



CO₂ fertilization, transpiration deficit and vegetation period drive the response of mixed broadleaved forests to a changing climate in Wallonia

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Received: 5 December 2019 / Accepted: 19 May 2020
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Abstract

• **Key message** The change in forest productivity was simulated in six stands in Wallonia (Belgium) following different climate scenarios using a process-based and spatially explicit tree growth model. Simulations revealed a strong and positive impact of the CO₂ fertilization while the negative effect of the transpiration deficit was compensated by longer vegetation periods. The site modulated significantly the forest productivity, mainly through the stand and soil characteristics.

• **Context** Forest net primary production (NPP) reflects forest vitality and is likely to be affected by climate change.

• **Aims** Simulating the impact of changing environmental conditions on NPP and two of its main drivers (transpiration deficit and vegetation period) in six Belgian stands and decomposing the site effect.

• **Methods** Based on the tree growth model HETEROFOR, simulations were performed for each stand between 2011 and 2100 using three climate scenarios and two CO₂ modalities (constant vs time dependent). Then, the climate conditions, soils and stands were interchanged to decompose the site effect in these three components.

Handling Editor: Céline Meredieu

Contributions of the co-authors Conceptualization: Louis DE WERGIFOSSE, Mathieu JONARD; Methodology: Louis DE WERGIFOSSE, Mathieu JONARD; Resources: Steven CALUWAERTS, Lesley DE CRUZ, Rozemien DE TROCH, Bert VAN SCHAEYBROECK; Writing – original draft: Louis DE WERGIFOSSE; Writing – review & editing: Louis DE WERGIFOSSE, Frédéric ANDRE, Hugues GOOSSE, Bert VAN SCHAEYBROECK, Mathieu JONARD; Supervision: Hugues GOOSSE, Mathieu JONARD

This article is part of the topical collection on *Mensuration and modelling for forestry in a changing environment*

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• **Results** In a changing climate with constant atmospheric CO₂, NPP values remained constant due to a compensation of the negative effect of increased transpiration deficit by a positive impact of longer vegetation periods. With time-dependent atmospheric CO₂, NPP substantially increased, especially for the scenarios with higher greenhouse gas (GHG) emissions. For both atmospheric CO₂ modalities, the site characteristics modulated the temporal trends and accounted in total for 56 to 73% of the variability.

• **Conclusion** Long-term changes in NPP were primarily driven by CO₂ fertilization, reinforced transpiration deficit, longer vegetation periods and the site characteristics.

Keywords Net primary production · Water stress · Vegetation period · Process-based modelling · Climate change · Climate projections · Site effect

1 Introduction

Forests affect the climate in various and complex ways, through biophysical and biogeochemical effects. They can have a warming or a cooling effect depending on the way they modify albedo and evapotranspiration compared with other land covers (Bonan 2008; Stocker et al. 2013). In addition, forest ecosystems decrease the concentration of atmospheric carbon dioxide (CO₂) by carbon storage in the soil and in tree biomass (Myhre et al. 2013; Le Quéré et al. 2018). On the other hand, most of the processes involved in forest ecosystem functioning are climate sensitive (Parmesan and Yohe 2003; Kint et al. 2012; Charru et al. 2017). Climate changes could therefore seriously affect forest dynamics and the provision of ecosystem services (Temperli et al. 2012; Mina et al. 2017) that in turn affect climate (Seidl et al. 2014; Thom et al. 2017).

Many environmental manipulation experiments and monitoring studies have highlighted the effects of atmospheric CO₂ concentration, air temperature and soil water availability on forest net primary production (NPP). The fertilizing effect of atmospheric CO₂ was pointed out from free-air or chamber CO₂ enrichment experiments (Ainsworth and Long 2005; Ainsworth and Rogers 2007; Thompson et al. 2017). Norby et al. (2005) found that NPP increased by 20–25% when the CO₂ level was elevated to 550 ppm. On the long run, however, this increase was constrained by nutrient availability (Norby et al. 2010; Warren et al. 2015).

Furthermore, global remote sensing and local observational studies have shown that the increase in air temperature tends to advance the budburst date and therefore lengthens the vegetation period (Menzel et al. 2006; Jeong et al. 2011; Richardson et al. 2013; Park et al. 2016; Flynn and Wolkovich 2018) and favours NPP (Baldocchi 2008; Dragoni et al. 2011; Richardson et al. 2013; Fu et al. 2017). Moreover, respiration and photosynthesis, which have an opposite effect on biomass production, are both stimulated by warmer temperatures (Zhang et al. 2017).

Concerning water availability, it is well known that soil water deficit during the vegetation period triggers stomatal closure and reduces carbon assimilation. In addition, it reduces the mineralization, uptake and transport of nutrients (Bréda et al.

2006; Lisar et al. 2012; Osakabe et al. 2014). Syntheses and meta-analyses of rainfall experiments generally report decreases in photosynthesis, NPP, aboveground biomass and soil respiration (Wu et al. 2011; Paschalis et al., 2020). During prolonged water stress periods, tree mortality may occur due to hydraulic failure or carbon starvation (McDowell et al. 2008; Adams et al. 2017). For instance, a particularly drastic rainfall exclusion experiment conducted during a 5-year period in a Mediterranean broadleaf forest (*Q. ilex*, *A. unedo* and *P. latifolia*) led to a 15% decrease in soil water content, lowered the aboveground biomass production by 83% and increased mortality rate by 46% (Ogaya and Peñuelas 2007). Similarly, different studies have highlighted the same trends but with a lower effect during the 2003 drought (Ciais et al. 2005; Bréda et al. 2006; Granier et al. 2007).

The Intergovernmental Panel on Climate Change (IPCC) has adopted different greenhouse gas (GHG) emission scenarios called Representative Concentration Pathway (RCPs). Two commonly used scenarios are RCP4.5 and RCP8.5 and feature CO₂ concentrations of 540 and 940 ppm in 2100, respectively. Regarding Atlantic Europe (see Fig. 1 in Jacob et al. 2014), the climate projections for the two abovementioned scenarios at the end of the twenty-first century are characterized by an increase in air temperature (between + 1.3 °C and + 4.2 °C), changes in annual precipitation (− 1% to + 9%), in high-temperature extremes, in drought events and by a decrease in summer precipitation (− 5 to − 25%) compared with the 1971–2000 period (Jacob et al. 2014; Kovats et al. 2014; Jacob et al. 2018).

The projected climate changes are likely to alter the forest dynamics (Lindner et al. 2014). However, the resulting trend is difficult to estimate due to the opposite and interacting effects of climate on the processes regulating forest productivity. To estimate tree growth in unprecedented conditions, process-based models (PBM), which integrate knowledge from in-situ experiments, are recommended since they allow the integration of a wide range of effects (Pretzsch et al. 2015). However, the future forest evolution will not be uniform but is more likely to be site dependent. Indeed, the different components of the site effect—climate, soil and stand—can modify the forest response to changing

conditions (Holdridge 1967; Tucker et al. 2008; Steenberg et al. 2015) and therefore, PBM must account for them.

The response of a given tree species to climate change depends on the local climate (first component of the site effect). For sites at the upper limit of the temperature distribution range of a tree species, an increase in temperature would be detrimental for the development of this tree species while it could be positive in colder sites. The same reasoning also holds for a rainfall reduction, which could induce water stress more frequently on drier sites but could be beneficial on wetter ones. In Wallonia, an increase in temperature of 2 °C would confine European beech (*Fagus Sylvatica* (L.)) in its tolerance limits while sessile oak (*Quercus petraea* (Matt.) Liebl.) would remain in optimal growing conditions (Petit et al. 2017). The climate change effect can then be modulated by the soil properties. Indeed, greater soil depth and water holding capacity decrease the negative impact of drought events on NPP (Phillips et al. 2016). Finally, the stand characteristics generate differences in the forest response to climate change. Different effects constitute the stand effect: the tree species identity and diversity and the stand structure and density. The tree species identity effect simply depicts that all tree species do not exhibit the same functional traits such as phenological timing (Vitasse et al. 2009; Cole and Sheldon 2017) or drought sensitivity (Leuzinger et al. 2005; Scherrer et al. 2011). Consequently, they display different phenological and stomatal responses to a rise of temperature (Primack et al. 2009) and a change in soil water content or in CO₂ levels (Medlyn et al. 2001; Jonard et al. 2011; Raftoyannis and Radoglou 2002). Additionally, when these tree species coexist in the same stand, the response to climate change is even more difficult to predict since it can be affected by complementarity, facilitation and selection effects (Grossiord 2019; Bello et al. 2019a). For instance, Anderegg et al. (2018) observed that mixing species with a high diversity of hydraulic traits decreases their sensitivity to drought. On the other hand, an intensive water use by some tree species mixtures could lead more rapidly to water stress (Pretzsch and Biber 2016). The stand structure modifies the response to climate change since trees respond differently depending on their size, age or social status. Dominant trees seem to be more sensitive to climatic stress than dominated ones, which can be explained by a higher vulnerability to hydraulic stress (McDowell and Allen 2015) and a stronger exposition to atmospheric conditions (Bennett et al. 2015). When soil water availability decreases, small trees keep their stomata open for longer since the position of their crown within the canopy limits the evaporative demand (Carl et al. 2018). Finally, tree density also affects the stand response to climate change as it is positively related to stand leaf area index and, consequently, to evapotranspiration (Bello et al. 2019b). During drought events, thinned broadleaved stands generally exhibit a lower growth decrease due to reduced competition for water among remaining trees (Sohn et al. 2016). Understanding the effect of stand

characteristics on forest response to climate change is essential since the forester can adapt it while the adaptability of the soil is much more limited and is practically inapplicable for the climate. In conclusion, sites subject to similar changes in climate conditions can display very different responses due to their climate, soil and stand characteristics. This was already pointed out based on observations by Boisvenue and Running (2006) and can be found in simulation studies (Reyer 2015).

In order to produce realistic projections of NPP for the twenty-first century, one must take into account the future climate under various GHG emission scenarios, the soil properties and the stand characteristics. Yet, most of the currently existing PBM are stand-scale models accounting for the climate and soil effects but only partly integrating the spatial and structural complexity of the stand. However, structurally complex stands (uneven aged and mixed) tend to be favoured by the foresters in order to improve the resilience of their forests (Bauhus et al. 2013; DeRose and Long 2014). To simulate correctly such stands, spatially explicit and individual-based approaches are required (Seidl et al. 2005).

In this study, we will address the question of how and to what extent changing climate and CO₂ conditions will impact forest productivity in six contrasting and structurally complex stands in Wallonia and assess how the site components and thinning operations modulate the response. To do so, we will use HETEROFOR (Jonard et al. 2020; de Wergifosse et al. 2020a), a process-based tree growth model running at the individual level with different climate projections based on three GHG emission scenarios.

Wallonia is within a climatic zone that deserves more studies on the impact of climate change on forests since this effect is quite uncertain there for several reasons. Under the current climate conditions, Wallonia is located at the transition between areas where forest growth is limited by temperature, and consequently by the length of the growing period, in the North and by water availability in the South (Bastrup-Birk et al. 2016). In the future, warmer temperatures are expected all over Europe, a rainfall increase in the Northern temperature-limited areas and inversely a precipitation decrease in the Southern water-limited areas (IPCC 2013; Kovats et al. 2014). Therefore, while most simulation studies agree that forest productivity should increase in Boreal forests and decrease or remain constant in Mediterranean area (Reyer et al. 2014; Reyser 2015), to what extent Walloon forest productivity will be constrained by water availability, on average and during extreme events, is not a consensual issue. In addition, an increased water stress could be partly compensated by a longer vegetation period in the future.

More precisely, the objectives of the paper are

- I. To simulate the temporal changes in the net primary production of six broadleaved stands in Wallonia (Belgium) and in two of its main drivers

(transpiration deficit and vegetation period) under various GHG scenarios.

- II. To differentiate the long-term trend from the inter-annual NPP variations and to evaluate the part of the NPP variability explained by transpiration deficit, vegetation period and atmospheric CO₂ concentration.
- III. To assess to which extent these temporal trends are modulated by the site and how thinning affects transpiration deficit.
- IV. To decompose the site effect in its three main components (climate, soil and stand) and see how they are accounted for by transpiration deficit and vegetation period.

2 Material and methods

2.1 Site description

For the simulation study, six long-term monitoring plots installed in sessile oak (*Quercus petraea* (Matt.) Liebl.) and European beech (*Fagus sylvatica* (L.)) stands were selected as case studies representative of the broadleaved forest in Wallonia (Belgium). Three plots are located in an experimental site in Baileux (50° 01' N, 4° 24' E) and have been monitored since 2001. The three other plots are part of the level II network of ICP Forests since 1998 (Ferretti and Fischer 2013) and are located in Louvain-la-Neuve (50° 41' N, 4° 36' E), Chimay (50° 07' N, 5° 34' E) and Virton (49° 32' N, 5° 34' E).

2.1.1 Stand characteristics

The three plots in Baileux were installed to study how species mixtures influence the forest ecosystem functioning (Jonard et al. 2006, 2007, 2008; André et al. 2008a, 2008b, 2010, 2011). Two are located in nearly monospecific stands dominated either by sessile oak (hereafter called Baileux-oak) or by European beech (Baileux-beech) and the third one is in a balanced mixture of both tree species (Baileux-mixed) (Table 1). The stand of Chimay originates from coppice-with-standards and is dominated by mature sessile oaks with a hornbeam understory. In Louvain-la-Neuve and Virton, European beech is the main tree species and is mixed with oaks. In Virton, other broadleaved species (maple, wild cherry, ash, hornbeam) are also present. All these stands cover a wide range in tree size (girth in 1999 or 2001: from 22.6 cm for hornbeam in Baileux-mixed to 190 cm for sessile oak in Virton), in stand density (basal area in 1999 or 2001: from 18.4 to 30.0 m² ha⁻¹) and in leaf area index (LAI) with values extending from 3.96 to 6.93 m² m⁻². Except for the Louvain-la-Neuve plot installed in an old even-aged beech forest, the

study stands display complex structure in terms of species composition and tree age (Table 1).

2.1.2 Soil properties

The soils in Baileux and Chimay are cambisols with moder humus (FAO soil taxonomy) developed in a bedrock of sandstone and shales mixed with loess deposits while the soil in Louvain-la-Neuve is an abruptic luvisol with moder humus formed in loamy loess deposits from the interglacial period. Finally, the soil of Virton is a calcareous cambisol with mull humus; it originates from the weathering of a hard limestone bedrock (Table 2).

This large range of soils is reflected in the soil texture. According to the USDA taxonomy, the soil of Baileux is silty clay loam and that of Chimay is intermediate between silty clay loam and clay loam. The soil in Louvain-la-Neuve is silty loam due to its high silt content (62–75%). The highest clay fraction was registered in Virton and it is therefore a clayey soil (Table 2). The soil texture influenced the soil hydraulic properties. In Baileux and Louvain-la-Neuve, the high silt content ensures good drainage. In Chimay, the presence of inflating clay favours the appearance of a perched water table near the surface during winter and drought cracks in the warm and dry period. In Virton, in spite of elevated clay content, the existence of faults in the bedrock enables an efficient drainage.

The stoniness varies a lot among plots. Baileux-beech, Baileux-mixed and Virton have the higher coarse fraction (> 50% in the deep horizons) while the soil in Louvain-la-Neuve contains hardly any large stones. The coarse fraction in the soils of Baileux-oak and Chimay is intermediate (between 30 and 45% at the bottom of the profile). These differences in soil texture and coarse fraction among sites lead to a great diversity of extractable water reserve on a 1.6-m depth. For example, the extractable water reserve in Louvain-la-Neuve is almost three times greater than that of Baileux-mixed and Virton (Table 2). A same soil depth of 1.6 m was retained for all site as it allows to account for most (if not all) the rooting zone and for the sake of comparability. The impact of using a same depth for all sites is limited since water uptake only occurs in the horizon where roots are present. In addition, the lower horizons of some sites are very stony and therefore the associated extractable water is limited.

2.1.3 Climate

Although entire Belgium being characterized by the same climate type (temperate maritime), the four sites of our study are all located in different bioclimatic zones (Van der Perre et al. 2015), which highlights their climate diversity (Table 2). Louvain-la-Neuve is characterized by the warmest (11.0 °C) and driest (818 mm) climate. Despite their proximity, Baileux

Table 1 Stand characteristics for the main tree species and for the whole stands

Stand inventory year (area)	Tree species	Tree density (N ha ⁻¹)	Basal area (m ² ha ⁻¹)	C ₁₃₀ (cm)	Dominant height (m)	LAI (m ² m ⁻²)
Baileux-oak 2001 (0.9 ha)	<i>Quercus petraea</i>	187	16.2	100.6 (26.5)	21.9	
	<i>Fagus sylvatica</i>	118	4.0	46.4 (35.6)	15.5	
	<i>Carpinus betulus</i>	152	1.3	31.4 (11.4)	11.6	
	Total	468	21.6	63.7 (40.4)	22.2	4.17
Baileux-beech 2001 (1.4 ha)	<i>Quercus petraea</i>	72	6.4	103.3 (18.1)	23.0	
	<i>Fagus sylvatica</i>	217	16.5	87.5 (41.5)	25.0	
	Total	297	23.1	90.3 (38.5)	24.8	4.86
Baileux-mixed 2001 (1.8 ha)	<i>Quercus petraea</i>	118	12.9	115.5 (21.0)	4.5	
	<i>Fagus sylvatica</i>	352	17.0	91.2 (39.3)	25.7	
	<i>Carpinus</i>	9	0.1	22.6 (17.3)	9.4	
	Total	484	30.0	101.2 (42.0)	25.9	5.99
Chimay 1999 (1.3 ha)	<i>Quercus petraea</i>	63	13.1	158.7 (35.0)	20.4	
	<i>Carpinus betulus</i>	634	5.3	30.5 (10.8)	15.8	
	Total	697	18.4	42.4 (40.1)	19.2	3.96
Louvain-la-Neuve 1999 (1.1 ha)	<i>Quercus petraea</i>	21	4.7	165.9 (23.0)	30.9	
	<i>Fagus sylvatica</i>	87	24.6	179.1 (53.6)	32.1	
	Total	108	29.4	176.6 (49.6)	32.9	6.34
Virton 1999 (1.4 ha)	<i>Quercus petraea</i>	5	1.3	190.0 (10.0)	24.1	
	<i>Fagus sylvatica</i>	340	16.8	70.9 (31.7)	24.0	
	<i>Carpinus betulus</i>	22	0.4	48.4 (15.4)	14.524.0	
	Total	425	23.3	73.6 (36.0)		6.93

Tree density is the number of trees per ha, basal area is the sum of the trunk radial area at 130 cm height per ha, C₁₃₀ is the average trunk circumference (cm) at a height of 130 cm, dominant height is the average height of the 100 biggest trees per ha and LAI (leaf area index) is the sum of tree leaf areas expressed by unit ground area

and Chimay display differences in terms of annual rainfall with 1075 mm in Baileux and 940 mm in Chimay probably due to the more elevated location of Baileux (between 305 and 312 m a.s.l.) than Chimay (260 m a.s.l.). However, yearly average temperatures are similar in both locations (9.8 °C in Baileux and 9.7 °C in Chimay). Finally, Virton features high precipitation values (1060 mm) and an intermediate yearly mean temperature of 9.9 °C (Table 2). Reference crop evapotranspiration was calculated for each site according to the FAO method (Allen et al. 1998) and showed a low variability

(between 712 and 745 mm year⁻¹) that can mainly be attributed to air temperature differences.

2.2 Simulation experiments

2.2.1 Model description and performances

For the simulations, we used the individual-based, spatially explicit and process-based model HETEROFOR that has been implemented in the Capsis simulator (Dufour-Kowalski et al.

Table 2 Soil and meteorological (2001–2016 period) characteristics of the different study sites

Stand	Location	Bioclimatic zone	Altitude (m)	Soil type	Soil texture (USDA)	Max extractable water over 1.6 m (mm)	Annual rainfall (mm)	Mean air temperature (°C)	Reference crop evapotranspiration (mm year ⁻¹)
Baileux (beech/mixed/oak)	50° 01' N, 4° 24' E	Basse et moyenne Ardenne	305-312	Cambisol	Silt (clay) loam	174/154/239	1075	9.8	712
Chimay	50° 06' N, 4° 16' E	Fagne, Famenne et Caletienne	260	Dystric Cambisol	(Silt) clay loam	205	940	9.7	723
Louvain-la-Neuve	50° 41' N, 4° 36' E	Hesbino-brabançon	130	Abruptic Luvisol	Silt loam	450	818	11.0	745
Virton	49° 31' N, 5° 34' E	Basse Lorraine	370	Calcaric Cambisol	Clay	167	1060	9.9	726

2012) and is especially convenient to simulate the evolution of structurally complex stands. Hereafter, we present a brief overview of the model functioning limited to the description of the options retained for the simulation experiments carried out in this study. For a more in-depth description, we refer the reader to Jonard et al. (2020) and de Wergifosse et al. (2020a).

To initialize the model, the user must provide different files: a tree species parameter file, an inventory (or stand) file with the tree coordinates and dimensions (tree circumference, total height, height to crown base, height of largest crown extension and crown radius in four cardinal directions), a soil file with the physical properties of each soil horizon (thickness, bulk density, coarse fraction, sand, silt, clay and organic carbon contents and fine root proportion) and a meteorology (or climate) file with hourly data for radiation, air temperature, precipitation, relative humidity and wind speed. After the initialization phase and at the end of each year, HETEROFOR calls the phenology routine that provides daily information concerning the foliage state for the coming year. From a fixed date, a sum of warm temperature is daily accumulated until reaching a threshold, which triggers the budburst and then, similarly, the progressive leaf expansion. From mid-summer, cold temperatures are accumulated until reaching a threshold, which triggers leaf yellowing occurring at a rate proportional to the photoperiod decrease. The leaf falling rate is calculated based on wind speed and accelerated in case of frost events. Phenology can be calculated at the species level or the individual scale to account for the extended vegetation period of understory trees. In this study, we chose to calculate phenology at the species level. Once phenology is fixed, HETEROFOR calculates the proportion of solar radiation intercepted by each tree using the SAMSARALIGHT library based on a ray tracing approach (Courbaud et al. 2003). From the photosynthetically active radiation (PAR) absorbed per unit leaf area and the soil water potential updated hourly with a water balance routine, the gross primary production (GPP) of each tree is estimated hourly with the photosynthesis model of the CASTANEA library (Farquhar et al. 1980; Dufrêne et al., 2005). The individual NPP is then obtained by using a NPP to GPP ratio to take the growth and maintenance respiration into account. NPP is first allocated to foliage and fine roots by ensuring a functional balance and then to structural components using allometric equations, which allows deriving tree dimensional growth. The water balance routine accounts for rainfall partitioning in throughfall, stemflow and interception (André et al. 2008a), for tree transpiration and evaporation from foliage, bark and soil using the Penman-Monteith equation (Monteith 1965), for root water uptake (Couvreur et al. 2012) and for soil water movements based on the Darcy law. This routine can be calculated at the stand or individual scale but calculation time considerably increases when the individual option is selected and consequently, we selected the stand scale in this study.

HETEROFOR was evaluated on the same sites as those used in this study. The evaluation of tree growth conducted in Jonard et al. (2020) demonstrated the model ability to reproduce size-growth relationships and individual radial growth. In the same study, the simulated GPP was related to the NPP reconstructed from tree growth measurement and this relationship displayed high Pearson's correlation coefficients (0.89 and 0.91 for sessile oak and European beech, respectively). Regarding water balance evaluated in de Wergifosse et al. (2020a), the model satisfactorily simulated the soil water content temporal dynamics (correlation coefficients between simulations and observations ranging from 0.83 to 0.95 according to the site) and the individual transpiration (0.85 and 0.89 for oak and beech, respectively). Finally, the budburst model previously described, a one-phase model based on the Uniforc model (Chuine 2000), which simulates the forcing period, has been chosen among two other budburst models (two-phase models accounting for the forcing and chilling periods) implemented in HETEROFOR as it reproduced best the inter-annual variability. With this budburst model, vegetation period was on average simulated with a RMSE of 6.7 days (unpublished data).

The parameters needed to initialize the model are those described in the two model description papers (Table 2 in Jonard et al. 2020 and Table 1 in de Wergifosse et al. 2020a). Only for Virton, a higher NPP to GPP ratio is used in the species parameter file to account for differences not considered by the model (probably due to a higher site fertility). This ratio was fixed to 0.6 and 0.75 for sessile oak and European beech, respectively. Yet, this parameterization difference is only applied in the first simulation experiment described below. Indeed, one of the objective of this first experiment is to estimate the future productivity of the site, for which as many site characteristics as possible must be integrated while the second simulations aimed at decomposing the site effects in its components without being affected by the parametrization.

2.2.2 First simulation experiment to highlight the climate change impact

One-year simulations were performed for different periods in order to assess the impact of climate change on stand NPP median value and variance, on transpiration deficit and on vegetation period (objectives I and II stated in Section 1) and to evaluate how site and thinning affected these changes (objective III). More specifically, each year, a new simulation was launched starting from the same initial stand. Stand characteristics were therefore reinitialized each year keeping thereby the focus on the climate impact, in contrast to multi-year simulations which could have given rise to diverging stand characteristics with time. Climate projections generated according to three Radiative Concentration Pathway (RCP)

scenarios (see below) were used to run simulations on the 2011–2100 period while the 1976–2005 period (called “historical” period) was used as reference for comparisons with RCP scenarios.

One of the major uncertainties when simulating long-term forest productivity is whether or not the positive response of forest to rising CO₂ concentration can persist. Indeed, it has been shown that the induced productivity gain may progressively be reduced when other factors such as nutrient availability become limiting (Körner 2006; Norby et al. 2010). In order to cover the range of possible tree responses, from a perfect acclimation to rising atmospheric CO₂ to no acclimation at all, the set of simulations was launched considering either a constant atmospheric CO₂ concentration (380 ppm) or time-dependent CO₂ concentrations corresponding to the RCP scenarios (Reyer et al. 2014). The first case can be seen as a response to increasing CO₂ concentration totally constrained by other limiting factors and the second as never constrained. Moreover, holding CO₂ concentration constant allowed us to have a better insight into the other climate effects.

The two simulation types were also run for each monitoring plot after applying a virtual thinning to reduce stand basal area by 25% and test the immediate thinning impact. The selection of thinned trees was made among the pool of trees that were effectively cut in each plot during the monitoring period. When the past thinning operations were insufficient to reach 25%, additional trees were randomly selected and removed.

2.2.3 Second simulation experiment to highlight and decompose the site effect

To further investigate the site effect on the NPP variability (objective IV stated in Section 1), a similar set of 1-year simulations was ran for the historical period (1976–2005) by combining the climate, soil and stand input files of all the monitoring plots according to a full factorial design (6 soil types × 6 stands × 4 climates × 30 years). The simulations were performed for a constant atmospheric CO₂ concentration in order to limit the number of variation factors. Then, the simulations were repeated for the 2071–2100 period considering the RCP8.5 scenario to test whether the NPP variance decomposition is affected by climate change.

2.2.4 Climate projections

As a basis, the climate projections of the global climate model (GCM) CNRM-CM5 were used here. These global simulations were also included in the Coupled Model Intercomparison Project (CMIP5) on which the IPCC bases most of its conclusions (Fifth Assessment Report: IPCC 2013; IPCC special report on 1.5 C: Masson-Delmotte 2018).

However, the horizontal resolution of CNRM-CM5 is 1.4° (≈ 155 km), which did not allow us to make any distinctions between our study plots. In a first step, the CNRM-CM5 projections were therefore downscaled over the European domain using the Regional Climate Model (RCM) ALARO-0 (Giot et al. 2016; Termonia et al. 2018) following the guidelines of the Coordinated Regional Downscaling Experiment (CORDEX; Giorgi et al. 2009; Jacob et al. 2014). This dynamic downscaling consisted in using ALARO-0 over 50-km resolution areas forced at their boundaries by projections of CNRM-CM5. In a second downscaling step, the simulations over Europe with 50-km resolution were downscaled to a 4-km resolution over Belgium (Rummukainen 2010).

The meteorological variables that served as input for HETEROFOR include hourly values of the longwave and shortwave radiations, air temperature, surface temperature, rainfall, specific humidity and wind speed. Finally, relative humidity was calculated based on temperature, specific humidity and atmospheric pressure. All values were taken at the grid points closest to the four sites for the historical period (1976–2005) and for the 2011–2100 period according to three RCP scenarios: RCP2.6, RCP4.5, RCP8.5. The scenario names depict the increase in radiative forcing in 2100 relative to pre-industrial levels (+ 2.6 W m⁻², + 4.5 W m⁻², + 8.5 W m⁻²). The climate projections should be considered as sensitivity experiments. In other words, the climate changes rather than the absolute climate values are of importance as the model climatology (during the historical period) is known to differ from the observed one (Maraun and Widmann 2018). However, for our case, there were important positive model biases in rainfall ranging from 7 to 35% when compared with the observed values at the considered sites. A bias correction was therefore performed (Maraun and Widmann 2018). More specifically, for air and soil temperatures, data were corrected according to

$$x_{\text{corr}_t} = x_{\text{simul}_t} + \left(\overline{x_{\text{obs}}} - \overline{x_{\text{simul}}} \right) \quad (1)$$

with

x_{corr_t} , the corrected value of a variable at time t

x_{simul_t} , the variable simulated by the regional model at time t

$\overline{x_{\text{obs}}}$ and $\overline{x_{\text{simul}}}$, the average observed and simulated values for the period 2001–2016.

This method is, however, not suitable for variables which cannot take negative values. For these variables (radiation, rainfall, relative humidity and wind speeds), data were corrected using a multiplicative scaling

$$x_{\text{corr}_t} = x_{\text{simul}_t} \frac{\overline{x_{\text{obs}}}}{\overline{x_{\text{simul}}}} \quad (2)$$

The same correction was applied to the three RCP scenarios using $\overline{x_{\text{obs}}}$ and $\overline{x_{\text{simul}}}$ based on the period 2001–2016. The average corrected mean air temperature, rainfall and reference evapotranspiration are presented in Table 3 for the three RCP

scenarios during the 2071–2100 period and also during the historical period.

2.2.5 Model simulation analysis

The HETEROFOR model generates many fluxes and stocks of carbon and water as outputs. For this study, we focus on the actual and potential tree transpiration (obtained without considering any limitation from soil water) to determine the transpiration deficit, the daily foliage status of each tree species to calculate the vegetation period length and the yearly NPP to characterize forest productivity (de Wergifosse et al. 2020b).

From the daily foliage status, the yearly vegetation period length was defined as the number of days between the day the green leaf proportion reaches 50% (budburst period) until the day it drops below this threshold (yellowing and then falling periods). Annual stand NPP values (gC m^{-2}) were simply the sum of individual tree NPP (gC) divided by the stand area (m^2), with NPP derived from GPP after accounting for the growth and maintenance respirations (see Jonard et al. 2020 for details). The annual transpiration deficit was calculated for each tree as the difference between actual and potential transpiration (in L). Then, individual transpiration deficits were summed and divided by the stand area to obtain a transpiration deficit in mm. As described in de Wergifosse et al. (2020a), the stomatal conductance is considered as decreasing exponentially with the soil water potential in the model. Therefore, this difference depicts the transpiration deficit induced by the soil water limitation. Using the vegetation period and the transpiration deficit is interesting since these variables are sufficiently integrative to summarize the model functioning but not too general so that we can disentangle the effect of two main mechanisms through which climate change affects forest ecosystems functioning (phenology and water).

In order to compare stand NPP, transpiration deficit and vegetation period (objective I) among RCP scenarios and time periods (1976–2005 for past climate and 2011–2040, 2041–2070 and 2071–2100 for the future climate), we used two different statistical tests to assess whether the distributions were significantly different. An unpaired Mann-Whitney test (Wilcoxon 1945) was performed when the two periods were not related (e.g. for the comparison of the 1976–2005 and 2041–2070), while a Wilcoxon signed-rank test (Wilcoxon 1945) was used when comparing RCP scenarios for a same period. These tests were chosen given the non-normality of the investigated variables. The Wilcoxon signed-rank test was also adopted to assess the effect of thinning on transpiration deficit. In order to test the equality of variance among distributions, a Levene test

Table 3 Mean annual rainfall, air temperature and reference crop evapotranspiration for the historical period (1976–2005) and the various RCP scenarios (2071–2100). Mean values for the vegetation period (fixed from the 1st of May to the 30th of September) are indicated between parentheses. For each site and climatic variable, same letters indicate that the scenarios are not statistically different (Student's *t* test)

Stand	Rainfall (mm)			Air temperature (°C)			Reference crop evapotranspiration (mm)				
	Historical (1976–2005)	RCP2.6 (2071–2100)	RCP4.5 (2071–2100)	RCP8.5 (2071–2100)	Historical (1976–2005)	RCP2.6 (2071–2100)	RCP4.5 (2071–2100)	RCP8.5 (2071–2100)	RCP4.5 (2071–2100)	RCP2.6 (2071–2100)	RCP8.5 (2071–2100)
Baileux	1075 ^A (449) ^A	1066 ^A (439) ^A	1145 ^B (431) ^A	1161 ^B (435) ^A	9.78 ^A (15.40) ^A	10.49 ^B (16.09) ^B	11.56 ^C (17.08) ^C	13.12 ^D (18.40) ^D	681.4 ^A (480.9) ^A	699.6 ^A (494.2) ^A	730.9 ^B (522.4) ^B
Chimay	940 ^{AB} (380) ^A	915 ^A (379) ^A	975 ^{BC} (366) ^A	995 ^C (372) ^A	9.74 ^A (15.37) ^A	10.48 ^B (16.06) ^B	11.55 ^C (17.04) ^C	13.10 ^D (18.35) ^D	689.1 ^A (485.2) ^A	706.6 ^A (498.5) ^A	739.3 ^B (527.2) ^B
Louvain-la-Neuve	818 ^A (354) ^A	799 ^A (341) ^A	868 ^B (352) ^A	901 ^B (360) ^A	10.99 ^A (16.71) ^A	11.67 ^B (17.37) ^B	12.75 ^C (18.37) ^C	14.30 ^D (19.68) ^D	716.0 ^A (502.0) ^A	729.9 ^A (513.2) ^{AB}	762.5 ^B (540.6) ^{BC}
Virton	1060 ^A (391) ^A	1013 ^A (381) ^A	1067 ^{AB} (345) ^B	1111 ^B (382) ^A	9.90 ^A (15.93) ^A	10.65 ^B (16.69) ^B	11.81 ^C (17.79) ^C	13.32 ^D (19.05) ^D	698.1 ^A (495.0) ^A	716.8 ^A (507.5) ^A	756.3 ^B (542.2) ^B
mean	958 ^A (394) ^A	948 ^A (385) ^A	1014 ^B (374) ^A	1042 ^B (387) ^A	10.11 ^A (15.85) ^A	10.82 ^B (16.55) ^B	11.92 ^C (17.57) ^C	13.46 ^D (18.87) ^D	696.2 ^A (490.8) ^A	713.2 ^A (490.8) ^A	747.3 ^B (533.1) ^B
											760.1 ^C (538.5) ^B
											767.1 ^B (541.9) ^B
											788.3 ^B (554.7) ^C
											784.2 ^B (556.1) ^B
											774.9 ^B (547.8) ^B

was performed as it is less sensitive to non-normality than other commonly used tests.

To differentiate the long-term effect of climate change on NPP from that of the inter-annual climate variability (objective II) while taking the site effect into account (objective III), a linear mixed model was fitted on the simulated stand NPPs of the first simulation experiment including both thinning modalities. For a same location, the thinned and unthinned stands were considered as two different sites in the linear mixed models. We have chosen to use linear mixed models to account for the correlation structure of the simulated dataset and to avoid an overparameterization of the model (for parsimony reasons). Some factors were important to consider to estimate their relative importance in explaining the NPP variability and to represent correctly the correlation structure of the data. However, we did not need to know accurately the value taken by each level of these factors, which, therefore, were considered as random and characterized with a limited number of parameters (one parameter per factor instead of one per factor level). In contrast, we wanted to accurately quantify the effects of other factors which were considered as fixed. For this reason, in the first mixed model, the temporal trend of each RCP scenario (time $\times$ scenario) is considered as a fixed effect and the site (site) and its effect on the temporal trend (site $\times$ time $\times$ scenario) as random factor effects. This model was applied for both atmospheric CO₂ modalities.

$$\text{NPP} \sim [\text{time} \times \text{scenario}]_{\text{fixed}} + [\text{site} + \text{site} \times \text{time} \times \text{scenario} + \epsilon]_{\text{random}} \quad (3)$$

The continuous variable characterizing the time effect is the number of years since 2011. In this way, no effect of the RCP scenario is considered in 2011, which allowed us to avoid considering the scenario as a main effect.

Besides, we adjusted another linear mixed model containing yearly vegetation period (VP), transpiration deficit (TD) and atmospheric CO₂ concentration (CO₂) as fixed effects in addition to the effects already considered in the previous model (Eq. (3)) in order to assess the extent to which these three variables accounted for the site effect, the long-term trend and the inter-annual variability:

$$\text{NPP} \sim [\text{time} \times \text{scenario} + \text{VP} + \text{TD} + \text{CO}_2]_{\text{fixed}} + [\text{site} + \text{site} \times \text{time} \times \text{scenario} + \epsilon]_{\text{random}} \quad (4)$$

This model was applied for both atmospheric CO₂ modalities, except that the atmospheric CO₂ concentration was logically not considered for the modality with constant atmospheric CO₂ concentration.

Using the outputs of the second simulation experiment, a linear mixed model was applied to decompose the site effect

in its climate, soil and stand components (objective IV). Three random factors were used to characterize the site components.

$$\text{NPP} \sim [\text{climate} + \text{soil} + \text{stand} + \epsilon]_{\text{random}} \quad (5)$$

Finally, to estimate how transpiration deficit and vegetation period accounted for the three components of the site effect, we fitted a linear mixed model containing these two drivers as fixed effects in addition to the effects considered in Eq. (5).

$$\text{NPP} \sim [\text{VP} + \text{TD}]_{\text{fixed}} + [\text{climate} + \text{soil} + \text{stand} + \epsilon]_{\text{random}} \quad (6)$$

For all the effects in the various models, the partial R^2 was calculated as the difference between the R^2 of the model with and without the considered effect. This method assumes that the effects are independent. As, in reality, this is not always the case, the sum of the partial R^2 can be lower than the R^2 of the full model. All the figures, statistical tests and linear mixed models were realized using R Studio software (RStudio Team 2015).

3 Results

3.1 Objective I: Climate change impact on NPP, transpiration deficit and vegetation period

Net primary production The differences in NPP between the RCP scenarios were generally non-significant when the atmospheric CO₂ concentration was kept constant. For this modality, the only significant difference with the historical period occurred between 2041 and 2070 for the RCP4.5 and 8.5 scenarios and remained limited: an increase of 3 and 5%, respectively (Fig. 1a). The site-by-site examination of the NPP projections revealed that the only sites with a significant positive effect of the RCP scenarios were Baileux-oak (RCP4.5 between 2071 and 2100) and Chimay (RCP4.5 and 8.5 for the 2041–2070 period and RCP8.5 during the 2071–2100 period) (Fig. 4).

For the simulations accounting for the time-dependent atmospheric CO₂, NPP increased significantly over time, especially for the scenarios with the higher CO₂ emission levels in 2100. Upon comparison with the historical period, NPP in 2071–2100 increased by 9%, 20% and 34% for RCP2.6, 4.5 and 8.5, respectively (Fig. 1b). The trends were similar for the different sites taken individually (Fig. 5).

The impact of climate change on NPP cannot be based solely on the change in its median value. The variability is a key component of the temporal evolution as well. However, as depicted by the boxplot width and whisker length of Fig. 1 and confirmed by the Levene tests, no consistent increase in NPP variability was observed in our simulations.

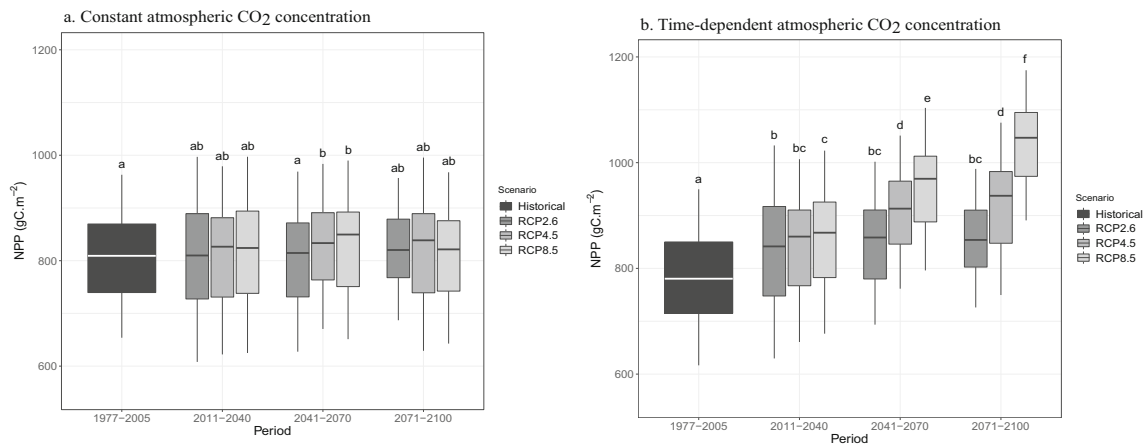


Fig. 1 NPP comparisons among RCP scenarios and with the historical period (1976–2005) for three 30-year periods considering all the sites together, with constant (a) and time-dependent (b) atmospheric CO₂ concentrations. The horizontal line corresponds to the median, the box ends indicate the upper and lower quartiles and the whiskers show the values

Transpiration deficit The results obtained for transpiration deficit were identical for the constant and time-dependent atmospheric CO₂ concentration since the way stomatal conductance for water was calculated does not account for the atmospheric CO₂ concentration effect. Therefore, only those of the constant atmospheric CO₂ were presented (Fig. 2a). Transpiration deficit did not change in comparison with the historical period during the 2011–2040 period. During the next period, the RCP2.6 and 8.5 scenarios displayed a significant increase in transpiration deficit of 24% and 19%, respectively. For this period, the only inter-scenario difference occurred between RCP2.6 and 4.5. During the last period, all scenarios were different from each other and the RCP4.5 and 8.5 scenarios showed respectively a 21% and 42% increase in transpiration deficit compared with the historical period (Fig. 2a).

The analysis of the temporal change in actual and potential transpiration enabled us to get a better insight in the origin of the transpiration deficit. It appeared that both variables were characterized by an increasing trend but with a more pronounced one for potential transpiration. The augmentation in actual transpiration ranged from 2.7 to 10.2% during the last period (2071–2100) while the rise in potential transpiration varied from 3.4 to 19.8% (Fig. 6).

Vegetation period As phenology is not CO₂ dependent in the HETEROFOR model, no distinction was made between atmospheric CO₂ modalities. Even though the length of the vegetation period differed between oak and beech (206 days for oak and 209 days for beech), its temporal change due to climate change was very similar for both tree species. The vegetation period length increased significantly with time for RCP4.5 and 8.5 while, for RCP2.6, it peaked between 2041 and 2070 before returning to the 2011–2040 level in 2071–2100. The increase of

above and below these quartiles within 1.5 interquartile. Common letters indicate that the distributions are non-significantly different according to a paired Wilcoxon signed-rank (between scenarios of the same period) or an unpaired Mann-Whitney (between scenarios of different periods) tests

the vegetation period length (calculated with regards to the last period) amounted to 0.6, 1.8 and 5.3 days per decade for RCP2.6, 4.5 and 8.5, respectively (Fig. 2 b and c).

3.2 Objective II: Long-term trend and inter-annual variations of NPP

When a constant atmospheric CO₂ concentration was considered for the model described by Eq. (3), no mean temporal trend in NPP was detected (time × scenario) though the random effect associated with this trend (site × time × scenario) explained 34% of the variability. This means that the temporal trend oscillated around 0, being slightly positive in some sites and slightly negative in others. The rest of the site effect accounted for 39% of the NPP variability and the unexplained variability amounted to 27% (Table 4 (a)).

For the simulations with changing atmospheric CO₂ concentrations, we observed a significant positive temporal trend dependent on both the RCP scenario (time × scenario) and on the site (site × time × scenario). These two effects accounted for 22% and 24% of the NPP variability, respectively. The remaining site effect explained 32% of the NPP variability while the unexplained variability was slightly lower than the simulations with constant CO₂, accounting for 23% of the NPP variability (Table 4 (b)).

3.3 Objective III: Influence of atmospheric CO₂ concentration, transpiration deficit, vegetation period, site and thinning on NPP

Relative importance of atmospheric CO₂ concentration, transpiration deficit, vegetation period and site in explaining NPP variability For both atmospheric CO₂ modalities, when

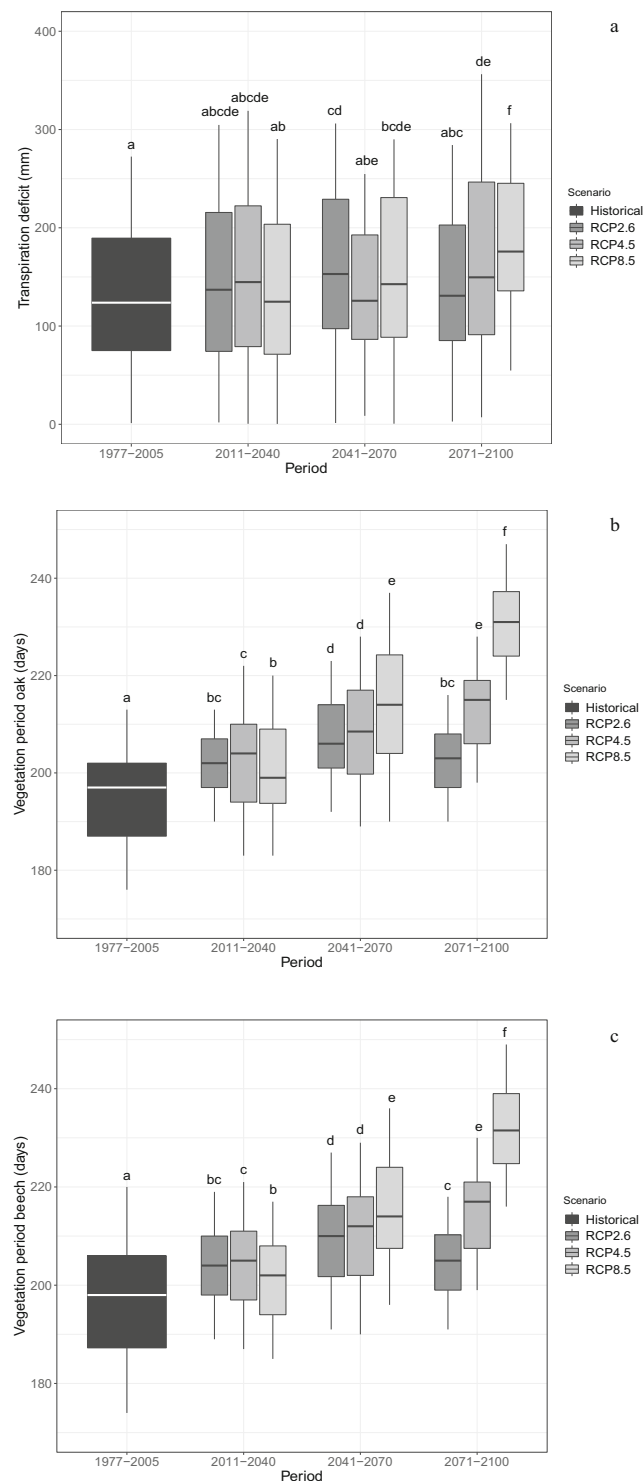


Fig. 2 Transpiration deficit (a), vegetation period of sessile oak (b) and European beech (c) comparisons among RCP scenarios and with the historical period (1976–2005) for three 30-year periods considering all the sites together, with constant atmospheric CO₂ concentrations. The horizontal line corresponds to the median, the box ends indicate the upper and lower quartiles and the whiskers show the values above and below these quartiles within 1.5 interquartile. Common letters indicate that the distributions are non-significantly different according to a paired Wilcoxon signed-rank (between scenarios of the same period) or an unpaired Mann-Whitney (between scenarios of different periods) tests

comparing the linear mixed models containing only the temporal trend and the site effect (Eq. (3)) with those including also transpiration deficit, vegetation period and atmospheric CO₂ concentration (Eq. (4)), one can observe that these variables explained the temporal trend (time $\times$ scenario) and its modulation by the site (site $\times$ time $\times$ scenario) and all the inter-annual variability (residuals). In addition, their inclusion slightly lowered the variability associated with the rest of the site effect. When atmospheric CO₂ concentration was held constant, the transpiration deficit effect was negative with a partial R^2 of 0.58 while the vegetation period effect was positive with a partial R^2 of 0.025 (Table 5 (a)). For the time-dependent atmospheric CO₂ simulations, the transpiration deficit and vegetation period effects had the same sign as for the constant atmospheric CO₂ modality but their partial R^2 was lower (0.43 and 0.016 respectively) since the atmospheric CO₂ concentration also explained a significant part of the variability (partial R^2 = 0.22, Table 5 (b)).

Thinning effect on transpiration deficit Transpiration deficit was much higher in beech dominated (between 205 and 267 mm) than in oak-dominated stands (between 75 and 104 mm) and this was observed after thinning as well (Fig. 3). Thinning significantly decreased transpiration deficit in all situations (P value < 0.001). For the historical period, RCP2.6, 4.5 and 8.5, the transpiration deficit in the thinned oak-dominated stands was 30, 34, 32 and 39 mm lower than in the unthinned ones (Fig. 3a) while in beech-dominated stands, this decrease amounted to 65, 82, 76 and 91 mm, respectively (Fig. 3b). The relative decrease was, however, more similar between the two tree species with a decrease between 35 and 40% for oak and between 32 and 34% for beech.

3.4 Objective IV: Decomposition of the site effect in its climate, soil and stand components

The second simulation experiment, aiming at decomposing the site effect in its climate, soil and stand components, was performed for two contrasted periods and RCP scenarios (i.e. the 1977–2005 historical period vs the 2071–2100 period for the RCP8.5 scenario). As the results were quite similar among periods, only the results for the historical period are presented. The stand and soil partial R^2 were close and amounted to 0.321 and 0.264, respectively, and were much higher than that of the climate effect (0.016) (Eq. (5)). Introducing the transpiration deficit and the vegetation period in the model (Eq. (6)) accounted for nearly the entire climate (94%) and soil (98%) effects but only partly for the stand effect (7%). The consideration of these drivers also strongly reduced the unexplained part of the variability (from 40 to 7%). The transpiration deficit had a negative effect while the

Table 4 Estimate, standard error, *P* value and partial R^2 of the parameters of the mixed linear model (Eq. (3): NPP~time*scenario + site + site*time*scenario) used to differentiate the temporal trend fromthe inter-annual variability in NPP (gC m^{-2}) for all sites, periods and RCP scenarios considering constant (a) and time-dependent (b) atmospheric CO_2 concentration

	Estimate	Standard error	<i>P</i> value	Partial R^2
a. Constant atmospheric CO_2 concentration				
Fixed effects				
Intercept	764.70	39.99	< .0001	/
Time $\times$ scenario [2.6, 4.5, 8.5]	[- 0.06, - 0.07, 0.06]	[0.07, 0.08, 0.08]	0.460	0.000
Random effects				
Site	0	138.13	/	0.392
Site $\times$ time $\times$ scenario [2.6, 4.5, 8.5]	0	[0.05, 0.15, 0.13]	/	0.336
Residuals	0	84.19	/	0.272
Total explained	/	/	/	0.728
b. Time-dependent atmospheric CO_2 concentration				
Fixed effects				
Intercept	777.24	41.38	< .0001	/
Time $\times$ scenario [2.6, 4.5, 8.5]	[0.32, 1.06, 2.52]	[0.08, 0.09, 0.10]	< .0001	0.216
Random effects				
Site	0	142.97	/	0.316
Site $\times$ time $\times$ scenario [2.6, 4.5, 8.5]	0	[0.10, 0.22, 0.27]	/	0.239
Residuals	0	85.84	/	0.229
Total explained	/	/	/	0.771

impact of vegetation period was positive, with a much higher partial R^2 for transpiration deficit (0.536) than for vegetation period (0.057) (Table 6).

4 Discussion

4.1 What are the possible evolutions of broadleaved forest NPP according to different climate projections?

At first glance, our results appear quite clear and easy to interpret. When the atmospheric CO_2 level was held constant, no long-term changes were observed but upon changing atmospheric CO_2 , NPP increased up to 34% for the 2071–2100 period. However, using a process-based model with many different outputs gave us the opportunity to understand more deeply the underlying mechanisms.

Based on the bias-corrected downscaled climate projections of Alaro-0 for our four sites in Wallonia, mean air temperature is expected to be significantly higher during the 2071–2100 period compared with the historical period (from 0.7 to 3.4 °C) while mean annual rainfall would remain stable or increase a bit. During the vegetation period, rainfall would slightly decrease but this decrease would be significant only for Virton under RCP4.5 scenario (Table 3). According to our simulations, these changing climate conditions would substantially increase the vegetation period (Fig. 2 b and c) since the budburst is triggered earlier when

late winter temperatures are warmer while leaf yellowing occurs later under warm conditions. The decrease of the vegetation period length between 2041–2070 and 2071–2100 for RCP2.6 scenario might look surprising but it is simply generated by the scenario that projects a temperature peak around the middle of the twenty-first century and a subsequent progressive decrease. Some limitations concerning the phenology date simulations are discussed hereafter. First, the budburst model is a one-phase model that only accounts for the accumulation of warm temperature to trigger budburst while it is commonly accepted that a chilling period is a prerequisite for the start of forcing period (corresponding to the endodormancy break) and then budburst. However, when no observations of endodormancy break are available and the species considered are not located at the margin of their species distribution area, one-phase models are often preferred to more complex ones (Chuine et al. 2016). In addition, our approach does not account for the impact of photoperiod on budburst, which can become significant when chilling requirements are not met (Vitasse and Basler 2013; Pletsers et al. 2015), the influence of late frost or water stress on the leaf development and senescence (Sanz-Perez and Castro-Diez 2010; Fu et al. 2014; Morin and Chuine 2014; Xie et al. 2018). However, as shown in the review of Piao et al. (2019), the modelling of these second order processes is extremely difficult and inaccurate because the interactions between these factors are still poorly known, observations are available only for a few

Table 5 Estimate, standard error, *P* value and partial R^2 of the parameters of the mixed linear model (Eq. (4): $\text{NPP} \sim \text{time} * \text{scenario} + \text{VP} + \text{TD} + \text{CO}_2 + \text{site} + \text{site} * \text{time} * \text{scenario}$) used to explain the NPP (gC m^{-2}) variability based on transpiration deficit, vegetation period and

CO_2 (only for time-dependent CO_2 modality) for all the sites, periods and RCP scenarios considering constant (a) and time-dependent (b) atmospheric CO_2 concentration

	Estimate	Standard error	<i>P</i> value	Partial R^2
a. Constant atmospheric CO_2 concentration				
Fixed effects				
Intercept	506.70	21.74	< .0001	/
Time $\times$ scenario [2.6, 4.5, 8.5]	[0.01, 0.04, 0.09]	[0.04, 0.05, 7.64]	0.748	0.000
Vegetation period	2.18	0.08	< .0001	0.025
Transpiration deficit	− 1.30	0.01	< .0001	0.582
Random effects				
Site	0	55.69	/	0.365
Site $\times$ time $\times$ scenario [2.6, 4.5, 8.5]	0	[0.05, 0.12, 26.5]	/	0.026
Residuals	0	39.54	/	0.002
Total explained	/	/	/	0.998
b. Time-dependent atmospheric CO_2 concentration				
Fixed effects				
Intercept	358.68	23.56	< .0001	/
Time $\times$ scenario [2.6, 4.5, 8.5]	[0.15, 0.56, 1.08]	[0.04, 0.07, 12.26]	0.310	0.001
Vegetation period	2.48	0.08	< .0001	0.016
Transpiration deficit	− 1.30	0.01	< .0001	0.432
CO_2 concentration	0.261	0.03	< .0001	0.220
Random effects				
Site	0	56.38	/	0.299
Site $\times$ time $\times$ scenario [2.6, 4.5, 8.5]	0	[0.05, 0.11, 42.5]	/	0.031
Residuals	0	42.69	/	0.001
Total explained	/	/	/	0.999

phenological stages and environmental modifying experiments have not been conducted to disentangle such a complexity.

In addition to the strong impact of climate change on the vegetation period, the model simulates that the transpiration deficit could be moderately reinforced through an in-

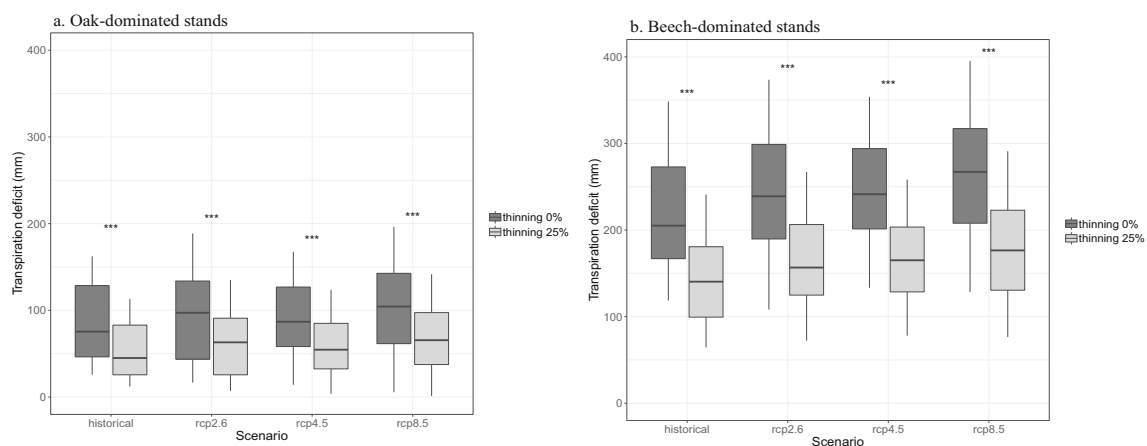


Fig. 3 Thinning effect on transpiration deficit for the historical period (1976–2005) and the three RCP scenarios (2011–2100) considering a constant atmospheric CO_2 concentration. Results are shown separately for oak-dominated stands (Baileux-oak and Chimay) (a) and beech-

dominated stands (Baileux-beech, Louvain-la-Neuve and Virton) (b). Significance of the Wilcoxon test evaluating the thinning effect by climate scenario is represented as NS (non-significant), * $p < 0.05$, ** $p < 0.01$ and *** $p < 0.001$

Table 6 Estimate, standard error, *P* value and partial R^2 of the parameters of (a) the mixed linear model (Eq. (5): NPP~stand + soil + climate) and (b) the mixed linear model (Eq. (6): NPP~VP + TD + stand + soil + climate) used to decompose the site effect in its climate, soil and stand components in order to explain the NPP (gC m^{-2}) variability for all the sites during the historical period, using simulations with constant atmospheric CO_2 concentration

	Estimate	Standard error	<i>P</i> value	Partial R^2
a. Historical period				
Random effects				
Stand	0	72.38	/	0.321
Soil	0	69.33	/	0.264
Climate	0	18.19	/	0.016
Residuals	0	82.57	/	0.397
Total explained	/	/	/	0.603
b. Historical period				
Fixed effects				
Intercept	305.11	39.94	< .0001	/
Transpiration deficit	- 1.30	0.014	< .0001	0.536
Vegetation period	3.45	0.067	< .0001	0.057
Random effects				
Stand	0	85.78	/	0.299
Soil	0	34.69	/	0.006
Climate	0	7.75	/	0.001
Residuals	0	46.04	/	0.072
Total explained	/	/	/	0.928

creased evapotranspiration (Fig. 2a). As the transpiration deficit was a stronger NPP driver than the vegetation period (Tables 5 and 6), their opposite effects on the long-term trends in NPP had more or less the same magnitude and were compensating. However, the long-term NPP evolution was slightly affected by the site: it tended to be slightly negative (positive) in sites with a low (high) soil holding capacity and for drought-sensitive (-tolerant) tree species such as beech (oak) (Fig. 4). Furthermore, by reducing the transpiration deficit, thinning contributed to make the climate change effect on NPP more positive. As the oak stomatal sensitivity to soil drying is lower than that of beech, the simulated impact of climate change was rather positive on oak and null on beech-dominated stands, which is consistent with simulation studies estimating that oak competitiveness could exceed that of beech under the projected future climate conditions in temperate European forests (Kint et al. 2012; Mette et al. 2013; Zimmermann et al. 2013; Rubio-Cuadrado et al. 2018).

With our simulations, we were unable to distinguish between the transpiration deficit under constant and time-dependent atmospheric CO_2 concentration since the water balance is calculated before photosynthesis in HETEROFOR and the stomatal conductance for water does not depend on atmospheric CO_2 concentration

contrary to that for CO_2 (Dufrêne et al., 2005; Jonard et al. 2020; de Wergifosse et al. 2020a). Therefore, our transpiration simulations are more reliable for the constant atmospheric CO_2 modality. For the time-dependent CO_2 modality, tree transpiration is probably slightly overestimated so that the increase in the transpiration deficit could still be lower than that simulated with HETEROFOR which is already limited. According to our simulations, water stress on Walloon broadleaved forests should not drastically increase in the future.

As stated in the description of the first simulation experiment (Section 2.2.2), the objective of running two similar sets of simulations with constant and changing atmospheric CO_2 concentrations was to define a possible range of NPP change depending on the way the fertilizing effect of CO_2 is constrained by other limiting factors. As soil water limitation was taken into account in the model, the more obvious constraint would come from the soil nutrient supply. The increased atmospheric CO_2 could potentially have no effect in sites where trees suffer from severe nutrient deficiencies. The CO_2 fertilization, on the other hand, would be manifested in full for stands with an optimal mineral nutrition (Oren et al. 2001; Fernandez-Martinez et al. 2014a). On average, this CO_2 fertilizing effect seems already constrained by nutrient availability since many European tree species, especially European beech and oak, are experiencing significant deterioration of their foliar nutrition (Jonard et al. 2015). Therefore, among our study sites, the plots in Chimay, Virton and Louvain-la-Neuve that already display some latent deficiency regarding P concentrations (Titeux et al. 2018) should behave closer to the simulations with constant CO_2 than the Baileux plots which present better foliar nutrition. On the other hand, one could also consider that a decreased soil water content would reduce nutrient availability and consequently NPP but this aspect is not taken into account in this study. However, as the simulated increase in transpiration deficit is limited, one can consider that the impact on nutrient availability would remain very low.

The dominant effect of the CO_2 fertilization in the long-term trend of forest productivity is consistent with similar studies. In his global review mainly focused on temperate and boreal forests in Europe and North America, Reyer (2015) showed that, for the simulation studies in which the atmospheric CO_2 levels were held constant, the simulated NPP change with regards to reference conditions varied between - 20 and + 33% for a median value of + 5%. When both climate change and atmospheric CO_2 rise were taken into account, most of the simulated biomass production increased relative to the historical period. In our simulations, when the atmospheric CO_2 was maintained constant, the NPP increase ranged from 0.1 to 5.0% (Fig. 1a), which is close to the value pointed out in the abovementioned review. When the atmospheric CO_2 concentration changed, the NPP

increase was between 7.8 and 34.2% (Fig. 1b), which is again in good agreement with Reyer (2015) that displayed a median value 20% higher than that of the historical period.

Fernandez-Martinez et al. (2014b) analysed an extensive global dataset and showed that NPP was mainly determined by water availability, warm period length and nitrogen deposition. These results, which come from temporally averaged measurements and therefore reflect spatial rather than temporal patterns, can be considered as a spatial corollary of our results that highlight the significance of the same variables or related ones.

We have mainly discussed here the average impact of climate change. However, many papers highlight the importance of extreme heat and drought waves on tree growth and mortality (Fuhrer et al. 2006; Lindner et al. 2010; Allen et al. 2010; Teskey et al. 2015). These extreme events are important because tree functioning is a complex set of non-linear mechanisms where threshold exceedance can generate feedbacks and totally deregulate their functioning (Thompson 2011; Reyer et al. 2015; D'Orangeville et al. 2018). In HETEROFOR, the leaf-level processes (photosynthesis, respiration and transpiration) are climate dependent and take the impact of heat or drought waves into account, especially on tree growth. In addition, as most processes in HETEROFOR are calculated at the hourly time scale, temperature peaks are not smoothed as in models working at the daily or monthly time scale. The impact of these extreme climate events is, however, only partly accounted for since mortality by hydraulic failure and leaf shedding is not considered. Furthermore, tree mortality driven by pests and diseases, which is often promoted by a succession of drought and heat waves (Allen et al. 2010) is not yet included in HETEROFOR. This could partly explain why we did not observe any changes in NPP variability in our simulations between the different scenarios and time periods. Moreover, as these elements are mostly detrimental, our simulation results should be seen as the upper estimates for NPP.

4.2 What can be learnt from the decomposition of the NPP variability?

The main originality of our study is the decomposition of the NPP variability, which allows estimating the relative importance of the temporal trend compared with the inter-annual variations and evaluating the extent to which site components (climate, soil and stand) could modulate the impact of climate change on NPP. The part of the NPP variability explained by the stand effect gives an idea of the leeway left to forest managers to adapt the forests to changing conditions. Furthermore, this is of primary

concern for forest managers because NPP can be considered as closely related to the timber volume under the hypothesis of allometry conservation and as a good proxy for forest health and the provision of most of the ecosystem services (e.g. Costanza et al., 1998; Dobbertin, 2005; Costanza et al., 2007; Van Oudenhoven et al., 2012; Vargas et al., 2019).

When the atmospheric CO₂ was kept constant, no overall temporal trend was observed but considering a trend randomly changing with the site explained 34% of the variability (Eq. (3) and Table 4 (a)). This random effect was ascribed to differences in soil water properties and in tree species sensitivity to drought and phenology since it almost totally disappeared when the transpiration deficit and the vegetation period were included in the linear mixed model (Eq. (4) and Table 5 (a)). These factors accounted also for some of the site effect that decreased from 39.2 to 36.5%. The remaining “unexplained” variability (27%) was mainly due to inter-annual climate variations since it totally vanished when the transpiration deficit and the vegetation period were added in the model (Tables 4 (a) and 5 (a)). Among these two drivers, the transpiration deficit had a much greater explanatory power than the vegetation period (partial R^2 of 0.582 vs 0.025).

Using a time-dependent atmospheric CO₂ concentration generated a strong temporal trend. This temporal trend accounted for 22% of the NPP variability while its modulation by the site explained another 24% (Eq. (3) and Table 4 (b)). The integration of the atmospheric CO₂ concentration, the transpiration deficit and the vegetation period in the linear mixed model made disappear the entire temporal trend and most of its variation among sites (3% remaining after the inclusion). The part of the variability explained by the atmospheric CO₂ concentration corresponded exactly to that associated with the temporal trend (22%) (Eq. (4) and Table 5 (b)). The site-dependent component of the trend was mainly ascribed to differences in transpiration deficit among sites with a minor role also played by the vegetation period. The rest of the NPP variability associated with the site amounted to 30%. As for the constant atmospheric CO₂ modality, we considered that the remaining “unexplained” variability (23%) was mainly due to inter-annual climate variations since it disappeared when the transpiration deficit and the vegetation period were added in the linear mixed model (Tables 4 (b) and 5 (b)). In this case, the transpiration deficit had also a much higher explanatory power than vegetation period (43% vs 2%).

Interchanging the climate, soil and stand files for the historical period under constant CO₂ concentration allowed us to get a deeper understanding of the site effect. According to Table 6 (a) (Eq. 5), when they were the only variables included, the stand and soil components had a

similar contribution in explaining the site effect (32 and 26%, respectively) while the part explained by differences in climate among sites was very low (1.6%). This was however not surprising as we examined a broad range of soils and stands but a much narrower range of climates. Anyway, integrating the transpiration deficit and the vegetation period in the linear mixed model explained most of the soil effect (which dropped to 0.6%) but only a little part of the stand effect, which remained at 30% (Eq. (6) and Table 6 (b)). These 30% represent the amount of freedom the forest managers have to influence the forest productivity under the current climate conditions. For the future, one must also consider the interaction between the site effect and the climate change (including atmospheric CO₂) whose relative importance in explaining the NPP variability is of the same order of magnitude than the site effect (Table 4). Foresters can also act on the transpiration deficit through tree species selection and thinning even if transpiration deficit is also strongly determined by climate conditions and soil water properties.

In all stands, thinning significantly decreased the transpiration deficit and this decrease was much more pronounced in beech-dominated stands. Still, the transpiration deficit levels before and after thinning were lower in oak-dominated than in beech-dominated stands (Fig. 3). This positive short-term effect of thinning on a stand response to drought was pointed out by various studies. For example, a Douglas-fir stand showed a decrease in evapotranspiration of 30 mm (17%) during the first year after thinning. This effect was progressively reduced during the next 4 years before evapotranspiration returned to its original level (Aussenac and Granier 1988). For broadleaved species, a meta-analysis highlighted the potential of thinning to mitigate growth reduction during drought events by increasing soil water availability (Sohn et al. 2016). As a result, thinning seems to be an interesting practice to reduce the projected increase in transpiration deficit and its detrimental effect on tree growth, especially for drought-sensitive tree species. However, one must keep in mind that thinning has a transitory effect and that its impact on drought resistance progressively decreases (Guillemot et al. 2015; Sohn et al. 2016). Thinning abruptly modifies stand characteristics and forest functioning due to tree removal. Then, the remaining trees react by expanding their crown and increasing their growth rate benefiting from the higher availability of resources per tree. With time, the openings in the canopy close and the effect of thinning decreases. In this study, we simulate the first year after the thinning when its effect is maximal and when the tree dimensions (especially the crown extension) are still those that characterize a stand with a higher density. Finally, in addition to thinning, some efforts to promote oak

regeneration could also be recommended to increase the stand resistance to drought as this tree species is more drought tolerant.

5 Conclusion

Understanding how NPP is going to be affected in the future due to environmental changes is crucial in order to create consistent climate change adaptation strategies and preserve the forest ecosystem services. This paper aimed at assessing, for six Belgian stands, the temporal change in NPP and in two of its main drivers: transpiration deficit and vegetation period length. Concomitantly, the influence of the CO₂ fertilization effect and the impact of thinning operations were evaluated. We did not detect any trend under the three contrasted GHG emission scenarios (RCP2.6, 4.5 and 8.5) when atmospheric CO₂ concentration was held constant but NPP showed a significant increase ranging from 9.4 to 34.2% for the time-dependent atmospheric CO₂ concentration. Behind the apparent lack of temporal trend in NPP for simulations with constant atmospheric CO₂ lies a compensatory effect of the transpiration deficit that slightly increased with time and had a pronounced negative effect on NPP and the vegetation period that became substantially longer but with a less marked impact on NPP. The site effect modulated these temporal trends and accounted for a substantial part of the NPP variability, which is encouraging for forest managers who have still a lot of possibilities to adapt their forest to changing conditions. Among others, thinning appeared very effective to decrease transpiration deficit, especially in beech-dominated stands. Forest practitioners could regularly decrease stand density or promote oak regeneration to limit the negative effect of the transpiration deficit. In the future, we plan to extend our methodology at the European scale to expand the validity of our results.

Acknowledgements We thank Rafiq Hamdi and Piet Termonia from Royal Meteorological Institute of Belgium for enabling the generation of the climate data.

Funding information This study was funded by FRIA (grant no. 1.E005.18).

Data availability The datasets generated during and/or analysed during the current study are available from the Zenodo repository <https://doi.org/10.5281/zenodo.3744345> and citable (de Wergifosse et al. 2020b).

Compliance with ethical standards

Conflict of interest The authors declare that they have no conflict of interest.

Annexes

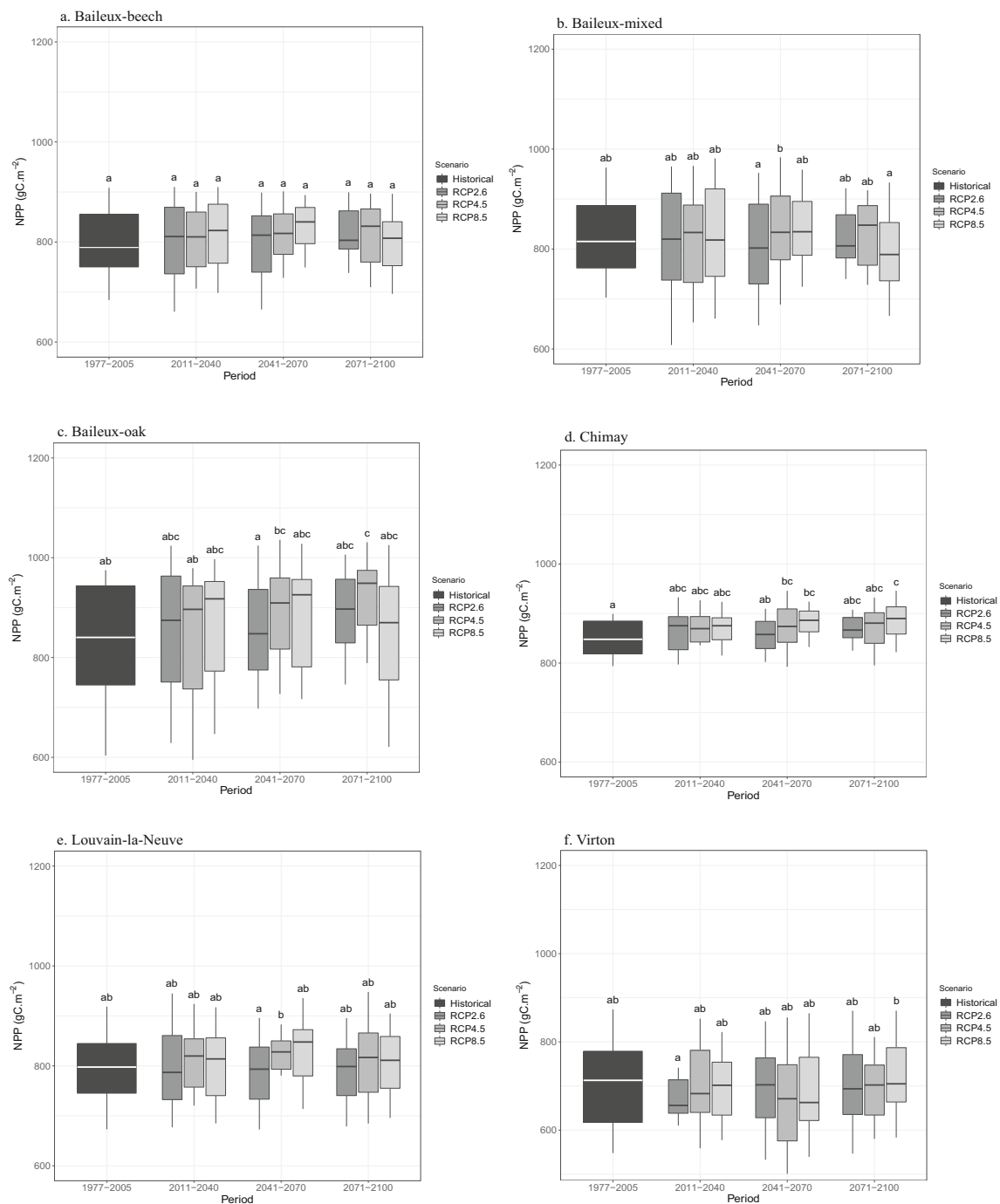


Fig. 4 NPP comparisons among RCP scenarios and with the historical period (1976–2005) for three 30-year periods in the different study sites (a–f) and with constant CO_2 atmospheric concentrations. The horizontal line corresponds to the median, the box ends indicate the upper and lower quartiles and the whiskers show the values above and below these

quartiles within 1.5 interquartile. Common letters indicate that the distributions are non-significantly different according to a paired Wilcoxon signed-rank (between scenarios of the same period) or an unpaired Mann-Whitney (between scenarios of different periods) tests

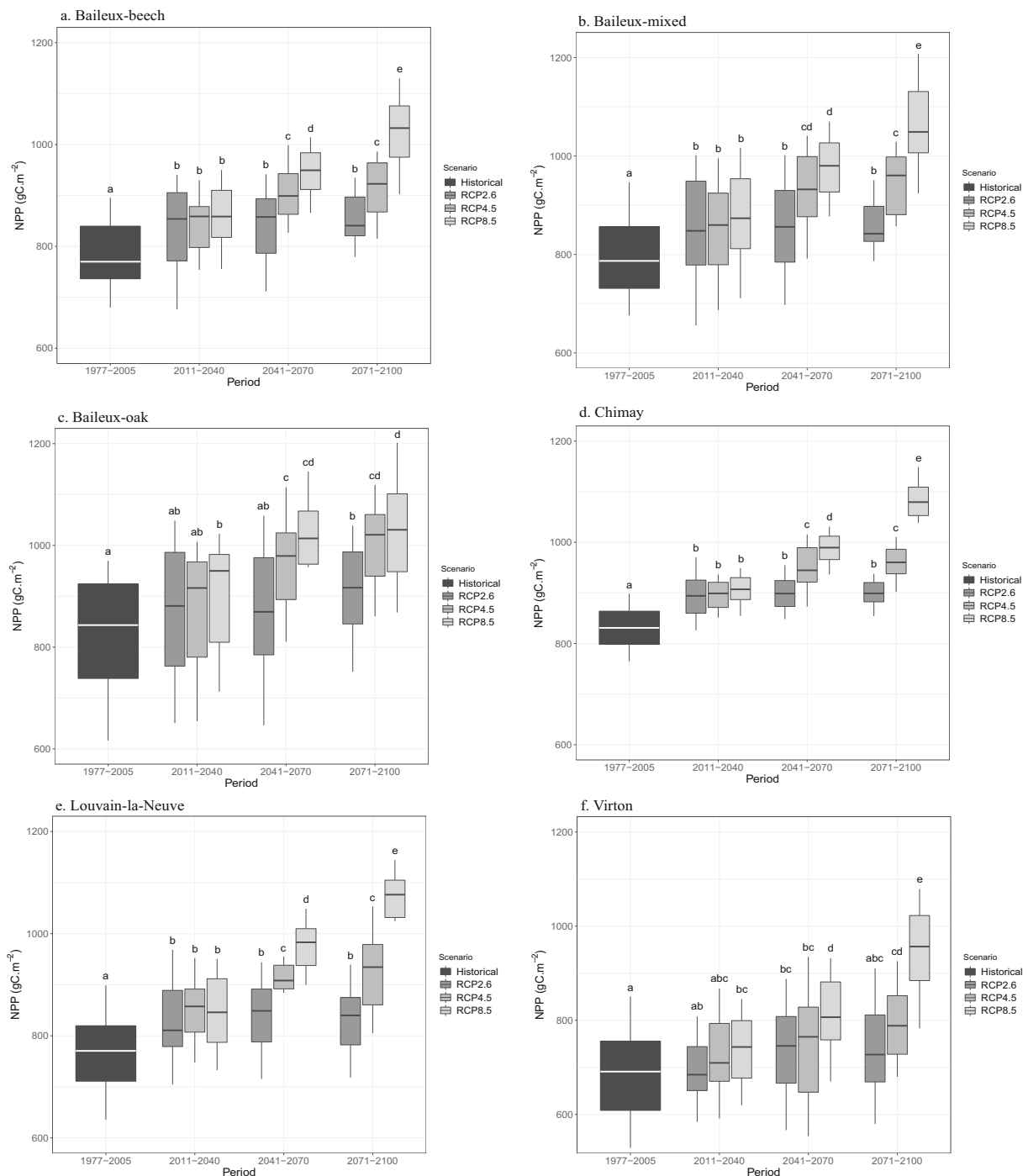


Fig. 5 NPP comparisons among RCP scenarios and with the historical period (1976–2005) for three 30-year periods in the different study sites (a–f) and with time-dependent CO_2 atmospheric concentrations. The horizontal line corresponds to the median, the box ends indicate the upper and lower quartiles and the whiskers show the values above and

below these quartiles within 1.5 interquartile. Common letters indicate that the distributions are non-significantly different according to a paired Wilcoxon signed-rank (between scenarios of the same period) or an unpaired Mann-Whitney (between scenarios of different periods) tests

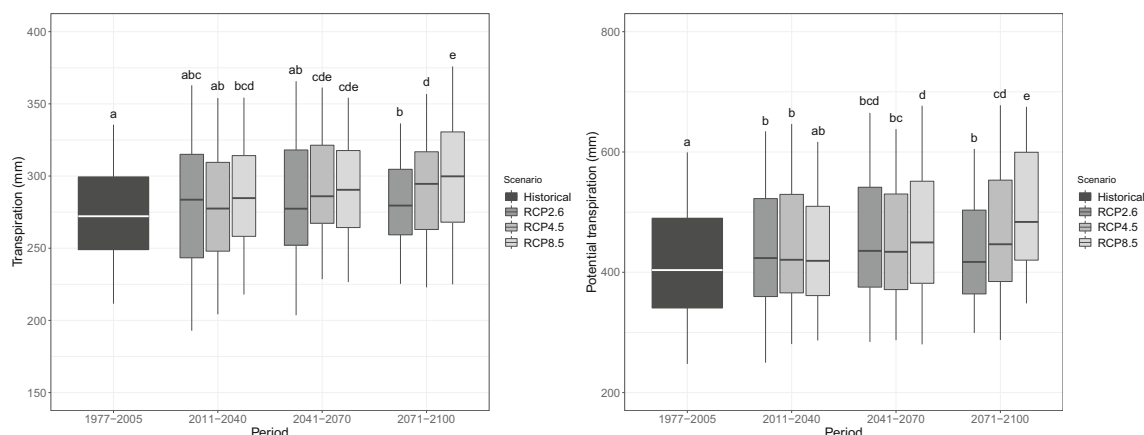


Fig. 6 Actual transpiration (left) and potential transpiration (right) comparisons among RCP scenarios and with the historical period (1976–2005) for three 30-year periods in the different study sites and with constant CO₂ atmospheric concentrations. The horizontal line corresponds to the median, the box ends indicate the upper and lower quartiles and the

whiskers show the values above and below these quartiles within 1.5 interquartile. Common letters indicate that the distributions are non-significantly different according to a paired Wilcoxon signed-rank (between scenarios of the same period) or an unpaired Mann-Whitney (between scenarios of different periods) tests

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