

The timing of snowmelt and amount of winter precipitation have limited influence on flowering phenology in a tallgrass prairie

Emma K. Chandler, Department of Biological Sciences, Dept. 2715, North Dakota State University, PO Box 6050, Fargo, ND 58108-6050

Steven E. Travers (Corresponding author), Department of Biological Sciences, Dept. 2715, North Dakota State University, PO Box 6050, Fargo, ND 58108-6050, steven.travers@ndsu.edu

Abstract

A growing body of work indicates that the timing of flowering of temperate angiosperms is demonstrably affected by shifts in climate since the 1970's. Sensitivity in flowering phenology to changing temperatures has been particularly well-documented. Precipitation patterns are also predicted to change with increasing greenhouse gasses, yet few studies of temperate communities have demonstrated widespread phenological sensitivity to precipitation changes. The exception is relationships between snowpack and early flowering in alpine environments, whereby the timing of flowering herbs has shown strong associations with winter precipitation amounts and the timing of snowmelt. Based on the results of alpine studies, we hypothesized that populations of plants in northern latitudes, characterized by strong seasonality and winter snowfall would similarly demonstrate significant effects of the timing of snowmelt on flowering phenology. We combined a historical data set of first flowering dates in Minnesota tallgrass prairie with climatic data to construct a structural equation model, testing hypotheses on the relationships between winter precipitation and temperature variables and flowering phenology. While temperature had a strong effect on flowering phenology for most species observed, winter precipitation had a significant relationship with only three of nineteen species. The three species affected by snow were later flowering species which is inconsistent with our prediction that winter precipitation affects early flowering phenology. These results further our understanding of the climatic cues that drive flowering phenology and improve our ability to predict how climate change will impact prairie species.

Introduction

One of the best documented biotic effects of climate change is changing flowering phenology, or flower timing (Cleland et al, 2007; Miller-Rushing & Primack, 2008; Parmesan, 2006; Schwartz et al, 2006; Wolkovich et al, 2012). Flowering phenology is important for plant-pollinator interactions, as asynchrony between flower timing and pollinator emergence can be detrimental for plant reproduction and pollinator health (Cleland et al, 2007; Kharouba et al, 2018; Kharouba & Wolkovich, 2020; Visser & Gienapp, 2019). Asynchrony is problematic for plant and pollinator populations, the communities they inhabit, and the ecosystem services they provide. Plant reproductive success has also been shown to be dependent on flowering phenology. Schemske et al. (1977) found that *Claytonia* sp. had peak seed set per ovary at the end of April with seed set per ovary decreasing in organisms with early or later maturation (Schemske, 1977). Thus, it is important to understand climate change effects on flowering phenology, in part because there is the potential for changes in evolutionary and conservation dynamics of natural populations.

Flowering can be triggered by several environmental cues such as photoperiod, amount and timing of precipitation or soil moisture, and temperature (Rathcke & Lacey, 1985). Climate change may alter these environmental cues resulting in the changing flowering phenology. A majority of studies on flowering phenology and global climate change have focused on the effects of temperature change (Wolkovich et al, 2012).

In prairies, flowering phenology has been strongly linked with temperature. Reed et al.(2019) found advancement of phenological events due to recent temperature increases in prairies of the Pacific Northwest (Reed et al, 2019). Dunnell and Travers (2011) also found prairie species shifting both earlier and later in response to temperature changes in the Midwest (Dunnell &

Travers, 2011). However, temperature is not the only climate or environmental variable affected by the accumulation of greenhouse gases. Changes in precipitation patterns have also been predicted as a result of a warming globe. For example, overall precipitation is expected to increase in the Midwest (IPCC, 2014). In the northern plains, where winters can be relatively long and harsh, changes in precipitation have the potential to influence plants primarily as snow. Snow could affect flowering phenology in several ways. During bud emergence, snow cover decreases the amount of sunlight plants receive but also insulates buds from frost events. When snow melts, soil temperature should increase quickly promoting plant growth. Additionally, substantial amounts of moisture are released into the soil and supply plants well into the summer.

Snowpack has been found to alter flowering phenology in montane and tundra species. Inouye et al. (2002) found a significant correlation between date of first bare ground and date of first flowering for *Delphinium barbeyi*, a subalpine species. Similarly, Sherwood et al. (2017) found advanced emergence, bud break, and flowering in a montane forb when snowpack was reduced. However, the snow removal treatment also resulted in increased frost damage among buds due to the lack of insulation from snow and freezing night temperatures (Sherwood et al, 2017). Species in the tundra had similar responses. Bjorkman et al. (2015) found that snowmelt was strongly related to flowering time for four arctic tundra species, while temperature was not a consistent driver of flowering phenology.

Though there have been several studies on the effects of snowpack on flowering phenology for montane and tundra species, from our understanding, no studies have been conducted on the effects of snowpack on the flowering of prairie species. This study examines the effect that snowpack and snow accumulation have on flowering phenology for 19 perennial prairie herbs that are typical of northern tallgrass prairies. The goals of this study are:

1. Simultaneously assess direct and indirect effects of temperature and winter precipitation variables on flowering phenology using path analysis.
2. Determine the importance of bare ground as an intermediate step between winter precipitation and flowering phenology.
3. Compare phenological responses to precipitation in the form of snow and temperature, whether advanced or delayed, across several species using a long-term data set.

Methods

Data collection

We used historical data collected by O.A. Stevens and SET to initially create a dataset of first flowering days (FFD) for 24 flowering plant species. The observations were made at Bluestem Prairie (<https://www.dnr.state.mn.us/snas/detail.html?id=sna00996>), a tallgrass prairie site in Clay county Minnesota that has been a Nature Conservancy preserve since 1975. Individual data points represent the day of the year on which a given plant species was observed flowering at the site, although all species were not observed in all years. The Stevens dataset represents continuous data from 1910 to 1961 (Dunnell & Travers, 2011); subsequent observations are from 2012 through 2020. Thus, there is a 52-year gap in data at the end of the past century. The plant species analyzed in this study were limited to those that met a series of minimum data requirements. The focal species had a minimum of five years of observations and at least one observation prior to 1962 and one after.

In order to quantify different environmental variables related to annual climate patterns, we used daily climate data collected in Fargo, North Dakota, USA, as part of the National Atmospheric and Oceanic Administration (NOAA) National Climatic Data Center (NCDC) observing network (<http://www.ncdc.noaa.gov/oa/ncdc.html>). The climate data collection site

(46 ° 56' N, 96 ° 49' W) is located at the Fargo International Airport, 32 km west of the flowering observation site. The climate dataset includes daily estimates of maximum and minimum temperature, snowpack (0 was considered bare ground), and snowfall beginning in 1942. However, snowpack data is unavailable for 1997 through 2004. As a result, we were able to analyze data for a total of 29 years (1942-1961 and 2012-2020).

Climate Variables

We used the raw climate data to calculate four variables regarding annual patterns of temperature or winter snowfall. The first climate variable we calculated for each year was intended to quantify the relative warmth of the late winter/early spring season, when the earliest flowering on the prairie is initiated. This variable, Accumulated Degree Growing Unit (AGDU), was calculated as the day of the year on which the sum of the growing units for a year exceeded 300. Growing units are defined as a daily measure of the difference between the average temperature and 35° F; units were set to zero if the average temperature was below 35°F (McMaster & Wilhelm, 1997). We chose 300 units as the cutoff because this number of units is typically accumulated by the end of March in the northern plains region. Thus, in years with warmer spring months the AGDU value will be relatively lower and vice versa.

Three different winter precipitation variables were calculated. The winter snowfall amount for a given year (TSNOW) was calculated as the sum of daily snowfall over the first 90 days. A second variable associated with winter snowfall was the Date of Bare Ground (DOBG) or the day of the year when snowpack first reached zero. Eight records indicated a short period, one to two days, of snowpack late in the season which were excluded. The third variable associated with winter snowfall was Snowpack on Day X (SPDX), a variable designed to estimate the extent of snowpack just prior to the growing season. To calculate SPDx for each

species we used linear regression and model selection to identify the day in March with snowpacks that best predicted the first flowering day (FFD) for that species. We ran separate linear regressions where FFD was the dependent variable and snowpack on day X was the independent variable for each day in March. AIC values were determined for each regression and the model associated with the lowest AIC value was chosen and used to assign the day in March consistently used for SPDX in that species. Thus, SPDX values increase with increasing snowpack and decrease with decreasing snowpack on the selected day of March. The most predictive day was determined separately for each plant species. We used this variable to maximize the explanatory power of snowpack on flowering in a month when temperatures and snowpack are rapidly changing. Each of the four climate variables were not independent of each other.

Model development

Our goal was to use Structural Equation Modelling (Grace, 2006) to simultaneously assess the relationships between each of the four climate variables and the first flowering day (FFD) of the focal plant species, given the covarying nature of the climate variables. We used the *lavaan* package (Rosseel, 2012) in R (R Core Team, 2020) to incorporate path analysis and examine the relationships among the climate variables and the dependence of FFD on each of the climate variables individually. In our initial, full model, we included AGDU and TSNOW as exogenous variables and DOBG, SPDX, and FFD as endogenous variables (Fig. 1). The assumption was that FFD could have direct and indirect effects from both temperature (AGDU) and winter snowfall (TSNOW), through their indirect effects on snowpack in March (SPDX) and the date at which the snow melted (DOBG). The model included regressions for each endogenous variable, variances within all variables, and residual covariances between the

exogenous variables. We considered both direct and indirect regressions. To best compensate for missing data points over the course of the 29 years analyzed, we applied full information maximum likelihood (FIML) estimation to determine path coefficients and model statistics. We used regression estimates for indirect and direct effects to interpret the relationships between latent variables in each of the species.

In order to identify the best overall structural equation model for analyzing relationships among climate and flowering variables we used a model selection approach and compared the fit of the full model (above) to three other reduced models that omitted either DOBG, SPDX, or AGDU. After using the *lavaan* program to conduct path analyses of the three reduced models, we used Akaike Information Criterion (AIC) to select the model of the four that best represented the data, based on the lowest AIC value.

Results

Variation in first flowering day (FFD)

We identified 24 flowering plant species in the Stevens Data set that met the criteria for analysis described in the methods. None of the species were observed in every year of the survey; sample size by species ranged from 5 to 13. The first flowering day (FFD) varied extensively both among years within a species and among species. Median FFD varied across the species from a low of 123 to a high of 206 and included early, mid, and late spring flowering species (Fig. 2).

Model selection

Model selection comparisons of AIC values among the three reduced models and the full model indicated that the best explanatory model was the reduced model which excluded DOBG. This indicates that the influence of temperature and snowfall on flowering date was relatively negligent through an indirect effect on when the ground first became bare of snow each spring.

Based on the chi-squared statistic estimating goodness of fit (Grace, 2006) (*lavaan*), the reduced model was a good representation of the relationships among the exogenous and endogenous variables for all but five species (*Anemone patens*, *Caltha palustris*, *Lithospermum canescens*, *Campanula rotundifolia*, and *Amorpha canescens*). These five species were removed from further analysis and consideration.

The results of path analysis are presented in Figure 3 and Table 1 for each of the remaining species arranged by order of seasonal flowering sequence. The direct relationship between AGDU and FFD was significant in 12 out of 19 species analyzed suggesting an important role of temperature in determining flowering time for a majority of species. All twelve species with significant AGDU effects had positive coefficients, indicating that warmer temperatures earlier in the year led to earlier flowering. The five first flowering species had strong and significant relationships between AGDU and FFD. Later flowering species typically had weaker, inconclusive relationships and few were significant. For the direct effect of AGDU on SPDX, only 5 of 19 were significant and all regression coefficients were weakly positive. Winter temperatures (AGDU) also had indirect effects on flowering time (FFD) through intermediary effects on the snowpack in March (SPDX) for 1 species (*Zigadenus elegans*).

The relationship between snowfall in the winter months (TSNOW) and snowpack in March (SPDX) was a predictably strong one. The path coefficient between the two variables was

positive and significant for all species. TSNOW was expected to be related to SPDX because both describe winter snowfall. However, only three out of the 19 species had a significant relationship between SPDX and FFD. In one species (*Cypripedium candidum*) the path coefficient was negative indicating that relatively large amounts of winter snowfall led to earlier flowering compared to years when there was less winter snowfall (Fig. 4). However, in the other two species (*Zigadenus elegans* and *Rosa arkansana*) the regression coefficients were positive indicating that greater snowpack delayed flowering. This is consistent with the pattern observed in other species in this analysis, though they were not significant (Fig. 4). There were significant indirect effects of TSNOW on FFD for the same three species through its effects on SPDX (Table 1).

Discussion

In this study we built a model to analyze relationships between temperature (AGDU), snowfall (TSNOW), snowpack (SPDX), date of first bare ground (DOBG), and first flowering day (FFD) for 19 prairie species. The model for all species improved when we excluded DOBG. We expected that the date of first bare ground would influence first flowering day as was reported by Inouye (2002) for montane species in Colorado. However, only a few of the species had a significant relationship between DOBG and FFD suggesting that when the winter snow melt occurs is not important for determining when plants begin flowering. An explanation for the lack of relationship between DOBG and FFD is that early DOBG could lead to increased frost damage in sensitive buds while later DOBG extends the date at which buds could emerge (Sherwood et al, 2017). Plants themselves may also compensate for a late start by shortening other growth stages, resulting in the same flower timing regardless of DOBG (Semenchuk et al, 2016). In contrast, temperature seems to be a consistent determinant of flower timing.

AGDU and FFD had a positive and significant relationship in most of the species. A higher AGDU means a colder spring suggesting that temperature is important for growth and development. This was especially the case for earlier flowering species. These results mirror other studies of plants in upper Midwestern prairies (Dunnell & Travers, 2011), Pacific Northwestern prairies (Reed et al, 2019), and other temperate communities (Cook et al, 2012). Interestingly, these results differ from previous research for areas that receive substantial amounts of snow, such as alpine and tundra environments. Moreover, Sherwood et al. (2017) found that temperature manipulations, specifically heating, had no effect on flowering phenology in montane species. Bjorkman et al. (2015) found that temperature was not strongly related to flowering phenology in tundra species. Temperature was a significant predictor for only one of four species observed (Bjorkman et al, 2015). Temperature may be more important than date of first bare ground for flowering phenology in tallgrass prairies compared to alpine settings because of the short, intense growing season in alpine communities. In a short growing season, there is a higher premium for every day of growth.

Snowpack in March was largely unimportant, with the exception of three later flowering species. Two species (*Rosa arkansana* and *Zigadenus elegans*) had positive regression coefficients meaning the deeper the snow on day X in March, the later the species flowered. This outcome would be expected if snow cover impaired earlier flowering. Since these species flower later in the summer, developmental processes earlier in the spring could be directly affected by snowpack, shifting flowering phenology. One species (*Cypripedium candidum*) had a negative regression coefficient meaning that increased snowpack led to earlier flowering. *Cypripedium candidum* is the only obligative wetland species used in this analysis, which may explain the strong relationship between flowering and winter precipitation. Since soil moisture from

snowpack can take months to dissipate, snowmelt and early evapotranspiration may affect the soil moisture available for species that flower later in the season (Wang et al, 2018). Whether due to impaired early development or quantities of soil moisture, these three species are compensating for the conditions that resulted from snowpack by shifting flowering phenology.

Overall, our results suggest that snowpack does not have a strong relationship with flower timing in Midwestern prairies. Snowpack may not inhibit flowering because, even with a late start, growing plants may be able to catch up by shortening earlier developmental phases (Semenchuk et al, 2016). We expected snowpack to influence early flowering species and not later flowering species but, our results indicate that growth and flowering begin regardless of snow cover. In comparison with snowpack, air temperature had a much stronger effect on when plants flower. The five earliest flowering species had significant regression coefficients for the effect of AGDU on FFD. However, there were also several other species with significant relationships between AGDU and FFD with flowering dates interspersed throughout the growing season. We can therefore draw the conclusion that temperature is more strongly associated with flowering phenology than snowpack for prairie species.

Further research is needed to better understand the relationships between changing climatic conditions and flowering phenology. We only considered snow cover and melt but, other forms of precipitation might be more tightly related to triggering flowering. Patricola and Cook (2013) found that precipitation is expected to increase for April and May with climate change and decrease for July and August. These changes could have implications for flowering phenology throughout the growing season.

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Table

Table 1. Table 1. Statistical summary of standardized regression coefficients for direct and indirect effects for reduced model. AD = indirect effect for TSNOW on FFD mediated by SPD, BD = indirect effect for AGDU on FFD mediated by SPD. Number of asterisks indicate level of significance for p-value: * $p \leq 0.05$, ** $p \leq 0.01$, *** $p \leq 0.001$.

Species	A SPD~TSNOW	B SPD~AGDU	C FFD~AGDU	D FFD~SPD	AD	BD
<i>Ranunculus rhomboides</i>	0.590**	0.244	0.696***	0.180	0.106	0.050
<i>Cerastium arvense</i>	0.653***	0.190	0.708***	0.200	0.131	0.038
<i>Ranunculus abortivus</i>	0.727***	0.173	0.693***	0.446	0.324	0.077
<i>Oxalis violacea</i>	0.680***	0.290*	0.544*	0.120	0.082	0.035
<i>Sisyrinchium angustifolium</i>	0.653***	0.190	0.618**	0.261	0.170	0.049
<i>Trillium cernuum</i>	0.759***	0.095	-0.113	0.405	0.308	0.039
<i>Lithospermum incisum</i>	0.759***	0.095	0.862***	-0.063	-0.048	-0.006
<i>Pedicularis canadensis</i>	0.469**	0.322*	-0.096	0.708	0.332	0.228
<i>Zizia aurea</i>	0.740***	0.220*	0.732***	0.161	0.119	0.035
<i>Vicia americana</i>	0.513***	0.388**	0.502	-0.129	-0.066	-0.050
<i>Cypripedium candidum</i>	0.745***	0.172	0.413	-0.689*	-0.514*	-0.118
<i>Achillea millefolium</i>	0.644***	0.113	0.731**	0.019	0.012	0.002
<i>Anemone canadensis</i>	0.745***	0.172	0.830***	-0.067	-0.050	-0.012
<i>Oxytropis lambertii</i>	0.763***	0.014	0.164	0.366	0.280	0.005
<i>Rosa arkansana</i>	0.745***	0.172	0.576**	0.478**	0.356**	0.082
<i>Penstemon grandifloras</i>	0.750***	0.206	-0.192	0.450	0.338	0.092
<i>Penstemon gracilis</i>	0.740***	0.212	0.633*	0.089	0.066	0.019
<i>Zigadenus elegans</i>	0.473***	0.371**	0.771***	0.294***	0.139*	0.109*
<i>Oenothera nuttallii</i>	0.566*	0.367	-0.099	0.336	0.190	0.123

Figure Legends

Figure 1. Full path diagram (a) and reduced path diagram excluding DOBG (b). The reduced path diagram was used for the structural equation modeling.

Figure 2. Box plots of the first flowering day (FFD) of 19 plant species from the Bluestem Prairie reserve in Clay county, MN. Observations were made between 1942-1961 and 2012-2020. Box plots indicate distribution quartiles and standard error bars.

Figure 3. Path diagrams with standardized regression coefficient estimates labeled. Number of asterisks indicate level of significance for p-value: * $p \leq 0.05$, ** $p \leq 0.01$, *** $p \leq 0.001$.

Figure 4. Simple linear regressions of FFD as a function of SPDX for each species with best-fit lines based on least-square estimates. Results for species are organized in order of flowering sequence over the season from early spring to late summer.

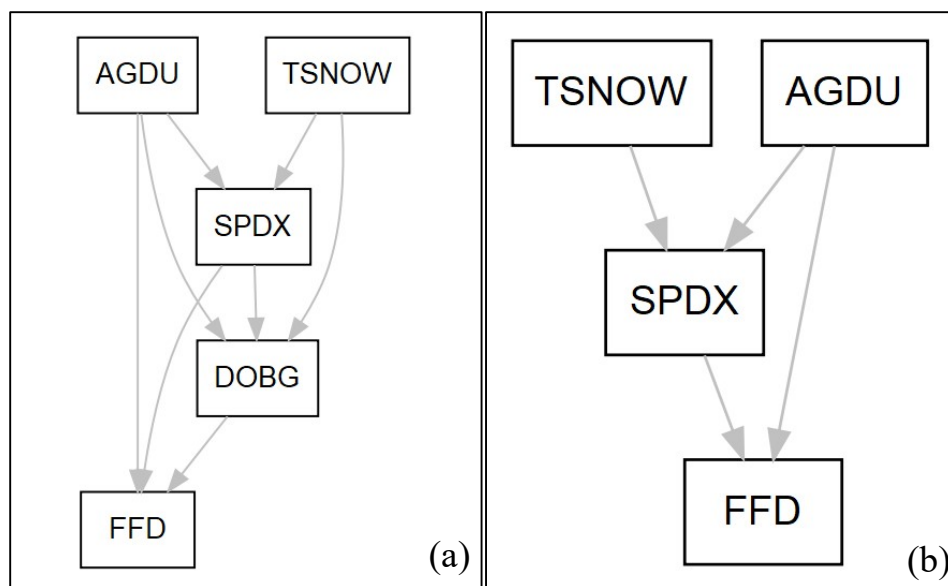


Figure 1.

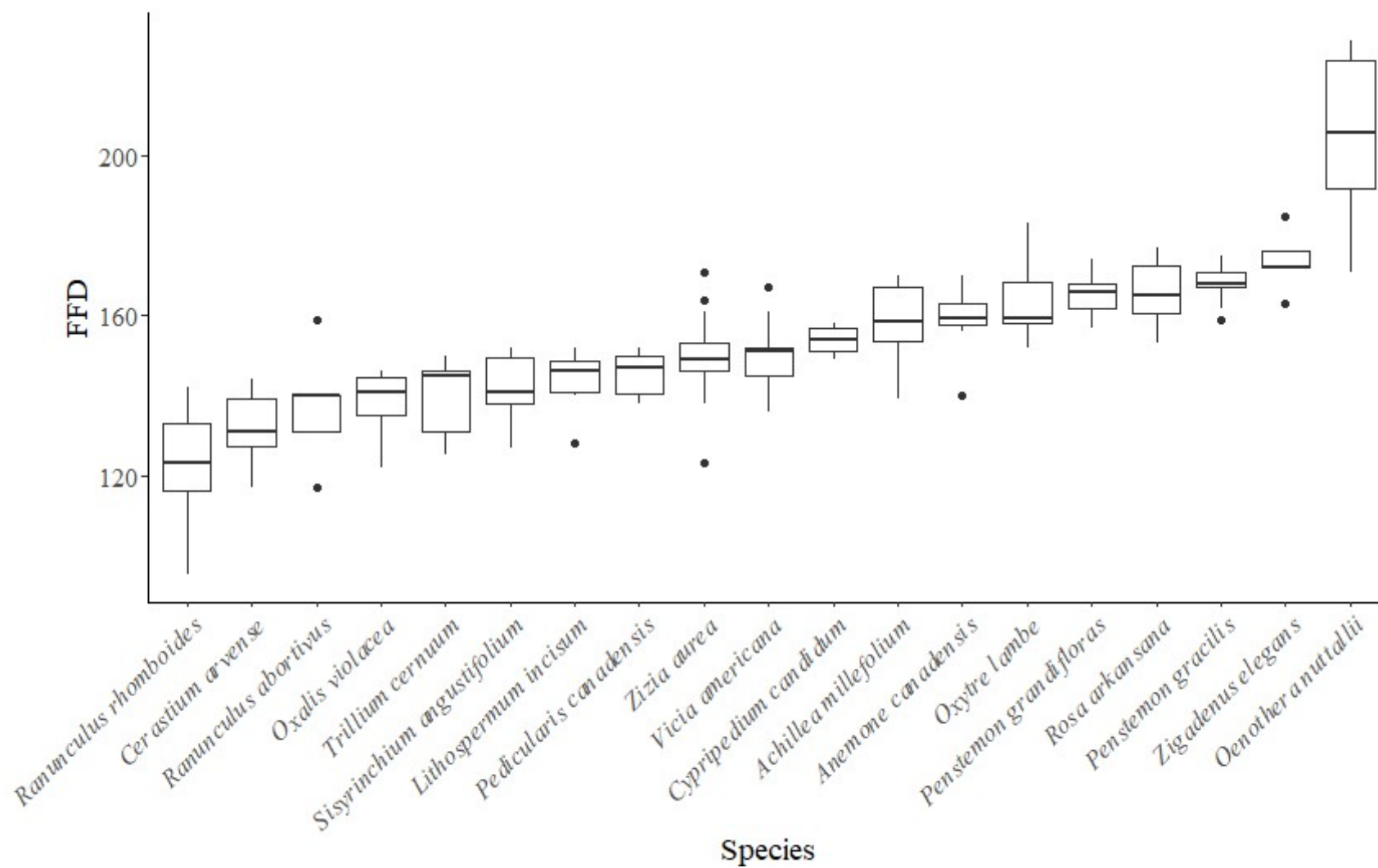


Figure 2.

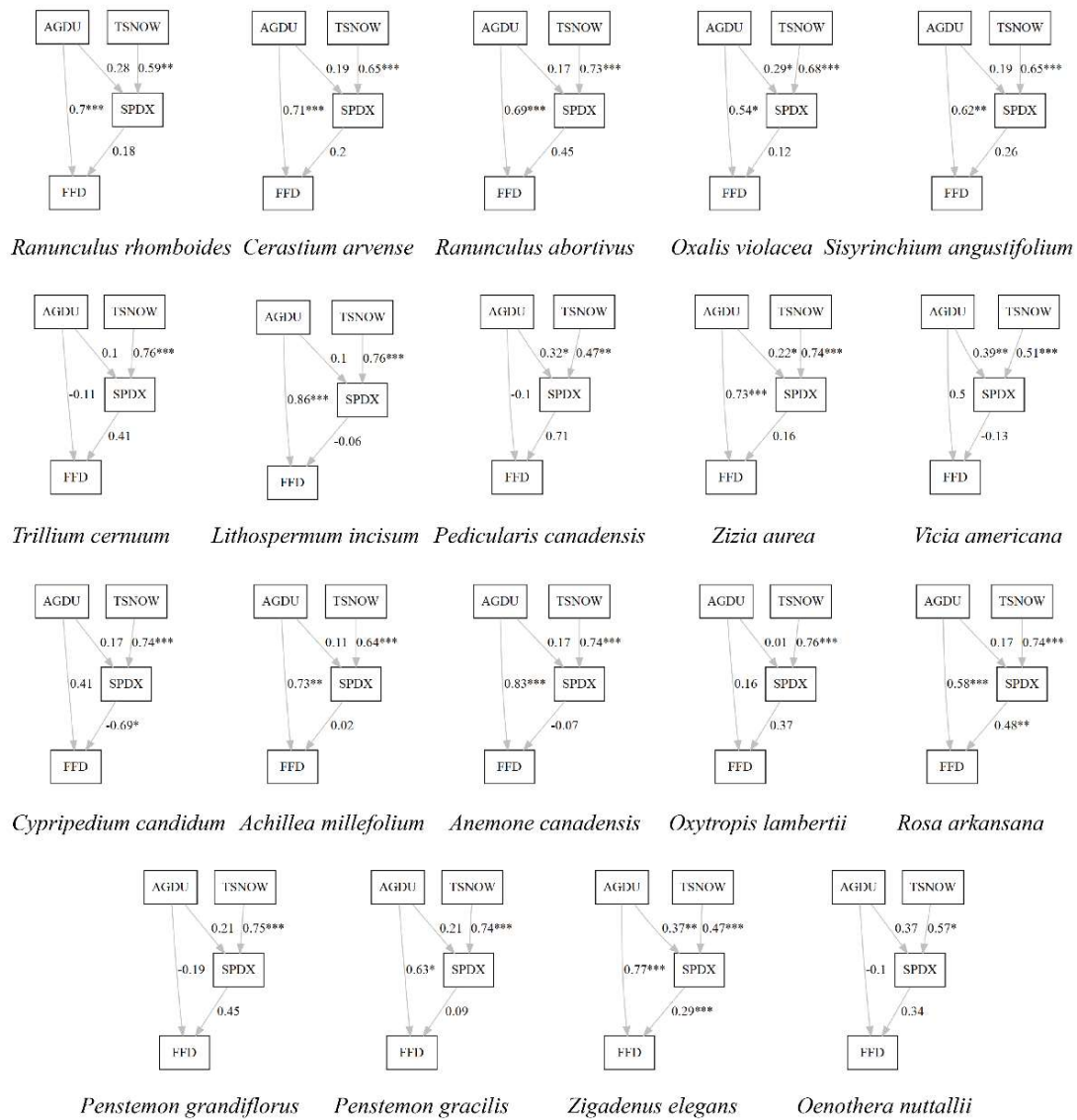


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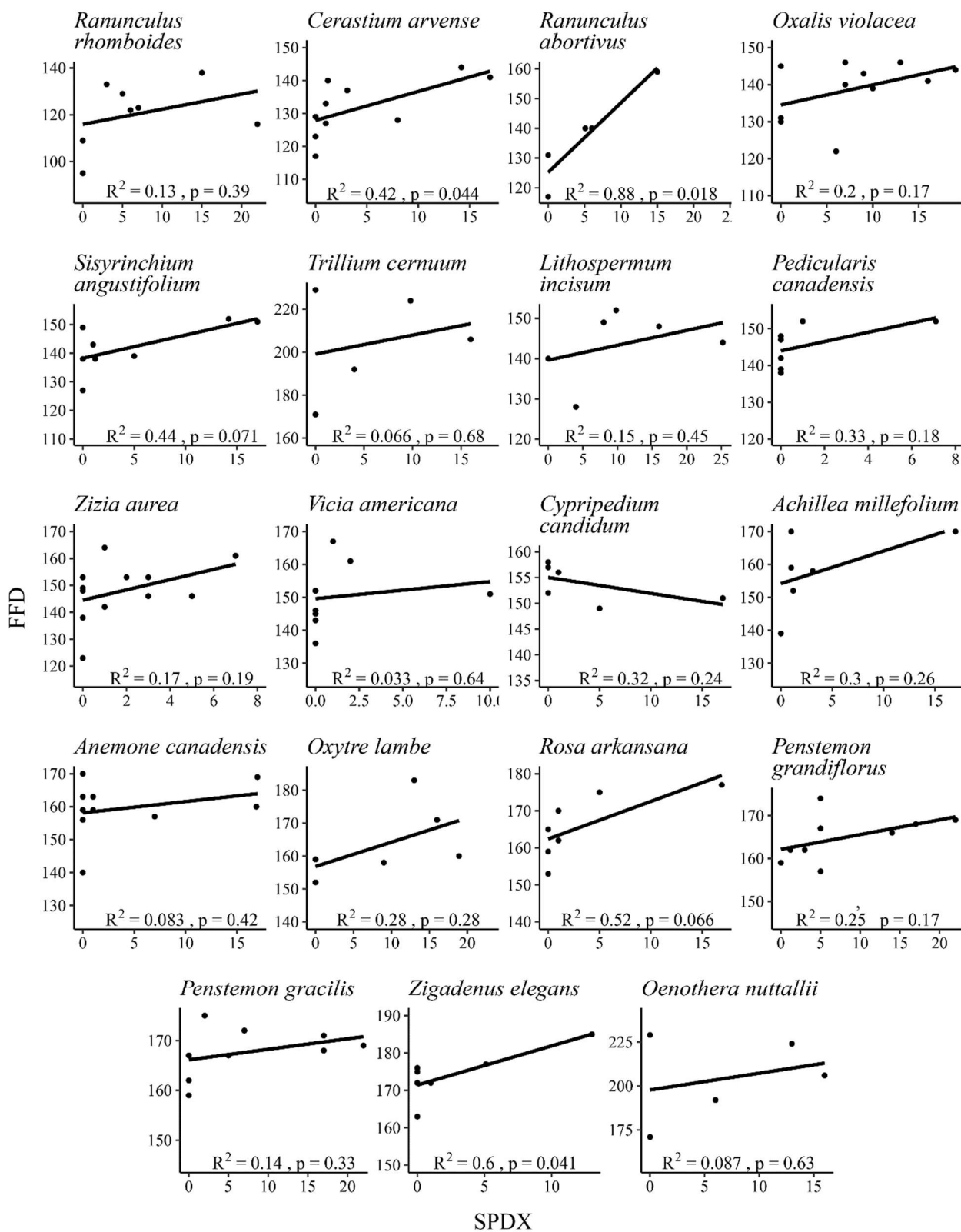


Figure 4.