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Monitoring and analysis of plant phenological responses in manipulative experiments and along natural gradients

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ABSTRACT

Background and Objectives. Due to human activities the concentrations of atmospheric greenhouse gases have increased markedly since the Industrial Revolution. Thus, in the last 100 years global average air temperature increased by 0.74 °C (± 0.18 °C) – with various consequences for ecosystems across the world. However, some ecosystems are much more vulnerable to impacts of global climate change than others. For the European Alps a temperature increase of about 2 °C has been detected since the end of the 19th century and it is predicted that future temperature rise in this region will remain above the global average. Moreover, it is expected that the date of snowmelt will strongly advance, thus snow cover duration will be drastically shortened. In Southern Germany a temperature increase of 1.1 °C was detected between 1931 and 2010. Since temperature is predicted to further increase in this region, it is expected that fen-peatlands in Bavaria, which naturally function as long-term sinks for atmospheric CO_2, may switch from carbon sinks to sources.

These shifts in the abiotic environment have already affected, and will further influence, processes and functioning of terrestrial ecosystems. Phenology, the science of recurrent seasonal natural events, plays a key role in the detection of shifts in ecosystem functions due to recent global climate change. Thus, the objective of this PhD thesis was to assess impacts of altered abiotic parameters along natural gradients and in manipulative experiments on plant phenology in the Bavarian Alps and in a temperate fen-peatland in Bavaria to better ascertain the effects of future climate change by addressing the following three leading research question:

a. How to estimate onset dates from BBCH scale recording?
b. How does plant phenology vary with altitude?
c. What effects do manipulative treatments have on plant phenological development?

Methods**.** In this PhD thesis one experimental study (in a fen-peatland in the Freisinger Moos), one experimental study along a natural (altitudinal) gradient (integrated study), and one natural (altitudinal) gradient study (both in the Berchtesgaden National Park) were conducted. Additionally, this dissertation comprises a methodological approach which constitutes the basis of the analysis of phenological observation data derived from both experimental studies.

In total, the frequency distribution of phenophases of 17 different grassland species were observed once a week according to the BBCH scale in the experimental studies in the Berchtesgaden National Park and in the Freisinger Moos between 2009 and 2011. The natural gradient study in the Berchtesgaden National Park has been running since 1994,

included 21 species (11 herbs and 10 woody species) and was based on the observation key of Ellenberg. For the simulation of altered abiotic parameters in the Freisinger Moos, temperature was manipulated passively by open-top chambers and the water table level was increased using a pumping system. Over the altitudinal gradient in the Berchtesgaden National Park a 1000-year extreme drought event was simulated with static rain-out shelters and shifts in snow melting date were achieved by shovelling snow from advanced to delayed snowmelt plots. The main statistical analyses used included *t*-tests, analysis of variance (ANOVA), (weighted) linear regressions, analysis of covariance (ANCOVA) and Tukey's HSD for multiple comparisons.

***Results and Discussion*.** The methodological study compared four different methods which can be used to estimate classical onset dates, as needed in climate change research, from the frequency distribution data of phenophases. For the analysis of observation data from the experimental studies reported in this thesis we decided to focus on Ordinal Logistic Regression since it appeared the most suitable method for our purposes.

Both experimental and natural gradient studies demonstrated that the overall development and / or key phenological phases of observed species were influenced in particular by temperature, showing a delay with altitude in the Berchtesgaden National Park and an advance for the warming treatment in the temperate fen-peatland in the Freisinger Moos. However, flowering duration was only modestly influenced by temperature in all observational approaches. For both studies in the Berchtesgaden National Park the date of snowmelt played a key role in plant phenology, showing a strong influence on leafing and flowering of species over the altitudinal gradient and a significant advance in the timing of flowering following earlier snowmelt. Flowering was more strongly affected by an advanced snowmelt at higher than at lower altitudes, whereas shifts appeared not to change with increasing altitude but with intensity of treatment in the integrated study. The timing and duration of flowering was not significantly influenced by delayed snowmelt and flowering duration was also not affected by earlier snowmelt in the integrated study. Additionally, drought and an elevated water table level did not influence the total development of plants and / or the timing and duration of key phenological phases (integrated and experimental study). Herbaceous species were more sensitive to temperature and snow than trees (natural gradient study), whereas species and phenophases later in the year were less sensitive to temperature (natural gradient and integrated study).

Conclusions. This PhD thesis introduced a new approach to phenological observation at remote study sites and highlighted findings on the impacts of altered abiotic parameters on plant phenology. Results showed that herbaceous species in particular will be strongly affected by global warming. A temperature increase of 1 °C already led to a 6-7 day earlier

flowering. However, raised water table levels in a fen-peatland in Bavaria as well as a 1000-year extreme drought event in the Bavarian Alps did not markedly influence plant flowering phenology. Duration of phases will mostly not be affected by altered abiotic factors. Thus, from a phenological perspective, elevating the water table level in fen-peatlands to reduce carbon loss, to levels where management is still feasible, is recommended. Furthermore, it is suggested that the risk of severe impacts of drought on flowering phenology will be rather low in the Alps. Thus, higher temperature and shifts in the date of snowmelt constitute the main drivers of altered plant phenology under future climate change; however, the magnitude of change will strongly depend on the species. Since there is some doubt that results from experimental studies really matches those from long-term observations, further research is recommended which combines natural gradients with experiments, for example by placing soil monoliths from along an altitudinal gradient in climatic chambers to simulate several levels of altered abiotic parameters under conditions made as natural as possible.

KURZFASSUNG

***Hintergrund und Zielsetzung*.** In den letzten 100 Jahren ist die durchschnittliche Lufttemperatur im globalen Mittel aufgrund der steigenden Emissionen anthropogener Treibhausgase um 0,74 °C (± 0,18 °C) angestiegen. Je nach Ökosystem machen sich diese Änderungen allerdings unterschiedlich stark bemerkbar. So wurde zum Beispiel in den europäischen Alpen sogar ein Temperaturanstieg von rund 2 °C seit Ende des 19. Jahrhunderts gemessen. In Zukunft soll die Temperatur in dieser Region weiterhin überdurchschnittlich stark ansteigen, wodurch die Schneeschmelze im Frühjahr stark verfrüht eintreten und sich die Dauer der Schneebedeckung deutlich verkürzen wird. In Süddeutschland wurde zwischen 1931 und 2010 ein Temperaturanstieg von 1.1 °C verzeichnet. Da die Temperatur auch hier in Zukunft weiterhin ansteigen soll, wird erwartet, dass Torfmoorgebiete in Bayern, die generell als langfristige Senken für atmosphärisches CO_2 gelten, zukünftig Kohlenstoff-Quellen darstellen.

Die Veränderungen in der abiotischen Umwelt hatten und werden auch weiterhin einen starken Einfluss auf die Prozesse und Funktionen terrestrischer Ökosysteme haben. Die Phänologie, die Wissenschaft der regelmäßig wiederkehrenden Ereignisse in der Natur, spielt eine zentrale Rolle bei der Erkennung von Veränderungen in Ökosystemen, die auf den rezenten Klimawandel zurückzuführen sind. Daher war es Ziel dieser Doktorarbeit, die Auswirkungen sich verändernder Klima- und Umweltparameter simuliert durch manipulative Experimente oder natürlich gegeben entlang eines Höhengradienten, auf die Entwicklung verschiedener Graslandökosystemarten in den Bayerischen Alpen und einem Torfmoorgebiet zu quantifizieren, um zukünftig die Folgen des Klimawandels auf die Natur besser einschätzen zu können. Dabei standen folgende drei Forschungsfragen im Vordergrund:

a. Wie lassen sich phänologische Eintrittstermine von einer, auf der BBCH Skala basierenden Beobachtungsmethode ableiten?
b. Wie stark beeinflusst die Veränderung abiotischer Faktoren über die Höhe die Phänologie von Pflanzen?
c. Wie wirken sich manipulative Experimente auf die Pflanzenentwicklung aus?

Methoden. Veränderte Klima- und Umweltparameter in dieser Doktorarbeit wurden entweder manipulativ durch Experimente in einem Torfmoorgebiet im Freisinger Moos simuliert oder waren entlang eines Höhengradienten im Nationalpark Berchtesgaden von Natur aus gegeben. Desweiteren wurde ein kombinierter Ansatz verfolgt, der manipulative Experimente entlang eines Höhengradienten im Nationalpark integrierte. Zusätzlich

beinhaltet diese Dissertation eine neue Methodik, die zur Auswertung der phänologischen Beobachtungsdaten aus beiden experimentellen Studien, herangezogen wird.

Auf den Experimentalflächen im Nationalpark Berchtesgaden und im Freisinger Moos wurden zwischen 2009 und 2011 einmal pro Woche die Häufigkeitsverteilung einzelner phänologischer Phasen von 17 verschiedenen Graslandökosystemarten, basierend auf der BBCH Skala, beobachtet. Desweiteren werden im Nationalpark seit 1994, phänologische Beobachtungen von 21 Arten (11 krautige und 10 verholzte Arten), basierend auf dem Schlüssel von Ellenberg, entlang eines Höhengradienten durchgeführt.

Zur Simulation veränderter abiotischer Parameter wurden im Freisinger Moos nach oben geöffnete Plexiglas-Kammern installiert, die die Temperatur passiv erhöhten. Gleichzeitig wurde hier der Grundwasserspiegel mit Hilfe eines Pumpsystems angehoben. Im Nationalpark Berchtesgaden wurde ein 1000-jähriges Dürreereignis durch das Aufstellen von Zelten simuliert. Durch Umschaufeln von Schnee wurden zudem entlang des Höhengradienten Flächen mit verfrühter und verzögerter Schneeschmelze geschaffen.

Die wichtigsten statistischen Analysen basieren auf *t*-Tests, Varianzanalysen (ANOVA), (gewichteten) linearen Regressionen, Kovarianzanalysen (ANCOVA) und auf Tukey's HSD Tests für multiple Vergleiche.

***Ergebnisse und Diskussion*.** In dieser Dissertation wurden vier Methoden angewandt, mit denen phänologische Eintrittstermine, wie sie in der Klimawandelforschung üblich sind, aus der beobachteten Häufigkeitsverteilung der phänologischen Phasen ermittelt werden können. Zur Auswertung der Daten aus den experimentellen Studien wurde in dieser Arbeit auf die ordinale logistische Regression zurückgegriffen, da sie für die Zwecke dieser Dissertation am geeignetsten erschien.

Sowohl die manipulativen Experimente, als auch die Studie entlang des Höhengradienten haben gezeigt, dass die Gesamtentwicklung und / oder einzelne phänologische Phasen maßgeblich von der Temperatur beeinflusst werden. Es zeigte sich eine Verzögerung der Entwicklung abhängig von der Höhenlage im Nationalpark Berchtesgaden und im Vergleich dazu ein Vorsprung in der Entwicklung auf den künstlich erwärmten Flächen im Freisinger Moos. Jedoch wurde die Andauer verschiedener phänologischer Phasen auf allen Beobachtungsflächen nur wenig von der Temperatur beeinflusst. Ein weiterer wichtiger Einflussfaktor auf die Phänologie der Pflanzen war der Zeitpunkt der Schneeschmelze. Sowohl entlang des Höhengradienten als auch auf den experimentellen Flächen wurden Blattaustrieb und Blühzeitpunkt stark durch Schnee beeinflusst. Nach verfrühter Schneeschmelze setzte auch der Blühzeitpunkt deutlich früher ein, wobei dies vor allem auf höher gelegenen Flächen beobachtet werden konnte. Dieser Umstand scheint nicht auf

unterschiedlichen Verhaltensmustern in der Entwicklung der Pflanzen im Flachland gegenüber den Pflanzen in der Höhe zu beruhen, sondern eher auf einen stärkeren Manipulationseffekt auf den höher gelegenen Flächen. Von einer verspäteten Schneeschmelze wurden Blühzeitpunkt und –dauer jedoch kaum beeinflusst. Auch auf den Flächen mit verfrühter Schneeschmelze konnte keine Veränderung der Blühdauer beobachtet werden. Dürre und ein erhöhter Grundwasserspiegel beeinflussten die Gesamtentwicklung und / oder den Zeitpunkt bzw. die Dauer der untersuchten phänologischen Phasen kaum. Krautige Arten reagierten stärker auf Temperatur und Schnee als Bäume, wohingegen Arten und phänologische Phasen später im Jahr weniger stark von der Temperatur beeinflusst wurden.

***Schlussfolgerungen*.** Diese Doktorarbeit beinhaltet eine neuartige Methode zur phänologischen Beobachtung an entlegenen oder nur schwer zugänglichen Versuchsflächen und zeigt den Einfluss sich verändernder abiotischer Faktoren auf die Pflanzenphänologie auf.

Die Ergebnisse dieser Doktorarbeit weisen darauf hin, dass besonders krautige Arten stark von einer zukünftigen globalen Erwärmung beeinflusst werden. Schon ein Temperaturanstieg von 1 °C hat zu einer Verfrühung des Blühzeitpunktes um 6-7 Tage geführt. Ein erhöhter Grundwasserspiegel in bayerischen Torfmooren, wie auch ein 1000-jähriges Dürreereignis in den Bayerischen Alpen haben hingegen keinen nennenswerten Einfluss auf die Phänologie der Pflanzen. Folglich kann vom phänologischen Standpunkt aus eine Erhöhung des Grundwasserspiegels in Torfmoorgebieten auf ein Niveau, das sowohl die Kohlenstofffreisetzung minimiert, als auch eine kommerzielle Nutzung ermöglicht, befürwortet werden. Weiterhin ist zu erwarten, dass ein 1000-jähriges Dürreereignis in den Alpen keine schwerwiegenden Auswirkungen auf die Blühphänologie der Pflanzen haben wird. Folglich sind vor allem Temperatur und Schneeschmelze die Haupteinflussfaktoren, die Veränderungen in der Phänologie der Pflanzen unter künftigen Klimabedingungen bestimmen. Das Ausmaß der Veränderung wird allerdings stark von der jeweiligen Art abhängen.

Neu aufkommende Zweifel, ob experimentelle Ansätze Ergebnisse aus Langzeitbeobachtungen wirklich widerspiegeln können, verstärken das Bedürfnis nach weiterführenden Forschungsvorhaben, die natürliche Gradienten mit Experimenten verbinden. Ein solcher Ansatz wäre beispielsweise die Entnahme von Bodensäulen entlang eines Höhengradienten, welche in Klimakammern veränderten abiotischen Faktoren unter möglichst natürlichen Bedingungen ausgesetzt werden.

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I.1.1.1 GLOBAL SCALE

Due to human activities the concentrations of atmospheric greenhouse gases such as carbon dioxide (CO_2), methane (CH_4) and dinitrogen monoxide (N_2O) have increased markedly since the Industrial Revolution (IPCC 2007a). The concentration of CO_2, which is regarded as the most important greenhouse gas (Hofmann *et al.* 2006; IPCC 2007a) has risen, mainly as a result of fossil fuel use and land use change, from 280 ppm in pre-industrial times to 394 ppm in 2012 (IPCC 2007a; NOAA 2012). The concentration of CH_4 and N_2O has also increased; primarily caused by agricultural intensification. The rise of anthropogenic greenhouse gases has already caused long-term changes in the climate, such as an increase in global mean temperatures, shifts in precipitation amounts and changes in wind patterns (IPCC 2007a, Zhang *et al.* 2007). Furthermore, an increase in the frequency of extreme weather events, such as drought, heat waves or heavy precipitation, has been observed (IPCC 2007a). Higher temperatures have consequently led to a reduction of snow and ice cover and a reduction in snow cover duration in both hemispheres (IPCC 2007a).

In the last 100 years global average air temperature increased by 0.74 °C (± 0.18 °C) (IPCC 2007a), however the global warming trend was especially high from the 1970s (Luterbacher *et al.* 2004; Hansen *et al.* 2006), increasing by 0.15 to 0.20 °C per decade (Hansen *et al.* 2010). Eleven of the 12 years from 1995 to 2006 were among the 12 warmest years since the beginning of the instrumental recording in 1850 (IPCC 2007a; Hansen *et al.* 2010; Jones & Stott 2011). For the future it is expected that the temperature rise will continue even if the concentration of greenhouse gases remains constant due to delayed reactions in climate feedback processes (IPCC 2007a; Solomon *et al.* 2009). Thus, a further increase in global average air temperature of 1.8 (likely range: 1.1 to 2.9 °C) to 4.0 °C (likely range: 2.4 to 6.4 °C), depending on the applied scenario, is predicted by the end of the 21st century (IPCC 2007a).

I.1.1.2 REGIONAL SCALE

A changing climate has been detected across the world; however its magnitude differs between regions. This PhD thesis dealt with two different types of ecosystems: grasslands in the Bavarian Alps and a temperate fen-peatland in the Freisinger Moos. Thus, in the following paragraph I focused on climate change impacts on these two ecosystems.

***European Alps*.** For the European Alps a temperature increase of about 2 °C has been detected since the end of the 19th century (Auer *et al*. 2007). However, the trend in snow amount has not substantially changed since the mid-1980s in the Swiss Alps. The reduction in the total amount and the duration of snow at sites below 1200 m has been within the range of background interannual variation in Säntis (Switzerland) since that time. For sites above 2000 m even an increase in the amount of snow has been detected since 1985 (Beniston 2006). However, it is predicted that winter temperature will rise faster than summer temperature (BMU 2008) which will affect the snow line in mountainous regions since the zero-degree isotherm will be displaced to higher altitudes. Thus, the date of snowmelt will further advance in spring and snow cover duration will be drastically shortened. In regions where snow is generally standard, precipitation will increasingly occur in the form of rain rather than snow (Beniston *et al.* 2003, Laghari *et al.* 2012). For Switzerland, depending on the underlying scenario, a temperature rise of 4.0 °C is predicted by the end of the 21st century (see PRUDENCE project described by Christensen *et al.* 2002) which will cause an earlier termination of snow cover duration of 50 to 60 days at 2500 m and of more than 100 days at 1000 m. This will result in severe consequences for the vegetation period and in a shift in the maximum water availability from snowmelt to the winter months (Beniston 2003).

Temperate peatlands. For Southern Germany, the region of the fen-peatland study site in this thesis, a temperature rise of 1.1 °C was detected in the period from 1931 to 2010, whereupon winter temperatures increased stronger than summer temperatures. Furthermore, mean annual precipitation amounts slightly increased for the same period (KLIWA 2011). Between 2021 and 2050 a temperature rise of 2.0 °C for the hydrological winter and of 1.4 °C for the hydrological summer is predicted for Bavaria. Moreover, precipitation amounts will increase in winter but will only little change in summer for the same region (KLIWA 2005). Since temperature is predicted to further increase, it is expected that peatlands which generally function as long-term sinks for atmospheric CO_2 switch from carbon sinks to carbon sources if not already done so (Byrne *et al.* 2004; for Arctic peatlands see Lund *et al.* 2012). Germany hosts only 3.2% of European peatlands, however, this country is already the second largest emitter (12% of European total) of NGHGB (net greenhouse gas balance of CO_2, CH_4, N_2O) from peatlands since most of the peatland area is drained and used for intensive farming (Byrne *et al.* 2004). Ise *et al.* (2008) showed that a further warming of 4 °C will result in a 40 to 86% loss of soil organic carbon depending on the peat layer. Thus, they suggested that peatland will react quickly to future warming with especially high loss of soil organic carbon in dry periods (Ise *et al.* 2008).

I.1.2 GENERAL PLANT RESPONSES

Several studies have demonstrated that global warming has already affected ecosystems worldwide (Parmesan & Yohe 2003; Root *et al.* 2003; IPCC 2007b; Rosenzweig *et al.* 2008). To handle changing environmental conditions, plant species may either respond by migration, persistence (through adaptation or phenotypic plasticity) or extinction (*e.g.*, Hampe & Petit 2005; Theurillat & Guisan 2001; Thuiller *et al.* 2008). Migration processes can either follow latitudinal or altitudinal gradients. Parmesan & Yohe (2003) showed, in a global meta-analysis, that species (including birds, butterflies and alpine herbs) shifted their range by about 6.1 km per decade towards the poles, whereas Chen *et al.* (2011) demonstrated a much greater shift of about 16.9 km per decade (also including plant and animal species). Differences in response rates were mainly explained by differences in data origin. Most of the data analysed by Chen *et al.* (2011) were derived from temperate ecosystems, where processes are mainly temperature driven, whereas ecosystems are mainly moisture limited for species analysed by Parmesan & Yohe (2003). Besides shifts along latitudinal gradients, migration processes were also detected along altitudinal gradients showing an upward shift of 2.7 m from 2001 to 2008 for several plant species across Europe's major mountain ranges (Pauli *et al.* 2012). A stronger shift was demonstrated by Lenoir *et al.* (2008) who compared data from 1905-1985 and 1986-2005 and demonstrated an upward shift of 29 m per decade for forest plant species in western Europe. Chen *et al.* (2011) showed a shift of 11 m per decade representing 1367 species responses across the world (Europe, North America, Malaysia, and Marion Island). Thus, depending on ecosystems or number and type of species, migration processes show differences in response intensity. For most mountainous regions, an upward shift of species often resulted in higher species richness (*e.g.*, Grabherr *et al.* 1994; Pauli *et al.* 2007; Erschbamer et *al*. 2009; Pauli *et al.* 2012) except for Mediterranean mountains (see Pauli *et al.* 2012). However, due to a reduction of habitat size at higher altitudes, it is expected that the number of high-mountain plant species will decline in future (*e.g.*, Korner 1995; Engler *et al.* 2011). Furthermore, it is suspected that some species will not be able to keep pace, by migration or also genetic adaptation, with future climate change (Jump & Penuelas 2005). Annual plants with a short generation time will be more able to adapt genetically than plants with longer generation times, such as tree species (Jump & Penuelas 2005). The decoupling between climate and local adaptation may result in a reduction in plant fitness and survival rates *inter alia* due to a lower resilience against pests and diseases or extreme weather events (Jump & Penuelas 2005). Thus, a temperature rise of up to 4.4 °C between 2051 and 2080 in Europe may, on average, result in a plant species loss of up to 42% by 2080 (no migration processes included; Thuiller *et al.* 2005).

To avoid species loss and hence conserve biodiversity it is necessary to understand plant responses to a changing environment (*e.g.*, to temperature or humidity). A close surveillance of plant phenological processes can help to understand those plant responses.

I.2 PHENOLOGY

Phenology, the science of recurrent seasonal natural events, plays a key role in the detection of shifts in ecosystem functions due to recent global climate change (Menzel 2002) since phenological events are highly dependent on temperature (*e.g.*, Sparks & Carey 1995; Menzel & Fabian 1999; Abu-Asab *et al.* 2001; Menzel *et al.* 2006). To quantify effects of climate change on plant development three different approaches to phenological research may be used.

I.2.1 RESEARCH TYPES

I.2.1.1 NATURAL GRADIENT STUDIES

Temporal. Temporal gradient studies (as described by Dunne *et al.* 2004) are either multidecadal (*e.g.*, Fitter *et al.* 1995; Sparks & Carey 1995; Crick & Sparks 1999; Inouye *et al.* 2000; Menzel *et al.* 2006) or based on site resampling (*e.g.*, Grabherr *et al.* 1994). Multidecadal records depend on long-term observation records which are mostly provided either by individuals (*e.g.*, Sparks & Carey 1995; Inouye *et al.* 2000; Fitter & Fitter 2002) or phenological networks (*e.g.*, Menzel 2000; Chmielewski & Roetzer 2001; Menzel *et al.* 2006). Datasets of individuals mostly cover only a small spatial area, whereas records of phenological networks span larger regions. The first phenological network was established by Carl von Linné in Sweden and Finland in the middle of the 18th century but was suspended after only three years of observations (Schnelle 1955). Currently, phenologcial networks are often incorporated into National Meteorological Services (*e.g.*, German Meteorological Service), and additionally, due to the importance of phenological records for climate change research, there is a great effort to launch more phenological networks such as the newly founded USA-National Phenology Network (USA-NPN).

However, the importance of phenology was already evident before climate change studies rediscovered the subject. From the very beginning, knowledge about phenology, especially the timing of ripening fruits, was essential for survival (Defila & Jeanneret 2007; Demarée & Rutishauser 2009). No wonder then that humans started a long time ago to record plant phenological events. One of the oldest and most famous records refers to the timing of the cherry flower in Kyoto, Japan, which was first noted in 705 AD and has continued for 1300 years (Aono & Kazui 2008).

Spatial. Spatial gradients can also be used to estimate impacts of changing environmental conditions on plant development. Spatial phenological studies mainly focus on altitudinal (Defila & Clot 2005; Dittmar & Elling 2006; Ziello *et al.* 2009), latitudinal (Parmesan & Yohe 2003; Badeck *et al.* 2004; Parmesan 2007) or urbanization gradients (Ziska *et al.* 2003; Zhang *et al.* 2004; Mimet *et al.* 2009; Jochner *et al.* 2012) since they provide *inter alia* natural temperature gradients. Temperature declines from warm city centres to a colder countryside for urbanization gradients and latitudinal gradients show an increase in temperatures from higher to lower latitudes. Altitudinal gradients are mainly characterized by a decrease of air temperature from *e.g.*, 0.54 to 0.58 °C per 100 m increase in altitude for the Alpine region (Rolland 2003).

Consequently, spatial gradients simulate climate change across sites, whereas temporal gradients reflect climate change over time. A substitution of space-for-time is therefore feasible and common in research. This thesis includes two phenological studies along altitudinal gradients to ascertain the effects of future climate change on plant phenology.

I.2.1.2 EXPERIMENTAL STUDIES

At present, manipulative experiments are a popular method to investigate the impacts of climate change on plant development. Most common is the simulation of higher temperatures, different snow melting dates, shifts in water availability or elevated CO_2 concentrations.

In field experiments, temperature is either manipulated actively by heaters (*e.g.*, Price & Waser 1998; De Valpine & Harte 2001; Dunne *et al.* 2003; Cleland *et al.* 2006) or heating cables (*e.g.*, Bokhorst *et al.* 2011; Moser *et al.* 2011) or passively in open-top chambers (OTCs; Marion *et al.* 1997; Arft *et al.* 1999; Totland & Eide 1999; Hollister & Webber 2000; Kudernatsch *et al.* 2008; De Frenne *et al.* 2010; Hoffmann *et al.* 2010; Liancourt *et al.* 2012) or greenhouses (*e.g.*, Shevtsova *et al.* 1997). Effects of passive warming techniques are variable because they are highly dependent on present meteorological conditions, whereas active warming is controllable. However, heaters and heating cables heat up the soil surface in particular which may result in an unrealistic heating difference between the above and below ground part of plants (De Boeck *et al.* 2010).

Studies simulating shifts in snow melting date use fences (Weaver & Collins 1977; Walker *et al.* 1999; Borner *et al.* 2008; Torp *et al.* 2010), active heaters (Price & Waser 1998; Dunne *et al.* 2003), passive heaters (OTCs; Aerts *et al.* 2006) or shovels (Galen & Stanton 1993; Galen & Stanton 1995; Starr *et al.* 2000; Dunne *et al.* 2003; Wipf *et al.* 2009) to modify melt dates. Delayed snowmelt is mostly simulated through snow accumulation using fences, within OTCs or by shovelling. Fences and OTCs are often favoured because once they are

installed they only need minor attention from researchers. In contrast, shovelling is much more labour-intensive since researchers need to make sure that the site remains snow-free. However, using passive melting techniques, snowmelt dates are hard to predict and vary from year to year (Wipf 2010). Advanced snowmelt is simulated either by active heaters or by removing snow through shovelling. Shovelling, again, is labour-intensive, whereas active heaters allow temperature control. However, due to the combination of warming and earlier snowmelt it might be difficult to attribute plant responses to a single effect afterwards (Wipf 2010).

Water availability of plants is mainly either manipulated by simulating drought events (*e.g.*, Llorens & Penuelas 2005; Prieto *et al.* 2008; Jentsch *et al.* 2009; Bernal *et al.* 2011) or by elevated precipitation (Phoenix *et al.* 2001; Cleland *et al.* 2006; Sherry *et al.* 2007; Jentsch *et al.* 2009). In field experiments drought is either simulated by mobile rain-out shelters which cover plots only during rain events (*e.g.*, Llorens & Penuelas 2005; Prieto *et al.* 2008; Bernal *et al.* 2011) or static rain-out shelters covering plots permanently during the drought period (*e.g.*, Jentsch *et al.* 2009). Mobile rain-out shelters have the advantage that radiation balance is only influenced during rain events when (solar) radiation is not crucial, whereas static rain-out shelters influence the radiation balance and PAR permanently. A few studies have increased water availability by additional irrigation. The added amount of water can range from a simulation of higher average precipitation up to heavy rain events (Phoenix *et al.* 2001; Cleland *et al.* 2006; Sherry *et al.* 2007; Jentsch *et al.* 2009).

In phenological studies the concentration of CO_2 is either elevated in glasshouses (*e.g.*, Ellis *et al.* 1995), in growth chambers (*e.g.*, Ward & Strain 1997) or under free-air with FACE (Free Air Carbon Enrichment; *e.g.*, Asshoff *et al.* 2006; Cleland *et al.* 2006; Hovenden *et al.* 2008a; Bloor *et al.* 2010) techniques (Springer & Ward 2007). FACE, in contrast to greenhouses or growth chambers, allows plants which growing under natural conditions to be exposed to elevated CO_2 concentrations without altering temperature, radiation, wind speed or humidity. However, both building and running of FACE systems are highly cost-intensive.

In this thesis, temperature was manipulated with OTCs and water availability was changed by elevating the water table level with a pumping system, both, singly and in a combined approach. With the help of static rain-out shelters the water availability was also influenced along the altitudinal gradient simulating a drought event. Furthermore, the date of snowmelt was manipulated by shovelling snow from advanced on delayed snowmelt plots. We did not concentrate on elevated CO_2 concentrations in this thesis.

I.2.2 OBSERVATION METHODS

Phenological records, from temporal, spatial or experimental studies are mostly based on observations in the field (recent or historical) or derived from satellite data (*e.g.*, Zhou *et al.* 2001; Stockli & Vidale 2004; Zhang *et al.* 2004; Jeong *et al.* 2011), photographs (*e.g.*, Miller-Rushing *et al.* 2006; Richardson *et al.* 2006; Sparks *et al.* 2006; Panchen *et al.* 2012) or herbarium specimens (*e.g.*, Primack *et al.* 2004; Miller-Rushing *et al.* 2006; Panchen *et al.* 2012). Field observation methods vary and include either single plants or populations (Jeanneret *et al.* 2011). The monitoring can either be carried out by a single observer who works at different plots and sites at different times (heterochron), by a single observer who works simultaneously on different plots on the same site (synchron) or by many observers who work at the same time on different sites (homochron; Zacharias 1972). Until 2003 many phenological networks, universities or individuals defined key phenological events in their own way. However, in order to make observations more comparable, European phenologists agreed on the BBCH code as a guideline for phenological observations (Van Vliet *et al.* 2003). The extended BBCH scale is a detailed growth stage key which was originally developed by four chemical companies, BASF, Bayer, Ciba-Geigy and Hoechst (Bleiholder *et al.* 1989), to standardize plant development recording especially for important agricultural crops. Besides key phenological events (*e.g.*, beginning of leaf unfolding or full flowering), the scale includes intermediate stages (*e.g.*, 20% of flowers open) as well as stages at the end of phenological phases (*e.g.*, end of flowering), which allows the observation of the entire development cycle of all mono- and dicotyledonous plants (Meier 2001).

I.2.3 PHENOLOGICAL PLANT RESPONSES

Several studies have already described various impacts on phenology of changed climatic parameters such as higher temperatures, changing date of snowmelt, low water availability or elevated CO_2 concentrations using temporal, spatial or experimental studies. Those impacts are summarized in the following paragraphs.

***Temperature*.** Especially in the last decades, consistent with a strong increase in temperature, a major advance in the timing of diverse phenological events for plant (and animal) species has been detected (*e.g.*, Fitter *et al.* 1995; Sparks & Carey 1995; Fitter & Fitter 2002; Menzel *et al.* 2006). Global meta-analyses demonstrated an advance of spring events by 2.3 or 5.1 days per decade, respectively (Parmesan & Yohe 2003; Root *et al.* 2003). For Europe a similar advance in spring and summer phenology of 2.5 days per decade was observed (Menzel *et al.* 2006), whereupon plant response to temperature change is strongest for spring phases and declines through the year (Fitter & Fitter 2002;

Menzel *et al.* 2006; Jeong *et al.* 2011). Menzel *et al.* (2006) showed that spring and summer phenophases advanced by up to 4.6 days per 1 °C warming whereas autumn phases such as leaf colouring were delayed by 2.4 days per 1 °C. The earlier the species, the stronger the sensitivity to temperature because early species are adapted to high temperature variability in spring and consequently react more sensitively to changes (Menzel *et al.* 2006). Due to a strong advance of spring and a smaller delay of autumn phenophases, the growing season, often defined as the time span between leaf unfolding and leaf colouring, has been extended over recent decades (*e.g.*, Menzel & Fabian 1999; Defila & Clot 2001; Stockli & Vidale 2004). For Europe, Stockli & Vidale (2004) demonstrated that the vegetation period was prolonged by 9.6 days per decade from 1982 to 2001. However, the growing season over the entire Northern Hemisphere was slightly less extended, by 6.5 days per decade, for the same period (Jeong *et al.* 2011). Menzel *et al.* (2006) further demonstrated that species phenology was more advanced in countries with a stronger temperature rise. Moreover, annuals were more sensitive to temperature than perennials, probably due to different life history strategies. The same was true for insect pollinated species compared to wind pollinated species in the study of Fitter & Fitter (2002), however, Ziello *et al.* (2012a) found contratictory results showing that the onset of flowering of wind-pollinated plants advanced stronger than for incect-pollinated species.

Comparing different methods to estimate plants' responses to climate change, the newly released meta-analysis of Wolkovich *et al.* (2012) demonstrated that phenological responses derived from experimental studies strongly underpredict advances in the timing of flowering or leafing by a factor of 8.5 or 4.0, respectively, compared with data derived from long-term observations. Furthermore, the authors showed that experiments cannot predict a higher response to temperature of early flowering species compared with species flowering later in the season as long-term observation studies can.

Even though there are several studies presenting an advance of the timing of phenophases due to higher temperatures, there is no detectable effect of experimental warming on flowering duration (Price & Waser 1998; Hovenden *et al.* 2008a). However, Dunne *et al.* (2003) showed a lengthening of the flowering duration due to experimental warming for several species, although the treatment effect was not significant.

***Snow*.** Timing, depth and duration of snow cover determine the beginning of the growing season in alpine areas (Inouye & Wielgolaski 2003). Thus, the development of many species in alpine or Arctic regions is highly dependent on the timing of snowmelt in order to exploit the whole season (Stinson 2004; Inouye 2008). In general, a prolongation in snow cover duration mainly delays plant phenology (Weaver & Collins 1977; Inouye 2008; Torp *et al.* 2010; Cooper *et al.* 2011), whereas a shortening of snow cover duration advances the

timing of plant development (*e.g.*, Price & Waser 1998; Dunne *et al.* 2003; Inouye *et al.* 2003; Wipf *et al.* 2009; Lambert *et al.* 2010; Wipf 2010; Chen *et al.* 2011). Dunne *et al.* (2003) demonstrated that flowering time was advanced by up to 11 days for every two weeks earlier snowmelt. The earlier the species in the season, the stronger the response of initial phenophases to snow melting dates (Dunne *et al.* 2003; Wipf 2010). There is evidence that early developing species or phenophases early in the growing season are mainly driven by snowmelt, whereas species and phenophases later in the season are especially influenced by growing degree days (GDD; cumulative temperature sum) (Wipf 2010). The response of plant flowering duration to shifts in snow melting date is rather equivocal, showing either an extension (Price & Waser 1998; Dunne *et al.* 2003) or no changes of flowering duration (Wipf 2010).

***Drought*.** Plant phenological responses to drought are not consistent. Jentsch *et al.* (2009) showed an advance of mid-flowering date by 4 days after a drought event, whereas Bloor *et al.* (2010) and Bernal *et al.* (2011) did not observe a significant effect of drought on grasses or shrub species. In contrast, a delay in flowering phenology under dry conditions was verified for Mediterranean plants (Penuelas *et al.* 2004; Llorens & Penuelas 2005; Prieto *et al.* 2008; Miranda *et al.* 2009). The effect of drought on the duration of flowering is contradictory, showing either an extension of the flowering period (Llorens & Penuelas 2005; Jentsch *et al.* 2009) or a shortening of the flowering duration for different species (Llorens & Penuelas 2005).

***CO_2*.** The impacts of elevated CO_2 on flowering, bud break or leaf fall varied strongly between species (*e.g.*, Asshoff *et al.* 2006; reviewed by Springer & Ward 2007) and are not well understood (Springer & Ward 2007). Flowering time of most crops and cultivated plants are advanced by elevated CO_2, whereas the response of wild species is evenly distributed between advanced, delayed or no change of flowering time (Springer & Ward 2007). Furthermore, the response of single species to higher CO_2 concentrations varies between studies depending on underlying growth conditions, such as light, water or nutrient availability (Springer & Ward 2007).

As became apparent in the last few paragraphs, there are plenty of studies dealing with impacts of altered abiotic parameters on plant phenology. However, there are still research gaps which need to be further investigated concerning, for example, the duration of phenophases, the response bias between experimental studies and long-term observations or inconsistent plant responses to drought events. Those gaps and further arising research questions of this thesis are described more precisely in Chapter I.3.2.

I.2.4 IMPACTS OF PHENOLOGICAL SHIFTS

Shifts in phenology affect various functions in ecosystems. Advanced or delayed onsets of phenophases influence interactions with animals, fungi or bacteria, which act as herbivores, pollinators, seed dispersers / predators or pathogens (reviewed by Donnelly *et al.* 2011). Moreover, shifts in the timing and duration of flowering may also interrupt plant-plant interactions by increasing competitive pressure, either with respect to pollinators or resources due to overlapping flowering times (*e.g.*, Molau 1997; Dunne *et al.* 2003). Shifts in phenology due to a changing climate will therefore not only influence plant species alone but also whole communities and ecosystems (Dunne *et al.* 2003). Additionally, people suffering from hay fever will be directly affected by shifts in phenology since several studies have demonstrated that an advance in flowering due to warmer temperatures consequently led to an earlier onset of the pollen season (Emberlin *et al.* 2002; Beggs 2004). Furthermore, it is evident that the pollen season of allergenic species has become longer and more intense (*e.g.*, Spieksma *et al.* 1995; Emberlin *et al.* 2002; Spieksma *et al.* 2003; Beggs 2004; Ziello *et al.* 2012b). Moreover, phenology also determines the LAI (leaf area index) of plants which in turn influences carbon fluxes of ecosystems (Menzel *et al*. 2002).

I.3 BACKGROUND AND OBJECTIVES

Since plant phenology affects all levels of ecosystems it is essential to understand phenological processes in as much detail as possible. Thus, the objective of this publication-based PhD thesis was to estimate the impacts of diverse abiotic environmental drivers at natural gradients and in manipulative experiments on plant development to better assess the effects of future climate change on plant phenology, especially herbs since in Central Europe only 7% of plant species are woody plants (shrubs and trees) (Pfadenhauer 1997) but most phenological studies focus on trees or shrubs (ISI Web of knowledge search of “phenology+tree”: 10.225 hits, “phenology+shrub”: 902 hits and “phenology+herbs”: 453 hits).

The research conducted in this PhD thesis was funded by the Bavarian Climate Program 2020 within the framework of the joint research centre FORKAST. Phenological observations were mostly carried out on experimental sites provided by our project partners who also were responsible for the infrastructure. Moreover, we closely collaborated with the Berchtesgaden National Park. The following paragraphs will briefly introduce the study design and will focus mainly on a detailed explanation of the objectives of this PhD thesis.

I.3.1 STUDY DESIGN

This PhD thesis included one experimental study in a fen-peatland in the Freisinger Moos, one integrated study with experiments along an altitudinal gradient in the Berchtesgaden National Park, and one altitudinal study in the same region (Fig. I.1). In those studies we concentrated on impacts of altered abiotic parameters such as temperature, snow and water availability in form of elevated water table level or drought on plant phenology. Additionally, this dissertation comprises a methodological approach which constitutes the basis of the analysis of phenological observation data derived from both experimental studies.

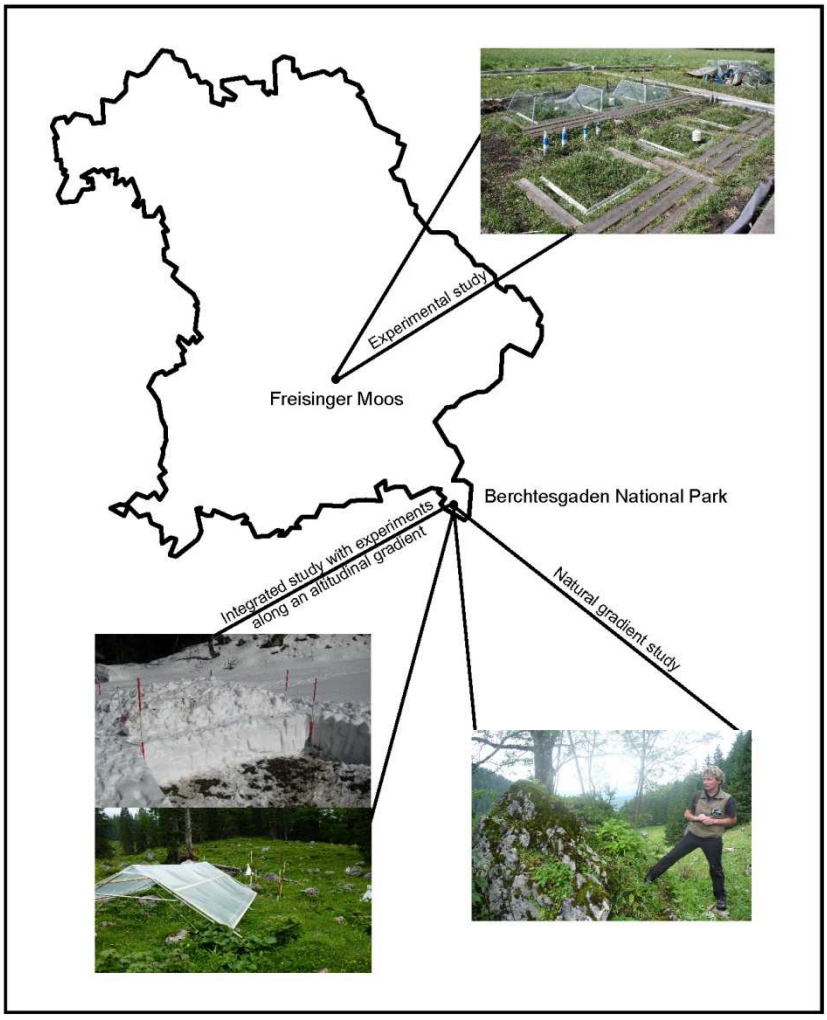

Figure I.1. Map of Bavaria (Germany) showing study sites and types.

***Phenology*.** Phenological observations at the experimental sites were conducted in the Freisinger Moos from 2009 to 2011 and in the Berchtesgaden National Park in 2010. Observations of the frequency distribution of phenophases were carried out once a week and based on the BBCH code. The natural gradient study in the Berchtesgaden National

Park has been running since 1994 and observations were conducted by park rangers two to three times a week based on the observation key provided in Ellenberg (1974). Our studies focused either on the total development and / or on single key phenological events such as leafing, flower development, flowering, ripening or fruit senescence (Table I.1). In total, 27 different herbs and 10 woody species (7 trees, 3 shrubs) were monitored (Table I.1) and observations were conducted either over the entire vegetation period or only for the duration of leafing and / or flowering.

Table I.1 List of studied species in this PhD thesis, including study type (N: natural gradient study, N/E: integrated altitudinal study with experiments, E: experimental study, M: methodological study), chapter number and observed phenophases (LU: leaf unfolding, LE: leaves fully expanded, BF: beginning of flowering, FF: full flowering, EF: end of flowering, TD: total development, FD: flower development, F: flowering, R: ripening and FS: fruit senescence). Further information is given about species in regard to its importance to humans (brief overview), risk of extinction and whether they are monitored by one of the phenological networks of the German Meteorological Service (DWD) or the International Phenological Gardens (IPG). Tree species are in bold, woody species in grey. Information was derived from the FloraWeb website of the BfN (2012), the PollenLibrary website (2012), the website of the DWD (2012) and the IPG (2012).

Species	Study	Chapter	Phenophases	DWD, IPG	Importance, allergenicity, risk of extinction
Aesculus hippocastanum L.	N	3	LU; LE	x	timber, medical plant, allergenic
Acer pseudoplatanus L.	N	3	LU; LE		allergenic
Alchemilla vulgaris L.	N/E	4	BF; FF; EF		population declining
Alnus incana (L.) Moench	N	3	LU; LE		allergenic
Alopecurus pratensis L.	M	2	TD	x	allergenic
Anemone nemorosa L.	N	3	LU; LE; BF; FF; EF	x	medical plant
Anthoxanthum odoratum L.	E	5	TD; FD; F; R; FS	x	allergenic
Aposeris foetida (L.) Less.	N	3	LU; LE; BF; FF; EF		
Briza media L.	N/E	4	BF; FF; EF		
Campanula scheuchzeri Vill	N/E	4	BF; FF; EF		
Dactylis glomerata L.	N/E; E; M	2;4;5	TD; BF; FF; EF; FD; R; FS	x	allergenic
Daphne mezereum L.	N	3	LU; LE; BF; FF; EF		medical plant
Festuca pratensis Huds.	M	2	TD		allergenic
Fragaria vesca L.	N	3	LU; LE; BF; FF; EF		medical plant
Fraxinus excelsior L.	N	3	LU; LE	x	timber, medical plant, allergenic
Helleborus niger L.	N	3	LU; LE; FF; EF		threatened
Holcus lanatus L.	E	5	TD		allergenic
Larix decidua Mill.	N	3	LU; LE	x	timber
Lotus corniculatus L.	N/E	4	BF; FF; EF		
Mercurialis perennis L.	N	3	LU; LE; BF; FF; EF		medical plant
Molinia caerulea L.	E	5	TD; FD; F		building material

Species	Study	Chapter	Phenophases	DWD, IPG	Importance, allergenicity, risk of extinction
Oxalis acetosella L.	N	3	LU; LE; BF; FF; EF		medical plant
Paris quadrifolia L.	N	3	LU; LE; BF; FF; EF		medical plant
Petasites albus L.	N	3	LU; LE; BF; FF; EF		
Picea abies (L.) H.Karst.	N	3	LU; LE	x	timber
Poa trivialis L.	M	2	TD		allergenic
Potentilla erecta (L.) Raeusch	N/E	4	BF; FF; EF		medical plant
Primula elatior Hill.	N	3	LU; LE; BF; FF; EF		medical plant
Prunella vulgaris L.	N/E	4	BF; FF; EF		medical plant, eatable
Ranunculus acris L.	N/E	4	FF; EF		
Ranunculus montanus Willd	N/E	4	FF; EF		threatened
Sambucus racemosa L.	N	3	LU; LE; BF; FF; EF		medical plant
Sorbus aucuparia L.	N	3	LU; LE; BF; FF; EF	x	allergenic
Trifolium pratense L.	N/E	4	BF; FF; EF		allergenic
Tussilago farfara L.	N	3	LU; LE; BF; FF; EF	x	allergenic, medical plant
Vaccinium myrtillus L.	N	3	LU; LE; BF; FF; EF		medical plant, eatable
Valeriana tripteris L.	N	3	LU; LE; BF; FF; EF		

***Manipulations*.** For the simulation of altered abiotic parameters in the Freisinger Moos, temperature was manipulated passively by open-top chambers since August 2009 and the water table level was increased using a pumping system to keep the water table 20 cm higher than on control plots since 2011. Over the altitudinal gradient in the Berchtesgaden National Park a 1000-year extreme drought event was simulated with static rain-out shelters and shifts in snow melting date were achieved by shovelling snow from advanced to delayed snowmelt plots in 2010.

***Environmental data*.** Meteorological data was derived from climate stations (temperature and precipitation data) next to the sites for the Freisinger Moos and the natural gradient study in the Berchtesgaden National Park or from mobile data loggers within the sites (temperature data) for the integrated study in the National Park. Soil moisture content for the same study was measured with a portable soil moisture meter.

***Data analysis*.** To estimate onset dates from the frequency distribution of recorded BBCH codes four different methods (Ordinal Logistic Regression (OLR), Cumulative Stage Development (CSD), Pooled pre / post Stage Development (PSD), Weighted Plant

Development (WPD)) were compared. Calculations were automated using MATLAB (R2009b, The Math Works) except for OLR which was run in R (R2.10.1 R Development Core Team). Statistical analyses of the dissertation were carried out using SPSS (17.0 and 19.0, SPSS Inc.). Analyses used in this PhD thesis included *t*-tests, analyses of variance (ANOVA), (weighted) linear regressions, analyses of covariance (ANCOVA) and Tukey's HSD for multiple comparisons.

I.3.2 RESEARCH QUESTIONS

The following leading research questions were addressed within this PhD thesis

a. How to estimate onset dates from BBCH scale recording?
b. How does plant phenology vary with altitude?
c. What effects do manipulative experiments have on plant phenological development?

The following section focuses on those questions in more detail and describes briefly the current state of research, illustrating gaps which were intended to be filled by this thesis.

I.3.2.1 FROM STATUS SAMPLING TO CLASSICAL ONSET DATES

Observation key. Phenological networks (*e.g.*, of the German Meteorological Service) often base their observation guidelines on the principle of event monitoring since they are reliant on volunteers who can only cover a small number of key phenological events, such as the beginning of leaf unfolding or full flowering. Only the newly founded USA-NPN switches from event to status monitoring by including phenophases covering the entire development of phenophases (*e.g.*, beginning of flowering, full flowering and end of flowering). However, until now, studies recording the end of phenophases (*e.g.*, end of flowering) were rare, although only these data allow an estimation of the duration of phenophases which is important since shifts in duration can affect plant-pollinator interactions (Memmott *et al.* 2007) or the pollen season (Emberlin *et al.* 1997; Van Vliet *et al.* 2002; Ziska *et al.* 2003). The BBCH code, on which European phenologists agreed, as a general guideline, unifies key phenological events (*e.g.*, full flowering), stages marking the end of phenophases (*e.g.*, end of flowering) and additionally intermediate stages (*e.g.*, 20% of flowers open) which further help to understand phenological development in more detail. Thus, in this study phenological observations were based on the BBCH code to switch from event to status monitoring and fill the gap of widely missing information about intermediate stages and stages marking the end of phenophases. Thus, in this study the following approach was taken:

- Observation of intermediate phenological stages and stages marking the end of phenophases.

Sampling. Most phenological networks (*e.g.*, of the German Meteorological Service) recommend revisiting selected plants every 2-3 days (DWD 1991); other studies even conduct their observations daily (*e.g.*, Yuan *et al.* 2007). However, the study design of this thesis required a less time intensive method for phenological observations since monitoring was carried out on several, partly remote (up to 2000 m a.s.l. in the Bavarian Alps) sites in 2010. Furthermore, in a natural meadow individuals grow very close together and can reach a height of more than one meter. Labelling and revisiting the same individuals, as recommended by phenological networks, appeared here as too time-consuming. Using the detailed BBCH code it is not necessary to be present at the exact start of the phenophases since it allows the observation of the frequency distribution of phenophases of populations instead of individuals. Hence, sampling intensity could be reduced to once a week. Thus, the following observation method was used for the first time within this thesis:

- Recording the frequency distribution of phenological stages in a population with an observation intensity of once a week.

Assessing onset dates. For climate change studies it is still necessary to determine classical onset dates of key phenological events in order to detect correlations between climatic parameters and phenology. However, since the above approach is not common in phenological studies there is no standard method to analyze frequency distribution data. Therefore, in this dissertation the following question was addressed (see also leading research question a):

- Development of a methodology to analyze the frequency distribution data.

I.3.2.2 FROM LOWER TO HIGHER SITES

Several phenological studies included data from a large latitudinal and longitudinal range (*e.g.*, Chmielewski & Roetzer 2001; Zhou *et al.* 2001; Menzel *et al.* 2006). However, only a few studies have dealt with altitudinal differences over a short latitudinal range (Migliavacca *et al.* 2008; Vitasse *et al.* 2009a; Ziello *et al.* 2009; Moser *et al.* 2010) even though those studies provide different natural temperature scenarios with which climate change impacts on plant phenology can be assessed while concurrently reducing photoperiodic differences (*e.g.*, Partanen *et al.* 1998; Keller & Korner 2003; Korner & Basler 2010). Since a substitution of space-for-time is common in research following question was fascinating to be investigated in this thesis:

- Do phenological responses to temperature over time match the phenological variability with altitude?

Moreover, most altitudinal studies, like the majority of phenological studies, especially consider tree species (Roetzer & Chmielewski 2001; Dittmar & Elling 2006; Richardson *et al.* 2006; Migliavacca *et al.* 2008; Vitasse *et al.* 2009b; Moser *et al.* 2010; Pellerin *et al*. 2012) studies focusing on herbaceous species are rare (but see Ziello *et al.* 2009 and Alexander 2010). Thus, this thesis especially focused on herbaceous species and addressed following questions:

- How does phenology of herbs vary with altitude? Are herbaceous species more sensitive to either variations with altitude or temperature than woody species (shrubs or trees)?

Furthermore, since the observation of stages marking the end of phenophases is not common in phenological research, this thesis also dealt with following question:

- How does the duration of phenophases vary with altitude?

I.3.2.3 FROM NATURAL TO EXPERIMENTAL APPROACHES

There have been many studies monitoring the phenological development of plants under manipulated conditions (reviewed by Wipf & Rixen 2010 or Wolkovich *et al.* 2012, supplementary information), however, they are biased geographically. A large number of experimental studies focusing on phenology were located in (sub-) alpine or Arctic ecosystems (*e.g.*, Totland & Alatalo 2002; Dunne *et al.* 2003; Aerts *et al.* 2006; Wipf *et al.* 2006; Wipf 2010), but less frequently in others, such as temperate forests, Mediterranean or low grassland ecosystems (but see Cleland *et al.* 2006; Prieto *et al.* 2008; De Frenne *et al.* 2010). As far as I am aware, there have been no phenological studies implementing manipulative experiments in a temperate fen-peatland area or covering an altitudinal gradient ranging from the foothill zone to alpine level. Only Dunne *et al.* (2003) combined an experimental study with a gradient approach, but just an altitudinal range of about 400 m was covered. Thus, besides leading research question c., this dissertation focused on the following questions:

- Do species respond to manipulative treatments differently at lower or higher altitudes?
- How do grassland species respond to manipulative treatments in a temperate fen-peatland?

Furthermore, since Wolkovich *et al.* (2012) demonstrated that phenological responses derived from experimental studies strongly underpredict advances in the timing of flowering or leafing compared with long-term observations, I also tried to discuss this topic in section VII. GENERAL DISCUSSION of this thesis.

Manipulations occur mainly at a single or very few levels of effect (Dunne *et al.* 2004). There have been several studies simulating a combination of different scenarios in order to test interaction effects, such as summer warming and earlier snowmelt (*e.g.*, Walker *et al.* 1999; Dunne *et al.* 2003; Aerts *et al.* 2006), drought and warming (Bloor *et al.* 2010; Beierkuhnlein *et al.* 2011) or warming and elevated CO_2 (Hovenden *et al.* 2008a; Bloor *et al.* 2010). However, there have been no phenological studies simulating higher temperatures and an elevated water table level. Thus, the following research question was intended to be answered in this study:

- What effect has the interaction of elevated water table level and higher temperatures on the development of grassland species?

Most phenological studies focus on key events such as leaf unfolding, beginning of flowering or full flowering, however, studies including other phenological phases such as flower development, fruit ripening or fruit senescence are rare (but see Price & Waser 1998; Hoffmann *et al.* 2010). Moreover, as already mentioned, the observation of stages marking the end of phenophases is not common. Thus, in this study the following questions were addressed:

- How do phenological events such as flower development, fruit ripening or fruit senescence respond to manipulative treatments?
- Do manipulative treatments influence the duration of phenophases?

I.4 OUTLINE OF THE THESIS

The main core of this PhD thesis consists of four peer-reviewed research papers, of which two are accepted (Chapter 2 and 3) and two are submitted (Chapter 4 and 5). Those papers follow the General Introduction (Chapter 1) and are deeply summarized in a General Discussion (Chapter 6).

The **General Introduction** (Chapter 1) describes changes in climate at a global and regional scale, general and phenological plant responses to changed environmental conditions, as well as types and methods of phenological research. This is followed by leading research questions and a brief description of the current state of research, illustrating gaps which were intended to be filled by this thesis.

The first publication (Chapter 2) "**A comparison of methods to estimate seasonal phenological development from BBCH scale recording**" (Cornelius *et al*., 2011, International Journal of Biometeorology 55: 867-877) presents and compares four different methods to estimate onset dates of phenological stages from frequency distribution data of populations which were recorded with the BBCH scale. The calculations were based on phenological data of four grass species which were observed weekly on a cultivated meadow next to the experimental site of Chapter 5 in the Freisinger Moos in 2009. We also tested, by omitting phenological stages, how detailed an observation key must be. Furthermore, we intended to answer the question whether the elimination of stages has an effect on the onset dates of other stages or if it is possible to estimate onset dates of stages which were not observed in the field. Additionally, we investigated whether an increased sampling interval results in similar estimates of onset dates. For both approaches we checked if estimates of all methods were consistent.

The second publication (Chapter 3) "**Linking altitudinal gradients and temperature responses of plant phenology in the Bavarian Alps**" (Cornelius *et al*., 2012, Plant Biology, doi: 10.1111/j.1438-8677.2012.00577.x) deals with the question how temperature affects key phenological events such as leafing or flowering of a range of species along an altitudinal gradient. Data were provided from the Berchtesgaden National Park and covered a time span of 14 years. In total 21 species spread over 24 sites were monitored over an altitudinal gradient from 680 to 1425 m a.s.l.. We examined if the response of woody plants to temperature was different to that of herbs. Additionally, we investigated if the duration of phenophases was affected by altitude. Finally, we focused on the question whether the response to temperature differed through the year and if phenological responses to temperature over time match the phenological variability with altitude.

The third publication (Chapter 4) "**Phenological response of grassland species to manipulative snowmelt and drought along an altitudinal gradient**" (Cornelius *et al*. 2012, submitted to Journal of Experimental Botany) focuses on single and combined effects of a natural gradient and experimental treatments on plant flowering (timing and duration) of 10 different grassland species. Observations sites (15) were located along an altitudinal gradient ranging from about 600 to 2000 m a.s.l. At each site a six week drought period using rain-out shelters and advanced and delayed snowmelt by shovelling were simulated. Phenological observations were carried out each week in 2010 based on the BBCH scale. We also examined if the response to experiments differed between lower and higher altitudes and if it changed through the season.

The fourth publication (Chapter 5) "**Impacts of temperature and water table manipulation on grassland phenology**" (Cornelius *et al*. 2012, submitted to Functional

Ecology) deals with the question whether an elevated water table level and higher temperatures affected either the entire plant development of four different grass species or single key phenophases such as flower development, flowering, ripening or fruit senescence. Phenological observations were conducted each week in the Freisinger Moos in 2010 and 2011. Furthermore, we tested if a combination of both an elevated water table level and higher temperatures influenced the total development or key phases of studied species. Moreover, we examined if the duration of phenophases or vegetation height were affected by manipulative treatments.

The **General Discussion** (Chapter 6) highlights the importance of my results in regard to research questions, integrates results over chapters and puts them in the context of other phenological studies.

The PhD thesis is summarized in a final **Summary and Conclusion** (Chapter 7). Further research perspectives are described in Chapter 8. All references are combined in Chapter 9. The publications and the candidate's individual contribution are listed in Chapter 10 and 11.

II A COMPARISON OF METHODS TO ESTIMATE SEASONAL PHENOLOGICAL DEVELOPMENT FROM BBCH SCALE RECORDING

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II.1 ABSTRACT

The BBCH scale is a two-digit key of growth stages in plants that is based on standardised definitions of plant development stages. The extended BBCH scale, used in this paper, enables the coding of the entire development cycle of all mono- and dicotyledonous plants. Using this key, the frequency distribution of phenological stages was recorded which required a less intense sampling frequency. The onset dates of single events were later estimated from the frequency distribution of BBCH codes. The purpose of this study was to present four different methods from which those onset dates can be estimated. Furthermore, the effects of (1) a less detailed observation key and (2) changes in the sampling frequency on estimates of onset dates were assessed. For all analyses, phenological data from the entire development cycle of four grass species were used. Estimates of onset dates determined by Weighted Plant Development (WPD), Pooled pre/post Stage Development (PSD), Cumulative Stage Development (CSD) and Ordinal Logistic Regression (OLR) methods can all be used to determine the phenological progression of plants. Moreover, results show that a less detailed observation key still resulted in similar onset dates, unless more than two consecutive stages were omitted. Further results reveal that the simulation of a less intense sampling frequency had only small impacts on estimates of onset dates. Thus, especially in remote areas where an observation interval of a week is not feasible, estimates derived from the frequency distribution of BBCH codes appear to be appropriate.

Keywords: Flowering, grassland, observation key, onset dates, sampling frequency

Table II.1 List of abbreviations

ANOVA	Analysis of Variance
BBCH	Biologische Bundesanstalt, Bundessortenamt and Chemical Industry
CSD	Cumulative Stage Development
DWD	German Meteorological Service
IPG	International Phenological Gardens
OLR	Ordinal Logistic Regression
PSD	Pooled pre/post Stage Development
USA-NPN	USA National Phenology Network
WPD	Weighted Plant Development

II.2 INTRODUCTION

Phenology, the science of recurrent seasonal natural events, may be a harbinger of changes in ecosystems arising from recent global climate change (Menzel 2002). Numerous authors have published articles on the effect of global warming on the timing of important developmental events in plants (*e.g.*, Sparks *et al.* 2000; Abu-Asab *et al.* 2001; Fitter & Fitter 2002; Menzel *et al.* 2005; Menzel *et al.* 2006). Most of these studies are based on long-term observation records which focus on key events such as leaf unfolding (Menzel *et al.* 2006) or first flowering (*e.g.*, Abu-Asab *et al.* 2001; Fitter & Fitter 2002). Datasets are often provided on an international (*e.g.*, Chmielewski & Roetzer 2001; Menzel *et al.* 2006) or national scale (*e.g.*, Defila & Clot 2001; Menzel *et al.* 2005) by phenological networks such as the International Phenological Gardens (IPG) or networks of National Meteorological Services. Because these networks are often reliant on volunteers, only a small choice of phenophases can be included in their monitoring programs. Intermediate stages (*e.g.*, 20% of all flowers open) as well as stages marking the end of phenophases (*e.g.*, end of flowering) are often not included. Thus, these datasets just provide information about onsets of key events without the possibility of analyzing the progression of phenophases. It is already known that higher temperatures cause an earlier start of plant flowering in spring and summer (*e.g.*, Menzel & Estrella 2001; Walther *et al.* 2002; Parmesan & Yohe 2003), an earlier onset of the pollen season in the Northern Hemisphere (Emberlin *et al.* 2002; Beggs 2004), and a longer and more intense pollen season for different species (*e.g.*, Spieksma *et al.* 1995; Emberlin *et al.* 2002; Spieksma *et al.* 2003). However, there are no studies based on other long-term records affirming a longer flowering period due to global warming because the end of flowering is often not monitored within phenological networks and therefore data are rare. Only the newly founded USA National Phenology Network (USA-NPN; www.usanpn.org) includes phenological stages covering the entire development cycle of phenophases (*e.g.*, beginning of flowering, full flowering and end of flowering) and

thus switches from event to status monitoring. The USA-NPN base their observation scheme on the extended BBCH scale (Meier 2001). The scale was originally developed jointly by four important chemical companies BASF, Bayer, Ciba-Geigy and Hoechst to standardize descriptions of plant development stages (Bleiholder *et al.* 1989). Later a slightly changed working group (BBCH: Biologische Bundesanstalt, Bundessortenamt and Chemical Industry) extended this scale to 27 crops and wild plants (Meier *et al.* 2009). The scale is a detailed growth stage key which includes intermediate stages as well as stages marking the end of phenophases. It allows the observation of the entire development cycle of all mono- and dicotyledonous plants using a decimal coding system. The first numeral of this system ranges from 0 to 9 in ascending order and corresponds to principal growth stages which describe longer-duration development phases such as bud development, leaf development or flowering. The second numeral also ranges from 0 to 9 and corresponds to secondary growth stages which refine the development stages such as the beginning of bud swelling or the end of flowering (Meier 2001).

Due to the advantages of a standardized observation system like this, which allows comparing homologous growth stages of different species, more and more phenological stages of existing datasets have been assigned to the BBCH scale as, for example, within the framework of COST action 725 (http://www.cost725.org), 'Establishing a European phenological data platform for climatological applications' (Menzel *et al.* 2006). Furthermore, several European phenological networks also modified their phenological guidelines according to the BBCH scale to provide higher compatibility between networks (Bruns *et al.* 2003).

Phenological networks such as the one of the German Meteorological Service (DWD; http://www.dwd.de) recommend making highly regular observations every 2-3 days and noting down the dates of occurrence of single phenological events. Where circumstances, such as remote research plots, difficult accessibility and limited financial resources, only allow a less frequent inspection, it seems more appropriate to refine the code by including intermediate stages, and to observe the phenological status of populations instead of single individuals. Thus, on each sampling date, the frequency distribution of phenological stages of a certain number of individuals could be recorded. The classical onset dates of key events can then be interpolated from these data and it is not necessary to be present at the exact start of the stage. This approach requires a less frequent observation intensity, *e.g*. once a week, in contrast to most other studies where observations are conducted every 2-3 days or even daily (*e.g*., Cleland *et al.* 2006; Yuan *et al.* 2007).

Despite these advantages, there have so far been no studies using the BBCH scale to observe the entire development cycle of wild plants. Most recent studies utilizing the BBCH scale either present further descriptions of phenological stages of certain species (*e.g.*, Salazar *et al.* 2006; Finn *et al.* 2007; Saska & Kuzovkina 2010) or deal with topics related to agricultural crop research (Bazok *et al.* 2009; Janusauskaite 2009; Kraska *et al.* 2009; Javier Rodriguez-Rajo *et al.* 2010) where single phenological events and not the entire development cycle of plants is considered. Consequently, there is no accepted methodology to analyze the frequency distribution of phenological stages.

Therefore, the purpose of this paper is to present and compare four different methods to analyze phenological data of populations recorded on a refined BBCH scale in order to estimate onset dates for each phenological stage. Calculations were based on phenological data of the entire development cycle of four grass species in the Freisinger Moos, Germany, in 2009.

Furthermore, it was tested whether a detailed observation key is necessary to estimate onset dates or if there are stages which are redundant. Moreover, the elimination of phenological stages from the observation key should help to answer the following questions: (1) What effect does the omission of a stage have on onset dates of other stages? (2) Is it possible to estimate onset dates of stages if that stage is not specifically recorded? (3) Are all methods consistent in this approach?

Finally, a simulated increased interval between consecutive recordings should help to answer the following questions: (a) Does an increased sampling interval of two or even three weeks reveal similar estimates of onset dates? (b) Are all methods consistent in this approach?

II.3 MATERIALS AND METHODS

II.3.1 PHENOLOGICAL OBSERVATIONS

Data were recorded from a cultivated meadow at a peatland site in the Freisinger Moos, Germany (48°22'N, 11°41'E). Records were taken separately from three 0.75 m x 0.75 m plots and one 0.75 m x 0.40 m plot. Differences in plot size were due to space restrictions on the site. All plots were contiguous. Four grass species, *Alopecurus pratensis* L. (meadow foxtail), *Dactylis glomerata* L. (cocksfoot), *Festuca pratensis* Huds. (meadow fescue) and *Poa trivialis* L. (rough-stalked meadow grass) were observed once a week from the beginning of April to the end of September in 2009. In each plot, 12 individuals of *A. pratensis*, *D. glomerata* and *F. pratensis* were randomly chosen every week to be observed. The number of individuals was considered large enough for further statistical analyses and

small enough to make all observations feasible in a single day. Only six individuals were observed of *P. trivialis* because of the small number of individuals in each plot. *D. glomerata* could only be monitored in three plots because the species did not exist in the remaining plot. As single individuals of each species were not marked, different individual plants were likely observed on consecutive sampling dates.

Phenological observations were conducted according to the BBCH scale for cereals (Meier 2001), which was slightly modified for wild grasses. In general, wild grasses grow closer together, often in combination with other species, and are much smaller than cereals. Therefore the distinction of secondary growth stages is more difficult and time-consuming than for cereals. Thus, some principal and secondary growth stages of the BBCH scale could not be transferred to the new key or needed to be redefined (Table II.2).

The BBCH principal growth stages 0, 2 and 7 were excluded completely from the new observation key. The principal growth stage 1 was not modified; stage 3 was included but rarely observed. The principal growth stages 4-6 were modified slightly for wild grasses. Principal growth stages 8 and 9 were redefined, because flowers of wild grasses are too small to test the development status of fruits, as it is done in the original BBCH scale for cereals, without destroying parts of the spike or panicle. The principal growth stages 5 and 9 were extended by one secondary growth stage because the resolution of the original key was not sufficient to describe development. The new stages were coded with the two-digit code of the stage they belonged to and with an additional index (59a, 95a, see Table II.2). Secondary growth stage 59a is only applicable for grass species with a panicle rather than a spike.

Table II.2 Description of the phenological growth stages of wild grasses according to the BBCH code for cereals (Meier 2001). Crosses for each species indicate secondary growth stages which were observed in the field in the Freisinger Moos in 2009. Stages not observed are omitted. Principal growth stages with the index a (=after) were added because the resolution of the original key was not sufficient to describe the development precisely.

BBCH code	Description	*Alopecurus pratensis* L.	*Dactylis glomerata* L.	*Festuca pratensis* Huds.	*Poa trivialis* L.
Principal growth stage 1:Leaf development					
11	First leaf unfolded	x	x	x	x
12	2 leaves unfolded	x	x	x	x
13	3 leaves unfolded	x	x	x	x
14	4 leaves unfolded		x		x
Principal growth stage 4: Booting					
43	Mid boot stage: sheath just visibly swollen	x	x	x	x
45	Late boot stage: flag leaf sheath swollen	x	x	x	x
47	Flag leaf sheath opening	x	x	x	x
Principal growth stage 5: Inflorescence emergence, heading					
51	Beginning of heading: tip of inflorescence emerged from sheath, first spikelet just visible	x	x	x	x
55	Middle of heading: half inflorescence emerged	x	x	x	x
59	End of heading: inflorescence fully emerged	x	x	x	x
59a	Panicle unfolded (in panicle forms only)		x	x	x
Principal growth stage 6: Flowering, anthesis					
61	Beginning of flowering: first anthers visible	x	x	x	x
65	Full flowering: 50% of anthers mature	x	x	x	x
69	End of flowering: all spikelet have completed flowering but some dehydrated anthers may remain	x	x	x	x
Principal growth stage 8: Ripening					
85	Inflorescence starts yellowing	x	x	x	x
89	Inflorescence yellow	x	x	x	x
Principal growth stage 9: Senescence					
93	First seeds fallen	x	x	x	x
95	50% or more seeds fallen	x	x	x	x
95a	All seeds are fallen	x	x	x	x
100	Reproductive period finished	x	x	x	x

Secondary growth stages 15-19 could not be detected in 2009 because species did not have more than four leaves simultaneously. Secondary growth stages 31-36 were also not detected because these stages proceed in parallel with more advanced growth stages which were recorded in preference. Secondary growth stage 97 was not observed until the end of September. All development stages occurring after secondary growth stage 95a were summarized as stage 100, indicating the end of development, which needed to be introduced for mathematical reasons to allow estimation of earlier growth stages. This stage was not considered further in analyses. The description of each secondary growth stage was further supported by digital photographs (Fig. II.1).

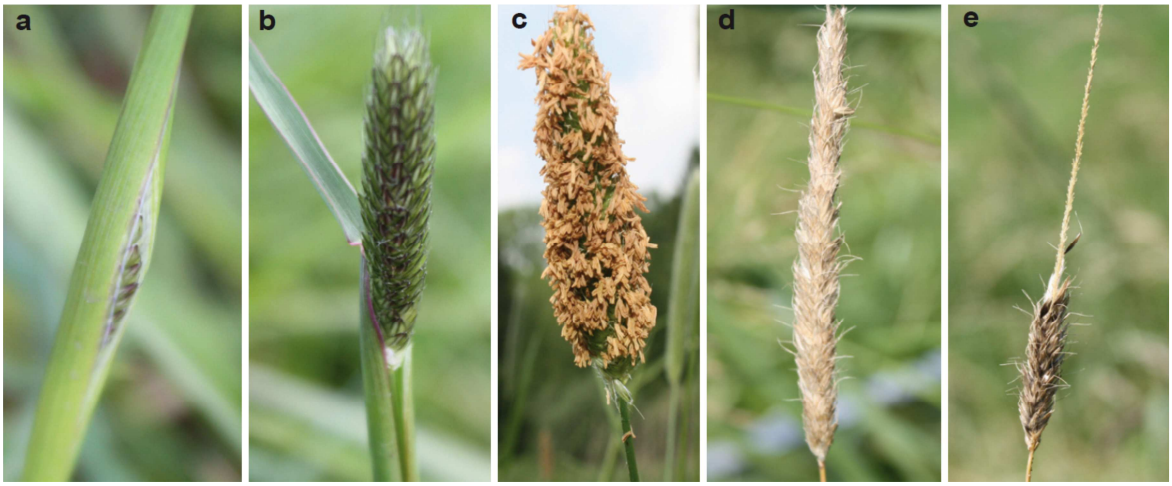

Figure II.1 Examples of the observation key of *Alopecurus pratensis* L., which is based on the BBCH code for cereals. a) BBCH code 47: flag leaf sheath opening, b) BBCH code 55: middle of heading*:* half inflorescence emerged, c) BBCH code 69: end of flowering: all spikelets have completed flowering but some dehydrated anthers may remain, d) BBCH code 89: Inflorescence yellow, e) BBCH code 95: 50% or more seeds fallen

II.3.2 DATA ANALYSIS

Weekly raw data (absolute frequencies of specimens within certain stages) were first converted into percentages. To estimate onset dates of secondary growth stages, four different methods were developed and compared (Fig. II.2). Calculations to determine onset dates were automated in MATLAB (R2009b; The MathWorks, Natick, MA, USA, 2009) except for the ordinal logistic regression method which was run in R (R2.10.1; R Development Core Team, Vienna, Austria, 2006). All observed dates were converted to day of year (1 January= 1 etc.). Calculations were done for each species and plot separately.

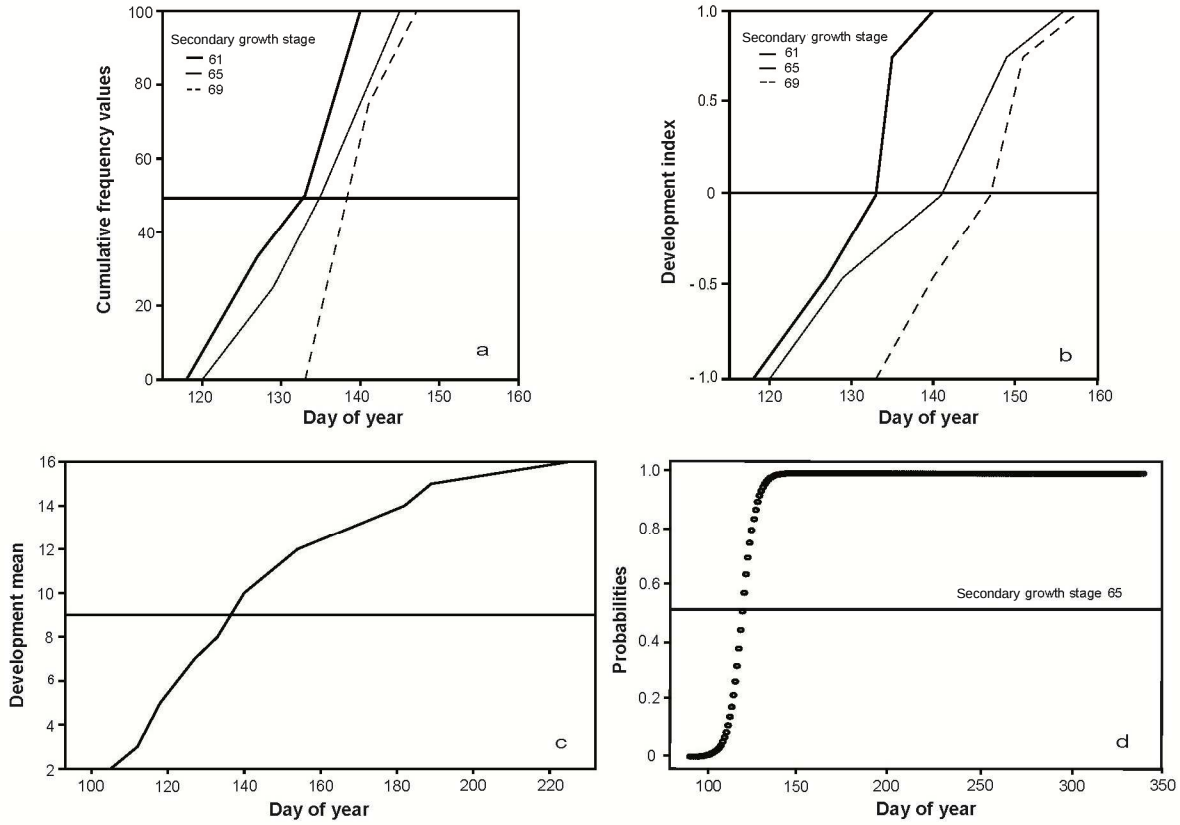

Figure II.2 Illustration of the different mathematical approaches of the four presented methods to estimate onset dates of secondary growth stages. a, b) Progression curves of single secondary growth stages 61-69 calculated by methods of Cumulative Stage Development (CSD) and Pooled pre/post Stage Development (PSD). Horizontal lines indicate thresholds used to define onset dates of corresponding growth stages. c) Progression curve of the entire plant development calculated by the method of Weighted Plant Development (WPD). The horizontal line indicates the threshold to define the onset date of secondary growth stage 65. Development mean values on the y-axis indicate converted BBCH codes to ranks. d) Progression curve of secondary growth stage 65 modelled by the method of Ordinal Logistic Regression (OLR). The horizontal line indicates the threshold used to define the onset date of secondary growth stage 65. Thresholds can be changed for CSD and OLR methods.

II.3.2.1 WEIGHTED PLANT DEVELOPMENT (WPD)

The basis of the method of weighted plant development is a linear interpolation between two consecutive sampling dates to determine onset dates of secondary growth stages. For this a phenological mean value (development mean; DM) per sampling date (t) was calculated from the relative frequency distribution data. First, the ordinal scaled, two-digit decimal code was converted to ranks (i) starting with 1. Each value on the new scale was then weighted by the corresponding relative frequency (x_i) between 0 and 1. The weighted values were finally summed over all secondary growth stages for each sampling date (Eq. 1).

$$DM(t) = \sum_{i=1}^{p} (x_i(t) \cdot i) \quad (1)$$

where p is the total number of phenological stages and i the corresponding phenological code. The dates of phenological stages were then estimated from linear interpolation between sampling date means.

II.3.2.2 POOLED PRE/POST STAGE DEVELOPMENT (PSD)

The method of pooled pre/post stage development is also based on linear interpolation between sampling dates. However, a development index (DI) per sampling date (t) and secondary growth stage (i) rather than a phenological mean was calculated. For each sampling date, the relative frequency distribution was divided into three groups in respect to the specific single secondary growth stage of interest (k). The first group was the percentage of secondary growth stages occurring before the stage of interest ($1 \ldots k-1$), the second group was the percentage occurring after the stage of interest ($k+1 \ldots p$). The third group was the percentage of observations exactly at the stage of interest. To calculate the development index all groups were weighted with a factor *f* in relation to their influence on the estimates of onset dates (Eq. 2). The first group was weighted with -1 because individuals in this group still needed to pass through the stage of interest. The bigger this group the later the onset date of the stage of interest. The second group was weighted with +1 because development of individuals was further advanced than the stage of interest. The bigger the influence of this group the earlier was the onset date of the stage of interest. The third group was weighted by 0 because these individuals are exactly at the stage of interest. The bigger this group the greater the probability that the date of onset equalled the sampling dates.

$$DI(t,k) = \sum_{i=1}^{p} x_i(t) \cdot f(k) \quad (2)$$

where $f = \begin{cases} -1, if\ (i < k) \\ 0, if\ (i = k) \\ 1, if\ (i > k) \end{cases}$

and $x_i(t)$ is the relative frequency of secondary growth stage i at sampling date t.

The resulting development indices were then linearly interpolated to estimate the onset date of each secondary growth stage as the date when the development index equalled zero. If more than one development index per secondary growth stage equalled zero the date of the first index was defined as the onset date.

II.3.2.3 CUMULATIVE STAGE DEVELOPMENT (CSD)

The method of cumulative stage development is analogous to the procedure of Brügger (1998) which, in turn, is based on the work of Schirone *et al.* (1990). Both studies used the method to determine the progression of phenophase development in tree crowns.

Onset dates of each secondary growth stage were determined with the help of summation curves. At each sampling date (t) relative frequency values from 0 to 1 at stage i ($x_i(t)$) were added to the relative frequency values at the following stages ($x(t,k)$) (Eq. 3).

$$CF_i(t) = x_i(t) + \sum_{k=i+1}^{p} x(t,k) \quad (3)$$

The resulting cumulative frequency values (CF) per sampling date and secondary growth stage were then linearly interpolated over time. Onset dates were defined as the point in time when 50% of all individuals were at the stage of interest. If this threshold was crossed twice because of later developing individuals observed at subsequent visits, the first date of crossing was defined as the onset date. If more than one cumulative frequency value per secondary growth stage equalled 50%, the date of the first value was defined as onset date.

II.3.2.4 ORDINAL LOGISTIC REGRESSION (OLR)

This method to determine onset dates of secondary growth stages is based on an ordinal logistic regression (Agresti 2007). First, the two-digit BBCH codes were ranked into ascending positive integers i as it was done for WPD. Frequency distribution data were then used in the following model (Eq. 4):

$$\log\left(\frac{P}{1-P}\right) = \alpha + \sum \beta_i \cdot x_i \quad (4)$$

where P= P(Y_i=1|x_i) is the probability and Y is the ordinal response variable, α is the intercept parameter, β_i the slope parameters and x_i the explanatory variable, in this case time.

The resulting intercept values for each secondary growth stage were put into a logistic regression function. Onset dates were defined as the date when the probability of a given individual to be in the considered stage is 50 %, i.e. the number of expected successes "observed stage" equals the half of a population; the rest of the population stays in earlier or later stages. In comparison to the other methods, OLR is based on the frequency distribution over time. WPD, PSD and CSD, however, are based on the frequency distribution over phenological stages at a fixed sampling date.

II.3.3 THE EFFECTS OF DEGRADED OBSERVATION KEYS AND REDUCED SAMPLING FREQUENCY

To test the effects of a less detailed observation key on estimates of onset dates of secondary growth stages, the key was degraded by sequentially leaving out a single secondary growth stage from the original observation data. Records of each omitted stage were redistributed to the previous and subsequent stages according to the proportion originally occurring in these stages. Percentages were reassigned in this way because field experience indicated that the developmental status of an individual would not always be allocated to the previous growth stage. Consequently, secondary growth stage 14 was the first stage from which observations could be properly redistributed. New, degraded data were then used to estimate onset dates. Furthermore, it was tested how similar onset dates are if two secondary growth stages were eliminated. For this, data were reassigned as described before but the percentages of two omitted stages were redistributed.

The influence of a reduced sampling frequency on onset dates of each secondary growth stage was tested by modifying the original data so that only observations of every second (both even and odd weeks) or third week were considered. These data were then used to estimate onset dates.

Analyses regarding the effects of degraded observation keys were only conducted on WPD and PSD methods because analyses showed that onset dates of stages can only be estimated with OLR and CSD if field data were collected. Consequently, effects regarding less intense sampling frequencies were also conducted only on these methods.

II.3.4 STATISTICAL ANALYSIS

An ideal method to assess accurate onset dates should deliver matching onset dates for the different plots in the same managed peatland meadow, thus produce repeatable results. Furthermore, the authors suppose that the ranking of the onset dates derived by the four methods should at least be constant across the four grassland species observed. To test differences between methods and plots on the estimated dates over all secondary growth stages and of each single secondary growth stage two-way analysis of variance (ANOVA) was used. Further two-way ANOVAs were conducted to test differences between methods and plots on estimated dates if a degraded observation key or a reduced sampling frequency was considered. All statistical analyses were performed using SPSS 17.0 (SPSS Inc., Chicago, Illinois, USA, 2008).

II.4 RESULTS

II.4.1 COMPARING ONSET DATES BY DIFFERENT METHODS

For all species, ANOVA revealed no significant differences in estimated dates between plots (Table II.3) which had been anticipated because they were all treated similarly. Estimated dates differed significantly between methods for *F. pratensis* and *P. trivialis* but not for *A. pratensis* or *D. glomerata* (Table II.3).

Table II.3 Results of a 2-way ANOVA showing effects of different methods and plots on the phenological progression of the four species. Values shown are p-values. Values in italics are significant (P< 0.05).

	Methods	Plots
Alopecurus pratensis L.	0.262	0.824
Dactylis glomerata L.	0.199	0.080
Festuca pratensis Huds.	*0.001*	0.075
Poa trivialis L.	*<0.001*	0.124

Figure II.3 shows phenological progression curves of onset dates estimated by the four methods for all species. Notably, for all species, onset dates of secondary growth stages showed minor differences (≤1 day) between WPD and PSD as well as between CSD and OLR. However, onset dates of secondary growth stages, especially from stage 51 on, were earlier if estimated by CSD or OLR compared to WPD and PSD (3-5 days on average depending on species). Differences in onset dates estimated by WPD/PSD and CSD/OLR were larger for stages at the very beginning (secondary growth stage 13) and later on in the development cycle, with differences between onset dates of more than a week. However, highly significant (P< 0.001) differences between methods, as determined by two-way ANOVA, were rarely detected for phenological stages towards the end of the development cycle (Fig. II.3). Differences were mostly found for stages of principal growth stages 4 and 5. Onset dates could not be estimated for secondary growth stage 12 because observations in 2009 started too late to survey the entire progression of this stage.

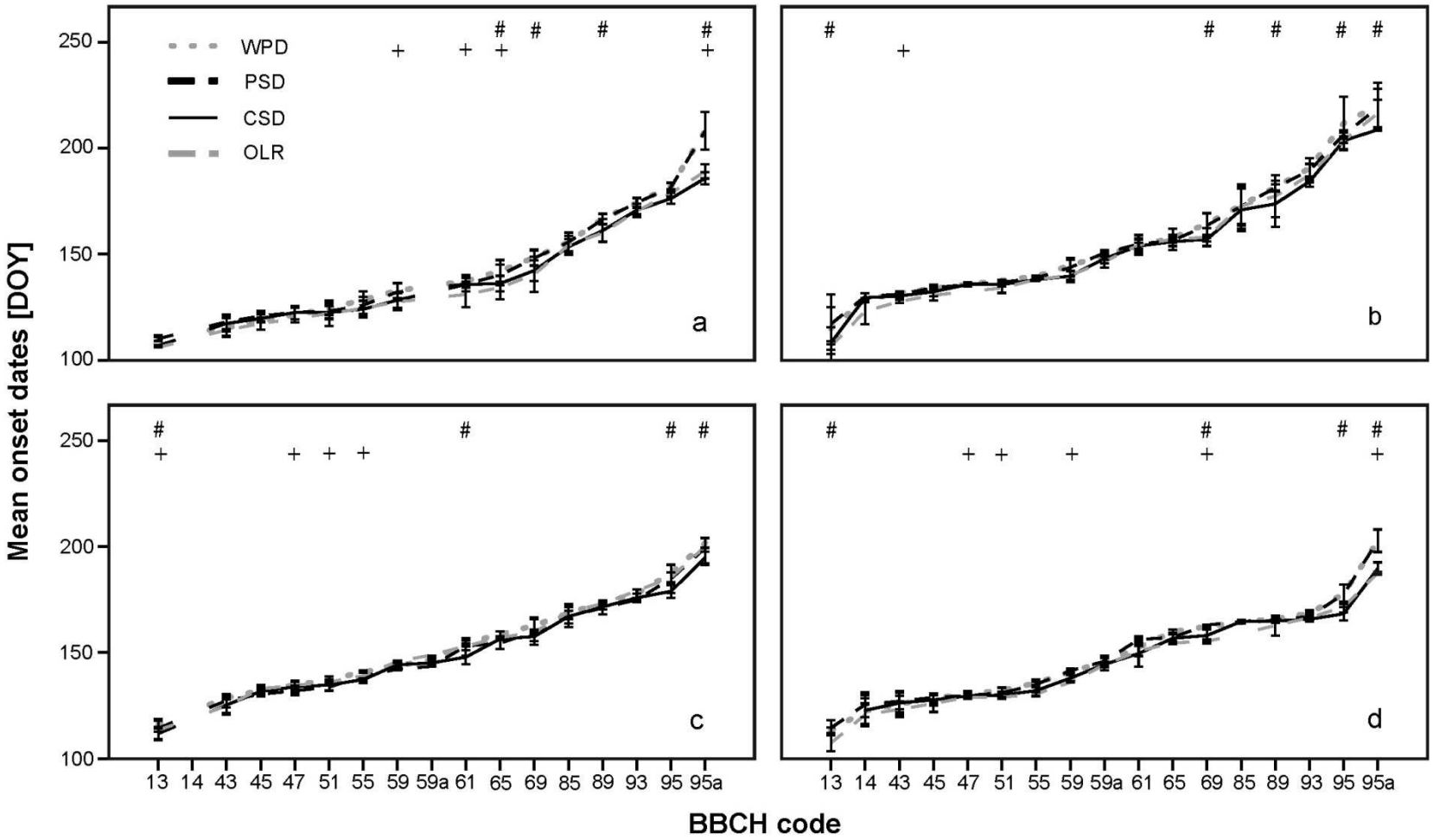

Figure II.3 Phenological progression curves of the four species in 2009 showing onset dates estimated by Weighted Plant Development (WPD), Pooled pre/post Stage Development (PSD), Cumulative Stage Development (CSD) and Ordinal Logistic Regression (OLR). Gaps in lines are due to different observation keys used for different species. Pluses indicate stages where onset dates were highly significantly ($P < 0.001$) different between methods. Hashes indicate stages where onset dates estimated by CSD and OLR differed by more than one week. Error bars indicate the standard error within the different plots. a) *Alopecurus pratensis* L., b) *Dactylis glomerata* L., c) *Festuca pratensis* Huds. d) *Poa trivialis* L.

II.4.2 EFFECTS OF DEGRADED OBSERVATION KEYS AND REDUCED SAMPLING FREQUENCY

Two-way ANOVA revealed no significant differences between WPD and PSD methods to estimate onset dates for all four species using degraded observation keys (P= 0.360 for *A. pratensis*, P= 0.906 for *D. glomerata*, P= 0.331 for *F. pratensis*, and P= 0.750 for *P. trivialis*).

Omitting the recording of single secondary growth stages affected onset dates of up to eight stages if WPD was used for estimation (Fig. II.4). The number and type of affected stages differed depending on which secondary growth stage was omitted. Using PSD, onset dates of up to three secondary growth stages were affected. The onset dates of the omitted and adjacent stages were always affected (Fig. II.4). Averaged over all plots and secondary growth stages, onset dates differed about 0.2-0.6 days for WPD and 0.9-1.2 days for PSD depending on species. Based on mean absolute deviations (averaged over plots) onset dates were affected by 2-9 days for WPD and 3-7 days for PSD depending on species. An effect of more than 2 days was noted if secondary growth stages 59a, 69, 93 and 95a were omitted. For PSD, the omission of secondary growth stages 43, 59, 61, 89 and 95 also affected onset dates by more than 2 days (Fig. II.4).

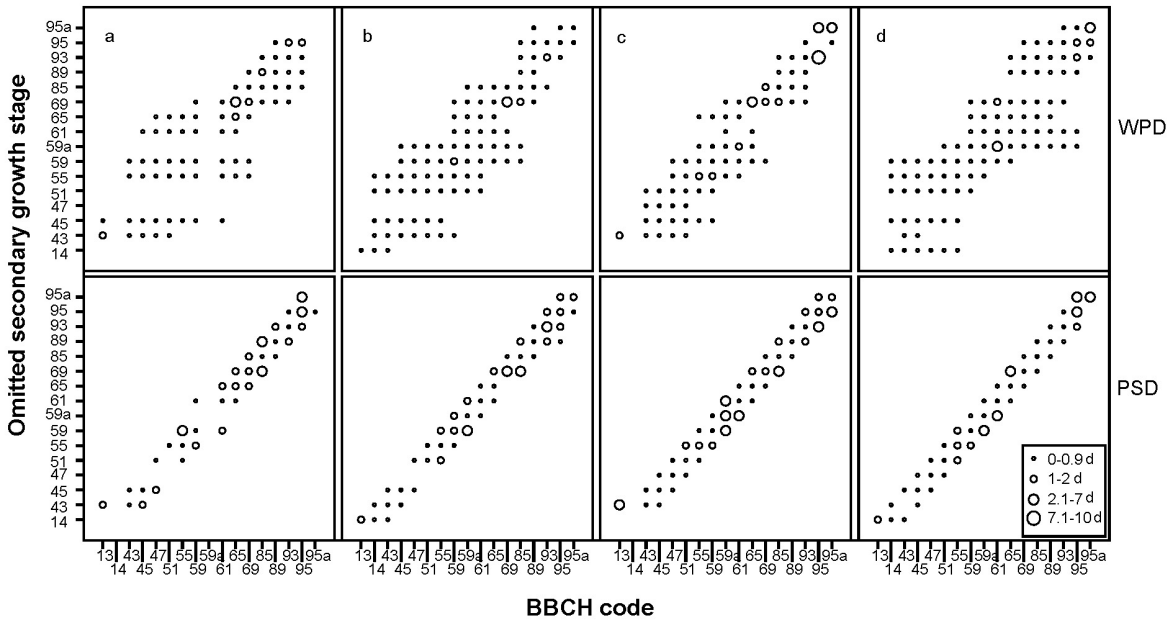

Figure II.4 Effects of a degraded observation key on onset dates of secondary growth stages estimated either by WPD (Weighted Plant Development) or PSD (Pooled pre/post Stage Development). Circle sizes indicate mean absolute deviations from original onset dates in days. Horizontal gaps indicate no change in onset dates even though one secondary growth stage was left out. Vertical gaps are due to different observation keys used for the four species. a) *Alopecurus pratensis* L. b) *Dactylis glomerata* L. c) *Festuca pratensis* Huds. d*) Poa trivialis* L.

When omitting the recording of two secondary growth stages, an estimation of onset dates with PSD was no longer possible. Using WPD for estimation, onset dates were affected by up to 14 days (depending on stage and species) if two stages were eliminated.

ANOVA showed no significant effect of methods (WPD and PSD) on onset dates of all four species (P= 0.856 for *A. pratensis*, P= 0.521 for *D. glomerata*, P= 0.650 for *F. pratensis* and P= 0.734 for *P. trivialis*) if sampling frequency was reduced.

Simulating observations every second week instead of every week changed estimates of onset dates by an average of 1-2 days for WPD and 1-3 days for PSD depending on species (Fig. II.5). Observations every 3 weeks affected estimates of onset dates by 2-4 days on average for both methods. Based on mean absolute deviations of each secondary growth stage, larger differences in onset dates of 5-9 days, depending on species, occurred when only every third week was considered. Observations conducted every second week caused a shift of 2-8 days depending on species. Onset dates for secondary growth stages could either be earlier or later in relation to onset dates estimated with the original data set.

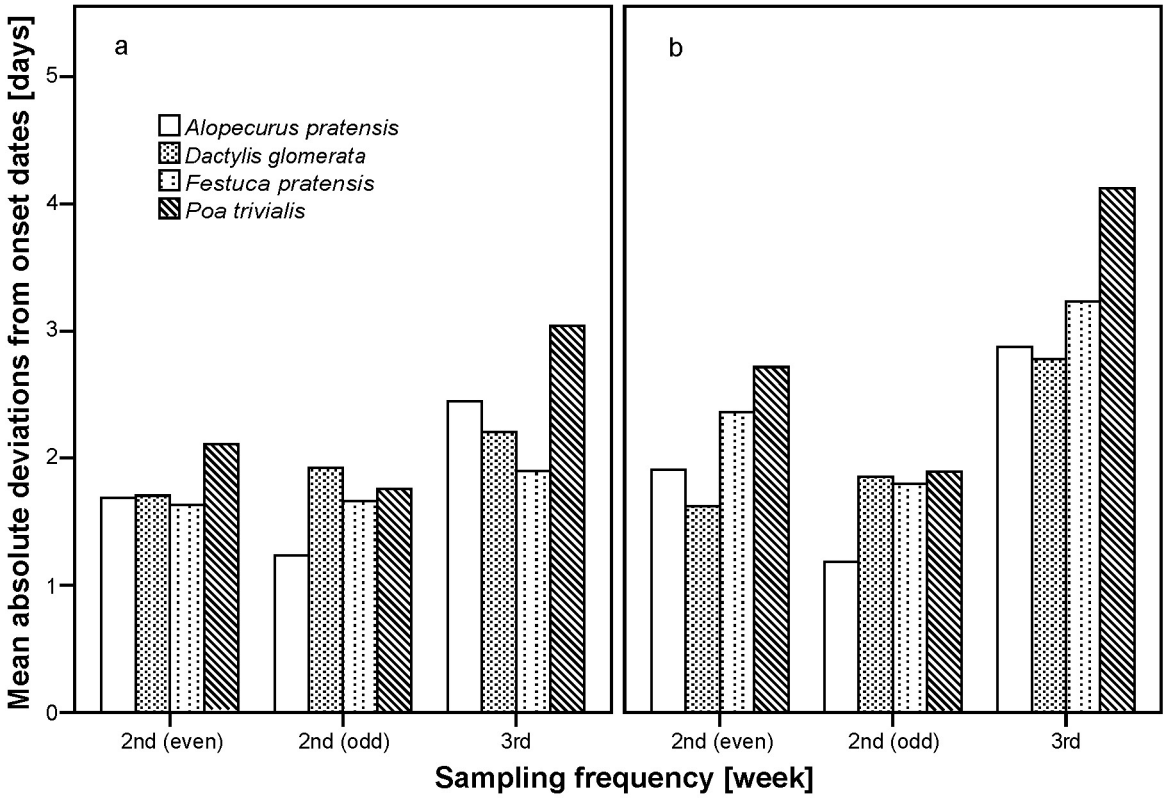

Figure II.5 Mean absolute deviations from original onset dates if sampling frequency is reduced to every second (even or odd) or third week. Onset dates were either estimated by Weighted Plant Development (a) or Pooled pre/post Stage Development (b) for all four species.

II.5 DISCUSSION

II.5.1 ADVANTAGES AND DISADVANTAGES OF METHODS

All four methods described in this paper can be used to determine the phenological progression of plants by estimating onset dates of secondary growth stages from recorded frequencies of BBCH codes. However, methods sometimes differed substantially in calculation effort and results.

The basic difference of WPD from all other methods lies in the fact that only one value per sampling date is calculated. This provides information only about the development of plants in general but no information about the progression of each secondary growth stage (Fig. II.2). However, this information allows the estimation of the beginning, the speed of passage and the end of single stages, which helps to understand the development of plants in more detail.

Furthermore, WPD is based on an interval-scaled observation key which presumes that all stages are of equal length. However, this contradicts reality because plants pass through some developmental stages faster than through others. This was quantified in a study by ÖKL (2006) where 2,749 phenological records of flowering stages of six important grass species in Austria in 2006 were analyzed. It was shown that *D. glomerata*, for example, needed 12 days from secondary growth stage 59 to 61 but just 5 days from growth stage 61 to 65 (ÖKL 2006). However, interval-scaled observation keys are often used in phenological approaches (*e.g.*, Price & Waser 1998; Vitasse *et al.* 2009b), so this method was also included in this study. The OLR method, in contrast, treats the observation key as ordinal scaled. Consequently, stages of different length are already considered in this approach. CSD and PSD are based on different calculation procedures. A switch to an interval-scaled observation key is not necessary.

CSD, in contrast to PSD, provides fewer data points to interpolate onset dates due to cumulative calculation procedures which often lead to steeper slopes resulting in earlier onset dates (Fig. II.2). Phenological progression is therefore often advanced if onset dates were calculated with CSD in comparison to PSD. A similar progression also occurs if onset dates were estimated by OLR. Onset dates between WPD/PSD and CSD/OLR differed most in stages at the very beginning and end of the development cycle of plants. Differences in onset dates of more than 1 week could be mostly detected for secondary growth stages 13, 69, 95 and 95a. A linear regression between the number of weeks a secondary growth stage lasts and the standard deviations of mean onset dates (averaged over methods and species) confirmed a strong positive relationship (R^2= 0.765, P< 0.001) between length of stage and difference in onset dates. Equally, the secondary growth stage 59 is also long

lasting which explains the highly significant differences in onset dates for two out of four species. All other highly significant differences between onset dates, as well as differences of more than 1 week, appear to be species specific and not connected to the duration of stages. Significant differences in onset dates between methods for *F. pratensis* and *P. trivialis*, as shown by ANOVA (Table II.3) are also due to differences between onset dates estimated by WPD/PSD and CSD/OLR, as post-hoc tests indicated (data not shown).

Both CSD and OLR methods have in common that different thresholds can be determined to define onset dates. In this study, a threshold of 50% is chosen because it is often used in other studies (*e.g.*, Vitasse *et al.* 2009b) and recommended for observations based on the BBCH code (Meier 2001). However, it is important to note that due to the sigmoidal nature of the progression of each secondary growth stage an interpolation error can occur, which is greatest at the beginning and the end of the curve. Thresholds defining onset dates of secondary growth stages should therefore be within the linear part of its course of the progression (Brügger 1998).

Onset dates estimated by PSD are sometimes identical for two consecutive secondary growth stages. This may happen because plants were not individually marked in the plots. Thus, due to recording of different individual plants, species can appear further advanced at one sampling date than at the following, which can result in the same onset dates. Equal onset dates as well as multiple crossing points could have been avoided if individuals had been marked. However, searching for marked individuals in a cultivated meadow, where plants grow close together and reach a height of almost a metre was regarded as too time-consuming. This was also the reason to limit the number of individuals to 12, even though it is known that larger sample sizes improve statistical estimates. Furthermore, data analyzed by CSD and OLR also result in the same onset dates if the first (for CSD) or second (for OLR) of two consecutive secondary growth stages was not observed in the field because these methods need field data for each secondary growth stage as a basis for estimating onset dates.

II.5.2 OBSERVATION KEY AND SAMPLING FREQUENCY

For WPD and PSD methods, onset dates of single secondary growth stages can be estimated even though no field data were collected. Using WPD compared to PSD, more stages are influenced if one secondary growth stage is left out but the error is smaller. For WPD, omission of most stages affects onset dates by less than 2 days. In the study by ÖKL (2006), the most rapid progression between secondary growth stages was observed for *Bromus erectus* Huds. which passed through secondary growth stage 61 in just 2 days. Thus, our simulated shift in onset dates of less than 2 days is still within the minimum range

of a short duration stage. For PSD, a slightly bigger influence on onset dates was observed. More than half of all stages affected onset dates by more than 2 days if left out. However, deviations were still small. In only two cases was the shift bigger than 5 days, which is within the time-span of most secondary growth stages in the ÖKL (2006) study. Those stages, whose onset dates differed most between estimates by WPD/PSD and CSD/OLR, were also identified as inducing complex shifts in the assessment of plant development when omitted from observation. Thus, long duration stages, if left out, influence changes of onset dates more than others. Estimates of onset dates determined by both methods are similar to the original estimates if a single secondary growth stage was left out. However, if more than one secondary growth stage was eliminated, onset dates of those stages could not be estimated by PSD. Using WPD for estimation, results are more promising; however deviations were larger (up to 14 days; data not shown). Thus, no further analyses regarding the elimination of more stages were conducted.

Simulating an increased observation interval of every 2 weeks caused a shift in onset dates of 2 days or less for almost all species and both methods. In comparison to the ÖKL (2006) study these shifts indicate that the onset dates are still within the range of a short duration stage. Sampling even less frequently (every third week) affected onset dates slightly more (≤5 days), which is again within the range of most secondary growth stages in the ÖKL (2006) study.

The DWD recommends a regular observation intensity of 2-3 days in peak season (DWD 1991). BBCH intensity, used for field observations in this study, is already a factor of three lower. Even recording intervals of every third week allow determination of onset dates although absolute error might be up to 1 week or slightly more. However, especially in remote areas where an observation intensity greater than once a week is not feasible, an observation method based on BBCH codes as described here seems to be appropriate.

II.6 CONCLUSION

Even though the BBCH scale has attracted attention of scientists outside agricultural plant science, there have been, so far, no studies using the BBCH code to investigate the entire development cycle of wild plants. Due to the lack of studies, there is no common method to determine onset dates for each secondary growth stage from frequency distributions of BBCH codes. In this study, four different methods were compared. WPD is fast and simple in calculation and onset dates can be estimated even though field data were not collected for each secondary growth stage. However, WPD provides no information about the progression of single secondary growth stages and the threshold for estimating onset dates is fixed. The progression of single secondary growth stages can be determined using PSD,

CSD and OLR methods. PSD, in contrast to CSD and OLR can estimate onset dates for each secondary growth stage even though no field data were collected. Both CSD and OLR methods allow different thresholds to define onset dates, PSD, however, does not.

WPD and PSD methods allowed determination of onset dates if a degraded observation key or a less frequent sampling intensity was used. However, deviations of onset dates estimated by PSD were often slightly bigger than those of onset dates estimated with WPD. Results showed that the observation key can be less detailed but neither method can estimate onset dates if two or more consecutive stages are left out. In particular, the omission of long duration stages influenced estimates of onset dates more than others. Thus, an observation key should preferably include long duration stages to avoid large errors in onset dates. Simulating a less intense sampling frequency leads to onset dates diverging only slightly from original estimates. For remote areas, in particular, recording a frequency distribution of BBCH codes with an interval of more than 1 week appears feasible to generate valid phenological observations on a less frequent but more intensive basis.

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III LINKING ALTITUDINAL GRADIENTS AND TEMPERATURE RESPONSES OF PLANT PHENOLOGY IN THE BAVARIAN ALPS

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III.1 ABSTRACT

Global climate change influences ecosystems across the world. Alpine plant communities have already experienced serious impacts, and will continue to do so as climate change continues. The aim of our study was to determine the sensitivity of woody and herbaceous species to shifts in temperature along an altitudinal gradient.

Since 1994 park rangers have been making phenological observations at 24 sites from 680-1425 m a.s.l. Each year 21 plant species were observed once or twice weekly from March to July; with a main focus on flowering and leaf unfolding.

Our study showed a very high degree of dependence of phenophases and species on inter-annual temperature variation and altitude. Averaged over all species and phenophases, there was a delay of 3.8 days with every 100 m increase in altitude and, across all elevations, an advance of phenophases of 6 days per 1 °C increase in temperature. Temperature lapse rates assessed indirectly by phenology, as the quotient of altitudinal to temperature response coefficients, were higher than directly calculated from March to July mean temperatures, most likely due to snow effects. Furthermore, a significant difference in sensitivity to temperature change was found between different growth forms (herbs *versus* trees). Sensitivity was less pronounced in events occurring later in the season.

Our results show that species reactions will differ in magnitude during global warming. Consequently, impacts of shifts in the timing of phenological events on plant migration and plant-pollinator interactions due to rising temperatures should be considered at the species level.

Key words: Alps, growth forms, herbs, phenology, sensitivity, trees

III.2 INTRODUCTION

Global climate change affects some regions more than others. In the past 100 years annual mean temperatures increased by about 1.1 °C in the European Alps compared to a global average increase of 0.7 °C (Böhm *et al*. 2001; IPCC 2007a). In future it is expected that temperatures in the Alpine region will continue to rise faster than average, rainfall distribution is expected to change and extreme weather events, such as torrential rain and drought, are also predicted to significantly increase in frequency (IPCC 2007a). Due to these changes, alpine plant communities will experience, and have already experienced, negative impacts (*e.g*., Korner 1992; Grabherr *et al.* 1994; Sala *et al.* 2000; Erschbamer *et al.* 2009). Abiotic factors such as climate, are more important than biotic factors, especially at high altitudes, therefore, the effects of climate change on alpine vegetation are more pronounced (Korner & Miglietta 1994; Theurillat & Guisan 2001).

Phenology, the study of the timing of recurring natural events, is a tool for assessing climate change impacts on plant growth and development. Several studies have already documented the effect of global warming in inducing advances in leaf unfolding and flowering during recent decades in Europe (Menzel & Fabian 1999; Menzel *et al.* 2006) and North America (Schwartz & Reiter 2000). Several of these studies include data from a large latitudinal and longitudinal range (Chmielewski & Roetzer 2001; Menzel *et al.* 2006); but far fewer have considered altitudinal differences over a short latitudinal range (Migliavacca *et al.* 2008; Vitasse *et al.* 2009b; Ziello *et al.* 2009; Moser *et al.* 2010). However, altitudinal gradients naturally provide different temperature scenarios, because atmospheric temperature decreases by an average of 0.55 °C per 100 m change in altitude, in summer by about 0.7 °C and in winter by about 0.4 °C (Ozenda & Bormann 1991). Thus, results from altitudinal studies can improve the understanding of changes in plant development under different temperature conditions. They can be particularly useful to estimate impacts of shifts in phenology on plant-pollinator interactions, which are expected to be disrupted (Memmott *et al.* 2007), or on plant community composition, which will change due to migration of different species in response to global warming (Grabherr *et al*. 1994; Parolo & Rossi 2008). Furthermore, studies along an altitudinal gradient within a short latitudinal range can reduce photoperiod effects that also influence plant phenology (*e.g*., Partanen *et al.* 1998; Keller & Korner 2003; Korner & Basler 2010).

Shifts in the phenology of tree species due to altitudinal change are well documented, showing *e.g*., a delay of 3 days 100 m^{-1} increase in elevation for leaf unfolding of *Acer pseudoplatanus* L. or *Fraxinus excelsior* L. (Vitasse *et al.* 2009b). However, altitudinal studies focusing on herbaceous species are rare and, as far as we are aware have not

examined any of the species observed in this study. However, for some herbaceous species, such as *Oxalis acetosella* L. and *Anemone nemorosa* L., the response to temperature change has been examined, showing an advance of different phenological events of 3-4 d $°C^{-1}$ (Sparks *et al.* 2009).

The aims of this work were to (i) investigate how temperature affects key phenological events of a range of plant species along an altitudinal gradient; (ii) determine the sensitivity of woody plants and herbs to temperature change; (iii) investigate if the length of the flowering or leafing period changes with altitude; and (iv) test if phenological events later in the year are less influenced by temperature than phenophases early in the year.

III.3 MATERIAL AND METHODS

III.3.1 STUDY AREA

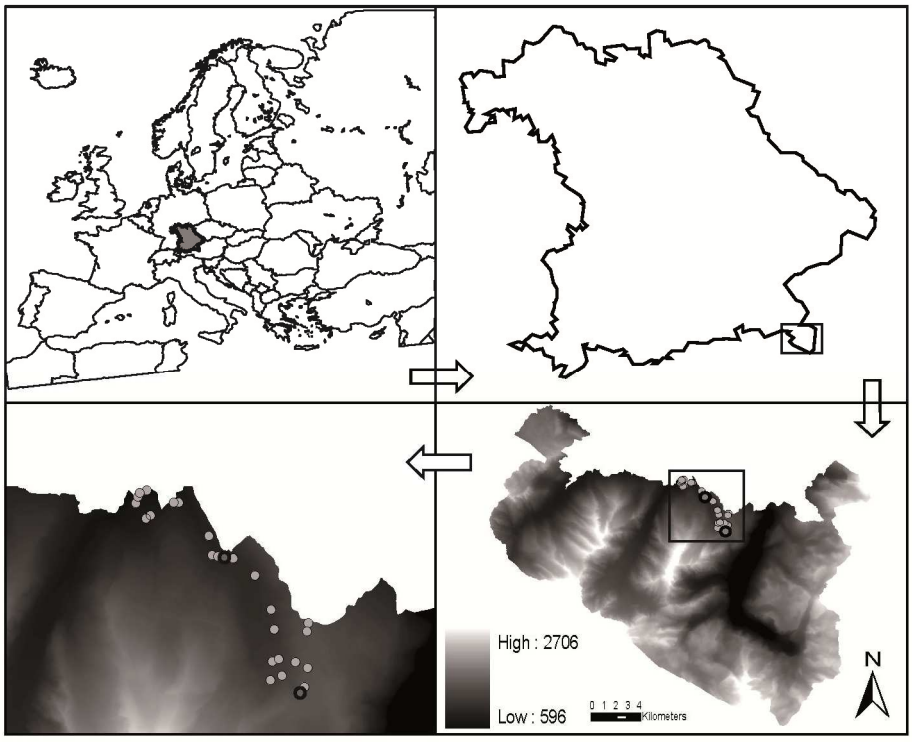

Figure III.1 Geographical position of the Berchtesgaden National Park in Bavaria/Germany and location of the observations sites (light grey) including two International Phenological Gardens (IPG, darker grey with thick black circles).

The study area was in the northern part of the Berchtesgaden National Park, which is the only German National Park in the Alps and is characterized by a large altitudinal range within a small area (StMUG 2001). Our altitudinal transect included 22 observation sites ranging from 680 m to 1390 m (Fig. III.1). Sites were not equally distributed along the

gradient but selected for accessibility, aspect and homogeneity (Schermaier & Hlousek 1994). However, in spite of these preconditions, the aspect of some sites differed. Most sites (15) faced north, three sites faced south and four sites west; two sites were on flat ground. Additionally, tree species in two International Phenological Gardens (IPG) at 950 and 1425 m were included in the observations. Due to snow removal alongside a forest road, ten sites received additional snow pack during winter and spring.

The mean annual temperature (calculated as the average of daily mean temperatures from 1994 to 2007; for more details see Meteorological data) in this study area was about 8° C at 600 m and about 5° C at 1400 m a.s.l. The lapse rate of atmospheric temperature (vertical decrease in temperature with elevation) was about 0.45 °C 100 m^{-1} elevation (mean from March to August; Konnert 2004). Growing season lengths (derived from days above a 10° C threshold) varied from 5 months at 600 m to 2 months at 1400 m. The annual sum of precipitation varied between 1650 mm at 600 m and 1825 mm at 1400 m (Konnert 2004).

III.3.2 SPECIES AND PHENOLOGICAL OBSERVATIONS

Along the altitudinal gradient, the leaf and flower development of 21 different species was monitored from 1994 (IPG sites) or 1995 (other sites) to 2007. The selected species should flower only once in the vegetation period. Due to restrictions in their natural distribution, altitudinal limits differ greatly between species. The average altitudinal range in this study is about 580 m, but can vary from 255 for *Aesculus hippocastanum* L. to 745 m for *Picea abies* (L.) H.Karst. (Table III.1). Among the 21 chosen species, there were ten woody (six deciduous trees, one evergreen tree, and three shrubs) and 11 herbaceous species.

Phenological observations of leaf and flower development were conducted once or twice weekly from March to July using the key provided by Ellenberg (1974). At each sampling date the phenological stage of the majority of individuals of herbaceous species was recorded. In the case of woody species the main phenological stage of the tree or shrub was recorded. The timing of the onset of phenophases of monitored stages was defined as the sampling date when the stage was first observed. Due to the observation method and interval, not all phenological stages could be monitored in each season. Thus, the timing of the onset of phenophases for missing stages was estimated by linear interpolation between onsets of previous and consecutive stages.

In this study we only focused on five key phenological events: beginning of leaf unfolding (LU), leaves fully expanded (LE), beginning of flowering (BF), full flowering (FF) and end of flowering (EF) (Table III.1). Leaf development and flowering periods were determined as the number of days between LU and LE or BF and EF, respectively.

Table III.1 Phenophases, altitudinal ranges (maximum amplitude of elevation) and adjusted mean dates (determined by two way ANOVA) of speciesNoS = number of sites; NoY = number of years; AMD = adjusted mean dates in days of the year of the different phenophases (± SE). ΔT is the difference in March-July temperature of the lowest and highest site (averaged from 1994-2007). Species altitudinal ranges and temperature differences match for all phenophases except for *Primula elatior,* which differs in altitudinal range for leafing and flowering. LU: beginning of leaf unfolding, LE: leaves fully expanded, BF*:* beginning of flowering, FF: full flowering, EF: end of flowering.

	LU	LE	BF	FF	EF	Altitudinal ranges [low-high] (m)	ΔT (°C)
Acer pseudoplatanus L. (Ap)							
NoS	10	11				710 [680-1390]	3.61
NoY	13	13					
AMD	**128**	**163**					
	(±1.7)	(±1.9)					
Aesculus hippocastanum L. (Ah)							
NoS	4	4				255 [695-950]	1.30
NoY	14	14					
AMD	**118**	**157**					
	(±0.9)	(±2.1)					
Alnus incana (L.) Moench (Ai)							
NoS	14	14				680 [680-1360]	3.45
NoY	13	13					
AMD	**119**	**158**					
	(±1.7)	(±1.3)					
Anemone nemorosa **L. (An)**							
NoS	10	10	10	10	11	470 [680-1150]	2.39
NoY	9	12	11	12	12		
AMD	**105**	**144**	**109**	**118**	**138**		
	(±3.7)	(±2.1)	(±3.4)	(±3.1)	(±3.1)		
Aposeris foetida (L.) Less. (Af)							
NoS	14	14	14	14	14	700 [680-1380]	3.56
NoY	13	13	13	13	13		
AMD	**115**	**162**	**141**	**152**	**172**		
	(±2.6)	(±2.1)	(±2.3)	(±2.2)	(±2.0)		
Daphne mezereum L. (Dm)							
NoS	9	9	9	9	9	510 [680-1190]	2.59
NoY	13	13	13	13	13		
AMD	**117**	**153**	**107**	**116**	**132**		
	(±3.9)	(±2.4)	(±4.5)	(±3.9)	(±3.7)		
Fragaria vesca L. (Fv)							
NoS	18	18	18	18	18	700 [680-1380]	3.53
NoY	13	13	13	13	13		
AMD	**114**	**162**	**136**	**151**	**172**		
	(±1.7)	(±1.9)	(±1.6)	(±1.7)	(±1.7)		
Fraxinus excelsior L. (Fe)							
NoS	5	5				280 [680-960]	1.42
NoY	13	13					
AMD	**129**	**162**					
	(±1.4)	(±1.2)					

	LU	LE	BF	FF	EF	Altitudinal ranges [low-high] (m)	ΔT (°C)
Helleborus niger L. (Hn)							
NoS	6	6		6	6	580 [780-1360]	2.95
NoY	9	9		9	9		
AMD	**127**	**155**		**101**	**123**		
	(±2.1)	(±2.4)		(±4.4)	(±2.4)		
Larix decidua Mill. (Ld)							
NoS	16	15				695 [685-1380]	3.53
NoY	13	13					
AMD	**119**	**163**					
	(±1.9)	(±1.6)					
Mercurialis perennis L. (Mp)							
NoS	17	16	16	16	16	680 [680-1360]	3.45
NoY	13	13	13	13	13		
AMD	**109**	**151**	**116**	**128**	**142**		
	(±2.6)	(±2.2)	(±1.8)	(±1.8)	(±2.4)		
Oxalis acetosella L. (Oa)							
NoS	11	12	11	12	12	680 [680-1360]	3.45
NoY	13	13	13	13	13		
AMD	**114**	**149**	**123**	**131**	**145**		
	(±3.9)	(±2.7)	(±3.1)	(±2.9)	(±3.3)		
Paris quadrifolia L. (Pq)							
NoS	12	12	12	12	12	700 [680-1380]	3.56
NoY	13	13	13	13	13		
AMD	**124**	**164**	**140**	**150**	**171**		
	(±2.2)	(±2.3)	(±2.2)	(±2.8)	(±2.1)		
Petasites albus L. (Pa)							
NoS	10	10	10	10	10	685 [695-1380]	3.48
NoY	13	13	13	13	13		
AMD	**122**	**172**	**113**	**122**	**138**		
	(±3.1)	(±1.8)	(±7.3)	(±3.2)	(±2.6)		
Picea abies (L.) H.Karst (Pia)							
NoS	20	20				745 [680-1425]	3.78
NoY	14	14					
AMD	**139**	**174**					
	(±2.0)	(±1.7)					
Primula elatior Hill. (Pe)							
NoS	14	15	15	15	15	700 [680-1380] (leafing)	3.56
NoY	13	13	13	13	13	600 [680-1280] (flowering)	3.05
AMD	**107**	**143**	**108**	**119**	**137**		
	(±2.2)	(±1.6)	(±1.7)	(±1.7)	(±1.6)		
Sambucus racemosa L. (Sr)							
NoS	5	5	5	5	5	320 [1060-1380]	1.63
NoY	13	13	13	13	13		
AMD	**121**	**170**	**138**	**148**	**161**		
	(±3.3)	(±1.8)	(±4.2)	(±5.1)	(±5.6)		
Sorbus aucuparia L. (Sa)							
NoS	10	10	10	10	10	430 [960-1390]	2.18
NoY	13	13	13	13	13		
AMD	**126**	**173**	**146**	**159**	**172**		
	(±2.1)	(±1.8)	(±2.8)	(±2.9)	(±1.9)		

	LU	LE	BF	FF	EF	Altitudinal ranges [low-high] (m)	ΔT (°C)
Tussilago farfara L. (Tf)							
NoS	18	18	18	18	18	695 [685-1380]	3.53
NoY	13	13	13	13	13		
AMD	**133**	**174**	**105**	**118**	**138**		
	(±1.9)	(±1.1)	(±2.6)	(±2.3)	(±2.5)		
Vaccinium myrtillus L. (Vm)							
NoS	10	11	9	10	11	700 [680-1380]	3.56
NoY	13	13	13	13	13		
AMD	**123**	**157**	**131**	**140**	**155**		
	(±2.8)	(±2.8)	(±2.5)	(±2.7)	(±2.9)		
Valeriana tripteris L. (Vt)							
NoS	12	11	10	11	10	695 [685-1380]	3.53
NoY	13	13	13	13	13		
AMD	**121** (±2.1)	**161** (±2.4)	**130** (±2.2)	**143** (±2.6)	**165** (±2.1)		

III.3.3 METEOROLOGICAL DATA

Meteorological data were obtained from two meteorological stations. One station (Kühroint) was located at 1415 m close to the International Phenological Garden, the second station (Ramsau) was 3 km west of the study area at 655 m. Mean temperature at each station was calculated as the mean daily temperature from March to July over the period 1994 to 2007, which corresponds to the observation period of the phenological study. From these mean temperatures a lapse rate between the two stations was determined for the same time period to define the exact temperature decreases per 100 m increase in altitude for this transect. In 2005 the manual station at Kühroint was replaced by an automatic one. Unfortunately, no data were available from the Ramsau station in 2006. Missing data due to technical faults at the weather stations were gap-filled with the help of linear interpolation based on data from the other weather station ($R^2 > 0.88$).

III.3.4 STATISTICAL ANALYSES

Overall mean dates for every key phenophase for each species and observation site were estimated by two-way analysis of variance (ANOVA, factors year and site) for each species/phenophase. This adjustment was made to compensate for missing data in an influentially cool or warm year. Linear regression analyses were conducted on these adjusted means to test the effect on phenophases of altitude (regression coefficients standardised to days 100 m^{-1}) and mean temperatures (regression coefficients in days $°C^{-1}$) for each species. Mean temperatures were calculated from the temperature data of the two calendar months preceding the mean onset date. However, if the mean onset date was after the 15th of the respective month, the mean temperature was calculated over the

month of onset and the previous month. In the altitudinal model the influence of additional snowpack and westerly exposed sites were considered as further factors because preliminary tests indicated their influence on the onset of phenophases. Both factors were included in models as binary categorical variables (snow: no/yes, westerly aspect: no/yes). We expected an advance in timing of phenological events on westerly exposed sites and a delay on sites with additional snowpack.

Temperature lapse rates were assessed by phenology as the quotient of altitudinal gradient to temperature response. To test if temperature and altitudinal coefficients varied with the mean timing of the phenophases, weighted linear regression was carried out of regression coefficients on mean date. We weighted the dependent variable in dependence on its residuals. A *t*-test was used to test whether the response to temperature change differed between woody plants (trees and shrubs) and herbaceous species. For the analysis we used altitudinal and temperature response coefficients. Due to missing flowering data for tree species, only the LU and LE phenophases were included in these analyses.

All statistical analyses were performed with SPSS 19.0 (SPSS, Chicago, IL, USA, 2010).

III.4 RESULTS

Mean annual temperatures in the observation period (March-July) ranged from 10.3 °C (in 1996) to 13.1 °C (in 2007) for the Ramsau station and from 6.5 °C (in 2004) to 9.1 °C (in 2003) for the Kühroint station. Averaged over all species, phenophases were earliest in 2007 and latest in 2004.

III.4.1 LEAF DEVELOPMENT AND FLOWERING PERIOD

Averaged over all altitudes and years, the earliest leaf unfolding of our species was for *An. nemorosa* (15 April, DOY 105) and the latest was *Pi. abies* (19 May, DOY 139, Table III.1). Leaf development was fastest for *Helleborus niger* L. (28 days) and slowest for *Petasites albus* L. (50 days, Fig. III.2a). Flowering began with *Tussilago farfara* L. (15 April, DOY 105) and ended with *Sorbus aucuparia* L. (26 May, DOY 146, Table III.1). Full flowering occurred first for *H. niger* (11 April, DOY 101) and last for *S. aucuparia* (08 June, DOY 159). The shortest flowering period was for *Vaccinium myrtillus* L. and *Sambucus racemosa* L. (22 days) while *Fragaria vesca* L. was longest (36 days, Fig. III.2b). The average period of leaf unfolding (40 days) was about 10 days longer than the average flowering period (29 days). *Daphne mezereum* L., *T. farfara* and *Pe. albus* develop flowers before leaves. On average, *Primula elatior* Hill. started to flower (18 April, DOY 108) and unfold its leaves (17 April, DOY 107) more or less simultaneously. All other species unfold their leaves before they started to flower (Fig. III.2).

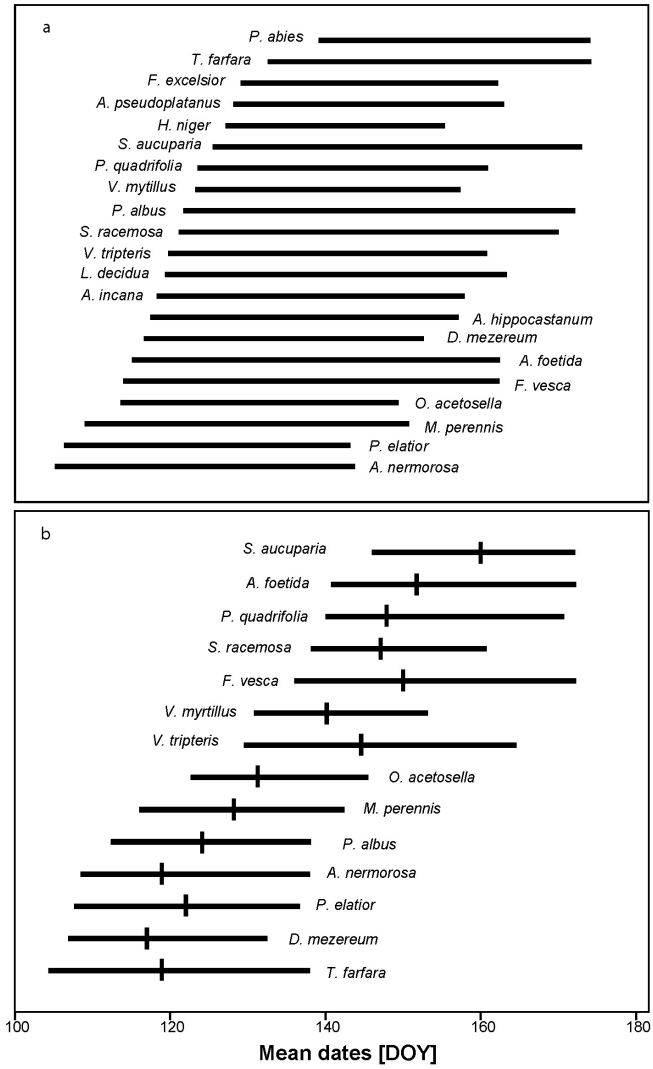

Figure III.2 Mean leaf development and flowering periods. a) leaf development (beginning of leaf unfolding to leaves full expanded) and b) flowering (beginning of flowering to end of flowering) period of studied species in days. Horizontal lines show full flowering dates.

III.4.2 SHIFTS IN PHENOLOGY DUE TO ALTITUDE

The mean temperature of March to July decreased by 0.51 °C for every 100 m increase in elevation on the observed transect. Differences in mean temperatures (March-July) along species' altitudinal ranges thus varied from 1.3 °C for *Ae. hippocastanum* to 3.8 °C for *Pi. abies* (Table III.1), reflecting restrictions in altitudinal range.

The altitudinal model showed that about 50% of all phenological events were significantly influenced only by altitude; neither snow nor aspect had a significant influence. For a further 42% significant models were achieved either with altitude and aspect, altitude and snow pack or aspect alone. The tested variables failed to produce significant models for only 8% of all phenophases: LU of *Ae. hippocastanum*, *H. niger* and *S. racemosa*; LE, BF and FF of

H. niger, and EF of *Pr. elatior* and *S. racemosa* (Table III.2). Flowering phases of *An. nemorosa* were significantly influenced by all three variables (altitude, snow and aspect). The timing of the onset of LE, BF and EF of *S. racemosa* could only be significantly explained by aspect, with a westerly aspect leading to onset of these phenophases 8 to 25 days earlier (Table III.2).

Table III.2 Slopes of two linear regression analyses. First, between station mean dates and altitude, and second, between annual mean dates of five phenological key events and mean temperatures of the two preceding months. The altitudinal model also includes aspect and snow as additional factors. In brackets is the SE. Species-specific lapse rates were calculated as the ratio of altitude and temperature coefficients (numbers in bold both coefficients are significant). LU: beginning of leaf unfolding, LE: leaves fully expanded, BF: beginning of flowering, FF: full flowering, EF: end of flowering. *** P≤ 0.001, ** P≤ 0.01, * P≤ 0.05. # No variation was recorded in this variable for this event.

Phenophase	Regression coefficients				Lapse rate [°C/100m]
	Altitude [days/100m]	Aspect [days]	Snow [days]	Mean temperature [days/°C]	
Acer pseudoplatanus					
LU	1.7 ** (±0.4)	#	0.1 (±2.1)	-5.0*** (±1.0)	**-0.34**
LE	2.5*** (±0.2)	#	0.5 (±1.2)	-3.5(±2.2)	-0.71
Aesculus hippocastanum					
LU	1.2 (±0.4)	#	#	-1.7 (±0.9)	6.00
LE	3.2** (±0.2)	#	#	-0.2 (±0.6)	-1.88
Alnus incana					
LU	2.4** (±0.7)	-1.4 (±3.7)	2.9 (±2.3)	-6.5***(±1.5)	**-0.37**
LE	2.0*** (±0.4)	-0.9 (±1.9)	1.6 (±1.2)	-3.6(±2.5)	-0.56
Anemone nemorosa					
LU	6.9*** (±0.4)	-9.5* (±0.4)	4.9 (±0.4)	-4.2(±3.3)	-1.64
LE	4.0** (±0.4)	-7.3* (±0.4)	1.2 (±0.4)	-0.9(±2.3)	-4.44
BF	5.5*** (±0.4)	-12.0** (±0.4)	9.1** (±0.4)	-5.0(±2.3)	-1.10
FF	5.3** (±0.4)	-10.8* (±0.4)	7.1* (±0.4)	-4.2*(±1.6)	**-1.26**
EF	4.9** (±0.4)	-13.7* (±0.4)	10.3* (±0.4)	-3.4*(±1.4)	**-1.44**
Aposeris foetida					
LU	4.4 *** (±0.4)	13.0*** (±2.2)	0.5 (±1.7)	-3.9*(±1.6)	**-1.13**
LE	3.5 *** (±0.4)	-5.9* (±2.1)	2.5 (±1.6)	-0.6(±2.7)	-5.83
BF	3.7*** (±0.6)	-12.41** (±3.1)	1.8 (±2.3)	-5.1**(±1.6)	**-0.73**
FF	3.6*** (±0.5)	-11.1** (±2.6	3.8 (±2.0)	-4.2*(±1.6)	**-0.86**
EF	3.2*** (±0.5)	-7.3* (±2.7)	3.5 (±2.1)	-3.4***(±1.1)	**-0.94**
Daphne mezereum					
LU	5.6** (±0.9)	-7.5 (±5.5)	-4.4 (±3.4)	-5.9*(±2.5)	**-0.95**
LE	3.6** (±0.5)	-3.9 (±2.9)	-2.0 (±1.8)	-4.5*(±2.0)	**-0.80**
BF	6.5** (±1.0)	-7.7 (±5.9)	-5.8 (±3.6)	-8.0*(±3.2)	**-0.81**
FF	5.4** (±1.1)	-11.6 (±6.7)	-3.7 (±4.1)	-6.4**(±2.1)	**-0.84**
EF	4.8** (±1.1)	-14.0 (±6.6)	-5.0 (±4.1)	-6.4**(±2.1)	**-0.75**
Fragaria vesca					
LU	3.1*** (±0.4)	-5.8* (±2.1)	1.9 (±1.5)	-6.4(±3.1)	-0.48
LE	3.3*** (±0.4)	-3.7 (±2.1)	4.5* (±1.6)	-1.9(±2.8)	-1.74
BF	1.5* (±0.7)	-6.0 (±3.8)	4.6 (±2.8)	-0.1(±1.7)	-20.00
FF	2.4** (±0.7)	-8.0* (±3.7)	3.4 (±2.7)	0.0(±1.4)	
EF	2.7** (±0.4)	-2.7 (±2.1)	5.0** (±1.5)	-1.0 (±1.1)	-2.82

Phenophase	Regression coefficients				Lapse rate [°C/100m]
	Altitude [days/100m]	Aspect [days]	Snow [days]	Mean temperature [days/°C]	
Fraxinus excelsior					
LU	3.1* (±0.6)	#	0.4 (±1.7)	-3.6* (±1.3)	**-0.86**
LE	2.4* (±0.6)	#	-1.5 (±1.5)	-2.1 (±2.4)	-1.14
Helleborus niger					
LU	2.5 (±0.8)	-4.9 (±3.1)	2.6 (±2.6)	-7.0 (±0.4)	-0.36
LE	1.1 (±1.4)	-1.4 (±5.5)	7.0 (±4.6)	-2.2 (±0.4)	0.50
BF			Insufficient data		
FF	5.2 (±1.7)	-10.7 (±6.7)	5.0 (±6.7)	-4.9 (±0.4)	-1.06
EF	3.1* (±0.7)	-6.8 (±2.6)	2.5 (±2.2)	-6.9 (±0.4)	-0.45
Larix decidua					
LU	3.3*** (±0.5)	-5.3 (±2.7)	3.7 (±1.9)	-5.9*** (±1.5)	**-0.56**
LE	2.5*** (±0.3)	-2.6 (±2.1)	1.5 (±1.2)	-3.8 (±2.7)	-0.66
Mecurialis perennis					
LU	5.1*** (±0.6)	-11.8** (±3.7)	1.0 (±2.2)	-0.3 (±2.9)	18.89
LE	4.4*** (±0.4)	-8.9** (±2.3)	1.5 (±1.5)	-1.0 (±1.7)	4.23
BF	3.5*** (±0.5)	-9.4** (±2.7)	2.3 (±1.7)	-0.3 (±2.6)	-11.86
FF	3.7*** (±0.4)	-9.5** (±2.1)	0.8 (±1.3)	-0.2 (±3.0)	-21.51
EF	5.0*** (±0.4)	-12.5*** (±2.3)	1.1 (±1.5)	-2.6 (±2.5)	-1.92
Oxalis acetosella					
LU	6.1** (±1.3)	-12.4 (±9.6)	0.2 (±4.8)	-4.3 (±4.0)	-1.42
LE	5.0*** (±0.3)	-10.7** (±2.3)	2.8* (±1.2)	-2.4 (±2.5)	-2.08
BF	5.3*** (±0.8)	-20.0* (±6.1)	-1.6 (±3.1)	-7.3*** (±1.5)	-0.73
FF	5.1*** (±0.9)	-15.0* (±6.5)	1.4 (±3.2)	-7.2*** (±1.5)	-0.71
EF	6.2*** (±0.7)	-18.8** (±5.0)	4.5 (±2.5)	-4.4** (±1.5)	-1.41
Paris quadrifolia					
LU	3.1** (±0.6)	-5.5 (±4.3)	2.3 (±2.5)	-5.8*** (±1.4)	-0.53
LE	3.5** (±0.5)	-4.5 (±3.7)	1.3 (±2.1)	-1.3 (±2.6)	-2.69
BF	3.4*** (±0.4)	-4.9 (±2.9)	2.1 (±1.7)	-3.8*** (±1.0)	-0.89
FF	4.2*** (±0.5)	-7.6 (±4.1)	1.9 (±2.3)	-3.6*** (±0.9)	-1.17
EF	3.3*** (±0.3)	-2.8 (±2.7)	2.5 (±1.5)	-3.3 (±1.5)	-1.00
Petasites albus					
LU	3.8** (±1.0)	-12.1 (±5.7)	-0.6 (±4.1)	-5.3** (±1.7)	-0.72
LE	2.4** (±0.4)	-3.2 (±2.6)	1.9 (±1.9)	-4.0 (±2.6)	-0.60
BF	4.5* (±1.4)	-16.7 (±8.2)	-6.7 (±6.0)	-2.5 (±2.4)	-1.80
FF	3.7** (±0.9)	-12.9* (±5.3)	-3.0 (±3.8)	-3.3* (±1.4)	**-1.12**
EF	3.6*** (±0.5)	-12.4** (±2.6)	0.4 (±1.9)	-4.1* (±1.8)	**-0.88**
Picea abies					
LU	3.6*** (±0.4)	-5.9 (±0.4)	0.8 (±0.4)	-5.0** (±1.7)	-0.72
LE	3.1*** (±0.3)	-3.3 (±2.4)	4.1** (±1.4)	-5.0* (±1.8)	-0.62
Primula elatior					
LU	3.3* (±1.4)	-3.9 (±5.4)	6.2 (±3.3)	-5.5 (±2.8)	-0.60
LE	3.2*** (±0.6)	-1.5 (±2.6)	1.4 (±1.6)	-0.5 (±2.6)	-6.27
BF	3.3** (±0.9)	-5.3 (±3.6)	3.9 (±2.2)	-5.1 (±2.1)	-0.65
FF	2.6* (±0.9)	-0.7 (±3.7)	4.1 (±2.2)	-5.0*** (±1.3)	-0.52
EF	2.1 (±0.1)	-0.1 (±4.0)	4.3 (±2.4)	-1.7 (±1.4)	-1.24

Phenophase	Regression coefficients				Lapse rate [°C/100m]
	Altitude [days/100m]	Aspect [days]	Snow [days]	Mean temperature [days/°C]	
Sambucus racemosa					
LU	2.0 (±1.0)	-11.4 (±3.0)	#	-8.4** (±2.4)	-0.24
LE	0.3 (±0.2)	-8.5** (±0.7)	#	-4.8** (±1.6)	-0.06
BF	2.2 (±0.7)	-25.0** (±2.0)	#	-7.1*** (±1.6)	-0.31
FF	0.6 (±1.7)	-23.7* (±5.0)	#	-6.1** (±2.0)	-0.10
EF	4.9 (±4.4)	-11.9 (±13.1)	#	-7.5*** (±1.7)	-0.65
Sorbus aucuparia					
LU	2.6** (±0.4)	-0.6 (±2.5)	#	-5.3*** (±1.2)	-0.49
LE	2.2*** (±0.3)	-2.8 (±1.7)	#	-4.4* (±1.5)	-0.50
BF	3.6*** (±0.4)	0.8 (±2.3)	#	-4.2** (±1.3)	-0.86
FF	3.6*** (±0.5)	1.2 (±3.0)	#	-4.9*** (±0.8)	-0.73
EF	2.3** (±0.4)	-0.8 (±2.3)	#	-5.0*** (±1.3)	-0.46
Tussilago farfara					
LU	3.2*** (±0.6)	-4.1 (±3.7)	1.1 (±2.4)	-5.6** (±1.6)	-0.57
LE	1.8*** (±1.1)	0.4 (±0.4)	0.4 (±0.4)	-5.7** (±2.2)	-0.32
BF	4.8*** (±0.6)	-6.8 (±3.9)	2.8 (±2.6)	-7.1 (±3.9)	-0.68
FF	4.4*** (±0.4)	-7.5** (±2.3)	-0.5 (±1.5)	-5.1 (±2.5)	-0.86
EF	4.7*** (±0.6)	-13.6** (±3.9)	-0.1 (±2.6)	-5.0 (±2.3)	-0.94
Vaccinium myrtillus					
LU	3.2** (±0.8)	-9.6 (±5.9)	0.01 (±3.6)	-7.1*** (±1.7)	-0.45
LE	3.8*** (±0.6)	-10.9* (±3.3)	3.5 (±2.6)	-3.2 (±1.8)	-1.19
BF	2.4* (±0.7)	-11.7 (±5.0)	-0.5 (±3.4)	-8.8*** (±1.2)	-0.27
FF	3.2** (±0.7)	-8.9 (±4.1)	-3.7 (±3.4)	-6.1*** (±1.3)	-0.52
EF	3.6** (±3.4)	-2.4 (±5.1)	-0.4 (±3.9)	-5.7** (±1.7)	-0.63
Valeriana tripteris					
LU	3.0** (±0.7)	-7.4* (±3.1)	4.3(±3.0)	-8.1** (±2.6)	**-0.37**
LE	3.9*** (±0.6)	-4.0 (±2.7)	6.8*(±2.6)	-2.2 (±2.8)	-1.77
BF	3.3** (±0.9)	-8.7* (±3.5)	5.6(±3.0)	-9.0*** (±1.6)	**-0.37**
FF	4.0** (±0.9)	-5.9 (±3.6)	9.7*(±3.4)	-6.2*** (±1.2)	**-0.65**
EF	3.2** (±0.7)	-3.6 (±3.1)	5.7(±3.0)	-6.6*** (±1.0)	**-0.48**

Averaged over all phenophases and species a delay of 3.8 days 100 m^{-1} increase in altitude was detected. However, species differed greatly in their altitudinal response. The strongest shift of 7 days 100 m^{-1} was for LU of *An. nemorosa*. In contrast, the altitudinal response for BF of *Frag. vesca* was just 1.5 days 100 m^{-1}.

Very few species showed a significant change in the length of leaf development and flowering period (Table III.3). Including all species, 15 out of 21 showed a shorter leaf development period (-0.2 to -2.9 days 100 m^{-1}) and six species a longer period (0.3 to 2.0 days 100 m^{-1}). Flowering period was shorter for eight species (-0.2 to -1.9 days 100 m^{-1}) and longer for six species (1.0 to 4.1 days 100 m^{-1}; Table III.3).

Table III.3 Regression coefficients of leaf development and flowering period with altitude. L: leaf development period, F: flowering period. Numbers in bold are significant (P≤ 0.05).

	R^2	*P*	Regression coefficients [days/100m]
Acer pseudoplatanus			
L	0.70	**0.003**	0.8
Aesculus hippocastanum			
L	0.93	**0.034**	2.0
Alnus incana			
L	0.05	0.426	-0.3
Anemone nemorosa			
L	0.74	**0.001**	-2.9
F	0.08	0.419	-0.5
Aposeris foetida			
L	0.08	0.316	-0.4
F	0.01	0.697	-0.2
Daphne mezereum			
L	0.50	**0.033**	-1.9
F	0.60	**0.015**	-1.9
Fragaria vesca			
L	0.04	0.406	0.3
F	0.44	**0.003**	1.4
Fraxinus excelsior			
L	0.07	0.625	-0.5
Helleborus niger			
L	0.06	0.637	-0.4
Larix decidua			
L	0.11	0.224	-0.5
Mercurialis perennis			
L	0.20	0.082	-0.6
F	0.43	**0.006**	1.1
Oxalis acetosella			
L	0.14	0.256	-1.0
F	0.19	0.182	1.0
Paris quadrifolia			
L	0.10	0.310	0.5
F	0.01	0.773	-0.1
Petasites albus			
L	0.10	0.374	-0.8
F	0.12	0.335	-1.0
Picea abies			
L	0.11	0.151	-0.5
Primula elatior			
L	0.01	0.808	-0.2
F	0.06	0.368	-0.3
Sambucus racemosa			
L	0.83	**0.031**	-2.4
F	0.40	0.256	4.1
Sorbus aucuparia			
L	0.12	0.320	-0.4
F	0.72	**0.002**	-1.3

	R^2	*P*	Regression coefficients [days/100m]
Tussilago farfara			
L	0.28	**0.023**	-1.0
F	0.07	0.293	-0.6
Vaccinium myrtillus			
L	0.19	0.211	0.6
F	0.33	0.106	1.1
Valeriana tripteris			
L	0.13	0.276	0.8
F	0.55	**0.015**	1.1

III.4.3 SENSITIVITY TO TEMPERATURE

Temperature significantly advanced the timing of phenophases for 56% of all species and events (Table III.2). Few significant models were produced for phenophase LE. Phenophases LU and FF were mainly (~72%) influenced significantly by temperature of the preceding months. The timing of the onset of phenophases BF and EF could less often be explained significantly by temperature change (~62%). *Frag. vesca* and *M. perennis* showed no significant response to temperature change for any phenophases (Table III.2). The greatest sensitivity to temperature was for BF of *Val. tripteris* (-9 days $°C^{-1}$), and least for FF of *Paris quadrifolia* L. (-4 days $°C^{-1}$) (Table III.2). Averaged over all phenophases, *Val. tripteris* (-8 days $°C^{-1}$) was most sensitive to temperature change. *An. nemorosa*, *P. quadrifolia*, *Pe. albus*, *F. excelsior* and *Aposeris foetida* L. were least sensitive, averaging -4 days $°C^{-1}$. Across all species and phenological events the temperature response was -5.6 days $°C^{-1}$.

Weighted linear regression analyses showed that phenophases occurring later in the year were significantly less sensitive to altitudinal change and temperature than phenophases early in the year ($P< 0.001$, $R^2= 0.213$ and $P= 0.007$, $R^2= 0.084$, respectively; Fig. III.3). The length of flowering and leaf development was almost the same in warm and cold years (2007: 31 days/ 45 days, 2004: 32 days/ 46 days, respectively).

The *t*-tests revealed a stronger influence of temperature on herbs than on trees if altitudinal coefficients (means: 3.7 days 100 m^{-1} and 2.7 days 100 m^{-1} respectively) were used ($P= 0.001$; $R^2= 0.199$) but not if temperature response coefficients were included ($P= 0.054$; $R^2= 0.023$; means: -6.0 days $°C^{-1}$ and -4.8 days $°C^{-1}$). The timing of the onset of phenophases of woody plants (shrubs and trees) did not significantly differ from herbs if tested variables were either altitudinal ($P= 0.066$; $R^2= 0.137$; means: 3.7 days 100 m^{-1} and 2.9 days 100 m^{-1}) or temperature ($P= 0.371$; $R^2= 0.042$; means:-5.8 days $°C^{-1}$ and -5.2 days $°C^{-1}$) response coefficients.

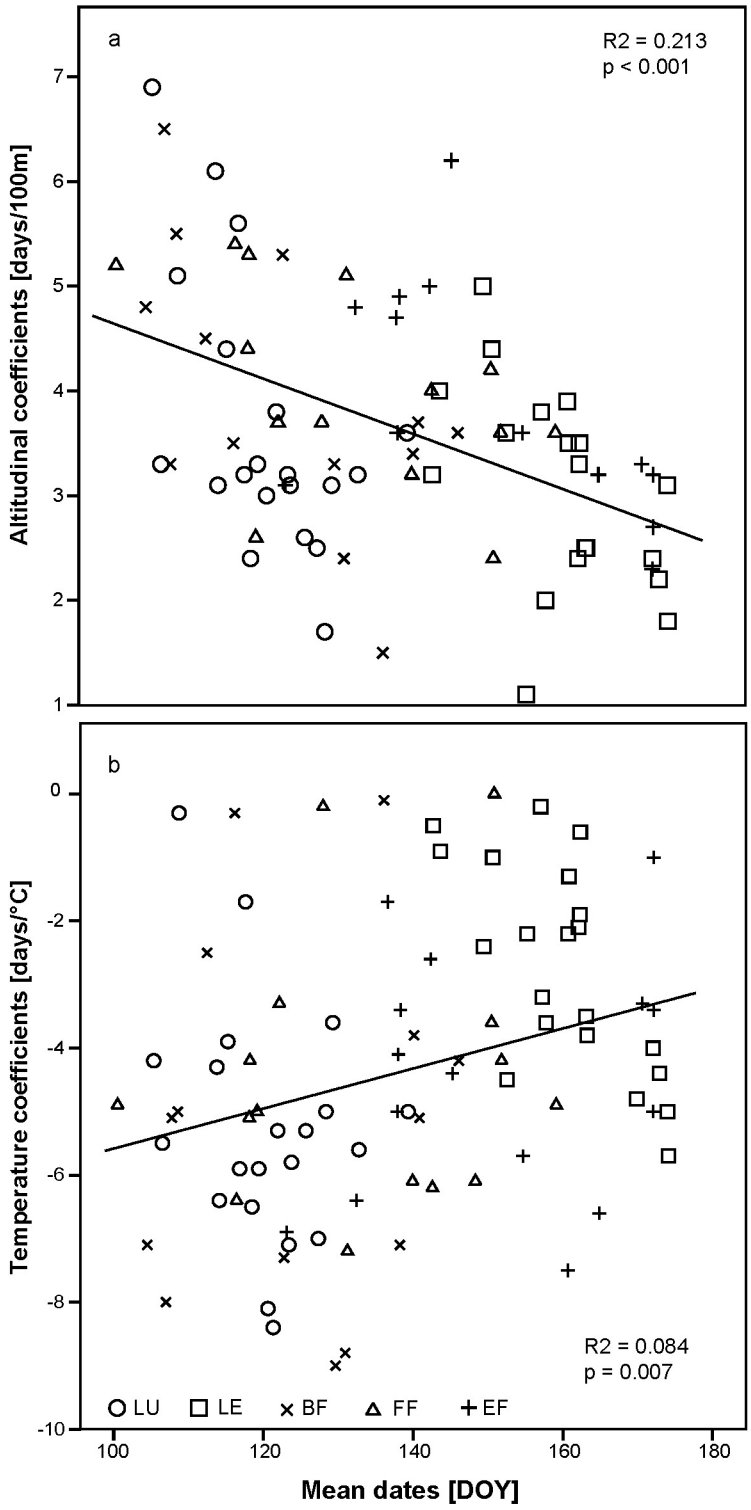

Figure III.3 Regression coefficients of timing of the onset of all species and phenophases on (a) altitude, and (b) temperature, plotted against mean onset date. LU: beginning of leaf unfolding, LE: leaves fully expanded, BF: beginning of flowering, FF: full flowering, EF: end of flowering.

III.4.4 INTEGRATION OF SENSITIVITY TO TEMPERATURE USING LAPSE RATES

Species-specific lapse rate (quotients including only significant coefficients of both temperature sensitivity and altitudinal gradients) were between -0.3 °C 100 m^{-1} for LE of *T. farfara* and -1.4 °C 100 m^{-1} for EF of *An. nemorosa*, the total range, including also non-significant results, was broader from -0.1 °C 100 m^{-1} for LE of *S. racemosa* to -21.5 °C 100 m^{-1} for FF of *M. perennis*. The average of the significant values was higher (-0.73 °C 100 m^{-1}) for all phenophases than the mean temperature lapse rate of March to July temperatures (-0.51 °C 100 m^{-1}; Table III.2; Fig. III.4).

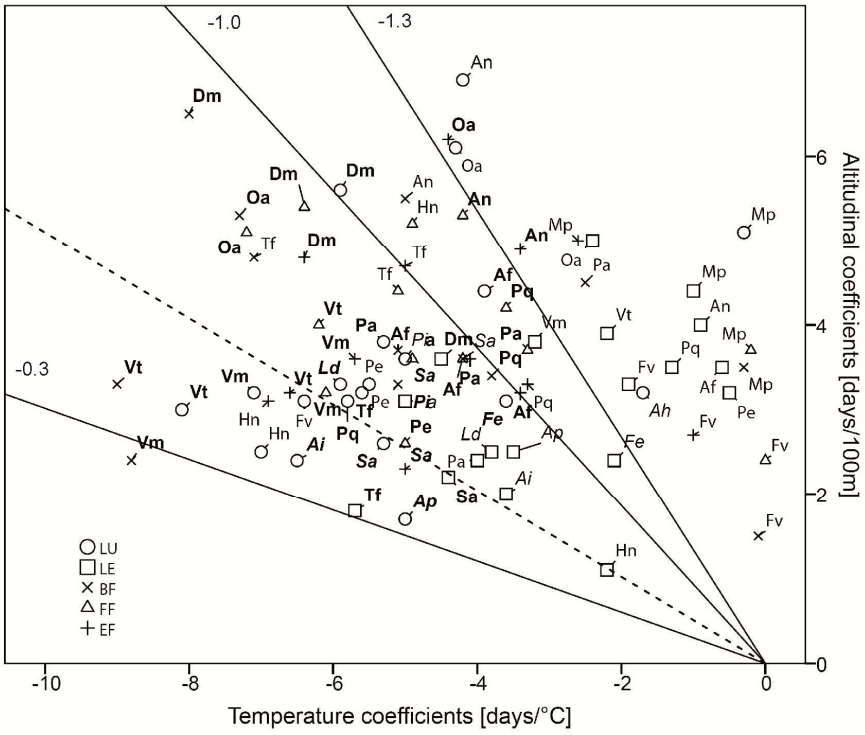

Figure III.4 Responses of events to altitude and temperature**.** Dashed diagonal line indicates the mean temperature lapse rate of March to July, other solid diagonal lines show lapse rates of -0.3, -1 and -1.3 (bottom to top) to better classify different species-specific lapse rates from Table III.2. LU: beginning of leaf unfolding, LE: leaves fully expanded, BF: beginning of flowering, FF: full flowering, EF: end of flowering. For abbreviations of species see Table III.1. Species in italics are tree species. For species in bold, both coefficients are significant.

III.5 DISCUSSION

As expected, this study clearly demonstrates the complex interrelationships between altitude and subsequent temperature changes, and the timing of plant phenology in the Bavarian Alps.

III.5.1 PHENOLOGICAL RESPONSE TO ALTITUDINAL CHANGE

Averaged over all species and phenophases there was a delay in the timing of plant phenology of 3.8 days 100 m^{-1}. This result is in accordance with Hopkin´s Law, which, based on phenological observations, states that for every 100 m increase in elevation, there was a 3.3 day delay in the onset of spring (Fitzjarrald *et al.* 2001). However, the delay in timing of the onset of phenophases varied strongly between species (1.7 to 6.9 days 100 m^{-1}); thus, Hopkin´s Law is not applicable to every species tested. For three tree species, Vitasse *et al.* (2009b) also found a delay of 1 day 100 m^{-1} for *Fagus sylvatica* L. and 3 days 100 m^{-1} for *A. pseudoplatanus* and *F. excelsior*. Other studies showed a delay of 2-4 days 100 m^{-1} altitudinal change for leaf unfolding of different tree species (Roetzer & Chmielewski 2001; Dittmar & Elling 2006; Richardson *et al.* 2006; Migliavacca *et al.* 2008; Moser *et al.* 2010). Most altitudinal studies refer to tree species; studies with herbaceous species are rare (*e.g.*, Alexander 2010). Ziello *et al.* (2009) showed, based on COST725 data for the Alpine region, a delay of BF for *Dactylis glomerata* L. of 2.8 days 100 m^{-1} and of BF for *Secale cereale* M.Bieb. of 3.2 days 100 m^{-1}, which is slightly less sensitive to altitudinal change than the average BF (3.8 days 100 m^{-1}) of all tested herbaceous species in our study.

For *S. racemosa*, three out of five phenophases (LE, BF, FF) were influenced more by aspect than by changes in altitude. Additional snow pack influenced the timing of the onset of phenophases of just a few species, mainly herbaceous species, such as *An. nemorosa*, *Frag. vesca*, *Pr. elatior* and *Val. tripteris*. Snowpack additions did not affect the entire site but only parts of it; thus, only plants that were located in such affected patches would experience delayed snowmelt.

III.5.2 PHENOLOGICAL RESPONSE TO TEMPERATURE

The sensitivity of species to temperature change has been frequently studied, however methodology differs in linking: (i) long-term records of phenology and temperature at one site, characterised by identical photoperiod; (ii) spatial network data of phenology and temperature including varying climate conditions and photoperiod; and (iii) altitudinal gradients of phenology and temperature, resulting in different climate conditions, but near-identical photoperiod as in the present study.

Sparks *et al.* (2009) found a temperature response of -7.6 d °C^{-1} for BF of *O. acetosella* in the UK; this is roughly consistent with the onset of BF for *O. acetosella* in the Berchtesgaden National Park. In Poland, plants showed a lower sensitivity to temperature change for BF and FF of *O. acetosella* (-4d °C^{-1} for both), however, *An. nemorosa* showed similar temperature responses (-5d °C^{-1} and -4d °C^{-1}, respectively; see Sparks *et al.* 2009). Tree

species such as *A. pseudoplatanus* or *F. excelsior* showed variation in the timing of onset for leaf unfolding of -5.4 d $°C^{-1}$ and -6.8 d $°C^{-1}$, respectively (Vitasse *et al.* 2009b). In the present study, *A. pseudoplatanus* showed a similar response (-5.0 days $°C^{-1}$) and *F. excelsior* was less sensitive to temperature change (-3.6 days $°C^{-1}$). Differences in temperature response of the same species at different observation sites might be caused by a non-linearity of temperature response over a wider temperature range (see Sparks *et al.* 2009; Sparks & Tryjanowski 2010), different amounts of winter chilling or photoperiodic differences (*e.g.*, Menzel *et al.* 2005; Rutishauser *et al.* 2009). In general, phenophase FF in this study was slightly more sensitive to temperature than found by Fitter *et al.* (1995) (-5 days $°C^{-1}$ and -4 days $°C^{-1}$, respectively).

III.5.3 PHENOLOGICAL RESPONSE TO OTHER FACTORS

For some species and phenophases mean temperatures of the two preceding months were not sufficient to significantly explain the variability of the timing of the onset of phenophases (Table III.2). Several modelling studies have shown that phenology is not simply related to mean temperatures (Schaber & Badeck 2003; Hanninen *et al.* 2007) and are strongly dependent on the chosen species (Vitasse *et al.* 2009b). It is suggested that leaf unfolding of *F. sylvatica* L., for example, is probably more triggered by photoperiod than temperature (Heide 1993a; Vitasse *et al.* 2009b). This is also true for onsets in some species in our study that also appeared to be influenced by factors other than temperature but which also varied with altitude such as snow, chilling requirements or photoperiod. Figure III.4 shows temperature and altitude responses for all studied species and phenophases. Species and phenophases that showed a strong response to altitude and a weak response to temperature are most likely influenced by snow. These are mainly herbaceous species and phases, which occur very early in the year, such as LU and BF of *An. nemorosa*, BF and FF of *T. farfara* or LU of *Pr. elatior* (Fig. III.4). In alpine and arctic ecosystems snowmelt and temperature after snowmelt mainly influence phenological development (Pop *et al.* 2000; Molau *et al.* 2005; Inouye 2008; Karlsen *et al.* 2008). An earlier snowmelt generally advances the timing of phenological events (Dunne *et al.* 2003), whereas greater snowpack leads to later snowmelt and timing of phenological events as well as less frost mortality (Inouye 2008). Unfortunately, the Berchtesgaden National Park started to measure snow height only in 2005. Thus, more data are needed to confirm the influence of snow on the timing of the onset of phenophases of these species.

Species and phenophases showing a strong altitudinal and temperature response are highly dependent on temperature (Fig. III.4). For example, *D. mezereum* shows early leafing and flowering, but as a shrub is less affected by snow. BF and FF of *O. acetosella* are also highly influenced by temperature; flowering of *O. acetosella* is later in the year than leafing. Thus,

leafing of this species is mainly influenced by snow whereas flowering is not affected. A weak response to temperature and altitude is mainly shown for tree species, phenophase LE, *Frag. vesca* and *M. perennis* (Fig. III.4). Tree species are most likely influenced by photoperiod or chilling requirements. Photoperiod mainly influences leaf senescence but several studies have shown that it can also affect spring leaf development (Caffarra & Donnelly 2011; Heide 1993b; Partanen *et al.* 1998; Worrall 1999). Accumulation of winter chilling influences tree bud burst (Caffarra & Donnelly 2011; Schaber & Badeck 2003); however, many authors have suggested that in alpine regions the winter chilling requirement can be neglected because it is easily fulfilled during winter (*e.g.*, Van Wijk *et al.* 2003; Chuine *et al.* 1999). However, in our study, elevation of sites is not extreme (~600-1400 m) thus winter chilling requirement is not necessarily fulfilled. Furthermore, recent studies showed that chilling temperatures could be insufficient in the 21st century for some tree species at lower altitudes (Morin *et al.* 2009; Vitasse *et al.* 2011). Thus, for these species chilling might be important.

Frag. vesca appears to be more influenced by photoperiod or chilling than temperature. Photoperiod might be especially relevant for herbs in warm years when the snow disappears earlier, because many species sensitive to photoperiod are not able to utilise periods of earlier snowmelt (Keller & Korner 2003; Migliavacca *et al.* 2011); *M. perennis* is more affected by snow and photoperiod. Strong temperature and weak altitudinal responses are especially shown by *V. myrtillus* and *Val. tripteris* (Fig. III.4); both of which flower and unfold their leaves in the middle of the observation period. Thus, these species are not influenced by snow and appear to be locally adapted.

Species-specific lapse rates show that the phenological shift with increasing altitude is generally related to temperature change but, as shown in this study, other factors can also influence phenology, thus these lapse rates can deviate from temperature lapse rates. In this study species-specific lapse rates are mainly higher than the temperature lapse rate from March to July temperatures (Table III.2, Fig. III.4). Higher lapse rates mean that species react more to altitude than can be explained through temperature change alone. Since most species and phenophases are influenced by other factors, such as snow higher lapse rates could be explained by those factors.

III.5.4 SENSITIVITY OF WOODY PLANTS AND HERBS

Differences in sensitivity to temperature change were significant between herbaceous species and trees using altitudinal coefficients but not if temperature coefficients were used. There were also no significant differences in onsets between herbs and woody species including shrubs. Thus, phenology of herbs was more sensitive to altitudinal change than

was that of trees. A lack of significant differences could be related to the small number of significant temperature response coefficients in the analysis (N = 9 for herbs and 12 for trees). Significant differences can be related to different morphological and/or physiological traits (Grime 2001). Iversen *et al.* (2009) showed that growth form predicts well variations in vegetative and flowering phenology and that it is generally a better predictor than topographical factors. Furthermore, these authors showed that vegetative phenological development such as recently burst leaves or fully developed leaves was fastest in forbs and slower in deciduous and evergreen shrubs (Iversen *et al.* 2009). Trees and shrubs are growth forms with a slow nutrient uptake and resistant tissues that require more energy for their development. These growth forms are expected to show slow and steady vegetative phenology. In contrast, species such as herbs use more energy for regrowth, which is based on a fast nutrient uptake (Grime 2001). Thus, it is suggested that species which are capable of fast regrowth in spring are more able to react to temperature change than species with slower growth. However, there are studies showing a phenological heterogeneity within life forms, either because within life forms resources are used have different timings or there may significant diversity of root morphology and leaf form (Golluscio *et al.* 2005).

III.5.5 PHENOLOGICAL RESPONSE TO TEMPERATURE OVER THE YEAR

Phenophases later in the year were significantly less sensitive to temperature change than phenophases early in the year; however, the relationship, indicated by R^2 (R^2= 0.084), was weak. A weak sensitivity to temperature of species flowering in May and June in regard to spring flowering species was also shown by Fitter & Fitter (2002) and Menzel *et al.* (2006), who found that because of high temperature variability in spring, the earlier the species, the stronger the sensitivity to temperature. The latest mean onset date of all tested phenophases in our study was June 11 (LE: DOY 162). Key phenological events in this study occurred between April and June and were correlated to temperatures of spring and early summer months (April to June). Thus, due to the lack of extreme early and late species or of phases occurring in late summer and autumn, dependencies between sensitivity to temperature and time of the year could not be demonstrated precisely.

III.5.6 LENGTH OF FLOWER AND LEAF DEVELOPMENT WITH ALTITUDE

Our study is most valuable for assessing variations in the length of flowering and leaf development, parameters that are rarely available from phenological networks. We found that the length of flowering and the leafing development changed significantly with altitude for some species. Flowering and leaf development period was mostly shorter for very early and very late flowering / leafing species. However, species that leafed and flowered in the middle of the observation period had a longer flowering / leafing period at higher altitudes.

Flowering and leafing early in the year is subject to the danger of late frost damage (*e.g.*, Weiser 1970; Rigby & Porporato 2008). Late flowering / leafing species need to finish their reproductive cycle before the first frost event of the next winter season occurs. Thus, in both cases an extended flowering / leafing period should be avoided. In contrast, an extension of the flowering and leafing period is unlikely to have effects on reproduction and growth for species flowering and leafing in the middle of the observation period. Length of flowering and leaf growth was similar in cold and warm years. Tyler (2001) found that the length of flowering period is little influenced by temperature because the timing of the onset of both critical phenophases (BF and EF) advances due to temperature increases; thus, the total length is not affected.

III.6 CONCLUSION

Our results suggest that species will react to global climate change but the magnitudes of these responses will differ. Most species showed a delay in the timing of phenophases with an increase in altitude and an advance with increase in temperature. Trees were less sensitive to temperature change than herbs, thus their reaction to climate change will be less pronounced. The length of flowering period and leaf development is little influenced by temperature change, and phenological events later in the year are less sensitive to temperature change. However, a large shift in the timing of the onset of phenophases such as in *Val. tripteris*, *V. myrtillus* or *S. racemosa* might potentially disrupt the temporal overlap between pollinators and host plants (Memmott *et al.* 2007). It is known that climate change can cause an upward migration in several alpine plant species (*e.g.*, Grabherr *et al.* 1994; Parolo & Rossi 2008); in a further study it would be interesting to test whether species that are more sensitive to temperature change are able to respond faster and migrate higher upslope than those that are less sensitive to warming.

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IV PHENOLOGICAL RESPONSE OF GRASSLAND SPECIES TO MANIPULATIVE SNOWMELT AND DROUGHT ALONG AN ALTITUDINAL GRADIENT

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IV.1 ABSTRACT

Alpine plant communities are assumed to be more vulnerable to impacts of global change than other ecosystems. It is predicted that the number of extreme weather events such as drought will increase and higher temperatures will lead to advanced snowmelt dates. The aim of this study was to determine the impacts of climate change scenarios, simulated by three different treatments (advanced or delayed snowmelt and drought) on flower phenology with a focus on impact variations with altitude. In 2010, flower phenology of 10 different grassland species, spread over 600 to 2000 m a.s.l., were observed in the Berchtesgaden National Park, Germany.

The study showed that there were high dependencies between flower phenology and altitude, however there were few effects of the treatments on flowering. The effects of advanced snowmelt were significantly greater on higher than on lower sites, but no significant difference in treatment effects was found between lower and higher altitudes for the other treatments. Furthermore, the response of flower phenology to temperature declined over the season and the length of flowering duration was largely not influenced by treatments.

The response to the examined treatments was highly species-specific and the effect of advanced snowmelt was stronger at higher altitudes possibly as response to differences in treatment intensity over the gradient. Consequently, shifts in the date of snowmelt due to global warming will affect species more at higher than at lower altitudes since changes will be more pronounced with increasing altitude.

Key words: Advanced snowmelt, Alps, BBCH, climate change, delayed snowmelt, flowering

IV.2 INTRODUCTION

In the past 100 years global annual mean temperatures increased by about 0.7 °C (IPCC 2007a), however, some regions were more affected by climate change than others. For the European Alps a much stronger temperature increase of about 2 °C was detected (Auer 2007). In the future, it is predicted that temperature will further rise, that rainfall distribution will change and that extreme weather events, such as torrential rain and drought will significantly increase in frequency (IPCC 2007a). Furthermore, a general reduction in snow cover duration will be caused by warmer temperatures, because the zero-degree isotherm will be displaced to higher altitudes (Beniston 2003; Laghari *et al.* 2012). Climate change scenarios for future snow conditions are rather vague. An increase in heavy snowfall events in winter may therefore also lead to a prolongation of snow cover duration.

Due to a changing environment, alpine plant communities will experience, and have already experienced, negative impacts (*e.g.*, Korner 1992; Grabherr *et al.* 1994; Sala *et al.* 2000; Erschbamer *et al.* 2009). Effects of climate change on alpine vegetation will be especially pronounced at high altitudes since abiotic factors such as climate prevail over biotic factors in those regions (Korner & Miglietta 1994, Theurillat & Guisan 2001).

Phenology, the study of the timing of recurring natural events, is a tool for assessing climate change impacts on plant growth and development. Several studies showed that the most important factors for plant development in alpine areas are temperature, date of snowmelt and photoperiod (*e.g.*, Blionis *et al.* 2001; Price & Waser 1998; Keller & Korner 2003). However, in the future, drought might also play an important role in the development of plants in the Alps due to an increasing probability of the occurrence of extreme weather events.

Shifts in plant phenology due to warmer temperatures have already been widely documented by analysing long-term datasets (*e.g.*, Sparks *et al.* 2000; Schwartz & Reiter 2000; Abu-Asab *et al.* 2001; Fitter & Fitter 2002; Menzel *et al.* 2005; Menzel *et al.* 2006) or have been confirmed by experimental studies (Marion *et al.* 1997; Hollister & Webber 2000; Kudernatsch *et al.* 2008; De Frenne *et al.* 2010). Higher temperatures mainly advance plant phenology (*e.g.*, Sparks *et al.* 2000; Menzel *et al.* 2006; Kudernatsch *et al.* 2008), which increases the risk of late frost damage in spring (Inouye 2000; Wipf *et al*. 2009) and may cause shifts in plant community composition due to die off (Molau 1997). Furthermore, changes in plant flowering patterns can cause an overlap of the flowering times of different species which, in early summer, can lead to greater competitive pressure, because pollinator activity is very low at this time of year (Molau 1997).

In general, a prolongation in snow cover duration delays plant phenology (Weaver & Collins 1977; Torp *et al.* 2010; Cooper *et al.* 2011) whereas a shortening of snow cover duration advances the timing of plant development (*e.g.*, Price & Waser 1998; Dunne *et al.* 2003; Inouye *et al.* 2003; Wipf *et al.* 2009; Lambert *et al.* 2010; Wipf 2010; Chen *et al.* 2011). However, phenological responses are highly species-specific and differ with functional groups (Wipf & Rixen 2010). An advanced snowmelt could potentially increase plant fitness by prolonging the growth period and hence resource allocation (Galen & Stanton 1993; Stinson 2004), however, an earlier start of flowering also increases the risk of late frost damage in spring.

Plant responses to drought are not consistent. Jentsch *et al*. (2009) showed an advance of mid-flowering date by 4 days after a drought event, whereas Bloor *et al.* (2010) and Bernal *et al.* (2011) did not detect a significant effect of drought on grasses or shrub species. In contrast, a delay in flowering phenology under dry conditions was reported for Mediterranean plants (Penuelas *et al.* 2004; Llorens & Penuelas 2005; Prieto *et al.* 2008; Miranda *et al.* 2009).

In general, there have been several studies dealing with the impacts of a changing abiotic environment (shifts in the date of snowmelt or the occurrence of drought) on plant phenology. However, as far as we know, there have been only a few studies combining manipulative experiments with an altitudinal gradient (but see Dunne *et al.* 2003; Stinson 2004) to assess whether impacts due to climate change differ between lower and higher altitudes. Altitudinal gradients naturally provide different temperature scenarios, because air temperature decreases by 0.54 °C to 0.58 °C per 100 m increase in altitude (Rolland 2003). Thus, this study not only focuses on treatment effects but also combines temperature changes which are indirectly derived from altitudinal change. Consequently, the aim of this study was to test whether shifts in the date of snowmelt or drought events affect (i) the timing and (ii) the length of flowering phenology of different grassland species. Furthermore we test if those impacts change with (iii) elevation or (iv) season.

IV.3 MATERIALS AND METHODS

IV.3.1 STUDY SITE AND EXPERIMENTAL DESIGN

The study area was located in the northern part of the Berchtesgaden National Park, which is the only German national park in the Alps and is characterized by a large altitudinal range within a small area (StMUG 2001).

Observation sites (11) were located along two valleys in the national park and ranged from ca. 800 m to ca. 2000 m a.s.l. To ensure a larger altitudinal gradient three sites below 800 m beyond the borders of the park were added, starting at ca. 600 m. One other site outside the two valleys was also included to ensure a site at ca. every 250 m altitude difference. Thus, observations were conducted at a total of 15 different sites. Aspects of sites were different, most sites (8) faced north, three faced west, three south and one was on flat ground.

Annual mean temperature in the park ranges between -2 °C and 7 °C, annual mean precipitation is 1500-2600 mm depending on altitude (StMUG 2001). For sites below 1000 m a.s.l. maximum snow cover is reached in February at a mean depth of about 50 cm. Sites over 1000 m have their maximum snow cover in March, ranging between 3 m and 5 m depth at highest altitudes (StMUG 2001).

The lapse rate of air temperature (vertical decrease in temperature with elevation) was about 0.45 °C 100 m^{-1} elevation (mean from March to August; Konnert 2004). Growing season lengths (derived from days above a 10 °C threshold) varied from 5 months at 600 m to ca. 1 month at 2000 m (Konnert 2004).

Experimental plots were established at each of the 15 study sites along the entire altitudinal gradient, consisting of three different treatments and a control, each plot sized 4 m x 4 m. Plots were contained within a 10 m x 10 m square, arranged in a 2 x 2 array. Treatments were the simulation of advanced and delayed snowmelt as well as a drought event.

IV.3.2 ADVANCED AND DELAYED SNOWMELT

Advanced and delayed snowmelt was simulated by shovelling snow from advanced snowmelt plots onto delayed snowmelt plots until only a thin snow layer was left on the former, thus the vegetation on the advanced snowmelt plots was not disturbed. Shovelling took place between the end of February and the beginning of April in 2010 depending on altitude. Snow depth along the gradient varied from 15 to 214 cm on advanced snowmelt plots before shovelling. After shovelling snow depth on delayed snowmelt plots ranged from 16 to 304 cm depending on altitude. Snow melting date was defined as the day when near-

surface air temperatures reached more than + 5 °C on at least three consecutive days (for description of temperature measurements see Environmental data).

IV.3.3 DROUGHT EVENT

The drought event was simulated by rain-out shelters which were installed, on average, four weeks after snowmelt in control plots depending on altitude (installed: end of April to end of June; removed: beginning of June to beginning of August). The drought period lasted 43 ± 1 days, which is regarded as a 1000-year extreme event in this region (Jentsch & Beierkuhnlein 2008). To allow air exchange rain-out shelters were open at the front and rear. Rain-out shelters were 125 cm high and constructed with aluminium tubes and cast-iron key clamps (B-One key clamps, Montfoort, Netherlands). Shelter poles were covered with a transparent plastic sheet (0.2 mm polyethylene, SPR 5, Hermann Meyer KG, Germany), which transfers nearly 90% of photosynthetically active radiation. After the drought period the tents were removed. Over the altitudinal gradient no significant difference in average near-surface air temperature (for description of temperature measurements see Environmental data) between drought and control plots was detected with a paired *t*-test (P= 0.6) for the drought period.

IV.3.4 SPECIES AND PHENOLOGICAL OBSERVATIONS

Phenological observations of 10 different species, 8 herbs and 2 grasses, were conducted once a week from April to September 2010 on each plot following the BBCH code (Meier 2001). The focus was on flower phenology, especially the beginning of flowering, full flowering and end of flowering. In each plot 20 individuals per species were observed where possible. The number of individuals was considered large enough for further statistical analyses and small enough to make all observations achievable within a week. As single individuals of each species were not marked, partly different individual plants were likely observed on consecutive sampling dates. Onset dates of each secondary growth stage were determined using the OLR method described by Cornelius *et al.* (2011). The average altitudinal range of species in this study was about 705 m but varied between 127 m for full flowering of *Ranunculus acris* L. and 1343 m for end of flowering of *Ranunculus montanus* Willd. (Table IV.1). All observed dates were converted to day of year (1 January = 1, etc.; DOY).

IV.3.5 ENVIRONMENTAL DATA

Temperature data was derived from iButton data loggers (Thermochron iButtons DS1921G#F5, Maxim Integrated Products, Inc., Sunnyvale, CA, U.S.) which were located in the middle of each treatment plot; recording temperature at 2 h intervals. For snowmelt

treatments iButton loggers were used to determine snow melting dates from subnivean temperatures, which were measured near soil surface. Due to technical faults of the iButton data loggers there is no information about snow melting dates for sites at 817 m and 1920 m. The amount of rain excluded from drought plots through rain-out shelters was estimated with the help of rain collectors next to the site. Averaged over all sites mean precipitation was 379 ± 71 l/m^2 during the drought period. Linear regression analysis showed no significant relationship in the amount of precipitation between sites along the altitudinal gradient (P= 0.3). Soil moisture content was measured with a portable soil moisture meter (Delta-T Devices type HH2 + ThetaProbe ML2x sensors, Cambridge, UK) on average four times per plot during the drought period.

IV.3.6 STATISTICAL ANALYSES

Linear regression models with data from control plots over the entire altitudinal gradient were conducted to test the effect of altitude on the timing of phenophases (beginning of flowering, full flowering and end of flowering) for each species. To test whether response to altitude changed with timing of mean onset dates weighted linear regression was carried out of significant altitudinal regression coefficients on mean dates. We weighted the dependent variable in dependence on its residuals. A mixed-effect analysis of covariance (ANCOVA) with Type I sums of squares was used for each species and phenophase (beginning of flowering, full flowering and end of flowering) separately to test whether there were differences in phenology due to experimental treatments. In this model site nested within altitude was considered as a random factor and treatment as a fixed factor. Altitude was included as a covariate to remove the effect of altitude from the treatment comparison. Tukey's HSD for multiple comparisons was used when the model was significant. Mean onset dates were derived from the adjusted means from the mixed-effect model. The ANCOVA was conducted separately for lower (600–1300 m) and higher sites (1300–2000 m) to detect changes in the response to experimental treatments over the altitudinal gradient.

Paired *t*-tests were used to see whether there were differences in treatment effects between lower and higher sites and to test whether soil moisture content differed between control and treated plots.

All statistical analyses were performed with SPSS 19.0 (SPSS, Chicago, IL, USA, 2010).

IV.4 RESULTS

IV.4.1 ABIOTIC TREATMENT EFFECTS

Averaged over the lower gradient from 600 m to 1300 m, snow melted ca. 18 days earlier on advanced snowmelt plots than on control plots (between 20 February (DOY 51) and 23 March (DOY 82)) (Figs. IV.1, IV.2). At higher altitudes (1300-2000 m) snow melting date on advanced snowmelt plots was between 23 March (DOY 82) and 8 April (DOY 98) which was about 40 days earlier in comparison to control plots (Figs. IV.1, IV.2). A *t*-test showed a significant difference in the advance of snow melting dates in comparison to control plots at lower and higher sites on advanced snowmelt plots (P< 0.014). On delayed snowmelt plots, mean snow melting date was about 2 days later at lower and about 5 days later at higher sites than on control plots (Fig. IV.2). Date of snowmelt was between 22 February (DOY 53) and 8 April (DOY 98) at lower sites and between 23 April (DOY 113) and 5 June (DOY 156) at higher sites. A *t*-test showed no significant differences in the delay of snowmelt in comparison to controls between lower and higher sites on delayed snowmelt plots (P< 0.157). During the drought period soil moisture content was, averaged over all sites, significantly different between control and drought plots (paired *t*-test, P< 0.001), however difference to control plots was not changing with altitude, since paired *t*-test is not significant different between lower and higher sites (P< 0.301, Fig. IV.3). No significant difference in soil moisture content was found between controls and either advanced or delayed snowmelt plots (paired *t*-test, P< 0.459 or P< 0.360).

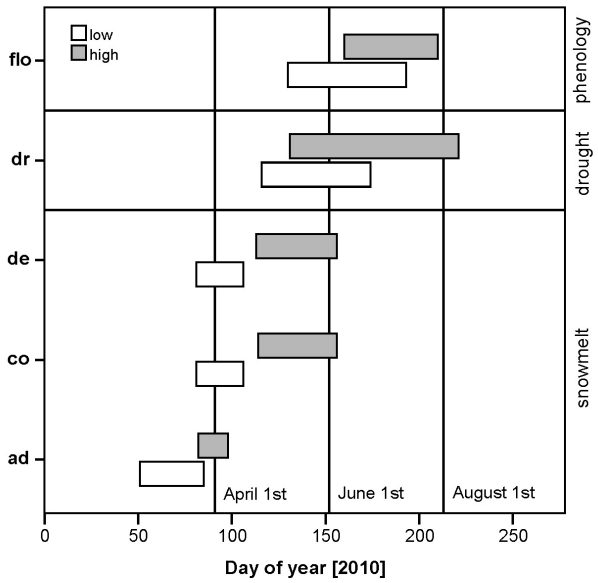

Figure IV.1 Range of the date of snowmelt (ad: advanced snowmelt, co: control, de: delayed snowmelt), duration of drought treatment (dr: drought) and flowering time (flo) of all species over the lower (600 m to 1300 m) and the higher (1300 m to 2000 m) altitudinal gradient in 2010.

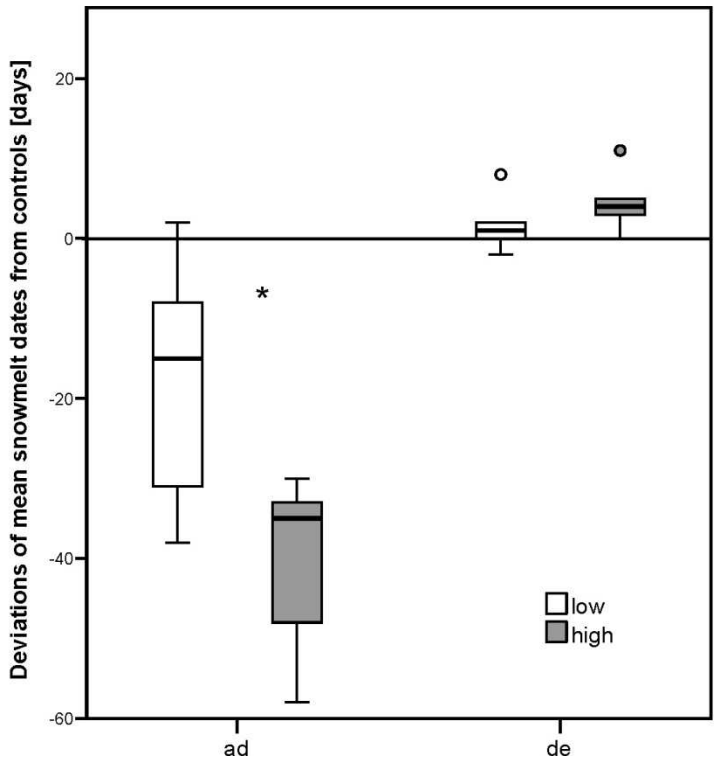

Figure IV.2 Deviations of mean snowmelt dates on advanced and delayed snowmelt plots from controls, derived from each altitudinal site singly and then separated in low (600-1300 m) and high altitudes (1300-2000 m). Asterisk indicates significant differences in snow melting date between lower and higher sites (P< 0.05).

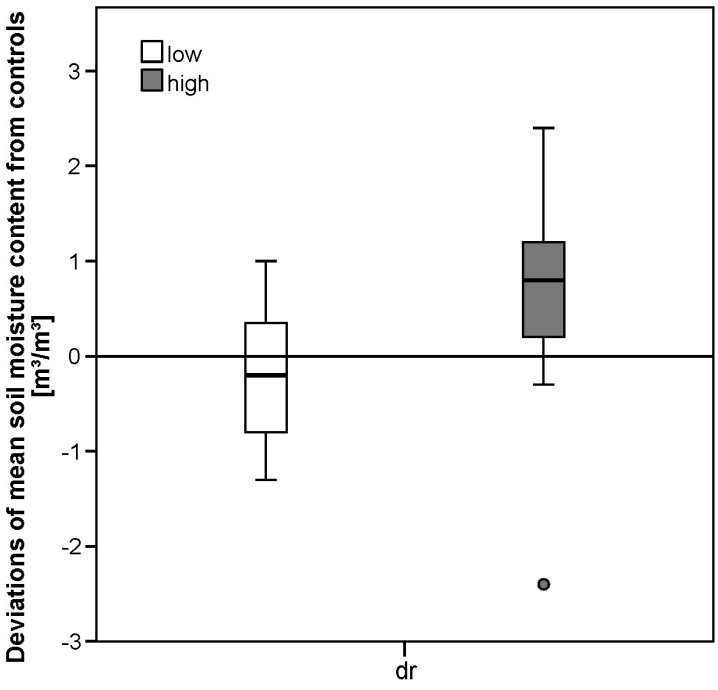

Figure IV.3 Deviations of soil moisture content on drought plots from controls, derived from each altitudinal site singly and then separated in low (600-1300 m) and high sites (1300-2000 m).

IV.4.2 PHENOLOGICAL SHIFTS WITH ALTITUDE

Linear regression models mostly showed significant responses of flowering phenology to altitude (Table IV.1). Averaged over all phenophases and species there was a delay in onset dates of 3.4 days 100 m^{-1} increase in elevation. However, the altitudinal response differed strongly between species, being greatest for the end of flowering of *R. acris* (5.7 days 100 m^{-1}), and the smallest for the end of flowering of *Lotus corniculatus* L. (1.7 days 100 m^{-1}).

Weighted linear regression analysis showed that phenophases occurring later in the year were significantly less responsive to altitudinal change than phenophases early in the year ($P< 0.043$, $R^2= 0.593$).

Table IV.1 Results of linear regression analysis of study site mean dates of three phenophases (BF: beginning of flowering, FF: full flowering, EF: end of flowering) on altitude. Numbers in bold are significant ($P< 0.05$). Altitudinal ranges showing the maximum amplitude of elevation for each species and phenophase. # No variation recorded in this variable for this event.

	N	R^2	P	Days/100m(±SE)	Altitudinal ranges [low-high] (m)
Alchemilla vulgaris L.					
BF	4	0.119	0.655	0.8 (± 1.6)	534 [1045-1579]
FF	7	0.827	**0.005**	4.8 (± 1.0)	865 [714-1579]
EF	7	0.550	**0.050**	2.4 (± 1.0)	619 [960-1579]
Briza media L.					
BF	7	0.844	**0.003**	3.4 (± 0.7)	689 [641-1330]
FF	7	0.731	**0.014**	2.4 (± 0.7)	689 [641-1330]
EF	7	0.853	**0.003**	3.2 (± 0.6)	689 [641-1330]
Campanula scheuchzeri Vill.					
BF	3	0.776	0.314	5.2 (± 2.8)	273 [1552-1825]
FF	5	0.535	0.160	1.4 (± 0.8)	865 [960-1825]
EF	8	0.642	**0.017**	1.9 (± 0.6)	865 [960-1825]
Dactylis glomerata L.					
BF	5	0.713	0.072	3.9 (± 1.4)	464 [641-1105]
FF	5	0.526	0.166	2.5 (± 1.4)	464 [641-1105]
EF	5	0.331	0.311	1.3 (± 1.1)	464 [641-1105]
Lotus corniculatus L.					
BF	6	0.794	**0.017**	3.6 (± 0.8)	1111 [714-1825]
FF	6	0.878	**0.006**	3.1 (± 0.6)	1111 [714-1825]
EF	1	0.683	**0.002**	1.7 (± 0.4)	1270 [714-1984]
Potentilla erecta (L.) Raeusch					
BF	4	0.917	**0.043**	3.6 (± 0.8)	762 [817-1579]
FF	5	0.916	**0.011**	3.1 (± 0.5)	762 [817-1579]
EF	9	0.074	0.479	0.8 (± 1.0)	1167 [641-1808]
Prunella vulgaris L.					
BF	3	0.900	0.205	7.0 (± 2.3)	288 [817-1105]
FF	5	0.816	**0.036**	2.7 (± 0.7)	865 [714-1579]
EF	8	0.769	**0.004**	2.5 (± 0.6)	938 [641-1579]

	N	R^2	P	Days/100m(±SE)	Altitudinal ranges [low-high] (m)
Ranunculus acris L.					
BF				#	
FF	3	0.894	0.211	7.9 (± 2.7)	127 [714-841]
EF	3	0.999	**0.019**	5.7 (± 0.2)	246 [714-960]
Ranunculus montanus Willd.					
BF				#	
FF	3	0.953	0.139	5.1 (± 1.1)	780 [1045-1825]
EF	8	0.954	**<0.001**	4.9 (± 0.4)	1343 [641-1984]
Trifolium pratense L.					
BF	5	0.648	0.100	3.4 (± 1.4)	984 [841 -1825]
FF	7	0.647	**0.029**	4.1 (± 1.3)	1111 [714-1825]
EF	1	0.684	**0.003**	4.1 (± 1.0)	1111 [714-1825]

IV.4.3 PHENOLOGICAL DIFFERENCES DUE TO TREATMENTS

ANCOVA showed significant differences in the timing of phenophases between treatments for five out of ten species, with differences mainly found at higher sites, except for *Prunella vulgaris* L. which showed a significant shift at the lower gradient (Table IV.2).

Tukey's HSD post-hoc tests showed a significant advance of 6-12 days for the beginning of flowering and full flowering of *Alchemilla vulgaris* L. on advanced snowmelt plots in comparison to control and other treatment plots. Full flowering and end of flowering of *R. montanus* were also 8-12 days earlier on advanced snowmelt plots in comparison to the other treatments (Table IV.2). A significant delay of 5-9 days in the end of flowering of *Campanula scheuchzeri* Vill. and *P. vulgaris* was recorded on delayed snowmelt plots. For *Potentilla erecta* (L.) Raeusch the end of flowering was significantly advanced on drought plots (-3 to -8 days) in comparison to advanced and delayed snowmelt plots (no data available for control plots).

Averaged over all species, including non-significant results, the timing of phenophases was, in comparison to control plots, advanced by about 1-7 days on advanced snowmelt plots, delayed by about 2-3 days on plots with delayed snowmelt and about the same (0 to -2 days) on plots with a simulated drought event. On advanced snowmelt plots, effects were much greater on higher than on lower sites (mean response of -1 day on lower and -5 days on higher sites). On delayed snowmelt plots the response was the same for lower and higher sites (mean delay of 3 days). Average response to drought was -1 day for lower sites but no significant difference in phenology was found at higher sites.

Table IV.2 Mixed-effect analysis of covariance (ANCOVA) showing differences in phenological onset dates (beginning of flowering, full flowering, end of flowering) between treatments (control (co), advanced snowmelt (ad), delayed snowmelt (de), drought (dr)) for a lower (l) (600–1300 m) and a higher (h) (1300–2000 m) altitudinal gradient. Numbers in bold are significant (P< 0.05). N/A data not available. Mean onset dates are derived as adjusted means from the model. Tukey's HSD was conducted for multiple comparisons if the model was significant; + ,- , x symbols indicate a significant difference between respective treatments (treat).

	Beginning of flowering					Full flowering					End of flowering				
	P	co	ad	de	dr	P	co	ad	de	dr	P	co	ad	de	dr
Alchemilla vulgaris L.															
mean (l)		**140**	**137**		**139**		**140**	**137**	**139**	**139**		**174**	**177**		**177**
treat (l)	0.622					0.153					0.369				
mean (h)		**160**	**154**	**166**	**161**		**170**	**161**	**172**	**169**		**187**	**187**	**189**	**185**
treat (h)	**0.005**	-	x + -	x	+	**0.028**	-	x + -	x	+	0.255				
Briza media L.															
mean (l)		**173**	**172**	**174**	**172**		**175**	**177**	**179**	**173**		**181**	**181**	**182**	**180**
treat (l)	0.485					0.236					0.103				
mean (h)								N/A							
treat (h)															
Campanula scheuchzeri Vill.															
mean (l)								N/A							
treat (l)															
mean (h)		**209**	**211**	**213**	**207**		**210**	**211**	**214**	**207**		**216**	**219**	**225**	**217**
treat (h)	0.122					0.123					**<0.001**	-	x	x + -	+
Dactylis glomerata L.															
mean (l)		**170**	**168**	**170**	**167**		**172**	**170**	**173**	**170**		**177**	**175**	**178**	**175**
treat (l)	0.106					0.354					0.265				
mean (h)								N/A							
treat (h)															
Lotus corniculatus L.															
mean (l)		**166**	**156**	**170**			**170**	**162**	**178**			**189**	**188**	**200**	**198**
treat (l)	0.253					0.223					0.160				
mean (h)					N/A							202	200	200	202
treat (h)											0.242				

	Beginning of flowering					Full flowering					End of flowering				
	P	co	ad	de	dr	P	co	ad	de	dr	P	co	ad	de	dr
Potentilla erecta (L.) Raeusch															
mean (l)		**149**	**153**	**153**	**152**		**156**	**158**	**158**	**158**		**189**	**189**	**192**	**187**
treat (l)	0.218					0.744					0.714				
mean (h)		**179**	**173**	**183**	**178**		**180**	**175**	**184**	**181**			**195**	**200**	**192**
treat (h)	0.318					0.192					**0.036**		-	x	x -
Prunella vulgaris L.															
mean (l)		**183**	**183**	**181**	**185**		**185**	**183**	**187**	**185**		**193**	**191**	**196**	**191**
treat (l)	0.800					0.290					**0.047**		-	x -	x
mean (h)								N/A							
treat (h)															
Ranunculus acris L.															
mean (l)		**143**	**140**	**144**	**141**		**144**	**143**	**144**	**142**		**159**	**157**	**158**	**158**
treat (l)	0.695					0.402					0.763				
mean (h)								N/A							
treat (h)															
Ranunculus montanus Willd.															
mean (l)							**130**	**128**	**130**	**130**		**136**	**133**	**137**	**136**
treat (l)						0.590					0.801				
mean (h)		**169**	**153**	**168**	**171**		**170**	**158**	**171**	**176**		**178**	**170**	**181**	**179**
treat (h)	0.092					**0.005**	-	x + -	x	+	**0.006**	-	x + -	x	+
Trifolium pratense L.															
mean (l)		**167**	**167**	**162**	**169**		**173**	**172**	**170**	**171**		**184**	**181**	**181**	**181**
treat (l)	0.391					0.147					0.634				
mean (h)			N/A				**199**	**196**	**201**	**198**		**210**	**207**	**211**	**210**
treat (h)						0.610					0.410				

The effect of an advanced snowmelt appeared to be more pronounced earlier in the year showing a response of -7 days on higher sites for the beginning of flowering and of only -2 days for the end of flowering. The effect of delayed snowmelt and drought appeared to be consistent throughout the year.

IV.4.4 CHANGES IN THE DURATION OF FLOWER PHENOLOGY

ANCOVA showed that, for all species, manipulative treatments had no significant effect on the duration of flower phenology except for *A. vulgaris* showing a prolongation of 7 days on advanced snowmelt plots in comparison to the control plots (Table IV.3). For *P. erecta* flower duration was much longer at lower altitudes (33 days) than at higher altitudes (18 days) averaged over all treatments (Table IV.3).

Table IV.3 Mixed-effect analysis of covariance (ANCOVA) showing differences in the length of flowering period (days from beginning of flowering to end of flowering) between treatments (control (co), advanced snowmelt (ad), delayed snowmelt (de), drought (dr) over a lower (l) (600–1300 m) and a higher (h) (1300–2000 m) altitudinal gradient. Numbers in bold are significant (P< 0.05). Tukey's HSD was conducted for multiple comparisons if the model was significant; +, -, x symbols indicate a significant difference between respective treatments (treatment). N/A data not available.

			Duration [days]			
		P	co	ad	de	dr
Alchemilla vulgaris L.	mean (l)			N/A		
	treatment (l)					
	mean (h)	**0.010**	30	37	25	27
	treatment (h)		-	x + -	x	+
Briza media L.	mean (l)		9	9	8	7
	treatment (l)	0.552				
	mean (h)			N/A		
	treatment (h)					
Campanula scheuchzeri Vill.	mean (l)			N/A		
	treatment (l)					
	mean (h)		11	11	12	14
	treatment (h)	0.253				
Dactylis glomerata L.	mean (l)		11	9	11	11
	treatment (l)	0.396				
	mean (h)			N/A		
	treatment (h)					
Lotus corniculatus L.	mean (l)		22	30	31	
	treatment (l)	0.696				
	mean (h)			N/A		
	treatment (h)					
Potentilla erecta (L.) Raeusch	mean (l)		33	31	35	31
	treatment (l)	0.591				
	mean (h)		18	22	17	15
	treatment (h)	0.082				

		Duration [days]				
		P	co	ad	de	dr
Prunella vulgaris L.	mean (l)		12	10	15	9
	treatment (l)	0.935				
	mean (h)			N/A		
	treatment (h)					
Ranunculus acris L.	mean (l)			N/A		
	treatment (l)					
	mean (h)			N/A		
	treatment (h)					
Ranunculus montanus Willd.	mean (l)			N/A		
	treatment (l)					
	mean (h)		10	20	16	9
	treatment (h)	0.241				
Trifolium pratense L.	mean (l)		12	12	15	10
	treatment (l)	0.283				
	mean (h)			N/A		
	treatment (h)					

IV.5 DISCUSSION

The present study showed strong responses on flower phenology of different grassland species to altitude. Furthermore, we demonstrated that advanced snowmelt had a greater influence on flower phenology on higher than on lower sites due to a stronger treatment effect at higher altitudes. However, altitude had no significant effect on responses to delayed snowmelt or drought, whereas treatment effects were rather small over the entire gradient. Flowering duration was mostly not influenced by manipulative treatments at both higher and lower sites.

IV.5.1 PHENOLOGICAL RESPONSE TO ALTITUDINAL CHANGE

Averaged over all species and phenophases, there was a delay in flower phenology of 3.4 days 100 m^{-1} increase. This is in accordance with Cornelius *et al.* (2012) who showed a delay of flower and leaf phenology of 3.8 days 100 m^{-1} increase for tree and herbaceous species in the same region. However, the response to altitude change is species-specific, ranging between 1.7 and 5.7 days 100 m^{-1} which is similar to the variation of 1.7 to 6.9 days 100 m^{-1} shown by Cornelius *et al.* (2012). Most altitudinal studies refer to tree species (*e.g.*, Roetzer & Chmielewski 2001; Dittmar & Elling 2006; Migliavacca *et al.* 2008; Vitasse *et al.* 2009a; Moser *et al.* 2010), however, Ziello *et al.* (2009) showed, based on COST725 data for the Alpine region, a delay in the beginning of flowering of *Dactylis glomerata* L. of 2.8 days 100 m^{-1}. This is slightly less sensitive to altitude than the non-significant response

of *D. glomerata* in our study (3.9 days 100 m $^{-1}$). We assume that had we had a higher number of observations in the present study these values would have been more similar.

Phenophases later in the year were significantly less sensitive to altitude than phenophases early in the year, which was also confirmed by Cornelius *et al.* (2012). A weaker response to temperature of species flowering in May and June in comparison to earlier spring flowering species was also shown by Fitter & Fitter (2002) and Menzel *et al.* (2006), who found that, because of high temperature variability in spring, the earlier the species, the stronger the sensitivity to temperature. However, in the present study as well as that of Cornelius *et al.* (2012) early (March to May) and late (September to October) species and phases were missing. Thus, it appears that response to temperature is declining not only in spring but consistently throughout the year.

IV.5.2 PHENOLOGICAL RESPONSE TO TREATMENTS

The experiment showed only a few significant differences in the timing of flowering due to the manipulative treatments. Earlier snowmelt advanced flower phenology in most cases although the effect was only significant for four species and phenophases. This is in accordance with other studies (Price & Waser 1998; Dunne *et al.* 2003; Lambert *et al.* 2010; Wipf 2010). For example, Wipf *et al.* (2009) showed an advance of flower phenology of up to 10 days (present study -1 to -7 days). The response of species to later snowmelt is rather small; only the end of flowering phenophases was sometimes significantly delayed. Delayed timing due to later snowmelt was also shown in other studies (Weaver & Collins 1977; Torp *et al.* 2010; Chen *et al.* 2011; Cooper *et al.* 2011) demonstrated a delay in beginning of flowering and peak flowering of about 6-8 days for alpine species. In our study the response was smaller with a non-significant delay of 2-3 days between delayed snowmelt and control plots. Hoye *et al.* (2007), however, showed that the result of delayed snowmelt was not necessarily later flowering but could also be unchanged. Thus, response to delayed snowmelt also appears to be species-specific. Wipf & Rixen (2010) suggested that, in general, the least responsive and least consistent responses to shifts in the date of snowmelt were in the grasses, while forbs were a little more responsive. Furthermore, the advanced snowmelt treatment was very early in the year, thus early flowering species such as *A. vulgaris* or *R. montanus* were affected, whereas an effect on late flowering species such as *C. scheuchzeri* or *P. vulgaris* was rather unlikely. Late-flowering species as well as phenophases later in the season were less responsive to snowmelt than early-flowering species or phenophases early in the season because those are controlled by temperature (Price & Waser 1998; Dunne *et al.* 2003; Wipf 2010).

Across species and phenophases the drought treatment did not influence flowering significantly except for *P. vulgaris.* No effect of drought on plant phenology was also found for different grass species in an alpine meadow in France (Bloor *et al.* 2010) or for the onset of growth of *Globularia alypum* L. in a Mediterranean shrubland area (Bernal *et al.* 2011). However, flowering of *G. alypum* was delayed by drought (Prieto *et al.* 2008). A delay in flowering time after a drought period was also demonstrated for other Mediterranean plants (Llorens & Penuelas 2005). In contrast, Jentsch *et al.* (2009) showed an advance of the midflowering-date of 4 days after a drought period of 32 days. Thus, plant response to drought appears to be highly species-specific (Bernal *et al.* 2011) and ecosystem dependent. In the present study, soil moisture content on drought plots was 0.420 m^3/m^3 on average, which was probably not low enough to simulate a drought event that affects plant phenology (Fig. IV.3).

The flowering durations of species were mostly not significantly affected by the manipulative treatments. As far as we know, studies dealing with the impacts of snowmelt date on flowering duration are rare and contradictory. Price & Waser (1998) showed that early snowmelt was associated with longer flowering duration which agrees with our prolongation of the flowering duration of *A. vulgaris* on advanced snowmelt plots. However, Wipf (2010) demonstrated that flowering duration was not affected by snowmelt timing which agrees with the results of all other species in our study. Studies dealing with the impacts of drought on flowering duration are also rare and contradictory. Jentsch *et al.* (2009) reported a lengthening of the flowering period after a drought event, whereas Llorens & Penuelas (2005) reported both a shortening and a lengthening of the flowering duration of two different Mediterranean dwarf shrubs. In our study, the intensity of drought was likely not sufficient to cause shifts in flowering duration. However, general conclusions from these ambiguous results should only be drawn with care since there are slight differences in flowering duration definitions between studies.

IV.5.3 SHIFTS IN THE PHENOLOGICAL RESPONSE DUE TO CHANGES IN ALTITUDE

For only a few species we had data for both the lower and the higher altitudes. Ideally, species would have been distributed over the entire altitudinal gradient and also located in each treatment plot. However, due to restrictions in their natural distribution, species are often not spread over the entire gradient. Thus, only four species were monitored on both lower and higher sites. For those species impacts of treatments on flower phenology were additionally illustrated in Fig. IV.4. For advanced snowmelt plots, treatment effects were more pronounced at higher sites; however other treatments showed no significant

difference between altitude bands. Thus, on advanced snowmelt plots the phenological response is most likely stronger at higher altitudes due to a larger treatment effect and not because species react more sensitively at higher than at lower altitudes. For delayed snowmelt and drought plots no significant difference in treatment effects between lower and higher altitudes were detected. Thus, phenological differences were not significant, which indicates that species responded similarly at different altitudes. Defila & Clot (2005) showed from a 50-year time series in Switzerland that the total proportion of significant trends is higher in the alpine (higher than 1000 m a.s.l.) regions (42%) and smaller in the lowland (lower than 600 m a.s.l, 33%). However, considering the intensity of trends, the results showed an advance of full flowering of 32 days in the lowland and 20 days in the alpine region.

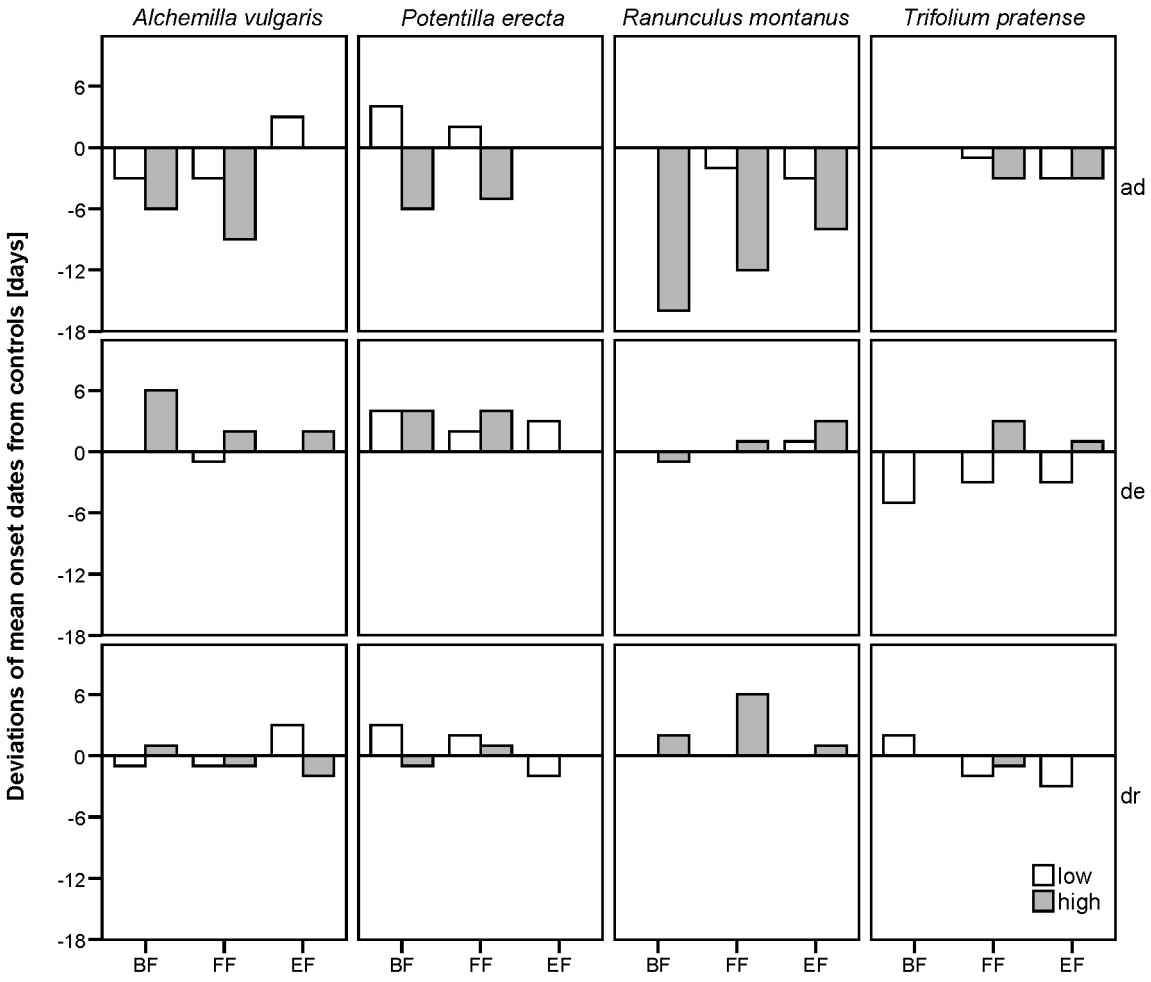

Figure IV.4 Deviations of mean onset dates from the ANCOVA model for each studied phenophase (BF: beginning of flowering, FF: full flowering, EF: end of flowering) from controls (ad: advanced snowmelt, de: delayed snowmelt, dr: drought) separately in low (600-1300 m) and high sites (1300-2000 m) for the four species (*Alchemilla vulgaris* L., *Potentilla erecta* (L.) Raeusch, *Ranunculus montanus* Willd, *Trifolium pratense* L.) observed on both low and high altitudes.

The length of flowering of *P. erecta* was greater at lower altitudes for all treatments which led to the conclusion that duration was probably influenced by higher temperatures at lower sites. Tyler (2001) showed that the length of the flowering period was only little influenced by temperature because the timing of the onset of both start and end of phenophases advances in response to temperature increase; thus, the total length is not affected. However, Cornelius *et al.* (2012) showed that although for most species flowering duration was not influenced by temperature, some species prolonged their flowering duration mainly due to a weaker response of end of flowering which is related to the declining sensitivity to temperature change over the season as also shown in the present study.

IV.6 CONCLUSION

Our results suggest that advanced or delayed snowmelt and drought only have an influence on the timing of flowering if the effect is rather distinctive. As this will mainly be the case at higher altitudes, species there will be more affected by global climate change. However, response sensitivity to changes in the abiotic environment appears not to shift with altitude but with effect intensity. Furthermore, response to treatments is highly species-specific as also shown in other studies because co-existing species may have different environmental constraints (Penuelas *et al.* 2002; Ogaya & Penuelas 2004; Llorens & Penuelas 2005). Phenology shifts along the altitudinal gradient and due to the experimental manipulations indicate severe changes in the studied ecosystems with changing climate within the next 50 years.

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V IMPACTS OF TEMPERATURE AND WATER TABLE MANIPULATION ON GRASSLAND PHENOLOGY

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V.1 ABSTRACT

Peatlands are naturally important carbon pools. Respiration of peat soils is positively related to both temperature and water table level which are likely to be affected by climate change. Since vegetation plays a key role in the carbon cycle of peatland ecosystems, it is important to know how plants will react to changed environmental conditions. The aim of this study was to test whether the phenological development of plant species in a peatland ecosystem changed with higher temperatures, increased water table level or with a combination of both. In 2010 manipulative experiments with two different treatments (control and warming) and in 2011 with four different treatments (control, warming, increased water table level and warming + increased water table level) were conducted in a fen-peatland in Bavaria, Germany. Temperature was manipulated with open-top chambers (OTCs) and water table level was continuously elevated by a pumping system. Phenological development of different grassland species was observed weekly using the BBCH code. Attention was focused on total development and on key single phenological phases such as flower development, flowering, ripening and fruit senescence as well as the duration of key phases. Additionally, the vegetation height was measured. Our study showed that higher temperatures advanced total development and most key phases except fruit senescence. Water table manipulations showed no significant influence on phenology. The duration of key phases was generally not significantly influenced by treatments, whereas vegetation height differed between control and higher temperature plots. In general, raising the water table to reduce carbon release from drained peatland sites will not affect phenological development of grassland species dramatically.

Key-words: BBCH, climate change, OTC, peatland

V.2 INTRODUCTION

Due to the rising atmospheric concentration of greenhouse gases, such as carbon dioxide (CO_2), global mean temperatures have increased by about 0.7 °C in the last 100 years which has already affected ecosystems across the world (IPCC 2007a; IPCC 2007b). Natural peatlands constitute a significant sink for atmospheric CO_2 because photosynthesis accumulation rates are an order of magnitude higher than carbon releases by respiration under waterlogged conditions. Thus, organic matter accumulates in those ecosystems as peat (Byrne *et al.* 2004). Germany contains only 3.2% of European peatlands, however it is the second largest emitter (12% of European total; European Russia included) of the NGHGB (net greenhouse gas balance of CO_2, CH_4, N_2O) from peatlands because most of the peatland area is used for intensive farming (Byrne *et al.* 2004). Peatlands turn from a carbon sink into a carbon source if drained because it enhances peat decomposition through increased soil aeration (Van Huissteden *et al.* 2006; Drösler *et al.* 2008). Respiration of peat soils is positively related to temperature (Billings *et al.* 1982; Moore & Dalva 1993; Updegraff *et al.* 1998) and water table level (Billings *et al.* 1982; Moore & Knowles 1989; Freeman *et al.* 1993; Moore & Dalva 1993) which are both likely to be affected by climate change (Strack *et al.* 2006). For Bavaria, climate change scenarios predict an increase in mean air temperature and an increase of precipitation in the winter months (KLIWA 2005) which will consequently influence the water table level in peatland ecosystems.

Since vegetation plays a key role in the carbon cycle of peatland ecosystems it is important to know how plants will react to these changing environmental conditions. Thus, in this study we simulated a changed environment to understand the impacts of higher temperature and water table level on ecological services of peatlands. The effects of these manipulations on the growth and development of the vegetation on peatland sites is analyzed in this paper. Most temperate grassland species flower at the time of maximum vegetative biomass (Mooney *et al.* 1986; Sun & Frelich 2011). Similar flowering times among species often lead to a competition for limiting soil resources and / or light. Shifts in phenology may change quality and quantity of resources at a given time, which may increase competitive pressure on species. Increased pressure often leads to shifts in plant composition which can influence the carbon cycle of peatland ecosystems.

Most climate change studies on peatland sites have either dealt with temperature manipulation (Chapin *et al.* 1995; Henry & Molau 1997 and see the running PEATWARM-experiment) or with water table changes (*e.g.*, Strack *et al.* 2004) focusing mainly on soil respiration aspects. Only the boreal APEX (Alaska peatland experiment) study and the Northern Peatlands Soil Warming Project in northern Minnesota, U.S. manipulated both

temperature and water table level. The latter was mainly focusing on soil respiration aspects (Updegraff *et al.* 2001) or plant community structures (Weltzin *et al.* 2000).

Future higher temperature conditions can be simulated by open-top chambers (OTCs) which are easy to handle and have been widely used in ecosystems such as tundra (Marion *et al.* 1997; Hollister & Webber 2000), alpine meadows (Totland & Eide 1999; Kudernatsch *et al.* 2008) or deciduous forests (De Frenne *et al.* 2010). OTCs are small greenhouses with Plexiglas and inclined walls which passively increase air temperatures by about 0.4-2.3 °C (Marion *et al.* 1997; Hollister & Webber 2000; Kudernatsch *et al.* 2008; Totland & Eide 1999; De Frenne *et al.* 2010). In our experiment water table level was increased by a pumping system keeping the water table level about 20 cm higher than the control plots.

It is already known that higher temperatures accelerate the onset of flowering of grassland species in different ecosystems such as subalpine (Hoffmann *et al.* 2010), temperate (Hovenden *et al.* 2008a) or tundra ecosystems (Arft *et al.* 1999; Hollister & Webber 2000). However, as far as we know there are no studies about the impacts of warming or water table manipulations on the development of grassland species in a temperate peatland site. Furthermore, in general, phenological studies mainly focus on the flowering of species. Studies dealing with other phenological phases of grassland species such as fruit ripening and fruit senescence are rare (but see Price & Waser 1998; Hoffmann *et al.* 2010). Little is also known about the length of key phenological phases, especially in manipulative experiments. However, some studies have examined the duration of the flowering period (Price & Waser 1998; Dunne *et al.* 2003; Jentsch *et al*. 2009; Hovenden *et al.* 2008b) under warming or drought conditions.

Plant growth is accelerated by warmer temperatures (*e.g.*, Hudson *et al.* 2011) and under flooded site conditions (Chivers *et al.* 2009). Moreover, plant height is positively correlated with peak flowering dates in alpine meadows (Jia *et al.* 2011). Thus, later flowering peak dates are associated with taller species. However, focussing on individuals of a single species, it is expected that warming will simultaneously advance flowering and lead to a higher plant growth.

The aims of the current work were to investigate how warming and an increased water table level, singly and in combination, affected (i) the total phenological development of grassland species (ii) single key phenological phases such as flower development, flowering, ripening and fruit senescence, (iii) the duration of those stages and (iv) vegetation height.

V.3 MATERIALS AND METHODS

V.3.1 STUDY SITE AND EXPERIMENTAL DESIGN

The study site was located in a peatland area in the Freisinger Moos, Germany (48°22'N, 11°41'E). The experiment was carried out with a control and three different types of manipulative treatments (warming (W), increased water table level (WT) and a combination of warming and increased water table level (WWT)). The setup consisted of three replicates of each treatment in a total of 12 plots each of 0.75 m x 0.75 m. All plots were contiguous (see Fig. V.1). A randomised plot design was not possible due to the complex engineering work needed to elevate the water table.

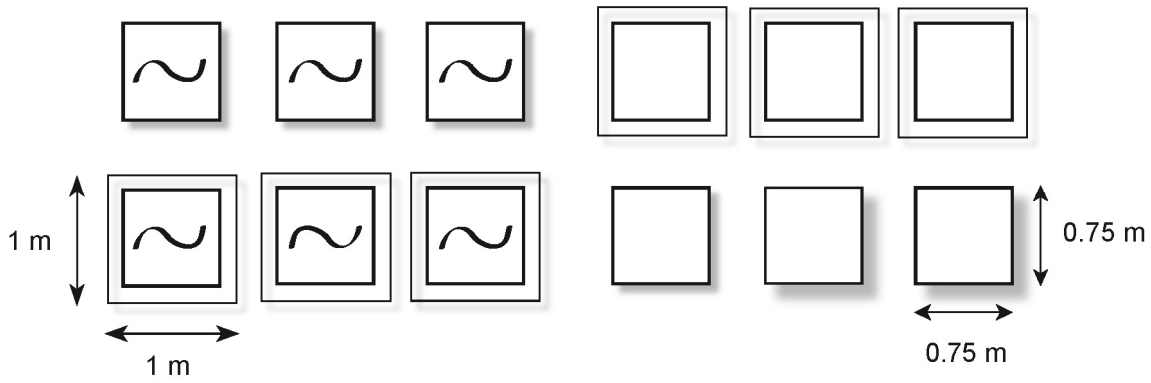

Figure V.1 Experimental design with 4x3 treatments. From top left to bottom right: Water level manipulations plots, temperature manipulation plots with open-top chambers (OTCs), temperature (OTCs) and water level manipulations plots, control plots. In 2010 the experiment consisted only of warmed and a control plot with six replicates each.

Temperature was manipulated with open-top chambers (OTCs) from August 2009 onwards. The OTCs were 50 cm high with 70° inwardly inclined sides made of UV permeable plastics (Quinn XT, Quinn plastics). Each chamber covered an area of 1 m^2 at the basis and an opening at the top of 0.75 m x 0.75 m, to equal the plot dimensions and was installed on 18 cm high feet. The construction of the OTCs increases temperature but humidity and soil moisture are not affected (Kudernatsch *et al.* 2008). Warming in 2010 was not as high as expected, thus the feet of the OTCs were shortened to 5 cm to reduce the cooling effect due to wind circulation within the chambers. The water table level was manipulated with a pumping system keeping the water table level constantly about 20 cm higher than that in control plots. Water was pumped from a nearby shallow well with similar chemistry to the groundwater in the control plots. Plots were enclosed by bulkheads to prevent water passing between treatments. A communication system consisting of pumps, relative pressure sensors and DT85 data loggers (dataTaker, Victoria, Australia) helped maintain the elevated water table levels by turning pumps on and off in reference to the control plots. The

pumping system operated from March 2011. Thus, in 2010 only warming could be simulated. The experiment consequently consisted of warmed and control plots with six replicates each in 2010.

Vegetation was cut annually between August and October as per local agricultural management regimes for extensive grasslands.

V.3.2 PHENOLOGICAL OBSERVATIONS

Observations started after snowmelt and ended when the vegetation was cut. Eleven different grassland species were observed weekly from the beginning of March to the end of September in 2010 and from the beginning of March to the end of August in 2011. Five species did not flower in the course of the experiment or flowers were partly destroyed due to trace gas measurements on site which were conducted with special chambers. Two other species either flowered irregularly or occurred in too few plots. These species were excluded from analysis, leaving four grass species (*Anthoxanthum odoratum* L., *Dactylis glomerata* L., *Holcus lanatus* L. and *Molinia caerulea* L.) for closer study. In 2010 phenological observations started in March, so leaf development stages and the mid boot stage of *A. odoratum* were missed. In both years, plots were cut before ripening and fruit senescence stages of *M. caerulea* could be observed. Phenological observations were conducted according to the extended BBCH scale (Meier 2001), which was adjusted to wild grass species (see Table V.1). In each plot 12 individuals per species were observed. The number of individuals was considered large enough for statistical analyses but small enough to allow all observations to be made in a single day. Since individual plants were not marked, different individual plants were likely observed on consecutive sampling dates. Grass species were not distributed equally over all treatments. *D. glomerata* were only observed on control and WWT plots, whereas *A. odoratum* were not found on WWT plots. *H. lanatus* and *M. caerulea* could be monitored on all plots (see Table V.2). Onset dates of each secondary growth stage were determined using the OLR method described by Cornelius *et al.* (2011).

Table V.1 Phenological key phases and affiliated secondary growth stages according to the BBCH code. Asterisks indicate secondary growth stages which were not observed on individuals of *Anthoxanthum odoratum* L.

Key phase	Secondary growth stage
Flower development	Flag leaf sheath just visibly swollen*
	Flag leaf sheath swollen
	Flag leaf sheath opening
	Beginning of heading
	Middle of heading
	End of heading
	Panicle unfolded*
Flowering	Beginning of flowering
	Full flowering
	End of flowering
Ripening	Inflorescence starts yellowing
	Inflorescence yellow
Fruit Senescence	First seeds fallen
	50% or more seeds fallen
	All seeds fallen

From May 2010 onwards vegetation height was measured five times within each plot with a meter, estimating by eye the height below which 80% of the vegetation was growing (Hodgson *et al.* 1971; 'tMannetje 1978).

V.3.3 METEOROLOGICAL DATA

Temperature was recorded from a weather station next to the site and mean temperature was calculated as the mean daily temperatures over the growing period from March to September. Missing data due to technical faults of the weather station were gap-filled with the help of linear interpolation based on data from a nearby weather station ($R^2 > 0.95$). Precipitation was calculated as the total precipitation from March to June.

Warming by the OTCs was measured with integrated relative humidity and air temperature sensors (HC2-S3, Rotronic AG, Switzerland) within plots 20 cm above ground level. Sensors were covered with non-ventilated radiation shields (AC1000, Rotronic AG, Switzerland) and were also used to measure temperature in control and WT plots. Temperature differences between treated plots and controls were calculated from the mean daily temperatures for the observation period from March to September in 2010 and March to August in 2011.

V.3.4 STATISTICAL ANALYSIS

To test if phenology has shifted as a consequence of experimental warming and water table manipulation a repeated measures analysis of variance (ANOVA) was conducted, with a Tukey's HSD for multiple comparisons where significant. Repeated measures ANOVAs were carried out for the entire development of plants or for key phases such as flower

development, flowering, ripening and fruit senescence (Table V.1). Moreover, we analysed the differences in the duration of key phases (flower development, flowering, ripening and fruit senescence) between treatments with a *t*- test for data in 2010 and *D. glomerata* in both years. An analysis of variance (ANOVA) was conducted to test whether there were differences in phenology between treatments for *A. odoratum*, *H. lanatus* and *M. caerulea* in 2011. For multiple comparisons Tukey's HSD was used. Phase durations were defined as the difference in days between the mean onset of panicle unfolded and flag leaf sheath just visibly swollen for flower development (for *A. odoratum*: end of heading and flag leaf sheath swollen), between the mean onset of end of flowering and beginning of flowering for flowering, between the mean onset of inflorescence yellow and inflorescence starts yellowing for ripening and between the mean onset of all seeds fallen and first seeds fallen for fruit senescence (Table V.1 and see Cornelius *et al.* 2011).

Furthermore, a *t*-test and repeated measures ANOVA were conducted to test whether there were differences in vegetation height between treatments in each year. For 2011 Tukey's HSD was used for multiple comparisons.

All observed dates were converted to Julian date (days after December 31). All statistical analyses were performed with SPSS 19.0 (SPSS, Chicago, IL, USA, 2010).

V.4 RESULTS

Mean temperature of the growing season (March to September) on the study site (measured by the weather station in 2 m above ground) was 12.5 °C in 2010 and 13.8 °C in 2011 with total precipitation (March to June) of 231.6 mm and 371.7 mm, respectively. Temperature differences between years were greater in spring (March-May: 2.6 °C) than in summer (June-September: 0.3 °C).

Mean temperatures of W and control plots differed by about 0.4 °C in March to September 2010 and 0.9 °C in March to August 2011. In 2011 mean temperature differences of 1.5 °C was found between WWTs and controls and -0.2 °C between WTs and controls for the same period (measured by sensors in 0.2 m above ground).

V.4.1 SHIFTS IN PHENOLOGY DUE TO MANIPULATIVE EXPERIMENTS

In 2010 passive warming significantly affected the total development of *D. glomerata* (P= 0.034) and *H. lanatus* (P= 0.008) (Table V.2). Averaged over all secondary growth stages, total development was -4 to -5 days earlier on plots with raised temperatures (Fig. V.2). Warming had no significant effect on the total development of *A. odoratum* (P= 0.099) and *M. caerulea* (P= 0.218) in 2010 (Table V.2). Furthermore, key phases such as flower

development and flowering of *A. odoratum* (P= 0.245; P= 0.807), *D. glomerata* (P= 0.161; P= 0.307) and *M. caerulea* (P= 0.388; P= 0.667) were not significantly affected by warming (Table V.2) in 2010. Only *H. lanatus* showed significant differences between the two treatments for flower development (P= 0.005) and flowering (P= 0.007). Key phases (flower development and flowering) were observed earlier on warmed plots (-2 to -7 days) for *D. glomerata* and *H. lanatus*, however, *A. odoratum* or *M. caerulea* flowered at about the same day on treated and non-treated plots (Fig. V.2). Ripening stages of *A. odoratum* (P= 0.090), *D. glomerata* (P= 0.237) and *H. lanatus* (P< 0.001) occurred 3-6 days earlier in plots with raised temperature than in controls (Table V.2, Fig. V.2). Fruit senescence was significantly earlier on warmed plots for *D. glomerata* (-9 days, P= 0.002) but not for *A. odoratum* (-4 days, P= 0.128) or *H. lanatus* (-1 day, P= 0.206) in 2010 (Table V.2, Fig. V.2).

In 2011 all studied species showed significant differences between treatments in the total development (*A. odoratum* P= 0.003, *D. glomerata* P= 0.014, *H. lanatus* P= 0.007 and *M. caerulea* P= 0.040) (Table V.2). Post-hoc tests confirmed that differences were especially strong between W and control plots. The total development of *A. odoratum* and *H. lanatus* was on average 5-6 days earlier on W than on control or WT plots. The effect was similar of the WWT treatment on the total development of *D. glomerata and H. lanatus* but slightly less for *M. caerulea* (only up to the secondary growth stage *end of flowering*) which advanced by 3 days (Table V.2). For *H. lanatus* total development was also significantly different between WT and WWT plots, showing an advance of 6 days on WWTs (Table V.2).

In general, warming has a greater influence than water table manipulations on single key phases in 2011. Phenology of grasses was earlier on warmed plots (-1 to -9 days) and slightly later on plots with higher water table level (1-2 days) (Fig. V.2). Post-hoc tests showed that flower development and flowering of *A. odoratum* and *H. lanatus* were significantly earlier (-5 to -9 days) on W compared to control and WT plots (Table V.2). A significant difference was also shown between WWT and controls and between WWT and WT for flower development of *H. lanatus* (advance by WWT: 10 days). Ripening was only significantly different between control and W plots for *A. odoratum* (advance of 8 days by W) and between WT and WWT plots for *H. lanatus* (7 days earlier on WWT) (Table V.2, Fig. V.2).

Warming and water table manipulations, singly and in combination, did not affect the key phase fruit senescence for all species in both years except for *D. glomerata* in 2010 which showed a significant advance of fruit senescence on W plots (-9 days) (Table V.2).

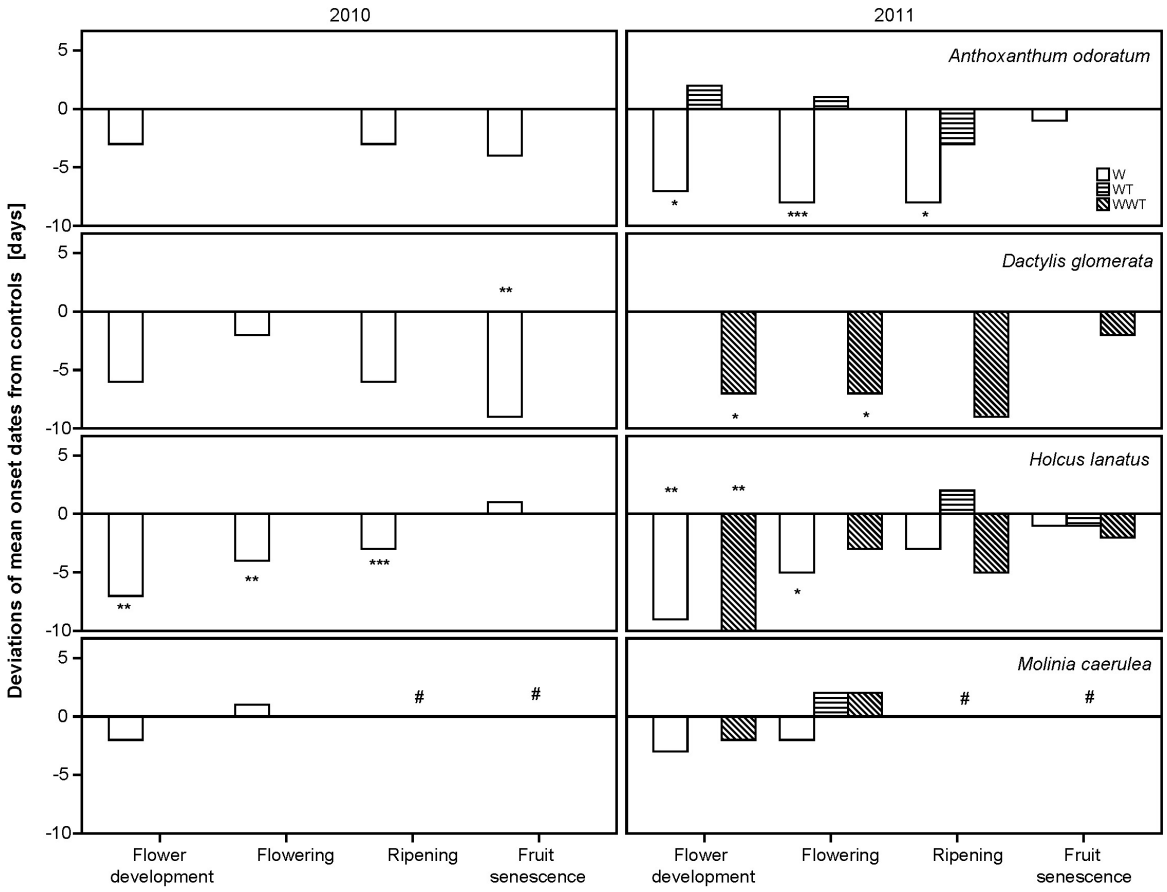

Figure V.2 Deviations of mean onset dates of key phases (flower development, flowering, ripening, fruit senescence) for different treatments from controls. Manipulative experiments were conducted in 2010 (W: warming) and 2011 (W, WT: water table rise, WWT: warming + water table rise). Asterisks indicate level of significance. *** P≤ 0.001, ** P≤ 0.01, * P≤ 0.05. #= Key phases could not be observed due to cutting activities on site.

Table V.2 Repeated measures ANOVA showing differences in the total development and in the timing of key phases (flower development, flowering, ripening and fruit senescence) between treatments in 2010 and 2011 for *Anthoxanthum odoratum* L., *Dactylis glomerata* L., *Holcus lanatus* L. and *Molinia caerulea* L.. N = Number of replicates on which different species could be monitored divided by treatment (C: control, WT: water table rise, W: warming, WWT: warming + water table rise). Numbers in bold are significant (P≤ 0.05). Asterisks show significant differences from Tukey's post-hoc tests. *** P≤ 0.001, ** P≤ 0.01, * P≤ 0.05. #= Key phases could not be observed due to cutting activities on site.

			Anthoxanthum odoratum			*Dactylis glomerata*			*Holcus lanatus*			*Molinia caerulea*		
		Treatment	Mean	N	P	Mean	N	P	Mean	N	P	Mean	N	P
Total development	2010	C	137	5	0.099	168	2	**0.034**	169	6	**0.008**	188	4	0.218
		W	133	3		163	5		165	6		187	4	
	2011	C	142	3	**0.003**	160	2	**0.014**	152	2	**0.007**	185	2	**0.040**
		WT	142	3			0		152	2		184	2	
		W	136	3			0		147	3		181	1	
		WWT		0		155	3		146	2		182	3	
Flower development	2010	C	124	5	0.245	148	2	0.161	152	6	**0.005**	179	4	0.388
		W	121	3		142	5		145	6		177	4	
	2011	C	117	3	**0.012**	145	2	**0.014**	143	2	**0.002**	193	2	0.072
		WT	119	3			0		143	2		193	2	
		W	110	3			0		134	3		190	1	
		WWT		0		138	3		133	2		191	3	
Flowering	2010	C	145	5	0.807	167	2	0.307	170	6	**0.007**	235	4	0.667
		W	145	3		165	5		166	6		236	4	
	2011	C	134	3	**<0.001**	161	2	**0.020**	160	2	**0.042**	229	2	0.199
		WT	135	3			0		160	2		231	2	
		W	126	3			0		155	3		227	1	
		WWT		0		154	3		157	2		231	3	

			Anthoxanthum odoratum			*Dactylis glomerata*			*Holcus lanatus*			*Molinia caerulea*		
		Treatment	Mean	N	P	Mean	N	P	Mean	N	P	Mean	N	P
Ripening	2010	C	171	5	0.090	185	2	0.237	181	6	**<0.001**			
		W	168	3		179	5		178	6				
	2011	C	155	3	**0.014**	176	2	0.079	168	2	**0.028**			
		WT	152	3			0		170	2				
		W	147	3			0		165	3				
		WWT		0		167	3		163	2				
Fruit senescence	2010	C	195	5	0.128	216	2	**0.002**	199	6	0.206		**#**	
		W	191	3		207	5		200	6				
	2011	C	168	3	0.910	193	2	0.629	179	2	0.316			
		WT	168	3			0		178	2				
		W	167	3			0		178	3				
		WWT		0		191	3		177	2				

* (WT, W)

* (170, 165)

V.4.2 CHANGES IN THE DURATION OF KEY PHENOLOGICAL PHASES

In general the length of phenological phases was longer in 2010 than in 2011. The duration of flower development and flowering was not significant different between treatments for all species and both years. Ripening differed significantly between W and controls for *D. glomerata* (P= 0.009) and *H. lanatus* (P= 0.004) in 2010. Fruit senescence was significantly different between treatments for *H. lanatus* (P= 0.004) in 2010 and for *A*. *odoratum* (P= 0.035 between W and controls, post-hoc tests) and *D. glomerata* (P= 0.001) in 2011 (Fig. V.3). Flower development mostly lasted longer on warmed plots (W) than on controls (1-7 days) except for *M. caerulea* in both years (2010: -4 days and 2011: -10 days) and *H. lanatus* in 2010 (-1 day) (Fig. V.3). Water table manipulations and the combined warming and water table manipulations also prolonged flower development (0-2 days and 3-4 days, respectively). Effects of warming on flowering (-1 to +5 days), ripening (-6 to +4 days) and fruit senescence (-5 to +12 days) (Fig. V.3) were inconsistent. Shifts in water table level also led to contradictory results showing a shortening of the duration of ripening and fruit senescence for *H. lanatus* (-2 days and -3 days), of flowering and ripening for *A. odoratum* (-3 days and -1 day) and of flowering for *M. caerulea* (-2 days), whilst lengthening fruit senescence for *A. odoratum* (+1 day) and flowering for *H. lanatus* (+1 day) (Fig. V.3) were detected. The combination of increased water table level and temperatures had no effect on the duration of ripening for *D. glomerata* but prolonged fruit senescence (+8 days) and shortened flowering (-1 day) of the same species. Furthermore, flowering of *M. caerulea* (-1 day) and ripening of *H. lanatus* (-3 days) were shortened. However, flowering and fruit senescence of *H. lanatus* were prolonged (+1 day and +2 days) (Fig. V.3).

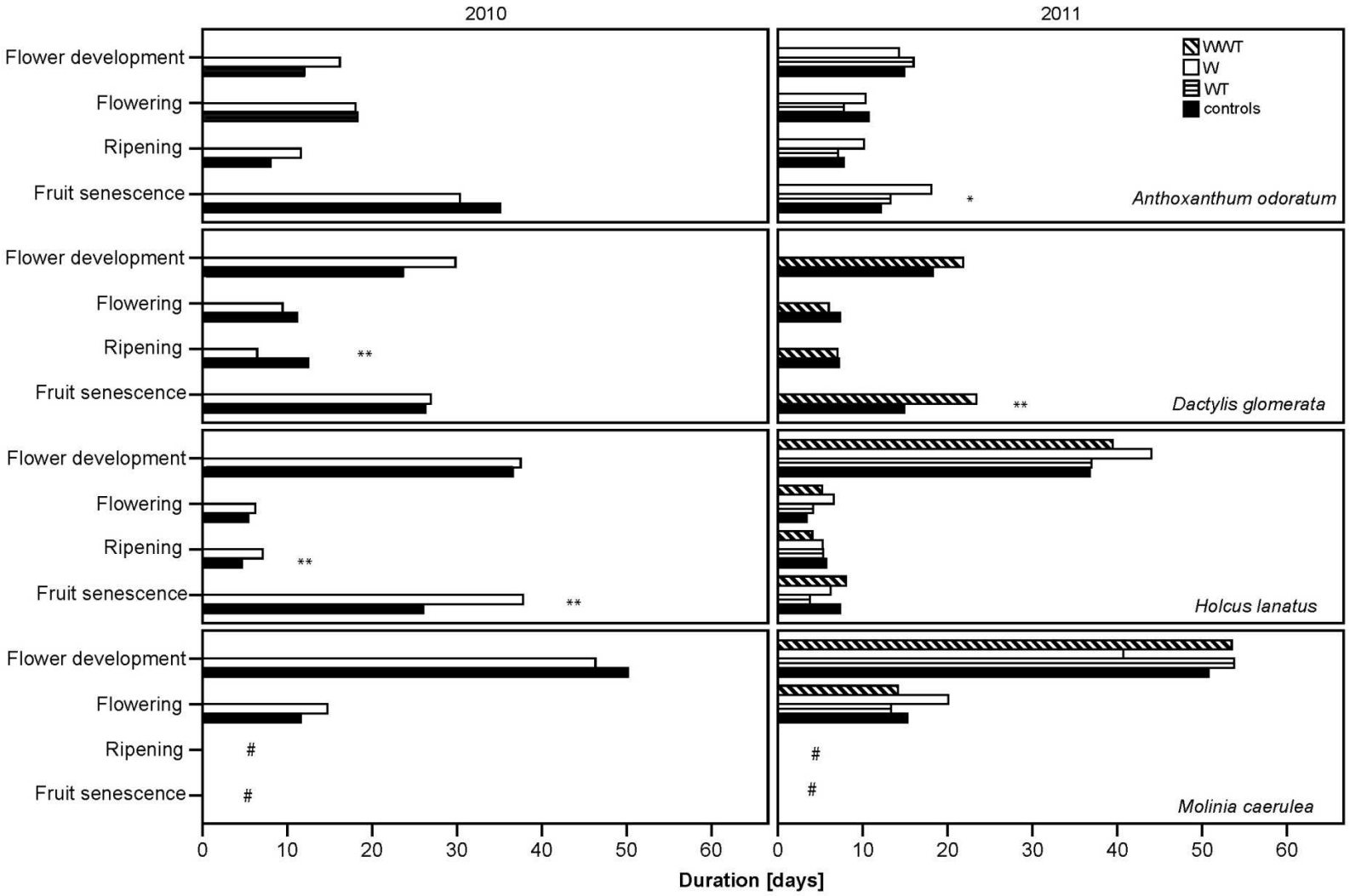

Figure V.3 Duration of key phases (flower development, flowering, ripening, fruit senescence) for control and treatments in 2010 (W: warming) and 2011 (W, WT: water table rise, WWT: warming + water table rise). Asterisks indicate level of significance. *** P≤ 0.001, ** P≤ 0.01, * P≤ 0.05. #= Key phases could not be observed due to cutting activities on site.

V.4.3 VEGETATION HEIGHT

In general, vegetation was higher in 2010 than in 2011. In 2010 vegetation was significantly higher on warmed plots than on controls (P= 0.044). After mid-July (DOY 200) vegetation height declined due to a thunderstorm on day 203 which flattened the plants. In 2011 vegetation height was not significantly different between treatments (P= 0.211). Plants were tallest on WWT plots in 2011 (Fig. V.4).

Full flowering was earlier on warmed plots with higher vegetation than on controls in 2011 (DOY 166 and 179, respectively) and about the same in 2010 (DOY 180 and 181, respectively).

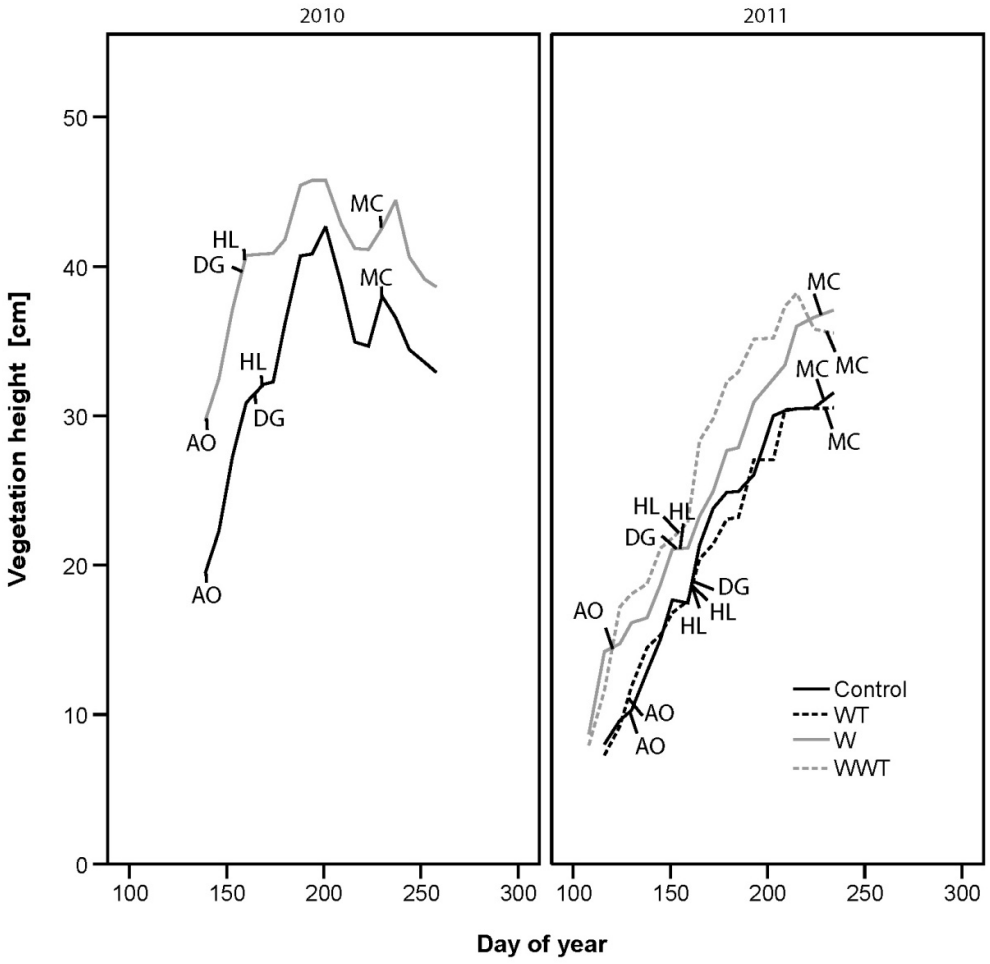

Figure V.4 Vegetation height on control and treated plots in 2010 (W: warming) and 2011 (W, WT: water table rise, WWT: warming + water table rise). Lines indicate full flowering dates of four grass species (AO: *Anthoxanthum odoratum* L., HL: *Holcus lanatus* L., DG: *Dactylis glomerata* L., MC: *Molinia caerulea* L.).

V.5 DISCUSSION

This study clearly demonstrates the relationship between warming and the timing of plant phenology in a peatland area. However, changes in the water table level had almost no effect on plant phenology.

In this study open-top chambers passively increased air temperatures by 0.4 °C (2010) and 0.9 °C (2011). A similar temperature rise of 0.4 °C was reported by De Frenne *et al.* (2010) for an understory experiment in a forest stand. Several studies showed a higher increase in air temperatures of about 0.7-1.8 °C for Arctic or alpine ecosystems (Marion *et al.* 1997; Kudernatsch *et al.* 2008). Differences in temperature rise can be due to higher plant growth of temperate grassland species relative to Arctic or alpine species, often leading to greater transpiration within chambers which has a cooling effect. On WWT plots, warming of OTCs was greater (difference from controls: 1.5 °C) probably due to differences in vegetation composition between plots or due to wind effects caused by meso-topographic differences.

In general, warming advanced total phenological development and single key phases of grasses. Total development and key phases were observed earlier in 2011 than in 2010 due to warmer temperatures, especially in spring. Response of plants to warming was greater in 2011 due to the greater warming effect of the OTCs that year. Flowering of grasses showed a mean response of -7 days per 1 °C. This is in agreement with several other studies showing a phenological advance of 1.3-11.0 days per degree warming for flowering (Arft *et al.* 1999; Cleland *et al.* 2006; Hovenden *et al.* 2008b). Flower development was slightly more sensitive to temperature change, showing a response of -9 days per 1 °C. Ripening and fruit senescence were less affected by temperature (-6 days/°C and -1 day/°C), which is in agreement with Menzel *et al.* (2006), who also showed a weaker response for fruit ripening compared to earlier spring phases. Furthermore, Hoffmann *et al.* (2010) showed that advanced flowering does not necessarily also advance seed maturation. Moreover, early budding and flowering can alter seed set since damage intensity from insect herbivores as well as the activity level of pollinators may shift (Both *et al.* 2009). Fruit senescence was only modestly influenced by temperature, probably because this phase is primarily controlled by mechanical factors such as wind or trace gas measurements on site.

On WWT plots temperature increase in OTCs was greatest, however, the phenological development resembled that in W plots. Results of phenological development on WT plots, led to the assumption that greater water availability delays the phenological development and thus, balances the warming effect in WWT plots. However, several other studies have shown that increased precipitation or heavy rainfall events have no significant impact on flowering phenology in grassland ecosystems (Cleland *et al.* 2006; Sherry *et al.* 2007;

Jentsch *et al*. 2009). In those studies increased water availability was only temporary, so plants were probably not able to adapt their development to the new conditions in such a short time. Grasses eventually need a permanently increased water table level for a longer time period in order to respond to changed conditions. Thus, we suggest continuing those experiments to test whether plants' reaction to water level manipulations is delayed.

In contrast to start of key phases, our manipulative experiment did not significantly influence the duration of most key phases. Results are contradictory, showing either a lengthening or shortening of the duration of key phases. Results from other studies which mainly focused on flower duration under warmer conditions were also inconsistent. Dunne *et al.* (2003) showed that warming led to longer flowering duration in subalpine meadows. Further studies showed no response of warming on flowering period for dwarf shrubs (Llorens & Penuelas 2005), subalpine angiosperms (Price & Waser 1998) and temperate grassland species (Hovenden *et al.* 2008b). Contradictory results, as also shown by Sherry *et al.* (2007) in a tallgrass prairie, led to the conclusion that the response of flowering period to warming is species-specific (Hovenden *et al.* 2008b). However, general conclusions from these ambiguous results should only be drawn with care since there are slight differences in flowering duration definitions between studies.

Heavy rain shortened flowering duration of grassland and heath species (Jentsch *et al.* 2009). However, changes in the duration of key phases due to water table manipulation were not consistent in our study. Duration of ripening and fruit senescence sometimes differed significantly between treatments. We suggest that differences in the length of fruit senescence are randomly depending on presence or absence of mechanical factors (*e.g.*, trace gas measurements with chambers) which may influence seed fall. Durations of key phases were mainly longer in 2010 than 2011 with a greater difference earlier in the year (21 days longer for flower development and 1 day longer for ripening in 2010 than 2011). These results lead to the conclusion that greater temperature differences (*e.g.*, 2.6 °C difference between spring 2010 and 2011) are probably necessary to show impacts of warming on the duration of key phases. Further investigations are needed to test whether greater temperature differences will have an impact on the duration of key phases.

Mean vegetation height was shorter in 2011 (23.4 cm) than in 2010 (37.2 cm) even though temperatures were higher in 2011. Several studies showed that higher temperatures accelerate plant growth (Hudson *et al.* 2011) especially of graminoids (Kudernatsch *et al.* 2008). Vegetation height was probably lower in this study due to trace gas measurements on site. Chambers with a height of 50 cm eventually damaged taller vegetation which restricted plant growth. Effects may accumulate after two years of measurements. However, manipulative experiments in this study confirmed findings of higher temperatures

accelerating plant height. Plants in OTCs were significantly taller; the tallest plants were found in WWT plots. This was probably due to the highest temperature differences being between WWT and control plots. However, the greater warming effect was not reflected in flower phenology which showed no further advance compared to WT plots. It appears that plant growth probably is more responsive to higher temperatures than phenology. An increased water table level had no impact on plant height. Thus, warming influences both vegetation height and timing of full flowering which led to the conclusion that resources were sufficient to produce taller plants and to reproduce earlier.

V.6 CONCLUSION

This study showed that only warming influenced grass phenology whereas changes in water table level did not significantly affect development. Thus, raising the water table (to reduce carbon losses) to levels which still allow grassland management would not substantially influence the phenology of grassland species. However, further investigations are needed to test whether grasses delay their response to water table rise and whether higher temperatures would influence the duration of key phases. Temperate peatland sites appear to provide sufficient resources to support all species. A shift in plant composition and therefore in the carbon cycle of the plants appears to be unlikely at the levels of water table rise established. Full restoration however, would be expected to shift plant composition and reduce significantly carbon losses from respiration.

Acknowledgments

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VI GENERAL DISCUSSION

VI.1 SAMPLING AND METHODOLOGY

A detailed observation key with both intermediate stages and stages marking the end of phenophases as used in Chapters 2, 4 and 5 in this thesis provides information about the entire phenological development of plants by switching from event to status monitoring. Thus, a first step was to modify the original BBCH scales created for important agricultural crops to the special needs of the wild species observed in this thesis. An important aspect was to consider that wild species grow closer together, often in combination with other species and are much smaller.

The phenological observer guidelines of the German Meteorological Service recommend that volunteers record the date of occurrence of phenophases in the field. This requires a frequent observation intensity of every 2-3 days, otherwise the observer misses the exact date of the beginning of the phenophases (DWD 1991). However, while using a detailed observation key such as the BBCH scale, it is not necessary to be present at the exact start of the stage since the key allows recording of the frequency distribution of phenophases of a certain number of individual plants on each sampling date. Classical onset dates as used in climate research studies could be interpolated from these data afterwards. Thus, sampling intensity could be reduced to once a week which was necessary in order to cover observations at each, partly remote, research site in this study. However, since this observation method is not common in phenological studies, a methodology was needed to determine the classical onset dates. Thus, in Chapter 2 we focused on the first leading research question of this PhD thesis: **How to estimate onset dates from BBCH scale recording?**

To estimate phenological onset dates from frequency distribution data, four methods were presented and compared in Chapter 2. All four methods can be used to determine onset dates; however, they sometimes differ greatly in result and complexity of calculation. For this thesis we decided to base our calculations on the OLR (Ordinal Logistic Regression) method (see Chapter 4 and 5) since compared to the Weighted Plant Development (WPD) method it provides information about the progression of stages (including the beginning, speed of passage and the end of secondary growth stages) and considers that stages are not of equal length (ordinal scale approach). Furthermore, compared to all other methods (WPD, Pooled pre/post Stage Development (PSD) and Cumulative Stage Development (CSD)), OLR is based on the frequency distribution over time which includes the entire progression of plants in the model and not only the progression of a single stage. However,

on the other hand, the OLR method can only estimate onset dates when observation data for the stage of interest exists. An observation intensity of once a week, as used in this thesis, can sometimes be too long to catch short-lasting growth stages such as flag leaf sheath opening of grass species. Thus, for those stages the observation data was sometimes missing. However, most key phenological events, such as full flowering or end of flowering, lasted longer than one week so that observation data were recorded, hence we accepted the disadvantage of the OLR method for this thesis. However, if short-lasting phenophases are of interest either an increased sampling intensity or another methodology for estimating onset dates (*e.g.*, WPD or PSD) should be used.

VI.2 NATURAL GRADIENTS

Since altitudinal gradients provide different natural temperature scenarios, those studies are useful for assessing plant responses to climate change by substituting space-for-time. However, compared to latitudinal studies, phenological approaches focusing on altitudinal gradients are rare. Thus, in Chapter 3 and 4 we addressed the second leading research question of this PhD thesis: **How does plant phenology vary with altitude?**, by analyzing phenological data monitored in the Berchtesgaden National Park, covering altitudinal gradients of about 800 m (Chapter 3) or 1400 m (Chapter 4), respectively. Phenological development was very similar in both studies, showing a delay, averaged over all species and phenophases, of 3.8 days (Chapter 3) or 3.4 days (Chapter 4) per 100 m increase in altitude. Slight differences occurred due to different species tested in both studies. These results were in agreement with other studies which showed a delay of 2-4 days per 100 m altitudinal change for leaf unfolding of different tree species (Roetzer & Chmielewski 2001; Dittmar & Elling 2006; Richardson *et al.* 2006; Migliavacca *et al.* 2008; Vitasse *et al.* 2009a; Moser *et al.* 2010; Pellerin *et al.* 2012) or of 3 days per 100 m increase in altitude for grass species (Ziello *et al.* 2009). Thus, as expected, plant species, including herbs and trees delayed their development with decreasing temperature. However, since it is common to apply gradient studies for assessing the effects of future climate change on plant phenology we considered in Chapter 3 ***if phenological responses to temperature over time match the phenological variability with altitude***, or if other factors than temperature influence phenology along altitudinal gradients. In Chapter 3, phenological response to altitude was slightly stronger than to temperature. This was shown by species-specific lapse rates which were derived by the ratio of significant altitude and temperature coefficients. The mean of these lapse rates (-0.73 °C / 100 m) were mainly higher than the mean temperature lapse rate of March to July (-0.51 °C / 100 m), which indicates that temperature is not sufficient to explain the variability in the timing, thus, also other factors influence plant phenology here. In this thesis tree species showed only a weak response to temperature and altitude

(Chapter 3). It is known that tree species in particular are also influenced *e.g.,* by photoperiod (Heide 1993a; Vitasse *et al.* 2011) or chilling (*e.g.*, Schaber & Badeck 2003; Caffarra & Donnelly 2011) thus, we also suggested a high dependency on photoperiod and chilling. Authors' suggestions that in alpine regions the winter chilling requirement can be neglected because it is easily fulfilled during winter (*e.g.*, Van Wijk *et al.* 2003; Chuine *et al.* 1999), is not necessarily true for our study since elevation of sites is not extreme (~600-1400 m) and hence winter chilling requirement may not be fulfilled. In alpine and Arctic ecosystems snowmelt and temperature after snowmelt mainly influence plant development (*e.g.*, Pop *et al.* 2000; Molau *et al.* 2005; Inouye 2008; Karlsen *et al.* 2008). In Chapter 3 of this thesis early herbs in particular showed a strong response to altitude, however the response to temperature was weak, which may indicate a strong influence of snow. Only a small number of species and phenophases showed a similar sensitivity to altitude and temperature, thus this study demonstrated that, in general, results of altitudinal studies should be used with caution to assess phenological plant responses to climate change by substituting space-for-time.

Since altitudinal studies dealing with herbaceous species are rare, we focused in Chapter 3 of this thesis on the research questions: ***How does phenology of herbs vary with altitude? Are herbaceous species more sensitive to either altitude or temperature than woody species (shrubs or trees)?*** For this we analyzed leaf development and flowering of 21 different species, including ten woody (six deciduous trees, one evergreen tree, and three shrubs) and eleven herbaceous species. The study demonstrated a delay of 3.9 days / 100 m for flowering and leafing of herbs and no significant difference in sensitivity between herbs and woody plants. This is in accordance with Wolkovich *et al.* (2012) who also showed no significant difference in the phenological response of both life forms, either in experimental or observational studies. However, in the current thesis a significant difference was detected between herbs and trees in altitudinal coefficients (3.7 days / 100m and 2.7 days / 100m, respectively) but not in temperature coefficients (-6.0 days / 1 °C and -4.8 days / 1 °C, respectively). Thus, even though herbs are more sensitive it appears that the reason for that is not temperature but other factors influencing herbal development. Since it is known that many species, especially herbs and shrubs, have synchronized their phenological development with snow melting dates (*e.g.*, Galen & Stanton 1995; Inouye *et al.* 2002; Dunne *et al.* 2003; Stinson 2004; Aerts *et al.* 2006), we suggested snow as the main influencing factor for differences in the sensitivity to altitude between herbs and trees.

In Chapter 3 of this thesis we additionally addressed the research question: ***How does the duration of phenophases vary with altitude?*** Only very few species showed a significant

change in the length of leaf development and flowering period with increasing altitude. However, the duration of flowering and leafing was mostly shorter at high altitudes for very early and late flowering species in this study. Species early in the year are likely to be subject to late frost damage (*e.g.*, Weiser 1970; Molau 1997; Inouye 2008; Rigby & Porporato 2008), whereas species late in the year are susceptible to the first frost event in the next winter season. Thus, an extension of flowering or leafing duration should be avoided. Species in the middle of the observation period showed no change in the duration of phenophases, which was in agreement with Tyler (2001) showing that both the beginning and the end of flowering advanced similarly to higher temperatures.

VI.3 MANIPULATIVE EXPERIMENTS

In addition to altitudinal gradients, manipulative experiments are also used to assess plant responses to climate change (*e.g.*, Price & Waser 1998; Dunne *et al.* 2003; Cleland *et al.* 2006; Wipf & Rixen 2010). Thus, in Chapter 4 and 5 of this PhD thesis we focused on the third leading research question: **What effects do manipulative experiments have on plant phenological development?** To answer this question we investigated six different manipulative treatments including, warming, elevated water table level, warming combined with elevated water table level, advanced snowmelt, delayed snowmelt and drought. Treatments were either carried out in a temperate fen-peatland (warming and water table level) or on meadows in the Berchtesgaden National Park covering an altitudinal gradient from the foothill zone to alpine level (ca. 600-2000 m; snowmelt and drought). In both studies 14 different species were observed, including 6 grass species and 8 herbs. We either monitored the entire plant development or single phenological key phases such as flower development, flowering, ripening or fruit senescence.

The six weeks of simulated drought (1000-year extreme drought event), conducted on meadows in the National Park, mostly did not affect flowering of tested species along the altitudinal gradient (Chapter 4). In other studies responses to drought varied and appeared ecosystem dependent. In agreement with our study, Bloor *et al.* (2010) showed no effect of drought on phenology of grass species in an alpine meadow in France. However, for drought sensitive plant species in the Mediterranean area a simulated drought delayed flowering (Prieto *et al.* 2008; Bernal *et al.* 2011). In contrast, Jentsch *et al.* (2009) showed an advance in the mid-flowering date for grassland and heathland species. Thus, it appears that in the Alps short-term drought periods, as conducted in this study and by Bloor *et al.* (2010), are not sufficient to reduce soil moisture content to a level which affects plant phenology. Dunne *et al.* (2003) suggested that soil moisture plays no or only a small role in the timing or duration of flowering as long as soil moisture conditions are not markedly dry

or wet. Thus, we suggested that a drought period probably needed to exceed a 1000-year extreme event to influence plant phenology significantly.

As already mentioned in section VI.2 NATURAL GRADIENTS, there is evidence that phenology of many species, especially herbs and shrubs, strongly reacts to snow melting date (*e.g.*, Galen & Stanton 1995; Inouye *et al.* 2002; Dunne *et al.* 2003; Stinson 2004; Aerts *et al.* 2006). Thus, we expected a high responsiveness of species tested in this study to shifts in the date of snowmelt. In general, a late date of snowmelt mainly delays plant phenology (Weaver & Collins 1977; Torp *et al.* 2010; Cooper *et al.* 2011) whereas an early date of snowmelt advances the timing of plant development (*e.g.*, Dunne *et al.* 2003; Price & Waser 1998; Inouye *et al.* 2003; Wipf *et al.* 2009; Lambert *et al.* 2010; Wipf 2010; Chen *et al.* 2011). However, in this thesis, phenological responses of species to later snowmelt were rather small (Chapter 4), either because the treatment effect was also small or because the response to snow melting dates were rather species-specific. In contrast, an earlier snowmelt advanced the flowering phenology of grassland species between 1-7 days in this study although the effect was only significant for a few species and phenophases (Chapter 4). Wipf *et al.* (2009) demonstrated similar effects of earlier snowmelt, showing an advance of flowering of about 3-10 days for different species. Since, in this study, impacts of delayed snowmelt on flowering phenology were not as large as expected we wondered even more ***if species respond to manipulative treatments differently at lower or higher altitudes.*** This question was addressed in Chapter 4, showing that effects were greater on higher (>1300 m) than on lower sites (<1300 m) for advanced snowmelt plots. However, for the other treatments, drought and delayed snowmelt, response was similar for both altitude classes. It is suspected that differences in phenology on lower and higher sites are due to large differences in treatment effects on advanced snowmelt plots and not due to a different response pattern of plants at lower and higher altitudes. Pellerin *et al.* (2012) support this idea since they found that thermal sums, required for budburst and leafing, increased with altitude for different tree species which is mainly due to the delaying effects of snow cover and melt and the fact that reduced snow cover will in particular have an influence at high altitudes since at low altitudes snow is mostly not a limiting factor. However, Defila & Clot (2005) showed from a 50-year time series in Switzerland that the total proportion of significant trends was higher in the alpine regions (above 1000 m a.s.l., 42%) than in the lowland (below 600 m a.s.l, 33%). Since temperature showed the same increase in the lowland and in the alpine regions (1.5 °C) for this period it is suspected that a higher sensitivity of plants at high altitudes to climate warming may be the reason for differences in phenological trends (Defila & Clot 2005). However, this could not be verified by other studies, which showed no statistical dependence on altitude for phenological trends (Ziello *et al.* 2009; Jochner *et al.* 2012). Defila & Clot (2005) also demonstrated a stronger

advance of full flowering in the lowland (32 days) than in the alpine region (20 days). However, due to a strong advance of leaf colouring at lower altitudes the photosynthetic period (from leaf unfolding to leaf colouring) was prolonged more in the alpine regions (9 days) than in the lowlands (3 days). The authors suggested that plants at higher altitudes have benefited more from climate change due to a longer photosynthetic period in those regions (Defila & Clot 2005).

Since phenological studies in temperate fen-peatlands are rare, in Chapter 5 of this thesis we focused on the research question: ***How do grassland species respond to manipulative treatments in a temperate fen-peatland?*** In 2011, the warming treatment in the Freisinger Moos, simulated by OTCs advanced both the total development and single key phenological events of studied grass species. The total development of all species was advanced by 5-6 days. The response of flowering to warming (-7 days / 1°C) was slightly higher in this thesis than demonstrated by experimental studies in other ecosystems which ranged between -1 to -3 days per 1 °C warming for a Californian annual grassland (Cleland *et al.* 2006) and -2 to -5 days per 1 °C warming for an Arctic grassland (Arft *et al.* 1999). In contrast, the response of flowering to warming was stronger for species in Australian grassland showing a mean advance of 11 days per 1 °C temperature increase (Hovenden *et al.* 2008b). Results in Chapter 5 also showed a higher sensitivity of species to temperature in comparison to long-term studies, demonstrating an advance of 4.5 days per 1 °C warming for flowering in the UK in the 1990s (Fitter & Fitter 2002) and 4.6 days per 1 °C temperature increase for spring and summer phases (plants and animals) in Europe between 1971 and 2000 (Menzel *et al.* 2006).

Chapter 5 in this thesis also demonstrated that an elevated water table level in the Freisinger Moos did not significantly influence the total development or key phenological events of grass species in 2011. This is in agreement with other studies showing no significant response to altered water availability such as higher precipitation or heavy rain events on flower phenology for grassland and heathland species (Jentsch *et al.* 2009), for species in a Californian annual grassland (Cleland *et al.* 2006) or grass species in a perennial grassland in Oklahoma (Sherry *et al.* 2007). Thus, higher water availability has only a small influence on the phenological development of grass species in a temperate fen-peatland, since species there can handle higher water table levels. Thus, raising the water table in order to reduce carbon losses to levels which still allow management would not substantially influence the phenology of grassland species.

Furthermore, in Chapter 5 we dealt with the research question: ***What effect has the interaction of elevated water table level and higher temperatures on the development of grassland species?*** The total phenological development in the Freisinger Moos in 2011

was advanced by 5-6 days on combined elevated water table level and temperature plots which resembles the advance of species on the warming-only treatment, even though the warming effect was greater on the combined plots (+0.9 *vs*. +1.5 °C). Thus, it appeared that a higher water table level delayed the phenological development and balanced the warming effect on combined plots. However, as already mentioned, elevated water table level (in Chapter 5), higher precipitation (*e.g*., Cleland *et al.* 2006) or heavy rain events (*e.g*., Jentsch *et al.* 2009) showed no effect on plant phenology. Thus, ambiguous results on single and mixed effect plots in Chapter 5 demonstrated the importance of studies focusing on the interaction of several aspects of climate change since plant phenological responses may be different if only single or combined factors are manipulated. Dunne *et al.* (2003) showed that mostly multivariate microclimate models (*e.g*., snowmelt date, soil temperature and soil degree-days) explained about 30 to 50% more variance for the timing of flowering than univariate models including, for example only date of snowmelt.

Since many studies have mainly focused on the flowering of plant species we wondered: ***How do phenological events such as flower development, fruit ripening or fruit senescence respond to manipulative treatments?*** Chapter 5 in this thesis demonstrated that warming treatment advanced all key phenological phases. However, the response varied strongly with phases showing the strongest effect for flower development (-8 days / 1 °C) and the smallest for fruit senescence (-1 day / 1 °C). Flowering was advanced by 7 days per 1 °C warming and fruit ripening by 6 days per 1 °C temperature increase. Thus, the response of phenophases to temperature declined through the year which is in agreement with results in Chapter 3 and 4 and other studies showing highest temperature responses for spring and summer phases (*e.g*., Sparks & Carey 1995; Fitter & Fitter 2002; Dose & Menzel 2004; Menzel *et al.* 2006). The phenophase fruit senescence was only modestly affected by temperature, which we attributed to a strong influence of mechanical factors such as wind in general or trace gas measurements in particular. An elevated water table level did not influence key phenological phases. Thus, differences in the sensitivity between phases could not be demonstrated.

In Chapter 4 and 5 of this PhD thesis we also dealt with the question: ***Do manipulative treatments influence the duration of phenophases?*** As in the altitudinal gradient study, the duration of key phases was also largely not significantly influenced by treatments in Chapters 4 (flowering duration) and 5 (flower development, flowering, fruit ripening or fruit senescence). In other studies effects of treatments on flowering / reproduction duration varied greatly. No detectable response to treatments on flowering duration was found after experimental warming by Price & Waser (1998), Tyler (2001) and Hovenden *et al.* (2008b), after shifting snow melting date by Wipf (2010) and after elevating CO_2 concentrations by

Hovenden *et al.* (2008b). However, an extension of flowering duration, especially for early flowering species was demonstrated by Dunne *et al.* (2003) after advancing the date of snowmelt or elevating temperature. In the grass genus *Festuca* warmer soil, decreased soil degree days and later snowmelt also extended the duration of flowering (Dunne *et al.* 2003). Simulated drought either compressed (Llorens & Penuelas 2005) or extended flowering duration (Llorens & Penuelas 2005; Jentsch *et al.* 2009) of herbaceous and shrub species. Partly contradictory results across literature appear highly treatment and species dependent. However, general conclusions from these ambiguous results should be only drawn with care since there are slight differences in flowering duration definitions between studies. In general, Tyler (2001) suggested that the duration of flowering is only slightly influenced by temperature since the timing of the onset of both the beginning of flowering and the end of flowering advances in response to temperature increase. This emphasizes most results in this thesis which show no alteration of flowering duration due to treatments. Duration of all other key phenological phases in this thesis, such as the duration of flower development, ripening or fruit senescence, also showed no detectable shift. This further supported the idea of Tyler (2001) that temperature influences the timing of the beginning and the end of phenophases to the same extent.

Combining the results from natural gradients and experiments, it finally can be concluded that a large number of herbaceous and tree species do not significantly change duration of key phenological phases due to higher temperature, shifts in snow melting date, higher water table level or drought.

VI.4 NATURAL GRADIENTS *VERSUS* EXPERIMENTS

In general, scientists normally focus their research interest either on natural climate gradients or climate manipulations to assess plant responses to climate change. A combination of both in field-based research is not common (Dunne *et al.* 2004).

Both approaches have advantages and disadvantages. In experimental studies novel conditions under climate change for which historical observations offer no comparison can be simulated, controlled, introduced immediately and applied either singly or with different levels of effect (Dunne *et al.* 2004; Wolkovich *et al.* 2012). However, manipulative experiments mostly fail to simulate one or few aspects of climate change without also altering other factors unexpectedly. Furthermore, field experiments mostly cover only a small area (Shaver *et al.* 2000) and due to often expensive or labour-intensive building and running costs, many manipulative experiments are conducted only over a short period of time, of one to ten years (Dunne *et al.* 2004; Leuzinger *et al*. 2011). However, longer term experiments are important since Leuzinger *et al.* (2011) showed, by combining several

long-term experimental studies including elevated CO_2, soil warming and nitrogen addition with four FACE experiments, that effect size of response variables either die out with time or even out at a lower steady state level.

Climate factors in natural gradient studies, on the other hand, cannot be controlled but long-term changes due to climate change are simulated across sites by substituting space-for-time. Thus, only if phenology responds to climate change over time to the same extent that ecosystems react now to changing climate conditions over space, a space-for-time substitution is reasonable (Dunne *et al.* 2004). In this thesis phenological response to altitude was stronger than to temperature (Chapter 3), thus, a space-for-time substitution should be only used with care here. Furthermore, in general, plant responses to natural gradients reflect long-term dynamics whereas responses to manipulative treatments are based on short-term reactions (Dunne *et al.* 2004). Several studies have cautioned about equating short-term responses of experimental studies with long-term mechanisms from gradient studies since results often only reflect parts of the potential dynamic of an ecosystem (Shaver *et al.* 2000; Dunne *et al.* 2004). Experiments may capture only plastic responses to temperature change whereas long-term studies may also include genotypic changes or shifts in community composition. Therefore, scientists repeatedly called for integrating gradient studies with field experiments (*e.g.*, Dunne *et al.* 2003; Wolkovich *et al.* 2012). A synthesis of both approaches would provide overall information about ecosystem responses to climate change on long- and short-term scales.

The necessity of integrated approaches was emphasized again by Wolkovich *et al.* (2012) showing that warming experiments underpredict the advance of spring phenophases compared with long-term observations. Advances in the timing of flowering was underestimated 8.5-fold and of leafing 4.0-fold. Flowering phenology was 0.5 days earlier per 1 °C warming for experiments and 4.5 days earlier per 1 °C temperature increase for long-term observations. Leafing was 1.6 days / 1 °C earlier on experimental sites and 6.4 days / 1 °C for observational studies. Surprisingly, experiments even predict a delay of flowering (1.6 days / 1 °C) and only small shifts in leafing (-0.2 days / 1 °C) if only those species common in both studies were taken into account. In this PhD thesis flowering of grass species was advanced by 7 days per 1 °C warming in a fen-peatland in the Freisinger Moos. Both natural gradients in this study (Chapter 3 and 4) resulted in an advance of 6 days per 1 °C temperature increase for flowering and / or leafing of different grassland species and trees in the Berchtesgaden National Park (if temperature coefficients were used). In both experimental and natural gradient studies a similar plant response to temperature was demonstrated even though sensitivity is stronger in this PhD thesis (except for leafing for long-term data) than shown by Wolkovich *et al.* (2012). The

comparison is not really representative since by contrast with Wolkovich *et al.* (2012) we could only contribute a small number of species, research sites and a short study duration of only one year for our experimental study in the Freisinger Moos and the integrated study in the Berchtesgaden National Park. However, Wolkovich *et al.* (2012) highlighted that mismatches between experimental and long-term studies were not caused by different habitats or study durations.

Additionally, Wolkovich *et al.* (2012) detected only a higher temperature sensitivity of early flowering species in long-term observation studies but not in experimental studies. In Chapter 5 of this PhD thesis due to only a small data set in our warming experiment we could not statistically test whether species sensitivity to temperature changes throughout the year but we detected an obvious decline in sensitivity from early to late flowering species (-8 days / 1 °C for *Anthoxanthum odoratum* L. flowering in May to -2 days / 1 °C for *Molinia caerulea* L. flowering in August).

Thus, for this PhD thesis a substitution of short-term and long-term observations appeared to be reasonable since the response to warming is similar for the gradient and the experimental studies. However, a substitution of space-for-time should be only used with care since the phenological response of species was slightly stronger to altitude due to snow effects than to temperature for the natural gradient study in the Berchtesgaden National Park.

VII SUMMARY AND CONCLUSION

This PhD thesis introduced a new approach to phenological observations at remote study sites and highlighted findings on the impacts of altered abiotic parameters on plant phenology to assess plant responses to climate change.

Phenological observations were based on the BBCH scale which was slightly modified for wild species. The observations were conducted once a week by recording the frequency distribution of a certain number of individuals. Classical onset dates, as needed for climate change research, were estimated subsequently with the Ordinal Logistic Regression method. Observation key, sampling procedure and analysis method made phenological observations feasible even at remote study sites in this thesis by reducing sampling effort and intensity (Chapter 2).

Total development and / or key phenological phases were in particular influenced by temperature, showing a delay with altitude in the Berchtesgaden National Park (Chapter 3 and 4) and an advance due to the warming treatment in the temperate fen-peatland in the Freisinger Moos (Chapter 5). Large shifts in the timing of the onset of phenophases, however, might potentially disrupt *inter alia* the temporal overlap between pollinators or herbivores and host plants (Donnelly *et al.* 2011) or plant-plant interactions (Molau 1997; Dunne *et al.* 2003). The duration of flowering was only slightly influenced by temperature (Chapter 3, 4 and 5). For both studies in the Berchtesgaden National Park, the date of snowmelt played a key role in plant phenology, showing a strong influence on leafing and flowering along the altitudinal gradient (Chapter 3) and a significant advance in the timing of flowering after earlier snowmelt (Chapter 4). Flowering was more strongly affected by an advanced snowmelt at higher than at lower altitudes, whereas shifts appeared not to change with altitude but with treatment intensity (Chapter 4). Timing and duration of flowering was largely not influenced by delayed snowmelt. Furthermore, flowering duration was also not affected by earlier snowmelt (Chapter 4). Additionally, drought and an elevated water table did not influence the total development of plants and / or the timing and duration of key phenological phases (Chapter 4 and 5). Thus, a 1000-year extreme drought event in the Bavarian Alps as well as an elevated water table in a temperate fen-peatland did not substantially influence the phenology of grassland species. Thus, from a phenological perspective, elevating the water table level in fen-peatlands to reduce carbon loss, to levels where management is still feasible, is recommended. Furthermore, it is suggested that the risk of severe impacts of droughts on flowering phenology will be rather low in the Alps. This thesis also demonstrated that herbaceous species are more sensitive to temperature and snow than trees whereas species and phenophases later in the year are

less sensitive to temperature (Chapter 3 and 5), hence herbaceous species in particular will be strongly affected by global warming.

Higher temperature and shifts in the date of snowmelt constitute the main parameters which will alter plant phenology under future climate change in Southern Germany; however, the magnitude will strongly depend on species. Thus, the expected consequences for those ecosystems in the next decades will be hard to quantify at a species level and further research in this field is still needed.

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VIII FUTURE RESEARCH PERSPECTIVES

The present PhD thesis demonstrated the impacts of global climate change on grassland species in two ecosystems detected by long-term and short-term observations. Out of these experiences some ideas arose on how to conduct and improve further phenological research.

First, I support the idea of further studies with increased numbers of levels of effects for experimental approaches since the interaction of treatments appeared to affect phenology differently than single treatments. However, levels should be kept to a dimension so that results are still possible to interpret. Furthermore, even though our study showed similar results in the natural gradient and the experimental study, I support Wolkovich *et al.* (2012), recommending a greater number of studies which integrate experimental and gradient approaches since the study of Wolkovich *et al.* (2012) showed that experimental results alone are not suitable to parameterize species distribution and ecosystem models. Additionally, I suggest further research focusing on shifts in treatment sensitivity at lower and higher altitudes since results so far appeared not to be uniform. Finally, since phenological response to natural gradients and experiments were highly species-specific in all studies of this thesis I recommend the inclusion of large numbers of species in further climate change studies. Thus, a substitution of results from species level to ecosystem level appears more feasible. This is in accordance with Wolkovich *et al.* (2012) also suggesting a higher number of species for accurate climate change forecasts.

A new research approach, which combines all these suggestions, is therefore recommended. This approach could be structured as follows: Soil monoliths with intact vegetation are removed along an altitudinal gradient and put into climate chambers. Soil monoliths have the advantage that species can be investigated within their natural community structure (with a high number of species), while in climate chambers, natural abiotic conditions as present along the gradient can be simulated. Simultaneously plants can be treated at different levels of climate change effects. Thus, an examination of species in respect to their response at high and low altitudes is feasible. Additionally, besides impacts on phenology whole mechanisms of exchange processes between biosphere, hydrosphere and atmosphere could be measured. I am aware that climate chamber studies cannot substitute natural conditions, however, I think this research approach is the best way to fulfil all criteria required in order to achieve results as close to natural as possible.

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X PUBLICATION LIST

Reviewed publications

Cornelius, C., H. Petermeier, N. Estrella, and A. Menzel. **2011**. A comparison of methods to estimate seasonal phenological development from BBCH scale recording. International Journal of Biometeorology 55: 867-877.

Cornelius, C., H. Franz, N. Estrella, and A. Menzel. **2012**. Linking altitudinal gradients and temperature responses of phenology in the Bavarian Alps. Plant Biology doi: 10.1111/j.1438-8677.2012.00577.x.

Submitted publications

Cornelius, C., J. Heinichen, M. Drösler, and A. Menzel. **2012**. Impacts of temperature and water table manipulation on grassland phenology. Submitted to Functional Ecology (09 July 2012).

Cornelius, C., A. Leingärtner, B. Hoiss, J. Krauss, I. Steffan-Dewenter, and A. Menzel. **2012**. Phenological response of grassland species to manipulative snowmelt and drought along an altitudinal gradient. Submitted to Journal of Experimental Botany (06 August 2012).

Further publications

Schleip C., C. Cornelius, and A. Menzel. **2011**. Wenn der Maitrieb zum Märztrieb wird. LWF aktuell 85: 15-18.

Conference proceedings and Abstracts

Oral presentations

Cornelius C., and A. Menzel. **2009**. Acquisition and analysis of phenological reactions of selected plants on extreme weather events. GfÖ. Bayreuth, Germany. 15 September 2009.

Cornelius C., N. Estrella, and A. Menzel. **2010**. Continuous monitoring of seasonal phenological development by BBCH- Code. International Conference on Phenology: Plant ecology and diversity. Edinburgh, UK. 08 April 2010.

Cornelius C., H. Franz, N. Estrella, and A. Menzel. **2010**. Phenological monitoring along an altitudinal gradient in the Berchtesgaden National Park, Germany. Phenology 2010: Climate change impacts and adaptation. Dublin, Ireland. 17 June 2010.

Cornelius C., I. Eschenlohr, N. Estrella, and A. Menzel. **2011**. Phenological response of herbs to manipulative experiments along an altitudinal gradient. International Conference on Biometeorology. Auckland, New Zealand. 5 December 2011.

Poster presentations

Cornelius C., N. Estrella, and A. Menzel. **2010**. Continuous monitoring of seasonal phenological development by BBCH- Code. EGU General Assembly. Vienna, Austria. 3-7 May 2010.

Cornelius C., H. Franz, R. Stocker, N. Estrella, and A. Menzel. **2011**. Phenological monitoring along an altitudinal gradient in the B erchtesgaden National Park, Germany. ForumAlpinum '10. Munich, Germany. Winner of the poster award. 6-8 October 2010.

Cornelius C., N. Estrella, and A. Menzel. **2011**. Short-term shifts in phenology due to experimental warming? EGU General Assembly. Vienna, Austria. 4-6 April 2011.

XI CANDIDATE'S INDIVIDUAL CONTRIBUTION

1. Cornelius, C., H. Petermeier, N. Estrella, and A. Menzel. **2011**. A comparison of methods to estimate seasonal phenological development from BBCH scale recording. International Journal of Biometeorology 55: 867-877.

Hannes Petermeier provided the R script of the OLR method as well as methodological and statistical advice. Annette Menzel and Nicole Estrella contributed with suggestions for statistical analyses, corrections and proof reading. Annette Menzel had the conceptual idea of the PSD method. About 80% of the work, including phenological observations, programming scripts for WSD, PSD and CSD methods, statistical analysis and the writing of the manuscript was done by me.

2. Cornelius, C., H. Franz, N. Estrella, and A. Menzel. **2012**. Linking altitudinal gradients and temperature responses of phenology in the Bavarian Alps. Plant Biology doi: 10.1111/j.1438-8677.2012.00577.x.

Helmut Franz provided the long-term observation data (climate and phenological data) of the Berchtesgaden National Park and helped with corrections. Annette Menzel and Nicole Estrella contributed with suggestions for statistical analysis, corrections and proof reading. About 80% of the work, including data processing, statistical analysis and the writing of the manuscript, was done by me.

3. Cornelius, C., J. Heinichen, M. Drösler, and A. Menzel. **2012**. Impacts of temperature and water table manipulation on grassland phenology. Submitted to Functional Ecology.

Jan Heinichen was engineering the side, provided temperature data and contributed with information about technical details and corrections. Matthias Drösler proof-read the manuscript and Annette Menzel provided suggestions for statistical analysis, corrections and proof reading. I did about 85% of the work, including phenological observations, data processing, statistical analysis and the writing of the manuscript.

4. Cornelius, C., A. Leingärtner, B. Hoiss, J. Krauss, I. Steffan-Dewenter, and A. Menzel. **2012**. Phenological response of grassland species to manipulative snowmelt and drought along an altitudinal gradient. Submitted to Journal of Experimental Botany.

Annette Leingärtner and Bernhard Hoiss were engineering the side, provided temperature and soil moisture data and helped with technical details and data analysis. Jochen Krauss provided statistical advice and suggestions for proof reading. Ingolf Steffan-Dewenter proof-read the manuscript and Annette Menzel provided suggestions for statistical analysis, corrections and proof reading. I did about 80% of the work, including data processing, statistical analysis and the writing of the manuscript.

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Ich erkläre an Eides statt, dass ich die der Fakultät Wissenschaftszentrum Weihenstephan für Ernährung, Landnutzung und Umwelt der Technischen Universität München zur Promotionsprüfung vorgelegten Arbeit mit dem Titel

„Monitoring and analysis of plant phenological responses in manipulative experiments and along natural gradients“

am Fachgebiet für Ökoklimatologie unter der Anleitung und Betreuung durch Prof. Dr. Annette Menzel ohne sonstige Hilfe erstellt und bei der Abfassung nur die gemäß § 6 Abs. 5 angegebenen Hilfsmittel benutzt habe.

Ich habe die Dissertation in keinem anderen Prüfungsverfahren als Prüfungsleistung vorgelegt.

Ich habe den angestrebten Doktorgrad noch nicht erworben und bin nicht in einem früheren Promotionsverfahren für den angestrebten Doktorgrad endgültig gescheitert.

Die Promotionsordnung der Technischen Universität München ist mir bekannt.

Freising, den _____ _____

Christine Cornelius