Arctic Plants Produce Vastly Different Numbers of Flowers in Three Contrasting Years at Lake Hazen, Quttinirpaaq National Park, Ellesmere Island, Nunavut, Canada

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To maximise reproductive success in the short Arctic growing season, plants pre-form flower buds the year prior to flowering. Flower bud production depends on warm ambient temperatures. Thus, although currently Arctic plants have low rates of sexual reproductive success, the warming climate may increase reproductive success. Following the long, warm growing season in 2012, plants at Lake Hazen, Ellesmere Island, produced many flowers in the short, cold growing season of 2013. Conversely, few flowers were produced in 2014, a long, warm growing season, but many flowers were produced in 2015, another long, warm growing season. Potentially higher rates of reproductive success in a warming climate could be compromised if consecutive years do not have long, warm growing seasons.

Key Words: Arnica angustifolia; Narrow-leaved Arnica; Cassiope tetragona; Arctic White Heather; Pedicularis capitata; Capitate Lousewort; climate change; flowering; flower abundance; reproductive success

Introduction

To maximise sexual reproductive success in the short Arctic growing season and to minimise time spent developing flower buds at the beginning of the growing season, many Arctic plants pre-form their flower buds in the year or years prior to flowering (Sørensen 1941). Of the complete flora of 184 species and varieties found in northeastern Greenland, for example, 80% pre-form their flower buds (Sørensen 1941). Given the circumpolar nature of Arctic flora, a similar proportion of the 125 species known to grow in the vicinity of Lake Hazen, Quttinirpaaq National Park, Ellesmere Island, Nunavut, Canada, likely also pre-form their flower buds (Sørensen 1941; Porsild and Cody 1980; Soper and Powell 1985; Elven 2003).

The extent to which the pre-formed flower bud primordia differentiate before the onset of winter varies among species but by August, differentiation has reached the extent to which it will differentiate in that year (Sørensen 1941). By winter, the flower buds of *Cassiope tetragona* (L.) D. Don (Arctic White Heather; Itsutit [Aiken *et al.* 2007]; Ericaceae) are fully formed with developed pollen visible, whereas those of *Arnica angustifolia* Vahl (Narrow-leaved Arnica; Qursuqtainnarmik nunaralik [Mallory and Aiken 2012]; Asteraceae) and some *Pedicularis* spp. L. (Orobanchaceae) are only partially formed, with anthers and petals visible and the ovary partially formed but no ovules visible (Sørensen 1941).

Flower abundance of some Arctic and alpine species is influenced by temperatures in the summer or autumn of the preceding year or by snow depth in the winter just prior to flowering. Flower abundance of *Dryas integrifolia* Vahl (Mountain Avens; Malikkaat [Aiken *et al.* 2007]; Rosaceae) and *Saxifraga oppositifolia* L. (Purple Saxifrage; Aupilattunnguat [Aiken et al. 2007]; Saxifragaceae) at Tanguary Fiord, Outtinirpaag National Park, Ellesmere Island, Nunavut, is influenced by August and October mean minimum temperature, respectively, in the year preceding flowering (Panchen and Gorelick 2015). In Zackenbergdale, Greenland, the flower abundance of C. tetragona, Salix arctica Pall. (Arctic Willow; Supitit [Aiken et al. 2007]; Salicaceae) and Papaver radicatum Rottb. (Arctic Poppy; Igutsat niqingit [Mallory and Aiken 2012]; Papaveraceae) are influenced by the sum of temperatures above 0°C (heat sum) in the preceding year's growing season, while flower abundance of Dryas species is influenced by snow depth in the preceding winter and heat sum in the preceding and current growing seasons (Høye et al. 2007; Ellebjerg et al. 2008). In Svalbard, Norway, C. tetragona flower abundance is influenced by snow depth in the context of extreme weather events, where shallow snow depth and an extremely warm spell mid-winter resulted in reduced flower numbers the following summer (Semenchuk et al. 2013). In the alpine setting of the Rocky Mountains in Colorado, flower abundance of Delphinium nelsonii Greene (Twolobe Larkspur; Ranunculaceae) was influenced by snow depth in the preceding winter, where it is thought that shallower snow depths in more recent years may have exposed the flower buds to frost damage (Inouye and McGuire 1991). In the same area, flower abundance of Androsace septentrionalis L. (Pygmyflower Rock Jasmine; Primulaceae), an annual or short-lived perennial, was influenced by the preceding year's summer precipitation and May temperature in the year of flowering but not the preceding year's growing season temperatures (Inouye et al. 2003).

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The Canadian Arctic Archipelago experienced dramatically different weather during each of the growing seasons from 2012 to 2015, leading to growing season lengths and temperatures that differed substantially over the four years. At Lake Hazen, Quttinirpaaq National Park, Ellesmere Island, Nunavut (81.82°N, 71.35°W), 2012 and 2015 were warm years with long growing seasons, while 2013 was a cold, snowy year with a short growing season and 2014 was a dry year with very little snow and a growing season length and temperatures intermediate between 2013 and 2015. Vastly more flowers were observed on plant species at Lake Hazen in 2013 and 2015 compared with 2014. This article presents critical baseline natural history data on Canadian high Arctic flowering phenology in a part of Canada that is rarely surveyed. Moreover, it documents the effects of variable weather conditions on Arctic plant flower production.

Methods

The flowering progression of three species, *A. angustifolia*, *C. tetragona* and *Pedicularis capitata* Adams (Capitate Lousewort; Kukiujait [Aiken *et al.* 2007]; Orobanchaceae), was monitored at Lake Hazen, Quttinirpaaq National Park, from 13th June to 31st July in 2013, 2014 and 2015 (Figure 1). A population of

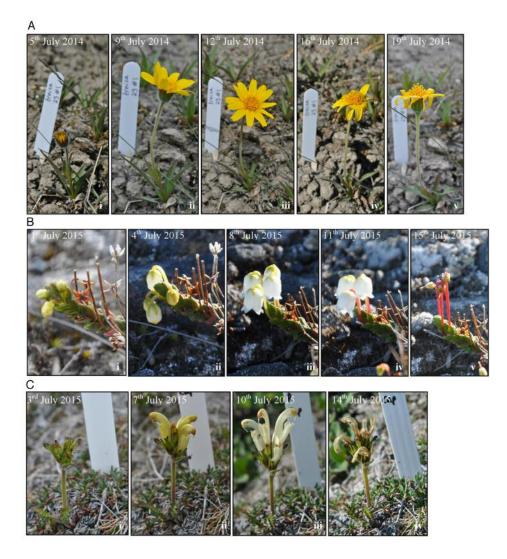


FIGURE 1. Flower progression of (A) Arnica angustifolia (Narrow-leaved Arnica) (B) Cassiope tetragona (Arctic White Heather) and (C) Pedicularis capitata (Capitate Lousewort) at Lake Hazen, Quttinirpaaq National Park, Ellesmere Island, Nunavut, Canada, showing flower(s) in bud (Ai, Bi and ii, and Ci), open flowers (Aii and iii, Biii and iv, and Cii and iii) and finish of flowering (Aiv and v, Bv and Civ). Photos: Zoe A. Panchen (panels A and C), Carly Cassey (B).

the perennial *A. angustifolia* was monitored on a southwest facing stream bank southeast of McGill Mountain (81.85°N, 71.35°W), a population of the woody species *C. tetragona* was monitored in a northeast facing gully on McGill Mountain (81.95°N, 71.49°W) and a population of the perennial *P. capitata* was monitored on the shores of Skeleton Lake (81.83°N, 71.48°W). Areas with established populations of each species were selected as monitoring sites before flowering began in 2013, except in the case of *A. angustifolia*, which only grows in a few locations at Lake Hazen and was not found until it was already in flower in 2013.

The sites were visited every 3–4 days in all 3 years. In 2013, monitoring was qualitative and subjective, following an approach successfully used by Panchen *et al.* (2012), wherein the date of first flower, peak flowering and finish of flowering of each population was recorded. After reviewing the 2013 results, the approach for subsequent years was changed to counting flowers to provide a more definitive date for start, peak and finish of flowering. Thus, in 2014 and 2015, monitoring was quantitative wherein 30 plants in each population were randomly tagged before flowering started and the number of flowers on each tagged plant was counted every 3–4 days. The inflorescence (capitulum holding many small flowers) of *A. angustifolia* was counted as a single flower.

The start, peak and finish of flowering for each species were determined from the flower count of the tagged plants. Start of flowering was defined as the date on which open flowers (Figure 1) were first observed on the 30 tagged plants, peak flowering as the date on which the greatest number of open flowers was counted and finish of flowering as the first date at the end of flowering on which no open flowers were observed. For each species, the peak number of flowers produced on the 30 tagged plants and the number of tagged plants that flowered in 2013–2015 were compared. For 2013, the peak number of flowers produced on 30 plants and the number of plants flowering out of 30 plants were estimated from observational field notes and pho-

tographs of the population or individual plants when they were in peak flower.

May to September mean monthly temperatures for the individual years 2012-2015 and the 10-year (2001– 2010) and 30-year (1981–2010) means at Eureka Weather Station, Ellesmere Island, Nunavut, Canada, were obtained or calculated from Environment Canada (2015) data. The Eureka Weather Station (79.59°N, 85.56°W) is the closest weather station to Lake Hazen and experiences a similar climate, with temperatures between the two locations well correlated (Soper and Powell 1985; Edlund and Alt 1989; Thompson 1994).

Results

Flower abundance of *A. angustifolia*, *C. tetragona* and *P. capitata* populations was much greater in 2013 and 2015 than in 2014 (Table 1, Figures 2 and 3). Compared with 2014, in 2013 and 2015 there were 1.5 times more flowers on tagged *A. angustifolia* plants and 1.5 times more *A. angustifolia* tagged plants flowering; 273 times more *C. tetragona* flowers and 2.5 times more *C. tetragona* plants flowering; and 6.3 times more *P. capitata* flowers and 2.3 times more *P. capitata* plants flowering (Table 1).

Of the 4 years 2012–2015, 2012 was the warmest growing season with the May–September mean temperature at Eureka 1.81°C and 2.32°C warmer than the 10- and 30-year means, respectively (Table 2). The coldest growing season occurred in 2013, with the May–September mean temperature 3.05°C and 2.54°C colder than the 10- and 30-year means, respectively. Mean monthly temperatures were above 0°C for a month longer in 2012, 2014 and 2015 than in 2013 suggesting that 2013 had a shorter growing season than the other 3 years.

Arnica angustifolia and P. capitata started, peaked and finished flowering earlier in 2014 and 2015 than in 2013 (Table 3), corroborating temperature data, which indicated that the growing season was likely longer in 2014 and 2015 than in 2013. Cassiope tetragona started flowering earlier in 2014 and 2015 than in 2013 and peaked and finished flowering earlier in 2015 than in

TABLE 1. Comparison of number of flowers per population on the date of peak flowering (Table 3) and number of tagged plants that produced flowers (30 tagged plants in each population) of *Arnica angustifolia* (Narrow-leaved Arnica), *Cassiope tetragona* (Arctic White Heather), and *Pedicularis capitata* (Capitate Lousewort) over 3 years at Lake Hazen, Quttinirpaaq National Park, Ellesmere Island, Nunavut, Canada.

Species	No. flowers on date of peak flowering			No. tagged plants that flowered		
	2013*	2014	2015	2013*	2014	2015
Arnica angustifolia	30	20	31	30	20	30
Cassiope tetragona	9000	33	9316	30	12	30
Pedicularis capitata	75	12	76	30	13	30

*2013 numbers are estimates.

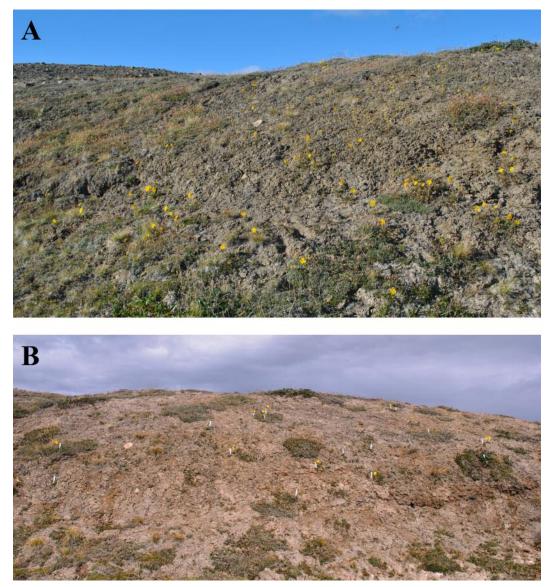


FIGURE 2. *Arnica angustifolia* (Narrow-leaved Arnica) population on a southwest facing stream bank, southeast of McGill Mountain, Lake Hazen, Quttinirpaaq National Park, Ellesmere Island, Nunavut, Canada. Over 100 flowers are visible in the 2013 photograph (A) and just 20 flowers (marked with white plastic plant tags) in 2014 (B). Both photos are of the same site taken from approximately the same position and angle but B is at a lower magnification than A. The patch of vegetation at the top right of A is on the centre skyline in B and the dip in the centre skyline in A is on the left in B. Photos: Zoe A. Panchen.

2013 and 2014. The *A. angustifolia* population was found on the last day at Lake Hazen in 2013 and was deemed to be at or close to peak flowering on that day because no flower buds remained and the majority of the plants had fresh-looking flowers, i.e., few of the ray

flowers around the edge of the capitulum were wilting. Given the time from start to peak flowering at Lake Hazen in 2014 and 2015 of 7 and 4 days, respectively (Table 3), *A. angustifolia* likely started flowering later in 2013 than in 2014 and 2015.



FIGURE 3. *Cassiope tetragona* (Arctic White Heather) in a northeast facing gully on McGill Mountain, Lake Hazen, Quttinirpaaq National Park, Ellesmere Island, Nunavut, Canada with over 300 flowers in 2013 (A) and with just three flowers in 2014 but over 100 flowers/fruits from 2013 still visible (B).

Month	2012	2013	2014	2015	10-year mean	30-year mean
May	-9.40	-12.31	-8.50	-12.60	-9.45	-10.20
June	5.40	0.50	1.00	4.30	3.49	3.00
July	8.60	4.45	5.85	9.60	5.50	6.10
August	5.10	-1.14	4.27	4.10	4.19	3.20
September	-2.40	-8.50	-4.62	-5.10	-5.47	-6.40
Average, May-Sept.	1.46	-3.40	-0.40	0.06	-0.35	-0.86
Average, June-Aug.	6.37	1.27	3.71	6.00	4.39	4.10

TABLE 2. Mean monthly temperature (°C) from May to September, 2012–2015, compared with 10-year (2001–2010) and 30-year (1981–2010) means at Eureka Weather Station, Ellesmere Island, Nunavut, Canada. Source: Environment Canada (2015).

TABLE 3. Dates for start, peak, and finish of flowering of *Arnica angustifolia* (Narrow-leaved Arnica), *Cassiope tetragona* (Arctic White Heather) and *Pedicularis capitata* (Capitate Lousewort) over 3 years at Lake Hazen, Quttinirpaaq National Park, Ellesmere Island, Nunavut, Canada.

Species	Year	Start of flowering	Peak flowering (days since start of flowering)	Finish of flowering (days since start of flowering)
Arnica angustifolia	2013	*	31 July	> 31 July†
ŭ ,	2014	5 July	12 July (7)	22 July (17)
	2015	9 July	13 July (4)	23 July (14)
Cassiope tetragona	2013	12 July	19 July (7)	> 31 July†
	2014	2 July	22 July (10)	> 31 July†
	2015	27 June	8 July (11)	23 July (26)
Pedicularis capitata	2013	18 July	21 July (3)	> 31 July†
*	2014	7 July	10 July (3)	13 July (6)
	2015	7 July	10 July (3)	20 July (13)

*Not found until after start of flowering.

†Not finished flowering when the Lake Hazen site was vacated on 31st July.

Discussion

The number of flowers in populations of three Arctic plant species at Lake Hazen was dramatically different in 2014 than in 2013 and 2015. There were many flowers in a year with a cold, short growing season (2013) following a year with a warm, long growing season (2012). There were few flowers in a year with a warm, long growing season (2014) following a year with a cold, short growing season (2013). There were many flowers in a year with a warm, long growing season (2015) following a year with a warm, long growing season (2014). Possible reasons for the low flower abundance in 2014 could be that the 2013 growing season might have been too short or temperatures may not have been warm enough for the species to pre-form flower buds (Sørensen 1941; Høye et al. 2007; Ellebjerg et al. 2008; Panchen and Gorelick 2015). In 2013, the mean temperature in August, the month in which flower bud differentiation is suspended (Sørensen 1941), was already below freezing but was above freezing in 2012, 2014 and 2015. Another possible reason is that the three species may have exhausted their available nutrient and carbohydrate resources in the sexual reproductive cycle in 2013 and, hence, did not have enough resources available to pre-form buds in 2013 for the 2014 flowering season. Arctic plants are generally resource limited and may not flower every year as they must build up enough nutrients and carbohydrates over 1 or more years for the resource-intensive sexual reproductive cycle (Mooney and Billings 1960; Fox and Stevens 1991; Wookey et al. 1993; Pielou 1994).

Of the three species studied, *C. tetragona* is the only one considered a snow bed species, it relies on the insulation of snow cover to protect the aboveground preformed flower buds from the harsh Arctic winters (Soper and Powell 1985). At Lake Hazen, it grows in gullies, depressions and on the lee side of hills where snow drifts form. In 2013, the gully on McGill Mountain was filled with approximately 30 cm of snow on 20th June and was not free of snow until 2nd July. In 2015 there was approximately 10 cm of snow in the gully on 13th June and it was snow free by 24th June. In 2014, however, the gully was snow free before 14th June. *Cassiope tetragona* may have had fewer flowers in 2014 than in 2013 and 2015 due to the absence of a protective snow layer and the resulting exposure may have killed the pre-formed flower buds (Inouye 2008; Semenchuk *et al.* 2013). *Arnica angustifolia* and *P. capitata* are perennials and their pre-formed buds are protected below ground from the cold air temperatures that are typically -40°C during the winter (Soper and Powell 1985; Thompson 1994).

The strategy to maximise sexual reproductive success by pre-forming flower buds in the prior year or years can only be effective if consecutive years have a long, warm growing season; the first year must be long enough and warm enough to pre-form sufficient flower buds (Høye *et al.* 2007; Ellebjerg *et al.* 2008; Panchen and Gorelick 2015), the second year must be long enough and warm enough to produce viable seed and a subsequent year must be long enough and warm enough to produce surviving seedlings (Muller *et al.* 2011).

Arctic plants have low rates of sexual reproductive success and, in theory, warmer temperatures and longer growing seasons resulting from recent climate change should increase sexual reproductive success (Bliss 1971; Wookey et al. 1993; Muller et al. 2011; Alsos et al. 2013). However, the extreme events and more varied climate, also associated with recent climate change (Easterling et al. 2000a, 2000b; Semenchuk et al. 2013), might be problematic for sexual reproductive success of Arctic plants given the 2+ year cycle to produce flowers (Inouye and McGuire 1991; Inouye 2008; Semenchuk et al. 2013). The observations did not test sexual reproductive success per se, however, flower abundance can be used as a proxy for reproductive success. If there are few flowers, then the possibility of sexual reproduction is lower.

The difference in methods between 2013 and 2014–2015 and the lack of quantitative measurements in 2013 introduces some uncertainty into the findings. However, the difference between the years is so dramatic that even if the flowers had been counted rather than estimated in 2013, the same results and conclusions would likely have been drawn.

The 2012–2015 observations at Lake Hazen may be indicative of larger-scale processes that could affect Arctic plant populations. Decreased rates of sexual reproduction resulting from increasingly greater year-toyear variation in growing conditions are likely to have important and long-lasting consequences in Arctic ecosystems (Soper and Powell 1985; Pielou 1994; Svoboda and Freedman 1994).

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