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Research Article

Life history stability under climate change: a wildflower at the northern edge of its range

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Stabilities of life history traits for a widespread native perennial wildflower, *Rudbeckia laciniata* L., are described for five populations near the northern edge of its range in North America. Theory proposes that such populations experience variable levels of stress as suitable abiotic conditions shift north or south from year to year, which destabilizes their life histories. With climate change, however, rising temperature may increase stability, by reducing the frequency or intensity of exposure to sub-optimal low temperatures. To investigate these ideas, stability was quantified as year-to-year variability in height, number of flower/seed heads, seasonal development, and density for flowering stems from 1999 to 2023. Proportional variability (PV) provided the most consistent estimates among three stability metrics that were tested. In all populations, three of four traits were remarkably stable (low PV), stem density less so. Monthly mean daily temperatures near the populations revealed climate change over 25 years: declining in April by 4.1°C, rising in June by 3.5°C. This local climate change, particularly rising June temperatures, caused declines in stem height and density. Contrary to expectations from life history theory, growth and development traits of *R. laciniata* were stable in the five northern populations, and climate change destabilized two traits: flowering stem height declined by 16% and stem density by 90% over two decades, threatening the future reproductive success of four wild populations.

Keywords: long-term study, phenology, population dynamics, *Rudbeckia laciniata* L., tall coneflower

Introduction

For populations near the boundary of a species' range, abiotic conditions most suitable for plant growth and development shift back and forth across this boundary, as weather changes from year to year. Such populations are subject to temporal variability in levels of environmental stress, which has led to the view that peripheral populations are less stable than those nearer the centre of their range (Nantel and Gagnon 1999, Parmesan et al. 2005, Parmesan and Singer 2022). At the northern boundary of a range in the Northern Hemisphere, however, rising temperatures due to climate

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change might reduce exposure to what otherwise would have been colder years, stabilizing life histories. The importance of weather and climate to population dynamics is widely acknowledged, particularly in the context of predicting the consequences of climate change for species in the natural world (Parmesan and Yohe 2003, Root et al. 2003, Dose and Menzel 2004, Parmesan et al. 2005, Shoo et al. 2006, Schleip et al. 2009, Sletvold et al. 2013, Wadgymar et al. 2018, Evers et al. 2021, Lindell et al. 2022, Parmesan and Singer 2022). However, identifying the effects of weather on individual population processes is challenging, particularly using the observational data from long-term studies which are needed to link population change and climate change (Wadgymar et al. 2015, Krebs et al. 2024, Williams et al. 2025).

To assess these ideas, we investigated the stability of life history traits for a wildflower, *Rudbeckia laciniata* L. (Asteraceae), a summer-blooming, sun-loving but shade-tolerant perennial, endemic to the southern half of North America (Urbatsch and Cox 2006, North American Plant Atlas 2014, USDA 2023). The northern limit of the plant's native distribution is in southern Canada, near Dauphin, Manitoba (Scoggan 1979, Cody 1988, University of Manitoba Herbarium 2024). The study was based on two decades of data for five populations of *R. laciniata* near the northern edge of its range, the most northerly population being 10 km south of this boundary.

Rudbeckia laciniata also inhabits areas of the continent (USDA 2023) with consistently higher temperatures than those in southern Manitoba, which led us to expect that climate change might have little impact, or perhaps a positive effect, on the fitness of northern populations. In the latter case, stability of these northern populations might increase with climate change. On the other hand, local populations may be adapted to conditions at the northern edge of the plant's range, without the genetic variation needed to adapt quickly to climate change (Wadgymar et al. 2015, Parmesan and Singer 2022). Climate change might then cause temporal trends in the traits, trends that reduce their year-to-year stability.

The stabilities of four life history traits were documented annually as stems matured, for individual flowering stems in each population: stem density, stem height, number of flower/seed heads per stem, and seasonal timing of development (phenology). As the ecology of the species has been little studied anywhere in its range, growth and development of individual stems were also assessed weekly in one of the populations. These weekly data provided information on the temporal and among-stem distributions of trait values, to assure us that the stability of trait means could be meaningfully compared (Pélabon et al. 2020), and were consistent with assumptions of statistical tests (Supporting information). Given uncertainty regarding the efficacy of metrics used to quantify stability (Lamb and MacKay 2010, Heath and Borowski 2013, Lobry et al. 2023), three metrics were compared, before settling on 'proportional variability' to quantify the stability of the traits (Heath 2006, Heath and Borowski 2013).

The life history theory relevant to stability at the northern edge of a range was investigated for *R. laciniata* by addressing two questions. Are life history traits unstable at the edge of the species' range? Does climate change stabilize life histories at the northern edge of the species' range? We expected to find that life history traits of the five *R. laciniata* populations would be unstable but stabilized by a warming climate.

Material and methods

Populations

Five populations in south-central Manitoba, Canada, were studied: four wild populations in Riding Mountain National Park (RMNP) and the fifth established 200–250 km to the southeast in an urban garden in Winnipeg. The physical details of the populations and their acronyms are in Table 1. The wild populations (BR, CC, BB, and BH) inhabit edges of four walking trails in RMNP, which extends 110 km east–west and 30 km south–north on the Manitoba Escarpment (Bird 1972). Three of the populations (BR, CC, and BB) are adjacent to trails through mature forest dominated by

Table 1. Five populations of *Rudbeckia laciniata* studied from 1999 to 2023, their locations along named trails in Riding Mountain National Park (RMNP), Manitoba, Canada, and in a Winnipeg wildflower garden. Data for assessing the effects of climate change on each population came from the nearest Environment Canada weather station, listed with the distance to each population. [a]For WH, the total area of five patches of *R. laciniata* is provided; this area is not comparable to that for RMNP trails which are calculated as 1 m on each side of the trail multiplied by the length of trail searched. [b]Wasagaming was included for additional comparisons because it has an elevation closer to that of BH and CC than other stations.

Location	Population (code)	Area[a] m^2	Longitude west	Latitude north	Altitude m a.s.l.
RMNP	Beach Ridges (BR)	1800	100°3′36″	51°0′36″	418–425
RMNP	Crawford Creek (CC)	5200	100°4′12″	51°0′0″	415–555
RMNP	Burls & Bittersweet (BB)	3600	99°33′36″	50°41′24″	392–410
RMNP	Bald Hill (BH)	1600	99°38′24″	50°41′24″	694–723
Winnipeg	Garden (WH)	29.4	97°7′48″	49°51′0″	247
Weather station		Distance to population, km	Longitude west	Latitude north	Altitude m a.s.l.
Dauphin		BR – 10, CC – 11	100°3′0″	51°6′0″	305
McCreary		BB – 3, BH – 7	99°31′48″	50°42′36″	351
Wasagaming[b]		BH – 21, CC – 33	99°56′24″	50°39′36″	627
Winnipeg (The Forks)		WH – 4	97°4′12″	49°31′48″	230

trembling aspen *Populus tremuloides* Michx. and unaffected by wildfire for 120–150 years. The fourth, BH, is near the top of the escarpment, where the trail passes through an area regenerating after a 1980 wildfire (Fire history records, RMNP Office, Wasagaming, Manitoba).

RMNP populations were assessed once per year in the third week of August 1999–2023, along trails that vary from 1 to 3 m wide. In 1999, a part of each trail with > 100 flowering stems was designated for sampling and divided into 100-m permanent sections defined by a global positioning system (GPS) (trail code – number of sections: BR – 9, CC – 26, BB – 18, BH – 8). Individual flowering stems (hereafter called stems) within 1 m of either edge of the trail were assessed. When stem density was high (e.g. at CC > 1000), all stems were counted, but other traits were assessed for individual stems in a sub-sample of 10 m for each section. At BH, stems were so abundant in the 1-m trail borders, and surrounding meadows, that assessments of all stems were impractical. For BH, sub-samples of stems were assessed in a total of 26 patches designated by GPS waypoints, with five stems closest to a waypoint assessed. In four later years, the total number of stems within 1 m of either edge of the trail was recorded for all BH sections. Mean annual counts of stems (n), and sub-samples of stems (S) for assessing growth and development were (population – n, S): BR – 100, 27; CC – 1005, 128; BB – 127, 53; BH – 4976, 190. Mean (range) August dates for annual assessments were BR – 18 (16–24); CC – 19 (16–26); BB – 19 (16–25); BH – 20 (16–28).

The Winnipeg population (WH) is in a private urban garden of mostly native wildflower species, where detailed observations could be made of stem growth and development through the season, protected from human disturbance. It was established in the mid-1980s using seed from wild plants growing in a riverine forest 5 km from the garden. By 1999, five patches of plants were established among mature deciduous trees near the Red River, to mimic the patches of tall coneflower that occur naturally in riverine forests around Winnipeg. This habitat is like that at BB in RMNP where the forest trail follows a streambank. The WH population, with an annual average of 145 stems, was similar in size to the BR and BB populations. The WH population was also assessed at the same time as the RMNP populations, between 16 and 26 August, (19 August on average), for comparison with the wild populations. In addition to the annual assessment, individual stems at WH were assessed approximately weekly (usually every 7–8 days, range of 3–12 days) through the growing season. This weekly assessment at WH provided data not available in the literature, that was used to define the plants' phenology and the statistical properties of life history traits. For all populations, assessments were non-destructive, with minimal contact with the plants. The WH population grew without interference except that it was maintained in fixed patches by removing seedlings or stem shoots at the edges of each patch. Herbivores were not controlled, nor were pesticides or fertilizer applied near the patches. Occasionally the patches were watered in dry periods, along with the rest of the garden.

Life history traits

From 1999 to 2023, four traits were documented annually in the third week of August as population means: stem density, stem height, number of flower/seed heads per stem, and phenological stage of stems. Stem density equalled the total number of stems in a population divided by sample area. At WH, the sample area was that of the five patches, 29 m^2. For RMNP, the total number of stems in a population was divided by the number of 100-m trail sections (a search area of 200 m^2 per section); the number of sections varied among populations but was fixed from year to year. This density is not comparable to that in the garden which is per m^2 of the patches of tall coneflower, not the density in the wider habitat. Stem heights and number of flower/seed heads per stem are means for the stems assessed in each population on a sample date. Plant phenology was measured as a mean stage in August, based on weekly observations of the stages at WH (Fig. 1a); development of the stems was divided into 12 successive visually recognizable stages (Table 2), named as integers 1–12. Each stage from 2–12 lasted 8–9 days. The frequencies of stages present in a population were recorded at each sample date and summarized by two metrics: the mean of integer values (for 'status' monitoring), and the median value for stages found on a date (for 'event' monitoring) (Denny et al. 2014). Recognizing the statistical uncertainties when phenological stages (categories) are quantified as numerical values (Schaub et al. 2022), temporal sequences of stages and their frequency distributions were assessed to determine the precision and validity of the two metrics for estimating seasonal stability of stem phenology.

Quantifying stability

Here, stability refers to the temporal variability of time series of annual estimates for each of the four traits and five populations (20 time series). Three metrics were considered to quantify stability: coefficient of variation (CV), Kvålseth's coefficient of variation (^{K}CV), and proportional variability (PV) (Heath 2006, Heath and Borowski 2013, Pélabon et al. 2020, Lobry et al. 2023). The relative merits of these metrics for quantifying stability of the populations were compared (Supporting information). PV (range of 0–1) was adopted to assess whether the life history traits are unstable at the edge of a species' range of *R. laciniata*: low PV (high stability) or high PV (low stability).

Influence of climate change on stability

Local climate change was identified as temporal trends in year-to-year variation of weather parameters over 25 years (1999–2023), using daily temperature and precipitation records from four Environment Canada, Government of Canada, weather stations within 3–33 km of the populations (Table 1). Weather parameters from the closest station were used for each population. A more distant station, Wasagaming, was included for additional comparisons because its elevation is more similar to that of the BH and CC populations, near the top of the escarpment, than the closest weather stations. For each station and year, the

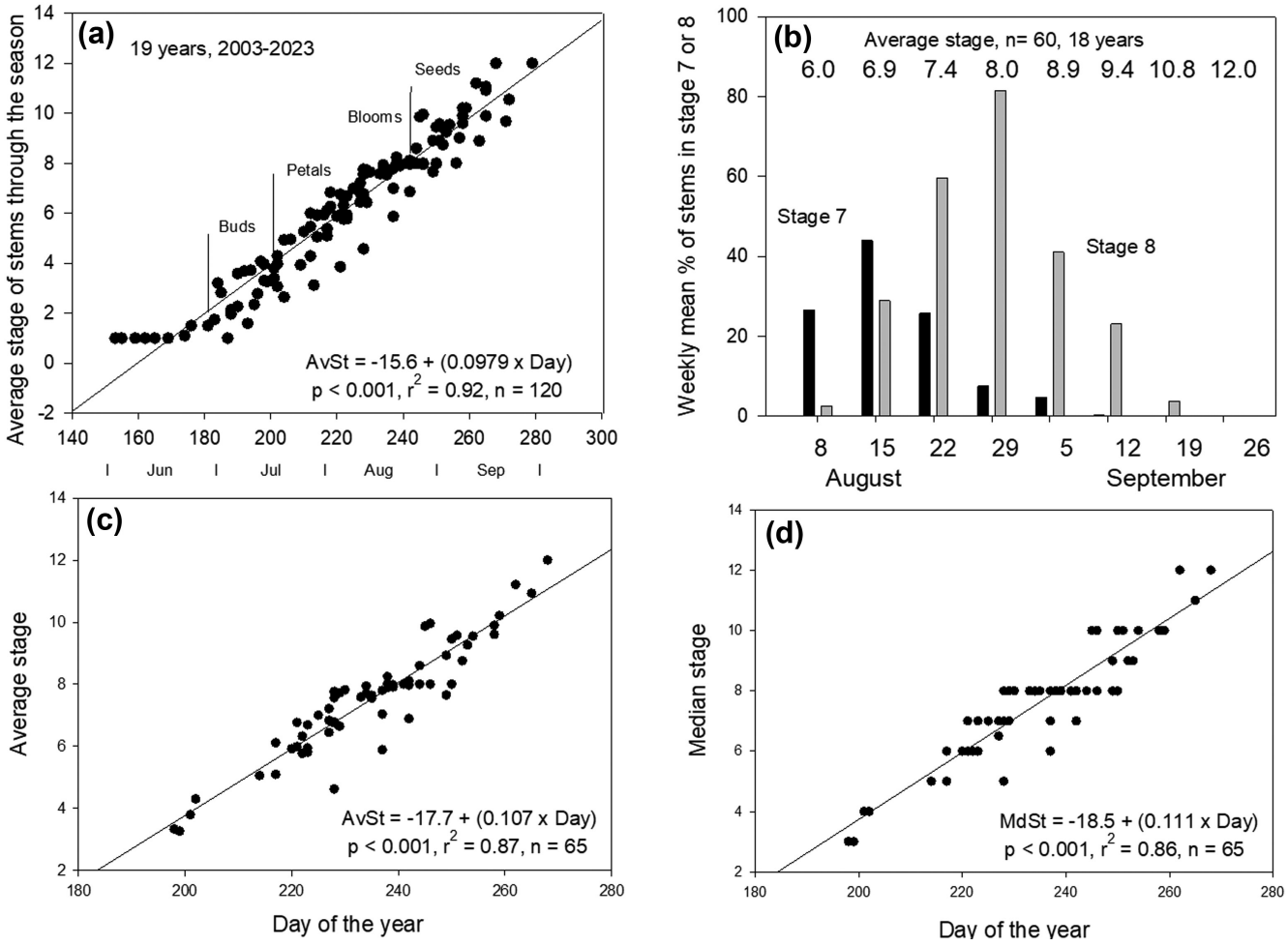


Figure 1. Developmental stages (Table 2) of stems through the season in a garden population of *Rudbeckia laciniata* in Winnipeg, Manitoba, Canada. (a) Average stage for stems through the growing season (120 sample days over 19 years; 69–257 individual stems per day); (b) weekly mean of the frequency (%) of stems dropping petals (stage 7) or without petals (stage 8) through August and September (60 sample days); (c) average stage for stems from early July through early September (65 sample days); (d) median stage for stems from early July through early September (65 sample days).

Table 2. Developmental stages, recorded as integers, used to characterize the phenology of individual flowering stems of *Rudbeckia laciniata* (adapted from Lamb and MacKay 2017). Stages 3–8 were assessed using the most advanced head on each stem. The average stage for a population is the mean of integer values of stages for individual stems on a particular day. Stages 2–12 were 8–9 days long.

Description of developmental stages for stems	Stage
Stem elongating but not yet in bud	1
Developing bud covered by bracts	2
Immature head visible	3
Petals of ray florets expanding	4
Some disc florets open	5
All disc florets open	6
Petals of ray florets dropping	7
No petals remain	8
Petioles yellow	9
Petioles brown	10
Stem yellow, yellowing occurs from top to bottom	11
Stem brown, browning occurs from top to bottom	12

following parameters were calculated: annual means of mean daily temperature; monthly means of daily minimum, daily maximum, and mean daily temperature; annual sums of daily precipitation, monthly sums of daily precipitation. Linear regressions (SigmaPlot 16 2025) of these parameters on year were used to identify any temporal trends in the weather parameters, which were then assumed to be exhibiting local climate change.

Temporal trends in the four plant traits were then identified using linear regression analysis. Our goal was to identify any trends in plant traits analogous to those of weather parameters. Except for stem density, estimates of the plant traits used in the models were annual means from large stem samples, and more likely to meet the assumptions of normality for the test than measurements for individual stems. A significance level of $p < 0.05$ was adopted to select models that might reflect real trends, recognizing that assumptions of normality were not met in all cases; models with $p < 0.10$ were also considered when they exhibited trends similar to

those with significant trends. Our assumption was that such a trend does not prove a role for climate change, but lack of a trend rules out local climate change as a factor in year-to-year variation of a trait.

To test whether a temporal trend in a plant trait was the result of climate change, the annual trait estimates were regressed, not on year, but instead on the annual value of a weather parameter that had been shown to reflect local climate change. If a local weather parameter affected by climate change, such as monthly mean temperature, explained as much of the annual variation in a trait (r^2, coefficient of determination; Sokal and Rohlf 1981) as the temporal or year-to-year trend for that trait, we concluded that climate change influenced annual variation in the trait. These data provided a test of the hypothesis inherent in the question: does climate change stabilize life histories at the northern edge of a species' range? For those life history traits affected by local climate change, the hypothesis is supported if the stability of a trait rises.

These analyses assume linearity. To assess the degree of non-linearity, polynomial quadratic regression models were also considered. In a few cases, non-linear models explained more of the variation (r^2, coefficient of determination) than linear ones, although not sufficiently so to change the interpretation of the role of climate change, but linear models detected more significant trends than non-linear ones. For ease of comparison of trends and relationships among parameters, linear models are presented.

Results

Phenology of flowering stems

At WH, shoots emerged from the soil between 1 April and 3 May 1998–2022 (19 April on average). By early May, shoots became individual acaulescent leaves on petioles that developed from subterranean rhizomes, forming a canopy at 40–50 cm by late June. Flowering stems emerged in late May and rose above the canopy of acaulescent leaves in early June. By late June, flower buds were produced, eventually forming a loose corymb of 1–24 heads. The number of stems increased to a maximum in early July, with a mean density of 4.9 stems per m^2 (± 0.406, n = 21 years). Stem height increased through June and July, reaching a maximum in early- to mid-August; stems bloomed through August. The number of heads on stems reached a maximum between the first and third week of August. Stems senesced by early October, usually before the first frost (< −1°C) in mid-October, and 3–4 weeks before a hard frost (< −5°C). Acaulescent leaves remained succulent until they froze. This phenology (Fig. 1a) was quantified based on developmental stages 1 to 12 (Table 2).

Properties of life history traits

Annual estimates of four life history traits differed among the five populations (Table 3). Stem density was high at CC and BH, and relatively low in the other two RMNP populations. Stem height and number of heads per stem were higher at WH and BH than in the other three populations. In all populations, the annual mean number of heads increased with mean stem height (linear regression, $p \leq 0.05$, n = 15 years), explaining 26% (r^2) of the annual variation, on average: BR-34%, CC-23%, BB-20%, BH-29%, WH-23%. Average stages of 6.9–7.0, near the end of full bloom, were uniform among populations. The year-to-year dynamics of stem populations were influenced by area-wide phenomena. Over 21 years, stem densities fluctuated together among three RMNP populations (BR, CC, BB: r = 0.55–0.76, p = 0.01 to $p < 0.001$; BH: $p > 0.05$), but not between RMNP and WH (r = 0.10–0.37, p = 0.13–0.69, n = 18). Similarly, stem heights were correlated from year to year between CC and BB or BH (r = 0.51, 0.58, p = 0.05, 0.02, respectively, n = 15; BR: $p > 0.05$). The numbers of heads per stem were correlated between CC and BB (r = 0.53, p = 0.04, n = 15). Neither stem height nor number of heads per stem were correlated between RMNP and WH populations ($p > 0.10$, n = 14 or 15).

In the third week of August at WH, annual estimates of the four traits (stem density, mean stem height, mean number of heads per stem, and average stage) were all normally distributed (Shapiro–Wilk mormality test, p = 0.97, 0.75, 0.35, and 0.10, respectively). For the four RMNP populations, stem height, number of heads, and average stage were also normally distributed, but stem density was not at BR, CC, and BB ($p < 0.01$). Stem density at BH was normally distributed (p = 0.90), but this estimate was based on only

Table 3. Annual mean, SE, and sample size (n, years) for four life history traits of *Rudbeckia laciniata* flowering stems in the third week of August 1999–2023, for five populations in Manitoba, Canada (see Table 1 for population site codes and locations). *Estimates of stem density per m^2 for plant patches at WH are not comparable to populations (BR, CC, BB, BH) at Riding Mountain National Park (RMNP), measured as stems per 100 m of trail, 200 m^2 of trail edges. For stem density at RMNP, means followed by a different letter differ, Kruskall–Wallis one-way analysis of variance on ranks ($p < 0.001$, n = 20 years). For the other three traits, means followed by a different letter differ: two-way analysis of variance for stem traits on site and year (site $p < 0.01$, n = 13–15 years).†For BH, the four estimates of stem density were insufficient to include in this analysis.

	Stem density			Stem height, cm			Heads per stem			Developmental stage		
Site	Mean*	SE	n	Mean	SE	n	Mean	SE	n	Mean	SE	n
BR	11.2[b]	3.033	23	105.0[b]	2.828	16	2.3[c]	0.135	18	6.9[b]	0.123	17
CC	37.3[a]	10.870	23	115.2[b]	2.141	17	2.9[c]	0.085	18	7.0[a]	0.116	17
BB	7.1[b]	1.278	22	113.4[b]	1.758	16	2.9[c]	0.132	16	7.0[a]	0.141	16
BH†	494.0	182.624	4	128.3[a]	2.673	17	3.9[b]	0.207	18	7.0[a]	0.186	17
WH	4.9	0.395	21	132.6[a]	2.86	21	6.3[a]	0.26	19	6.9[b]	0.289	13

four years, compared with 22–23 years for the other three RMNP populations.

Average stage is the mean of the integer values of stages for individual stems present in a population on a particular date (Table 2, Fig. 1b). It reflects the relative frequency of stages present in the population at a particular time, providing a metric for the phenology of the population (Fig. 1b). Stage is a category, not a continuous variable, and therefore may not meet assumptions of standard statistical analyses. Nevertheless, the transition from stage 7 to stage 8 in the population in late August illustrates their symmetrical frequency distributions, with the peak frequency of a stage close to the center of the normal distribution for that stage (Shapiro–Wilk normality test, $p = 0.054$, $p = 0.368$, respectively) (Fig. 1b). For July–September when stems matured, average stage for each sample date in all years was linearly related to the day of the year (Fig. 1c); Stages 2–12 each lasted 8–9 days. Median stage exhibited a similar pattern for stage over the growing season (Fig. 1d), but this metric provided a less precise description because it consists of only integer values: the median was 8 on 22 and 29 August, compared with 7.4 and 8.0 for average stage (Fig. 1b). Median stage quantified the mid-point of stages present, as did average stage, but the median did not reflect the relative frequency of stages above or below the dominant stage. Furthermore, year-to-year values of median stage were not normally distributed (Shapiro–Wilk normality test, $p = 0.006$), whereas average stage was ($p = 0.310$).

Table 4. Stability metrics for four life history traits (Table 3) of *Rudbeckia laciniata* measured annually in the third week of August for flowering stems in five populations (Table 1) in Manitoba, Canada (1999–2023). Stability (temporal variability) is quantified from time series of annual means for trait values as: proportional variability (PV, proportion on a scale of 0–1), coefficient of variation (CV, standard deviation/mean), and Kvålseth's CV (^{K}CV, proportion on a scale of 0–1). See Table 1 for explanation of population codes.

Trait	Population	PV	CV	^{K}CV
Density	BR	0.728	1.301	0.793
Density	CC	0.573	1.399	0.814
Density	BB	0.577	0.843	0.644
Density	BH	0.637	0.739	0.595
Density	WH	0.340	0.369	0.346
Height	BR	0.110	0.108	0.107
Height	CC	0.085	0.077	0.076
Height	BB	0.066	0.062	0.062
Height	BH	0.093	0.086	0.086
Height	WH	0.108	0.099	0.098
Heads	BR	0.244	0.249	0.242
Heads	CC	0.131	0.126	0.125
Heads	BB	0.167	0.180	0.177
Heads	BH	0.212	0.226	0.220
Heads	WH	0.177	0.181	0.178
Stage	BR	0.079	0.074	0.074
Stage	CC	0.073	0.068	0.068
Stage	BB	0.088	0.080	0.080
Stage	BH	0.115	0.109	0.108
Stage	WH	0.155	0.151	0.150

Stability of year-to-year variation for life history traits

Three metrics, PV, CV, and ^{K}CV, provided similar values for 16 estimates of stability when $PV < 0.4$ (Table 4). Linear regression of ^{K}CV (y) on PV (x) explained 99.7% of the variation ($y = -0.011 + 1.056 \pm 0.016 * y$, $n = 16$, $p < 0.0001$), with the slope close to 1:1. Above $PV = 0.5$ (stem densities at RMNP), the three metrics diverged substantially and inconsistently among metrics and populations (Table 4). PV is adopted as the stability metric, because it does not assume a Gaussian distribution for trait values as do CV and ^{K}CV, and because PV values did not vary as erratically as the other two metrics (Supporting information).

Of the four life history traits, stem height and average stage were remarkably stable (low year-to-year variability) in all populations (average $PV = 0.09$ and 0.10, respectively, on a scale of 0–1) (Table 4). Stability was lower but still relatively high for the number of heads per stem (average $PV = 0.19$); stem density was less stable (average $PV = 0.57$), particularly in RMNP (Table 4).

Local climate change

From 1999 to 2023, four weather stations near populations of *R. laciniata* showed similar patterns of weather through the growing season (April–September) but differed in monthly mean temperatures (two-way ANOVA, $n = 4$ stations and 25 years, $p = 0.001$). On average, The Forks was 1°C warmer than McCreary, 2–3°C warmer than Dauphin, and 3–4°C warmer than Wasagaming. Monthly precipitation also differed among stations for April–May ($p < 0.05$), but not from June–August ($p > 0.05$); Dauphin usually had the lowest rainfall.

Annual means for daily temperature and annual sums of daily precipitation showed no trends over 25 years that might reflect climate change at the four stations. For annual daily mean, maximum, and minimum temperatures ($p = 0.36$–0.96) and precipitation ($p = 0.11$–0.42), linear regression slopes on year explained little of the year-to-year variation in the parameters ($r^2 = 0$–0.11). In contrast to annual parameters, monthly mean temperatures showed significant temporal trends for April and June. For April, temperature declined ($p < 0.05$, $r^2 = 0.16$–0.25). For June, temperatures rose ($p < 0.001$, $r^2 = 0.40$–0.52). Slope coefficients were also consistently positive for one or more of these parameters and stations in May, July, and September ($p > 0.05 < 0.10$, $r^2 < 0.16$). The cooling trend for April and warming trend for June had numerically similar but opposite slopes (Fig. 2); at the annual scale, the monthly trends cancelled each other, leading to the lack of a trend for annual mean temperature. At the four stations, the decline in April temperature was 3.8–4.4°C, and the increase in June temperature was 3.1–3.9°C, over 25 years (Fig. 2), whereas for other months, although similar among stations, increases or decreases were numerically smaller and did not differ significantly from 0.

Monthly precipitation showed indefinite trends over 25 years. Five of 48 slopes for regressions of monthly precipitation on year had $p < 0.05$, one positive and four negative: e.g. the highest slopes were −1.05 ($p = 0.006$, $r^2 = 0.28$) for November at McCreary, and −0.70 ($p = 0.02$, $r^2 = 0.22$) for January in Dauphin. Most trends, 32 of 48, were negative, particularly for winter months. Based on monthly estimates of precipitation, effects of climate change were not evident for any station from April to September, the months when plants were actively growing.

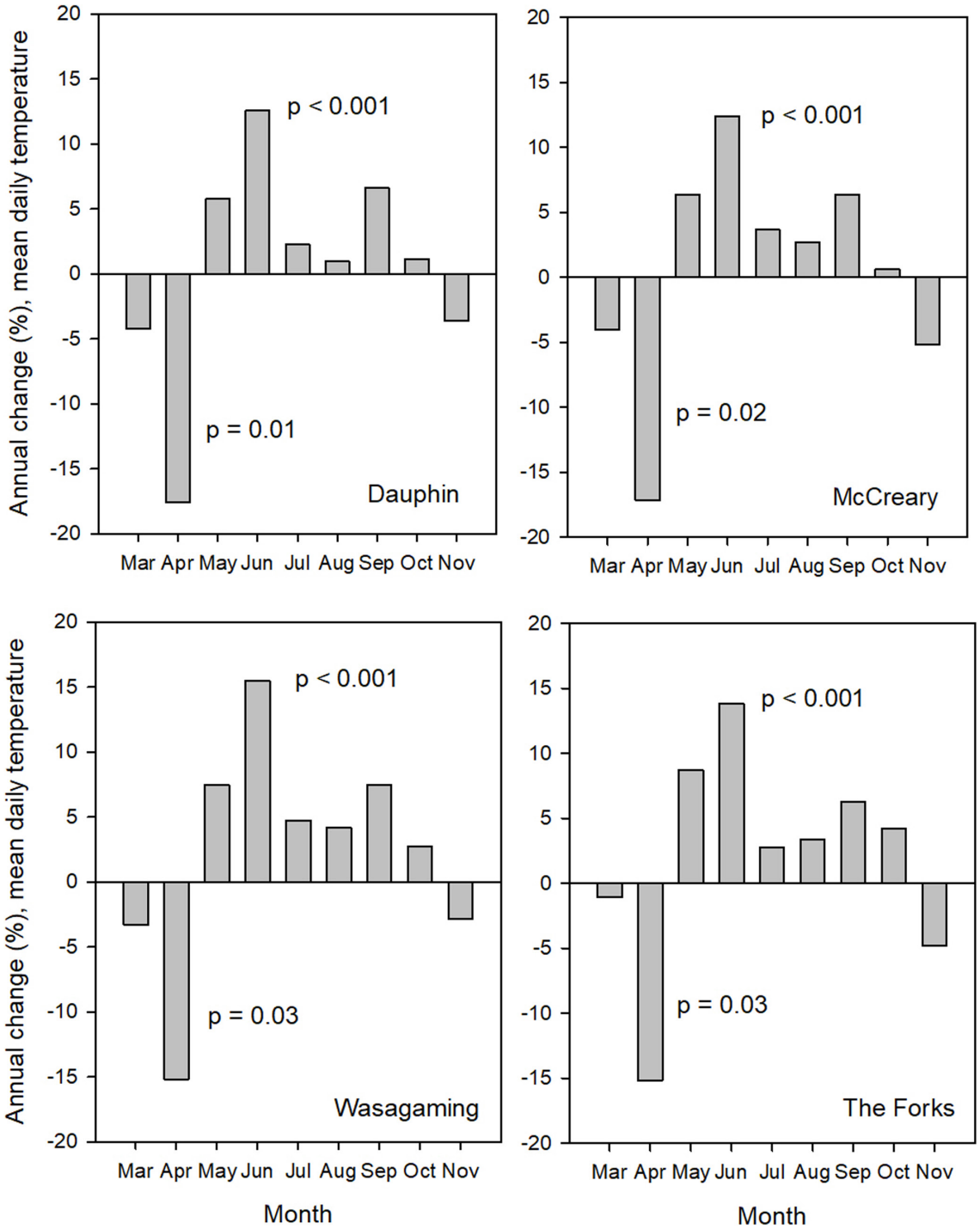


Figure 2. Local climate change measured as the change in mean monthly temperature over 25 years, at four Environment Canada weather stations near populations (Table 1) of *Rudbeckia laciniata*, during its growing season. Unless indicated, the change in temperature did not differ from 0 ($p > 0.05$).

Temporal trends of life history traits

Of four life history traits, stem density and stem height showed negative temporal trends from 1999 to 2023 in all five populations (Table 5). Of these 10 negative trends, nine had $p < 0.10$ and six had $p < 0.05$ (Table 5). Stem density (Fig. 3) and stem height (Fig. 4) declined from 1999 to 2023. No consistent or significant temporal trends occurred for the number of heads per stem or average stage (Table 5).

These temporal trends document declines in stem density for all four RMNP populations of 3.1–4.3% per year over 25 years, based on the regression slopes, explaining 12–90% (r^2) of the annual variation (Table 5). In contrast, at WH, no significant temporal trend in stem density was detected (Fig. 3), with no correlations in annual stem density (Pearson product moment correlation, $p = 0.13–0.67$) between WH and RMNP populations. For stem height, stems lost 0.44–0.83% of their height per year over 25 years; negative temporal trends for the RMNP populations explain 19–47% (r^2) of the annual variation (Fig. 4, Table 5). Although WH showed no temporal trend in stem density, stem height declined (Fig. 4), by 0.77% per year or 17% over the study, similar to that at BH (Table 5). Year-to-year variation in stem height was correlated among BR, CC, and BH (Pearson product moment correlation, $r = 0.48–0.65$, $p = 0.01–0.07$), and between BH and WH ($r = 0.49$, $p = 0.06$).

Climate change and temporal trends in plant life history traits

The decline in monthly mean temperature in April and rise in June at weather stations near the populations (Fig. 2) reflect local climate change that may be affecting life history traits of *R. laciniata*. Stem density and height showed consistent and often significant temporal trends, all declining over two decades (Table 5). For stem density no consistent or significant response to mean monthly temperature in April was detected (Table 6), and so this aspect of local climate change did not affect the decline in stem density. However, stem height increased with April temperature in all populations, significantly so at BB (Table 6), consistent with an effect of this aspect of climate change. In contrast to April temperature, high June temperature reduced stem density and stem height, except for stem density at WH, with three populations showing significant or near significant trends for each trait ($p < 0.001–0.06$; Table 6). Thus, for some populations, declines in both stem density and height are consistent with effects of climate change, particularly with rising June temperatures.

Table 5. Temporal trends of annual means for four life history traits of flowering stems of *Rudbeckia laciniata* from five populations in southern Manitoba, Canada (1999–2023). Trends are defined by linear regression of each trait on year, with regression parameters. Regression slopes (b) are indicated as positive (+) or negative (–). Traits were observed in the third week of August when stem density, height, and number of heads have reached annual maximums. Annual declines for stem density and height are provided as % per year, over 25 years. See Table 1 for explanation of population codes.

Linear regression, trait = a + (b * year)						
Population	a	b	n, years	p-value	r^2	% per year
Stem density, per 200 m^2 (WH, in 29 m^2)						
BR	2069.8	−1.024	23	0.01	0.25	−4.3
CC	5123.5	−2.529	23	0.10	0.12	−3.6
BB	844.3	−0.416	22	0.03	0.22	−3.1
BH	1 11 551	−55.03	4	0.05	0.90	−3.4
WH	37.5	−0.016	21	0.81	0	−0.3
Stem height, cm						
BR	2182.9	−1.032	16	0.04	0.27	−0.83
CC	1525.8	−0.701	17	0.06	0.21	−0.54
BB	1235.2	−0.557	16	0.09	0.19	−0.44
BH	2539.3	−1.198	17	< 0.01	0.47	−0.80
WH	2553.9	−1.203	21	< 0.01	0.32	−0.77
Heads per stem						
BR	77.1	0.037	18	0.09	0.17	
CC	−12.4	0.008	18	0.61	0.02	
BB	−56.7	0.030	16	0.25	0.09	
BH	160.6	−0.051	18	0.12	0.14	
WH	−80.4	0.043	19	0.32	0.06	
Developmental stage (mean, 1–12 stages)						
BR	38.0	−0.016	17	0.48	0.03	
CC	−13.4	0.010	17	0.64	0.02	
BB	−46.0	0.026	16	0.34	0.07	
BH	40.6	−0.019	17	0.60	0.02	
WH	−112.8	0.060	13	0.23	0.13	

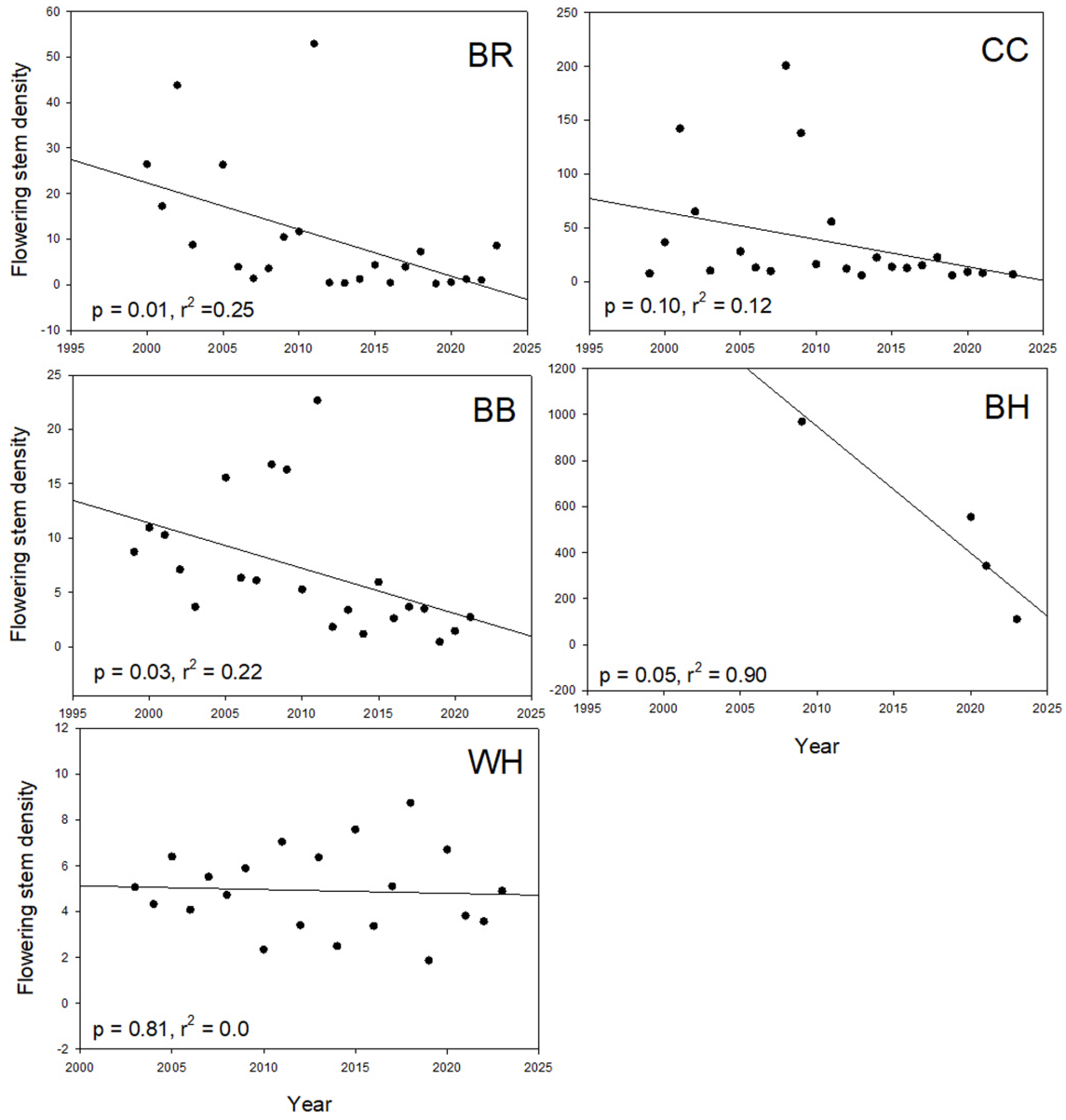


Figure 3. Temporal trends of annual density for flowering stems (1999–2023), in five populations of *Rudbeckia laciniata* (Table 1). For CC, BR, BB, and BH, stem density equals the mean number of stems in 100-m sections of trail, or per 200 m^2; for WH, stem density equals the total number of stems in five patches with a total area of 29 m^2.

The proportion of variation (r^2) in stem density explained by June temperature exceeded that for temporal trends at CC, BB, and BH, and so are consistent with an effect of climate change, but not at BR (Tables 5–6). Similarly, the proportion of variation (r^2) in stem height explained by April or June temperature equalled or exceeded that for temporal trends at CC, BB, BH, and WH, and so are consistent with an effect of climate change, but that for BR did not (Tables 5–6). Declines in tall coneflower stem densities at CC, BB, and BH, and stem heights at CC, BB, BH, and WH are consistent with the hypothesis that climate change resulting in falling April (one case) or rising June temperatures (six cases) caused these seven declines.

The other two life history traits, number of heads per stem and developmental stage, showed no consistent or significant temporal trends over 25 years, and so provided no evidence of an impact of climate change on these traits (Table 5). The number of heads per stem did increase with April temperature in the RMNP populations, but not significantly so, and the increase explained little of the annual variation (Table 6). Similarly, any effects of June temperature on this trait are not significant, nor are the relationships consistent among populations (Table 6). For average stage, nine of ten slopes are positive for the relationship between this trait and April or June temperature, and sometimes significantly so (Table 6). Although warm temperatures in April and June may have

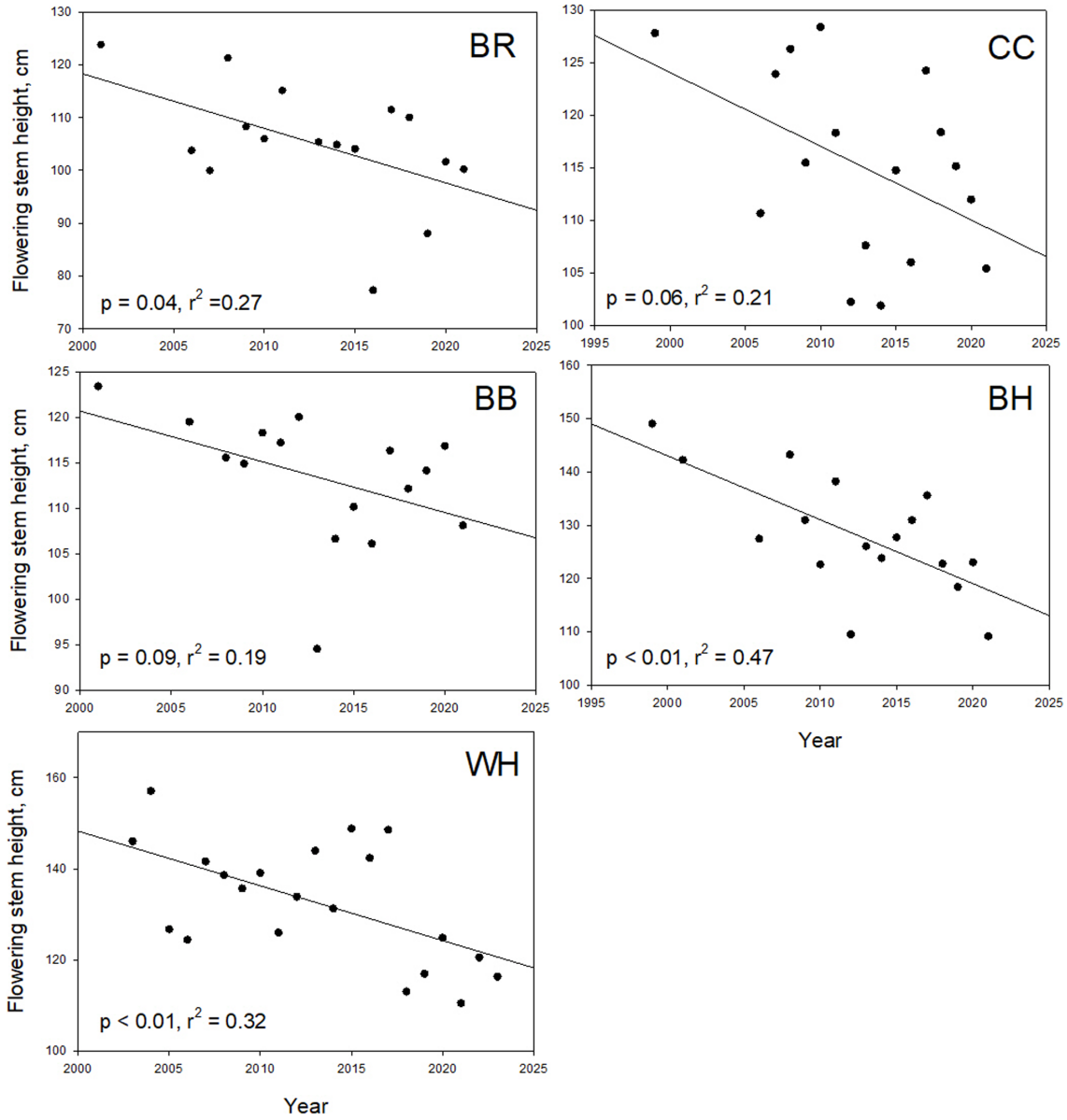


Figure 4. Temporal trends of annual mean heights, cm, of flowering stems (1999–2023), for five populations of *Rudbeckia laciniata* (Table 1).

increased head production or accelerated development (Table 6), no temporal trends were detected for these two life history traits (Table 5), and so climate change is not implicated.

Discussion

Rudbeckia laciniata has a wide distribution in the southern part of North America, reaching its northern limit in southern Manitoba (Scoggan 1979). In a continental climate, these 'northern' populations are exposed to long cold winters, short summers with occasional high temperatures, and wide fluctuations in temperature from year to year (Price et al. 2013). Based on the long-held view that peripheral populations are less stable than those more central in their range (Nantel and Gagnon 1999, Parmesan et al. 2005), we expected life history traits of *R. laciniata* in southern Manitoba to be unstable from year to year as habitat suitability near the range boundary shifted back and forth in warm versus cool, wet versus dry years. A direct test of this hypothesis might include populations from further south closer to the centre of the *R. laciniata* range, but including such populations as part of this long-term study was impractical. Studies from North Carolina, USA, do not provide comparable data (Service and Lenski 1982, Service 1984, Davison et al. 2003). In a comparison of a peripheral and more southern population (2° of latitude difference) for two plant species over three years, Nantel and Gagnon (1999) found higher demographic variability in the

Table 6. Trends of annual means for life history traits of flowering stems of *Rudbeckia laciniata* from five populations in southern Manitoba, Canada (1999–2023) on local climate change. Linear regression of annual means for traits on mean monthly temperatures in ºC for April and June. Traits were observed in the third week of August when stem density, height, and number of heads, have reached maximum values each year. See Table 1 for explanation of population codes.

	Trait = a + (b * April mean temperature)					Trait = a + (b * June mean temperature)				
Pop.	a	b	n, years	p-value	r^2	a	b	n, years	p-value	r^2
Stem density, per 200 m^2 (WH, in 29 m^2)										
BR	0.047	0.003	23	0.56	0.02	0.273	−0.01	23	0.24	0.07
CC	0.203	−0.005	23	0.80	0	293.1	−15.53	23	0.04	0.19
BB	5.629	0.398	22	0.42	0.03	45.4	−2.35	22	0.02	0.26
BH	362.3	70.42	4	0.75	0.06	3718.9	−182.4	4	0.02	0.97
WH	158.2	−2.740	21	0.53	0.02	17.3	+6.82	21	0.42	0.03
Stem height, cm										
BR	104.6	0.318	16	0.78	0.01	156.2	−3.08	16	0.20	0.11
CC	111.9	1.097	17	0.16	0.13	172.2	−3.45	17	0.06	0.22
BB	107.4	1.713	16	< 0.01	0.43	136.4	−1.41	16	0.38	0.06
BH	126.9	0.403	17	0.68	0.01	225.8	−5.92	17	0.002	0.48
WH	128.2	0.900	21	0.40	0.04	254.5	−6.50	21	< 0.001	0.51
Heads per stem										
BR	2.2	0.013	16	0.82	0	2.9	−0.04	16	0.77	0.01
CC	2.8	0.013	18	0.69	0.01	4.2	−0.08	18	0.30	0.06
BB	2.8	0.014	16	0.79	0.01	0.4	+0.15	16	0.19	0.12
BH	3.4	0.118	17	0.19	0.11	7.8	−0.24	17	0.25	0.09
WH	6.6	−0.062	19	0.51	0.03	5.1	+0.06	19	0.75	0.01
Developmental stage (mean, 1–12 stages)										
BR	6.5	0.121	16	< 0.01	0.41	4.8	+0.13	16	0.29	0.08
CC	6.8	0.095	17	0.02	0.33	3.9	+0.19	17	0.05	0.23
BB	6.7	0.093	16	0.07	0.21	3.1	+0.23	16	0.05	0.26
BH	6.7	0.117	17	0.08	0.20	3.6	+0.21	17	0.18	0.12
WH	7.5	−0.138	13	0.28	0.10	1.5	+0.28	13	0.15	0.18

peripheral population than the more central one, consistent with the hypothesis.

In contrast, levels of stability for three life history traits of *R. laciniata* related to growth and development are not consistent with the edge-of-range hypothesis. For populations in RMNP, stem height, number of heads per stem, and average stage in late August are as stable as or more stable than at WH. Given that WH is only 126 km south (1º of latitude) of the northern RMNP populations, a difference in stability might be difficult to detect. Nevertheless, the PV values for these traits are remarkably low on a scale of 0–1 (highly stable): PV = 0.09 for stem height, PV = 0.10 for average stage, and 0.19 for the number heads per stem. These PV values are so low that finding higher levels of stability (lower PV) further south is unlikely.

A fourth trait of *R. laciniata*, stem density, is less stable, PV = 0.63 on average in RMNP populations. For this trait, the higher stability of the more southern population at WH, PV = 0.34, is consistent with the hypothesis. At WH, however, this higher stability might be due to factors such as: the density estimate used (density in defined patches at WH compared with density in the wider habitat at RMNP), or the additional water applied at WH. Stabilities of stem density for *R. laciniata* populations are similar to those of the orchid *Platanthera praeclara* (Sheviak and Bowles) in southern Manitoba where, as for *R. laciniata*, it lives near the northern limit of its range (Bleho et al. 2015). Over 21 years at multiple sites, proportional variabilities of *P. praeclara* stems are PV = 0.51 (calculated from Table 2 in Bleho et al. 2015), compared with PV = 0.57 for *R. laciniata* at CC or PV = 0.58 at BB. Whether or not a PV > 0.5 for plant density is characteristic of peripheral populations or characteristic of plant densities in wild populations in any part of their range remains to be determined.

For the three stable life history traits related to growth and development, we hypothesize that northern populations of *R. laciniata* have evolved a pace of development that helps assure flowering stems reach maturity before damaging early frosts occur. This hypothesis is consistent with the early maturity of stems in these populations, their high stability (low PV) for phenology from year to year, and the similarity in the pace of their development among populations. In 22 of 25 years in southern Manitoba, the rates of development in response to summer temperatures resulted in flowering stems senescing before fall frosts ended the season. This hypothesis predicts that southern populations of *R. laciniata* will delay maturity and utilize their longer season to increase seed production. Data to test this hypothesis are not available from southern parts of this plant's distribution. However, Service (1984) reports that in North Carolina, USA, flowering occurs from early August to October, at least a month

longer than in Manitoba, with stems sometimes remaining green into January, compared with senescence in Manitoba which is complete by late October.

Of the three traits related to growth and development, the number of heads per stem is the least stable (PV = 0.19 versus PV = 0.09, 0.10). The number of heads per stem increases with stem height, and so the stability of number of heads includes variability in stem height (height explains $r^2 = 0.26$ of the variation in number of heads, on average, for the five populations). Therefore, a mean population PV = 0.19 overestimates year-to-year stability of the number of heads per stem by about 26% and would be closer to PV = 0.14, and closer to the high stability traits. Stability estimates for phenology based on average stage, a mean of integers that name categories, are suspect (Schaub et al. 2022), until it is recognized that the frequency distributions of stages are normally distributed over time, and average stage is linearly related to time over most of the growing season. The weekly records of phenology at WH show that a sampling date in the third week in August occurs when stem height, number of heads per stem, and stem density have reached maximum seasonal values. Thus, these traits are not confounded by developmental stage at the time of the annual assessment.

As climate warms, local environmental conditions at the northern edge of a range in the Northern Hemisphere may become more favourable for a species by ameliorating the most unsuitable weather and so stabilizing its life history (Nantel and Gagnon 1999, Parmesan et al. 2005, Parmesan and Singer 2022). Temporal trends in ecological traits often are consistent with an effect of climate change resulting from global warming (Parmesan and Yohe 2003, Root et al. 2003, Sletvold et al. 2013, Wadgymar et al. 2018, Lindell et al. 2022, Williams et al. 2025). If these trends are positive, for example, increasing plant performance in years that would have had sub-optimal temperatures without climate warming, then the trend would be stabilizing. Such temporal trends, however, are often correlated with trends of traits or environmental variables other than rising temperatures, making causal relationships uncertain (Krebs 1991, Evers et al. 2021, Williams et al. 2025). Krebs et al. (2024) conclude that causal factors must be identified through experimental manipulation, a challenge for processes such as climate change that occur over decades (Lindell et al. 2022). Ecological trends and their relationships to climate change have been investigated using detailed analyses of multiple weather variables and their effects on ecological traits, leading to models of the ways that such traits respond to variation in the weather (Sletvold et al. 2013, Evers et al. 2021, Lindell et al. 2022, Williams et al. 2025). The resulting models have then been used to predict likely future effects of climate change on organisms, assuming that the models reflect the effects of climate change on the test species (Sletvold et al. 2013, Lindell et al. 2022, Williams et al. 2025).

A different approach for assessing the effect of climate change on ecological traits of *R. laciniata* was adopted here: 1) identify temporal trends in local weather to determine the habitat-specific characteristics of climate change; 2) identify temporal trends in life history traits of the plant; 3) assess whether variation in a plant trait is affected by the variation of a local weather parameter known to reflect climate change, irrespective of year; and 4) assess whether variation explained by the weather parameter alone, ignoring year (in 3, above), is consistent with the amount of variation explained by the temporal trend for the trait (in 2, above). When the coefficient of determination of the regression model (r^2 in 3, above) explains all the year-to-year variation in a trait that is explained by the regression of the trait on year (r^2 in 2, above), then a causative relationship between trait and local climate change is the simplest explanation.

Local climate change is expressed differently at different locations, and is beginning to be mapped for latitudes, biomes, and times of the year (Parmesan and Singer 2022, Neale and Rudolf 2025). From 1999 to 2023 in southern Manitoba, at four weather stations adjacent to populations of *R. laciniata*, no significant trends consistent with climate change are detected for annual means of daily weather parameters. When monthly mean daily temperatures are considered, however, a seasonal pattern of climate change is evident. In southern Manitoba, local climate change does not result in a simple rising trend in temperature, but a seasonal pattern of rising and falling temperatures. For precipitation, monthly trends are less consistent than is the case for temperature. The geographical scale of these local effects of climate change includes the five study sites and four weather stations in an area of south-central Manitoba from Winnipeg to Dauphin. Although some weather stations are consistently cooler or warmer than others, they all show similar patterns of climate change from month to month, supporting the conclusion that a cooling trend in early spring, and warming trend in late spring, summer, and early autumn are climate phenomena, expressed most strongly in April and June.

For comparison, three weather stations in the Boreal Forest biome of south-eastern Manitoba, showed a positive annual temperature trend of 0.05°C per year from 1971 to 2004, with significant positive trends for monthly temperature for September, December, and January (Westwood and Blair 2010). In our study from 1999 to 2023, in the Aspen Parkland 50–400 km further west, no annual trend was detected; temperature trends for September, December, and January were also positive but weak. The part of the Boreal Forest studied by Westwood and Blair (2010) showed neither the April decline nor the June rise in temperature that characterize local climate change further west in southern Manitoba. The pattern of local climate change in the Aspen Parkland also contrasts with that of the Boreal Forest in southern Yukon, Canada (Krebs et al. 2024): winter temperatures (November–February) increased by 0.70°C per decade (1970 to 2022) in southern Yukon, but decreased by 0.24°C per decade in southern Manitoba; summer temperatures (June to August) increased by 0.28°C per decade in the Yukon, but by 0.66°C per decade in southern Manitoba. These differences in local climate change emphasize the importance of documenting local weather conditions when assessing the role of climate change in ecological processes. These comparisons

are based on weather station data, close to but not in the habitats of the study organism. Christiansen et al. (2024), however, find that weather data recorded at a distance from study sites reduce the precision of estimates, which emphasizes the importance of defining the local characteristics of climate change.

Temporal trends in weather parameters that most clearly reflect local climate change in the populations of *R. laciniata* are a declining mean monthly temperature for April and a rising mean monthly temperature for June. Of the four life history traits, the annual number of heads per stem and average stage, recorded in the third week of August, showed no temporal trends from year to year, and therefore provided no evidence that local climate change affected their stability. Stem height, however, declined in all five populations, by 0.4–0.8% per year, as did stem density in the four RMNP populations, by 3.1–4.3% per year. As June temperature increased, stem height and density declined. The relationships between June temperatures and stem height and density ($r^2 = 0.19–0.97$) explained the same amount of the variation as the temporal trends ($r^2 = 0.12–0.90$) in three of five populations. Thus, for stem height and density, 6 of 10 declining trends in the populations are explained by climate change related to June temperatures that rose 3.4°C over 25 years.

Climate change, as reflected in declining April temperatures, influenced only stem height in the BB population. In this case, warm Aprils – which were more frequent early in the study – resulted in taller stems at the end of the season. The negative trend for height at BB was due to declining April temperatures in combination with rising June temperatures. In RMNP, average stage in the third week of August was more advanced when April was warm, but not sufficiently so to be detected as a temporal trend that could be attributed to climate change.

The mechanisms underlying the relationships between stem height or density and April or June temperatures are unlikely to be a direct effect of mean monthly temperature, but rather aspects of daily temperature that contribute to, and are correlated with, the monthly mean. Lagging effects of temperature on the plant from the previous growing season and/or from the winter dormant season might also be important (Evers et al. 2021) but were not considered here.

For *R. laciniata*, we suspect that rising June temperatures interact with soil moisture; stems often wilt when exposed to direct sunlight on hot days, which may slow growth and reduce stem height. In June, the number of hot days when soil moisture is limiting for growth might better reflect the effects of climate change on plant growth than monthly mean temperature. Precipitation data available from weather stations, however, do not readily predict local soil moistures in habitats with differing slopes, soil types, plant densities, and canopy covers.

An interaction between soil moisture and June temperatures might explain the temporal trends for stem height and density in the BR population which were negative ($p < 0.05$), as they were for the nearby CC population, but unlike at CC, the relationships between traits and June temperature were not detected at BR ($p > 0.2$). BR is relatively flat, near the base of the escarpment, whereas CC is 1 km to the south and climbs 130 m a.s.l. up the escarpment. Climate was assumed to be the same for these two populations, given their proximity. This may be an example of a situation where more localized records of temperature (Christiansen et al. 2024) and soil moisture would have more precisely defined their importance in a changing climate, and their role in the declining stem height and density of *R. laciniata* in both populations.

At the northern edge of its range, *R. laciniata* might be expected to benefit from climate warming, through more rapid development and increased growth. These populations might also be expected to be adapting to climate change, to take advantage of a longer growing season (Westwood and Blair 2010, Wadgymar et al. 2015). In fact, stem height is declining in all five populations of *R. laciniata*, and in the RMNP populations, stem density is also declining. Over the past 25 years the phenology of the plant shows no evidence of adapting to warming temperatures. Climate change, as it affects stem density and height, is not stabilizing for these populations. The negative temporal trends in these traits, due primarily to rising June temperatures, explains 12–47% of the annual variation of the populations, variation that reduces stability (increases the year-to-year variability). Over the past two decades in RMNP, stem heights have declined by 16%, and stem densities by 90% of their peak densities, threatening these wild populations at the northern edge of the plant's range.

Conclusions

Our original expectations were that life history traits of *R. laciniata* would be unstable at the northern edge of its range but be stabilized by a warming climate. In fact, populations of *R. laciniata* exhibit high levels of stability (low levels of year-to-year variability) in three life history traits that quantify aspects of growth and development: stem height, number of heads per stem, and phenological stage. This stability calls into question the generality of the hypothesis that populations at the edge of their range are unstable. These observations indicate *R. laciniata* is well adapted to the high variability in weather it experiences at the northern edge of its range in a continental climate. The discovery that rising June temperature, reflecting climate change, affects the life history of the plant, led us to expect that rising temperatures would ameliorate the variability of abiotic factors, and therefore further stabilize the life history of the plant. In fact, climate change has no detectable stabilizing or destabilizing effect on flower head production or phenology of the plant. However, rising June temperatures cause a decline in stem height and density; these negative trends contribute to temporal variability, rather than stabilizing these two traits.

Rudbeckia laciniata, as evidenced by the decline in stem height and density in the populations, has not adapted over the past two decades to moderate levels of climate change. Climate change is causing significant declines in flowering stem height and density in wild populations of a native perennial, living near the northern edge of its wide north–south

distribution in North America. As a result, in four RMNP populations, stem height has declined by 16% and density by 90% over the past two decades. threatening the reproductive success of *R. laciniata* and the long-term persistence of these populations in Manitoba.

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Author contributions

Robert J. Lamb: Conceptualization (equal); Data curation (equal); Formal analysis (lead); Funding acquisition (equal); Investigation (equal); Methodology (equal); Project administration (equal); Resources (equal); Software (equal); Supervision (equal); Validation (equal); Visualization (equal); Writing – original draft (lead); Writing – review and editing (equal). **Patricia A. MacKay**: Conceptualization (equal); Data curation (equal); Formal analysis (supporting); Funding acquisition (equal); Investigation (equal); Methodology (equal); Project administration (equal); Resources (equal); Software (equal); Supervision (equal); Validation (equal); Visualization (equal); Writing – original draft (supporting); Writing – review and editing (equal).

Data availability statement

Data are available from the Dryad Digital Repository: https://doi.org/10.5061/dryad.6q573n6f1 (Lamb and MacKay 2026).

Supporting information

The Supporting information associated with this article is available with the online version.

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