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USING RECORDINGS OF CYCLING RACES AS INNOVATIVE METHOD TO QUANTIFY THE EFFECTS OF CLIMATE CHANGE ON THE PHENOLOGY OF TREES

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Voorwoord

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List of abbreviations

ANOVA	analysis of variance
AVHRR	Advanced Very High Resolution Radiometer
BGS	beginning of the growing season
C	carbon
CO_2	carbon dioxide
DOY	day of the year
EVI	Enhanced Vegetation index
ExG	Excess Green Index
GDH	growing degree hours
GHG	greenhouse gas
GPS	Global Positioning System
IPCC	Intergovernmental Panel on Climate Change
IPG	International Phenological Gardens
IPO	Interdecadal Pacific Oscillation
LCT	local clock time
LOWESS	locally weighted scatterplot smoothing curve
MODIS	Moderate Resolution Imaging Spectroradiometer
N	nitrogen
NA	not available
NAO	North Atlantic Oscillation
NASA	National Aeronautics and Space Administration
NDVI	Normalized Difference Vegetation Index
NOAA	National Oceanic and Atmospheric Administration
P	phosphorus
pH-H_2O	pH in H_2O solution
RMI	Royal Meteorological Institute of Belgium
VI	vegetation indices
VRT	Vlaamse Radio- en Televisieomroeporganisatie

Abstract

Phenology is a major determinant of species dynamics and fitness, ecosystem structure and functions. Hence, it is of paramount importance to examine the effects of climate change on phenology of plants. Different studies already indicated that an increase of mean annual air temperature in Europe by 1 °C has led to an advancement of phenological spring events with five days. However, there is still a lack of data for many plant species to get a better understanding on the effects of climate change. In this study, recordings of video footage of the annual cycling race the "Tour of Flanders" between 1980 and 2016 are used to collect phenological data of 46 tree individuals of 19 different species occurring along the route of the race. The aim was to link these data about leaf unfolding and flowering of the trees with climatic data such as temperature and precipitation, in order to (i) establish the possibilities of this approach and (ii) better understand the trend in phenological variation among species. The influence of site characteristics, such as soil properties and surrounding land use, was also examined. Moreover, the growth pattern of six trees was determined using dendrochronology (growth ring-measurements) and linked to the variation in phenology.

The results show that the growing degree hours between the first of January and the date of the Tour of Flanders had a strongly significant positive effect on leaf unfolding and flowering. Therefore, spring phenology would advance as a consequence of the increasing surface temperature in spring. However, a weakening of this trend was observed since 2003 to 2016, caused by the global warming hiatus, whereby the increase in surface temperature diminished compared to the previous decades. The effect of changes in precipitation and site characteristics was less important. Species specificity plays an important role in the advancement of spring phenology. Early leaf-out species are sensitive to variation in temperature, while late leaf-out species are less dependent of the spring temperature. The growth pattern showed no clear link with the variation in phenology.

It can be concluded that the use of this unique data source can significantly contribute to a better understanding and estimation of the effects of climate change on the phenology of trees. The data can be extended to other plant species groups that appear in the video footage, such as agricultural crops and wild road verge plants. This method can also be used to examine autumn phenology using autumn cycling races or other footage (e.g. news events, other sport events such as running races, CCTV cameras, etc.)

Samenvatting

Fenologie is een belangrijke determinant voor de dynamiek en fitness van soorten en de structuur en functies van ecosystemen. Daarom is het van groot belang de effecten van de klimaatverandering op de fenologie van planten te bestuderen. Verscheidene studies hebben reeds aangetoond dat de start van het groeiseizoen in Europa ongeveer vijf dagen per stijgende °C vervroegd is. Effecten van klimaatverandering zijn er dus ongetwijfeld, maar er is nog een gebrek aan data van vele plantensoorten om hier een beter beeld van te krijgen. In deze thesis worden video-opnamen van de jaarlijkse wielerwedstrijd de “Ronde van Vlaanderen” van 1980 tot en met 2016 gebruikt om fenologische gegevens van 46 bomen van 19 verschillende soorten die voorkomen langs de route van deze race, te verzamelen. Het doel was de gegevens omtrent het ontluiken van het blad of de bloem te linken aan klimatologische gegevens als temperatuur en neerslag, om zo (i) de mogelijkheden van deze aanpak na te gaan en (ii) een beter beeld te verkrijgen van de variatie in fenologie van verschillende soorten. Ook de invloed van omgevingsparameters, zoals bodemeigenschappen en het voornaamste landgebruik in de nabije omgeving, werd onderzocht. Tot slot werd het groeipatroon van zes bomen bepaald aan de hand van dendrochronologie (jaarringanalyse) om te linken aan de variatie in fenologie.

Resultaten tonen aan dat de groeigraaduren van één januari tot en met de datum van de Ronde van Vlaanderen een sterk significant positief effect hadden op het ontluiken van het blad of de bloem. Als gevolg van de stijgende oppervlaktetemperatuur in het voorjaar, zal het ontluiken dus steeds vroeger plaatsvinden. Een afzwakking van deze trend was echter op te merken vanaf 2003 tot 2016, als gevolg van de globale opwarming hiatus, waarbij de oppervlaktetemperatuur minder sterk toenam dan de decennia voordien. Het effect van veranderingen in neerslag en omgevingsparameters was minder belangrijk. Soortspecificiteit speelt een belangrijke rol in deze fenologieverschuivingen. Vroege soorten zijn gevoelig aan temperatuurvariatie, terwijl late soorten minder afhankelijk zijn van de lentetemperatuur. Het groeipatroon en de variatie in fenologie vertoonde geen duidelijk verband.

Het gebruik van deze unieke databron kan aanzienlijk bijdragen om de effecten van de klimaatverandering op de fenologie van bomen beter in te schatten. Deze data kan uitgebreid worden naar andere plantengroepen die voorkomen in de videobeelden, zoals landbouwgewassen en wilde wegbermplanten. Deze methode kan ook gebruikt worden om fenologieveranderingen in de herfst te bestuderen door wielerwedstrijden in het najaar of ander beeldmateriaal (e.g. nieuwsgebeurtenissen, andere sportevenementen zoals loopwedstrijden, CCTV camera’s, etc.) te gebruiken.

Introduction

The global climate is changing, mainly as a result of enhanced greenhouse gas concentrations. Land and ocean surface temperatures showed a global increase of 0.85 °C between 1980 and 2012 (IPCC, 2014). Precipitation patterns are changing, with an increasing trend in northern Europe and a decrease in southern Europe (Dore, 2005). Overall, the amount of extreme events, such as droughts, heat waves and heavy precipitation is rising (IPCC, 2014).
Species adapt to this climate change by physiological changes, shifting their spatial distribution and shifting their phenology, i.e. changes in the timing of life cycle events such as budding, flowering and fruiting (Bellard et al., 2012). Previous studies showed that the impact of climate change would lead to an advancement of spring as a response to warming, resulting in an extended growing season (Chmielewski & Rötzer, 2001; Menzel & Fabian, 1999; Parmesan & Yohe, 2003; Root et al., 2003; Wolkovich et al., 2012). Phenological shifts of plants affect ecosystem functioning, such as the synchrony between plants and pollinators, food web structure, shading and have an impact on agriculture, forestry, biodiversity conservation, urban applications and gardening. Therefore, it is important to get a better understanding of these changes to forecast future ecosystem dynamics.

In this study, historical images from the Tour of Flanders cycling event are used to collect phenological data. These images provide a large time span of 36 years, 46 tree individuals and data of 19 different species. The trend in the variation of spring phenology, more particular leaf unfolding and flowering of trees, between 1980 and 2016 will be examined. The main purpose is to examine the effect of climatic variables, such as temperature and precipitation, on spring phenology. The possible influence of biotic and abiotic site characteristics measured during different site visits, as well as the influence of species specificity will be considered as well. Moreover, the link between the growth pattern and the variation in phenology of six trees is determined.

1 Literature review

1.1 Climate change

1.1.1 Defining climate change

Long-term data of weather stations worldwide show a significant warming trend of surface temperatures since the start of the instrumental record in the 19th century. The Intergovernmental Panel on Climate Change (IPCC) stated that, since the 1950s, many of the observed changes are unprecedented. The atmosphere and ocean have warmed, the amounts of snow and ice have diminished, and sea level has risen 0.19 m over the 1901-2010 period (IPCC, 2014). In their Fifth Assessment Report, the IPCC noted that the globally averaged combined land and ocean surface temperature data showed a warming of 0.85 [0.65 to 1.06] °C between 1880 and 2012 (IPCC, 2014). This warming trend of the surface temperature is experienced over almost the entire globe (**Figure 1**).

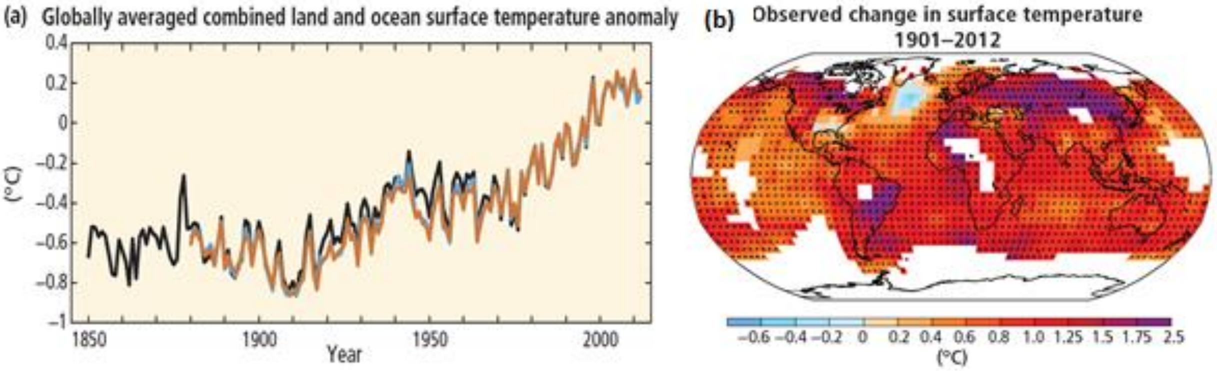


Figure 1. (a) Annually and globally averaged combined land and ocean surface temperature anomalies 1850-2012, relative to the mean of 1986 to 2005. Colours indicate different data sets. (b) Map of the observed surface temperature change, from 1901 to 2012 (IPCC, 2014).

The total precipitation worldwide has also increased since 1901, mainly after 1951 (IPCC, 2014) **(Figure 2**). Due to climate change, precipitation is increasing in high latitudes and decreasing in China, Australia and the Small Island States in the Pacific. Precipitation in equatorial regions becomes more variable. For Europe, the precipitation has increased in the 20th century by 10-40% for northern Europe and decreased by 20% in some parts of southern Europe (Dore, 2005). Overall, heavy and extreme precipitation events increased, even in regions where the total precipitation has decreased or remained constant (IPCC, 2014).

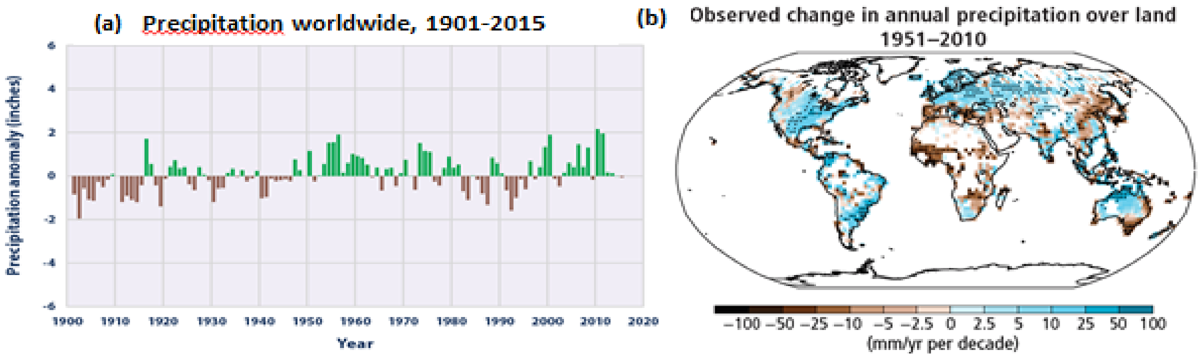
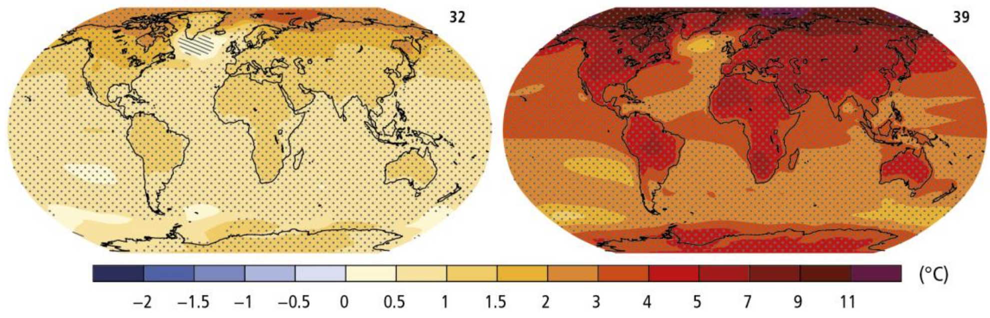


Figure 2. (a) The total annual amount of precipitation over land worldwide 1901-2015, relative to the mean of 1901 to 2000 (Blunden and Arndt, 2016). (b) Map of the observed precipitation change, from 1951 to 2010 (IPCC, 2014).

Based on Earth System Models, the IPCC estimated further changes of climatic parameters under different scenarios. By the end of the 21st century (2081-2100), the increase of the global mean surface temperature relative to 1986-2005 is likely to be 0.3 °C to 1.7 °C under a stringent mitigation scenario[1] and 2.6 °C to 4.8 °C under a scenario without additional efforts to constrain emissions (**Figure 3a**). Changes in precipitation will not be uniform in the future (**Figure 3b**). Even beyond 2100, the warming will continue under all scenarios, except under very stringent mitigations[1]. Many aspects of climate change will continue for centuries and the risks of abrupt or irreversible changes like heat waves, droughts, floods, cyclones and wildfires increase as the magnitude of the warming increases (IPCC, 2014).


(a) Change in average surface temperature (1986–2005 to 2081–2100)

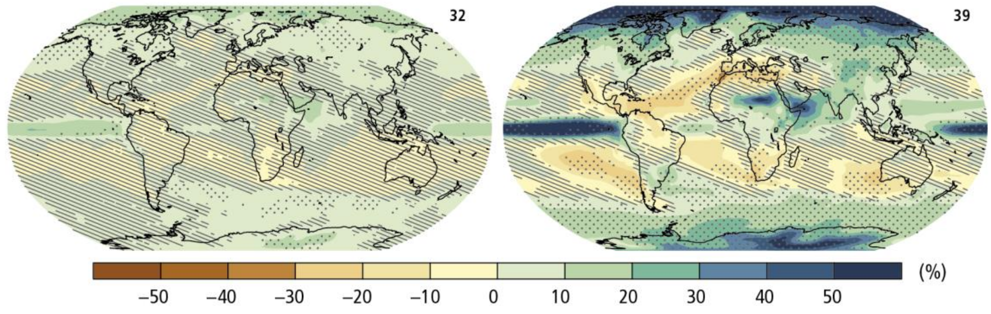

(b) Change in average precipitation (1986–2005 to 2081–2100)

Figure 3. Change in average surface temperature (a) and average precipitation (b), based on multi-model mean projections for 2081-2100 relative to 1986-2005 under a stringent mitigation scenario (left) and a scenario without additional efforts to constrain emissions (right) (IPCC, 2014).

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[1] Very stringent mitigations aiming to keep the warming below 2 °C relative to the 1861-1880 period. In order not to surpass this limit, the cumulative anthropogenic CO_2 emissions should stay below 2900 $GtCO_2$ (IPCC, 2014).

1.1.2 Drivers of climate change

Natural causes of climate change, such as changes in solar energy, volcanic eruptions and natural changes in greenhouse gas (GHG) concentrations, explain climate changes that have occurred before the Industrial Revolution in the 1700s (EPA, 2016). Changes of Earth's orbit, as well as the tilt and position of Earth's axis, also affect temperature, but only on very long timescales of tens to hundreds of thousands of years. However, sensors on satellites have measured the intensity of the sun during the past half century, but no overall increase was found (USGCRP, 2014). Volcanic eruptions release aerosols, these are small particles or liquid droplets in the atmosphere that reflect sunlight and therefore have a cooling effect. So climate changes, as occurring in the last decades, cannot be explained by natural causes only. Models that account both for natural and human factors are able to explain the recent warming (EPA, 2016) (**Figure 4**). The IPCC stated that the anthropogenic increase in GHG concentrations and other anthropogenic forcings caused more than half of the observed increase in global average surface temperature from 1951 to 2010 (IPCC, 2014).

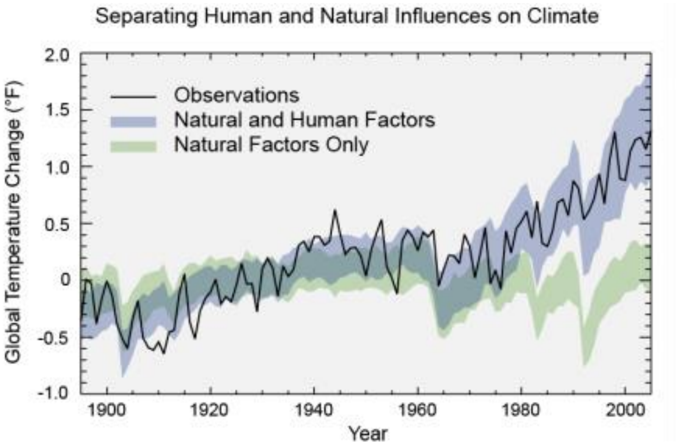

Figure 4. The global temperature change predicted by models when only natural factors are involved (green line) and when both natural and human factors are involved (blue line). The black line represents the observations (EPA, 2016).

GHGs tend to warm the surface of the planet because they absorb energy radiating from Earth's surface, slowing or preventing the loss of heat to space. The warmer atmosphere then increases the temperature of plants and soils through convection and conduction (Amthor et al., 2010). Driven by economic and population growth, anthropogenic GHG emissions have increased since the pre-industrial era. Concentrations of carbon dioxide, methane and nitrous oxide have shown increases from 40%, 150% and 20% respectively since 1750 (IPCC, 2014) (**Figure 5**). CO_2 emissions from fossil fuel combustion and industrial processes contributed about 78% of the total GHG emissions increase from 1970 to 2010. About 40% of these emissions remained in the atmosphere, the rest was stored on land and in the ocean (IPCC, 2014). Water vapour is the most abundant GHG and the most important for the natural greenhouse effect. The concentration of H_2O is controlled by temperature, therefore causing a positive feedback mechanism that induces further warming, because the rate of evaporation and the ability of air to hold water vapour both rise as the Earth warms (EPA, 2016).

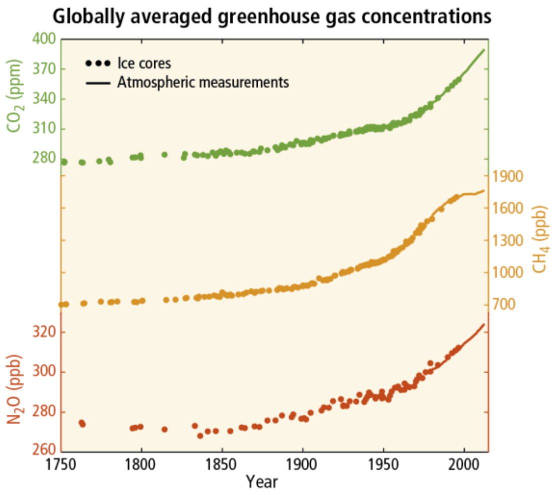

Figure 5. Observed changes in atmospheric greenhouse gas concentrations. Atmospheric concentrations of carbon dioxide (green line), methane (orange line) and nitrous oxide (red line) (IPCC, 2014).

Figure 6 represents the contributions of different factors to the observed surface temperature change over the 1951-2010 period. No net effect of natural factors on surface temperature was detected. The surface temperature was mainly affected by anthropogenic forcings. GHGs are the main cause of the observed warming. This is partly compensated by other anthropogenic forcings, including the effect of aerosols and land use change (IPCC, 2014). Aerosols, such as sulphur emissions from burning coal, can reflect the sunlight and thus have a cooling effect. But other aerosols that absorb the sunlight, such as black carbon from soot, have a warming effect. Overall, the human-generated aerosols, formed mainly by burning fossil fuels and biomass, show a net cooling effect. This effect offsets about one-third of the total warming associated with anthropogenic GHG emissions (EPA, 2016).

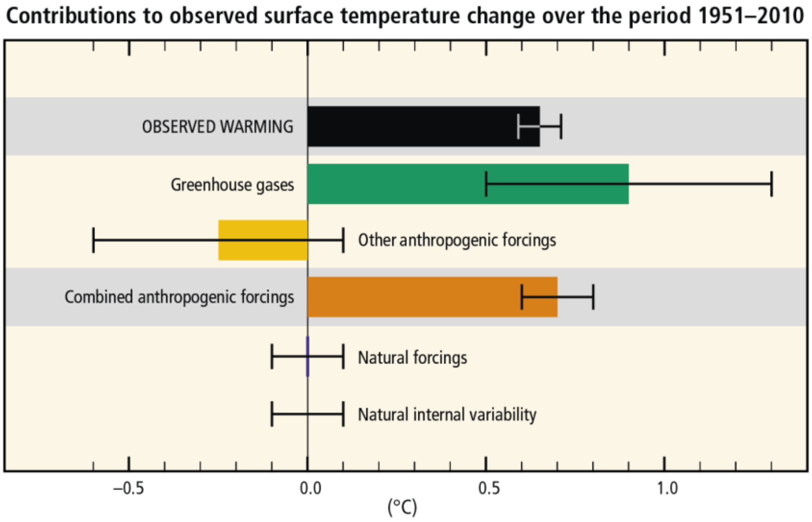

Figure 6. Warming trends over the 1951-2010 period from well-mixed greenhouse gases, other anthropogenic forcings (including the cooling effect of aerosols and the effect of land use change), combined anthropogenic forcings, natural forcings and natural internal climate variability. The observed surface temperature change over the 1951-2010 period is shown in black and is almost completely caused by anthropogenic forcings (IPCC, 2014).

To conclude, the ongoing changes in the climate system are most visible in the increasing temperature worldwide. Precipitation patterns are changing and the CO_2 concentration is rising. This warming is mainly induced by humans through increased GHG emissions. The changing climate has a broad impact on both individual species and the whole ecosystem. The most important responses to climate change, specifically for trees, will be discussed in the next chapter.

1.2 Responses of trees to climate change

Species can respond to climate change and these responses have already been observed across the globe. According to Bellard et al. (2012) these changes can be categorized along three axes: temporal (e.g. phenology), spatial (e.g. range) or self (e.g. physiology).

1.2.1 Phenological shifts

Climate change affects the timing of cyclical abiotic factors such as temperature on a daily or yearly period. Species can adapt to these changes by shifting their phenology, i.e. the timing of life cycle events such as budding, flowering and fruiting (Bellard et al., 2012). Phenological changes affect ecosystem functioning and have an impact on agriculture, forestry and gardening. Therefore, it is important to understand these changes to forecast future ecosystem dynamics. To predict plant responses to climate change, two main research methods have been applied. The first method relies on observations, either in situ or by remote sensing, while the second method relies on experiments on a small scale. Results of both approaches show an advancing phenology trend as a response to warming (Wolkovich et al., 2012).

1.2.1.1 Studies based on observations

The International Phenological Gardens (IPG) are a Europe-wide network where observational data of different phases, such as leaf unfolding, flowering and leaf fall, have been collected since 1959 (Linderholm, 2006). Menzel and Fabian (1999) analysed this observational data and revealed that spring events had advanced on average 6.3 days in four decades (1959-1999). According to the same studies, autumn events are now delayed on average by 4.5 days, resulting in an average lengthening of the growing season by 10.8 days. The data from the IPG was also utilised by Chmielewski and Rötzer (2001) to investigate the beginning of the growing season (BGS) across Europe for the 1969-1998 period for four tree species (*Betula pubescens* Ehrh., *Prunus avium* L., *Sorbus aucuparia* L. and *Ribes alpinum* L.).

Figure 7 represents the trends in the BGS, the end of the growing season and the length of the growing season. The end of the growing season shows smaller annual variations compared to the BGS. For the 1969-1998 period, the length of the growing season has increased with 10.5 days, which is mainly the result of an earlier onset of spring. The strongest trends of earlier BGS were observed in central Europe, while weak trends were found in northern Scandinavia and in southeast Europe.

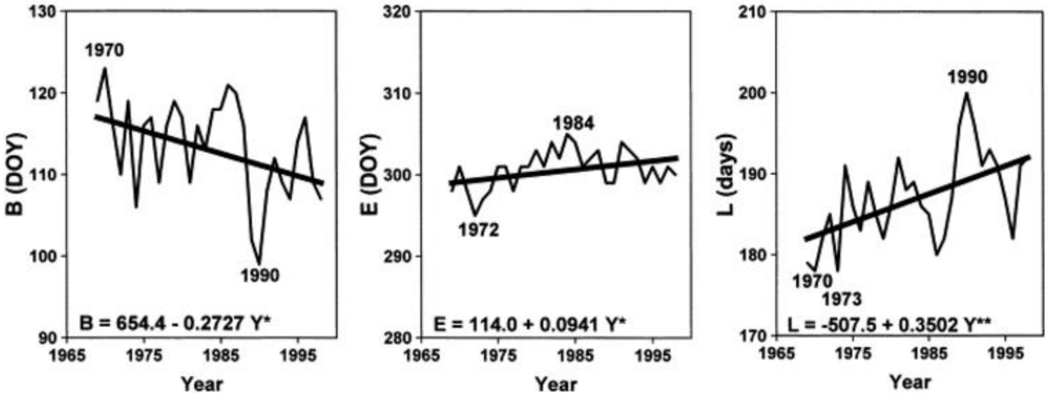

Figure 7. Trends in the average beginning (B), end (E) and length (L) of growing season in Europe, 1969-1998, Y: year, DOY: day of the year (Chmielewski & Rötzer, 2001).

Root et al. (2003) examined the results of 143 phenological studies with a time span of at least 10 years and an average of 34.5 years. The results showed an estimated mean number of 5.1 ± 0.1 days earlier timing of spring events per decade for all species showing change in spring phenology. However, trees show an estimated mean of only 3.0 ± 0.1 days earlier timing of spring events per decade, which is a lower advancement than the cluster (**Figure 8**). Another global meta-analysis of 677 species over a time period range of 16-132 years showed advancement of spring events by 2.3 days per decade (Parmesan & Yohe, 2003). This dissimilarity between the two studies is a consequence of the fact that nonresponsive species were excluded in the study of Root et al. (2003), while these stable species (27% of the 677 species) were included in the study of Parmesan & Yohe (2003) (Parmesan, 2007).

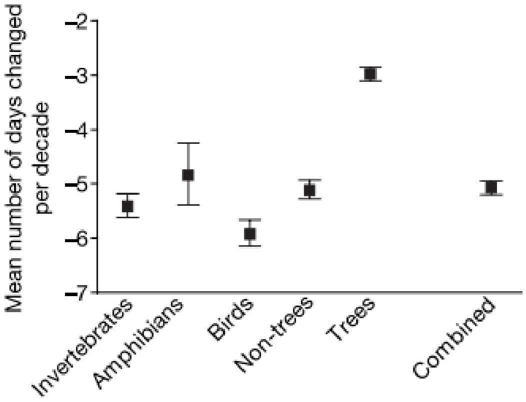

Figure 8. Mean number of days changed per decade for the given groups of species (Root et al., 2003).

Recent spring phenology shifts for trees and shrubs in western Central Europe were measured by Fu et al. (2014). In situ observations showed a significant advancing trend over the 1982-1999 period (-0.67 days per year), while the advancement was significantly slower over the 2000-2011 period (-0.38 days per year). The uniformly advancing trend also decreased between 2000 and 2011, where different temporal patterns were found (**Figure 9**). Delaying trends were found mainly in plants with earlier leaf unfolding or flowering, in contrast with the species with late unfolding and flowering, which still showed advancing trends. These directions of changes in spring phenology are likely to be related to the cooling trend in late winter (February and March) for early spring species and the warming trend during spring months (mainly April) for the late spring species.

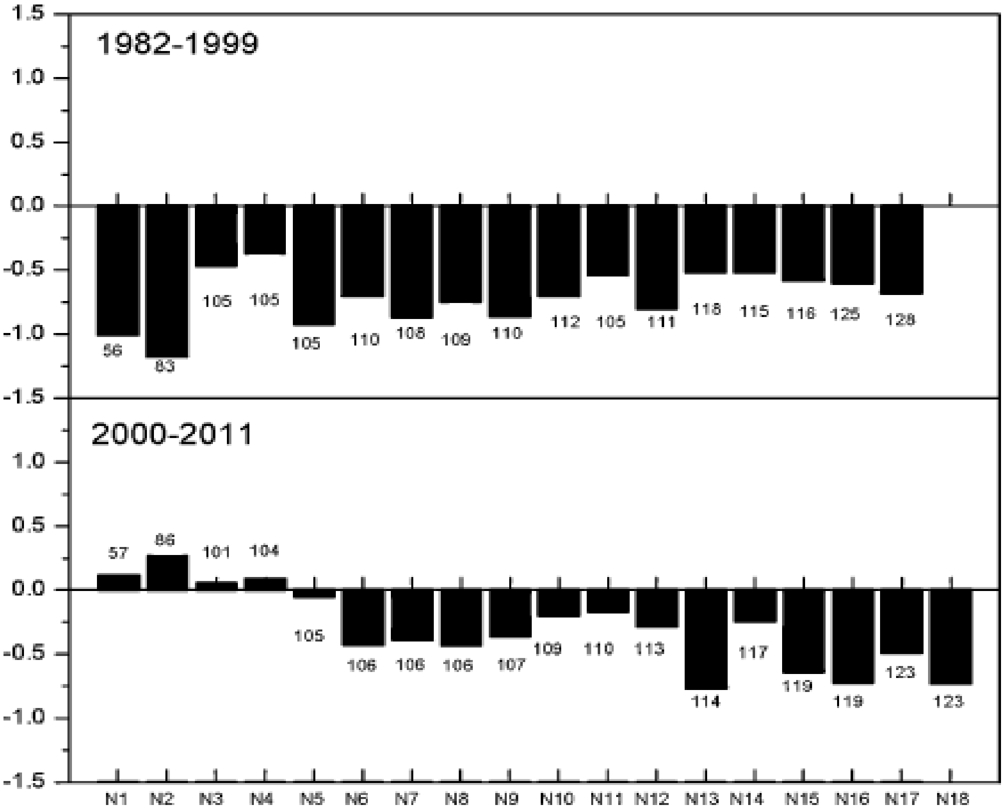

Figure 9. The species specific trends of spring leaf unfolding during the two periods (1982-1999 and 2000-2011). The numbers above or below the column are the average dates of species-specific phenological events for the study period. The number N1 to N18 indicates the id of these study species. N1: *Prunus amygdalus*; N2: *Sambucus nigra*; N3: *Prunus spinosa*; N4: *Prunus avium*; N5: *Syringa vulgaris*; N6: *Aesculus hippocastanum*; N7: *Alnus glutinosa*; N8: *Betula pendula*; N9: *Sorbus aucuparia*; N10: *Corylus avellana*; N11: *Prunus domestica*; N12: *Pyrus communis*; N13: *Fagus sylvatica*; N14: *Tilia cordata*; N15: *Acer pseudoplatanus*; N16: *Quercus robur*; N17: *Fraxinus excelsior*; N18: *Robinia pseudoacacia* (Fu et al., 2014).

Research from Beaubien and Freeland (2000) in Canada showed that the timing of the flowering was largely a response to temperature, with earlier blooms seen in years of higher spring temperature. Early flowering correlated with stronger El Niño[2] events, warmer ocean

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[2] El Niño is a naturally phenomenon which causes the warming of the seawater along the equator in the eastern Pacific Ocean. El Niño normally lasts for six months, with the peak in December, and the temperature of the sea surface around the equator can rise 3 °C above the normal temperature (KNMI, 2015).

temperatures and warmer winter-spring temperatures. In Europe, warming in late winter and early spring (February to April) by 1 °C causes an advance in the BGS (earlier leaf unfolding) of seven days. An increase of mean annual air temperature in Europe by 1 °C led to an extension of the growing season of five days (Chmielewski & Rötzer, 2001). These results coincide with the findings of White et al. (1999) for the US stations.

In the northern Atlantic region, a significant proportion of inter-annual climate variability is attributed to the dynamics of the North Atlantic Oscillation (NAO), which is a measure of the pressure difference between the Azores and Iceland and hence affects westerly winds blowing across the North Atlantic. Seasons of high positive NAO are associated with warming and increased rainfall over northwest Europe (Linderholm, 2006). D'Odorico et al. (2002) found that spring phenology in Europe was significantly affected by the NAO, where high NAO winters speeded up the occurrence of bud burst and bloom. In Germany, the January-February NAO in 1951-2000 explained ca. 40% of the variance in the length of the growing season (Menzel, 2003). This influence of the NAO decreased later in spring and with increasing distance from the Atlantic coast and in mountainous terrains (Scheifinger et al., 2002).

At lower latitudes closer to the tropics, rainfall and evapotranspiration must be taken into account, while in temperate zones the reproductive cycles of plants is foremost controlled by temperature and day length (Linderholm, 2006). Because the warming trend is higher at higher latitudes, separate analyses for different latitudinal belts (32°N-49.9°N and 50°N-72°N) resulted in lower advancement in the phenological phases (4.2 ± 0.2 days per decade) for the lower belt than for the higher belt (5.5 ± 0.1 days per decade). This significant difference suggests that species at higher latitudes are reacting more strongly to the more intense change in temperature (Root et al., 2003). Phenological changes are less pronounced at high altitudes. Over the 1975-1999 period, no significant change in the beginning of the growing season was found in the Colorado Rocky Mountains, USA (Inouye et al., 2000). The beginning of the growing season in these mountains is associated with the melting of the previous winter's snowpack, which does not melt earlier, despite the warmer spring temperatures, due to an increase in winter precipitation. Roetzer et al. (2000) compared phenological trends between urban and rural sites from 1951-1995. Urban sites showed stronger shifts in spring timing, between two and four days earlier than nearby rural sites.

Temporal changes in autumn seem to be less pronounced and show more heterogeneous patterns (Menzel, 2002). Leaf fall in autumn is a more complex process than leafing in spring, for the reason that leaf fall is also induced by lack of light and chilliness. It is therefore not possible to explain leaf fall only by temperature (Chmielewski & Rötzer, 2001).

1.2.1.2 Studies based on experiments

Studies based on experiments allow researchers to estimate the effect of only one variable, e.g. temperature. Wolkovich et al. (2012) examined the data of different warming experiments, representing a total of 115 species. This resulted in estimates of changes in phenology of 1.9-3.3 days per °C, which is below the estimates for observations (2.5-5 days per °C). Thus, warming experiments underestimate plant phenological responses. This discrepancy could arise from complex interactions among multiple drivers in the observational data, or could be explained by the experimental designs that tend to reduce irradiance and soil moisture, which can delay plant phenology.

Besides the effect of temperature, the effect of rainfall and elevated CO_2 concentrations can also be tested by experiments. Ecosystem field experiments in a Mediterranean forest, where rain and runoff were excluded during the growing season (15-20% decrease in soil water availability), were implemented by Peñuelas et al. (2004). Of the four species in this study, two showed delayed flowering and two remained unaffected. This species-specificity of the response to changes in rainfall would suggest that new dominance patterns may appear. Experiments with CO_2 enrichment also indicate strong species specific changes. Asshoff et al. (2006) documented phenology and leaf duration from 2002 to 2004 for *Carpinus sp.*, *Fagus sp.* and *Quercus sp*. under current ambient CO_2 concentrations and in CO_2-enriched zones. No effect on bud break was observed, but the mean leaf duration increased under elevated CO_2 concentrations for *Carpinus sp.* (by five days) and *Fagus sp.* (by six days) and decreased for *Quercus sp.* (by five days).

The phenological changes of an earlier beginning and lengthening of the growing season can also be disruptive, e.g. by increasing asynchrony in insect-plant systems, which may lead to species extinction (Bellard et al., 2012). Earlier blossom of fruit trees also holds the risk of damage by late frosts, which can harm the blossoms so total crop failure can occur (Chmielewski et al., 2004). Persistent lengthening of the growing season may lead to long-term increases in carbon storage, as a consequence of the increase in photosynthetic activity of terrestrial vegetation (Linderholm, 2006). Plants will also need more water when the growing season extends, which increases the risk of failed crops and wildfires (EEA, 2017).

Warmer winters and springs and earlier last frosts has caused already significantly advancing of spring, concluded by the majority of phenological studies. Although there are limitations to these changes in phenology, beyond which ecosystems have to adapt by changes in species composition (EEA, 2017). Increasing temperatures of 1.4-5.8 °C in the next century will most certainly have large consequences, some species will benefit while others will disappear due to warmer and longer growing seasons (Linderholm, 2006).

1.2.2 Spatial shifts

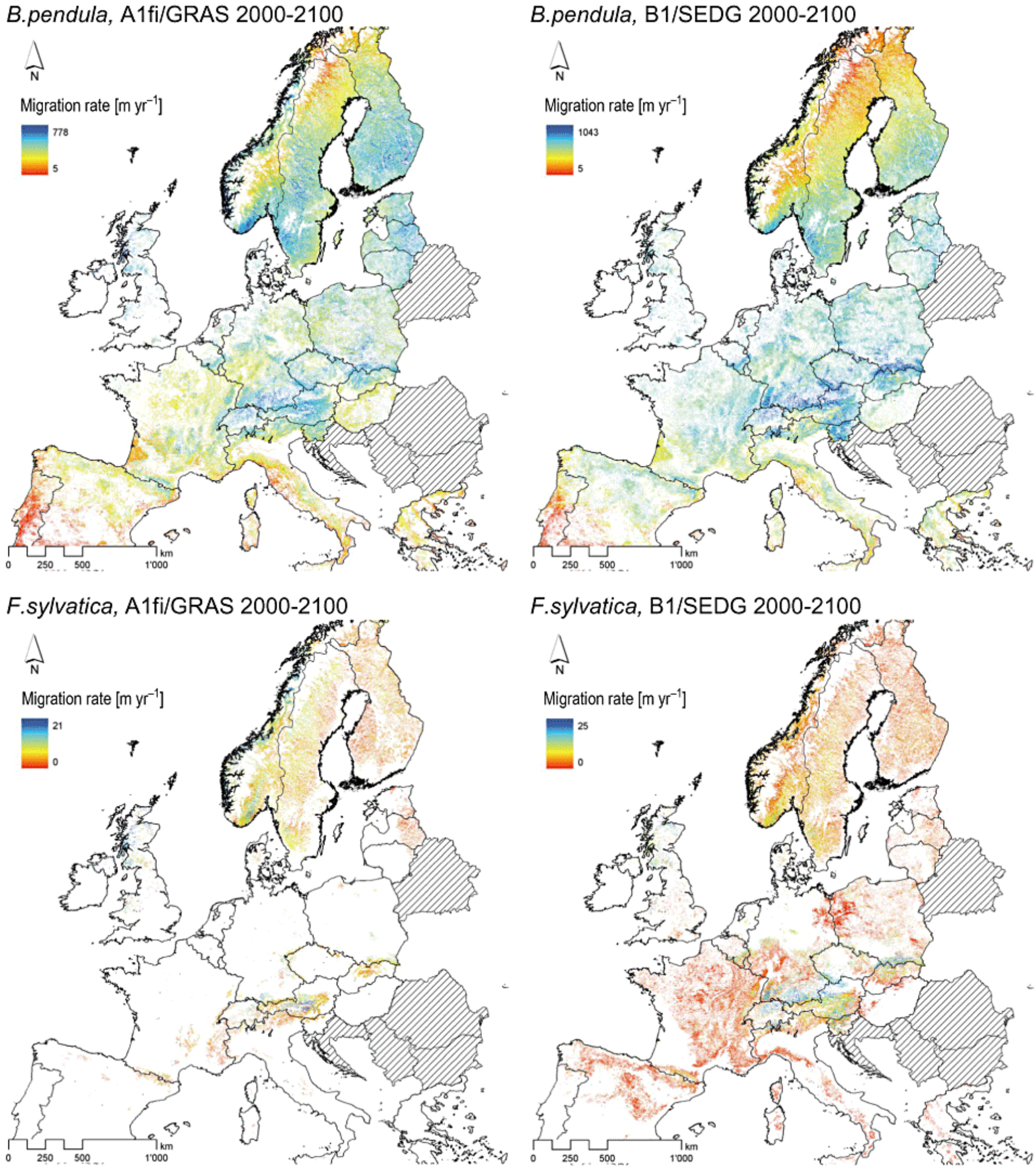
Besides adjusting the phenology, plant species can also track climate change by shifting their distribution to stay in quasi-equilibrium with the climatic conditions they are adapted to (Bellard et al., 2012). The causes of these range shifts can be direct (e.g. drought) or indirect (e.g. drought-induced pests or diseases) effects of climate change whereby the area becomes unsuitable for plant species. The shifts in the distribution of tree species can have consequences in forestry, human health, biodiversity and ecosystem functions and services (EEA, 2017).

1.2.2.1 Shifts measured in the past

Poleward range shifts and upward shifts in elevation have been documented for many species on all continents (Parmesan, 2006). Global meta-analyses of more than 1700 plant and animal species reported range shifts averaging 6.1 km per decade towards the poles (Parmesan & Yohe, 2003). Lenoir et al. (2008) studied the altitudinal distribution of 171 forest plant species along an elevation range of 0-2600 m using data from 1905 to 2006. The results showed a significant upwards shift in species optimum elevation averaging 29 m per decade. In the Montseny mountain range in northeast Spain for instance, the altitude range of beech (*Fagus sylvatica* L.) extended by 70 m upwards between 1940 and 2001 (Penuelas & Boada, 2003).

1.2.2.2 Predictions of shifts in the future

The impact of climate change on 38 European tree species was analysed by an array of models to predict their range shift. More drought-tolerant species such as sessile oak (*Quercus petraea* (Matt.) Liebl.), pubescent oak (*Quercus pubescens* Willd.) and Scots pine (*Pinus sylvestris* L.) can be expected to become more abundant at lower altitudes throughout Europe, while other species such as beech (*Fagus sylvatica* L.), sycamore maple (*Acer pseudoplatanus* L.), lime (*Tilia sp.*), elm (*Ulmus sp.*) or silver fir (*Abies alba* Mill.) are likely to see further reductions in their ranges (EEA, 2017). Meier et al. (2012) also focused on the migration rates of European tree species under projected future climates. Four coniferous trees and ten deciduous trees were divided in early-successional (rapid growth rates, large amounts of seed and long seed-dispersal distances) and mid- to late-successional species. Early-successional species (e.g. *Betula pendula* Roth) had a significantly higher migration rate (108.2 ± 69.3 m per year) than mid- to late-successional species (e.g. *Fagus sylvatica* L.) (11.7 ± 8.6 m per year) (**Figure 10**). Loarie et al. (2009) estimated the rate of climate change, using temperature change calculated from 2000-2100 under an intermediate emissions scenario. The geometric mean velocity of the changing climate was 420 m per year, implicating that both early- and late-successional species would not be able to keep pace with the changing climate. Especially biomes with less topographic variation in the terrain such as flooded grasslands, mangroves and deserts require great velocities, in contrast with mountainous biomes, which require the slowest velocities. Despite this low velocity requirements on mountaintops, a lot of species face extinction near the top because the uphill movement is limited (Colwell et al., 2008).


B.pendula, A1fi/GRAS 2000-2100

B.pendula, B1/SEDG 2000-2100

F.sylvatica, A1fi/GRAS 2000-2100

F.sylvatica, B1/SEDG 2000-2100

Figure 10. Mean migration rate (including time lags due to forest fragmentation) for the 2000-2100 period across potentially suitable habitats of an exemplary early-successional broadleaf species (*Betula pendula* Roth) and an exemplary late-successional broadleaf species (*Fagus sylvatica* L.) for the A1fi/GRAS and B1/SEDG climate and land-use scenarios[3]. 'Striped' countries indicate additional areas for model calibration. The migration rates are especially high in the Alps, where abandoned land promotes species migration, and particularly low in northern and southern Europe, where the climate is either very cold or very dry. 12 out of the 14 species examined showed a similar pattern (Meier et al., 2012).

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[3] A1fi/GRAS and B1/SEDG are climate scenarios outlined by the Intergovernmental Panel on Climate Change. A1fi/GRAS holds a scenario with growth, deregulation, free trade and globalization with a fossil fuel intensive energy production. B1/SEDG stands for Sustainable European Development Goal with reductions in material intensity and the introduction of clean and resource-efficient technologies (IPCC, 2017).

The rates of range shifts vary greatly among and within species. Consequently, the composition of many plant communities is changing. This also leads to disruptions or alterations of currently existing species interactions such as pollination, symbiosis, competition, predation and parasitism (EEA, 2017). The forest structure will change quite considerably as a consequence of the projected range shifts and therefore affect the functioning of forest ecosystems (Fitzgerald & Lindner, 2013).

The observed northwards and uphill movement of many plant species is projected to continue in the current century. Yet, the migration rates of species are likely to be limited and do not only depend on effects of climate, but also on interspecific competition and landscape fragmentation. The rate of climate change is thus expected to exceed the ability of many plant species to migrate. Especially mid- to late-successional species may not be able to keep pace with future climate change (Meier et al., 2012).

1.2.3 Physiological shifts

Next to tracking their current optimal conditions in space or time, species can also adapt themselves to the new climatic conditions in their local range to cope with the changing climate (Bellard et al., 2012). A study from 1953-2002 in northern Russia showed a shift in tree allometry. In areas where summer temperatures and precipitation have both increased, a general increase in biomass (9%) was found, primarily as a result of increased leaf biomass. This is in contrast with the areas that have experienced warming and drying trends, were greenery has decreased, while roots and stems have increased (Lapenis et al., 2005).

Of course, every phenotypic response reaches a physiological limit in extreme environments, so strong selection is needed (Bellard et al., 2012). Warm-adapted communities expand on all continents for all well-studied plant groups (Parmesan, 2006). Consequently, regions may become more favourable to the establishment and survival of alien species (EEA, 2017). Southern Switzerland, for example, is gaining more and more exotic evergreen broadleaved species that profit from milder winter conditions (Walther et al., 2002) (**Figure 11**).

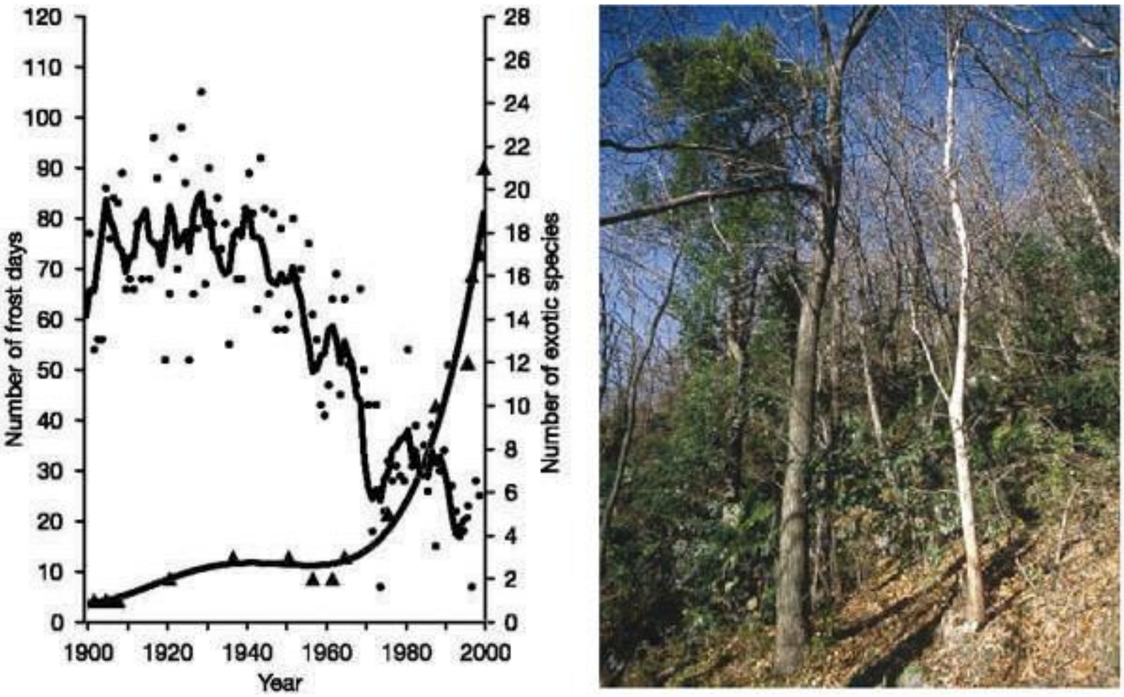

Figure 11. Left: decreasing number of days with frost per year (●) and increasing number of exotic species (▲) in southern Switzerland. Right: vegetation shift from native deciduous to exotic evergreen broadleaved vegetation in southern Switzerland (Walther et al., 2002).

1.3 Characterizing phenology

Understanding phenological changes is helpful to forecast future ecosystem dynamics (Fu et al., 2014). It is therefore important to characterize phenology as accurately as possible, to estimate the impact of this changing trend. Traditionally, different methods have been used to measure phenological data: ground observations, remote sensing and modelling. These methods are discussed below, along with some other and innovative methods.

1.3.1 Ground observations

The oldest method used to characterize phenology is the ground observation. In this approach, observers, mostly volunteers, collect *in situ* observations of various phenophases at numerous stations. The longest records come from the Far East and Europe, including the more than 1300-year Kyoto cherry blossom time series, the more than 670 years of grape harvest dates in Central Europe and the more than 200 year record of plant phenology in Marsham, UK. Most observation networks are located in temperate ecosystems, while long-term phenological observations are lacking in the tropics (Cleland et al., 2007). Different organisations, e.g. the USA National Phenology Network (USA-NPN), the GLOBE (Global Learning and Observations to Benefit the Environment) science network and the French RENECOFOR (Réseau National de suivi à long terme des ecosystèmes forestiers), attempt to expand and extend the phenological records (Hufkens et al., 2012). In Europe, the International Phenological Gardens (IPG) offer the most important phenological network. F. Schnelle and E. Volkert founded these gardens in 1957 and in 1959 the first IPG started its phenological observations. It is now a Europe-wide network of 89 gardens with a large spatial coverage (42°N-69°N, 10°W-27°E) which holds genetic clones from 21 species of trees and shrubs. Eight different phenological phases are measured: leaf-unfolding, May shoot[4], St. John's sprout[5], beginning of flowering, general flowering, first ripe fruits, autumn colouring and leaf fall (Humboldt-University of Berlin, 2012). As mentioned earlier, many studies used these observational data to examine phenological changes (Menzel & Fabian, 1999; Chmielewski & Rötzer, 2001).

The main advantage of *in situ* observations is providing information of specific plants and species. On the other hand, extrapolating over large scales is difficult (Fu et al., 2014). Another shortcoming of ground observations is the subjectivity, because the quality of the data depends on the skills and precision of the observers (Schnelle, 1955). Other methods can complement ground observations, thereby making high spatial coverage possible.

1.3.2 Remote sensing

Remote sensing includes all methods where information is obtained from a distance. The sensors collect the data by detecting the energy that is reflected from Earth (NOAA, 2015). For measuring phenology, remote sensing is mainly carried out by satellites, but also near-surface remote sensing by photography or webcams is applied.

1.3.2.1 Near-surface remote sensing

Near-surface remote sensing means that digital red-green-blue cameras are mounted on instrumentation towers or installed at look-outs, drones, airplanes, etc., resulting in horizontal or oblique views of vegetation canopies (**Figure 12**). Then, these cameras take repeated images of the landscape at high frequencies (mostly several images per day) (Sonnentag et al., 2012). Each image gets number values for the red, green and blue colour planes allowing to calculate the average excess green index (ExG). This index is widely used to describe canopy greenness and is defined as:

$$ExG = 2G - (R + B) \qquad (1)$$

whereby G, R and B are the green, red and blue content in the regions of interests (Hufkens et al., 2012). Especially webcams are attractive as they are easy to use and maintain and easy

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[4] The first spring sprout of conifers (firs, pines). The buds open and the protecting involucres come off the bud edges. The needles are not yet expanded (Humboldt-University of Berlin, 2012).

[5] The second sprout of oaks and mountain ashes. Buds that are already developed for the next year are caused to sprout prematurely by weather factors (Humboldt-University of Berlin, 2012).

accessible through the internet. Although they minimize site visits, they can involve relatively high technical concerns. The approach of near-surface remote sensing overcomes the limitations of ground observations by individuals, like lack of consistency and objectivity, and provides a cost effective way to monitor green leaf phenology. However, cloudiness or other weather effects, scene illumination changes due to the daily rotation of the Earth and other changes could negatively influence the quality of the images and thereby the quality of phenological data (Sonnentag et al., 2012). Nevertheless, digital repeat photography has emerged as a valuable tool for characterizing phenology at local scales and is often used to complement satellite remote sensing (Hufkens et al., 2012).

Figure 12. Example of digital JPEG images of an abandoned pasture in the north-western Italian Alps collected by the CC640 Campbell digital camera during the 2009 growing season. More green content means a higher excess green index (Migliavacca et al., 2011).

1.3.2.2 Satellite remote sensing

Since the mid-1980s, satellite data have been used to study vegetation phenology. For almost 20 years, the Advanced Very High Resolution Radiometer (AVHRR), carried out by meteorological satellites in the NOAA/NASA Earth Observing System, provided the only source of global data suited to analyse seasonal- to decadal-scale dynamics (Linderholm, 2006; Zhang et al., 2003). However, calibration of this data lacked and cloud screening resulted in high levels of noise (Zhang et al., 2003). The Moderate Resolution Imaging Spectroradiometer (MODIS) on board NASA’s Terra and Aqua spacecraft has provided new daily reflectance data since the early 2000s. With spatial resolutions of 250 m, 500 m and 1 km (instead of 1.1-8 km of AVHRR), substantially improved calibration and atmospheric corrections, MODIS data provides an improved basis for monitoring global ecosystem dynamics (Zhang et al., 2006). Different vegetation indices (VI) have been used to quantify the spatial and temporal variation in vegetation growth and activity. The oldest VI derived from satellite remote sensing was the Normalized Difference Vegetation Index (NDVI). This index captures the contrast between red (R) and near-infrared (NIR) reflectance of vegetation, thereby indicating the energy absorption by leaf pigments such as chlorophyll (Linderholm, 2006):

$$NDVI = \frac{(NIR-R)}{(NIR+R)} \tag{2}$$

The Enhanced Vegetation index (EVI) is more responsive to canopy structural variations, canopy type and canopy architecture. The EVI improved the NDVI by making a clearer distinction between bare soil and vegetation. This index has been defined as:

$$EVI = G * \frac{(NIR-R)}{(NIR+C1*R-C2*R-C2*B+L)} \tag{3}$$

where NIR (near-infrared), R (red) and B (blue) are atmospherically corrected surface reflectances, L is the canopy background adjustment, C1 and C2 are the coefficients of the aerosol resistance term and G is the gain factor. The coefficients adopted in the MODIS-EVI algorithm are: L=1, C1=6, C2=7.5 and G=2.5 (Huete et al., 2002).

Satellite remote sensing combines large spatial coverage and regularly repeated observations, which offers a great potential to monitor phenology at regional to global scales. On the other hand, it cannot be used for monitoring individual plants or species and phenophases such as flowering and fruiting cannot be discerned (Cleland et al., 2007). In addition, VI cannot be used in areas with evergreen vegetation, since the annual variation in VI is too subtle to retrieve phenology (Zhang et al., 2006). Another obstacle of satellite data is the noise caused by several factors such as atmospheric disturbances, solar radiation effects, clouds or snow cover (Studer et al., 2007). Some possibilities to remedy these problems has been developed: linear interpolation of the nearest available values (in time) to replace missing values due to clouds and values containing snow are replaced with their most recent snow-free value (Zhang et al., 2006). Still, more work is required to develop formal, uniform protocols for evaluating, calibrating and validating satellite remote sensing data (Hufkens et al., 2012).

Fu et al. (2014) compared *in situ* observations with satellite-based datasets, to measure the recent spring phenology shifts in western Central Europe. Both observations showed significant advancement over 1982-1999, however satellite-based observations showed leaf flushing advancement two times larger than the *in situ* observations (-1.2 days per year and -0.67 days per year). There are two possible explanations for this weak correlation. First, the NDVI-based start of season dates mainly reflect the phenology of the earliest species within the pixel, which are often understory plants that green up earlier. A second explanation is the altered quality of the satellite data. The combination of both ground observations and satellite-based data is thus the preferred approach for observing spring phenology changes.

1.3.3 Phenology modelling

Accurate predictions of species phenology changes have some important benefits. First, productivity of ecosystems and gas exchanges with the atmosphere can be predicted more accurate, thereby leading to better predictions of our future climate. It also enables a better understanding of interactions, especially between animals and plants. Another application of forecasting phenology is supporting farmers and foresters to select varieties adapted to the new climatic conditions. Finally, it also increases the accuracy of predicting the changing species distribution. To predict the timing of particular phenological events, three main types of phenological models have been used. The first are theoretical models, which are based on the trade-off of producing leaves to optimize resources. Secondly, statistical models are used to relate climatic factors and observations of phenophases with mathematical linear equations. The third models are process-based models, describing cause-effect relationships between biological processes and driving environmental factors (Cleland et al., 2007). An example of this last category is the PHENOFIT model that predicts species distribution on a continental scale. This distribution depends on the survival probability and reproduction success, which are both influenced by species phenology (Chuine & Beaubien, 2001).

The POSITIVE project (Phenological Observations and Satellite Data: Trends in the Vegetation Cycle in Europe) compared satellite data of spring green-up with the projections of phenological models that made regional predictions of spring leaf-out based on ground observations of birch leaf unfolding. An acceleration of spring has been found in both methods, but the correlation between the phenological models and satellite data was poor. This highlights the difficulty of scaling phenology from species- to ecosystem-level (Cleland et al., 2007).

1.3.4 Other methods

Global change experiments are experiments where the environmental changes are controlled to observe the response of species. This method allows researchers to estimate the effect of only one parameter, e.g. warming experiments where the influence of temperature is tested. Experimental warming is a valuable tool to increase the understanding of the temperature effect, but are limited to specific locations and provide seldom data from more than ten years (Cleland et al., 2007). The most common passive warming structures are open-top chambers, where the plant can be grown under realistic field conditions. However, these chambers are seldom used for trees and it is not possible to recreate a forest ecosystem and its atmospheric environment in these chambers (Norby et al., 1997). Active warming experiments are mostly carried out using above-canopy heaters, which are influenced by wind. As described earlier, warming experiments underestimate plant phenological responses due to experimental designs, as both active and passive designs reduce soil moisture and irradiance, and due to the lack of complex interactions among multiple drivers (Wolkovich et al., 2012).

Also other approaches to study phenology are tested to **supplement commonly used methods** such as **eddy-covariance monitoring**, measuring carbon and other biogeochemical fluxes in and out of vegetation, which can then be linked to phenology. Another method is **aerobiology**, where pollen composition is studied to examine the phenology of trees. Although there is still uncertainty around the long-distance pollen transport and determination at species level is not possible (identification at genus or family level) (Estrella et al., 2006; Cleland et al., 2007). **Innovative methods are important to improve our predictions of future plant performance under climate change**. An example of a new, innovative approach is the study of Munson and Long (2016). They used **herbarium** records across ecoregions of the western USA to study grass reproductive phenology. This herbarium-based approach allows researchers to gather phenological data covering broad geographic and temporal ranges (Primack & Gallinat, 2017). Another method is the use of **historical images**, e.g. the study of Miller-Rushing et al. (2006). This study revealed advances in the date of woody-plant flowering in New England, consistent with the warming temperatures, using herbarium records and photographs of the Arnold Arboretum (Harvard University) dating to the early 1900s. Besides their usefulness for characterizing phenology, historical images can also be used to quantify other ecological variables such as habitat types, community composition and shifts in treelines. Understanding the changes that have occurred in the past will improve our ability to predict forward (Vellend et al., 2013).

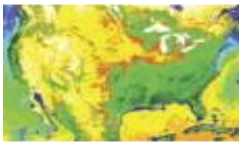
Each approach contributes to the understanding and forecasting of phenological changes, but each are suited to a particular scale (**Table 1**). Synthesizing these different scales is important to make accurate estimates about climate change impacts (Cleland et al., 2007).

1.4 Aims

The aim of this master thesis is to assess the impact of climate change on plant phenology, as well as the influence of other possible drivers, using historical images (legacy data sensu Vellend et al.). In particular, the following research questions will be addressed to improve our understanding of the changing phenology.

[1] Is this method useful to examine variation in phenology?
[2] Is there a significant variation in the timing of leaf unfolding and flowering phenology between 1980 and 2016?
[3] Is there a significant effect of the temperature and precipitation metrics on the variation in leaf and flowering phenology?
[4] Does species specificity has a significant influence on the variation in phenology and which species are more sensitive to the different climatic variables?
[5] Are the effects of characteristics of the tree and of the environment significant?
[6] Is there a link between the growth pattern of the tree and the variation in phenology?

Table 1. The utility, advantages and limitations of approaches used to investigate the influence of global change on plant phenology.

Approach[a]	Utility	Advantages	Limitations
(i) Ground observations 	Various phenological events are observed at numerous sites	Long records available; specific species and plants	Limited spatial coverage; quality depends on observational effort
(ii) Near-surface remote sensing 	Digital cameras take repeated images at high frequencies	objective and consistent; suited to complement satellite data	Quality influenced by weather effects: high technical concerns
(iii) Satellite remote sensing 	Satellite data on spectral reflectance is used to calculate vegetation indices	High spatial coverage; regularly repeated observations	Limited time series; not suited for individual plants and species; noise caused by atmospheric disturbances
(iv) Phenology modelling	Scales phenology of the past, present and future across space and time	Convenient method to project into the future	Numerous phenological data are required to fit parameters
(v) Global change experiments 	Observations in response to controlled environmental changes	Possibility to estimate the effect of only one parameter	Underestimates plant phenology responses; limited locations; seldom more than ten years
(vi) Eddy-covariance monitoring 	Measures carbon fluxes in and out of vegetation	Data used in simulation models; to complement other data	Expensive method; not on species-level

[a] Photographs highlight: (i) flowering of individual species (Cleland et al., 2007); (ii) example of digital repeat photography (Sonnentag et al., 2012); (iii) MODIS satellite image of NDVI; (v) experimental plot in the Jasper Ridge Global Change Experiment; (vi) an AmeriFlux eddy-covariance flux tower at the University of Michigan Biological Station (Cleland et al., 2007).

2 Materials and methods

2.1 Archive work

To assess the phenology of trees over time, recordings of the Tour of Flanders (‘Ronde van Vlaanderen’), provided by Vlaamse Radio- en Televisieomroeporganisatie (VRT) and access in close collaboration with them, were used. The Tour of Flanders is a major annual road cycle race in Belgium, held every spring around early April. The cycling race is part of the UCI World Tour and one of the five ‘monuments’. The event started in 1913, with interruptions from 1915-1918 due to World War I, and celebrated its 100th edition in 2016. Only recordings of sufficient quality were examined in this study, with the result that the editions of 1980-2016 were selected because of the availability of colour in film. After comparing the different routes of these 36 editions, 12 frequently occurring climbs were picked as reference points. **Figure 13** illustrates the map of the study area, together with the locations of the 12 selected climbs.

The archive work was performed in Avid Interplay Media Asset Manager Desktop (Avid technology, 2011). Images of the trees occurring on or around these climbs were saved for each year where the tree was clearly visible in the recorded film. **Table 2** shows the 46 different, selected trees and the number of images that are available, classified according to the nearest climb. A dataset of 531 images of (part of) these trees was obtained and every image was given a phenology score from zero to four (**Figure 14**):

[0] no leaves visible
[1] 1-25% of the leaves/flowers visible
[2] 26-50% of the leaves/flowers visible
[3] 51-75% of the leaves/flowers visible
[4] 76-100% of the leaves/flowers visible

Figure 14. Example of phenology scores for *Betula sp.* From left to right: score 0, 1, 2, 3 and 4.

Figure 13. Map of the study area (50°52’14”N-50°46’2”N, 3°30’59”E-3°56’16”E) with the 12 selected climbs around the cities of Oudenaarde and Geraardsbergen that are (nearly) annually part of the route of the Tour of Flanders cycling race (Geopunt Vlaanderen, 2017).

Table 2. Selected trees and their number of images. Each image represents one replicate year.

climbing	Tree ID	tree species	number of images
Bosberg	BOSvoor	Oriental cherry – *Prunus serrulata* Lindl.[2]	15
	BOS3	*unknown tree species*[2, 4]	9
Eikenberg	EIK1	*unknown tree species*[1, 2, 4]	5
	EIK4	Common ash – *Fraxinus excelsior* L.	20
	EIK6	Common ash – *Fraxinus excelsior* L.[2]	11
	EIK8	Birch – *Betula sp.*[2]	9
	EIK10	European beech – *Fagus sylvatica* L.[2]	20
Koppenberg	KOP2	European beech – *Fagus sylvatica* L.[2, 3]	5
	KOP3	English oak – *Quercus robur* L.	10
Kwaremont	KWA2	Carolina poplar – *Populus x canadensis* Moench	15
	KWA5	English oak – *Quercus robur* L.[3]	17
	KWA6	European pear – *Pyrus communis* L.[1, 2, 3]	23
	KWA7	Magnolia – *Magnolia sp.*[1, 2]	14
	KWA8	Birch – *Betula sp.*	3
	KWAx	Hawthorn – *Crataegus monogyna* Jacq.[2]	6
Leberg	LEB1	Birch – *Betula sp.*	11
	LEB2	European beech – *Fagus sylvatica* L.	11
	LEB3	English oak – *Quercus robur* L.	11
	LEB4	European beech – *Fagus sylvatica* L.	6
	LEB6	Weeping willow – *Salix sp.*[2, 3]	10
Molenberg	MOL3l	Silver linden – *Tilia tomentosa* Moench[3]	14
	MOL3e	Sycamore maple – *Acer pseudoplatanus* L.[3]	14
	MOL5	*unknown tree species*[4]	7
	MOL6	Southern catalpa – *Catalpa bignonioides* Walt.	15
	MOLkap	*unknown tree species*[4]	7
	MOL7	Weeping willow – *Salix sp.*[2]	8
Muur	MUU2	Lombardy poplar – *Populus nigra* L.	7
	MUUkap1	Black locust – *Robinia pseudoacacia* L.	18
	MUUkap2	Weeping willow – *Salix sp.*[2, 3]	7
Paterberg	PAT1	Carolina poplar – *Populus x canadensis* Moench[2,3]	21
	PAT2	Carolina poplar – *Populus x canadensis* Moench[2]	19
	PAT3b	Birch – *Betula sp.*[2, 3]	22
	PAT3.5	European hornbeam – *Carpinus betulus* L.[2]	23
Steenbeekdries	STE2	Silver linden – *Tilia tomentosa* Moench[2, 3]	11
	STE3	Weeping willow – *Salix sp.*[2]	9
Taaienberg	TAA1	Birch – *Betula sp.*[2, 3]	18
	TAA3	Silver linden – *Tilia tomentosa* Moench	17
	TAA10	*unknown tree species*[2, 4]	20
Valkenberg	VAL2	Weeping willow – *Salix sp.*[2]	5
	VAL3	Cherry - *Prunus sp.*	6
	VAL5	*unknown tree species*[4]	5
Wolvenberg	WOL1	Birch – *Betula sp.*	6
	WOL2	Border forsythia - *Forsythia x intermedia* Zab.[1, 2]	10
	WOL4	Common walnut – *Juglans regia* L.	7
	WOL5	Lombardy poplar – *Populus nigra* L.	8
	WOL6	Birch – *Betula sp.*[2]	6

(1) species where flowering was examined instead of leaf unfolding; (2) trees showing variation in phenology score; (3) trees where samples of the stem were taken; (4) determination was not possible, because the tree was cut or access was restricted or denied.

2.2 Site characteristics

Characteristics of the different trees and of their environment were assessed during site visits in September and October 2016. An overview of the variables and their unit is given in **Table 3**. First, the exact GPS location and species of each tree was determined. For 11 of the 46 trees that were recently cut, determination was done with the help of older images and Google Street View (Google, 2007). It was, unfortunately, not possible to determine the species for six of these 11 individuals. Different characteristics for each of the trees were determined during the site visit: plant height, diameter at breast height, crown size, vitality, and key characteristics of the surroundings (aspect, main land use surrounding the tree). The height of the tree (m) was estimated with a Vertex IV (Haglöf, Sweden). The tree canopy crown size was measured with a tape measure and the diameter of the stem at breast height with callipers. Also a score of vitality was given by estimating the percentage of defoliation and discolouration.

Characteristics of the environment were also assessed: position of the tree (garden, roadside, edge of a forest…), main land use surrounding the tree (meadow, arable land or paved) within a radius of 25 m around the tree, as well as the number of trees within this same radius with their percentage of canopy cover were noted. The distance to the nearest tree was measured using a tape measure and the aspect was determined with a compass.

Table 3. Characteristics of the trees and of their environment, assessed during the site visits.

characteristic tree	**unit**	**characteristic environment**	**unit**
species		GPS location	°
height	m	position	
diameter stem at 1.30 m	m	nearest tree	m
crown size	m	canopy cover	%
vitality		surrounding land use	
defoliation	%	aspect	
discolouration	%	soil	
		P	mg/kg
		N	%
		C	%
		pH	

For each tree (unless this was impossible due to access restrictions or paved surroundings), a soil sample (20 cm depth) was taken with the use of a soil auger. The soil was dried at 40 °C until a constant weight was obtained. After grinding and passing through a 1 mm sieve, Olsen-P, CN and pH analyses were conducted. Available inorganic soil P was measured by extraction in $NaHCO_3$ (Olsen-P according to ISO 11263:1994(E)). Total C and N contents were measured by dry combustion using an elemental analyser (Vario MAX CNS, Elementar, Germany) and pH-H_2O was measured using a glass electrode (Orion, Orion Europe, Cambridge, England, model 920A) following the procedure described in ISO 10390:1994(E).

Finally, to determine the age of the tree and growth patterns over time, samples of the stem were taken with a pressler borer, when allowed, for all trees that showed variation in phenology. In total, 22 samples of 11 trees (i.e. two samples per tree perpendicular to each other), were taken. Due to a lack of experience and other circumstances such as steep slopes, a worn borer..., not all samples were useful. Two different samples of each tree were examined to analyse the growth patterns of six trees. The year ring width (10^{-2} mm/year) was determined with Lintab (Rinntech) for the two samples separately and were cross dated afterwards.

2.3 Climatic data

The best available temperature and precipitation data with high spatial resolution were provided by the Royal Meteorological Institute of Belgium (RMI). The RMI network relies on voluntary and professional observers, civil and military aerodromes, regional and federal agents and employees of private companies. Maximum and minimum temperatures for the previous 24 hours, are recorded at 08:00 LCT (local clock time) and precipitation amounts were mostly measured with a manual rain gauge. Data quality control procedures were applied to ensure that only valid measurements will be involved in the gridding process. Afterwards, the set of unevenly distributed temperature data was interpolated using the method of kriging on a 4 km x 4 km regular grid over Belgium (Delvaux et al., 2015). This gives a very accurate dataset, with one of the best resolutions available worldwide. Each location and thus each tree has specific data values of maximum temperature (in °C), minimum temperature (in °C) and precipitation amounts (in mm/hour) per day from January 1, 1979 up to December 31, 2016. The mean temperature (in °C) per day was obtained by dividing the sum of the maximum and minimum temperature by two.

Based on these climatic data, six different temperature metrics were calculated per tree and year: the mean annual temperature, the mean temperature between January 1st and March 31st, the mean temperature between January 1st and the date of the cycling event (which can change each year), the mean temperature between October 1st and December 31st of the previous year, the cumulative growing degree hours (GDH) of the whole year, and, finally, the cumulative GDH from January 1st up to the date of the cycling event. Growing degree hours (GDH) were calculated using the formula of Lindsey and Newman (1956) (**Figure 15**). In addition to the six temperature metrics, two precipitation metrics were calculated: the mean precipitation rate between January 1st and March 31st and the mean precipitation rate between October 1st and December 31st of the previous year. **Table 4** gives an overview of the eight different metrics.

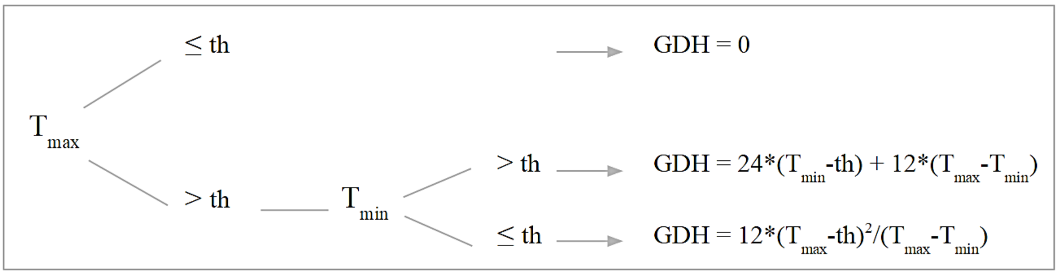


Figure 15. Formula based on Lindsey and Newman (1956) to calculate GDH of one day. T_{max} stands for the maximum temperature of that day, T_{min} stands for the minimum temperature of that day and th represents the threshold value, assumed to be 5 °C for most plant species.

Table 4. The different metrics calculated with the climatic data.

metric	**data**	**unit**
T_{year}	mean annual temperature	°C
T_{spring}	mean temperature January 1st-March 31st	°C
T_{date}	mean temperature January 1st-date of cycling event	°C
$T_{autumnwinter}$	mean temperature October 1st-December 31st of the previous year	°C
GDH_{year}	cumulative growing degree hours of the whole year	
GDH_{date}	cumulative growing degree hours January 1st-date of cycling event	
P_{spring}	mean precipitation rate January 1st-March 31st	mm/hr
$P_{autumnwinter}$	mean precipitation rate October 1st-December 31st of the previous year	mm/hr

2.4 Statistical analyses

First, the spread of the date of the cycling event and the temperature on that date was checked. Also, the variation of the temperature and GDH through the years was examined using locally weighted scatterplot smoothing curves (LOWESS) (gplots package 3.0.1, 2016). To minimise possible mistakes in calculations, not the average, but the temperature data of the Leberg station was used for these calculations, since this climb lies approximately in the middle of the study area.

To analyse the effect of the climatic metrics on tree phenology, only the trees showing variation in phenology scores (i.e., not trees who had no leaves/flowers at all during all 36 years) were taking into account. This resulted in 20 (leaf unfolding) and 4 (flowering) individual trees remaining for the rest of these analyses. Each statistical analysis was carried out for both the leaf unfolding and the flowering dataset separately. First, a linear mixed effects model (nlme package 3.1-131, 2017) was used eight times to explain the variation in phenology scores on the basis of the previously calculated climatic variables mentioned in Table 4. A random factor was added each time to the TreeID, because of the hierarchical non-independence of data from the same tree. The phenology scores were related to the climatic variable of the same year, except for the mean temperature and precipitation between October 1st and December 31st, where the phenology scores were compared with the data of the previous year. To determine the relationship between the phenology scores and the time, again the linear mixed effects model was used with a random factor for TreeID. As for determining the influence of the characteristics of the tree and of the environment on the phenology score.

Linear regressions were carried out for every tree separately and the GDH between the 1st of January and the date of the cycling event. Also, a heatmap was constructed to illustrate the correlation between the eight climatic variables and the phenology of the different species. For each year, an average of the different phenology scores was determined for each species and compared with the climatic data of the Leberg station. Pearson's r was calculated and illustrated using the ggplot function (ggplot package 2.2.1, 2016).

To analyse the growth ring data, the pointRes package (pointRes 1.1.3, 2016) in R was used to calculate the mean deviation away from the average in growth (%) of each year for each tree separately and combined. The normalisation function was used for this purpose, which provides the tree growth deviation in individual years from the moving window average of five years (Cropper, 1979). Afterwards, a linear mixed effects model was used to check the effect of the spring temperature and precipitation between January 1st and the 31st of March on this data and the link between the mean growth deviation with the variation in phenology. Again, a random factor was added each time to the TreeID, because of dependency of the data coming from the same tree (see above). All statistical analyses were performed in RStudio 3.3.2 (R Development Core Team, 2016).

3 Results

3.1 Variation in temperature

The date of the Tour of Flanders can differ a few days from year to year. The spread of the data between 1980 and 2016, as well as the minimum and maximum temperature on that date, is shown in **Figure 16**. These dates range between the 90th and 98th day of the year.

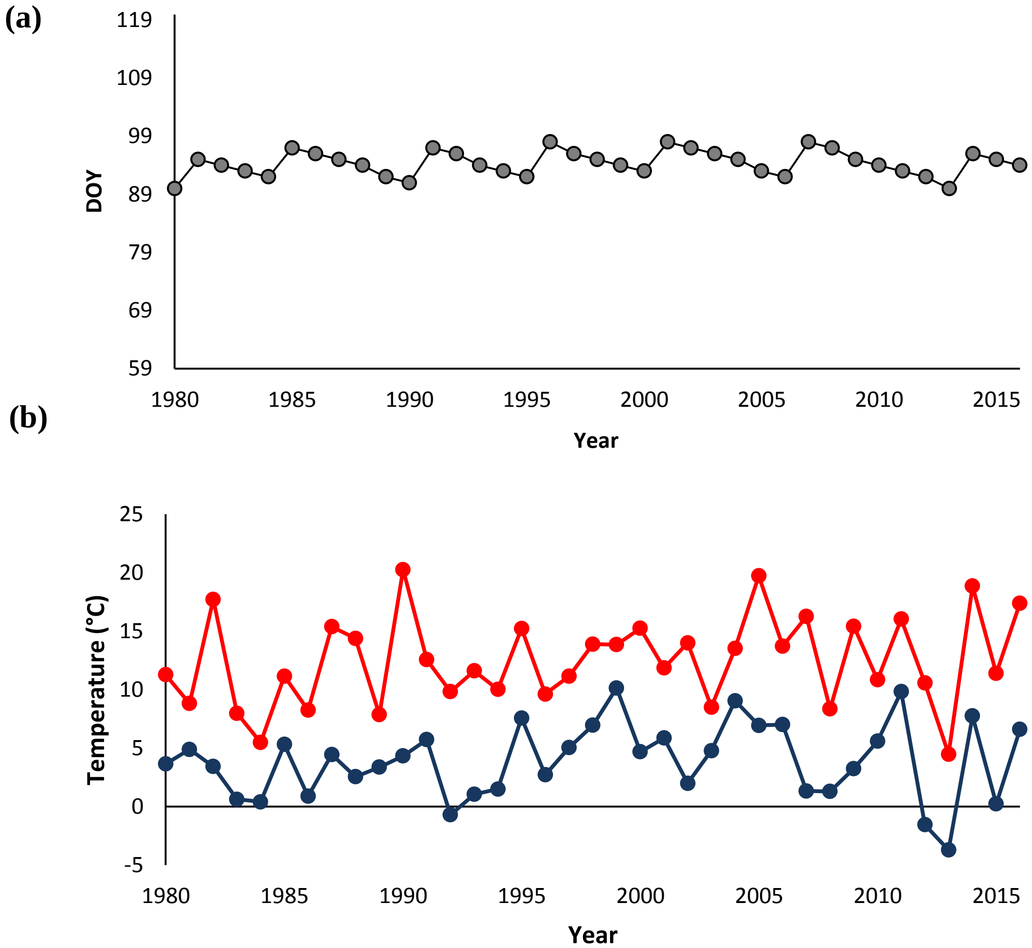


Figure 16. The dates of the Tour of Flanders between 1980 and 2016 (a) and the minimum (blue line) and maximum (red line) temperature at the Leberg station on that day (b).

Figure 17 illustrates the variation in mean annual temperature and the cumulative GDH of the whole year between 1980-2016 for the Leberg station. The locally weighted scatterplot smoothing curve on this figure clearly illustrates the rising mean annual temperature until 2002. Thereafter, the trend flattens. The same pattern can be observed for the cumulative GDH of the whole year, with even a small decreasing trend toward the last years.

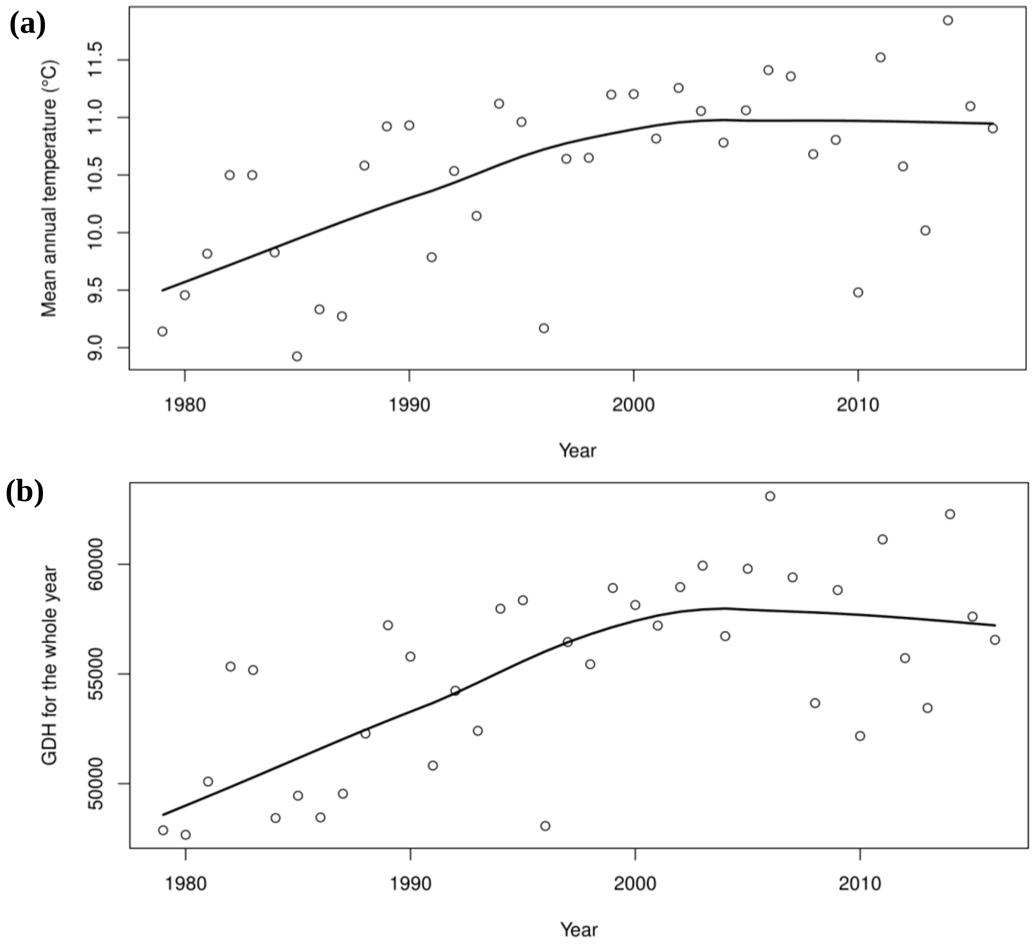


Figure 17. The variation in mean annual temperature at the Leberg station (a) and in cumulative GDH of the whole year at the Leberg station (b). The black line represents the LOWESS curve.

3.2 Variation in phenology

3.2.1 Species specificity

Not all trees showed variation in the phenology score on the date of the cycling event. Of the 46 trees examined, 20 showed variation in the phenology of leaf unfolding and four in the phenology of flowering (**Table 5**). The phenology score of the trees not showing variation was always zero. This difference was mostly related to species specificity or the number of images that is available.

Table 5. Distinction between trees showing variation in phenology score on the images that are available and trees not showing variation in phenology score on the images that are available.

Variation in phenology score		**No variation in phenology score**	
Species	**number of trees**	**Species**	**number of trees**
Leaf unfolding			
Betula sp.	3	*Acer pseudoplatanus* L.	1
Carpinus betulus L.	1	*Betula sp.*	3
Crataegus monogyna Jacq.	1	*Catalpa bignonioides* Walt.	1
Fagus sylvatica L.	2	*Fagus sylvatica* L.	2
Fraxinus excelsior L.	1	*Fraxinus excelsior* L.	1
Populus x canadensis Moench	2	*Juglans regia* L.	1
Prunus serrulata Lindl.	1	*Populus x canadensis* Moench	1
Salix sp.	4	*Populus nigra* L.	2
Tilia tomentosa Moench	1	*Prunus sp.*	1
unknown	2	*Quercus robur* L.	3
Flowering		*Robinia pseudoacacia* L.	1
Forsythia x intermedia Zab.	1	*Tilia tomentosa* Moench	1
Magnolia sp.	1	*unknown*	3
Pyrus communis L.	1		
unknown	1		

3.2.2 Effect of time

Time and phenology score showed a correlation for both leaf unfolding and flowering (**Figure 18**). However, the effect of time on phenology for the 1980-2016 period was not significant (**Table 6**). If only the 1980-2002 period was taken into account, since this is the period with an increase in temperature (Figure 17), the effect of time was significant for the phenology of leaf unfolding, but still non-significant for the effect on the phenology of flowering.

Table 6. Effect of the year on the phenology score. With respect to the significance codes, the following symbols were used: * for P < 0.001, ** for P < 0.01, * for P < 0.05 and . for P < 0.1.**

Effect		**numDF**	**denDF**	**F-value**	**p-value**
leaf unfolding	year 1980-2016	1	217	2.586087	0.1093
	year 1980-2002	1	95	6.356304	0.0134 *
flowering	year 1980-2016	1	45	2.290677	0.1371
	year 1980-2002	1	22	2.802881	0.1083

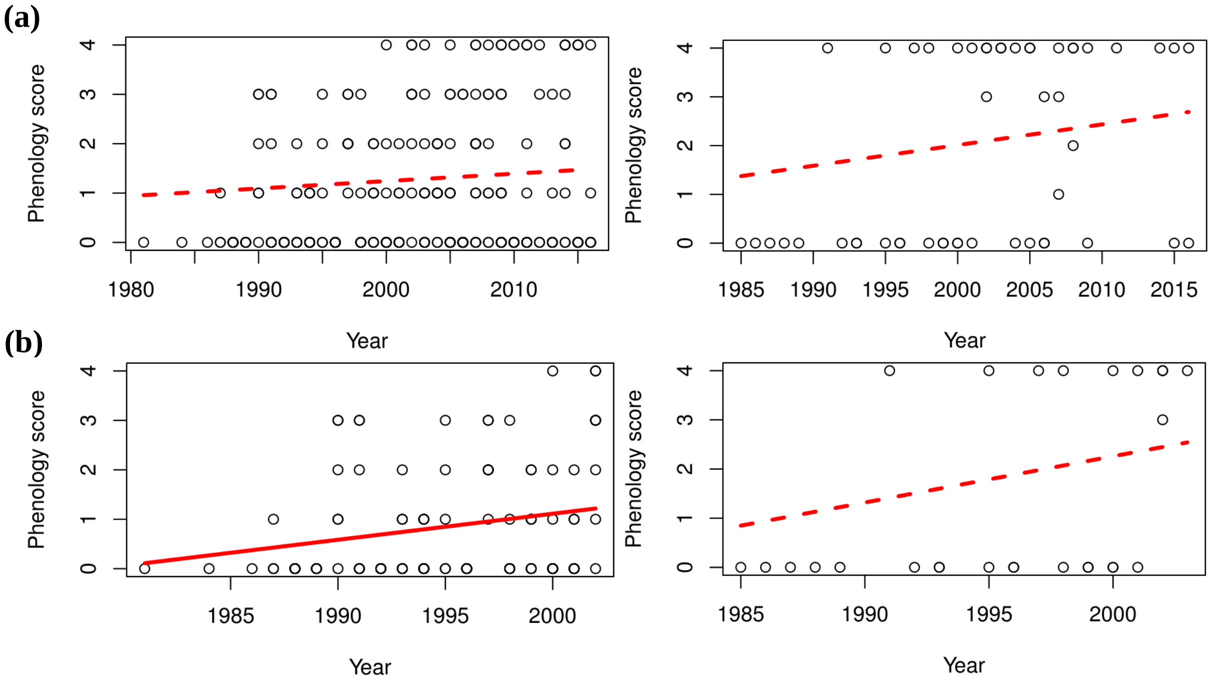


Figure 18. The effect of time on the phenology score of leaf unfolding (left) and flowering (right) for the 1980-2016 period (a) and the 1980-2002 period (b). The red line represents the fit of the linear mixed effects model and is dashed if the effect is non-significant.

3.3 Effects of climate on phenology

3.3.1 Effects of temperature and precipitation

Regarding **Figure 19**, the eight different metrics had a positive effect on earlier leaf unfolding. The GDH from January 1st up to the date of the cycling event (GDH_{date}), which is strongly related to the mean temperature from January 1st up to the date of the cycling event and the mean temperature between January 1st and March 31st, had the largest effect on variation in phenology. The effects of the other temperature metrics were also strongly significant (**Table 7**). Except for the mean temperature between October 1st and December 31st, which showed a very small effect and this effect was not significant. Precipitation rates, both in spring and in autumn and winter, showed only slight, non-significant effects on earlier leaf unfolding.

The temperature metrics showed similar effects on the phenology of flowering (**Figure 20**). Again, the GDH_{date} showed the largest effect with strongly significant effects on tree phenology (**Table 7**). Only the mean temperature between October 1st and December 31st had now a non-significant, negative effect. Precipitation had a slightly larger effect on flowering than on leaf unfolding, but the effects were either non-significant.

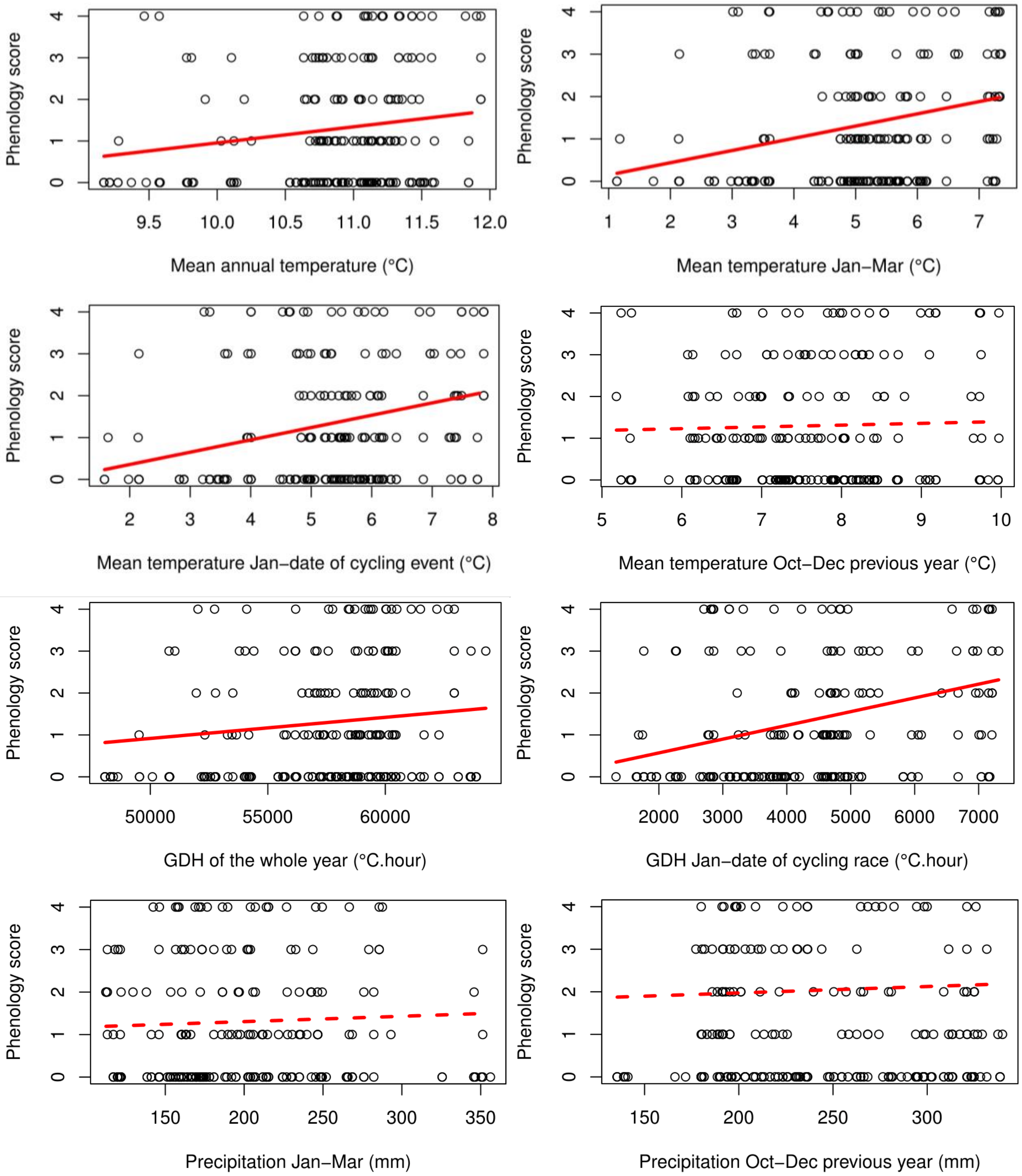


Figure 19. The effects of the eight different climatic variables on the phenology score of leaf unfolding. The red line represents the fit of the linear mixed effects model and is dashed if the effect is non-significant.

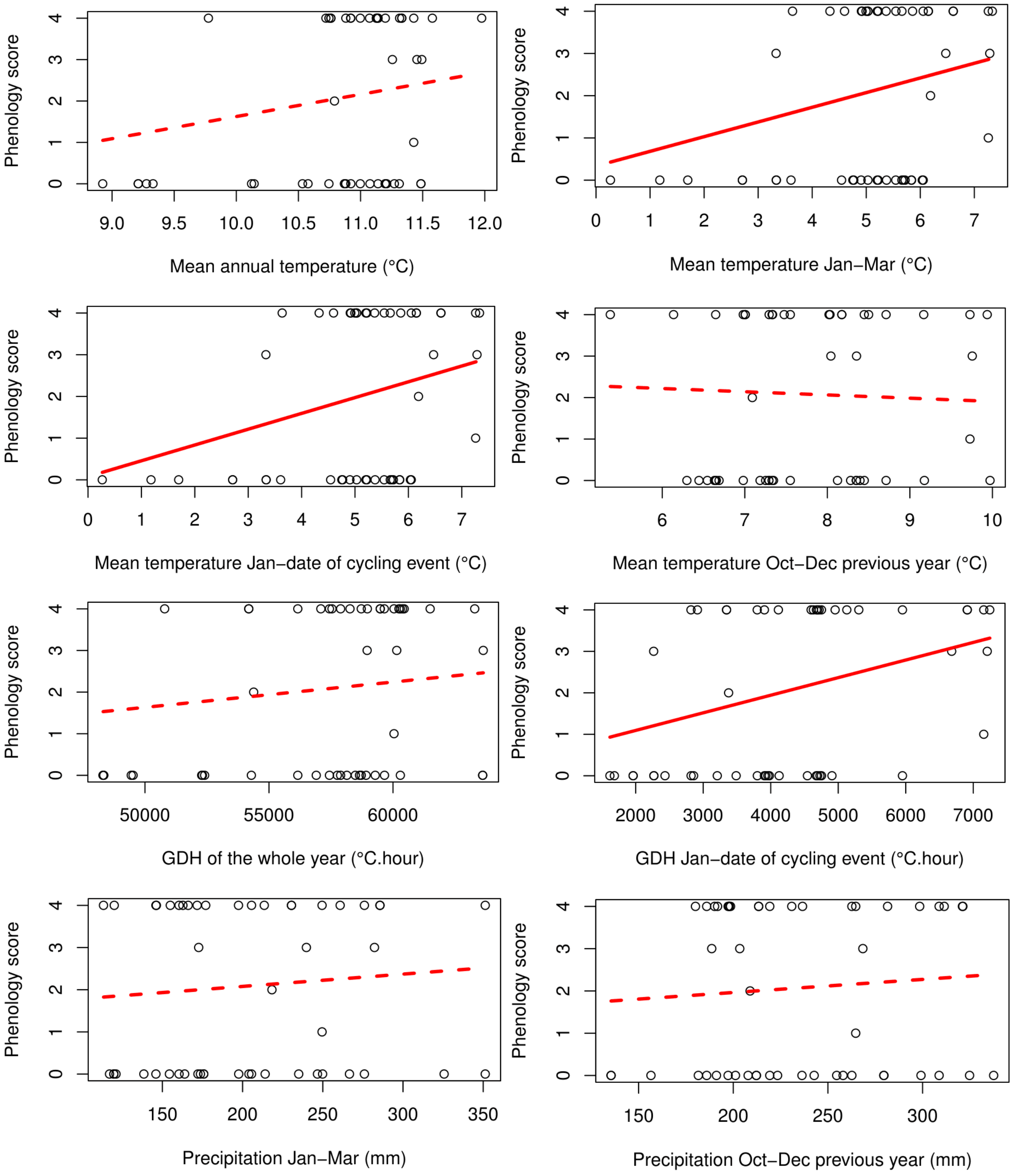


Figure 20. The effects of the eight different climatic variables on the phenology score of flowering. The red line represents the fit of the linear mixed effects model and is dashed if the effect is non-significant.

Table 7. Effects of the eight climatic metrics on the phenology score of leaf unfolding (a) and flowering (b). With respect to the significance codes, the following symbols were used: * for P < 0.001, ** for P < 0.01, * for P < 0.05 and . for P < 0.1.**

Effect	numDF	denDF	F-value	p-value
(a) Leaf unfolding				
T_{year}	1	217	13.19137	4e-04 ***
T_{spring}	1	217	39.55232	<0.0001 ***
T_{date}	1	217	42.32927	<0.0001 ***
$T_{autumnwinter}$	1	217	0.445548	0.5052
GDH_{year}	1	217	7.665646	0.0061 **
GDH_{date}	1	217	69.67429	<0.0001 ***
P_{spring}	1	217	1.104757	0.2944
$P_{autumnwinter}$	1	217	1.475819	0.2258
(b) Flowering				
T_{year}	1	45	3.068802	0.0866 .
T_{spring}	1	45	7.578491	0.0085 **
T_{date}	1	45	8.706236	0.0050 **
$T_{autumnwinter}$	1	45	0.158778	0.6922
GDH_{year}	1	45	1.349697	0.2515
GDH_{date}	1	45	13.156721	0.0007 ***
P_{spring}	1	45	0.791271	0.3784
$P_{autumnwinter}$	1	45	0.59356	0.4451

3.3.2 Species specificity

Every species and every tree showed a different variation in phenology and a different sensitivity to the climatic metrics. This is clearly shown by **Figure 21**, where each line represents one tree for the effect of the GDH_{date} (since this metric showed the largest effect) on the phenology of leaf unfolding and flowering.

Figure 22 illustrates the sensitivity from the different species to the climatic metrics in a heatmap. Most species showed no deviation from the previously found effects, which were strong positive correlations with the temperature metrics, but different non-significant precipitation effects. Only the correlations found for the phenology of *Forsythia x intermedia* Zab. and the metrics with the largest effect (T_{spring} and T_{date}) were slightly negative, but slightly positive with GDH_{date}.

3.4 Effects of abiotic and biotic site characteristics

Table S1 in the appendix represents the assessed characteristics of the tree and of the environment. However, the effect of these characteristics on the phenology score was never significant (**Table 8**).

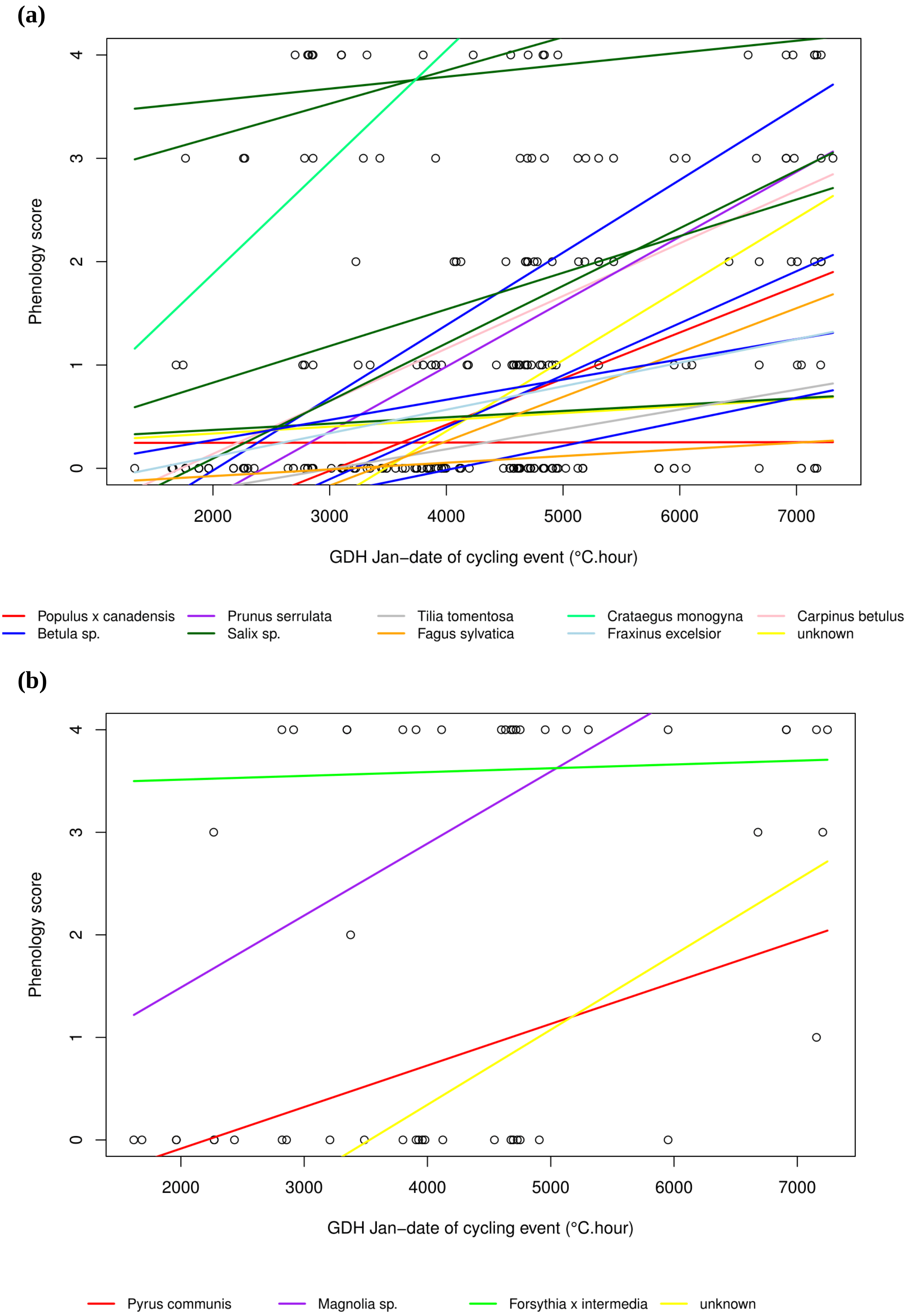


Figure 21. The linear regression between the GDH from January 1st up to the date of the cycling event on the phenology score of leaf unfolding (a) and flowering (b), each line with a different colour represents one individual tree.

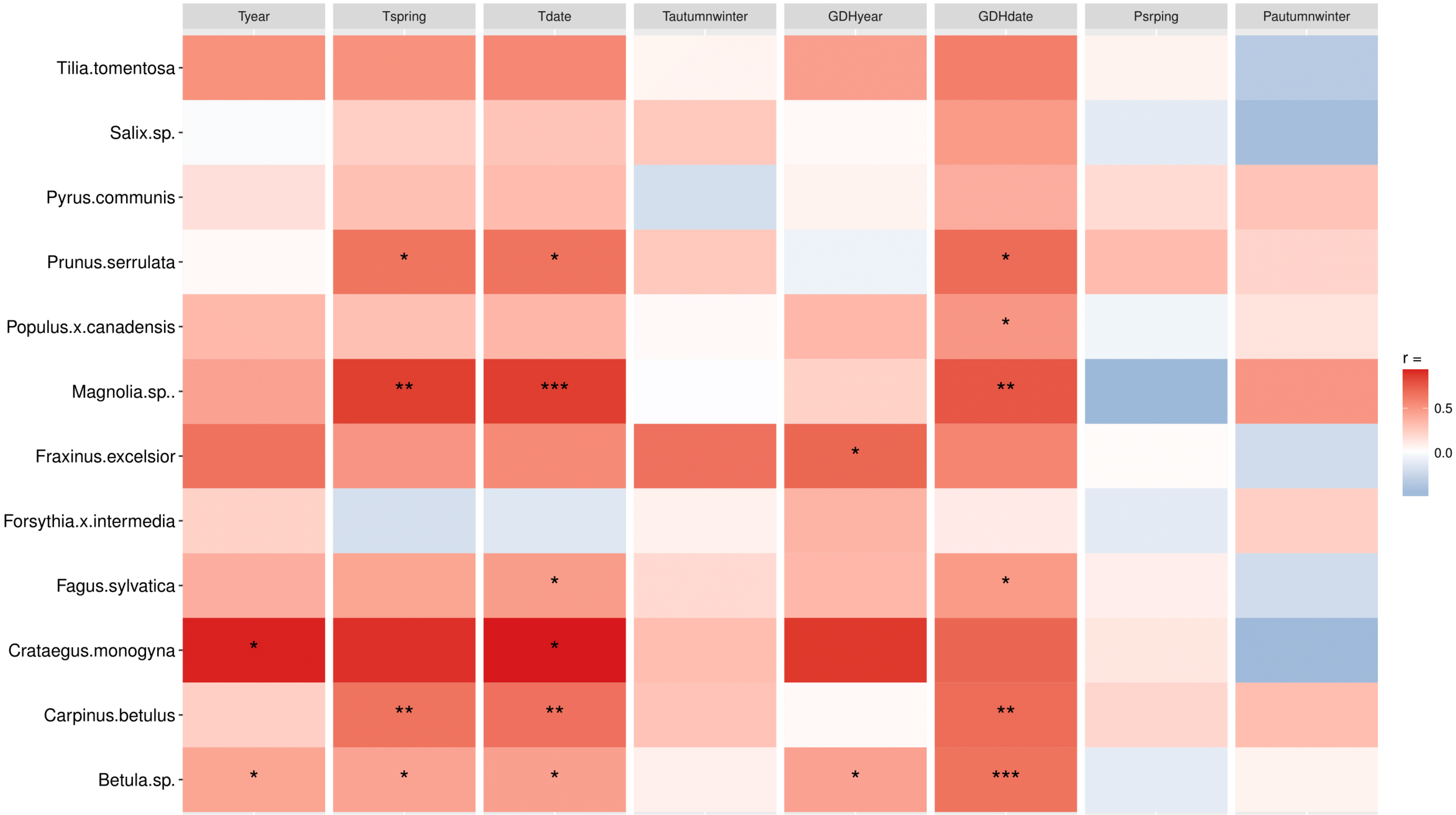


Figure 22. Correlation between leaf unfolding and flowering (*Pyrus communis* L., *Magnolia sp.*, *Forsythia x intermedia* Zab.) for different species and climate variables. Positive correlations (red) and negative correlations (blue), dark red or blue represents strong correlations (Pearson's r). With respect to the significance codes, the following symbols were used: * for P < 0.001, ** for P < 0.01, * for P < 0.05 and . for P < 0.1.**

Table 8. Effects of the site characteristics of the tree and of the environment on phenology of leaf unfolding (a) and flowering (b).

	(a) leaf unfolding				(b) flowering			
Effect	**numDF**	**denDF**	**F-value**	**p-value**	**numDF**	**denDF**	**F-value**	**p-value**
height	1	140	1.160587	0.2832	1	41	0.230675	0.6336
diameter stem[a]	1	140	0.118302	0.7314	-	-	-	-
crown size[a]	1	10	1.01335	0.3378	-	-	-	-
defoliation	1	11	1.055299	0.3263	1	1	1.929271	0.3972
discoloration	1	11	0.085184	0.7758	1	1	0.227284	0.7168
Position[a]	4	15	1.546948	0.2393	-	-	-	-
nearest tree	1	12	0.934024	0.3529	1	1	28.60151	0.1168
trees around	1	13	0.328123	0.5765	1	1	5.55749	0.2554
canopy cover	1	13	0.055729	0.8171	1	1	28.49836	0.1169
land use	2	17	0.575033	0.5733	1	2	0.885143	0.4461
aspect	6	13	0.272296	0.9402	2	1	0.557586	0.6876
soilP[a]	1	10	1.090949	0.3209	-	-	-	-
soilN[a]	1	10	0.369487	0.5568	-	-	-	-
soilC[a]	1	10	0.607938	0.4536	-	-	-	-
pH[a]	1	10	0.024879	0.8778	-	-	-	-

[a] Calculating the effect on the phenology of flowering was not possible, since there was not enough variation in the data.

3.5 Growth analysis

The growth pattern was examined for six trees of which three showed no variation in phenology (*Acer pseudoplatanus* L., *Quercus robur* L. and *Tilia tomentosa* Moench), two showed variation in leaf unfolding phenology (*Populus x canadensis* Moench and *Tilia tomentosa* Moench) and one showed variation in flowering phenology (*Pyrus communis* L.). The growth pattern of these trees is illustrated in **Figure 23**.
The mean growth deviation was never larger than 60% for positive growth deviation or lower than 40% for negative growth deviation (**Figure 24**). Thus, no pointer years (years with extraordinary growth responses) occurred between 1980 and 2016.

Figure 25 shows that spring temperature and precipitation showed only a weak, non-significant effect on the mean growth deviation (**Table 9**). The link between this mean growth deviation and the phenology score of these six trees was also small and non-significant.

Table 9. Effects of spring temperature and precipitation on the mean growth deviation and the link between mean growth deviation and the phenology score of leaf unfolding and flowering.

Effect	**numDF**	**denDF**	**F-value**	**p-value**
T_{spring}	1	209	0.4352	0.5102
P_{spring}	1	209	0.5365	0.4647
Phenology score	1	90	1.2048	0.2753

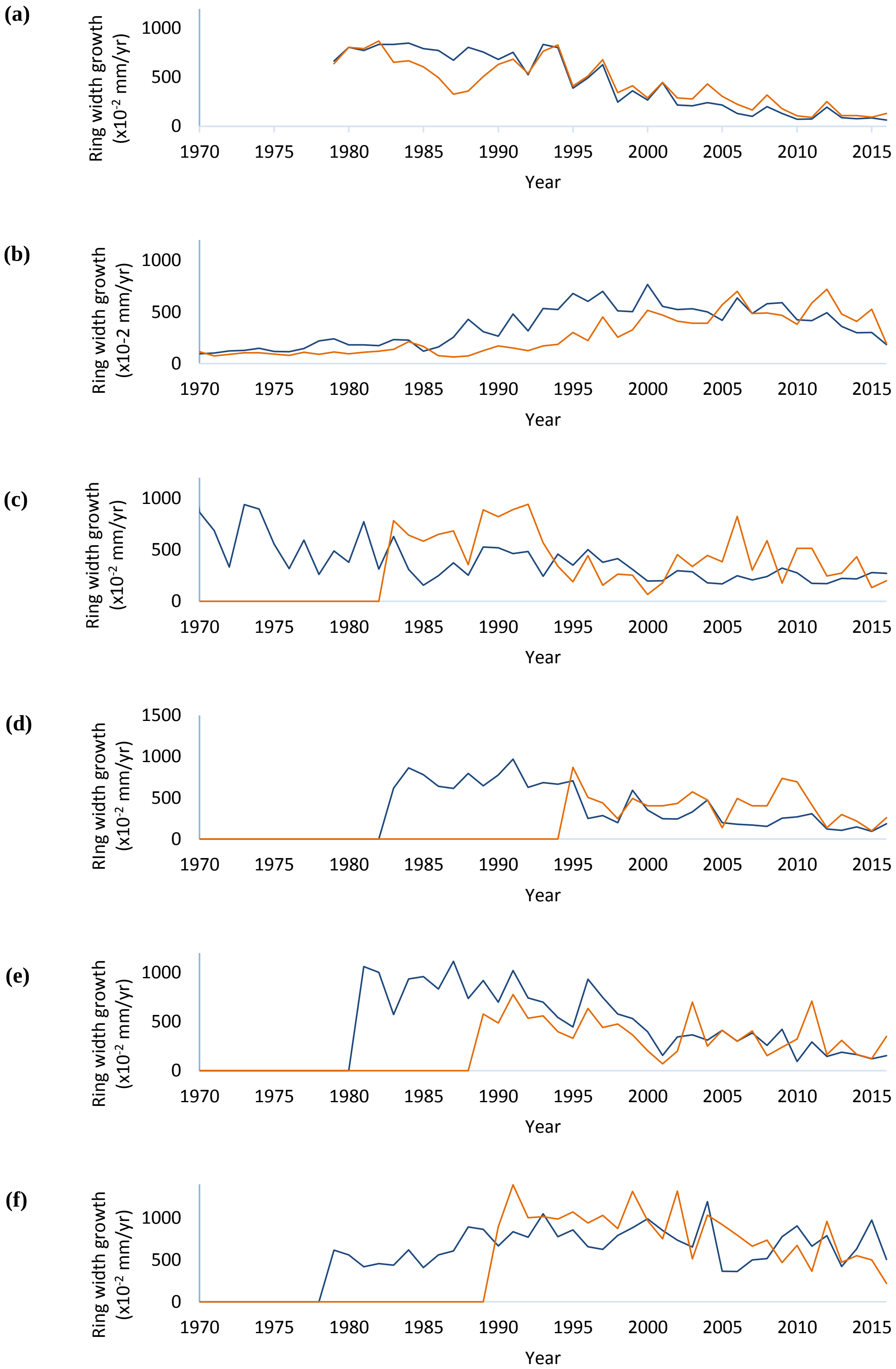


Figure 23. The growth pattern of the trees of which two different samples were examined. (a) MOL3e: *Acer pseudoplatanus* L. on the Molenberg; (b) KWA5: *Quercus robur* L. on the Kwaremont; (c) KWA6: *Pyrus communis* L. on the Kwaremont; (d) MOL3l: *Tilia tomentosa* Moench on the Molenberg; (e) PAT1: *Populus x canadensis* Moench on the Paterberg; (f) STE2: *Tilia tomentosa* Moench on the Steenberg.

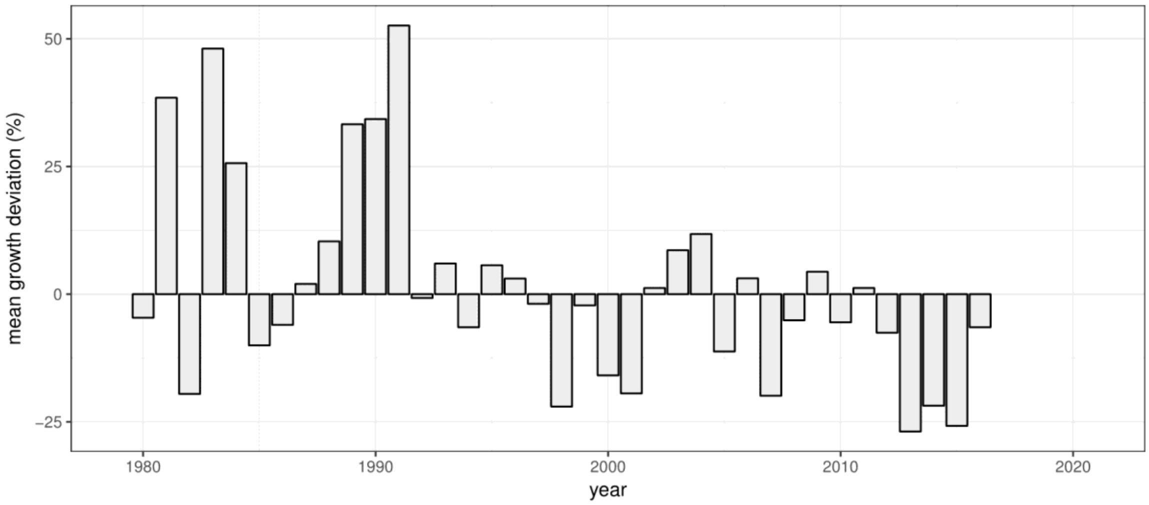


Figure 24. The mean growth deviation of the six trees combined for the 1980-2016 period.

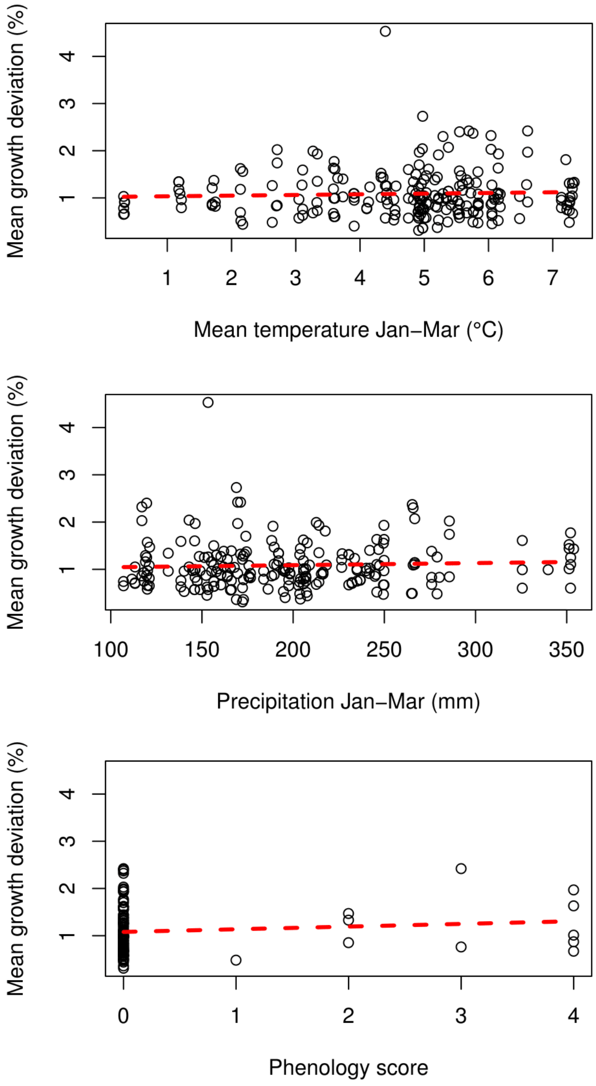


Figure 25. The effects of the spring temperature and precipitation on the mean growth deviation and the link between the mean growth deviation and the phenology score of leaf unfolding and flowering. The red line represents the fit of the linear mixed effects model and is dashed if the effect is non-significant.

4 Discussion

4.1 Changes in climate

The observed temperature increase in the study area between 1980 and 2002 (1.2 °C) is comparable with the increase of annual temperature in the rest of the world (0.8 °C). The flattening out of the temperature increase after 2002 was also observed in the global annual temperature. Only in the last few years (2014-2016) the temperature data at the study area (still no increase) differed from the global annual temperature trend (increased with 0.24 °C) (NASA, 2017; NOAA, 2017).

The change in the warming trend in the early twenty-first century is referred to as the global warming hiatus. The global temperature has not risen, despite the continued increase of GHG concentrations in the atmosphere (Kosaka & Xie, 2013). Regarding the cause of this hiatus, two major theories have been described. One considers the slowdown in radiative forcing, due to a decreased water vapour concentration in the stratosphere (Solomon et al., 2010), changes in solar insolation and rapid increase of aerosols, to be partially responsible (Maher et al., 2014). The other suggests that natural variability may be a factor, especially the influence of the negative cooling phase of the Interdecadal Pacific Oscillation (IPO) (Liu et al., 2016). The IPO is a 15-30 year time scale fluctuation in sea surface temperatures and circulation across the whole Pacific basin (Power et al., 1999). Another aspect of natural variability is the surface wind variability, causing a vertical redistribution of the heat in oceans. Research of Balmaseda et al. (2013) confirmed this theory by measuring the warming in the ocean, which amounted to 30% below 700 m between 2002 and 2012 and thereby contributed to a significant acceleration of the warming trend.

Since these different causes of the warming hiatus had an effect on the temperature and the temperature had an effect on tree phenology, the warming hiatus had an indirect effect on the variation in phenology. This effect is perceptible in our data of between 2002 and 2016, where phenology shifts are less significant than before 2002. Jochner & Menzel (2015) confirmed these findings by concluding that seven of nine phenological phases slowed down their advancing trends between 2002 and 2012. Fu et al. (2015) studied leaf unfolding dates for seven dominant European tree species at 1245 sites and found that the advance of leaf unfolding per °C decreased by 40% from 4.0 ± 1.8 days $°C^{-1}$ during 1980–1994 to 2.3 ± 1.6 days $°C^{-1}$ during 1999–2013. This reduction is probably also partly attributable to reduced chilling, which will be discussed further on.

The IPCC stated that the mean global surface temperature will start to increase again (IPCC, 2013) (**Figure 26**), along with the frequency of extreme events (IPCC, 2014). These extreme events, such as heat waves and droughts, were found to influence phenological development dramatically (Jochner & Menzel, 2015). According to the data of the NASA, the increase in mean global surface temperature started already the last few years with an increase of 0.24 °C between 2014 and 2016. Thus, it is very likely that the impact of the climate on the variation in phenology will also increase again.

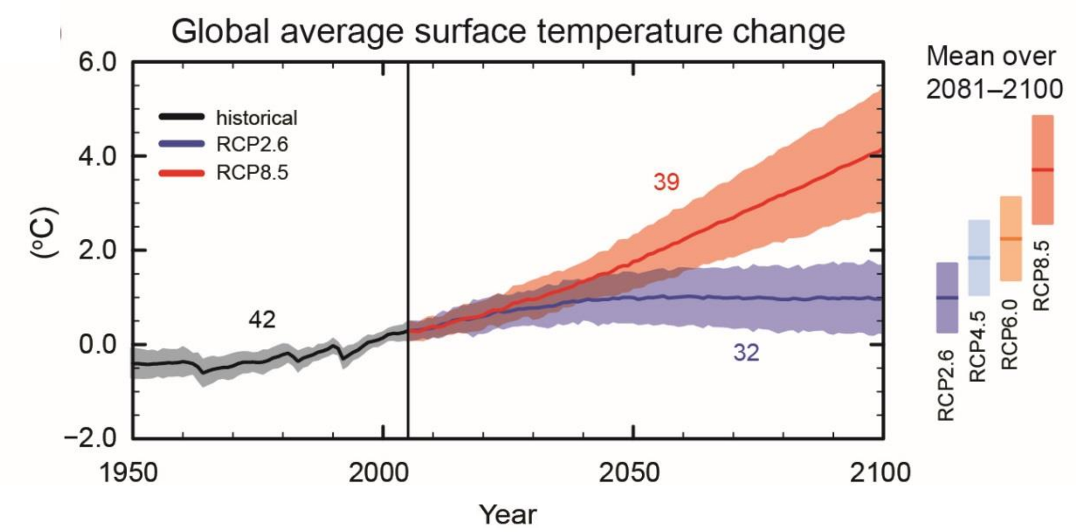


Figure 26. Model mean global average surface temperature change relative to the 1986-2005 period, for the representative scenario with modest commitments RP8.5 (red) and the scenario with a transition to a non-carbon economy RP2.6 (blue) with a measure of uncertainty (shading). The black line is the modelled historical evolution using historical reconstructed forcings (IPCC, 2013).

4.2 Effects of climatic variables on phenology

4.2.1 Effects of temperature

In this study, temperature is clearly the most important climatic variable to explain the variation in plant phenology. This is in agreement with most previous studies, especially in mid- and high latitudes where water is not the limiting factor (Chmielewski & Rötzer, 2001; Doi & Katano, 2008; Gordo & Sanz, 2010; Menzel, 2002). The GDH in particular show the highest correlation with leaf unfolding and flowering phenology. This relationship between GDH and plant phenology has also been demonstrated before (Chuine, 2000; Diekmann, 1996; Valentini et al., 2001).

The magnitude of the effect depends on the timing of the increase in temperature. The results in this study show that the temperature between January and March had the largest influence on leaf unfolding and flowering. Menzel (2002) stated that the phenological onset of spring, such as leaf unfolding, correlated very well with the air temperature of the preceding months. Thus, the increase in early spring temperatures has the biggest influence on the variation in spring phenology. This corresponds with the findings of Chmielewski et al. (2005) and the results in this study. More disagreement exists about the effect of the increase in autumn and winter temperature. In our study, the mean temperature between October 1st and December 31st showed a small positive effect on leaf unfolding and a small negative effect on flowering, both non-significant. According to research of Chmielewski et al. (2005), increasing winter temperatures should cause earlier leafing and flowering. Although, winter warming may reduce the advancing of tree spring phenology, because of the lack of required chilling temperatures (Fu et al., 2015). These chilling temperatures are necessary to break winter dormancy (Menzel, 2002). The study of Heide (2003) suggests that warmer winters would increase the depth of dormancy because of the decrease in chilling temperatures, thereby leading to a slowdown in the advancement of spring. The degree to which future warming will influence the depth and timing of winter dormancy in trees is still unclear and may differ between species and ecotypes (Way, 2011).

4.2.2 Effects of precipitation

The cumulative precipitation amount showed no significant effect on both leaf unfolding and flowering phenology. Although, different studies indicated that precipitation does have an effect on phenological events (Gordo & Sanz, 2009, Piao et al., 2006; Zhang et al., 2005). However, these results were mainly found in areas coping with water shortage and droughts, where water availability is the primary limitation of vegetation growth. Such as in arid and semiarid regions of Africa, where a higher cumulative rainfall stimulates an earlier vegetation green-up (Zhang et al., 2005). In Mediterranean ecosystems precipitation accounted for less than ten percent of the phenological variability (Gordo & Sanz, 2009). Piao et al. (2006) stated that the effect of precipitation differs among vegetation types and phenological phases. This corresponds with the large differences of the precipitation effect between species in this study. As well as with the fact that the impact on the phenology of flowering was larger than the impact on the phenology of leaf unfolding.

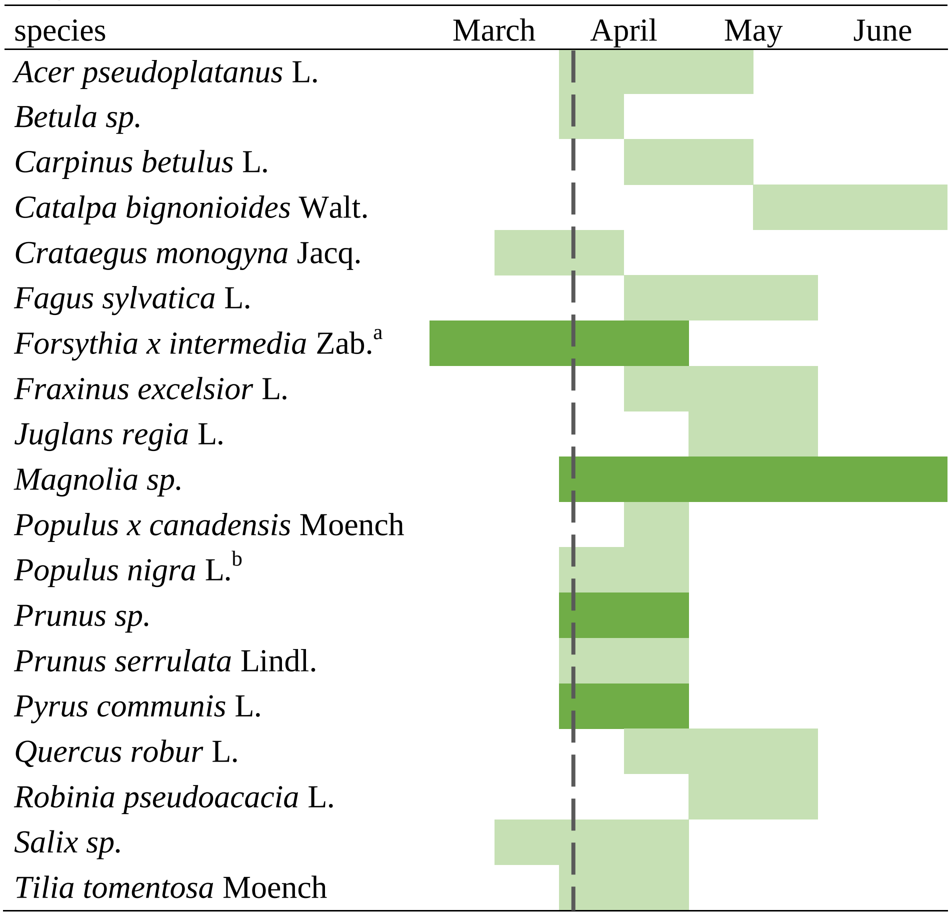
To conclude, the variation in tree phenology is primarily controlled by temperature. Spring phenological phases, such as leaf unfolding and flowering, are mostly influenced by early spring temperatures, while there is more unclearness about the effect of the winter temperatures. The precipitation factor has also an influence on phenological events, which varies abruptly across different ecosystems and climate regions. In temperate, humid climate regions, the effect of precipitation on the phenology of trees is rather limited and depends on species and phenological phases. On the other hand, in water-limited regions, changing precipitation patterns are expected to strongly influence the annual cycle of plant activity. Besides temperature and precipitation, also the degree of winter chilling and the photoperiod play an important role to control spring phenology (Körner & Basler, 2010). Their effect is strongly dependent on the tree species and will be discussed in the next chapter.

4.3 Species specificity

4.3.1 Variation in phenology

In this study, 19 different species were examined, of which seven always showed variation in the phenology score, seven species always scored zero and five species belonged to both variation and no variation categories. This difference in phenology variation could be explained by the difference in early and late leaf unfolding or flowering species. **Table 10** illustrates the average dates of leaf unfolding and flowering in Belgium for each species examined in this study. The average date of the Tour of Flanders between 1980 and 2016, and thus the average date on which the phenology score was determined, is the 4th of April.

Table 10. Average period of leaf unfolding (light green) and flowering (dark green) in Belgium of each species examined (Inverde, 2011); [a](Willaert, 2015); [b](WWF, 1988). The dashed line represents the average date of the cycling event the Tour of Flanders (i.e. DOY 94, or the 4th of April).



species	March	April	May	June
Acer pseudoplatanus L.		░░	░	
Betula sp.		░		
Carpinus betulus L.		░	░	
Catalpa bignonioides Walt.			░	░░
Crataegus monogyna Jacq.	░	░		
Fagus sylvatica L.		░	░░	
Forsythia x intermedia Zab.[a]	▓▓	▓▓		
Fraxinus excelsior L.		░	░░	
Juglans regia L.			░░	
Magnolia sp.		▓▓	▓▓	▓▓
Populus x canadensis Moench		░		
Populus nigra L.[b]		░░		
Prunus sp.		▓▓		
Prunus serrulata Lindl.		░░		
Pyrus communis L.		▓▓		
Quercus robur L.		░	░░	
Robinia pseudoacacia L.			░░	
Salix sp.	░	░░		
Tilia tomentosa Moench		░░		

Late leaf unfolding species (*Acer pseudoplatanus* L., *Catalpa bignonioides* Walt., *Fagus sylvatica* L., *Fraxinus excelsior* L., *Juglans regia* L., *Quercus robur* L., *Robinia pseudoacacia* L.), scored mostly zero for all images. Except for *Fagus sylvatica* L. and *Fraxinus excelsior* L. respectively four and two trees were examined of which half of the examined individuals of both species showed variation in leaf unfolding phenology. However, it must be noticed that

Fagus sylvatica L. only scored different from zero in 2014, which was a rather warm year. Species unfolding their leaves mainly in March or April (*Betula sp*., *Carpinus betulus* L., *Crataegus monogyna* Jacq., *Populus x canadensis* Moench, *Populus nigra* L., *Prunus serrulata* Lindl., *Salix sp*. and *Tilia tomentosa* Moench), showed variation in phenology scores. Except for *Populus nigra* L., where the one tree scored zero on all seven images. Variations in flowering scores were determined for *Forsythia x intermedia* Zab., *Magnolia sp.* and *Pyrus communis* L., which are all early flowering species. *Prunus sp*. also starts flowering in April, but scored zero on all six images. This is probably a consequence of the older age, regarding the high defoliation (40%) and discolouration (10%) of the tree, which is expected to correlate with delayed spring events (Menzel & Fabian, 1999).

4.3.2 Variation in temperature sensitivity

Based on the correlation between the different temperature metrics and the phenology scores, the temperature sensitivity for leaf unfolding and flowering differs among species. *Magnolia sp.* and *Crataegus monogyna* Jacq. showed the highest sensitivity in this study, followed by *Carpinus betulus* L., *Tilia tomentosa* Moench, *Prunus serrulata* Lindl. and *Betula sp*. Slightly negative correlations were found for *Forsythia x intermedia* Zab.

An explanation for this variation is found in the difference between early and late leaf unfolding species, their photoperiod-sensitivity and chilling requirements. Early leaf unfolding species are more temperature sensitive and require less chilling days (Zhang et al., 2015). On the other hand, late leaf unfolding species are more photoperiod controlled and require more chilling days (Körner & Basler, 2010). Intermediate leaf unfolding species (e.g. *Carpinus betulus* L.) are unaffected by the photoperiod, but require more chilling temperatures than early species, thereby showing intermediate temperature sensitivity (Heide, 1993; Vitasse et al., 2009). Research of Murray et al. (1989) explained this difference in temperature sensitivity by calculating the thermal time needed to unfold the leaves of 15 different woody plant species. A relationship between the required thermal time (days > 5 °C) and the chilling days (days ≤ 5 °C) was found (**Figure 27**). Decreased chilling greatly increased the required thermal time for late leaf-out species (e.g. *Fagus sylvatica* L.), but slowly increased the required thermal time for early leaf-out species (e.g. *Crataegus monogyna* Jacq.). This results in a larger effect of temperature on early leaf unfolding species.

The results in this study confirm the findings mentioned above. Early leaf-out species show the highest positive correlation with the spring temperature metrics, while late leaf-out species show a lower positive correlation. Although, *Salix sp*. shows no high positive correlation as an early leaf-out species and *Forsythia x intermedia* Zab. even shows negative correlations with spring temperatures. Both correlations are non-significant.

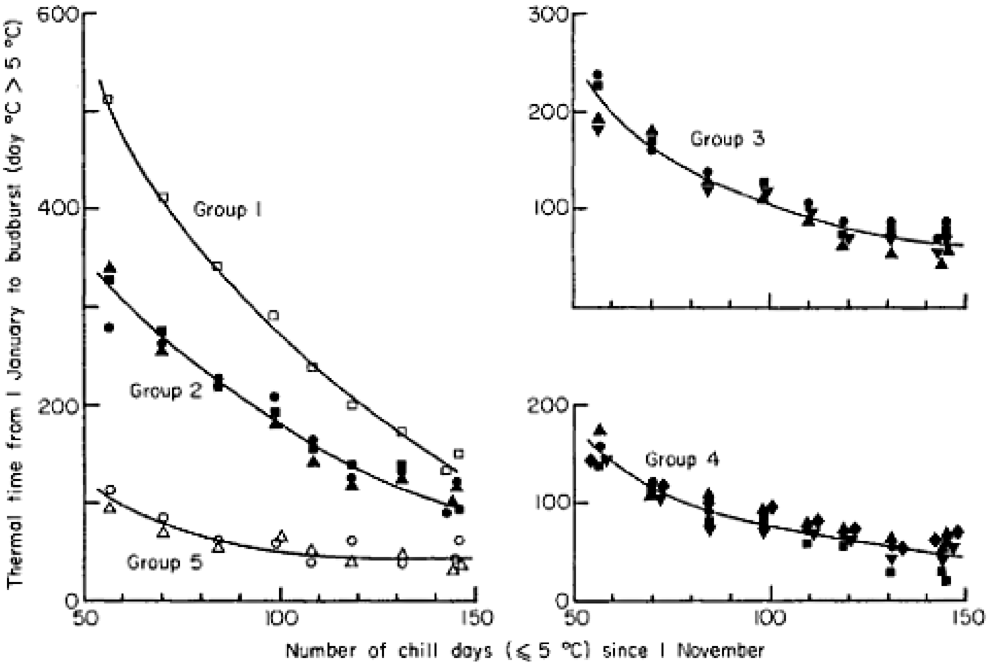


Figure 27. The relationship between the thermal times to budburst and the accumulated number of chill days for fifteen perennial woody species, arranged into five groups. Group 1: *Fagus sylvatica* L. (□); group 2: *Robinia pseudoacacia* L. (▲), *Tsuga heterophylla* Sagh. (■), *Picea sitchensis* Carrière. (●); group 3: *Rubus idaeus* L. (▲), *Sorbus aucuparia* L. (▼), *Betula pendula* Roth. (■), *Corylus avellana* L. (●); group 4: *Sambucus nigra* L. (▲), *Rosa rugosa* Thunb. (▼), *Salix viminalis* L. (♦), *Larix decidua* Mill. (■), *Prunus avium* L. (●); group 5: *Populus trichocarpa* Hook. (△), *Crataegus monogyna* Jacq. (○) (Murray et al., 1989).

4.4 Effects of abiotic and biotic site characteristics on phenology

No single characteristic of the tree or of the environment showed significant effects in our study. Yet, different sources in the scientific literature described that, besides climatic variables, several other factors can also have an influence on plant phenology (Honour et al., 2009; Jochner & Menzel, 2015; Seiwa, 1999; Wielgolaski, 2001).

The height of the tree showed a slight negative, non-significant effect in this study. This is in corroboration with the study of Seiwa (1999) about the effect of tree height of *Acer mono* Maxim. on leaf phenology in a temperate forest in Japan. Results showed that larger tree height correlated with delayed leaf unfolding. This is probably a consequence of the fact that plant height of *Acer mono* Maxim. is strongly correlated with age, and the latter is expected to correlate with delayed spring phenology (Ishikawa, 1987; Menzel & Fabian, 1999). In our study, the effects of soil characteristics were very diverse: the concentration of nitrogen and carbon in the upper soil layer showed slight negative, non-significant results, while the concentration of phosphorus and the pH of the upper soil layer showed slight positive, non-significant results. This is in contradiction with the findings of Wielgolaski (2001), that the amount of phosphorus, as well as other ions, often showed negative correlations with earlier phenophases. The same study found similar results for pH: high pH delayed leaf unfolding of *Betula pubescens* Ehrh., *Sorbus aucuparia* L., *Syringa vulgaris* L. and *Prunus domestica* L. The tendency to this negative correlation seemed to be weakest for plant species strongly dependent on high temperature for their development (e.g. *Fraxinus excelsior* L.), indicating that the influence of soil parameters is partly related to the influence of climatic factors.

Some abiotic and biotic site characteristics or characteristics of the tree could have a positive or negative (e.g. tree height, pH) effect on earlier spring phenology. However, these effects are small, relative to the temperature effect (Badeck et al., 2004).

4.5 Growth analysis

Tree ring growth is highly dependent of the temperature and the moisture content of the soil. Narrow rings occur during years of low moisture and high temperatures (Fritts, 1966). According to the study of Lebourgeois et al. (2005) on the tree ring growth of *Fagus sylvatica* L. in France, the soil water deficit in June and July is the dominant climatic factor controlling tree ring width. In North-America, the tree ring width of *Quercus alba* L. was found to be related to the moisture availability during the preceding September and current June and July (Fritts, 1962). High temperatures in August and September favour wide tree rings, though the effect of temperature on tree ring widths is less frequent and significant than the moisture content of the soil (Lebourgeois et al., 2005). This differs from the influences of the climatic variables on the variation in leaf unfolding and flowering, where spring temperature plays the main roll and precipitation is less important in temperate, humid climate zones. **Figure 28** illustrates the changes in stem size of six *Pinus longaeva* Bailey trees during 1962, 1963 and 1964, together with the phenological changes. Regarding this figure, the phenological phase of bud opening and the emerging of the needles shows no link with the stem growth of the tree for these three years.

In our study, the link between the variation in flowering and leafing phenology and the growth pattern was non-significant. However, it must be taken into account that the measurements of the growth pattern based on tree rings were not very reliable. This is a consequence of several factors: two representative samples of only six trees (due to access restrictions and samples of unusable quality) and many species with unclear tree rings. A possible solution is the use of dendrochronomics, where a non-destructive visualization with high resolution is made, using X-ray tomography (Van den Bulcke, 2009). The density profile, obtained by this X-ray computed tomography, allows accurate tree ring analysis (De Mil, 2016).

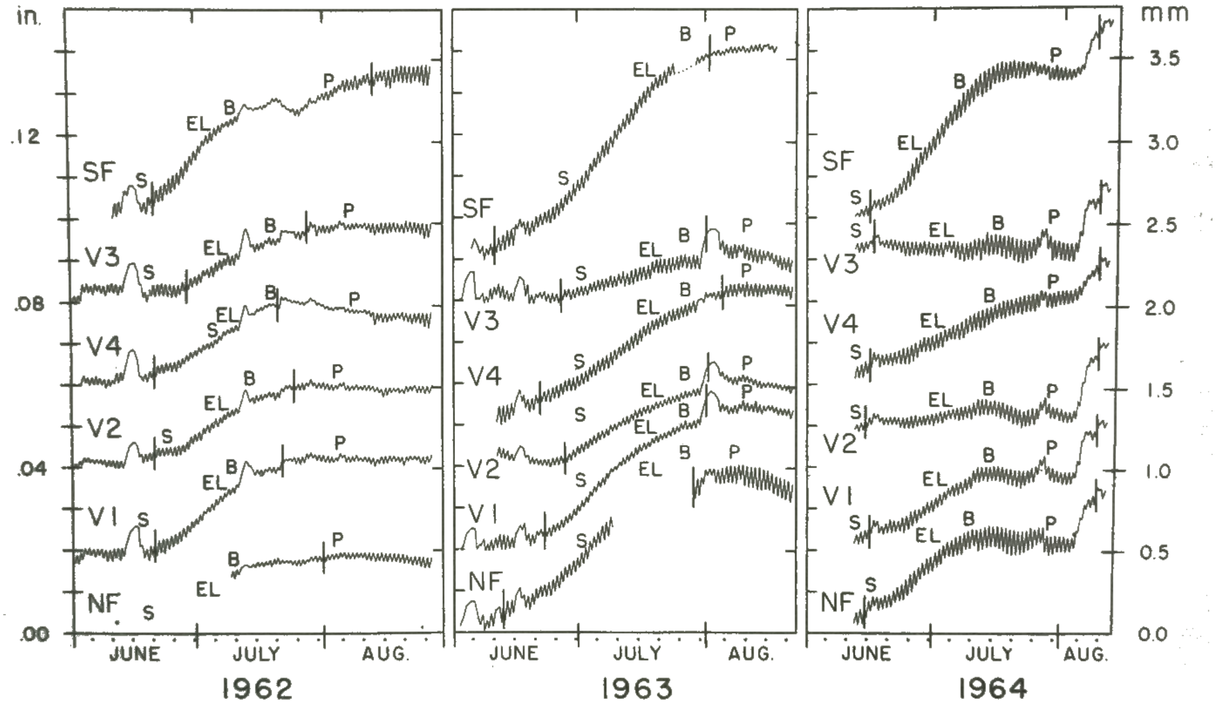


Figure 28. The daily maximum and minimum stem size measured by dendrographs mounted on six *Pinus longaeva* Bailey trees during 1962, 1963 and 1964. Phenological changes in each tree are indicated: S – bud swelling; EL – buds elongating; B - buds opening, needles beginning to emerge; P – pollen shedding. Trees V1 through V4 are in the valley floor, SF on a south-facing slope and NF on a north-facing slope (Fritts, 1976).

5 Conclusion

The mean annual temperature, derived from the high-resolution climatic data of the RMI, showed a strong increasing trend between 1980 and 2002. Thereafter, warming across the route of the Tour of Flanders slowed down and the mean annual temperature remained constant around 11 °C. These observations correspond with global measurements and the current global warming hiatus. Out of the 46 trees examined, 24 showed variation in leaf unfolding or flowering phenology and 20 trees scored zero on all images. This is largely a consequence of the difference between early and late leaf unfolding or flowering species. Because the Tour of Flanders is a cycling event held around the 4th of April every year (between the 90th and 98th day of the year), it is not possible to study very late species with images of this event. The phenology scores of leaf unfolding showed a significant positive correlation with time during the warming period, meaning an advancement of leaf unfolding between 1980 and 2002. This clear positive correlation ended after 2002, where non-significant effects were found. A positive correlation was also found between the phenology scores of flowering and time, but this was before and after 2002 non-significant.

From the eight climatic metrics tested, the amount of growing degree hours between January 1st and the date of the cycling event (GDH_{date}) had clearly the largest positive effect. GDH_{date} is strongly related with the temperature between January 1st and March 31st and the temperature between January 1st and the date of the cycling event, both showing significant positive effects. Therefore, it can be concluded that spring temperature shows the largest effect on leaf unfolding and flowering phenology, which is consistent with scientific literature. Annual temperatures and the GDH of the whole year also showed significant positive effects, while the temperature between October 1st and December 31st showed a non-significant effect on both leaf unfolding and flowering. Precipitation rates, both in spring and in autumn and winter, showed only slight, non-significant effects on spring phenology. Not all trees showed the same response to the different climatic variables. This is partly due to species specificity and the variation in temperature sensitivity. Early leaf unfolding species showed higher temperature sensitivity than late leaf unfolding species, because these late species are more dependent on chilling requirements. The effect of the assessed characteristics of the tree and of the environment remained unclear, since no significant effect was found. As for the growth analysis, where no significant link was found between the growth pattern and the variation in phenology scores.

By using historical images, it is not possible to quantify the advancement in spring phenology, since it is not exact known when leaf unfolding or flowering started. Although, the determined correlation can be used to calculate the required amount of GDH for each species to achieve the first phenology score. In conclusion, the use of video footage or images from recurring events is a valuable method to study phenological variations, which contributes to a better understanding and estimation of the effects of climate change on the phenology of trees.

6 Future research perspectives

Since temperatures tend to increase again and the global climate is still changing, the shift of phenological events will continue in the future. More research is required to understand these shifts for all species to estimate further impacts on ecosystem functioning. The use of historical images allows to examine different species and long periods in a short time span. Therefore, new innovative sources, such as the use of footage from recurring events, are valuable additions to commonly used methods.

However, there are still possibilities to optimize the phenological data obtained from this video footage. The quality of the images, for example, is important. Events were less different camera angles are used should provide easier comparison and thereby more objective phenological data. Also, missing images in the data could be avoided when using the same camera angle every year. This thesis showed that innovative methods could be an excellent way to study phenological variations. It is therefore important to continue to seek for additional events or new methods, such as news events, other sport events and CCTV cameras, so reliable models can be made. These models could then provide more insight into the impact of climate change on the phenology of trees and our capacity to project future impacts would be improved.

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8 Appendix

Table S1. Characteristics of the trees and their environment. NA: the tree was cut or access was restricted or denied.

tree ID	latitude (N)	longitude (E)	height (m)	diameter breast height (m)	crown size (m)	defoliation (%)	discolouration (%)	position	nearest tree (m)	number of trees around	canopy cover (%)	surrounding land use	aspect	soil P (mg/kg)	soil N (%)	soil C (%)	soil pH
KOP2	50°48'69"	3°34'61"	33.9	1.01	20	10	0	roadside	8.7	6	30	meadow	NW	62.1	0.321	3.591	6.19
KOP3	50°49'20"	3°36'12"	11.7	0.41	9.5	0	0	roadside	25.4	0	5	arable	flat	11.4	0.203	2.617	6.715
WOL4	50°50'34"	3°38'32"	11.1	0.42	7.8	50	20	roadside	28	0	5	paved	ZW	NA	NA	NA	NA
WOL5	50°50'33"	3°38'29"	33	1.05	4	0	0	garden	1.8	23	50	paved	ZW	165.8	0.429	5.112	7.419
WOL6	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	paved	flat	NA	NA	NA	NA
WOL1	50°50'30"	3°38'13"	9.1	0.21	6	0	0	garden	7.7	6	15	paved	flat	43.4	0.162	1.785	7.08
WOL2	50°50'31"	3°38'18"	3.8	NA	NA	10	5	garden	0.5	10	15	paved	W	35.4	0.101	0.984	7.846
KWA2	50°46'58"	3°31'33"	8.2	0.52	5	0	0	roadside	4.3	4	10	meadow	NW	81.7	0.27	2.858	6.721
KWA6	50°46'20"	3°31'42"	11.4	0.56	9	25	5	garden	9.5	4	20	meadow	NW	62.3	0.14	1.307	5.13
KWA8	50°46'20"	3°31'41"	16	0.43	8	0	0	roadside	1	9	30	meadow	NW	7.7	0.192	1.855	5.128
KWAx	50°46'20"	3°31'41"	3.6	0.24	5.1	0	0	roadside	4.5	10	30	meadow	NW	33.5	0.218	2.551	5.782
KWA7	50°46'32"	3°31'33"	4.2	0.3	5.2	20	0	garden	2	13	15	paved	flat	NA	NA	NA	NA
KWA5	50°46'44"	3°31'31"	NA[6]	1.05	NA[1]	50	20	roadside	1.5	6	15	meadow	NW	100.7	0.303	3.269	5.5
PAT1	50°46'57"	3°32'39"	32	0.6	7.5	0	0	roadside	5.1	10	25	meadow	flat	27.4	0.322	4.042	7.412
PAT3b	50°46'57"	3°32'48"	12.9	0.24	3.8	10	40	garden	1.8	13	20	meadow	W	47.8	0.139	1.181	7.635
PAT2	50°46'57"	3°32'48"	NA	NA	NA	NA	NA	garden	NA	NA	NA	meadow	W	NA	NA	NA	NA
PAT3,5	50°46'55"	3°32'56"	NA	NA	NA	NA	NA	roadside	7	7	20	arable	W	NA	NA	NA	NA

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[6] This tree was partly cut, measuring the current height and crown size would lead to a distorted picture.

EIK1	50°49'06"	3°38'23"	NA	NA	NA	NA	NA	garden	NA	NA	NA	paved	flat	NA	NA	NA	NA
EIK4	50°49'20"	3°38'27"	17.2	1.08	3.8	50	0	roadside	14.1	8	30	arable	ZW	101.5	0.183	1.74	7.133
EIK6	50°49'38"	3°38'35"	6.3	0.2	4	50	0	roadside	17.5	2	5	meadow	Z	42.5	0.252	2.842	7.268
EIK8	50°49'32"	3°38'25"	NA	NA	NA	NA	NA	garden	NA	NA	NA	paved	Z	NA	NA	NA	NA
EIK10	50°49'29"	3°38'18"	25.6	1.03	16	10	0	roadside	0.4	15	50	arable	flat	22.9	0.43	5.02	7.14
STE2	50°48'7"	3°34'56"	12.6	0.64	12	0	2	garden	250	0	5	arable	ZO	9.6	0.387	5.948	5.834
STE3	50°48'3"	3°37'10"	7.8	0.64	6.5	0	0	garden	4.4	6	20	paved	flat	20.9	0.392	5.742	6.696
TAA1	50°47'39"	3°37'29"	21.5	0.47	9	5	30	roadside	1.1	18	25	paved	NO	98.3	0.329	4.101	5.476
TAA3	50°47'41"	3°37'32"	16.3	0.48	12.8	5	45	garden	9	7	40	paved	NW	93.3	0.181	2.211	6.389
TAA10	50°47'44"	3°38'4"	14	0.7	NA	20	0	garden	2	10	40	paved	flat	NA	NA	NA	NA
BOSvoor	50°46'05"	3°55'56"	NA	NA	NA	NA	NA	roadside	NA	NA	NA	arable	ZW	NA	NA	NA	NA
BOS3	50°45'11"	3°56'35"	NA	NA	NA	NA	NA	garden	NA	NA	NA	paved	flat	NA	NA	NA	NA
MUU2	50°46'19"	3°53'22"	28	0.76	5	5	5	forest	1.5	15	50	paved	W	35.1	0.252	2.704	6.46
MUUkap1	50°46'21"	3°53'25"	21.4	0.8	12	5	10	park	10.1	1	10	meadow	W	32.3	0.414	4.875	4.469
MUUkap2	50°46'22"	3°53'28"	15.3	1.02	10	10	5	park	13.7	7	15	paved	flat	123	0.4	3.58	6.673
LEB6	50°49'38"	3°43'25"	6.6	0.4	5.5	0	0	garden	4	7	15	arable	ZW	92	0.349	4.608	7.187
LEB4	50°49'29"	3°43'15"	23	0.86	10	5	0	forest	2	16	40	meadow	Z	45.8	0.278	3.834	7.266
LEB3	50°49'33"	3°43'16"	9.8	0.28	6.7	0	0	roadside	1.5	13	20	meadow	flat	53.9	0.284	3.944	7.003
LEB2	50°49'8"	3°42'44"	21	1	16	5	5	garden	5	2	15	meadow	W	54.6	0.313	4.586	6.888
LEB1	50°49'10"	3°42'13"	14.1	0.33	6	0	5	garden	10	4	20	paved	flat	81.2	0.192	3.298	5.557
VAL2	50°48'54"	3°45'15"	21	1.1	14	0	0	garden	4	6	40	paved	Z	103.4	0.161	1.643	6.465
VAL3	50°49'19"	3°45'30"	6.9	0.3	5.6	40	10	garden	2.5	10	35	paved	flat	NA	NA	NA	NA
VAL5	50°49'01"	3°45'15"	NA	NA	NA	NA	NA	roadside	NA	NA	NA	paved	flat	NA	NA	NA	NA
MOL3e	50°51'30"	3°41'60"	20.1	0.4	10	5	10	roadside	1	17	65	paved	Z	NA	NA	NA	NA
MOL3l	50°51'30"	3°41'60"	20.1	0.4	10	0	0	roadside	1	17	65	paved	Z	NA	NA	NA	NA
MOL5	50°51'31"	3°42'02"	NA	NA	NA	100	NA	garden	8	6	30	meadow	Z	NA	NA	NA	NA
MOL6	50°51'35"	3°42'10"	7.5	0.76	6.8	20	20	garden	15	1	10	meadow	ZW	NA	NA	NA	NA
MOLkap	50°31'36"	3°42'11"	NA	NA	NA	NA	NA	garden	NA	3	10	meadow	ZW	NA	NA	NA	NA
MOL7	50°51'37"	3°34'12"	NA	NA	NA	NA	NA	garden	NA	8	30	meadow	flat	NA	NA	NA	NA