Response of an *Isotria medeoloides* **Population to Canopy Thinning**

William E. Brumback¹, Sara Cairns², Molly B. Sperduto^{3,*}, and Carol W. Fyler¹ (deceased)

Abstract - *Isotria medeoloides* (Small Whorled Pogonia) is a globally rare woodland orchid. Observed population declines in this species may be related to decreased light availability resulting from forest maturation. In East Alton, NH, a population of Small Whorled Pogonia was partitioned into two groups, with one left as a control and the other subjected to canopy-reduction management. The removal of all shrubs and 25% of the tree basal area approximately doubled light transmission to the managed group. The number of stems and seed capsules significantly increased in this group relative to the control group. While this was not a replicated experiment, our observations suggest that canopy thinning may help promote the long-term conservation of this federally threatened species.

Introduction

Isotria medeoloides (Pursh) Rafinesque (Small Whorled Pogonia) is a rare perennial woodland orchid that is designated as federally threatened under the Endangered Species Act of 1973, as amended. The majority of the world's populations occur in Maine and New Hampshire, often in second- or third-growth forests. Several lines of evidence suggest that observed declines in population size ([Mehrhoff 1989](https://www.researchgate.net/publication/222002811_Reproductive_vigor_and_environmental_factors_in_populations_of_an_endangered_North_American_orchid_Isotria_medeoloides_Pursh_rafinesque?el=1_x_8&enrichId=rgreq-86eb862f7b0e04fcd783a9b06c18f78b-XXX&enrichSource=Y292ZXJQYWdlOzIzMjY2NDM0MztBUzoyNzE3NTkzMzczMjQ1NDRAMTQ0MTgwMzg4MzU3NQ==)) could be caused by decreased light availability resulting from the maturation of forests in the region.

At one site in NH, an increase in population size and flowering was observed after gypsy moth defoliation (Brackley 1985), and [Mehrhoff \(1989\)](https://www.researchgate.net/publication/222002811_Reproductive_vigor_and_environmental_factors_in_populations_of_an_endangered_North_American_orchid_Isotria_medeoloides_Pursh_rafinesque?el=1_x_8&enrichId=rgreq-86eb862f7b0e04fcd783a9b06c18f78b-XXX&enrichSource=Y292ZXJQYWdlOzIzMjY2NDM0MztBUzoyNzE3NTkzMzczMjQ1NDRAMTQ0MTgwMzg4MzU3NQ==) found that both plant size and flower production in 11 populations were positively correlated with estimated light levels. In the winter of 1990–91 at East Alton, NH, the vegetation along power lines above or adjacent to a group of Small Whorled Pogonia plants was cut down as part of the electric company's maintenance program, thus creating open corridors. This cutting increased ambient light to the plants, which had been growing in relatively dense forest cover. Possibly as a result of the increased light, the number of stems emerging and the percent of flowering stems increased in this population. In six years of monitoring before the vegetation removal (1985–1990), the average annual stem count was 53, with 17% of the stems flowering. In the six years afterwards (1991–1996), average annual stem counts increased to 111, with 33% flowering (B. Brumback and C. Fyler, New England Wildflower Society, Framingham, MA, unpub. data).

¹New England Wild Flower Society, 180 Hemenway Road, Framingham, MA 01701. ²New Hampshire Natural Heritage Bureau, DRED, PO Box 1856, Concord, NH 03302-1856. ³Molly Sperduto, US Fish and Wildlife Service, 70 Commercial Street, Suite 300, Concord, NH 03301-5087. *Corresponding author – molly sperduto@fws.gov.

186 *Northeastern Naturalist* Vol. 18, No. 2

 Based on these observations, we hypothesized that canopy thinning resulting in increased light could be an effective management tool to increase vigor and reproduction in a declining population of Small Whorled Pogonia.

Field-Site Description

 We chose as our study site a secondary, mixed deciduous-coniferous forest in East Alton, NH, which supported a Small Whorled Pogonia population that had been monitored yearly since 1986. From 1986 to 1996 the total number of stems had declined from 64 to 13. Increased canopy cover due to succession was suspected as a factor in the decline.

Methods

We identified two groups of the orchid occurring at the site $(X \text{ and } Y)$, which were naturally separated by a 20-m-wide stand of *Tsuga canadensis* (Eastern Hemlock) trees. We chose Group Y as the treatment group because access for canopy manipulation was easier and because removing trees that shaded the Small Whorled Pogonia in Group Y did not appear to increase light to Group X. Removing trees associated with Group X would have resulted in thinning the hemlock stand between the two groups and may have increased light to Group Y. In both groups, we established a 30- by 40-m grid, consisting of twelve 10- by 10-m plots on a north–south alignment (Group Y is displayed in Fig. 1). Starting in September 1997, a more intensive search was used for the annual monitoring, and all the stems were mapped relative to the grid. In 1997, we also mapped tree locations and measured the basal area $(m^2/h$ ectare) of all live stems greater than

Figure 1. Group Y: grid layout showing the location of plots, *I. medeoloides* plants, and removed trees.

2.54 cm diameter at breast height (DBH). We made quantitative measurements of site features (e.g., forest composition and structure and snow depth during cutting) to help inform management decisions at other locations.

 Trees that cast the most shade and that blocked light from the east and south were selected for removal. Generally, most evergreen species, particularly Eastern Hemlock, were removed based on these criteria. However, while there were a number of tall *Pinus strobus* (White Pine) over 30 m in height, they had few lower limbs and in general did not appear to block as much light from reaching the orchid population. The White Pines also tended to be very large-diameter trees, i.e., 41–61 cm DBH. Because their size would have made them problematic for removal, and because they did not appear to provide as much shade, they were not selected for removal. Deciduous trees with low branches, such as *Acer rubrum* (Red Maple), contributed heavily to shading and were removed. In total, 48 trees were marked for removal in Group Y.

Tree and shrub removal

 In October 1997, we hand cut and removed all shrubs and saplings in Group Y over 1 m in height and less than 2.54 cm DBH (Table 1). Tree removal was deferred until later in the winter, when frozen ground and snow cover would protect underground over-wintering plants from damage caused by removal activities.

 In January 1998, we removed trees in Group Y, during a time when there was substantial snow and ice accumulation. At the time of the cutting, we measured the depth of both snow and ice at two locations in Group Y. At one location, there

Table 1. Number of shrubs and saplings over 1 m in height and less than 2.54 cm DBH removed from Group Y by Plot.

188 *Northeastern Naturalist* Vol. 18, No. 2

were 18 cm of snow above 21 cm of hardpacked snow and ice, and at the other location snow depth was 17 cm above a hardpacked snow and ice layer that was 22 cm thick.

 Forty-eight trees (Table 2), comprising approximately 25% of the total basal area, were cut with a chain saw and winched out of the plot using a tractor that only crossed a small section of the plot's southeast corner. There was no disturbance to the hemlock stand that existed between Groups X and Y. The thick layer of ice and snow effectively protected the soil during tree removal, except in small areas where some of the larger trees (up to 20 cm DBH) fell and were winched off the plots. No shrubs, saplings, or trees were removed from Group X.

Canopy photography

 To get an estimate of the amount of ambient light reaching each group, we took photographs of the canopy at 16 of the 20 plot corners in late September 1997 before leaf drop (prior to tree and shrub removal). The weather ranged from partly sunny to cloudy, so we took photographs early or late in the day to minimize glare and distortion from the sun. Photographs were taken on black-and-white film (Kodak Tri-x 400) using a Nikon F4 camera with a multi-control back (MF-23) and a Sigma fisheye lens (160, 8 mm/4.0). We mounted the camera on a tripod 1 m directly above each plot corner. We leveled and aligned the camera to have the top of each photograph face true north. We photographed the canopy at three different exposures: the camera's automatic exposure, and one and two stops below. In September 1998, nine months after the experimental cutting, we repeated canopy photographs of both Group X and Y. Methods, materials, and locations of photographs were the same as in 1997, with the exception of a Filtermatic 022.5 (filter) on the camera. The weather was cloudy with periods of rain, thus the sun was not a factor when the 1998 photographs were taken.

 In September 2003, six growing seasons after the experimental cutting in January 1998, we collected a third set of canopy photographs in both groups. Methods, materials, and locations were the same as in 1997, and photographs were taken without a filter. We took photographs in the morning or late afternoon to minimize effects of the sun since both days were bright and sunny.

Table 2. Number and basal area of tree species cut and removed from Group Y.

Canopy photograph analysis

 Black-and-white canopy photos from 1997, 1998, and 2003 were scanned using a Nikon Super Cool Scan 4000 ED and Nikon Scan 4.0 software. In general, photos taken at an f-stop of -1.0 best distinguished sky from vegetation and were thus used for analysis. Digitized photos were analyzed using Gap Light Analyzer (GLA) imaging software (Frazer et al. 1999), with growing season set to May 15–September 15. Pixel brightness used to distinguish sky from vegetation was

Figure 2. *Isotria medeoloides* in bloom. Photo © Ben Kimball.

set separately in areas of the photographs that had sunspots or reflections. No correction was used for the filter that was present in the 1998 photos, since it blocked an area (ca. 15 degrees above the horizon) with little to no light transmission ([Canham et al. 1994](https://www.researchgate.net/publication/216800507_Canham_C_D_A_C_Finzi_S_W_Pacala_and_D_H_Burbank_Causes_and_consequences_of_resource_heterogeneity_in_forests_interspecific_variation_in_light_transmission_by_canopy_trees_Can_J_Forest_Res?el=1_x_8&enrichId=rgreq-86eb862f7b0e04fcd783a9b06c18f78b-XXX&enrichSource=Y292ZXJQYWdlOzIzMjY2NDM0MztBUzoyNzE3NTkzMzczMjQ1NDRAMTQ0MTgwMzg4MzU3NQ==), Frazer et al. 1999).

 Light transmission through the canopy was estimated using a gap light index (GLI; [Canham 1988](https://www.researchgate.net/publication/216800499_An_Index_For_Understory_Light_Levels_in_and_Around_Canopy_Gaps?el=1_x_8&enrichId=rgreq-86eb862f7b0e04fcd783a9b06c18f78b-XXX&enrichSource=Y292ZXJQYWdlOzIzMjY2NDM0MztBUzoyNzE3NTkzMzczMjQ1NDRAMTQ0MTgwMzg4MzU3NQ==)). This index measures the percent transmission of global (diffuse + direct) solar radiation and is calculated as the fraction of pixels showing unobscured sky multiplied by the fraction of growing season radiation orginating in a given region of the sky ([Canham et al. 1994](https://www.researchgate.net/publication/216800507_Canham_C_D_A_C_Finzi_S_W_Pacala_and_D_H_Burbank_Causes_and_consequences_of_resource_heterogeneity_in_forests_interspecific_variation_in_light_transmission_by_canopy_trees_Can_J_Forest_Res?el=1_x_8&enrichId=rgreq-86eb862f7b0e04fcd783a9b06c18f78b-XXX&enrichSource=Y292ZXJQYWdlOzIzMjY2NDM0MztBUzoyNzE3NTkzMzczMjQ1NDRAMTQ0MTgwMzg4MzU3NQ==)). This product was summed over 648 regions for each hemispherical photograph (36 azimuth or compass angle divisions x 18 zenith divisions) to generate the GLI. Differences between Groups X and Y each year in the GLI were examined using separate variance *t*-tests (Systat Version 9, SSP Corp.).

Monitoring of Small Whorled Pogonia

 Beginning in 1986, we conducted yearly monitoring of Small Whorled Pogonia stems in both Groups X and Y. We marked individual stems with colored plastic toothpicks. Each stem was checked for emergence in late May or early June, checked for bloom (Fig. 2) in early or mid-June, and checked again in late July or August for seed capsule formation. Each area was thoroughly searched in August or early September to detect any new stems that may have appeared during the growing season.

Population effects analysis

 To test for the effects of the canopy manipulation on population size, we calculated correlations (Sokal and Rohlf 1981) between Group X and Group Y: a positive correlation would indicate that the two groups were acting like one population during the time period used for the correlation. One correlation was calculated for the 10 years before canopy thinning (excluding 1997, when a more comprehensive search method was used), and one for the 11 years after thinning. To examine effects on reproductive output, Resampling Stats software (Blank et al. 2001) was used to simulate seed capsule production under the null hypothesis that stems in both groups had the same probability of producing a capsule in any one year. A random draw from a binomial distribution was used to determine whether a stem produced a capsule. The probability used for a given year was calculated as total seed capsules divided by total stems for that year, summed over both groups. Two statistics were calculated: the difference between Group Y and Group X in total capsules produced in the 12 years before thinning, and the difference in the 11 years after. Each statistic was generated for 1000 repetitions of the simulation.

Results

Habitat characteristics

 Before habitat manipulation, both the tree species composition and the basal area were similar between the two groups (Table 3, Fig. 3). The total basal area was $40.5 \text{ m}^2/\text{hectar}$ in Group X and $39.9 \text{ m}^2/\text{hectar}$ in Group Y.

Canopy photograph analysis

number of stems of each species in each group.

 There was no difference in the percent transmission of global solar radiation (GLI) between the two groups in 1997 ($t = -1.419$, df = 23.7, $P = 0.169$; Fig. 4). Both groups had slightly higher index values in 1998 than in 1997, possibly due to an ice storm in January 1998. However, in 1998, Group Y received significantly more light than Group X ($t = -4.874$, df = 28.6, $P < 0.001$). Mean GLI values were twice as high in Group Y vs. Group X in 1998 (10.0 vs. 5.0). By 2003, the difference in GLI between the two groups had declined (7.4 vs. 4.7; Fig. 4), but Group Y still had a significantly higher value.

Table 3. Percent of total basal area of each tree species in Groups X and Y prior to cutting and the

Percent of total basal area Number of stems Species Group X Group X Group Y Group X Group Y *Pinus strobus* (White Pine) 33.8% 38.8 % 16 26 *Acer rubrum* (Red Maple) 28.9 % 26.0 % 58 32 *Tsuga canadensis* (Eastern Hemlock) 14.2 % 16.3 % 22 21 *Acer saccharum* (Sugar Maple) 6.9 % 2.8 % 9 10 *Betula lenta* (Black Birch) 6.2% 5.9 % 6 3
Betula alleghaniensis (Yellow Birch) 4.1% 4.3 % 8 7 *Betula alleghaniensis* (Yellow Birch) 4.1% 4.3% *Betula papyrifera* (White Birch) 2.5 % 0.0 % 2 0 *Fagus grandifolia* (American Beech) 2.4 % 0.2 % 3 6 *Picea rubens* (Red Spruce) 0.6 % 5.4 % 1 4 *Quercus rubra* (Red Oak) 0.4% 0.0 % 2 0 *Fraxinus americanus* (White Ash) 0.0% 0.3 % 0 1 Total 100.0 % 100.0 % 127 110

Figure 3. Composition of dominant tree species (basal area $> 2\%$) in Group X (control) and Group Y (pre- and post-treatment).

Figure 4. Gap light index (GLI) at 16 photo points for Group X (circles: left) and Group Y (crosses: right): A. before canopy thinning (1997), B. one year after thinning (1998), and C. six years after thinning (2003). Each graph shows the actual distribution of GLI values (circles and crosses), boxplots displaying the median and range of values, and a normal curve for comparison. (SYSTAT Version 9, two-sample *t*-test).

Small Whorled Pogonia: stems

 Two years after the tree and shrub removal, more Small Whorled Pogonia stems emerged in Group Y than Group X, for the first time in 14 years of monitoring (Fig. 5A). Group Y continued to have 7 to 34 more stems emerge than Group X for the next nine years.

 During 10 years of changes in population size before the canopy thinning, Group X and Group Y were highly correlated $(R^2 = 0.77, P < .01)$; each year they usually either both increased or both decreased in size (Fig. 5A). During 11

Figure 5. Number of stems (A) and number of stems producing seed capsules (B) in each group. Tree and shrub removal occurred in Group Y in the winter of 1997–1998 (vertical dotted line).

post-thinning year-to-year changes, there was no significant correlation between the two groups $(R^2 = 0.002)$.

Small Whorled Pogonia: seed capsule production

 Between 1986 and 1991, Group X produced more seed capsules each year than did Group Y (Fig. 5b). With two exceptions, neither group produced any seed capsules in the five years before the canopy thinning, or in the first year afterwards. Starting in 1999, however, Group Y produced more seed capsules each year than Group X. Calculated as a percent of emerged stems, to control for differences in total number of stems, there was no significant difference in seed capsule production between Group X and Group Y in the 12 years before thinning occurred $(P > 0.05)$. In the 11 years after thinning, however, stems in Group Y had a significantly higher probability of producing a seed capsule than those in Group $X (P < 0.01)$; the average annual proportion of stems with seed capsules was 22% in Group Y vs. 5% in Group X.

Discussion

 The selective removal of 25% of the basal area of trees in Group Y, along with removal of shrubs, approximately doubled the amount of direct and diffuse light being transmitted to the forest floor in this area compared to the control.

 Where the canopy was reduced, the number of stems had more than doubled over a ten-year period, whereas the number of stems in the control area had declined. An increase in number of stems could be due to any of three effects: more new plants becoming established; longer periods of emergence for individual plants (lower likelihood of death or dormancy); or previously dormant plants breaking dormancy. Dormancy, a phenomenon common to some terrestrial orchid species ([Mehrhoff 1980](https://www.researchgate.net/publication/35130773_The_reproductive_biology_of_the_genus_Isotria_Orchidaceae_and_the_ecology_of_Isotria_medeoloides?el=1_x_8&enrichId=rgreq-86eb862f7b0e04fcd783a9b06c18f78b-XXX&enrichSource=Y292ZXJQYWdlOzIzMjY2NDM0MztBUzoyNzE3NTkzMzczMjQ1NDRAMTQ0MTgwMzg4MzU3NQ==)), including Small Whorled Pogonia, where individual plants have remained below-ground for up to three years before re-emerging (Vitt 1991), seems unlikely to have accounted for the observed increase in stems in Group Y because very few plants had entered dormancy in either group in the 3–4 years before the thinning occurred. More new plants and longer periods of emergence were both more common in Group Y than in Group X after the canopy thinning, so both apparently contributed to the significant increase in population size.

 Factors other than canopy maturation and the canopy thinning could also have affected emergence patterns. This study does not exclude other possible explanations, including reduced root competition and leaf-litter depth and increased dead organic matter in the soil. The control group appeared to start to increase three years before the thinning occurred (Fig. 5a). The jump in both groups between 1996 and 1997 was largely due to the pre-thinning intensive search in 1997, but Group X had begun to increase before that and continued afterwards, even in the absence of canopy thinning. The post-thinning increase in Group X, however, was small compared to Group Y, and was not sustained.

 After canopy thinning, reproductive effort in Group X remained low, whereas a major, sustained increase in seed capsule production occurred in Group Y

(Fig. 5b). The increase was due to both an increase in total stems in Group Y and to an increase in the likelihood that any one stem would produce a seed capsule. Although we did not measure stem size in this study, the plants receiving more light in Group Y appeared to be larger on the whole. Past research ([Mehrhoff](https://www.researchgate.net/publication/35130773_The_reproductive_biology_of_the_genus_Isotria_Orchidaceae_and_the_ecology_of_Isotria_medeoloides?el=1_x_8&enrichId=rgreq-86eb862f7b0e04fcd783a9b06c18f78b-XXX&enrichSource=Y292ZXJQYWdlOzIzMjY2NDM0MztBUzoyNzE3NTkzMzczMjQ1NDRAMTQ0MTgwMzg4MzU3NQ==) [1980](https://www.researchgate.net/publication/35130773_The_reproductive_biology_of_the_genus_Isotria_Orchidaceae_and_the_ecology_of_Isotria_medeoloides?el=1_x_8&enrichId=rgreq-86eb862f7b0e04fcd783a9b06c18f78b-XXX&enrichSource=Y292ZXJQYWdlOzIzMjY2NDM0MztBUzoyNzE3NTkzMzczMjQ1NDRAMTQ0MTgwMzg4MzU3NQ==), Vitt 1991) has shown that larger plants are more likely to bloom.

 We have observed an apparent increase in the herbaceous vegetation and small shrubs under one meter tall in Group Y and concomitant shading and competition for nutrients and water since the canopy was thinned, which might have contributed to the leveling off of the number of stems emerging starting in 2003, after four years of steady increases. After seven seasons, a reduction in seed capsule production began, possibly due to the effects of competing vegetation.

 The flush of re-growth that followed the canopy thinning apparently attracted *Odocoileus virginianus* Zimmermann (White-tailed Deer) to this area, and intensified browsing impacts to herbaceous cover. We confirmed browsing by White-tailed Deer through observation of tracks and scat. Browsing of Small Whorled Pogonia by White-tailed Deer was very evident in some years in Group Y, but not apparent in Group X. When browse occurred, usually the entire top of the Small Whorled Pogonia plant, including the leaf whorl, was taken, leaving only a bare stem that eventually withered away. Observations of browse in this study were anecdotal rather than systematic, but if browse is heavy, the potential reproductive gains achieved through increased light could be offset by destruction through browse.

 The increased emergence and reproduction of stems in Group Y, following a non-random removal of 25% of the tree basal area (focusing on trees that cast the most shade), has important implications for long-term maintenance of populations of Small Whorled Pogonia. This management approach could be particularly useful on parcels of land protected specifically for the conservation of this species. It should be noted that since shade-producing trees were preferentially selected for removal, a slightly larger percentage of the basal area might need to be removed if a random tree selection was utilized for future management efforts. The technique used to open the canopy in this study, i.e., cutting the dominant shade-causing trees and winching them off the plots, minimized impacts to the plants and to the site and could be adapted to other sites in which shade could be a factor of apparent decline. Mechanized logging equipment used during times of the year when the ground isn't frozen or when snow cover is absent would likely have considerably more direct impact on the plants and soils.

 Although this was not a replicated experiment, this study and anecdotal evidence from other Small Whorled Pogonia sites suggest that opening the canopy through the removal of trees or other means within or adjacent to the occurrence, may prove beneficial to the long-term maintenance of the species. Additional systematic observations and field tests are needed to check the validity of this conclusion, and to identify specific habitat changes that lead to increases in the growth and reproduction of this rare orchid.

196 *Northeastern Naturalist* Vol. 18, No. 2

Acknowledgments

 Many thanks to Peter Farrell, New England Forestry Consultants, Inc. for tree removal, and to Tom Hoopes and the Town of Alton, NH for granting permission for the project. We thank Charles D. Canham and Lynn Schnurr, Cary Institute of Ecosystem Studies, for their analyses of hemispherical photography. We also thank Susi von Oettingen, Jessica Korecki, Danielle Ogurcak, and Chris Mattrick for their help, guidance, and support. Support for this project came from the Harold Whitworth Pierce Charitable Trust, the US Fish and Wildlife Service, the New England Wild Flower Society, and the New Hampshire Natural Heritage Bureau.

Literature Cited

- Blank, S., P. Bruce, and C. Seiter. 2001. Resampling stats in Excel (version 2). Resampling Stats Inc., Arlington VA. 185 pp.
- Brackley, F.E. 1985. The orchids of New Hampshire. Rhodora 87:1–115.
- [Canham, C.D. 1988. An index for understory light levels in and around canopy gaps.](https://www.researchgate.net/publication/216800499_An_Index_For_Understory_Light_Levels_in_and_Around_Canopy_Gaps?el=1_x_8&enrichId=rgreq-86eb862f7b0e04fcd783a9b06c18f78b-XXX&enrichSource=Y292ZXJQYWdlOzIzMjY2NDM0MztBUzoyNzE3NTkzMzczMjQ1NDRAMTQ0MTgwMzg4MzU3NQ==) [Ecology 69:1634–1638.](https://www.researchgate.net/publication/216800499_An_Index_For_Understory_Light_Levels_in_and_Around_Canopy_Gaps?el=1_x_8&enrichId=rgreq-86eb862f7b0e04fcd783a9b06c18f78b-XXX&enrichSource=Y292ZXJQYWdlOzIzMjY2NDM0MztBUzoyNzE3NTkzMzczMjQ1NDRAMTQ0MTgwMzg4MzU3NQ==)
- [Canham, C.D., A.C. Finzi, S.W. Pacala, and D.H. Burbank. 1994. Causes and conse](https://www.researchgate.net/publication/216800507_Canham_C_D_A_C_Finzi_S_W_Pacala_and_D_H_Burbank_Causes_and_consequences_of_resource_heterogeneity_in_forests_interspecific_variation_in_light_transmission_by_canopy_trees_Can_J_Forest_Res?el=1_x_8&enrichId=rgreq-86eb862f7b0e04fcd783a9b06c18f78b-XXX&enrichSource=Y292ZXJQYWdlOzIzMjY2NDM0MztBUzoyNzE3NTkzMzczMjQ1NDRAMTQ0MTgwMzg4MzU3NQ==)[quences of resource heterogeneity in forests: Interspeci](https://www.researchgate.net/publication/216800507_Canham_C_D_A_C_Finzi_S_W_Pacala_and_D_H_Burbank_Causes_and_consequences_of_resource_heterogeneity_in_forests_interspecific_variation_in_light_transmission_by_canopy_trees_Can_J_Forest_Res?el=1_x_8&enrichId=rgreq-86eb862f7b0e04fcd783a9b06c18f78b-XXX&enrichSource=Y292ZXJQYWdlOzIzMjY2NDM0MztBUzoyNzE3NTkzMzczMjQ1NDRAMTQ0MTgwMzg4MzU3NQ==)fic variation in light transmis[sion by canopy trees. Canadian Journal of Forest Research 24:337–349.](https://www.researchgate.net/publication/216800507_Canham_C_D_A_C_Finzi_S_W_Pacala_and_D_H_Burbank_Causes_and_consequences_of_resource_heterogeneity_in_forests_interspecific_variation_in_light_transmission_by_canopy_trees_Can_J_Forest_Res?el=1_x_8&enrichId=rgreq-86eb862f7b0e04fcd783a9b06c18f78b-XXX&enrichSource=Y292ZXJQYWdlOzIzMjY2NDM0MztBUzoyNzE3NTkzMzczMjQ1NDRAMTQ0MTgwMzg4MzU3NQ==)
- Frazer, G.W., C.D. Canham, and K.P. Lertzman. 1999. Gap Light Analyzer (GLA) imaging software to extract canopy structure and gap light-transmission indices from true-colour fi sheye photographs: Users manual and program documentation. Simon Fraser University, Burnaby, British Columbia, and the Institute of Ecosystem Studies, Millbrook, NY. 40 pp.
- [Mehrhoff, L.A. 1980. The reproductive biology of the genus](https://www.researchgate.net/publication/35130773_The_reproductive_biology_of_the_genus_Isotria_Orchidaceae_and_the_ecology_of_Isotria_medeoloides?el=1_x_8&enrichId=rgreq-86eb862f7b0e04fcd783a9b06c18f78b-XXX&enrichSource=Y292ZXJQYWdlOzIzMjY2NDM0MztBUzoyNzE3NTkzMzczMjQ1NDRAMTQ0MTgwMzg4MzU3NQ==) *Isotria* (Orchidaceae) and the ecology of *Isotria medeoloides*[. M.Sc. Thesis. University of North Carolina, Cha](https://www.researchgate.net/publication/35130773_The_reproductive_biology_of_the_genus_Isotria_Orchidaceae_and_the_ecology_of_Isotria_medeoloides?el=1_x_8&enrichId=rgreq-86eb862f7b0e04fcd783a9b06c18f78b-XXX&enrichSource=Y292ZXJQYWdlOzIzMjY2NDM0MztBUzoyNzE3NTkzMzczMjQ1NDRAMTQ0MTgwMzg4MzU3NQ==)[pel Hill, NC. 65 pp.](https://www.researchgate.net/publication/35130773_The_reproductive_biology_of_the_genus_Isotria_Orchidaceae_and_the_ecology_of_Isotria_medeoloides?el=1_x_8&enrichId=rgreq-86eb862f7b0e04fcd783a9b06c18f78b-XXX&enrichSource=Y292ZXJQYWdlOzIzMjY2NDM0MztBUzoyNzE3NTkzMzczMjQ1NDRAMTQ0MTgwMzg4MzU3NQ==)
- [Mehrhoff, L.A. 1989. Reproductive vigor and environmental factors in populations of an](https://www.researchgate.net/publication/222002811_Reproductive_vigor_and_environmental_factors_in_populations_of_an_endangered_North_American_orchid_Isotria_medeoloides_Pursh_rafinesque?el=1_x_8&enrichId=rgreq-86eb862f7b0e04fcd783a9b06c18f78b-XXX&enrichSource=Y292ZXJQYWdlOzIzMjY2NDM0MztBUzoyNzE3NTkzMzczMjQ1NDRAMTQ0MTgwMzg4MzU3NQ==) [endangered North American orchid,](https://www.researchgate.net/publication/222002811_Reproductive_vigor_and_environmental_factors_in_populations_of_an_endangered_North_American_orchid_Isotria_medeoloides_Pursh_rafinesque?el=1_x_8&enrichId=rgreq-86eb862f7b0e04fcd783a9b06c18f78b-XXX&enrichSource=Y292ZXJQYWdlOzIzMjY2NDM0MztBUzoyNzE3NTkzMzczMjQ1NDRAMTQ0MTgwMzg4MzU3NQ==) *Isotria medeoloides* (Pursh) Rafinesque. Biologi[cal Conservation. 47:281–296.](https://www.researchgate.net/publication/222002811_Reproductive_vigor_and_environmental_factors_in_populations_of_an_endangered_North_American_orchid_Isotria_medeoloides_Pursh_rafinesque?el=1_x_8&enrichId=rgreq-86eb862f7b0e04fcd783a9b06c18f78b-XXX&enrichSource=Y292ZXJQYWdlOzIzMjY2NDM0MztBUzoyNzE3NTkzMzczMjQ1NDRAMTQ0MTgwMzg4MzU3NQ==)
- Sokal, R.R., and F.J. Rohlf. 1981. Biometry: The Principles and Practice of Statistics in Biological Research. Second Edition. W.H. Freeman and Company, San Francisco, CA. 859 pp.
- Vitt, P. 1991. Conservation of *Isotria medeoloides*: A federally endangered terrestrial orchid. M.Sc. Thesis. University of Maine, Orono, ME. 40 pp.