

Effects of Forest Cover on Fruit Set in the Woodland Herb, *Maianthemum canadense* (Liliaceae)

HISATOMO TAKI^{1,3}, PETER G. KEVAN¹ and YUICHI YAMAURA²

¹Department of Environmental Biology, University of Guelph, Guelph, Ontario N1G 2W1 Canada

²Department of Forest Entomology, Forestry and Forest Products Research Institute, Tsukuba, Ibaraki 305-8687 Japan

³Corresponding Author and Present address: Hisatomo Taki, Department of Forest Entomology, Forestry and Forest Products Research Institute, 1 Matsunosato, Tsukuba, Ibaraki 305-8687 Japan

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Animal pollination has been recognized as an essential ecosystem function that is potentially under various environmental stresses. We investigated the landscape effects of forest cover at multiple spatial scales on the sexual reproductive success of a common woodland herb in North America, *Maianthemum canadense*. This species is a self-incompatible species and pollinated by insects requiring natural landscapes. Nine populations were selected in deciduous forests within agricultural fields of southern Ontario, Canada. We investigated whether fruiting success decreases as forest cover surrounding the plant populations increases at the landscape scale. Forest cover was quantified by the proportion of forest within six different radii from 250 to 1500 m. Analyses showed relationships with the proportion of forest at 750- and 1000-m radii and fruiting success in populations of *M. canadense*. These findings suggest potential local extirpation of *M. canadense* and indicate that forest loss can negatively impact on even some common woodland herbs.

Key Words: Carolinian forest, forest fragmentation, habitat isolation, habitat loss, pollinator, Ontario.

Reproductive success of many plants is negatively affected by habitat loss and fragmentation, and such habitat alterations have the potential to influence the reproductive outputs of plants pollinated by animals (Aguilar et al. 2006). Animal pollination is a critical component of ecosystem services, and most of the animal pollinators require natural landscapes (Daily 1997; Losey and Vaughan 2006). To manage such an essential and threatened function in terrestrial ecosystems, understanding the scales at which the reproductive output of plants is influenced is central to the management of pollination services (Kremen 2005).

In this study, we examined the landscape effects of spatial scale on Canada Mayflower, *Maianthemum canadense* (Desf.) (Liliaceae). This species is a widespread, perennial forest-understory herb with genets of dimorphic ramets (shoots; Silva et al. 1982; Ross and Laroi 1990; McCully et al. 1991; Ganger 2004). Vegetative shoots have a single leaf, and flowering shoots have two or three leaves with a terminal inflorescence of 6 to 40 white flowers (McCall and Primack 1987; Ganger 1997). In eastern Canada, the flowers bloom in late spring and fruits appear in late summer (Helenurm and Barrett 1987). Each fruit contains one to four seeds, and usually only fruit with seeds develop. *Maianthemum canadense* is self-incompatible (Worthen and Stiles 1986, 1988; Barrett and Helenurm 1987; McCall and Primack 1987; Wheelwright et al. 2006) and is pollinated by insects (Thomson et al. 1985; Barrett and Helenurm 1987). Several populations of *M. canadense* in Canada have suffered reductions in sexual reproductive output from loss of pollinators

caused by pesticides used to control forest insect pests (Kevan and Plowright 1995).

Knowing that forests provide potential habitat area for pollinating insects, we quantified forest cover surrounding populations of *M. canadense* and investigated whether forest cover affects sexual reproductive success. We determined whether fruiting success decreases as forest cover increases. If so, we then determined at what scale(s) it is affected.

Methods

Study region

The study was conducted within a restricted geographical area of Norfolk County, Ontario, Canada (42°37' to 42°48'N, 80°25' to 80°39'W), to reduce the potential problems associated with differences in climate (Lipow et al. 2002) and edaphic factors (Mix et al. 2006). This region is located in southern Ontario's deciduous forest ecosystem, the Carolinian forest. The unique warm and dry climate of this region is suitable for this deciduous ecosystem, which is not found elsewhere in Canada. The landscape is rather flat, with patches of forest ecosystems, which were most of the natural ecosystems in the study region, distributed within intensively managed agricultural fields of crops, mainly tobacco, corn, and soybeans (Taki and Kevan 2007; Taki et al. 2008). Many plants with priority for conservation in Canada exist in this Carolinian forest zone (Allen et al. 1990; Argus 1992; Waldron 2003).

Plant selection

Nine populations of *M. canadense*, each existing within varying amounts of forest cover, were selected.

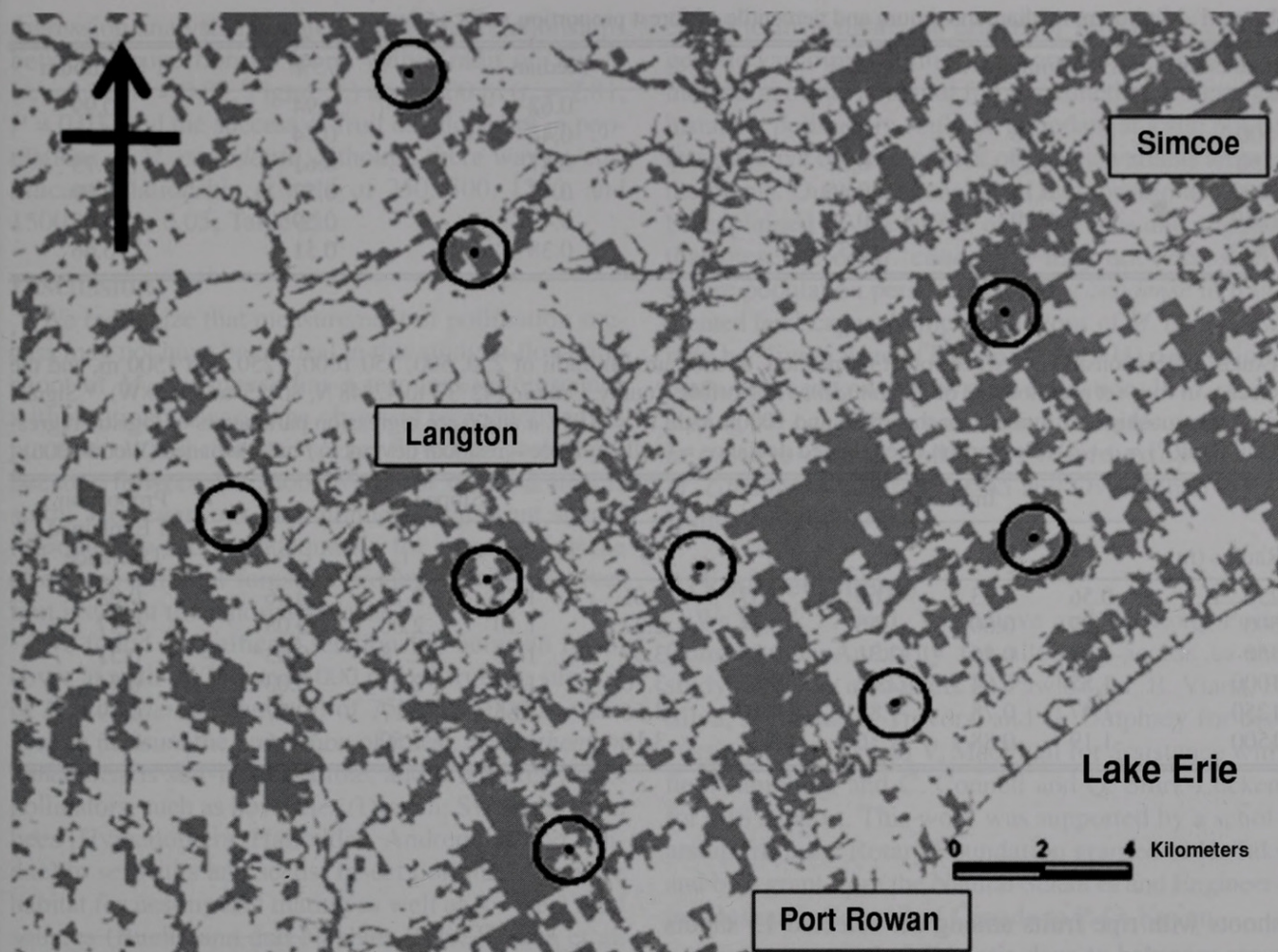


FIGURE 1. Nine study sites of *M. canadense* used to evaluate amounts of forest cover and forest in Norfolk County, Ontario. The 750-m radius, one of the six study scales, is also shown. Shaded areas indicate forested areas. The geospatial data were obtained from the Ontario Base Map Series (Ontario Ministry of Natural Resources, Peterborough, Ontario, Canada).

The study populations had variable numbers of flowering shoots, and the mean number of flowering shoots among the nine sites was 66.2 ± 30 (mean $\pm$ SD), ranging from 40 to 125. To reduce the potential effects of forest edges, all populations were selected at least 30 m from edges of forest patches. All populations of *M. canadense* were selected by 5 May 2004, prior to blooming. They were separated by a distance of at least 4000 m from other study populations. This was ensured with the aid of a global positioning system (GPS; Garmin International, Olathe, Kansas, USA) and a Geographical Information System (GIS), ArcView (version 3.3, ESRI, Redlands, California, USA). The geospatial data on forest cover produced using aerial photography (1:30 000 and 1:50 000) were obtained from the Ontario Base Map Series in 2003 (Ontario Ministry of Natural Resources, Peterborough, Ontario, Canada).

Forest cover

To determine the landscape effects of forest cover, each of the nine populations of *M. canadense* was marked on a map as the center of circles having radii of 250, 500, 750, 1000, 1250, and 1500 m (Figure 1)

to measure the amount of forest surrounding the populations. Within the circles, quantification of forest cover (m^2) was carried out using GPS coordinates obtained from the field sites and ArcView. Forest cover within the circles was then determined and treated as an explanatory variable in the statistical analysis (Table 1). Edges of forest were not actual woodlands in the study region, but we considered those natural lands as forest cover. The selected radii were selected as the scales corresponding to the landscape scale response of solitary bees (Gathmann and Tschamntke 2002; Steffan-Dewenter et al. 2002), which are one of the major pollinator groups of *M. canadense* (Thomson et al. 1985; Barrett and Helenurm 1987).

Fruiting success

Within each of the nine populations of *M. canadense*, 15 individual shoots with unopened flowers were randomly selected on 13 and 14 May 2004. After blooming, on 19 June, all of the shoots were covered with polypropylene mesh bags (product number ON-6200, InterNet, Minneapolis, Minnesota, USA) with 3-mm square holes to prevent potential damage to fruits by herbivorous mammals and birds. On 29 June,

TABLE 1. Minimum, median, maximum and percentile of forest proportion at six scales.

Radius (m)	Minimum	25%	Median	75%	Maximum
250	0.36	0.53	0.62	0.94	0.99
500	0.18	0.25	0.48	0.74	0.85
750	0.12	0.32	0.47	0.61	0.75
1000	0.15	0.40	0.47	0.57	0.69
1250	0.20	0.39	0.43	0.59	0.68
1500	0.20	0.33	0.38	0.51	0.66

TABLE 2. Relationships between forest proportion, as measured in radii of 250, 500, 750 1000, 1250, and 1500 m, and the success in fruit set per shoot (*p*) of *M. canadense* in Norfolk County, Ontario (42°37' to 42°48'N, 80°25' to 80°39'W). * Significant relationships are evident for the 750m and 1000m radii (*P* < 0.05). *a* and *b* are regression parameters of logistic regression: $\text{logit}(P) = a + bX$. Proportion of explained deviance = (null deviance – residual deviance) / null deviance (Wood 2006).

Radius (m)	Intercept				Slope				Proportion of Explained Deviance
	<i>a</i>	SE	<i>t</i> ₇	<i>P</i>	<i>b</i>	SE	<i>t</i> ₇	<i>P</i>	
250	-0.56	0.93	-0.60	0.57	1.01	1.28	0.79	0.46	0.08
500	-0.99	0.60	-1.66	0.14	2.27	1.10	2.06	0.08	0.37
750	-1.28	0.56	-2.31	0.05*	3.07	1.10	2.78	0.03*	0.53
1000	-1.55	0.64	-2.42	0.05*	3.70	1.32	2.81	0.03*	0.54
1250	-1.47	0.78	-1.88	0.10	3.56	1.65	2.17	0.07	0.39
1500	-1.19	0.88	-1.36	0.22	3.12	1.97	1.59	0.16	0.25

shoots with ripe fruits among the selected 15 shoots were recorded at each site. All fruits were taken to a laboratory at the University of Guelph, Ontario, where they were dissected and checked for the presence of developed seeds. To quantify the success of fruit set in each population, the proportion of shoots exhibiting fruits with developed seeds was then calculated for each set of 15 shoots.

Statistical analysis

Before we tested for landscape effects of forest cover on the fruiting success of *M. canadense*, a logistic regression analysis was used to examine the relationship between population size, indicated by the number of flowering shoots, and fruiting success (Faraway 2006; Crawley 2007). We used a quasi-binomial distribution rather than a binomial distribution to avoid over-dispersion problems (Faraway 2006; Crawley 2007). The number of flowering shoots was transformed to avoid high leverage problems (Quinn and Keough 2002). We used logarithmic transformation rather than square-root transformation because logarithmic transformation effectively reduced the frequency of a few populations that were quite large (Legendre and Legendre 1998). A logistic regression analysis was then performed to examine relationships between the proportion of forest and the fruiting success of *M. canadense*. Statistical computations were performed using R Ver. 2.4.1 (R Development Core Team 2006*). For all analyses, a Type I error rate of 0.05 was used.

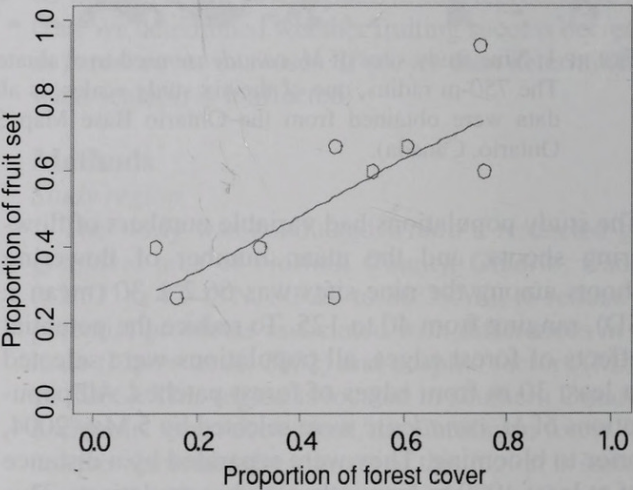


FIGURE 2. Relationship between forest cover measured within a circle radius of 750 m and the success of fruit set in *M. canadense* in Norfolk County, Ontario. Regression analysis shows $\text{logit}(p) = -1.28 + 3.07X$, *t*₇ = 2.78, *P* = 0.03. A similar trend was found for forest cover measured within a radius of 1000 m.

Results

Logistic regression analysis indicated no significant relationship between fruiting success in *M. canadense* and the number of flowering shoots in a population (proportion of explained deviance = 0.04, slope = -0.46, SE = 0.80, *t*₇ = -0.57, *P* = 0.59). Logistic

regression analysis indicated significant relationships between proportion of forest within radii of 750 m ($t_7 = 2.78$, $P = 0.03$; Figure 2.) and 1000 m ($t_7 = 2.81$, $P = 0.03$) and the success of fruit development in populations of *M. canadense*, although there was no significant relationship at radii of 250, 500, 1250, and 1500 m ($P > 0.05$; Table 2).

Discussion

We recognize that measurement of pollination success may not have been ideal in this study. A flowering shoot of *M. canadense* has a terminal inflorescence with multiple flowers. The observed reproductive output does not indicate fruit set per flower on each shoot because flowers per shoot were not counted in this study. However, our measurements represent sexual reproductive success adequately for investigating the effects of different forest environments on conservation issues at the landscape scale.

We found a significant relationship between forest cover at radii of 750 and 1000 m and fruiting success of *M. canadense*. The radii of 750 and 1000 m were used to measure the proportion of forest. *Maianthemum canadense* is self-incompatible, and it requires insect pollinators, such as hoverflies (Diptera: Syrphidae) and bees (Hymenoptera: Halictidae, Andrenidae and Apidae) to set fruits and seeds. Insect pollinators require habitat for nesting and mating as well as for their food sources (Buchmann and Nabhan 1996; Kearns et al. 1998; Kevan 1999). Loss of forest area within a radius probably reflects the distance containing the habitats of insect pollinators of *M. canadense*. Although we did not observe the abundance of flower visitors to our study populations of *M. canadense*, forest cover would likely influence to these insects. For example, Taki et al. (2007) found that the abundance and species richness of bees collected in pan traps in nearby sites and forest cover at the scale of the 750-m radius showed a significant relationship. Our findings also indicate that the consideration of the pollinators in Acadian and boreal forests, where *M. canadense* is found, are necessarily the same as those in the Carolinian zone of Norfolk.

Although *M. canadense* can maintain large populations through genets consisting of multiple clonal ramets, maintaining and increasing genetic diversity in *M. canadense* populations rely on pollen exchange. Seed dispersal by animals also positively influences genetic diversity in plants of other disturbed habitats (Ibrahim et al. 1996; Austerlitz and Garnier-Géré 2003), but dispersal is contingent on satisfactory fruit set through pollination. Therefore, lack of sufficient pollination could directly and indirectly impede genetic diversity in populations of *M. canadense* inhabiting areas with high loss of forest cover. This may become an issue concerning local extirpations of *M. canadense*; therefore, as in another clonal species of *Maianthemum* in Europe (Honnay et al. 2006), it would be inter-

esting to investigate the effects of forest loss and on genetic variation within and among populations as an indication of the potential for an extinction vortex. For instance, pollinators could be abundant at a site but be less effective because of lack of genetic variants among the plants. Our results suggest a relationship that may be explained by the effect of forest loss and suggest that presence of *M. canadense* may not necessarily assure population persistence of *M. canadense* in fragmented landscapes. Some populations of *M. canadense* may be "living dead" (Tilman et al. 1994) populations that are already on their way to extinction. If so, maintaining *M. canadense* would require restoring forests in order to recover pollinators before extirpation of *M. canadense* occurs (Hanski and Ovaskainen 2002; Bulman et al. 2007).

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