The Influence of Caterpillars and Climate on Tree Growth

How caterpillar abundance, with the resulting defoliation, and changes in climatic conditions affect the seasonal growth of *Quercus sp.*.

Abstract

Some species of forest caterpillars have been observed to exhibit cyclical outbreaks and defoliate entire forests during the peaks of outbreaks. The defoliation of *Quercus* spp. and drought conditions throughout the year have a negative impact on trees development, which becomes an important factor for oak survival as climate change advances. While this topic has been under investigation there are still areas and factors that need attention.

In this study core samples from 12 individual *Quercus robur* from the Dwingelderveld, in Drenthe, the Netherlands, have been taken and the ring width variation between 2007 and 2019 been analysed. For each individual tree, annual caterpillar peak abundance was known and we investigated how much of the variance is explained by either caterpillar biomass or drought. It was found that caterpillar biomass negatively affects the growth of a tree and to a lesser extend drought also has a negative impact.

Introduction

Herbivores in tree canopies are an integral part of the forest ecosystem. They are both prey and can defoliate entire forests. Normally the numbers are kept low by food availability, predation, parasites and climatic factors, but every few years the numbers explode and can have a significant negative impact on the host tree's growth and mortality (Futuyma and Wasserman, 1980; Sarvašová *et al.*, 2020). Such cyclical outbreaks can be observed in Lepidoptera that can be found in high abundance on *Q. robur* (Tikkanen and Julkunen-Tiitto, 2003), and even within the species do the herbivores actively select their target host (Mopper and Simberloff, 1995).

Tree growth can be categorized into two different mechanisms (axial and radial growth), tree trunk growth is the increase in size and number of wood cells (Mahmood, 1971). Growth is limited in temperate climates to certain seasons, spring and summer, and depends on endogenic and exogenic factors (Phipps, 1985; Savidge, 1996). Growth of a tree occurs to sustain life giving functions within an individual. This happens mostly in spring. Later in the growing season, summer, a tree produces excess photosynthates and then the extra energy is used to produce new growth (Phipps, 1985).

The growth of a tree can be determined by analysing the growth rings, which each represent a growth cycle (Mäkinen *et al.*, 2008). When a tree is exposed to stress and the growth season is impacted white or light rings are formed, which are also known as inter annual rings (Hogg, Hart and Lieffers, 2002).

Tree ring width has been shown to vary, depending on climatic influences (King *et al.*, 2013). Oak (*Quercus*) species show a decline in growth during droughts, as at lower elevations precipitation is more important than temperature for growth, while the opposite is true at higher elevations (Di Filippo *et al.*, 2010). In recent years climate change has led to the advanced spring phenological development (Chen *et al.*, 2019). Budburst of oaks, in temperate regions, heavily depends on the temperature. Sufficiently chilling at temperatures, between 6°C to 12°C during winter and temperatures above 12°C in spring, are needed to kick start budburst (Polgar and Primack, 2011; Fu *et al.*, 2015; Chen *et al.*, 2019).

Earlier leaf unfolding has been linked to climate change (Fu et al., 2015). Furthermore, it has been found that outbreaks of gypsy moth and subsequent defoliation show a correlation with warmer temperatures. With climate change and the warming of the winter months the eggs of the caterpillars are less likely to die during winter, resulting in more caterpillars during outbreaks (Hunter, 1991). Also, less cumulative heat units are needed for both budburst and hatching of the caterpillars (Buse and Good, 1996). Furthermore, climate change causes a movement of caterpillars latitudinal north affecting the forests in the north of Europe (Tenow et al., 2007; Jepsen et al., 2008; Wenden et al., 2020). Overall climate change is causing an increased difference between spring and autumn phenology and causes a decrease in temperature sensitivity of leave unfolding (Chen et al., 2019). However, no change in the synchro between budburst and caterpillar emergence has been recorded (Buse and Good, 1996), but spring phenology does continue to advance earlier into the year (Vitasse et al., 2009; Polgar and Primack, 2011; Fu et al., 2015; Chen et al., 2019; Denéchère et al., 2019; Wenden et al., 2020). On the other hand, many northern tree species need a chilling period for budburst to start, and as a consequence of climate change counter act the overall warming (Polgar and Primack, 2011; Fu et al., 2015; Chen et al., 2019; Wenden et al., 2020). This makes it important to understand the impact of climate on the functions of the cyclical outbreaks and subsequent defoliation and the impact on growth of trees, which are impacted by defoliation. As climate change impacts this cycle it can affect the insects directly, by changing their ecosystem, food and climate (Cornelissen, 2011).

Climatic parameters can be used to predict the chemical and physical defences of deciduous trees against herbivores (Pearse and Hipp, 2012). With low temperature seasonality a tree develops more defences against herbivores. This affects trees in the tropics and in the temperate zone deciduous trees (Pearse and Hipp, 2012). Herbivory early in the growth season leads to an increased investment into defences and results in less late season herbivory (Wold and Marquis, 1997). Toughness, evergreeness, and condensed tannins are defences used by leaves against predation (Pearse, 2011). Another method is to reduce leaf digestibility, by increasing tannins and toughness (Wold and Marquis, 1997). Furthermore, plants can track biotic and abiotic influences over macro evolutionary time, in order to adapt their defences (Pearse and Hipp, 2012).

Herbivores depend on the phenology of the host in order to not starve when insect herbivores start hatching. Early phenology caterpillars depend on a synchronous outbreak and budburst, with asynchronous outbreak between caterpillars and budburst having severe impacts on caterpillar population dynamics, with even a few days increasing the risk of mortality and impacting future fecundity during the adult stage (Hunter, 1991). Early phenology is always a target of herbivory, and late phenology only during severe out breaks. Delaying phenology is used as a defence mechanism, since defoliation of a tree is costly and can lead after consecutive defoliation to death (Wesołowski and Rowiński, 2008). Furthermore, defoliated oaks shown less growth and after defoliation have an increased risk of death and a lower resistance to biotic and abiotic influences (Foss and Rieske, 2003).

A common herbivore found on oak (*Quercus spp.*) are caterpillars belonging to the Geometridae family (FAO, 2014). Geometridae larvae are classified as a spring to early summer feeder, and thus feeds during the main growth season of oak (Naidoo and Lechowicz, 2001). Furthermore, larvae tend to avoid high tannin concentrations and feed preferably on oaks. Two of the most common species are *Operophtera brumata* (winter moth) and *Erannis defoliaria* (mottled umber) (Sarvašová *et al.*, 2020). *O. brumata* is one of the most abundant insect herbivores on *Q. robur*, with caterpillars emerging in early spring (Tikkanen and Julkunen-Tiitto, 2003) and show a roughly 10-year outbreak cycle (Jepsen *et al.*, 2008). Another common species known to completely defoliate oaks is *Tortrix viridana* (European oak leafroller) (Ghirardo *et al.*, 2012).

The aim of this study is to investigate the impact of caterpillar biomass on the radial growth on the tree and what role climate plays in this integration. It is expected that growth within a tree is uniform enough to be repeatable. Since the effects of defoliation affect the growth negatively for up to three years (Dulamsuren *et al.*, 2010; Wiley, Casper and Helliker, 2017), it is expected that with increasing caterpillar biomass a growth in tree rings reduces for the host tree. Precipitation is expected to be the main influence besides herbivores, due to the low elevation of the study site (Di Filippo *et al.*, 2010).

Methods

Study Site

The study area Dwingelderveld (Coordinates: 224000/537000), Figure 1, is a mosaic of wet heathlands with forests with an area of 37km², located near Dwingeloo, Drenthe a province in northern Netherlands. Dwingelderveld is a national park, established 1991, managed by Staatsbosbeheer (Forestry Commission), Natuurmonumenten and private entities (van Roon, 201?). The national park is open to the public with designated walking paths through the area. The national park is under both the conservation of natural habitats and of wild fauna and flora directive (92/43/EEC) and the conservation of wild birds directive (2009/147/EC).

The annual average precipitation is around 840mm, with a relative even spread around the year, with slightly lower rates of precipitation during the spring months compared to the rest of the year. The monthly maximum temperature is at its lowest during the winter months around 6°C and can reach a maximum monthly average temperature of 23°C during the summer months (KNMI, 2020).



Figure 1 - Map of the study site in the National Park Dwingelderveld, Drenthe the Netherlands. The inset map shows the location of the study site in the context of the Netherlands. The main map shows the study site in Dwingelderveld with the 12 sampled *Quercus sp.* distributed from the west to northeast of the study site.

The heathlands are predominantly covered by *Caluna vulgaris, Empetrum nigrum* and *Genista sp.*, the forests compromise of *Quercus robur* (oak) and *Pinus sylvestris* (scots pine), which are the tree types selected for this study, and various grasses and mosses. The soil of the area is poor quality with low nutrient levels and predominantly sandy top soils (European Environment Agency, 2019).

The larval stages of species within the Lepidoptera order are known to be able to defoliate entire forests (Tikkanen, Niemelä and Keränen, 2000). For this study the exact species of caterpillar that causes in the Dwingelderveld the defoliation of the oaks is not known. It is very likely that species within the Geometridae family, especially different winter moth species, are the cause for the defoliation, as they are among the most prevalent herbivores (Sarvašová *et al.*, 2020). Field observations show that in recent years Orthosia species (most notably *O. cruda*), and that locally *Agriopis leucophaearia, Tortricodes alternella, Phycita roborella* seem to be abundant.

Original Dataset

An unpublished dataset, from Both, consisting of the droppings of caterpillars from 12 individual *Quercus robur* trees, collected over a period of 13 years, starting in 2007, was used as part of this study. The caterpillar frass was collected using the methods as described by Tinbergen (1960). Frass nets with an area $0.25m^2$ were placed under a tree and samples were collected every 2-3 days. Afterwards the droppings were collected, dried at 60°C for 24h, cleaned of debris, finally weighed and caterpillar biomass calculated. The biomass, referred to in this study as peak max, was calculated based on an adjusted formula from the one published by Tinbergen and Dietz (1994). This formula aims at correcting for the effect of temperature on the amount of frass that is being produced by caterpillars. Data for this formula were obtained both from the Veluwe area as from Drenthe (caterpillar biomass= frass/m2/24hr * exp (5.0742 – 0.2646* Mean temperature)). As the caterpillar peak per individual tree depends on both the density of caterpillars per leaf, as on the crown volume, it is not necessarily true that values between trees can easily be compared quantitatively in terms of the herbivore pressure. In an attempt to scale the caterpillar pressure among trees, the lowest peak height per tree for the period 2007-2019 (in all cases in 2016), and divided each annual peak with this tree specific base value. This scaled peak thus runs from a value of 1 to almost 200.

Part of the analysis was using climate data. The climate data that was used was drought/precipitation surplus. This factor was calculated based on the monthly precipitation minus the monthly evaporation and then averaged across the whole year. The data used, was provided from the Royal Netherlands Metrological Institute of the nearest measuring station to the National Park Dwingelderweld, which was at Hoogeveen.

Sampling Method

A standard Swedish increment borer was used for collecting tree cores of the individual oaks for which we had caterpillar frass data. All 12 oaks were revisited during the summer and autumn of 2020 to take cores from the trunk. In addition each oak was paired, if possible, with a pine tree nearby and a core was also taken. The cores were taken at chest height with a tree corer. Three to two replicates were taken additionally, from different cardinal directions, giving a total of either 3 or 4 samples per tree. The corer was inserted, at chest height, into the tree trunk as far as possible, and the vertical direction of the cells were marked. The cores were stored in small paper envelopes, see figure 2.



Figure 2 – A, Swedish increment borer inserted into an oak tree. B, the hole left after the removal of the borer. C, the core retrieved from the sampled tree with the top of the core marked and a paper envelope, which is used to store the core.

Laboratory Analysis

For the preparation of the wood cores the method described by Asherin and Mata (2001) was used. First, the cores are aligned so that the cell structure was visible from the top. Second, the core is glued with wood glue into a mount. Third, after the glue dried the core was sanded to get a flat surface. The core was sanded using first 120 grid sanding paper followed by 240 grid and lastly a smooth finish was achieved by using a 400 grid sanding paper. Third, the core was then cleaned by using pressurised air to remove wood dust from the sanding process. Lastly, the cores were stained using Fehling's Solution. The solution contained 3.5 g copper sulphate (CuSO4 5H2O), 17.3 g potassium sodium tartrate, 6.0 g sodium hydroxide, and 100.0 ml water. A processed core can be seen in figure 3.



Figure 3 – Two processed cores, with a flat smooth finish and blue greenish hue, that results from the staining process. The top is a pine core and the bottom an oak core. The oak core shows a clear difference between the lighter sapwood and the darker latewood and light round vessels that are the tree rings. Tree ring width is significantly negatively correlated with caterpillar biomass and drought conditions. The white X shows where markers for measuring a ring width would be set.

Statistical Analysis

For this project three research questions were formulated. Firstly, how repeatable are rings from the same tree-year and between different trees at the same year? Secondly, to what extent is variation in ring width explained by the variation of caterpillar biomass by growth of the individual tree or all trees? Thirdly, how does climate together with caterpillar biomass influence annual variation in tree ring growth?

Based on these three research questions four hypotheses were formulated. First, there is a significant positive correlation in tree ring width within a sample across the same tree, showing a high repeatability. Second, annual growth in oak and pine tree rings of at the same location are positively

correlated due to similarity of growing conditions. Third, most of the variation in ring width within a sample is explained by the year of the tree rings. Lastly, tree ring width is significantly negatively correlated with caterpillar biomass and drought conditions.

These four null hypotheses have been made: There is no significant positive correlation in tree ring width within a sample across the same tree, showing a low repeatability. Annual growth of tree rings of oak and pine at the same location are not positively correlated due to similarity of environmental conditions. Most of the variation in ring width within a sample is not explained by the year of the tree rings. Lastly, tree ring width is significantly positively correlated with caterpillar biomass and drought conditions.

The prepared samples were then one by one photographed using a Sony ILCE-6000, with a focal length of 50mm. The camera was mounted on a stand, taking pictures from the top as seen in figure 4. Extra lighting was used to get a well-lit photo. The photos were then transferred over to a pc and, since a raw data format was used, converted into a JPG file format.



Figure 4 – The setup used to photograph the cores.

For the dating and marking of rings the programme ImageJ with the ObjectJ plugin was used. Within ObjectJ for each core every tree ring was marked and dated. First completed ring after the bark was assumed to be the growth ring of 2019. This was done for each ring starting at 2019 and any subsequent ring following until the end of the core. For the oak tree a marker was set in the centre of the large pores (figure 3), which are the end of a growth increment (Kollmann and Côté, 1968). For pine the marker was set at the end of the growth increment, which appears to be darker in colour (Kollmann and Côté, 1968). After scanning the pine tree samples an unexpected pattern was found within most of the pine cores. In figure 5 two cores of different pine trees are given, and it can be seen

that the rings in the bottom core show a normal ring formation with a gradual transition from a lighter wood colour to a darker, but in the top core the rings are very narrow and distinct. The reason why these rings have formed are unknown and thus the pine cores needed to be removed from the study as analysing these samples was not possible, and thus the second hypothesis has been dropped. The resulting dataset with distance between each core and ring year, was then transferred into excel. Since the measurements from ImageJ did not match up with the actual ring widths, the ratio between the width of one ring from the software and a physical measurement of the same ring was calculated. This ratio was then multiplied with each measurement from ObjectJ and lastly multiplied by 0.01 to get a final measurement in millimetres. In the dataset the following categories were recorded and are referred to under these names in this study Tree Number, identification number of the same for each of the cores; Year, the year of each tree ring within a sample across all the sampled trees and Tree-Year, the year of each ring within a certain tree.



Figure 5 – Two pine cores from different trees. The top core shows unusual ring formation with narrow and distinct rings. The bottom shows a normal ring formation with a gradual ring growth from light into dark wood colour.

After conversion was done and a corrected dataset was compiled, each core was then transcribed into Tellervo development version 2.1, a tree core management software, since the data had to be in a .rwl, ring width length, file format for further analysis. The data was entered in micrometres.

After the transcription the data was imported into R Studio version 1.1.463. The imported dataset was limited to the years from 2007 to 2019. Since for this time range caterpillar biomass data was available. Ring width might decrease over time at the same time as tree diameter and volume increase, resulting in narrower rings but also a volume increase. Thus, the data has to be standardized by detrending the data series in order to take this increase in overall volume into account (Fritts, 1976).

The analysis on the cores was done in the R package dplR. The analysis followed the methods outlined in "An introduction to dplR" by Bunn and Korpela (2019). First all the cores were combined into one dataset and checked for any naming or conversion/import errors. Next the core for each corresponding tree were combined into one dataset. The data of each tree was detrended using "ModNegExp" method. "ModNegExp" method tries to fit the same nonlinear model of biological growth to the whole dataset (Bunn and Korpela, 2019). The model is $f(t) = a \exp(bt) + k$, with time being the argument of the function, see Fritts (1976) for a detailed description.

To test how the data correlated within a tree, a Spearman's overall interseries correlation was carried out, for each tree. In an overall interseries correlation a master series is built and the individual series are then correlated to the master series (Bunn and Korpela, 2019). A master series is a tree core that gets created based on the mean ring year, of the different cores within a tree, creating an average tree core. To find the within correlation of a tree each tree core then is correlated to the corresponding tree master series (Bunn and Korpela, 2019). In addition, the annual rings for each core within a tree have been correlated to the annual rings of another core of the same tree, to find the best estimate of annual ring width variation between each other to see how the different core in a tree compares to each other. A lower correlation coefficient, of 0.5 or less, was assumed to be the result of an unknown error outside of natural variation and was then noted within the dataset, so that easy possible exclusion in further analysis was possible. In total six cores from six different trees were removed this way and the resulting set of cores was then marked as selected cores for the variance partitioning models. The removed cores were, 599_O_N, 607_O, 699_O, 712_O, 867_O_E and 1021_O. The full result tables of each tree can be seen in appendix 1.

A mixed effect model was used to find out how within and between individual variance components were explained by different factors (Dingemanse and Dochtermann, 2013). For the mixed model the Ime4 package in R was used, using the Imer function to build the model. Three different models were run. First set of models were null models with just random effects of Tree-Year and Year, with either all cores or selected cores, 2 models. Second set of models included a fixed effect either Peak Max or Peak Scaled and the random effects of year and tree-year and were also done once with all or selected cores, 4 models. Third set of models included, in addition to Peak Max or Scaled, also Drought as a fixed effect, 4 models. In all ten different models Ring Width Length Detrend was the predictor. The selected cores, are the samples that were not removed from the dataset based on the selection procedure previously described. After the variance partitioning models were run the residuals were tested for normality using a Kolmogorov-Smirnov test (Dytham, 2011).

The Peak Max and Peak Scaled models were then compared to see which gives a better picture of the caterpillar influence on the tree. The results of the models with all tree cores and the selected tree cores were then compared to see, which method would deal better with possible errors that have occurred during tree ring width measurements. In the end only the null model, Peak Max and Peak Max & Drought models with the selected cores were presented in this study, since differences between the ten variations were negligible and all the full results can be found in appendix 2.

Results

In table 1 the results of the overall interseries correlations for each tree can be seen. Overall, eight tree series did not give any significant correlation within the tree, whereas four gave some significant positive correlations. Cores that show a significant correlation, also show a high positive correlation coefficient. The cores of the tree 1055 show all together a negative correlation coefficient and p values greater than 0.5 suggesting that there is something wrong with that series. There is only one tree, 683, that has a consistent significant correlation throughout the tree. There are three series, 599, 930 and 1055, which have no significant correlating cores within a tree, based on the respective master series. This suggests that a tree does not grow evenly and that possible data collection errors have an important impact on the ring width, this has to be kept in mind during analysis. This is further supported by the correlation coefficients gained from the selection procedure, appendix 1. These pair wise correlations show certain cores within a tree correlate better with other, but that there is always one or two cores that do not show a significant correlation to the rest. Lastly, 1055 samples will be excluded from any further analysis due to the negative correlation.

With the majority of cores showing a non-significant correlation, the first hypothesis, there is a significant positive correlation in tree ring width within a sample across the same tree, showing a high repeatability, is therefore mostly rejected.

Table 1 – Overall interseries correlation (Spearman) based on the master series of each core series within a tree. Significance values: * P < 0.05; Core ID: 599_O_N – Tree Number (599), Tree Species (Oak), Cardinal Direction of Sample (North)

| Core ID | Correlation Coefficient | Core ID | Correlation Coefficient | Core ID | Correlation Coefficient |
|---------|----------------------------|---------|----------------------------|----------|----------------------------|
| 599_O | 0.4196 | 699_O | 0.3916 | 867_O_W | 0.5664* |
| 599_O_N | 0.0979 | 699_O_E | 0.3776 | 930_O_N | 0.3776 |
| 599_O_W | 0.4615 | 699_O_N | 0.2797 | 930_O_E | 0.4273 |
| 607_O | 0.4056 | 699_O_S | 0.6084* | 930_O_W | 0.2797 |
| 607_O_E | 0.4690 | 699_O_W | 0.4406 | 944_O_E | 0.7198* |
| 607_O_N | 0.6923* | 712_0 | 0.9230* | 944_O_N | 0.4545 |
| 607_O_S | 0.2545 | 712_O_E | 0.5385 | 944_O_S | 0.7363* |
| 623_O | 0.8951* | 712_0_N | 0.7747 | 1021_0 | 0.0934 |
| 623_O_N | 0.3364 | 712_0_S | 0.4476 | 1021_O_E | 0.5824* |
| 623_0_W | 0.7692* | 736_O_E | 0.6713* | 1021_O_W | 0.4670 |
| 683_O | 0.6273* | 736_O_N | 0.8364* | 1055_0 | -0.0165 |
| 683_O_E | 0.8127* | 736_O_W | 0.4126 | 1055_O_N | -0.1758 |
| 683_O_N | 0.8391* | 867_O_E | 0.3986 | 1055_O_S | -0.3297 |
| 683_O_S | 0.7565* | 867_O_N | 0.4615 | | |

In the null model, table 2, it was found that a substantial part of the variance was explained by the tree-year combination (ca 37%, which can be viewed as the repeatability), and by year (ca 33%), which suggests that there is an overall environmental covariate that explains annual variation in tree width growth. When adding caterpillar biomass as a fixed effect most of the variance is then explained by the year of the tree rings (ca 38%) with tree year explaining ca 32%. The same trend can be seen with both caterpillar biomass and drought as a fixed effect, but with both random effects year ca 35% and tree year ca 33% showing a slight decrease in explained variance.

Both models with fixed effects show that year of the tree rings explain most of the variation, with this the third hypothesis, most of the variation in ring width within a sample is explained by the year of the tree rings, is accepted.

In both models with fixed effects the caterpillar biomass explains a significant amount of the variation in tree ring width. This can be seen in table 2, as both peak max estimate values (-0.0261 and -0.0272) and their respective confidence intervals are negative values (-0.0389, -0.0128 and -0.0398, -0.0140). The drought factor indicates that it has a negative effect on the variation of ring width since the confidence interval of -0.0468 to 0.0042 overlaps with 0 and the estimate is -0.0212. This shows that an increase in caterpillar biomass has a negative effect on ring width growth i.e. that the growth of the tree is slowed during years with a high density of caterpillars. Drought indicates that it also has a negative impact, since either an overall precipitation shortage or surplus has a different effect on the growth. A precipitation shortage would mean that growth is less and a surplus would mean that growth can take place.

Adding the fixed effects to the model has shown that growth is indeed impacted by both caterpillar biomass and drought conditions. However due to the overlap with 0 of the confidence intervals of drought, the fourth hypothesis, tree ring width is significantly negatively correlated with caterpillar biomass and drought conditions, is accepted if drought conditions are present.

Overall is the Peak Max model with selected cores the best option in investigating the effect on tree ring growth, as this model is the only one that shows the best significance and has a significant normality of the residuals. Drought does appear that it is for this model an over simplification of the climatic and environmental conditions, but still gives an indication on the effect on growth.

Table 2 – Results of the variance partitioning model with Peak Max as the fixed effect. All Cores model includes all sampled cores, Selected Cores model includes the cores that have not been removed from the selection procedure. Normality of Residuals tested with Kolmogorov-Smirnov. Significance values: * P < 0.05

| Models | Null Model | | Peak Max | | Peak Max & Drought | | |
|--------------|------------|------------|----------|------------|--------------------|------------|--|
| Random Effe | cts | | | | | | |
| | Variance | Std. Dev. | Variance | Std. Dev. | Variance | Std. Dev. | |
| Tree Year | 0.049 | 0.2206 | 0.042 | 0.2055 | 0.042 | 0.2054 | |
| Year | 0.043 | 0.2066 | 0.050 | 0.2229 | 0.043 | 0.2084 | |
| Residual | 0.040 | 0.1992 | 0.039 | 0.1973 | 0.039 | 0.1973 | |
| Fixed Effect | | | | | | | |
| | Estimate | Std. Error | Estimate | Std. Error | Estimate | Std. Error | |
| Peak Max | | | -0.0261 | 0.0065 | -0.0272 | 0.0065 | |
| Drought | | | | | -0.0212 | 0.0131 | |
| Confidence I | ntervals | | | | | | |
| | 2.50% | 97.50% | 2.50% | 97.50% | 2.50% | 97.50% | |
| .sig01 | 0.1878 | 0.2589 | 0.1721 | 0.2420 | 0.1721 | 0.2420 | |
| .sig02 | 0.1296 | 0.3197 | 0.1402 | 0.3425 | 0.1225 | 0.3065 | |
| .sigma | 0.1836 | 0.2172 | 0.1815 | 0.2156 | 0.1815 | 0.2155 | |
| (Intercept) | 0.8800 | 1.1279 | 0.9359 | 1.2066 | 0.7970 | 1.1412 | |
| Peak Max | | | -0.0389 | -0.0128 | -0.0398 | -0.0140 | |
| Drought | | | | | -0.0468 | 0.0042 | |
| Normality of | Residuals | | | | | | |
| Statistic | | 0.059 | | 0.069* | | 0.064 | |

Plotting the tree rings from all tree cores, as a time series, against the average caterpillar biomass a pattern can be seen, figure 6. It appears that the sampled time period of 2007 to 2019 falls exactly within one caterpillar outbreak and tree recovery cycle. The graph starts out with an average ring width of ca 1.25mm and an average caterpillar biomass value of ca 2.5. In the following 2 years there is an increase in average caterpillar biomass to above 3 and a constant decrease in average tree ring width to below 1mm. In the subsequent two years the average caterpillar biomass crashes to a value of less than 0.25 and then remains mostly constant for six years until 2017. In this time period the tree ring width slowly increases again to its maximum in 2018 (ca 1.25mm). In 2018 the average caterpillar biomass then started to increase again as tree growth also increased. The time line ends in 2019 the same way it started in 2007, with a sharp increase of caterpillar biomass and a decline in tree growth. This graph suggests that caterpillar biomass lags about one year behind the tree growth and that one cycle takes ten years.



Figure 6 – Time series of the tree rings from all tree cores, with the average tree ring width as the grey line, against the average caterpillar biomass (average peak max) in red, which is a fraction of 3 of the ring width scale.

Discussion

The outbreak of caterpillars is dependent on the phenology of the host tree. Early phenology provides more nutrients and is more palatable for the caterpillar. Younger foliage thus supports a better development of the caterpillar (Hunter, 1991; D. Coley, L. Bateman and A. Kursar, 2006). Early phenology is not just more susceptible to predation and early frost (Utkina and Rubtsov, 2017), but also to the hatching of the caterpillars, which is synchronized with the budburst (Hunter, 1991). This may be an effect of assortative mating (Baltensweiler, 1993), since asynchronous outbreaks of caterpillars and budburst could have a negative impact on the mortality and fecundity of the adult moths (Hunter, 1991).

Different caterpillar species have been found to exhibit a cyclical outbreak of nine to ten years, with *E. autumata* nine to ten years (Babst, Esper and Parlow, 2010), *O. brumata* ten years (Jepsen *et al.*, 2008) and larch bud moth 9.3 years (Esper *et al.*, 2007). This ten-year cycle also fits with the observed cycle in figure 6, in which a ten-year cycle can be observed. Furthermore, since the figure shows a clear cycle it can be assumed that in the Dwingelderveld one dominant species of caterpillars is causing the defoliation, as different winter moth species show a difference in outbreak cycles of around one to two years (Tenow *et al.*, 2007; Jepsen *et al.*, 2008).

Furthermore, it has been shown that specialists species show faster development on their respective host tree than generalists (D. Coley, L. Bateman and A. Kursar, 2006), which is important since caterpillars have only a short time window to develop (Tikkanen, Niemelä and Keränen, 2000). This is due to changes in leave chemistry and physics, which makes the leaves less palatable over time and with the hatching of birds' predation pressure also increases on caterpillars (Visser, Holleman and Gienapp, 2006).

The host trees have a wide array of defences against caterpillar predation. Oaks have shown to attract caterpillar predators by causing the herbivore to release plant volatiles, which attracts predators (Ghirardo *et al.*, 2012). One of the defences from outside is from bird predation on caterpillars, to feed

their chicks (Gunnarsson, Wallin and Klingberg, 2018). This bird predation then increases in trees with damaged leaves, which leads to more predation in trees with open crowns and easier predation by the birds (Gunnarsson, Wallin and Klingberg, 2018), and as a side effect of this, apart from fewer caterpillars, is that winter moths tend to avoid feeding on damaged leaves (Fenny, 1970).

A major influence on the feeding behaviour of caterpillars is the presence of tannins within the leaves (Fenny, 1970; Foss and Rieske, 2003). Tannins inhibit the growth of winter moth caterpillars (Fenny, 1970). As a result, *Q. robur* does increase the tannin concentrations within the leaves unfolded leaves as the feeding season progresses (Fenny, 1970). Other changes to the leaves include increase in toughness and decrease the palatability for the caterpillars (Fenny, 1970; Baltensweiler, 1993; Wold and Marquis, 1997; Lovett *et al.*, 2002; Pearse, 2011). As a result, generalist herbivores do change host to diffuse host specific toxins (D. Coley, L. Bateman and A. Kursar, 2006; Pearse, 2011). In the case of the Dwingelderveld given the two dominant tree species are *Q. robur* and *P. sylvestris* and the synchrony of the caterpillar biomass and tree growth (figure 6) suggests that the caterpillar species found there is a specialist species.

Another defence mechanism is late phenology and leave flushing, since caterpillars depend on food availability at the time of hatching (Wesołowski and Rowiński, 2008), but as earlier mentioned caterpillars can also hatch at a later time. Overall older trees are more resilient to herbivory (Wagner *et al.*, 2012). Climactic factors are an important factor in the development and deployment of defences and low seasonality results in more defences being used (Pearse and Hipp, 2012). As individual trees can track abiotic factors over a macro evolutionary time frame to develop defences (Pearse, 2011; Pearse and Hipp, 2012).

The defoliation of entire forests (Tikkanen, Niemelä and Keränen, 2000), does not only affect the defoliated tree itself but the whole ecosystem. The defoliation of a tree is part of the natural succession of a forest (Jedlicka et al., 2004). Furthermore, is the whole nutrient cycle of that ecosystem influenced as more leave litter and frass are being added to the top soil, resulting in higher quantities of nutrients and nitrogen being available (Kolb, Dodds and Clancy, 1999; Lovett et al., 2002; Grüning et al., 2018). However, for the tree it results in fewer acorns being produced (Canelo et al., 2018) and less nitrogen available for regeneration as storage nitrogen is being depleted (Lovett et al., 2002; Piper, Gundale and Fajardo, 2015; Canelo et al., 2018). Another result is that overall nutrient concentration, in the year of defoliation, within the leaves increase since there is less biomass to support with nutrients making the leaves more palatable for herbivores (Kolb, Dodds and Clancy, 1999), and that early leaves act as storage and then later leaves are to support the growth of the tree (Kulman, 1971). Defoliated trees have as a result a lower biomass as nutrients go directly to regeneration (Kolb, Dodds and Clancy, 1999). This decrease in biomass can be related to the reduction of growth that can be seen in figure 6 for 7 years, in the years between 2009 and 2016. Such decreases in growth in Quercus spp. were also found by Muzika and Liebhold (1999) and Wiley, Casper and Helliker (2017). The defoliation and resulting increase of stress then in turn leads to an increased probability of mortality (Kulman, 1971; Jepsen et al., 2008; Wesołowski and Rowiński, 2008). The effect of the defoliation is site specific depending on local scale variations within a woodland and is likely to have an effect on local phenology of different tree species such as Quercus spp. (Cole and Sheldon, 2017; Khasanov and Sandlersky, 2018). With earlier season damage less damage is then inflicted later on (Wold and Marquis, 1997; Utkina and Rubtsov, 2017).

Radial growth is one of the most measurable impacts from defoliation as defoliation decreases the growth rate of the tree (Kulman, 1971; Muzika and Liebhold, 1999; Piper, Gundale and Fajardo, 2015; Khasanov and Sandlersky, 2018). Since growth is the result of excess photosynthates (Kulman, 1971) it is strongly dependent on the available storage and energy produced by the leaves. This is also seen in variance partitioning, table 2, where it is shown that a greater caterpillar biomass, as such more

leaves being eaten, decrease significantly the growth of the host tree. On a cellular level, vessels are used to transport water and energy throughout the tree. These cells are formed during growth periods of a tree (Mäkinen *et al.*, 2008). This part is taken over by the large vessels in the early wood and are formed using energy storage from the previous season (Muzika and Liebhold, 1999; Dulamsuren *et al.*, 2010). As a result, the tree grows more when there are fewer caterpillars feeding on it and drought is not adding an additional stress factor.

Oak trees, which have been completely defoliated can show 50% and with a defoliation of 30% growth can be reduced by 30 to 40% (Kulman, 1971; Muzika and Liebhold, 1999; Naidoo and Lechowicz, 2001; Simmons *et al.*, 2014; Arbellay *et al.*, 2018) and growth can decrease for one to five years (Alfaro and MacDonald, 1988; Muzika and Liebhold, 1999; Dulamsuren *et al.*, 2010; Wiley, Casper and Helliker, 2017), which can be seen in figure 6 where the growth decreases for two times, first time for four years with a reduction of 0.5mm and second time for two years with a reduction of 0.25mm. With the reduction of growth again the mortality increases (Foss and Rieske, 2003), as the tree develops less and is less resilient, as less nitrogen and water are being transported and fewer nutrients are being stored (Lovett *et al.*, 2002).

Growth away from the equator is seasonal, and most of the growth comes from early wood during before the budburst (Michelot *et al.*, 2012). The early growth season shows little variation in growth between trees within *Quercus* spp. (Puchałka *et al.*, 2017). Less starch is available for *Quercus* spp. during April to June (Michelot *et al.*, 2012), and as a result growth slows down after April with the bud swelling (Puchałka *et al.*, 2017). Defoliation is not the only factor that causes the reduction of growth, but also climate (Kulman, 1971; Muzika and Liebhold, 1999; Piper, Gundale and Fajardo, 2015; Khasanov and Sandlersky, 2018).

Other effects on growth are climactic factors such as water availability and temperature (King et al., 2013; Cole and Sheldon, 2017). Growth of trees reduces during drought periods (Di Filippo et al., 2010; Matisons, Elferts and Brumelis, 2012). This effect was found in the variance partitioning, table 2, as drought conditions showed to decrease radial growth. In addition, also leave senescence also depends on climate (Chen et al., 2019; Denéchère et al., 2019). The summer soil water can be used as a predictor for radial growth the following months (Naidoo and Lechowicz, 2001). Also, there is a difference between old and young trees how they are affected when they are affected by temperature (Vitasse et al., 2009). Young oak growth is predominantly limited by temperature during summer and spring. Older oak growth shows a negative response to summer and winter temperature (Rozas, 2005). The effect of droughts on growth depends on the soil depth (Helama et al., 2009), with older oaks having a deeper root system and in turn can access more water (Wagner et al., 2012). Another effect of drought is the reduction of available nitrogen (Wagner et al., 2012). Quercus ilex shows a plastic response to drought. However, severe drought still affects the growth and leave growth negatively, which makes climate and especially water availability an important factor for radial growth (Corcuera, Camarero and Gil-Pelegrín, 2004). Overall, are climatic influences and defoliation the biggest influencers of growth rate on a tree (Naidoo and Lechowicz, 2001; King et al., 2013).

The process of recreating caterpillar outbreaks is highly scalable and with a larger dataset with more trees and longer climactic data (Rolland, Baltensweiler and Petitcolas, 2001) even reconstructions of the past are possible, with studies going back more than 1000 years (Esper *et al.*, 2007). If climatic data is not available stable carbon isotopes from late wood can be used to reconstruct past temperatures (Young *et al.*, 2012).

For better climatic analysis a model can be used, CLIMTERG V.6, which calculates the impact of the climate on the trees within a study (Beck and Heinzig, 2018). With this model a more detailed analysis of the different climatic influences, i.e. temperature, precipitation, radiation and more, could have been carried out for this study.

Conclusion

It has been found in this study that annual variation in tree ring width of oak correlates negatively with caterpillar density and to some extend drought. Also, the repeatability of ring width within a tree shows too much variation to be considered uniform. This suggests that other factors than just caterpillar biomass and drought influence the width of a tree ring. Lastly, a cycle of caterpillar outbreak und subsequent growth reduction over a span of ten years was observed.

For this study initially the oak cores were supposed to be compared to a non-host tree species, in this case Scots Pine. However, to an unknown factor, which caused the control cores to grow in an unexpected way and made them not comparable to the oak cores. This would be a whole other possible investigation. Also, since the CLIMTERG V.6 program was unavailable at the time the climatic investigation had to be drastically simplified, but was still able to show some indications. Overall, this study showed the expected result of the effect from caterpillar outbreaks and the study also shows potential to be further developed.

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Appendix 1

| cor\P | 599_O | 599_O_N | 599_0_W | | cor | \P | 607_O | 607_O_E | 607_0_N | 607_0_S | |
|----------|---------|----------|----------|---------|-----|--------------|---------|----------|----------|---------|---------|
| 599_O | 1.00 | 0.7407 | 0.0095 | | 607 | _0 | 1.00 | 0.3228 | 0.0003 | 0.2086 | |
| 599_O_N | 0.10 | 1.00 | 0.2792 | | 607 | ′_O_E | 0.30 | 1.00 | 0.0711 | 0.0244 | |
| 599_0_W | 0.69 | 0.32 | 1.00 | | 607 | ′_0_N | 0.85 | 0.52 | 1.00 | 0.0673 | |
| | | | | | 607 | ′_0_S | 0.37 | 0.62 | 0.52 | 1.00 | |
| | | | | | | | | | | | |
| cor\P | 623_0 | 623_0_N | 623_0_W | | cor | \P | 683_O | 683_O_E | 683_O_N | 683_0_S | |
| 623_0 | 1.00 | 0.0022 | 0.0004 | | 683 | 8_0 | 1.00 | 0.0009 | 0.0000 | 0.0098 | |
| 623_O_N | 0.77 | 1.00 | 0.0263 | | 683 | 3_0_E | 0.81 | 1.00 | 0.0000 | 0.0004 | |
| 623_0_W | 0.83 | 0.61 | 1.00 | | 683 | 3_0_N | 0.91 | 0.90 | 1.00 | 0.0048 | |
| | | | | | 683 | <u>_0_</u> s | 0.69 | 0.83 | 0.73 | 1.00 | |
| | | | | | | | | | | | |
| cor\P | 712_0 | 712_0_E | 712_0_N | 712_0_S | cor | \P | 699_O | 699_O_E | 699_O_N | 699_O_S | 699_0_W |
| 712_0 | 1.00 | 0.5171 | 0.4706 | 0.694 | 699 | 0_0 | 1.00 | 0.8585 | 0.0707 | 0.4262 | 0.3344 |
| 712_0_E | -0.20 | 1.00 | 0.0055 | 0.0576 | 699 | 0_E | 0.05 | 1.00 | 0.0027 | 0.0001 | 0.0080 |
| 712_0_N | 0.22 | 0.72 | 1.00 | 0.022 | 699 | _O_N | 0.52 | 0.76 | 1.00 | 0.0061 | 0.0087 |
| 712_0_S | -0.12 | 0.54 | 0.63 | 1.00 | 699 | _0_S | 0.24 | 0.87 | 0.71 | 1.00 | 0.0000 |
| | | | | | 699 | _0_W | 0.29 | 0.70 | 0.69 | 0.90 | 1.00 |
| | | | | | | | | | | | |
| cor\P | 867_O_E | 867_0_N | 867_0_W | | cor | \P | 736_O_E | 736_O_N | 736_0_W | | |
| 867_O_E | 1.00 | 0.5053 | 0.5533 | | 736 | 6_0_E | 1 | 0.0030 | 0.0367 | | |
| 867_O_N | 0.20 | 1.00 | 0.0013 | | 736 | 5_0_N | 0.75 | 1 | 0.0005 | | |
| 867_0_W | 0.18 | 0.79 | 1.00 | | 736 | 5_0_W | 0.58 | 0.82 | 1 | | |
| | | | | | | | | | | | |
| cor\P | 944_O_E | 944_O_N | 944_0_S | | cor | \P | 930_O_N | 930_O_E | 930_O_W | | |
| 944_0_E | 1.00 | 0.0153 | 0.0178 | | 930 | _O_N | 1.00 | 0.0398 | 0.0252 | | |
| 944_0_N | 0.65 | 1.00 | 0.0346 | | 930 |)_O_E | 0.57 | 1.00 | 0.1269 | | |
| 944_0_S | 0.64 | 0.59 | 1.00 | | 930 | _0_W | 0.62 | 0.45 | 1.00 | | |
| | | | | | | | | | | | |
| cor\P | 1055_0 | 1055_O_N | 1055_O_S | | cor | \P | 1021_0 | 1021_O_E | 1021_0_W | 1 | |
| 1055_0 | 1.00 | 0.578 | 0.4821 | | 102 | 21_0 | 1.00 | 0.6031 | 0.8166 | | |
| 1055_0_N | 0.17 | 1.00 | 0.2233 | | 102 | 21_0_E | 0.16 | 1.00 | 0.0027 | | |
| 1055_O_S | -0.21 | -0.36 | 1.00 | | 102 | 21_0_V | 0.07 | 0.76 | 1.00 | | |

The different correlation tables follow the same layout. Each table is for one individual tree and the top row and first column being the cores within that tree. The values above the 1.00 being the p value and below the 1.00 being the correlation coefficient.

| All Core Models | Null Mode | | Peak Max | | Peak Max & Drought | | | | |
|--------------------|-----------|------------|----------|------------|--------------------|------------|--|--|--|
| Random Effects | | | | | | | | | |
| | Variance | Std. Dev. | Variance | Std. Dev. | Variance | Std. Dev. | | | |
| Tree Year | 0.037 | 0.1920 | 0.031 | 0.1773 | 0.031 | 0.1772 | | | |
| Year | 0.033 | 0.1817 | 0.038 | 0.1947 | 0.033 | 0.1817 | | | |
| Residual | 0.052 | 0.2275 | 0.051 | 0.2260 | 0.051 | 0.2260 | | | |
| Fixed Effect | | | | | | | | | |
| | Estimate | Std. Error | Estimate | Std. Error | Estimate | Std. Error | | | |
| Peak Max | | | -0.02344 | 0.005951 | -0.0245 | 0.0059 | | | |
| Drought | | | | | -0.0187 | 0.0115 | | | |
| Confidence Interv | als | | | | | | | | |
| | 2.50% | 97.50% | 2.50% | 97.50% | 2.50% | 97.50% | | | |
| .sig01 | 0.1603 | 0.2282 | 0.1449 | 0.2120 | 0.1449 | 0.2119 | | | |
| .sig02 | 0.1132 | 0.2817 | 0.1217 | 0.2997 | 0.1059 | 0.2677 | | | |
| .sigma | 0.2116 | 0.2454 | 0.2099 | 0.2441 | 0.2099 | 0.2441 | | | |
| (Intercept) | 0.8934 | 1.1123 | 0.9448 | 1.1826 | 0.8230 | 1.1244 | | | |
| Peak Max | | | -0.0351 | -0.0114 | -0.0360 | -0.0125 | | | |
| Drought | | | | | -0.0411 | 0.0036 | | | |
| Normality of Resid | luals | | | | | | | | |
| Statistic | | 0.054 | | 0.054 | | 0.051 | | | |

Appendix 2

| Selected Core Models | Null Model | | Peak Max | | Peak Max & Drought | |
|------------------------|------------|------------|----------|------------|--------------------|------------|
| Random Effects | | | | | | |
| | Variance | Std. Dev. | Variance | Std. Dev. | Variance | Std. Dev. |
| Tree Year | 0.049 | 0.2206 | 0.042 | 0.2055 | 0.042 | 0.2054 |
| Year | 0.043 | 0.2066 | 0.050 | 0.2229 | 0.043 | 0.2084 |
| Residual | 0.040 | 0.1992 | 0.039 | 0.1973 | 0.039 | 0.1973 |
| Fixed Effect | | | | | | |
| | Estimate | Std. Error | Estimate | Std. Error | Estimate | Std. Error |
| Peak Max | | | -0.0261 | 0.0065 | -0.0272 | 0.0065 |
| Drought | | | | | -0.0212 | 0.0131 |
| Confidence Intervals | | | | | | |
| | 2.50% | 97.50% | 2.50% | 97.50% | 2.50% | 97.50% |
| .sig01 | 0.1878 | 0.2589 | 0.1721 | 0.2420 | 0.1721 | 0.2420 |
| .sig02 | 0.1296 | 0.3197 | 0.1402 | 0.3425 | 0.1225 | 0.3065 |
| .sigma | 0.1836 | 0.2172 | 0.1815 | 0.2156 | 0.1815 | 0.2155 |
| (Intercept) | 0.8800 | 1.1279 | 0.9359 | 1.2066 | 0.7970 | 1.1412 |
| Peak Max | | | -0.0389 | -0.0128 | -0.0398 | -0.0140 |
| Drought | | | | | -0.0468 | 0.0042 |
| Normality of Residuals | | | | | | |
| Statistic | | 0.059 | | 0.069* | | 0.064 |

| All Core Models | Null Mode | l | Peak Scaled | | Peak Scaled & Drought | | | | |
|--------------------|-----------|------------|-------------|------------|-----------------------|------------|--|--|--|
| Random Effects | | | | | | | | | |
| | Variance | Std. Dev. | Variance | Std. Dev. | Variance | Std. Dev. | | | |
| Tree Year | 0.037 | 0.1920 | 0.037 | 0.1927 | 0.037 | 0.1927 | | | |
| Year | 0.033 | 0.1817 | 0.032 | 0.1778 | 0.029 | 0.1717 | | | |
| Residual | 0.052 | 0.2275 | 0.051 | 0.2260 | 0.051 | 0.2260 | | | |
| Fixed Effect | | | | | | | | | |
| | Estimate | Std. Error | Estimate | Std. Error | Estimate | Std. Error | | | |
| Peak Max | | | -0.0009 | 0.0007 | -0.0011 | 0.0007 | | | |
| Drought | | | | | -0.0145 | 0.0111 | | | |
| Confidence Interv | als | | | | | | | | |
| | 2.50% | 97.50% | 2.50% | 97.50% | 2.50% | 97.50% | | | |
| .sig01 | 0.1603 | 0.2282 | 0.1597 | 0.2286 | 0.1597 | 0.2286 | | | |
| .sig02 | 0.1132 | 0.2817 | 0.1087 | 0.2750 | 0.0972 | 0.2541 | | | |
| .sigma | 0.2116 | 0.2454 | 0.2100 | 0.2442 | 0.2100 | 0.2442 | | | |
| (Intercept) | 0.8934 | 1.1123 | 0.9139 | 1.1373 | 0.8126 | 1.1018 | | | |
| Peak Max | | | -0.0024 | 0.0005 | -0.0026 | 0.0003 | | | |
| Drought | | | | | -0.0360 | 0.0069 | | | |
| Normality of Resid | duals | | | | | | | | |
| Statistic | | 0.054 | | 0.051 | | 0.052 | | | |

| Selected Core Models | Null Model | | Peak Scaled | | Peak Scaled & Drought | |
|------------------------|------------|------------|-------------|------------|-----------------------|------------|
| Random Effects | | | | | | |
| | Variance | Std. Dev. | Variance | Std. Dev. | Variance | Std. Dev. |
| Tree Year | 0.049 | 0.2206 | 0.050 | 0.2229 | 0.050 | 0.2230 |
| Year | 0.043 | 0.2066 | 0.041 | 0.2022 | 0.038 | 0.1960 |
| Residual | 0.040 | 0.1992 | 0.039 | 0.1973 | 0.039 | 0.1973 |
| Fixed Effect | | | | | | |
| | Estimate | Std. Error | Estimate | Std. Error | Estimate | Std. Error |
| Peak Max | | | -0.0008 | 0.0008 | -0.0010 | 0.0008 |
| Drought | | | | | -0.0161 | 0.0126 |
| Confidence Intervals | | | | | | |
| | 2.50% | 97.50% | 2.50% | 97.50% | 2.50% | 97.50% |
| .sig01 | 0.1878 | 0.2589 | 0.1885 | 0.2612 | 0.1885 | 0.2612 |
| .sig02 | 0.1296 | 0.3197 | 0.1244 | 0.3122 | 0.1120 | 0.2895 |
| .sigma | 0.1836 | 0.2172 | 0.1815 | 0.2156 | 0.1815 | 0.2156 |
| (Intercept) | 0.8800 | 1.1279 | 0.8979 | 1.1505 | 0.7838 | 1.1125 |
| Peak Max | | | -0.0025 | 0.0007 | -0.0027 | 0.0006 |
| Drought | | | | | -0.0405 | 0.0082 |
| Normality of Residuals | | | | | | |
| Statistic | | 0.059 | | 0.086 | | 0.063 |