**Extreme Warm Temperatures Alter Forest Phenology and Productivity in Europe**

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**Abstract**

Recent climate warming has shifted the timing of spring and autumn vegetation phenological events in the temperate and boreal forest ecosystems of Europe. In many areas spring phenological events start earlier and autumn events switch between earlier and later onset. Consequently, the length of growing season in mid and high latitudes of European forest is extended. However, the lagged effects (i.e. the impact of a warm spring or autumn on the subsequent phenological events) on vegetation phenology and productivity are less explored. In this study, we have (1) characterised extreme warm spring and extreme warm autumn events in Europe during 2003-2011, and (2) investigated if direct impact on forest phenology and productivity due to a specific warm event translated to a lagged effect in subsequent phenological events. We found that warmer events in spring occurred extensively in high latitude Europe producing a significant earlier onset of greening (OG) in broadleaf deciduous forest (BLDF) and mixed forest (MF). However, this earlier OG did not show any significant lagged effects on autumnal senescence. Needleleaf evergreen forest (NLEF), BLDF and MF showed a significantly delayed end of senescence (EOS) as a result of extreme warm autumn events; and in the following year’s spring phenological events, OG started significantly earlier. Extreme warm spring events directly led to significant (p=0.0189) increases in the productivity of BLDF. In order to have a complete understanding of ecosystems response to warm temperature during key phenological events, particularly autumn events, the lagged effect on the next growing season should be considered.

**Key words**: Land surface phenology, Envisat MTCI, Anomalous temperature, Climate variability, Lagged effect, Forest ecology

# Introduction

Land surface phenology can be defined as the seasonal pattern of variation in vegetation growth as observed by remote sensing data; and this has been used as a surrogate measure of global change in many studies (eg. Piao et al., 2006; White et al., 2009; Atzberger and Eilers, 2011; Tan et al., 2011). Monitoring the growth and development dynamics of temperate and boreal vegetation is essential in understanding the impacts of climate on a vast range of terrestrial life-forms (Reed et al., 1994; Menzel, 2000; Morisette et al., 2009; Morin et al., 2009). Forest phenology sets the tone for competition and interactions (via the complex food chain and food web processes) among plant and animal species. Additionally, the amount and quality of vegetation cover regulates land-atmosphere interactions such as albedo and carbon, water and energy exchanges (Wilson and Baldocchi, 2000; Molod et al., 2003; Richardson et al., 2013) , as well as key ecosystem services such as food, fibre, fuel, medicine and recreation (Badeck et al., 2004; Kauserud et al., 2012). Consequently, shifting in the dates at which leaves unfold and fall is of paramount importance from an ecological point of view. As a result, numerous earlier studies have tried to characterise the land surface phenology at different spatial scales (eg. Brown et al., 2010; Atzberger and Eilers, 2011; Jones et al., 2012; Rodriguez-Galiano et al., 2015).

Although photoperiod influences the phenology of certain northern high latitude forest species (Heide, 1993; Fracheboud et al., 2009; Sanz-Pérez et al., 2009; Vitasse and Basler, 2013; Way and Montgomery, 2015), air temperature was found to be the most crucial cue in determining the seasonal onset and senescence (Vitasse et al., 2009b; Shen et al., 2014). A sequence of normal temperature range ensures optimal growth of plants by indirectly supplying energy (via photosynthesis and respiration) for metabolic processes and development. Temperature directly regulates the dynamics of plant development via the processes of chilling and forcing requirements during dormancy (Luedeling et al., 2013).

The timing of vegetation phenology directly influences forest productivity by regulating the duration available for carbon fixation (Chang et al., 2013; Sakuraba et al., 2014). For example, biochemical compositions of the leaf such as foliar nitrogen enhance carbon fixation process during the growing seasons and hence, results in an increase in forest productivity (Smith et al., 2002; Charrier and Améglio, 2011). Other factors such as stand age (Ryan et al., 1997; Bond, 2000; Smith and Long, 2001; Song et al., 2014), soil quality (Pastor et al., 1984; Reich et al., 1997), latitudinal differences (Gillman et al., 2015) and species richness (Zhang et al., 2012; Gillman et al., 2015) also determine variations in forest productivity.

Regional and global changes in temperatures (Hurrell and VanLoon, 1997; Overland et al., 2008) have shifted the timing of forest phenology in mid and high latitudes of Europe (Sparks and Menzel, 2002; Vitasse et al., 2011). Many forest ecosystems in Europe have thus experienced prolongation of active growing season and consequent increase in photosynthetic activity (Myneni et al., 1997; Tucker et al., 2001) and in turn ecosystem productivity (Richardson et al., 2010; Pilegaard et al., 2011). More importantly, recent temperature anomalies in mid and high latitude Europe (Tuomenvirta et al., 2000; Xoplaki et al., 2005; Luterbacher et al., 2007; Van Oldenborgh, 2007; Cattiaux et al., 2009) have been responsible for earlier onset of greening (OG) and later end of senescence (EOS) (Roetzer et al., 2000; Walther et al., 2002; Parmesan and Yohe, 2003; Mimet et al., 2009); altering ecosystem functions and services (Hanninen et al., 1990; Kellomaki et al., 1995; Inouye, 2008; Piao et al., 2008; Hufkens et al., 2012).

Spring season sets out the start of the productive time in temperate and boreal forest ecosystem; and hence, gained the attentions of many researchers. Many studies have looked into the consequences of a warmer spring on the tree phenology and productivity (Richardson et al., 2010; Polgar and Primack, 2011; Way, 2011; Clark et al., 2014; Guo et al., 2015). Recently, the relationship between spring and autumn leaf phenology in the conditions of warming climate in temperate forest ecosystems has been reported (Fu et al., 2014; Keenan and Richardson, 2015). It has been shown that a warmer winter affects spring and autumn vegetation phenology the subsequent year (this is often termed as the ‘lagged’ effect) (Fu et al., 2014). Further, Keenan and Richardson (2015b) demonstrated a strong association between the spring greening and autumn senescence within a growing season and this relationship was used to predict autumn senescence. Studies analysing the impact of warm temperature during spring and autumn phenological events mostly focus on the ‘direct’ effect of changes in spring and autumn temperatures on vegetation phenology, but studies investigating lagged effects are limited. In northern high latitude regions of Europe where temperature mostly controls vegetation phenology (Gulen and Eris, 2004; He et al., 2005); it has thus become imperative to investigate the extent to which extreme warm temperatures in spring and autumn phenology directly affect forest greenness (productivity) and also to investigate if this direct effect translates to a lagged effect in subsequent spring or autumn phenology. This would provide a better understanding of forest ecosystem response to these warm climatic events and resulting change (if any) in the forest productivity. To this end, this study aimed to: (1) characterise the extremely warm spring and autumn events in the whole of Europe between the years 2002 and 2012, and (2) investigate the effects of these warmer events on phenology and productivity of different forest types. This study was limited to extreme warm spring (EWS) and extreme warm autumn (EWA) events only and not to cold events because the former were more widespread within the study period and the spatial resolution of satellite data limited the detection of extreme cold events.

# Materials and methods

## Data

### Temperature Data

Daily mean temperatures for the periods 2003-2011 and 1961-1990, called study temperature and reference temperature respectively hereafter, were obtained from the E-OBS dataset (http://eca.knmi.nl/). The E-OBS temperature data are part of the Europe’s ENSEMBLE project (Haylock et al., 2008). They are daily gridded data sets with 0.25o x 0.25o pixel size and 25o N-75o N x 40o W-75o E areal coverage. This reference temperature was used to determine the standardised anomalies because it is the climate with the best estimate per the World Meteorological Organization (WMO) quality assessment work (WMO, 1996).

### GlobCover Land Cover

This GlobCover Land Cover map (http://due.esrin.esa.int/globcover) of 2005-2006 was used to identify the spatial locations of key forest types such as broadleaf deciduous forest (BLDF), needleleaf evergreen forest (NLEF) and mixed forest (MF) in Europe. GlobCover is a global land cover map developed by the European Space Agency from ENVISAT Medium Resolution Imaging Spectrometer (MERIS) imagery at a 300 m spatial resolution (Bontemps et al., 2011).

### The Envisat MERIS Terrestrial Chlorophyll Index

Time series of the Envisat MERIS Terrestrial Chlorophyll Index (MTCI) was used to estimate the land surface phenology over Europe. The MTCI makes use of spectral reflectance in the red edge position to estimate this chlorophyll content of the vegetation cover. It is a ratio expressed as:

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|  | = | (**1**) |

where R753.75, R708.75, and R681.25 refer to the bands 10, 9 and 8 respectively in the MERIS standard band setting (Dash and Curran, 2004). The use of MTCI has the following advantages: (i) unlike other vegetation indices it is not saturated at high biomass and limited sensitivity to atmospheric effects, view angle and soil background (Dash, 2010), (ii) the time series data has been used in many studies to detect land surface phenology at regional scales (Dash et al., 2010; He et al., 2015; Rodriguez-Galiano et al., 2015) and (iii) due to its direct relationship with canopy chlorophyll contents, it is a strong indicator of vegetation primary productivity (Harris and Dash, 2010; Boyd et al., 2012; Ogutu et al., 2013). The MTCI composite data used in this study has an approximate spatial resolution of 1 km2 and 30o N-70o N to 15o W- 45o E areal coverage. Weekly and dekad time-series of MTCI spanning 2003 to 2011 were obtained from NERC Earth Observation Data Centre (NEODC (http://neodc.nerc.ac.uk/)). These dataset were supplied by the European Space Agency and were processed by Airbus Defence and Space. The MTCI data, from 2003 to 2007, corresponded to 8-days composite period whereas data from 2008 to 2011 were processed with a10-days composite period.

### Eddy Covariance Flux Data

Flux tower data were used to demonstrate the relationship between the MTCI and gross primary productivity (GPP) for dominant forest types in this study. These data were obtained from the CarboEurope website (www.carboeurope.org) for Hainich, Davos and Brasschaat flux towers. The Hainich tower is located in Germany and it is associated to deciduous broadleaf tree species. The Davos flux site is located in Switzerland. This site is predominantly composed of Norway spruce forest. The Brasschaat site in Belgium is a mixed forest site. The carbon flux data were measured in a half-hourly time step. The Hainich and Davos flux sites cover the period from 2003 to 2005 whereas the data of Brasschaat site from 2004 to 2005.

## Methods

### Conceptual Models

This study dwelt on certain assumptions to investigate the link between vegetation phenology, forest productivity, and changes in spring and autumn temperature. The study assumed that, temperate and boreal forests would generally experience earlier start of growing season and thus, increase in forest productivity in EWS events. The extreme warm temperatures might increase the rate of nitrogen mineralisation and this might eventually increase photosynthetic activity since more nitrogen might be present in the leaves (Reich et al., 1997; Richardson et al., 2009). Additionally, late start of leaf fall as a result of warm autumn could facilitate longer growth of tree foliage which may lead to increased trapping of solar radiation, in the absence of cloud, for further canopy photosynthetic activity (Jolly et al., 2004; Vitasse et al., 2009b). On the other hand, the study expected that the event of a warmer spring might delay senescence of leaves in autumn to demonstrate a lagged effect (Fu et al., 2014; Keenan and Richardson, 2015b). Similarly, the warmer autumn might lead to earlier or later spring phenology in the following year (Estiarte and Peñuelas, 2015) as a consequence of lagged effect.

The extreme warm temperatures have generally resulted in immediate increase in forest productivity; and this effect is what we referred to as direct effect in this study. However, in some cases, the effects are deferred, and hence, known as lagged effects. The study recognized three possible effects in forest phenology and productivity (measured through greenness) due to the extreme warm spring and autumn temperatures: (1) no lagged effect, when the forest productivity for normal spring or autumn is equal to the productivity for EWS or EWA and no significant change in spring and autumn phenological events; (2) positive lagged effect, when the forest productivity for extreme warm season is greater than the forest productivity for normal season and significant change in spring and autumn phenological events preceding the extreme warm season; and (3) negative lagged effect, when the forest productivity for extreme warm season is less than the normal season and significant change in spring and autumn phenological events preceding the extreme warm season . These conceptual models are presented in detail in Figure 1.

### Anomaly Detection and Processing of Envisat MTCI Time Series Data

Missing temperature data were masked out before grouping them into spring (March, April and May) and autumn (September, October and November) seasons. Mean and standard deviation maps of spring and autumn were created for reference temperature while only mean maps were created for study temperature. Standardised anomalies were computed as:

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|  |  | (**2**) |

X was the mean temperature of the spring or autumn of a particular year. and respectively represented the long-term mean and the standard deviation of the same period of time over the whole time-series. EWS and EWA seasons were defined as events that showed a temperature in that season is more than 1.5 standard deviation away from the long-term mean. Additionally for the purpose of the study and to provide some controlled conditions, EWS or EWA seasons were considered for further analysis under the following scenarios: (i) the season immediately preceding it (EWS or EWA) was normal, (ii) the season(s) succeeding was normal, and (iii) both the spring and autumn of the following year was normal. These conditions were made to investigate if the extreme warm events engendered lagged effects in a very conservative way. As a result of these control conditions, this paper was focused on EWS events in 2004, 2007 and 2009; and EWA events in 2003, 2005 and 2009 (**Figures 2a and b**).

The MTCI pixels in the extreme warm temperature regions were extracted for the entire study period. Missing values were present in the MTCI time-series as a consequence of sensor drop out, snow cover over the tree canopy and cloud cover. Pixels with more than 10 consecutive missing values during the growing season were discarded to preserve the quality of the signal. A linear interpolation was used to fill any individual missing values (Dash et al., 2010).

### Sampling Forest Types

Globcover land cover map was used to discard non-homogeneous forest pixels at the resolution of MTCI data (~1 km2). MTCI time-series signal of BLDF, NLEF and MF were extracted for the areas identified as EWS and EWA (Figure 3). NLEF samples were not considered for EWS events, as all the NLEF areas were smaller than 1 km2. However, samples for BLDF, NLEF and MF were obtained for EWA study sites. A further filter was applied to select the samples that belong exclusively to one extreme warm event. Twenty and thirty-five pixels for EWS were randomly resampled for BLDF and MF respectively. In the case of EWA, eighteen and twenty-six pixels for BLDF, NLEF and MF were selected, respectively (**Table 1**).

### Extraction and Validation of Phenological and Productivity Variables

A number of different approaches have been proposed to derive phenological variables from satellite data (eg. Jonsson and Eklundh, 2002; Atzberger et al., 2013). In this study, the methodology of Dash et al. (2010) was adapted to estimate phenological variables as it has previously shown to suit the MTCI data set. The extraction of vegetation phenological variables from MTCI time-series involves two steps: (i) data smoothing using inverse Fourier transformation and (ii) derivation of phenological variables. The Fourier transformation based smoothing was preferred as it outperformed other smoothing algorithms when applied to MTCI data (Atkinson et al., 2012) and limits subjectivity to only the specification of number of harmonics to reconstruct the smoothed time-series. In this study, the first four Fourier harmonics and the mean were used to reconstruct the smoother time series. The extraction of phenological variables required the detection of the peak (i.e. Maximum MTCI) in the time-series. From this peak the algorithm searches forward and backward in the time-series for the valley point to estimate Onset of Greenness (OG) and End of Senescence (EOS). OG was defined by the valley point found at the backward end of the peak (as result of change in derivative value from positive to negative) whereas the EOS was determined by the valley point at the forward end (derivative value changed from negative to positive). In EWS events, the OG was used to determine the immediate effect in spring phenology whereas the EOS variable determined the lagged effect from the EWS. Conversely, in the EWA events, the OG variable was used to estimate lagged effect in spring phenology and the EOS estimated the direct effect in autumn phenology.

Validation of satellite derived land surface phenology is always challenging mostly due to the spatial mismatch between the ground observation (i.e. individual points) and satellite pixel (i.e. 1 km2). For Europe, PEP725 (http://www.pep725.eu/) provides one of the largest database of ground phenological observation. Unfortunately, no ground phenology observation data in the PEP725 database coincided with the study sites for the EWS and EWA events; therefore, it was not possible to validate the phenological variables in this particular study. The reliability of the land surface phenology variables in this study has already been assessed in a previous study (Rodriguez-Galiano et al., 2015) using PEP725 database for different deciduous tree species collected across Europe.

The integrated MTCI (I-MTCI, the summation of all the MTCI values of the area under certain part of the phenology curve), which measures the total greenness of forest under the season, was used as a proxy for forest productivity for spring and autumn phases of the growing season. For spring productivity, I-MTCI was estimated as an integration of MTCI values from the OG to the peak of the phenology curve, whereas for autumn productivity, MTCI was integrated from the peak of the phenology curve to the EOS. I-MTCI value is dimensionless and its high value indicates increase in forest productivity and vice-versa. In earlier studies, MTCI has been shown to be strongly associated with GPP across different vegetation types in Europe and North America (Harris and Dash, 2010; Boyd et al., 2012; Ogutu et al., 2013). The MTCI for three dominant forest types (i.e. BLDF, NLEF and MF) across Europe were further compared with flux tower GPP estimates to demonstrate its association with forest productivity.

### Statistical Analysis

Median statistic for OG, EOS and I-MTCI was computed for arrays of individual pixel values of each of the areas experiencing EWS or EWA. The median was used to curtail the influence of outliers in the data. The median values of the extreme warm events were compared to the median values of normal events. Regarding direct and lagged effects, the mean I-MTCI values for all regions of interest for each forest type were estimated for each extreme warm event. Similarly, the mean I-MTCI value for normal phenological events was then compared to the mean I-MTCI value of the extreme warm phenological events. Further, the study performed Welch’s t-test at a confident level of 95% for OG and EOS for each forest type under each extreme warm event. Similar analyses were performed for productivity variables but, with relative change estimated.

# Results

## Extreme warm spring and autumn events in Europe

EWS events were found for the years 2004, 2007 and 2009 where the specific season temperature was more than 1.5 standard deviation away from the long-term mean. The EWS events occurred extensively in Fennoscandia and Russia (**Figure 2a**). On the other hand, the EWA events occurred predominantly in Russia, Spain, France and United Kingdom in 2003, 2005 and 2009 (**Figure 2b**).

## Effects of extreme warm spring and autumn events in phenology

### Extreme warm spring events

All forest types showed early OG for the direct positive effect as expected in the conceptual models and reported in literature (eg. Menzel and Fabian, 1999; Roetzer et al., 2000; Walther et al., 2002; Parmesan and Yohe, 2003; Mimet et al., 2009). BLDF started greening up 12 days earlier in 120± 14 DOY whereas MF was three days earlier in 129±3 DOY. Both BLDF and MF showed a significant earlier OG date (**Figure 5**)**.** Considering the lagged effect of EWS, the end of greening delayed seven (311±17 DOY) and four (295±11 DOY) days for BLDF and MF, respectively. However, these changes were not significant (**Figure 6**)**.**

### Extreme warm autumn events

In EWA events, all forest types showed a delayed EOS due to the direct effect. Particularly, EOS for the BLDF was delayed by five days with a median EOS 291±8 DOY during EWA events. For NLEF, the median EOS date was 316±10 DOY with a 15 days delay compared to normal year. Similarly, MF extended EOS by 10 days to 296±8 DOY. These delays in EOS for all forest types due to EWA were statistically significant (**Figure 7**)**.**

In terms of lagged effects, MF showed an early OG in the following year whereas BLDF and NLEF delayed the OG. The OG for MF began six days earlier in 133±4 DOY and was significantly different from the OG for normal years (**Figure 8**). The start of spring in the following year for BLDF was 130±4 DOY which meant the OG was three days late. However, this was not statistically significant. Similarly, for NLEF the OG for the next spring was seven days late and this difference was statistically significant compared to normal years (**Figure 8)**.

## Effects of extreme warm spring and extreme warm autumn events in productivity

### Relationship between MTCI and GPP

For the three dominant forest types, MTCI showed a strong positive correlation with flux tower GPP (r = 0.78) **(Figure 4)**. Between these forest types both BLDF at Hainich and MF at Brasschaat had a stronger correlation compared to the NLEF. In addition, for BLDF and MF, both MTCI and GPP followed a similar phenological pattern. Therefore, the I-MTCI used in this study can be used as a proxy for productivity.

### Extreme warm spring events

Significant difference in mean I-MTCI values for spring was observed when the forest types were under normal spring seasons and when they experienced extreme warm temperatures. During the EWS events, the forest spring productivity (as measured using I-MTCI) for BLDF and MF was equal to 173±43 and 171±23, representing relative increments in mean I-MTCI of about 17 % and 2 % respectively compared to normal years. However, it was only in BLDF the differences in productivity were statistically significant (**Table 2**).

Early OG had a negative lagged effect on autumn productivity in BLDF. The mean I-MTCI during autumn (166±32) for BLDF was about 1% lower than the mean I-MTCI (167±41) for years with normal spring (negative lagged) (**Table 3**).However, MF experienced a positive lagged effect in autumn productivity as the mean I-MTCI (168±14) for normal autumn productivity was 4% lower than the mean I-MTCI for EWA. However, these differences were not statistically significant (**Table 3**).

### Extreme warm autumn events

Autumnal productivity was expected to experience a positive effect as a result of the extreme warmer temperatures in autumn. BLDF and MF increased autumn productivity by 3% and 7% respectively whereas NLEF showed no change in autumn productivity (**Table 4**). Further, no statistically significant difference was found in the autumnal productivity for any of the forest types (**Table 4**).

Late EOS had a negative lagged effect on spring productivity in NLEF. The mean I-MTCI during spring that followed EWA (185±15) for NLEF was about 5% lower than the mean I-MTCI (194±17) for years with normal spring. However, this difference was not statistically significant (**Table 5**). In contrast, BLDF and MF experienced a positive lagged effect in spring productivity as their mean I-MTCI (185±16 for BLDF and 139±4 for MF) for normal spring productivity was lower (~1% for BLDF and ~6% for MF) than the mean I-MTCI for the spring that followed EWA. However, it was only in MF the difference was statistically significant (**Table 5**).

# Discussion

## Extreme warm spring and autumn events in Europe

The warmer spring events largely occurred in Scandinavia and northern Russia. This observation is congruent with the findings from literature showing warm spring events in Northern and Arctic Europe (Serreze et al., 2000; Tingley and Huybers, 2013; IPCC, 2014). Regarding EWA events, previous studies showed a pervasive warmer autumn in Europe (Luterbacher et al., 2007; Van Oldenborgh, 2007; Cattiaux et al., 2009) which agrees with the results of this work.

These extreme warm spring and autumn events have been attributed to anthropogenic greenhouse gas forcing (Stott et al., 2001; Klein Tank et al., 2005). However, extreme strong positive North Atlantic Oscillation (NAO) since the 1980s in Northern Europe might be partly responsible for the temperature anomalies (Hurrell and VanLoon, 1997). This is because the strong positive phase of NAO brings along extreme anticyclones and warm air advection from subtropical middle latitude which tends to raise the land surface temperatures (Luterbacher et al., 2007).

## Effects of extreme warm spring and autumn events in phenology

In this study, we anticipated that warmer spring and autumn events would directly result in early leaf-out in spring and late leaf senescence in autumn which demonstrates the direct effect. Also, we expected that the EWS or EWA events would show lagged effects in the immediate normal autumn or spring phenology. Some of the forest types met these assumptions; for instance, BLDF and NLEF delayed leaf flushing whereas MF was earlier in determining lagged effect as a result of EWA (**Figure 8**). This observation is similar to earlier studies(Richardson et al., 2009;Vitasse et al., 2009b;Vitasse et al., 2011)**.** Air temperature might explain the variation in spring leaf-out in temperate and boreal woody plants. However, the response of forest ecosystems to temperature is species-specific (Luedeling et al., 2013). Temperate and boreal forests depend on chilling temperatures in winter and forcing temperatures in spring to recycle leaf flushing; and it varies depending on species (Morin et al., 2009;Vitasse et al., 2009a). The earlier OG observed in BLDF and MF for episodic warmer spring might be attributed to the relation between species and temperature. The delayed leaf senescence date observed in extreme warm events for BLDF, NLEF and MF **(Figure 7)** was expected to delay the set-in time of endodormancy in forests; and consequently, delay the timing of leaf flushing in the following year. This was observed in NLEF but not in MF; because MF started leaf flushing significantly earlier (**Figure 8**). The delayed timing of leaf flushing in NLEF for the spring that followed EWA possibly suggests that the species constituting NLEF require a critical amount of daylight, irrespective of the extent of prevailing air temperature, to start leaf flushing (Way and Montgomery, 2015). MF might have reached warmth accumulation earlier because of the warmer autumn and as a result started earlier leaf flushing in the following year. Further, the earlier leaf flushing observed in MF might be explained by their total carbohydrate content. A recent study reported a close relationship between the total carbohydrate of plants and their leaf flushing process (Charrier and Améglio, 2011). It may thus suggest that MF had accumulated rich amount of non-structural carbohydrates. However, if this is the case then how the non-structural carbohydrates control leaf phenology remains to be investigated.

Plant species differ in terms of their response to environmental cues in leafing out. Some species are photoperiodic (eg. Norway spruce), others are more temperature-dependent (eg. poplar) or combine both temperature and photoperiod (eg. some species of oak). Some species need to meet a certain amount of photoperiod before leaf-out begins irrespective of the degree of prevailing air temperature. The species that do not need photoperiod requirement to break endodormancy (dormancy as a result on internal inherent factors), but still have a chilling requirement, may take advantage of warmer events to start earlier leaf flushing (Körner and Basler, 2010).

There have been several debates about factors responsible for leaf senescence. However, environmental factors including extreme temperature and photoperiod (Fracheboud et al., 2009; Sanz-Pérez et al., 2009) have been noted for initiating leaf senescence. Also, internal factors such as age (Song et al., 2014) and phytohormones (Sakuraba et al., 2014) regulate leaf senescence. Extreme warm temperatures can cause premature leaf senescence in plants. Earlier studies have found that extreme warm temperatures catalyse the process of protein degradation in plants (Jiang and Huang, 2002; Gulen and Eris, 2004; He et al., 2005) and in turn promotes early leaf senescence (Zavaleta-Mancera et al., 1999; Ueda et al., 2000). However, in this study, we observed extension in leaf senescence under extreme warm temperatures (**Figure 7**). This may imply that other factors regulating leaf senescence might be at work instead of exclusive temperature.

## Effects of extreme warm spring and autumn events in productivity

Earlier start of spring is noted to enhance forest ecosystem productivity (Richardson et al., 2009; Pilegaard et al., 2011). We observed in this study that the EWS caused immediate increase in productivity for all forest types; although, not always significant. The EWS had a mixed (negative and positive) lagged effect into autumn productivity within the same growing year. It was not surprising to see a negative lagged effect since high temperature could cause respiration to exceed photosynthesis in some ecosystems thus resulting in overall lower productivity (Piao et al., 2008; Chang et al., 2013). Depending on the geographic location, natural forests are expected to differ in their soil quality. Forests on nitrogen-rich (or other macronutrient) soils might have leaves that are as well rich in nitrogen and thus, experience effective photosynthesis. However, sudden frost damage could account for the lower spring productivity in warmer events. Previous studies showed that premature OG as a result of EWS events make forest cover susceptible to decline in productivity by way of leaf loss and late canopy development (Hanninen et al., 1990; Kellomaki et al., 1995; Inouye, 2008; Hufkens et al., 2012). EWA events precipitate a lagged effect in MF in the following spring productivity (**Table 5**). This is possibly because of nutrient resorption by plants before leaf fall in autumn. At spring, nutrients resorbed from leaves during the preceding autumn period might have to be spent to generate new leaves (Estiarte and Peñuelas, 2015).

The observations of this study feed back into the conceptual models expressing negative, positive and no lagged effects by extreme warm events in growing seasons.

# Conclusions

This study applied OG and EOS phenological variables to investigate the shifting in the timing of spring and autumn phenologies as a result of extreme warm temperature events and their impacts on forest productivity. The study started on the assumption that warmer spring or autumn results in direct positive effect on the forest greenness (productivity); and then, evaluated how the direct positive effects performed on the dynamics of the following spring or autumn forest greenness. An intuitive method was applied to the phenological variables to derive a proxy for forest productivity, named I-MTCI.

Under EWS events, both BLDF and MF started earlier leaf flushing. Although the warmer temperatures in spring prolonged autumnal senescence in BLDF and MF, the extension was not significantly different from the autumn of normal years. The EWS events sparked an increase in the productivity of BLDF and MF. However, it was only in BLDF the differences in productivity were statistically significant. Early OG revealed a negative lagged effect on autumn productivity in BLDF whereas MF experienced a positive lagged effect in autumn productivity. Nevertheless, these lagged effects in productivity of BLDF and MF were not significant.

Under EWA events, all the forest types investigated showed a significant delayed EOS. Additionally, the OG for MF as a result of lagged effect occurred significantly earlier whereas for NLEF this was delayed. The OG for BLDF also delayed but was not statistically significant. Regarding direct positive effect on autumn productivity, save NLEF, the rest of forest types showed increase in productivity; however, these were not statistically significant. BLDF and MF experienced positive lagged effect of EWA in productivity but only MF was statistically significant. NLEF experienced a non-significant negative lagged effect in productivity.

The OG, EOS and I-MTCI variables that constitute the core of this study are important spatial information that may assist in effective management and conservation of forest ecosystems. This study was carried out at a coarse spatial resolution (~1 km2). Therefore, future studies may consider the use of higher spatial resolution data to better describe the forest dynamics. Finally, this study could be improved if narrowed down to a species scale while other factors such as photoperiod, stand age and disturbance history could be considered.

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**ist of tables**

**Table 1.** The number of broadleaf deciduous forest (BLDF), mixed forest (MF) and needleleaf evergreen forest (NLEF) pixels randomly sampled from extreme warm spring (EWS) and extreme warm autumn (EWA) locations.

|  |  |  |  |
| --- | --- | --- | --- |
|  | BLDF | NLEF | MF |
| EWS | 20 | - | 35 |
| EWA | 48 | 18 | 26 |

**Table 2.** Comparing the mean spring productivity of broadleaf deciduous forest (BLDF) and mixed forest (MF) in a normal spring (NS) to mean spring productivity during extreme warm spring (EWS) events using integrated MTCI (I-MTCI). The increase or decrease of productivity as a result of the extreme warm spring is determined by the relative changes in per cent.

|  |  |  |  |  |
| --- | --- | --- | --- | --- |
| Forest types | I-MTCI, NS | I-MTCI, EWS | Relative change (%) | p- value |
| BLDF | 148±25 | 173±43 | 16.89 | 0.0189 |
| MF | 168±14 | 171±23 | 1.79 | 0.7295 |

**Table 3.** Comparing the mean autumn productivity of broadleaf deciduous forest (BLDF) and mixed forest (MF) in a normal autumn (NA) to mean autumn productivity of the autumn that immediately followed extreme warm spring events (Aut) using integrated MTCI (I-MTCI). The increase or decrease of productivity as a result of the extreme warm spring is determined by the relative changes in per cent.

|  |  |  |  |  |
| --- | --- | --- | --- | --- |
| Forest types | I-MTCI, NA | I-MTCI, Aut | Relative change (%) | p- value |
| BLDF | 167±41 | 166±32 | -0.60 | 0.9558 |
| MF | 168±14 | 175±18 | 4.17 | 0.3083 |

**Table 4.** Comparing the mean autumn productivity of broadleaf deciduous forest (BLDF), mixed forest (MF) and needleleaf evergreen forest (NLEF) in a normal autumn (NA) to mean autumn productivity during extreme warm autumn (EWA) events using integrated MTCI (I-MTCI). The increase or decrease of productivity as a result of the extreme warm autumn is determined by the relative changes in per cent.

|  |  |  |  |  |
| --- | --- | --- | --- | --- |
| Forest types | I-MTCI, NA | I-MTCI, EWA | Relative change (%) | p- value |
| BLDF | 194±21 | 199±25 | 2.58 | 0.5306 |
| NLEF | 222±22 | 222±18 | 0 | 0.9911 |
| MF | 146±7 | 156±16 | 6.85 | 0.1270 |

**Table 5.** Comparing mean spring productivity of broadleaf deciduous forest (BLDF), mixed forest (MF) and needleleaf evergreen forest (NLEF) in a normal spring (NS) to mean spring productivity of the spring that immediately followed extreme warm autumn events (Spr) using integrated MTCI (I-MTCI). The increase or decrease of productivity as a result of the extreme warm autumn is determined by the relative changes in per cent.

|  |  |  |  |  |
| --- | --- | --- | --- | --- |
| Forest types | I-MTCI, NS | I-MTCI, Spr | Relative change (%) | p- value |
| BLDF | 185±16 | 186±13 | 0.54 | 0.8334 |
| NLEF | 194±17 | 185±15 | -4.64 | 0.1975 |
| MF | 139±4 | 148±8 | 6.47 | 0.0132 |

**List of figures**

Direct positive effect on spring productivity

No lagged effect on autumn productivity

Direct positive effect on spring productivity

Negative lagged effect on autumn productivity

Direct positive effect on spring productivity

Positive lagged effect on autumn productivity

No lagged effect on spring productivity in the following year

Direct positive effect on autumn productivity

Direct positive effect on autumn productivity

Negative lagged effect on spring productivity in the following year

Direct positive effect on autumn productivity

Positive lagged effect on spring productivity in the following year

**b**. Extreme warm spring: Positive lagged effect model. This model indicates that direct positive effect in spring forest productivity as a result of extreme warm spring season might lead to positive lagged effect in autumn productivity. The arrow at the right hand shows a shift from normal autumn productivity to extreme warm autumn productivity in the positive direction indicating increase in autumn forest productivity when compared to normal.

**a.** Extreme warm spring: No lagged effect model. This model theorizes that earlier OG in spring, as a result of extreme high temperatures, ensures direct positive effect on spring productivity which in turn may not have any lagged effect on autumn productivity. The broken lines show extreme warm spring productivity whiles the arrow depicts a shift from normal spring productivity to extreme warm spring productivity; thus indicating direct positive effect on spring productivity.

**d.** Extreme warm autumn: No lagged effect. This model theorizes that delayed EOS in autumn, as a result of extreme high temperatures, ensures direct positive effect on autumn productivity which in turn may not have any lagged effect on subsequent spring productivity. The broken lines show extreme warm autumn productivity whiles the arrow depicts a shift from normal autumn productivity to extreme warm autumn productivity; thus indicating direct positive effect on autumn productivity but without any lagged effect on spring productivity

**e.** Extreme warm autumn: Positive lagged effect model. This model indicates that direct positive effect in autumn forest productivity as a result of extreme warm autumn events might lead to positive lagged effect in spring productivity. The arrow at the right hand shows a shift from normal spring productivity to extreme warm spring productivity in the positive direction indicating increase in spring forest productivity when compared to normal.

**f**. Extreme warm autumn- Negative lagged effect. This model indicates that direct positive effect in autumn forest productivity as a result of extreme warm autumn events might lead to negative lagged effect in spring productivity. The arrow at the right hand shows a shift from normal autumn productivity to extreme warm autumn productivity in the negative direction indicating decrease in autumn forest productivity when compared to normal.

**c.** Extreme warm spring: Negative lagged effect. This model indicates that direct positive effect in spring forest productivity as a result of extreme warm spring season might lead to negative lagged effect in autumn productivity. The arrow at the right hand shows a shift from normal autumn productivity to extreme warm autumn productivity in the negative direction indicating decrease in autumn forest productivity when compared to normal.

**Figure 1:** Conceptual models theorizing the extreme warm events and the plausible impacts they may have on forest phenology and productivity.



**Figure 2 (printed version)**. **a**. Areas in Europe that experienced extreme warm spring. The extreme warm spring events occurred in 2004, 2007 and 2009. These events extensively occurred in Russia, Finland, Sweden and Norway.

**b**. Areas in Europe that experienced extreme warm autumn events. These events happened in Spain, France and the United Kingdom. Also, these events occurred in Russia, Sweden and Norway. Largely, extreme warm autumns in 2003 and 2005 overlapped same area.



**Figure 2 (web version)**. **a.** Areas in Europe that experienced extreme warm spring. The extreme warm spring events occurred in 2004, 2007 and 2009. These events extensively occurred in Russia, Finland, Sweden and Norway.

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**Figure 3 (print version).** The samples of forest pixels selected from regions of interest for extreme warm spring and extreme warm autumn events. The forest types are broadleaf deciduous forest (BLDF), needleleaf evergreen forest (NLEF) and Mixed forest (MF).



Figure 3 (web version). The samples of forest pixels selected from regions of interest for both extreme warm spring and extreme warm autumn events. The forest types are broadleaf deciduous forest (BLDF), needleleaf evergreen forest (NLEF) and Mixed forest (MF).



Figure 4 (print version). Relationship between Meris Terrestrial Chlorophyll Index (MTCI) and Gross Primary Productivity (GPP) for a broadleaf deciduous forest in Hainich (Germany), a needleleaf evergreen forest in Davos (Switzerland) and a mixed forest in Brasschaat (Belgium).



Figure 4 (web version). Relationship between Meris Terrestrial Chlorophyll Index (MTCI) and Gross Primary Productivity (GPP) for a broadleaf deciduous forest in Hainich (Germany), a needleleaf evergreen forest in Davos (Switzerland) and a mixed forest in Brasschaat (Belgium).

**Figure 5.** Direct effect of extreme warm spring. Onset of Greenness for normal spring (white) vs Onset of Greenness for extreme warm spring (grey). These bars represent the mean onset of greenness for normal spring and extreme warm spring for broadleaf deciduous forest (BLDF) and mixed forest (MF). The error bars on top of each bar show the standard deviation whereas S indicates where these differences are statistically significant.

**Figure 6.** Lagged effects of extreme warm spring. End of Senescence for normal spring (white) vs End of Senescence for extreme warm spring (grey). These bars represent the mean end of senescence for normal spring and extreme warm spring for broadleaf deciduous forest (BLDF) and mixed forest (MF). The error bars on top of each bar show the standard deviation whereas NS indicates where these differences are statistically not significant.

**Figure 7**. Direct effect of extreme warm autumn. End of Senescence for normal autumn (white) vs End of Senescence for extreme warm autumn (grey). These bars represent the mean onset of greenness for normal autumn and extreme warm autumn for broadleaf deciduous forest (BLDF), needleleaf evergreen forest (NLEF) and mixed forest (MF). The error bars on top of each bar show the standard deviation whereas S indicates where these differences are statistically significant.

**Figure 8.** Lagged effect of extreme warm autumn. Onset of Greening for normal spring (white) vs Onset of Greening for spring that immediately followed extreme warm autumn event (grey). These bars represent the mean onset of greening (OG) for normal spring and spring that immediately followed extreme warm autumn events for broadleaf deciduous forest (BLDF), needleleaf evergreen forest (NLEF) and mixed forest (MF). The error bars on top of each bar show the standard deviation whereas S indicates where these differences are statistically significant and NS represents not significant.