# Earlier and increased growth of tundra willows after a decade of growth in a warmer common garden environment

## Abstract

1. The expansion of woody shrubs, known as shrubification, is one of the most widely observed patterns of vegetation change in the tundra. Yet, we do not know the relative importance of plant plasticity and genetic change in determining shrub responses to warming. Plastic responses to the environment can be rapid, while genetic differentiation is much slower.
2. We established a common garden experiment, using three tundra willow species (two tall willow shrubs: *Salix richardsonii*, *S. pulchra,* and one prostrate willow: *S. arctica*). We transplanted cuttings from southern (alpine, high elevation) and northern (Arctic) source populations to a 5ºC warmer environment in southern boreal Yukon, simulating projected future Arctic conditions. We monitored growth, phenology and functional traits in the common garden over a ten-year period from 2013 to 2023 and measured the same variables in the source populations.
3. The three willow species responded differently to a warmer environment. Southern *S. richardsonii* shrubs in the common garden grew almost seven times faster than the northern willows of the same species. Neither common garden populations of *S. pulchra* increased in height, but southern individuals grew wider. *S. arctica* growth patterns were similar between southern and northern common garden populations. All shrubs in the garden advanced their date of leaf bud burst by approximately one month compared to source populations. All northern willows growing in the garden also advanced senescence timing, resulting in less change to overall growing season length

for northern willows. We suggest local adaptation to source population conditions as a likely cause of early senescence and limiting growth of northern willows in the common garden.

4. *Synthesis:* Our findings suggest longer growing seasons due to the advancement of leaf bud burst but not delayed senescence, and potential for rapid shrub growth as tundra ecosystems continue to warm. However, responses to warming vary by species and population, as we observed varied levels of plasticity for traits, phenology and growth. Local adaptation to past climatic conditions and slow genetic change may limit future shrub growth and determine which shrub species proliferate with future warming.

Key words: shrubs, climate change, phenotypic plasticity, phenology, plant traits, Arctic warming, vegetation change, local adaptation

Authors and affiliations:

- **Corresponding author:** Madelaine J. R. Anderson, madelaine.anderson@usherbrooke.ca Département de Biologie, Université de Sherbrooke, Sherbrooke, QC, J1K 2R1, Canada.
- Isla H. Myers-Smith, 1) School of GeoSciences, University of Edinburgh, Edinburgh, EH8 9XP, United Kingdom, 2) Department of Forest and Conservation Sciences, Faculty of Forestry, University of British Columbia, Vancouver, V6T 1Z4, Canada
- Erica Zaja, 1) School of GeoSciences, University of Edinburgh, Edinburgh, EH8 9XP, United Kingdom , 2) UK Centre for Ecology & Hydrology, Bush Estate, Penicuik, Midlothian EH26 0QB, United Kingdom
- Haydn J. D. Thomas, School of GeoSciences, University of Edinburgh, Edinburgh, EH8 9XP, United Kingdom
- Mariana García Criado, School of GeoSciences, University of Edinburgh, Edinburgh, EH8 9XP, United Kingdom
- Gergana Daskalova, 1) School of GeoSciences, University of Edinburgh, Edinburgh, EH8 9XP, United Kingdom, 2) Department of Conservation Biology, University of Goettingen, Bürgerstrasse 50, 37073 Goettingen, Germany
- Elise Gallois, 1) School of GeoSciences, University of Edinburgh, Edinburgh, EH8 9XP, United Kingdom, 2) Natural History Museum of London, Cromwell Rd, South Kensington, London SW7 5BD, United Kingdom
- Jiří Šubrt, School of GeoSciences, University of Edinburgh, Edinburgh, EH8 9XP, United Kingdom
- Mark Vellend, Département de Biologie, Université de Sherbrooke, Sherbrooke, QC, J1K 2R1, Canada

## Introduction

Rapid Arctic warming at a rate of up to four times the global average (IPCC, 2022, Rantanen *et al.*, 2022) is having profound impacts on tundra landscapes and plant communities (Myers-Smith *et al.*, 2019, Elmendorf *et al.*, 2012a). As the Arctic warms, the snow-free period each year is extending to earlier in the spring and later in the autumn (Box *et al.*, 2019). Both warming and altered snow dynamics interact to influence growing season length, plant growth, phenology, and ecosystem productivity (Bjorkman *et al.*, 2015, Frei & Henry, 2022, Rixen *et al.*, 2022, Kelsey *et al.*, 2021, Oberbauer *et al.*, 2013, Zona *et al.*, 2022). Understanding the effects of warming on plant communities is essential to safeguard the human livelihoods and wildlife populations that depend on the function and productivity of tundra ecosystems (Ford *et al.*, 2021, Bjorkman *et al.*, 2020, IPCC, 2022).

One of the most widely observed examples of warming-induced vegetation change in Arctic and alpine tundra is shrubification: the increased growth, distribution and abundance of woody plants (Myers-Smith *et al.*, 2011a, Mekonnen *et al.*, 2021, García Criado *et al.*, 2020). Shrubification is largely driven by tall deciduous shrubs such as willow (*Salix* spp.), birch (*Betula* spp.), and alder (*Alnus* spp.) (Myers-Smith *et al.*, 2011a), and it contributes to both positive and negative feedbacks on local climate and carbon cycles (Mekonnen *et al.*, 2021, García Criado *et al.*, 2020, Frost & Epstein, 2014, Elmendorf *et al.*, 2012a, 2012b, Myers-Smith *et al.*, 2011a). As shrubs are the canopy-forming species in most tundra landscapes, shrub responses to future warming will have cascading impacts to other plants and wildlife communities (Zhou *et al.*, 2020, Hollister *et al.*, 2015).

As conditions are warmer and more benign at lower latitudes or altitudes, plants there tend to be larger, leaves tend to have less mass per area and lower leaf dry matter content (LDMC) suggesting lower stress tolerance, and phenological events (life cycle timings) are less contracted within a season (Bjorkman *et al.*, 2018). We might thus expect warming to lead to similar changes over time, with the potential for some interactions among traits. For example, altered phenology can extend the growing seasons and thereby increase plant growth and size (Choi *et al.*, 2019, Körner *et al.*, 2023). However, predicting changes in tundra plant populations and communities will depend on the degree to which plants respond to their changing environments via plasticity versus genetic differentiation (Bjorkman *et al.*, 2017, Lajoie & Vellend 2018, Thomas *et al.*, 2020).

Genetic differentiation and plastic responses to the environment occur at different rates (Siefert *et al.*, 2015, Thomas *et al.*, 2020). Heritable, genetic changes in trait values happen slowly, as populations of long-lived individuals are subject to natural selection and locally adapt to environmental conditions. Plastic responses to the environment can be much more rapid (i.e., within an individual's lifetime). While there is considerable variation in both inter- and intra-specific plant trait values across the tundra, identifying the contributions of genetic differentiation and plasticity to intraspecific trait variation remains challenging (Elmendorf *et al.*, 2012a, 2012b, García Criado *et al.*, 2023). If trait differences among populations under different climate conditions are largely due to plasticity, we might expect rapid plant trait responses to environmental change. Alternatively, if genetic differentiation dominates, the potential rate of plant trait response is much slower.

Experiments that bring individuals from different environments together in a common garden have long been used in ecology as an effective tool to study genetic differentiation versus plastic responses to environmental variation (Lortie & Hierro 2021). Trait differences between populations that persist in a common garden are attributed to fixed genetic differences, likely but not necessarily due to local adaptation. Trait differences between plants from the same population growing in different environments (e.g., the source population *in situ* versus in the common garden) are attributed to phenotypic plasticity. The few experiments of this nature that have been conducted in the tundra provide evidence of both plasticity and genetic differentiation with potential local adaptation in plant growth patterns, trait expression, and phenology (Parker *et al*., 2021, Bjorkman *et al*., 2017, DeMarche *et al*., 2017, Table S1). These studies have focused on herbaceous plants (Parker *et al*., 2021, Bjorkman *et al*., 2017, DeMarche *et al.*, 2017, but see Tumajer *et al*., 2021), yet it is shrubs that respond most to climate change in the Arctic (Mekonnen *et al.*, 2021, García Criado *et al.*, 2020, Myers-Smith *et al*., 2011). Capturing responses of shrubs in a warmer common garden environment provides estimates of growth rates and phenological timings under conditions that will likely occur with future warming.

Plasticity is often most obvious for phenological traits. For example, temperature and snowmelt timing are dominant cues for plastic changes in spring leaf bud burst in northern woody plants (Polgar & Primack, 2011, Flynn & Wolkovich, 2018). With warmer temperatures, the timing of leaf bud burst is advancing across the circumpolar region (Collins *et al*., 2021, Myers-Smith *et al*., 2019). However, late-season phenology is less understood, complicating predictions of how growing season length might change. Photoperiod and temperature are considered the two main cues for senescence (Gill *et al*., 2015, Lang *et al*., 2019, Keenan & Richardson 2015), and plant growth and growing season lengths can also be limited by the amount of carbon plants are physically able to accumulate referred to as physiological sink limitations (Cerasuolo *et al.*, 2015, White *et al.*, 2015). The remaining knowledge gaps around how the overall length of the growing season may change hinder predictions of future ecosystem productivity and effects on trophic interactions, particularly in high latitude and elevation ecosystems such as the tundra (Collins *et al.*, 2021, Zona *et al.*, 2022).

Here, we investigated responses of three species of tundra shrubs to growing in a common garden that is warmer than their northern and southern source populations. Over one decade, we measured responses in terms of 1) growth and plant size (canopy height and width, stem elongation measured as incremental growth each season), 2) phenology (timing of leaf bud burst, leaf yellowing, growing season length), and 3) functional traits (specific leaf area or SLA, leaf area, and leaf length) in two tall willow species (*Salix richardsonii* Chamisso and *Salix pulchra* Marshall; maximum heights up to 127 cm and 101cm in common garden, respectively) and one prostrate willow species (*Salix arctica* Pallas; maximum height up to 15 cm in common garden). We tested the following predictions (see Table S2 for variables measured to test each prediction):

1. In the common garden, southern willows will grow more rapidly and achieve larger sizes than northern willows, as is the case in their respective source populations. This would be indicative of genetic differentiation.
2. Shrubs in the common garden will have an overall longer growing season (period of photosynthetically active leaves) than in their respective source populations, indicative of phenotypic plasticity.
3. For functional traits, both northern and southern willows will respond plastically to the warmer common garden environment (i.e., higher SLA, lower LDMC, and larger leaves relative to source populations).

## Methods

## Study Sites

### ***Qikiqtaruk-Herschel Island: the northern source population habitat***

Qikiqtaruk-Herschel Island (hereafter Qikiqtaruk, 69.6°N, -138.9°E) is an island off the north slope of the Yukon Territory in the Inuvialuit Settlement Region of Inuit Nunangat in the northwestern edge of the Canadian Arctic. The island falls at the northern extent of tall shrubs (i.e., those reaching heights of over 50 cm) and is underlain by ice-rich permafrost. The three *Salix* species in the experiment are widely found across the island. Willows have dominated the island's shrubification over the past two decades (Myers-Smith *et al*. 2011b, Myers-Smith *et al.* 2019). *Salix pulchra* is often found in tussock tundra vegetation (Herschel Vegetation Type), *S. richardsonii* is widespread in floodplains and moist areas (Orca Vegetation Type), and *S. arctica* is found in recently disturbed forb- and grass-dominated areas (Komakuk Vegetation Type) (Smith *et al*., 1989).

### ***Alpine Kluane: the southern source population habitat***

The Kluane region (61.0°N, -138.4°E) is in the southwest part of the Yukon Territory, approximately 1,000 km south of Qikiqtaruk (Figure 1), on the traditional territory of the Kluane First Nation, Champagne and Aishihik First Nation and White River First Nation. The area is mountainous and above 1,200 – 1,400 m elevation is characterized by increasingly shrub-dominated alpine tundra (Myers-Smith & Hik, 2018). Here, the three willow species that we studied are widely distributed, although *S. arctica* is generally more restricted to higher elevation zones.

### ***Common garden experiment***

We established a common garden experiment in 2013 near Kluane Lake, Yukon Territory (61.0° N, -138.4° E, elevation: 690m) in the boreal zone. Cuttings from the two tall shrub species (*S. richardsonii, S. pulchra*) and the prostrate shrub species (*S. arctica*) were taken from shrubs growing in two source populations: 1) on Qikiqtaruk and 2) from alpine Kluane sites (Figure 1). For both tall willow species, cuttings were on average longer from the southern (alpine) source site due to larger mother shrubs, resulting in larger canopy heights in year one for southern *S. richardsonii* and *S. pulchra* populations (see below, Figure 2A, B). We did not record the width of the cuttings when planted, although qualitatively we observed no major difference in widths (the cuttings were not complex and branched). Over 800 cuttings were sampled from unique individuals at least 10 m apart, in varied plant communities, microhabitats and elevations across the two sites (Table S3). Willows are dioecious and cuttings usually were collected from female shrubs, although in some cases catkins were not present to determine the plant sex. Cuttings from the Kluane Region were collected from alpine slopes between 1,400 - 1,900 m elevation within 30 km of the Outpost Research Station, located outside Kluane National Park in the Kluane Front and Ruby Ranges (Figure S1). Cuttings from Qikiqtaruk were collected within 5 km of the Pauline Cove Settlement across the north-eastern part of the island. Cuttings were then planted in the common garden environment with root growth hormone (bottom tips of cuttings dipped in Roots Liquid Stimulator, Wilson Control) and fertilizer (Golf Green Shrub Fertilizer or mix of similar) to facilitate establishment (see supplementary methods for more information on propagation methods).

Within the garden there are 15 planting areas (“beds”), with beds separated from one another by approximately 50 cm. There was one willow species per bed from both source sites with up to 27 individuals per bed separated by approximately 30 cm. Cuttings were established in the common garden in 2013 with more individuals added from unique shrubs (from both source sites) each year until 2018, resulting in a variety of ages within each bed (Figure S3). Plantings of *S. arctica* started in 2015 so the maximum age in either population of this species is eight years. The garden is fenced to limit herbivory and trampling from large animals. In each garden bed, the ground was covered with black garden shade cloth topped with a layer of gravel to limit non-experimental plant growth. The beds were regularly weeded during summer. Mortality rates differed across the 10 years of the experiment although the number of surviving northern and southern willows for a given species has remained relatively balanced over time (Table S3). At the end of summer 2023, the garden contained 208 alive shrubs composed of 69 *S. richardsonii*, 89 *S. pulchra* and 50 *S. arctica* individuals.

We refer to shrubs measured on Qikiqtaruk as the “northern source populations” and shrubs sampled in alpine sites around the Kluane region as the “southern source populations”. Individuals grown in the common garden that come from Qikiqtaruk are referred to as “northern shrubs in the garden”, and those from alpine Kluane sites as “southern shrubs in the garden” (Figure 1).

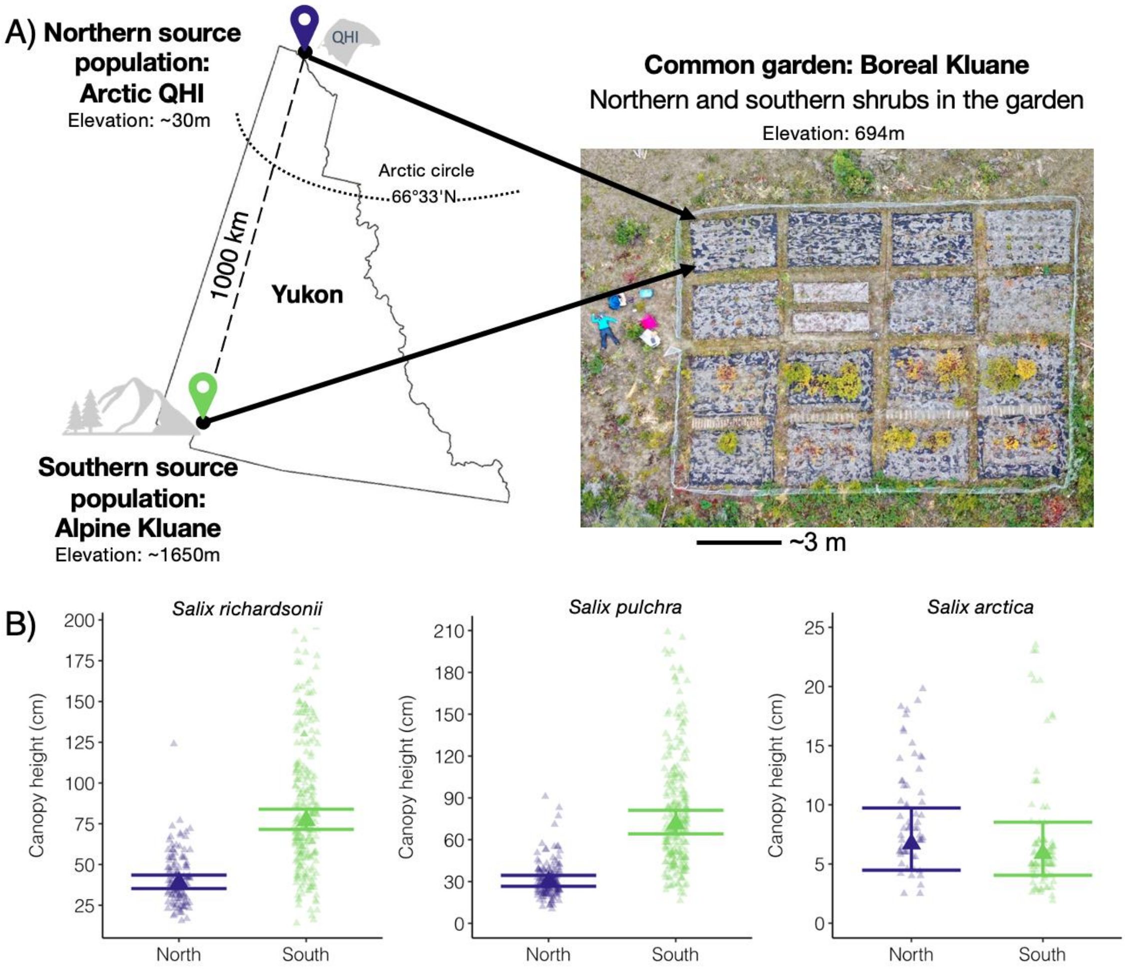

Figure 1. A) Left: the source population sites in the Yukon Territory are separated by approximately 1,000 km. Right: aerial picture of the common garden experiment in boreal Kluane. B) The two tall willow species were taller in the southern (alpine) source population than the northern (Arctic) source population. Raw data points (transparent triangles) and means (solid triangles) ± 95% credible interval bars from Bayesian model output (Table S7).

The northern and southern source population sites experience similar average July temperatures of 9-10ºC, which are 4-5ºC cooler than the common garden site (Table 1, Figure S2), confirmed by *in situ* data loggers and gridded climate data (CHELSA; Karger *et al.*, 2017). The common garden site has lower soil moisture over the summer than the source population sites (Table 1). The common garden also has a mean snow free duration of 155 days, longer than both the northern (108 days) and southern (88 days) source population sites, as determined by manual observations from timelapse cameras set up in the garden and source populations to monitor phenology (Moultrie Wingscapes TimelapseCam Pro, hereafter ‘phenocams’) (Table 1). Seasonal variation in photoperiod is the same between the southern source population and the common garden, but is different in the northern source population, where there is 24-hour sun from 19 May to 26 July, with significantly longer days (than in the south) preceding and following those dates. The common garden receives less annual precipitation than both source populations (Table 1).

**Table 1**. Site environmental conditions, including standard deviations (±) from means and/or ranges. CHELSA data extracted from Karger *et al*. (2017). *In situ* temperature and soil moisture data from data loggers deployed during study. Snowmelt and snow return timings from manual phenocam observations.

| | **Common garden** | **Alpine Kluane (southern source)** | **Qikiqtaruk (northern source)** |
|---|---|---|---|
| Mean July surface temperature (°C) - *in situ* | 14.1 ± 3.3 | 9.2 ± 1.2 | 10.0 ± 3.5 |
| Mean July soil temperature (°C) - *in situ* | 14.0 ± 1.2 | 5.4 ± 1.6 | 5.7 ± 2.6 |
| Mean July long term temperature (°C) (1999-2019) (CHELSA) | 13.7 ± 1.0 | 7.3 ±1.0 | 6.2 ± 1.9 |
| Mean July soil moisture (%) *in situ* | 32.3 ± 10.9 | 45.4 ± 3.2 | 55.6 ± 2.1 |
| Mean July long term precipitation (kg/m$^2$) (1998-2018) (CHELSA) | 52.9 ± 19.9 | 71.2 ± 26.9 | 81.2 ± 45.4 |
| Mean snowmelt DOY | 115 (range 109-124) | 165 (range 147-177) | 154 (range 135-183) |
| Mean snow return DOY | 270 (range 269-276) | 253 (240-269) | 262 (range 242-270) |

## Data collection

### *Growth, traits and phenology in the common garden*

From 2013 to 2023, we monitored growth, morphological traits and timing of phenophases in the common garden at varying frequencies (Table S4). We measured two resource-use traits (SLA and LDMC), and two leaf size traits (leaf length and leaf area). Leaves for trait analyses were selected from the top of the shrub canopy and were representative of the shrub, healthy, and fully green (Laliberté, 2018; see Supplementary methods for additional trait processing information). Ten phenocams were installed in the garden to monitor phenology using manual sequential image browsing to determine. The phenocams captured daily images from which we extracted day of year for first leaf bud burst (also called leaf emergence, first green leaf visible) and day of year of the first yellowing leaf. We used phenological phases defined in the International Tundra Experiment protocols (Molau and Mølgaard, 1996). We calculated growing season length as the difference between day of the year of first leaf yellowing and day of the year of first leaf bud burst.

### *Growth, traits and phenology in the source populations*

Plant growth, traits, and phenology were also measured in both the southern and northern source populations of the three willow species. All plant trait and size measurements were collected on healthy individuals during peak growing season between July to early August. We followed the same protocols to estimate plant size, phenology and trait measurements as in the common garden (Table S4). Plant size (height, width) measurements were not collected repeatedly on the same individuals over time and because we did not know the age of the shrubs that were measured, we did not compare growth rates in the common garden with those in the source populations. There were nine phenocams set up in the southern source population and

18 in the northern source population. Day of year for leaf bud burst and the first yellowing leaf were extracted as described above using manual observations of tagged individuals in the image viewsheds. We also included data from long-term phenology monitoring plots set up in the northern source population for *S. arctica* to compare leaf bud burst and leaf yellowing dates (2013 to 2023, methods described in Myers-Smith *et al*., 2019). Because *S. arctica* shrubs occur at higher elevations not suitable for phenocam installation, we did not have southern source population phenology data for this species.

### Data analysis

We used Bayesian hierarchical mixed effects models and carried out all analyses in R version 4.2.2 (R Core Team, 2022). We separated our analyses by species because the three species in the garden have known differences in their trait expression and growth patterns. Model convergence was assessed by visually examining tracing plots and by assessing $R_{hat}$ values (ratio of effective sample size to overall number of iterations, all close to 1.0). We used the package 'brms' (Bürkner, 2017, version 2.20.4) and for all models ran three chains of 3,000 to 5,000 iterations, with 1,000 iterations as warmup. We log-transformed the response variables or centred variables on zero where appropriate to improve model fit and convergence. We report back-transformed model estimates for visualisation and clarity. See Table S5 in supplementary material for summary of model structures for each research question and variable.

Before analysing growth over time or maximum size of shrubs in the garden, we tested for relationships between the length of the cutting taken from the parent shrub and the maximum size of the shrub in the garden (supplementary methods). We found no significant relationships between cutting length and maximum size achieved in the garden for any population or species and therefore did not include cutting length as a covariate in our models (Figure S5, Table S6).

### *Source population shrub size*

To test whether northern and southern population shrubs have different size and growth patterns in the wild, we compared plant height, stem elongation and width by source population site (southern versus northern; Table S5). To account for lack of consistent measurements across all years for the source population shrubs, we included year as a random effect when we had data collected over more than three years. We only compared source stem elongations for the tall willow species because we lack data for the southern *S. arctica* population.

### *Common garden growth rates and maximum size*

To test whether northern and southern population shrubs had different growth and size patterns in the common garden, we analysed three response variables (canopy height, stem elongation, maximum width; Table S5). Because southern shrub cuttings were longer than northern cuttings for both tall willow species, we focused on change in shrub size (height, stem elongation) rather than only final sizes achieved in the garden. We also analysed maximum widths achieved by shrubs in the garden as we did not have width measurements over the full experimental period. Canopy height and stem elongation were analysed as repeated measurements to test for growth differences over time, while maximum width was analysed as a single estimate per shrub.

For the growth models, we ran models with random intercepts and random slopes to allow for each shrub individual to have a separate relationship with time. This approach also accounts for the non-independence of repeated measurements and for age differences, given that plantings were established in multiple years. We reported growth rates as the slope of the sample age term (for both southern and northern populations) in the canopy height models (incremental height over time). We also report the mean growth per year as the log transformed difference in start and end heights divided by the number of years of growth (units are presented back transformed). We then tested for differences in maximum shrub width between the southern and northern populations growing in the common garden. We extracted the maximum width value for each shrub in the garden from the three-year period we collected width measurements (2020 to 2023), rather than only 2023 widths to account for any shrubs that were pruned back due to disease in later years.

### *Common garden and source population trait and phenology models*

We tested for differences in trait expression between populations in the common garden and the natural source populations with separate models for each trait (Table S5). We included year as a random effect to account for interannual variation across measurement years. We log-transformed specific leaf area data to fit a Gaussian distribution, which we then back transformed to report outputs. Finally, to examine differences in phenology between southern and northern willows and their respective source populations, we tested for differences in shrub phenophases (separate models for leaf bud burst and leaf yellowing) between populations in the common garden and in their respective source populations. We again included year as a random effect to account for interannual variation in environmental conditions when we had more than three years of observations (Table S5). We report growing season length as the number of days between model estimates for leaf bud burst and leaf senescence for each species.

## Results

### Southern willows grew up to seven times faster than northern willows in the common garden

For *S. richardsonii*, southern willows grew larger and at a faster rate than their northern counterparts in the common garden across all metrics – height, stem elongation, and maximum width (Figure 2A, D, G, Table S8). Southern *S. richardsonii* shrubs grew up to seven times faster than northern willows in the common garden (southern sample age slope: 0.21, CI: 0.09 to 0.32 log scale), increasing in height 8.2 cm on average per year, compared to 0.7 cm per year for northern *S. richardsonii*. The tallest shrub in the garden was a southern *S. richardsonii* individual that reached a height of 127 cm in nine years. Southern *S. richardsonii* willows in the garden were also 3.9 times wider on average than their northern counterparts (Figure 2, Table S9). Stem elongation values were also consistently greater for the southern *S. richardsonii* population in the garden across the 10-year period, similar to the higher stem elongation values we observed in the southern source populations (Figure S4, Table S7). Annual height gain values declined slightly with increasing sample age in each population (Figure 2D, Table S8), from 22 mm (CI year one: 16 to 32) to 11 mm (CI year ten: 7 to 17) in the northern population, and from 83 mm (CI year one: 61 to 112) to 64 mm (CI year ten: 44 to 93) for the southern population.

*Salix pulchra* height did not increase on average (credible intervals spanned zero) for either northern or southern populations during the 10 years of the experiment in the common garden (Figure 2B, Table S8). Maximum *S. pulchra* width in the garden was 3.4 times greater for the southern population with a mean maximum width of 36.3 cm (estimates from model comparing northern and southern shrub widths in garden, CI: 22.4 to 58.5 cm, Figure S4, Table S9), unlike the similar widths we observed between the two natural source populations (Figure S4, Table S7). Stem elongation for *S. pulchra* in the garden was consistently greater for southern willows in the source populations (Figure S4, Table S7) and in the garden populations (Table S8). Mean stem elongation estimates in the garden at year 10 reached 40 mm (CI: 89 to 57 mm), while the estimate for northern willows was 12 mm (CI: 8 to 16; Figure 2). Sample age did not significantly influence stem elongation in either *S. pulchra* population (Table S8).

The prostrate willow species, *S. arctica,* showed steady increases over time in canopy height (Figure 2C, 2I, Table S8) and stem elongation (Figure 2F, Table S8) for both northern and southern populations. The differences between the populations were not statistically significant, with credible intervals for all growth metrics (height, stem elongation, width) overlapping between populations. This result mirrors patterns in the natural source populations, where we found similar sizes among sites (Figure 1B, S4, Table S7). Southern *S. arctica* grew at a rate of 0.66 cm on average per year (sample age slope: 0.14, CI: 0.10 to 0.18), while northern individuals grew slightly slower (0.39 cm per year, sample age slope: 0.18, CI: 0.09 to 0.28), although credible intervals overlapped between populations. Northern and southern *S. arctica* willows growing in the garden also reached similar maximum canopy widths after up to eight years: 16.5 cm (CI: 13.2 to 20.6 cm) for the northern population and 18.4 cm (CI: 10.8 to 30.2 cm) for the southern population (Figure 2I). Stem elongation increased for both populations over the eight-year period (Figure 2F).

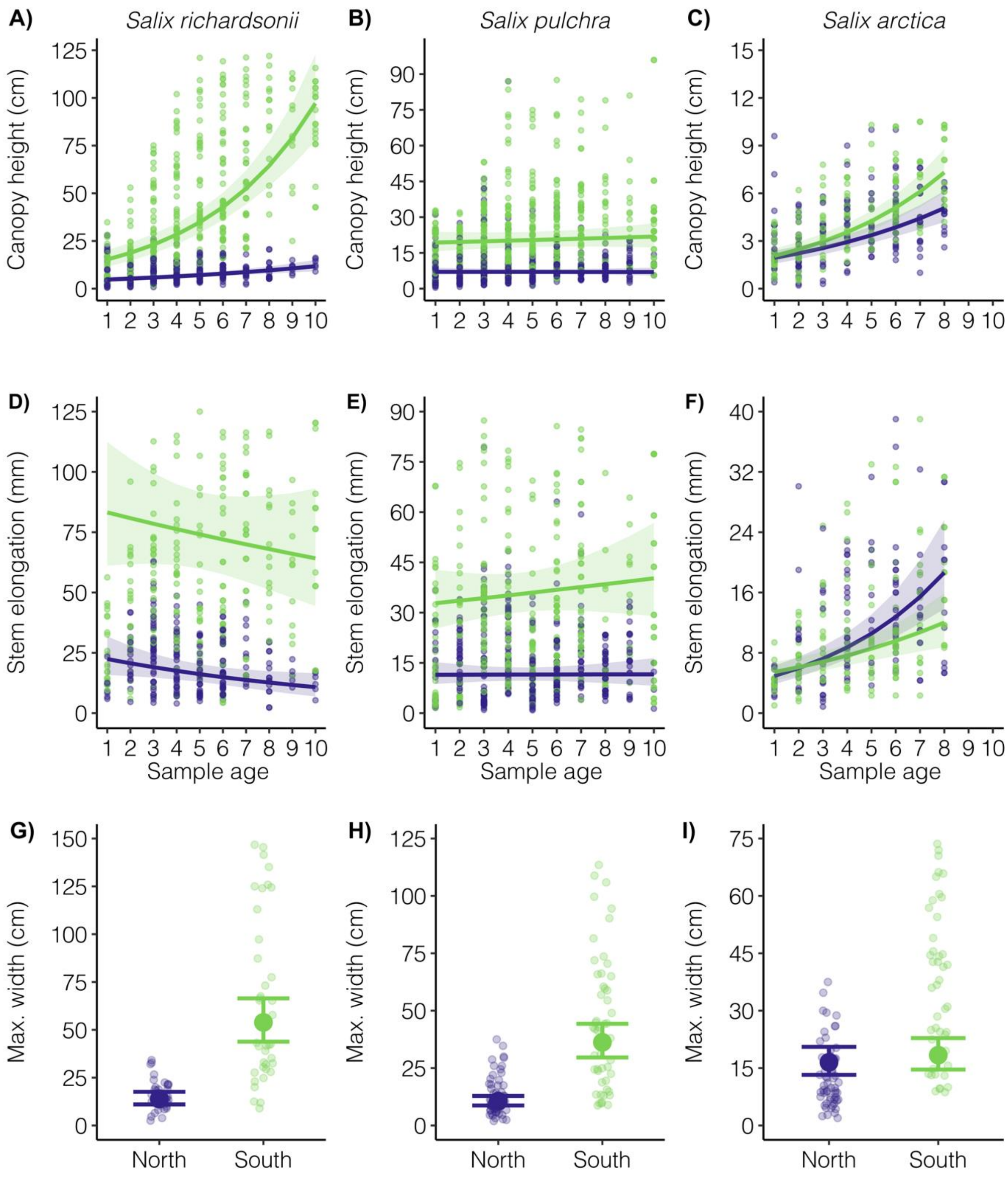

Figure 2. Southern tall shrub species grew faster and larger in the common garden. Southern willows growing in the garden (green) started at taller heights than northern (purple) willows growing in the garden at the time of planting (year one). Top: Canopy height (cm) over time. Middle: stem elongation (mm) over time. A-F): Raw data points and fitted lines from back transformed hierarchical Bayesian linear model outputs with 95% credible interval bands. Bottom: maximum canopy width (cm). G-I): Bayesian linear model outputs (back transformed estimate point plus 95% credible interval error bars) over raw data.

### Shrubs green up earlier in warmer conditions

In natural populations, leaf bud burst occurred at approximately the same time in the south and north for both tall willows: in mid-June with mean bud burst dates ranging from day 169 to 173 of the year (Figure 3, Table S10). First leaf bud burst tended to occur around 30 days earlier in the common garden than in the natural source populations. This was the case for both northern willows (33 days earlier for *S. richardsonii*, 32 days earlier for *S. pulchra*, 33 days earlier for *S. arctica*) and southern willows (32 days earlier for both *S. richardsonii* and *S. pulchra*; Table S10).

The first signs of leaf yellowing occurred around 10 days earlier (9 days earlier for *S. richardsonii* and 11 days earlier for *S. pulchra*) in natural northern source populations (late July) than in natural southern source populations (early August) (Figure 4, Table S10). The same tendency was observed for both *S. richardsonii* and *S. pulchra* (we had no southern source population phenology data for *S. arctica*), although the credible intervals between populations overlapped. For all species in the common garden, first leaf yellowing occurred later for southern willows than northern willows: up to 40 days later for S. richardsonii, 21 days for *S. pulchra*, and 19 days for *S. arctica*. For northern willows of all three species, first yellowing occurred earlier in the common garden than in the source populations: 24 days for *S. richardsonii*, 14 days for *S. pulchra* and 13 days for *S. arctica*. For southern willows, first yellowing occurred slightly later in the garden than in the source populations for *S. richardsonii* (7 days later), with no difference for *S. pulchra*.

Between the natural source populations, growing season length was seven to nine days longer in the south than the north for both *S. pulchra* and *S. richardsonii*. In the common garden, growing season length was longer for southern willows than for northern willows across all species; up to 48 days for *S. richardsonii*. The differences in growing season lengths between the source populations and common garden populations were greater for southern willows. For southern willows of both tall species, the growing season lengthened in the garden relative to their source populations (39 days for *S. richardsonii*; 29 days for *S. pulchra*). For northern willows growing in the common garden, the growing season lengthened by 20 days for *S. arctica*, 18 days for *S. richardsonii*, and nine days for *S. pulchra* relative to the northern source population.

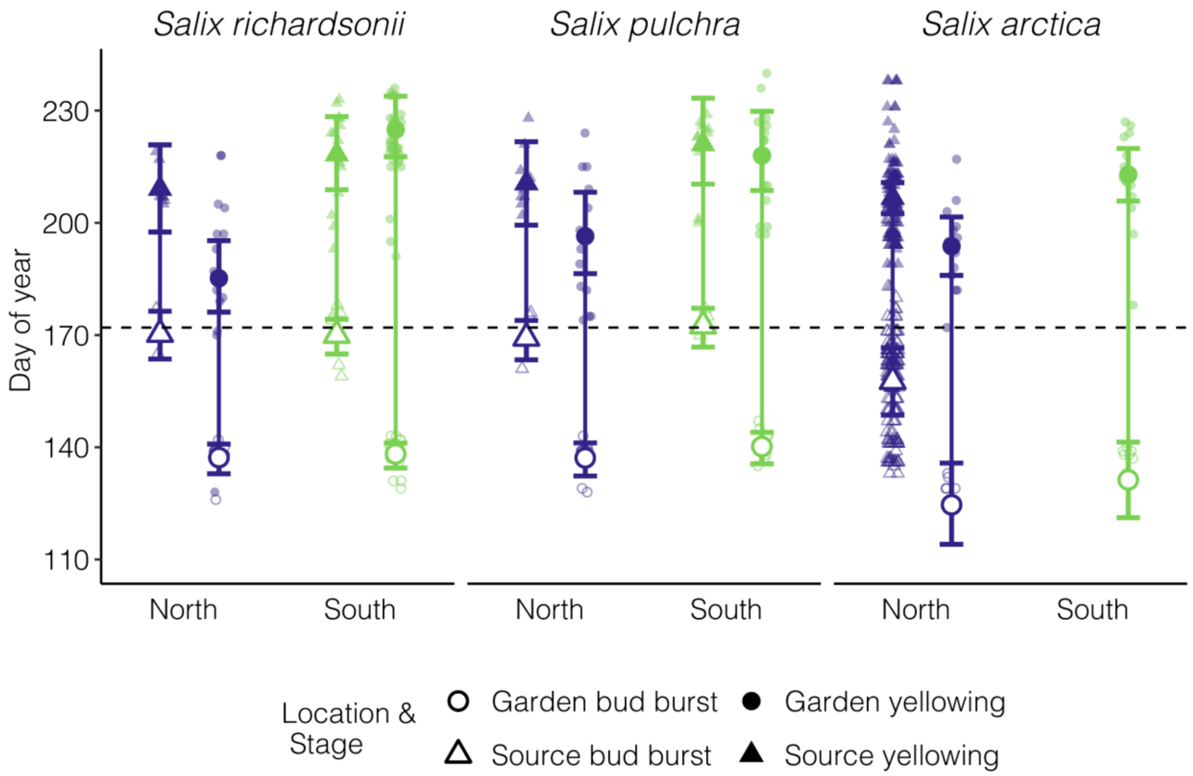

Figure 3. Willow growth starts earlier in the warmer common garden. Growing season length (line connecting points) measured by day of year of first leaf bud burst (hollow lower point) and day of year of first yellowing leaf (solid upper point) for populations in the common garden and source populations. Horizontal dashed line indicates summer solstice (21 June, day 172). Common garden populations represented by circles and source populations represented by triangles. Symbols represent hierarchal Bayesian linear model estimates and error bars represent the 95% credible intervals over raw data.

## Leaves grow larger in source populations than in the garden

Leaves tended to be larger (greater area and length) in natural source populations than in the common garden, for both northern and southern sites and for all species (Figure 4, Table S11). The differences in leaf area were significant for the tall willows, *S. richardsonii* (22.80 cm$^2$ larger) and *S. pulchra* (17.53 cm$^2$ larger), but not for the prostrate *S. arctica* (credible intervals between populations overlapped). In the common garden, mean leaf areas for northern *S. richardsonii* and *S. pulchra* were less than half the mean in the natural northern source populations (*S. richardsonii* 25.22 cm$^2$ smaller, *S. pulchra* were 20.17 cm$^2$ smaller) but credible intervals still overlapped for both species. For southern *S. richardsonii,* leaf areas in the garden were 18.59 cm$^2$ smaller than those in the source population (albeit with overlapping credible intervals). For southern *S. pulchra*, garden leaf areas were 23.62 cm$^2$ smaller than leaves in the source population. Consistent with the leaf area results, leaf lengths tended to be greater in the natural source populations than in the common garden, for both northern and southern sites and across species (Figure 4, Table S11).

For traits related to resource acquisition (SLA, LDMC), we observed no significant differences between populations measured either at their natural source sites or in the common garden, for any species (Figure 4, Table S11). These traits showed some small differences across species (for each species, all credible intervals overlapped across all populations; Table 11, Figure 4).

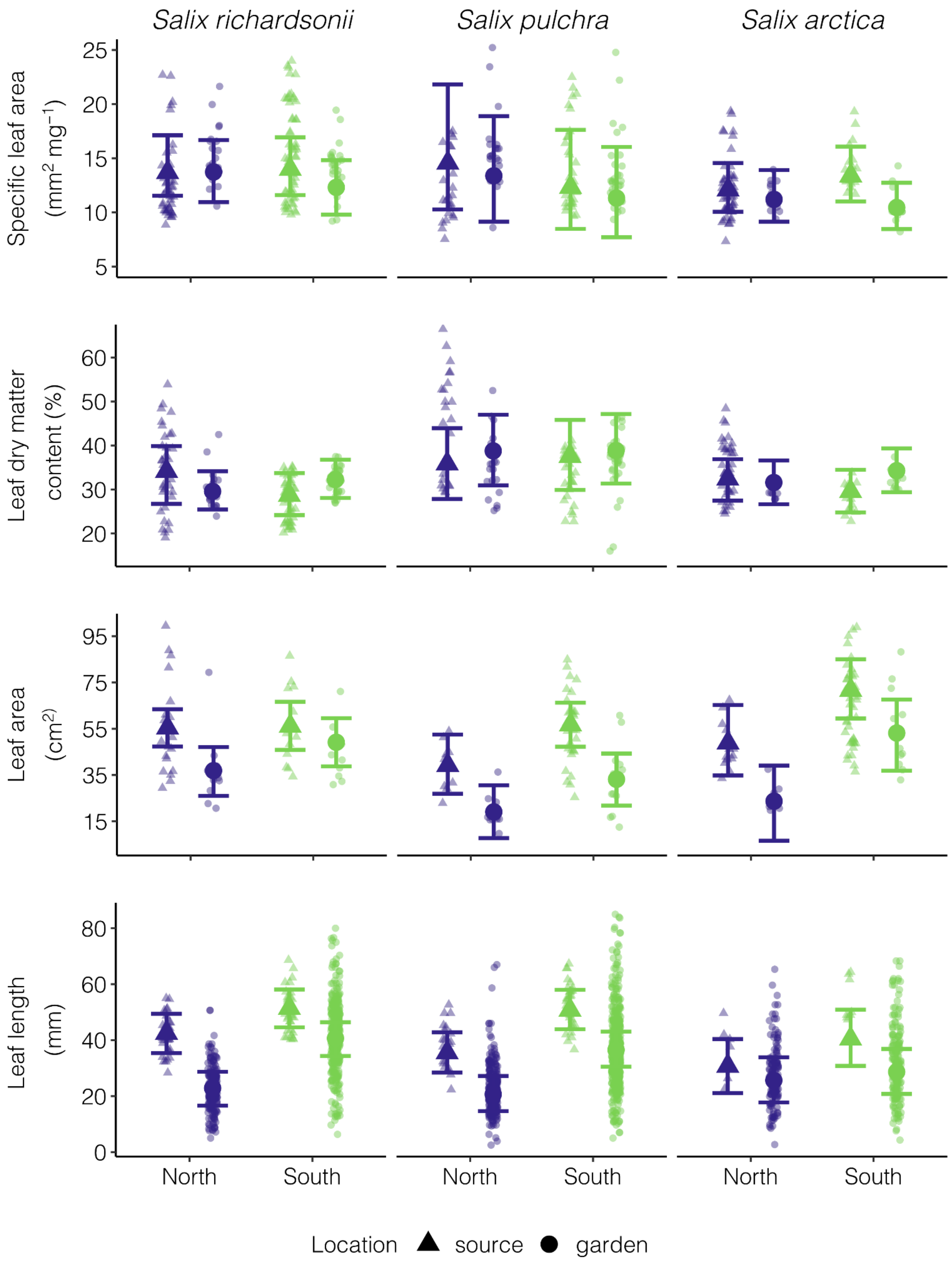

Figure 4. Leaves were larger in the cooler northern and southern source population environments than in the common garden. Leaf traits top to bottom: specific leaf area (mm$^2$ mg$^{-1}$), leaf dry matter content (%), leaf area (cm$^2$), leaf length (mm). Common garden

populations represented by circles and source populations represented by triangles. Symbols represent Bayesian linear model estimates and error bars represent the 95% credible intervals over raw data.

## Discussion

### Southern tall willows grew faster in a warmer environment

After ten years in the common garden, southern individuals of one species grew up to seven times faster than northern individuals, while all species of southern willows experienced longer growing seasons than their northern counterparts. The warmer conditions and longer snow-free period of the common garden simulates predicted future Arctic conditions (Rantanen *et al.*, 2022, Rixen *et al.*, 2022, IPCC 2022, Table 1). Overall, our findings showed that some willows grew rapidly – at rates of up to 8.2 cm per year (vertical height increase in *S. richardsonii*) – under warmer temperatures, while bud burst advanced by approximately one month across species, although the degree of plasticity to warming was species-specific (Elmendorf *et al.*, 2012b). The heterogeneous responses across species are consistent with the literature suggesting that with warming temperatures, responses of Arctic plants will vary across species, driven by complex biotic and abiotic interactions (Angers-Blondin *et al.*, 2018, Alexander *et al.*, 2015, Elmendorf *et al.*, 2012a). Given the clear growth and phenological differences between the southern and northern willows in a common garden (for two of three species), our findings also indicate genetic differences between populations, potentially due to local adaptation to photoperiod or other environmental conditions. If local adaptation is to past conditions, future maladaptation could limit shrub growth and expansion in a warmer future, as could physiological source-sink limitations.

We generally found support for our prediction of southern willows growing faster and reaching larger sizes than northern willows when growing in a warmer, common environment, although there was variation across species. Southern *S. richardsonii* shrubs grew taller than northern conspecifics; neither *S. pulchra* population showed increased individual height over time, but the southern population showed greater annual growth and were wider; shrubs from the two *S. arctica* populations grew at similar rates. This variation highlights the varied responses and climate sensitivities of tundra plants to warming (Figure 2, Myers-Smith *et al.*, 2015a, Elmendorf *et al.*, 2012a).

Previous research using growth rings found climate sensitivity of shrub growth across the tundra biome (Myers-Smith *et al*. 2015a). Specific studies in the Yukon, Nunavut and Alaska for our three species found that growth and size were positively associated with warmer temperatures (Boyle *et al.*, 2022, Buchkowski *et al*., 2020, Myers-Smith & Hik, 2018, Ackerman *et al*., 2017, Boulanger-Lapointe *et al*., 2016, Blok *et al*., 2011, Walker, 1989). The rapid growth response for southern *S. richardsonii* that we observed in the common garden could be due to the elevated temperatures. While we did not directly compare stem elongation values from the garden populations with the source populations due to unknown ages of source population shrubs, after just ten years in the garden, the southern *S. richardsonii* population had comparable annual stem elongation with the southern source population (~64 to 66 mm per season; Figure 2D). These findings demonstrate the potential for some willow species and populations to grow rapidly under warmer conditions.

## Willow species differ in their growth responses to warming

We found that species and populations respond differently to warming, but that patterns vary across growth metrics. We expected consistent patterns across growth metrics, which was the case for *S. richardsonii* and *S. arctica,* but not for *S. pulchra*. We found no increases in height for either garden population of *S. pulchra,* although stem elongation rates were consistently up to three times greater for the southern population (Figure 2), which contributed to increased width (southern willows were wider than northern willows). While *S. pulchra* growth has been previously linked to summer temperatures, its growth may be limited by other factors like soil moisture (Ackerman *et al*., 2017, Blok *et al*., 2011) and disease (Pie & McCracken 2005, Smith *et al*., 2004). As the common garden site had lower soil moisture than both source sites (Table 1), shrubs of all species and populations may have experienced water stress, with consequences for growth (Boulanger-Lapointe *et al*., 2016, Myers-Smith *et al*., 2015a). Some shrubs in the garden (notably southern *S. richardsonii* individuals) grew large enough to shade smaller shrubs, which were often but not necessarily, northern conspecifics. Field observations have similarly noted that tall, deciduous shrubs often have a competitive advantage under warmer conditions (Mekonnen *et al*., 2021). The varied growth results among willow species indicate that we should expect different shrub species, even those that are closely related to each other, to respond differently to changing climate conditions (García Criado *et al.*, 2023).

Different environmental conditions favour different growth strategies across the tundra, likely helping to explain why we observed taller (Figure 1) but not necessarily wider (Figure S4) shrubs in the natural southern source populations compared to the natural northern source populations of *S. richardsonii* and *S. pulchra*. Comparing natural source environments, we observed similar heights between *S. pulchra* and *S. richardsonii* in both southern and northern populations (Figure 1). However, in the warmer common garden, southern *S. richardsonii* clearly grew faster and larger than southern *S. pulchra* (Figure 2). In contrast, *S. arctica* growth, traits, and phenology, were more similar between southern and northern willows growing in the common garden. In wild environments, *S. arctica* growth generally declines with increasing latitude (Boulanger-Lapointe *et al*., 2016, Wilson, 1964), and the movement of *S. arctica* cuttings to the common garden appeared to stimulate growth for both sources about equally. As we observed vertical and lateral growth in both populations in the warmer common garden, we might expect *S. arctica* to grow rapidly in warming conditions across latitudes. The success of both populations of *S. arctica* in the garden may be due in part to its prostrate growth form, which keeps individuals insulated under snow for longer each season and reduces exposure to freezing spring temperatures, compared to tall shrubs (Kuprian *et al.*, 2014). While the three focal species are geographically widespread, given the range of responses we observed across and within species, we cannot easily predict how other species of *Salix* or other common shrubs like *Betula* spp. or *Alnus* spp. will respond to warming (García Criado *et al.*, 2023).

### Growing season lengthens in warmer conditions

Changes to the growth periods for Arctic plants are expected to occur via earlier bud burst coupled with either: 1) maintenance of senescence timing, or 2) later senescence (Collins *et al.*, 2021). As predicted, we found that growing seasons were longer for willows in the common garden relative to their source populations, although the difference was far more pronounced for southern willows than for northern willows. All species demonstrated earlier leaf bud burst in the warmer common garden relative to their source populations, which agrees with experimental and ambient tundra warming studies that generally find a positive relationship between warming and leaf bud burst (Collins *et al*., 2012, Elmendorf *et al*., 2012, Flynn & Wolkovich, 2018). advances in bud burst timing that we observed suggests that the timing of this event is strongly plastic and may be triggered by temperature and snowmelt timing (Assmann *et al.*, 2019). For the end of the growing season, the southern common garden populations maintained or slightly delayed their initiation of senescence compared to the source population (with the same day lengths as their source populations), but the northern willows in the garden populations senesced up to 24 days earlier than the northern source populations. As a result, the growing season lengths for northern willows were shorter (up to 48 days for *S. richardsonii*) than for southern willows growing in the common garden. Our results thus suggest that changes to the growing season may not be consistent across species and populations.

The difference in senescence timing between southern and northern willows growing in the common garden suggests potential genetic differentiation of the underlying cue (Miryeganeh, 2022, Guo *et al.*, 2021, Parker *et al.*, 2021). Northern willows may be adapted to northern photoperiod, thus their physiological processes may have been disrupted by the move 1,000 km south corresponding with a substantial shift in photoperiod. The day length for the mean timing of senescence for northern *S. richardsonii* growing in the garden (day 185 or 4 July) was just under 19 hours, while for that same day of year in the northern source location there is 24-hour daylight. The importance of photoperiod as a cue for senescence (along with temperature) has been suggested to increase in importance with increasing latitude (Lang *et al.*, 2019, Gill *et al.*, 2015). In their reciprocal transplant experiment, Parker *et al.* (2021) also found evidence of genetic differentiation of senescence cues, showing that ecotypes from different sources of a common sedge, *Eriophorum vaginatum,* maintained the timing of senescence even in warmer conditions. Similarly, Bjorkman *et al.* (2017) observed that within their common garden experiment, *Oxyria digyna* and *Papaver radicatum* plants retained the same phenologies as plants from their source latitudes. As photoperiod varies across the latitudinal gradient of the tundra, if daylength is a dominant cue for senescence, we should expect spatial variation in changes to growing season length as the biome continues to warm.

Early senescence of northern willows in the garden could also be due to earlier bud burst and leaf life spans (Edwards et al., 2014), physiological growth capacity limitations (sink dynamics) or environmental stress (Kumar *et al.*, 2023, Campany *et al.,* 2017). Growth and energy storage (“sink”) and photosynthetic (“source”) capacities vary across species and individuals, and can influence senescence timing, since there is no benefit to additional photosynthesis once "sinks" have been filled (Kumar *et al.*, 2023, Thomas, 2013). Larger shrubs (e.g., southern *S. richardsonii* growing in the garden) with more leaves or larger leaves have greater photosynthetic capacities than smaller shrubs (Díaz *et al.*, 2016), which in turn influences growth and the capacity to store energy (Körner *et al.*, 2015). If willows are limited by seasonal growth and photosynthetic capacities, performance can in part be controlled by the size of the individual, which changes over the shrub's lifespan (White *et al.*, 2015). The disparity in growth and photosynthetic capacities between northern and southern willows in the garden could have increased over time as some southern willows grew larger. Environmental stress, such as the drier conditions of the garden or reduced light exposure period (northern willows only) can also constrain growth and have contributed to early senescence (Guo *et al.*, 2021, Sade *et al.*, 2018, Körner, 2015). We suspect the smaller leaves we observed in the common garden (relative to natural source populations) were due to a stress response to the warmer, drier (lower soil moisture) conditions of the experiment (Bjorkman *et al.*, 2018, Díaz *et al.*, 2016). The consistent timing of senescence (early July) for *S. richardsonii* and *S. pulchra* from the northern source populations among years with different summer temperatures and precipitation suggests that senescence timing is primarily controlled by photoperiod rather than capacity limitations or stress when these willows are moved into a common garden environment away from source populations at higher latitudes.

In the common garden, the shorter period between leaf bud burst and senescence is likely a main factor explaining low growth in the northern tall willows compared to the southern population. Shorter periods of active leaves for the northern populations reduced the potential for photosynthesis and growth each summer compared to southern individuals growing in the garden (Gregerson *et al.*, 2013). In their Alaskan common garden experiment containing ecotypes of *E. vaginatum* from different latitudes, Parker *et al*. (2017) observed that southern ecotypes accumulated more biomass over time due to a longer growing season (southern ecotypes senesced later than northern ones). Experimental work on *Salix* spp. grown for wood harvest has also identified daylength as a dominant cue for growth (Cerasuolo *et al*., 2015). While the relocation of Arctic shrubs to the boreal zone in our experiment represents a major environmental change, plants will naturally experience shifts in photoperiod during range expansion (Collins *et al.*, 2021, Ettinger *et al*., 2021, Prevéy *et al*., 2019). Our results suggest that in natural environments without daylight manipulation, warming could lengthen the growing season by advancing leaf bud burst, and maintaining or slightly delaying senescence timing, but range expansions may involve different processes that may lead to maladaptation of the timing of phenological events and constrain future performance (Collins *et al*., 2021, Ettinger *et al*., 2021).

## Shrubs respond rapidly to warmer conditions

Our ten-year experiment exceeds the duration of many existing tundra common garden or reciprocal transplant experiments and provides a sufficiently long period to draw conclusions about plasticity and genetic differentiation influencing plant responses to warming (Bennington *et al*., 2012). Northern willows may have a reduced response to warming than southern willows, consistent with our observations that southern willows experienced longer growing seasons and achieved larger sizes (Prevéy *et al*., 2017, DeMarch *et al*., 2016). As tundra shrubs are long lived, over an individual's lifetime, they will continue to experience increasing temperatures and must adjust growth or resource use strategies (i.e., plasticity) to maximise carbon accumulation (Crous, 2019, Myers-Smith *et al*., 2015b, Way & Oren, 2010). We observed rapid plastic responses to the warmer, drier environment for some traits (e.g., smaller leaves the first year of the experiment), enabling plants to adjust their strategies to cope with sudden change (Moran *et al.*, 2016). Contrary to our second prediction, however, we did not observe plastic responses in resource management traits and found no differences in SLA or LDMC values between the garden and source populations. Community trait shifts to more resource acquisitive strategies (higher SLA, lower LDMC) were previously found to be greater in warmer wet environments compared to warmer drier conditions like our common garden (Bjorkman *et al.*, 2018). While plastic responses may slow the process of natural selection by weakening selective pressures in the short term, plasticity may also help populations persist in environments in which they can subsequently undergo evolutionary change (Crispo, 2008). Our results demonstrate that some phenological and morphological traits can quickly (plastically) respond to a warmer environment, but responses vary across species and populations.

Genetic differentiation between populations may be due to local adaptations to factors like photoperiod, which varies across species ranges (DeMarch *et al.*, 2017). If the cue for triggering senescence is genetically regulated and willows are adapted to local photoperiod, future changes to the growing season may be limited by advances in spring phenology without evolution of senescence cues. Other common garden experiments support the argument that Arctic plants can exhibit strong local adaptation to photoperiod and climate, potentially limiting the ability of plant populations to respond quickly to a rapidly changing climate (Bennington *et al.*, 2012, DeMarche *et al.*, 2017, Jump & Peñuelas, 2005). As the climate warms, more southern adapted *Salix* spp. genotypes from warmer locations may ‘rescue’ northern populations through gene flow and confer beneficial adaptations for warmer environments (Anderson *et al.*, 2012, Norberg *et al.*, 2012, Parker *et al.*, 2021). However, as factors other than temperature (e.g., photoperiod) influence the fitness of tundra plants and also vary with latitude - but do not shift with climate change - maladaption of southern genotypes may hinder their success at more northern latitudes (Bjorkman *et al.,* 2017). Alpine and Arctic ecosystems will also experience and respond to different changes (e.g., range expansions will not occur at the same rates) as the climate warms (Rixen *et al.,* 2022, Ernakovick *et al*., 2014, Loarie *et al*., 2008). If not constrained by dispersal or environmental conditions, southern willow shrubs may grow more rapidly with future warming and could extend their ranges northwards.

## Conclusions and implications

Our findings suggest that as temperatures warm and the snow-free period lengthens in the Arctic, we can expect rapid *Salix* growth across the tundra with potential increases to growing season length due to bud burst advancement (Walker *et al.,* 2006, Collins *et al.,* 2021). However, we found that responses to warming differed among species and populations, complicating future predictions of tundra vegetation change using temperature alone. The differences we observed between shrubs growing in the common garden and their respective source populations provide evidence of both phenotypic plasticity and genetic differentiation potentially caused by local adaptation and thus demonstrate the ability of some but not all shrub traits to respond rapidly to a warmer environment. All species in our experiment demonstrated some plastic responses to the warmer environment like earlier leaf bud burst, but northern tall willows grew notably less and experienced shorter growing seasons than southern tall willows likely due to genetic differentiation. Future reciprocal transplants and measurements of willow fitness (e.g., catkin counts) across species and populations over the long term would enable us to make stronger evolutionary inferences and test directly for local adaptation. Local adaptation to photoperiod and/or physiologic limitations may limit future shrub growth and influence which species succeed in a warmer tundra as shrubs disperse with northward range expansion (García Criado *et al*., 2020, Seider *et al*., 2022). In the short term, local adaptation to photoperiod may limit the future success of some species and populations, and changes to growing season length may be constrained by genetically fixed senescence timing. Future rates of shrub growth and success thus depend on the species and its distribution, as well as the expansion of southern populations further north. Improving our predictions of increases in growing season lengths, shrub growth and expansion and tundra primary productivity is critical for projecting the impact of climate change on wildlife populations and ultimately the livelihoods and sustainability of Arctic Communities (Ford *et al.*, 2021, Post *et al.*, 2019).

## REFERENCES

Ackerman, D., Griffin, D., Hobbie, S. E. & Finlay, J. C. Arctic shrub growth trajectories differ across soil moisture levels. *Glob Chang Biol* **23**, 4294–4302 (2017).

Anderson, J. T., Panetta, A. M. & Mitchell-Olds, T. Evolutionary and Ecological Responses to Anthropogenic Climate Change: Update on Anthropogenic Climate Change. *Plant Physiology* **160**, 1728–1740 (2012).

Angers-Blondin, S., Myers-Smith, I. H. & Boudreau, S. Plant–plant interactions could limit recruitment and range expansion of tall shrubs into alpine and Arctic tundra. *Polar Biol* **41**, 2211–2219 (2018).

Assmann, J. J. *et al.* Local snow melt and temperature—but not regional sea ice—explain variation in spring phenology in coastal Arctic tundra. *Global Change Biology* **25**, 2258–2274 (2019).

Baruah, G., Molau, U., Bai, Y. & Alatalo, J. M. Community and species-specific responses of plant traits to 23 years of experimental warming across subarctic tundra plant communities. *Sci Rep* **7**, 2571 (2017).

Bennington, C. C. *et al.* Home site advantage in two long-lived arctic plant species: results from two 30-year reciprocal transplant studies. *Journal of Ecology* **100**, 841–851 (2012).

Billings, W. D. & Mooney, H. A. The Ecology of Arctic and Alpine Plants. *Biological Reviews* **43**, 481–529 (1968).

Bjorkman, A. D., Elmendorf, S. C., Beamish, A. L., Vellend, M. & Henry, G. H. R. Contrasting effects of warming and increased snowfall on Arctic tundra plant phenology over the past two decades. *Global Change Biology* **21**, 4651–4661 (2015).

Bjorkman, A. D. *et al.* Status and trends in Arctic vegetation: Evidence from experimental warming and long-term monitoring. *Ambio* **49**, 678–692 (2020).

Bjorkman, A. D. *et al.* Plant functional trait change across a warming tundra biome. *Nature* **562**, 57–62 (2018).

Bjorkman, A. D., Vellend, M., Frei, E. R. & Henry, G. H. R. Climate adaptation is not enough: warming does not facilitate success of southern tundra plant populations in the high Arctic. *Global Change Biology* **23**, 1540–1551 (2017).

Blok, D. *et al.* What are the main climate drivers for shrub growth in Northeastern Siberian tundra? *Biogeosciences* **8**, 1169–1179 (2011).

Boulanger-Lapointe, N., Lévesque, E., Baittinger, C. & Schmidt, N. M. Local variability in growth and reproduction of Salix arctica in the High Arctic. *Polar Research* (2016).

Box, J. E. *et al.* Key indicators of Arctic climate change: 1971–2017. *Environ. Res. Lett.* **14**, 045010 (2019).

Buchkowski, R. W. *et al.* Warmer temperatures promote shrub radial growth but not cover in the central Canadian Arctic. *Arctic, Antarctic, and Alpine Research* **52**, 582–595 (2020).

Bürkner, P.-C. brms: An R Package for Bayesian Multilevel Models Using Stan. *Journal of Statistical Software* **80**, 1–28 (2017).

Campany, C. E., Medlyn, B. E. & Duursma, R. A. Reduced growth due to belowground sink limitation is not fully explained by reduced photosynthesis. *Tree Physiology* **37**, 1042–1054 (2017).

Cerasuolo, M. *et al.* Development of a sink–source interaction model for the growth of short-rotation coppice willow and in silico exploration of genotype × environment effects. *Journal of Experimental Botany* **67**, 961–977 (2016).

Choi, R. T., Beard, K. H., Leffler, A. J., Kelsey, K. C., Schmutz, J. A., & Welker, J. M. (2019). Phenological mismatch between season advancement and migration timing alters Arctic plant traits. *Journal of Ecology*, *107*(5), 2503–2518.

Collins, C. G. *et al.* Experimental warming differentially affects vegetative and reproductive phenology of tundra plants. *Nat Commun* **12**, 1–12 (2021).

Crispo, E. Modifying effects of phenotypic plasticity on interactions among natural selection, adaptation and gene flow. *Journal of Evolutionary Biology* **21**, 1460–1469 (2008).

Crous, K. Y. Plant responses to climate warming: physiological adjustments and implications for plant functioning in a future, warmer world. *Am J Bot* **106**, 1049–1051 (2019).

DeMarche, M. L., Doak, D. F. & Morris, W. F. Both life-history plasticity and local adaptation will shape range-wide responses to climate warming in the tundra plant Silene acaulis. *Global Change Biology* **24**, 1614–1625 (2018).

Díaz, S. *et al.* The global spectrum of plant form and function. *Nature* **529**, 167–171 (2016).

Edwards, E. J., *et al.* Leaf life span and the leaf economic spectrum in the context of whole plant architecture. *Journal of Ecology*, *102*(2), 328–336 (2014).

Elmendorf, S. C. *et al.* Global assessment of experimental climate warming on tundra vegetation: heterogeneity over space and time. *Ecology Letters* **15**, 164–175 (2012a).

Elmendorf, S. C. *et al.* Plot-scale evidence of tundra vegetation change and links to recent summer warming. *Nature Clim Change* **2**, 453–457 (2012b).

Elmendorf, S. C. & Hollister, R. D. Limits on phenological response to high temperature in the Arctic. *Sci Rep* **13**, 208 (2023).

Ernakovich, J. G. *et al.* Predicted responses of arctic and alpine ecosystems to altered seasonality under climate change. *Glob Chang Biol* **20**, 3256–3269 (2014).

Ettinger, A. K., Buonaiuto, D. M., Chamberlain, C. J., Morales-Castilla, I. & Wolkovich, E. M. Spatial and temporal shifts in photoperiod with climate change. *New Phytologist* **230**, 462–474 (2021).

Flynn, D. F. B. & Wolkovich, E. M. Temperature and photoperiod drive spring phenology across all species in a temperate forest community. *New Phytologist* **219**, 1353–1362 (2018).

Ford, J. D., Pearce, T., Canosa, I. V., & Harper, S. (2021). The rapidly changing Arctic and its societal implications. *WIREs Climate Change*, *12*(6), e735.

Frei, E. R. & Henry, G. H. R. Long-term effects of snowmelt timing and climate warming on phenology, growth, and reproductive effort of Arctic tundra plant species. *Arctic Science* **8**, 700–721 (2022).

Frost, G. V. & Epstein, H. E. Tall shrub and tree expansion in Siberian tundra ecotones since the 1960s. *Glob Chang Biol* **20**, 1264–1277 (2014).

García Criado, M. G., Myers-Smith, I. H., Bjorkman, A. D., Lehmann, C. E. R. & Stevens, N. Woody plant encroachment intensifies under climate change across tundra and savanna biomes. *Global Ecology and Biogeography* **29**, 925–943 (2020).

García Criado, M. *et al.* Plant traits poorly predict winner and loser shrub species in a warming tundra biome. *Nat Commun* **14**, 3837 (2023).

Gill, A. L. *et al.* Changes in autumn senescence in northern hemisphere deciduous trees: a meta-analysis of autumn phenology studies. *Ann Bot* **116**, 875–888 (2015).

Guo, Y. *et al.* Leaf senescence: progression, regulation, and application. *Molecular Horticulture* **1**, 5 (2021).

Hollister, R. D., May, J. L., Kremers, K. S., Tweedie, C. E., Oberbauer, S. F., Liebig, J. A., Botting, T. F., Barrett, R. T., & Gregory, J. L. (2015). Warming experiments elucidate the drivers of observed directional changes in tundra vegetation. *Ecology and Evolution*, *5*(9), 1881–1895.

IPCC. *Climate Change 2022: Impacts, Adaptation, and Vulnerability*. https://www.ipcc.ch/report/ar5/wg2/ (2022).

Jump, A. S. & Peñuelas, J. Running to stand still: adaptation and the response of plants to rapid climate change. *Ecology Letters* **8**, 1010–1020 (2005).

Karger, D. N. *et al.* Climatologies at high resolution for the earth's land surface areas. *Sci Data* **4**, 170122 (2017).

Keenan, T. F. & Richardson, A. D. The timing of autumn senescence is affected by the timing of spring phenology: implications for predictive models. *Global Change Biology* **21**, 2634–2641 (2015).

Kelsey, K. C. *et al.* Winter snow and spring temperature have differential effects on vegetation phenology and productivity across Arctic plant communities. *Global Change Biology* **27**, 1572–1586 (2021).

Körner, C. Some Often Overlooked Plant Characteristics as Determinants of Plant Growth: A Reconsideration. *Functional Ecology* **5**, 162–173 (1991).

Körner, C. Paradigm shift in plant growth control. *Current Opinion in Plant Biology* **25**, 107–114 (2015).

Körner, C., Möhl, P. & Hiltbrunner, E. Four ways to define the growing season. *Ecology Letters* **26**, 1277–1292 (2023).

Kumar, R. *et al.* Genetic architecture of source–sink-regulated senescence in maize. *Plant Physiology* **193**, 2459–2479 (2023).

Lajoie, G. & Vellend, M. Characterizing the contribution of plasticity and genetic differentiation to community-level trait responses to environmental change. *Ecology and Evolution* **8**, (2018).

Lang, W., Chen, X., Qian, S., Liu, G. & Piao, S. A new process-based model for predicting autumn phenology: How is leaf senescence controlled by photoperiod and temperature coupling? *Agricultural and Forest Meteorology* **268**, 124–135 (2019).

Lortie, C. & Hierro, J. A synthesis of local adaptation to climate through reciprocal common gardens. *Journal of Ecology* (2021).

Martin, A. C., Jeffers, E. S., Petrokofsky, G., Myers-Smith, I. & Macias-Fauria, M. Shrub growth and expansion in the Arctic tundra: an assessment of controlling factors using an evidence-based approach. *Environ. Res. Lett.* **12**, 085007 (2017).

Mekonnen, Z. A. *et al.* Arctic tundra shrubification: a review of mechanisms and impacts on ecosystem carbon balance. *Environ. Res. Lett.* **16**, 053001 (2021).

Miller, T. E. X. *et al.* Eco-evolutionary dynamics of range expansion. *Ecology* **101**, e03139 (2020).

Miryeganeh, M. Epigenetic Mechanisms of Senescence in Plants. *Cells* **11**, 251 (2022).

Molau, U., and Mølgaard, P. 1996. ITEX Manual. 2nd ed. Danish Polar Center. Available from https://www.gvsu.edu/itex/

Moran, E. V., Hartig, F. & Bell, D. M. Intraspecific trait variation across scales: implications for understanding global change responses. *Glob Chang Biol* **22**, 137–150 (2016).

Myers-Smith, I. H. *et al.* Climate sensitivity of shrub growth across the tundra biome. *Nature Clim Change* **5**, 887–891 (2015a).

Myers-Smith, I. H. *et al.* Shrub expansion in tundra ecosystems: dynamics, impacts and research priorities. *Environ. Res. Lett.* **6**, 045509 (2011).

Myers-Smith, I. H. *et al.* Methods for measuring arctic and alpine shrub growth: A review. *Earth-Science Reviews* **140**, 1–13 (2015b).

Myers-Smith, I. H. & Hik, D. S. Climate warming as a driver of tundra shrubline advance. *Journal of Ecology* **106**, 547–560 (2018).

Myers-Smith, I. H. *et al.* Expansion of Canopy-Forming Willows Over the Twentieth Century on Herschel Island, Yukon Territory, Canada. *Ambio* **40**, 610–623 (2011).

Myers-Smith, I. H. *et al.* Eighteen years of ecological monitoring reveals multiple lines of evidence for tundra vegetation change. *Ecological Monographs* **89**, e01351 (2019).

Niittynen, P., Heikkinen, R. K. & Luoto, M. Decreasing snow cover alters functional composition and diversity of Arctic tundra. *Proc Natl Acad Sci USA* **117**, 21480–21487 (2020).

Oberbauer, S. F. *et al.* Phenological response of tundra plants to background climate variation tested using the International Tundra Experiment. *Phil. Trans. R. Soc. B* **368**, 20120481 (2013).

Olofsson, J. & Post, E. Effects of large herbivores on tundra vegetation in a changing climate, and implications for rewilding. *Philosophical Transactions of the Royal Society B: Biological Sciences* **373**, 20170437 (2018)..

Parker, T. C., Tang, J., Clark, M. B., Moody, M. M. & Fetcher, N. Ecotypic differences in the phenology of the tundra species Eriophorum vaginatum reflect sites of origin. *Ecol Evol* **7**, 9775–9786 (2017).

Parker, T. C., Unger, S. L., Moody, M. L., Tang, J. & Fetcher, N. Intraspecific variation in phenology offers resilience to climate change for Eriophorum vaginatum. *Arctic Science* **8**, 935–951 (2021).

Pei, M. H. & McCracken, A. R. *Rust Diseases of Willow and Poplar*. (CABI, 2005).

Polgar, C. A. & Primack, R. B. Leaf-out phenology of temperate woody plants: from trees to ecosystems. *New Phytologist* **191**, 926–941 (2011).

Post, E., Alley, R. B., Christensen, T. R., Macias-Fauria, M., Forbes, B. C., Gooseff, M. N., Iler, A., Kerby, J. T., Laidre, K. L., Mann, M. E., Olofsson, J., Stroeve, J. C., Ulmer, F., Virginia, R. A., & Wang, M. (2019). The polar regions in a 2°C warmer world. *Science Advances*, *5*(12), eaaw9883.

Potter, C. & Alexander, O. Changes in Vegetation Phenology and Productivity in Alaska Over the Past Two Decades. *Remote Sensing* **12**, 1546 (2020).

Prescott, C. E. *et al.* Surplus Carbon Drives Allocation and Plant–Soil Interactions. *Trends in Ecology & Evolution* **35**, 1110–1118 (2020).

Prevéy, J. S. *et al.* Warming shortens flowering seasons of tundra plant communities. *Nat Ecol Evol* **3**, 45–52 (2019).

Prevéy, J. *et al.* Greater temperature sensitivity of plant phenology at colder sites: implications for convergence across northern latitudes. *Global Change Biology* **23**, 2660–2671 (2017).

Rantanen, M. *et al.* The Arctic has warmed nearly four times faster than the globe since 1979. *Commun Earth Environ* **3**, 1–10 (2022).

Reich, P. B. The world-wide 'fast–slow' plant economics spectrum: a traits manifesto. *Journal of Ecology* **102**, 275–301 (2014).

Rivest, S., Inouye, B. D. & Forrest, J. R. K. Warmer springs increase potential for temporal reproductive isolation among habitat patches in subalpine flowering plants. *Journal of Ecology* **111**, 2257–2268 (2023).

Rivest, S., Lajoie, G., Watts, D. A. & Vellend, M. Earlier spring reduces potential for gene flow via reduced flowering synchrony across an elevational gradient. *Am J Bot* **108**, 538–545 (2021).

Rixen, C. *et al.* Winters are changing: snow effects on Arctic and alpine tundra ecosystems. *Arctic Science* **8**, 572–608 (2022).

Sade, N., del Mar Rubio-Wilhelmi, M., Umnajkitikorn, K. & Blumwald, E. Stress-induced senescence and plant tolerance to abiotic stress. *Journal of Experimental Botany* **69**, 845–853 (2018).

Samplonius, J. M. *et al.* Strengthening the evidence base for temperature-mediated phenological asynchrony and its impacts. *Nat Ecol Evol* **5**, 155–164 (2021).

Schmidt, N. M. *et al.* Little directional change in the timing of Arctic spring phenology over the past 25 years. *Current Biology* **33**, 3244-3249.e3 (2023).

Seider, J. H., Lantz, T. C. & Bone, C. Tundra shrub expansion in a warming climate and the influence of data type on models of habitat suitability. *Arctic, Antarctic, and Alpine Research* **54**, 488–506 (2022).

Siefert, A. *et al.* A global meta-analysis of the relative extent of intraspecific trait variation in plant communities. *Ecology Letters* **18**, 1406–1419 (2015).

Smith, J. A., Blanchette, R. A., & Newcombe, G. (2004). Molecular and morphological characterization of the willow rust fungus, Melampsora epitea, from arctic and temperate hosts in North America. *Mycologia*, *96*(6), 1330–1338.

Smith, C. A. S., Kennedy, C. E., Hargrave, A. E. & McKenna, K. M. *Soil and Vegetation of Herschel Island*. https://sis.agr.gc.ca/cansis/publications/surveys/yt/yt15/yt15_report.pdf (1989).

Thomas, H. J. D. *et al.* Global plant trait relationships extend to the climatic extremes of the tundra biome. *Nat Commun* **11**, 1351 (2020).

Thomas, H. Senescence, ageing and death of the whole plant. *New Phytologist* **197**, 696–711 (2013).

Tuomi, M. *et al.* Stomping in silence: Conceptualizing trampling effects on soils in polar tundra. *Functional Ecology* **35**, 306–317 (2021).

Walker, D. A. Height and growth rings of *Salix lanata* ssp. *Richardsonii* along the coastal temperature gradient of northern Alaska. *Can. J. Bot.* **65**, 988–993 (1987).

Walker, M. D. *et al.* Plant community responses to experimental warming across the tundra biome. *Proceedings of the National Academy of Sciences* **103**, 1342–1346 (2006).

White, A. C., Rogers, A., Rees, M. & Osborne, C. P. How can we make plants grow faster? A source–sink perspective on growth rate. *Journal of Experimental Botany* **67**, 31–45 (2016).

Wilson, J. W. Annual Growth of Salix arctica in the High-Arctic1. *Annals of Botany* **28**, 71–76 (1964).

Wright, I. J. *et al.* The worldwide leaf economics spectrum. *Nature* **428**, 821–827 (2004).

Zona, D. *et al.* Earlier snowmelt may lead to late season declines in plant productivity and carbon sequestration in Arctic tundra ecosystems. *Sci Rep* **12**, 3986 (2022).

Zhou, J., Tape, K. D., Prugh, L., Kofinas, G., Carroll, G., & Kielland, K. (2020). Enhanced shrub growth in the Arctic increases habitat connectivity for browsing herbivores. *Global Change Biology*, *26*(7), 3809–3820.

## AUTHOR CONTRIBUTIONS

Isla Myers-Smith designed the experiment. Data collection occurred over ten years: Isla Myers-Smith (2013-2023), Madelaine Anderson (2021-2023), Haydn Thomas (2015-2017), Gergana Daskalova (2017-2019), Mariana García Criado (2018), Erica Zaja (2022), Jiří Šubrt (2022), Elise Gallois (2022). Madelaine Anderson, Erica Zaja, Isla Myers-Smith, Gergana Daskalova, Mariana García Criado and Haydn Thomas contributed to model design and data analysis. Madelaine Anderson and Erica Zaja led manuscript writing. All authors provided critical input on drafts and final approval for publication.

## ACKNOWLEDGEMENTS

Over the ten years of this experiment, many people have contributed to its success. We would like to thank everyone that helped in the common garden over the years including Kelly Hurley, John Godlee, Megan Grabowski, Sian Williams, Sandra Angers-Blondin, Jakob Assmann, Beth Scott, Izzy Rich, Cameron Cosgrove, Matt Little, Noah Bell, Sophie Noel, Joe Boyle, Eleanor Walker, Zabrina Leslie, Clara Surprenant, Diana Jerome, Calum Hoad, Joseph Everest, Ashley Bradley, Else Radeloff and Andrew Cunliffe. We thank the Inuvialuit people, Kluane First Nation, White River First Nation and Champagne and Aishihik First Nations for their permission to work on their lands. We thank Outpost Research Station, the Kluane Lake Research Station and Qikiqtaruk-Herschel Island Territorial Park and Park Rangers for logistical support.

This research was funded by the NERC Shrub Tundra (NE/M016323/1) and Tundra Time (NE/W006448/1) projects. MA was funded by the Canadian Airborne Biodiversity Observatory Project (NSERC; #509190- 2017). EZ was funded by the Canadian Mountain Network Knowledge Hub Project. MGC was funded by the EU Horizon 2020 Research and Innovations Programme through the CHARTER project (Grant #869471).

**Data availability statement:**

Data and code are publicly available online:

# SUPPLEMENTARY MATERIALS

## Supplementary methods

### Propagation

Cuttings were collected during the growing season (July and August) over years between 2013 and 2018. Tips of cuttings were kept moist in paper towel or submerged (approaches varied depending on year) during transport from source location (alpine or Arctic site). Because the northern, Arctic site is approximately 1000 km from the common garden and the southern alpine sites are in the same region, northern cuttings had a longer transport time. Application of rooting hormone (Roots Liquid Stimulator, Wilson Control) and fertilizer (Golf Green Shrub fertilizer, 18N:8P:8K) varied by year, but within a given year all cuttings across the source sites were treated the same during planting in the garden.

### Propagation analysis

We tested for relationships between cutting size and maximum size achieved in the garden because we hypothesised there may be a positive relationship where larger cuttings may have an advantage in establishment because they can acquire resources more rapidly. Alternatively, there may be a negative relationship, where smaller cuttings perform better because they have less plant material to support while establishing roots. We used maximum size values (height and width) for the shrubs in the garden from the entire ten-year growth period in the common garden, given that some shrubs experienced die back in recent years. We included ‘source site’ as an interactive term to test how relationships varied between northern and southern source populations (Table S5).

### Trait processing

We followed a standard protocol by Laliberté (2018) for measuring specific leaf area, leaf dry matter content, and leaf area measurements. Briefly, we collected healthy leaves from the top of the shrub canopy, removed the petioles and recorded fresh mass, rehydrated mass (after twelve hours rehydration), scans of the leaves, and dried leaf mass (drying time minimum of 72 hours in a 65ºC oven). Leaf area scans were collected on a Cannon scanner (CanoScan LiDE 220) with WinFOLIA software (Régent Instruments) using the rehydrated leaves. Calculations for SLA and LDMC are outlined in Laliberté (2018). Three leaves were measured per shrub for leaf length and between six to twelve leaves were measured for SLA, LDMC, and leaf area measurements (Laliberté, 2018, Table S4).

## Supplementary Figures

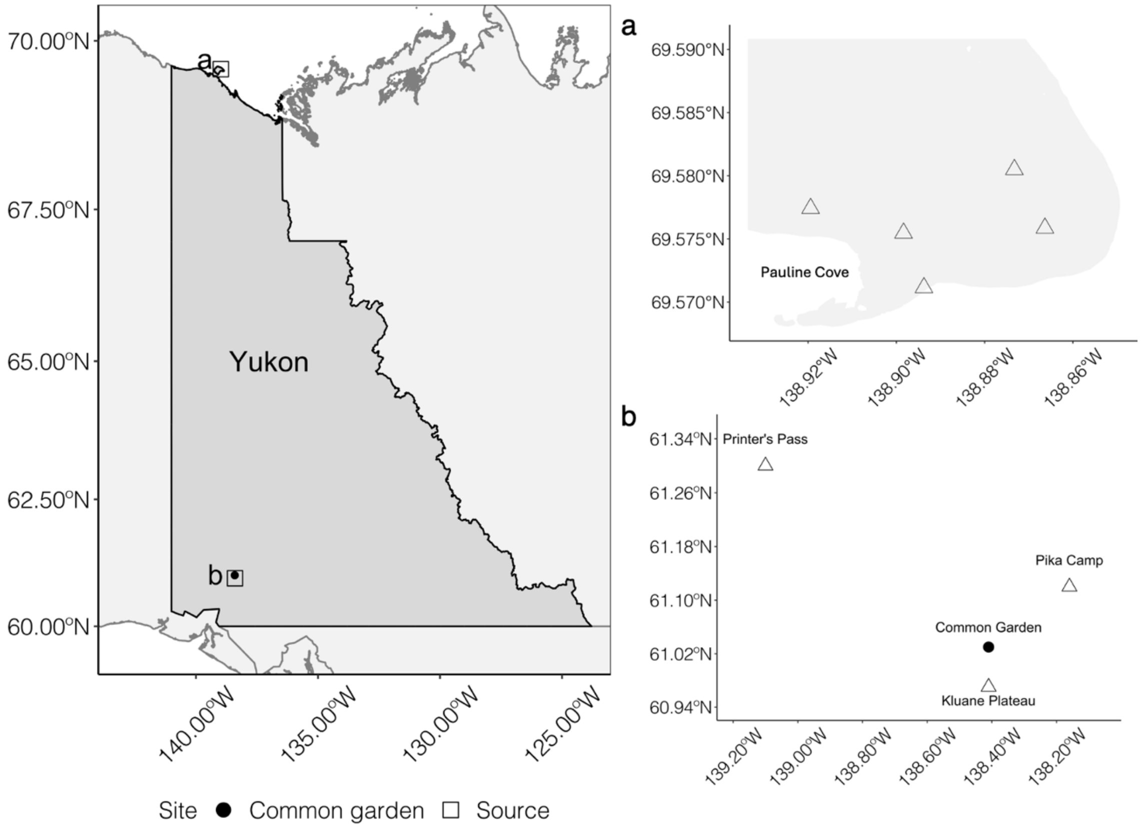

**Figure S1.** The common garden and its relative position to the southern alpine source site and northern Arctic source site. Left: map of the Yukon Territory in Canada and positions of source sites (a: Qikiqtaruk, northern source, b: alpine Kluane, southern source). Right top a) Region of Qikiqtaruk where cuttings and size, phenology, and trait measurements were collected from. Triangle icons represent areas where cuttings and/or monitoring took place between 2013-2023. Right bottom b) map of alpine Kluane sites (triangles, 1400 - 1900 m elevation) and location of common garden (circle). Cuttings were collected from areas at high elevation from Printers Pass, Pika Camp (Myers-Smith and Hik, 2018), and the Kluane Plateau. Phenology, trait and growth measurements in the field were collected on the Kluane Plateau.

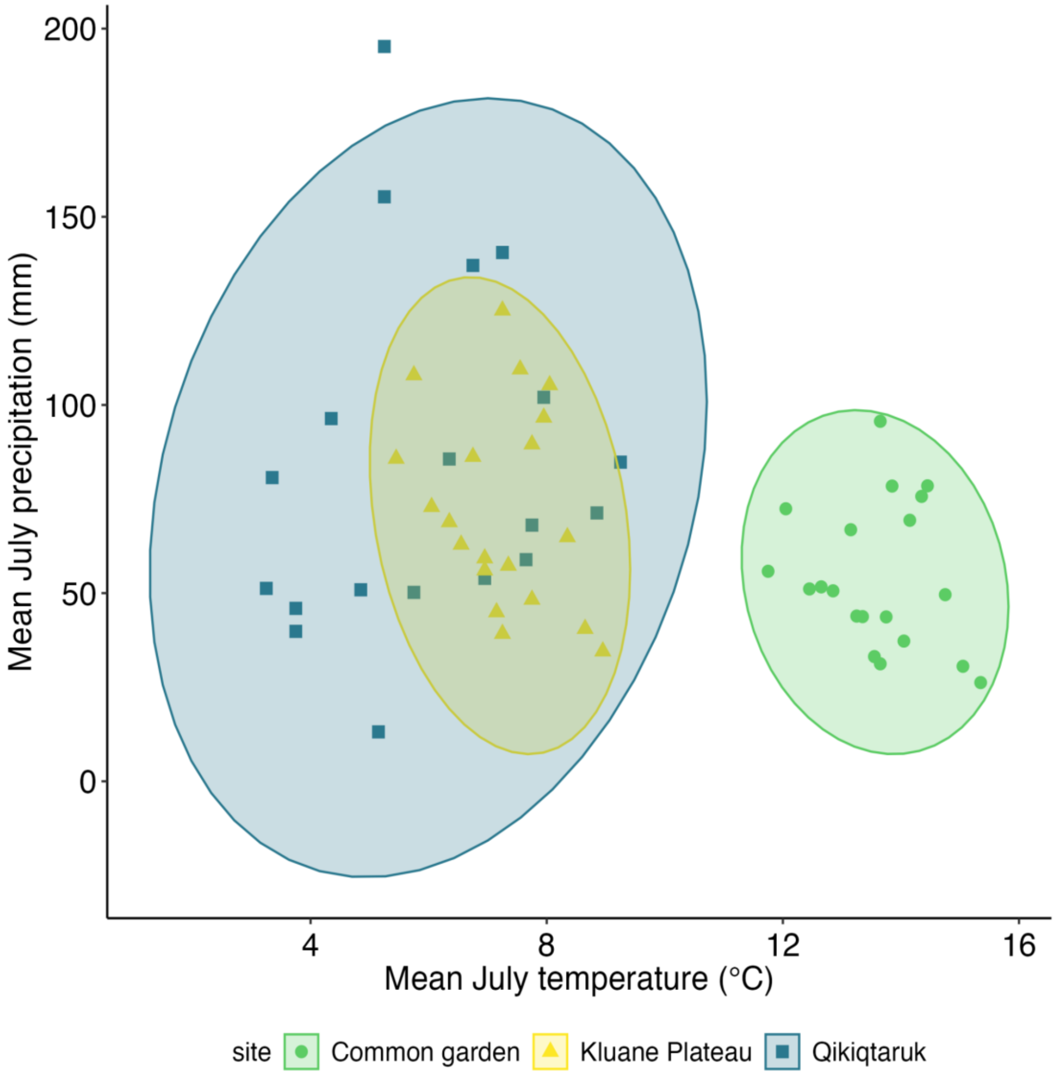

**Figure S2.** The common garden temperatures were on average 6.4 to 7.5ºC warmer, but precipitation was similar across the three sites. Mean July temperature (ºC) and precipitation (mm) in Qikiqtaruk (northern source population, squares), Kluane Plateau (southern source population, triangles) and in the common garden (circles) over 20 years (1999-2019), from CHELSA gridded climate data (Karger et al. 2017). Each data point is the yearly mean July temperature and precipitation per site. Large variation in Qikiqtaruk temperature and precipitation could be due to fog and sea ice coming and going, making the island rapidly change temperature and moisture levels.

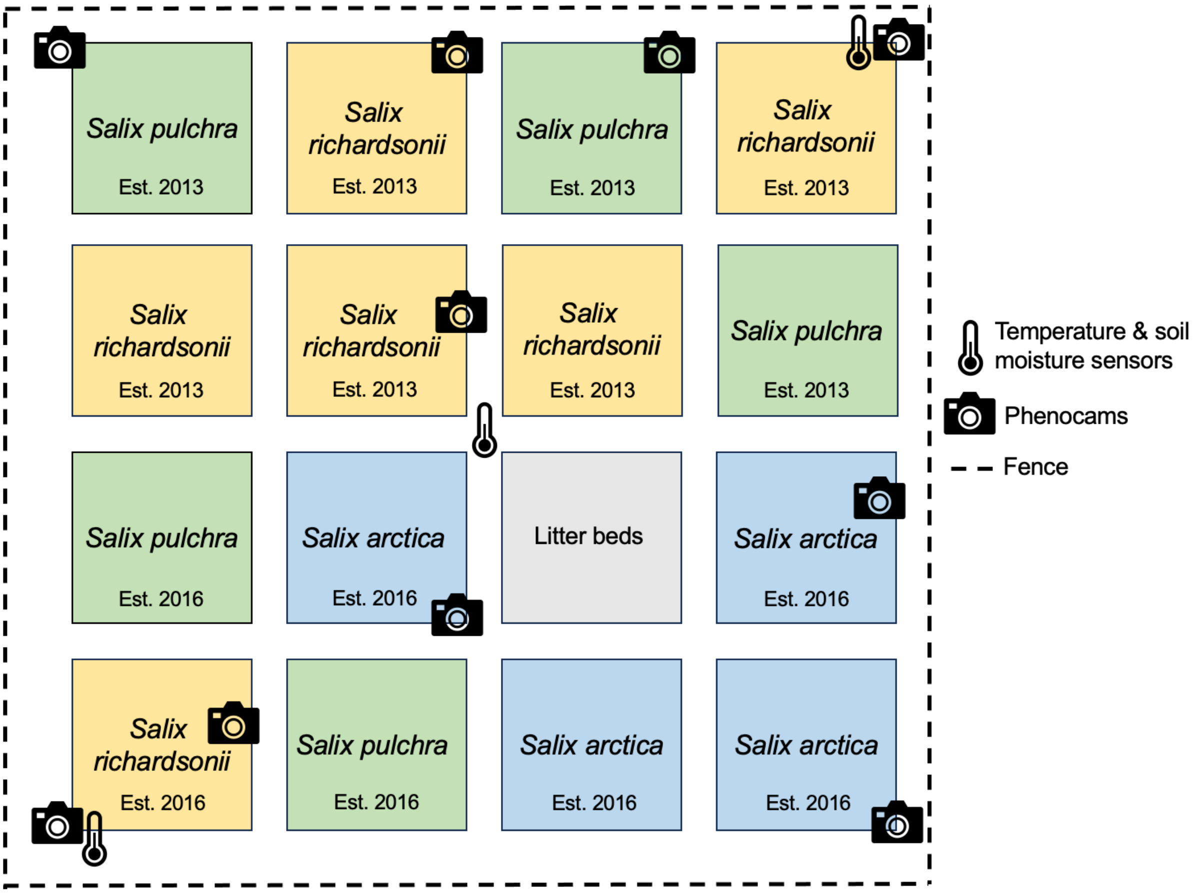

**Figure S3.** Common garden schematic with relative positions of temperature and moisture sensors and phenocams in the garden. Species and the year each garden bed was established indicated on each garden bed. Litter beds are from a separate experiment finished in 2017.

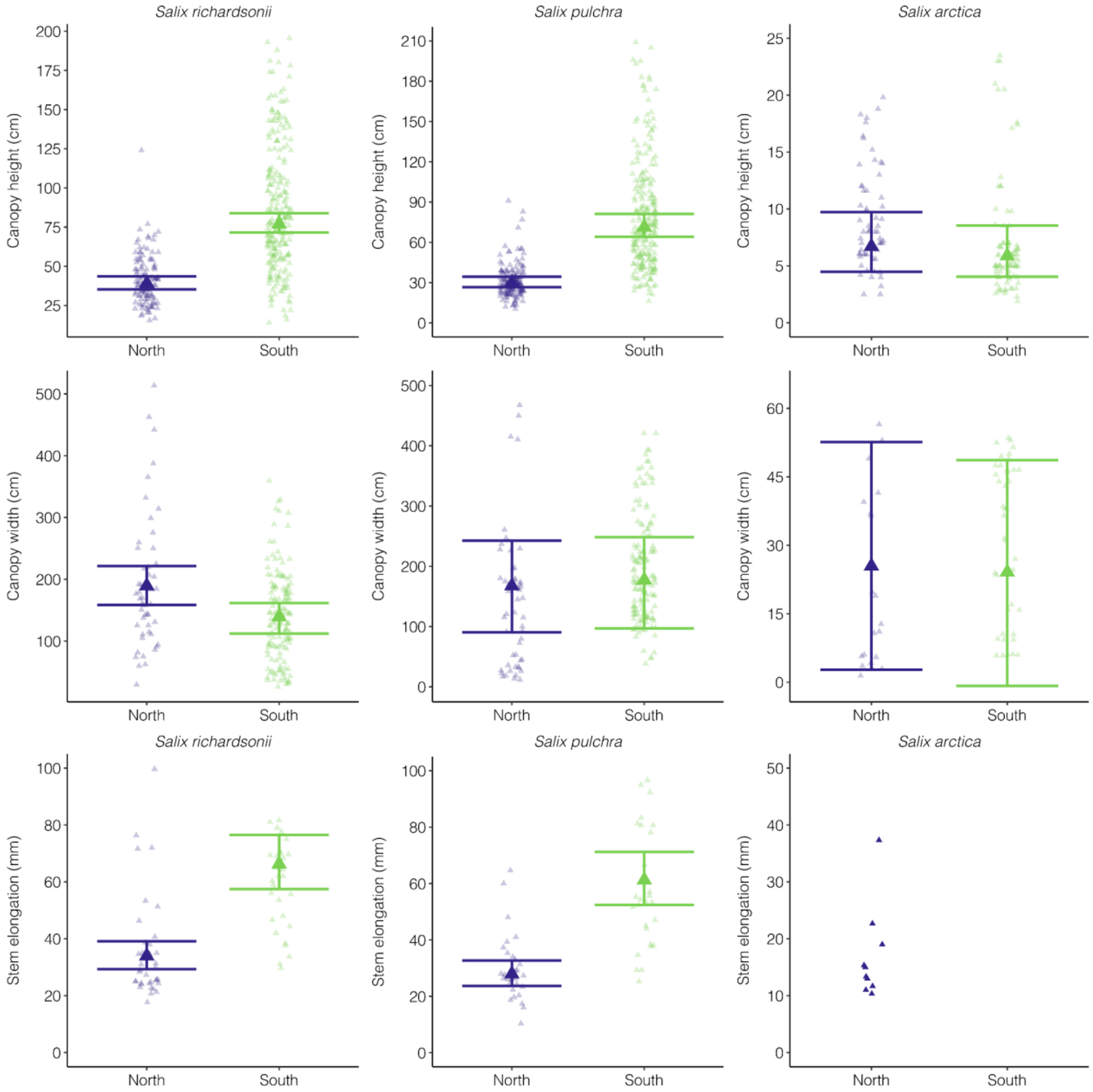

**Figure S4.** Southern source population tall willows grew faster (stem elongation) and taller but not wider in the source populations. Canopy height (top), width (middle), and stem elongation (bottom) of willow species in the source populations: Southern source (S. Source, Kluane, green), and Northern Source (N. Source, Qikiqtaruk, purple). Bayesian model outputs (point plus standard error bars) over raw log transformed data points (from all years). Only raw data shown for *S. arctica* stem elongation for reference. From left to right: *Salix richardsonii*, *Salix pulchra*, *Salix arctica.*

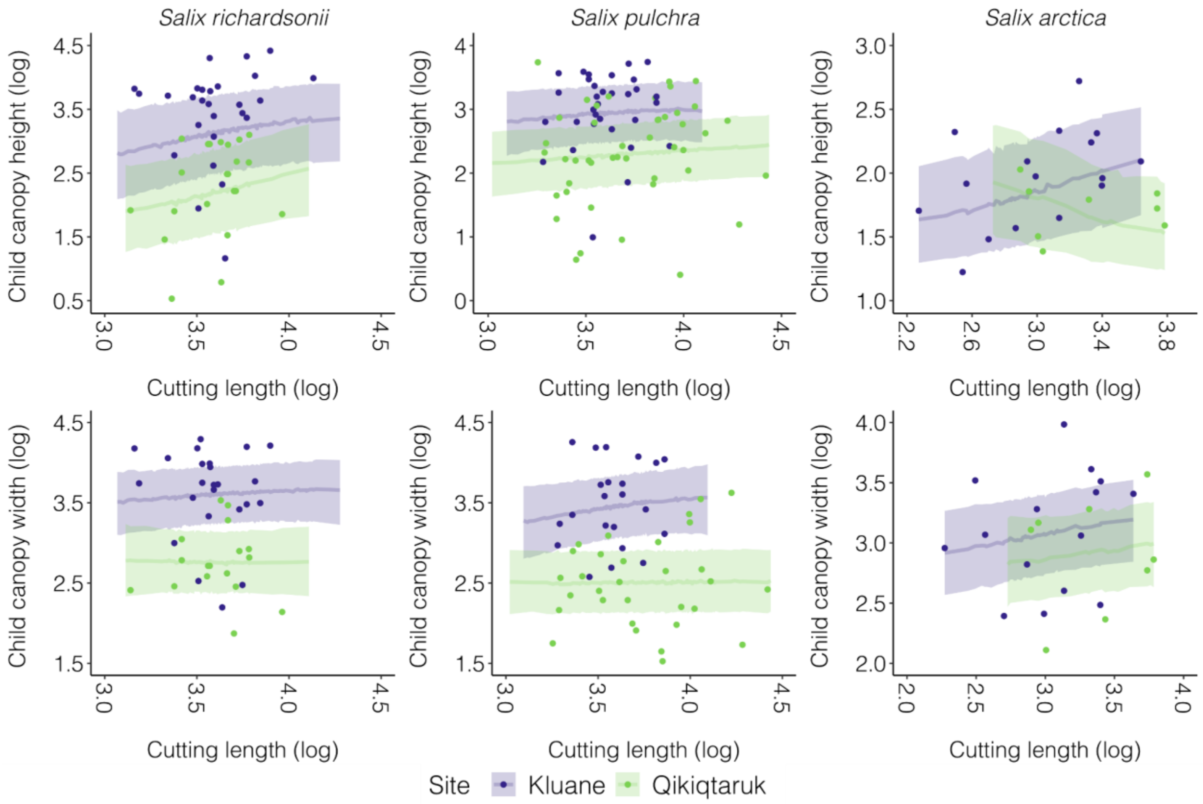

**Figure S5.** Longer cuttings did not lead to significantly larger (taller, wider) shrubs in the common garden. Top: maximum canopy height achieved by offspring in the garden by initial cutting length. Bottom: maximum canopy width achieved by offspring by initial cutting length. Raw data were measured in cm and were converted to log scale for analysis and visualisation. Bayesian model outputs (line and ribbon) over raw log transformed data points. From left to right: *Salix richardsonii*, *Salix pulchra*, *Salix arctica.*

## Supplementary Tables

Table S1: Key findings of common garden or reciprocal transplant studies focused on tundra plants.

| Study design | Species | Variables | Main findings | Citation |
|---|---|---|---|---|
| Reciprocal transplant experiment | *Eriophorum vaginatum* | Phenology, traits, growth | Northern ecotypes showed longer growing seasons in warmer conditions, but biomass and growing season length remained shorter than southern ecotypes.<br>Northern and southern ecotypes maintained timing of senescence suggesting genetic control.<br>Warming did not impact early or late season phenology. | Parker et al., 2021 |
| Revisit 30 years after snow exposure transplant (*Dryas octopetala*) and reciprocal transplant experiment (*Eriophorum vaginatum*) | *Eriophorum vaginatum* and *Dryas octopetala* | Survival, phenology | Evidence of local adaptation found for *D. octopetala*, where local individuals had greater survival rates in snow transplants after thirty years.<br>Differential survival of *E. vaginatum* found after 17 years at home sites.<br>Found no evidence that plasticity increased survival for either species. | Bennington et al., 2012 |

| | | | | |
|---|---|---|---|---|
| Field data across latitudinal range and experimental warming | *Silene acaulis* | Growth | Plants showed compensatory responses to warming across latitudinal ranges.<br>Evidence of local adaptation to climate with populations having differing temperature responses across the latitudinal gradient.<br>Warming negatively affected plants from cooler regions before negatively impacting the same species from warmer regions. | DeMarche et al., 2017 |
| Field observations at species' range edges | *Juniperus communis* | Growth, phenology | Shrubs responded plastically to warming across species range.<br>Shrubs intensified growth rates in the short Arctic growing season. | Tumajer et al., 2021 |
| Experimental warmed common garden established from seeds across latitudinal gradient | *Oxyria digyna* and *Papaver radicatum* | Growth, survival, phenology | Local individuals had higher survival and growth rates regardless of warming treatment.<br>Phenology varied by source latitude of seeds. Southern individuals leafed out and senesced later than northern individuals.<br>Differences in phenology from warming were not significant for *O. digyna*. Warming was associated with earlier leaf out and later senescence for some *P. radicatum* populations. | Bjorkman et al., 2017 |

Table S2. Research questions, variables of interest and predictions.

| **Research Questions** | **Variables** | **Predictions** |
|---|---|---|
| 1. How does shrub growth vary between southern and northern willow shrubs when grown in a warmer, common environment? | Canopy height, shrub width, stem elongation | **H1**: Southern willows grown in the garden will achieve larger sizes (taller, wider) and grow more rapidly than northern willows in the garden across all species, as seen in their respective source populations. |
| 2. How do shrub traits vary between southern and northern willow shrubs when grown in a warmer, common environment, and how do these compare to their respective source populations? | Specific leaf area (SLA), leaf dry matter content (LDMC), leaf length, leaf area | **H2.1:** Shrubs from southern and northern populations growing in the common garden will respond plastically to the warmer environment and demonstrate trait values associated with more resource acquisition strategies and less stressful environments (i.e., higher SLA, lower LDMC), relative to their southern and northern source populations.<br>**H2.2**: Shrubs from southern and northern populations will grow larger (longer leaves, greater area) leaves in the warmer environment than in their respective source populations. |
| 3. How does shrub phenology vary between southern and northern willow shrubs when grown in a warmer, common environment, compared to their respective source populations? | Timing of leaf bud burst and first leaf yellowing, growing season | **H3**: Shrubs growing in a warmer common environment will have an overall longer growing season (earlier leaf bud burst and later leaf yellowing) than in their source populations. |

**Table S3**. Number of individuals of each species and their source locations in common garden experiment as of July 2023.

| Species | Population | Year | Number of individuals |
|---|---|---|---|
| *Salix arctica* | Southern | 2016 | 7 |
| | | 2017 | 13 |
| | | 2018 | 21 |
| | | 2019 | 26 |
| | | 2020 | 26 |
| | | 2021 | 26 |
| | | 2022 | 26 |
| | | 2023 | 26 |
| *Salix arctica* | Northern | 2016 | 15 |
| | | 2017 | 20 |
| | | 2018 | 42 |
| | | 2019 | 33 |
| | | 2020 | 29 |
| | | 2021 | 26 |
| | | 2022 | 24 |
| | | 2023 | 24 |
| *Salix pulchra* | Southern | 2014 | 21 |
| | | 2015 | 20 |
| | | 2016 | 21 |
| | | 2017 | 35 |
| | | 2018 | 52 |
| | | 2019 | 56 |
| | | 2020 | 55 |
| | | 2021 | 53 |
| | | 2022 | 47 |
| | | 2023 | 47 |
| *Salix pulchra* | Northern | 2014 | 19 |
| | | 2015 | 14 |
| | | 2016 | 42 |
| | | 2017 | 50 |
| | | 2018 | 66 |
| | | 2019 | 61 |
| | | 2020 | 55 |
| | | 2021 | 49 |
| | | 2022 | 42 |
| | | 2023 | 42 |
| *Salix richardsonii* | Southern | 2014 | 15 |
| | | 2015 | 15 |
| | | 2016 | 16 |
| | | 2017 | 26 |
| | | 2018 | 42 |

|  |  |  |  |
|---|---|---|---|
|  |  | 2019 | 42 |
|  |  | 2020 | 42 |
|  |  | 2021 | 42 |
|  |  | 2022 | 38 |
|  |  | 2023 | 38 |
| *Salix richardsonii* | Northern | 2014 | 18 |
|  |  | 2015 | 14 |
|  |  | 2016 | 26 |
|  |  | 2017 | 22 |
|  |  | 2018 | 48 |
|  |  | 2019 | 43 |
|  |  | 2020 | 38 |
|  |  | 2021 | 35 |
|  |  | 2022 | 33 |
|  |  | 2023 | 31 |

**Table S4**. Shrub growth and trait measurements collected in the common garden experiment and in source populations.

| RQ | Variable | Dates measured common garden | Dates measured source populations | Description |
|---|---|---|---|---|
| 1 | Plant height (cm) | All shrubs measured since 2013 | Randomly selected shrubs in Kluane 2013-2017 and in 2021-2022; and 2014-2017, 2022 and 2022 in Qikiqtaruk. | Vertical measurement from base of shrub to highest point of canopy |
| 1 | Plant width (cm) | All shrubs measured since 2020 | Randomly selected shrubs in Kluane in 2013, 2016-2017, 2022; and in 2016-2017, 2022 in Qikiqtaruk. | Two radial measurements, one from widest point of shrub and second perpendicular to first measurement |
| 1 | Stem elongation (mm) | All shrubs measured since 2016 | Recorded for mother willow plants and some willows in wild environments, but not consistently over time and at different times of the summer, so we did not use these data in this manuscript | Mean length of three terminal regions of new growth from the season, measured from growth scar from previous years |
| 2 | Leaf length (mm) | All shrubs measured since 2013 | Randomly selected shrubs on KP / Pika Camp in 2017 and 2022; and in 2017 and 2022 in Qikiqtaruk. | Mean length of three longest leaves |
| 2 | Specific leaf area ($mm^2 mg^{-1}$) | Subset of shrubs sampled in summers 2017, 2021, 2022 | Subset of shrubs on KP summers 2014, 2015, 2021, 2023; and on Qikiqtaruk in 2014, 2015, 2022, 2023 | Ratio of leaf area to total leaf dry mass. Followed protocol described by Laliberté (2018) |
| 2 | Leaf matter dry content ($mg\ g^{-1}$) | Subset of shrubs sampled in summers 2017, 2021, 2022 | Subset of shrubs on KP summers 2014, 2015, 2021, 2023; and on Qikiqtaruk in 2014, 2015, 2022, 2023 | Ratio of leaf dry mass to leaf fresh mass. Followed protocol described by Laliberté (2018) |

| | | | | |
|---|---|---|---|---|
| 2 | Leaf area (cm$^2$) | Subset of shrubs sampled in summers 2017, 2021, 2022 | Subset of shrubs on KP summers 2014, 2015, 2021, 2023; and on Qikiqtaruk in 2014, 2015, 2022, 2023 | Total area of fresh leaf. Followed protocol described by Laliberté (2018) |
| 3 | Leaf bud burst and yellowing | Cameras in the garden capture daily images with phenocams extraction in years 2021, 2022, 2023 | Cameras capture daily images with phenocams extraction in 2021-2023 for KP and 2016-2023 for Qikiqtaruk. Long term phenological monitoring plots of *S. arctica* on Qikiqtaruk (Myers-Smith *et al.*, 2019). | Day of the year of leaf bud burst and first yellow leaf. |
| 3 | Growing season length | Data from phenocams images (above) leaf bud burst and leaf yellowing. | Data from phenocams images (above) capture leaf bud burst and leaf yellowing. | Day of the year first leaf yellowing – day of the year leaf bud burst |

Table S5: List of analyses structures for research questions and testing for propagation effects. Population refers to northern source, northern in the garden, southern source and southern in the garden. Sample age refers to year of measurement – year planted in common garden.

1. Did longer cuttings lead to larger (taller, wider) shrubs in the common garden?
    a. Bayesian linear model for each species: log(*offspring size) ~ log(cutting length) * site*

2. How does shrub size (height, width, stem elongation) differ in source populations?
    a. Hierarchical Bayesian linear model for each species (sample year was included as random effect when more than three years of data were available): *growth variable ~ source site + (1/Sample_Year)*

3. How does shrub growth vary between southern and northern willow shrubs when grown in a warmer, common environment?
    a. Hierarchical Bayesian linear model for maximum width achieved in common garden for each species: log(*maximum width) ~ garden population + (1|Sample_age)*
    b. Hierarchical Bayesian linear model for growth (height, stem elongation) over time (up to 10 years) in common garden for each species: log(*Growth variable) ~ Sample_age*population + (Sample_age|SampleID_standard)*

4. How do shrub traits vary between southern and northern willow shrubs when grown in a warmer, common environment, and how do these compare to their respective source populations?
    a. Hierarchical Bayesian linear models for specific leaf area, leaf dry matter content, and leaf area trait values measured in four populations for each species: *trait variable ~ population + (1|year).* Specific leaf area data were log transformed before analysis to meet Gaussian distribution.
    *b.* Hierarchical Bayesian linear models for leaf length (measured repeatedly each year in common garden) measured in four populations for each species: *trait variable ~ population + (1|year) + (1|Sample_ID)*
*5.* How does shrub phenology vary between southern and northern willow shrubs when grown in a warmer, common environment, compared to their respective source populations?
    a. Hierarchical Bayesian linear model for each phenology variable (leaf bud burst, leaf yellowing for each species: *Scaled phenology variable ~ population + (1|Year).*

Table S6 Statistical results for propagation analyses. Outputs of Bayesian linear models relating maximum shrub height and width (separate models) with cutting length. Data were log transformed before analysis.

Shrub height and cutting length. *S. richardsonii* N = 54, *S. pulchra* N = 81, *S. arctica* N = 31.

|  | **Species** | **Estimate (log)** | **Error** | **L95% CI** | **U95% CI** | **Rhat** | **Bulk ESS** | **Tail ESS** | **Effect** |
|---|---|---|---|---|---|---|---|---|---|
| Intercept | *Salix richardsonii* | 0.51 | 3.41 | -6.26 | 7.08 | 1.00 | 2751 | 3410 | fixed |
| log(Cutting length) |  | 0.77 | 0.95 | -1.05 | 2.65 | 1.00 | 2745 | 3354 | fixed |
| Site: Qikiqtaruk |  | -1.53 | 5.37 | -12.50 | 8.93 | 1.00 | 2113 | 3065 | fixed |
| log(Cutting length) * Site |  | 0.10 | 1.49 | -2.80 | 3.12 | 1.00 | 2110 | 3056 | fixed |
| Sigma |  | 1.05 | 0.11 | 0.87 | 1.29 | 1.00 | 3612 | 3028 | residual |
| Intercept | *Salix pulchra* | 2.07 | 2.82 | -3.39 | 7.51 | 1.00 | 1484 | 2319 | fixed |
| log(Cutting length) |  | 0.27 | 0.78 | -1.25 | 1.79 | 1.00 | 1492 | 2348 | fixed |
| Site: Qikiqtaruk |  | -0.55 | 2.90 | -6.04 | 5.13 | 1.00 | 1514 | 2507 | fixed |
| log(Cutting length) * Site |  | -0.06 | 0.80 | -1.62 | 1.47 | 1.00 | 1517 | 2428 | fixed |
| Sigma |  | 0.72 | 0.06 | 0.62 | 0.85 | 1.00 | 2712 | 2949 | residual |
| Intercept | *Salix arctica* | -0.73 | 1.58 | -3.91 | 2.40 | 1.00 | 2641 | 3306 | fixed |
| log(Cutting length) |  | 0.81 | 0.53 | -0.22 | 1.88 | 1.00 | 2647 | 3189 | fixed |
| Site: Qikiqtaruk |  | 5.38 | 2.99 | -0.48 | 11.25 | 1.00 | 1850 | 2214 | fixed |
| log(Cutting length) * Site |  | -1.84 | 0.91 | -3.66 | -0.06 | 1.00 | 1829 | 2394 | fixed |
| Sigma |  | 0.85 | 0.12 | 0.65 | 1.12 | 1.00 | 3199 | 3276 | residual |

Shrub width and cutting length, *S. richardsonii* N = 42, *S. pulchra* N = 57, *S. arctica* N = 23

| | **Species** | **Estimate (log)** | **Error** | **L95% CI** | **U95% CI** | **Rhat** | **Bulk ESS** | **Tail ESS** | **Effect** |
|---|---|---|---|---|---|---|---|---|---|
| Intercept | *Salix richardsonii* | 3.00 | 1.97 | -0.75 | 6.95 | 1.00 | 2624 | 3076 | fixed |
| log(Cutting length) | | 0.18 | 0.55 | -0.91 | 1.22 | 1.00 | 2641 | 3073 | fixed |
| Site:Qikiqtaruk | | -0.18 | 3.39 | -6.90 | 6.42 | 1.00 | 2236 | 2614 | fixed |
| log(Cutting length) * Site | | -0.20 | 0.94 | -2.02 | 1.65 | 1.00 | 2238 | 2585 | fixed |
| Sigma | | 0.56 | 0.07 | 0.45 | 0.71 | 1.00 | 3212 | 3337 | residual |
| Intercept | *Salix pulchra* | 2.14 | 2.79 | -3.27 | 7.73 | 1.00 | 1701 | 1884 | fixed |
| log(Cutting length) | | 0.38 | 0.78 | -1.19 | 1.90 | 1.00 | 1708 | 1969 | fixed |
| Site:Qikiqtaruk | | 0.24 | 2.86 | -5.48 | 5.82 | 1.00 | 1683 | 2031 | fixed |
| log(Cutting length) * Site | | -0.35 | 0.79 | -1.90 | 1.23 | 1.00 | 1685 | 1959 | fixed |
| Sigma | | 0.60 | 0.06 | 0.50 | 0.74 | 1.00 | 2881 | 2942 | residual |
| Intercept | *Salix arctica* | 2.28 | 1.12 | 0.19 | 4.49 | 1.00 | 2752 | 3298 | fixed |
| log(Cutting length) | | 0.27 | 0.37 | -0.46 | 0.96 | 1.00 | 2759 | 3613 | fixed |
| Site:Qikiqtaruk | | -0.08 | 2.11 | -4.33 | 3.97 | 1.00 | 2014 | 2656 | fixed |
| log(Cutting length) * Site | | -0.06 | 0.65 | -1.31 | 1.26 | 1.00 | 1965 | 2696 | fixed |
| Sigma | | 0.53 | 0.10 | 0.39 | 0.75 | 1.00 | 3098 | 3298 | residual |

Table S7. Statistical results for Bayesian models comparing source populations shrub canopy height, stem elongation and width. Data were log-transformed for analysis, outputs presented in log units and back transformed for clarity.

Canopy height *S. richardsonii* N = 361, *S. pulchra* N = 371, *S. arctica* N = 150.

| | **Species** | **Est. (log)** | **Error** | **L95% CI log** | **U95% CI log** | **Est.** | **L95% CI** | **U95% CI** | **Rhat** | **Bulk ESS** | **Tail ESS** | **Effect** |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Intercept | | 4.35 | 0.04 | 4.27 | 4.43 | 77.11 | 71.58 | 83.94 | 1.00 | 3620 | 3020 | fixed |
| Northern Source | *Salix richardsonii* | -0.68 | 0.05 | -0.79 | -0.57 | 39.07 | 32.61 | 47.31 | 1.00 | 5809 | 4124 | fixed |
| Sample year | | 0.05 | 0.05 | 0.00 | 0.17 | 1.05 | 1.00 | 1.18 | 1.00 | 1763 | 2516 | random |
| Sigma | | 0.46 | 0.02 | 0.43 | 0.50 | 1.59 | 1.54 | 1.65 | 1.00 | 6168 | 4574 | residual |
| Intercept | *Salix pulchra* | 4.27 | 0.06 | 4.16 | 4.40 | 71.53 | 64.19 | 81.11 | 1.00 | 1885 | 1660 | fixed |
| Northern Source | | -0.87 | 0.05 | -0.98 | -0.77 | 29.88 | 24.19 | 37.59 | 1.00 | 4424 | 4420 | fixed |
| Sample year | | 0.10 | 0.08 | 0.01 | 0.30 | 1.10 | 1.01 | 1.35 | 1.00 | 1084 | 2110 | random |
| Sigma | | 0.47 | 0.02 | 0.44 | 0.51 | 1.60 | 1.55 | 1.66 | 1.00 | 4610 | 4145 | residual |
| Intercept | | 1.77 | 0.19 | 1.40 | 2.14 | 5.90 | 4.05 | 8.53 | 1.00 | 1565 | 1841 | fixed |
| Northern Source | *Salix arctica* | 0.13 | 0.10 | -0.07 | 0.33 | 6.69 | 3.76 | 11.82 | 1.00 | 4247 | 3587 | fixed |
| Sample year | | 0.41 | 0.21 | 0.16 | 0.96 | 1.51 | 1.18 | 2.61 | 1.00 | 1254 | 1700 | random |
| Sigma | | 0.49 | 0.03 | 0.44 | 0.56 | 1.64 | 1.55 | 1.75 | 1.00 | 3791 | 3545 | residual |

Stem elongation *S. richardsonii N = 76, S. pulchra N = 61.*

| | **Species** | **Est. (log)** | **Error** | **L95% CI log** | **U95% CI log** | **Estimate** | **L95% CI** | **U95% CI** | **Rhat** | **Bulk ESS** | **Tail ESS** | **Effect** |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Intercept | | 4.19 | 0.07 | 4.05 | 4.34 | 66.34 | 57.45 | 76.51 | 1.00 | 4338 | 3747 | fixed |
| Northern Source | *Salix richardsonii* | -0.67 | 0.10 | -0.87 | -0.47 | 33.92 | 24.07 | 48.01 | 1.00 | 4182 | 3800 | fixed |
| Sigma | | 0.46 | 0.04 | 0.39 | 0.54 | 1.58 | 1.48 | 1.72 | 1.00 | 4866 | 3511 | residual |
| Intercept | *Salix pulchra* | 4.11 | 0.08 | 3.96 | 4.27 | 61.23 | 52.42 | 71.25 | 1.00 | 8853 | 6751 | fixed |
| Northern Source | | -0.79 | 0.11 | -1.01 | -0.57 | 27.87 | 19.10 | 40.44 | 1.00 | 8563 | 6594 | fixed |
| Sigma | | 0.44 | 0.04 | 0.37 | 0.53 | 1.55 | 1.44 | 1.70 | 1.00 | 7882 | 6525 | residual |

Canopy width *S. richardsonii* N = 193, *S. pulchra* N = 169, *S. arctica* N = 60.

| | **Species** | **Estimate** | **Error** | **L95% CI** | **U95% CI** | **Rhat** | **Bulk ESS** | **Tail ESS** | **Effect** |
|---|---|---|---|---|---|---|---|---|---|
| Intercept | *Salix richardsonii* | 139.0 | 12.8 | 110.81 | 161.5 | 1.00 | 2904 | 2628 | fixed |
| Northern source | | 50.7 | 14.0 | 24.41 | 78.7 | 1.00 | 5634 | 4427 | fixed |
| Sample year | | 15.6 | 15.4 | 0.54 | 56.3 | 1.00 | 1623 | 2769 | random |
| Sigma | | 83.0 | 4.3 | 75.07 | 92.0 | 1.00 | 5469 | 3429 | residual |
| Intercept | *Salix pulchra* | 176.5 | 37.2 | 97.0 | 248.3 | 1.00 | 2222 | 2335 | fixed |
| Northern source | | -9.3 | 18.1 | -44.6 | 25.9 | 1.00 | 5987 | 4316 | fixed |
| Sample year | | 77.1 | 35.8 | 32.5 | 167.4 | 1.00 | 1835 | 2904 | random |
| Sigma | | 104.9 | 5.3 | 95.3 | 115.7 | 1.00 | 6298 | 3762 | residual |
| Intercept | *Salix arctica* | 24.4 | 11.9 | -0.3 | 49.4 | 1.00 | 2013 | 2630 | fixed |
| Northern source | | 1.7 | 6.2 | -10.4 | 13.9 | 1.00 | 4221 | 3492 | fixed |
| Sample year | | 20.8 | 12.7 | 5.53 | 51.9 | 1.00 | 1910 | 2435 | random |
| Sigma | | 16.2 | 1.6 | 13.51 | 19.7 | 1.00 | 5207 | 4235 | residual |

Table S8 Statistical results for the Bayesian models comparing canopy height and stem elongation over time (sample age) of southern and northern willows in the common garden. Estimates and 95% credible intervals presented in log scale and back transformed for clarity.

Canopy height over time *S. richardsonii* N = 601, *S. pulchra* N = 819, *S. arctica* N = 326.

| | **Species** | **Est. (log)** | **Error (log)** | **L95% CI (log)** | **U95% CI (log)** | **Rhat** | **Bulk ESS** | **Tail ESS** | **Est.** | **L95% CI** | **U95% CI** | **Effect** |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Intercept | *Salix richardsonii* | 1.5 | 0.2 | 1.1 | 1.8 | 1.00 | 1415 | 2501 | 4.3 | 3.1 | 6.0 | fixed |
| Sample age | | 0.1 | 0.0 | 0.1 | 0.1 | 1.00 | 1749 | 3739 | 1.1 | 1.1 | 1.2 | fixed |
| Southern population | | 1.1 | 0.2 | 0.6 | 1.5 | 1.00 | 1388 | 3024 | 2.9 | 1.8 | 4.5 | fixed |
| Sample age:Southern population | | 0.1 | 0.0 | 0.0 | 0.2 | 1.00 | 1700 | 3593 | 1.1 | 1.0 | 1.2 | fixed |
| Random intercept | | 1.1 | 0.1 | 1.0 | 1.3 | 1.00 | 2522 | 3967 | 3.1 | 2.7 | 3.8 | random |
| sd(Sample age) | | 0.1 | 0.0 | 0.1 | 0.2 | 1.00 | 2302 | 3784 | 1.2 | 1.1 | 1.2 | random |
| cor(Intercept, Sample age) | | -0.9 | 0.0 | -0.9 | -0.8 | 1.00 | 2627 | 5709 | 0.4 | 0.4 | 0.4 | random |
| sigma | | 0.3 | 0.0 | 0.3 | 0.3 | 1.00 | 6925 | 8534 | 1.4 | 1.3 | 1.4 | residual |
| Intercept | *Salix pulchra* | 2.0 | 0.1 | 1.7 | 2.2 | 1.00 | 2746 | 4835 | 7.1 | 5.6 | 9.0 | fixed |
| Sample age | | 0.0 | 0.0 | 0.0 | 0.0 | 1.00 | 3411 | 5868 | 1.0 | 1.0 | 1.0 | fixed |
| Southern population | | 1.0 | 0.2 | 0.7 | 1.3 | 1.00 | 2764 | 4713 | 2.7 | 1.9 | 3.8 | fixed |
| Sample age:Southern population | | 0.0 | 0.0 | 0.0 | 0.1 | 1.00 | 3266 | 4896 | 1.0 | 1.0 | 1.1 | fixed |
| Random intercept | | 0.9 | 0.1 | 0.8 | 1.1 | 1.00 | 3586 | 6445 | 2.5 | 2.2 | 2.9 | random |
| sd(Sample age) | | 0.1 | 0.0 | 0.1 | 0.1 | 1.00 | 2653 | 4782 | 1.1 | 1.1 | 1.2 | random |
| cor(Intercept, Sample age) | | -0.8 | 0.1 | -0.8 | -0.6 | 1.00 | 3874 | 7004 | 0.5 | 0.4 | 0.5 | random |
| sigma | | 0.3 | 0.0 | 0.3 | 0.4 | 1.00 | 7947 | 8370 | 1.4 | 1.4 | 1.4 | residual |
| Intercept | *Salix arctica* | 0.5 | 0.1 | 0.3 | 0.8 | 1.00 | 5049 | 5681 | 1.7 | 1.3 | 2.1 | fixed |
| Sample age | | 0.1 | 0.0 | 0.1 | 0.2 | 1.00 | 7328 | 8185 | 1.1 | 1.1 | 1.2 | fixed |
| Southern population | | 0.0 | 0.2 | -0.3 | 0.3 | 1.00 | 4795 | 6370 | 1.0 | 0.7 | 1.4 | fixed |
| Sample age:Southern population | | 0.0 | 0.0 | 0.0 | 0.1 | 1.00 | 6664 | 6966 | 1.0 | 1.0 | 1.1 | fixed |
| Random intercept | | 0.5 | 0.1 | 0.4 | 0.7 | 1.00 | 3053 | 4756 | 1.7 | 1.5 | 2.0 | random |
| sd(Sample age) | | 0.0 | 0.0 | 0.0 | 0.1 | 1.00 | 1988 | 2717 | 1.1 | 1.0 | 1.1 | random |
| cor(Intercept, Sample age) | | -0.8 | 0.2 | -1.0 | -0.2 | 1.00 | 5340 | 4585 | 0.5 | 0.4 | 0.8 | random |
| sigma | | 0.4 | 0.0 | 0.4 | 0.5 | 1.00 | 5303 | 7752 | 1.5 | 1.5 | 1.6 | residual |

**Stem elongation over time.** *S. richardsonii* N = 526, *S. pulchra* N = 742, *S. arctica* N = 272.

| | Species | Est. (log) | Error (log) | L95% CI (log) | U95% CI (log) | Rhat | Bulk ESS | Tail ESS | Est. | L95% CI | U95% CI | Effect |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Intercept | *Salix richardsonii* | 3 | 0 | 3 | 4 | 1.00 | 3945 | 5862 | 24 | 16 | 36 | fixed |
| Sample age | | 0 | 0 | 0 | 0 | 1.00 | 3555 | 5935 | 1 | 1 | 1 | fixed |
| Southern population | | 1 | 0 | 1 | 2 | 1.00 | 3500 | 5633 | 4 | 2 | 6 | fixed |
| Sample age: Southern population | | 0 | 0 | 0 | 0 | 1.00 | 3491 | 5793 | 1 | 1 | 1 | fixed |
| Random intercept | | 1 | 0 | 1 | 1 | 1.00 | 4016 | 6815 | 3 | 2 | 4 | random |
| sd(Sample age) | | 0 | 0 | 0 | 0 | 1.00 | 2054 | 3936 | 1 | 1 | 1 | random |
| cor(Intercept, Sample age) | | -1 | 0 | -1 | -1 | 1.00 | 3760 | 6405 | 0 | 0 | 1 | random |
| sigma | | 1 | 0 | 1 | 1 | 1.00 | 6607 | 8267 | 2 | 2 | 2 | residual |
| Intercept | *Salix pulchra* | 2 | 0 | 2 | 3 | 1.00 | 7010 | 8729 | 11 | 8 | 16 | fixed |
| Sample age | | 0 | 0 | 0 | 0 | 1.00 | 6293 | 8085 | 1 | 1 | 1 | fixed |
| Southern population | | 1 | 0 | 1 | 1 | 1.00 | 6855 | 7459 | 3 | 2 | 4 | fixed |
| Sample age:Southern population | | 0 | 0 | 0 | 0 | 1.00 | 5975 | 6804 | 1 | 1 | 1 | fixed |
| Random intercept | | 1 | 0 | 1 | 1 | 1.00 | 2564 | 3556 | 2 | 2 | 3 | random |
| sd(Sample age) | | 0 | 0 | 0 | 0 | 1.00 | 1902 | 2536 | 1 | 1 | 1 | random |
| cor(Intercept, Sample age) | | -1 | 0 | -1 | -1 | 1.00 | 3019 | 3784 | 0 | 0 | 1 | random |
| Sigma | | 1 | 0 | 1 | 1 | 1.00 | 7036 | 8295 | 2 | 2 | 3 | residual |
| Intercept | *Salix arctica* | 1 | 0 | 1 | 2 | 1.00 | 6628 | 7784 | 4 | 3 | 5 | fixed |
| Sample age | | 0 | 0 | 0 | 0 | 1.00 | 6551 | 7766 | 1 | 1 | 1 | fixed |
| Southern population | | 0 | 0 | 0 | 1 | 1.00 | 5755 | 7241 | 1 | 1 | 2 | fixed |
| Sample age:Southern population | | 0 | 0 | 0 | 0 | 1.00 | 5797 | 6523 | 1 | 1 | 1 | fixed |
| Random intercept | | 0 | 0 | 0 | 1 | 1.00 | 4150 | 4200 | 1 | 1 | 2 | random |
| sd(Sample age) | | 0 | 0 | 0 | 0 | 1.01 | 762 | 1696 | 1 | 1 | 1 | random |
| cor(Intercept, Sample age) | | 0 | 0 | -1 | 1 | 1.00 | 1621 | 2338 | 1 | 1 | 3 | random |
| sigma | | 1 | 0 | 0 | 1 | 1.00 | 5179 | 7629 | 2 | 2 | 2 | residual |

Table S9: Statistical results for the hierarchical Bayesian models comparing maximum widths achieved by northern and southern willows in the common garden. Estimates and 95% credible intervals presented in log scale. *S. richardsonii* N = 78, *S. pulchra* N = 109, *S. arctica* N = 53.

| | **Species** | **Est. (log)** | **Error** | **L95% CI log** | **U95% CI log** | **Estimat** | **L95% CI** | **U95% CI** | **Rhat** | **Bulk ESS** | **Tail ESS** | **Effect** |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Intercept | *Salix richardsonii* | 2.63 | 0.12 | 2.40 | 2.87 | 13.91 | 11.01 | 17.60 | 1.00 | 9058 | 7099 | fixed |
| Southern Garden | | 1.36 | 0.16 | 1.05 | 1.67 | 53.92 | 31.37 | 93.94 | 1.00 | 8761 | 6037 | fixed |
| Sigma | | 0.70 | 0.06 | 0.60 | 0.82 | 2.02 | 1.82 | 2.28 | 1.00 | 8755 | 7162 | residual |
| Intercept | *Salix pulchra* | 2.36 | 0.10 | 2.16 | 2.55 | 10.56 | 8.71 | 12.87 | 1.00 | 8657 | 7340 | fixed |
| Southern Garden | | 1.23 | 0.14 | 0.95 | 1.51 | 36.26 | 22.64 | 58.47 | 1.00 | 8801 | 7270 | fixed |
| Sigma | | 0.74 | 0.05 | 0.64 | 0.85 | 2.09 | 1.90 | 2.33 | 1.00 | 8849 | 7259 | residual |
| Intercept | *Salix arctica* | 2.80 | 0.11 | 2.58 | 3.02 | 16.51 | 13.24 | 20.56 | 1.00 | 8008 | 6958 | fixed |
| Southern Garden | | 0.11 | 0.16 | -0.20 | 0.42 | 18.35 | 10.79 | 31.19 | 1.00 | 8300 | 7117 | fixed |
| Sigma | | 0.57 | 0.06 | 0.47 | 0.70 | 1.78 | 1.61 | 2.02 | 1.00 | 8536 | 6033 | residual |

Table S10 Statistical results for Bayesian models comparing day of year leaf bud burst and day of year first leaf yellowing across four populations per species. Data were scaled to be centered on zero before analyses and we present outputs in scaled and unscaled units for clarity.

Leaf bud burst *S. richardsonii* N = 40, *S. pulchra* N = 36, *S. arctica* N = 173.

| | **Species** | **Est. (scaled)** | **Error** | **L95% CI scaled** | **U95% CI scaled** | **Rhat** | **Bulk ESS** | **Tail ESS** | **Est.** | **L95% CI** | **U95% CI** | **Effect** |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Northern Garden | *Salix richardsonii* | -9 | 2 | -13 | -5 | 1.00 | 2198 | 1788 | 137 | 133 | 141 | fixed |
| Northern Source | | 33 | 3 | 26 | 40 | 1.00 | 4420 | 4036 | 170 | 159 | 181 | fixed |
| Southern Garden | | 1 | 2 | -3 | 5 | 1.00 | 4019 | 4320 | 138 | 130 | 146 | fixed |
| Southern Source | | 33 | 2 | 28 | 38 | 1.00 | 4202 | 3910 | 170 | 161 | 179 | fixed |
| Year | | 2 | 2 | 0 | 6 | 1.00 | 1596 | 1948 | 148 | 146 | 152 | random |
| Sigma | | 5 | 1 | 4 | 6 | 1.00 | 4461 | 3908 | 151 | 150 | 153 | residual |
| Northern Garden | *Salix pulchra* | -11 | 2 | -16 | -7 | 1.00 | 2250 | 2983 | 137 | 132 | 141 | fixed |
| Northern Source | | 32 | 3 | 27 | 37 | 1.00 | 4024 | 3993 | 169 | 159 | 179 | fixed |
| Southern Garden | | 3 | 2 | 0 | 6 | 1.00 | 4792 | 4150 | 140 | 132 | 147 | fixed |
| Southern Source | | 35 | 2 | 31 | 40 | 1.00 | 4820 | 4360 | 172 | 163 | 181 | fixed |
| Year | | 3 | 2 | 0 | 8 | 1.00 | 1191 | 1626 | 151 | 148 | 156 | random |
| Sigma | | 4 | 1 | 3 | 5 | 1.00 | 3549 | 4356 | 152 | 151 | 153 | residual |
| Northern Garden | *Salix arctica* | -31 | 5 | -41 | -20 | 1.00 | 1761 | 2493 | 125 | 114 | 136 | fixed |
| Northern Source | | 33 | 3 | 26 | 39 | 1.00 | 3472 | 3413 | 158 | 140 | 175 | fixed |
| Southern Garden | | 6 | 4 | -1 | 14 | 1.00 | 3479 | 3597 | 131 | 113 | 150 | fixed |
| Year | | 14 | 4 | 8 | 23 | 1.00 | 1377 | 2702 | 169 | 164 | 178 | random |
| Sigma | | 7 | 0 | 6 | 7 | 1.00 | 4422 | 3581 | 162 | 161 | 163 | residual |

Leaf yellowing *S. richardsonii* N = 78, *S. pulchra* N = 49, *S. arctica* N = 154.

| | **Species** | **Est. (scaled)** | **Error** | **L95% CI scaled** | **U95% CI scaled** | **Rhat** | **Bulk ESS** | **Tail ESS** | **Est.** | **L95% CI** | **U95% CI** | **Effect** |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Northern Garden | *Salix richardsonii* | -27 | 5 | -36 | -17 | 1.00 | 2773 | 2987 | 185 | 176 | 195 | fixed |
| Northern Source | | 24 | 6 | 11 | 36 | 1.00 | 4549 | 4668 | 209 | 188 | 231 | fixed |
| Southern Garden | | 40 | 4 | 31 | 49 | 1.00 | 3947 | 4282 | 225 | 207 | 244 | fixed |
| Southern Source | | 33 | 5 | 23 | 44 | 1.00 | 4176 | 3839 | 218 | 199 | 239 | fixed |
| Year | | 5 | 5 | 0 | 17 | 1.00 | 2020 | 2188 | 217 | 213 | 230 | random |

|  |  |  |  |  |  |  |  |  |  |  |  |  |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Sigma |  | 15 | 1 | 13 | 18 | 1.00 | 5125 | 4078 | 228 | 226 | 231 | residual |
| Northern Garden | *Salix pulchra* | -13 | 5 | -24 | -2 | 1.00 | 2345 | 2357 | 197 | 186 | 208 | fixed |
| Northern Source |  | 14 | 6 | 2 | 27 | 1.00 | 3346 | 3780 | 211 | 188 | 235 | fixed |
| Southern Garden |  | 22 | 5 | 12 | 32 | 1.00 | 3468 | 3621 | 218 | 198 | 240 | fixed |
| Southern Source |  | 25 | 6 | 14 | 36 | 1.00 | 3925 | 3922 | 221 | 200 | 244 | fixed |
| Year |  | 7 | 5 | 0 | 20 | 1.00 | 1294 | 2024 | 217 | 210 | 230 | random |
| Sigma |  | 13 | 1 | 11 | 17 | 1.00 | 4085 | 3967 | 223 | 221 | 227 | residual |
| Northern Garden | *Salix arctica* | -13 | 4 | -20 | -5 | 1.00 | 2871 | 3493 | 194 | 186 | 202 | fixed |
| Northern Source |  | 13 | 4 | 5 | 20 | 1.00 | 3729 | 4109 | 207 | 191 | 222 | fixed |
| Southern Garden |  | 19 | 4 | 11 | 28 | 1.00 | 4289 | 3714 | 213 | 197 | 229 | fixed |
| Year |  | 5 | 2 | 2 | 10 | 1.00 | 1931 | 2640 | 211 | 209 | 216 | random |
| Sigma |  | 11 | 1 | 9 | 12 | 1.00 | 5011 | 4156 | 217 | 216 | 218 | residual |

Table S11 Statistical results for the hierarchical Bayesian models comparing trait values (specific leaf area, lead dry matter content, leaf area, leaf length) across populations per species. Estimates and 95% credible intervals presented in log scale and back transformed for clarity when necessary.

Specific leaf area *S. richardsonii* N = 152, *S. pulchra* N = 110, *S. arctica* N = 96**.**

| | **Species** | **Est. (log)** | **Error** | **L95% CI log** | **U95% CI log** | **Est.** | **L95% CI** | **U95% CI** | **Rhat** | **Bulk ESS** | **Tail ESS** | **Effect** |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Intercept | *Salix richardsonii* | 2.62 | 0.11 | 2.39 | 2.81 | 13.67 | 10.94 | 16.68 | 1.00 | 3739 | 5026 | fixed |
| Northern Source | | 0.01 | 0.10 | -0.18 | 0.20 | 13.79 | 9.10 | 20.39 | 1.00 | 4905 | 5902 | fixed |
| Southern Source | | 0.02 | 0.08 | -0.12 | 0.18 | 14.00 | 9.67 | 19.89 | 1.00 | 5893 | 7733 | fixed |
| Southern Garden | | -0.11 | 0.07 | -0.24 | 0.02 | 12.25 | 8.64 | 16.95 | 1.00 | 7965 | 8230 | fixed |
| Year | | 0.19 | 0.10 | 0.06 | 0.45 | 1.20 | 1.06 | 1.57 | 1.00 | 2574 | 3985 | random |
| Sigma | | 0.22 | 0.01 | 0.20 | 0.25 | 1.25 | 1.22 | 1.28 | 1.00 | 8336 | 8151 | residual |
| Intercept | *Salix pulchra* | 2.60 | 0.22 | 2.20 | 2.99 | 13.40 | 9.01 | 19.99 | 1.00 | 1315 | 1495 | fixed |
| Northern Source | | 0.10 | 0.11 | -0.11 | 0.31 | 14.81 | 8.07 | 27.33 | 1.00 | 3199 | 3737 | fixed |
| Southern Source | | -0.08 | 0.08 | -0.22 | 0.07 | 12.40 | 7.20 | 21.53 | 1.00 | 3431 | 4035 | fixed |
| Southern Garden1 | | -0.17 | 0.06 | -0.29 | -0.05 | 11.33 | 6.74 | 19.03 | 1.00 | 4061 | 4030 | fixed |
| Year1 | | 0.37 | 0.26 | 0.13 | 1.02 | 1.44 | 1.13 | 2.79 | 1.00 | 1115 | 1603 | random |
| Sigma1 | | 0.22 | 0.02 | 0.19 | 0.25 | 1.24 | 1.21 | 1.28 | 1.00 | 4306 | 3683 | residual |
| Intercept | *Salix arctica* | 2.42 | 0.10 | 2.21 | 2.63 | 11.23 | 9.14 | 13.91 | 1.00 | 2046 | 2215 | fixed |
| Northern Source | | 0.07 | 0.07 | -0.07 | 0.22 | 12.10 | 8.54 | 17.27 | 1.00 | 2790 | 3842 | fixed |
| Southern Source | | 0.17 | 0.07 | 0.03 | 0.31 | 13.37 | 9.43 | 19.02 | 1.00 | 2879 | 3714 | fixed |
| Southern Garden | | -0.07 | 0.07 | -0.20 | 0.06 | 10.45 | 7.46 | 14.73 | 1.00 | 3759 | 3555 | fixed |
| Year | | 0.17 | 0.11 | 0.06 | 0.44 | 1.18 | 1.06 | 1.55 | 1.00 | 1669 | 2462 | random |
| Sigma | | 0.16 | 0.01 | 0.14 | 0.18 | 1.17 | 1.15 | 1.20 | 1.00 | 5341 | 4041 | residual |

Leaf dry matter content *S. richardsonii* N = 133, *S. pulchra* N = 110, *S. arctica* N = 75.

| | **Species** | **Estimate** | **Error** | **L95% CI** | **U95% CI** | **Rhat** | **Bulk ESS** | **Tail ESS** | **Effect** |
|---|---|---|---|---|---|---|---|---|---|
| Intercept | *Salix richardsonii* | 29.63 | 2.17 | 25.45 | 34.14 | 1.00 | 2343 | 3257 | fixed |
| Northern Source | | 33.97 | 3.43 | 22.74 | 44.86 | 1.00 | 3209 | 3668 | fixed |
| Southern Source | | 28.77 | 1.63 | 21.50 | 36.53 | 1.00 | 5635 | 4468 | fixed |
| Southern Garden | | 32.29 | 1.10 | 25.92 | 38.95 | 1.00 | 6621 | 4303 | fixed |
| Year | | 4.65 | 2.13 | 1.76 | 9.68 | 1.00 | 1990 | 2915 | random |
| Sigma | | 4.55 | 0.29 | 4.03 | 5.16 | 1.00 | 5826 | 4246 | residual |

| | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|
| Intercept | *Salix pulchra* | 38.83 | 4.06 | 30.94 | 47.00 | 1.00 | 2044 | 2702 | fixed |
| Northern Source | | 35.90 | 2.87 | 22.32 | 49.60 | 1.00 | 4131 | 4134 | fixed |
| Southern Source | | 37.62 | 2.10 | 25.59 | 49.95 | 1.00 | 3943 | 3604 | fixed |
| Southern Garden | | 38.96 | 1.67 | 27.81 | 50.39 | 1.00 | 4441 | 4036 | fixed |
| Year | | 9.81 | 3.62 | 5.11 | 18.60 | 1.00 | 1853 | 2986 | random |
| Sigma | | 5.99 | 0.43 | 5.21 | 6.92 | 1.00 | 4600 | 3721 | residual |
| Intercept | *Salix arctica* | 31.60 | 2.50 | 26.65 | 36.60 | 1.00 | 4866 | 5678 | fixed |
| Northern Source | | 32.36 | 1.73 | 24.01 | 40.81 | 1.00 | 8056 | 7930 | fixed |
| Southern Source | | 29.59 | 1.60 | 21.53 | 37.72 | 1.00 | 8890 | 8434 | fixed |
| Southern Garden | | 34.31 | 1.39 | 26.61 | 42.03 | 1.00 | 10857 | 8999 | fixed |
| Year | | 5.19 | 2.25 | 2.42 | 10.69 | 1.00 | 5223 | 6682 | random |
| Sigma | | 3.37 | 0.29 | 2.87 | 4.00 | 1.00 | 10032 | 8133 | residual |

Leaf area *S. richardsonii* N = 66, *S. pulchra* N = 66, *S. arctica N* = 56.

| | **Species** | **Estimate** | **Error** | **L95% CI** | **U95% CI** | **Rhat** | **Bulk ESS** | **Tail ESS** | **Effect** |
|---|---|---|---|---|---|---|---|---|---|
| Intercept | *Salix richardsonii* | 23.53 | 8.12 | 6.63 | 39.10 | 1.00 | 2228 | 2636 | fixed |
| Northern Source | | 49.16 | 8.78 | 15.27 | 82.14 | 1.00 | 2897 | 3493 | fixed |
| Southern Source | | 71.80 | 7.17 | 41.10 | 101.55 | 1.00 | 2904 | 3806 | fixed |
| Southern Garden | | 53.00 | 8.01 | 20.61 | 84.39 | 1.00 | 3406 | 3583 | fixed |
| Year | | 7.29 | 7.29 | 0.16 | 26.20 | 1.00 | 1435 | 1616 | random |
| Sigma | | 19.46 | 1.53 | 16.73 | 22.72 | 1.00 | 4060 | 3395 | residual |
| Intercept | *Salix pulchra* | 19.03 | 5.80 | 7.75 | 30.58 | 1.00 | 2552 | 2642 | fixed |
| Northern Source | | 39.29 | 7.03 | 13.87 | 64.50 | 1.00 | 3109 | 3707 | fixed |
| Southern Source | | 56.75 | 5.31 | 35.08 | 78.72 | 1.00 | 3002 | 3695 | fixed |
| Southern Garden | | 33.15 | 5.95 | 10.06 | 56.57 | 1.00 | 3308 | 3788 | fixed |
| Year | | 5.13 | 5.72 | 0.14 | 21.01 | 1.00 | 1684 | 2197 | random |
| Sigma | | 14.88 | 1.38 | 12.48 | 17.89 | 1.00 | 4462 | 4041 | residual |
| Intercept | *Salix arctica* | 36.83 | 5.42 | 25.99 | 47.08 | 1.00 | 3057 | 3342 | fixed |
| Northern Source | | 55.43 | 6.83 | 31.54 | 79.18 | 1.00 | 3289 | 4004 | fixed |
| Southern Source | | 56.23 | 7.69 | 30.50 | 81.97 | 1.00 | 3408 | 3825 | fixed |
| Southern Garden | | 49.19 | 7.67 | 23.33 | 74.80 | 1.00 | 3442 | 4133 | fixed |
| Sigma | | 18.66 | 1.83 | 15.48 | 22.75 | 1.00 | 4243 | 3939 | residual |

Leaf length *S. richardsonii* N = 620, *S. pulchra* N = 793, *S. arctica N* = 319.

| | **Species** | **Estimate** | **Error** | **L95% CI** | **U95% CI** | **Rhat** | **Bulk ESS** | **Tail ESS** | **Effect** |
|---|---|---|---|---|---|---|---|---|---|
| Intercept | *Salix richardsonii* | 23 | 3 | 17 | 29 | 1.00 | 1251 | 1546 | fixed |
| Northern Source | | 43 | 2 | 33 | 52 | 1.00 | 5058 | 4426 | fixed |
| Southern Source | | 51 | 2 | 42 | 61 | 1.00 | 4999 | 4205 | fixed |
| Southern Garden | | 41 | 1 | 33 | 48 | 1.00 | 5133 | 4083 | fixed |
| Year | | 9 | 3 | 5 | 15 | 1.00 | 1576 | 2520 | random |
| Sigma | | 9 | 0 | 9 | 10 | 1.00 | 5636 | 4022 | residual |
| Intercept | *Salix pulchra* | 21 | 3 | 15 | 27 | 1.00 | 1235 | 1701 | fixed |
| Northern Source | | 36 | 2 | 25 | 46 | 1.00 | 6058 | 4408 | fixed |
| Southern Source | | 51 | 2 | 41 | 61 | 1.00 | 5236 | 4028 | fixed |
| Southern Garden | | 37 | 1 | 29 | 45 | 1.00 | 5485 | 4142 | fixed |
| Year | | 9 | 3 | 6 | 15 | 1.00 | 1674 | 2852 | random |
| Sigma | | 10 | 0 | 10 | 11 | 1.00 | 6986 | 3746 | residual |
| Intercept | *Salix arctica* | 26 | 4 | 18 | 34 | 1.00 | 1154 | 2073 | fixed |
| Northern Source | | 31 | 4 | 16 | 46 | 1.00 | 1838 | 2938 | fixed |
| Southern Source | | 41 | 4 | 25 | 56 | 1.00 | 2276 | 3891 | fixed |
| Southern Garden | | 29 | 2 | 16 | 41 | 1.00 | 1059 | 1776 | fixed |
| Year | | 9 | 3 | 5 | 18 | 1.00 | 2044 | 2767 | random |
| Sigma | | 6 | 0 | 6 | 7 | 1.00 | 5378 | 4578 | residual |

1144