

How Caterpillar Outbreaks Affect Radial Increment in Differing Phenology of English Oak (*Quercus robur*)

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Abstract

Caterpillar outbreaks can cause severe defoliation of their host trees. There is a strong synchronisation between the emergence of winter moth caterpillars (*Operophtera brumata*) with the bud burst of English oak (*Quercus robur*). However, individual oaks vary in phenology, allowing oaks with a late bud burst to endure less defoliation. Severe defoliation leads to a decrease in radial increment in years following a caterpillar outbreak. These effects have been widely studied, yet no research has been done on the difference in effect of outbreaks on trees with differing phenology of the same species. Here, the effects of caterpillar outbreaks on English oak with differing phenology have been studied using tree-ring analyses. Additionally, caterpillar growth was monitored *in natura* on early and late oaks, as well as the development of leaf toughness. I found that oak trees produced thinner rings in years after a caterpillar outbreak, and that trees with an early phenology were more affected by this than late oaks. I found no difference in growth of caterpillars between early and late trees, despite finding a stark difference in leaf toughness development indicating that leaves of late trees become tougher more quickly than early tree leaves. The future role of climate change and global warming on the effects of caterpillar outbreaks remain uncertain.

1. Introduction

Plants and herbivores are subjected to an ongoing arms race, in which plants aim to protect themselves against herbivory, whereas herbivores are selected to break these defences (Barbehenn & Constabel, 2011). Deciduous trees often have lower defences when their leaves are growing in early spring, and many caterpillar species have adapted to match their growing season with this relatively unprotected phase (van Asch & Visser, 2007).

However, there are species such as the English oak (*Quercus robur*) that are partly successful in avoiding damage induced by caterpillars. This is accomplished by having a relatively broad range of the timing of bud burst, which can differ up to as much as two to three weeks between individuals of the species (Feeny,

1970; Tikkanen & Julkunen-Tiitto, 2003). As a consequence of the variance in bud burst, trees with early phenology (i.e. trees that start bud burst early in the season) tend to host higher insect populations in contrast to late trees. This possibly allows late trees to “escape” defoliation to a certain degree, even in so-called outbreak years in which insect abundances are extremely high (Feeny, 1970; Kulfan, Sarvašová, Parák, Dzurenko, & Zach, 2018). Moreover, the differences within the varying phenotypes are consistent between years, meaning that early trees are on average always early and late trees on average late (Tikkanen & Julkunen-Tiitto, 2003). Trees also defend themselves against defoliation by producing chemical compounds in their leaves that are toxic to their defoliators, such as tannins which increase in concentration during the summer (Feeny, 1970). Research on evergreen trees of differing species and

phenology - 'early' *Schima superba* which regenerates its leaves in February and the 'late' *Engelhardia roxburghiana* which regenerates its leaves in May - has also shown that leaf phenology plays an important role in host resistance to defoliation by insects. This is due to the relative differences that were found in the chemical composition and toughness between the two species (Chen, Wang, Dai, Wan, & Liu, 2017).

However, despite the trees' efforts, there are years when caterpillars are able to successfully breach their defences. These years are also known as outbreak years and have been recorded in multiple species of Lepidoptera across the world (Cooke & Lorenzetti, 2006; Hódar & Zamora, 2004; Tikkanen & Roininen, 2001), The Netherlands being no exception.

Caterpillar abundance has been recorded in the Netherlands for over two decades, namely in the Veluwe and Dwingelderveld (Appendix A.1, Figure 11). During this time, multiple outbreaks have been observed following roughly a 10-year cycle. However, defoliation rates were not measured (C. Both, personal communication, 2021). Caterpillars are able to cause severe defoliation of their hosts during outbreak years (Wesołowski & Rowiński, 2006). Higher levels of defoliation have been found to be associated with increased mortality as well as decreased (radial) growth (in years following an outbreak) (Alfaro & MacDonald, 1988; Baker, 1941; Wickman, 1980). Such decreases in radial growth can be measured using tree-ring analysis. In dendroecology, tree-rings of trees growing in seasonal climates (e.g. mid and high latitudes and areas with a pronounced dry or wet season) are used as a natural record of environmental events. More specifically, in dendroentomology tree-rings are used to identify insect outbreaks (Speer, 2010e). Usually trees in seasonal climates grow one yearly ring which can be separated in earlywood (EW; produced in spring and early summer) and latewood (LW; produced in late summer) (Speer, 2010d). The production of latewood suffers as a result of folivory induced defoliation, which directly results in a lowered

cambial activity during the summer (Rubtsov, 1996).

This study focuses on the effects of the entire spring caterpillar community, of which the winter moth (*Operophtera brumata* L.) is one of the important species, on the growth of English oak, also known as Pedunculate oak. Oaks (*Quercus* spp.) are trees with a ring-porous wood structure, which is defined by a distinct row of vessels. These vessels are produced early in the growing season and are completed before leaf-out. Due to this formation taking place before leaf-out, trees have to use the stored reserves produced in the previous year since no photosynthates have been produced yet. In oak, these vessels form the earlywood (Speer, 2010d).

It is highly likely that the winter moth contributes to the caterpillar outbreaks in the Netherlands. The species has a cyclic population dynamic with peaks in abundance every nine to ten years (i.e. a frequency similar to the observed outbreaks in The Netherlands), accompanied by annual increases in caterpillar abundance three to four years prior to an actual outbreak (Wesołowski & Rowiński, 2006). The winter moth is a polyphagous insect, however, its preferred food plant is the oak (*Quercus* spp.) (Buse, Dury, Woodburn, Perrins, & Good, 1999). One of the species's distinctive traits compared to other host-insect systems, is the ability of the winter moth to adapt to one individual host tree and its corresponding bud burst phenology (van Dongen, Backeljau, Matthysen, & Dhondt, 1997). In their early instar, larvae are able to balloon to neighbouring vegetation. However, the act of ballooning is a passive mechanism leading to uncontrolled selection of a new host. The larvae usually pupate near the base of their host, and after pupation the flightless adult females ascend the trees once more to mate and lay their eggs. Contrary, the males are capable of flying short distances, while also staying within a relatively small area. Thus, both caterpillars and adults of the winter moth have neither high, nor effective mobility and are unlikely to disperse to another host tree (Tikkanen & Julkunen-Tiitto, 2003). This combination of traits may suggest that despite the array of phenology phenotypes on a site, individual host trees might not per se be

protected against caterpillar herbivory. In particular this could mean that late trees that have otherwise been suggested to be able to escape defoliation, are in fact being predated on.

The aim of this study was to establish whether oak trees varying in bud burst phenology are differently affected by caterpillar folivory. To this aim, the effects of a time series on caterpillar outbreaks on the radial increment of English oak were studied, with the focus on the difference between early and late phenology bud burst. Previous studies have shown that early oaks host more caterpillars than late oaks, causing more defoliation (Wesołowski & Rowiński, 2008), and that annual variation in tree ring width could be used to study outbreak frequencies of caterpillars (Speer, 2010b), but it has not been studied whether within one species of oak these effects are related to tree phenology.

A decrease in ring-width, characterised by an increase in the ratio EW:LW, was expected in years following caterpillar outbreaks. Additionally, it was expected that trees with early phenology are more affected compared to trees with late phenology. As I was also interested in the possible cause of less caterpillars on late trees, leaf toughness was studied as a defence mechanism, with the expectation that the leaves of trees with a late phenology grow and mature faster, and thus become tougher more quickly, than leaves of trees with an early phenology. With the above expectation in mind, it was also expected that caterpillars would grow slower on late trees compared to early trees, as leaves of late trees would thus become harder to digest more quickly.

2. Materials and Methods

2.1 Study area

All experiments and sampling were conducted in the mixed forest of National Park

Dwingelderveld (Drenthe, the Netherlands) (Figure 1). Caterpillar outbreaks have been observed in the study area in the years 2008/'09 and 2018/'19/'20 (Appendix A.1, Figure 11 and 12) (C. Both, personal communication, 2021). In the year of this study's experiments (2021) caterpillar densities were still relatively high. The subset of trees that were sampled for this study are representative of the site-level conditions concerning both caterpillar peak height and caterpillar peak day (Appendix A.1, Figure 12; Appendix A.2, Figure 13).

2.2 Tree phenology

For the purpose of this study, the phenology was calculated for each oak tree using existing bud burst data. Bud burst has been scored for a selection of trees in the study area since 2007 (C. Both, personal communication, 2021). Buds were scored every four days. The unfolding of the leaves is divided into five different stages, ranging from dormant buds to fully developed leaves (Müller, Seifert, & Finkeldey, 2015). Of these five stages, the date when stage three (i.e. the start of leaf development of the buds) was reached, was used as a measure of tree phenology. However, stage three was not always recorded for each tree, or trees would remain at the stage for multiple recordings in one year. Therefore, a loop was constructed in RStudio in order to specify a single date for each year where the bud burst stage first equaled three (R Core Team, 2020). The result is a dataset with one bud burst date per tree per year. Phenology was then calculated per tree by taking the average bud burst of all years. Additionally, the year phenology was calculated by taking the average of the bud burst of all trees per year.

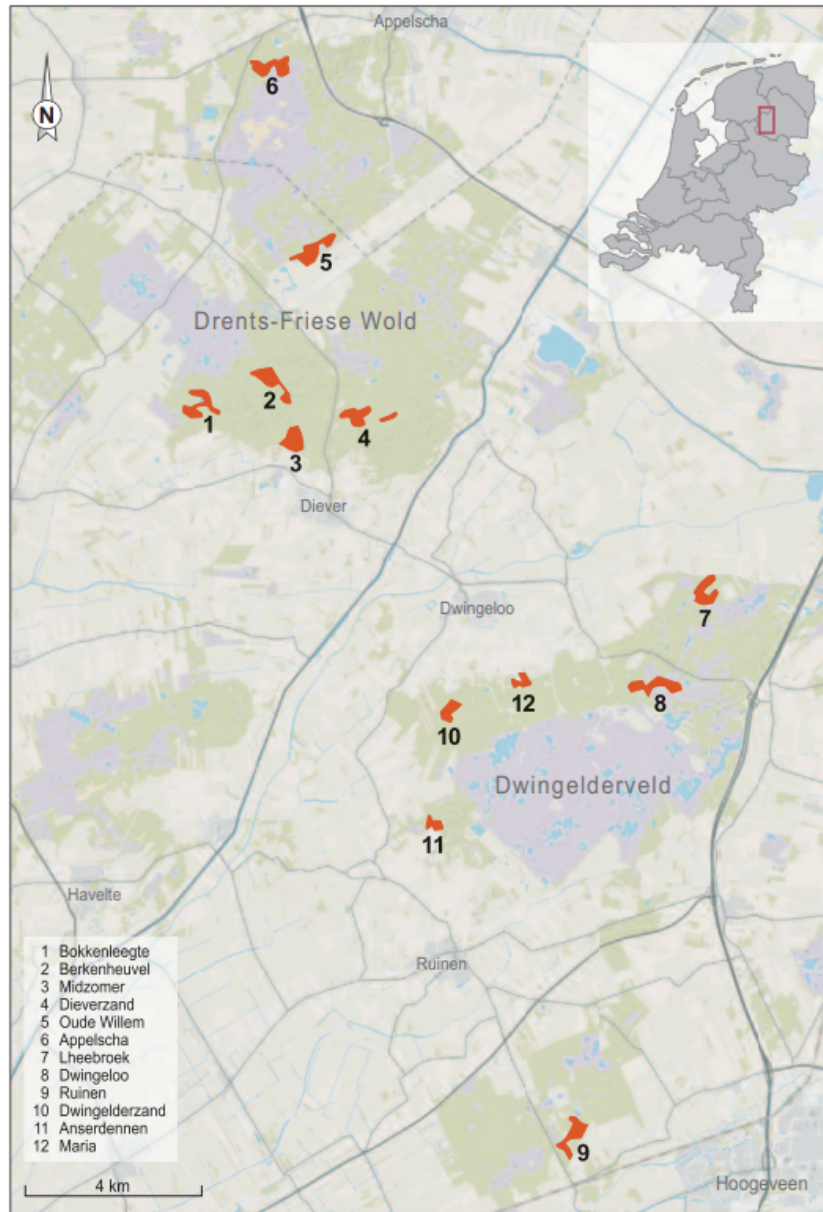


Figure 1. Locations of study plots in Drenthe, The Netherlands (Both et al., 2017). Plot 8 (Dwingeloo) was used for the experiments described in this study.

2.3 Caterpillars

2.3.1 Growth

Caterpillars of the winter moth were initially selected as a proxy for general caterpillar abundance. However, a limited number of frass samples from the year 2020 have been analysed using DNA-barcoding and showed that the winter moth was a prevalent species on some trees, whereas it was scarce on others (C. Both, personal communication,

2022). Despite the relatively high caterpillar density in 2021, caterpillars of the winter moth were scarce on the sampled trees, resulting in insufficient numbers for the species to be used as the sole test subject. Therefore, caterpillars of various species and sizes were collected from oak branches that were within arm's reach (ca. 1.5-2 metres from the ground up). Collected caterpillars were identified as either crawlers or geometridae. Subsequently, the caterpillars were placed back in the tree on caterpillar-free tufts of leaves in fruit protection sleeves (30 x 40 cm

bags made from a fine fabric which prevents insects from entering, and thus leaving, the bag whilst allowing light and air to pass through) (Buse et al., 1999). The sleeves prevented the caterpillars from being predated and enabled the tracking of the same individuals over a longer period of time. Each sleeve initially contained at least three caterpillars, however, over time caterpillars were added to some sleeves to make up for caterpillars dying, or getting lost. Lost caterpillars are individuals that fell during transport from and to the sleeve, or were presumed to have escaped. The caterpillars added at a later time were of similar size as the caterpillars already present in the sleeves, and mostly of the same species as the caterpillars that either died or were lost. In the statistical models that were run for mortality, the replacement of lost and dead caterpillars with living caterpillars was not taken into account in the sense that there is no differentiation between the original caterpillars and the later additions to the sleeve.

In total, 17 sleeves were put up divided over seven oak trees with differing phenology (3 early, 1 intermediate, 3 late trees), with respectively 7, 3, and 7 sleeves. Of the 17 sleeves, there are four that will be referred to as translocation sleeves. These sleeves had caterpillars taken from early trees that have been relocated to late trees and vice versa. Two sleeves were used for each of the translocation treatments.

Every four days, the sleeves were emptied and searched for caterpillars. Despite searching the tufts for caterpillars before placing the sleeves, new caterpillars were occasionally found in the sealed off sleeves. On other occasions not all caterpillars were found back while checking the sleeves. Of these caterpillars some were assumed to be lost, whereas others were found again in the next check. The caterpillars were photographed (using either the macro or regular lens on the Xiaomi Mi 10 lite) on millimetre paper and afterwards put back on the tree (in total 365 photographed caterpillars, of which 153 crawlers, 131 geometridae, 17 dead, and 63 pupae). The photographs were later analysed to determine caterpillar length and

growth. Additionally, caterpillar frass was collected each time the sleeves were emptied, however, it was not used for this study.

2.3.2 Biomass

Caterpillar biomass has been recorded since 2007 (C. Both, personal communication, 2021). Frass nets (0.25 m²) were used to collect caterpillar droppings, as described by Visser *et al.* (2006) with the exception that only one net was used per tree instead of two (Visser, Holleman, & Gienapp, 2006). Subsequently, the biomass can be calculated from the collected frass data by using the formula of Tinbergen and Dietz (1994) (Tinbergen & Dietz, 1994; Visser et al., 2006).

2.4 Tree cores

English oak, was selected for tree-ring analysis to study the effects of caterpillar folivory on radial growth. Scots Pine (*Sylvestris pinus*) was chosen to serve as a control for any environmental factors that could have influenced radial increment for all species on site, as they likely do not suffer from defoliation caused by (winter moth) caterpillars and are abundant in the study area.

Cores were collected during late summer 2020, early autumn 2020, and spring 2021 using a Swedish increment borer (∅5 mm) (in total 58 cores, of which 39 cores from 13 oaks (early, intermediate, and late phenology) and 19 cores from 6 pines). The samples were taken by coring perpendicular to the tree at breast height (ca. 140 cm) as this allows for the whole body to be used to build momentum (Speer, 2010c). Cores were taken with at least a 60° angle between them (Simmons et al., 2014). Three cores were collected for each tree, with the exception of one tree (oak 710) only having two cores and two trees (oak 699 and pine 699) having four cores each. After extraction, the fresh cores were rolled up in a small piece of paper notated with tree ID, date of extraction, species, and cardinal direction at which the core was taken. The cores were stored in a refrigerator at ca. 5 °C until further processing.

Final preparations for the analyses were done by mounting the cores onto pre-slotted

wooden slats. Wood glue and clamps were used to secure the cores in place. After the glue had dried, the cores were sanded down to their broadest point using sandpaper with increasingly finer grit (respectively grits 100, 240, 320, 400) as described by Asherin & Malta (2001). Compressed air was used to remove any dust remaining from the sanding before staining the cores with Fehling's solution, which improves the detectability of tree-rings as it darkens the latewood (Asherin & Mata, 2001).

To properly date wood samples, it is of importance that dendrochronologists check their dating quality, which is why at least two attempts should be made to date each sample such as skeleton plotting, a second analysis by another dendrochronologist, or COFECHA (note that COFECHA should not be used as the singular attempt at dating a wood sample, or as a replacement for crossdating) (Speer, 2010a). In the attempt to properly date the samples, each core was analysed in three different ways.

(1) Skeleton plots were constructed from each individual core by studying the rings under a stereo microscope, as described by Swetnam *et al.* (1985). Subsequently, composite plots were made for each tree by averaging the individual skeleton plots of the cores sampled from the same tree. From these composite plots, a master chronology was created by averaging all composite plots (Stokes & Smiley, 1996; Swetnam, Thompson, & Sutherland, 1985). This was done separately for oak and pine, thus resulting in two master chronologies for the site.

(2) Photos were taken of all cores and analysed in ImageJ Fiji (Schindelin *et al.*, 2012). Measurements were performed using the straight-line measuring option combined with the ROI manager tool. The scale was determined by measuring an object in the photograph of a known length (i.e. the width of the mount) and subsequently assigning this value to the measured length. Each line was drawn from the beginning to the end of each ring, measuring earlywood and latewood separately to later determine the ratio EW/LW. The ring-width data was rounded up to a thousandth.

(3) COFECHA (version COF12K_XP) was used as a second corrector for the

identification of measurements that should be reviewed for possible errors (Holmes, 1983). In addition to quality control, COFECHA is also able to calculate if any possible missing or false rings occur in a core, and if so, where they would be. COFECHA works by taking the ring-width measurements obtained from the measuring stage (i.e. ImageJ) and fitting a cubic smoothing spline to the cores for standardisation. In the next step, it creates the master chronology by averaging all of the index series for all of the cores together. It subsequently removes the core that is then to be analysed and cuts it into overlapping segments. Each segment is then statistically correlated against the master chronology. COFECHA checks the level of correlation between each segment and the master chronology and flags any segments that have a higher correlation if matched better within +10 to -10 lag years, or flagging segments with a low correlation to the master chronology. The aforementioned calculated index value for each year can be used to identify exceptionally small year-rings that might be missing in other cores (Speer, 2010a). The sample depth was set to a minimum of 10 cores as a measure of quality for obtaining a well-replicated stand-level signal (Speer, 2010a). For this reason some measurements of relatively long cores were cropped if there were less than 10 cores representing the same year-ring. The ring-width measurements gathered from ImageJ were used in COFECHA, however, the programme is unable to read in Excel spreadsheet datafiles in the common formats .xlsx and .csv (Microsoft Corporation, 2018). Therefore, the data had to be transformed to an adequate format. One of the formats accepted by COFECHA is the Tucson format (also referred to as Decadal, RWL, CRN, ITRDB, Time series format, or TSF) (Brewer, Murphy, & Jansma, 2011; Grissino-Mayer, 2001). A useful tool that performs the transformation from .xlsx to Tucson is the `write.tucson()` function from the R package `dplR` (A. Bunn *et al.*, 2021; A. G. Bunn, 2008, 2010). The result of running the `write.tucson()` function is a temporary text file with the data in the format needed to run COFECHA. It may be necessary to manually edit parts of the text file

before converting it to the format .rwl and running COFECHA to avoid mishaps in reading in the data. COFECHA was run separately for the oak and pine data, as described by James H. Speer's (2010) keystroke tutorial, using the default options presented by the programme (Grissino-Mayer, 2001; Speer, 2010a). From the COFECHA output, the predicted missing rings for certain cores and the index values for each year were used in further analyses. The 'missing' rings were manually added as a zero to the ring-width data alongside the original measurements. For example, if COFECHA suggests a missing ring for the year 2006, it would be added to the data by inserting a zero between 2006 and 2007, and subsequently moving the measured ring-widths down a year (i.e. the value originally measured for 2006 is now the ring-width for 2005).

After running COFECHA, the programme EDRM (Edit Ring Measurements) was supposed to be run. In EDRM, the input data (i.e. the same file used for the first COFECHA run) would be edited using the information gathered from the COFECHA output. For example, missing rings can be added in EDRM (Speer, 2010a). After undergoing the editing done in EDRM, the new datafile would be used in COFECHA again. This cycle would continue until COFECHA no longer detects missing rings (Speer, 2010a). When this point is reached, the file would then be transferred to the programme ARSTAN to make any concluding tweaks to the data (Speer, 2010a). The result is a final data file. If done separately for oak and pine, both final files would be entered in the programme OUTBREAK. OUTBREAK allows for the quantification and differentiation of insect outbreaks using a host species chronology (oak) and comparing this to the chronology of a control species (pine) (Speer, 2010a). However, due to an unfixable malfunction in EDRM, it was impossible to continue with this initial plan from thereon.

2.5 Leaf toughness

Leaf toughness is used as a proxy for palatability, as it is known that tougher leaves are less desirable to eat for caterpillars (Feeny,

1970). Leaves were collected every four days from a total of seven oak trees with differing phenology (3 early, 1 intermediate, 3 late). A total of 15 leaves were measured per tree per day, taken from three different tufts with each at least five leaves that were within reach (ca. 1.5-2 metres from the ground up). Leaves were selected based on their size and state. Damaged and small leaves were avoided. When penetrating smaller leaves, it is more likely to hit (close to) a vein. The veins and midribs of a leaf are tougher than the lamina and can therefore negatively influence the results (Choong, 1996).

After harvest, each leaf was immediately measured in length (excluding the stem), and subsequently measured for toughness. Individual leaves were clamped between two perspex plates (5 x 7 cm with each a \varnothing 1.5 cm hole in the centre). A handheld penetrometer (model NEWTRY GY-3) was used to puncture the leaves, measuring toughness (max. 25 kg/cm²). The GY-3 model comes with two types of test heads (\varnothing 8 mm and \varnothing 11 mm, scale values respectively 1~24 kg/cm² and 0.5~12 kg/cm²) that can be mounted onto the device. The larger test head was used at first, however, it had to be replaced by the smaller test head as the leaves got too tough to measure within the scale range of the large test head. Each leaf was measured once (in total 677 measured leaves, 420 of which were measured in length).

2.6 Data analysis and visualisation

Apart from COFECHA, all analyses were performed using RStudio (Holmes, 1983; R Core Team, 2020).

Linear Mixed-Effect Models were used to determine which variables had the greatest effect on caterpillar length and ring-width using the function `lmer()` from the R package `lme4` (Bates, Mächler, Bolker, & Walker, 2015). For the models concerning caterpillar length, sleeve ID and tree ID were added as random effects, whereas April day (i.e. date) and tree phenology were added as fixed effects (Table 1.A). For the models concerning ring-width, tree ID and year were added as random effects, whereas the caterpillar peak height (CPH), CPH of the year prior (CPH_1), and tree phenology were added

as fixed effects (Table 3.A and Table 4.A). Restricted maximum likelihood (i.e. REML) was set to FALSE for all models.

The leaf toughness measurements were transformed into the relative proportion of toughness by dividing the values by 25 (i.e. maximum toughness measurement). Similarly, the mortality of caterpillars was calculated by dividing the number of dead caterpillars by the number of alive caterpillars for each day the sleeves were checked. This allowed for statistical analysis with Generalised Linear Mixed-Effects models, using the function `glmer()` (with family set to binomial) from the R package `lme4` (Bates et al., 2015). For the leaf toughness models, tree ID and `day_rnd:tree` were added as random effects, whereas `day` (as covariate) and tree phenology were added as fixed effects (Table 7.A). For the caterpillar mortality models, tree ID was added as a random effect, whereas leaf toughness and tree phenology were added as fixed effects (Table 2.A).

From the candidate models, the best model fits were selected using Akaike's Information Criterion (AIC) (Bozdogan, 1987). The R package `lmerTest` provided p-values in the summary tables for the `glmer()` and `lmer()` models (Kuznetsova, Brockhoff, & Christensen, 2017).

Linear Models were used to determine which variables had the greatest effect on the index value using the built-in function `lm()` in RStudio (R Core Team, 2020).

Data was visualised using the R packages `ggplot2` (Wickham, 2016).

3. Results

3.1 Caterpillar development

3.1.1 Caterpillar growth

Caterpillar length was linearly and positively related to date ($p < 0.001$, Table 1.B, Figure 2). Including tree phenology in the model did not result in any improvement of the model (also see Appendix A.3, Figure 14), and hence there was no evidence found that caterpillars grow less well on earlier or later trees (Table 1.A). None of the variance in length is explained by the individual sleeves, however, tree identity explained ca. 25% of the variance found in caterpillar length (Table 1.B). Thus, there are other variables, either untested or not included, at play that cause a variation in caterpillar growth.

Table 1. A) Candidate models explaining which variables affect caterpillar length. B) Estimates of the best model fit ($n = 91$). Models are linear mixed effect models (`lmer`).

1.A

Candidate models	AIC
(1) <code>length ~ 1 + (1 tree_ID) + (1 sleeve_ID)</code>	552.7
(2) <code>length ~ aprilday + (1 tree_ID) + (1 sleeve_ID)</code>	506.3
(3) <code>length ~ aprilday + tree_phenology + (1 tree_ID) + (1 sleeve_ID)</code>	508.0
(4) <code>length ~ aprilday * tree_phenology + (1 tree_ID) + (1 sleeve_ID)</code>	508.8

Best model: (2)

1.B

Random effects	Variance	Std. Dev.		
Sleeve_ID	0.000	0.000		
Tree_ID	4.078	2.019		
Residual	12.074	3.475		
Fixed effects	Estimate	Std. Error	DF	p-value
Intercept	-12.599	3.240	90.989	<0.000
April day	0.406	0.050	85.452	<0.000

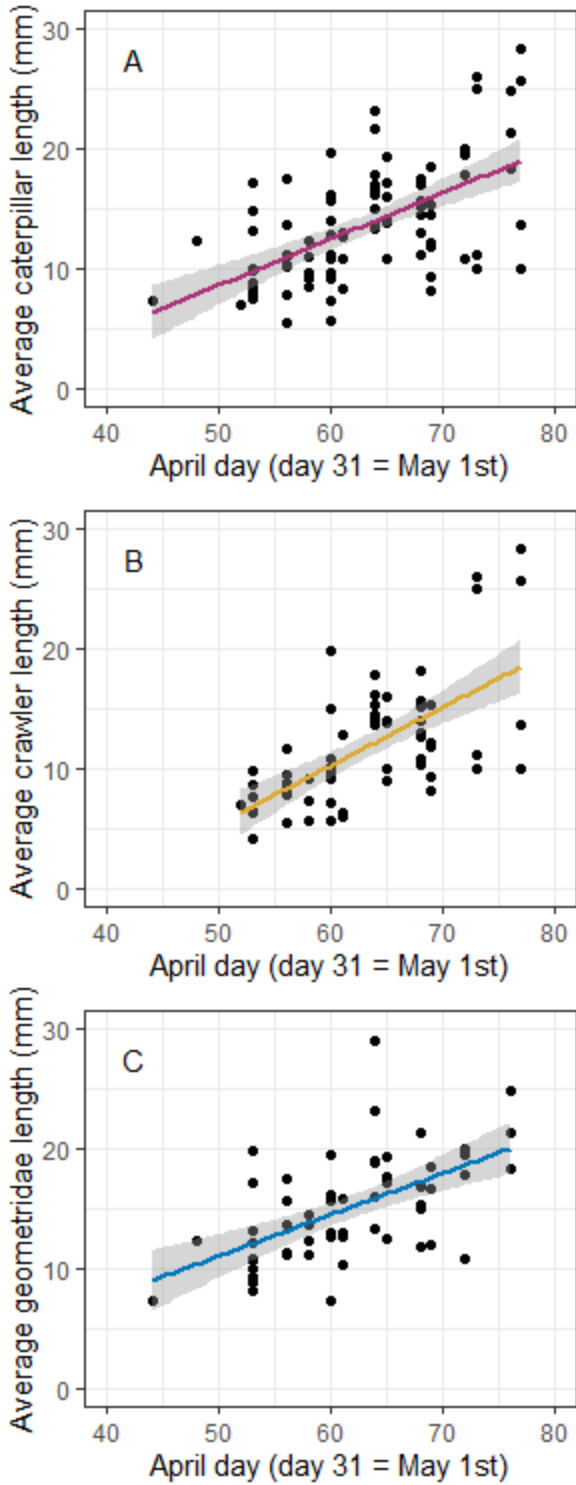


Figure 2. Caterpillar growth over the course of May and June. A) The average growth of crawlers and geometridae combined (n = 91). B) The average growth of crawlers (n = 65). C) The average growth of geometridae (n = 58).

3.1.2 Caterpillar mortality

In total, 17 caterpillars were found dead in the sleeves during the experiment. As can be seen in Figure 3, mortality gradually increased as of April day 64/65 (June 4th/5th), aside from two outliers on Day 48 (May 18th) and Day 58 (May 28th). When visually comparing Figure 3 with Figure 18 (Appendix A.7) there seems to be a correlation between the development of leaf toughness and caterpillar mortality, however, while running the models for mortality, neither including the leaf toughness nor the tree phenology in the model improved the simplest

candidate model (Table 2.A). The simplest model was chosen over the model including toughness, as their AIC values barely differ (<2) and AIC prefers models with fewer parameters between models that explain the same amount of variation (Bevans, 2021). However, due to the small difference in AIC there is still some uncertainty about the role of leaf toughness as an explanation of variance in caterpillar mortality.

None of the variance in caterpillar death is explained by the individual sleeves (Table 2.B).

Table 2. A) Candidate models explaining which variables affect mortality. B) Estimates of the best model fit ($n = 101$). Tree_phenology = average phenology of each tree. Models are generalised linear mixed-effects models (glmer) with family = binomial.

2.A

<i>Candidate models</i>	<i>AIC</i>
(1) mortality ~ 1 + (1 sleeve_ID)	31.0
(2) mortality ~ toughness + (1 sleeve_ID)	29.8
(3) mortality ~ tree_phenology + (1 sleeve_ID)	32.9
(4) mortality ~ toughness + tree_phenology + (1 sleeve_ID)	31.8
(5) mortality ~ toughness * tree_phenology + (1 sleeve_ID)	33.6

Best model: (1)

2.B

<i>Random effects</i>	<i>Variance</i>	<i>Std. Dev.</i>	
Sleeve_ID	0.000	0.000	
<i>Fixed effects</i>	<i>Estimate</i>	<i>Std. Error</i>	<i>p-value</i>
Intercept	-3.486	0.586	0.000

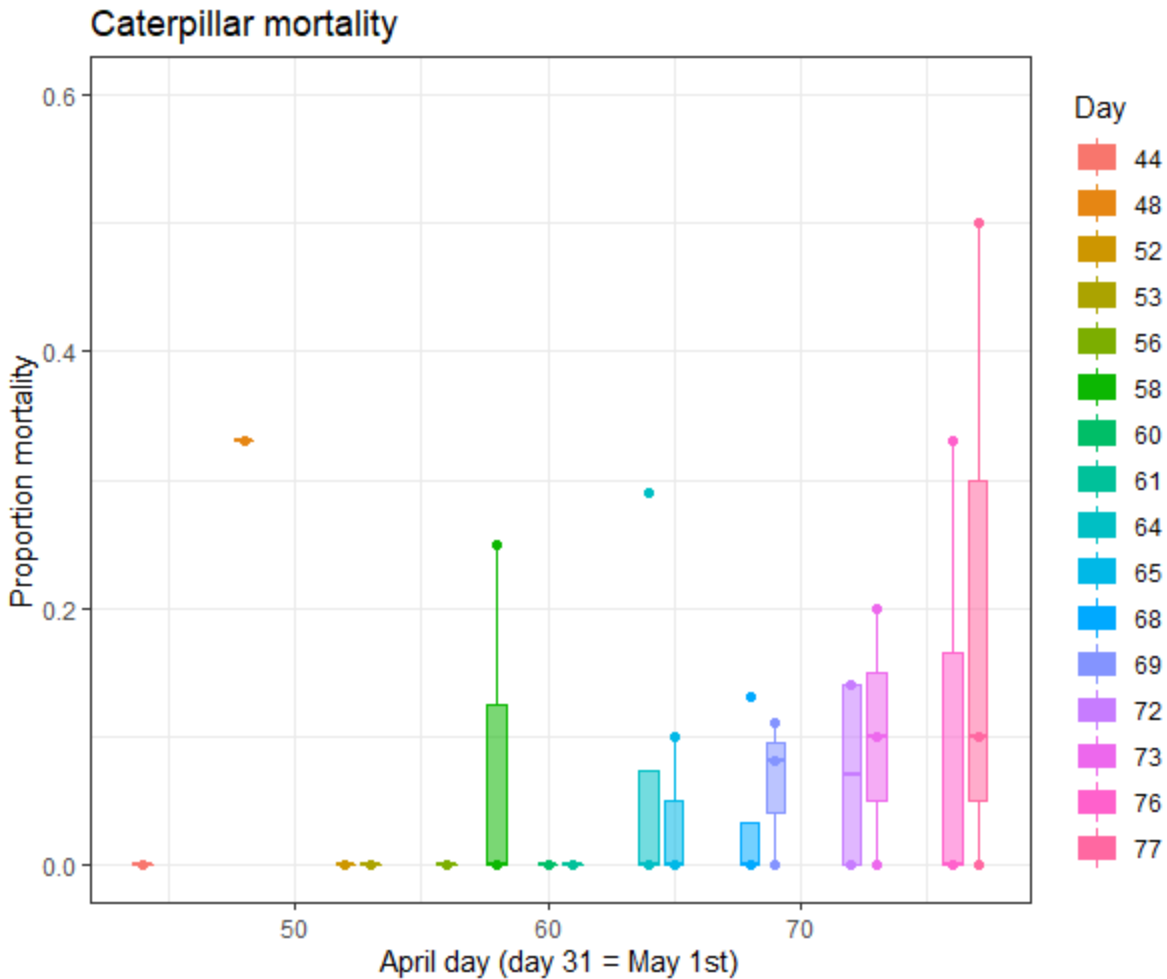


Figure 3. Caterpillar mortality over the course of May and June (n = 51). ‘Day’ in the legend refers to the date on which the sleeves were checked.

3.2 COFECHA output

3.2.1 English Oak

Out of 39 oak cores, 10 were reported to have possible missing rings (Figure 4). These rings were added to the raw data if (more than) half of the cores (i.e. two cores, with the exception of one core being sufficient for oak 710) of a tree were listed as having the same missing ring. For example, in Figure 4 all three cores of tree 751 are suspected to have a missing

ring for 2019, which should thus be inserted between 2019 and 2020 when adding it to the data. However, only one core of 751 is suspected to be missing a ring for 2009, therefore, this ring will not be added to the data.

Of the trees that are suspected to have a missing ring, three have a late phenology (>30), whereas only one has an early phenology (<25) (Figure 4).

ABSENT RINGS listed by SERIES:			
684os	1 absent rings:	1999	
688os	2 absent rings:	1999	2009
688ow	1 absent rings:	1999	
710os	1 absent rings:	2019	
751os	1 absent rings:	2019	
751ow	2 absent rings:	2009	2019
751on	1 absent rings:	2019	
700os	1 absent rings:	2019	
700oe	1 absent rings:	2019	
700on	1 absent rings:	2019	

Figure 4. COFECHA output of the oak cores. Individual cores are shown in the left column with unique identification codes (e.g. 684os = tree 684, oak, core taken from the south side). Phenology per tree, noted as (tree, phenology) is (684, 35.4); (688, 36.3); (710, 21.4); (751, 33.8); (700, 37.2).

3.2.2 Scots Pine

Out of 19 pine cores, 4 were reported to have possible missing rings (Figure 5). Only one ‘missing’ ring was added to the pine data, which is for tree 710 for the year 2019.

ABSENT RINGS listed by SERIES:			
736pe	1 absent rings:	2019	
710pn	2 absent rings:	2009	2019
710ps	1 absent rings:	2019	
710pw	1 absent rings:	2019	

Figure 5. COFECHA output of the pine cores. Individual cores are shown in the left column with unique identification codes (e.g. 736pe = tree 736, pine, core taken from the east side).

3.3 Ring-width

3.3.1 English Oak

There is clear support in the candidate models that tree phenology explains variation in annual tree-ring increment (e.g. model 3 versus model 1, Table 3.A; also see Figure 6). Furthermore, there is some support for the caterpillar peak in the previous year to explain variation in tree-ring width, especially in interaction with tree phenology (model 8 versus model 3, Table 3.A; also see Appendix A.4, Figure 15). However, model 8 is only 0.6 AIC

better than model 3, and therefore there is still uncertainty about the role of caterpillar abundance as an explanation for annual variation in tree-ring growth. The most supported model (model 8) shows that caterpillar abundance of the previous year negatively affects tree-ring growth ($p = 0.032$, Table 3.B). Additionally, the model gave clear support for trees with early phenology having more growth than trees with late phenology ($p = 0.007$, Table 3.B; Figure 6), and shows a trend that these earlier trees were more negatively

affected by caterpillar abundance in the previous year than later trees ($p = 0.073$, Table 3.B).

46.0% of the variance in ring-width is explained by tree identity, whereas 10% is explained by yearly variation (Table 3.B).

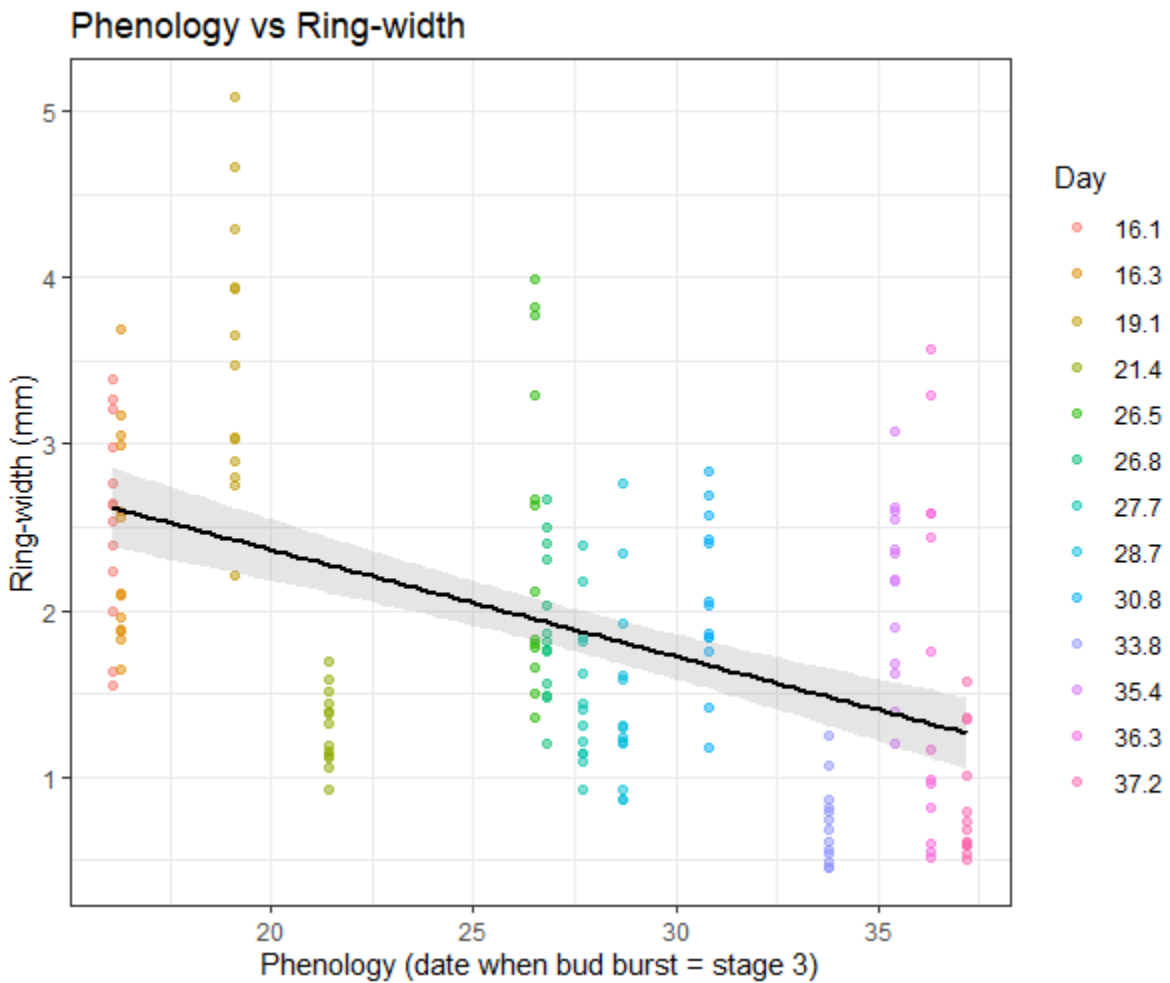


Figure 6. The correlation between tree phenology and ring-width ($n = 169$). Each tree has its own phenology represented by Day (in April day) in the legend, and has one data point per year (total of 13 data points per tree).

Table 3. A) Candidate models explaining which variables affect ring-width in English oak. B) Estimates of the best model fit (n = 169). rw = ring-width; rwm = ring-width including predicted missing rings; cph = caterpillar peak height; cph_1 = caterpillar peak height of the year prior; tree_phenology = average phenology of each tree. Models are linear mixed effect models (lmer).

3.A

Candidate models	AIC
(1) $rw \sim 1 + (1 tree_ID) + (1 year)$	346.7
(2) $rw \sim cph + (1 tree_ID) + (1 year)$	348.3
(2) $rw \sim tree_phenology + (1 tree_ID) + (1 year)$	342.5
(4) $rw \sim cph + tree_phenology + (1 tree_ID) + (1 year)$	344.1
(5) $rw \sim cph * tree_phenology + (1 tree_ID) + (1 year)$	356.0
(6) $rw \sim cph_1 + (1 tree_ID) + (1 year)$	347.3
(7) $rw \sim cph_1 + tree_phenology + (1 tree_ID) + (1 year)$	343.2
(8) $rw \sim cph_1 * tree_phenology + (1 tree_ID) + (1 year)$	341.9

Candidate models	AIC
(1) $rwm \sim 1 + (1 tree_ID) + (1 year)$	356.0
(2) $rwm \sim cph + (1 tree_ID) + (1 year)$	357.9
(2) $rwm \sim tree_phenology + (1 tree_ID) + (1 year)$	352.2
(4) $rwm \sim cph + tree_phenology + (1 tree_ID) + (1 year)$	354.0
(5) $rwm \sim cph * tree_phenology + (1 tree_ID) + (1 year)$	356.0
(6) $rwm \sim cph_1 + (1 tree_ID) + (1 year)$	356.5
(7) $rwm \sim cph_1 + tree_phenology + (1 tree_ID) + (1 year)$	352.6
(8) $rwm \sim cph_1 * tree_phenology + (1 tree_ID) + (1 year)$	351.4

Best model: (8) with raw data

3.B

Random effects	Variance	Std. Dev.		
Tree_ID	0.315	0.562		
Year	0.070	0.265		
Residual	0.300	0.548		
Fixed effects	Estimate	Std. Error	DF	p-value
Intercept	3.660	0.338	14.971	0.000
CPH_1	-0.099	0.046	125.552	0.032
Tree_Phenology	-0.073	0.023	14.362	0.007
CPH_1:Tree_Phenology	0.003	0.001	143.884	0.073

3.3.2 Scots Pine

The candidate models show no strong support that caterpillar peak height, neither of the current year or the previous year, explain variation in tree-ring increment (Table 4.A; also see Appendix A.5, Figure 16). Similar to the model selection in 3.1.2 *Caterpillar mortality*, the simplest model for ring-width was chosen as 'best' model (model 2, with raw data) only differs 0.7 AIC from the simplest model. Moreover, there is only a difference of 0.4 AIC between the two simplest models (model 1 using raw (rw)

data versus model 1 using edited (rwm) data). It thus seems that editing the original data to add the predicted missing rings from COFECHA does not improve the models. Therefore, the simplest model for ring-width using the unedited (raw) data was chosen over the simplest model for ring-width with the added possibly missing rings to the data.

80.3% of the variance in ring-width can be explained by yearly variation, whereas there seems to be no variance explained by tree identity (Table 4.B).

Table 4. A) Candidate models explaining which variables affect ring-width in Scots Pine. B) Estimates of the best model fit ($n = 78$). rw = ring-width; rwm = ring-width including predicted missing rings. Models are linear mixed effect models (lmer).

4.A

Candidate models	AIC
(1) $rw \sim 1 + (1 tree_ID) + (1 year)$	160.4
(2) $rw \sim cph + (1 tree_ID) + (1 year)$	159.7
(3) $rw \sim cph_1 + (1 tree_ID) + (1 year)$	161.2

Candidate models	AIC
(1) $rwm \sim 1 + (1 tree_ID) + (1 year)$	160.8
(2) $rwm \sim cph + (1 tree_ID) + (1 year)$	161.7
(3) $rwm \sim cph_1 + (1 tree_ID) + (1 year)$	162.2

4.B

Random effects	Variance	Std. Dev.
Tree_ID	0.000	0.000
Year	1.240	1.114
Residual	0.304	0.551

Fixed effects	Estimate	Std. Error	DF	p-value
Intercept	2.540	0.459	6.000	0.001

Best model: (1) with raw data

3.3.3 Earlywood and latewood

Pine has an overall higher ratio EW:LW compared to oak. On average, oak trees grow less earlywood than latewood per year-ring, whereas pine trees on average grow less latewood than earlywood per year-ring. However, the difference between the production of early- and latewood is bigger in oak than in pine (Figure 8).

The ratio EW:LW dips in 2012 for both pine and oak, indicating that both species produced a relatively high amount of latewood that year. Furthermore, only the ratio EW:LW of pine dips once in 2017 and peak in 2019/'20 (Figure 7). In contrast, the ratio EW:LW of oak remained relatively constant after slowly decreasing from 2013 to 2016 (Figure 7).

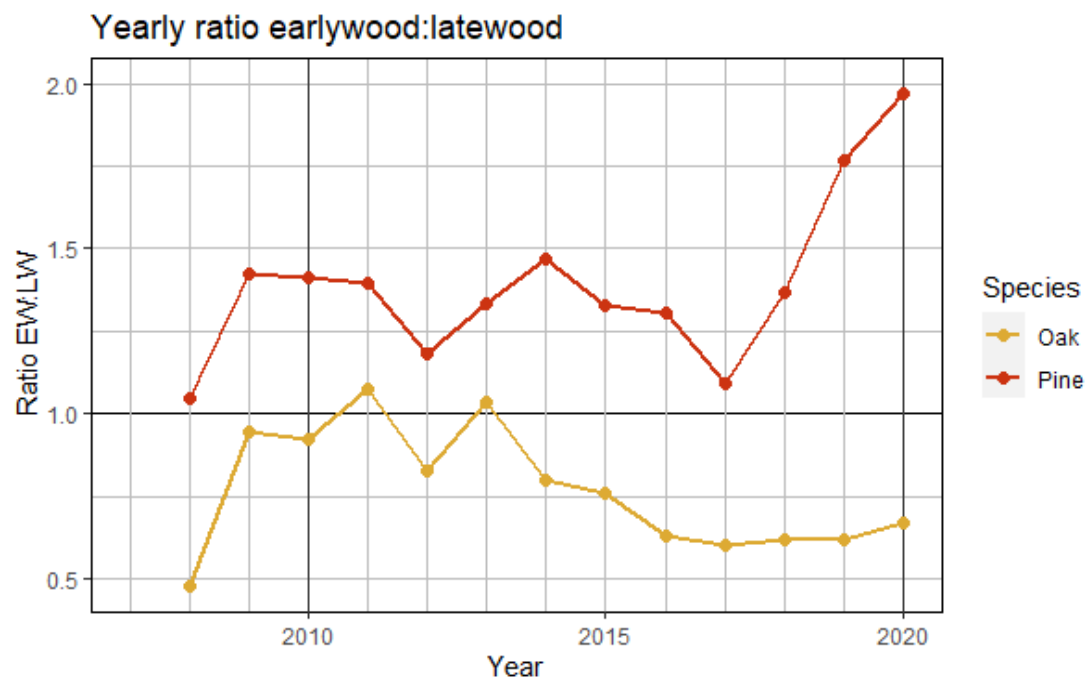


Figure 7. Yearly average ratio of earlywood to latewood in oak and pine. The average ratio was calculated for each year from 13 oaks (39 cores) and 6 pines (19 cores).

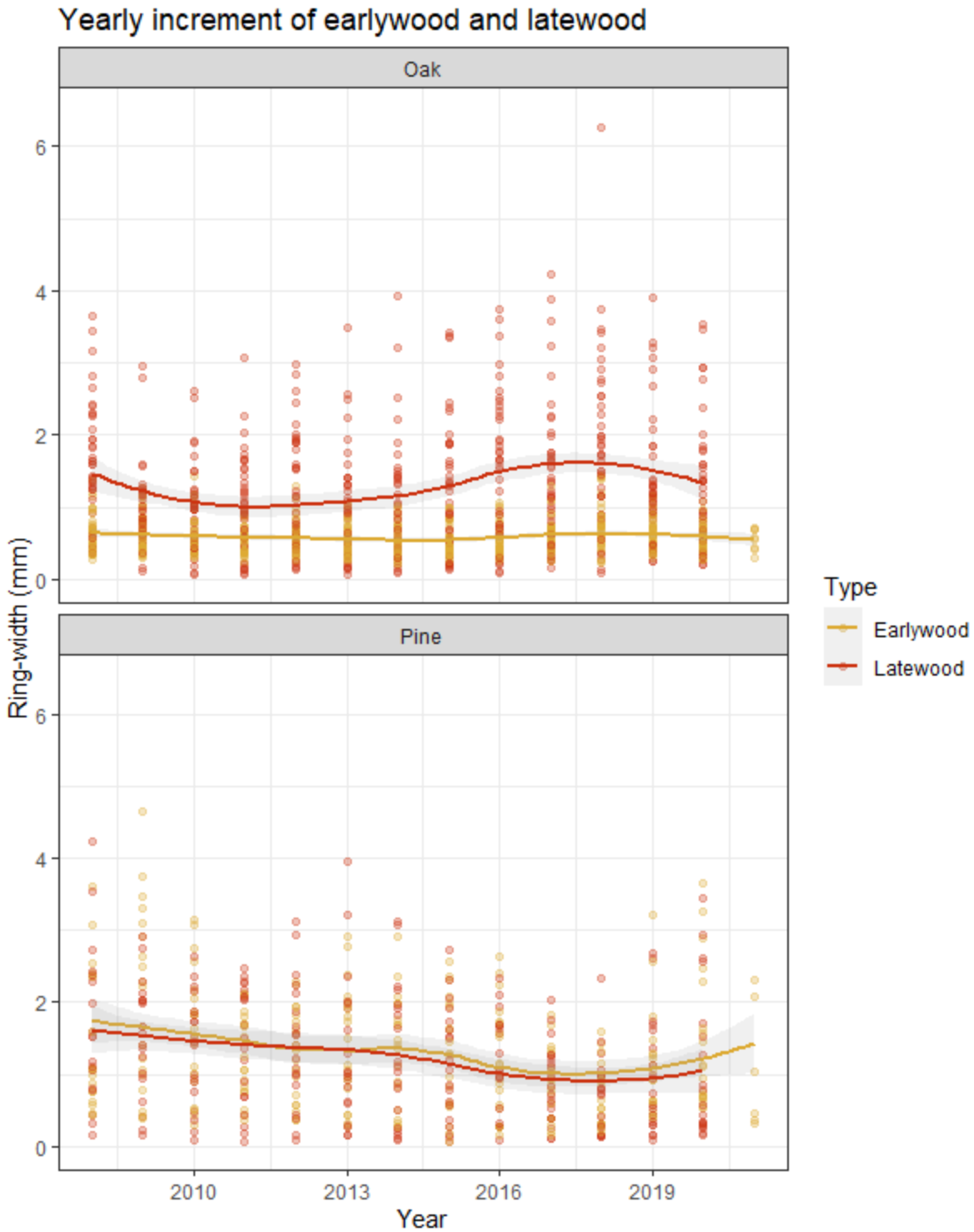


Figure 8. Yearly ring-width increment separated into growth of earlywood and latewood for oak ($n = 1016$) and pine ($n = 498$), cropped from 2007 (see Appendix A.6, Figure 17 for all measured tree-rings).

3.4 Index value

3.4.1 Comparing English Oak and Scots Pine

In the event of an environmental factor influencing growth of all species in a specific area, there would be a universal thick (in case of a good growing season) or thin (in case of a bad growing season) year-ring that can be identified in all trees. Such events would show up in plots of index values as peaks or dips in both the host species as well as the control species. As can be seen in Figure 9, there seem to be no similarities in pattern between oak and pine index values.

Upon closer inspection there are three instances where the different species do show a similar pattern. In the years 2006 to 2007, 2011 to 2012, and 2013 to 2014 both species showed an increase in index value. However, these years meander around the average (index value = 0) and exhibit no noticeable peaks or dips indicating a particularly thick or thin year. Therefore, any rings that are found to be (extremely) small in oak trees are likely not due to environmental factors, but rather insect outbreaks, for example.

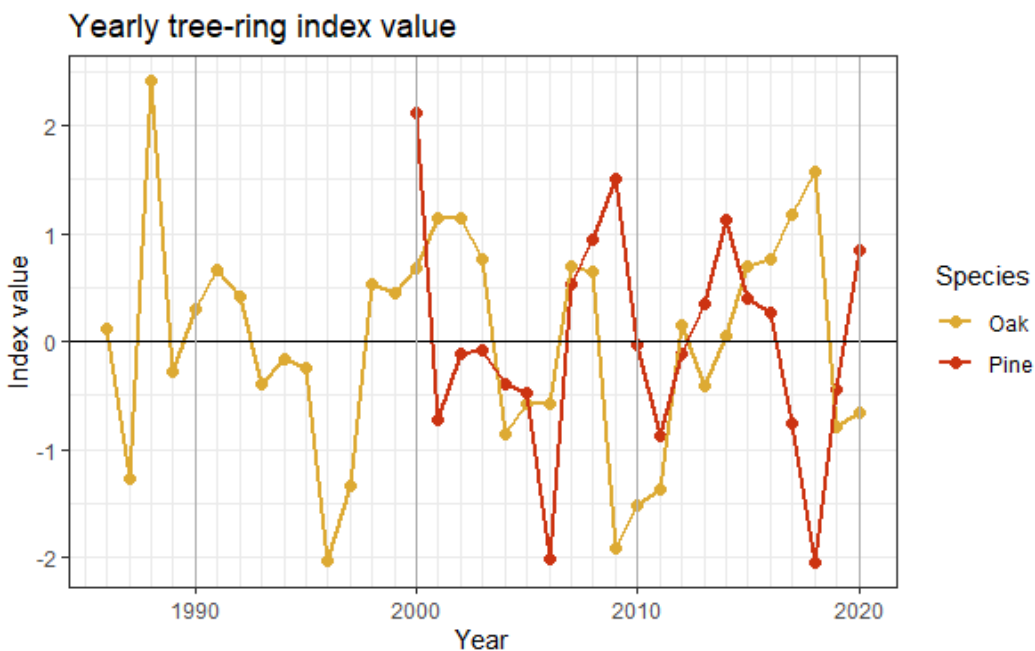


Figure 9. Yearly tree-ring index value in oak and pine. The index value per year was calculated in COFECHA from 39 oaks cores and 19 pine cores. Values above zero indicate relatively big year-rings, values below zero indicate relatively small year-rings.

3.4.2 English Oak

The candidate models show strong support that the index value is affected by the caterpillar peak height of the previous year (e.g. model 6 versus model 1, Table 5.A). Additionally, there is some support that year phenology (i.e. the average phenology of all trees in the area per year) affects the index value, in particular in

interaction with the caterpillar peak of the previous year (e.g. model 8 versus model 3, Table 5.A). However, the most supported model (model 6) shows that only caterpillar abundance of the year prior affects the index value ($p < 0.004$, Table 5.B), with higher numbers of caterpillars leading to a lower index value in the following year.

Table 5. A) Candidate models explaining which variables affect the index value in English Oak. B). Estimates of the best model fit (n = 13). index = index value; cph = caterpillar peak height; cph_1 = caterpillar peak height the year prior; year_phenology = average phenology of all trees in one year. Models are linear models.

5.A

<i>Candidate models</i>	<i>AIC</i>
(1) index ~ 1	42.1
(2) index ~ cph	42.2
(3) index ~ year_phenology	41.9
(4) index ~ cph + year_phenology	43.2
(5) index ~ cph * year_phenology	44.1
(6) index ~ cph_1	33.8
(7) index ~ cph_1 + year_phenology	35.2
(8) index ~ cph_1 * year_phenology	36.7

5.B

<i>Residuals</i>				
<i>Min</i>	1Q	<i>Median</i>	3Q	<i>Max</i>
-1.374	-0.436	0.207	0.541	1.169
<i>Coefficients</i>	<i>Estimate</i>	<i>Std. Error</i>	<i>p-value</i>	
Intercept	0.559	0.283	0.074	
CPH_1	-0.194	0.053	0.004	

Best model: (6)

3.4.3 Scots Pine

The candidate models show no clear support that the index value is affected by caterpillar peak height of either the corresponding or the previous year (Table 6.A). The simplest model (model 1) is the most

supported model. However, due to the small differences in AIC between model 2 and 1 (0.8 AIC), and model 3 and 1 (0.6 AIC), there is still some uncertainty about the role of caterpillar abundance as an explanation of variance in index value in pine.

Table 6. A) Candidate models explaining which variables affect the index value in Scots Pine. B) Estimates of the best model fit (n = 13). iv = index value; cph = caterpillar peak height; cph_1 = caterpillar peak height the year prior. Models are linear models.

6.A

<i>Candidate models</i>	<i>AIC</i>
(1) index ~ 1	38.9
(2) index ~ cph	39.7
(3) index ~ cph_1	39.5

6.B

<i>Residuals</i>				
<i>Min</i>	1Q	<i>Median</i>	3Q	<i>Max</i>
-2.146	-0.528	0.182	0.750	1.415
<i>Coefficients</i>	<i>Estimate</i>	<i>Std. Error</i>	<i>p-value</i>	
Intercept	0.090	0.267	0.742	

Best model: (1)

3.5 Leaf toughness

Leaf size (i.e. leaf length) did not significantly affect leaf toughness measurements ($p = 0.803$) (derived from the model $glmer(\text{proportion toughness} \sim \text{length} + (1|\text{tree_ID}/\text{day_random}), \text{family} = \text{binomial})$). After this had been established, it was decided to not include length in further candidate models.

From the candidate models it seems that the effects of date on leaf toughness are clearly

supported (e.g. model 2 versus model 1, Table 7.A), and that there seems to be no support for the effects of tree phenology on leaf toughness (e.g. model 3 versus model 1, Table 7.A). However, the most supported model (model 5) shows that later trees grow tougher leaves than early trees ($p < 0.001$, Table 7.B), and that these late trees produce leaves that get tougher more quickly ($p < 0.001$, Table 7.B).

Table 7. A) Candidate models explaining which variables affect leaf toughness in English Oak. B) Estimates of the best model fit (n = 677). prop = proportion toughness (range 0 - 1); day_rnd = day as random effect (factor); day_cov = day as fixed effect (numeric); tree_phenology = average phenology of each tree. Models are generalised linear mixed-effects models (glmer).

7-A

Candidate models	AIC
(1) prop ~ 1 + (1 tree_ID/day_rnd)	547.7
(2) prop ~ day_cov + (1 tree_ID/day_rnd)	292.5
(3) prop ~ tree_phenology + (1 tree_ID/day_rnd)	548.6
(4) prop ~ day_cov + tree_phenology + (1 tree_ID/day_rnd)	289.5
(5) prop ~ day_cov * tree_phenology + (1 tree_ID/day_rnd)	274.2

Best model: (5)

7.B

Random effects	Variance	Std. Dev.	
Day_rnd:Tree_ID	0.000	0.000	
Tree_ID	0.171	0.413	
Fixed effects	Estimate	Std. Error	p-value
Intercept	19.459	12.763	0.127
Day_cov	-0.340	0.194	0.080
Tree_Phenology	-2.755	0.629	0.000
Day_cov:Tree_Phenology	0.044	0.010	0.000

By taking the values from the best fitting model (Table 7.B), a formula can be constructed fitting an S-curve for the development of leaf toughness dependent on tree phenology. In Figure 10, 15 (early phenology) and 30 (late phenology) were chosen as examples to demonstrate the

difference in leaf toughness development between early and late trees. As can be seen in the figure, early trees will initially produce tougher leaves compared to late trees, as well as reach full toughness more gradually and later than late trees.

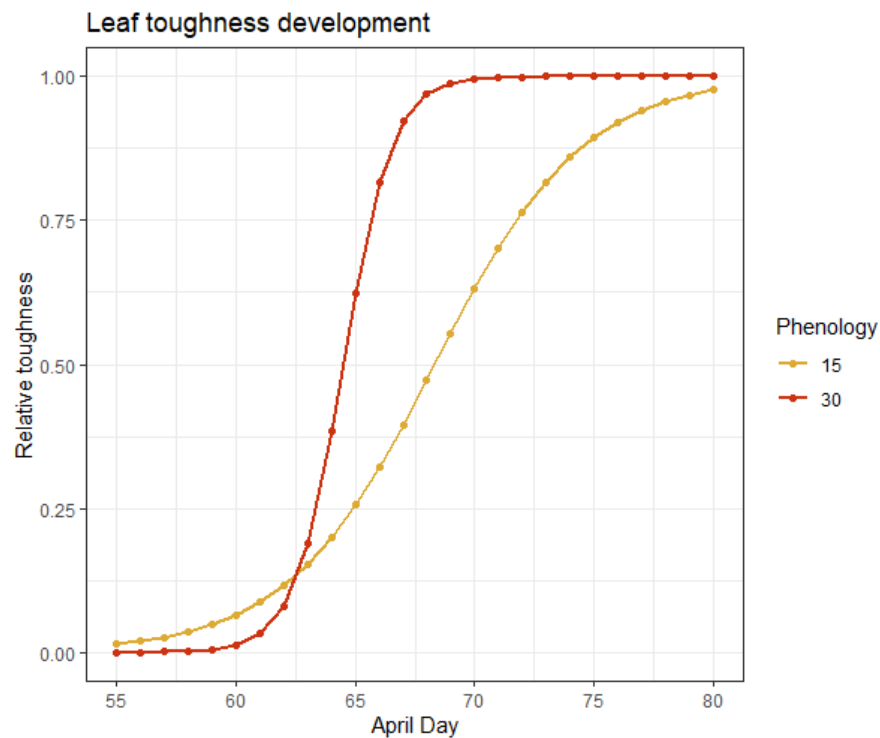


Figure 10. Development of leaf toughness over time. Phenology is measured in April Days. Yellow (15) = early tree phenology; Red (30) = late tree phenology.

4. Discussion

Different phenology phenotypes in English oak seem to vary in vulnerability for folivory, where early trees are more susceptible than late trees. Previously it has indeed been shown that early phenotypes carry higher densities of caterpillars and suffer more defoliation than late phenotypes (Wesołowski & Rowiński, 2008), and this study shows that this could be partly due to a later start in defence of leaves in early oaks compared to late oaks. This would suggest that there is a trade-off between early bud burst and defence against herbivores. Morecroft & Roberts (1999) found that the photosynthetic capacity in English oak takes a substantial amount of time to develop. They described that there is a lag between bud burst and total photosynthetic capacity of the mature leaf of 52 days, which takes up roughly a fourth of the potential growing season (Morecroft & Roberts, 1999). Taking into account that caterpillar outbreaks are relatively rare, it is possible that by producing leaves early in the season rather than late, net photosynthetic yields are higher for early trees as they are able to produce at full capacity for longer than late trees. A similar suggestion was made by Tikkanen and Julkunen-Tiitto (2003), who proposed that a possible cost of late phenology could be a reduction in length of the growing season. Additionally, they suggest that late trees might be disadvantaged due to more shade from surrounding trees (Tikkanen & Julkunen-Tiitto, 2003).

As has been previously mentioned, caterpillar outbreaks are relatively rare events, and this study found that on average early oaks grew bigger tree-rings than late oaks. This raises the question of why late oaks still exist, since apparently there is a general benefit of being early. Despite caterpillar peaks occurring only once every 9-10 years, studies found that oak trees with an early phenology suffer at least some degree of defoliation every single year, with nearly complete defoliation during certain outbreak years (Wesołowski & Rowiński, 2008). In contrast, oak trees with a late phenology were

found to only suffer visible defoliation during caterpillar peak years (Wesołowski & Rowiński, 2008). Thus, by relinquishing early bud burst, late trees might make up for lost days of the growing season by escaping defoliation a majority of the time.

Another drawback to earlier bud burst in oak species is the decreased production of acorns in the following year as a result of heavier defoliation (Pearse, Funk, Kraft, & Koenig, 2015), whereas oaks that were protected against folivory produced more acorns (Canelo, Gaytan, González-Bornay, & Bonal, 2018). Caterpillars are able to both directly and indirectly negatively affect acorn production. Directly, they can destroy the embryos and flowers (Wesołowski, Rowiński, & Maziarz, 2015). Indirectly they can increase the energy expenditure of trees by upping the costs of developing a second flushing of leaves (Canelo et al., 2018; Wesołowski et al., 2015).

The results show a strong support that the index values of oak were negatively correlated with caterpillar abundance in the previous year. However, support at the individual tree level for an effect of caterpillars on ring-width was not unequivocal. This difference might be explained by the fact that the index value is calculated from all individual tree cores, whereas ring-widths were averaged per tree. It is possible that on the site-level there are a considerable number of outliers that significantly affect the determination of the index values, but that said outliers are (evenly) distributed among the individual trees (e.g. only one of three cores per tree being an outlier). If this is true, it could explain how the effects of caterpillar abundance do show on site-level, whereas on tree-level these effects would not be as evident since any outliers would be smoothed out through the averaging of cores per tree.

It was expected that the ratio earlywood to latewood would increase in oak trees in years after a caterpillar outbreak, however, the results in Figure 7 do not show this. Instead it shows a relatively stable, low ratio of EW:LW in oak for the past five years. When inspecting the growth of oak, it can be seen that the production of earlywood is constant throughout the years,

whereas the production of latewood fluctuates (Figure 8). This is in conformity with Rubtsov (1996) who also found that in English oak the production of earlywood was less closely related to defoliation than latewood (Rubtsov, 1996). In Figure 8, it can also be seen that after 2008 (outbreak 2008/'09) the production of latewood somewhat decreased before gradually increasing again after 2011/'12. Additionally, the production of latewood seems to be decreasing once more after 2018 (outbreak 2018/'19/'20). Thus, the decrease in latewood does not show in the averaged data used to calculate the ratio, yet there is some evidence of a decreased production of latewood when looking at the individual cores.

There seems to be a lagged response to the caterpillar outbreak by one year regarding the production of latewood from 2008 to 2009. Whereas there is only a very faint, if any, response to the caterpillar outbreak starting in 2018. This raises the question of what could cause this difference in response of latewood production to the start of a caterpillar peak. One possible explanation for the difference in response might be that in recent years the growing conditions were simply better than ten to fifteen years ago. Another possible explanation is the difference in caterpillar peak height between the outbreak of 2008 and 2018. As can be seen in Figure 11 (Appendix A.1), the caterpillar outbreak of 2008 reaches a considerably higher caterpillar peak height (CPH of respectively 2007; 2008; 2009 = 21.4; 54.8; 71.2 g/m²/day) compared to the outbreak of 2018 (CPH of respectively 2018; 2019; 2020 = 23.0; 54.5; 36.1 g/m²/day). However, the outbreak of 2008 only lasted two years, whereas the outbreak of 2018 lasted three years. These results might suggest that the intensity of a caterpillar outbreak plays a bigger role in the growth of latewood than the duration of an outbreak. Therefore, it would be interesting to replicate the tree-ring analysis experiment performed in this study elsewhere in an area that has undergone similar outbreak patterns (i.e. a short, yet intense outbreak followed by a longer, less intense outbreak or vice versa).

Here, no clear support was found that non-host species (i.e. Scots pine) benefited from

caterpillar outbreaks, which concurs with the findings of Tikkanen and Roininen (2001), who found no increased radial growth in less-preferred trees in a mixed forest stand (Tikkanen & Roininen, 2001).

Against the expectation, no difference was found between the growth of caterpillars on early trees compared to late trees despite the stark difference in leaf toughness development. It is known that caterpillars are strongly synchronised with the bud burst of their host (Van Dongen et al., 1997), however, these results might suggest an ever deeper level of host-insect interaction. Caterpillars are able to tolerate a certain level of tannins by virtue of their guts, which provide a variety of physical and biochemical defences (e.g. antioxidants, high pH, surfactants and a protective lining of the midgut consisting of a peritrophic envelope) (Barbehenn & Constabel, 2011). Caterpillar guts have been studied before (Campbell, Cao, Hines, East, & Gordon, 2008; Gross, Brune, & Walenciak, 2008), however, literature research yields no studies that have focused on possible differences between gut composition in caterpillars (of the same species) growing on early versus late trees. Yet, a difference in gut biome might offer some explanation as to why caterpillars on late trees are able to grow without any apparent inhibition.

With the prediction that climate change will lead to a global rise in temperature, studies have investigated the possible effects of climate warming on oak trees and caterpillar growth. There does not seem to be a consensus in the literature when it comes to how warmer temperatures will affect the synchronisation of bud burst of oaks and egg hatching of caterpillars. Buse *et al.* (1999) propose that at the predicted levels of climate warming, there will overall be little effect on the host-insect interaction between oak and winter moth. They found that oaks bud earlier and their leaves develop faster at elevated temperatures. However, they found that the same is true for the winter moth, as the caterpillars emerged earlier and also developed faster. Thus, any advantages that trees would have by budding earlier would be negated, maintaining the same

effect of caterpillars on trees (Buse, Good, Dury, & Perrins, 1998, 1999). On the other hand, more recent studies are less certain about the effects climate warming will have on the synchrony between hosts and caterpillars. Asch and Visser (2007) propose that global climate change will lead to a disturbance in the synchronisation of host and herbivore interactions. They suggest that unless natural selection is capable of restoring synchrony, population viability may be severely impacted (van Asch & Visser, 2007).

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Appendix A - Additional figures

A.1 Caterpillar peak height

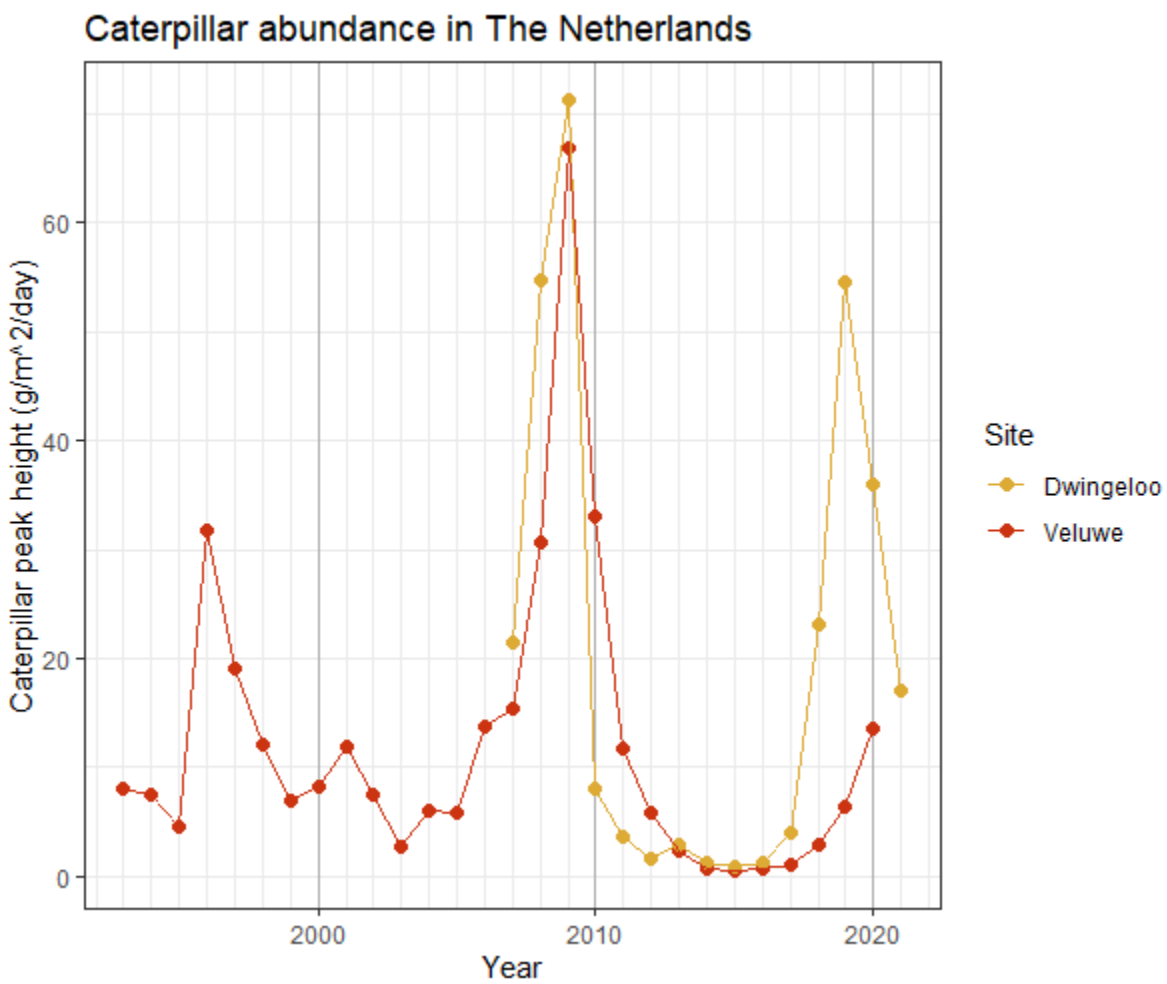


Figure 11. Caterpillar peak height in The Netherlands, measured in National Park the Veluwe (red, n = 28) and National Park Dwineldervel (yellow, n = 15).

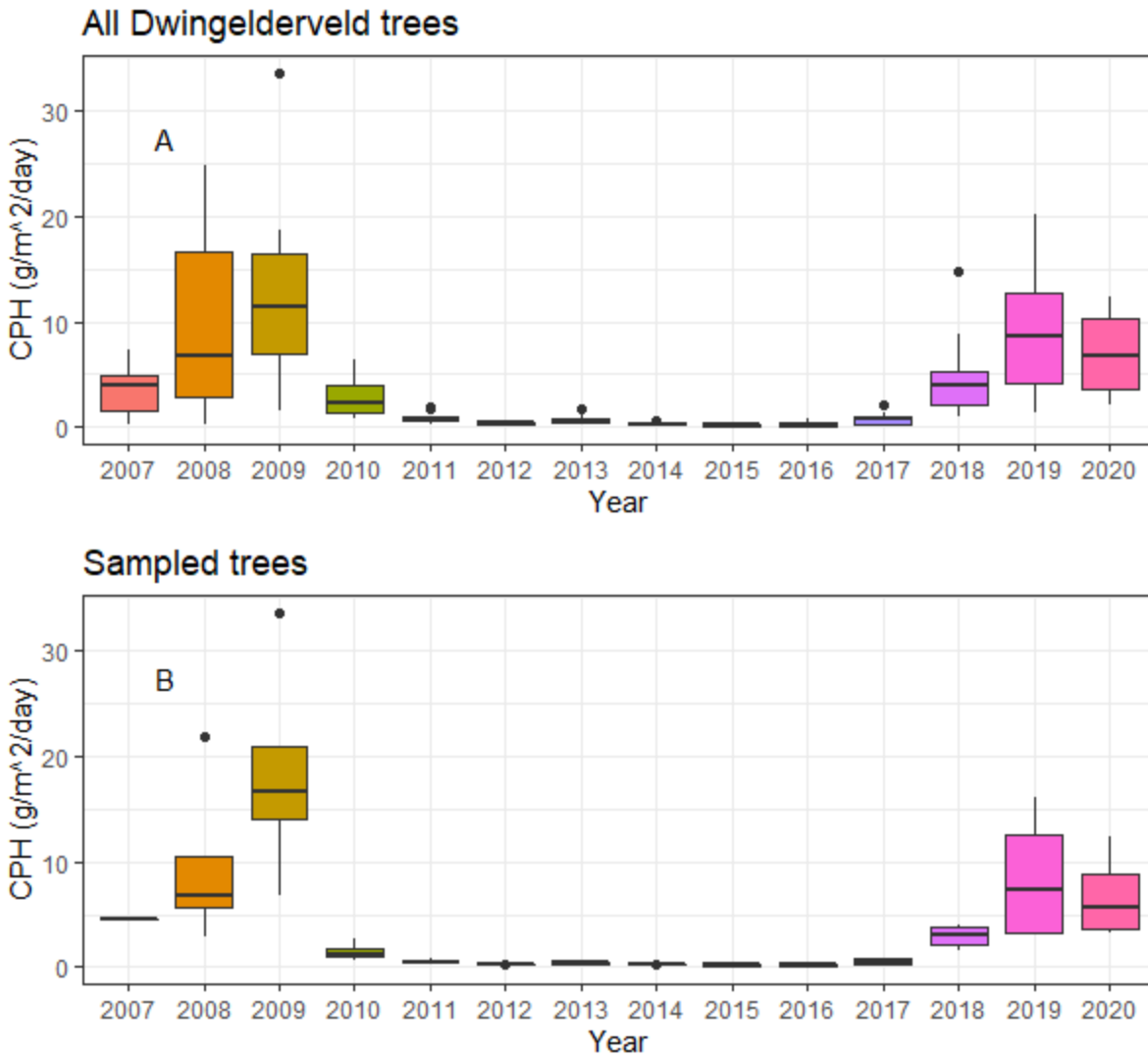


Figure 12. Caterpillar peak height (CPH) in National Park Dwingelderveld for; A) all trees with frass nets in the area (n = 159), and B) the subset of trees that were sampled with the increment corer (n = 52).

A.2 - Caterpillar peak day

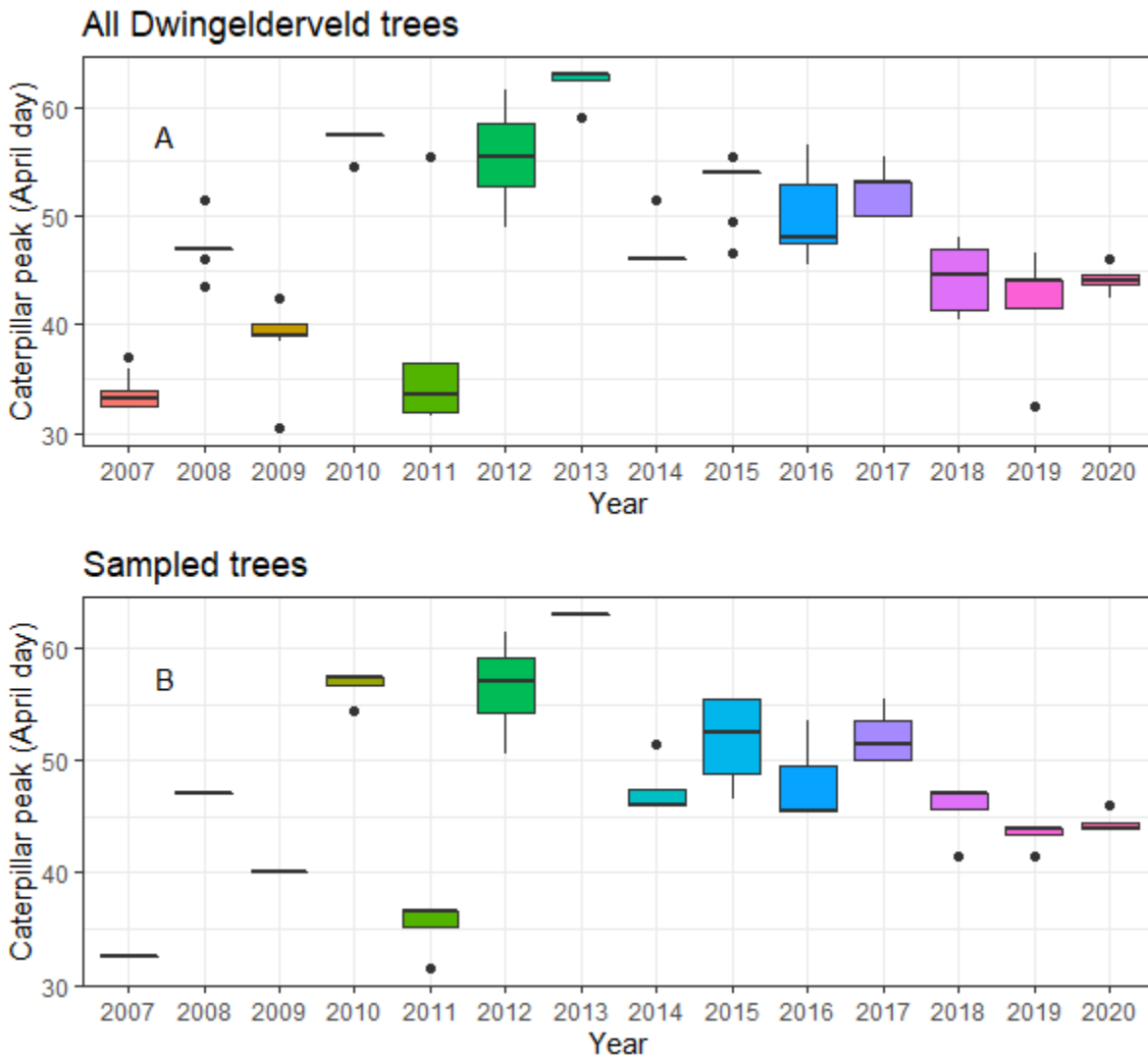


Figure 13. Caterpillar peak day per year for; A) all trees with frass nets in the area ($n = 159$), and B) the subset of trees that were sampled with the increment corer ($n = 52$).

A.3 - Caterpillar growth

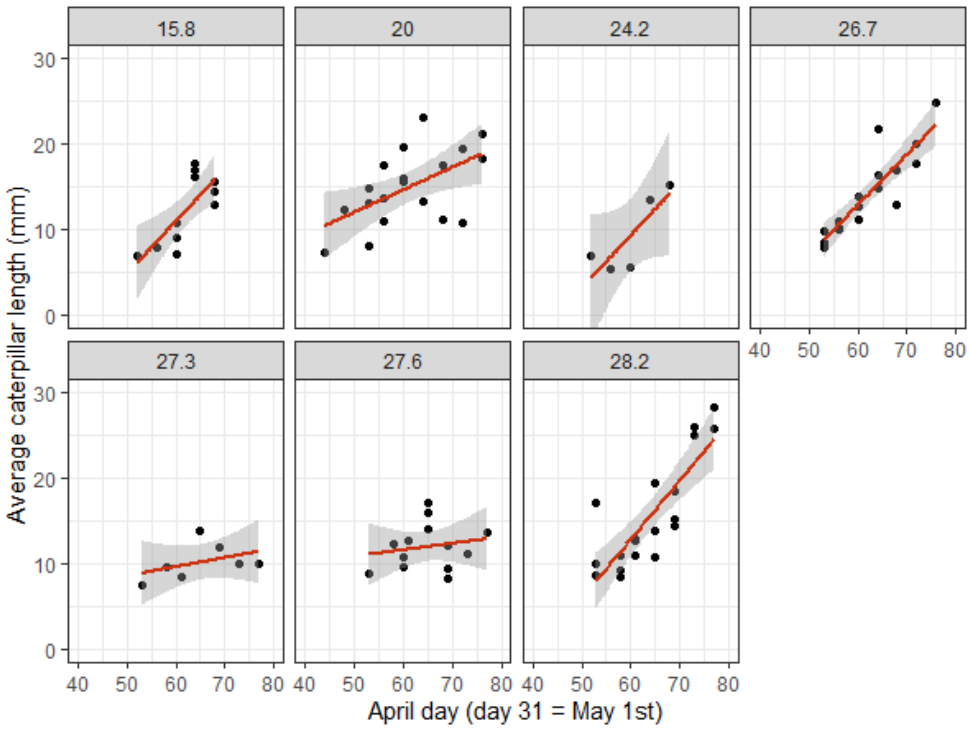


Figure 14. Average caterpillar growth (crawlers and geometridae combined) per individual tree. Tree phenology, represented by the average date of all measured years at which each tree reaches bud burst stage 3, is presented in the grey box above each plot.

A.4 - Caterpillar peak height and Ring-width in oak

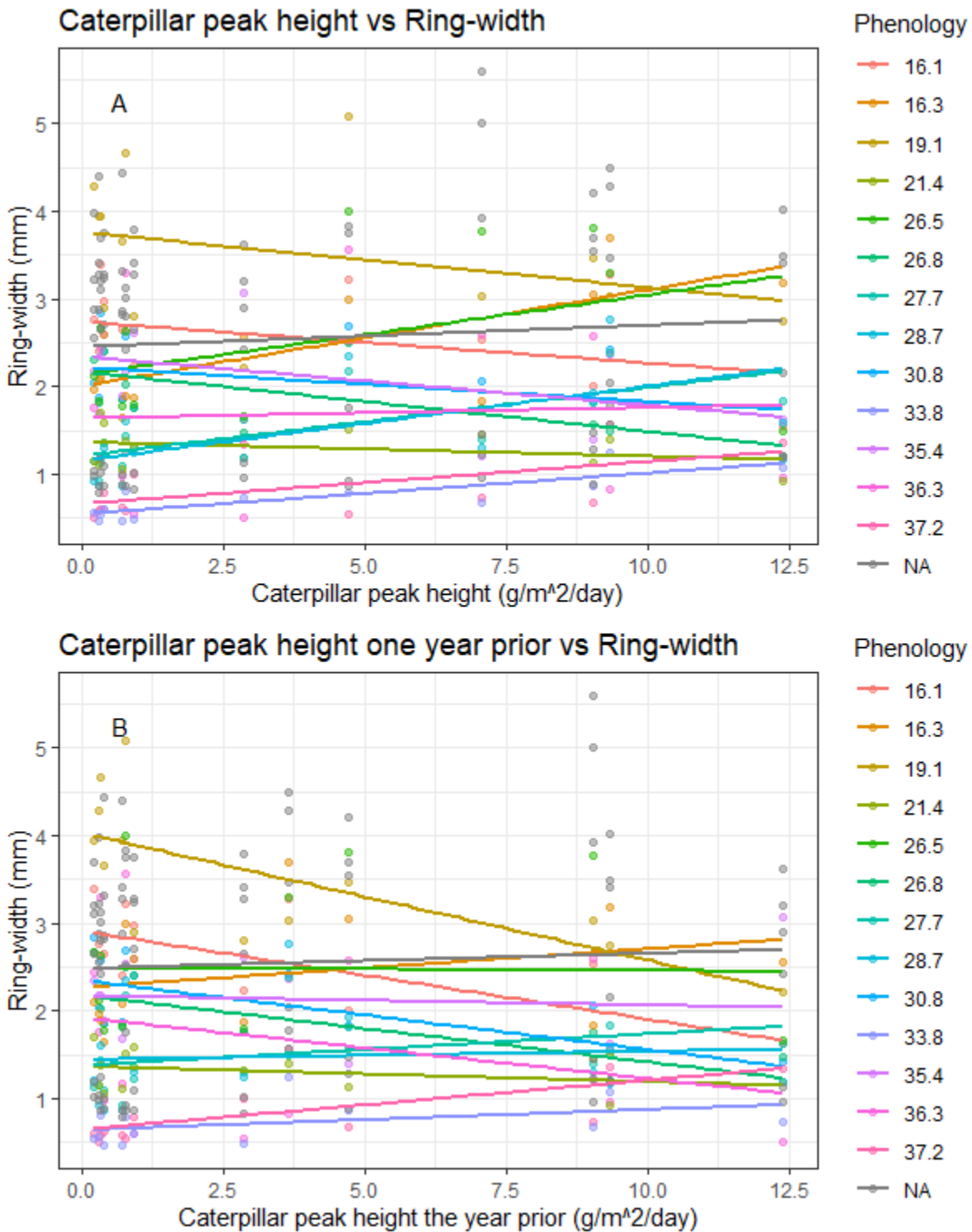


Figure 15. The correlation between A) caterpillar peak height and ring-width ($n = 247$), and B) caterpillar peak height of the previous year and ring-width ($n = 247$). The 'Phenology' in the legend refers to individual oak trees and represents the average date (April day) at which the tree reaches bud burst stage 3; 'NA' in the legend represents the pine trees, as they were not given a bud burst score.

A.5 - Caterpillar peak height and Ring-width in pine

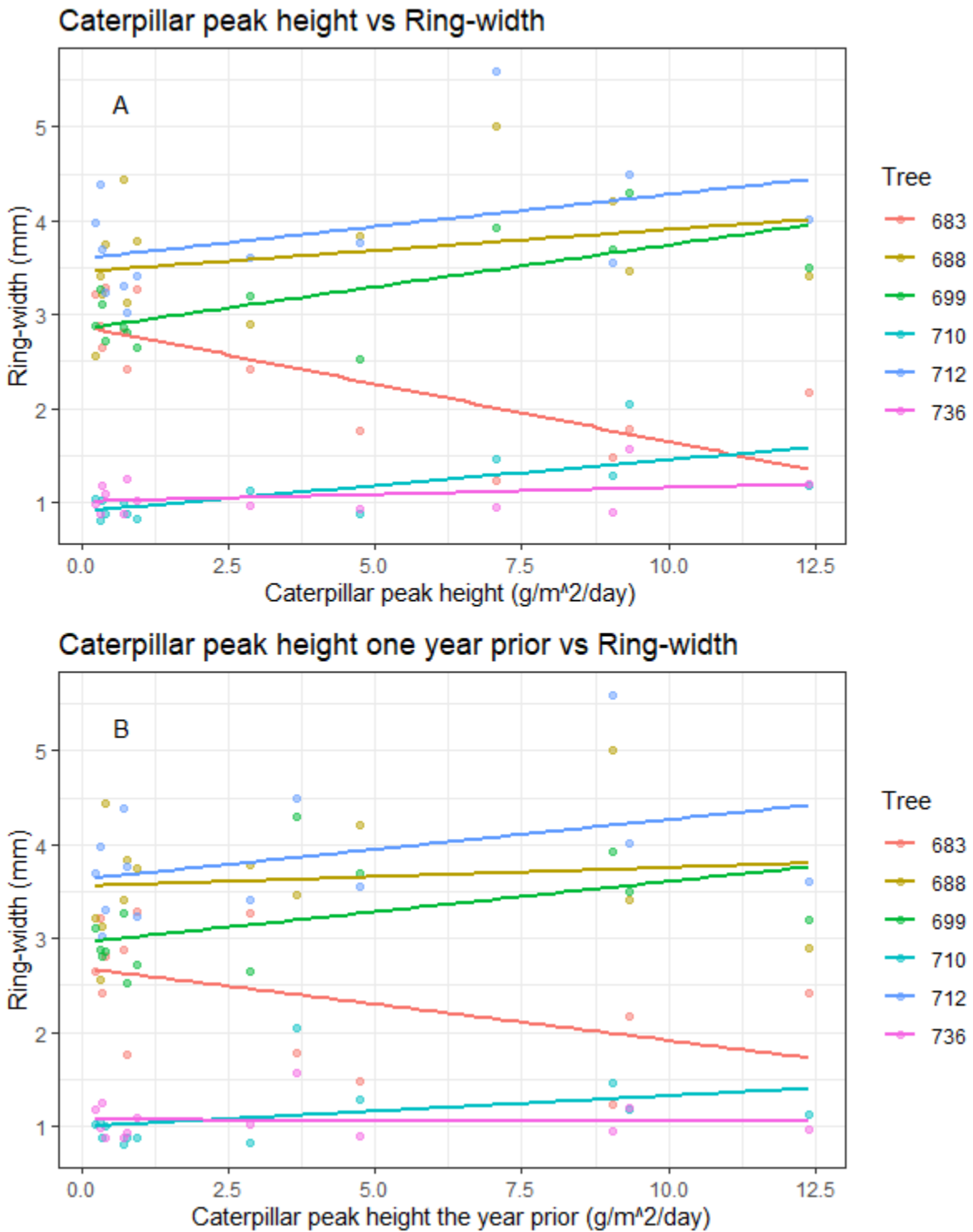


Figure 16. The correlation between ring-width of pine and A) caterpillar peak height ($n = 78$), and B) caterpillar peak height of the previous year ($n = 78$). 'Tree' in the legend represents the individual pine trees.

A.6 - Earlywood and latewood increment

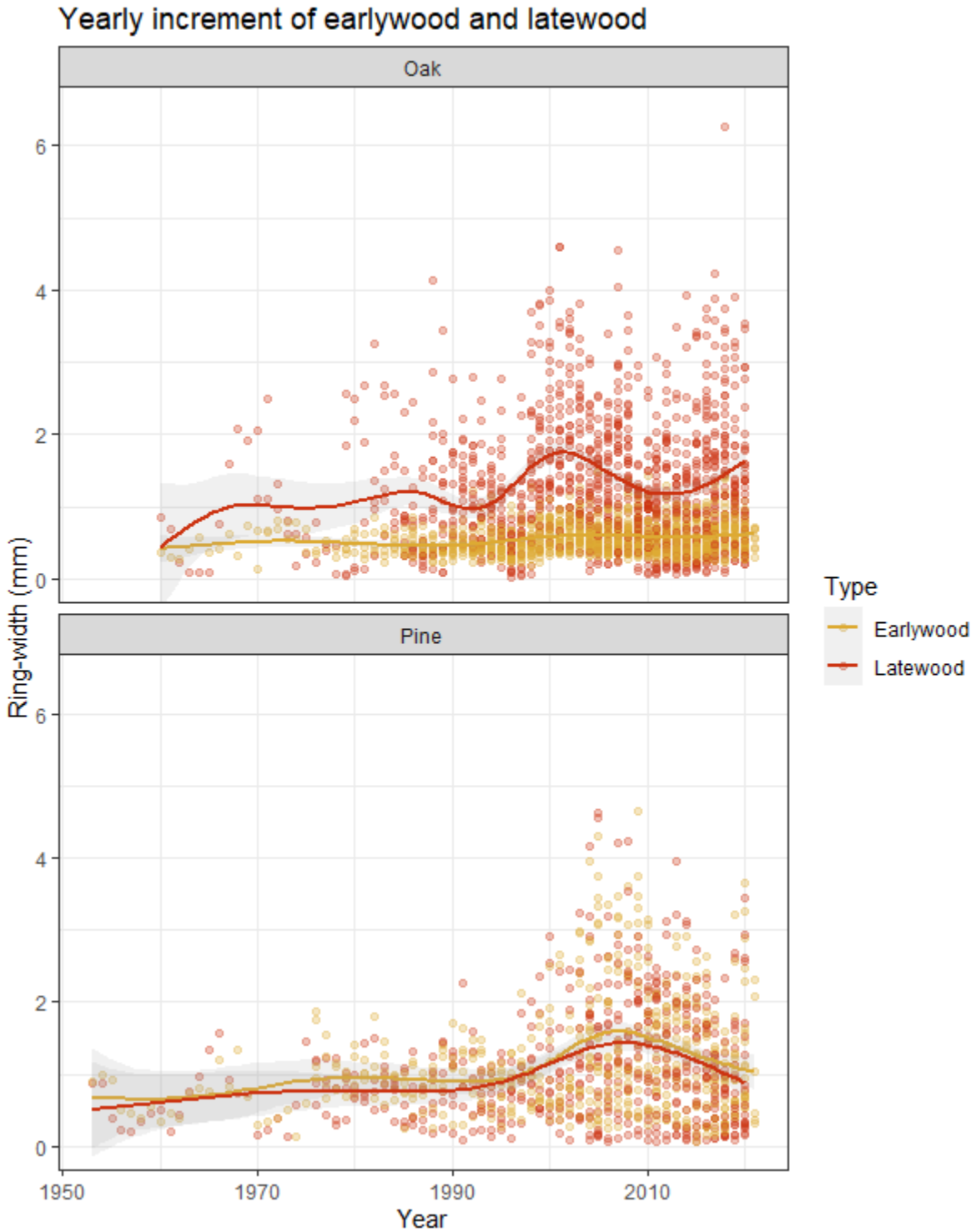


Figure 17. Yearly ring-width increment separated into growth of earlywood and latewood for oak ($n = 2174$) and pine ($n = 1052$) for all measured tree-rings.

A.7 - Leaf toughness

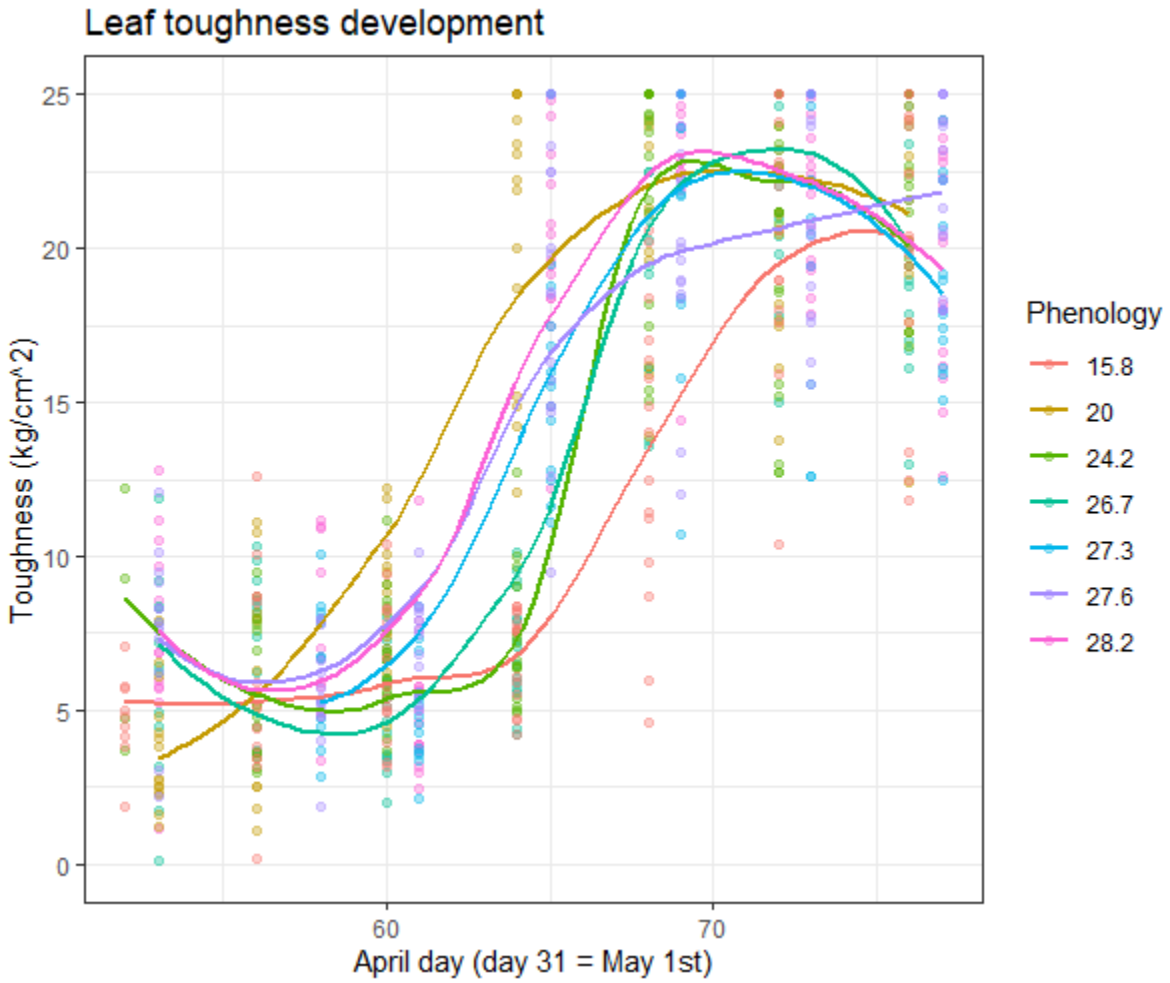


Figure 18. Leaf toughness development of the seven individual trees on which the caterpillar sleeves were kept ($n = 677$). 'Phenology' in the legend refers to the average date (April day) at which each tree reaches bud burst stage 3.