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Delayed response of spring phenology to global warming in subtropics and tropics

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ABSTRACT

Climate drivers of plant phenology in the subtropics and tropics are still unclear, which significantly hinders accurate prediction of climate change impacts on vegetation growth and carbon balance in these unique ecoregions. The basic hypothesis of process-based phenology models is that spring tree phenology is regulated by temperature and triggered by chilling temperatures during the dormancy period, followed by forcing temperatures during the growth period. That is, trees require cool temperatures during a chilling period to break endodormancy, and then enter the phase of ecodormancy during which the rate of ontogenetic development increases with increasing air temperature. Therefore, insufficient chilling requirements may slow bud growth and consequently delay budburst. Many studies have shown that chilling requirement is at present sufficient to release bud dormancy fully in temperate regions, and thus forcing temperatures play a dominant role in triggering spring tree phenology. To identify differences in mechanisms of spring tree phenology responses to air temperature between the subtropics/tropics and the temperate zone, and their possible effects on future phenological trends under global warming, we used leaf unfolding and flowering data from a tree species of tropical origin, *Melia azedarach*, and output daily mean air temperature data from a regional climate model (HadGEM3-RA) for the period 1981–2005 at 42 stations in southeastern China to fit unified forcing and chilling phenology models. Then, we selected optimum models for each phenophase at each station. Moreover, we predicted leafing and flowering dates across the research region over 2021–2100 under global climate warming scenarios. The results show a previously unreported phenological phenomenon: chilling will often be insufficient to break bud dormancy in the northern tropical zone and may become a crucial factor limiting leafing and flowering responses to spring warming. However, chilling will still be sufficient to break bud dormancy in the warm temperate zone, and thus may not limit leafing and flowering responses to spring warming there. Consequently, predicted leafing and flowering dates both will be delayed in the northern tropical zone but will advance in the warm temperate zone from 2021 to 2100. In the subtropical zone, the effect of chilling temperature on spring phenology will be reduced gradually from earlier to later phenophases. Thus, predicted leafing and flowering dates show decreased delaying trends and increased advancing trends from earlier to later phenophases in the subtropical zone. Our findings suggest that insufficient chilling temperature accumulation during the dormancy period may counteract the forcing temperature accumulation during the growth period in the northern tropical zone and parts of the subtropical zone, resulting in delayed leafing and flowering dates.

1. Introduction

The changing rate and direction of plant phenology in response to climate change are diversified, depending highly on geographical locations, time scales, and specific species (Menzel, 2003; Matsumoto et al., 2003; Gordo and Sanz, 2010; Chen and Xu, 2012; Chen et al., 2015). Therefore, revealing environmental and biological mechanisms of the diversified phenological responses across different climate zones is key to predicting accurately vegetation phenology at regional and continental scales (Morin et al., 2009; Xu and Chen, 2013). Process-based phenology models provide a reliable and effective tool to identify external and internal mechanisms of phenological responses.

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Numerous studies have shown that spring phenology is highly dependent on temperature during both the endodormancy phase and the ecodormancy phase (Hänninen and Kramer, 2007; Chuine et al., 2003). Photoperiod may also influence budburst but the magnitude of the effect is generally minor (Bernier, 1988; Mouradov et al., 2002; Laube et al., 2014). So far, no evidence has demonstrated that photoperiod is more dominant than temperature when predicting leafing and flowering, even in beech—one of the species most sensitive to photoperiod (Kramer, 1994a; Vitasse et al., 2009; Chuine et al., 2010). Thus, the basic hypothesis of process-based phenology models is that spring tree phenology is controlled by air temperature and triggered by a period with chilling temperatures followed by a period with forcing temperatures (Chuine, 2000). Because chilling temperatures may accelerate bud growth from the state of quiescence to the state of budburst, in addition to breaking dormancy (Nelson and Lavender, 1979; Cannell and Smith, 1983; Murray et al., 1989; Hänninen et al., 1993), insufficient chilling due to rapid late winter-early spring air temperature increase may slow bud growth and consequently delay budburst. By contrast, forcing temperatures may also promote bud growth after bud dormancy has been released in spring (Cannell and Smith, 1983; Hunter and Lechowicz, 1992; Kramer, 1994b; Chuine, 2000), and early fulfilment of forcing requirements under rapid spring air temperature increase may speed up bud growth and advance budburst. Therefore, budburst timing might be attributed to the net effect of temperature variations on the fulfilment of chilling and forcing requirements.

Generally speaking, the less chilling temperatures are received, the more forcing temperatures are subsequently needed to trigger budburst (Chuine, 2000). To date, many process-based phenology models have been established to simulate and predict spring phenology of temperate-zone trees, and its responses to regional and global climate change (Cannell and Smith, 1983; Murray et al., 1989; Hänninen, 1990; Kramer, 1994a, 1994b; Chuine et al., 1998, 1999; Chuine, 2000; Linkosalo et al., 2008; Morin et al., 2009; Richardson and O'Keefe, 2009; Luedeling et al., 2011; Fu et al., 2012; Xu and Chen, 2013). Overall, results show that the fulfilment of forcing requirements is not necessarily influenced by the fulfilment of chilling requirements in triggering spring tree phenology. That is, models excluding chilling requirements were best supported by the data, while models including both forcing and chilling requirements were less well supported (Chuine, 2000; Linkosalo et al., 2008; Morin et al., 2009; Richardson and O'Keefe, 2009; Parker et al., 2011; Vitasse et al., 2011; Fu et al., 2012; Xu and Chen, 2013). This implies that chilling requirements are currently sufficient to release fully bud dormancy of trees in many temperate regions of the world even though dramatic late winter-early spring temperature increases have occurred. Therefore, forcing temperature is currently the main trigger of spring phenology.

Observed spring phenological advancement and its response to forcing temperature in the Northern Hemisphere over the past decades (Fitter et al., 1995; Peñuelas and Filella, 2001; Fitter and Fitter, 2002; Walther et al., 2002; Parmesan, 2007; Cook et al., 2012) verify the above process-based modeling. Recently, a few studies based on statistical models and experimental approaches found that several temperate species are responsive to cold temperature in the previous autumn and winter (Cook et al., 2012; Laube et al., 2014; Roberts et al., 2015). Species that are highly sensitive to chilling, such as hawthorn and birch, were predicted to be delayed or advance less (Roberts et al., 2015). However, sensitive species detected by statistical models and experimental approaches were inconsistent (Laube et al., 2014; Roberts et al., 2015). Moreover, responses to autumn and winter temperatures were strongest for early-flowering species, and declined for species that normally flower later in spring and summer (Cook et al., 2012; Roberts et al., 2015).

By contrast, climate drivers of plant phenology in the subtropics and tropics are still unclear (Hatta and Darnaedi, 2005; Sanchez-Azofeifa et al., 2013), which significantly hinders accurate prediction of climate change impacts on vegetation growth and carbon balance in these unique ecoregions. A statistical analysis of data from the northern tropical zone of China detected a dominant delaying trend in budburst and flowering dates of tropical plants, which are mainly influenced by increasing temperature. In contrast, rainfall showed little effect on spring phenological variation (Zhao et al., 2013). Nevertheless, whether the delayed spring phenology in tropics of China is induced by insufficient chilling requirement is unknown. Moreover, a process-based rough estimate of winter chilling for temperate fruit and nut trees across the entire terrestrial globe indicates that warm regions are likely to experience severe reductions in available winter chilling, potentially threatening production there (Luedeling et al., 2011). However, no robust surface evidence has been detected so far for a warmer winter-induced insufficient chilling requirement and delayed spring phenology in the subtropics and tropics. To address this gap in our knowledge, which hinders assessments of how spring phenology in the subtropics and tropics is responding to climate warming, this study presents the results of process-based modeling using first leaf unfolding (FLU), 50% leaf unfolding (50% LU), first flowering (FF) and 50% flowering (50% F) data from a tree species of tropical origin, *Melia azedarach*, and daily mean air temperature data at 42 stations across southeastern China from 1981 to 2005 (Fig. 1 and Table 1). The scientific questions we intend to answer are: 1) Whether mechanisms of spring tree phenology response to air temperature are different in different climate zones and different seasonal stages (phenophases), and if so, why?; 2) Do occurrence dates of spring tree phenology indicate a delayed trend in response to global warming in the subtropics and tropics, and if so, why?; and 3) How do effects of chilling and forcing temperatures on spring tree phenology interact?

2. Materials and methods

2.1. Study area and tree species

The study area is located in southeastern China from 19.0°N to 35.4°N and from 106.6°E to 120.5°E, covering approximately 1.58 million km^2, which accounts for 16.5% of China's land area (Fig. 1, Table 1). The climate is characterized by monsoonal winds and a variety of climatic types. There are five climate zones from south to north, namely, northern tropical, southern subtropical, middle subtropical, northern subtropical and warm temperate zones (China Meteorological Administration, 1979). The annual mean air temperature decreases from 23.8 °C in the south to 11.9 °C in the north and the annual mean total precipitation decreases from 1878.7 mm in the southeast to 579.5 mm in the northwest. The topographic structure in this area is composed of fluvial plains, low mountains, and hills with an average elevation less than 500 m. The dominant vegetation types from south to north include rain forest, evergreen broadleaf forest, deciduous and evergreen broadleaf mixed forest, and deciduous broadleaf forest on the low mountains and hills, as well as cultivated vegetation on the plains.

To detect the diversified responses of spring tree phenology to climate warming over the large geographical ranges, we selected *Melia azedarach* (Meliaceae) as the indicator species. *Melia azedarach* is a deciduous tree with odd-pinnate leaves, about 10 m tall. The leaflets are opposite, blades ovate or elliptic. The thyrsus is similar in length to leaves. Flowers are fragrant and lilac-colored. It grows widely in mixed evergreen broad-leaved and deciduous forests, sparse forests, field margins, roadsides at elevations between 500 and 2100 m from warm temperate to northern trop-