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FORBIO Climate

**Adaptation potential of biodiverse forests in the face of
climate change**

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NETWORK PROJECT

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Adaptation potential of biodiverse forests in the face of climate change

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FINAL REPORT

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ABSTRACT

Context

Climate change is expected to have a large impact on the distribution, composition and functioning of forest ecosystems worldwide as trees have only little opportunities to migrate and adaptation via natural selection happens very slowly. Hence, creating resistant and resilient forests is a key challenge for forest management. More insight into the adaptive capacity of trees and forests in their consecutive life and development stages, respectively, and the potential buffering effect of tree species admixing to climate change is thus urgently needed.

Objectives

FORBIO Climate aimed at scrutinizing the adaptive capacity of pedunculate and sessile oak (*Quercus robur* and *Q. petraea*, respectively) and European beech (*Fagus sylvatica*) and at predicting the future performance of these tree species in Belgium under climate change. More specifically, the project aimed at testing the following hypotheses: (1) epigenetic inheritance mechanisms can increase the adaptive capacity of trees to climate change during the reproduction stage; (2) across subsequent tree development stages, tree performance is more resistant and resilient to climate change in more biodiverse forests.

Conclusions

Belgian's future climate is projected to be warmer, with a higher frequency of extreme precipitation events. Parental temperature influenced the germination success, bud phenology and growth of oak and beech seedlings, but we did not observe DNA methylation that could help to explain the phenological change mediated by the parental temperature. Studies on both saplings and mature trees suggested that drought may influence ecosystem processes in young and mature forests, affecting the growth and vitality of trees. Despite the high awareness of climate change as an issue in forest management and the need to adjust management practices, we found a lack of knowledge on how to adapt forest management in order to mitigate the vulnerability of forests under changing climate conditions. The results of this project confirm that admixing tree species in oak and beech stands is a good adaptation measure across all forest development stages.

Keywords

Adaptive capacity; climate change; epigenetics; Europe; *Fagus sylvatica*; forest management; mature trees; phenology; *Quercus* sp.; seedlings; saplings; temperate forests; tree diversity

1. INTRODUCTION

Biological signals of climate change are already discernible in a wide array of ecosystems (Parmesan 2006). In Western Europe, including Belgium, projections indicate that winters will become warmer and wetter, and summers warmer and drier. In addition, a higher incidence of extreme weather events is expected (IPCC 2007; IPCC 2018). Forests are expected to be especially vulnerable to climate change since trees are sessile organisms with long generation times that result in slow adaptation via natural selection and that have little opportunities to migrate (Jump and Peñuelas 2005).

Projection models of future forest distribution and composition generally show large distribution range shifts (e.g. Hanewinkel et al. 2013). However, these projections are usually based on models that do not take into account the adaptive capacity of trees, which may be larger than anticipated (e.g. Jump et al. 2008). More and more indications arise that trees dispose of specific mechanisms to improve their survival chances in a changing environment. Notably, epigenetic inheritance mechanisms can contribute to the phenotypic plasticity and adaptive capacity of trees and may increase their capacity to respond quickly to an altering climate (Bräutigam et al. 2013). Epigenetic inheritance occurs when phenotypic variations that do not stem from variations in DNA base sequences are transmitted to subsequent generations (Jablonka and Raz 2010).

Besides the adaptive capacity of trees, the diversity of the forest neighbourhood surrounding a tree may also mitigate the effects of climate change during the subsequent tree establishment and development stages. Functional biodiversity research in grasslands (Cardinale et al. 2011), and more recently also in forests (Gamfeldt et al. 2013; van der Plas et al. 2016; Ratcliffe et al. 2017), has shown that more complex, mixed systems generally perform better, exhibit higher levels of ecosystem functioning and are more resistant and resilient to disturbances. The underlying mechanisms include better access to limited resources due to more complementary resource use in space and time (Meißner et al. 2012), facilitation (Scherer-Lorenzen et al. 2005) and lower susceptibility to pest and pathogen attacks (Castagneyrol et al. 2013).

2. STATE OF THE ART AND OBJECTIVES

The extent and importance of epigenetic mechanisms for the rapid creation of better-adapted offspring is still unknown. More insight into the adaptive capacity of trees and forests to climate change is urgently needed to be able to make more accurate predictions about their fate in a changing world and to allow building in resistance and resilience in forest ecosystems through proper management (Messier et al. 2013). Since the nature of adaptive responses and underlying mechanisms varies between life stages, it is key that life-stage specific adaptive capacities are quantified (cf. Clark et al. 2011). However, studies that integrate climatic responses of trees over multiple life stages are, to the best of our knowledge, still lacking.

The general objective of FORBIO Climate was to scrutinize the adaptive capacity of trees to climate change and to make predictions about their future performance in Belgium under scenarios of climate change. We hypothesized that: (1) epigenetic inheritance mechanisms can increase the adaptive capacity of trees to climate change during the reproduction stage; (2) across subsequent tree development stages, more biodiverse forest environments generate higher resistance and resilience to climate change.

3. METHODOLOGY, SCIENTIFIC RESULTS AND RECOMMENDATIONS

The project was structured in five work packages (WPs) (Figure 1). WP1 provided past climate data from selected weather stations in Belgium that were linked to the measurements on seedlings, saplings and mature trees in WP2-4 to assess the effects of climate variation on tree performance. WP1 also provided high-resolution simulations of the future climate. In WP5, drought and diversity responses were scaled up to a national level and stakeholders were inquired about their perception of climate change effects and adaptation.

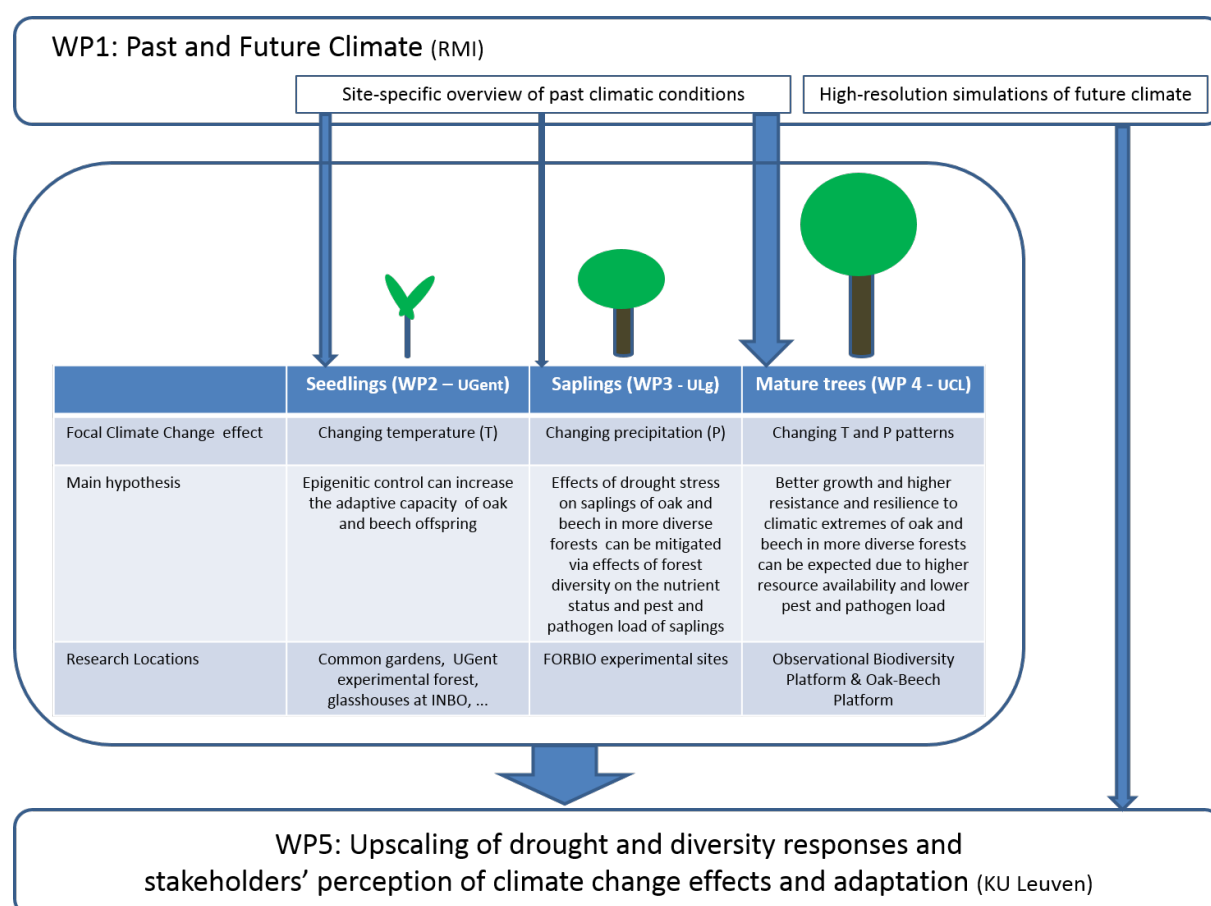


Figure 1. Overview of the Work Packages (WPs) in FORBIO Climate, how they were interlinked and who was the main responsible. The width of the arrows linking WP1 with WP2-5 and WP2-4 with WP5 indicate the importance of the data flows.

WP1 Past and future climate

WP1 provided data on the past climate. A set of suitable weather stations were selected, and quality control tests were applied on the resulting observational dataset. This WP also provided high-resolution simulations of the future climate by using the high-resolution Regional Climate Model ALARO-0.

Past climate: observational climate dataset

Since 1913, the official Belgian climatological network is operated by the Royal Meteorological Institute (RMI). This network is mainly relying on volunteers and collects observations of daily precipitation amount and daily maximum and minimum temperatures. The network currently counts 145 thermometric stations and 226 pluviometric stations but the number of climatological stations maintaining daily precipitation amount and temperature records has varied over the time. A total of 278 thermometric and 539 precipitation stations were identified in the RMI central database for the time period 1980-2016. For each of them, the station's name, code, latitude, longitude, altitude and observer were verified thoroughly. The inventory of station metadata has been completed by additional information (e.g. station's instruments, station's environment, station relocations, etc.) when available. However, not all stations in the network were suitable for the climate analysis (i.e. most had too little data, while other had excessive missing data, poor site characteristics or unreliable observations). For example, among the selected stations, only 65 thermometric stations and 131 pluviometric stations had less than 5 % of missing records over the considered 1980-2016 period.

Errors can occur in meteorological observations for a wide variety of reasons, the most common being instrument faults, observer errors, errors in data transmission and clerical error in data processing. As the use of uncorrected data might lead to misinterpretations about the evolution of the climate, quality assurance procedures were developed to ensure the quality of the daily records. Automated quality control tests were applied to daily extreme temperature records and precipitation amounts from the selected stations to isolate and flag potentially erroneous values as well as for ensuring internal consistency and temporal and spatial coherence of the data. More than 5 million values were analysed. About 97 % of temperature data and 99 % of the precipitation data were validated at the highest confidence level. Such high scores result from the routinely manual check of the climatological data operated by the RMI quality control staff. At the end of the quality control process, the number of valid temperature (precipitation) records per day varied between 109 (226) and 175 (337) over the considered period of 1980-2016. All validated records on precipitation amount, daily maximum and minimum temperature were then interpolated on a regular 4 x 4 km grid over Belgium. To predict the unknown values from the unevenly distributed records observed at known locations, performances of different interpolation methods (i.e. inverse distance weighting, ordinary kriging and kriging with external drift(s) - topography and/or land cover types -) were evaluated by leave-one-out cross-validation. Based on the analysis of several cross validation scores, kriging using the topography as drift was selected for the interpolation of the daily temperature data (e.g. root mean square error of 0.818 °C for daily minimum temperature and of 0.601°C

for daily maximum temperature). By contrast, for precipitation the most relevant result was obtained by ordinary kriging (e.g. root mean square error of 1.089 mm). Spatial interpolation was performed for each day of the considered 1980-2016 time period to produce a high-resolution 37-year long quality controlled daily gridded observational climate dataset for Belgium (TABLE I). The procedure and associated results are described in detail in Delvaux et al. (2015).

Future climate: model climate dataset

The model climate dataset has been obtained through a dynamical downscaling of global climate data using the Regional Climate Model ALARO-0 (Berckmans et al. 2017). Three different downscaling approaches for climate simulations over Western-Europe with the ALARO-0 model were validated: 1) the commonly used continuous approach, where the atmosphere and land surface are modelled in a continuous way; 2) an approach with daily reinitialisations for both the atmosphere and the land surface, and 3) an approach with daily reinitialisations of the atmosphere while the land surface is kept continuous (FS approach). Spatial distributions over Western Europe and annual cycles of 10-year times series (1991-2000) of daily mean 2-m temperature and precipitation were compared with observations. The performance of the three downscaling approaches depended on the climate regime and thus the geographical region under consideration. In general, for the whole study region of Western Europe, the approach with daily reinitialisation of the atmosphere showed an improvement in the simulation of 2-m temperature for all seasons. For precipitation, the impact of the daily reinitialisation was neutral for the winter, and for summer the results were improved when the land surface was kept continuous. However, for Belgium, the results showed a similar performance of the three approaches. Hence, for the climate simulations within the FORBIO Climate project, the continuous approach was used.

As a first step, the ALARO-0 model was validated for present climate conditions (1980-2010). For this, global climate model data from so-called “perfect boundary conditions” or reanalyses were dynamically downscaled using the regional ALARO-0 model over a domain centred on Belgium at 4x4 km resolution. More specifically, maximum and minimum temperature, and precipitation from this ERA-Interim driven simulation (hereafter denoted as ERA-INT) were compared to the high-resolution (4 km) daily gridded climatological observation dataset which has been obtained in the first part of this WP (Delvaux et al. 2015). In a next step, the ALARO-0 model was applied for a dynamical downscaling of climate change projection, by driving the model with a global climate model that takes into account the historical and future changes in greenhouse gases. For the historical simulation (hereafter denoted as HIST), a constant value for the CO₂-equivalent value was used. The future evolution was implemented by the so-called Representative Concentration Pathways (RCPs) as defined by the Intergovernmental Panel of Climate Change (IPCC): RCP 2.6, RCP 4.5 and RCP 8.5. These RCPs describe the radiative forcing from greenhouse gases. RCP 8.5 shows a strong increase in CO₂-equivalent by the end of the century, RCP 4.5 shows a strong increase and gradual stabilisation, and RCP 2.6 shows an increase followed by a decrease of the concentrations of CO₂-equivalent by the end of the century (Figure 2). In this way, four climate runs with the ALARO-0 model were done

(TABLE I): (i) a 30-yr historical simulation for the period 1976-2005, and (ii) three RCP simulations for the period 2007-2100. The climate change signals were then quantified by calculating the differences between the respective RCP and HIST simulations.

Table I. Overview of the observational data and model data.

Period	Observation	Model				
		ERA-INT	HIST	RCP 2.6	RCP 4.5	RCP 8.5
1980-2010	✓	✓	-	-	-	-
1976-2005	-	-	✓	-	-	-
2007-2100	-	-	-	✓	✓	✓

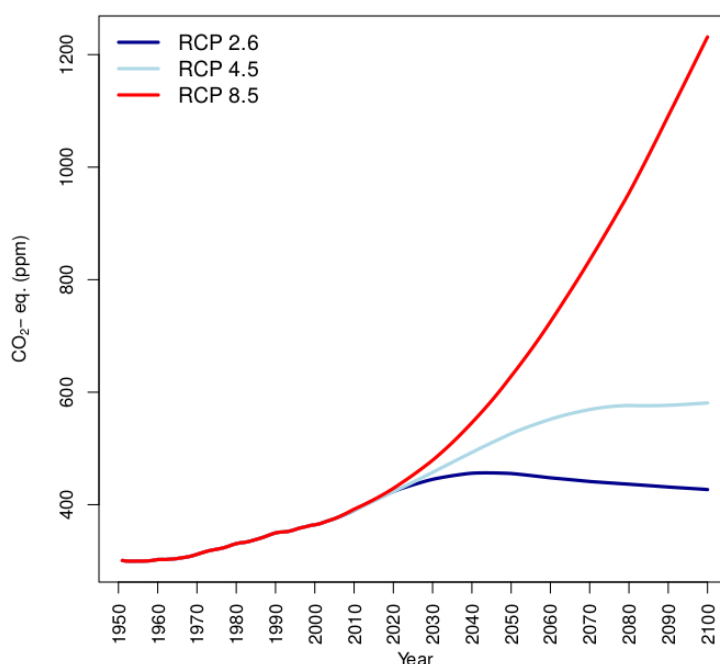


Figure 2. Evolution of the equivalent CO_2 for the three RCPs that describes the radiative forcing from greenhouse gases as used for the future simulations.

In general, the modelled maximum temperature (both ERA-INT and HIST) showed a systematic cold bias with regard to the observations for the whole year (Figure 3), and all seasons (result not shown). The ERA-INT driven simulation showed cold biases that vary between 1 °C up to almost 3 °C in spring (not shown). Nevertheless, it can be seen from Figures 4 and 5 that the model was able to capture the overall spatial distribution, with lower temperatures at the higher altitudes in the southeast compared to the rest of the country. For minimum temperature, the spatial distributions for both the ERA-INT driven and HIST simulation also showed an orographic dependency, which is very similar to the observed minimum temperature distributions (Figure 4). Compared to maximum temperature, the ERA-INT model simulation was able to capture very well the observed spatial distribution of minimum temperature. Only for the inland locations, a slight cold bias was still present. The spatial distribution of the historical minimum temperature showed minimum values that are much colder than the observations, especially for the summer and autumn (not shown). The

larger bias in the HIST simulation compared to the ERA-INT driven simulation can be partly attributed to the GCM that was used as driving model, and hence introduces additional biases to the 4 km high-resolution simulation. The spatial distribution of the ERA-INT driven precipitation approached the observations very close (Figure 5). Both the observed and simulated precipitation showed a clear topographical dependency, with a gradual increase in precipitation going from the northwest (low altitudes) to the southeast (high altitudes) of Belgium. Furthermore, similar as the ERA-INT driven simulation, the historical precipitation showed also very small biases with regard to the observations. In general, the observed temperature and precipitation showed a less heterogeneous distribution compared to the modelled ones. The reason for this could be the smoothing effect due to the kriging method used to obtain the gridded observation data set.

In consultation with the other partners of the FORBIO Climate consortium, a number of relevant meteorological variables were selected; i.e. (i) 2-m mean temperature [$^{\circ}\text{C}$], (ii) 2-m maximum temperature [$^{\circ}\text{C}$], (iii) 2-m minimum temperature [$^{\circ}\text{C}$], (iv) precipitation [mm], (v) 10-m wind speed [m s^{-1}], (vi) and 2-m relative humidity [%].

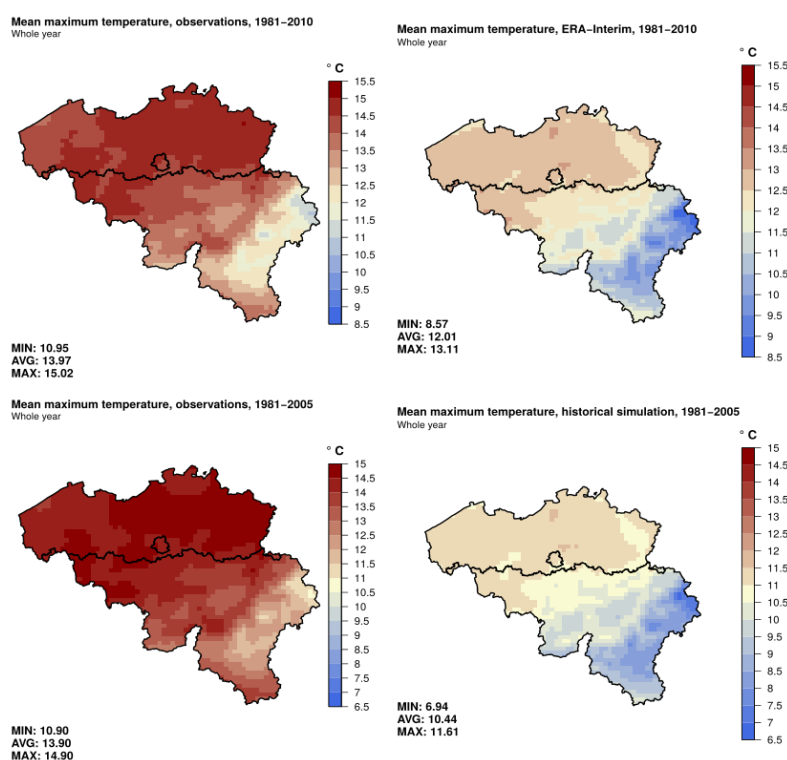


Figure 3. Spatial distribution of 30-year mean observed maximum temperature (top left) and modelled ERA-INT maximum temperature (top right), and 25-year mean observed maximum temperature (bottom left) and modelled HIST maximum temperature (bottom right). Both the observed and modelled values have a spatial resolution of 4x4 km.

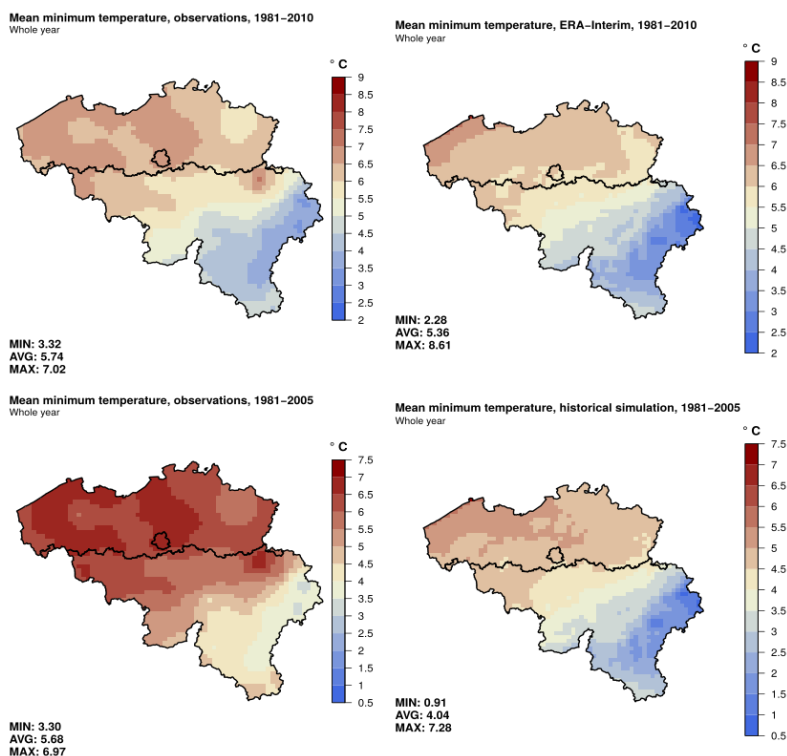


Figure 4. Spatial distribution of 30-year mean observed minimum temperature (top left) and modelled ERA-INT minimum temperature (top right), and 25-year mean observed minimum temperature (bottom left) and modelled HIST minimum temperature (bottom right). Both the observed and modelled values have a spatial resolution of 4x4 km.

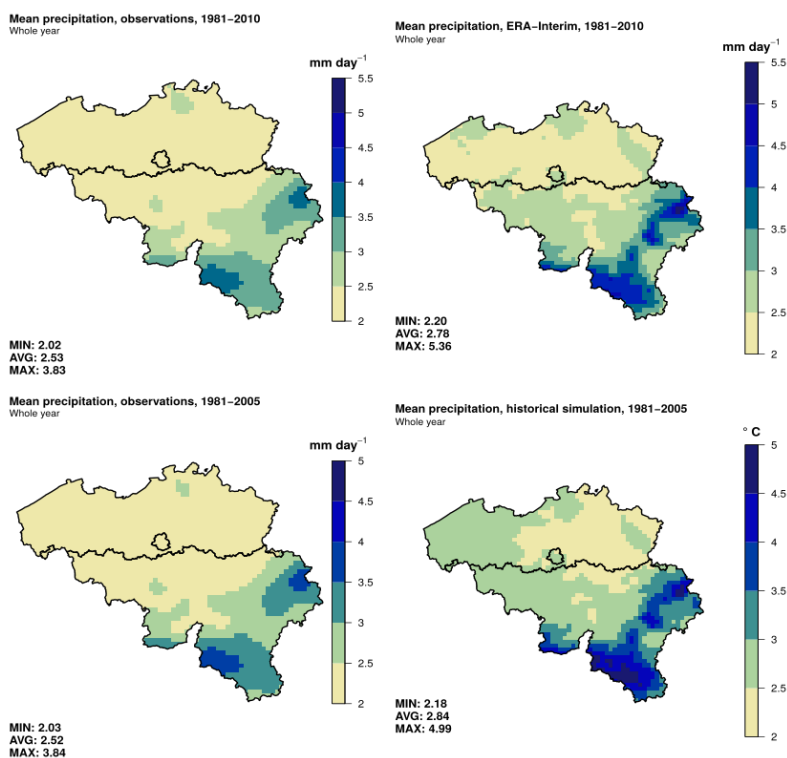


Figure 5. Spatial distribution of 30-year mean observed precipitation (top left) and modelled ERA-INT mean precipitation (top right), and 25-year mean observed precipitation (bottom left) and modelled HIST precipitation (bottom right). Both the observed and modelled values have a spatial resolution of 4x4 km.

For Belgium, a consistent increase in temperature (maximum and minimum) ranging between 0.3 and 4.2 °C, can be expected by the end of the century (Figure 6). The positive temperature changes were obviously larger for the most extreme scenario (RCP 8.5), while for the RCP 2.6 scenario the temperature changes stayed below 1 °C by the end of the century (not shown). Finally, the 30-yr mean temperature distributions showed a larger warming for the Ardennes (forested areas). These results, showing a shift towards higher mean temperatures, were in line with previous scenario results obtained with the ALARO-0 model for Belgium (e.g. Hamdi et al. 2014), as well as with the general tendency found by regional climate modelling initiatives for Europe (e.g. EUROCORDEX; Jacob et al. 2014).

This shift of mean temperature values towards higher temperatures also implied a shift of the tails of the distribution where the extreme temperature values were located. Hence, to provide a measure for the change in the extreme temperature values, four temperature indices were calculated: number of days per year with a T of 25 °C or more, number of days per year with frost, 99th percentile of the daily maximum temperature and 1st percentile of the daily minimum temperature. The number of days per year with a 2-m mean temperature of at least 25 °C as simulated by the model approached the observed number of days relatively well. Overall, relatively small changes in the number of days with minimum 25 °C were found for the three RCPs. The number of days per year with a 2-m mean temperature of less than 0 °C (i.e. number of frost days) was expected to decrease consistently for the three scenarios by the end of the century. However, the number of frost days present in the historical simulation was strongly overestimated compared to the observations. Therefore, it is important to stress that this result can only be interpreted as a sensitivity of the ALARO-0 model to the two different sets of historical and RCP boundary conditions. Both the 99th percentile of daily maximum temperature as well as the 1st percentile of daily minimum temperature showed a positive change (up to ± 4 °C) by the end of this century for all RCPs.

Mean precipitation changes for RCP 8.5 for the end of this century showed an overall tendency towards slightly wetter conditions. The largest positive changes were found for the winter and autumn precipitation (not shown) and for the most pessimistic scenario RCP 8.5 (up to 45 %). These large positive changes could be attributed to the extreme precipitation amounts that are present in the RCP 8.5 simulation and not in the HIST simulation. This shift towards more extreme precipitation was also confirmed by the results from the extreme precipitation indices (i.e. number of days per year with at least 10 mm and 99th percentile of daily precipitation). Both indices were indeed expected to increase by the end of the century for RCP 8.5 (not shown). Furthermore, for both indices the HIST simulation reproduced the observed index values and its respective spatial distribution relatively well.

For 10-m wind speed and relative humidity no pronounced changes were found, and hence no clear statements could be made on the changes in the spatial distribution or frequencies of both meteorological variables. However, for summer, both the RCP 4.5 and RCP 8.5 showed a consistent decrease in 2-m relative humidity by the end of the century (not shown). This finding is in line with a previous study of Hamdi et al. (2014), where future climate changes as modelled by the ALARO model were studied under one of the previous IPCC emission scenarios.

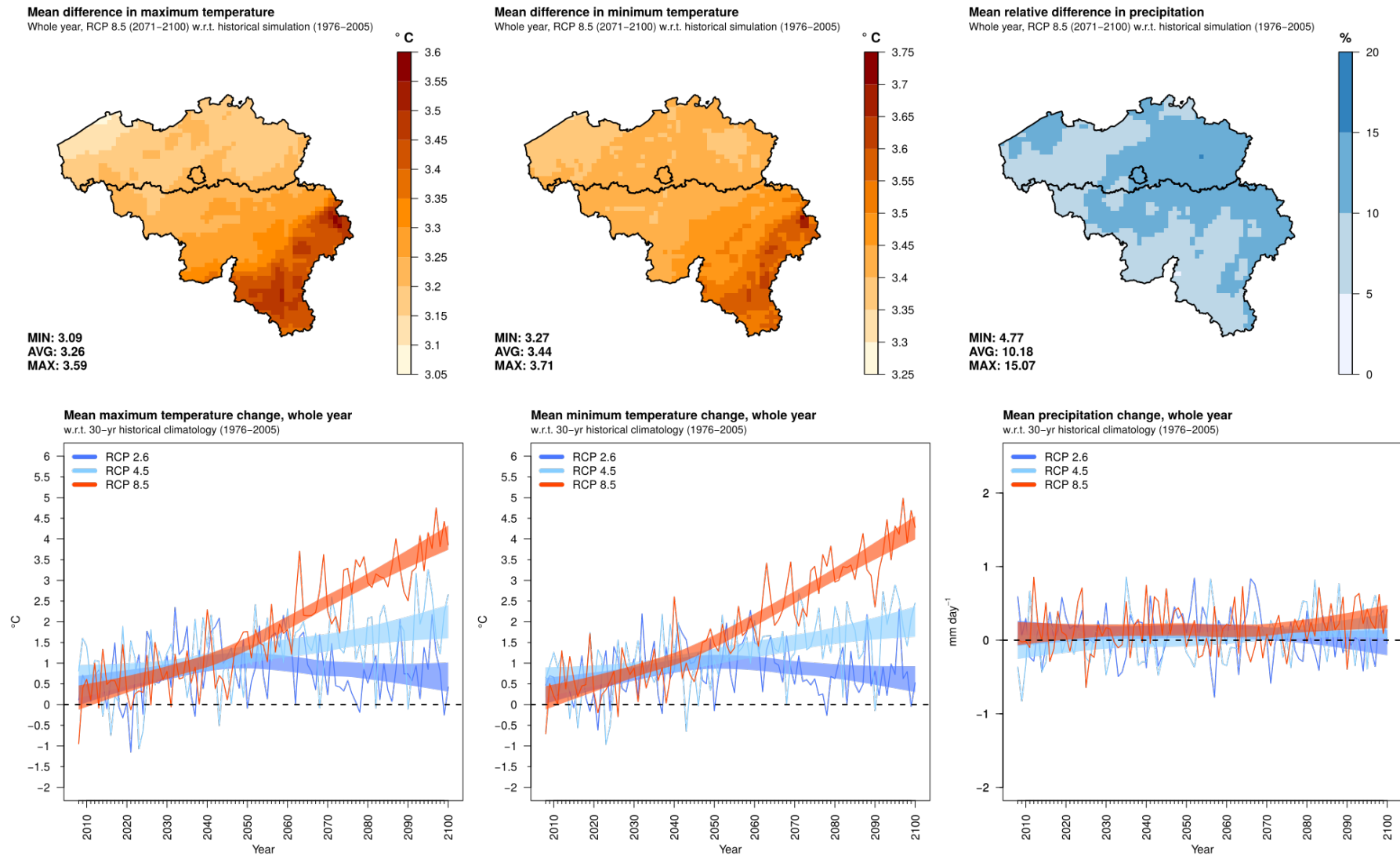


Figure 6. Mean change in 2-m maximum temperature change (left), 2-m minimum temperature (middle) change, and precipitation (right) over 30 years for RCP 8.5. The spatial distributions (top row) have a spatial resolution of 4x4 km.

WP2 Effects of temperature on progeny performance

This WP aimed to quantify the extent to which epigenetic mechanisms can affect the adaptive capacity of oak and beech seedlings to climate change. It focussed on the epigenetic effects of increased temperatures during seed development. Five tasks, varying between descriptive with little scientific control and experimental with a high level of scientific control, were completed. First, we looked at phenological responses of oak and beech seedlings to the temperature variation during seed maturation. Second, phenological shifts between seedlings and mother trees of translocated provenances in comparison to local provenances were examined in two common gardens. Third, we assessed the germination success of control and warmed seeds after fructifying twigs on 'in situ' trees were experimentally warmed. In the fourth task, we performed controlled crosses at different temperatures in greenhouse conditions. Fifth, a common garden experiment was performed to assess the maternal effect on budburst and bud set time of vegetative offspring (stem cuttings) and to search for DNA methylation as a potential epigenetic variation induced by the environment. The WP1 climate data were used to link weather patterns during seed development with seedling performance.

In a first step, we assessed the interactive effect of parental temperature and warming of the seedlings on the relative growth, budburst and leaf discoloration in pedunculate oak and European beech seedlings. In October 2014, we sampled 12 beech and 13 oak mother trees from five forests in Belgium and collected 335 oak and 296 beech seedlings ranging from 1-5 years old based on visual observations of scars on the stem, the height, and diameter from the base of the mother trees and planted the seedlings in 1.5 L pots in a common garden. Half of the seedlings were experimentally heated by circa +2.5 °C, using 150 W infrared heating lamps (Eider Landgeräte GmbH) during the period of end of January to April in both 2015 and 2016. We monitored bud phenology and growth of the seedlings in 2015 and 2016 (Kimball et al. 2007). We assessed the bud phenology using a score from 0 to 5 following the method of Schüler et al. (2012) and Wesolowski and Rowiński (2006). We observed an interaction effect of parental temperature and warming treatment on budburst time in 2016. For oak, higher parental temperature advanced or did not affect budburst time of oak seedlings when they were heated, while budburst time was delayed in control conditions (Figure 7d, 7e). For beech seedlings, higher parental temperature advanced or did not affect budburst time in control conditions, while budburst time was delayed when they were heated (Figure 7j). We did not observe a change in leaf discoloration with higher parental temperature and warming treatment for oak or beech.

Second, we studied the influence of parental effects regarding local adaptation to local temperature and photoperiod on germination, budburst, and biomass of pedunculated oak seedlings. In 2015, we collected seeds from four different provenances (two Danish, namely Bregentved and Wedellsborg, one Dutch and one Swedish, namely Visingso) in a mature Danish provenance trial (55.33° N, 12.07° E), that was established between 1940 and 1947 (Jensen 2010). There were two replicate plots for the Bregentved provenance and we kept the plots separate and recognized them as Bregentved 1 and Bregentved 2. We planted seeds in two common gardens at different latitudes. One common garden was located in Denmark (55.68° N, 12.54° E), circa 50 km away from the provenance trial, and the other common

garden was located in Belgium (50.98° N, 3.81° E), hence at a more southern latitude, with a mean temperature difference of 1.6 °C (Fick and Hijmans 2017). In both gardens, we monitored germination, budburst, and aboveground biomass of the seedlings for two years. We also followed the budburst time of the individual mother trees to compare the variability in budburst time between mother trees and seedlings. In the Belgian common garden, we observed reduced germination success. There was no difference in germination success among the provenances. There was a significant interaction between provenances and common gardens in budburst time indicating seedlings' budburst time was dependent on both the environment at origin (provenance) and seedlings growing environment (Figure 8). Budburst was significantly advanced in the southern common garden suggesting increased temperatures advanced budburst of the seedlings. We also observed earlier budburst in seedlings resulting from heavier acorns. Seedlings' biomass was higher in the northern common garden compared to the southern common garden with marginal difference among the provenances (Figure 9).

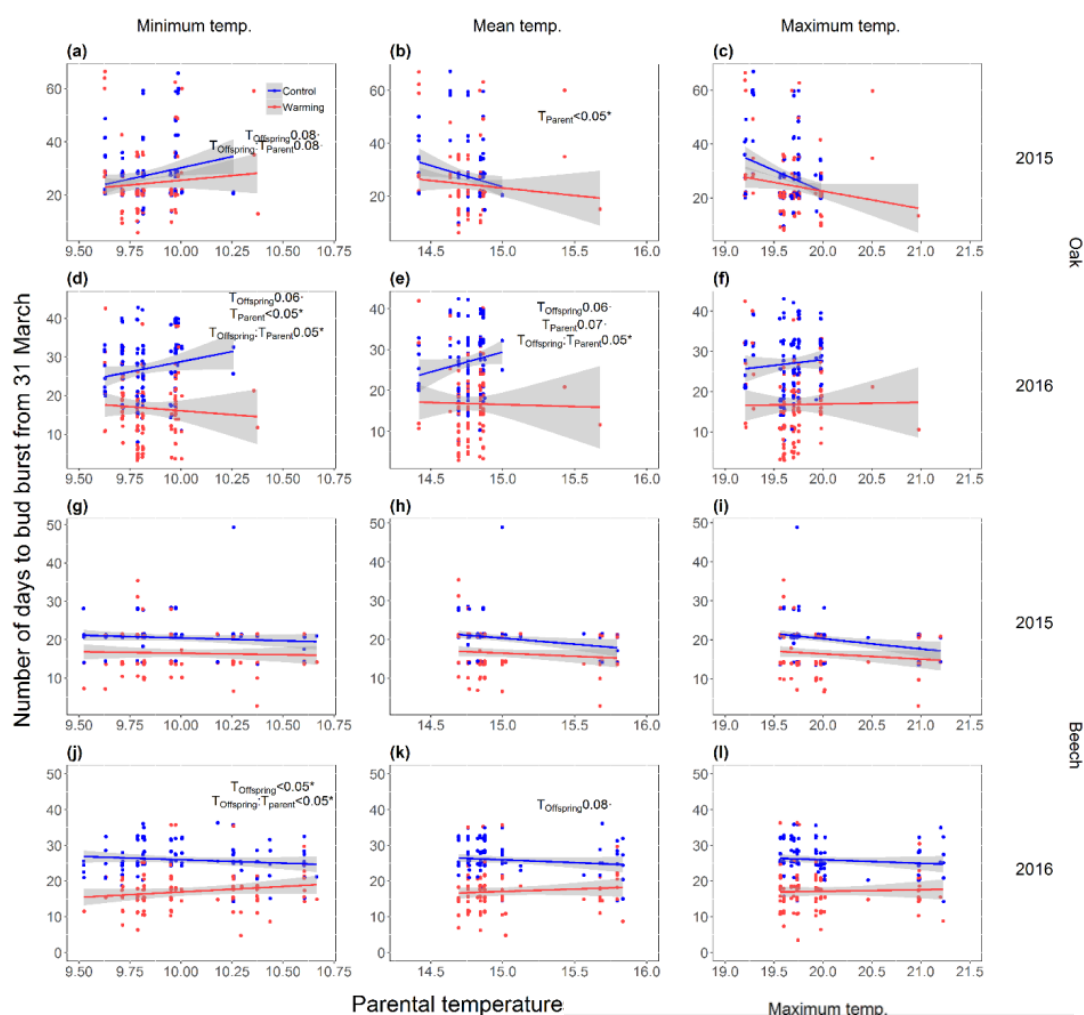


Figure 7. Effects of parental temperature (April-September, T_{Parent}) and warming of the offspring ($T_{\text{Offspring}}$) on the budburst time in oak (a-f) and beech (g-l) seedlings. Red denotes heated seedlings, blue the control seedlings. Values in the figures are p values for the effect of $T_{\text{Offspring}}$, T_{Parent} and the interaction between $T_{\text{Offspring}}$ and T_{Parent} from linear mixed effect models. Significance levels are denoted by ‘.’ for $0.05 < p < 0.1$ and ‘*’ for $p < 0.05$.

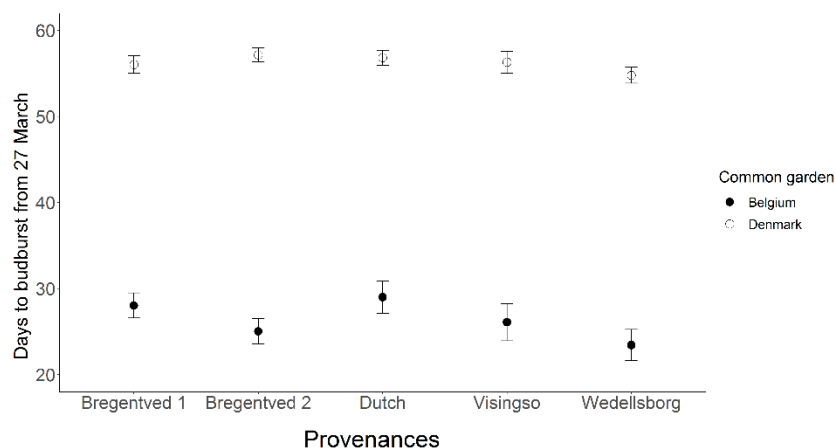


Figure 8. Days to bud burst (counted from 27 March 2017) for the five provenances in the Danish and Belgian common garden. The seedlings in the Belgian common garden displayed earlier bud burst than Danish common garden. The error bars denote the standard error.

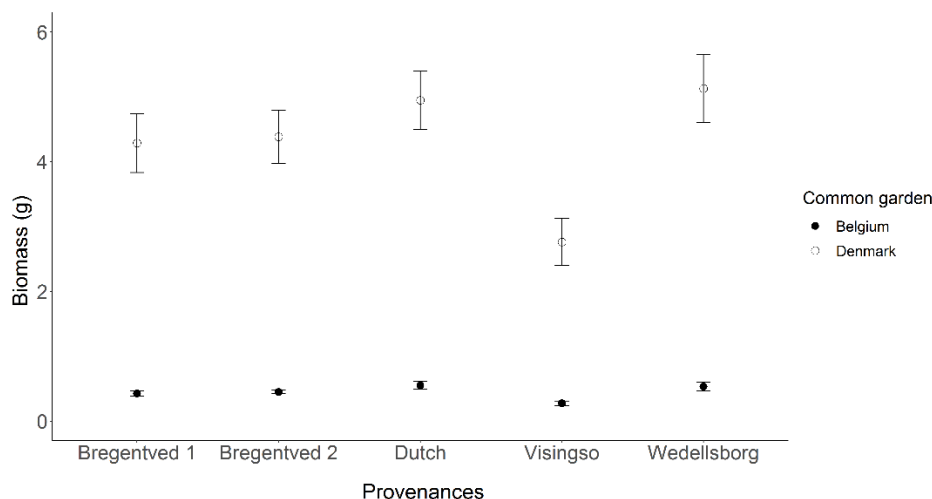


Figure 9. Aboveground biomass of the seedlings for the five provenances in the Danish and Belgian common garden. Error bars denote the standard error.

In a third experiment, we examined the germination success, budburst, leaf discoloration and biomass of pedunculate oak and beech seedlings. We looked at the response to the combined application of warming (+1.5 °C) to three pedunculate oak branches and four beech branches of an individual tree during the reproductive period (April-September), and subsequent warming of the soil in which their offspring were grown (+3 °C). For oak, the combination of branch warming during the reproduction period and soil warming treatment of the seedlings did not affect the germination success (Figure 10). For beech, the soil warming treatment significantly increased germination success of nuts from controlled branches (Z value = 2.024, $p = 0.043^*$). We did not observe a difference in germination success in response to branch warming.

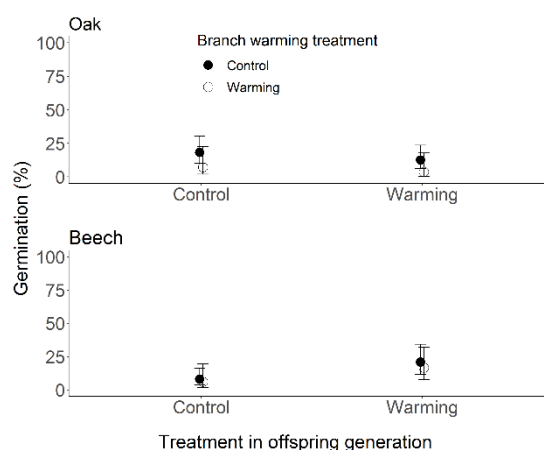


Figure 10. Seed germination in control and warming treatments in offspring and parental reproduction period (branch warming). Germination percentage was accounted based on total number of seedlings emerged from sowed acorns. Error bars denote the confidence intervals.

For the fourth and the fifth task, we used *Populus* species because of the well-suited characteristics of this dioecious species to perform controlled crosses to study the parental temperature effect in a single genotype. *Populus* is also ideal species to study tree molecular biology and biotechnology (Brunner et al. 2004; Cronk 2005). Therefore, understanding the responses of asexually reproducing plants (vegetative cuttings) of *Populus* to climate change will extend our knowledge, which can be implemented in the breeding programme.

In the fourth task, we assessed the effect of elevated parental temperature on the germination, timing to budburst and bud set, and growth of the full-sib seedlings of black poplar (*Populus nigra*). There were three pairs of genotypes used for three different experiments. In 2013, we performed crosses between genotypes Proven (female) and Horrues (male; Cross 1) in control (C) and warm (+10 °C) (W) environments and let the seed mature in the same environment (experiment 1). In 2014, we repeated experiment 1 in February, including one extra treatment where we performed the crosses in a cold (control) environment and let the seeds develop and mature in a warm (+10 °C) environment to disentangle the effect of temperature during pollination vs. during seed maturation (experiment 2). We performed the third experiment in 2014 using crosses between genotypes Meers (female) and Elst (male; Cross 2) and between genotypes Oosterzele (female) and Remicourt (male; Cross 3) following the same method and temperature treatments as described above in the second experiment (see Dewan et al. 2018 for a detailed description). Higher reproductive temperature reduced germination of black poplar across all three pairs of genotypes, but reduced bud set time in only one genotype, suggesting that black poplar responses to parental temperature differed among genotypes (see Tables 3 and 4 and Figures 1-4 in Dewan et al. 2018).

Finally, to assess the transgenerational effect on budburst and bud set time of vegetative offsprings (stem cuttings), a common garden experiment was performed in 2015. We used the vegetative cuttings of five hybrid poplars (hybrids of *Populus trichocarpa* and *P. deltoides*) of the same provenance but with different history (parental plant growing at different latitudinal gradient of >2100 kilometres, which corresponds with a 4.9 °C temperature difference and a

difference in photoperiods of up to 3.5 hours). We assessed the global DNA methylation in the vegetative cuttings as a potential epigenetic variation induced by the environment (Bräutigam et al. 2013, Guarino et al. 2015). Epigenetic modifications, such as methylation of DNA by methyltransferases, are principal regulatory mechanisms that translate developmental cues into differential gene expression programs. Methylation of DNA inhibits the binding of transcription factors to DNA and thereby influence gene expression. Methylation events are in turn regulated by noncoding RNAs, and modifications of RNA itself can induce plasticity. Here, Methylation Sensitive Amplified Fragment Length Polymorphism (MSAP) was used to understand the natural variation in genome-wide DNA methylation patterns within individuals plants of a single poplar hybrid clone (genotype) (Guarino et al. 2015). We found that the life history of the vegetative clones altered the budburst time of hybrid poplars. Warmer parental environment in winter advanced budburst time of the vegetative cuttings (Figure 11). Warmer mean annual temperature of the parental environment advanced bud set time (Figure 12). However, the advanced bud set time was observed only on one observation day during the second growing season. There was no significant epigenetic variation (DNA methylation) in the cuttings. Further research using more powerful molecular methods, such as whole-genome bisulphite sequencing techniques, are needed to explore the mechanism of transgenerational effects.

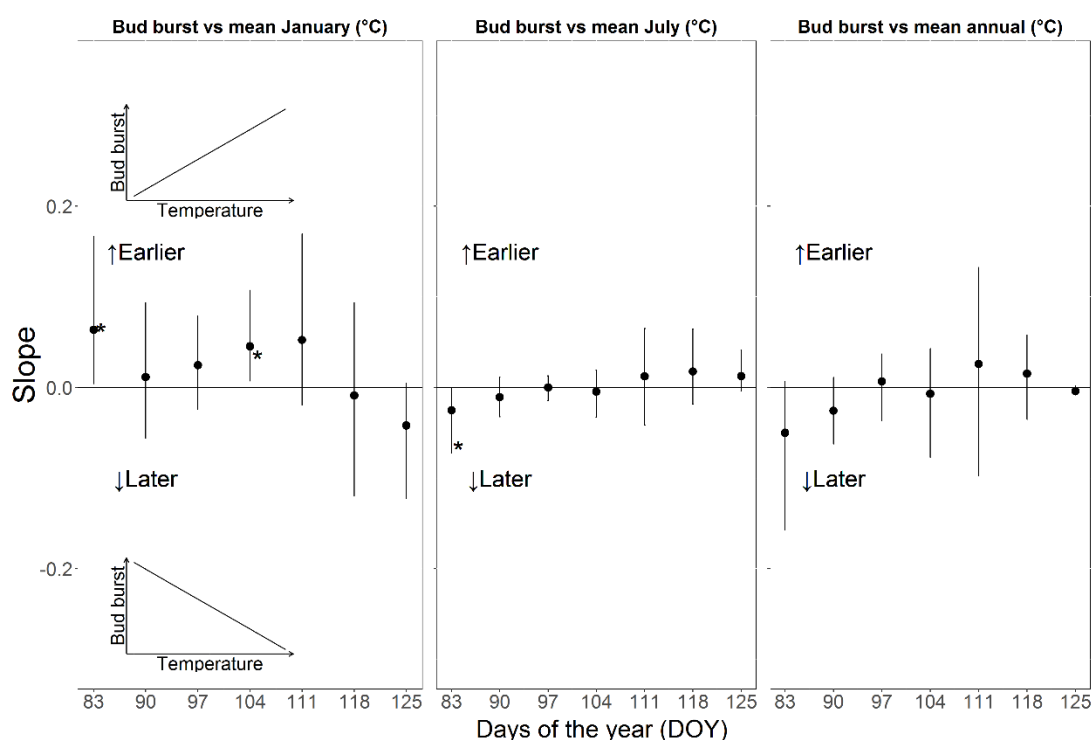


Figure 11. Mean weighted (bootstrapped) slopes of the relationship between the mean bud burst score in 2015 and mean January, July and mean annual temperatures experienced by the parent trees. Error bars denote 95% confidence intervals (upper and lower) across the 500 bootstrapped values. Significances at the 95% level are denoted by '*'. 'Earlier' means that buds burst earlier (higher bud burst score) with increasing temperatures and 'Later' means that buds burst later (lower bud burst score) with increasing temperatures.

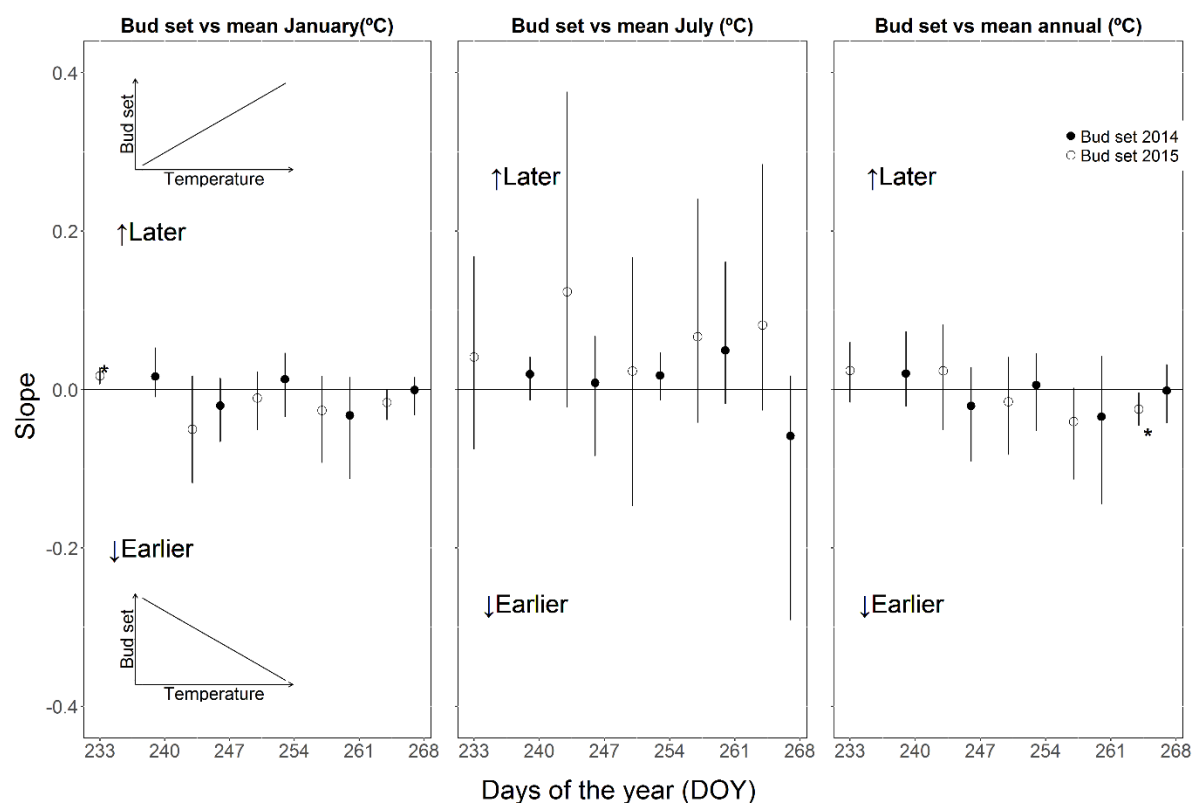


Figure 12. Mean weighted (bootstrapped) slopes of the relationship between the mean bud set score in 2014 and 2015 and mean January, mean July and mean annual temperatures experienced by the parent trees. Error bars denote 95% confidence interval (upper and lower) across the 500 bootstrapped values. Significances at the 95% level are denoted by '*'. 'Earlier' means that buds set earlier (lower bud set score) with increasing temperatures and 'Later' means that buds set later (higher bud set score) with increasing temperatures.

To conclude, parental temperature influenced the germination percentage, bud phenology and growth of seedlings of *Populus nigra*, *Q. robur* and *Fagus sylvatica* and this effect depended on the environmental conditions in the offspring generation. Hence, there is a need to consider the life history and parental environmental conditions to predict the response of trees to climate change. We investigated DNA methylation as a potential epigenetic mechanism for transgenerational effects but we could not confirm that methylation helps to explain the phenological changes mediated by the parental temperature.

WP3 Sapling resistance and resilience to drought in more or less diverse neighbourhoods

This WP focused on the performance of oak and beech saplings under drought stress. It also examined the hypothesis that effects of drought stress are less pronounced in forest stands with a higher tree diversity. More specifically, this WP examined the impact of drought and tree diversity on sapling growth and vitality, abiotic soil variables, soil microorganisms and soil organic matter transformation. For this purpose, a drought experiment using rainout shelters was installed on the FORBIO-site in Zedelgem. WP3 used WP1 data to design realistic experimental drought treatments.

A precipitation reduction (drought) experiment was established at the Zedelgem site of the FORBIO experiment (51°9' N 3°7' E) (<http://www.treedivbelgium.ugent.be>), a previously agricultural site on sandy to moderately wet loamy sand soil. The site was planted in 2009-2010 with one to four tree species in 40 plots (42 m × 42 m; five plots for each diversity level, two replications). Five functionally dissimilar site-adapted species (*Fagus sylvatica* hereafter beech, *Betula pendula*, *Pinus sylvestris*, *Tilia cordata*, *Quercus robur* hereafter oak) have been planted following a synthetic community approach (Verheyen et al. 2013). Twelve drought and twelve control subplots (three for each diversity level; 3 m × 3 m) were installed in spring 2015 within 14 plots in the south-east side of the site, around central oak or beech saplings. The central (focal) tree was surrounded by trees of the same species or by trees of one to three other tree species, creating a tree diversity gradient of one to four. Drought was imposed by installing rainout shelters (Yahdjian and Sala 2002), consisting of PVC gutters placed at a height of 0.95 m (in the upper part) and 0.75 m (in the lower part) from the soil (Figure 13). The gutters covered approximately 50% of the sub-plot surface and intercepted about 50% of total precipitation. Intercepted water was channelled to the downward side of the plot (6 m away). In addition, three “reverse gutter” subplots of same size were installed to assess the potential shading effects of rainout shelters. Soil moisture (0-30 cm) was continuously measured from June 2015 onwards using a Time-Domain Reflectometry instrument in three drought and three control subplots. The 50% precipitation reduction reduced the soil moisture in the drought plots by 4% on average. Soil temperature (0-5 cm) was measured during the growing season in 2015 and 2016 at three control, three drought and three reverse gutter subplots. Air temperature did not differ significantly between these subplots, indicating that the rainout shelter did not alter the microclimate under the canopy.



Figure 13. Rainout shelter in Zedelgem. Twenty-four similar drought subplots were installed with a plot size of 3m x 3m and heights in the upper and lower site of 0.95 m and 0.75m, respectively.

Diameter and height of the central oak and beech trees were measured in April 2015 and May 2017. Amount of dead shoots, leaf discoloration and pest and pathogen damage were assessed for the central trees in both drought and control subplots in June, August & October of 2015 and July, August & October of 2016. Tree vitality was visually assessed following the ICP forest protocol (<http://icp-forests.net>) and the procedure followed by Setiawan et al. (2014). Different leaf traits and leaf nutrient content of the central trees were also measured in August 2015 & August 2016.

Soil was sampled three times from both drought and control subplots. Top 0-5 and 5-10 cm soil were sampled using a plastic soil corer at the beginning (April 2015) and at the end of first and second growing season (October 2015 and 2016) after installation of rainout shelters. The following soil analyses were performed: soil moisture, soil pH_{H2O}, soil organic matter (SOM) content, soil respiration potential, net N mineralization & net nitrification, soil microbial biomass C and N, total soil C, N, C/N, metabolic diversity of soil bacteria and exchangeable cations in soil. In addition, *in situ* soil N availability was assessed by placing resin bags in the soil during the growing season (June-September) in 2015 and 2016.

Soil organic matter transformation was assessed by measuring two indices, namely the decomposition rate *k* and the stabilization factor *S*, using green and rooibos tea bags as described by Keuskamp et al. (2013). Four tea bags of each kind were weighed and placed at 5-7 cm soil depth in the drought and control subplots for 100 days (June to September). In addition to the Zedelgem site, tea bags were also buried in the ORPHEE experiment, that is located close to Bordeaux, France (44.74° N, -0.80° E; Castagneyrol et al. 2013). The ORPHEE experiment consists of eight blocks, and each block has 32 plots (10 m x 10 m). Tree diversity varied from monocultures to five species mixtures. This region is subjected to natural summer drought condition. An irrigation experiment has started in 2015 where half of the blocks were irrigated every night during the summer. One set of tea bags was buried at the centre of the plots for 90 days. Tea bags were collected, dried and re-weighed. Based on the weight loss of the green and rooibos tea, *k* and *S* were calculated (Keuskamp et al. 2013).

To assess the drought legacy effects on soil microorganisms under oak, soil samples were taken at a depth of 0-5 cm after two years of drought (May 2017). Bacterial and fungal growth rates, soil respiration, soil microbial biomass and soil microbial PLFA (Phospholipid-derived Fatty Acids) composition were measured. Further, a soil drying-rewetting experiment was performed in the laboratory to assess the drought legacy effects on bacterial growth and soil CO₂ emission.

Tree species admixing affected several above-and belowground processes, but the magnitude of the effect depended on the focal tree (oak or beech) and sampling time. For beech, tree species admixture reduced height increment and increased specific leaf area (SLA), possibly due to the competition for light of this shade-tolerant species with the neighbourhood trees. For oak, tree species admixture reduced the amount of dead shoots, crown damage from pests and pathogens, and leaf area index (2015 and 2016), Na and Zn content (2015). Tree species admixing increased soil nitrogen mineralization, nitrification, N content and total exchangeable cation concentration but the effect was not consistent between sampling time nor between soil layers. Soil microbial PLFA composition under oak was significantly affected by tree species admixing: it was similar between monocultures and two species mixtures, but different from three and four species mixtures.

Drought decreased SOM decomposition rate under beech at Zedelgem and at ORPHEE. Under drought, SOM stabilization rate was increased at Zedelgem while it decreased at ORPHEE. Drought also decreased the microbial metabolic quotient *q*CO₂ (i.e. ratio of

respiration to biomass) under oak in October 2016 soil sampling. Tree growth, photosynthesis rates, leaf traits and soil nutrient availability were not affected by drought.

Under oak, significant interactions between drought and tree species admixture were found for leaf K, Mg content (2015), soil nitrification rates (2015: 0-5 cm), soil microbial biomass carbon (MBC), microbial quotient (qMic; 2016: 0-5 cm) and soil organic matter decomposition rates. Under beech, significant interactions were found for leaf Cu, N content (2015), soil potential respiration (2015: 5-10 cm), metabolic diversity of soil bacteria (2016:0-5 cm), soil MBC and qmic (2016: 5-10 cm). Most of these interactions were driven by the drought effects on monocultures and two species mixtures, indicating a potential stabilizing effect of tree species admixing against drought.

Under oak, drought legacy reduced soil bacterial growth rates, soil potential respiration, and soil microbial biomass, without an effect of tree species admixing. An interaction between drought legacy and tree species admixture was found for bacterial to fungal growth ratio. This interaction was driven by the drought effects on bacterial growth rates in monocultures and two species mixtures.

To conclude, results suggest that both tree species admixing and drought have the potential to influence ecosystem processes in young forests. Growth and vitality of both beech and oak could benefit from admixing with functionally dissimilar tree species. Tree species admixing could offset the effects of drought on different ecosystem processes, and hence, stabilize ecosystem processes under drought, among others via changes in soil biogeochemical processes and microbial composition.

WP4 Effect of drought stress on growth of mature oak and beech trees growing in more or less diverse forest stands

WP4 examined the performance of mature oak and beech trees under drought stress. For this purpose, we focused on the growth history of oak and beech trees, derived from tree ring chronologies and stable carbon isotopes. Long-term, site-specific historical climate data provided by WP1 were used to link the growth responses of oak and beech to climate variation in pure versus mixed stands.

In order to isolate effects of species mixing from other stand and site effects that impact tree growth, we used the triplet method (Forrester and Pretzsch 2015). On each of eight study sites we identified three forest stands, i.e. a mixed stand of sessile oak and beech, and a pure stand of each of both species. The three stands are comparable in tree dimensions, stand density and abiotic conditions. Each of the study sites is located in Belgium, most of them in or around the Ardenne region (Figure 14, TABLE II). Based on the soil map, each site was classified as either wet (tendency towards a water excess), dry (tendency towards a water deficit) or optimal. In every site, at least 40 dominant target trees were selected (10 per species and stand). Two wood cores were extracted, on which tree rings were dated and measured. Within an 18 m radius of the target trees, we performed dendrometric measurements on each tree of which

the circumference at 130 cm was at least 50 cm. The aim was to characterize the neighbourhood of the trees under study, in terms of competition and species composition. The establishment of this network of eight oak-beech triplets, together with a collection of data on the tree growth and neighbourhood is an important outcome of this WP. In fact, these sites already serve as soil sampling sites for other studies on tree species mixing in forests.



Figure 14. Location of the eight study sites in Belgium.

Table II. Site characteristics of the eight triplets. The triplets of Ave-et-Auffe and Eupen have two sets of coordinates as these triplets are spread over two locations.

Triplet	Longitude	Latitude	Ecological territory (Wallonia)/ Ecodistrict (Flanders)	Altitude (m)
Baileux	4° 23' 59"	50° 1' 23"	Atlantic Ardenne and Ardenne basins	300
Ave-et-Auffe	5° 8' 56"	50° 6' 9"	Calestienne	250
	5° 7' 44"	50° 7' 3"		
Grune	5° 24' 28"	50° 9' 2"	Centro-Eastern Ardenne	420
Eupen	6° 6' 30"	50° 36' 39"	Centro-Eastern Ardenne	440
	6° 3' 47"	50° 33' 53"		
Buggenhout	4° 13' 5"	50° 59' 39"	Mid-Flemish sloping sandy-loamy district	20
La Roche	5° 35' 32"	50° 11' 45"	Centro-Eastern Ardenne	450
Vecmont	5° 28' 37"	50° 9' 37"	Centro-Eastern Ardenne	450
Arlon	5° 32' 54"	49° 38' 45"	Côtes de Florenville	340

In the isotopic study, we examined the effects of the summer drought in 2003 using stable carbon isotopes, by selecting from a subset of the wood samples the wood produced during the 2003 summer, and the wood produced during the summer of 2001 as a reference without drought. This was analysed for ^{12}C and ^{13}C content, from which we calculated $\delta^{13}\text{C}$. Under soil water limiting conditions, an increased $\delta^{13}\text{C}$ reflects the higher water use efficiency due to

stomatal regulation (a greater decrease in stomatal conductance compared to that of photosynthetic activity). $\delta^{13}C$ is thus a measure for the extent to which drought is experienced by the tree. Because other factors (like shading) impact $\delta^{13}C$ as well, we used the difference in $\delta^{13}C$ between 2003 and 2001, which represents drought exposure, as main variable. Unlike most research on stable carbon isotopes in tree rings, we performed measures on a tree-scale (rather than pooling samples to obtain a stand signal). This allowed us to carefully assess the relationships between mixing, growth and drought exposure. Additional variables characterizing site and tree environment were taken into account. We observed that stable carbon isotope ratios in late wood were closely linked to summer drought. We observed an effect of mixing on drought exposure ($\delta^{13}C_{2003} - \delta^{13}C_{2001}$) in beech, but not in oak. Drought exposure of beech was higher in mixed than in pure stands (Figure 15), though this effect lost its statistical significance when tree growth was taken into account. Regardless of mixing, beech trees were more exposed to drought as they grew faster in the years prior to the 2003 summer drought year, probably because growing fast requires more water. As a consequence, faster growing trees use up the available water more quickly under droughts. Because beech trees generally grew faster in the mixed stands, they were more exposed to the summer drought. We also assessed the stable carbon isotope ratios ($\delta^{13}C$) in the two years separately. Predrought beech growth was positively related to $\delta^{13}C$ in the reference year of 2001, while there was no relation with $\delta^{13}C$ in 2003. This suggests that fast growing trees have beneficial water relations in reference conditions, which they lose under conditions of drought.

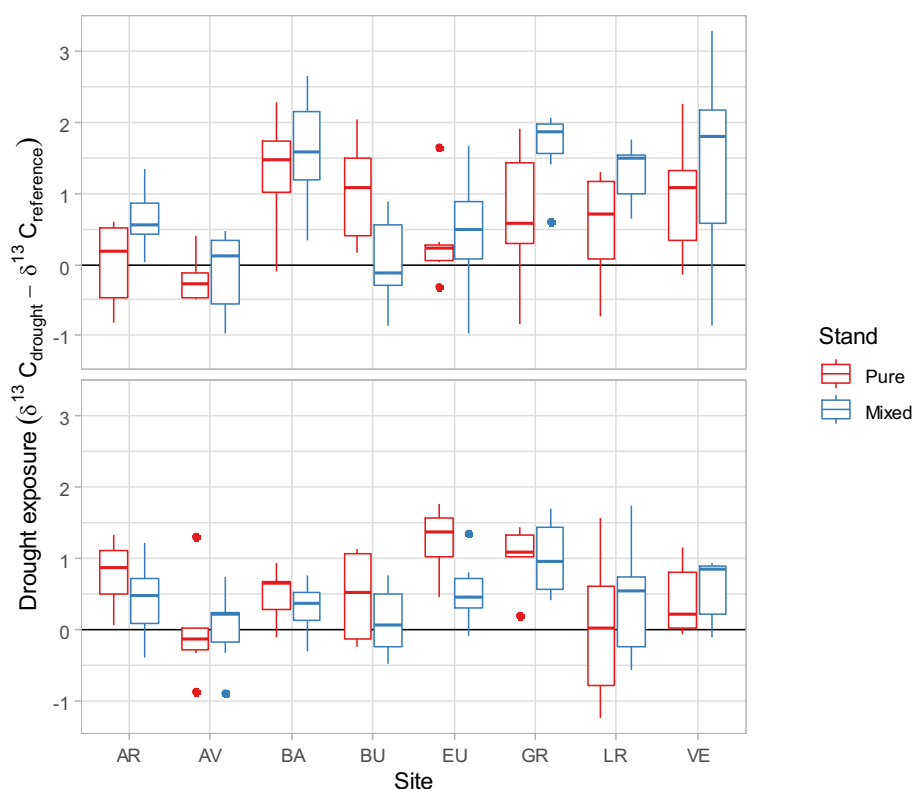


Figure 15. Drought exposure of individual trees in pure and mixed stands for beech (upper panel) and oak (lower panel). Site abbreviations stand for Arlon, Ave et Auffe, Baileux, Buggenhout, Eupen, Grune, La Roche and Vecmont respectively.

In the dendrochronological study, tree ring measurements (1953-2014) were used to test whether mixing has an impact on individual tree growth, more specifically on the sensitivity of growth to stresses like drought. We chose to avoid detrending our tree ring time series, which is usually done in dendrochronology, as this would remove part of the variation in the data, thereby possibly masking mixing effects. Instead, we used linear mixed models to explain tree growth in terms of climate. As climatic variables, we used mean temperature and accumulated precipitation, calculated on time windows that are multiples of 15 days. Data on oak and beech were kept separately. First, a linear mixed model was constructed, aiming to explain growth solely by climatic variables and using site as a random effect. Afterwards, we added interactions with a mixing variable (binary variable with values 0 for monocultures and 1 for mixtures). This approach allowed us to examine whether the effect of climate on growth depended on mixing. Unfortunately, there was a low explanatory power of the climatic variables. In a second step, we calculated a mixing index per site, year and species, as $(\text{mixed} - \text{pure})/(\text{mixed} + \text{pure})$, where mixed and pure are the average ring widths in the mixed and the pure stand, respectively. Then, a second linear mixed model was constructed, aiming to explain this mixing index by site-level water availability and tree growth. Tree growth was averaged per stand and per year and serves as a proxy for growing conditions. This allowed us to test the hypothesis that mixing effects become positive as conditions become less favorable. The effect of mixing on oak growth ranged from positive (on soils that are often deficient in water) to negative (on sites that rather have a water excess). A similar trend was observed for beech though this was not statistically significant. Climatic variables that represented spring precipitation showed a significant positive effect on growth of both oak and beech. This indicated that growth of both species was limited by precipitation in spring, though this effect was small. The sensitivity of beech to drought was higher than that of oak. We did not find a clear mixing effect on drought sensitivity, but this may be due to limitation of individual climate variables to express the sensitivity. From the models explaining the mixing effect on growth directly without considering climate, we observed that the effect of mixing on growth was generally positive for beech. For oak, this effect ranged from negative on wet sites, to neutral on dry sites. However, there was an important effect of yearly growth conditions. When conditions become less favorable (as indicated by a slower growth in general), mixing tends either to become advantageous, or the already existing advantage becomes larger. This was the case for both species on almost all sites. Mixing can stabilize the community-level growth, because positive and negative peaks in growth of different species are not aligned and can compensate for each other to some extent. This effect is independent of a potential mixing effect on the stability of growth on the population level (del Río et al. 2017).

We conclude that in mixed oak-beech stands, beech grew faster compared to its monoculture, while oak grew more slowly due to the competition with beech. This faster growth of beech is related to a higher exposure to drought conditions. However, in dry conditions, mixing turned out to be beneficial for the growth of both species. The data we collected on growth and neighbourhood will further be used to calculate population-level (tree species) and community-level (forest stands) growth.

WP5 Upscaling drought and diversity responses to a national level and stakeholders' perception on climate change effects and adaptation

This WP worked on a more integrated level, in terms of time, space and forest development stage, on the role of tree diversity in a context of climate change. First, nation-wide effects of climate change on stand dynamics of beech and oak stands were investigated. More specifically, multiple datasets were used to assess tree health and growth and to examine whether drought resilience was correlated with increased tree diversity and whether mixed-species stands can overyield monospecific stands. Next, to overcome the well-documented mismatch between research and management, we conducted a survey to identify which responses to climate change are being implemented and, from the perspective of forest managers, which impediments limit their ability to prepare and respond to these changes. In the final step that is still ongoing, we are performing a literature review to synthesize knowledge on tree diversity effects in a climate change context

In a first step, we examined the temporal variation in forest condition at the national scale using data from the ICP Forests monitoring plots network (<http://icp-forests.net>). This comprises data on health and growth of over 2,700 trees across 119 long-term forest plots, monitored between 1990 and 2016. Additionally, we used the regional forest inventory data of Flanders and Wallonia to explore potential overyielding in mixed-species stands (Annexes Figure A1). Climate data were obtained from the FORBIO Climate dataset, prepared in WP1 (Delvaux et al. 2015). Soil data were obtained from the digital soil map of Belgium (Dondeyne et al. 2014; Dondeyne, *unpublished raw data*) and complemented, when necessary, with data from the Walloon forest inventory (Rondeux and Lecomte 2010). Topographic variables were extracted from a LiDAR-derived digital terrain model at a spatial resolution of 1 m (AGIV 2015; SPW 2015). To better understand the interactive effects of tree species richness and drought on crown defoliation and radial growth, we used mixed-effects models for all analyses. Mixed-effects models have become increasingly popular for fitting models to structured data (Schielzeth and Nakagawa 2013), as is the case with inventory plots. In continuous forest inventories, measurements are nested within a tree (i.e. repeated measurements) and trees are nested within a plot. Furthermore, repeated observations in longitudinal studies are typically correlated. Mixed-effects models explicitly model hierarchical data structures by featuring random effects that allow clustering observations into groups (Zuur et al. 2009), thus accounting for the potential correlation of trees within plots.

Our findings point to the pivotal role of tree diversity for increasing growth resilience to drought events. We showed that mixed species forests can better withstand drought stress, which adds further evidence to the overall positive impact of diversity on forest productivity. Increased species richness can insure against a decline in forest productivity, as the long-term resilience of forest ecosystems is increased when species exhibit a diversity of responses to a disturbance (here drought) (Elmqvist et al. 2003; Folke et al. 2004). Species interactions may reduce susceptibility to drought stress via facilitative mechanisms, such as hydraulic lift and canopy shading, or via a reduction in competition due to spatial and temporal partitioning of resources (Forrester & Bauhus 2016). Responses of trees to drought are therefore highly context-dependent. In this work, and in the literature, beech was shown to be more resistant

and resilient against drought and to exhibit higher growth rates when growing in mixtures than in monocultures. This positive effect of mixing on beech has been attributed to its low self-tolerance (del Río et al. 2014), superior space sequestration efficiency (Dieler & Pretzsch 2013), and specific root system architecture (Leuschner et al. 2001), which give the species a competitive advantage in mixtures. For sessile oak, we observed no significant differences between trees growing in mixtures and monocultures, neither before, during, nor after the drought events. The mixture effect on sessile oak growth has been found to depend on the shade tolerance of the surrounding species, i.e. positive effects when the surrounding species are shade-intolerant and negative effects when the surrounding species are highly shade-tolerant (Toigo et al. 2018). Sessile oak is a light-demanding species with low shade tolerance; thus, the more shade-intolerant the surrounding species, the more sessile oak may benefit from the mixture. Maintaining forest diversity has, therefore, major implications for forest management practices and efforts to mitigate the vulnerability of forests to drought under changing climate conditions. In addition, we have shown that standardized, long-term monitoring of forest vitality is an effective method to detect climate change-induced and tree diversity-mediated trends in forest health and productivity. The continuous improvement in the quality of data that has been achieved so far has proven to be an effort that merits improved and extended continuation.

One of our main findings was that crown defoliation of beech and oak trees has significantly increased since 1990s. The severity of defoliation was lower at higher tree diversity levels when considering long-term responses to changes in temperature and precipitation (Figure 16). The observed shift from a negative to a positive effect of species richness on forest condition, caused by increased water stress, although implicit in previous studies, has never been reported from real ecosystems outside experimental conditions.

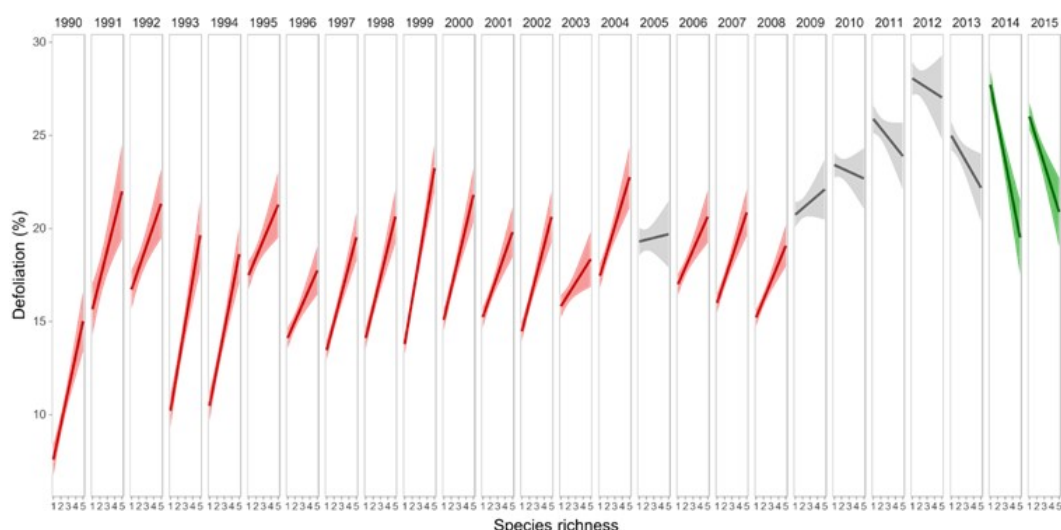


Figure 16. Annual trends in plot-averaged tree defoliation along a tree species richness gradient. Defoliation severity was expressed as the proportion (percentage 0–100%, with intervals of 5%) of leaf loss. Solid lines and shaded areas represent the mean and 95% confidence intervals for each year of the study. Positive slopes (red) indicate an increase in defoliation with increased species richness (ranging from 1 to 5), whereas negative slopes (green) denote a decrease in defoliation in more diverse stands. Non-significant slopes are shaded grey ($P \geq 0.05$). $N = 37,800$ observations.

A second important outcome of the upscaling work was that drought caused a marked growth reduction in deciduous trees, especially for beech (Figure 17). We also found that trees growing in mixtures were more resilient to drought than those growing in monocultures (Annexes Figure A2): they displayed a lower disturbance impact (higher resistance) and they returned faster to their pre-disturbance state (higher recovery rate). Besides, drought resilience tended to be lower in defoliated trees.

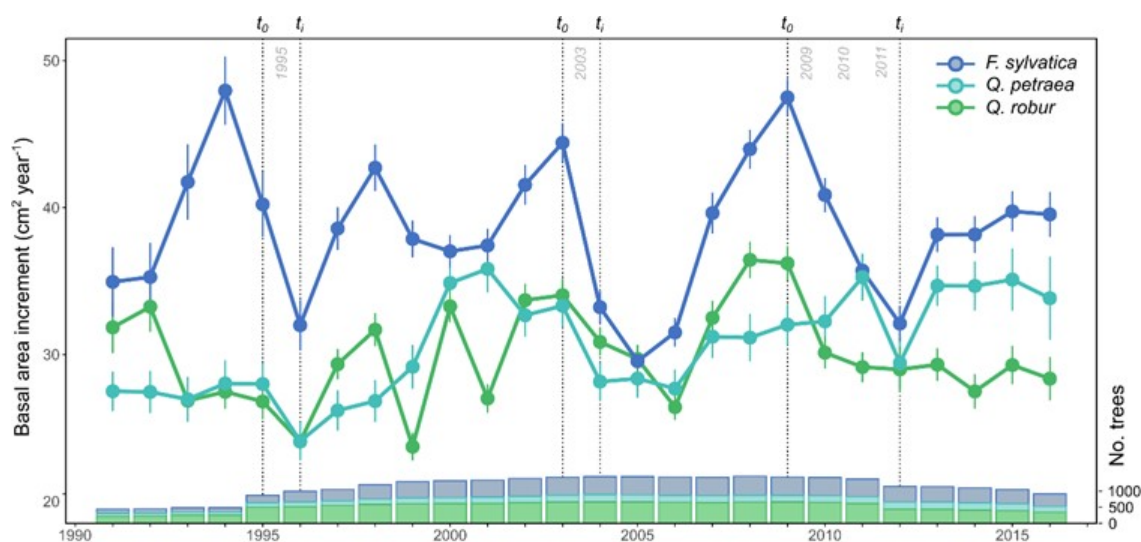


Figure 17. Annual basal area increment from 1991 to 2016 for the three studied tree species. Values are means with standard errors (left y axis), and the bars show the sample depth, i.e., the annual number of assessed trees (right y axis) for beech (*F. sylvatica*; dark blue), sessile oak (*Q. petraea*; light blue), and pedunculate oak (*Q. robur*; green). Vertical dotted lines encompass the immediate effect of the drought event; t_0 and t_1 correspond to the time immediately before and immediately after the main disturbance effect.

In a second step, we administered a questionnaire to 391 forest practitioners, either private forest owners or managers of public and private forests in Belgium, to inform on their perception on climate change effects and adaptation. The same questionnaire was later used in other countries, providing the possibility of performing some cross-national comparisons, and especially to compare findings for Belgium with those in other countries. An important result was that there is a marked imbalance between the large awareness about climate change impacts and the adaptation practices put in place by forest managers for coping with it (Figure 18). A lack of locally relevant and practical information about potential climate impacts and a lack of technical expertise on how to adapt are barriers that hinder adaptation to climate change.

As a third chapter in this WP, we made efforts to synthesize knowledge on tree diversity effects in a climate change context. A systematic review of the published literature on this subject, coupled with the results attained with WP2-4, is still ongoing.

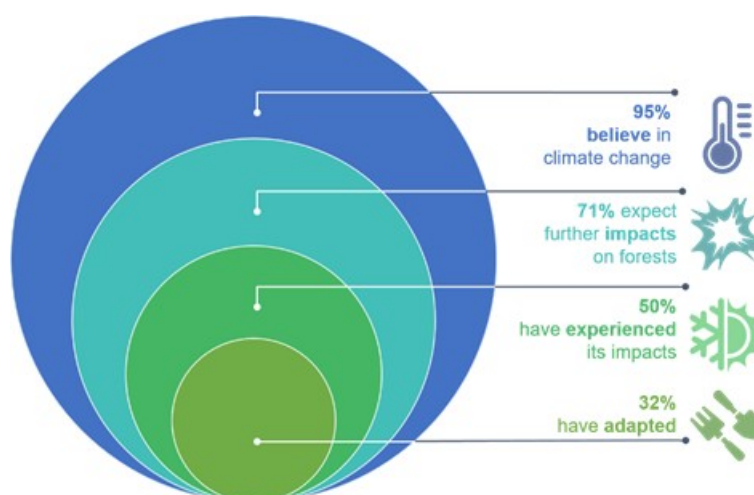


Figure 18. Key findings from the survey carried out in this research to assess how forest practitioners in Belgium perceive the role of their forest management in the context of climate change and the impediments that limit their ability to prepare and respond to these changes. Circle areas are proportional to the number of responses (N = 391).

To conclude, we demonstrated that the crown condition of the three species has declined appreciably over the past decades, in parallel with increasing water stress, and that this change has triggered a regime shift from healthy monocultures to resilient tree species mixtures. A strong and clear link has also emerged between a decline in tree productivity and the occurrence of drought events, associated with longer recovery times. Noteworthy, trees growing in mixtures showed greater capacity to recover after drought events than trees growing in monocultures. Our results indicate that mixed species forests can better withstand drought stress, which confirms their greater resilience to projected changes in climate extremes and disturbance regimes. Furthermore, managing forests to retain or increase diversity has the additional potential benefit to provide managers with more options for future stand development. Altogether, the new knowledge generated allows us to meet some of the forest managers' knowledge needs, detailed in our survey, and hence may explain the lack of adaptation responses, despite their relatively high awareness of climate change as an issue in forest management.

General conclusions and recommendations

Simulation results showed a clear climate change over the next 80 years, with a shift towards higher temperatures and slightly wetter conditions due to more extreme precipitation amounts in winter and autumn. We hypothesized that epigenetic inheritance mechanisms can increase the adaptive capacity of trees to this climate change during the reproduction stage. In general, warmer environments for seeds and offspring led to increased germination success for beech but reduced germination and seedling biomass for oak. Higher offspring temperatures also accelerated bud burst, especially for oaks. However, we did not observe any significant DNA methylation that might help us understand the mechanism behind the phenological changes

due to maternal environment. Further investigation using more powerful molecular methods like whole-genome bisulphite sequencing techniques, is thus necessary.

We also hypothesized that across subsequent tree development stages, more biodiverse forest environments generate higher resistance (initial response) and resilience (recovery) of beech and oak trees to climate change. Beech is able to invade pure forests of sessile oak and has a tendency to dominate mixed oak-beech forests, as beech grows faster in mixtures, compared to its monocultures (Pretzsch and Schütze 2009). Oak, on the other hand, generally grows more slowly when mixed with beech, because beech trees are better competitors that cast a deep shade, in this way reducing light availability for the neighbouring oak trees. A drawback to fast beech growth is the high water use, which might cause them drying out the soil quicker. This could increase the vulnerability of these mixed oak-beech stands, because beech is more sensitive to drought than sessile oak, especially in summer (Scherrer et al. 2011; Vanhellemont et al. 2019). However, studies on saplings and mature trees (WP3-5) showed that tree species admixing to oak and beech showed some degree of stabilization against drought, probably resulting from facilitation and complementarity among tree species (Loreau and de Mazancourt 2013; Jucker et al. 2014). We have shown that mixing is *de facto* beneficial for the growth of beech trees in tough years (i.e., years of slow growth, regardless of whether this is caused by droughts or other environmental factors). The disadvantage of slower growth for oak also becomes smaller in harsher conditions, and may even be reversed, for example on dry sites. Complementary rooting of oak and beech trees leads to more complete use of available water resources and this higher soil water depletion, resulting in a stronger negative effect of drought on beech in mixtures with oak (Vanhellemont et al. 2019). In these cases, oak growth actually benefits from growing in a mixture with beech trees. This also means that, when conditions harshen, oak growth will be less affected in mixture than in pure stands. In this sense, mixing can be seen as a safety measure. Thus, the overall effect of tree diversity on the productivity of mixed stands including oak and beech remains positive. Indeed, we found that the more diverse a stand is, the lower mean defoliation for all species and the higher the overall growth rate. These conclusions are also consistent with our observations that tree health and productivity increased at high tree species richness (WP5), as well as with those described in the literature for multiple ecosystem services (e.g. van der Plas et al. 2016; Ratcliffe et al. 2017).

Silvicultural interventions may be needed to maintain a certain degree of tree diversity. For example, as mentioned higher, beech is a species that both casts and tolerates deep shade and tends to develop rather monospecific stands in which other tree species occur only sporadically (Hobi et al. 2015). This is often the case in mixtures of beech and oak, where thinning at appropriate intervals is often needed to reduce or eliminate strong interspecific competition and help to maintain or even favor oak over beech, both by limiting the suppression of oak by beech, and by promoting oak regeneration. These interventions should aim at keeping a balance between a minimum stand density, that ensures a certain level of productivity and maintain interactions among species, and a maximum density in which competitive effects may outweigh complementarity effects (Bauhus et al. 2017). Controlling stand density is also an effective way to prevent forest stands from severe drought stress since water consumption is intrinsically related to the stand density (Forrester 2015).

To conclude, our results corroborate evidence that managing oak and beech forests to retain or increase taxonomic, functional and/or genetic tree diversity is a step forward to mitigate the vulnerability of these forests to climate change. Mixed stands grant managers with more options for future stand development, as they decrease the vulnerability posed on monocultures in light of future climate changes. Standardized, long-term monitoring of forest vitality is an effective method to detect climate change-induced and tree diversity-mediated trends in forest health and productivity. The continuous improvement in the quality of data that has been achieved so far has proven to be an effort that merits improved and extended continuation. Further research may focus on a wider range of tree species and multiple climate change drivers across various ecosystems to predict the response of trees to climate change better.

5. DISSEMINATION AND VALORISATION

Delvaux, C., Journée, M., Bertrand, C. (2014) The FORBIO Climate data set for climate analyses. Poster at the 14th EMS Annual Meeting & 10th European Conference on Applied Climatology (ECAC), 6-10 October 2014, Prague, Czech.

Dewan, S., De Frenne, P., Vander Mijnsbrugge, K. & Verheyen, K. (2014) Effect of maternal temperatures on the performance of tree seedlings. Poster presentation at the Joint Annual Meeting of the British Ecological Society (BES) and Société Française d'Ecologie (SFE), 09-12 December 2014, Lille, France.

Dewan, S., De Frenne, P., Vander Mijnsbrugge, K., Verheyen, K. (2015) Does phenology of beech and oak seedlings varies with the prevailing environment of seed development? Oral presentation at Seminar on Global Forestry Trends, 7-10 October 2015, Joensuu, Finland.

Rahman, M.M., Verheyen, K., Carnol, M. (2015) The role of tree species diversity in drought resistance of oak and beech sapling. Poster presentation at the Congress of the Graduate School BEE (Biodiversity, Ecology, Evolution), 21 March 2015, Brussels, Belgium.

de Streel, G. Jacobs, K., Nickmans H. (2016) Le mélange d'espèces: l'avenir des forêts? Poster presentation at the Journée bio-ingénieurs (midi étudiants-chercheurs), 25 October 2016, Louvain La Neuve, Belgium.

Sousa-Silva, R., Van Meerbeek K., Sioen G., Laurent C., Kint V., Ponette Q., Verheyen K., Muys B. (2016) *How do tree species mixtures modulate climate effects on tree vitality in Belgian forests? Poster presentation at the EcoSummit 2016 on Ecological Sustainability: Engineering Change.* 29 August – 1 September 2016. Montpellier, France.

De Troch, R., Duchêne, F., Hamdi, R., Van Schaeuybroeck, B., De Cruz, L., Termonia, P., Bauwens, M., Stavrou, T., Gobin, A. (2017) CORDEX.be: a Belgian framework to close the gap between regional climate model information and local-impact assessment for climate services. Poster at the Climateurope Festival, 5-7 April 2017, Valencia, Spain.

Dewan, S., De Frenne, P., Steenackers, M., Vander Mijnsbrugge, K., Verheyen, K. (2017) Temperature memory effects persistently alter the phenology of tree clones. Oral presentation at Starters in het Natuur- en Bosonderzoek, 24 March 2017, Ghent, Belgium.

Dewan, S., Vander Mijnsbrugge, K., De Frenne, P., Steenackers, M., Michiels, B., Verheyen, K. (2017) Maternal temperature affects the germination success and the phenology of tree seedlings. Oral presentation at the Conference on Restoring Forests, 12-14 September 2017, Lund, Sweden.

Rahman, M.M., Verheyen, K., Castagneyrol, B., Jactel, H., Carnol, M. (2017) Does tree species richness attenuate the effect of experimental irrigation and drought on decomposition rate in young plantation forests? Poster presentation at the European Geo-science Union General Assembly, 23-28 April 2017, Vienna, Austria.

Sousa-Silva, R., Verheyen, K., Ponette, Q., Muys, B. (2017) Unveiling the role of tree diversity on forest growth and resilience to drought. Oral presentation at the British Ecological Society Joint Annual Meeting: Ecology Across Borders. 11-14 December 2017, Gent, Belgium.

Sousa-Silva, R., Van Meerbeek, K., Van de Peer, T., Sioen, G., Laurent, C., Ponette, Q., Verheyen, K., Muys, B. (2017) Contrasting vulnerability and resilience to drought-induced defoliation in mixed versus pure stands. Oral presentation at the IUFRO 125th Anniversary Congress, 18-22 September 2017, Freiburg, Germany.

Sousa-Silva, R., Boogers S., Van de Peer, T., Govaere, L., Lecomte, H., Ponette, Q., Verheyen, K., Muys, B. (2017) Friend or Foe? Assessing the diversity-productivity relationship using forest inventory data. Oral presentation at the IUFRO 125th Anniversary Congress. 18-22 September 2017, Freiburg, Germany.

Sousa-Silva, R., Van Meerbeek, K., Van de Peer, T., Sioen, G., Laurent, C., Ponette, Q., Verheyen, K., Muys, B. (2017) Does tree diversity matter for defoliation trends of oak and beech? Keynote oral presentation at the 6th ICP Forests Scientific Conference, 16-17 May 2017, Bucharest, Romania.

Sousa-Silva, R., Verbist, B., Ponette, Q., Verheyen, K., Muys, B. (2017) A line made by walking: adaptation to climate change in forestry across Europe. Invited oral presentation at the International Workshop on Forests and Climate Change: adaptation initiatives and new management practices, 8-9 March 2017, Nancy, France.

Sousa-Silva, R., Van Meerbeek, K., Van de Peer, T., Sioen, G., Laurent, C., Ponette, Q., Verheyen, K., Muys, B. (2017) Contrasting vulnerability and resilience to drought-induced defoliation in mixed versus pure stands. Communications in Agricultural and Applied Biological Sciences: vol. 82(1), 42. Oral presentation at the 22nd National Symposium on Applied Biological Sciences, 7 February 2017, Leuven, Belgium.

Jacobs, K. (2018) Effects of mixing (oak-beech) on drought exposure. Oral presentation at the Séminaire sur les forêts mélangées, 5-6 June 2018, Nancy, France.

Rahman, M.M., Hicks, L.C., Verheyen, K., Rousk, J., Carnol, M. (2018) Effect of drought legacy and tree species admixing on bacterial growth and soil respiration rates upon drying-rewetting in a young tree plantation. Oral presentation at the BioLink meeting, 14-16 March 2018, Granada, Spain.

Sousa-Silva, R., Verheyen, K., Ponette, Q., Bay, E., Laurent, C., Sioen, G., Titeux, H., Vanhellefont, M., Muys, B. (2018) *The impact of forest diversity on tree growth and recovery to drought*. Oral presentation at the 7th ICP Forests Scientific Conference, 22-23 May 2018, Riga, Latvia.

6. PUBLICATIONS

PhD theses (C2 publications)

Sousa-Silva, R. (2018) Adaptation to climate change: the importance of tree diversity for the resilience of forest ecosystems. Doctoral thesis. Faculty of Bioscience Engineering, KU Leuven. 30 August 2018.

Rahman, M.M. (2018) Effects of tree species diversity and drought on ecosystem functioning in a young forest. Doctoral thesis. Faculty of Science, University of Liege. 7 September 2018.

Dewan, S. (*in preparation*). Effects of parental temperature on offspring performance of temperate forest trees. Doctoral thesis. Faculty of Bioscience Engineering, UGent.

Jacobs, K. (*in preparation*). Does mixing change the performance of oak and beech to drought? Doctoral thesis. Université catholique de Louvain, Louvain-La-Neuve.

A1 publications (peer reviewed)

Delvaux, C., Journée, M., Bertrand, C. (2015). The FORBIO Climate data set for climate analyses. *Advances in Sciences and Research* 12, 103-109. doi:10.5194/asr-12-103-2015

Sousa-Silva, R., Ponette, Q., Verheyen, K., Van Herzele, A., Muys, B. (2016) Adaptation of forest management to climate change as perceived by forest owners and managers in Belgium. *Forest Ecosystems* 3, 22. doi: 10.1186/s40663-016-0082-7

Berckmans, J., Giot, O., De Troch, R., Hamdi, R., Ceulemans, R., Termonia, P. (2017) Reinitialised versus continuous regional climate simulations using ALARO-0 coupled to the land surface model SURFEXv5. *Geoscientific Model Development* 10, 223-238. doi: 10.5194/gmd-10-223-2017

Dewan, S., De Frenne, P., Leroux, O., Nijs, I., Vander Mijnsbrugge, K., Verheyen, K. (2018) Phenology and growth of *Fagus sylvatica* and *Quercus robur* seedlings in response to

temperature variation in the parental vs. offspring generation. *Plant Biology*, *resubmitted after major revisions*.

Dewan, S., De Frenne, P., Vanden Broeck, A., Steenackers, M., Vander Mijnsbrugge, K., Verheyen K. (2018) Transgenerational effects in asexually reproduced offspring of *Populus*. *Plos One*, *resubmitted after major revisions*.

Dewan, S., Vander Mijnsbrugge, K., De Frenne, P., Steenackers, M., Michiels, B., Verheyen, K. (2018) Maternal temperature during seed maturation affects seed germination and timing of bud set in seedlings of European black poplar. *Forest Ecology and Management* 410, 126–135. doi: 10.1016/j.foreco.2018.01.002

Hicks, L.C.*, Rahman, M.M.*, Carnol, M., Verheyen, K., Rousk, J. (2018) The legacy of mixed planting and precipitation reduction treatments on soil microbial activity, biomass and community composition in a young tree plantation. *Soil Biology and Biochemistry* 124, 227–235. doi: 10.1016/j.soilbio.2018.05.027 (* equal contributions)

Rahman, M. M., Castagneyrol, B., Verheyen, K., Jactel, H., Carnol, M. (2018) Can tree species richness attenuate the effect of drought on organic matter decomposition and stabilization in young plantation forests? *Acta Oecologica* 93, 30-40. doi.org/10.1016/j.actao.2018.10.008

Rahman, M. M., Hicks, L. C., Verheyen, K., Rousk, J., Carnol, M. (2018) Effects of drought legacy and tree species admixing on bacterial growth and respiration in a young forest soil upon drying and rewetting. *Soil Biology and Biochemistry* 127, 148-155. doi: 10.1016/j.soilbio.2018.09.026

Sousa-Silva, R., Boggers, S., Verheyen, K., Muys, B. (2018) Partitioning of tree biodiversity effects on forest growth using national forest inventory data. *Forest Ecology & Management*, *will be submitted in December 2018*.

Sousa-Silva, R., Verbist, B., Lomba, Â., Valent, P., Suškevičs, M., Picard, O., Hoogstra-Klein, M.A., Cosofret, V.-C., Bouriaud, L., Ponette, Q., Verheyen, K., Muys, B. (2018) Adapting forest management to climate change in Europe: Linking perceptions to adaptive responses. *Forest Policy and Economics* 90, 22–30. doi: 10.1016/j.forpol.2018.01.004

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A3 publications (peer reviewed)

Sousa-Silva, R. (2017) Klimaatadaptatie in het bosbeheer: een mythe of een feit? *Bosrevue* 59a.

A4 publications

Sousa-Silva, R. (2017) L'adaptation de la gestion forestière au changement climatique : est-ce un mythe ou une réalité ? *Silva Belgica* n° 1/2017.

Other C2 publications

Saeren, A. (2016) Is climate change affecting our forests? Perceptions and responses to climate change among forest managers and owners in Belgium and EU. Master thesis. KU Leuven.

Boogers, S. (2017) The interplay of facilitation and competition on tree growth in mixed versus pure stands. Master thesis. KU Leuven.

Navare, K. (2017) Assessment of changes in the Flemish forest through the analysis of Forest Inventory data. Master thesis. KU Leuven.

Vermeulen, J. (2017) Quantifying the evidence for biodiversity effects on tree growth and mortality in Belgian forests. Master thesis. KU Leuven.

Sousa-Silva R, Verheyen K, Muys B (2018). Does tree diversity influence defoliation trends of oak and beech? In: *Forest Condition in Europe: 2018 Technical Report of ICP Forests*. *In press*.

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ANNEXES

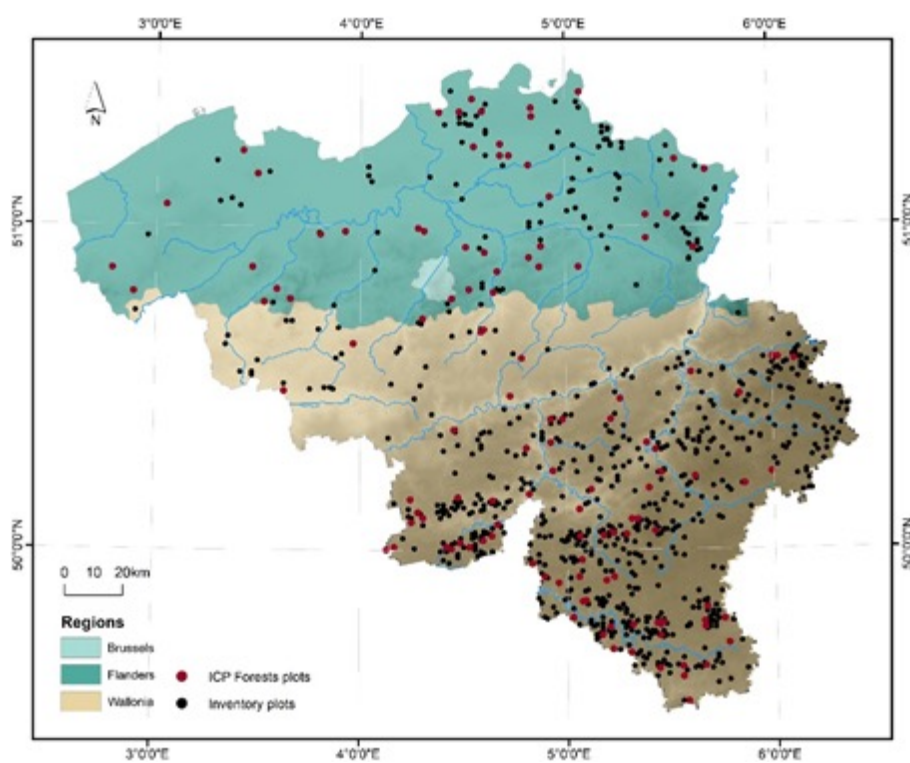


Figure A1. Distribution of sample plots across Belgium. In total, data were used from 119 ICP Forests monitoring plots (Level I and Level II) and 743 plots from the regional forest inventories of Flanders and Wallonia.

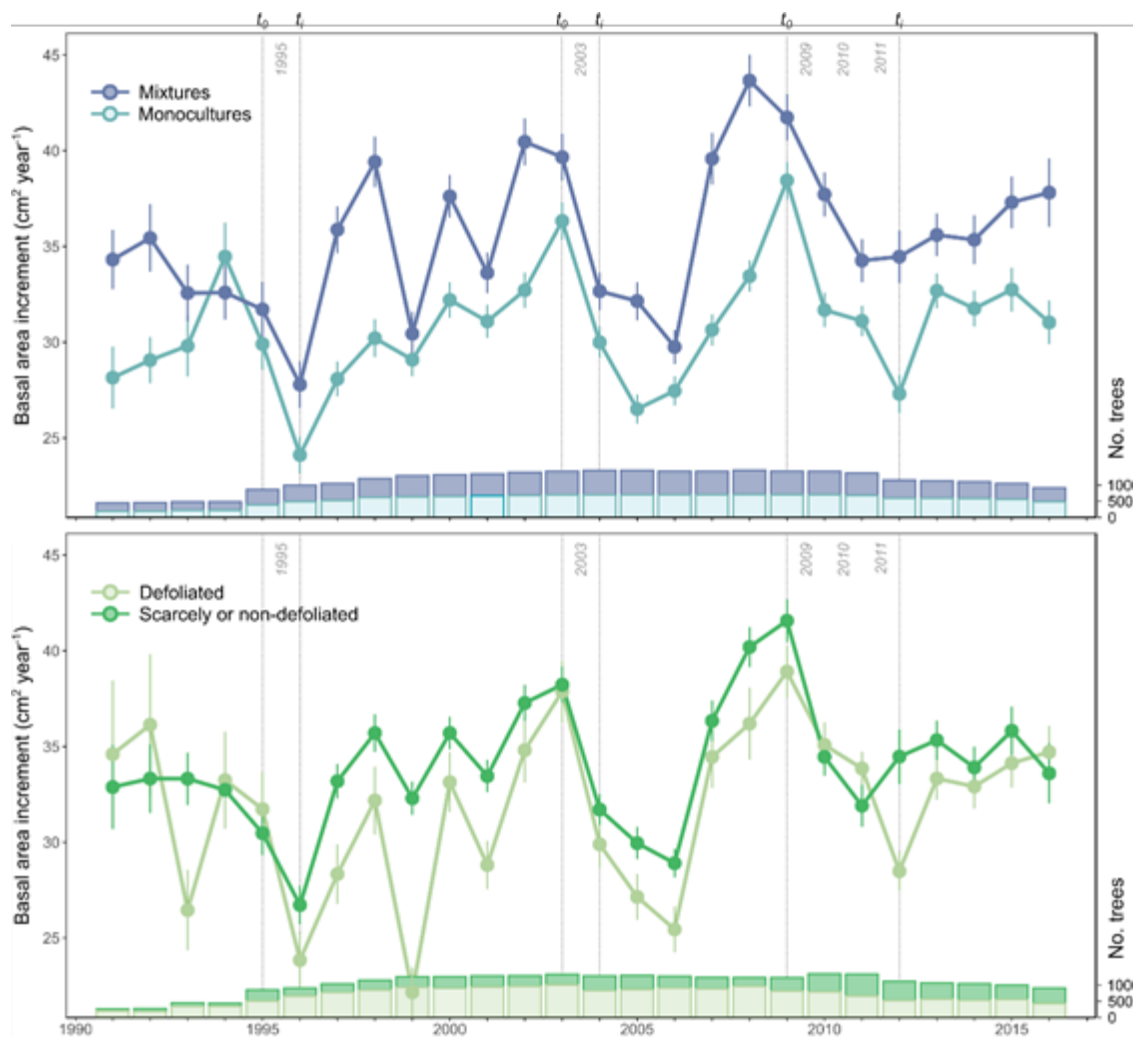


Figure A2. Basal area increment for trees in mixtures and monocultures (top) and for defoliated and non-defoliated trees (bottom). Values are means with standard errors (left y axis), and the bars show the sample depth, i.e., the annual number of assessed trees (right y axis). Vertical dotted lines encompass the immediate effect of the drought event; t_0 and t_1 correspond to the time immediately before and immediately after the main disturbance effect. Mixtures are stands composed of two or more tree species, and trees were considered defoliated when their defoliation was higher than 25% at time t_0 .