UNIVERSITÉ DU QUÉBEC À MONTRÉAL

BIRD'S-FOOT VIOLET (VIOLA PEDATA) OPTIMAL MICROHABITAT CHARACTERISTICS IN ONTARIO TALLGRASS PRAIRIE REMNANTS

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DE LA MAÎTRISE EN BIOLOGIE

PAR

MELINDA J. THOMPSON

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UNIVERSITÉ DU QUÉBEC À MONTRÉAL

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THESIS

PRESENTED

AS A PARTIAL REQUIREMENT

FOR THE MASTERS IN BIOLOGY

BY

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Résumé

La violette birds-foot (*Viola pedata*) est une plante herbacée qui occupe les milieux ouverts, perturbés, bien drainés et à sols sableux de l'Est de l'Amérique du Nord. Au Canada, où cette espèce est désignée «en voie de disparition», toutes ses populations se retrouvent uniquement dans le sud de l'Ontario dans des habitats extrêmement rares, les prairies à hautes herbes et/ou savanes de chênes. Les objectifs de cette étude étaient de déterminer les exigences de microhabitat optimales permettant à *Viola pedata* de survivre, fleurir et produire des graines, ainsi que de fournir des valeurs seuil pour recommander des brûlages dirigés ou d'autres formes d'aménagement. Des données détaillées d'habitat, en particulier la quantité de lumière disponible sous le couvert des arbres, les espèces associées, les caractéristiques du sol et le recouvrement de différents types de litière, ont été récoltées dans 180 microquadrats localisés dans quatre populations de *Viola pedata* en Ontario. Ces données ont été utilisées pour évaluer trois catégories de conditions d'habitat de *Viola pedata* (microquadrats avec *Viola pedata*; microquadrats sans *Viola pedata*, mais à proximité de microquadrats avec *Viola pedata*; microquadrats sans *Viola pedata*, mais très éloignés de microquadrats avec *Viola pedata*) dans un site récemment brûlé et dans trois sites non brûlés. Des analyses de régression indiquent que le nombre de feuilles produites par les plants de *Viola pedata* est corrélé positivement avec le pourcentage d'ouverture du couvert arborescent. L'analyse canonique des correspondances révèle que les microquadrats qui contiennent *Viola pedata* sont associés à un pourcentage de sol à nu plus élevé. La perturbation par le feu produit une augmentation du nombre de fleurs et de la vigueur des plants de *Viola pedata*, ainsi qu'une augmentation des probabilités de germination des graines suite à la réduction de la quantité de litière. Les analyses ont déterminé que les facteurs écologiques les plus importants affectant *Viola pedata*, sur tous les sites, étaient le pourcentage d'ouverture du couvert arborescent et de sol à nu. L'ouverture du couvert arborescent affecte directement la survie, la vigueur et la production de fleurs, alors que le sol à nu affecte la régénération et la germination en réduisant la compétition. De ces analyses, il ressort qu'une valeur seuil d'au moins 15 pourcent d'ouverture du couvert arborescent est requis pour assurer la survie d'individus reproducteurs de *Viola pedata* dans le sud de l'Ontario. Les résultats de cette étude seront utilisés pour développer des critères d'aménagement pour la conservation de *Viola pedata* au Canada.

Mots clés : *Viola pedata*, plante menacée, habitat, vestiges de prairie, conservation

Abstract

Birds-foot Violet (*Viola pedata*) is an herbaceous plant that occurs in open, disturbed, well-drained, sandy sites in Eastern North America. In Canada, where it is listed as an Endangered species, all known populations occur in southern Ontario in extremely rare tallgrass prairie/oak savanna habitats. The objectives of this study were to determine the optimal microhabitat requirements for *Viola pedata* to survive, flower and produce seed, and provide threshold values for recommending prescribed burns or other management activities. Detailed habitat data, with a focus on light availability from the canopy, co-occurring species, soil characteristics and litter type cover, were collected from 180 microplots placed at four Ontario populations of *Viola pedata* and used to evaluate three types of habitat conditions (microplots with *Viola pedata*; microplots without *Viola pedata* but nearby microplots with *Viola pedata*; microplots without *Viola pedata* and distant from microplots with *Viola pedata*) at one recently burned and three unburned sites. Regression analyses indicated that the number of leaves produced by *Viola pedata* is positively correlated with percent canopy openness. Canonical Correspondance Analysis showed that plots which contained *Viola pedata* were associated with higher percent bare soil. Fire disturbance produces a definite increase in number of flowers and vigour of *Viola pedata*, as well as an increased chance of successful germination due to the removal of litter. Analyses determined that the most important ecological factors affecting *Viola pedata* at all sites were canopy openness and percent bare soil. Canopy openness directly affects survival, vigour and flower production, while bare soil affects regeneration and germination by reducing competition. From these analyses, it appears that a threshold value of at least 15 percent canopy openness is required to maintain reproducing individuals of *Viola pedata* in Southern Ontario. The results of this study will be used to develop management policies for the conservation of *Viola pedata* in Canada.

Key words: *Viola pedata*, endangered plant, habitat, prairie remnants, conservation

1. Introduction

In Canada, more than 400 animal and plant species are considered "at risk" according to the Committee on the Status of Endangered Species in Canada (COSEWIC). Nearly 40 percent of these species are found in Ontario. In southern Ontario, there is increasing pressure on all natural habitats from agriculture and urban development. Natural habitats that are under pressure include forests, grasslands (including tallgrass prairies), wetlands, and the Great Lakes and their watersheds. In many areas of southern Ontario, the loss or degradation of natural habitats has displaced many wild plants and animals, and many populations known in the past no longer occur.

Tallgrass prairies and savannas are some of the most endangered ecological communities in Canada (Rodger 1998). Tallgrass communities once covered a significant part of southern Ontario's landscape, yet owing to degradation and destruction through urban development, agriculture, pollution and mismanagement, less than three percent of their original extent remains (Rodger 1998).

Diverse assemblages of plants are found in tallgrass communities in southern Ontario. As these communities themselves are rare and threatened, many of the wildlife species that depend on these communities for their survival are threatened in turn. Approximately 156 plants associated with tallgrass communities in Ontario have been granted one or more official rare designations at the global, national, and/or provincial levels (Rodger 1998). One of these species is *Viola pedata*, a species limited to tallgrass prairie remnants in southern Ontario.

1.1 Status of Tallgrass Communities

Tallgrass communities, composed of prairies and savannas, are ecological communities native to central North America, including extreme southern Manitoba and southern Ontario. Prairies are open, generally treeless communities dominated by grasses such as big bluestem (*Andropogon gerardii*), little bluestem (*Schizachyrium scoparium*), and Indian grass (*Sorghastrum nutans*), along with many other native graminoids and forbs (Bakowsky 1993). Savannas are communities dominated by both prairie grasses and open-grown oak trees (Bakowsky 1993).

Historically, tallgrass prairie and savanna covered vast expanses of eastern central North America. These communities are some of the most endangered ecosystems in Canada, part of a vast system of tallgrass prairie and oak savanna communities that once formed a rough triangle extending north into southern Manitoba, south into northeastern Texas, and east into Indiana, southern Michigan and Ontario (Long 2000). Most of the original prairie has been destroyed through conversion to farmland and urbanization (Rodger 1998). In Ontario, the prairie peninsula may more accurately be described as an archipelago, since historically tallgrass communities dotted the landscape throughout the southern part of the province (Goodban *et al.* 1996; Bakowsky and Riley 1994). Tallgrass prairie and oak savanna communities occupied approximately 1000 km^2 of southern Ontario prior to European settlement (Bakowsky, pers. comm.); now less than 21 km^2 exists as small, isolated remnants (Long 2000).

As it is one of the most endangered ecosystems in North America, the imperative to conserve and restore tallgrass communities is clear. While concerted efforts have been going on for some 60 years in the U.S., prairie restoration on a large scale is a relatively new activity in Ontario. However, there has been increasing interest and activity, including the development of a region-wide recovery plan

(Rodger 1998) and the organization of «Tallgrass Ontario» to help provide coordinated leadership to achieve the recovery plan goals (Rodger 1998).

The destruction of tallgrass prairie and oak savanna communities has been a result of urban development, agricultural practices, and mismanagement. Remaining vestiges of tallgrass prairie and oak savanna occur in isolated patches, mostly less than two hectares in size. Many of these remnants occur in and around the open and abandoned spaces within the highly urbanized and agricultural landscape of southern Ontario and face the risk of continued destruction or damage from uninformed planning decisions (Long 2000).

Interest is growing in southern Ontario to preserve and restore these endangered communities as they are becoming recognized as important elements of southern Ontario's natural heritage. The Natural Heritage Information Centre has identified provincially significant tallgrass prairie and savanna remnants for inclusion in a system of provincially recognized and protected Areas of Natural and Scientific Interest (ANSIs) (Long 2000). Tallgrass prairies in North America are given ranks ranging from G3 to G1 (either very rare and local throughout its range or found locally in a restricted range; between twenty-one to one hundred occurrences globally) (Rodger 1998, Natureserve 2004).

It is vital to save all of the prairie remnants since so little native grassland and savanna habitat remains. Opportunities for protection and restoration exist in parks and on lands owned by conservation-minded organizations and individuals. However, we are faced with the realities of a densely populated region, intensively used land, and private land ownership. It is impractical to think that southern Ontario can or will be converted to many extensive tracts of "untouchable" wilderness. Finding practical solutions to bringing back native grassland will involve incorporating it into our working landscape. Getting many involved will have the added benefit of reacquainting people with the native flora and hopefully increasing interest in the natural world (Rodger 1998).

1.2 Light Availability Factor

Light is one of the major environmental factors influencing growth and distribution in plant species (Boardman 1977, Lambers *et al.* 1998), and is a primary limiting resource in forest environments (Frost *et al.* 1986, Hoffmann and Franco 2003, Elemans 2004). Many species are adapted to low light levels, but some herbaceous species evade periods of light limitation in two ways; by growing in treeless gaps or at forest edges where there is more available light, or by growing earlier in the spring before tree foliage is fully developed. Analysis of oak savanna communities in Wisconsin revealed that most species reached peak coverage under sunny or partly shaded conditions, and flowering and fruiting was often skewed towards sunnier microsites (Leach and Givnish 1999).

Tallgrass prairie habitats are characterized by high light availability, low soil nitrogen availability and seasonal water stress, especially after a fire event (Turner and Knapp 1996). Competition for resources, particularly light and water may be very important for individual species. In oak savanna habitats, the amount of light reaching the soil surface can be reduced greatly once the tree foliage has fully developed in early summer. This reduction in light may severely limit plant growth and reproduction because of major reductions in carbon gain (McKenna and Houle 1998).

Light availability can vary on a fine spatial scale within populations and can be substantially reduced for smaller plants, which are shaded by their taller neighbours (Schmitt 1993). The small stature of *Viola* species could make fine scale environmental variation more important for them than it is to larger species (Griffith

1996). In a study of *Viola blanda*, Griffith (1998) found that shading reduced growth and reproduction.

1.3 Other Microhabitat Factors

Rare plants typically have quite specific requirements for survival – unique soils, unique habitats, or restricted distributions (Gaston and Kunin 1997). Understanding the factors that restrict the establishment and growth of such species could aid in conservation efforts by identifying suitable occupied sites for protection or restoration efforts (Schemske *et al.* 1994, Maschinski and Holter 2001, Maschinski *et al.* 2004). According to Hutchinson (1957) the realized niche of a species is smaller than its fundamental niche, and a species may frequently be absent from portions of its fundamental niche because of competition with other species (Pulliam 2000).

Recent studies place emphasis on quantifying the essential and potentially limiting factors in the same sites where population growth rates are measured (Pulliam 2000). Such information is particularly useful in developing successful management strategies for rare and endangered species (Schemske *et al.* 1994, Aleric and Kirkman 2005) before actually establishing what does and does not constitute suitable habitat for the survival and growth of a species (Pulliam 2000).

Most studies of microhabitats have focused on spatial distribution and seed and seedling ecology (Winn 1985; Hilton and Boyd 1996). A number of studies have researched the link between seed germination and seedling establishment to particular safe sites by examining microsite variation in light. Microsite variation in terms of litter depth, physical stresses, microtopography, disturbance, soil temperature, plant density and fire intensity have also been studied (Silvertown and Smith 1989; Griffith 1996; Hilton and Boyd 1996).

Variation can affect plants during many parts of their life cycle, influencing demographic parameters, fitness, and reproduction. The restriction of plants to particular microsites has been explored for a number of species of conservation concern (Boyd and Hilton 1994). According to Menges and Kimmich (1996), small-statured plants may be particularly sensitive to microsite variation, especially in habitats dominated by larger shrubs or trees, which can affect the availability of resources such as water, nutrients, light and space.

To determine a species' ecological niche breadth, the crucial information is the range of conditions (e.g., light, moisture, soil nutrients, and temperature) the species may successfully occupy. These conditions represent the highest and lowest resource states that occur in sites inhabited by viable populations, rather than the mean or frequency distribution of particular environmental states (Sultan *et al.* 1988).

Abiotic resources in habitats are often patchily distributed, with demonstrated allocation of different resource levels to different microsites. If plant growth and reproduction depend heavily on access to specific resources, then plants may only occur on the microsites within a habitat that exhibit certain characteristics. In oak savannas, resources are often irregularly distributed, even at small scales (Leach & Givnish 1999). If resources are irregularly distributed (patchy) and are strongly affecting growth or reproduction, plants may be non-randomly "selecting" sites through germination and establishment with respect to resources. It follows then that microsites in patchy habitats may be unoccupied because the resource levels that they provide are inadequate for survival and reproduction. Conversely, some microsites may be suitable for habitation, but may be unoccupied due to a lack of seed dispersal (Griffith 1998).

It is possible to determine what the ideal habitat conditions are for specific species by studying the environmental variables that are most likely to be limiting to the species. By sampling as many environmental variables as possible from sites which support viable populations of the species, as well as sampling nearby sites that do not support the species, one can determine the significance of small variations in habitat. These small variations can ultimately be the factors that limit a species survival.

Within this framework, we have examined the habitat characteristics of a species associated with tallgrass communities in southern Ontario. Bird's-foot Violet (*Viola pedata*) is considered Endangered in Canada, and occurs only within a few small remnants of tallgrass prairie. The results of this study will allow us to determine the optimal microhabitat characteristics of Bird's-foot Violet habitat in tallgrass prairie habitat remnants in Ontario.

1.4 Study Species

Bird's-foot Violet (*Viola pedata*) is currently designated as Endangered in Canada by the Committee on the Status of Endangered Wildlife in Canada (COSEWIC) (White 2002). This species has a rank of S1 in Ontario, a National rank of N2, and a Global rank of G5 (Conservation status ranks are based on a one to five scale, ranging from critically imperiled (G1) to demonstrably secure (G5). Status is assessed and documented at three distinct geographic scales - global (G), national (N), and state/province (S)). These status assessments are based on the best available information, and consider a variety of factors such as abundance, distribution, population trends, and threats (Natureserve 2004). *Viola pedata* is considered an Endangered species in Ontario and it has recently been regulated under the *Endangered Species Act* (Natural Heritage Information Centre 2005).

1.4.1 Description

The Bird's-foot Violet (*Viola pedata*) is a spring and autumn flowering perennial herb named for its finely dissected leaves, which resemble the splayed toes of a bird. The leaves and stalks rise from a rhizome. The leaves are divided into many sections, which are principally three parted. The lilac or lilac and purple flowers (Figure 1) occur singly at the end of stalks. In Canada, the Bird's-foot Violet flowers from mid-May until mid-June and again from the end of September to mid-October.

1.4.2 Distribution

The Bird's-foot Violet occurs in scattered populations in eastern North America north of Florida: from southwestern Ontario and northern New England, west to Iowa, eastern Kansas, eastern Oklahoma and Louisiana (Natureserve, 2004). It is secure throughout most of its primary range in the United States (Figure 2). In Canada, the Bird's-foot Violet is found only in extreme southern Ontario (Figure 3). The Canadian populations are isolated pockets separated from the main Bird's-foot Violet populations found in the United States. In Ontario, the species occurs in Brant County and Haldimand-Norfolk Regional Municipality (R.O.M. 1997). Seventy-five percent of its historical distribution in Ontario is now eliminated (Natural Heritage Information Centre 2005).

1.4.3 Habitat

Viola pedata grows in open, disturbed, well-drained, sandy sites, and in Ontario, is found only in oak savanna habitats. In southern Ontario, the Bird's-foot Violet is at the northernmost margin of its range. Ontario populations of *Viola pedata* are confined to the Carolinian or Deciduous Forest Region, the warmest and most species-rich hardwood forest ecosystem in Canada (Rowe 1972). Topography is mostly undulating to flat (Rowe 1972). Work done by O'Dell (1996) indicates that site is the most important factor influencing reproduction in *Viola pedata*, affecting flowering, fruiting and seed production. Plants growing in forested sites or openings were found to have fewer flowers per plant, fewer fruits per plant, and fewer filled seeds per fruit than those growing in field edges or meadows (O'Dell 1996).

1.4.4 Biology

Bird's-foot Violet is pollinated by insects such as butterflies and bumblebees (Beattie 1974). This species is believed to be the larval host plant for the Regal Fritillary (*Speyeria idalia)* butterfly, a prairie dependent species. Many tiny, copper-coloured seeds are produced in smooth green capsules. When the capsules open, the seeds are catapulted up to five metres away from the parent plant (Beattie and Lyons 1975). Seeds are often picked up by ants and brought to nests, which reduces predation on seeds and increases the chances of seed germination and seedling establishment (Culver and Beattie 1978).

Possibly because of their dependence on specific soil fungi, Bird's-foot Violets do not transplant well, and relocation of plants is not a management option (R.O.M. 1997). In addition, Bird's-foot Violet is highly sensitive to shading. Even at light intensities where plants are partially shaded, flowering is significantly reduced. This is evident at the Brantford Savanna (Location 1 on Figure 3). Another hindrance to the reproduction of this species is that it does not reproduce vegetatively and it does not produce cleistogamous flowers, as in most violets, making it self-incompatible (Kavanaugh *et al.* 1990; Beattie and Culver 1979).

The type of pollination of a species can also limit reproduction and population growth. Chasmogamy is defined as cross pollination between open flowers, whereas cleistogamy is the self pollination of closed flowers (O'Dell 1996). Waller (1980) determined that average cleistogamous seed mass in *Viola* increased under shaded conditions, a result that has been observed in other herbaceous species. This effect does not occur in *Viola pedata*, as reproduction is limited to chasmogamous flowers. Field and greenhouse experiments by Beattie and Culver (1979) show that in the absence of insect visits, chasmogamous flowers fail to set seed. Beattie (1974) suggests that *Viola pedata* is in transition from sternotriby to nototriby and may experience reduced pollination.

Seed dispersal distance in diplochorous *Viola* species is approximately two metres, from the combined actions of ballistic dispersal and myrmecochory (Culver and Beattie 1978). Mature seed pods of *Viola pedata* explode, spreading the seeds an average of 140 cm (Culver and Beattie 1978). This evidence suggests that distribution within sites is not limited by dispersal.

Myrmecochory also adds to the dispersal of seeds in *Viola pedata*. Ants have been known to move seeds approximately 35 cm (Culver and Beattie 1978). Seed dispersal by myrmecochory often results in seeds remaining in the ants nest after the removal of the elaiosome, which may explain the association of *Viola* species with higher levels of soil phosphorus (Griffith 1996). Research suggests that ant nests exhibit higher levels of phosphorus in comparison to samples of undisturbed soil (Oostermeijer 1989).

1.4.5 Limiting Factors

Historically, the destruction of habitat through the conversion of oak savanna to farmland was the main factor responsible for decline of the Bird's-foot Violet in Ontario. Competition from woody species is also a major problem for this species. In the past, the savannas occupied by Bird's-foot Violet burnt frequently. When European settlers prevented the fires, fire-intolerant woody species of plants started invading savannas, modifying the habitat of this violet. Human activities such as mowing and the use of herbicides are also detrimental to populations of the Bird's-foot Violet. Six historical populations have been extirpated in Ontario due to destruction of critical habitat by agricultural land use. At Turkey Point, it was observed that virtually no *Viola pedata* survived in an area that was used as a path, indicating a high sensitivity to trampling (Kavanaugh, *et al.* 1990).

Seed germination is reportedly relatively poor in *Viola pedata*. Low soil nutrient conditions, full sunlight and ants appear to play important roles in the successful germination of this species (Kavanaugh *et al.* 1990; O'Dell 1996). *Viola pedata* is sensitive to several fungal pathogens and is easily outcompeted by woody plant species (Kavanaugh *et al.* 1990).

1.4.6 Recovery Efforts

Currently, there is no species-specific recovery plan for Bird's-foot Violet. However, this species is listed under the Tallgrass Recovery Plan, which aims to protect and recover tallgrass communities in southern Ontario. In 1994, the Ontario Ministry of Natural Resources implemented a prescribed burn in a small area of Turkey Point Provincial Park to reverse succession towards forest in oak savanna habitat. This burn was not performed specifically for Bird's-foot Violet, but had a beneficial impact on the plant. The Ministry conducted a second burn in 1999 as an activity under the park's Management Plan. No recovery or management actions had been attempted at the other sites prior to 2004.

While a distinct suite of flora and fauna having an affinity to tallgrass communities in southern Ontario can be determined, individual species have dissimilar requirements and tolerances to the range of environmental conditions and processes existing in these communities. In addition, some species at risk have particular management needs that need to be addressed. Schemske *et al.* (1994) recognized that for most rare plant taxa, research to identify the limiting life history stages and the factors affecting them needs to begin before recovery can take place.

2. Study Objectives and Hypotheses

2.1 Objectives

Our objectives were to determine the optimal microhabitat requirements for *Viola pedata* to grow, flower and produce seed, and provide threshold values for recommending prescribed burns or tree/shrub removal. With this knowledge, public agencies will have a better capacity to manage *Viola pedata* populations, and thus lower the threat of extirpation for *Viola pedata* in Canada. Also, we will have quantified the amount of unoccupied suitable *Viola pedata* microhabitat in existing populations. Thus, this project should also contribute to the conservation of *Viola pedata* by:

(1) documenting the ecological characteristics of known populations (survey of *Viola pedata* individuals (demographic categories) and microhabitat (site and vegetation characteristics),

(2) providing necessary knowledge (threshold values) for fire/vegetation removal management or restoration work,

(3) identifying unoccupied suitable habitat (for possible augmentation actions),

(4) providing a solid baseline of information (habitat and ecology) for conservation managers, and,

(5) accomplish, or contribute to the accomplishment of, several of the objectives of the Tallgrass Recovery Strategy.

2.2 Hypotheses

1. We predict that increased light availability will have a positive influence on *Viola pedata* distribution.

Results should reveal a minimum threshold of canopy openness required for *Viola pedata* to occur. Plants that are now surviving below this threshold probably became established when light conditions were more favourable (more open canopy).

2. We predict that increasing light availability has a direct influence on the ability of *Viola pedata* to sexually reproduce.

Results should reveal that a minimum threshold of canopy openness, higher than the threshold for survival (presence), is required for *Viola pedata* to flower and set seed.

3. We predict that soil characteristics within sites will not determine *Viola pedata* distribution and flowering status. However, between sites, soil nutrient characteristics may be linked to higher reproductive output in burned sites.

Light availability should be the determining factor for distribution and flowering status of *Viola pedata*, with soil factors having a secondary or non-significant role. In burned sites, soil factors may influence vigour, flowering and seed set in *Viola pedata*. Such factors may not be detectable if the burn occurred many years ago (pulse of resources occurred right after fire and is no longer detectable by soil analysis, but long term effect on plants may still be seen).

3. Methods

3.1 Study Sites

We conducted in-depth studies of four populations of *Viola pedata* in Southern Ontario. We had planned to study all sizeable populations across the species range, but permission to access the only other large population in Ontario (Brantford) was denied by the landowner. Populations that were studied are listed in Table 1. All are located in the vicinity of Sites 2 and 3 on Figure 3.

3.2 Field Sampling and Soil Sample Analysis

In early May 2004, the four study populations were visited to record flowering of *Viola pedata* plants. A rapid mapping of each population was made in order to include all plants. Sites were visited twice a week from May to September 2004. These plots (approximately 20m X 20m) covered an area including *Viola pedata* plants, but also an area without them (approximate ratio of area with:without, 1:2), in order to include site conditions not favourable to *Viola pedata* (Figure 4). Precise position of each *Viola pedata* plant (flowering and non-flowering) was mapped in 1 m^2 permanent microplots (two corners marked with large nails pushed into soil). For each plant, presence and number of flowers was recorded. In each population, 15 microplots with *Viola pedata* were mapped (Type 1). Microplot position and general site features (trees, large rocks, logs, paths, etc.) were also rapidly mapped (1 cm to 1 m) using a Sonin electronic distance finder and a measuring tape laid out along the longest axis of each plot. The number of flowers and leaves present was recorded for each individual. Later in the summer, each plant was relocated using the maps in order to count the number of large leaves (greater than 2 cm in width).

Our objective was to determine ecological factors in all $1m^2$ microplots containing *Viola pedata* (approx. 60), and in other $1m^2$ microplots within the populations and around them, but without *Viola pedata* (approx. 120 "absence" microplots). In each study population, 15 absence microplots were selected within a core area (minimum distance of 1m from any presence microplot) (Type 2), and 15 more outside of this area, presumably in microhabitats unsuitable to *Viola pedata* (Type 3). "Absence" plot locations were randomly selected from map grid coordinates in each population, in the two categories (core area and periphery). In all microplots ("absence" as well as "presence") the following data and samples were recorded or taken: (1) percent canopy opening, (2) soil samples, (3) vegetation data, (4) soil cover categories (bare soil, litter, moss, etc.). Canopy photos were taken 50 cm above each microplot using a digital camera (Nikon Coolpix 950) equipped with a fisheye lens (Nikon FC-e*). Photos were analyzed using a Gap Light Analysis software package (Version 2.0, Frazer *et al.* 1999) in order to determine percent canopy openness.

Soil samples (400 ml) were air dried and analyzed in the lab for pH, as well as soil cations (K, Ca, Mg, Mn). Soil cations were extracted using the method of Hendershot *et al.* (1993) and concentrations were determined by atomic absorption analysis. Vegetation cover was recorded in each microplot for each vascular species and for species of *Polytrichum* moss. Cover was estimated using seven cover classes (1, 0-1% cover; 2, 1-5%; 3, 5-25%; 4, 25-50%; 5, 50-75%; 6, 75-100%; 7, 100%).

Percent cover was estimated (also in seven cover classes) for the categories of bare soil (%), moss cover (%), cover of organic layer (FH) (%), branch litter (L) cover (%), leaf litter (L) cover (%), and pine needle litter (L) cover (%). Leaf litter thickness (T) (cm) was also measured four times in each microplot and averaged. In addition, all tree and large shrub stems were identified, measured (DBH) and located on site maps. Exact geographical coordinates of each population was recorded (GPS) (Table 1).

3.3 Data Analysis

Canonical Correspondence Analysis (CCA) was applied on a vegetation data matrix and an environmental data matrix for all 180 microplots using the CANOCO v 4.0 software package (Ter Braak and Smilauer 1998). Forty species were analysed to determine how they were associated with the presence of *Viola pedata* and with the recorded environmental variables. A list of species encountered during the study can be found in Appendix 1. Only species that were recorded in more than seven microplots were used for CCA analyses. Environmental variables included in the analysis were pH, bare soil (%), moss cover (%), cover of organic layer (FH) (%), branch litter (L) cover (%), leaf litter (L) cover (%), and pine needle litter (L) cover (%). Confidence interval ellipses were created using Systat software package Version 11. Comparisons between datasets were undertaken using analysis of variance (ANOVA). Bivariate fits were calculated by entering data into an Excel spreadsheet, plotting the data, creating a trendline and displaying its R-squared value.

4. Results and Discussion

4.1 Canonical Correspondence Analysis

Results from the CCA on species and environmental variables indicate that *Viola pedata* was most strongly associated with *Oenothera pilosella, Rumex acetosella* and *Panicum acuminatum. Rumex acetosella* is an introduced species that is commonly found on bare ground, gravel, or sand. Since *Viola pedata* appears to be strongly correlated with the presence of bare soil, it is expected that these species would be associated in disturbed environments. Several other rare prairie plant species, i.e. *Tephrosia virginiana, Phlox subulata* were recorded in the vegetation data and their relationships to *Viola pedata* and ecological factors can be seen in Figure 5.

All of the litter variables which were recorded in the microplots indicate that they are strongly correlated with one another, as they all are generally influenced by the presence of trees (ie. *Pinus strobus, Prunus serotina, Quercus* spp; right side of CCA) in an area. Conversely, environmental variables indicating the absence of litter (FH and bare soil) are correlated with open canopy (absence of trees; left side of CCA). The first axis (horizontal) of CCA is therefore a gradient of very open prairie/savanna environment to the left of the axis, towards a more closed canopy savanna or forest to the right of the axis.

All sampled microplots were plotted on the CCA in order to analyze the relationships between the plot types and the recorded environmental variables (Figure 6). Environmental variable vectors defined non-suitable habitat plots as plots characterized by high levels of various types of litter. Plots with *Viola pedata* appear to be widely scattered but in general were positively associated with open canopy, bare soil, moss cover (which has almost the same characteristics as bare soil for seed germination) and FH cover (soil covered with a thin organic layer). Plots that occurred in *Viola* habitat but which did not contain *Viola* were also scattered but many exhibited characteristics that were not correlated with *Viola* presence, which may explain why these plots have not been colonized.

The relative size of the 75% confidence interval ellipses for each plot type (Figure 6) is an indicator of habitat suitability. Plots in *Viola* habitat that do not contain *Viola pedata* have the largest ellipse, indicating that it has the highest level of habitat variability among the microplots studied. Points from all three plots types fall into the area encompassed by this ellipse. The ellipse which represents plots that are unsuitable for *Viola pedata* is restricted to the right half of the CCA, and overlaps slightly with the ellipse representing plots which contain *Viola pedata*. This overlapping area represents degraded habitat which currently supports *Viola pedata*, but where *Viola pedata* is not likely to survive or reproduce. The smallest ellipse surrounds plots which contain *Viola pedata*, and it is centered towards the left of the CCA. The small size of the ellipse may be an indication that *Viola pedata* has a narrow range of suitable habitat characteristics. This ellipse may also represent the realized niche of *Viola pedata*.

In general, we can observe from the CCA that there are two dominant factors (or at least, two factors related to variables measured) controlling the presence of *Viola pedata* at the study sites: one is the presence of forested vs. open conditions (canopy openness), and the other is the presence of bare soil (bare soil vs. litter). A third factor that might be influencing *Viola pedata* presence is soil pH, since its vector is roughly orthogonal to the open canopy and bare soil gradient of the first axis. However, examining the data reveals that this pH gradient is linked to site differences and not to *Viola pedata* presence or absence.

Some of the recorded environmental variables were evaluated in order to determine if they varied between plot types. Total litter for all plot types was assessed by adding the cover values for percent leaf litter, percent coniferous needle litter, and percent FH (decayed litter). Between plot types, total litter was shown to differ considerably (r^2=0.37, p<0.001); plot type 3 consistently had higher coverage of litter. The percent bare soil was also assessed for microplots by plot type. Bare soil was higher in plots that contained *Viola pedata* (Figure 7). Conversely, an increase in total litter cover was associated with a reduction in percentage of flowering *Viola pedata* plants ($r^2 = 0.12$).

A study of *Prunella vulgaris* conducted by Winn (1985) determined that in general, litter and herbaceous cover inhibited emergence. Emergence is likely inhibited differentially depending on the quantity and composition of litter present at different sites. Tree leaf litter inhibits germination by blocking out light or by physically preventing emergence. O'Dell (1996) noted that *Viola pedata* plants were only found in areas with little or no ground cover in early spring. It is likely that *Viola pedata* has not become established in plots with high percent cover of leaf litter due to a lack of bare soil available for seed germination.

Microsites are not static, as the quantity and distribution of litter and herbaceous cover can change from year to year. Increase in population sizes of rare plants may be achieved by manipulating habitat to increase preferred microsite availability. It seems that much of the habitat near Turkey Point would support growth of *Viola pedata* with the exception of closed canopy forests. Indeed, *Viola pedata* may be solely dispersal-limited in between sites. While growth and survival were greatest in the areas in which *Viola pedata* persists today, the physical environment in terms of light and soil quality suggested the possibility that *Viola pedata* might grow in other areas. This is important knowledge for future population augmentation interventions, as well as attempts at re-establishing *Viola pedata* populations where it once occurred or in other suitable habitats.

4.2 Vigour Ranking

Twelve categories were created in order to rate studied *Viola pedata* populations based on demographic vigour. The *Viola pedata* "presence" microplots were ranked in demographic vigour categories by number of leaves per plant, number of large leaves (greater than 2 cm wide), and total number of flowers present (Table 2). Results indicate that all sites except for St. Williams #2 (SW2) had the majority of individuals categorized as plants having 6-10 leaves in total, with 1-5 of those leaves defined as large leaves. Individuals falling into the category described above were the plants which were most likely to produce flowers; this was true for all sites. It appears as though plants with more than six large leaves will always produce flowers, whereas plants with no large leaves rarely produce flowers.

Plants at Turkey Point #1 (TP1), Turkey Point #2 (TP2) and St. Williams #1 (SW1) were distributed across the demographic vigour categories, with individuals present in both the smaller and larger size classes. A number of plants at TP2 were very large in size, with more than sixteen leaves. TP2 also had the greatest number of small individuals, which may be an indicator of recent recruitment. Plants at St. Williams #2 were almost entirely confined to the smaller size classes. Unlike the smaller plants at TP2, which are likely a result of seed germination, it is probable that individuals at SW2 are small because of decline as a result of lower light levels (diminishing vigour).

Hutchison and Kavanaugh (1994) examined individuals of *Viola pedata* occurring at Turkey Point and Brantford and determined that individual plants of *Viola pedata* are likely to be long-lived. They also suggested that plants require two or more years to become established before flowering. This slow maturation process may reduce the species ability to colonize new areas.

A summary of the numbers of plants, flowers and leaves recorded from each site can be found in Table 3. Preliminary site assessments indicate that the "healthiest" population is that occurring at Turkey Point #2 (TP2). This site exhibited the greatest number of plants and leaves, although not the greatest number of flowers. It is interesting to note that the burn site (TP1) displayed the greatest number of flowers, even though it supported fewer plants overall. Table 4 also shows the difference in demographic data collected at the sites in St. Williams (SW1, SW2). Although each site had a similar number of plants, the number of flowers and leaves differed significantly between these two sites; St Williams #2 (SW2) was definitely the poorest quality.

Results of the *Viola pedata* population sampling indicate that there was a distinct "burn effect" shown for *Viola pedata*, even after a period of 6 years. Fire rapidly releases trapped nutrients within dead plant matter, as well as creating a slightly higher soil pH by releasing alkaline metals (Vogl 1974). This soil alteration may be evident as plants in burned areas may be larger and healthier. *Viola pedata* plants at TP1 (the only burned site) had a greater number of flowers per plant than any other site (Figure 8). There is a definite improvement in abundance of flowers and vigour in *Viola pedata* related to fire disturbance. O'Dell (1996) determined that plants at burned sites also tended to produce greater numbers of seeds than plants growing at unburned sites.

Fire can significantly alter the accumulation of plant litter at a particular site. Burns are successful in removing tree and sub-canopy layers and reducing shrub cover. Burns are also known to increase bare soil cover (Rickey 2004). The build-up of litter can reduce the growth and production of plants, alter species diversity, and create greater competition for space and light within species (Vogl 1974). Percent total litter varied significantly between plots. Absence microplots had significantly more leaf litter, which would hinder the establishment of *Viola pedata* seedlings. Plots that contained *Viola pedata* had significantly higher percent bare soil. Plots that were in *Viola* habitat but which did not contain *Viola pedata* had less percent bare soil than those containing *Viola pedata*.

A significant role for fire as a disturbance mechanism maintaining the environmental conditions required for pioneer plant species, and promoting habitat renewal in grasslands is well documented from several studies (Vogl 1977, Bazzaz 1983, Grime 1987, Abbadie *et al.* 1992, Sinclair *et al.* 1995). Following a fire, there is often a flush of growth (Ehrenreich and Aikman 1963). This is a result of increased nutrients, made available by the burning of living and dead biomass. These nutrients become available due to mineralization (release by burning), or because of an increase in soil pH (Ehrenreich and Aikman 1963, Stock and Lewis 1986, Whelan 1995). Post-burning effects include increased incident light conditions, higher temperature, higher water availability due to reduced transpiration, and reduced competition (Ehrenreich and Aikman 1963). The fact that fire can alter the outcome of plant competition, invasion and succession (Vogl 1977, Rowe 1983), suggests that fire frequency could be manipulated as part of an integrated restoration program.

4.3 Canopy Openness

Results of the bivariate analyses indicate that the number of leaves per microplot (with presence of *Viola pedata*) is positively correlated with percent canopy openness (Figure 9). Mean percent canopy openness varied between sites, with SW2 having the lowest average canopy values and SW1 and TP2 having the highest values (Figure 10a). Between plot types, canopy openness was significantly higher in plots that were in *Viola* habitat (no difference between presence and absence plots) than in those that were in adjacent "unsuitable" habitat (Figure 10b).

In this study, canopy openness of greater than 15% was associated with the greatest increase in percent of plants flowering and number of leaves present in *Viola pedata* (Figure 9 and Figure 11). Nutrient levels in all the savanna habitats sampled were very similar to each other (see section 4.4 Soil Factors). Clearly, an increase in nutrients (presumably caused by burning) would enhance the vigour of *Viola pedata*, which in turn might enhance reproduction and viability, but it would also enhance the vigour of some herbaceous competitors.

As part of his research on seed production, O'Dell (1996) artificially shaded plants in order to test the effects of light levels on reproductive output. O'Dell (1996) determined that site was the most significant independent variable affecting the reproductive characteristics of *Viola pedata*. O'Dell (1996) reported that *Viola pedata* plants growing in forested areas had significantly fewer flowers per plant than plants growing in cleared sites. Artificially shaded plants differed from un-shaded plants in respect to flower number, fruit number and average filled seed mass. Plants growing in forested sites also produced fewer filled seeds per fruit. These differences were attributed to the decreased amount of sunlight reaching the plants.

Hutchison and Kavanaugh (1994) investigated the effects of shading on *Viola pedata* at Turkey Point and at Brantford. They determined that even low-density oak canopies are sufficient to eliminate *Viola pedata*. In addition, they observed that even small amounts of shading were sufficient to reduce the number of flowering individuals in a population. Hutchison and Kavanaugh (1994) did not measure actual light levels, but did observe that plants were less likely to occur in shaded habitats, and that plants were less likely to flower under shaded conditions.

A "shade effect" is visible between the two sites located within St. Williams forest tract. Although the sites are less than 1 km apart and have similar numbers of plants, there is a marked decrease in flowering and number of leaves at SW2. SW2 was the most shaded site sampled during this study (Figure 10). It is likely that the plants at SW2 were established at a time when the canopy was more open. The plants appear to be surviving but are suffering from low levels of light, which is leading to diminished vigour, including reduced flowering, reduced plant size (number of leaves) and reduced reproduction (Table 4). A shade effect was also noted at the Brantford population where the number of flowers per plant was very low (Hutchison and Kavanaugh 1994).

As *Viola pedata* leaves remain green throughout the year, it was speculated initially that this might allow them to take advantage of more light for their growth as compared to grasses and other understory herbs early in the season before leaf out of the forest canopy. However, the number of large leaves present was reduced in shaded sites (SW2, TP1). The narrowly divided structure of the leaf of *Viola pedata* would allow for even less light capture, especially where only small leaves are present.

The absence or elimination of *Viola pedata* from shaded sites can be explained not only by the reduction in available light, but also by additional factors such as competition in the ground layer, litter accumulation and litter burial. Many studies have suggested that litter burial frequently becomes an important recruitment constraint for open-dune species during old-field succession (Lichter 2000). In *Viola pedata,* vulnerability of seedlings to light limitation may be increased by burial in litter falling over the year. This may be compounded by the fact that oak leaves are large and have a very slow rate of decomposition. It is also suggested that tolerance-based competitive strategies are best expressed in habitats with more litter accumulation and less disturbance (MacDougall and Turkington 2004). Findings of

Fynn *et al.* (2005) suggested that *Themeda triandra*, a litter and shade-intolerant small herb, shows a 'suppression-based' competitive strategy, requiring regular disturbances to reduce shading and remove litter. This would appear to be very similar to the competitive strategy of *Viola pedata.*

4.4 Soil Factors

Mean pH values for each site are presented in Table 5. Analyses indicate a significant difference ($r^2=0.57$, $p<0.0001$) for pH between sites, but no significant difference between microplots with and without *Viola pedata*. The soil pH values were highest at TP1, likely due to past burning, and TP2, possibly due to disturbance or fertilizer application. TP2 is located within Turkey Point Provincial Park, directly adjacent to a day use picnic area. Parts of the site have been used to dump brush. This area was mown continuously during the summer months until 2001 after which the practice was discontinued. Average pH values recorded at St. Williams were very similar to each other.

Soils were analyzed in order to determine values for Mn, Ca, Mg, and K. Table 5 shows the range of values and mean values of the soil variables (major cations) collected for the presence and absence plots for all sites. Absence plots at SW1 exhibited higher mean levels of potassium and manganese (Table 5). The soils at SW1 have never been disturbed. High levels of calcium at TP2 can likely be attributed to the addition of fertilizer (lime) to the nearby mown lawn areas. No clear pattern emerges in relation with soil nutrients and *Viola pedata* presence.

Analyses of microhabitats occupied by *Viola blanda* performed by Griffith (1996) determined that soil samples taken beneath the violets had more phosphorus, while the soil beneath random points had more magnesium. Soil samples taken during this study were not taken from beneath plants as caution was taken not to damage plants during the study.

Many studies in which soil cations at burned sites were measured (Knoepp *et al.* 2004, Binkley *et al.* 1992, Lynham *et al.* 1999) indicate that concentrations of soil extractable cations (Ca, Mg, K) increase after a burn. Increases in these cations can vary with the intensity and frequency of burning. No significant difference was determined between cations measured in the burned site (TP1) and the non-burned sites during this study. The increase in soil cations that may have occurred at TP1 after the fire is no longer quantifiable because of the number of years that have passed since the burn.

This study highlights the role of habitat-specific factors on *Viola pedata*, and reveals the effects of light availability and litter accumulation levels on survival and growth of this endangered species. The tolerance of this species to the range of conditions found at sites near Turkey Point reflects its fundamental niche. Our findings suggest that *Viola pedata* would only be able to inhabit a narrow range of habitats and microhabitats within Ontario, as is confirmed by its present distribution. *Viola pedata* plants respond to environmental conditions in a manner that supports other assessments of the suitability of the current habitats within Ontario, from optimal habitat (open prairie or recently burned savanna), through sub-optimal (unburned savanna) to unsuitable (forest). Although light is a critical factor for reproduction, low light levels do not necessarily result in immediate extirpation of *Viola pedata* from sites.

A limitation of the present investigation is that populations throughout the North American range of *Viola pedata* were not studied. Therefore, we are not able to fully document the variable habitats or climates in which this taxon occurs. Nevertheless, the limiting factors of specificity of habitat, lack of flower production, and limited colonization of new habitat are primarily responsible for the few populations present in southern Ontario, and are the most likely reasons why *Viola pedata* is rare in Canada.

5. Conclusion

The most important findings of the present study are:

1. The presence of leaf litter on the soil surface will hinder growth and reproductive capability of *Viola pedata.*
2. Areas that have greater than 15% canopy openness increase flowering and therefore improve the possibility of successful reproduction for *Viola pedata.*

In defining habitat requirements for an endangered species, it is useful to determine its edaphic and climatic tolerances, such as nitrogen supply, soil pH, tolerance to drought, and shade (Ellenberg and Mueller-Dombois 1974), and to track floristic changes in the surrounding plant communities (Grime 2001). The objectives of this study aimed at identifying optimal conditions for the survival and growth of *Viola pedata,* but the same niche-based methodological framework could readily be applied to other species. Processes causing extinction at a local scale may be very complex; therefore, even within a single species the particular causes of extinction are not always the same at all sites (Grime 2001). It will therefore be important for the protective management of *Viola pedata* to continue the surveys initiated by this study, in order to detect (and anticipate) symptoms of declining vigour at different sites.

Clearly survival, vigour, and reproduction in *Viola pedata* in Canada depend on the availability of sites where its particular niche requirements are best met (Higashi 1993, Brown *et al.*1995, Anthony and Connolly 2004). This work supports the notion that plant species segregate along one or more environmental niche axes (Silvertown 2004), in this case axes correspond to light and bare soil availability. It is important that sites in the vicinity of existing sites that have close to ideal conditions should not be overlooked, as they may serve as suitable habitat if conditions are improved or if seeds of *Viola pedata* are sown. At the nearby James Property, *Viola pedata* was located after a burn, where previously it had not been recorded (G. Buck, pers. comm., 2004). It is possible that *Viola pedata* seeds have long soil seedbank viability, and that they will germinate in the future if conditions become favourable (nutrient flush signal following fire, or light quality changes perceived by seed).

Sites currently occupied by *Viola pedata* will undoubtedly continue to change as succession progresses. The savanna at Turkey Point #1 (TP1) and the degraded savanna at St. Williams #2 (SW2) (the successional savanna sites) require close monitoring to detect the point where *Viola pedata* is experiencing more than 85% shade, as growth and reproduction will be greatly reduced. Noting that stress from competition will be added to effects of low light, managers should probably become concerned if light levels reach less than 10% canopy openness. At that point, either thinning of the surrounding canopy or burning of the site would be advisable. The population of *Viola pedata* at SW2 was doubly shaded, first by the canopy and secondly by bracken fern (*Pteridium aquilinum*). This secondary shading would not be eliminated by canopy thinning, but might be reduced through burning.

The survival of healthy populations of *Viola pedata* in southern Ontario is threatened in several ways. Natural disturbances within the habitat may not create enough favourable microhabitats within extant populations to maintain viable populations. Progressing succession and forest closure caused by fire suppression will continue to have adverse effects on *Viola pedata*. Additionally, several populations are extremely small in area, which increases the chance of destruction of a population by a single catastrophic event. It is essential that the remaining populations of *Viola pedata* be properly protected and managed to ensure their long-term survival.

Table 1: *Viola pedata* study populations, locations and burn sites.

Study Populations	Geographical Coordinates (UTM NAD83)	Burn Status
Turkey Point Provincial Park #1 (TP1)	17 T 553979 4728535	Burned in 1999
Turkey Point Provincial Park #2 (TP2)	17 T 554842 4728056	Not Burned
St. Williams Forestry Station #1 (SW1)	17 T 553642 4728390	Not Burned
St. Williams Forestry Station #2 (SW2)	17 T 553559 4728532	Not Burned

Table 2. *Viola pedata* abundance and flowering status among two types of vigour indices (number of leaves per plant; number of large leaves per plant). Data recorded in 15 microplots at each of four Ontario populations.

Turkey Point #1		Leaves per Plant			
		1-5	6-10	11-15	16+
Number of Large Leaves	0	p=36 f=2	p=4 f=2	p=1	
	1-5	p=32 f=10	p=56 f=34	p=6 f=7	p=2 f=2
	6+		p=14 f=11	p=11 f=10	p=5 f=5

Turkey Point #2		Leaves per Plant			
		1-5	6-10	11-15	16+
Number of Large Leaves	0	p=73 f=2	p=12		
	1-5	p=33 f=10	p=104 f=45	p=15 f=12	p=5 f=2
	6+		p=13 f=10	p=23 f=18	p=9 f=9

St. Williams #1		Leaves per Plant			
		1-5	6-10	11-15	16+
Number of Large Leaves	0	p=33	p=9 f=1		
	1-5	p=26	p=39 f=14	p=11 f=8	
	6+		p=4 f=3	p=12 f=11	p=16 f=13

St. Williams #2		Leaves per Plant			
		1-5	6-10	11-15	16+
Number of Large Leaves	0	p=59 f=2	p=2		
	1-5	p=44 f=4	p=42 f=15	p=5 f=3	
	6+			p=4 f=3	p=1 f=1

p = number of plants
f = number of plants with flowers

Table 3. *Viola pedata* abundance, flowering status and leaf number summary for four study populations (totals for 15 microplots per site/population).

Site	Number of Plants	Number of Flowers	Number of Leaves	Number of Large Leaves
TP1	167	256	1167	520
TP2	287	217	2090	833
SW1	150	176	1247	483
SW2	157	27	769	272

Table 4. Mean soil pH values for *Viola pedata* study populations and microplot type.

Site	Plots with *Viola pedata*	Plots in *Viola pedata* habitat, but no plants	Unsuitable habitat plots
TP1	4.7	4.7	4.6
TP2	5.2	5.2	4.9
SW1	4.2	4.3	4.4
SW2	4.4	4.5	4.5

Table 5. Comparison of soil cations for presence and absence plots located within *Viola pedata* habitat at four study populations. Means are presented with the range in parentheses.

a) Presence plots

	TP1	TP2	SW1	SW2
K (ppm)	36.6 (16.7-59.7)	48 (6.8-96.2)	48.7 (26.6-83.3)	46.0 (13.5-128.9
Mg (ppm)	39.0 (17.0-77.8)	59.3 (19.4-146.3)	48.5 (23.0-111.2)	42.8 (12.2-191.1)
Mn (ppm)	30.5 (10.4-136.5)	16.7 (1.8-40.3)	60.0 (11.2-180.7)	44.7 (2.0-169.0)
Ca (ppm)	4821.2 (2027.6-10298.4)	10300.6 (2361.6-22765.3)	6090.6 (3106.6-13800.1)	4944.2 (1330.3-21038.1)

b) Absence plots

	TP1	TP2	SW1	SW2
K (ppm)	39.0 (28.0-85.3)	51 (9.4-119.3)	84.4 (33.9-191.7)	38.9 (20.9-75.4)
Mg (ppm)	44.0 (14.5-84.0)	64.2 (9.5-182.6)	55.6 (27.4-99.7)	42.1 (19.5-66.6)
Mn (ppm)	26.6 (14.6-43.6)	18.4 (-2.6-72.1)	74.7 (15.8-138.5)	45.0 (12.5-94.2)
Ca (ppm)	5789.1 (1295.4-12150.4)	11089.7 (1377.9-34898.1)	6606.2 (2902.9-14594.4)	5205.7 (1619.2-13219.0)

Figure 1. Flower of *Viola pedata* (photo by M.J. Thompson).

Figure 2. Distribution of *Viola pedata* (based on White 2002). Populations studied are at the northern edge of the species range in North America.

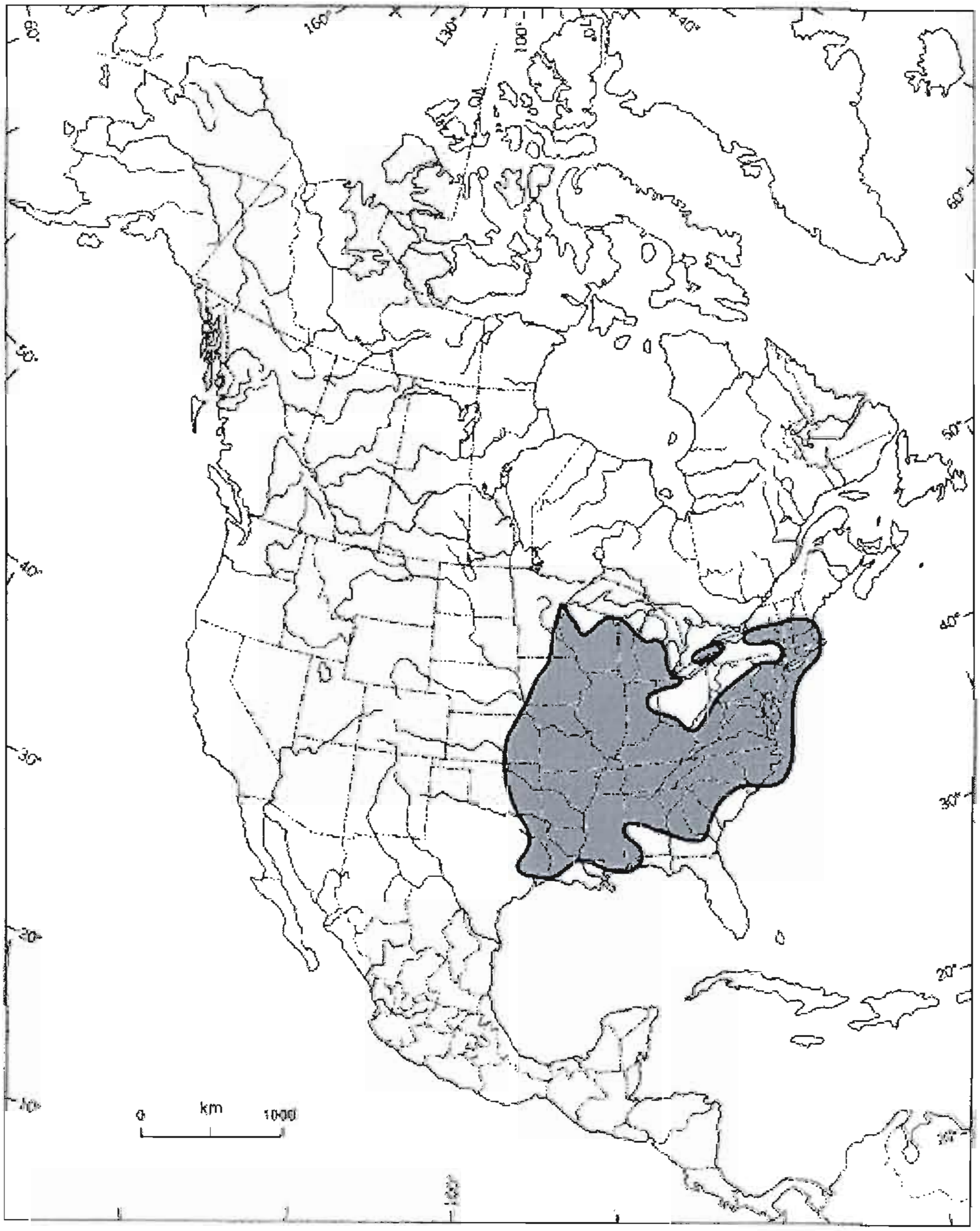


Figure 3. Current distribution of *Viola pedata* in Ontario (Based on White, 2002). Sites 2 and 3 (Turkey Point and St. Williams) were investigated during this study. Permission to access Site 1 (Brantford) was denied. The population at Site 4 was considered too small for the purposes of the study.

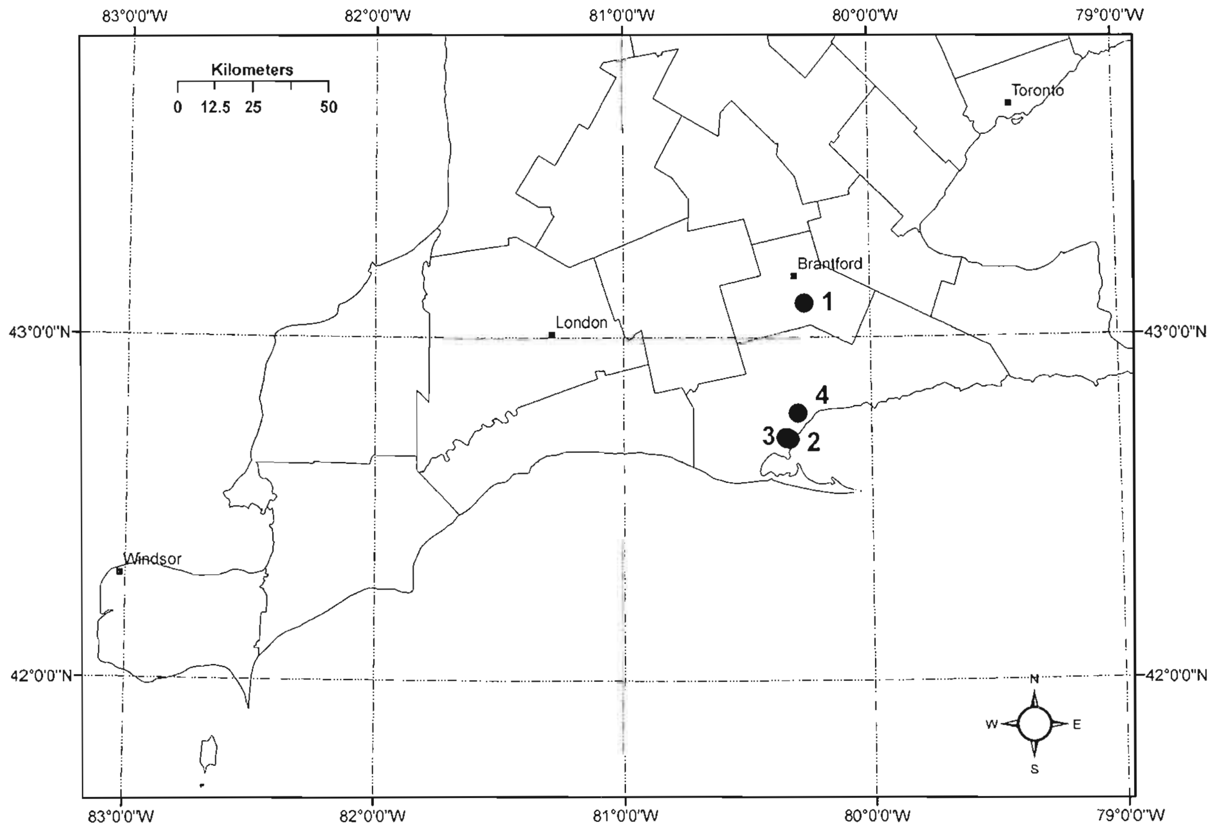


Figure 4. Example of microplot positioning. Diagram detailing the exact positioning of microplots at Turkey Point #1 site. A similar diagram was prepared for each of the study sites.

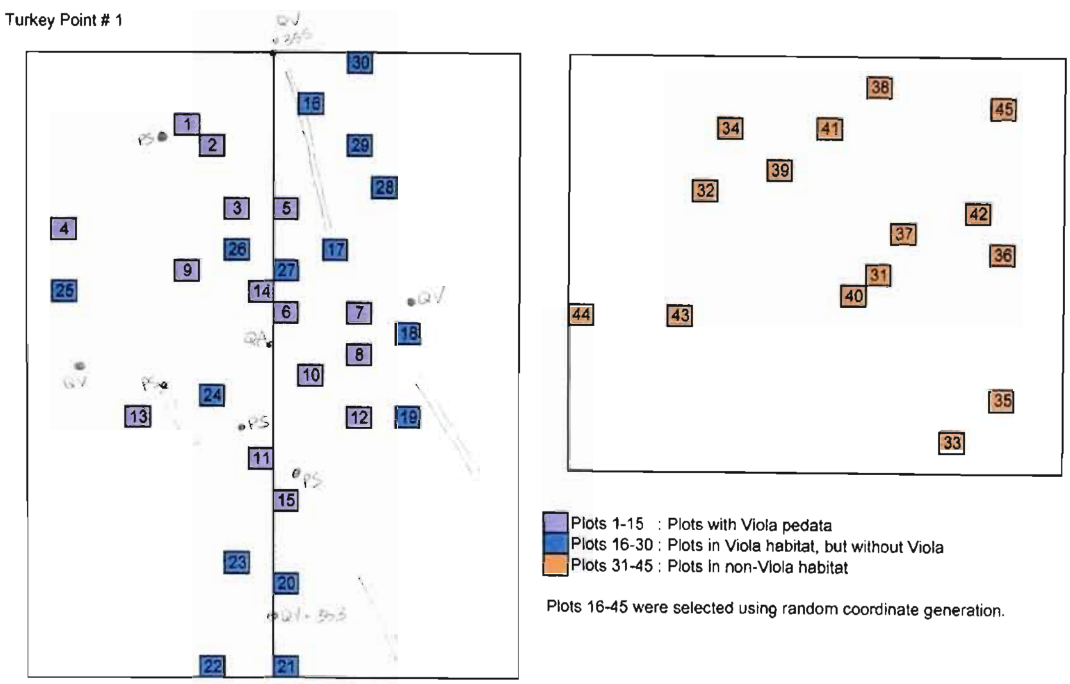


Figure 5. Canonical Correspondence Analysis (CCA) of plant species and environmental variables in *Viola pedata* population sites. Environmental variables: soil pH, canopy openness (%), bare soil (%), moss cover (%), cover of organic layer (FH) (%), branch litter (L) cover (%), leaf litter (L) cover (%), pine needle litter (L) cover (%), leaf litter thickness (T) (cm).

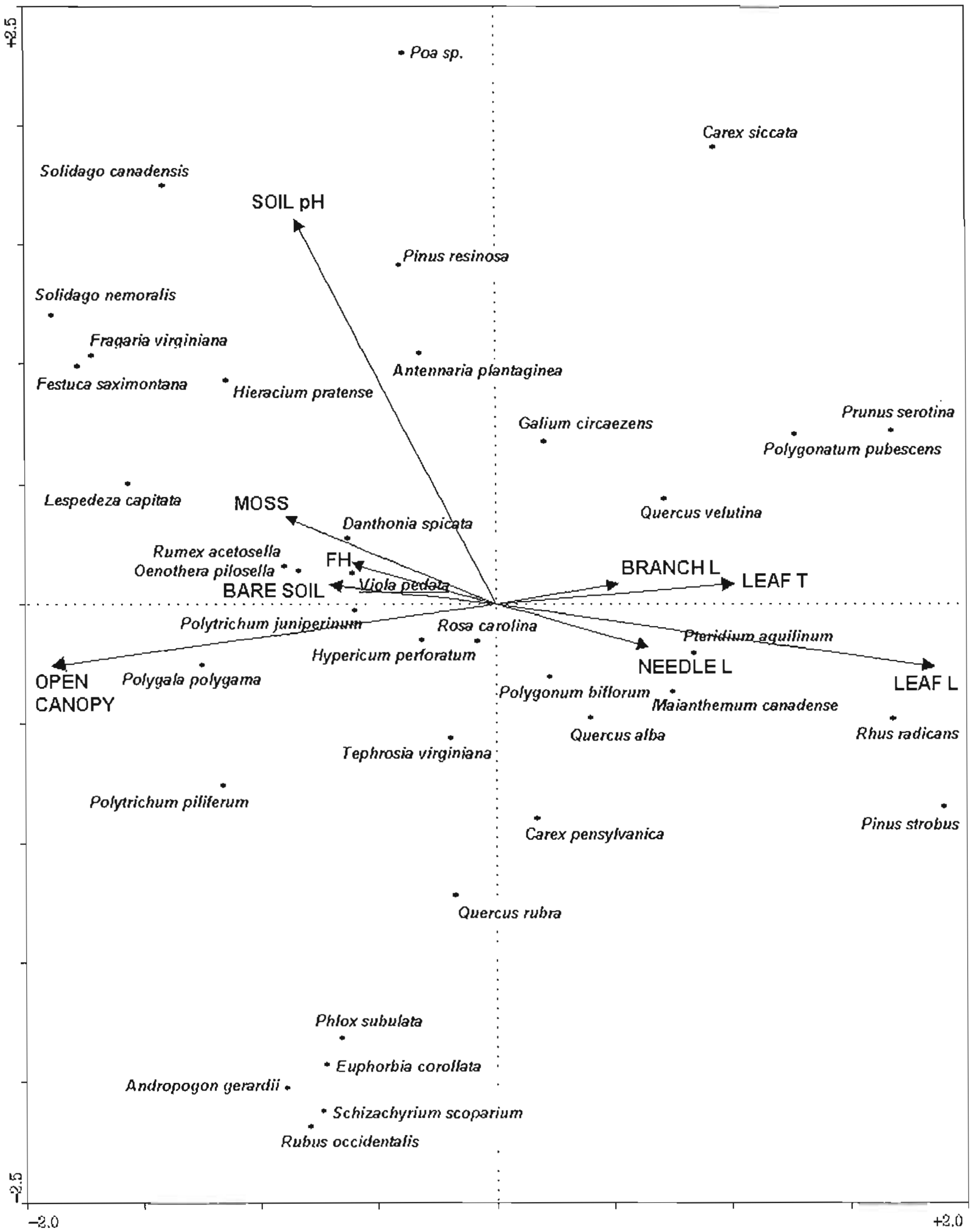


Figure 6. Canonical Correspondence Analysis (CCA) of plot types and environmental variables in *Viola pedata* population sites. a) each point represents one microplot. b) ellipses represent 75% confidence intervals for plot types. See Fig. 5 for a list of environmental variables.

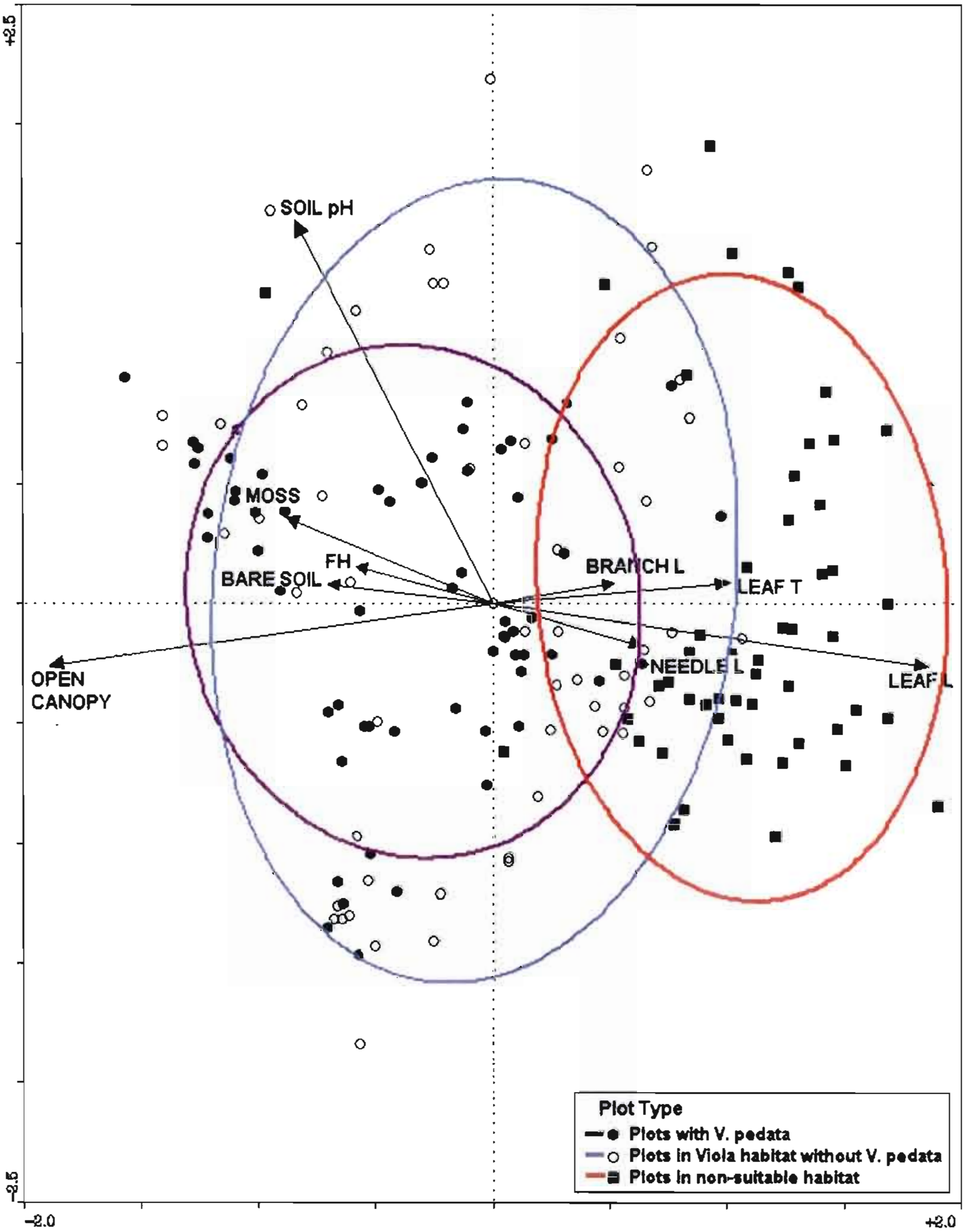


Figure 7. Percent cover of bare soil according to microplot type. Microplot types: plots with *Viola pedata*; plots in *Viola* habitat without *Viola pedata;* plots in non-suitable habitat.

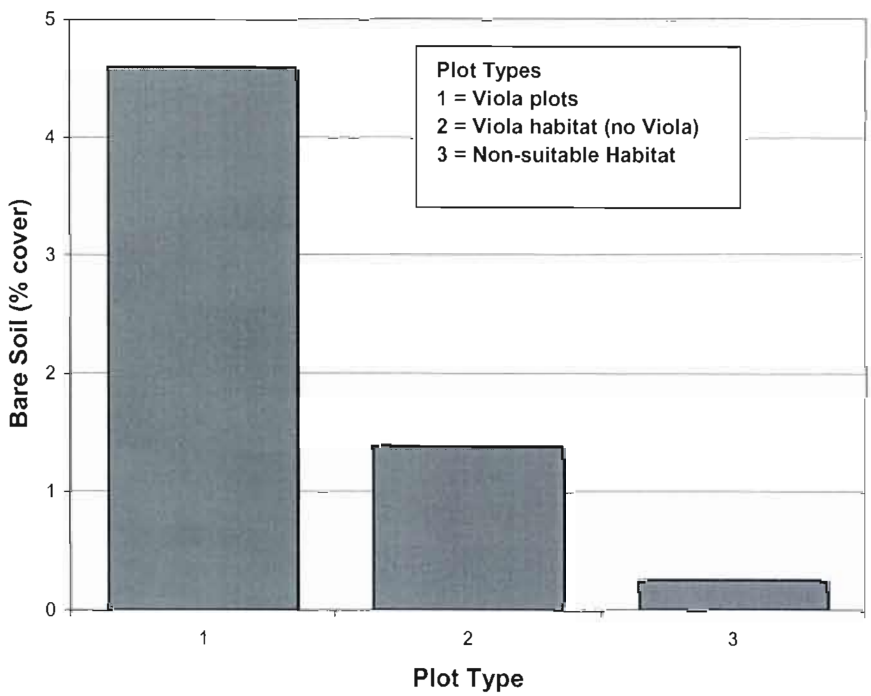


Figure 8. Proportion of flowering to non-flowering *Viola pedata* plants by site.

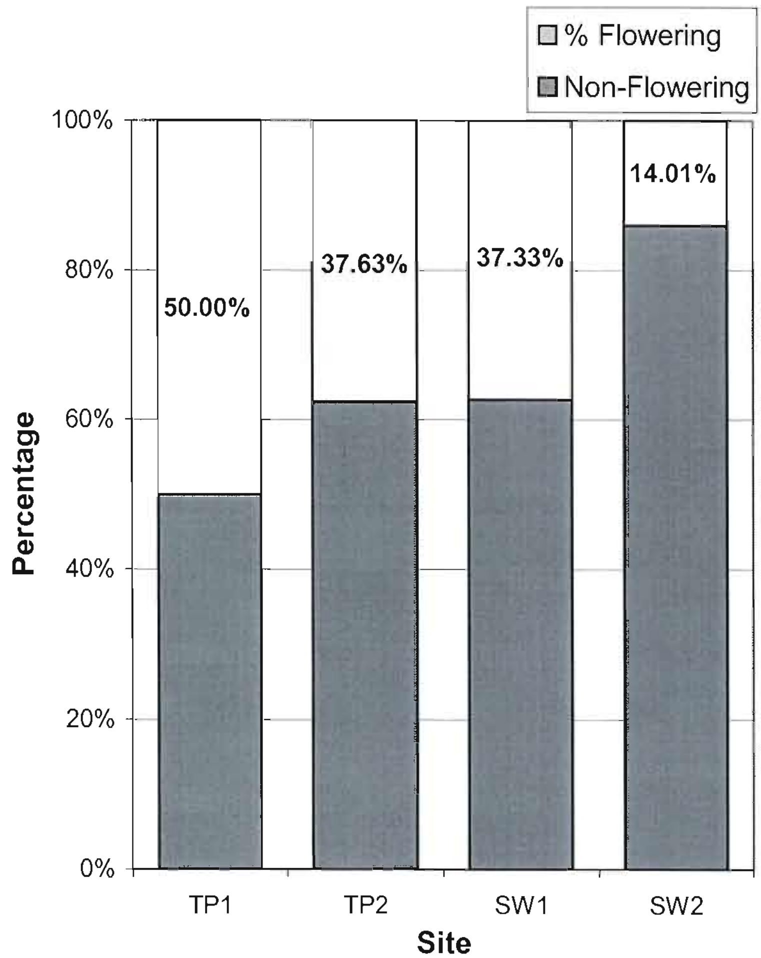


Figure 9. Bivariate fit of number of leaves of *Viola pedata* per microplot vs percent canopy openness in *Viola pedata* population sites. Points represent all microplots with *Viola pedata* sampled in 4 sites.

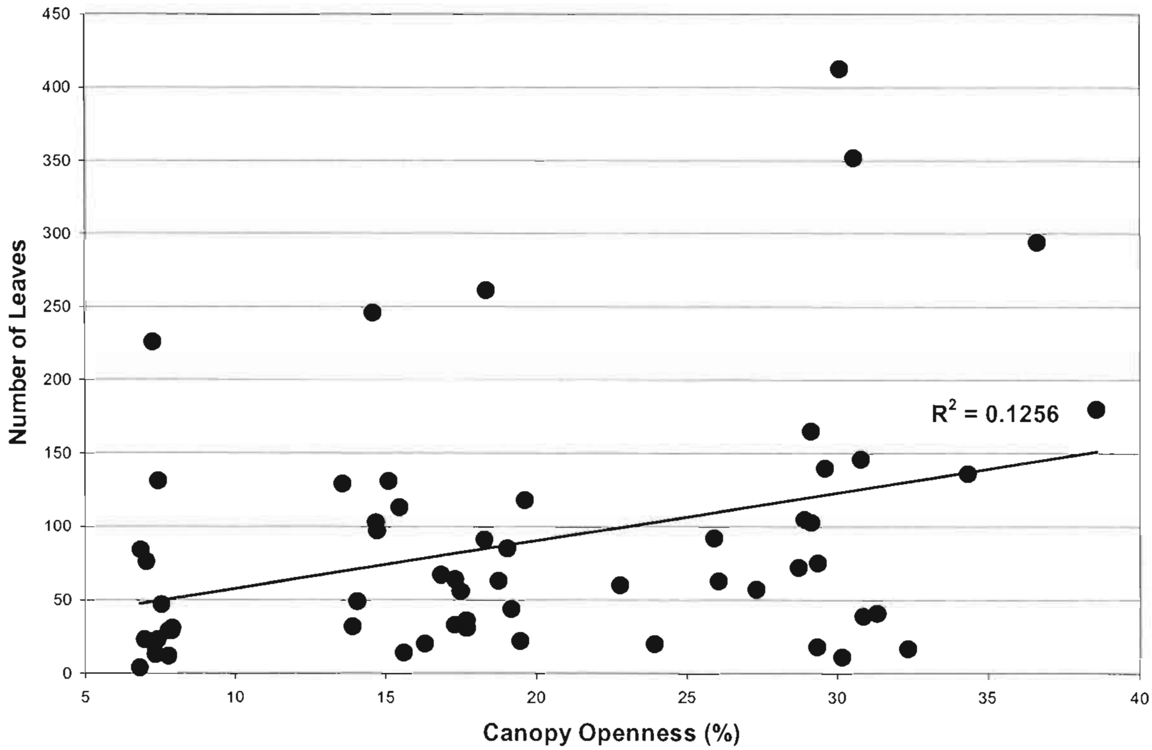
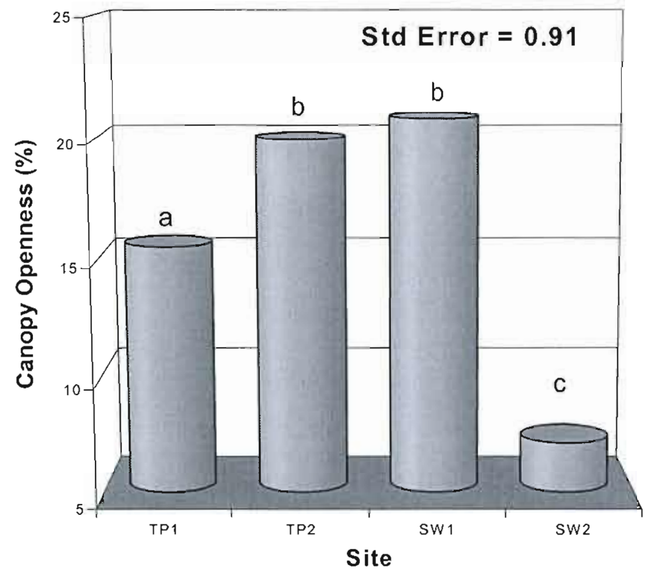


Figure 10. Comparison of canopy openness among sites (A) and between plot types (B).

A)



B)

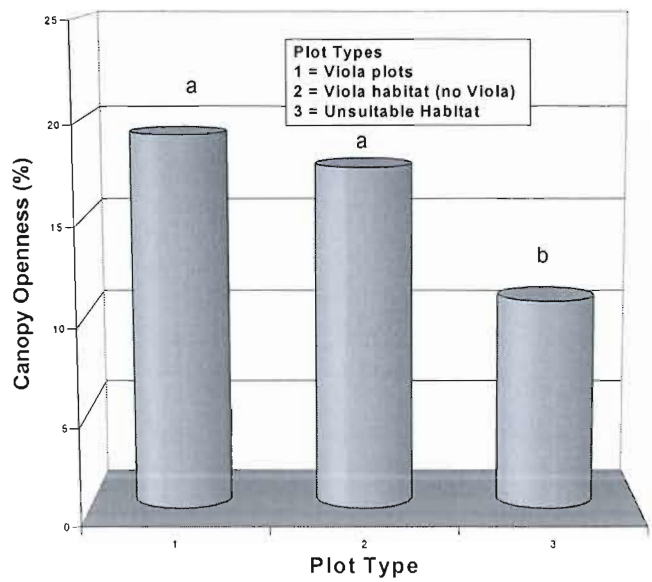
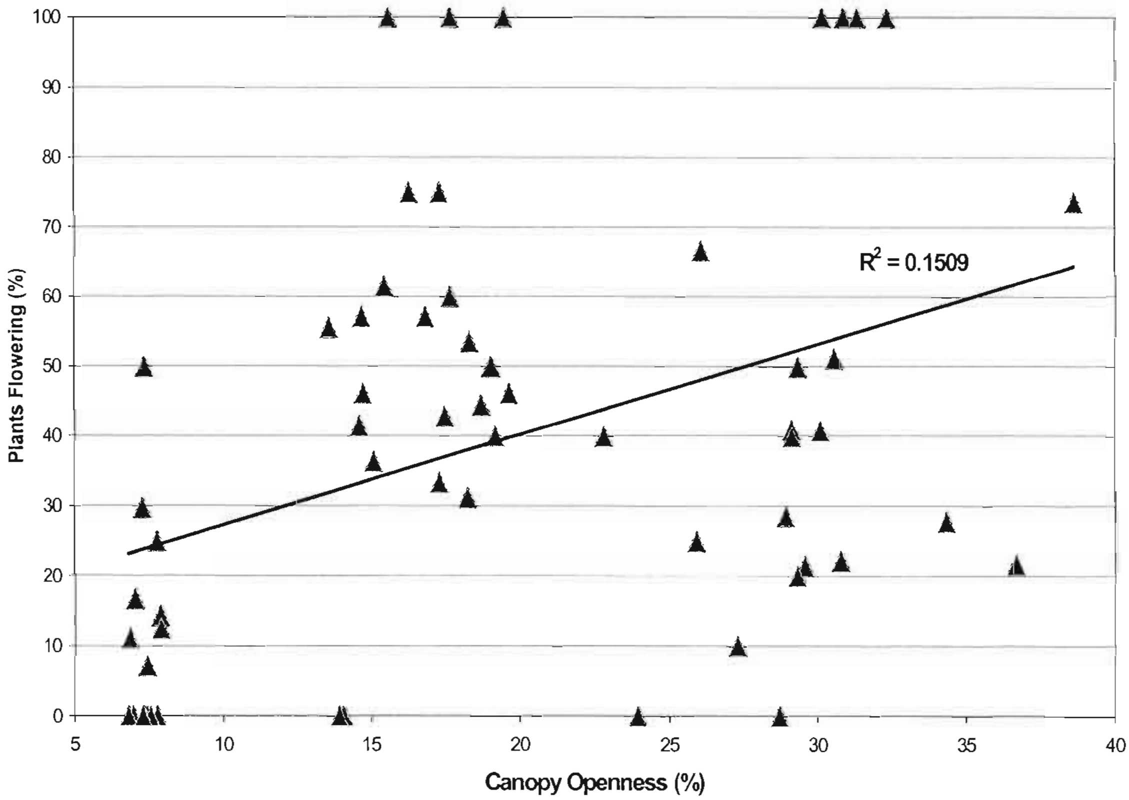


Figure 11. Bivariate fit of percent of *Viola pedata* plants flowering vs. percent canopy openness in *Viola pedata* population sites. Points represent all microplots with *Viola pedata* sampled in 4 sites.



6. Appendix.

List of species present at study sites (nomenclature for vascular plants from Ontario Plant List (Newmaster *et. al.*, 1998)).

Acer rubrum
Alliaria petiolata
Ambrosia artemisiifolia
Andropogon gerardii
Anemone virginiana
Antennaria neglecta
Antennaria plantaginea
Apocynum androsaemifolium
Asclepias tuberosa
Asclepias verticillata
Aster lateriflorus
Carex pensylvanica
Carex siccata
Celastrus scandens
Cornus racemosa
Cyperus filiculmis
Danthonia spicata
Euphorbia corollata
Festuca saximontana
Fragaria virginiana
Fraxinus americana
Galium circaezans
Geum canadense
Glechoma hederacea
Hieracium pratense
Hypericum perforatum
Juniperus virginiana
*Larix decidua**
Lespedeza capitata
Maianthemum canadense
Melilotus officinalis
Monotropa uniflora
Muhlenbergia spp.
Oenothera pilosella
Panicum acuminatum
Pedicularis canadensis
Phlox subulata
*Pinus resinosa**
Pinus strobus
*Pinus sylvestris**
Plantago major
Poa spp.
Polygala polygama
Polygonatum biflorum
Polygonatum pubescens
Polytrichum juniperinum
Polytrichum piliferum
Potentilla recta
Prunus serotina
Pteridium aquilinum
Pyrola elliptica
Quercus alba
Quercus rubra
Quercus velutina
Ranunculus acris
Rhus radicans
Rosa carolina
Rubus flagellaris
Rubus occidentalis
Rumex acetosella
Schizachyrium scoparium
Solanum dulcamara
Solidago canadensis
Solidago nemoralis
Solidago speciosa
Solidago squarrosa
Tephrosia virginiana
Trifolium pratense
Vaccinium angustifolium
Viburnum cassinoides
Viburnum lentago
Viola lanceolata
Viola pedata
Vitis aestivalis

* planted species found in Turkey Point Provincial Park

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