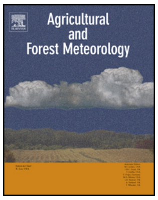
Agricultural and Forest Meteorology 181 (2013) 33–42

Contents lists available at ScienceDirect

Agricultural and Forest Meteorology

journal homepage: www.elsevier.com/locate/agrformet



Differential responses of trees to temperature variation during the chilling and forcing phases☆

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ARTICLE INFO

Article history:
Received 12 April 2013
Received in revised form 21 June 2013
Accepted 25 June 2013

Keywords:
Chestnut
Cherry
Walnut
chillR
Partial Least Squares regression
Phenology

ABSTRACT

Temperate-zone trees must fulfill cultivar-specific chilling and heat requirements during the dormant period, in order to produce leaves and flowers in the following growing season. Timing and accumulation rate of chill and heat are understood to determine the timing of spring events, but both processes are difficult to observe in dormant tree buds. Where long-term phenological observations are available, Partial Least Squares (PLS) regression offers a statistical opportunity to delineate phases of chill and heat accumulation and determine the climatic requirements of trees. This study uses PLS regression to explore how the timing of spring events of chestnut in China, cherry in Germany and walnut in California is related to variation in the daily rates of chill and heat accumulation, as calculated with horticultural models. Dependent variables were 39 years of flowering dates for chestnuts in Beijing (China), 25 years of cherry bloom in Klein-Altendorf (Germany) and 54 years of walnut leaf emergence in Davis (California, USA). These were related to daily accumulation rates of chill, calculated with the Dynamic Model, and heat, calculated with the Growing Degree Hours Model. Compared to an earlier version of the procedure, in which phenological dates were related to unprocessed temperature data, delineation of chilling and forcing phases was much clearer when using horticultural metrics to quantify chill and heat. Chestnut bloom in the cold-winter climate of Beijing was found to depend primarily on the rate of heat accumulation, while cherry bloom in the temperate climate of Germany showed dependence on both chill and heat accumulation rates. The timing of walnut leaf emergence in the mild-winter climate of California depended much more strongly on chill accumulation rates. Chilling (in Chill Portions = CP) and heat (in Growing Degree Hours = GDH) requirements determined based on PLS regression were 79.8 ± 5.3 CP and 13,466 ± 1918 GDH for chestnut bloom in Beijing, 104.2 ± 8.9 CP and 2698 ± 1183 GDH for cherry bloom in Germany, and 37.5 ± 5.0 CP and 11,245 ± 1697 GDH for walnut leaf emergence in California. Spring phases of cherry in Klein-Altendorf and especially chestnut in Beijing will likely continue to advance in response to global warming, while for walnut in California, inadequate chilling may cause delays in flowering and leaf emergence. Such delays could serve as an early-warning indicator that future productivity may be threatened by climate change. The R package 'chillR' makes the method used in this study available for wider use.

1. Introduction

Plants in temperate climates have responded to recent climatic changes (Chmielewski and Rötzer, 2001; Menzel et al., 2006; Parmesan and Yohe, 2003). Spring phases in particular have been affected, with leaf emergence and bloom of many species occurring significantly earlier now than a few decades ago (Fitter and Fitter, 2002), and showing clear advancing trends (Parmesan, 2007). However, there are notable exceptions to these developments (Cook et al., 2012). At some locations, for vegetation at high altitudes (Yu et al., 2010, 2012) and high latitudes (Frich et al., 2002; Kozlov and Berlina, 2002), spring phases have in fact occurred later in recent years, in spite of clear warming trends. Some fruit trees grown in areas that are substantially warmer than their native habitat have also responded with delayed spring phases to extraordinarily warm conditions during the winter (Elloumi et al., 2013). The

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http://dx.doi.org/10.1016/j.agrformet.2013.06.018

most likely explanation for these exceptions to common trends is the need for climatic cues during plant dormancy (Campoy et al., 2011; Saure, 1985). Especially perennial plants from temperate and cold climates, but also seeds of many annuals, undergo dormancy in winter to avoid frost damage to sensitive tissue (Vegis, 1964). Perennial plants lose their leaves and reduce physiological activity substantially to withstand cold winter temperatures (Saure, 1985). Come spring, plants must emerge from this protective state, develop leaves and flowers, and resume full physiological activity. Temperature has been found to be the most important environmental variable influencing plants' progression through dormancy (Campoy et al., 2011; Luedeling, 2012), possibly modulated by daylength for many species (Blümel and Chmielewski, 2012). It is commonly assumed that two separate temperature responses are responsible for ending dormancy in perennial species: a chilling requirement, which is fulfilled by a phase of cool conditions, and a heat requirement (forcing), which is satisfied by high temperature (Luedeling et al., 2009f).

Depending on the particular climatic requirements of species and the location where they are grown, increasing temperatures may not necessarily have a phenology-advancing effect (Luedeling, 2012). While warming during the heat accumulation (forcing) phase almost certainly advances budbreak and flowering, increasing temperatures during the previous chilling phase may have the opposite effect (Guo et al., 2013; Luedeling and Gassner, 2012; Luedeling et al., in press). If chill accumulates more slowly during the winter, chilling requirements may be fulfilled later, delaying heat accumulation and ultimately leading to later bloom or leaf emergence. This effect can be compensated, at least in part, if warming occurs during both the chill and heat accumulation phases. Heat is then accrued faster in spring, so that plants may be able to make up for delays during the chilling phase (Luedeling, 2012). Strongly delayed spring phases can also be observed, when chilling requirements are not completely fulfilled (Erez, 2000). At least for some species, greater heat accumulation can then compensate for insufficient winter chill (Harrington et al., 2010).

Several recent studies have shown that winter chill has been declining in many temperate and subtropical regions throughout the world and is likely to continue decreasing in the future (Baldocchi and Wong, 2008; Darbyshire et al., 2011, 2013; Luedeling, 2012; Luedeling et al., 2009b,d, 2011a). This trend will almost certainly affect perennials from temperate and cool subtropical locations that depend on winter chill for completion of their annual cycles. For fruit and nut trees in particular, these developments could precipitate into substantial problems in the future that will require many growers to adapt by revising their choice of tree species or cultivar (Darbyshire et al., 2011, 2012; Luedeling et al., 2009b,d). Unfortunately, prominent knowledge gaps currently constrain the ability of researchers and growers to project impacts of climate change on tree phenology (Campoy et al., 2011; Dennis, 2003; Luedeling, 2012). Models commonly used to quantify winter chill are fairly inaccurate (Luedeling and Brown, 2011; Luedeling et al., 2009e), and there is considerable uncertainty about the chilling and heat requirements of species and cultivars. It has also been shown that chilling requirements estimated with common models may not be valid in a different climate or at a location that is different from where the trees' climatic needs were determined (Luedeling and Brown, 2011; Luedeling et al., 2009f). Furthermore, it is unclear, which phases during the dormancy season are relevant for chill and heat accumulation. The main reason for these knowledge gaps is the lack of visible indicators for chill and heat accumulation during dormancy. While some change occurs in buds during this period, it is difficult to detect and does not as yet allow clear differentiation between chill and heat accumulation phases.

Where long-term temperature and phenology records are available, Partial Least Squares (PLS) regression has recently been used to statistically determine and visualize different stages during dormancy progression (Luedeling and Gassner, 2012; Luedeling et al., in press). This method, which is widely used in the fields of chemometrics (Wold, 1995) and hyperspectral remote sensing (Luedeling et al., 2009c; Min and Lee, 2005), allows the establishment of correlations between a large number of independent factors and one or several dependent variables. The procedure is based on latent factors, a form of principal components, which are constructed as linear combinations of the independent variables and then correlated with the dependent variables (Wold, 1995; Wold et al., 2001). In contrast to more conventional regression approaches, this strategy avoids problems with autocorrelation between independent variables, and it works well even when the number of independent variables substantially exceeds the number of observations. PLS regression thus allows the correlation of daily temperatures with spring phenological dates. The resulting models describe the effects of deviation from normal temperature conditions during the winter on phenological dates.

In previous studies, distinct temperature response phases have been detected by PLS regression for walnuts in California (Luedeling and Gassner, 2012; Luedeling et al., in press), for cherries in Germany (Luedeling et al., in press) and for chestnuts in China (Guo et al., 2013). In all of these studies, daily temperatures were used as independent variables. The results from these analyses provided valuable clues about temperature response timing during dormancy. However, they did not consider quantifications of the temperature-dependent effectiveness of chill and heat effects, which have been derived by horticultural researchers from experiments and observations (Anderson and Seeley, 1992; Fishman et al., 1987a,b). In this study, we refine the PLS approach by relating spring phenology dates not directly to day-to-day variation in temperature, but to daily accumulation of chill and heat units according to common horticultural models. This additional analysis step helps define chilling and forcing periods during dormancy more clearly than earlier approaches. We use the resulting delineations to update earlier estimates of chilling and forcing requirements.

2. Materials and methods

2.1. Phenology and temperature records

Three phenology datasets were used in the analysis. Bloom dates of chestnuts were collected from the garden of the former Royal Summer Palace in Beijing, China (40.02°N, 116.33°E, 50 m a.s.l.) (Guo et al., 2013). The dataset contains data for 39 years between 1963 and 2008 (no observations were available for 1969–1971 and 1997–2000). Daily minimum and maximum temperature were sourced from an official weather station in Beijing, just 2.5 km from the observation site.

Bloom data of cherry cv. 'Schneiders späte Knorpelkirsche' were collected at Klein-Altendorf, Germany, at the research station of the University of Bonn (50.40°N, 6.99°E, 160 m a.s.l.). Twenty-five years of observations were available, collected between 1984 and 2008 (no observations were available for 1985) (Luedeling et al., in press). Daily weather data were recorded on the same station (Blanke and Kunz, 2009; Luedeling et al., 2011b).

Phenology data for several walnut cultivars have been recorded at the University of California Davis, USA (38.54°N, 121.78°E, 20 m a.s.l.) since 1953. We selected leaf emergence dates of the cultivar 'Payne' as the spring phenology indicator with the greatest number of available observations. Data for 54 years between 1953 and 2007 were available (no observations for 1996) (Luedeling et al., 2009f). Daily weather data were obtained from the university's weather