

Heliotropism in *Trillium grandiflorum* provides increased reproductive success

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Abstract

Heliotropism of flowers is thought to provide a reproductive advantage to individuals of many species; yet, there are few clear demonstrations of a fitness advantage provided by heliotropism, most of which are almost completely restricted to plants from the arctic or alpine regions where a heat gain provides an advantage to the plants. In this study, we report heliotropism in the white trillium, an early spring blooming species from the temperate forests of eastern North America. The white trillium shows horizontal seasonal heliotropism with flowers mainly facing south throughout the summer, but it also exhibits daily horizontal and vertical heliotropism with the orientation of the flower tracking the sun during the day. The study of 479 tethered plants indicated that seasonal heliotropism provides a reproductive advantage to the white trillium, with south-facing individuals showing a 12% increase in fertilized ovules compared to north-facing plants. The ecology of this long-lived perennial is, in many aspects, similar to that of alpine and arctic heliotropic species. Indeed, white trilliums are insect-pollinated and they flower when the weather is cold, before the trees leaf out. This suggests that there are potentially more species for which heliotropism is advantageous amongst early spring flowers from the temperate forest.

Key words: heliotropism, white trillium, fertilized ovules, fitness, plant reproduction

Résumé

On pense que l'héliotropisme des fleurs procure un avantage reproductif aux individus de nombreuses espèces. Pourtant, il existe peu de démonstrations claires de l'avantage de l'héliotropisme sur le plan de la valeur adaptative, et ces démonstrations sont presque toutes limitées aux plantes des régions arctiques ou alpines, où un gain de chaleur procure un avantage aux plantes. Dans cette étude, nous décrivons l'héliotropisme chez le trille blanc, une espèce à floraison printanière précoce des forêts tempérées de l'est de l'Amérique du Nord. Le trille blanc montre un héliotropisme saisonnier horizontal avec des fleurs principalement orientées vers le sud tout au long de l'été, mais il présente également un héliotropisme horizontal et vertical quotidien avec l'orientation de la fleur suivant le soleil pendant la journée. L'étude de 479 plantes attachées a indiqué que l'héliotropisme saisonnier procure un avantage reproductif au trille blanc, les individus orientés vers le sud présentant une augmentation de 12 % d'ovules fécondés par rapport aux plantes orientées vers le nord. L'écologie de cette plante vivace à longue durée de vie est, sous de nombreux aspects, similaire à celle des espèces héliotropes alpines et arctiques. En effet, les trilles blancs sont pollinisés par les insectes et ils fleurissent lorsque le temps est froid, avant l'apparition du feuillage des arbres. Cela suggère qu'il y a potentiellement plus d'espèces pour lesquelles l'héliotropisme est avantageux parmi les fleurs printanières précoces de la forêt tempérée. [Traduit par la Rédaction]

Mots-clés : héliotropisme, trille blanc, ovules fécondés, valeur adaptative, reproduction végétale

Introduction

The heliotropism of flowers has attracted curiosity and interest amongst evolutionary ecologists for more than 50 years (Hocking and Sharplin 1965; Hocking 1968; Kevan 1972, 1975). Heliotropism is the process that modifies an organ's orientation in response to the sun's position. At present, more than 96 plant species from several families have been reported as showing floral or inflorescence heliotropism (Serrano et al. 2018). Different forms of he-

liotropism exist (Serrano et al. 2018): flowers could orient themselves parallel (paraheliotropism) or perpendicular (diaheliotropism) to the sun's rays; they can track the sun on a daily basis (diurnal heliotropism) or remain relatively constant once they have acquired their position (seasonal heliotropism); and finally they could track the sun horizontally or vertically from the horizon to the zenith (horizontal and vertical heliotropism, respectively).

Three hypotheses have been proposed to explain the presence of heliotropism. First, the pollinator attraction hypothesis holds that flower heliotropism contributes to attracting more pollinators. Indeed, several studies have reported increased pollinator visitation rates due to heliotropism (Smith 1975; Stanton and Galen 1989; Kudo 1995; Luzar and Gottsberger 2001; Atamian et al. 2016). The cause is unclear, but temperature seems to play a role, at least in some species (Atamian et al. 2016). Moreover, increased temperature of flowers tracking the sun sometimes augment pollinator residency time (Stanton and Galen 1989; Luzar and Gottsberger 2001). Second, the growth promotion hypothesis proposes that the increase of internal temperature could promote seed development or pollen tube germination and growth (Kevan 1972, 1975; Kudo 1995; Galen and Stanton 2003). Indeed, some experiments demonstrated the impact of flower temperature on seed number and size (Kudo 1995; Zhang et al. 2010). Third, the cooling hypothesis that originated from studies in tropical regions suggests that flowers adopt a position to avoid overheating during the day, which contributes to increasing pollinator visitation rates (Patiño et al. 2002).

While all these hypotheses received some empirical support, it nevertheless appears that none of them can explain heliotropism in all situations, especially given that heliotropism occurs in various environments. Indeed, some studies failed to find evidence for increased pollinator visits (Totland 1996), pollen removal or deposition (Wilson 1994; Galen and Stanton 2003), or differences in flower temperature in heliotropic species (Luzar and Gottsberger 2001). In contrast, other studies have highlighted that more than one of the proposed hypotheses were responsible for the advantages provided by heliotropism (Kudo 1995).

Whichever the mechanism, it is generally believed that heliotropism should increase the fitness of the plants; yet, the number of studies that directly tested for such a fitness advantage is relatively small. Some found that heliotropism provided a fitness advantage (Stanton and Galen 1989; Kudo 1995; Zhang et al. 2010) as estimated by an increase in seed numbers, seed mass, or seed:ovule ratios. Nevertheless, at least one study that tested for a fitness advantage did not find any (Totland 1996). We exclude here many studies that have documented increased pollinator visit rates or residency time because, although these are components of the plant fitness, they do not provide a direct assessment.

Most studies that investigated the ecological significance of heliotropism have focused on species from arctic and alpine regions where temperature can be a limiting factor to plant growth and pollinator activity. Many species from temperate regions are known to be heliotropic (Knutson 1981; Kudo 1995; Lino 2001; Atamian et al. 2016); however, apart from the spring ephemeral *Adonis ramosa* Franch. from deciduous forests in Japan (Kudo 1995), we have little evidence as to the fitness advantages of heliotropism in these regions. In addition, the vast majority of studies on the ecological significance of heliotropism have involved species of the Ranunculaceae and Papaveraceae families. There is thus a need to test if heliotropism provides a fitness advantage in more species coming from a broader range of ecosystems and plant families to better understand this phenomenon.

One of us (S.J.) recently noticed potential seasonal heliotropism in the white trillium, *Trillium grandiflorum* (Michaux) Salisbury (Melanthiaceae), a long-lived understory perennial plant of the deciduous forests of eastern North America (Fig. 1A). The white trillium starts to flower early in the spring before the trees have leafed out when outside temperatures are still cool and its flowers last for 2–3 weeks. It is mostly pollinated by bees and bumblebees (Irwin 2000) and the species often occurs in dense patches. Its reproduction can be limited by several factors, such as deer grazing, low population density, and low pollinator visitation rates (Knight 2003b). The percentage of fertilized ovules typically varies between 0.3 and 0.8 in natural populations, even when pollen is manually applied to the stigma (Irwin 2000; Griffin and Barrett 2002). Consequently, a strategy like heliotropism that would increase reproductive fitness could be of advantage for this species. In this study, we describe heliotropism in *T. grandiflorum* and demonstrate that it provides a reproductive fitness advantage in this species.

Methods

Research sites

Our research was conducted in eight populations of white trillium located in the urban forests of Laval (Québec, Canada). Laval is a city of 422 993 people with a density of 1700 people per square kilometre (Statistics Canada 2017) located on an island just north of Montreal. We chose our field sites there because of the low density of white-tailed deer (*Odocoileus virginianus*) on the island that are known to graze intensively on trillium populations (Augustine and Frelich 1998; Knight 2003a, 2004). The populations are located in mature deciduous forests (Table 1). We chose the location of the study sites so that they were under a full canopy to avoid potential border effects. At the latitude of the studied populations, the sun elevation reaches approximately 63° at midday in mid-May when the white trillium is in flower. Experiments were performed over four consecutive years (2018–2021).

Estimation of the density of reproductive individuals

To estimate the density of reproductively active individuals in the populations, we ran four random transects in each population in 2020 along which five quadrats of 1 m² were equally spaced. All plants in flowers included in the quadrats were counted.

Seasonal horizontal orientation of *Trillium* flowers in natural populations

We measured the horizontal orientation of *Trillium* flowers in each population with a compass. To quantify the error associated with measuring flower orientation, 30 measurements of a single flower were taken. This experiment was carried out in the First Nations Garden at the Montreal Botanical Garden. The horizontal orientation of flowers and fruits was performed in different populations over three years. Sampling was done by measuring all plants present within arm-length along a transect in the populations. The number of

Fig. 1. (A) A *Trillium grandiflorum* population in the Edimbourg urban forest. The camera was oriented towards the north when the photo was taken on 20 May 2019. (B) Tethered flower with electric wire. Photo credits: S.J. [Colour online]



Table 1. Names of the urban forests with latitude and longitude of the studied populations as well as the mean density (and standard deviation) of the number of reproductive individuals in each population.

Forest name	Latitude	Longitude	Density $\times m^{-2}$ (\pm SD)
La Source (East)	45.560128	-73.84697	11.0 (\pm 4.8)
La Source (West)	45.55975	-73.848725	9.8 (\pm 6.6)
Equerre (South)	45.608917	-73.761095	3.4 (\pm 3.6)
Equerre (North)	45.613078	-73.760345	3.9 (\pm 3.4)
Edimbourg	45.590255	-73.72602	16.5 (\pm 9.0)
Orée-des-bois	45.573363	-73.845688	19.6 (\pm 9.6)
38th Avenue	45.57315	-73.84318	20.3 (\pm 10.4)
Papineau	45.59082	-73.68312	1.6 (\pm 1.5)

individuals measured per population varied between 100 and 300. Measurements were done in mid-May when flowers were in full bloom in 2018 and 2019, whereas the orientation was measured at the fruiting stage (mid-June, using the main axis of the fruit) in 2020.

Variation in horizontal and vertical flower orientation

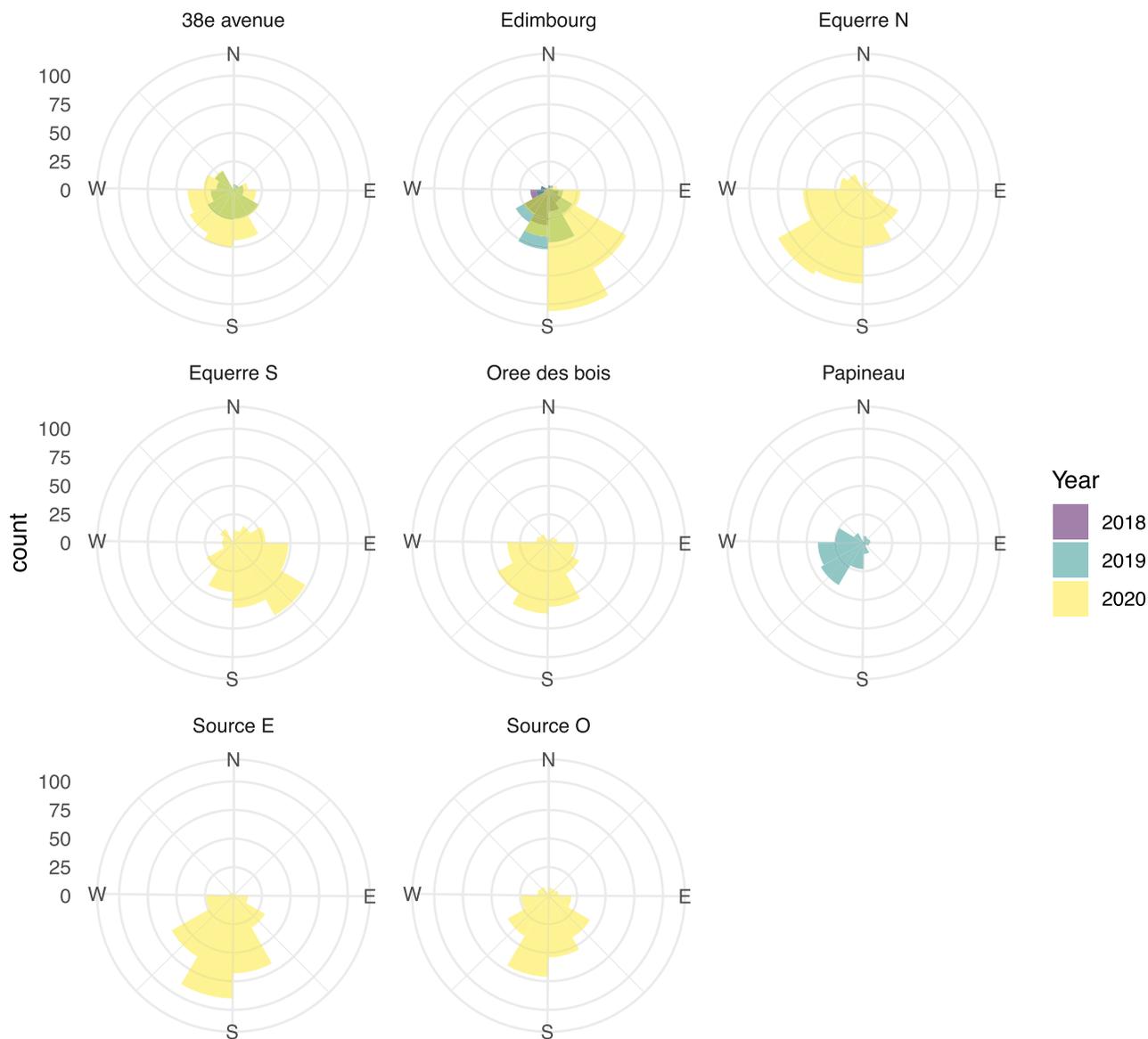
To determine if the horizontal and vertical orientation of the white trillium varies throughout the day, we tracked the orientation of 100 flowers at anthesis in the Edimbourg population on 2 and 3 May 2021. The skies were mostly clear throughout the experiment. For the horizontal orientation, we measured the orientation of each flower using a compass from 06:00 to 19:00 every two hours, then re-measured the flowers the next morning at 06:00. The vertical orientation was estimated using a clinometer application on a smartphone (iLevel—Protractor and Level, iOS, version 3.85, JRSoft-Worx), thus estimating the angle relative to the horizon line. The vertical orientation of flowers was measured on the same flowers and on the same day as for the horizontal orientation at 07:00, 13:00, and 19:00. We tested whether orientation var-

ied during the day using linear mixed-effects models using the plants as a random effect to account for repeated measures.

We set up an experiment in 2019 to estimate the effect of flower orientation on the white trillium reproduction by identifying plants facing each of the four cardinal points (south, east, west, north) to come back and collect the fruits later. However, other data collected at the same time suggested that the plants could change direction during the day or during the flowering season, compromising the experiment. Instead, we used this experiment to test if the orientation of plants changes during the season. We thus re-estimated the orientation of the plants initially identified 1.5 months later at the fruiting stage to compare the orientation of the fruits with that of the flower previously measured.

Impact of orientation on the internal temperature

To test the effect of flower orientation on flower internal temperature, we measured the temperature at the base of the corolla for 15 flowers facing each of the four cardinal directions ($\pm 15^\circ$) on 22 May 2019, between 11:30 and 12:45,

Fig. 2. The horizontal orientation of the individuals of *Trillium grandiflorum* in the studied populations. [Colour online]

using a temperature sensor with a flexible probe (Model HH23, Omega, St-Eustache, Canada). The external temperatures ranged from 18.8 to 21.5 °C during the experiment. The effect of the orientation on temperature was tested using a linear model with the square root of the temperature to ensure normality of the residuals.

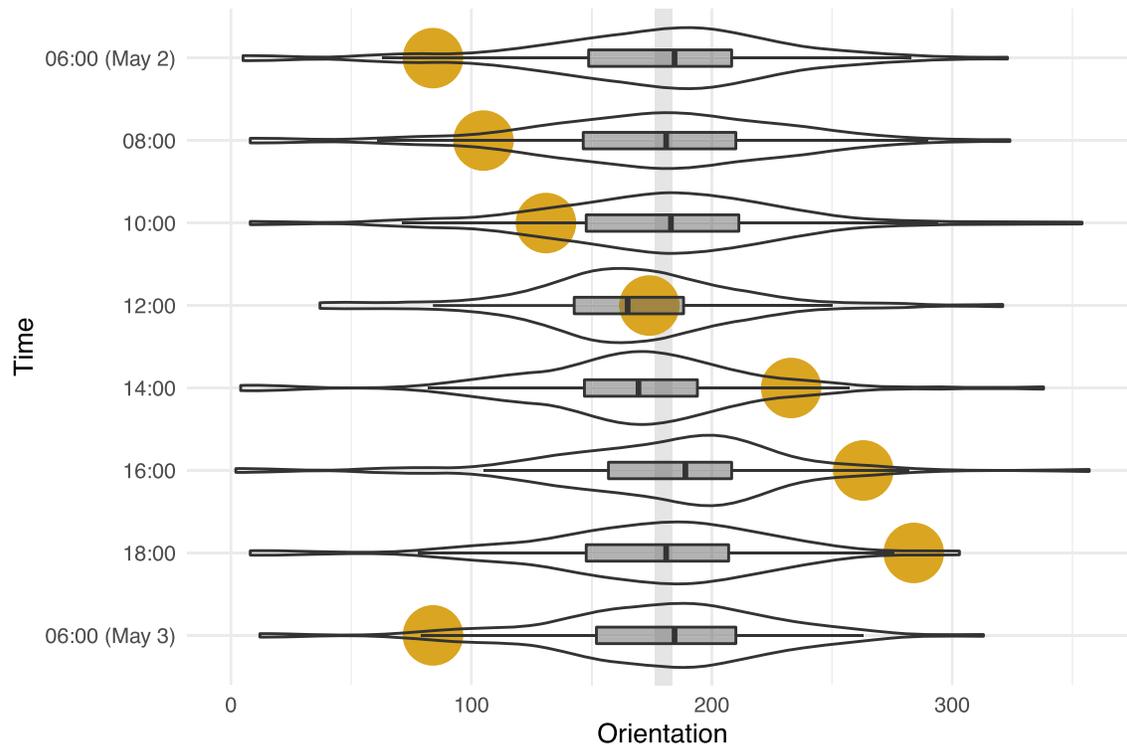
Evaluating the impact of seasonal heliotropism on the percentage of fertilized ovules

To test whether seasonal heliotropism provides a reproductive advantage, we evaluated the effect of orientation on the proportion of fertilized ovules. Before the flowers had a receptive stigma (6–11 May 2020), we tethered 100 plants in seven populations to fix an equal proportion of flowers facing east, west, north, south by using electrical wire, making a loop in the wire to make sure the flower stays in the intended direction (Fig. 1B). To allow the plants to continue to

grow freely after fecundation, the wires were removed at the early fruit stage (8 June 2020), making sure that the flowers were still pointing in the proper direction. Fruits were harvested when fertilized ovules could be easily distinguished from nonfertilized ones but when the latter were still easy to count (17 June 2020). The number of fertilized and unfertilized ovules were counted by two persons under a dissecting microscope.

We used linear mixed-effects models to test if flower orientation has an impact on the proportion of fertilized ovules. We treated plant density and the number of ovules as random effects in the model and orientation, population and their interaction as fixed effects. We proceeded by backward selection to choose the best model. We first tested the random effects with all fixed effects included in the models using restricted maximum likelihood (REML) optimization and the Akaike information criterion (AIC) for model comparison. We

Fig. 3. Variation in flower horizontal orientation of 100 individuals of *Trillium grandiflorum* for a 24 hour period. The yellow circle indicates the position of the sun for the same population. The vertical bar represents the south (180°). The data are from the Edimbourg population in 2021. [Colour online]



then tested the fixed effects using maximum likelihood (ML) optimization and the AIC criterion. The percentage of fertilized ovules was arcsin transformed to ensure the normality of the residuals, but the results are presented on the original scale. We also tested whether heliotropism had an effect on the number of ovules per fruit. We proceeded as for the percentage of ovules except that the number of ovules was log-transformed.

All statistical analyses were performed using the nlme R package (Pinheiro et al. 2020). Analysis of variance (ANOVA) tests used type III sums of squares and were performed with the car R package (Fox and Weisberg 2019) and Tukey's tests for significant factors and marginal means were estimated with the emmeans R package (Lenth 2020).

Results

The density of plants in flower varied considerably in the studied populations, from 1.6 to more than 20 reproductive plants per square metre (Table 1).

Our 30 estimations of orientation on a single flower using a compass gave a standard deviation of 3.014° . The white trillium flowers showed variation in horizontal orientation in the populations, but the mean orientation was very close to the south (180°) in all populations and few individuals were closer to the north than the south (Fig. 2). There was some variation amongst populations in the mean orientation, which ranged between 158° (Edimbourg) and 219° (Papineau) (Fig. 2). The results were relatively constant between

years, including when orientation was estimated at the fruiting stages.

Daily variation

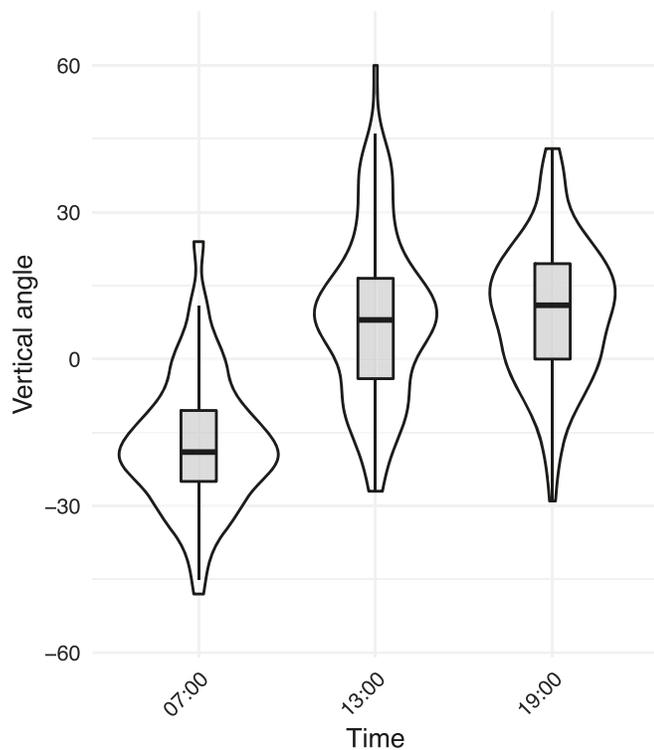
We found a significant variation in mean horizontal flower orientation during the day ($p < 0.0001$, ANOVA, $\chi^2 = 40.56$, 7 df, $n = 800$). The mean horizontal orientation in the population was fixed until the end of the morning, after which the flowers turned towards the east in the sun's direction and then shifted to the west during the afternoon (Fig. 3). From a population mean of ca. 176° in the early morning, the mean orientation shifted to 165° at midday and reached a maximum of 181° at 16:00 to come back at ca. 176° at 18:00. This makes a total variation of approximately 32° for the day.

We also observed significant variation in mean vertical orientation during the day ($p < 0.0001$, ANOVA, $\chi^2 = 299.81$, 2 df, $n = 300$). Early in the morning the flowers were inclined towards the soil (mean of -16° relative to the horizontal axis) and they had shifted upwards by mid-day (8°) and maintained this position until the sun was about to set (Fig. 4).

Seasonal variation

In 2019, we tagged individuals in bloom according to their orientation (north, east, west, south) and came back to re-estimate the orientation of the plants at the fruiting stage. The majority of the fruits were in a similar direction to that initially measured at the flowering stage (Fig. 5).

Fig. 4. Variation in flower vertical orientation of 100 individuals of *Trillium grandiflorum* for a 24 hour period. The angle was measured relative to the horizontal axis, so negative values mean that the flowers are facing the ground. The data are from the Edimbourg population in 2021.



Impact on the internal temperature of flowers

The orientation of the flower could potentially have an effect on the flower internal temperature as the median temperature measured for flowers facing the north was lower than for those facing other directions, but the results were not significant ($p = 0.6489$, ANOVA, $\chi^2 = 0.033$, 3 df, $n = 60$; Fig. 6).

Impact on the proportion of fertilized ovules

We were able to collect fruits from 479 of the 700 plants that were initially tethered. A few could not be found, a few died, and several got out of the wire either because of normal growth or because animals pushed the plants out. The population Orée-des-bois occurs alongside a dense population of grey squirrels and was particularly affected with only 45 recovered plants. The number of plants in the other populations ranged from 63 to 86.

We found that neither the total number of ovules in the fruit nor the plant density in the population significantly improved the model to explain the proportion of fertilized ovules so both random terms were dropped. Similarly, we did not find a significant interaction between orientation and population, so the interaction was also dropped from the model. The final model showed that both population ($p < 0.0001$, ANOVA, $F = 8.509$, 6 df, $n = 479$) and orientation ($p = 0.04856$, ANOVA, $F = 2.646$, 3 df, $n = 479$) were found to be significant in explaining the percentage of fertilized

ovules. The effect was relatively important for orientation, with flowers facing south having 11.6% more fertilized ovules than north-facing flowers (Tukey's test, $p = 0.0368$; Fig. 7). However, south-facing flowers had less advantage over west-facing (2.6% increase; Tukey's test, $p > 0.05$) or east-facing flowers (5.4% increase; Tukey's test, $p > 0.05$).

For the analysis of the number of ovules per fruit, including population density as a random effect did not significantly improve the model and the same was observed for the population-orientation interaction. The final model only had orientation and population as fixed effects. Orientation did not have a significant effect on the number of ovules per fruit when all orientations were considered ($p = 0.102$, ANOVA, $F = 2.078$, 3 df, $n = 479$).

Discussion

The white trillium is an iconic species of the deciduous forest of eastern North America and has been the subject of many research projects. It is thus surprising that we could not find a reference to its heliotropism in the scientific literature, especially given that its population density makes this behaviour particularly striking when walking in the forest. Moreover, heliotropism has been reported in a congener, *Trillium nivale* Riddell (Knutson 1981), suggesting that other *Trillium* species might also be heliotropic.

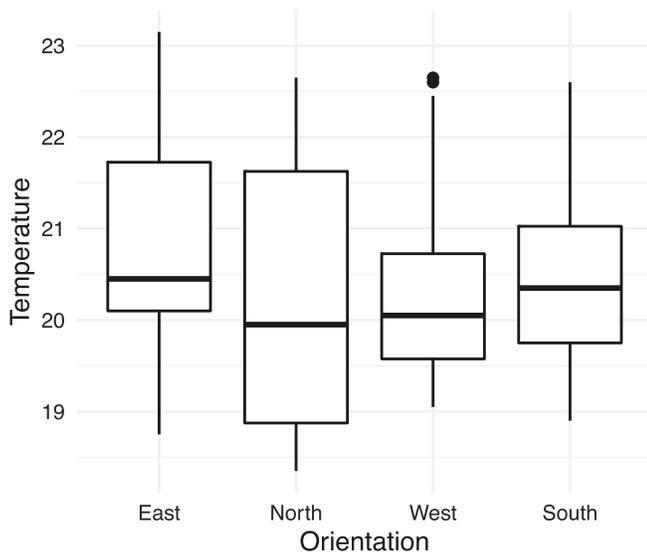
Our observations suggest that the white trillium possesses characteristics that correspond to both seasonal and daily heliotropism (Patiño et al. 2002; Serrano et al. 2018). We found that white trillium flowers face mainly south in populations and that they maintain this orientation throughout the season (Figs. 2 and 5), which suggests seasonal heliotropism. Yet, we also found daily variation in mean horizontal and vertical orientation of the flowers just as expected for daily heliotropic species (Figs. 3 and 4). The daily orientation was relatively modest and not necessarily observed for all individuals of the population. Similarly, a south-facing orientation was not observed for all individuals, although there was a declining trend in frequency as the orientation went closer to the north. This suggests that heliotropism in the white trillium is not a very strict mechanism.

The term seasonal heliotropism was first mentioned in a study of tropical plants (Patiño et al. 2002) and has not been reported very often (see Serrano et al. 2018). However, it might be a more widespread phenomenon given that previous reports may not have made the distinction between seasonal and diurnal heliotropism. This seems to be the case for *Dryas integrifolia* Vahl, an arctic plant that has movements that are closer to seasonal heliotropism than to diurnal heliotropism, but that has not been reported as seasonal heliotropism (Serrano et al. 2018). In addition, it is possible that many cases of seasonal heliotropism remain undocumented because it is a less spectacular behaviour than diurnal heliotropism. For instance, *Tropaolum majus* L. is a seasonal heliotropic species (S.J., personal observation), although only the negative heliotropism of its fruits appears to be

Fig. 5. Seasonal variation in the orientation of *Trillium grandiflorum*. Each plot represents the orientation of individual plants at the fruiting stage for plants that were oriented towards a specific cardinal point at the flowering stage. Data pooled from three populations in 2019.



Fig. 6. Impact of the orientation on the internal temperature of flowers.

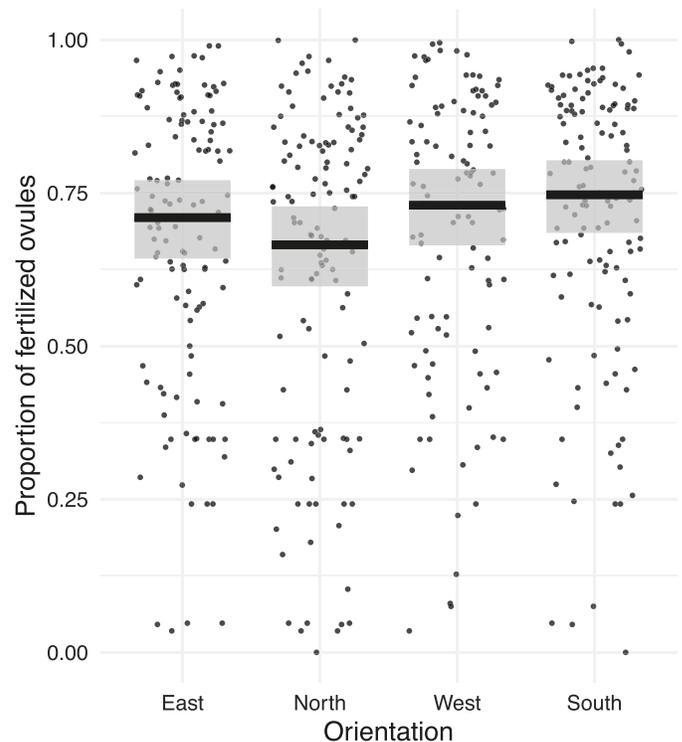


mentioned in the scientific literature (Oehlkers 1922; Serrano et al. 2018).

Impact on reproductive fitness

A natural reaction when facing a phenomenon such as the southward orientation of the vast majority of flowers in a population is to search for the advantage provided by such behaviour. However, we need to refrain from quickly jumping to adaptive explanations in front of a striking phenomenon as it could also be the result of other processes (Gould et al. 1979). For instance, heliotropism could be a correlate of the impact of light on auxin transport in pedicels without necessarily providing a fitness advantage. Here, however, we found that south-facing flowers had an 11.5% increase in fertilized ovules compared to north-facing flowers. This is significant for a species that has very low pollinator visitation rates and that essentially never reaches 100% seed set even after manual pollen supplementation (Irwin 2000; Griffin and Barrett

Fig. 7. Percentage of fertilized ovules for *Trillium grandiflorum* plants oriented towards the east, the north, the west, or the south. The black line is the expected (fitted) value as predicted by the model and the grey regions the standard errors. The points represent the observed data, pooled from seven populations.



2002). The advantage of south-facing flowers was not significant compared to west- and east-facing flowers, but the effect was nevertheless positive.

Our study does not provide a mechanism for the reproductive advantage of seasonal heliotropism. As mentioned in the introduction, both pollinator attraction and increased developmental growth have been found to increase the reproductive success of heliotropic species and both might

also explain the increased fitness observed in the white trillium. The sun rays hitting the petals could increase their temperature and bumblebees, the main pollinator of the white trillium, are known to prefer warm flowers when given the choice (Dyer et al. 2006). Indeed, a preference for warm flowers has been observed many times in heliotropic species living in cold environments either in terms of visitation rates (Smith 1975; Stanton and Galen 1989; Kudo 1995; Luzar and Gottsberger 2001; Atamian et al. 2016) or residency time (Stanton and Galen 1989; Luzar and Gottsberger 2001). Although the effect of flower orientation on internal flower temperature was not significant in our study, there was a tendency for south-facing flowers to have higher internal temperature (Fig. 6) and this aspect warrants further investigation. Yet, petal reflectance could play a role similar to that of temperature given that plant reproductive fitness has been shown to vary in different conditions of solar radiation (Arista et al. 2013).

Alternatively, the higher temperature provided by heliotropism could also promote pollen germination and growth as previous studies showed (Kevan 1972, 1975; Kudo 1995; Galen and Stanton 2003). We did not find a significant difference in numbers of ovules per fruit for the plants fixed in the different orientations, but this could be because plants were tethered just before anthesis when the ovary is already almost completely developed. Several other factors could affect the ovule or seed production such as soil composition (nutrients and moisture) or the microbiome of the plants. Yet, previous studies did not find that plant resources affected the seed:ovule ratio in the white trillium (Griffin and Barrett 2002). Moreover, the randomization of the treatments should have partially controlled for soil factors that could affect ovule and seed production within populations. Finally, we note that although heliotropism is less likely to have an impact on seed development in the white trillium because this occurs after the trees have leafed out (when the light is more diffused) we did not evaluate it at the fruiting stage.

Our experiment using tethered plants only tested for the fitness effect of seasonal heliotropism. We did not test if the daily movement of flowers also affects the plant fitness, though this would be interesting to test in the future. We might actually find that the fitness advantage of the combination of seasonal and daily heliotropism in the white trillium is more important than that of seasonal heliotropism alone.

Significance for early spring blooming plants from the temperate regions

The white trillium starts to bloom in early May, when the temperature is low in North America (mean min and max temperatures in May at the Montreal International Airport (1983–2013) are 8.0 ± 4.1 °C and 18.9 ± 5.1 °C, respectively). The importance of an increase in solar radiation for the flowers in such conditions is thus similar to that of alpine and arctic species for which the ecological importance of heliotropism has been frequently demonstrated. This would

only be true, however, of species that flower in early spring, before the trees leaf out, to benefit from the sun. This is the case of *Adonis ramosa* Franch., a spring ephemeral from Japan, in which heliotropic movements increased floral temperature and improved reproductive success through pollination, fertilization, and (or) seed development (Kudo 1995). But to date, this is the only species from temperate forests other than *T. grandiflorum* for which a fitness advantage for heliotropism has been demonstrated. There are certainly several other similar cases out there, especially given the putatively high number of heliotropic species in these environments (Lino 2001).

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Data availability

Data and scripts to reproduce the analyses presented in this study were deposited in FigShare under digital object identifier (doi): [10.6084/m9.figshare.12994355](https://doi.org/10.6084/m9.figshare.12994355).

Author information

Author contributions

M.G., C.F., and S.J. collected and analyzed the data. M.G. wrote the first draft of the manuscript. M.G. and S.J. edited the final version of the manuscript.

Competing interests

The authors have declared that no competing interests exist.

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