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ORIGINAL PAPER

Climate change, more than management, drives short- and long-term changes in iWUE in a sub-Alpine beech forest

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Abstract The present study aims to determine the potential impact of recent past, present-day and future climate conditions—along with silvicultural interventions—on the "intrinsic Water Use Efficiency" (iWUE). iWUE, defined as the amount of carbon assimilated per unit of water lost through stomata, is a valuable metric that reflects the combined effects of climate change and forest management on carbon and water balance in forest ecosystems. We studied these effects on a European beech (*Fagus sylvatica* L.) forest, one of the most common tree species in Europe, in a unique pre-Alpine site in Italy subjected to different silvicultural treatments in the past. Therefore, we analyzed iWUE derived from the $\delta^{13}C$ measured isotope for the period 2013–2019 under three different silvicultural schemes observed at the study site. Opposite to what was expected, no statistically significant differences were found on iWUE between the treatments (ANOVA: p-value = 0.21) with a mean value for all treatments ranging from 94 µmol mol^{-1} and 98 µmol mol^{-1}. To explore future dynamics, we used a validated process-based biogeochemical model to simulate iWUE under two climate scenarios (RCP4.5 and RCP8.5) and the same three silvicultural treatments. Again, silvicultural practices showed little effect on iWUE, while differences were evident between climate scenarios and time periods. iWUE increased between the first (2019–2029) and last (2040–2050) decades of simulation by 20.9%, 20.5% and 19.5% for the "Control", "Traditional" and "Innovative" treatments, respectively. In conclusion, in the past and for the next half-decade, silvicultural treatments, at least at the study site, may not influence much the iWUE of beech forests even if it will increase remarkably under climate change.

Keywords Intrinsic Water-Use-Efficiency · Tree-rings · Isotopes · Silvicultural treatments · Forest Modelling · *Fagus sylvatica L*

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Introduction

A plant's metabolic demand for growth and other physiological functions relies on the assimilation of carbon, a trade-off that regulate gas exchange with the absorption of carbon dioxide and the loss of water through stomata regulation (Cowan and Farquhar 1977). The metric used to quantify the amount of water lost to the amount of carbon fixed is commonly defined as "Water Use Efficiency" (WUE), a concept introduced more than a century ago in accordance with Briggs and Shantz (1913). The intrinsic Water Use Efficiency (iWUE), one of the more recently derived WUEs metrics, is defined as the rate of net carbon assimilation (A_n) and stomatal conductance (g_s) and characterizes the physiological controls of carbon and water coupling processes (Farquhar et al. 1982; Bacon 2009). Nowadays, the carbon isotope $\delta^{13}C$ composition is a highly effective and widely used indicator to estimate the iWUE in plant tissues as, for instance, the tree-rings (Farquhar et al. 1989; Saurer et al. 2014; Du et al. 2021). According to Linares and Camarero (2012), iWUE is linked to the inherent adaptive capacity of species to withstand drought. A complex interplay of physiological mechanisms governs iWUE, balancing carbon fixation with water loss in trees (Gessler et al. 2018). Increases in iWUE are often achieved through enhanced photosynthetic capacity or through a reduction in stomatal conductance, a common response to water stress that minimizes transpiration without proportionally lowering CO_2 uptake. However, excessive stomatal closure can lead to a reduction in carbon sequestration and, in turn, to growth reduction and ultimately, if this persists over long periods, to carbon starvation and tree mortality (Sevanto et al. 2014; Hammond et al. 2019). Conversely, if stomatal conductance remains high under limiting water conditions, iWUE may decline, resulting in disproportionate water loss relative to carbon gain, which can lead to reduced photosynthetic activity and culminate in hydraulic failure and soon after in tree mortality (McDowell et al. 2008). This connection highlights the importance of iWUE in assessing the vulnerability of forest ecosystems to climate change. Radiative forcing due to climate change is altering atmospheric water circulation by intensifying atmospheric moisture fluxes. This shift is changing precipitation patterns, with projections indicating that the terrestrial water cycle over land may undergo strong alterations in terms of heavy precipitation and extreme drought events (Allan et al. 2020; IPCC 2023).

Forests worldwide have become increasingly susceptible to warming and drought, even in regions traditionally not considered water-limited, resulting in higher rates of tree mortality (Allen et al. 2010; Camarero et al. 2015). At the same time, across the Alpine region, a seasonal shift is foreseen to occur, which will lead, on average, to an increment in winter and a reduction of summer precipitation (Kotlarski et al. 2023). This shift, combined with an increasing temperature at different altitudes, is expected to strongly affect water availability for vegetation (Nigrelli and Chiarle 2023). However, the capacity to withstand more extreme climate conditions, such as drought, varies depending on the specific traits of each tree species (Eilmann and Rigling 2012). For instance, the anisohydric behaviour of *Fagus sylvatica* L., (European beech) i.e., the tendency to maintain stomatal openness despite decreasing leaf water potential, combined with its root system predominantly concentrated in the topsoil, heightens the species" vulnerability to drought stress (McDowell et al. 2008; Puchi et al. 2024). This predisposition increases the risk of catastrophic hydraulic failure during prolonged dry periods (Leuschner 2020). Dolar et al. (2023) demonstrated, through tree-ring analysis, a declining growth trend in European beech forests, one of the most common tree species in Europe and in Italy, primarily affecting the edges of the beech's geographical distribution, particularly in the sub-Mediterranean regions, considered as vulnerable area, due to high summer temperatures (Noce et al. 2016). Similarly, using tree-ring analysis, Puchi et al. (2024) demonstrated that beech forests at higher latitudes in the Italian peninsula are more vulnerable to extreme drought events than those at lower latitudes but showing, at the same time, a drastic increase in iWUE in the last two decades. In this context, it is largely demonstrated that forest management can have profound effects on processes that drive and control carbon (Nolè et al. 2014; Zhang et al. 2023) including photosynthesis (Merino et al. 2007; Collalti et al. 2018, 2020; Dalmonech et al. 2022; Testolin et al. 2023) and water dynamics, including stomatal regulation (Ferraz et al. 2013; Grant et al. 2013; Del Campo et al. 2022), acting on tree competition for resources such as light and water (Boncina et al. 2007; Goetz et al. 2011; Ammer 2016; Niccoli et al. 2021). Therefore, iWUE is expected to be particularly influenced by management interventions, climate change, ageing, thinning, and changes to stand structure (Rezaie et al. 2018; Fernández-de-Uña et al. 2016; Zhang et al. 2023). However, most of the studies focus on carbon and water fluxes at ecosystem scales, making it difficult to disentangle the direct effect of silvicultural intervention at the ecophysiological level of plants, because of confounding factors such as changes in forest cover, land use or dominant effect on soil evaporation (Cui et al. 2024; Hu et al. 2024). For these reasons, modeling efforts to simulate forest carbon and water processes are essential for understanding the iWUE long-term dynamics under the effect of a changing climate and silvicultural interventions.

Detailed ecophysiological forest models are particularly effective mathematical tools for investigating tree response to changing environmental conditions due to meteorology and increasing atmospheric CO_2 and silviculture, by linking key processes, such as growth, mortality and water- (H_2O)

and carbon- (C) use-efficiency, which are critical variables for assessing the forest's mitigation potential but which are, unfortunately, often understudied (Pilli et al. 2022; Testolin et al. 2023, Boukhris et al. 2025). Therefore, this study aims to examine: (i) potential differences in the iWUE of European beech forests and present-day climate conditions because forest management and the possible (if any) differences between different treatments; and, (ii) to what extent future climate changes may impact iWUE, and whether it will vary across different management scenarios. We tested the hypotheses that forest management significantly influences iWUE and that different management schemes result in distinct iWUE responses, using a pre-Alpine beech forest in Cansiglio, Italy, as our study site. This location provided a unique opportunity, having undergone various silvicultural treatments in recent years and offering multi-source observational data for each treatment, an approach, to our knowledge, not previously documented in the literature. To this aim, we analysed observed carbon isotope signals from the differently managed monitored plots of European beech for the recent past and present-day climate. Subsequently, we applied a validated state-of-the-science biogeochemical, biophysical, process-based model, namely 3D-CMCC-FEM, to simulate recent past, present-day, and future climate, combined with different forest management and their effects on iWUE.

Materials and methods

Site description

The study was conducted in a pure beech forest, even-aged, approximately 120 years old, located in the northeastern Alps in the Cansiglio site, Veneto region, at latitude 46°02′ N and longitude 12°22′ E, Italy (Fig. 1). The site, located at an elevation of 1300 m a.s.l., experiences a mean annual precipitation (MAP) of 2219 mm and a mean annual air temperature (MAT) of 6.7 °C for the reference period 2010–2022. The site is characterized by the presence of an oceanic climate and an absence of significant summer drought, maintaining a copious precipitation regime throughout the year (Fig. S1). According to the USDA soil classification system, soils are classified as Haplic luvisols.

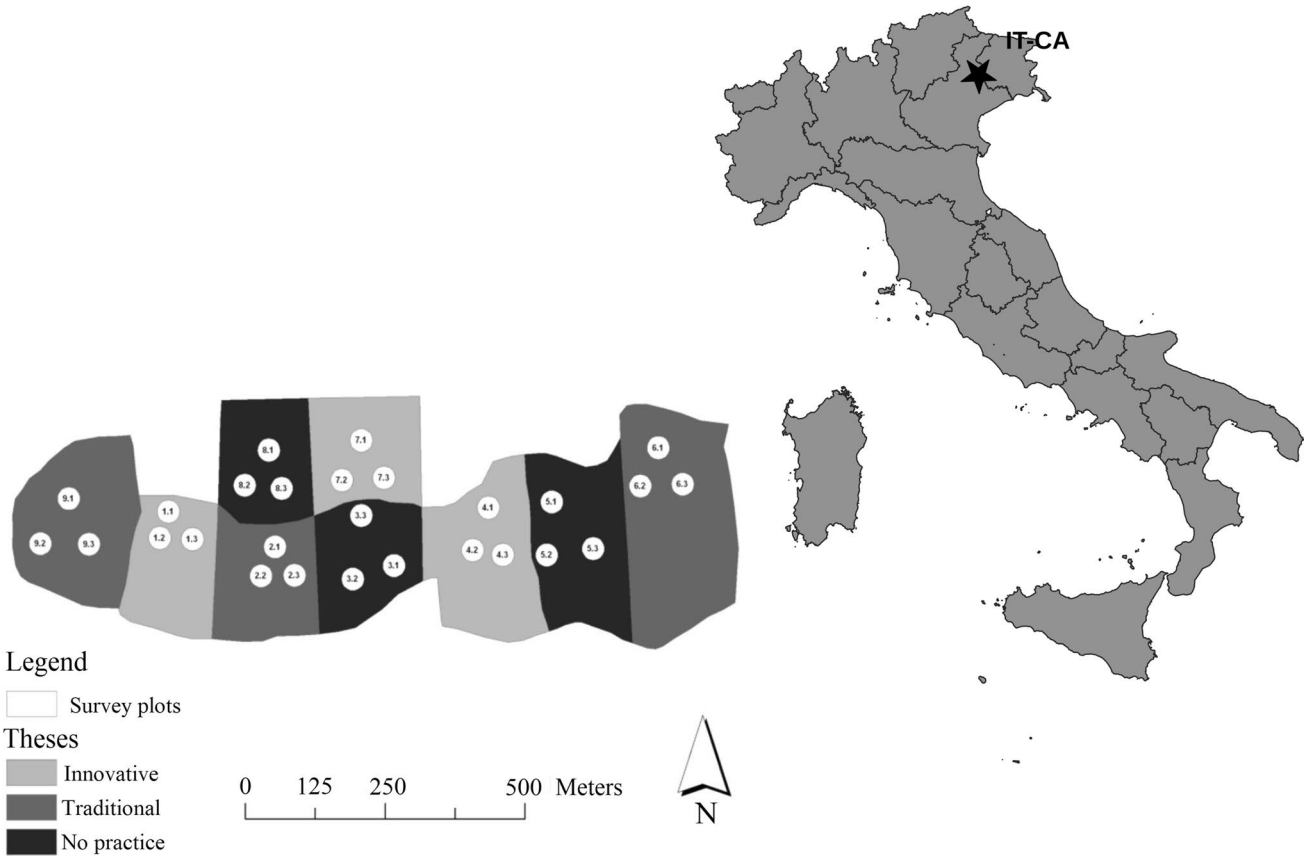

Fig. 1 Location of the Cansiglio site in the Italian peninsula and treatment scheme. The "Control" plots (black), the Traditional plots (dark-grey) and the Innovative ones (light-grey). The white circles represent the sampling sub-plots within the plots (from https://www.manfor.eu/new/?page_id=379)

The experimental area comprises nine monitored plots, each exceeding 3 ha and previously unmanaged, covering a total of approximately 27 ha. In 2012, out of the nine plots, three were left unmanaged, allowing for natural stand development, and designated as "Control" plots, three plots were managed using the shelterwood system ("Traditional"), and the remaining three with the innovative cutting regime ("Innovative") selecting a variable number of well-shaped candidate trees and thinning neighbouring competitors (Fig. 1, Table 1).

Dendrochronological data processing

In September 2019, three out of nine plots in the forest stand for isotopic analysis, where silvicultural treatments had been conducted earlier, were selected. From each plot, five co-dominant trees were sampled using a 10 mm increment borer. This included five trees from the "Control" plot, five from the traditional plot, and five from the innovative plot. Standard dendrochronological methods were employed to date the tree rings using a LINTAB measuring table (Rinntech, Heidelberg, Germany) equipped with a Leica MS5 stereoscope (Leica Microsystems, Wetzlar, Germany) and analyzed with TSAPWin software.

Cellulose extraction from the individual tree-rings, for the period 2010–2019 was performed according to Boettger et al. (2007), which was later used to determine the isotopic composition of tree carbon ($\delta^{13}C_{tree}$) calculated using the following Eq. 1:

$$\delta^{13}C_{tree} = \delta^{13}C_{atm} - a - \frac{[(b-a)\cdot c_i]}{c_a} \quad (1)$$

where $\delta^{13}C_{atm}$ is the proportion of ^{13}C in the atmosphere (approximately 8‰ during the twentieth century), a (4.4‰) and b (27‰) the fractionations associated with the diffusion of $^{13}CO_2$ in air and in vitro estimations of Rubisco carboxylation, respectively, according to Farquhar et al. (1982), the two terms C_a and C_i represent the mole fraction of CO_2 in the air and the intercellular spaces, respectively (Farquhar and Richards 1984).

Subsequently, following Francey and Farquhar (1982), we determined c_i as Eq. 2:

$$c_i = c_a \cdot \frac{(\delta^{13}C_{atm} - \delta^{13}C_{tree} - a)}{(b - a)} \quad (2)$$

and the iWUE was calculated as Eq. 3:

$$iWUE = \frac{(c_a \cdot b - \delta^{13}C_{atm} - \delta^{13}C_{tree})}{1.6(b - a)} \quad (3)$$

where 1.6 is the ratio of water and CO_2 diffusivity in the atmosphere. However, due to lack of species-specific parameters data and large uncertainties in determining the mesophyll conductance we applied the simplified model of isotopic discrimination, which does not account for mesophyll conductance or photorespiration.

The values of $\delta^{13}C_{atm}$ used for the period 2010–2019 were obtained from (https://gml.noaa.gov/ccgg/arc/index.php?id=134), while the annual atmospheric CO_2 concentration from the Mauna Loa station data (https://gml.noaa.gov/ccgg/trends/).

The process-based model 3D-CMCC-FEM

The eco-physiological, biogeochemical and biophysical model 3D-CMCC-FEM v.5.6.06 (Collalti et al. 2014, 2024; Marconi et al. 2017; Dalmonech et al. 2022, 2024; Morichetti et al. 2024; Vangi et al. 2024a, 2024b) was designed to simulate carbon, nitrogen and water fluxes by incorporating key ecohydrological processes within forest ecosystems. The model provided robust evidence in simulating carbon and water fluxes across different sites populated by beech forests, as described in, e.g., Collalti et al. (2016), Mahnken

Table 1 Forest structure before and after thinning, based on sample data in 2011 and 2019, respectively

Sample	Before Thinning (2011)			After Thinning (2019)		
	n (ind.$^{-1}$)	Mean DBH (cm)	Mean Height (m)	n (ind.$^{-1}$)	Mean DBH (cm)	Mean Height (m)
Plot1	360	40.34	26.55	196	45.83	27.47
Plot2	310	40.41	26.59	244	42.97	26.86
Plot3	363	38.39	26.11	347	40.51	26.28
Plot4	283	43.37	27.18	145	49.44	28.14
Plot5	244	42.39	27.03	244	44.4	27.17
Plot6	339	41.51	26.84	238	44.45	27.18
Plot7	315	41.2	26.77	175	45.92	27.5
Plot8	387	37.91	26	387	39.47	26.03
Plot9	326	36.84	25.71	209	42.13	26.64

"n" represents the number of trees in the forest stand, while DBH refers to the mean diameter at breast height. The table also includes the mean tree height for each sampling period

et al. (2022) and Saponaro et al. (2025) even at the National level Vangi et al. (2025) The model employs species-specific parameterization and simulates at a consistent spatial resolution of 1 ha, with temporal scales ranging from daily to monthly and annual, depending on the simulated process. The 3D-CMCC-FEM model simulates photosynthesis (A_n), according to the biochemical model of Farquhar et al. (1980), with temperature acclimation as in Kattge and Knorr (2007) and soil moisture influence as in Bonan et al. (2011) as shown in Eq. S1, S2 and S3.

Daily stomatal regulation follows the Jarvis stomatal regulation model (Jarvis 1976) where the maximum stomatal conductance (m sec^{-1}, i.e., the stomatal conductance with no limitations) multiplied by a list of factors "*f*" influencing the degree of the stomatal opening degree varying from 0 (total limiting) to 1 (not limiting) (Eq. S4). All these variables have a direct effect on the conductance and are described in Collalti et al. (2018, 2024). Autotrophic respiration (R_a) is computed explicitly through the "growth and maintenance-respiration-paradigm", which accounts for maintenance (that supports the maintenance of existing tissues) and growth respiration (that supports the synthesis of new tissues) (Amthor 2000). Net primary production (NPP) is the difference between gross primary production (GPP) and R_a. Whenever during the year plant respiration exceeds photosynthesis, i.e., when NPP < 0, non-structural carbohydrates (NSC; sugar and starch, undistinguished) support growth (for leaf expansion and fine root growth during spring) or metabolism (all other periods of the year, Collalti et al. 2020). When the vegetative season begins, which depends on the species-specific thermal sum, the model allocates non-structural carbon to leaves and fine roots as a primary process (Puchi et al. 2026). The daily fraction of carbon allocated to leaves (both sunlit and shaded), the specific leaf area value, and the single-tree canopy coverage, based on the current sapwood area regulated by the "pipe-model" theory (Shinozaki et al. 1964a, 1964b, Puchi et al. 2026), determine the maximum leaf carbon allocation and the maximum Leaf Area Index (LAI). At the tree level, the 3D-CMCC-FEM takes account environmental variability, including extremes such as edaphic and atmospheric drought and increase in temperature, on the tree physiology in both direct way by acting on the photosynthetic process, i.e., the rate of carboxylation and stomatal conductance, and indirectly regulating carbon allocation paths and on increasing in autotrophic respiration respectively and, thus, on NSC usage.

iWUE, is determined as the ratio of net CO_2 assimilation rate (excluding dark respiration, A_n) to stomatal conductance (g_s) as shown in Eq. S5.

This calculation is performed on a daily scale and considers the average tree within the stand, as the model is not individual-based. We considered the whole vegetative period simulated by the model for the iWUE calculation, and these values were compared to the estimates by means of the isotopic signature of the interested plots.

Input data, management schemes and simulation set-up

To perform the simulations, the model requires essential stand-level variables, namely the species, tree density (ind ha^{-1}), mean tree diameter at breast height (DBH, cm), tree height (m), and stand age at the beginning of the simulation. Soil texture, quantified as the percentage of sand, silt and clay, and soil depth are also essential inputs for the models and were derived directly from field campaigns. A comprehensive species traits information is provided to the model, considering physiological parameters specific to the species within the stand (Table S1 of model parameters and the sensitivity analysis to parameters in Collalti et al. 2019). The meteorological datasets utilized as forcing for the 3D-CMCC-FEM model were the recent past and present-day climate (called "historical") and two representing future climate scenarios, under the representative concentration pathways RCP4.5 and RCP8.5 (Van Vuuren et al. 2011) as used in the Coupled Model Intercomparison Project Phase 5 (CMIP5). The historical observed climate data was obtained at a daily temporal resolution from the relevant Regional Environmental Protection Agencies (ARPAs) in Italy, which track meteorological variables via ground weather stations. The climate scenario data for RCP4.5 and RCP8.5 were derived from climate data dynamically downscaled by means of the regional climate model COSMO-CLM provided at a high spatial resolution of approximately 2.2 km over Italy (Raffa et al. 2023). Specifically, variables such as mean solar radiation, maximum and minimum air temperature, and precipitation were retrieved for both databases (ARPA and COSMO-CLM). Mean relative air humidity was calculated using modelled atmospheric pressure and dewpoint temperature, following Upreti and Ojha (2017) for the historical climate. The simulations were conducted for each plot from 2010 to 2022 for the observed historical climate, using data from the first sampling campaign for stand structural data to initialize the forest model. For the RCP4.5 and RCP8.5 climate scenarios, simulations were performed from 2019 to 2050, incorporating data from the second sampling campaign (after thinning) for stand structural data. The model uses daily meteorological forcing as mean solar radiation at the surface (MJ m^{-2} d^{-1}), maximum and minimum air temperature (°C), precipitation (mm d^{-1}), and mean relative air humidity (%). Simulations were conducted following the management protocol established by the LIFE-ManFor project (De Cinti et al. 2016), which involved the removal of a specified percentage of the basal area (BA) where for the "Traditional" is around 33% and for "Innovative" plots 47% (Table 2 of Management protocol). A "Control" scenario,

Table 2 Year of thinning and average percentages of basal area (BA) removed for each plot

Year of thinning	Management type								
	Innovative			Traditional			Control		
	Plot 1	Plot 4	Plot 7	Plot 2	Plot 6	Plot 9	Plot 3	Plot 5	Plot 8
2012	40%	40%	40%	33%	33%	33%	–	–	–
2027	–	–	–	30%	30%	30%	–	–	–
2032	40%	40%	40%	–	–	–	–	–	–
2042	–	–	–	30%	30%	30%	–	–	–

Plots 3, 5 and 8 correspond to the "Control" treatment, which includes no cutting, while plots 2, 6 and 9 correspond to the "Traditional" treatment, and plots 1, 4 and 7 correspond to the "Innovative" treatment

which includes no cutting and leaving the stands to natural development with no interventions, was also considered. The simulation period for the historical climate scenario spanned from 2010 to 2022, with the first thinning occurring in 2012. Simulations for the RCP4.5 and RCP8.5 climate scenarios began in 2019 and extended to 2050, incorporating the management scheme that involves the periodic removal of a fixed percentage of BA, every 15 years for "Traditional" and 20 years for "Innovative" following the initial thinning in 2012, up to 2050, i.e., the future scenario (Table 2).

Statistical analysis

To identify the effects and the relative significant differences, if any, between the different treatments considered in this study on the observed iWUE, we performed the analysis of variance (ANOVA) test for normal data. Before performing ANOVA, we tested assumptions such as Shapiro–Wilk and Levene analysis to determine the normal distribution and homogeneity. The post-hoc Tukey's HSD analyses were carried out to detect further differences between silvicultural treatments. Analyses were conducted over a defined period (2013–2019) for the observed data to assess iWUE signals following biomass removal in 2012 and to capture potential differences in the treatments. In addition, we performed the Kruskal–Wallis and post-hoc Dunn test on the modelled iWUE to determine the differences in iWUE between treatments. This choice was based on the nature of the data (e.g., normal or non-normal), as determined by the assumption tests.

Furthermore, we used the non-parametric Wilcoxon rank-sum test to assess the significance of differences, if any, in distributions over various years and between the observed and modelled iWUE based on the treatments.

Differently, to analyze the effects of silvicultural interventions and climate within the same climate scenarios but between treatments and within the same treatment but between different climate scenarios, a linear mixed model (LMM) analysis was performed. This approach, generalize ANOVA by accommodating random effects and temporal correlations, allows understanding the important effects between and within levels for the time series data and also the interactions between the various factors (the predictors). Assumption tests were conducted first, including the Shapiro–Wilk test for normality, the homoscedasticity of residual variance, and, finally, the Durbin-Watson test for residual autocorrelation.

Statistical analyses were performed using *SciPY* and *Statsmodels* modules (Python version 3.12.4; Python Software Foundation).

Results

iWUE differences between the silvicultural treatments

No differences were observed in iWUE for the period 2013–2019. The ANOVA analysis for iWUE observed, revealed no statistically significant differences across the various management practices (p-value = 0.21, Table 3). This is supported by the Tukey HSD test which indicated limited variability between the treatments of observed iWUE (Table 3), thus, no management effects. In line with the observed iWUE data, modelled iWUE showed similar results. All the results are shown in Fig. 2, Table 3 and Table S2 for the assumption tests.

Model evaluation

Tree-ring $\delta^{13}C$-derived iWUE was compared with the iWUE simulated by the model (Fig. 3, Table 4). During the period 2010–2019, the annual observed iWUE values ranged from 91.6 to 107.6 µmol mol^{-1} for the "Control", from 92.4 to 102.6 µmol mol^{-1} for the "Traditional", and from 85.9 to 100.6 µmol mol^{-1} for the "Innovative" treatment. Similarly, the annual simulated iWUE values varied from 84.7 to 112.8 µmol·mol^{-1} for the "Control", from 89.8 to 112.8 µmol mol^{-1} for the "Traditional", and from 87.2 to 112.8 µmol mol^{-1} for the "Innovative" treatment, respectively. In addition, the observed and modeled data

Table 3 In the top table ANOVA and TUKEY-HSD analysis conducted over the period from 2013 to 2019 for observed iWUE (µmol mol^{-1})

ANOVA						
	sum_sq	df	F	*p*-value		
variable	64.49	2.0	1.66	0.21		
Residual	348.15	18.0				
Multiple Comparison of Means-Tukey HSD, FWER = 0.05						
Group 1	Group 2	mean_diff	*p*-adj	lower	upper	Reject
Control	Traditional	−0.87	0.92	−10.07	1.92	False
Control	Innovative	−4.07	0.22	−6.87	5.12	False
Innovative	Traditional	3.20	0.38	−2.79	9.20	False
Kruskal–Wallis test						
	F	*p*-value				
variable	4.83	0.09				
Multiple Comparison-Dunn test, FWER = 0.05						
	Control	Traditional	Innovative			
Control	1	0.08	0.90			
Traditional	0.08	1	0.73			
Innovative	0.90	0.73	1			

In the bottom table Kruskal–Wallis test and Dunn-test analysis conducted over the period from 2013 to 2019 for modelled iWUE (µmol mol^{-1}). In each test has been considered various management scenarios, show the difference between "Innovative", "Traditional" and "Control" treatments. The significance level is set at a *p*-value of less than 0.05

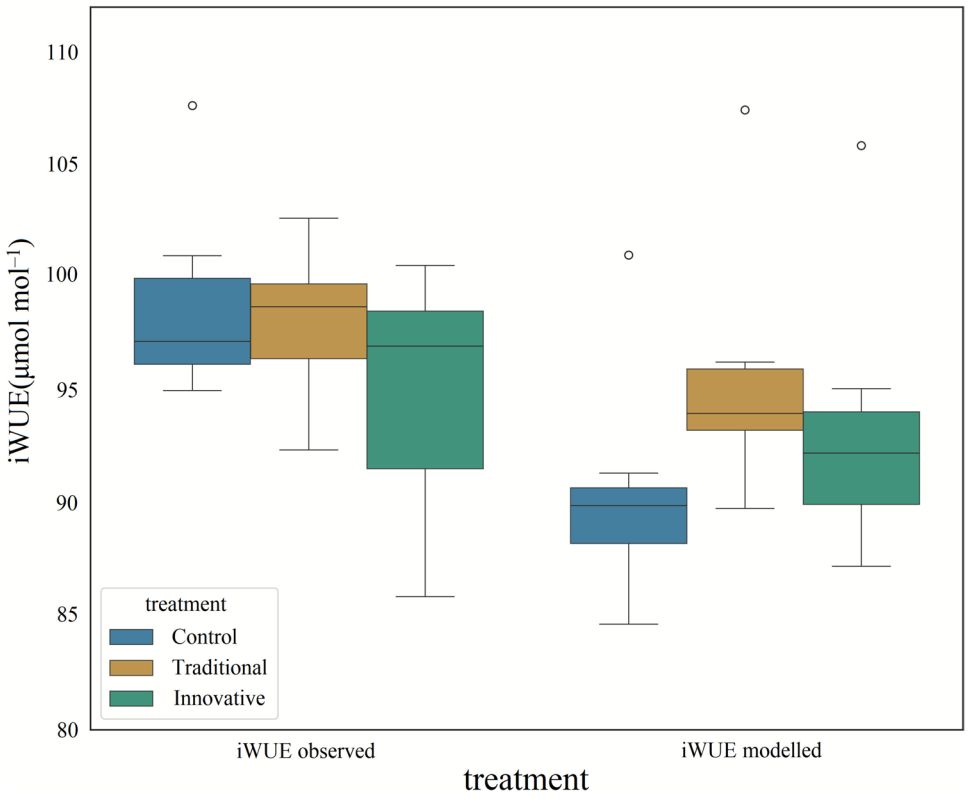

Fig. 2 Boxplots between treatments in terms of intrinsic Water Use Efficiency (iWUE) µmol mol^{-1} of the observed (on the left) and modelled (on the right) data for the period 2013–2019. The central mark represents the median, while the lower and upper edges of the box correspond to the 25th and 75th percentiles, respectively. The "whiskers" extend beyond the box to indicate the data range, excluding outliers, which are plotted as individual points beyond the whisker length

showed similar distribution patterns, with no significant differences detected, as indicated by the *p*-values from the Wilcoxon rank-sum test (Table 4) for the "Control", "Traditional" and "Innovative" treatment, respectively. In addition, daily C fluxes were evaluated against daily Sentinel2 products for the reference period (2015–2022)

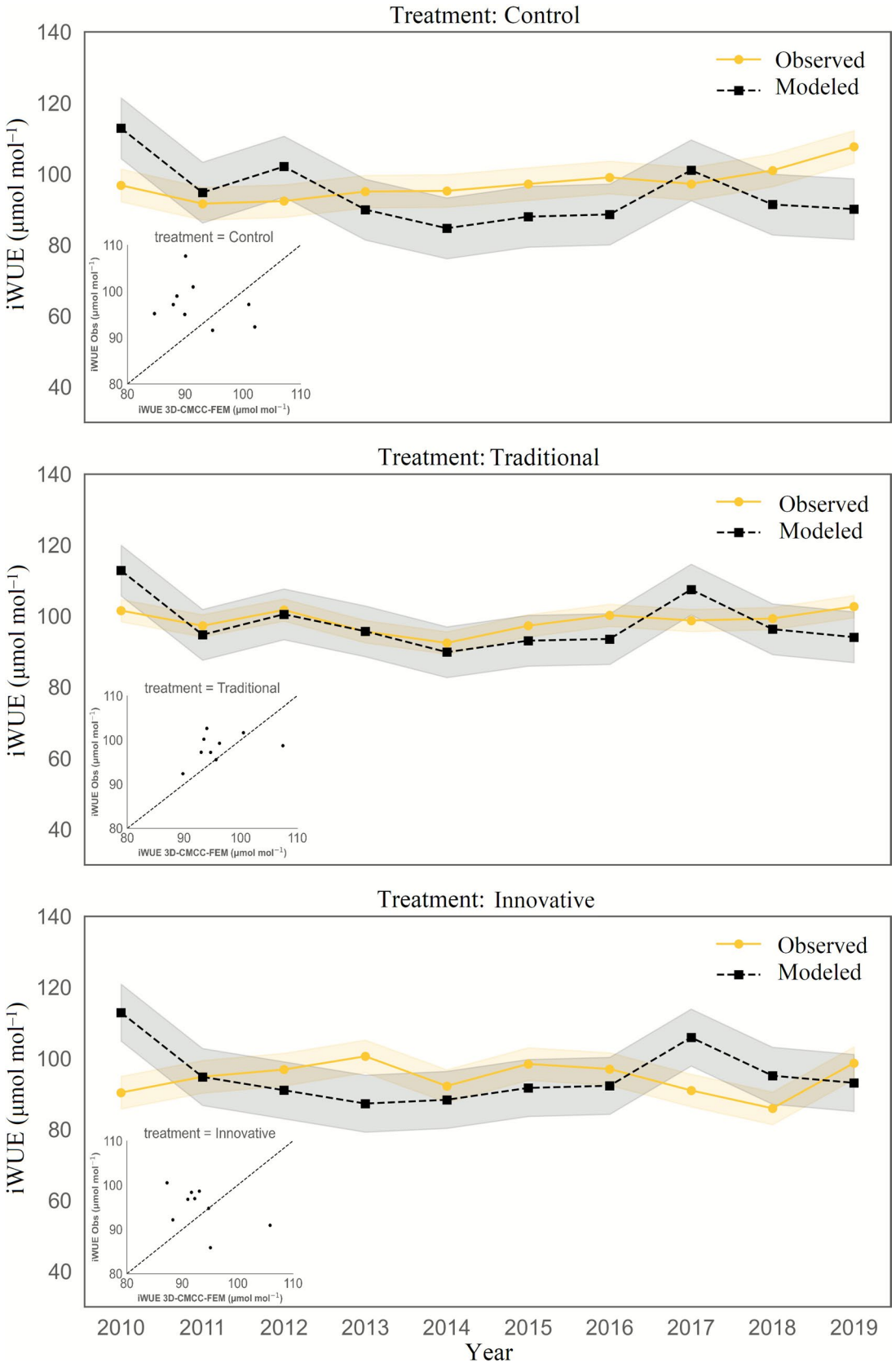

Fig. 3 iWUE (µmol mol^{-1}) modelled by the 3D-CMCC-FEM model and observed from tree-ring between treatments for the period 2010–2019. The shaded area represents the standard deviation. Each panel inside also shows the regression plot

Table 4 The Root Mean Square Error (RMSE, µmol mol^{-1}), the Mean Absolute Error (MAE, µmol mol^{-1}), the Wilcoxon rank-sum test statistics and *p*-value for, the iWUE (µmol mol^{-1}) of the daily simulations at Cansiglio site performed by the 3D-CMCC-FEM and compared with tree-ring data in the beech forest plots

Sample	RMSE	MAE	Wilcoxon stat	Wilcoxon *p*-value
Control	4.23	3.34	−1.51	0.13
Traditional	3.64	2.7	−0.38	0.71
Innovative	2.61	2.12	−1.13	0.26

Statistical significance was defined as $p > 0.05$

using historical climate data and Sentinel2-provided data at the plot level and for each single plot. The evaluation is shown in the supplementary materials (Fig. S2, Table S3).

iWUE results under climate change scenarios and silvicultural treatments

The inter-annual variation of iWUE based on silvicultural systems and climate scenarios was evaluated. No statistically significant differences were observed between the different treatments (Table 5). In addition, no differences were found across both RCP scenarios until 2050 (Fig. 4, Fig. S4). During the period 2019–2050, the annual mean iWUE under the RCP4.5 scenario was 141.6 ± 31.0 µmol·mol^{-1} (here and elsewhere, ± denotes one standard deviation) for the "Control", 137.0 ± 24.9 µmol·mol^{-1} for the "Traditional" and 137.8 ± 27.4 µmol mol^{-1} for the "Innovative" treatment, respectively. Under the RCP8.5 scenario, the iWUE values were 141.7 ± 33.3 µmol mol^{-1}, 137.0 ± 28.3 µmol mol^{-1} and 137.6 ± 30.6 µmol mol^{-1} for the "Control", "Traditional" and "Innovative" treatments, respectively. The LMM analysis showed a significant increase in iWUE for the decade 2019–2029 compared to the decade 2040–2050

Table 5 Results of the mixed linear model regression for the effect of treatment ("Control", "Traditional" and "Innovative") and climate scenario (RCP4.5, RCP8.5) over years of simulation on the iWUE variable

Effect	Coefficient	Std. Error	*z*-value	*p*-value	95% CI Lower	95% CI Upper
Intercept	−3374.80	591.66	−5.70	< 0.001*	−4534.44	−2215.15
Innovative *vs* Control	−3.75	5.32	−0.71	0.48	−14.18	6.67
Traditional *vs* Control	−4.55	5.32	−0.85	0.39	−14.97	5.87
RCP4.5 *vs* RCP8.5	0.14	5.32	0.03	0.98	−10.28	10.57
Innovative × Scenarios	−0.33	7.52	−0.04	0.96	−15.07	14.4
Traditional × Scenarios	−0.19	7.52	−0.02	0.98	−14.92	14.55
YEAR	1.73	0.29	5.94	< 0.001*	1.16	2.3
Group Variance	155.3	3.06	–	–	–	–

The table reports the main effects of the three factors and their interactions. The significance level is set at a *p*-value of less than 0.05. *p*-values with * indicate statistically significant variables.

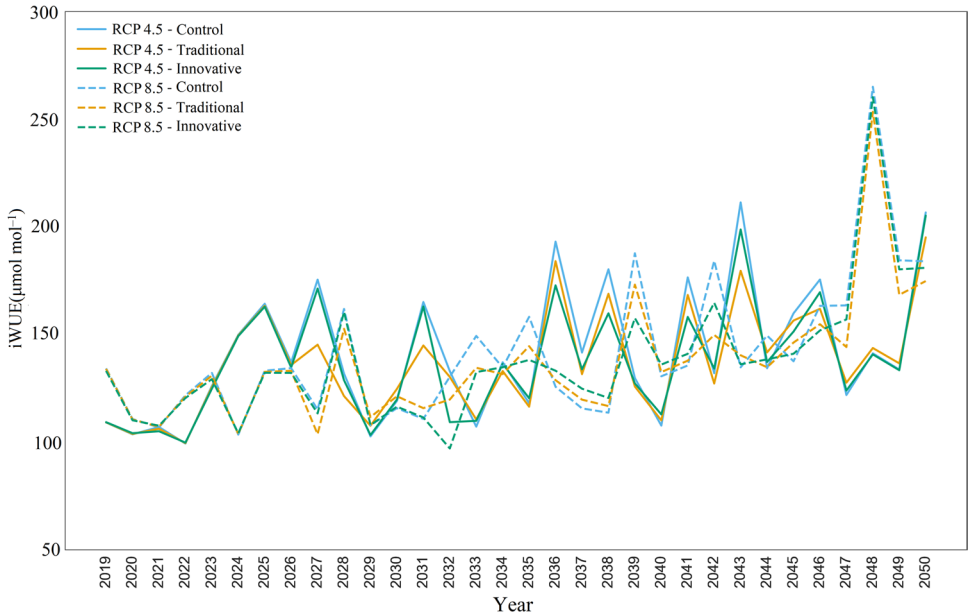

Fig. 4 Projected iWUE (µmol mol^{-1}) simulations using the 3D-CMCC-FEM model under different silvicultural systems ("Control", "Traditional" and "Innovative", averaged across all plots within each treatment) and under future climate scenarios (2019–2050). These projections are derived from COSMO-CLM simulations at ~ 2.2 km spatial resolution over Italy. The solid blue line represents the "Control" treatment, the solid orange line denotes the "Traditional" treatment, and the solid green line indicates the "Innovative" treatment under the RCP 4.5 climate scenario. Dashed lines in the same colors correspond to the RCP 8.5 climate scenario

(assumptions tests are shown in Fig. S3). Under the RCP4.5 scenario, the "Control" showed an increase of 20.9%, the "Traditional" treatment 20.5%, and the "Innovative" treatment 19.5%. Under the RCP8.5 scenario, the "Control" showed an increase of 34.6%, the "Traditional" treatment 29.5% and the "Innovative" treatment 32.3% (Fig. 4, Fig. S4 and Table 5).

Discussion

Overview

Despite increasing interest in forest responses to climate change and management (and its different treatments), relatively few studies have questioned about their role on iWUE. This study addresses that gap by investigating the effects of three silvicultural treatments on iWUE, using tree-ring-derived field data from a European beech in an Italian pre-Alpine forest under recent-past and present-day climate. By integrating these empirical observations with a mechanistic modelling framework, the study explores both historical and projected future dynamics of iWUE under the same different management scenarios, providing insights, at least for the test site, into the long-term impacts of forest management strategies under changing climatic conditions.

Observed and Modelled iWUE in the present-day climate

The effects of forest management on iWUE remain a debated yet unresolved topic. Based on the ANOVA analysis of observed iWUE tree-ring α-cellulose data, there are no differences between different silvicultural treatments. Similarly, modelled iWUE values did not show any treatment-related variation. Our analysis is in line with Martín-Benito et al. (2010) for a *Pinus nigra* (Arnold.) forest stand, showing no significant differences between silvicultural treatments (Fig. 2, Table 3 and Table S2), which, maybe, could be reflected in other types of WUE as seen e.g. for AGB-WUE (Forrester et al. 2012). Conversely, Rezaie et al. (2018) suggested that silvicultural treatments can enhance iWUE, based on the hypothesis that thinning alters canopy structure by increasing the ratio of sunlit to shaded leaves, thereby boosting the proportion of sunlit foliage, which exhibits higher photosynthetic rates (Scartazza et al. 2016). Moreover, the canopy openings, created by thinning, can temporary increase the available light, along with the "remaining trees" ability to expand their canopy, also laterally (Granier et al. 2008; Bayer & Pretzsch 2017). However, an increase in the light availability due to thinning could not necessarily and automatically be mirrored in a significant increase in the net assimilation because of light saturation. European beech is, indeed, a very shade-tolerant tree species (Szwagrzyk et al. 2012). Moreover, the canopy openings created by thinning allows precipitation, both as liquid or as snow, to reach the forest floor more directly. This leads to a greater increase in soil water content and availability compared to un-thinned forests, where interception by the canopy is higher. As a result, the enhanced soil moisture can be sustained even during drier periods, such as summer (Dalsgaard 2007; Gao et al. 2022). However, according to Saurer et al. (2014), this increase is not spatially uniform across the sites and is strongly dependent on soil water availability, which, in turn, much depends on soil characteristics. At the opposite, whether an increase in light availability would lead to an increase in assimilation rate without saturation effects, this would also necessarily result in an increase in stomatal water loss. Ultimately, these two factors (increased assimilation and increased water loss), rising in parallel, may compensate each other, resulting in no net differences between the iWUE across the different silvicultural treatments. In addition, variables such as air temperature, precipitation, the main driver of evaporative demand (VPD) and soil water content (SWC) are important factors controlling the spatial pattern of iWUE in forest ecosystems as well as the stomatal response, especially during the vegetative period (Yu et al. 2008; Sulman et al. 2016; Yuan et al. 2019). The sub-Alpine Cansiglio site exhibits an abundant precipitation regime, unaffected by low summer rainfall, with mean annual temperatures within the optimal growth range for *Fagus sylvatica* and no drought events have been reported so far ("SPEI" in Supplementary information and Figs. S9, S10). Since the Cansiglio site did not experience drought years during the analyzed period, this positive feedback, as a result of the management, does not appear to have significantly impacted the iWUE from the "Control". Moreover, in even-aged mature forest stands, the effectiveness of thinning to the remaining trees may be limited, as mature trees have a reduced capacity to respond further to management interventions, and their productivity may unavoidably decline with ageing (Pregitzer and Euskirchen 2004). This may result in a weak iWUE response within the stand to thinning regimes independently of its intensity and frequency as found here.

Modelled iWUE under present-day climate

When comparing the annual iWUE in modelled values, the slight disagreement in interannual variability in iWUE values may lie in the model's high sensitivity to multiple meteorological factors, including temperature, precipitation, solar radiation and some parameters related to forest structure (Collalti et al. 2018, 2019). Notably, model evaluation against Sentinel-2-derived GPP data reveals a tendency to slightly overestimate daily GPP, a pattern consistent with findings from previous studies in other, few, sites (e.g.,

Collalti et al. 2016; Saponaro et al. 2025). Since iWUE is intrinsically linked to the ratio of carbon assimilation to stomatal conductance, any bias may directly influence iWUE outputs. However, the model was not specifically calibrated for the site, which may further contribute to these discrepancies.

Overall, the model demonstrates, as already done at other sites and for different species and management schemes with generic (not site-specific) parameterizations (Mahnken et al. 2022; Testolin et al. 2023; Morichetti et al. 2024), good predictive capability for these ecological variables. However, the statistical analyses show that measured and modelled iWUE values between the different treatments are, in absolute terms, comparable.

iWUE under climate change scenarios and implications for management

Under future climate scenarios (RCP4.5 and RCP8.5), which imply warmer and drier conditions but even higher atmospheric CO_2 concentrations, we found no substantial differences in iWUE as confirmed by the LMM analysis between the different treatments (Table 5). Both the "Traditional" and "Innovative" treatments resulted in unaffecting the iWUE compared to the "Control" treatment, with p-value = 0.39 for the "Innovative" treatment and p-value = 0.48 for the "Traditional" treatment. Furthermore, neither the RCP4.5 nor the RCP8.5 climate scenarios produced statistically significant effects (p-value = 0.98) within the management framework. Moreover, the interaction terms between treatments and climate scenarios were non-significant (p-value = 0.96 and p-value = 0.98, respectively), suggesting that the iWUE reductions due to management were not consistent across both climate scenarios (Table 5).

An increase in iWUE over years observed in our simulations is consistent with what described in the text books and the literature (Frank et al. 2015; Keenan et al. 2013), due to a physiological response to rising atmospheric CO_2 concentration (C_a) and not counterbalanced by an increase in water loss through stomata. An increase in atmospheric CO_2 concentration, which in turn leads to an increase in intercellular CO_2 concentration (C_i), is itself influenced by climatic variability. Indeed, a closer analysis of the modeled assimilation rate (A_n) reveals statistical differences (indicating an increase in assimilation rate ranging from 1.6% to 8.42%) for the "Control", "Traditional" and "Innovative" treatments between the two climate scenarios and over years of simulation (Fig. S5 and S6 for the assumptions test, and the LMM analysis presented in Table S4). In addition, stomatal conductance (g_s) showed statistical differences (decreasing) just over years of simulation, indicating a reduction ranging from 11 to 18% for both silvicultural treatments and climate scenarios (Fig. S7 and S8 for the assumptions test, and the LMM analysis presented in Table S5). The percentage differences are calculated considering the decades 2019–2029 and 2040–2050. Unfortunately, the literature offers few studies for direct comparison with our results. To the best of our knowledge, this is one of the first studies to simultaneously examine the effects of different forest management schemes and climate change on iWUE.

Summary, limitations and uncertainties

The isotopic approach assumes that C_a and C_i (the mole fraction of CO_2 in the air and in the intercellular spaces) are the only non-constant factors that control the isotope fractionation occurring at the leaf level. Consequently, in the iWUE calculation we did not consider two aspects that, at the same time, lacks also in the model, i.e., the mesophyll conductance of CO_2 (Seibt et al. 2008; Márquez and Busch 2024) and post-photosynthetic processes that may potentially affect tree-ring α-cellulose $\delta^{13}C$ (Gessler et al. 2014; Frank et al. 2015; Lavergne et al. 2019). This can create additional variability that may not be fully captured and reproduced by the model. In addition, the effects of increased atmospheric CO_2 on plant drought response are complex and can strongly influence physiological processes such as stomatal behaviour and mesophyll conductance for Rubisco activity (De Kauwe et al. 2021; Sun et al. 2014) and more generally, also to primary productivity (Dunkl et al. 2023). The warmer and drier conditions of the climate scenarios will likely influence iWUE in the next decade in our study site. Nevertheless, different thinning regimes will likely not affect iWUE in this mature, even-aged beech stand. Importantly, based on these findings, no early warning signs of water stress were detected and foreseen. This could suggest that as in the recent-past and present-day climate, as even under future environmental conditions (up to 2050), water availability will not be a limiting factor for beech stands at the Cansiglio site (in Supplementary information and Figs. S9 and S10) and that species-specific traits, such as its anisohydric behavior, may ensure synchronicity to optimize (and even increase) the trade-off between photosynthesis and water loss. Furthermore, several factors not directly considered in this study could influence the regulation of iWUE, such as nitrogen deposition (Adams et al. 2021; Du et al. 2025), tropospheric ozone (Holmes 2014), and non-anthropogenic disturbances (Zhao et al. 2021). Although our findings are based on a single site without comparable replications in the pre-Alpine region, a thorough literature review revealed no other studies that provide multi-source observational data for each silvicultural treatment simultaneously, making this site uniquely valuable for such analyses. While the results may appear site-specific, we believe they are broadly representative—not only for this location—but also scalable to other

Europena beech forests, as they are grounded in fundamental principles discussed in detail in the Discussion section.

Conclusion

To assess the short- and long-term impacts of different silvicultural schemes and climate change scenarios on iWUE, we analyzed responses in a single, mature, even-aged beech forest stand located in a pre-Alpine area of northern Italy. The analysis of $\delta^{13}C$ in tree-ring α-cellulose samples from the observed period (2013–2019) showed no differences between treatments, as also confirmed by a state-of-the-science, validated process-based model. The model effectively simulated iWUE data under the "Control", "Traditional" and "Innovative" treatments, both under recent-past present-day and future climate, without revealing differences in the data distribution, consistent with previous observations from tree-ring data. This suggests that, at least in our site, even-aged mature beech forests may not be affected by management practices, but only when environmental conditions and/or soil nutrient availability are not limiting factors. We showed that silvicultural treatments cannot influence the iWUE, regardless of future climate scenarios considered in the Cansiglio site. This study concludes that, over the coming decades, silvicultural treatments may be unlikely to affect intrinsic Water Use efficiency in pre-Alpine beech forest. Instead, an increase in iWUE is expected as a result of climate change, regardless of the specific climate scenario and forest management scheme. Future research should aim to disentangle the potential age-related effects on iWUE, including uneven-aged forest structures, and to explore alternative management approaches such as "close-to-nature" practices. Moreover, since our study site does not experience pronounced drought stress, it would be especially valuable to investigate how forest management influences iWUE in beech-dominated stands located in drought-prone regions or under future climate scenarios characterized by increased water limitation.

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