of this population (10200 flowering plants) is much larger than those required to maintain high seed production (1000; Tomimatsu and Ohara, 2002) and high allelic diversity (550; Tomimatsu and Ohara, 2003). Thus the effects of edge orientation also provide management implications for reserve design. On the northern side of the forest, the density of young stages was high in the sample points even at 10–20 m from the forest edges (Fig. 2). The results suggest that edge effects on recruitment can be greatly ameliorated if the shape and orientation of remnant forests are taken into consideration.

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