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**Flowering phenology and survival of two annual plants *Impatiens noli-tangere* and
Persicaria thunbergii co-occurring in streamside environments**

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Abstract Flowering phenology of cleistogamous annual plants *Impatiens noli-tangere* and *Persicaria thunbergii* was studied with reference to their mortality in streamside environments in northern Japan. *Impatiens noli-tangere* produced flower-buds and flowers from late June to October, whereas *P. thunbergii* did from mid August to October. Both species were often killed by rapid current and submergence after heavy rainfall which was unpredictable in the timing and intensity. *Persicaria thunbergii* was more tolerant to rapid current and submergence than *I. noli-tangere*. Some individuals of *I. noli-tangere* were killed by herbivory from sawfly larvae in summer, but *P. thunbergii* individuals were seldom killed by herbivory. In consequence, the percentage of individuals that survived until the end of September was higher in *P. thunbergii* than in *I. noli-tangere*. These situations are assumed to select a long reproductive life in *I. noli-tangere* and autumn flowering in *P. thunbergii*.

Keywords Annual plants • Flowering phenology • Herbivory • Rapid current • Submergence • Survival

Introduction

Annual plants are often found in floodplains, marshes, and sand dunes where disturbances often occur, and their life history characteristics such as small size, rapid growth and large reproductive effort are suggested as adaptations to disturbances (Grime 1979). In addition, their reproductive timing, another important life history trait, is expected to be tuned to cope with disturbances. Plants that reproduce after the occurrence of disturbances would suffer fitness loss due to severe mortality during the disturbances, but those that finish reproduction prior to disturbances may suffer fitness loss due to shortened growth period. Satake et al. (2001), assuming a semelparous annual plant that reproduces once and dies, developed a theoretical model on the evolutionary stable reproductive timing under disturbance. They predicted that when disturbance is serious and its timing is predictable, plants evolve a timid strategy – plants reproduce prior to the major disturbance season. When the timing of disturbance is unpredictable, plants exhibit phenotypic variability in reproductive timing (a mixture of early and late reproduction, or dates of reproduction spreading over a wide interval). On the contrary, when disturbance is not serious, a bold strategy evolves – plants reproduce only when they are fully grown.

Some of these predictions are confirmed in foregoing studies. For example, Schemske (1984) reported that a forest population of *Impatiens pallida* subjected to catastrophe (100 % mortality) in July due to herbivory from beetles reproduces in June, prior to catastrophe; i.e., it exhibits a timid strategy. On the other hand, Mack and Pyke (1983, 1984) and Watkinson et al. (1998, 2000) reported that annual grasses

Bromus tectorum and *Vulpia ciliata* reproduce at the end of growing season (i.e., they exhibit a bold strategy), although they are subjected to temporally and spatially variable disturbances. It is assumed that the intensity of disturbances on these two grasses is lower than the threshold above which a mixture of early and late reproduction evolves. However, available data on the intensity of disturbances are not sufficient to test this assumption.

In this study, we assessed the timing and intensity of disturbances in two annual species *Impatiens noli-tangere* L. (Balsaminaceae) and *Persicaria thunbergii* (Sieb. et Zucc.) (Polygonaceae) to test the model of Satake et al. (2001). These two species often co-occur on streamsides or roadsides in central and northern Japan, but *I. noli-tangere* reproduces from early summer to autumn whereas *P. thunbergii* does in autumn (Hiratsuka 1984; Kawano et al. 1990; Momose and Inoue 1993; Masuda and Yahara 1994; Hatcher 2003).

Materials and methods

Study area and flowering phenology

The study was carried out in a cool-temperate deciduous forest in Nopporo Forest Park (43.1 °N, 141.5 °E) located about 15 km east of the center of Sapporo City. In this forest, *I. noli-tangere* and *P. thunbergii* were observed along streams, paths and roads. Other major undergrowth plants in this forest are *Sasa senanensis* (Franch. et Savat.),

Cryptotaenia japonica Hassk., *Chrysosplenium graynum* Maxim., *Petasites japonicus* (Siebold et Zucc.), *Smilacina japonica* Gray, *Anemone flaccida* Fr. Schm. and *Lilium cordatum* Koidz.

The flowering phenology of *I. noli-tangere* was studied at seven sites along streams in 2004 (Fig. 1). At each site, a 50 cm×50 cm plot was set in mid May. A total of 65 individuals grew in these seven plots, and they were monitored for the formation of flower buds once a week. However, three individuals died before flower-bud formation, and then data were obtained from 62 individuals.

The flowering phenology of *P. thunbergii* was studied at ten sites in 2004 (Fig. 1). At each site, more than 100 individuals grew, and at a number of sites the density was very high (about 10 individuals per 100 cm²). In such dense patches, checking of the presence or absence of flower buds sometimes damages plants. Then, once a week, fifty individuals were randomly chosen at each site and checked for the formation of flower buds.

Survival of natural populations

Survival of these two annual plants was studied in areas A and B along streams (Fig. 1). Area A was located under dense canopy with small gaps. The relative light intensity was measured at 11 points in this area on August 19, 2003 using quantum sensor (LI-190SA, LI-COR, Lincoln, USA); it ranged from 0.8 to 2.6 % of the regime in open area. In this area, *I. noli-tangere* grows singly or in small patches, and *P. thunbergii* forms patches variable in size and density. Area B was located in a relatively large gap.

The relative light intensity in this area was 3.6 – 3.9 % of the regime in open area. The two study species formed large mixed colonies in this area.

The study was made with 50 cm×50 cm plots, which were set in mid May when seedlings of the study species appeared. In area A, *I. noli-tangere* plots were set in all (five) patches with >5 individuals in 1999 and 2000, and in 63 patches that varied in the density in 2001 (Table 1). In 2002, *I. noli-tangere* was not studied since only few individuals were observed in this area probably due to serious damages by heavy rain in the last year (see Results). For *P. thunbergii*, a number of plots were set in patches with various densities in 1999, 2001 and 2002 (Table 1). In 2000, *P. thunbergii* was not studied because of our circumstances. In area B, several plots were set in mixed patches in 2001 and 2002.

The study plots were divided into two categories according to the height from the water level of streams, those at high locations (>25 cm above the water level in late May) and those at low locations (<25 cm). On plots at low locations, only few plants were found except for sparsely distributed individuals and populations of the present study species, probably because of frequent submergence. Plots at high locations were usually covered by vegetation including some perennials. The number of plots and the range of individual number in plots were shown in Table 1. Survival and leaf damage of *I. noli-tangere* and *P. thunbergii* in the study plots were monitored every one or two week(s) from early May until the end of October when almost all individuals died.

The difference in survival was analysed by χ^2 and two-dimensional log likelihood ratio tests with JMP 4.0 (SAS Institute, Cary, USA).

Mortality factors

Four different types of mortality factors were classified.

1) Rapid current and submergence: In the present streams, heavy rainfall often caused rapid current and increased levels of water for few to several days, and a number of individuals were carried away or buried under silt. In addition, some fallen individuals experienced submergence and died. They were determined to be killed by rapid current and submergence.

2) Herbivory: *Impatiens noli-tangere* leaves were often heavily attacked by larvae of two sawfly species. In Japan, two species of sawfly have been reported to attack *Impatiens* leaves, *Aglaostigma nebuosa* (André) and *Siobla ferox* (Smith) (Okutani 1967). Larvae observed in the study area were considered to be these two species according to their morphology, but were not confirmed since they were not successfully raised to the adults. Some lepidopteran larvae were observed on *I. noli-tangere* and *P. thunbergii*, but their attacks were much less serious. These lepidopteran larvae were not identified to species. In this study, individuals of *I. noli-tangere* and *P. thunbergii* disappeared after complete defoliation by these insects were assigned to be killed by herbivory. Individuals that died due to rapid current and submergence before they were completely defoliated were assigned to be killed by rapid current and submergence. Rapid current, submergence and herbivory are also expected to lower the fitness of plants by retarding their growth, but these effects were not determined in this study.

3) Ageing: In mid to late October, most plants withered. Some of them were

infected by pathogens, but it was not determined whether the infection caused death or not. In this study, they were categorized to have died due to aging.

4) Unidentified factors: Shading and competition would also be important mortality factors, but it was difficult to determine whether these factors acted as a direct cause of death or not. In this study, mortality factors other than rapid current, submergence, herbivory and aging were categorized as “unidentified factors”.

Submergence experiments

Tolerance to submergence was compared between *I. noli-tangere* and *P. thunbergii*. Seedlings of *I. noli-tangere* were collected in the campus of Hokkaido University and those of *P. thunbergii* were collected from Nopporo Natural Forest in early May. They were planted in flowerpots (ten individuals per flowerpot) and raised in a grove located in the campus of Hokkaido University. The flowerpots with plants were submerged in a pond in the campus of Hokkaido University on May 28, 2001 for 1, 3, 8, 16 or 32 days, and plants were examined for survival after they were allowed to recover for one month. A flowerpot with ten individuals was used in each treatment for each species. Plant height at the time of submergence was 15-20 cm in *P. thunbergii* and 20-30 cm in *I. noli-tangere*. Water temperature during the experiment was 17-20 °C.

Results

Flowering phenology

In 2004, *I. noli-tangere* produced flower buds and/or flowers from late June to October, whereas *P. thunbergii* from mid August to October (Fig. 2).

Survival and mortality factors

In the study areas, most individuals of *I. noli-tangere* and *P. thunbergii* germinated in May, and the number of survivors gradually decreased until October (Fig. 3). The percentage of individuals survived until the end of September was always higher in *P. thunbergii* than in *I. noli-tangere* (Table 2), and the difference was significant (χ^2 test with sequential Bonferroni correction, $P < 0.01$) except for the case at low plots in 2002. Rapid current and submergence after heavy rainfall caused very high mortality to both species in September 2001, and moderate mortality from July to October in 2002. In 2000, no individual of *I. noli-tangere* was killed by rapid current or submergence, although heavy rainfall occurred in July (data not shown). This is because all of the study individuals occurred at high locations (>25 cm from the water level of the streams) (Table 1). In 1999, some *I. noli-tangere* individuals were killed by rapid current and submergence, although they occurred at high locations (Table 1).

After heavy rainfall in September 2001, mortality was significantly higher at lower plots (<25 cm from the water level of the streams) than at higher plots (>25 cm) in both species (two-dimensional log likelihood ratio test, $P < 0.01$ for areas A and B), and also in *I. noli-tangere* than in *P. thunbergii* on areas A ($P < 0.001$) and B ($P = 0.02$).

(Fig. 4).

Some *I. noli-tangere* individuals were killed by herbivory from sawfly larvae in summer (Figs. 3 and 5). The pattern of herbivory was not uniform but spatially and yearly varied; among the plots with more than five individuals of *I. noli-tangere*, the mortality by herbivory ranged from 0 to 60 % in 1999, 0 to 86 % in 2000 and 0 to 50 % in 2002, and the locations where severe herbivory occurred changed from year to year (Fig. 5). In contrast to *I. noli-tangere*, a very small number of *P. thunbergii* individuals were killed by herbivory (Fig. 3).

Submergence experiments

None of *I. noli-tangere* individuals survived when they were submerged for 8 days or longer, while 90 % of *P. thunbergii* individuals survived even when they were submerged for 16 days (Fig. 6).

Discussion

Rapid current and submergence after heavy rainfall often caused high mortality to *Persicaria thunbergii* and *Impatiens noli-tangere* in the study area. The occurrence of heavy rainfall was unpredictable, and therefore mortality due to heavy rainfall varied seasonally and yearly. In these two species, *I. noli-tangere* was less tolerant to rapid current and submergence and received more serious damages from heavy rainfall. In

addition, *I. noli-tangere* often received serious damages from herbivory by sawfly larvae from July to September in the study area, and the degree of herbivory varied spatially and yearly. Thus, mortality was higher and more fluctuating in *I. noli-tangere* than in *P. thunbergii*. According to the model of Satake et al. (2001), annual plants like *I. noli-tangere* are likely to exhibit phenotypic variability in the timing of reproduction, whereas those like *P. thunbergii* are likely to evolve a bold strategy – they reproduce when they are fully grown, if they are semelparous, i.e., they reproduce once and die. In the present study, the prediction for *P. thunbergii* is supported; this species started flower-bud formation in mid to late August, much later than *I. noli-tangere*.

On the other hand, *I. noli-tangere* did not exhibit a semelparous lifestyle with phenotypic variability in reproductive timing, but it exhibited a long reproductive life; i.e., it started flower-bud formation in late June and reproduced until late autumn. These two strategies are similar at least in the seasonal pattern of seed production at the population level; i.e., seeds are produced from early to late seasons. Therefore, a long reproductive life would also be an option of annual plants under unpredictable environmental conditions. The choice between a semelparous lifestyle and a long reproductive life is dependent on a tradeoff between current and future reproduction (Pianka 1983; Roff 1992; Stearns 1992), but little is known why *I. noli-tangere* has not evolved a semelparous lifestyle but evolved a long reproductive life.

It should be noted that the Satake et al.'s (2001) prediction is based on a tacit assumption that fecundity increases as plants grow their size with age. Although it is not known whether or not this is the case in *P. thunbergii* and *I. noli-tangere*, but this relation is reported in a wide range of plant species (Kawano and Miyake 1983; Rees

and Crawley 1989; Aarssen and Taylor 1992; Herrera 2004).

In addition to demography, the availability and behaviour of pollinators are known to affect the evolution of flowering phenology (Faegri and van der Pijl 1971; Augspurger 1981; Feinsinger 1983; Rathcke 1983; Waser 1983; Bell 1985; Primack 1985; Zimmerman 1988; Brody 1997). The present study species differ in floral characteristics, although both are cleistogamous; *I. noli-tangere* usually produces few, large chasmogamous flowers and many, small cleistogamous flowers near the tip of stems, whereas *P. thunbergii* produces many, small chasmogamous flowers at the tip of stems and few cleistogamous flowers under the ground (Hiratsuka 1984; Kawano et al. 1990; Momose and Inoue 1993; Masuda and Yahara 1994; Hatcher 2003). Therefore, availability and behaviours of pollinators would be different between these species. These differences may be reflected in the difference of flowering timing, but little is understood on this issue.

In the present study, thus, it appeared that *I. noli-tangere* and *P. thunbergii* adapt themselves to streamside environments in different ways. *Persicaria thunbergii* has evolved tolerance to flood and submergence, while *I. noli-tangere* starts reproduction early in the season, probably at a cost of tolerance to rainfall and/or defense against herbivores. Relative fitness of these two strategies would be dependent on environmental conditions such as the frequency, predictability and intensity of flooding and herbivory. In the study area, these two species co-occur along streams, suggesting that these two strategies are approximately balanced in fitness.

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Table 1 Numbers of high (>25 cm above the water level in late May) and low (<25 cm) study plots in areas A and B, and the range of numbers of individuals in the plots (in parentheses).

	Area A		Area B	
	High	Low	High	Low
<i>I. noli-tangere</i>				
1999	5 (6-21)	-	-	-
2000	5 (6-24)	-	-	-
2001	47 (1-20)	16 (1-6)	3 (33-76)	4 (32-91)
2002	-	-	5 (4-29)	1 (20)
<i>P. thunbergii</i>				
1999	3 (15-56)	-	-	-
2001	44 (1-146)	33 (1-164)	3 (12-60)	4 (68-230)
2002	7 (18-33)	8 (9-41)	5 (4-44)	2 (13-52)

Table 2 The percentage of individuals survived until the end of September in *I. noli-tangere* and *P. thunbergii* at high and low plots. Data on plots along areas A and B were pooled.

	High plots	Low plots
<i>I. noli-tangere</i>		
1999	37.1 (62)	-
2000	9.2 (65)	-
2001	4.9 (408)	0 (171)
2002	17.2 (64)	30.8 (39)
<i>P. thunbergii</i>		
1999	64.5 (110)	-
2001	33.5 (1264)	9.3 (1121)
2002	48.3 (236)	37.8 (246)

Numbers in parentheses refer to the total number of individuals that germinated in the plots.

Captions to figures

Fig. 1 Study sites. Arrows indicate sites where flowering phenology was studied (solid arrows; *I. noli-tangere*, broken arrows; *P. thunbergii*). Survival was studied in areas A and B.

Fig. 2 Seasonal changes in the percentage of individuals with flowers and/or flower buds in *I. noli-tangere* and *P. thunbergii* in 2004.

Fig. 3 Survival of *I. noli-tangere* and *P. thunbergii*. Mortality factors were also shown. White bars indicate survivors. Data on all study plots were pooled.

Fig. 4 Mortality due to rapid current and submergence at high and low plots in area A (white bars) and area B (shaded bars) in September, 2001.

Fig. 5 Locations of *I. noli-tangere* plots with more than 5 individuals in area A in 1999, 2000 and 2001, and proportions of individuals died due to herbivory by sawfly larvae (dark areas).

Fig. 6 Survival (%) of *I. noli-tangere* and *P. thunbergii* after submergence for 1, 3, 8, 16, or 32 days in a pond. Plants were raised in pods for about one month after germination and submerged on 28 May, 2001.

Fig. 1

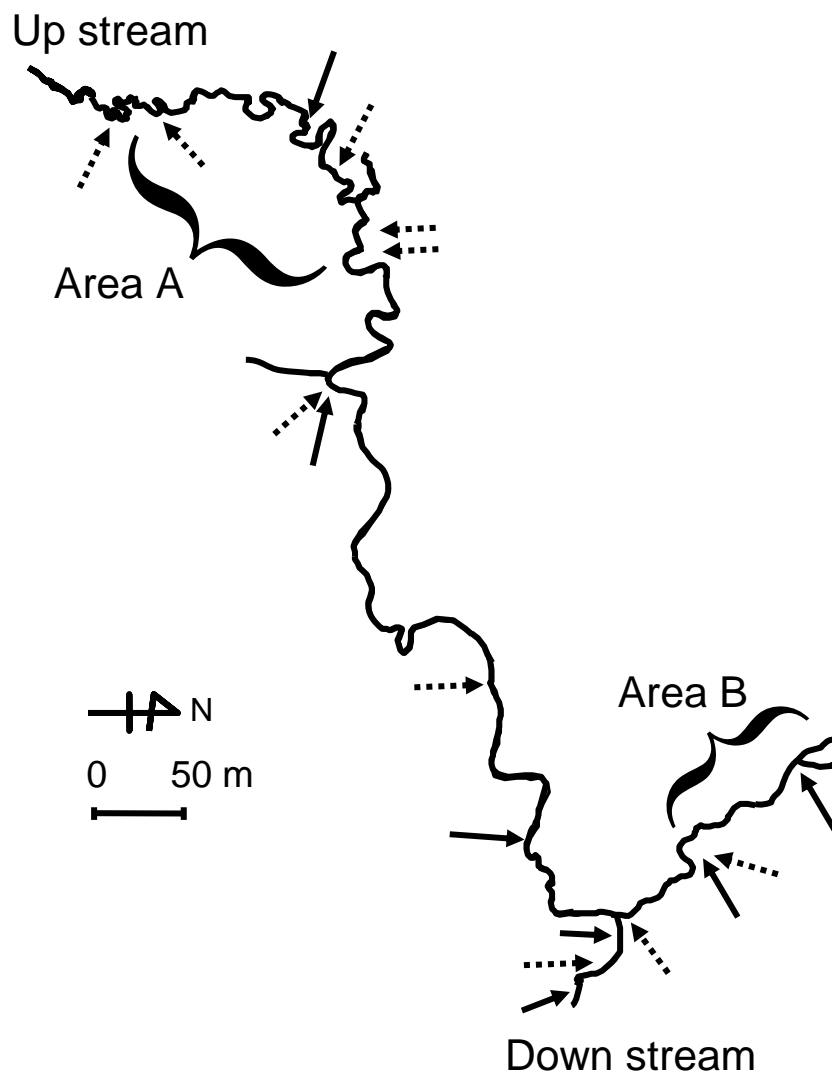


Fig. 2

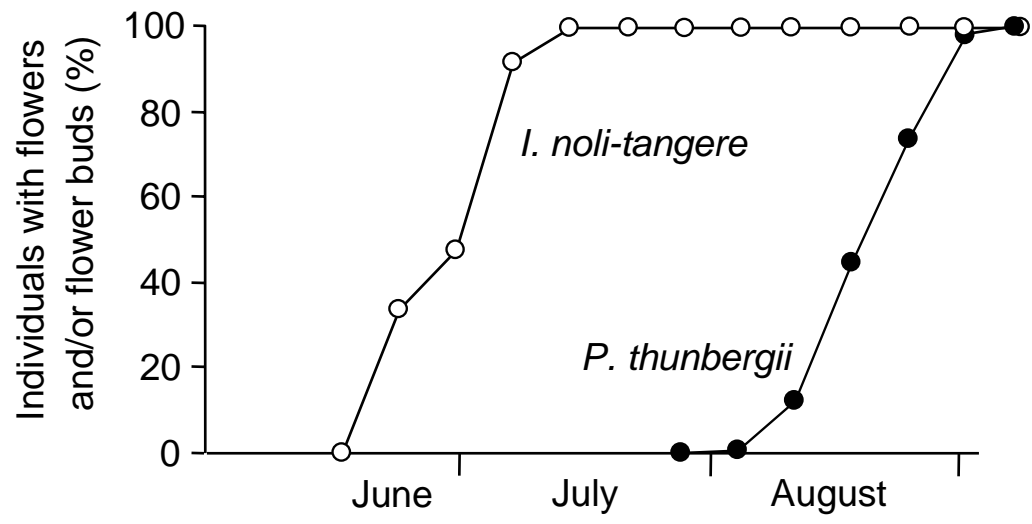


Fig. 3

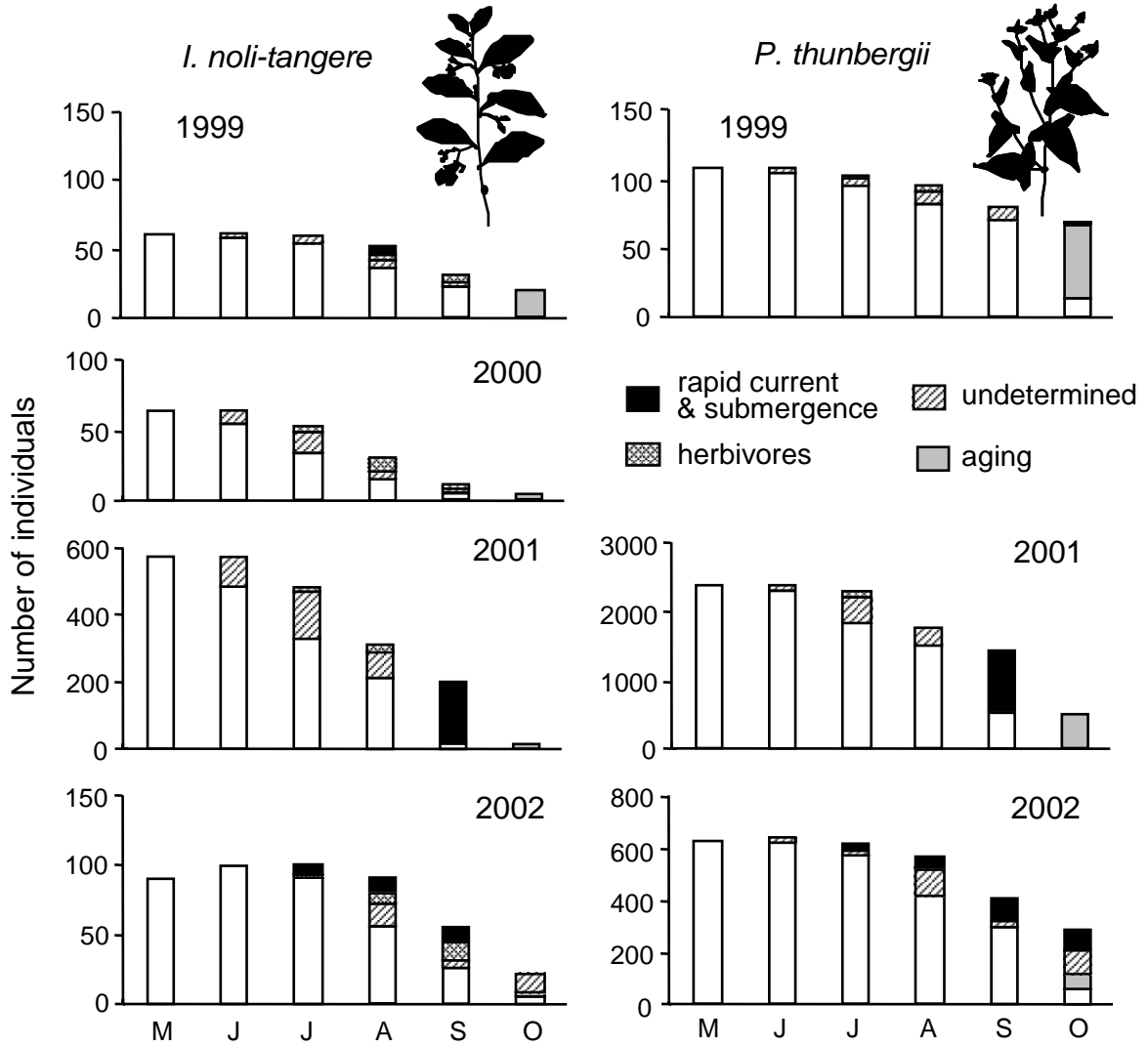


Fig. 4

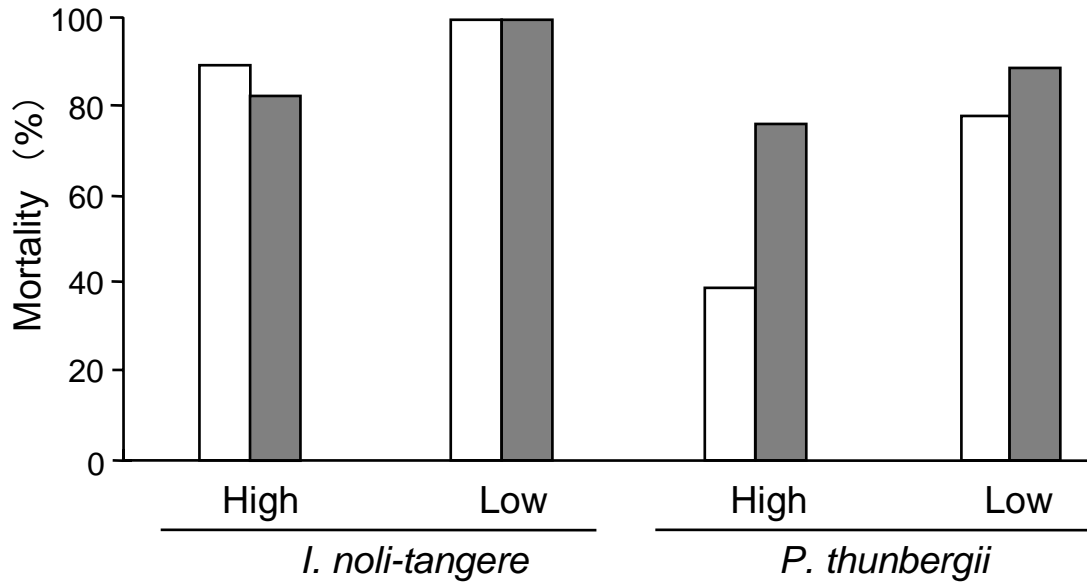


Fig. 5

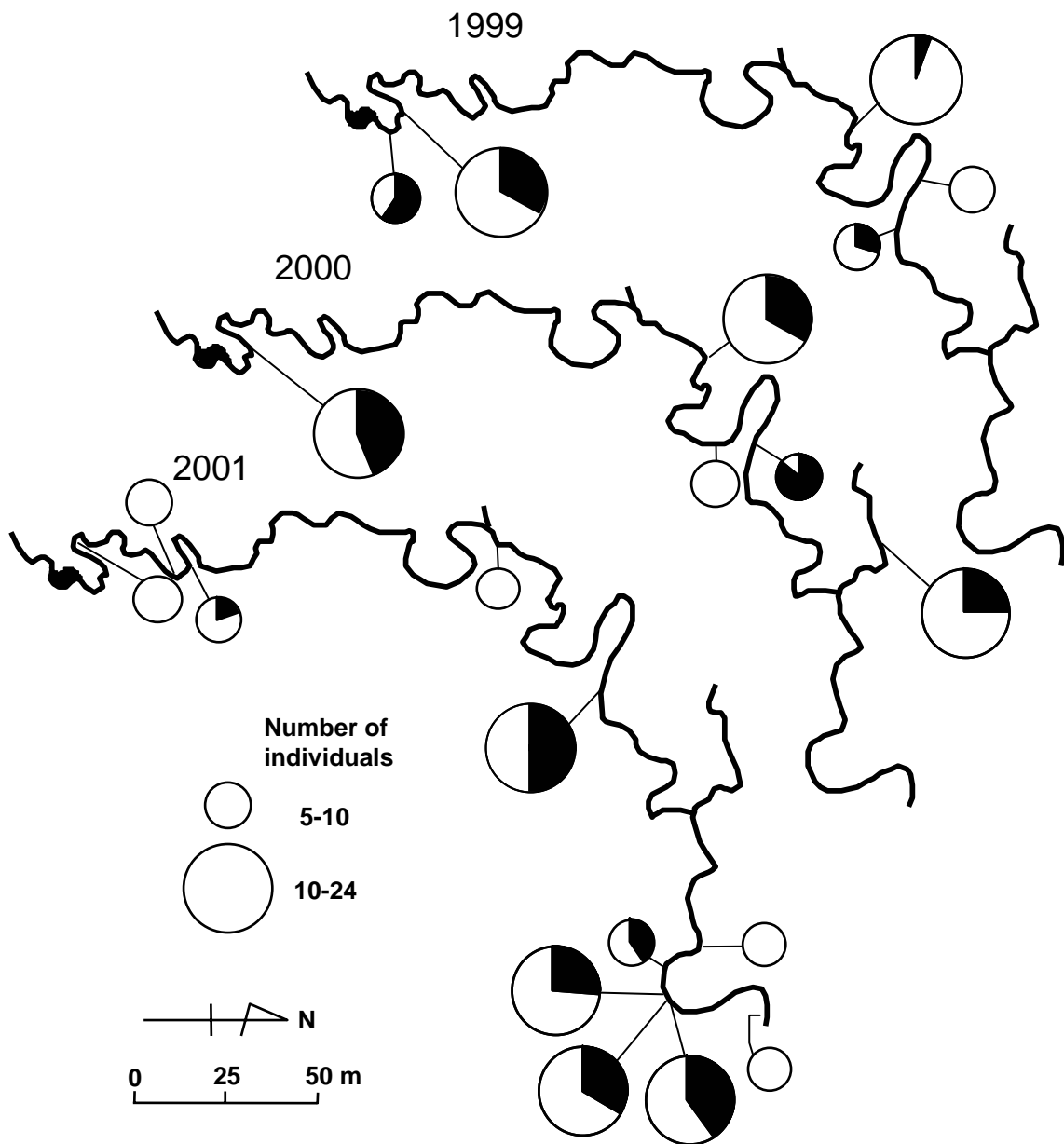


Fig. 6

