Fitness of *Maianthemum canadense*, *Trientalis borealis,* and *Cornus canadensis* under canopy gaps

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Abstract

The importance of canopy gaps in promoting forest biodiversity and regeneration has been well documented. A majority of forest plant biodiversity is located in the herbaceous layer. However, the link between canopy gaps and fitness of the herbaceous plant layer has not been fully explored. Three common herbaceous plants in the Wisconsin area are Canada mayflower (*Maianthemum canadense)*, starflower (*Trientalis borealis)*, and bunchberry dogwood (*Cornus canadensis).* In this study, the fitness of these three species in relation to three canopy gap locations (center, edge, and outside of gap) was analyzed. Leaf length, stem height, and flower presence were used as proxies of fitness. These three factors, as well as the abundance of the three plant species, were collected from twenty-six canopy gap study sites. Though there were no significant differences in leaf length, stem height or flowering plant presence among the three gap locations, plant abundance of *T. borealis* and *C. canadensis* did vary significantly per location. This suggests that different herbaceous plant species respond to canopy gaps in unique manners. Some may compete with growing saplings inside canopy gaps, and thus thrive on the edge of a canopy gap, while others are able to thrive in the center of a gap. Overall, fitness did not vary between location, though interesting trends of abundance were present.

Keywords: canopy gap, edge effect, fitness, herbaceous plants, *M. canadense, T. borealis, C. canadensis*

Introduction

A forest canopy gap is an open area formed by fallen branches and trees (Whitmore 1989). Conditions provided by canopy gaps have been shown to increase levels of biodiversity in forest ecosystems for both shade tolerant and intolerant species (Beckage and Clark 2003, Einecker 2014, Nuttle et al. 2013, Schnitzer and Carson, 2001). One important component of forest biodiversity is the herbaceous layer. This paper explores how the fitness of herbaceous plant species is impacted by forest canopy gaps.

Higher biodiversity in canopy gaps is related to the environmental conditions they provide. During a comparative study of sunlight levels, light levels were 7.3 $\pm$ 1.7% higher in canopy gaps than beneath closed canopy (Beckage and Clark 2003). Along with increased light levels, canopy gaps also provide the space necessary to establish high levels of both woody and herbaceous plants (Schnitzer and Carson 2001, Schleuning et al. 2008, Royo et al. 2010). The gap hypothesis, set forth by Schnitzer et al. 2008, makes predictions about canopy gaps, stating that (1) resources are more heterogeneous within a gap, (2) some species need this increase in resource heterogeneity to survive, (3) some species will need the resources found within a gap to initiate reproduction, and (4) some species in a gap have higher levels of fecundity. A trend of regeneration hubs being located under a canopy gap has been seen in black cherry (*Alseis blackiana),* wild daffodil (*Narcissus pseudonarcissus),* and the herb *Heliconia metallica* (Dalling et al. 2001, Barkham 1980, Schleuning et al. 2008). However, the specific mechanisms behind this observed increases in fitness within gaps are not entirely understood (Schnitzer et al. 2000).

While canopy gaps and associated trees are well studied, there is limited research on the herbaceous layer in general (Schnitzer et al. 2008). It is known that the diversity of understory species decreased 25% at the 1-m^2 scale in southern Wisconsin from 1949-2004 as a result of shifts in canopy and understory composition (Rogers et al. 2008). This is concerning, and the herbaceous layer must be included when considering the stability of forest ecosystems. It makes up less than 1% of forest biomass, but accounts for up to 90% of temperate forest plant species (Gilliam 2007). Within the ecosystem, the herbaceous layer cycles nutrients and provides food for vertebrates and invertebrates alike. By better understanding the relationship between canopy gaps and the herbaceous layer, one can be better informed when discussing forest biodiversity and conservation implications.

Little research has been performed on the specific regenerative patterns of herbaceous plants in response to canopy gaps in the northern Michigan region. Three common herbaceous plants in this region include Canada mayflower (*Maianthemum canadense),* starflower *(Trientalis borealis),* and bunchberry dogwood (*Cornus canadensis). M. canadense* is an abundant perennial member of Family Liliaceae with a 5-20cm height (Gleason et al 1991) and spreads along the forest floor through vegetative reproduction by rhizomes (Silva et al 1982). *T.*

borealis is a member of Family Primulaceae with a 10-20cm height (Gleason et al 1991) and relies on asexual reproduction by tubers to maintain population size, and sexual reproduction by seeds to incorporate genetic diversity (Anderson and Beare 1983). *C. canadensis* is a member of Family Cornaceae with a 4-8cm height (Gleason et al 1991) and grows laterally by underground rhizomes while also producing fruit consumed by migratory birds and small mammals (Burger 1987). Because of their high regional abundance, these three plants are ideal model organisms to use in order to study fitness trends of herbaceous plants under canopy gaps.

This study investigated how the fitness of the herbaceous plants *M. canadense*, *T. borealis*, and *C. canadensis* in the Wisconsin-Michigan area compare inside, on the edge of, and outside canopy gaps. The flowering rate, plant abundance, and leaf width of the three herbaceous plants was analyzed. The results tested the gap hypothesis, especially points (3) and (4) which state that some species will need the resources found within a gap to initiate reproduction, and that some species in a gap have higher levels of fecundity (Schnitzer et al. 2008). I hypothesized that (1) *M. canadense, T. borealis,* and *C. canadensis* would have the highest level of fitness (indicated by flower presence, tall stem height, and longer leaves) in the center of canopy gaps, and that (2) the highest abundance of each species would occur inside the canopy gap.

Materials and Methods

This study took place at the University of Notre Dame Environmental Research Center (UNDERC), located on the border of Wisconsin and the Upper Peninsula of Michigan. The selection of the species *M. canadense, T. borealis,* and *C. canadensis* was based on previous research performed indicating strong presence of these species in the area (Einecker 2014). Canopy gaps were defined as an opening in the canopy due to a fallen tree where sunlight can reach an area $>50m^2$.

Twenty-six canopy gaps were selected as sampling sites (Figure 1). At each site, a circular plot with a one-meter radius was established in the center of the gap, on a randomly selected edge of the gap, and fifteen meters outside the gap (Figure 2). Random selection was performed using cardinal directions and a random number generator. Within each circular plot, I located every individual of the three target species and measured height and longest leaf length, and recorded whether or not the individual was flowering. Previous studies have shown flower presence and plant size to be appropriate proxies for fitness (Charles-Dominique et al. 2012, Tanaka et al. 2008).

Flowering abundance was calculated on a per-plot basis by dividing the number of flowering individuals by the total number of individuals present in a given species. Plant density was calculated by dividing number of plants by plot area, which was πm^2 for all plots.

A one-way ANOVA was run to analyze the relationship between location (center of gap, edge of gap, outside gap) and average stem height for *T. borealis*. The remainder of the data was not normally distributed (Shapiro Wilk, all $W>0.436$, all $p<0.036$). Thus, the remainder of the data was analyzed using nonparametric Kruskal-Wallis tests. Three Kruskal-Wallis tests analyzed the relationships between location and leaf length, flowering plant abundance, and plant density for *T. borealis.* Four Kruskal-Wallis tests per *C. canadensis* and *M. canadense* analyzed the relationship between location and stem height, leaf length, flowering plant abundance, and plant density. Two post-hoc Nemenyi tests were run for both *T. borealis* and *C. canadensis* to further analyze pairwise comparisons. Data was analyzed using R software (R Core Team 2013).

Results

A total of 1,977 herbaceous plants from twenty-six canopy gaps were studied. The average stem heights did not differ significantly by location for any species (*M. canadense*, H_2=5.041, p=0.080; *C. canadensis*, H_2=5.50, p=0.064; *T. borealis*, F_2=0.15 p=0.86) (Table 1).

The average longest leaf length also did not differ significantly by location for any species (*M. canadense*, H_2=5.068, p=0.079; *T. borealis*, H_2=0.304, p=0.859; *C. canadensis*, H_2=1.55, p=0.461) (Table 2). Additionally, flowering rate did not differ significantly by location (*M. canadense*, H_2=0.063, p=0.969; *T. borealis*, H_2=1.168, p=0.558; *C. canadensis*, H_2=3.396, p=0.183) (Table 3).

Abundance did not differ by location for *M. canadense* (H_2=1.637, p=0.441). However, there were significant differences for both *T. borealis* and *C. canadensis* (*T. borealis*, H_2=10.657, p=0.005; *C. canadensis*, H_2=8.586, p=0.014). A post-hoc Nemenyi test analyzed pairwise comparisons and showed that *T. borealis* was significantly more abundant on the edge than the center (p=0.021) and outside the gap (p=0.012) (Table 4). *C. canadensis* was significantly more abundant at the center of the gap than outside the gap (p=0.047) (Table 4).

In both Figures 5 and 6, *C. canadensis* follows a trend separate from *M. canadense* and *T. borealis.* It has more plants and flowers in the center of the gap than on the edge. Both *M. canadense* and *T. borealis* had the highest number of plants on the canopy gap edge, though in the case of *M. canadense*, this difference was not significant.

Discussion

I hypothesized that *M. canadense*, *T. borealis,* and *C. canadensis* would have the highest levels of fitness in the center of canopy gaps. Experimental results did not support this hypothesis. Rather, average stem height and longest leaf length were similar between the three locations (Figures 3-4). There was also no significant difference between the number of plants with flowers and each canopy gap location (Figure 5). It is likely these trends can be explained by growth patterns of these plant species. In the case of *T. borealis,* asexual reproduction by underground tubers is more important than reproduction by seed (Anderson and Beare 1983). Both *C. canadensis* and *M. canadense* have rhizome structures that may limit the reliance on sunlight for reproduction by flowering (Hall and Sibley 1976, Silva et al 1982). Thus, the proxies for fitness used in this study of flowering, leaf length and stem height did not account for all methods of reproduction for these three plant species. Future studies measuring the impact of canopy gaps on herbaceous plant reproduction should consider factors both above and below ground. Also, the species studied were short, herbaceous plants featuring leaf growth in whorls, basal shapes, and leaves on umbrellas (Gleason et al 1987). While there may be leaf changes in relation to shifting moisture and nutrient levels, natural methods to minimize self-shading may prevent the need to change leaf length and stem height in order to use sunlight most efficiently (Givnish 1987). A future study analyzing the physiology of herbaceous plants in response to shifting nutrient levels would be interesting, as would a study tracking spatial shifts in soil composition under different canopy gap locations.

I also hypothesized that the highest abundance of each species would occur in the center of the gap. Experimental support for this hypothesis varied by species. Results for *C. canadensis* supported the hypothesis, as it had significantly more plants in the center of the gap than outside the gap (Figure 6). *C. canadensis* may dominate areas under open canopy because of its rhizome structure and colonial growth patterns. These rhizomes can grow up to 30 cm per year, and will dominate an area until the rhizomes are removed (Hall and Sibley 1976). Along with producing fruit for dispersal, it is also a colonial plant, meaning it grows in colonies of aerial stems from underground connections (Gleason et al 1991). It is likely this type of reproductive strategy takes advantage of the increased levels of sunlight and space provided by a canopy gap.

Meanwhile, *T. borealis* had significantly higher plant abundance on the edge than the center and outside gap (Figure 6). When looking at Figure 6, it appears *M. canadense* followed a trend similar to *T. borealis* even though it was not significant. In this way, while *T. borealis* and *M. canadense* had unexpected results. This may be due to growth strategies and competition. In the case of hardwood tree species, literature has shown that there is a hub of regeneration under high light gap areas. For example, there was increased clumping of the tropical canopy tree *Alseis blackiana* seedlings inside rather than outside a canopy gap (Dalling et al. 2001). However, herbaceous plants must compete with hardwood seedlings to obtain resources needed for growth. This occurred in a canopy gaps when the number of yellow trout lily (*Erythronium americanum*) decreased as the height of black cherry tree (*Prunus serotine*) seedlings increased (Collins et al 1988). When there were fewer sugar maple (*Acer saccharum)* seedlings near the edge of a gap, there was an increase in patch size of *E. americanum (*Marchand et al 2006). In the Sylvania Wilderness Area of the Ottawa National Forest in Upper Michigan, greater plant species evenness correlated with a low number of sugar maple saplings (Miller et al 2002). In this way, competition between herbaceous plants and hardwood saplings, specifically deep shade casting saplings such as *A. saccharum*, impacts abundance trends of herbaceous plants. The canopy gaps in this study were in areas with high levels of *A. saccharum* saplings, and competition with these and other hardwood tree saplings could explain the increased edge plant abundance for *M. canadense* and *T. borealis*.

In this study, the three plant species did not exhibit significant differences in fitness between locations, thus these results did not support the gap hypothesis. However, there were interesting trends in plant abundances. The gap hypothesis (when applied to the herbaceous layer) does not account for the significance of the gap edge. Because of competition for resources, the regeneration and reproduction of herbaceous plants may require the unique gap edge environment. Thus, the edge provides an area for the herbaceous layer to thrive, and this edge would not be possible without the formation of canopy gaps. More research is needed to explore how competition within a canopy gap impacts spatial forest composition. This study indicated how different growth patterns of herbaceous plants respond to disturbances in different ways. As forests continue to shift, it is important to be aware of these differences in order to understand how the ecosystem as a whole will change.

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Tables and figures

Table 1. Stem heights (cm) of 1,977 plants from twenty-six study sites were measured. Average stem height was compared between location of center, edge, and outside canopy gap. Means reported as ± SE.

Species	**Center**	**Edge**	**Outside**
M. canadense	5.23±0.09	5.26±0.09	5.01±0.11
T. borealis	9.97±0.38	10.2±0.23	10.06±1.27
C. canadensis	10.76±0.23	10.13±0.22	9.74±0.34

Table 2. Longest leaf lengths (cm) of 1,977 plants from twenty-six study sites were measured. Average length was compared between location of center, edge, and outside canopy gap. Means reported as ± SE.

Species	**Center**	**Edge**	**Outside**
M. canadense	4.13±0.05	4.3±0.05	4.28±0.06
T. borealis	4.95±0.19	5.1±0.12	5.1±0.64
C. canadensis	4.3±0.07	4.42±0.08	4.36±0.14

Table 3. Average number of flowering plants for each plant species by location. Means reported as ± SE.

Species	**Center**	**Edge**	**Outside**
M. canadense	1.42±0.41	2.23±0.48	1.12±0.28
T. borealis	0.19±0.25	0.31±0.22	0.15±0.23
C. canadensis	3.31±0.65	1.35±0.42	0.19±0.25

Table 4. Average number of plants for each plant species by location. Means reported as ± SE.

Species	**Center**	**Edge**	**Outside**
M. canadense	14.08±0.61	17.85±0.54	14.58±0.43
T. borealis	3±0.45	7.35±0.45	2.58±0.37
C. canadensis	9.65±0.83	5.58±0.51	1.38±0.64

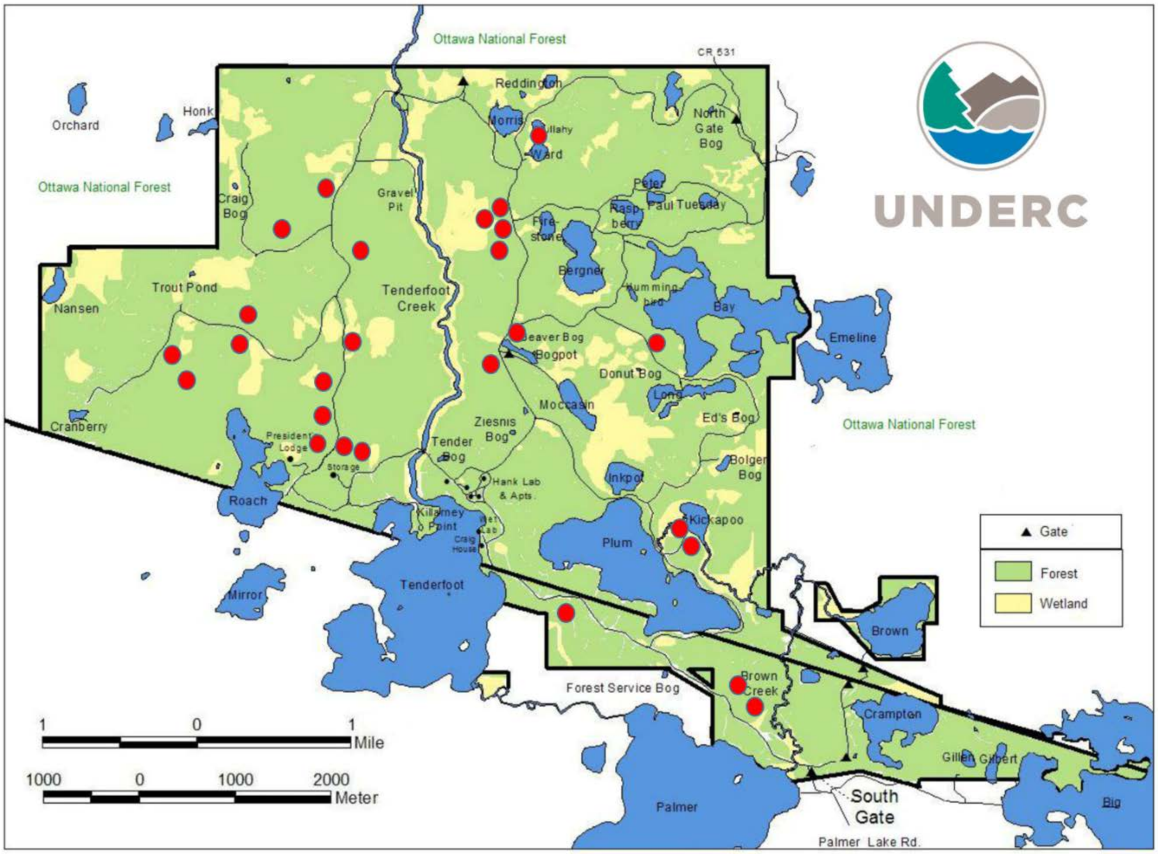

Figure 1. Map of twenty-six canopy gap sites on UNDERC property.

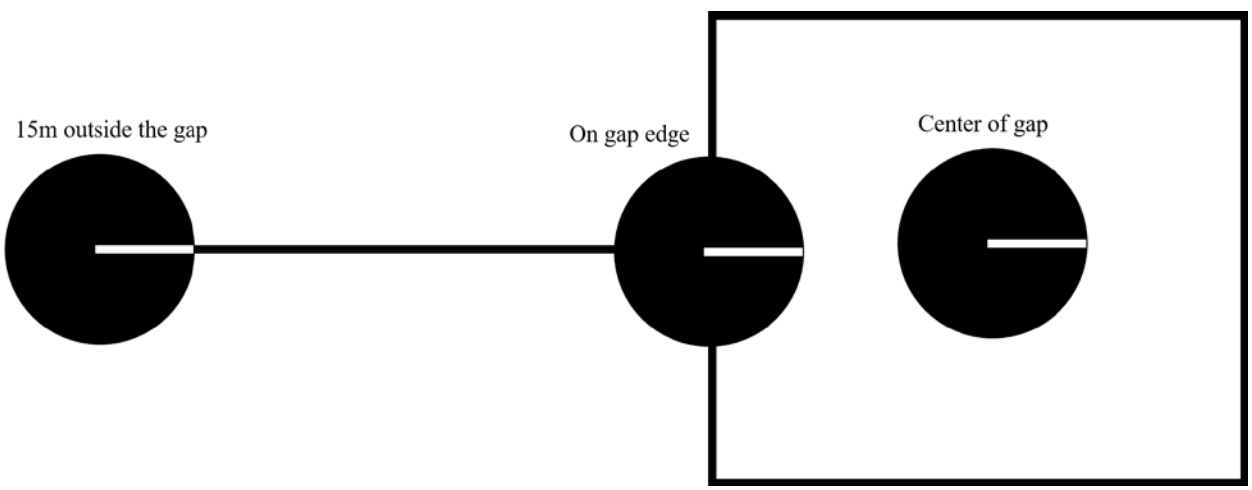

Figure 2. Set up of sampling plots. A 1m radius circle was made in the center, on the edge, and outside each canopy gap. Data for leaf length, stem height, flower presence, and abundance for the three plants was collected in each circle. A random cardinal direction was generated to determine location for circles on the edge and outside the gap.

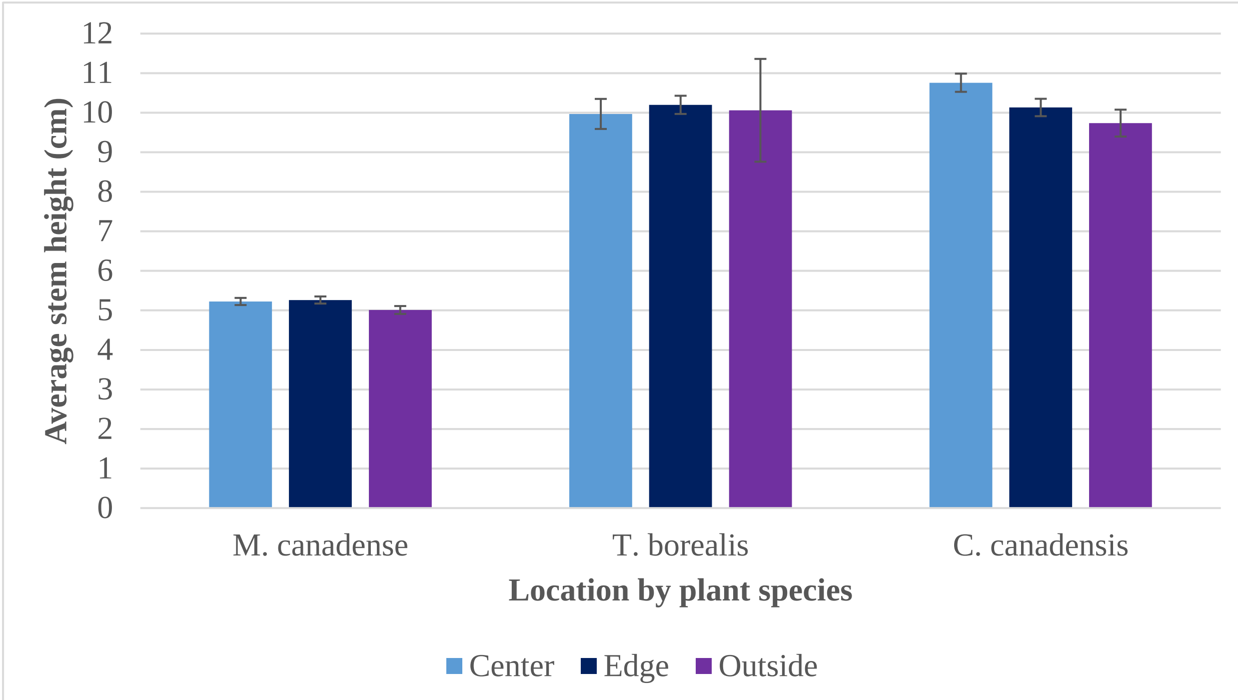

Figure 3. Average stem height of each plant species in each canopy gap site location. There were no significant differences between the locations (*M. canadense,* H_2=5.041, p=0.080; *T. borealis*, F_2=0.15 p=0.86; *C. canadensis*, H_2=5.50, p=0.064).

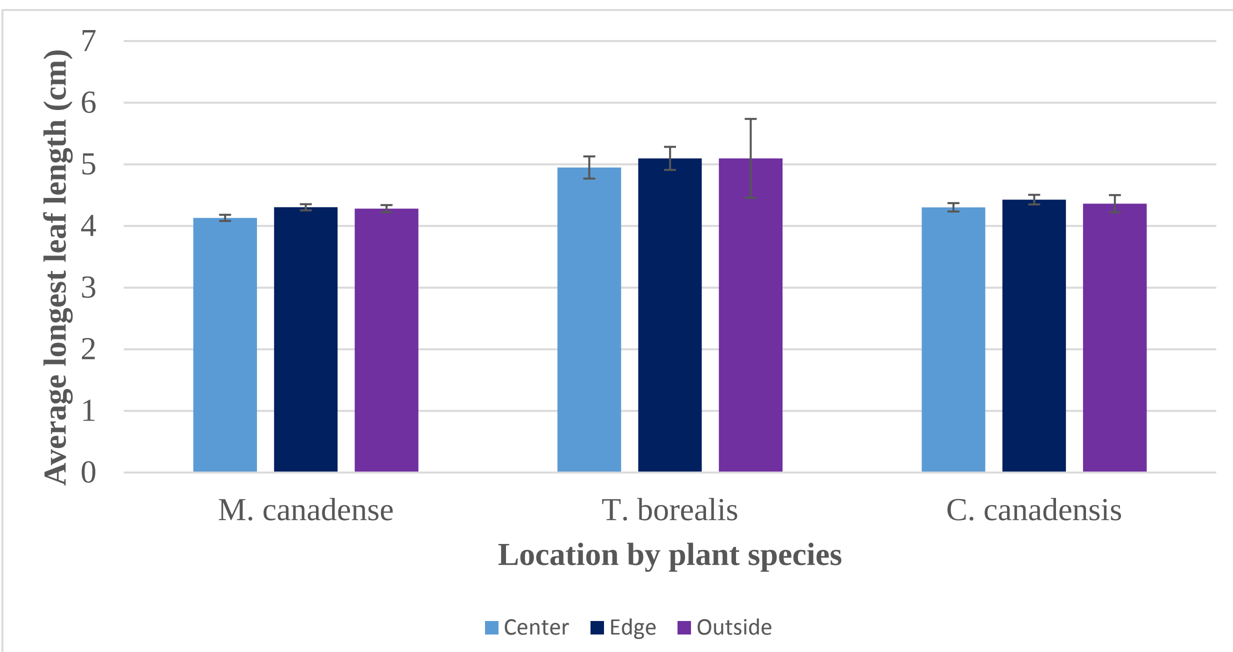

Figure 4. Average longest leaf length of each plant species in each canopy gap site location. There were no significant differences between the locations (*M. canadense*, H_2=5.068, p=0.079; *T. borealis*, H_2=0.304, p=0.859; *C. canadensis*, H_2=1.55, p=0.461).

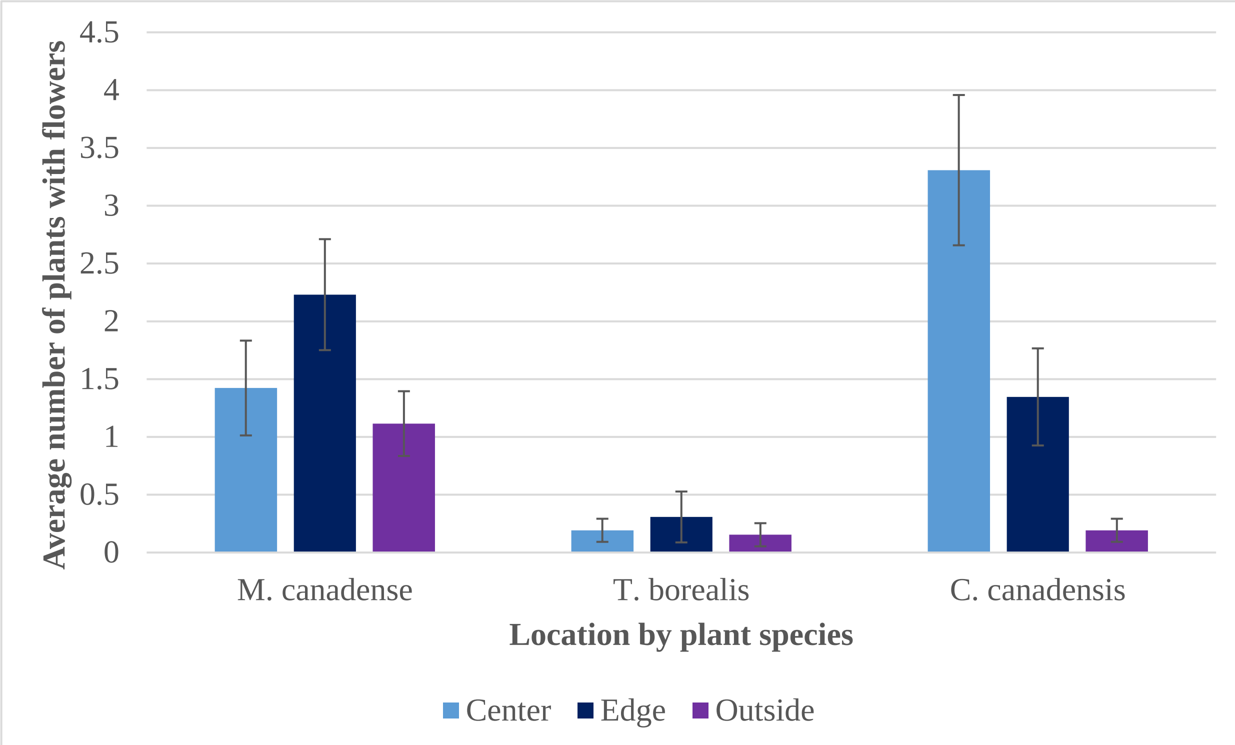

Figure 5. Average number of plants with flowers of each plant species in each canopy gap site location. There were no significant differences between the locations (*M. canadense*, H_2=0.063, p=0.969; *T. borealis*, flowering plant, H_2=1.168, p=0.558; *C. canadensis*, H_2=3.396, p=0.183).

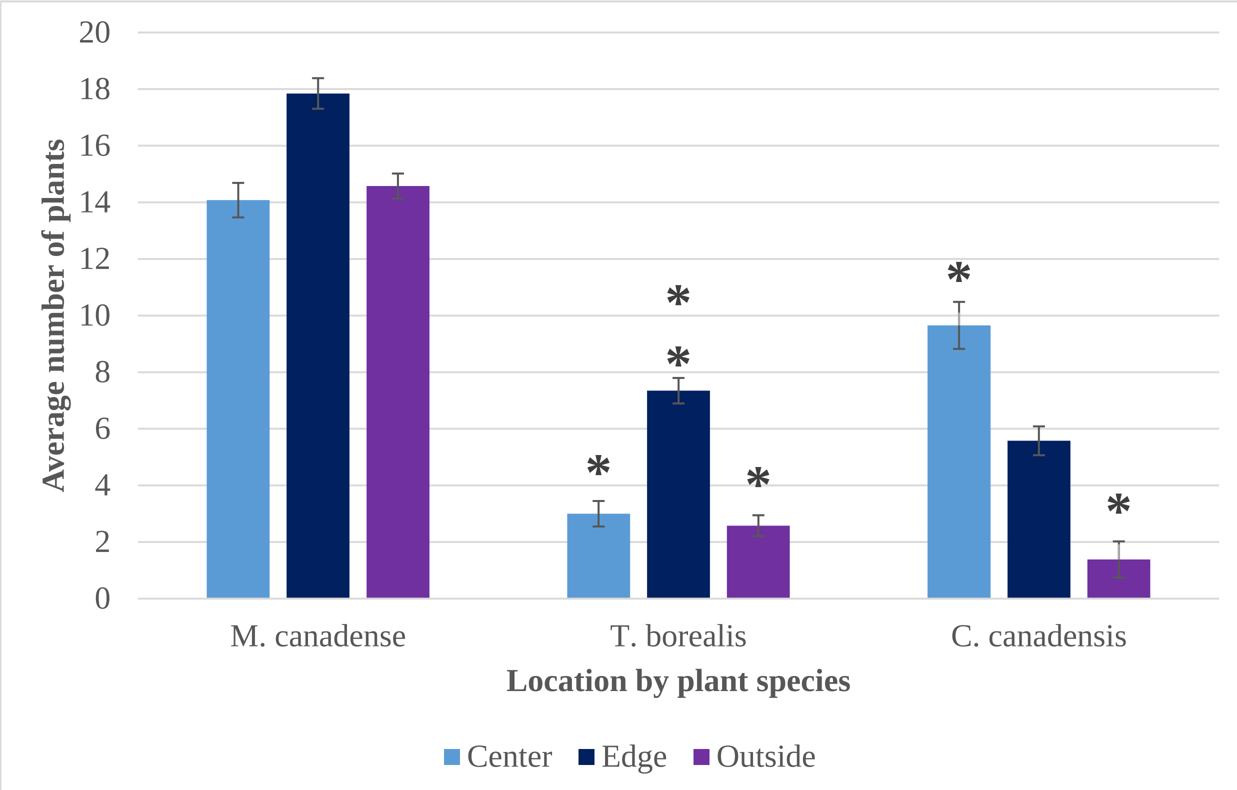

Figure 6. Average number of each plant species in each canopy gap site location. There were no significant differences for *M. canadense* between the locations (H_2=1.637, p=0.441). There were significant differences (denoted by *) for *T. borealis* between edge and center (p=0.021) and edge and outside (p=0.012). There was a significant difference for *C. canadensis* between center and outside (p=0.047).