RESEARCH PAPER

Latitudinal patterns in the phenological responses of leaf colouring and leaf fall to climate change in Japan

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ABSTRACT

Aim To estimate the potential effect of global climate change on the phenological responses of plants it is necessary to estimate spatial variations at larger scales. However, previous studies have not estimated latitudinal patterns in the phenological response directly. We hypothesized that the phenological response of plants varies with latitude, and estimated the phenological response to long-term climate change using autumn phenological events that have been delayed by recent climate change.

Location Japan.

Methods We used a 53-year data set to document the latitudinal patterns in the climate responses of the timing of autumn leaf colouring and fall for two tree species over a wide range of latitudes in Japan (31 to 44 N). We calculated single regression slopes for leaf phenological timing and air temperature across Japan and tested their latitudinal patterns using regression models. The effects of latitude, time and their interaction on the responses of the phenological timings were also estimated using generalized linear mixed models.

Results Our results showed that single regression slopes of leaf phenological timing and air temperature in autumn were positive at most stations. Higher temperatures can delay the timing of leaf phenology. Negative relationships were found between the phenological response of leaves to temperature and latitude. Single regression slopes of the phenological responses at lower latitudes were larger than those at higher latitudes.

Main conclusions We found negative relationships between leaf phenological responsiveness and latitude. These findings will be important for predicting phenological timing with global climate change.

Keywords

Air temperature, ginkgo, Japan, latitude, maple, phenology, spatial variation.

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INTRODUCTION

Recent changes in climate such as increases in air temperature have been found to affect plant phenological events such as earlier onset of flowering and leaf unfolding in the spring and delayed onset of leaf colouring and leaf fall in the autumn (e.g. Menzel *et al.*, 2001, 2006a; Walther *et al.*, 2002; Parmesan & Yohe, 2003; Root *et al.*, 2003; Gordo & Sanz, 2005; Wolfe *et al.*, 2005).

To estimate the potential effect of global climate change on the phenological response of a plant it is necessary to estimate spatial variations at larger scales (i.e. global and continental scales). Root *et al.* (2003) analysed global patterns of phenological responses to recent climate changes. Their meta-analysis

suggested that the mean phenological shifts between latitudes 50 and 72 N were larger than those between 32 and 50 N. However, Menzel *et al.* (2006a) suggested that the phenological responses of plants to temperature in warmer countries were stronger than those in colder countries of Europe.

This discrepancy indicates that the responses of phenological events in plants to climate change, including increases in air temperature, may vary with latitude. Most previous studies, however, did not estimate latitudinal patterns in phenological responses, although phenological responses at sites with similar latitudes have been analysed. Data analyses of phenological responses as a function of latitude are still uncommon, and the phenological response to latitude remains one of the big

questions unanswered by previous studies (Peñuelas *et al.*, 2002; Menzel, 2003; Menzel *et al.*, 2006a).

We hypothesized that the phenological response of plants varies with latitude, and estimated the phenological response to long-term climate change using autumn phenological events that have been delayed by recent climate change. The phenological response of trees in Germany was determined by temperature in several months preceding the phenological event (Estrella & Menzel, 2006). Changes in leaf colouring and leaf fall during the past several decades have been similar to changes in spring phenology, such as flowering and leaf unfolding in the Mediterranean region (Peñuelas *et al.*, 2002). In Japan, the timing of leaf fall clearly changed with latitude (e.g. Matsumoto *et al.*, 2003).

The aim of the present study was to estimate latitudinal patterns in leaf phenological responses to climate change in autumn. Using a 53-year data set for the phenological timing of leaf colouring and leaf fall of trees, we estimated the latitudinal patterns in phenological responses to air temperature. In addition, the relationships between phenological events and climate change have been principally studied in North America and Europe (e.g. Walther *et al.*, 2002; Menzel, 2003; Root *et al.*, 2003; Gordo & Sanz, 2005; Menzel *et al.*, 2006a,b; Richardson *et al.*, 2006), while published studies in Asian regions are still very limited (but see Chen & Pan, 2002; Matsumoto *et al.*, 2003; Doi, 2007; Doi & Katano, 2008; Doi *et al.*, 2008). Moreover, studies of the autumn phenological response are limited (but see Estrella & Menzel, 2006; Menzel *et al.*, 2006a; Richardson *et al.*, 2006). The present study focused on the phenological response to recent climate change in autumn across Japan. It also contributes to the understanding of patterns of phenological change in Asia and of autumn phenological responses.

MATERIALS AND METHODS

Phenology data set

The Japan Meteorological Agency (JMA) monitored leaf colouring and leaf fall dates across Japan for *Ginkgo biloba* and *Acer palmatum* from 1953 to 2005. The JMA defined 'leaf colouring day' as the date when most of the leaves of *G. biloba* and *A. palmatum* were yellow or red, with no green leaves. Additionally, 'leaf fall day' was defined as the date when approximately 80% of leaves had fallen at each JMA observation station (JMA, 1985).

Many studies have focused on the growth periods (e.g. periods from leaf unfolding day to leaf fall day) of plants in response to recent climate change (e.g. Menzel & Fabian, 1999; Matsumoto *et al.*, 2003); however, other phenological periods, such as the period of leaf colouring, are still unknown. Thus, we calculated 'leaf fall periods' (unit: days) from leaf colouring and leaf fall day (Julian date) at each site as follows:

leaf fall periods (in days) = leaf fall day − leaf colouring day

We selected JMA stations across Japan based on two criteria: consistent data collection must have occurred over 25 years and the altitude must be lower than 300 m above sea level. These

constraints limited the effect of air temperature due to altitudinal differences (Kaneko, 1965). By preliminary analysis, we analysed four stations over 300 m (altitude 418–610 m), and the phenological responses were different from those of stations at similar latitude but lower altitude. Consequently, 63 JMA station records were selected for *G. biloba* and 64 for *A. palmatum* (*G. biloba* 31.3–43.0 N, 128.5–141.6 E, altitude 0.5–273 m; *A. palmatum* 31.3–44.0 N, 128.5–144.2 E, altitude 1.6–155 m). Fifty-two stations were selected for both *A. palmatum* and *G. biloba*. The 63 JMA stations for *G. biloba* were the same as those used by Matsumoto *et al.* (2003).

Climate data set

The monthly mean air temperature at each JMA site was calculated for August to December from 1953 to 2005. We also used the monthly mean air temperature of the sites in spring (March to May), since increased spring temperatures can delay leaf colouring (Menzel *et al.*, 2003).

Statistical analysis

Phenological responses to temperature were analysed using simple linear regression of the phenological timings (leaf colouring day, leaf fall day and leaf fall period) against the mean temperatures of the following four periods: (1) in the month of the mean date of phenology (leaf colouring day, leaf fall day and starting date of leaf fall period), (2) in the month and the preceding month, (3) in the month and the preceding 2 months, and (4) in spring (March to May). We tested the Pearson correlation coefficients and linear regression slopes of the relationships by one-way analysis of variance (ANOVA, factors; four periods) and Tukey multiple comparison. To estimate the latitudinal patterns of phenological responses, we used single linear, exponential, logarithmic and quadratic regression models. The best model was selected based on the Akaike information criterion (AIC) values.

To analyse the effects of latitude, time (year) and their interaction on the responses of phenological timing (leaf colouring day, leaf fall day and leaf fall period), generalized linear mixed models (GLMMs) were run by the statistical software program R version 2.5.1 (R Development Core Team, 2007) using the lmer function with a Gaussian distribution of the lme4 library. The model fit was calculated using maximum likelihood methods. The explanatory variables – latitude and year – were mean centred and the site number assigned to each JMA observation station was included as a random effect in the GLMMs. Models with and without the interaction term of latitude and year were compared based on AIC values to determine whether the effect of the interaction was supported by the data.

RESULTS

Latitudinal patterns in climate and leaf phenology

Air temperature was significantly correlated with latitude across Japan. From 1953 to 2005, the mean temperature from August to
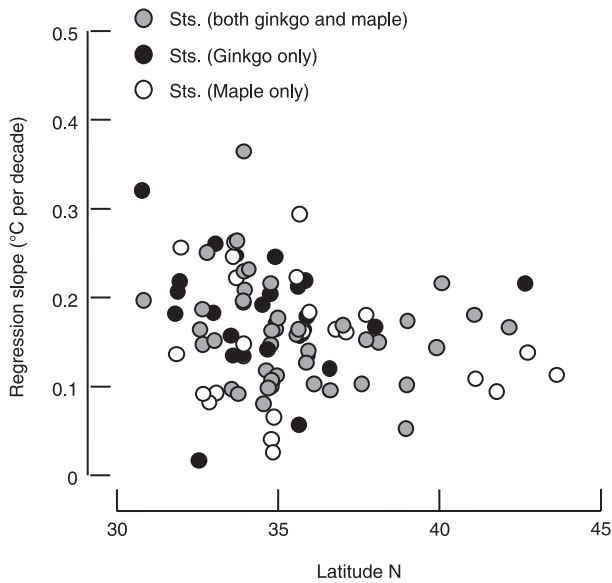
Figure 1 Latitudinal trends in regression slope (°C per decade) between air temperature from October to December and time from 1953 to 2005 at the sites for *Ginkgo biloba* and *Acer palmatum.*
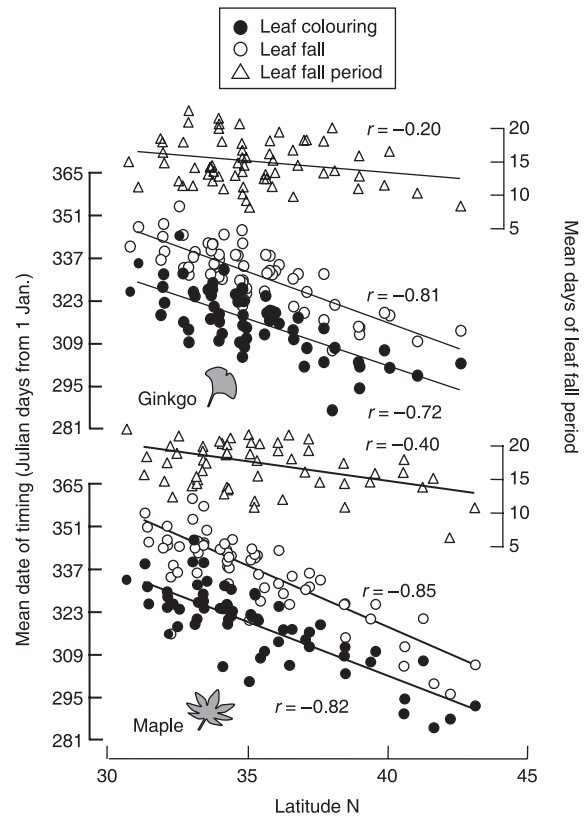

Figure 2 Mean date of leaf colouring (closed circles), fall (open circles) and fall period (open triangles) for *Acer palmatum* and *Ginkgo biloba* from 1953 to 2005. Dates are shown as Julian days (1 January = 1). The *r* values are shown as Pearson's correlation coefficient (all *P* values < 0.05).

December for the *G. biloba* sites ranged from 10.7 to 20.5 °C, and those for the *A. palmatum* stations ranged from 8.7 to 20.5 °C. The mean air temperature in autumn over the observed period decreased significantly with latitude ($r = -0.90$ for *A. palmatum* and -0.92 for *G. biloba*, $P < 0.001$). Spring mean air temperatures (March to June) varied among the stations for *G. biloba* and *A. palmatum* (13.3–22.0 °C and 10.6–22.0 °C, respectively), and significantly decreased with latitude ($r = -0.94$ and -0.96, respectively, $P < 0.001$, data not shown). The mean regression slopes of the autumn temperature against time at the *G. biloba* and *A. palmatum* stations were positive: 0.22 ± 0.08 °C and 0.20 ± 0.08 °C per decade, respectively. At lower latitudes, the regression slope of air temperature in autumn tended to be higher than those at higher latitudes (Fig. 1).

Mean leaf colouring and leaf fall day in autumn from 1953 to 2005 correlated significantly with latitude ($r = -0.72$ to -0.85, $P < 0.001$, Fig. 2). Among stations at lower latitudes, the leaf colouring day and leaf fall day tended to differ slightly, while they were appreciably different at stations at higher latitudes. The mean leaf fall periods from 1953 to 2005 at each station tended to decrease with latitude ($r = -0.20$, $P = 0.2$, for *G. biloba* and $r = -0.40$, $P < 0.01$, for *A. palmatum*, Fig. 2).

The effects of latitude, year and their interaction on the responses of phenological timing were estimated by GLMMs (Table 1). The model with the interaction term of latitude and year was selected as the best model for the leaf colouring day and leaf fall day of both *A. palmatum* and *G. biloba*. These results suggested that the phenological timing of colouring and fall of *G. biloba* and *A. palmatum* should differ with latitude. For example, the leaf colouring day of *G. biloba* was delayed for 0.16 days per decade with decreasing latitude, in addition to the delay of 2.6 days per decade regardless of the latitude.

Relationships between leaf phenology and air temperature

Among the four periods of mean air temperature, the correlation and regression slopes between leaf colouring and leaf fall and mean temperature in the month of the mean date of phenology and the two preceding months were significantly higher than those in the other three periods, except those of leaf colouring of *G. biloba* (ANOVA, $F = 130.5$, $P < 0.001$, and Tukey multiple comparison, $P < 0.05$, Table 2). With air temperature in spring, regression slopes for leaf colouring and leaf fall day of *G. biloba* and *A. palmatum* were positive at most stations, but they were not significant at 32–42 sites. The results showed that spring temperature did not strongly influence leaf phenology. In fact, the leaf phenology of both trees was considered to be correlated mainly with autumn air temperature (Matsumoto & Fukuoka, 2002).

Latitudinal pattern of changes in the leaf phenological response

The regression slopes for leaf colouring day of *G. biloba* and *A. palmatum* against air temperature in the month of the mean

Table 1 Generalized linear mixed models (GLMMs) to estimate the effects of latitude, year and their interactions on phenological trends. The lowest Akaike information criterion (AIC) value per model is given in bold.

Species	Phenology	Coefficients				
		Latitude	Year	Latitude × year	Intercept	AIC
Ginkgo biloba	Colouring	−2.790	0.259	−0.016	317.6	**18,603**
		−2.798	0.257		317.6	18,612
	Fall	−3.010	0.168	−0.009	331.5	**17,867**
		−3.019	0.167		331.5	17,870
	Fall period	−0.250	−0.093	0.009	13.7	**16,476**
		−0.243	−0.093		13.7	16,480
Acer palmatum	Colouring	−3.620	0.330	−0.012	320.7	**20,018**
		−3.620	0.330		320.7	20,029
	Fall	−4.090	0.206	−0.012	337.8	**19,176**
		−4.100	0.206		337.8	19,184
	Fall period	−0.449	−0.138	0.002	16.7	17,714
		−0.448	−0.138		16.7	**17,712**

Table 2 Mean correlation coefficients and regression slope (mean ± 1 SD) between leaf phenology and mean air temperature. Mean air temperature was represented by monthly mean temperature in the month of mean date of phenology (leaf colouring day, leaf fall day and starting date of leaf fall period), in the month and a preceding month, in the month and two preceding months, and in spring (March to May). Bold numbers indicate the highest significant values in Tukey multiple comparisons ($P < 0.05$).

		Leaf colouring	Leaf fall	Fall period
Correlation				
Ginkgo biloba	Month of mean phenology	0.32 ± 0.17	0.27 ± 0.16	−0.02 ± 0.18
	Month + preceding month	**0.42 ± 0.15**	0.34 ± 0.16	−0.08 ± 0.17
	Month + preceding 2 months	**0.42 ± 0.16**	**0.44 ± 0.17**	−0.05 ± 0.19
	Spring (March–May)	0.28 ± 0.18	0.26 ± 0.19	−0.09 ± 0.18
Acer palmatum	Month of mean phenology	0.37 ± 0.13	0.20 ± 0.15	−0.06 ± 0.19
	Month + preceding month	0.38 ± 0.11	0.30 ± 0.18	−0.10 ± 0.20
	Month + preceding 2 months	**0.47 ± 0.13**	**0.42 ± 0.19**	−0.10 ± 0.19
	Spring (March–May)	0.27 ± 0.18	0.23 ± 0.20	−0.09 ± 0.19
Regression slope				
Ginkgo biloba	Month of mean phenology	2.26 ± 1.39	1.59 ± 1.05	−0.14 ± 0.77
	Month + preceding month	3.73 ± 1.72	2.34 ± 1.24	−0.40 ± 0.86
	Month + preceding 2 months	**4.27 ± 2.04**	**3.76 ± 1.89**	−0.40 ± 1.45
	Spring (March–May)	3.45 ± 2.37	2.65 ± 2.09	−0.82 ± 1.45
Acer palmatum	Month of mean phenology	2.97 ± 1.45	1.46 ± 1.26	−0.41 ± 1.09
	Month + preceding month	3.71 ± 1.68	2.56 ± 1.83	−0.90 ± 1.67
	Month + preceding 2 months	**5.28 ± 2.21**	**4.35 ± 2.41**	−0.88 ± 1.62
	Spring (March–May)	3.84 ± 2.91	2.86 ± 2.76	−0.90 ± 1.83

date of phenology and the two preceding months decreased significantly with latitude ($r = -0.46$ for *G. biloba* and $r = -0.34$ for *A. palmatum*, $P < 0.05$, Fig. 3). For leaf fall day, the regression slopes for *G. biloba* and *A. palmatum* with air temperature decreased significantly with latitude ($r = -0.44$ for the exponential model and $r = -0.36$ for the linear model, respectively, $P < 0.05$). Except for 5–10 sites, leaf colouring day and leaf fall day correlated with air temperature ($P < 0.05$). At lower latitudes, the regression slopes for leaf colouring day and leaf fall day varied, while at

higher latitudes the variability of the slopes was small. For leaf fall periods, the regression slopes for *G. biloba* and *A. palmatum* with air temperature were not significantly related to latitude ($r = 0.13$ and $r = 0.01$, $P > 0.1$, Fig. 3).

DISCUSSION

In this study, we identified negative relationships between leaf phenological responsiveness and latitude. The leaf phenological
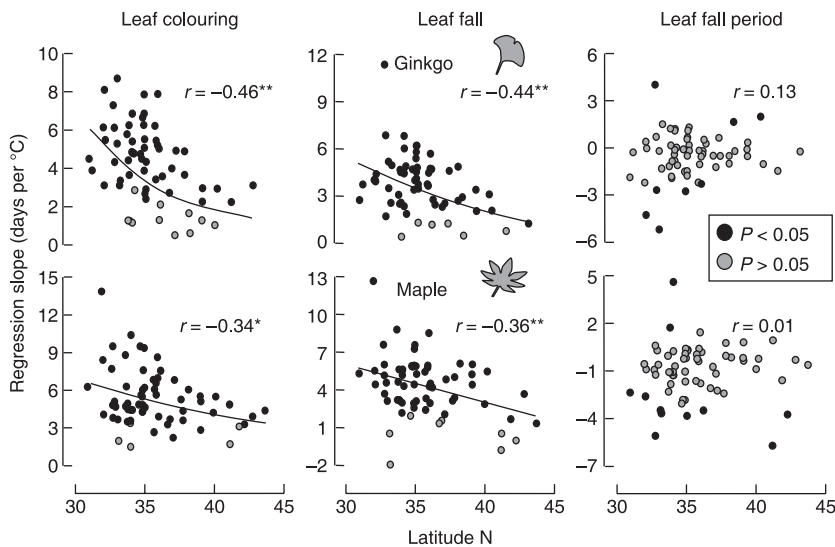
Figure 3 Latitudinal patterns of regression slope (days per C) between leaf phenological event (leaf colouring, fall and fall periods) for *Ginkgo biloba* and *Acer palmatum* and air temperature in the month of mean phenology and two preceding months from 1953 to 2005. Black and grey circles indicate the results of regression analysis; $P < 0.05$ and $P > 0.05$, respectively. The regression lines shown for leaf colouring and leaf fall represent slope as an exponential function of latitude. *, ** and no asterisk indicate $P < 0.05$, $P < 0.01$, and $P > 0.05$, respectively.

responses at lower latitudes were larger than those at higher latitudes. Menzel *et al.* (2006a) also suggested that the phenological response of plants to temperature in warmer countries was stronger than that found in colder countries, although Root *et al.* (2003) have suggested the opposite. Thus, our findings support the hypothesis of Menzel *et al.* (2006a). Root *et al.* (2003) compared the phenological response between 50 and 72 N and 32 and 50 N. Most study sites (31–44 N) were between 32 and 50 N; however, such latitudinal variation in Japan makes a difference to the phenological response of plants. These findings will be important in predicting changes in phenological timing in response to global climate change.

The phenological responses of leaves of both *G. biloba* and *A. palmatum* to air temperature were positive at most stations. Warmer temperatures might delay the timing of leaf phenology. The phenological response of leaves to air temperature at lower latitudes was larger than that at higher latitudes. Latitudinal patterns in temperature may cause latitudinal patterns in phenological responses of leaves. Air temperature at lower latitudes has increased more than at higher latitudes over the past five decades in Japan. Thus, differing changes in temperature between latitudes may cause latitudinal patterns in the responses of leaves to temperature. Day length is also different at different latitudes (Forsythe *et al.*, 1995) and affects plant phenology (e.g. Nizinski & Saugier, 1988; Schaber & Badeck, 2003). In Japan, the timing of leaf fall in of trees including *Acer* is affected by day length (Misawa & Takakura, 1990); however, seasonal and latitudinal patterns in day length have not changed during the last five decades. Therefore we did not consider day length to be a factor that would change the latitudinal patterns of the phenological response in the last five decades.

To summarize, the present study showed that latitudinal patterns in the responses of leaf colouring and leaf fall phenology correlate with air temperature. The phenological responses at lower latitudes were stronger than those at higher latitudes. Our findings indicate that we should consider phenological responses to differ with regard to latitude and climate change.

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Editor: Martin Sykes