

Climatic factors controlling plant sensitivity to warming

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Abstract Plant sensitivity to warming can be expressed as β or the number of days of advance in leafing or flowering events per 1 °C of Mean Annual Temperature (MAT) change. Many local studies demonstrate that β estimates for spring flowering species are usually larger than estimates for plants flowering in summer or fall. Until now, however, neither observational nor experimental estimates of this parameter were considered to be climate or geographically dependent. Here we question this paradigm through reanalysis of observational β estimates and mathematical modeling of the seasonal warming signal. Statistical analysis of a large number of bulk (averaged over species) estimates of β derived from the Pan European Phenology Data network (PEP725) revealed a positive spatial correlation with MAT, as well as a negative correlation with the Seasonal Temperature Range (STR). These spatial correlations of bulk β values as well as interseasonal variability in β were explained using a simple deterministic model of the Thermal Growing Season (TGS). More specifically, we found that the geographic distribution of bulk plant sensitivity to warming as well as the seasonal decline of β were controlled by the seasonal patterns in the warming signal and by average soil thermal properties. Thus, until recently, plants managed to keep pace with climate warming by shifting their leafing and flowering events by the same number of days as the length of the period of weather suitable for their growth. Our model predicts, however, an even greater increase in the TGS for subsequent increases in MAT. Depending on how they interact with other factors such as changes in precipitation and increased temperature variability, these longer thermal growing seasons may not be beneficial for plant growth.

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1 Introduction

In the geologic past, changes in temperature and precipitation significantly altered the distribution of plant species and had a strong impact on their evolution (e.g., Tivy 1996). Modern climate warming, however, occurs much more rapidly. During the last 3–4 decades the average MAT in the Northern Hemisphere (NH) increased at the rate of 0.2–0.3 °C per decade (Lugina et al. 2007; Hansen et al. 2006; Jones et al. 2013). By the end of this century, MAT in the NH could increase by another 2–4 °C (IPCC 2007). In central and northern Europe, this increase could be even larger and might exceed 5 °C (IPCC 2007). The time scale of these changes is comparable to the life span of many long-lived plants. Trees might become extinct or acclimate to new conditions depending on their phenotypic plasticity and the magnitude of warming (Rosenzweig et al. 2007). Phenotypic plasticity can manifest itself, for example, through the adjustment of leafing and/or flowering dates to warmer climates. The exact limits of this type of adjustment are not, however, known.

For the bulk of wild and horticultural species, mostly from mid-latitudes of the NH, the average observed plant sensitivity to warming is 2.5–6.0 days per 1 °C (e.g., Chmielewski and Rötzer 2001; Menzel 2003; Menzel et al. 2006). Recently, Wolkovich et al. (2012) estimated the sensitivities of wild plants and found a similar range of average β : 4–6 days per °C MAT change, which is 4–8 times higher than estimates of β from controlled warming experiments. This finding is important, because numeric values of β from controlled warming experiments are often used in carbon cycle and climate models to predict future changes in atmospheric carbon dioxide and climate.

Wolkovich et al. (2012) did not find any significant correlations between observed β and climatic variables. Instead, they found that wild plants that flower/leaf out early in the season exhibit greater sensitivity than plants that flower/leaf out late in the season. This particular finding is not new. Analysis of long-term phenologic records has demonstrated a stronger response to warming by early blooming plants compared to plants which bloom/leaf later in season (e.g. Menzel and Fabian 1999; Menzel 2000; Moeller 2004; Sherry et al. 2007; Sparks et al. 2010; Cook et al. 2012).

Here, we show that most of these findings can be explained not through some inherited features of individual species, but rather through seasonality of the warming signal itself. In other words, different responses of species to the same change in MAT might not depend on differences in species genotypes, but on the shift in the thermal regime that controls their growth during a particular season or at a specific geographic location.

2 Materials and methods

2.1 Data and statistical model

We use observational estimates of β derived from the Pan European Phenology data base (PEP725). These estimates were derived by Wolkovich et al. (2012). For individual locations, PEP725 often presents multiple records of the First Flowering Day (FFD) and the First Leafing Day (FLD) events covering various observational periods. Wolkovich et al. (2012) paired these records with the corresponding MAT records from a gridded set of daily climatic data available from the European Climate Assessment (ECA). For each pair of phenological and MAT records, the long-term sensitivity of plants to MAT change was estimated as the linear regression coefficient between variations in flowering/leafing events and MAT.

Only about 50 % of all estimates by Wolkovich and others were statistically significant ($p < 0.05$); however, in their analysis of the dependence of β on MAT they used both statistically significant and insignificant estimates. Their primary motivation for this approach was to avoid a bias towards species with high sensitivity to warming (Wolkovich et al. 2012). The low statistical significance of their β estimates, however, may not have necessarily been caused by a weak response of some species to a strong warming signal, but could also have resulted from sampling over regions with very weak warming trends, where such large changes in flowering or leafing dates would not be expected, or simply by high variability in the data. Analysis of regional temperature trends from 1976 to 2000 demonstrate, for example, a much stronger increase in MAT at high latitudes and over interior continental regions, while coastal areas, as well as relatively low latitudes, show weaker MAT trends (Lugina et al. 2007). The western UK, for example, has experienced weak warming of 0.2 °C per decade, whereas central and eastern Europe have experienced much stronger warming of 1 °C MAT per decade (Hansen et al. 2006). Weak local warming should lead to smaller shifts in FFD/FLD, and thus, to a low signal to noise ratio, causing low statistical significance in the regression. High noise in the data could have been caused by the short period of some FFD and FLD records, which often were limited by 1–5 years of observations. Therefore, in order to avoid the inclusion of records without a clear climatic signal into the analysis, we filtered the results of Wolkovich et al. (2012) by statistical significance, and found 57,272 FFD- and 11,771 FLD-based estimates of statistically significant β ($p < 0.05$). These are individual estimates of β which were collected at 1,587 locations with FFD records and at 1,288 locations with FLD records. The latter locations mostly overlapped with the earlier locations. Most of the statistically insignificant values of β that were filtered out were derived from records of 15 y or shorter, while statistically significant results were obtained via records with an average length of greater than 25 y (see [Supplementary Information](#)). Because some sites are located within 0.5° latitude or longitude from each other, the gridded climatological dataset from ECA gives the same MAT values for locations with various β values. In order to reduce noise in β estimates caused by coarse climatic resolution, we sorted β estimates by average MAT values and found 693 unique FFD- and 653 FLD-based estimates of β . These estimates were assigned to individual clusters within a 0.5° radius. Each cluster was characterized by the central coordinates, β , MAT, STR and by the number of records used to obtain average values (see [Supplementary Information](#)).

Most of these records were concentrated over Western and Central Europe, including Germany, Belgium, Austria and the Czech Republic. Despite a rather small geographic region covered by the bulk of the data, the maps exhibited a rather high spatial variability of β estimates as well as average MAT and STR values (see Fig. 1S, 2S in [Supplementary Information](#)). The large variability in climatic data could be explained not only by the difference in climatic conditions between coastal and interior continental regions, but also by the effect of mountain ridges. Overall, however, the data showed an increase in plant sensitivity towards coastal areas, and towards southern Europe (Fig. 2S in [Supplementary Information](#)).

We began our statistical analysis by estimating the covariance between the MAT and STR records. The next step was to estimate the values of the coefficients for the multiple linear regressions between plant sensitivity and the climatic variables:

$$\beta = \alpha_0 + \alpha_1 MAT + \alpha_2 STR + \varepsilon, \quad (1)$$

where α_0 – intercept, $\alpha_{1,2}$ – coefficients of the variables MAT and STR, and ε - residuals. Finally, we estimated the spatial autocorrelation of residuals in Eq. 1. More specifically, we used ArcGIS to calculate Moran's index (Moran 1950) for regions with clusters of PEP725

sites (Fig. 1). Moran's index can change from -1 (perfect dispersion) to $+1$ (perfect clustering). A Moran's index of zero indicates a random spatial pattern or absence of spatial autocorrelation. Absence of spatial autocorrelation of residuals indicates robustness of multiple regression models, but a low autocorrelation of residuals does not necessarily prove that the regression reflects on a direct physical linkage among variables. A strong regression between β and MAT and STR, for example, could be a result of climate-regulated distribution of species with distinctly different, inherited responses to MAT. It would be difficult, if not impossible, through statistical analysis alone, to separate these inherited biological traits of species from species-invariant, direct biophysical controls of plant sensitivity by MAT and/or STR. Therefore, we conducted additional tests by employing of a simple, deterministic model, where β was calculated only from climatic variables, and did not depend on any biological factors.

2.2 Model of plant sensitivity to warming based on the concept of the Thermal Growing Season

Dependence of mean annual β on the geographic location: all other conditions being equal, plants bloom early in warm climates, and/or in unusually warm years. During the past four decades the surface air temperature in extratropical land areas increased in winter and early spring at twice the pace of the summer increase (Lugina et al. 2007; IPCC 2007; Jones et al. 2013). Therefore, the apparently stronger response to warming of early flowering plants might be a manifestation of warming signal seasonality, rather than a difference in phenotypic plasticity between early and late blooming species. It is important to keep in mind, however, that plants should respond not to MAT per se, but rather to changes in the length of the growing season.

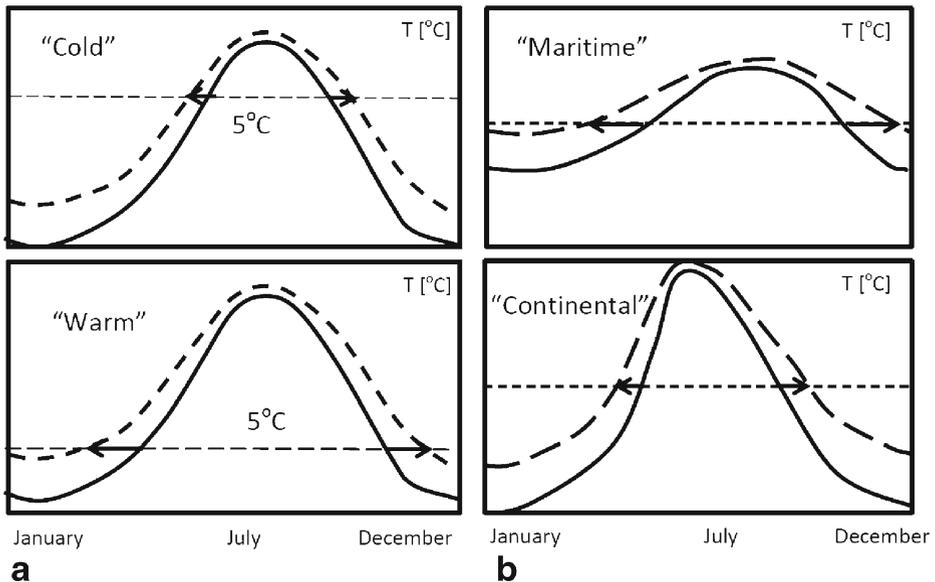


Fig. 1 The impact of a hypothetical 1 °C MAT warming on the length of the Thermal Growing Season in “cold” versus “warm” climates with the same seasonal temperature range (a), and in “continental” and “maritime” climates with the same MAT but contrasting STR values (b). The solid and dashed curved lines represent the pre-warming and post-warming distribution of seasonal temperatures, respectively. The dashed horizontal lines represent the level of the Biological Zero temperature. The arrows show extension of the TGS due to warming

Here, we hypothesize that the bulk sensitivity of plants (i.e. the average flowering or leafing for all species during the first part of the year) to MAT change (β) is controlled by the length of the Thermal Growing Season or the length of the period when soil temperature exceeds the so-called “Biological Zero” temperature. Biological Zero is “the soil temperature at a depth of 50 cm below which the growth and function of locally adapted plants are negligible” (NTCHS 2003). This concept works well in middle and high latitude climates with a pronounced cold season with temperatures below 5 °C (Rabenhorst 2005). At a given geographic location, various species typically bloom on different days (see below, where we modify our model to account for interannual variation in plant sensitivity to the warming signal). The main point of our hypothesis, however, is that if the start of the TGS shifts, for example, 5 days earlier, then it should trigger a similar advance in the annual average for spring flowering and leaf out.

In the case of hypothetical seasonally-differentiated warming (Fig. 1a), the sensitivity to warming should be highest in a “warm” climate (bottom panel) with a relatively long growing season that extends into the period with the maximum warming signal. Another climatologic variable which should control the length of the TGS, and thus the sensitivity of the growing season to warming, is the Seasonal Temperature Range. Normally, the seasonal amplitude of temperature increases towards the continental interior. Therefore, maritime climates may have the same or similar MAT as continental climates, but much weaker seasonality (Fig. 1b). As it follows from Fig. 1b, in climates with the same MAT, the sensitivity to warming should be highest in climates with low STR.

The detailed description of the deterministic model of average plant sensitivity to warming, which includes all of the features of the seasonal warming signal we discussed above, can be found in the Supplementary Information (Eqs. 1–8).

2.3 Model of intraseasonal variability of β at any single geographic location

Numerous observations demonstrate that plants blooming early have greater sensitivity to warming than plants which leaf or bloom later (Fitter et al. 1995; Miller-Rushing and Primack 2008; Mazer et al. 2013). Typically, these observations are viewed through the paradigm of “species-specific” sensitivity, meaning that the difference in sensitivity to warming between early and late blooming plants can be explained by inherited traits of these species. Here, however, we investigate an alternative explanation, namely that the weakening in the response of these different species to warming from spring to fall results from the weakening of the warming signal itself.

In this seasonal model, we postulated that the flowering or leaf-out events are regulated, at any given location, by some specific threshold temperature. This suggestion does not contradict, for example, the results of a recent analysis where the warming-related shifts in the phenologic stages of plants were linked directly to daily temperature and day length (Siebert and Ewert 2012). We can test this suggestion by comparing local data of seasonal changes in plant sensitivity with the seasonal distribution of the warming signal, as modeled by our seasonal model (see description of seasonal model in Supplementary Information (Eqs. 9–12)).

3 Results

Statistical estimates of β dependence on MAT and STR Results of the multiple regressions (Eq. 1) for FFD and FDL events versus MAT and STR are shown in Table 1. As it follows from Table 1, both datasets of observational estimates of plant sensitivity to warming (FFD and FLD-based) show a statistically significant negative correlation with MAT (coefficient α_1) and

Table 1 Coefficients of the multiple linear regressions (Eq. 1) of β dependence on MAT and STR for two phenological events: the First Flowering Day (FFD) and the First Leafing Day (FLD)

Event	α_0	$\pm\sigma_0$	α_1	$\pm\sigma_1$	α_2	$\pm\sigma_2$	r	F	p
FFD	-19.07	0.99	-0.26	0.05	0.52	0.04	0.46	97	<0.001
FLD	-11.55	0.99	-0.10	0.06	0.25	0.04	0.25	59	<0.001

positive correlation (coefficient α_2) with STR. Thus, our multiple regression model supports the suggestion we made earlier that increases in MAT or decreases in STR should increase the value of β (Fig. 1). Furthermore, analysis of the MAT and STR datasets revealed no significant correlation between MAT and STR. The Pearson Correlation Coefficient (PCC) between MAT and STR was -0.057 for FFD, and +0.005 for the FLD dataset. Thus, we can conclude that the regression we derived supports the suggested linkage between β and the climatic variables.

Our estimates reveal that the coefficient α_1 , obtained through analysis of the FFD dataset, was not different within a 95 % confidence interval from the α_1 estimated through analysis of the FLD dataset. Dependence on STR (coefficient α_2), as well as constants in both equations, were different between the FFD and FLD datasets. Overall, the dependence of β on STR was stronger than on MAT (see regression coefficients, Table 1).

Furthermore, we estimated the spatial autocorrelation of the residuals in the multiple regression (Eq. 1) and found statistically significant, near-zero values of Moran's coefficient for FFD as well as for the FLD dataset (Table 2). The low spatial autocorrelations of residuals demonstrated that the regressions we derived (Table 1) explained the major causes for spatial clustering of plant sensitivity to warming (e.g. increase towards coastal areas and towards the south). This analysis does not exclude that some mechanism other than climate may be controlling β . A species with high sensitivity to MAT, for example, could predominantly grow in warm regions within maritime climates, while species with inherited low sensitivity would grow mainly in cold, interior continental regions. Therefore, to better understand the contributions of physical versus biological factors to the result of this statistical analysis, we employed a deterministic model where the response of plants to warming was calculated solely from climatic variables.

Deterministic model of the average plant sensitivity to warming in spring (β) In Fig. 2 we show the results of the calculations for Eq. 8 (Supplementary Information). These calculations were completed for the case of a constant advance in the phase shift ($m=-1.35$ days per 1 °C MAT), and constant winter amplification of the warming signal ($n=2$). The two panels on this figure represent two extreme values of the thermal diffusivity coefficient K : 10^{-7} (a) and 1.5×10^{-6} m²/s (b). These values cover a large range of natural and agricultural soils: from moisture-saturated, dense mineral soils to dry, low density organic soils. According to this model, the entire range of β_m estimates is from -6 to -24 days per 1 °C MAT change (Fig. 2). This range

Table 2 Spatial autocorrelation of residuals in the multiple regression model (see maps and details in Supplementary Information)

Event	Moran's coefficient	p	Z score
FFD	0.045	<0.001	18
FLD	0.097	<0.001	18

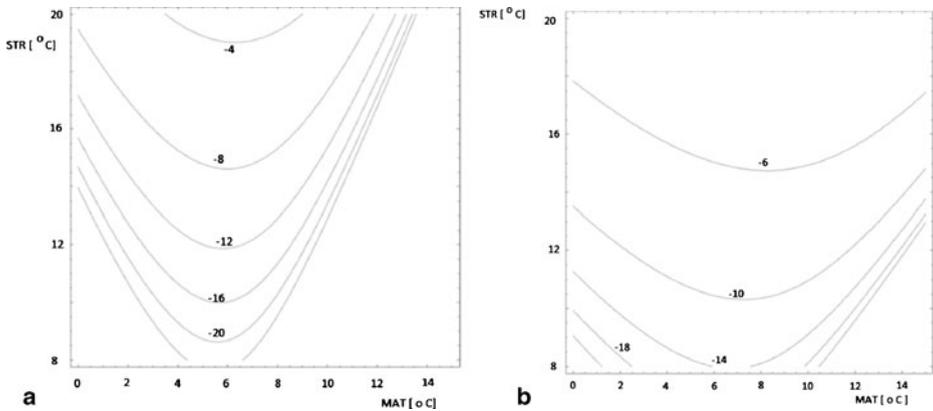


Fig. 2 Model-based plant sensitivity to warming (β_m) as function of MAT and STR for two extreme values of the soil thermal diffusivity coefficient K : 10^{-7} (a), and $1.5 \cdot 10^{-6}$ m^2/s (b)

is within the range of observed values of β found through the PEP 725 analysis: +9.1 to –30.1 days per 1°C MAT (see [Supplementary Information](#)).

The concept of the TGS as a control of the biological growing season works well only in climates with a prolonged period with soil temperature below the Biological Zero temperature (Rabenhorst 2005). Therefore, our model has some limitations. Blank areas on the right and left lower corners of Fig. 2 represent climates with extremely low STR, and either extremely high MAT (right corners), where TGS is already equal to 365 days, or extremely low MAT (left corners), where a small increase in MAT cannot form a growing season with MAT above the Biological Zero Temperature (5°C). These exceptions, however, are rare for European midlatitudes, where most of the PEP 725 data were collected (see [Supplementary Information](#)). Only 10 sites from 693 FFD and 653 FLD clusters fell into these exceptions.

The absence of a physically meaningful solution for Eq. 8 ([Supplementary Information](#)) for the extreme climatic regions does not mean, of course, that these regions should not respond to warming. It means, however, that the concept of the TGS should not be used in very warm or very cold climates. Perhaps other variables such as duration of photoperiod, moisture regime or the sum of degree days could serve as better descriptors of the growing season in these regions. Here, however, we limit our study to the midlatitudes, where we can use the concept of the TGS to depict the length of biological growing season.

3.1 Deterministic model of seasonal changes in plant sensitivity (β_s)

The dependence of plant sensitivity on the Day of Year (DoY) demonstrated by Wolkovich et al. (2012) was derived from geographically aggregated information averaged over species. It follows from our model (Eq. 12 in [Supplementary Information](#)) that changes in the DoY at a specific temperature depend on local conditions such as MAT and STR, soil physical properties and patterns of the seasonal warming signal such as the parameters “m” and “n” (see above). Therefore, to test this model we used data collected from a single location at the Poznan Botanical Garden in Poland from 1976 to 2006 (Sparks et al. 2010). These data demonstrated several features that are typical for many locations. First, they showed an overall decline in plant sensitivity from late winter to summer (Fig. 3). Second, they showed a change in the sign of sensitivity during the second part of the year after the summer temperature

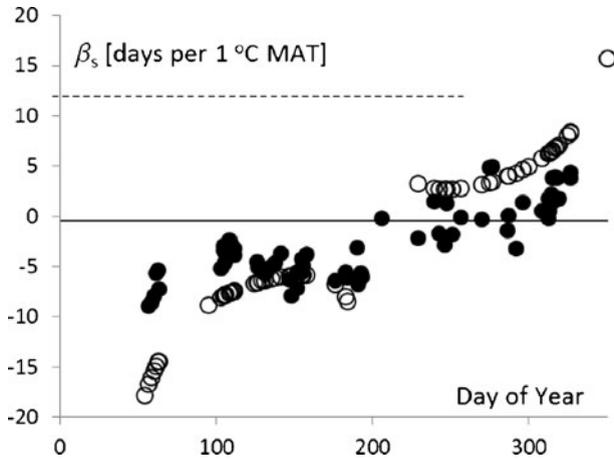


Fig. 3 Seasonal changes in plant β (vertical scale) measured using long-term records (1976–2006) of phenological and climatic observations at the Poznan Botanical Gardens (Sparks et al. 2010). The negative values of β correspond with the advance of phenological phases towards winter, while positive values of the same parameter reflect the extent of phenologic phases during the second half of year. The open circles represent model estimates of β_{s1} (negative) and β_{s2} (positive). The model calculations were performed using $K=1 \times 10^{-6} \text{ m}^2/\text{s}$; $m=1.6$ and $n=0.6$. The values of these two parameters were calculated as trends in the date of the seasonal temperature maximum (m) and the seasonal temperature range (n) from daily weather records available for this particular location through the NOAA National Climatic Data Center (www.ncdc.noaa.gov)

maximum (in Poznan, this maximum occurred around late July). The change in the sign of sensitivity means that plants flowering leafing out before the summer maximum in response to increase in the MAT shift the start of their phenologic phase towards the winter months. The positive sensitivity after the summer maximum results from shifts in the phenologic phase towards fall due to the extension of the growing season. The latter represents responses of phenologic phases such as the last day of flowering or the last day with leaves (Sparks et al. 2010). Third, overall the absolute values of plant sensitivity in the fall are lower than the absolute values of plant sensitivity in spring. As can be seen in Fig. 3, our model (open circles), with various degrees of accuracy, reproduced all these important features. There are, of course, some limitations to the model. Because seasonal temperature reaches its maximum in mid-summer, the model has asymptotic discontinuity around late July. Apparently, the actual response of plants to warming cannot show “infinite” sensitivity or have discontinuities. All of these are mathematical artifacts caused by the approximation of finite changes in plant phenologic phases with derivatives of smooth mathematical functions. Therefore, our seasonal model predicts shifts in the DoY for a specific temperature well, with the exception of about a 1 week period around the local temperature maximum which coincides with the point of discontinuity in the model.

Sensitivity of β_m to parameters It follows from Eq. 8 (Supplementary Information) that β_m is directly proportional to the value of m with a multiplier of 1. From 1950 to 2000, the average value of m was 1.35 days per 1°C of MAT (above). After 2000, the additional phase shift of seasonal temperature changes declined and became negligible, while warming in the fall months caught up with the rate of spring warming (Barichivich et al. 2013). Therefore, the entire range of possible errors in β_m due to uncertainty in the estimate of m should be from 0 to -1.35 days per 1°C MAT.

Although β_m and n are related in a non-linear manner, the impact of uncertainties in the parameter n cannot cause large errors in β_m . To constrain the sensitivity of β_m to n , we varied the latter from 1 to 3 ($\pm 50\%$) from the average estimate of 2. These calculations demonstrated that β_m could change a maximum of 10 % in response to 50 % variation in the parameter n (see Fig. 3S in Supplementary Information).

The sensitivity of the model to uncertainties in K , however, was much stronger than to the previous two parameters (comparison of panel (a) with (b) in Fig. 2). Here, we attempted to reduce uncertainty in K via calibration of the model using observational data.

3.2 Sensitivity of β_s to parameters

The decline in the absolute value of β_s with DoY can be explained by two main factors: a) decline in the STR with warming, as described by the parameter “ n ”, and b) by an asymmetrical warming signal that is stronger in the spring than in the fall (parameter “ m ”). Therefore, the decline of β with seasons weakens when both “ n ” and “ m ” decline. Another parameter of significance is the thermal diffusivity of soil (K). We choose of value of K typical for saturated garden soil (1×10^{-6} [m²/s])(Kasuda and Archenbach 1965). Changes in K , however, can influence the length of the period around the summer maximum where the model predicts much larger sensitivities than are observed (Fig. 3). For example, this region increases by a factor of two with a decrease in K by one order of magnitude. Increases in K , in turn, decrease the region around the point of asymptotic discontinuity.

Calibration of K using PEP 725 observational data At any single location K can be defined based on information about soil type and moisture regime, as we did for the case of the Poznan Botanical Garden (above). However, because soil properties change from site to site, in our estimates of the average modeled plant sensitivity for Central Europe, we calibrated K in Eq. 7 based on PEP 725 data (Supplementary Information). In other words, we estimated a value of K which allowed for the best possible agreement with the PEP 725 data by using average MAT and STR values for each location from the PEP 725 dataset to calculate corresponding values of β_m . Then, we calculated the Pearson Correlation Coefficient between β and β_m . This was done for an extremely large range of K values from 10^{-7} to 1.5×10^{-6} m²/s (Fig. 4S).

Our results demonstrated that the best agreement between the model and the observed data could be found at values of K of about 2×10^{-7} m²/s, where the correlation coefficients between β_m and β reached their maxima of about 0.52 for FFD and 0.32 for the FLD sites (Fig. 4S). At lower or higher K values the agreement with observations for both FFD and FDL sites deteriorated.

Finally, we analyzed the spatial autocorrelation of the difference between the estimate of plant sensitivity by the deterministic model (at $K=2 \times 10^{-7}$ m²/s), and the observational value of plant sensitivity: $\beta_m - \beta$. This difference represents the residual of plant sensitivity to warming, which cannot be explained by the deterministic model. Estimates of Moran’s coefficient demonstrated that the residuals of the deterministic model had a random spatial distribution (Table 3). Thus, we concluded that the deterministic model provided an adequate explanation for the patterns of geographic distribution of plant sensitivity to warming.

Overall, the deterministic model described variability in observed plant sensitivity to warming better than statistical modeling. The goodness of fit of the multiple regressions to the data was characterized by the coefficient of multiple regression r (Table 1). We marked values of these coefficients for the FFD and FDL records as parallel dashed lines in Fig. 3. The goodness of the fit of the multiple regressions was lower than the correlation coefficients between β_m and β at an optimum value of $K=2 \times 10^{-7}$ m²/s.

Table 3 Spatial autocorrelation of residuals in the deterministic model (the difference between β_m and β)

Event	Moran's coefficient	<i>p</i>	<i>Z score</i>
FFD	0.079	<0.001	4
FLD	0.064	<0.001	12

The better overall agreement of the data with the deterministic model could be explained by the strong, non-linear dependence of β on MAT (Fig. 2); at sites with a MAT of less than 4–6 °C, the dependence of β on MAT had the opposite slope compared to warmer sites. Therefore, if our deterministic model holds true, a simple linear regression can be biased towards positive or negative slopes depending on the median MAT and STR values. The median values of MAT in the FFD and FLD datasets were 8.7 and 8.8 °C, and STR values were 10.6 and 10.4 °C, respectively. The dependence of modeled plant sensitivity on MAT in the vicinity of these coordinates is positive: increases in MAT should lead to increases in the absolute value of β_m (Fig. 2). This prediction of the deterministic model was consistent with results of the statistical analysis we obtained earlier (Table 1). There were only 35 sites in the FFD and FLD aggregated datasets with MAT below 5 °C. The rest of the 693 FFD and 653 FLD sites had MAT in the range of 5 to 15° C. Therefore, it is plausible that the multiple linear regression models were biased towards a positive correlation with MAT due to a much larger number of sites located in “warm” relative to “cold” climates. The direct comparison of average observational values of β inside the clusters of PEP725 sites with corresponding modeled estimates are shown on the Fig. 5S (see Supplementary Information).

4 Discussion and conclusions

The models we employed for our analysis of average plant sensitivity (the statistical and deterministic models) predicted a strong dependence of plant sensitivity β and modelled plant sensitivity β_m on MAT and STR. More specifically, they both predicted an increase in plant response to warming with a decline in average STR and with an increase in average MAT (for sites with MAT greater than 4–6 °C). The linear regression model demonstrated a similar sensitivity to STR as the deterministic model of about 0.3–0.5 days per 1 °C change in STR (Table 1, Fig. 5S). The sensitivity to MAT in the multiple regression models (0.3 to 0.5 days per 1 °C MAT change (Table 1)) was lower than the sensitivity of the deterministic model (up to 5.0 days per 1 °C MAT change, depending on the STR value). However, the linear regression model might have underestimated the sensitivity to changes in MAT due to the non-linear nature of this dependence (Fig. 2). Therefore, the deterministic model was a better instrument for estimating the potential thermal forcing of growing season due to future warming.

The averaged observational β estimates for the aggregated FFD and FLD datasets were -9.9 ± 2.45 days per 1 °C MAT and -7.3 ± 2.1 days per 1° C MAT, respectively. The deterministic model predicted for the same PEP 725 sites an average of -7.2 ± 2.6 days per 1 °C MAT and 7.9 ± 1.9 days per 1 °C MAT, respectively. Thus, we concluded that the deterministic model successfully reproduced the average values for the PEP 725 dataset, and adequately described geographic variation in β in this dataset (above).

The seasonal changes in β_s we calculated by employing the deterministic model for a single location (Eq. 12 in Supplementary Information) at single site (Poznan Botanical Gardens,

Poland) demonstrated a good agreement with long-term observations of plant sensitivity (Fig. 4S).

Thus, all 3 models showed reasonable agreement between the model-based plant sensitivity derived only from climatic data and the actual sensitivity as observed from phenological records. This observation suggests that until recently plants have managed to keep the pace with climate warming by shifting their leafing and flowering days by the same number of days as shifts in thermal growing season. In other words, geographic changes in plant sensitivity or changes at any single location during seasons (i.e. declines in sensitivity with seasons) do not require any additional explanation. The latter hints that potential differences in biological traits among plant species have played a much smaller role in their responses to warming than seasonal patterns in the warming signal itself or than soil thermal properties. There is no guarantee, however, that plants will continue to respond to warming in the future with the same degree of plasticity.

According to IPCC projections, the average MAT in Central Europe could increase by 3–5 °C by the end of the 21st century (IPCC 2007). The same scenarios, however, do not predict an amplification of future warming in winter months. Instead, they demonstrate a monotonic warming through all seasons (IPCC 2007). Here we used a deterministic model with values typical for Central European MAT and STR to calculate possible changes in β_m due to 3–5 °C of warming. For these calculations we used values of $m=0$ and $n=1$ (no additional shift in the phase of winter amplification), and average $K=2 \times 10^{-7}$ m²/s. Our results demonstrated that warming of 3–5 °C in MAT should increase β_m by 4–7 days per 1 °C MAT, or nearly double the modern average value of plant sensitivity to warming in Central Europe. By multiplying these new estimates of plant sensitivity by the projected degree of warming, we demonstrate that the advance of flowering/leafing events by the end of the 21st century is on the order of an additional ½ –2 months. This potentially large advance of the growing season could cause immense stress for modern perennial plants with life spans greater than 70–100 years.

As global warming continues plants might not be able to keep pace with warming by shifting their leafing or flowering days. Without exact knowledge of the physical forcing of these changes, such as relationships between MAT, STR and TGS, it will be difficult, if not impossible, to estimate the species-specific thresholds of this type of phenotypic plasticity.

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