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Delayed chilling appears to counteract flowering advances of apricot in southern UK

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ABSTRACT

Temperatures are rising across the globe, and the UK is no exception. Spring phenology of perennial fruit crops is to a large extent determined by temperature during effective chilling (endo-dormancy) and heat accumulation (eco-dormancy) periods. We used the apricot flowering records of the UK National Fruit Collections (NFC) to determine the influence of temperature trends over recent decades (1960–2014) on apricot (*Prunus armeniaca* L.) flowering time. Using Partial Least Squares (PLS) regression, we determined the respective periods for calculating chill and heat accumulation.

Results suggested intervals between September 27th and February 26th and between December 31st and April 12th as the effective chilling and warming periods, respectively. Flowering time was correlated with temperature during both periods, with warming during chilling corresponding to flowering delays by 4.82 d °C^{-1}, while warming during heat accumulation was associated with bloom advances by 9.85 d °C^{-1}. Heat accumulation started after accumulating 62.7 ± 5.6 Chill Portions, and flowering occurred after a further 3744 ± 1538 Growing Degree Hours (above a base temperature of 4 °C, with optimal growth at 26 °C). When examining the time series, the increase in temperature during the chilling period did not appear to decrease overall chill accumulation during the chilling period but to delay the onset of chill accumulation and the completion of the average chill accumulation necessary to start heat accumulation. The resulting delay in heat responsiveness appeared to weaken the phenology-advancing effect of spring warming. These processes may explain why apricot flowering time remained relatively unchanged despite significant temperature increases. A consequence of this may be a reduction of frost risk for early flowering crops such as apricot in the UK.

1. Introduction

Phenological records provide valuable data for characterizing the effect of variation in environmental conditions on plant development. Frequently, these records cover a longer time span than any defined experiment, making them one of the most valuable pieces of evidence of the impacts of global warming over past decades or even centuries (Fitchett et al., 2015; Menzel et al., 2008). Flowering time of fruit crops is one of the most widely used indicators of climate change, because of the availability of such records, but also because of the strong temperature dependence of the fruit crop life cycle (El Yaacoubi et al., 2014; Martínez-Lüscher et al., 2016). Although the vast majority of case studies have reported significant advances in flowering times over the years (Chmielewski et al., 2011; Chmielewski and Rotzer, 2001; Fitter and Fitter, 2002; Fu et al., 2015; Legave and Clauzel, 2006; Menzel et al., 2006; Parmesan, 2007; Parmesan and Yohe, 2003; Root et al., 2003; Wolfe et al., 2005), the literature includes a considerable number of records describing observations of flowering times that have remained unchanged or even experienced delays (Cook et al., 2012; Elloumi et al., 2013; Fitter and Fitter, 2002; Kozlov and Berlina, 2002; Legave et al., 2013; Menzel et al., 2006; Yu et al., 2010). Recent studies have indicated that the response of plant phenology to temperature is more complex than simply an advance due to warming

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(Andreini et al., 2014; Chuine et al., 2016; Cook et al., 2012; Guo et al., 2015; Pope et al., 2014).

Temperate deciduous trees enter a period of winter dormancy, during which they are leafless and their buds stay dormant awaiting suitable conditions to resume growth when temperatures rise. Apricots (*Prunus armeniaca* L.), like most temperate fruit crops, have an obligatory chilling requirement that must be fulfilled before trees can produce flowers (Campoy et al., 2011b; Luedeling, 2012). This means that they need a period of cool temperatures during the winter before normal budburst takes place (Campoy et al., 2011b; Campoy et al., 2013). The need to fulfil this chill requirement prevents these plants from flowering during short warm spells in winter, since flower development is prevented even when temperatures are favourable. The time when the chill requirement has been met marks the end of endo-dormancy. Subsequently, during the eco-dormant period, budburst can be induced by warm temperatures (Lang et al., 1987). It occurs after sufficient accumulation of heat above a base temperature (measured in Growing Degree Days or Growing Degree Hours), which is often cultivar/species dependent (Campoy et al., 2011a; Luedeling, 2012).

For modelling purposes, chill and heat requirements have been conceptualized in different ways. The most common concept is one of sequential fulfilment of chilling and heat requirements, in which there is a period, before fulfilment of the chilling requirement, when buds are insensitive to heat accumulation, followed by the warming phase, when additional chilling has no effect. After sufficient heat has then accumulated to fulfil the heat requirement, bud burst occurs (Darbyshire et al., 2013; Guedon and Legave, 2008; Luedeling et al., 2009). A rather different concept proposes that chilling and heat accumulation start at a similar time and budburst is possible after a combination of chilling and heat accumulation. This indicates a trade-off between chill and heat accumulation, with abundant heat being able to compensate for low chilling, and vice versa (Harrington and Gould, 2015; Harrington et al., 2010; Murray et al., 1989). This model assumes that plants with an obligatory chill requirement must first receive a minimum chilling dose (critical chilling units). Subsequently, high heat accumulation might induce bud burst. However, this heat requirement is reduced by exposure to additional chilling. Other modelling efforts for almonds have described this as an overlap between chilling and warming period, with a model assuming a budbreak-advancing effect of additional chilling until fulfilment of 75% of the heat requirement being best supported by field data (Pope et al., 2014). Experiments under controlled environment conditions also suggest that additional chilling during the early warming period may decrease the heat requirement (Couvillon and Erez, 1985). Since previous delineations between chilling and warming periods through PLS regression have also indicated an overlap between the phases, it seems plausible to differentiate between three temperature-responsive phases between the onset of bud dormancy and flowering: 1) only chilling accumulation has a flowering-advancing effect, 2) both chilling and heat accumulation are effective, and 3) only heat accumulation may promote bud development (Guo et al., 2014; Guo et al., 2015; Luedeling et al., 2013).

Although the effects of temperature on the fulfilment of chilling and heat requirements have been addressed by a large number of studies (e.g. Anzanello et al., 2014; Campoy et al., 2013; Carew et al., 2001; Mahmood et al., 2000), at the mechanistic level, the process responsible for chill accumulation is not fully understood (Campoy et al., 2011a).

In climates such as those encountered in the United Kingdom (145 Chill Portions [CP] accumulated on average from 1st September to 31st April), chilling is not typically assumed to be a limiting factor of flowering or crop yield of apricots (Guo et al., 2015; Viti et al., 2010). In addition, a calculation of chilling according to the Dynamic Model for future climate projections did not forecast major changes in the seasonal number of accumulated Chill Portions in the UK (Luedeling et al., 2011). However, assuming sequential completion of chilling and heat requirements, the current trend of climate warming may have an effect on the timing of the initiation of chilling, fulfilment of chilling, initiation of heat accumulation and completion of heat requirement, with all these factors having potential for major impacts on flowering dates (Luedeling et al., 2009). This leaves significant uncertainty about future trends in spring flowering of fruit species in the UK. In fact, studies conducted on wild species show a change in the order of flowering among species as temperatures increase (Roberts et al., 2015). It is also worth considering that, at present, apricots in the UK already flower relatively early, so that their timing often coincides with low activity of pollinators during anthesis, whilst buds, flowers and fruitlets face substantial risk of frost damage (Else and Atkinson, 2010). Further advances in apricot flowering dates may reduce their suitability for commercial plantings, whereas a delay in flowering may make them more suitable, particularly when associated with an increase in temperatures around flowering time (Cannell and Smith, 1986).

The aim of this study was to determine the influence of fluctuations in chill and heat accumulation on recorded flowering dates of apricots of the UK National Fruit Collections (NFC) in the SE England. We used Partial Least Squares (PLS) regression to determine the start and end of the effective chill and warming periods and to give an outlook of how variation in daily chill and heat accumulation rates affect the flowering date.

2. Materials and methods

2.1. Phenology and climate data

This study used a 35-year discontinuous record of the flowering dates of 14 apricot varieties at the UK NFC at Brogdale Farm, Faversham, UK (51.30° N, 0.87° E, 12 m a.s.l.) observed between 1960 and 2014 (Table A.1 in Supplementary material). Trees were generally monitored at least twice weekly (more frequently during particularly warm spells) and time of flowering was determined as the date when 10% of the flowers had fully opened. Dates were converted to Julian days (day of the year) for further analysis. There were no signs of any variety flowering earlier than the others (average range of 5.9 days; Fig. A.1 in Supplementary material). During several years, all varieties flowered on the same day or over a very short period (Fig. 1). The order in which different varieties flowered was not consistent throughout the record. For instance, the two varieties creating the largest flowering spread in the record (13 days in 1967 between Alfred and Sun-Glo), flowered only 2 days apart in the previous year. Another example is that Sun-Glo was the latest variety in 1981 but also the earliest three years later. Therefore, average flowering time for all varieties was used for the analyses. Among the 14 varieties, 'Alfred', 'Early Moorpark' and 'Farmingdale' were represented in most of the 35 years when flowering was recorded (Table A.1 in Supplementary material), allowing meaningful trend analysis for these varieties.

Daily minimum and maximum temperatures were collected from a meteorological station located near the apricot orchard. A gap in the meteorological data, from March 1st of 1990 to April 30th of 1998, was filled with data from the nearest weather station available (East Malling, 51.29° N; 0.45° E, 78 m a.s.l., ca. 30 km away). These data were corrected for the 0.19 and −0.19 °C difference in mean daily minimum and maximum temperatures determined by analysing differences between the records for overlapping periods. Minor gaps in the meteorological data were filled by linear interpolation. These gaps were 14 recordings of daily