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Douglas-fir as a Climate Adaptation Option for Central European Lowland Forests

Die Douglasie – eine Option der Klimaanpassung in mitteleuropäischen Wäldern im Tiefland

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Schlüsselbegriffe: *Pseudotsuga menziesii*, Klimawandel, Trockenstress, Waldbewirtschaftung, Biome-BGC, stomatäre Leitfähigkeit

Abstract

The increasing impacts of climate change require adaptation strategies for sustainable forest management. One potential adaptation measure is the promotion of new tree species, such as Douglas-fir, which originates from northwestern North America. In contrast to European beech and Norway spruce, which depend on regular precipitation during the growing season, Douglas-fir is better able to withstand drought, particularly during the summer months. In this study, we investigate the drought stress response of Douglas-fir in comparison with European beech and Norway spruce under future climate conditions. As a diagnostic tool, we employ the species-specific biogeochemical flux model Biome-BGC, which has been calibrated for all major tree species in Central Europe. To assess future drought stress until the year 2100, we consider four climate scenarios:

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(i) a baseline scenario assuming no climate change, (ii) RCP 4.5, (iii) RCP 8.5, and (iv) an extreme RCP 8.5 scenario that assumes a substantial reduction in summer precipitation by 2100. The results indicate that the physiological drought stress response, expressed as relative stomatal opening, is less sensitive in Douglas-fir and oak species than in European beech and Norway spruce. This lower sensitivity suggests higher productivity of Douglas-fir during seasonal drought periods. Accordingly, simulations under the RCP 4.5 and RCP 8.5 scenarios show no decline in Douglas-fir productivity. Under the extreme RCP 8.5 scenario, net primary production declines markedly for European beech and Norway spruce, whereas Douglas-fir exhibits only a minor reduction in productivity.

Zusammenfassung

Die zunehmenden Auswirkungen des Klimawandels erfordern geeignete Anpassungsstrategien für eine nachhaltige Waldbewirtschaftung. Eine mögliche Maßnahme stellt die verstärkte Förderung bislang weniger verbreiteter Baumarten wie der Douglasie (*Pseudotsuga menziesii*) dar, die ursprünglich aus dem westlichen Nordamerika stammt. Im Vergleich zu der Rotbuche (*Fagus sylvatica*) und der Gemeinen Fichte (*Picea abies*), deren Wachstum während der Vegetationsperiode in hohem Maße von einer ausreichenden und regelmäßigen Wasserversorgung abhängt, weist die Douglasie insbesondere gegenüber sommerlicher Trockenheit eine höhere Toleranz auf. In der vorliegenden Studie wird die Reaktion der Douglasie auf Trockenstress unter zukünftigen Klimabedingungen mit jener von Rotbuche und Fichte verglichen. Als diagnostisches Instrument dient das artspezifisch parametrisierte biogeochemische Prozessmodell Biome-BGC, das für die wichtigsten Baumarten Mitteleuropas kalibriert wurde. Zur Abschätzung des Trockenstresses bis zum Jahr 2100 werden vier Klimaszenarien untersucht: (i) ein Referenzszenario ohne Klimaänderung, (ii) RCP 4.5, (iii) RCP 8.5 sowie (iv) ein extremes RCP 8.5 Szenario, das bis zum Jahr 2100 von einer starken Abnahme der Sommerniederschläge ausgeht. Die Ergebnisse zeigen, dass die physiologische Reaktion auf Trockenstress, ausgedrückt durch die relative stomatäre Öffnung, bei Douglasie und Eichenarten weniger stark ausgeprägt ist als bei Rotbuche und Fichte. Die geringere Sensitivität gegenüber Trockenstress deutet darauf hin, dass die Douglasie ihre Produktivität während saisonaler Trockenperioden vergleichsweise gut aufrechterhalten kann. Entsprechend zeigen die Simulationen unter den Szenarien RCP 4.5 und RCP 8.5 keinen Rückgang der Produktivität der Douglasie. Unter dem extremen RCP 8.5 Szenario nimmt die Nettoprimärproduktion von Buche und Fichte hingegen deutlich ab, während für die Douglasie lediglich eine geringfügige Produktivitätsminderung simuliert wird.

1 Introduction

Europe is the fastest-warming continent (ESOTC 2025). While rising temperatures have enhanced tree growth in some regions (Pretzsch *et al*. 2014), other areas experience increasing drought stress associated with bark beetle outbreaks (Jandl 2020), wildfires, and elevated tree mortality (Neumann *et al*. 2017). At the same time, precipitation patterns are shifting toward drier springs and wetter late summers and autumns (Myhre *et al*. 2019; Tabari 2020), further intensifying summer drought conditions (Vitali *et al*. 2017) and the associated risks for forest ecosystems.

Austria, located in central Europe, encompasses a highly heterogeneous landscape characterized by large elevational gradients and two distinct climate regimes. The western part of the country is influenced by an oceanic climate with abundant rainfall and snowfall, whereas eastern Austria experiences a more continental climate characterized by lower precipitation and hot, dry summers, particularly in the lowlands surrounding Vienna (Hasenauer *et al*. 2003). Under projected climate change, rising temperatures combined with altered precipitation regimes are expected to substantially increase drought stress in these regions. Consequently, the lower elevational limit for economically viable forestry may shift upward, with potentially severe consequences for timber production and forest management.

Historically, Austrian lowland forests were dominated by broadleaved species such as European beech (*Fagus sylvatica* L.) and oaks (*Quercus* spp.). However, large areas have been converted to agricultural land or replanted with so-called secondary coniferous forests dominated by Norway spruce (*Picea abies* (L.) Karst.) because of its high productivity and commercial value. Recent climatic trends indicate longer and more frequent summer droughts, substantially increasing drought stress and reducing soil water availability during the growing season (Lebourgeois 2007; Ge *et al*. 2013; Hartl-Meier *et al.* 2014). Consequently, Norway spruce has become increasingly susceptible to bark beetle infestations (Rehschuh *et al*. 2017).

A commonly proposed adaptation strategy is the conversion of secondary spruce forests into European beech forests, which are generally considered more resilient to climate change. However, recent studies suggest that even beech forests growing in the European lowlands may experience substantial drought stress and productivity losses under future climatic conditions (Zhang *et al.* 2025; Verdonck *et al*. 2025). Consequently, alternative tree species with greater drought tolerance warrant further evaluation.

One promising candidate is Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco), a species native to North America that was introduced into European forests at the end of the nineteenth century (Hintsteiner *et al.* 2017). Douglas-fir was widely planted across Western Europe for reforestation until the mid-twentieth century (van Loo and Dobrowolska 2019). In addition to its high productivity (Thomas *et al.* 2022), Doug-

las-fir exhibits remarkable tolerance to prolonged summer drought (Nicolescu *et al.* 2023), resulting in higher aboveground biomass production (Čihák and Vejpustková 2022) and radial growth than many native European tree species (Vitali *et al.* 2017; Levanič and Štraus 2022). Unlike species such as European beech and Norway spruce, Douglas-fir is adapted to maintain physiological activity during extended periods of limited water availability, making it a potential adaptation option for drought-prone lowland forests.

The objective of this study is to evaluate Douglas-fir as a climate change adaptation option for lowland forests in central Europe. Specifically, we investigate its physiological response to increasing drought stress and compare its productivity with that of European beech and Norway spruce. As a diagnostic tool, we employ the biogeochemical ecosystem model Biome-BGC (White *et al.* 2000; Thornton *et al.* 2002), using the species-specific parameterizations developed for the major tree species of central Europe (Pietsch *et al.* 2005). Biome-BGC simulates ecosystem responses to climatic variability by representing the coupled energy, water, nutrient, and carbon cycles, thereby allowing the assessment of physiological processes such as water-use efficiency, carbon uptake, and productivity under changing environmental conditions.

Our work is structured as follows:

(i) We develop and validate species-specific eco-physiological parameters for Douglas-fir suitable for Biome-BGC simulations. Since no validated parameter set is currently available for Douglas-fir growing in Europe, published parameter values are compiled and evaluated using observations from 28 Douglas-fir stands located in the lowland forests (<1000 m a.s.l.) of Austria and southern Germany.
(ii) Using the validated parameterization, we compare simulated physiological responses among Douglas-fir, European beech, and Norway spruce across 32 lowland forest plots with detailed soil information. Specifically, we evaluate relative stomatal opening, plant transpiration, net primary production, and stem carbon productivity under present-day climatic conditions.
(iii) Finally, we assess the effects of future climate change on drought stress and forest productivity using the same 32 plots and species-specific parameterizations under four climate scenarios extending to the year 2100: (a) baseline, (b) RCP4.5, (c) RCP8.5, and (d) an extreme RCP8.5 scenario assuming a 50% reduction in precipitation by 2100.

2 Methods and Materials

2.1 The Biome-BGC model

The biogeochemical mechanistic ecosystem model Biome-BGC (Running and Coughlan 1988; Thornton *et al.* 2002), including species-specific parameterizations for European beech and Norway spruce (Pietsch *et al.* 2005), simulates daily carbon,

nitrogen, water, and energy fluxes at stand scale (m^2). The model has been widely validated and applied in central Europe for simulating forest biomass and ecosystem carbon and water dynamics (Pietsch *et al.* 2003; Merganičová *et al.* 2005; Eastaugh *et al.* 2011; Hasenauer *et al.* 2012; Pötzelsberger and Hasenauer 2015). For Douglas-fir, parameters were derived within the Biome-BGC framework (Thornton *et al.* 2002) and adapted and evaluated for central European conditions (see next chapter and appendix).

Biome-BGC requires daily meteorological input (Tmin, Tmax, precipitation, solar radiation, vapor pressure deficit, day length), and site data including soil depth, soil texture, coordinates, elevation, atmospheric CO_2 concentration, and nitrogen deposition. The model runs on a daily time step and is initialized per unit area (m^2) using a spin-up procedure until steady-state equilibrium is reached (Pietsch and Hasenauer 2006), representing an undisturbed forest condition. Management history (*e.g.*, rotations, planting, thinning) can be included prior to simulation (Pietsch and Hasenauer 2006). Carbon fluxes are simulated using the Farquhar *et al.* (1980) photosynthesis formulation. Gross primary production (GPP) represents total carbon uptake, and net primary production (NPP) is calculated as GPP minus autotrophic respiration.

The present study focuses on hydrological processes. Precipitation is partitioned into rainfall (>0 °C) and snowfall (≤0 °C). Snow is subject to sublimation and melt; rainfall is either intercepted or infiltrates into the soil. Canopy interception depends on leaf area index (LAI) (Jones 2013), species-specific interception parameters, and precipitation intensity (Thornton 1998). After evaporation of intercepted water, transpiration is initiated.

Evapotranspiration and transpiration are computed separately for sunlit and shaded canopy fractions using the Penman–Monteith equation (Allen *et al.* 1998). Stomatal conductance regulates coupling between water loss and carbon uptake. Soil water holding capacity is derived from pedotransfer functions based on soil depth and texture (Clapp and Hornberger 1978; Cosby *et al.* 1984; Saxton *et al.* 1986). Soil water potential and volumetric soil water content follow Cosby et al. (1984) and Saxton *et al.* (1986). Infiltration occurs when soil water content is below saturation. Further model description is provided in Hasenauer *et al.* (2003), Pietsch *et al.* (2005), and Thornton (1998).

2.2 Douglas-fir validation data

Since the eco-physiological parameterization for Douglas-fir (Thornton *et al.* 2002) has not been validated under European forest conditions, we compiled data from Douglas-fir stands for model evaluation from Austria and southern Germany (Eckhart 2019). Data were collected following the guidelines of the Austrian National Forest Inventory (Gabler and Schadauer 2008) using fixed-area circular plots (20 m radius). For each tree, species, diameter at breast height (dbh), height (h), age, and spatial

position were recorded.

Stand age was determined by increment cores extracted from the tree with quadratic mean dbh at each angle-count sampling point. Elevation ranged from 290 to 890 m a.s.l., mean annual precipitation from 596 to 1802 mm, and mean annual temperature from 6.8 to 10.2 °C (Eckhart *et al.* 2014). All stands originate from a single provenance, sourced from the coastal and western Cascade regions of Oregon and Washington (Eckhart 2019). Summary statistics of the Douglas-fir stands used for model validation are provided in Table 1.

2.3 Soil data for scenario analyses

Soil data were available for 32 sites across Austrian lowland forests (<1000 m a.s.l.; Fig. 1). Eleven sites were obtained from the AlpS project (Eckhart *et al.* 2014), and 21 sites from the Biosoil database (Mutsch *et al.* 2013a, b), maintained by the Austrian Forest Research Centre. Soils are developed on siliceous and carbonate parent material (Eckhart 2019).

Across all sites, soil depth ranges from 50 to 150 cm, with sand contents of 1–60%, silt contents of 27–70%, and clay contents of 6–47%. Dominant soil types include Cambisols, Luvisols, and Regosols (Mutsch *et al.* 2013a, b). Elevation ranges from 290 to 820 m a.s.l. Long-term climate (1960–2022) is characterized by mean annual precipitation of 849 mm and mean annual temperature of 8.8 °C.

Table 1: Summary statistics of the available Douglas-fir forest inventory data, including stand and site characteristics. Min. and Max. represent the minimum and maximum values, respectively; sd denotes the standard deviation; and SDI is the Stand Density Index according to Reinecke (1933).

Tabelle 1: Verfügbaren Daten der Douglasienbestände, einschließlich der Bestandes- und Standortmerkmale. Min. und Max. bezeichnen den Minimal- bzw. Maximalwert; sd steht für die Standardabweichung; und SDI bezeichnet den Stand Density Index (Bestandesdichteindex) nach Reinecke (1933).

Variables	Douglas-fir stands N=28 plots			
	Min.	Max.	Mean	sd
Elevation (m)	290	890	554	156
Precipitation (mm)	596	1802	906	261
Annual average Temperature (°C)	6.8	10.2	8.6	0.95
Age	38.0	121.0	73.1	27.2
Diameter at Breast Height (cm)	31.6	82.2	53.8	15.8
Tree height (m)	20.2	50.1	34.8	8.9
Stem number (N/ha)	60.5	748.3	284.3	165.5
Basal area (m^2/ha)	17.0	65.0	42.0	12.6
Volume (m^3/ha)	219.0	1317.2	640.7	289.8
Above ground biomass (ton/ha)	109.5	658.6	320.4	144.9
SDI (Stand Density Index)	256.8	1441.0	803.9	259.2

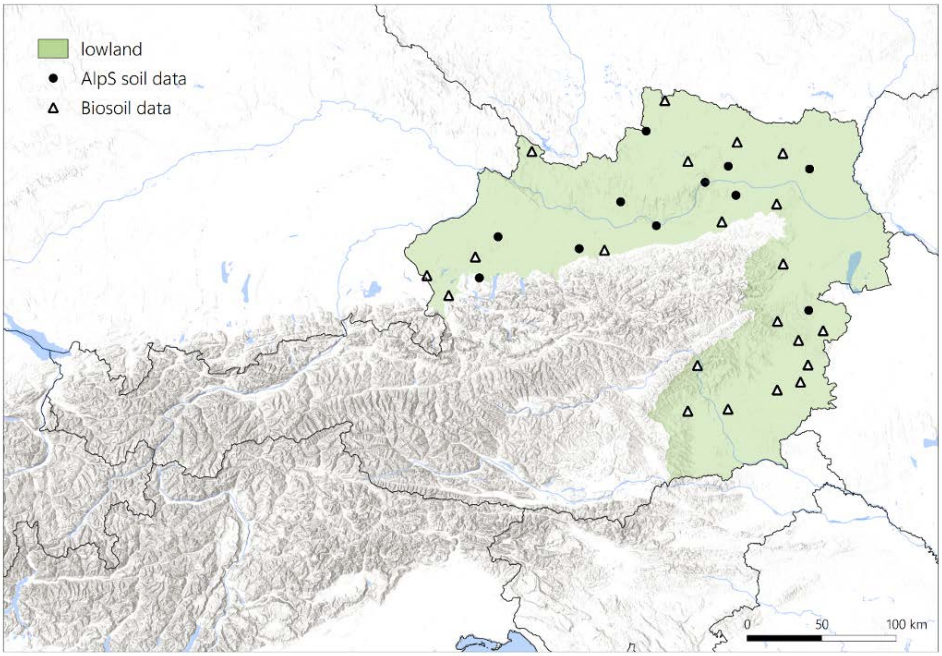


Figure 1: Distribution of the 32 soil plots across the Austrian lowlands (elevation < 1000 m). Eleven plots originate from the AlpS project and 21 plots from the Biosoil database. Both datasets provide comparable soil information and were used for the species-specific drought stress analyses.

Abbildung 1: Verteilung der 32 Bodenprobeflächen in Tiefland von Österreich (Seehöhe < 1000 m). Elf Probeflächen stammen aus dem AlpS-Projekt und 21 aus der Biosoil-Datenbank. Beide Datensätze liefern vergleichbare Bodeninformationen und wurden für die artspezifischen Analysen des Trockenstresses verwendet.

2.4 Climate data

Historical daily climate data

For the period 1960–2022, daily minimum (Tmin) and maximum (Tmax) air temperature as well as precipitation (Prcp) data were obtained from climate stations operated by the Austrian Central Institute for Meteorology and Geodynamics (ZAMG) and the German Weather Service (DWD). These data were used as input for DAYMET, a climate interpolation and simulation tool (Hasenauer *et al.* 2003; Thornton *et al.* 1997, 2000), to

(i) interpolate daily weather variables, including Tmin (°C), Tmax (°C), and Prcp (mm), and
(ii) derive vapor pressure deficit (VPD; Pa), solar radiation (SRAD; W m^{-2}), and day length (DL; s) for each forest site.

The historical climate data were analyzed to assess climate development over the past 62 years in the Austrian lowlands (Fig. 2). In addition, they were used as input for Biome-BGC simulations to validate the model and assess the physiological responses of different tree species to climatic variation.

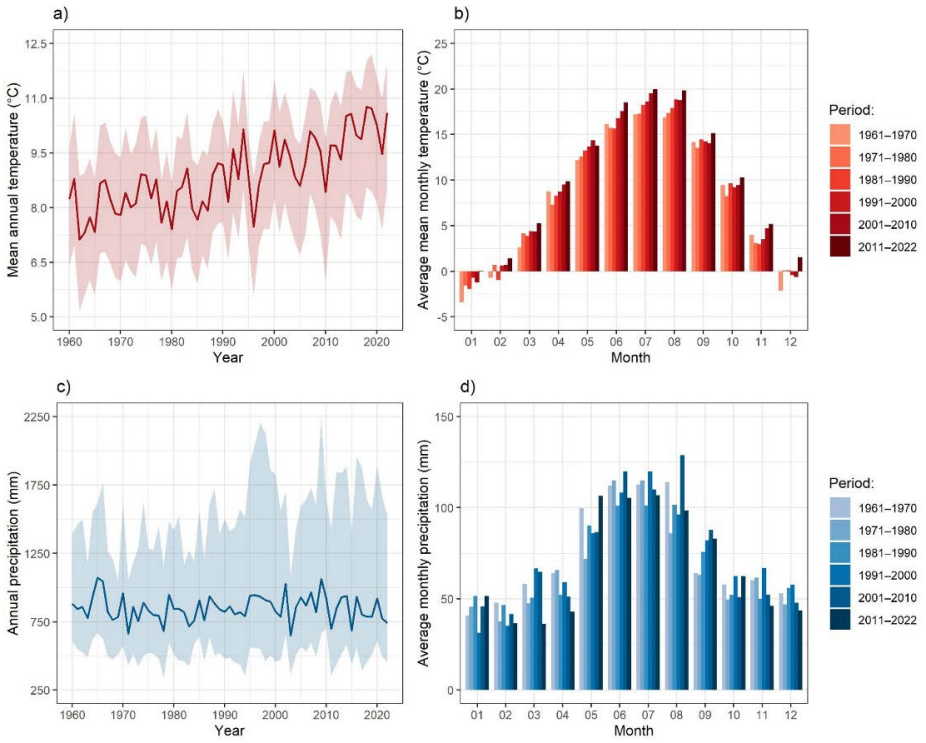


Figure 2: Climate variation across the 32 locations (see Fig. 1) representing lowland forest areas in Austria from 1960 to 2022. Mean annual temperature (a) and annual precipitation totals (c) are shown for the period 1960–2022, while mean monthly temperature (b) and cumulative monthly precipitation (d) are presented for 10-year intervals between 1961 and 2022. The ribbons in the left panels represent the variability within each 10-year period.

Abbildung 2: Klimatische Variation der 32 Standorten (siehe Abb. 1) im Zeitraum von 1960 bis 2022. Dargestellt sind die mittlere Jahrestemperatur (a) und die jährliche Niederschlagssumme (c) für den Zeitraum 1960 bis 2022 sowie die mittlere Monatstemperatur (b) und der kumulierte monatliche Niederschlag (d) für 10-Jahres-Intervalle zwischen 1961 und 2022. Die grauen Bereiche in den linken Abbildungen zeigen die Variabilität innerhalb der jeweiligen 10-Jahres-Perioden.

Climate Change scenarios

For the analysis extending to 2100, one baseline dataset and three climate change scenarios were used. The baseline scenario was derived from the ERA5 dataset (C3S 2017; Hersbach *et al.* 2020; Bell *et al.* 2021) and covers the reference period 1981–2010. Whole years from this 30-year period were randomly sampled to generate a detrended climate dataset for 1981–2100, thereby preserving the occurrence of historical extreme events such as heat waves and droughts (Hasel and Formayer 2020).

The climate change scenarios for the period 1960–2100 were obtained from EURO-CORDEX (Moss *et al.* 2010) and comprise three regional climate projections based on Representative Concentration Pathways (RCPs). These scenarios are classified according to the projected radiative forcing in 2100 (W m^{-2}) relative to historical climate conditions (IPCC 2014), including RCP 4.5 and RCP 8.5.

An additional scenario, RCP 8.5 Extreme, was developed within the ZEUS project and assumes a substantial reduction in precipitation by 2100. It was selected because it exhibits the greatest Euclidean distance from the ensemble mean with respect to projected temperature and precipitation changes (Hasel and Formayer 2020). The three climate change scenarios used in this study represent the following projected changes for Central Europe by 2100:

1. RCP 4.5: Mean annual temperature increase of 1.5 °C, with no change in annual precipitation.
2. RCP 8.5: Mean annual temperature increase of 3.4 °C, with no change in annual precipitation.
3. RCP 8.5 Extreme: Mean annual temperature increase of 4.1 °C, an 11% reduction in annual precipitation, and a 50% reduction in summer precipitation (June–August).

Except for the RCP 8.5 Extreme scenario, no changes in precipitation were considered. The annual and monthly mean temperature and precipitation trends for the four scenarios (Baseline, RCP 4.5, RCP 8.5, and RCP 8.5 Extreme) at the selected Austrian lowland forest sites are presented in Fig. 3. All RCP scenarios were bias-corrected to minimize systematic errors, while both the baseline and climate scenario datasets were statistically downscaled and originally developed within the ZEUS project (Hasel and Formayer 2020).

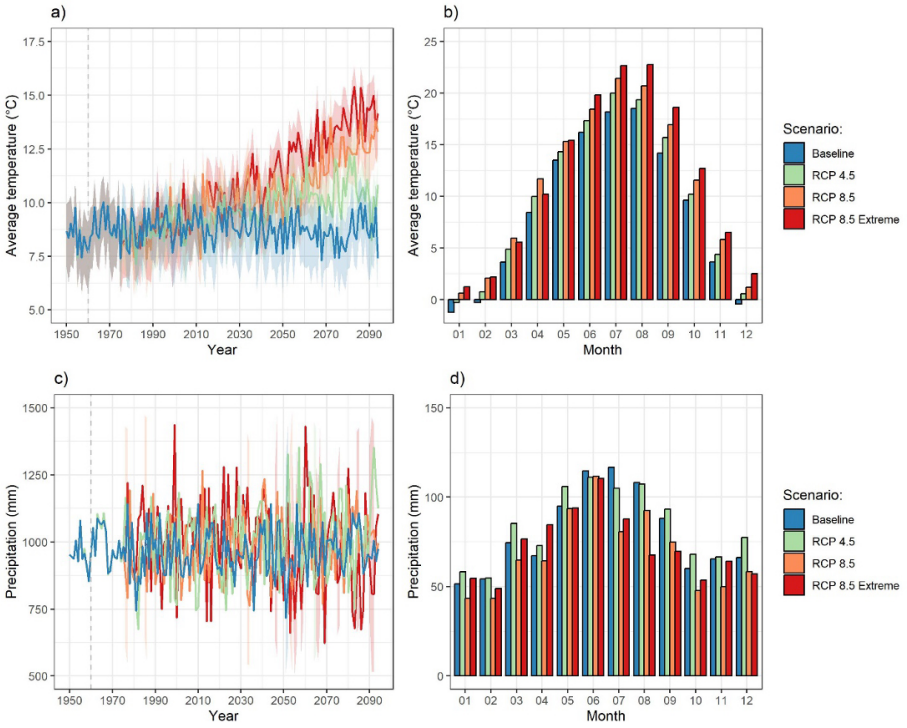


Figure 3: Mean annual temperature (a) and precipitation (c), as well as mean monthly temperature (b) and precipitation (d), under the projected climate change scenarios for the Austrian lowlands (Fig. 1) from 1960 to 2100. The Baseline scenario represents current climate conditions without changes in temperature or precipitation. The RCP 4.5 scenario assumes an annual temperature increase of 1.5 °C, while the RCP 8.5 scenario assumes an increase of 3.4 °C. The RCP 8.5 Extreme scenario represents a temperature increase of 4.1 °C combined with reduced precipitation (−11% in annual precipitation and −50% in summer precipitation) for Central Europe by 2100.

Abbildung 3: Mittlere Jahrestemperatur (a) und jährlicher Niederschlag (c) sowie mittlere monatliche Temperatur (b) und monatlicher Niederschlag (d) unter den projizierten Klimawandelszenarien für die österreichischen Tieflagen (siehe Abb. 1) für den Zeitraum von 1960 bis 2100. Das Baseline-Szenario repräsentiert die gegenwärtigen Klimabedingungen ohne Veränderungen der Temperatur oder des Niederschlags. Das RCP-4.5-Szenario geht von einem Anstieg der Jahrestemperatur um 1,5 °C aus, während das RCP-8.5-Szenario einen Anstieg um 3,4 °C annimmt. Das Szenario RCP 8.5 Extreme beschreibt für Mitteleuropa bis zum Jahr 2100 einen Temperaturanstieg um 4,1 °C in Kombination mit einem Rückgang der Niederschläge (−11 % des Jahresniederschlags und −50 % des Sommerniederschlags).

The baseline and climate change scenario datasets (Fig. 3) consist of daily ERA5 and EURO-CORDEX data, providing minimum and maximum air temperature as well as precipitation through 2100. To run the Biome-BGC model, additional climate variables, including vapor pressure deficit (VPD), solar radiation (SRAD), and day length (DL),

were required. These variables were derived using DAYMET (Thornton et al. 1997, 2000), which interpolates daily Tmin, Tmax, and precipitation data for each selected forest stand location. Missing VPD, SRAD, and day length values were subsequently calculated for each plot for the baseline and all three climate change scenarios (Hasenauer *et al.* 2003).

2.5 Simulation procedure

Biome-BGC simulations began with a spin-up procedure (Pietsch and Hasenauer 2006) to initialize ecosystem carbon, nitrogen, and water pools for each site based on local climate and soil conditions. For each of the 28 Douglas-fir sites and 32 lowland Austrian soil sites (Fig. 1), the parameterization for European beech was applied, assuming that beech represents the potential natural vegetation under the prevailing site conditions. Historical climate data were repeatedly cycled until the ecosystem pools reached a steady state.

Following the spin-up, three consecutive 100-year rotations representing historical forest management with Norway spruce were simulated to account for legacy effects of past management and the historical shift in dominant tree species from European beech to Norway spruce. The actual simulation was then performed using the species-specific parameterization for each target species. This procedure ensured identical initial conditions with respect to management history, soil properties, and climate for all species-specific ecophysiological response analyses.

The impacts of the climate scenarios on Douglas-fir, European beech, and Norway spruce were evaluated using net primary production (NPP), water balance, and soil water potential. Results are presented as mean summer (June–August) values averaged over the period 2050–2100. Water balance was calculated as the mean daily difference between precipitation and actual evapotranspiration. Soil water potential was calculated as the mean daily soil water potential during the summer months, while net primary production was calculated as the mean daily NPP during the same period. All variables were derived from the Biome-BGC model outputs.

3 Results

3.1 Douglas-fir model validation

The mean observed stem volume across the 28 forest stands was 640.7 $m^3\ ha^{-1}$, whereas the corresponding mean simulated volume was 853.0 $m^3\ ha^{-1}$ (Fig. 4a), indicating that Biome-BGC overestimated stem growth. Biome-BGC assumes fully stocked

stands and simulates ecosystem carbon fluxes under the absence of density-related management effects. Previous studies (Petritsch 2008; de Bastos and Hasenauer 2023) have shown that this assumption may lead to an overestimation of stem carbon accumulation when changes in stand density resulting from forest management are not considered.

To account for management-induced differences in stand density, the simulated stem carbon values were corrected using the Stand Density Index (SDI) according to Reineke (1933). The SDI is defined as:

$$SDI = N\left(\frac{dg}{25}\right)^{1.605} \quad (1)$$

where N is the number of trees per unit area [ha^{-1}], dg is the quadratic mean stand diameter at breast height [cm], 25 is a reference dg and 1.605 is the slope parameter defining the maximum carrying capacity. The SDI has been shown to be independent of site quality and stand age, while the SDImax provides an estimate of the carrying capacity of a given forest type (Hasenauer 1994).

After calculating the difference Δ between predicted (simulated) versus observed stem volume, a density-related pattern is evident (Fig. 4b) and a logarithmic correction function of the following form can be applied:

$$\Delta Volume = a + b \cdot ln(SDI) \pm \varepsilon \quad (2)$$

The results (Fig. 4b) exhibited negative exponential behavior with an $R^2 = 0.41$, and coefficient estimates for a = 3164.2 and for b = - 445.2.

After correcting the simulations (predictions) for stand density, the mean corrected predicted stem volume was 640.7 m^3/ha, closely matching the field observations (Fig. 4c). A paired t-test indicated no significant difference or bias between the corrected predicted and observed stem volume, $t_{(\alpha=0.05,\ n=28)} = 6.87e\text{-}05$ and p-value = 0.99. The critical t-value at $\alpha = 0.05$ was ±2.05, confirming that, after accounting for stand density effects, the Biome-BGC simulations provided unbiased and consistent estimates of stem volume (Fig. 4c).

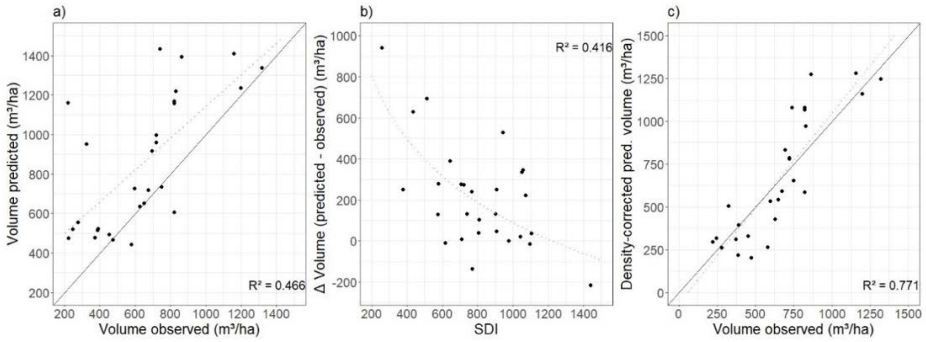


Figure 4: Predicted versus observed stem volume for the 28 Douglas-fir stands (a); relationship between the difference in volume (Δ volume = predicted – observed) and the Stand Density Index (SDI) (b); and density-corrected predicted volume versus observed volume (c). Solid lines in panels (a) and (c) represent the 1:1 reference line for assessing agreement between predicted and observed values. Dashed lines represent fitted linear trendlines in panels (a) and (c) and a logarithmic trendline in panel (b).

Abbildung 4: Geschätzte versus beobachtetes Stammvolumen für die 28 Douglasienbestände (a); Zusammenhang zwischen der Volumendifferenz (Δ Volumen = vorhergesagt – beobachtet) und dem Bestandesdichteindex (SDI) (b); sowie dichtekorrigiertes vorhergesagtes Volumen im Vergleich zum beobachteten Volumen (c). Die durchgezogenen Linien in den Abbildungen (a) und (c) stellen die 1:1-Referenzlinie zur Beurteilung der Übereinstimmung zwischen vorhergesagten und beobachteten Werten dar. Die gestrichelten Linien zeigen angepasste lineare Trendlinien in den Abbildungen (a) und (c) sowie eine logarithmische Trendlinie in Abbildung (b).

3.2 Drought stress response by tree species

This analysis focuses on the physiological drought responses of Douglas-fir, European beech, and Norway spruce and their effects on

(i) relative stomatal opening,
(ii) plant transpiration,
(iii) net primary production (NPP), and
(iv) stem carbon.

These variables were evaluated for 32 forest soil plots (Fig. 1) representing typical forest growth conditions in the Austrian lowlands. Three years representing contrasting climatic conditions were selected for the analysis:

(i) 2010, representing average climatic conditions in the study region, with an annual precipitation of 920.4 mm and a mean annual temperature of T_{avg}=8.4 °C,
(ii) 2011, a dry year, with an annual precipitation of 697.4 mm and a mean annual temperature of T_{avg}=9.7 °C, and
(iii) 2015, another dry year, with an annual precipitation of 685.1 mm and a mean annual temperature T_{avg} of 10.6 °C.

Differences in precipitation resulted in species-specific physiological responses and associated changes in ecosystem fluxes. As shown in Fig. 5, relative stomatal opening varied among years (average versus dry years), tree species, and seasons. European beech and Norway spruce exhibited greater day-to-day variability in stomatal opening than Douglas-fir, indicating a stronger physiological response to drought. This increased sensitivity was associated with reduced carbon assimilation and consequently lower net primary production.

Under the average climatic conditions of 2010, Douglas-fir maintained higher daily productivity during late summer and autumn than the other species, resulting in an annual NPP of 0.8431 kg m^{-2}, compared with 0.7449 kg m^{-2} for Norway spruce. In the dry years 2011 and 2015, annual NPP declined for all three species relative to 2010 (Fig. 5).

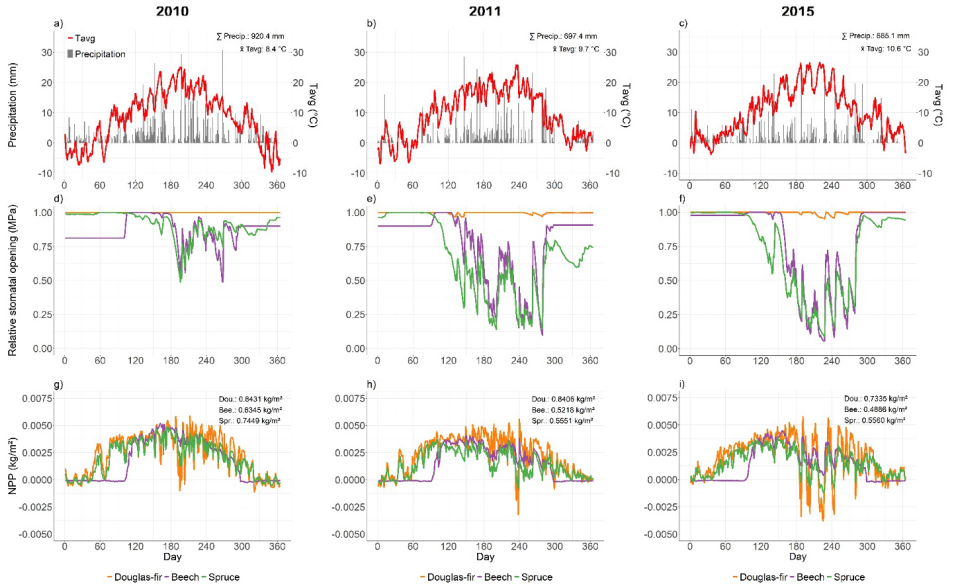


Figure 5: Daily precipitation and mean temperature during a normal year (2010) and two dry years (2011 and 2015) (a–c). Daily simulated plant responses, including relative stomatal opening (MPa) (d–f) and net primary production (kg m^{-2}) (g–i), for Douglas-fir (Dou), European beech (Bee), and Norway spruce (Spr) in the Austrian lowlands (n = 32). Values represent the mean across the 32 simulated stands. A relative stomatal opening value of 1 MPa indicates fully open stomata, whereas a value of 0 MPa indicates completely closed stomata.

Abbildung 5: Täglicher Niederschlag und mittlere Temperatur während eines Normaljahres (2010) und zweier Trockenjahre (2011 und 2015) (a–c). Dargestellt sind die täglich simulierten Pflanzenreaktionen, einschließlich der relativen Stomataöffnung (MPa) (d–f) und der Nettoprimärproduktion (kg m^{-2}) (g–i), für Douglasie (Dou), Rotbuche (Bee) und Fichte (Spr) in den österreichischen Tieflagen (n = 32). Die Werte entsprechen dem Mittelwert über die 32 simulierten Bestände. Ein Wert der relativen Stomataöffnung von 1 MPa entspricht vollständig geöffneten Stomata, während ein Wert von 0 MPa vollständig geschlossene Stomata anzeigt.

3.3 Changes in drought stress due to climate change

As shown in Fig. 5, Douglas-fir was less sensitive to drought stress than European beech and Norway spruce. We therefore simulated carbon and water flux dynamics using Biome-BGC under four climate scenarios (Baseline, RCP 4.5, RCP 8.5, and RCP 8.5 Extreme) for each of the three species (Douglas-fir, European beech, and Norway spruce). Simulations were conducted for the 32 study plots with detailed soil information, representing the lowland forest regions of Austria (elevation < 1000 m; Fig. 1).

As a first step, we calculated the mean summer (June–August) water balance for the period 2050–2100 (50-year average) for each species (Fig. 6a). Higher temperatures and drier summer conditions resulted in a negative water balance for European beech and Norway spruce, whereas Douglas-fir maintained a positive mean summer water balance under all four climate scenarios (Fig. 6a).

To assess drought susceptibility under future climate conditions, we analyzed the mean summer (June–August) soil water potential (MPa) for each species (Fig. 6b). Soil water potential declined under increasingly severe climate scenarios for all species. However, Douglas-fir exhibited only minor changes across the scenarios. In contrast, European beech and Norway spruce approached the permanent wilting point (–1.5 MPa) under the RCP 8.5 Extreme scenario, indicating substantially greater drought stress.

The mean summer NPP under the RCP 8.5 Extreme scenario declined for all species relative to the Baseline scenario (Fig. 6c). In contrast, mean annual NPP increased slightly under the RCP 4.5 and RCP 8.5 scenarios but decreased under the RCP 8.5 Extreme scenario for all three species (Fig. 7). Douglas-fir exhibited the smallest variation in annual NPP across the climate scenarios, whereas Norway spruce showed the greatest variability (Fig. 7). The relationship between annual NPP and precipitation for each species under the four climate scenarios over the simulation period (2050–2100) is presented in Fig. 8.

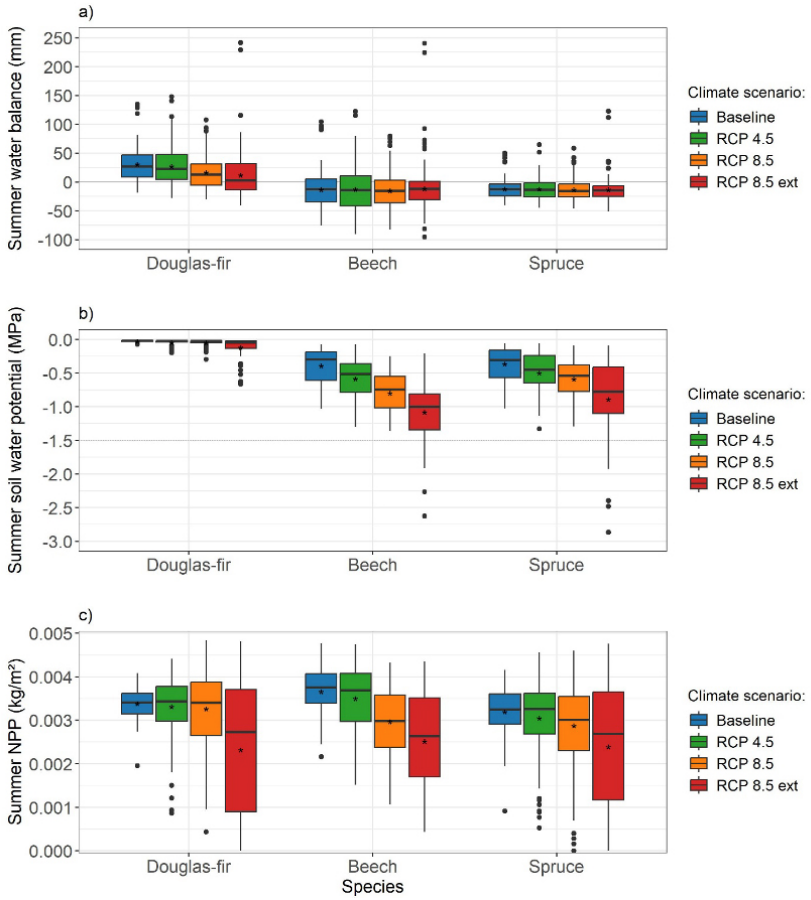


Figure 6: Fifty-year (2050–2100) averages of summer (June–August) water balance (mm) (a), soil water potential (MPa) (b), and net primary production (NPP, kg m^{-2}) (c) by tree species and climate change scenario. The summer water balance was calculated as the mean daily difference between precipitation and actual evapotranspiration. Soil water potential represents the mean daily soil water potential for each species during the summer months. Both variables were derived from species-specific simulations for the 32 plots (Fig. 1) representing Austrian lowland forest areas. Each box represents the distribution of values, with the point indicating the mean, the horizontal line indicating the median (50th percentile), and the lower and upper boundaries representing the 25th and 75th percentiles, respectively.

Abbildung 6: 50-Jahres-Mittelwerte (2050–2100) der Sommer–Wasserbilanz (Juni–August; mm) (a), des Bodenwasserpotenzials (MPa) (b) und der Nettoprimärproduktion (NPP; kg m^{-2}) (c), aufgeschlüsselt nach Baumart und Klimawandelszenario. Die sommerliche Wasserbilanz wurde als mittlere tägliche Differenz zwischen Niederschlag und tatsächlicher Evapotranspiration berechnet. Das Bodenwasserpotenzial entspricht dem mittleren täglichen Bodenwasserpotenzial der jeweiligen Baumart während der Sommermonate. Beide Variablen wurden aus artspezifischen Simulationen für die 32 Probeflächen (Abb. 1) der Tiefalgenwaldgebiete berechnet. Jede Box stellt die Verteilung der Werte dar, wobei der Punkt den Mittelwert, die horizontale Linie den Median (50. Perzentil) und die untere bzw. obere Begrenzung das 25. bzw. 75. Perzentil kennzeichnet.

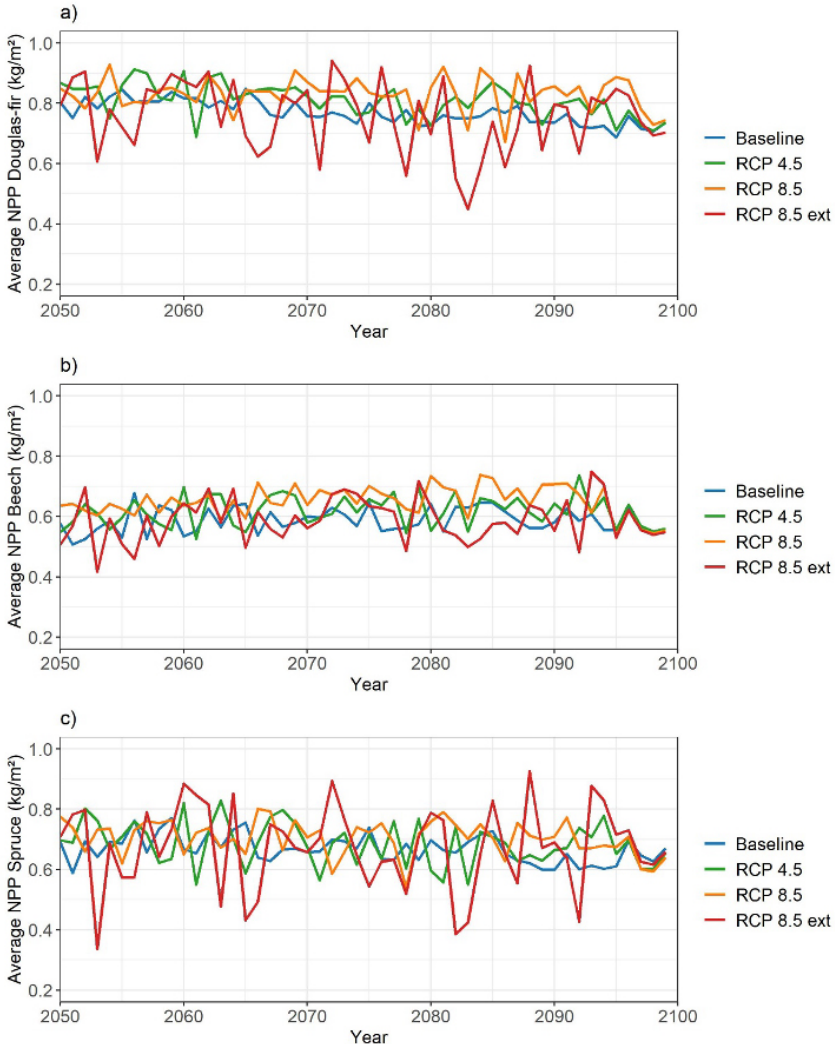


Figure 7: Average annual net primary production (NPP) of the 32 lowland forest locations (Fig. 1) representing Douglas-fir (a), European beech (b), and Norway spruce (c) from 2050 to 2100 under four climate change scenarios: Baseline (blue), RCP 4.5 (green), RCP 8.5 (orange), and RCP 8.5 Extreme (red). The same soil and climate conditions were applied for all species; therefore, differences among species result from species-specific ecophysiological characteristics affecting flux calculations as implemented in the model.

Abbildung 7: Mittlere jährliche Nettoprimärproduktion (NPP) der 32 Waldstandorte der österreichischen Tieflagen (Abb. 1) für Douglasie (a), Rotbuche (b) und Fichte (c) im Zeitraum 2050 bis 2100 unter vier Klimawandelszenarien: Baseline (blau), RCP 4.5 (grün), RCP 8.5 (orange) und RCP 8.5 Extreme (rot). Für alle Baumarten wurden die identen Boden- und Klimabedingungen zugrunde gelegt; Unterschiede zwischen den Baumarten ergeben sich daher aus artspezifischen ökophysiologischen Eigenschaften, die die im Modell implementierten Flussberechnungen beeinflussen.

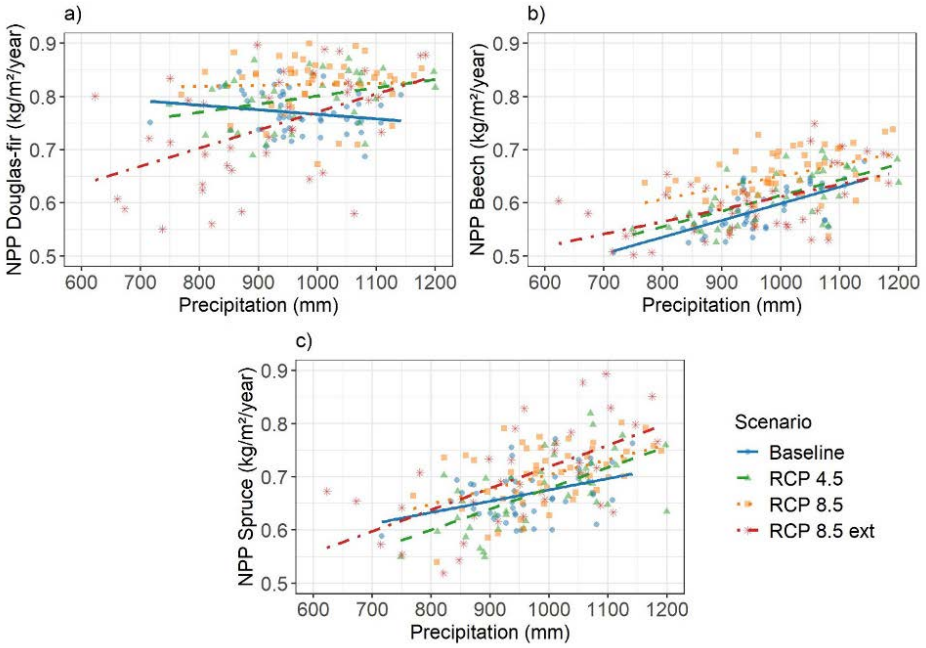


Figure 8: Relationship between annual net primary production (NPP) and annual precipitation in the Austrian lowlands for Douglas-fir (a), European beech (b), and Norway spruce (c) from 2050 to 2100 under four climate change scenarios: Baseline (blue), RCP 4.5 (green), RCP 8.5 (orange), and RCP 8.5 Extreme (red).

Abbildung 8: Zusammenhang zwischen der jährlichen Nettoprimärproduktion (NPP) und dem jährlichen Niederschlag in den österreichischen Tieflagen für Douglasie (a), Rotbuche (b) und Fichte (c) von 2050 bis 2100 unter vier Klimawandelszenarien: Baseline (blau), RCP 4.5 (grün), RCP 8.5 (orange) und RCP 8.5 Extreme (rot).

4 Discussion

Relative stomatal opening, a physiological indicator of drought stress, differed markedly among the three species, with European beech and Norway spruce exhibiting greater sensitivity than Douglas-fir. During the dry years (2011 and 2015), relative stomatal opening declined, accompanied by reduced net primary production (NPP), particularly in beech and spruce (Fig. 5). For these two species, reduced precipitation induced stomatal closure from summer to early autumn, indicating severe drought stress.

In contrast, Douglas-fir exhibited a much smaller reduction in relative stomatal opening, particularly during the summer months. Consequently, simulated NPP declined only slightly compared with European beech and Norway spruce (Fig. 5). Similar responses have been reported by Ditmarová *et al.* (2009), who found that decreasing

water potential in Norway spruce seedlings reduced stomatal conductance and CO_2 exchange. For Douglas-fir, the small reduction in relative stomatal opening suggests that the simulated decline in NPP was primarily related to increasing air temperature rather than water limitation. Kunert *et al.* (2022) reported no significant differences in thermal tolerance between Norway spruce and Douglas-fir, although the combined effects of heat stress and water limitation in forest ecosystems remain insufficiently understood. Under both average and dry climatic conditions, Douglas-fir maintained the highest annual NPP (Fig. 5), which may be explained by its relatively stable stomatal regulation and lower sensitivity to climatic variability.

Douglas-fir also maintained higher productivity during the summer months, resulting in greater annual NPP than European beech and Norway spruce. This may partly reflect a longer effective growing season, allowing sustained carbon assimilation later into the growing season (Fig. 5g–i). Rising temperatures can enhance tree growth provided that soil water availability is not limiting.

Between 1960 and 2022, the mean annual temperature in the Austrian lowland forest zone (elevation < 1000 m) increased by approximately 2 °C, reaching a 10-year average of 10.2 °C for the period 2012–2021 (Fig. 2). During the same period, the annual precipitation total remained relatively constant at approximately 850 mm yr^{-1}, whereas the seasonal distribution of rainfall shifted towards the second half of the year (Fig. 2). Higher temperatures increase plant respiration and atmospheric evaporative demand through a higher vapour pressure deficit, thereby increasing the likelihood that water becomes the primary limiting factor for forest growth. Consequently, drought stress is expected to become an increasingly important driver of forest productivity in Austrian lowland forests (Fig. 2).

Although total annual precipitation has changed little, alterations in seasonal rainfall distribution, such as longer dry periods during the growing season, may substantially increase drought stress. European beech and Norway spruce are physiologically less adapted to prolonged summer droughts and require annual precipitation exceeding approximately 500 mm, together with relatively frequent rainfall events during the growing season, to avoid severe water stress (Leuschner, 2020).

Douglas-fir differs fundamentally in this respect. Although native to the humid Pacific Northwest of North America, it has evolved under a Mediterranean-type seasonal precipitation regime characterized by wet winters and prolonged summer dry periods. Consequently, its ecophysiological adaptations differ from those of European beech and Norway spruce, making Douglas-fir a promising species for climate change adaptation in Austrian lowland forests.

The selected climate scenarios indicate a continued increase in temperature accompanied by further changes in seasonal precipitation patterns (Fig. 3). These projections emphasize the importance of adapting forest management by considering more

drought-tolerant species such as Douglas-fir to maintain forest productivity under future climatic conditions.

The simulated mean summer water balance for the second half of the twenty-first century (Fig. 6) further demonstrates the lower drought sensitivity of Douglas-fir compared with European beech and Norway spruce. The two native species responded similarly across all four climate scenarios, suggesting comparable thresholds with respect to water availability. Consequently, further reductions in precipitation or longer summer dry periods are likely to affect both species to a similar extent.

An even stronger distinction among species is evident from the simulated summer soil water potential (Fig. 6), which represents an important indicator of plant water stress. Whereas Douglas-fir exhibited only minor changes across the climate scenarios, European beech and Norway spruce experienced a substantial decline in soil water potential, approaching the permanent wilting point under the RCP 8.5 Extreme scenario.

Because summer water balance and soil water potential strongly influence plant productivity, the simulated annual NPP responded accordingly (Fig. 7). Douglas-fir showed the smallest reduction in productivity under future climate conditions, consistent with findings by Štraus (2022) for Slovenian forests and Vitali *et al.* (2017) for southwestern Germany, both of whom reported lower drought sensitivity of Douglas-fir compared with Norway spruce.

Long-term declines in productivity generally indicate reduced tree vitality and forest health. Our simulations suggest that Austrian lowland forests may increasingly become water-limited ecosystems as precipitation patterns shift towards drier growing seasons and wetter autumns. Therefore, the relationship between annual precipitation and annual NPP is of particular interest. In the Baseline, RCP 4.5 (approximately +1.5 °C), and RCP 8.5 (approximately +3.4 °C) scenarios, total annual precipitation was assumed to remain unchanged, whereas the RCP 8.5 Extreme scenario (+4.1 °C) assumed an 11% reduction in annual precipitation together with a 50% reduction in summer (June–August) rainfall. Under all precipitation regimes, Douglas-fir maintained higher NPP than European beech and Norway spruce (Fig. 8). Furthermore, Douglas-fir exhibited lower sensitivity to changes in precipitation patterns, particularly under the Baseline and RCP 8.5 scenarios.

Overall, Douglas-fir exhibited the highest productivity among the evaluated species under both average and dry conditions and was less sensitive to changes in precipitation than European beech and Norway spruce. However, our simulations did not account for biotic disturbance agents that may become more important under climate change. In particular, drought-induced bark beetle outbreaks in Norway spruce stands may further reduce forest productivity beyond the effects simulated by Biome-BGC (Jandl, 2020).

5 Conclusion

Drought stress affects important eco-physiological parameters, including

(i) relative stomatal opening,
(ii) plant transpiration,
(iii) net primary production (NPP), and
(iv) stem carbon productivity, for Douglas-fir, European beech, and Norway spruce.

The results indicate that, under future climate conditions, Douglas-fir is expected to exhibit lower sensitivity of stomatal regulation to climatic stress, resulting in higher productivity compared with European beech and Norway spruce during both average and dry periods.

Net primary production increased or remained relatively stable for all species under the RCP 4.5 and RCP 8.5 climate scenarios. However, under the RCP 8.5 Extreme scenario, characterized by a 50% reduction in summer precipitation, NPP declined, with the strongest negative effects observed for Norway spruce. Douglas-fir maintained the highest productivity under both average and dry conditions and showed lower sensitivity to changes in precipitation compared with European beech and Norway spruce. These findings suggest that Douglas-fir may represent a suitable future tree species for supporting sustainable forest management in Central European lowland forests under increasing drought pressure.

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Appendices

Table A.1: Species-specific parametrization of Douglas-fir (Pseudotsuga menziesii).

Parameter	Value	Unit	Reference
Phenological parameters			
Transfer growth period	30	%	Given as fraction of growing season
Litterfall period	30	%	
Annual turnover rates			
Leaves and fine roots	0.167	$year^{-1}$	(White et al. 2000)
Live wood	0.7	$year^{-1}$	(White et al. 2000)
Whole plant mortality	0.005	$year^{-1}$	
Fire mortality	0	$year^{-1}$	
Allocation ratios			
Fine root C/leaf C	1	ratio	(WR in Thornton et al. 2002)
Stem C/leaf C	2.57		(WR in Thornton et al. 2002)
Live wood C/total wood C	0.073		(White et al. 2000 cit. Panshin et al. 1964)
Coarse root C/stem C	0.1		(WR in Thornton et al. 2002)
Current growth C/storage C	0.5		
C/N ratios			
C/N leaves	45	kgC/kg N	(WR in Thornton et al. 2002)
C/N of falling leaf litter	92		(WR in Thornton et al. 2002)
C/N of fine roots	79		(WR in Thornton et al. 2002)
C/N of live wood	50		(Thornton et al. 2002)
C/N of dead wood	600		(WR in Thornton et al. 2002)
Leaf litter proportions			
Labile proportion	0.31	DIM	(Biomes Mean from White et al. 2000)
Cellulose proportion	0.49	DIM	(Biomes Mean from White et al. 2000)
Lignin proportion	0.2	DIM	(Biomes Mean from White et al. 2000)
Fine roots proportion			
Labile proportion	0.223	DIM	(ENF Mean from White et al. 2000)
Cellulose proportion	0.577	DIM	(ENF Mean from White et al. 2000)
Lignin proportion	0.2	DIM	(WR in Thornton et al. 2002)
Dead wood proportions			
Cellulose proportion	0.76	DIM	(White et al. 2000 cit. Edmonds 1987)
Lignin proportion	0.24	DIM	(Thornton et al. 2002)
Canopy parameters			
Water interception coefficient	0.01	$LAI^{-1}\ d^{-1}$	(Thornton et al. 2002)

Light extinction coefficient	0.5	DIM	(White et al. 2000 cit. Black et al. 1991)
Average specific leaf area	10	$m^2\ kg^{-1}$ C	(WR in Thornton et al. 2002)
Ratio sunlit to shaded LAI	2	DIM	(Thornton et al. 2002)
Ratio all sided to projected LAI	2.36	DIM	(Thornton et al. 2002)
Fraction of leaf N in Rubisco	0.06	DIM	(Thornton et al. 2002)
Conductance parameters			
Maximum stomatal conductance	0.0015	$m\ s^{-1}$	(WR in Thornton et al. 2002)
Cuticular conductance	0.00003	$m\ s^{-1}$	(Thornton et al. 2002)
Boundary layer conductance	0.1	$m\ s^{-1}$	(Thornton et al. 2002)
Boundaries for conduction reduction			
Leaf water potential: start of reduction	-0.6	MPa	(Thornton et al. 2002)
Leaf water potential: complete of reduction	-2.3	MPa	(Thornton et al. 2002)
VPD: start of reduction	500	Pa	Personal assessment
VPD: complete reduction	2000	Pa	Personal assessment
Night temperature: start of reduction	0	°C	Personal assessment
Night temperature: end of reduction	-8	°C	Personal assessment

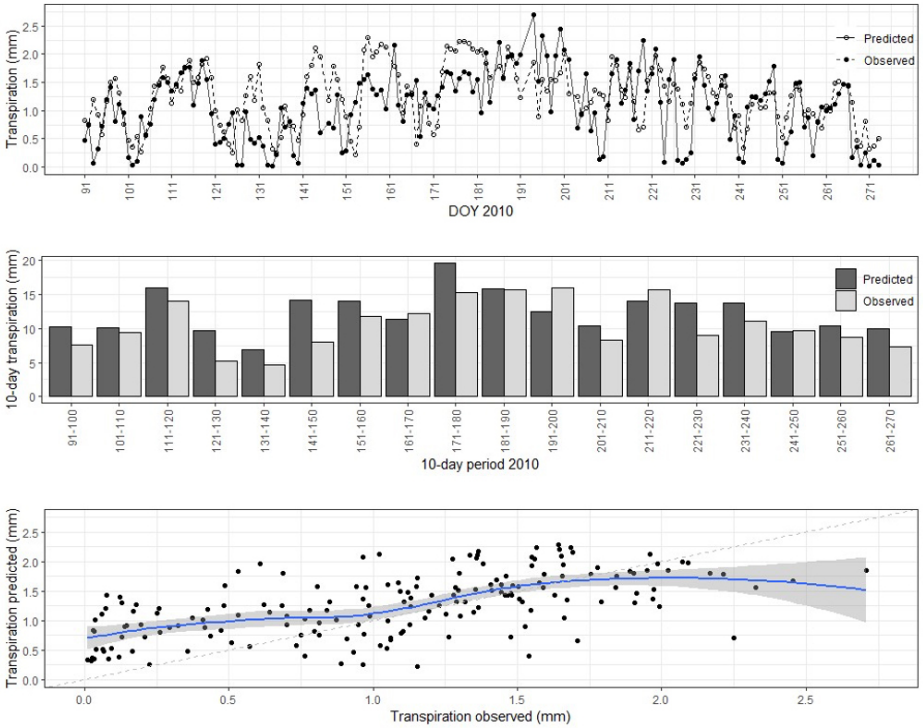


Figure A.1: Predicted and observed daily transpiration rates and 10-day transpiration sums from day of the year (DOY) 91 to 270 in 2010. Predicted transpiration represents the average across the 28 Douglas-fir stands simulated with Biome-BGC, whereas observed transpiration was obtained from the Sapfluxnet database. The correlation between observed and predicted transpiration is shown, with the blue smoothed line representing the general trend between the variables and the gray shading indicating the 95% confidence intervals.

Figure A.1: Geschätzte versus beobachtete tägliche Transpirationsraten sowie 10-Tages-Summen der Transpiration vom 91. bis zum 270. Tag des Jahres (DOY) im Jahr 2010. Die vorhergesagte Transpiration entspricht dem Mittelwert der 28 mit Biome-BGC simulierten Douglasienbestände, während die beobachtete Transpiration aus der Sapfluxnet-Datenbank stammt. Dargestellt ist zudem die Korrelation zwischen beobachteter und vorhergesagter Transpiration, wobei die blaue geglättete Linie den allgemeinen Zusammenhang zwischen den Variablen und die graue Schattierung die 95%-Konfidenzintervalle darstellt.