Does dry soil promote earlier flowering in Arctic tundra plants?

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Abstract

Arctic soil moisture conditions span a wide spectrum from permanently wet, bog-like conditions, to cold desert landscapes, and many Arctic plant species manage to persist across this environmental heterogeneity. It is unknown however, whether these plants exhibit a phenological shift to earlier flowering times as an adaptive response to water stress, which is seen in some hot desert and Mediterranean plants. Here we use an Arctic phenological dataset to address this question by examining differences in the flowering time of four Arctic forb species (*Pedicularis hirsuta, Polygonum viviparum, Draba lacteal*, and *Papaver radicatum*) across wet and dry soil conditions. Our results indicate that there is no significant difference in the flowering time of these four species between wet and dry soil, likely due to the existing adaptations that Arctic species possess to combat abiotic stress and the unique biogeographic features of the Arctic.

Introduction

Arctic plants are faced with a wide variety of harsh abiotic conditions that shape the ecological communities in these regions. It has been posited that the greatest constraints on plant reproduction in the Arctic are low air and soil temperatures, low soil nutrient availability, and a short growing season (Klady et al., 2011). It is less clear, however, how soil moisture influences plant reproduction in these regions. Soil moisture is highly variable in the Arctic due to complex hydrology; it is mainly dependent on precipitation, which largely falls and is stored as snow, and on the rates of melting and evapotranspiration during the spring and summer months. (Bring et al., 2016). The rates of precipitation and evapotranspiration remain highly variable throughout the Arctic, however, and depend on conditions such as vegetative canopy, the length of the growing season, and the length of the snow cover period (Bring et al., 2016). In addition to these sources of variation in the amount of precipitation a region receives and loses during a season, soil moisture is highly dependent on the topographic conditions of the landscape, which can vary between mountain sides, shallow slopes, and flat terrain. (Bring et al., 2016).

The result of such complex hydrological processes is a highly variable mosaic of soil moisture conditions across the Arctic. Within the tundra, regions such as sedge-dominated wet meadows are wet throughout the entirety of the growing season, whereas dry heath ecosystems, which are also common throughout much of the tundra, are characterized by extremely dry soil conditions due to low levels of precipitation and snow cover (Gough et al., 2002; Henry, 1998). Many common Arctic species, however, manage to persist across this wide variety of soil moisture conditions, which suggests that they possess adaptations to cope with this extreme environmental heterogeneity.

Plant adaptations to low soil moisture conditions have been observed in Mediterranean and hot desert adapted plants, where it was shown that water stress acts to accelerate phenology (the timing of biological events), specifically flowering time, by triggering an earlier-than-average shift from vegetative to reproductive growth (Aronson et al., 1992; Desclaux & Roumet, 1996). This response is thought to maximize reproductive output in unfavourable environmental conditions, such as low water availability (Aronson et al., 1992; Desclaux & Roumet, 1996). It is unknown however, whether this effect is environment-specific, or whether plants in dry Arctic communities show a similar adaptive response to water stress as plants in Mediterranean and hot desert communities.

Here we address this question using an open-source Arctic ecological dataset to test the response of flowering time to soil moisture conditions within four forb species across seven Arctic locations. We hypothesize that plants in dry soil will flower at a significantly different time from plants in wet soil, and that flowering time will shift to be earlier in dry soil than in wet to maximize reproductive output under abiotic stress.

Methods

Sampling & Data Description

We assessed the effects of soil moisture type on the phenology of tundra plants using the tundra Phenology Database provided by the International Tundra Experiment (ITEX). The ITEX is a collection of multi-year experiments that investigate the impacts of global warming on tundra vegetation throughout time. The database contains over 150,000 phenology observations of 278 plant species from 28 different tundra locations. The data set includes information such as treatment type, study area, subsite, latitude and longitude coordinates, elevation, ecosystem type, year, species, functional group, phenophase (the observable stage in a plant's life cycle), day of year (DOY), and soil moisture type. These observations were reported either daily, once weekly, or twice weekly for periods of 1 to 26 years (Prevéy et al., 2021).

For the purpose of our study, we narrowed the dataset to observations of the following plant species: *Pedicularis hirsuta* (referred to as PEDHIR), *Polygonum viviparum* (referred to as POLVIV), *Draba lacteal* (referred to as DRALAC), and *Papaver radicatum* (referred to as PAPRAD). These species were sampled from 1992 to 2018 from the following study sites: Alexandra Fiord, Canada; Zackenberg, Greenland; Endalen, Norway; Adventdalen, Norway; Latnjajaure, Sweden; Atqasuk, Alaska, United States; and Utqiagvik, Alaska, United States (Figure 2).

We selected our study organisms because they all fall under the same functional group: forbs. Forbs are herbaceous flowering plants found in numerous habitats and are especially abundant throughout the tundra biome (Snow, 2005). In addition, the four species had numerous observations in both wet and dry soils, which is essential for investigating phenological shifts between the two soil moisture types. In addition to filtering for our species of interest, we further refined the dataset by filtering the "phenophase" column for "flowering", the "soil moisture" column for "wet" and "dry", the "treatment" column for "CTL" (control), and the "functional group" column for "forb". All data manipulations were performed in R Studio (version 4.0.3 R, 2020-10-10).

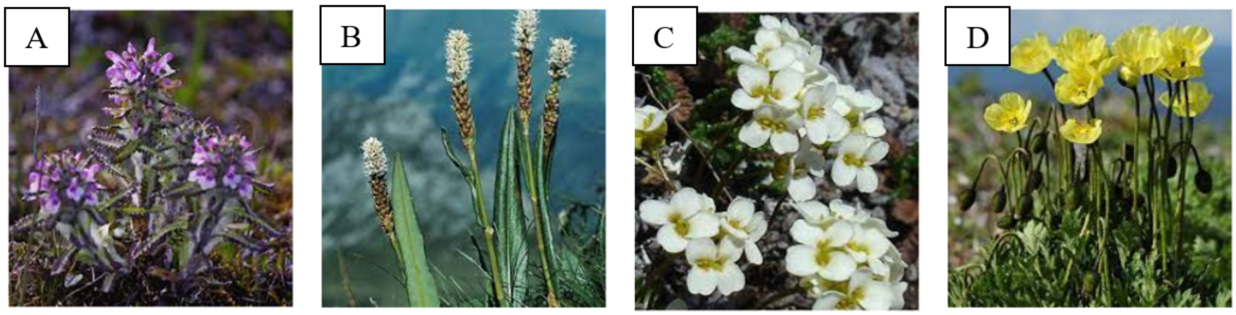

Figure 1: The four tundra plants investigated in this study. A) *Pedicularis hirsuta* (referred to as PEDHIR), B) *Polygonum viviparum* (referred to as POLVIV), C) *Draba lacteal* (referred to as DRALAC), D) *Papaver radicatum* (referred to as PAPRAD).

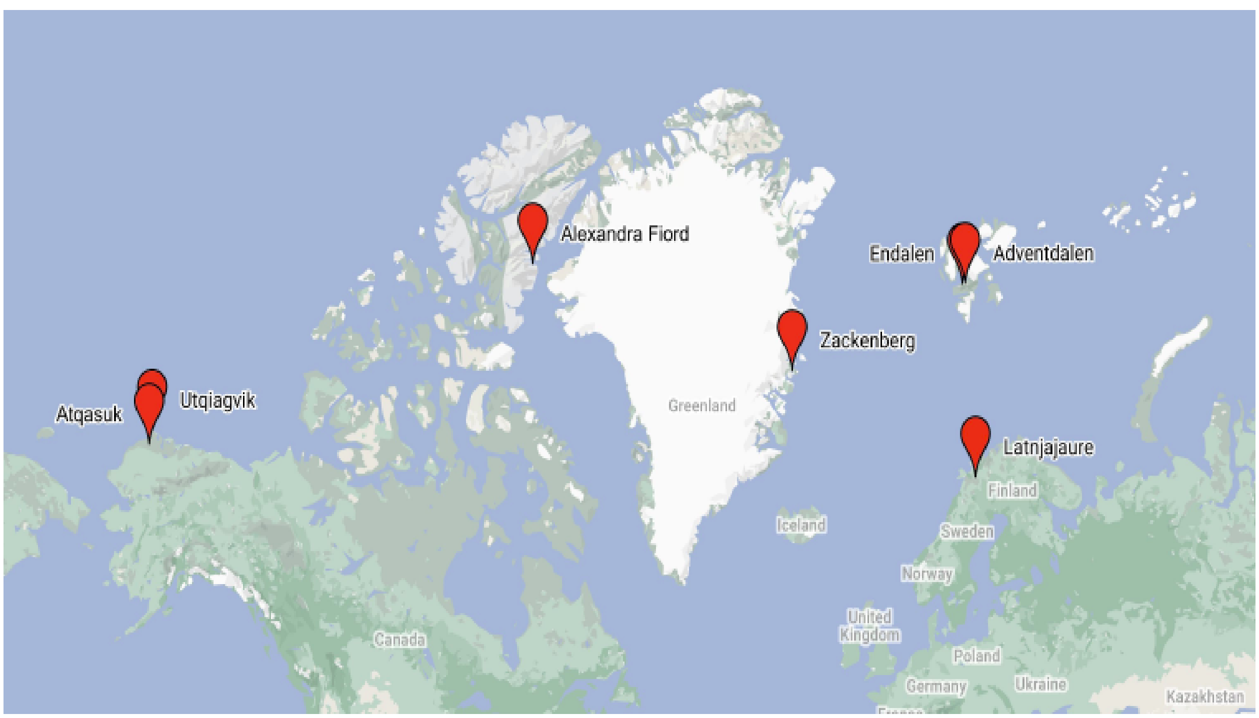

Figure 2: Map showing the seven study sites included in our filtered dataset: Alexandra Fiord, Canada; Zackenberg, Greenland; Endalen, Norway; Adventdalen, Norway; Latnjajaure, Sweden; Atqasuk, Alaska, United States; and Utqiagvik, Alaska, United States.

Data Analysis

All statistical analyses were performed in R Studio. We initially tested the assumptions of a t-test using the Shapiro-Wilk test for normality of data, as well as the F-test for homogeneity of variances. Four smaller datasets were created for each species from the original dataset to perform data transformations to satisfy the assumptions. We applied a log base 10 transformation to the PAPRAD dataset, an inverse transformation to the POLVIV dataset, an inverse transformation to the PEDHIR dataset, and no transformations to the DRALAC dataset, as it was already normally distributed. Using the smaller datasets, we then performed four separate t-tests for each species to compare the mean day-of-year of flowering of individuals in dry soils to those in wet soils.

Using the original dataset, we tested the assumptions of a linear model (normality, homogeneity of variances, and independence of observations). Six linear mixed effects models were then constructed, each with a different combination of fixed and random effects. All models, however, had soil moisture with a species interaction as a fixed effect, as we were aiming to compare the effects of soil moisture type within species, not across species . These models are shown and explained in Table 1. To compare all models, the second-order Akaike Information Criterion (AICc) was used to evaluate which model best fit the data.

Table 1: Six linear mixed effects models used with various combinations of fixed and random effects alongside the model explanations. All models had soil moisture with a species interaction as a fixed effect.

Model	**Model Explanation**
DOY~soil moisture * species + (1|subsite)	Modelling the relationship between DOY and soil moisture with a species interaction as a fixed effect, and subsite as a random effect
DOY~soil moisture * species + (1|study area)	Modelling the relationship between DOY and soil moisture with a species interaction as a fixed effect, and study area as a random effect
DOY~soil moisture * species + (1|subsite) + (1|study area)	Modelling the relationship between DOY and soil moisture with a species interaction as a fixed effect, and subsite and study area as random effects

DOY~soil moisture * species + year + (1|subsite) + (1|study area)	Modelling the relationship between DOY and soil moisture with a species interaction, as well as year as fixed effects, and study area as a random effect
DOY~soil moisture * species * year + (1|subsite)	Modelling the relationship between DOY and soil moisture with a species and year interaction as a fixed effect, and subsite as a random effect
DOY~soil moisture * species * year + (1|study area)	Modelling the relationship between DOY and soil moisture with a species and year interaction as a fixed effect, and study area as a random effect

Lastly, we created a boxplot to visualize flowering day across all species in both wet and dry soils, as well as a graph to show the mean flowering day of each year for individuals in dry soils and individuals in wet soils, faceted by species.

Results

An initial visualization of the data indicated that two species, DRALAC and PAPRAD, had an earlier median flowering day in dry soil compared to wet soil, while the other two species, PEDHIR and POLVIV, had an earlier median flowering day in wet soil compared to dry soil (Figure 3).

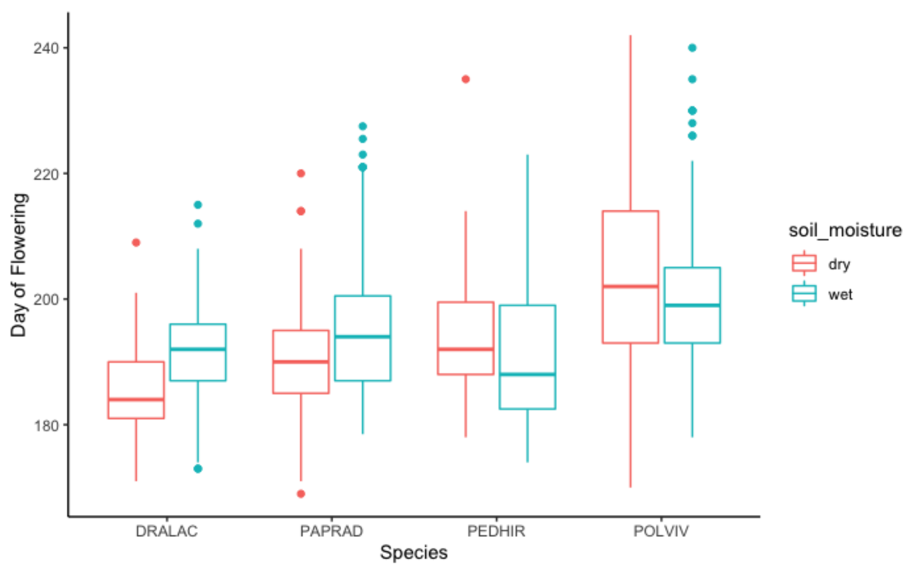

Figure 3: A comparison of the flowering day of each species in dry soil compared to wet soil, with the median, interquartile range, and minimum and maximum values indicated. DRALAC and PAPRAD have an earlier median flowering day in dry soil compared to wet soil, while PEDHIR and POLVIV have an earlier median flowering day in wet soil compared to dry.

DRALAC had a median flowering day of 184 Julian days (JD) in dry soil, and 193 JD in wet soil; PAPRAD had a median flowering day of 190 JD in dry soil and 194 JD in wet soil; PEDHIR had a median flowering day of 192 JD in dry soil and 188 JD in wet soil; and POLVIV had a mean flowering day of 202 JD in dry soil and 199 JD in wet soil. A visual analysis revealed that there was no evident shift in average flowering day for each species throughout the years of observation (Figure 4).

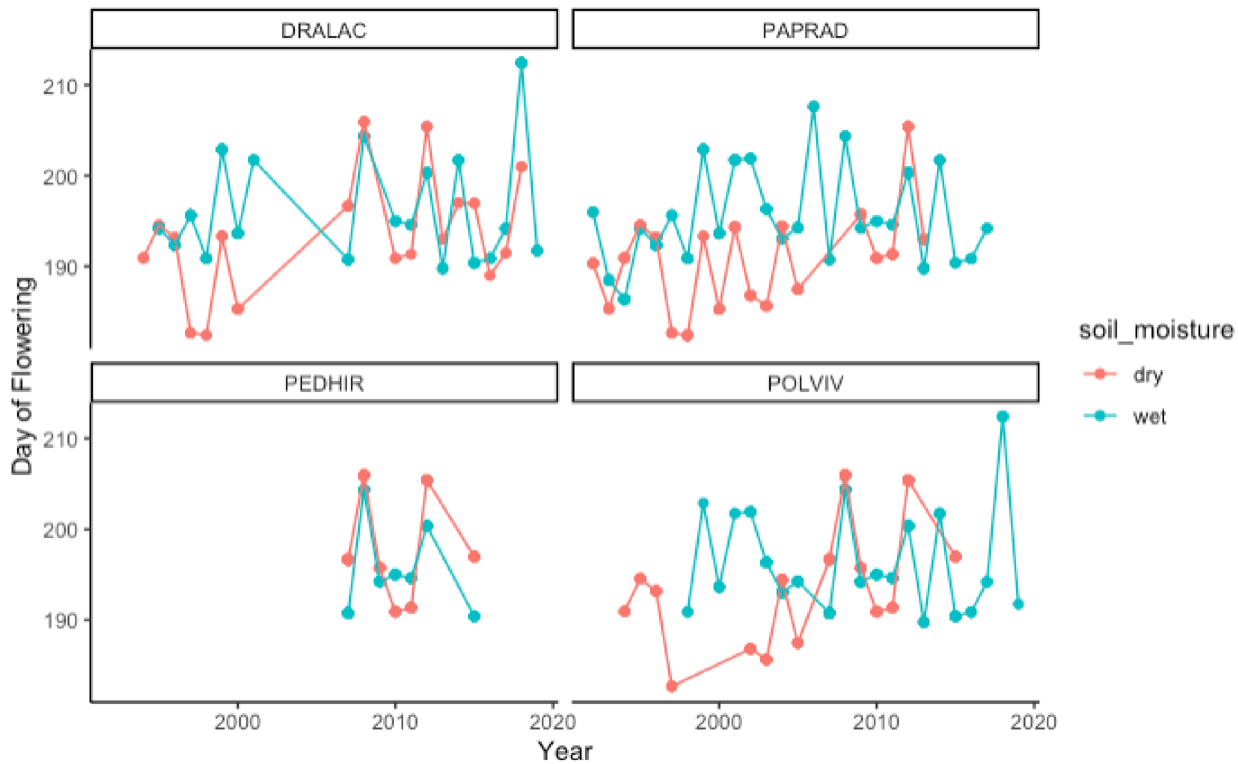

Figure 4: Average flowering day of each species over each year of observation. A visual examination revealed no apparent trend in the day of flowering over time.

The results of our t-test comparing mean flowering day in dry soil compared to wet indicated a significantly earlier flowering time in dry soil for all species (POLVIV: $t(251.2) = -2.4679$, $p = 0.005$; PEDHIR: $t(180.07) = -2.4679$, $p = 0.015$; PAPRAD: $t(361.59) = -5.7346$, $p = 2.066\text{e-}08$; DRALAC: $t(62.946) = -4.2071$, $p = 8.354\text{e-}05$) (Table 2). Our data, however, did not meet the assumption of normality or of homogeneity of variances required for a t-test. Following the transformations described in *Methods* to increase the normality of the data, a Shapiro-Wilk test indicated that the data remained significantly non-normal for all species except for DRALAC (DRALAC: W = 0.98979, $p = 0.1$; PAPRAD: W = 0.96096, $p = 2.405\text{e-}08$; POLVIV: W = 0.98747, $p = 0.0006$; PEDHIR: W = 0.96723, $p = 3.598\text{e-}05$). The data was assessed to be qualitatively normal, however, through examination of a histogram for each species. Similarly, the homogeneity of variance assumption was violated for PAPRAD, POLVIV, and PEDHIR, however the variance was assessed to be qualitatively even for each between the wet and dry groups (PAPRAD: F = 0.68351, *p-value* = 0.01232; POLVIV: F = 2.0363, *p-value* = 1.611e-07; PEDHIR: F = 0.68736, *p-value* = 0.04568). DRALAC was found to have homogenous variance between the two groups (F = 1.2373, *p-value* = 0.3374).

Table 2: Results from t-tests for each species. For all species, the mean flowering day in wet soil was found to be significantly later than the mean flowering day in dry soil. Note that the units of the means for each species are reflective of the transformations that were performed on each species' data.

Species	**Dry soil mean**	**Wet soil mean**	***t*-statistic**	***df***	***p*-value**
POLVIV	0.004924713	0.005015719	-2.4679	251.2	0.004792
PEDHIR	0.005198867	0.005279747	-2.4679	180.07	0.01452
PAPRAD	2.278568	2.290284	-5.7346	361.59	2.066e-08
DRALAC	185.7556	191.8056	-4.2071	62.946	8.354e-05

The linear mixed effects model with the lowest AICc value, and therefore selected for analysis, considered soil moisture with an interaction with species as fixed effects, and study area and subsite as separate random effects (Table 3). The results of the model found that all species flowered, on average, five days later in wet soil compared to dry soil, however this effect was non-significant for all species (Table 4).

Table 3: The AICc and degrees of freedom for each of the models tested for analysis. The best performing model (bolded), considered soil moisture with an interaction with species as fixed effects, and study area and subsite as separate random effects.

Model	**AICc**	***df***
soil_moisture * spp + (1|subsite)	9354.858	10
soil_moisture * spp + (1|study_area)	9407.855	10
soil_moisture * spp + (1|study_area) + (1|subsite)	**9353.501**	**11**
soil_moisture * spp + year + (1|study_area) + (1|subsite)	9359.146	12

soil_moisture * spp * year + (1|subsite)	9364.245	18
soil_moisture * spp * year + (1|study_area)	9411.569	18

Table 4: A subset of results from the best performing model, comparing the flowering time of each species in dry soil and wet soil. The negative estimates indicate that each species flowers earlier in dry soil than in wet soil, however, this effect is non-significant ($p > 0.05$).

Contrast	Estimate	*df*	P-value
DRALAC dry - DRALAC wet	-5.4972	6.82	0.9918
PAPRAD dry - PAPRAD wet	-4.1316	5.09	0.9949
PEDHIR dry - PEDHIR wet	-9.3442	9.59	0.4219
POLVIV dry - POLVIV wet	-3.3183	7.44	0.9845

Table 5: The full results of the best performing model. The estimate for *soil_moisturewet* indicates that all species, on average, flowered 5 days earlier in dry soil than in wet, however, this effect is non-significant ($p > 0.05$).

Predictor	Estimate	*t*-value	*df*	P-value
soil_moisturewet	5.497	0.837	1	0.426
sppPAPRAD	5.578	0.554	3	0.595
sppPEDHIR	-6.369	-0.748	3	0.479
sppPOLVIV	11.028	1.304	3	0.235
soil_moisturewet:sppPAPRAD	-1.366	-0.153	3	0.882
soil_moisturewet:sppPEDHIR	3.847	0.524	3	0.611
soil_moisturewet:sppPOLVIV	-2.179	-0.303	3	0.768

Discussion

Although the results from the t-test indicated a significant difference in flowering day between wet and dry soils for each species, these results should be considered with caution, as the t-test fails to account for important confounding variables that can lead to an increase in Type 1 error. Variables such as study site and subsite varied between the four species studied and may have had an important impact on the flowering day for the individuals at each site, but this effect is not considered in the t-test. Our linear mixed model, however, did account for study site and subsite as random effects (refer to Table 3). The results of this model showed that across all species, plants flowered approximately 5 days earlier in dry soils than in wet soils. While this finding seems to support our hypothesis and prediction, none of the results were significant (p-value>0.05). Therefore, we cannot conclude that soil moisture has a significant effect on the flowering day of tundra plants, which rejects our hypothesis.

Although the tundra desert differs from warm desert climates, both biomes suffer from water stress. Water stress has been shown to impact the phenology of warm-climate plants, where plants under dry soil conditions have been observed to flower earlier in the season to increase their reproductive output (Aronson et al., 1992; Desclaux & Roumet, 1996). The hydrological complexities of the tundra may lead to unexpected outcomes for plants facing water stress, however, that lead to a differential response to dry soil moisture conditions in tundra plants compared to hot-desert plants. Plants in the tundra often rely on cryptogamic soil crusts (soil top layers formed by microorganisms), which have access to surface runoff from melting snow from the short growing season. Crusted regions in the polar desert aid plant communities not by relieving water stress, but by facilitating nitrogen fixation, and growth and development activities (Gold and Bliss, 1995). These benefits target vascular plants, and may thus offset the abiotic stress imposed by low moisture conditions.

Furthermore, vegetation lifeforms in the tundra are well equipped with adaptations to thrive in the various soil conditions of the Arctic. Many plants have small waxy leaves to prevent water loss in the drier conditions, as well as dark coloured leaves to improve the absorption of heat (Snow, 2005). Moreover, the shallow permafrost layer can impose limits to plant root growth, especially in regions where the permafrost layer is only 10 cm to 1 m below the surface. Because of this, the root networks of plants generally spread out laterally, which can improve water and nutrient absorption (Snow, 2005). Peterson (2014) notes that very few tundra plant species experience water stress, even though the Arctic is climatologically a desert. Instead, the main limiting factor of tundra plant communities does appear to be a lack of heat, which results in very short growing seasons.

Although we did not detect any significant trends, the effects of soil moisture on the phenology of tundra plants should be further explored. Future studies should investigate these effects using a larger sample size, seeing that the four species used in our study are not representative of all forb plants in the tundra. In addition, the effects of soil moisture can be compared between different plant functional groups to test if certain functional groups are better adapted to harsh abiotic conditions than others. Lastly, future studies should compare whether the phenological response of plants to variation in soil moisture differs between geographically distant tundra regions, to better understand the effect of location on plant responses.

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