



Canopy nitrogen application effects on *Quercus petraea* L. and *Fagus sylvatica* L. ring width and wood density

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Received: 29 December 2023 / Revised: 8 April 2024 / Accepted: 15 April 2024
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Abstract

As an essential nutrient, Nitrogen (N) availability is fundamental in evaluating forest productivity, and as such, understanding the effects of changing atmospheric N inputs in forest ecosystems is of high significance. While most field experiments have been employing ground fertilization as a method to simulate N deposition, two experimental forest sites in Italy have adopted the more advanced canopy N application approach. Here we present findings from a case study of wood core analyses of predominantly pure, even aged, Sessile oak (*Quercus petraea* L.) and European beech (*Fagus sylvatica* L.) forest stands, treated with either below or above canopy N fertilization, comparing between the two simulation pathways of increased N deposition. The potential effects of elevated N availability on total ring width, mean ring density, and their corresponding earlywood and latewood fractions are examined. Our results indicate inconclusive effects of the treatments on the ring width traits of both *Q. petraea* or *F. sylvatica*, although basal area increment patterns appeared to be affected divergently between the species and treatments. Mean and earlywood, but not latewood, densities on the other hand, exhibited a decrease in certain years of the treatment period in *Q. petraea* as result of the above canopy N application only, whereas *F. sylvatica* wood density showed no clear response to any of the treatments. Thus, we are describing distinct reactions of the two broad-leaved species to the different experimental N deposition approaches, discussing potential growth patterns under increased N availability, and emphasizing the importance of considering wood density in assessments of tree biomass accumulation and essentially Carbon storage capacities.

Keywords Nitrogen deposition · Canopy Nitrogen · Ring width · Wood density · Sessile oak · European beech

Introduction

With ongoing anthropogenic meddling in the natural Nitrogen (N) cycle, elevation in atmospheric N deposition has been fairly steady in the past decades. Despite of existing evidence suggesting a decline in the total averaged European N deposition rate, the trends are spatially divergent, where certain areas still experience an upsurge (Schmitz et al. 2019). On a global scale, rates of inorganic N deposition were shown to increase by 8% between 1984–2016 from 86.6 to 93.6 Tg N yr⁻¹ (Ackerman et al. 2019). Thus, propelling the interest of investigating its function in forests worldwide (Galloway et al. 2008; Bobbink et al. 2010; Etzold et al. 2020), in an attempt to uncover and define its underlying mechanisms (Khaine and Woo 2015; Carter et al. 2017), and consequent effects on Carbon (C) storage (Högberg 2007; Janssens et al. 2010; Quinn Thomas et al. 2010).

Communicated by Miren del Río.

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When examining plant C and N dynamics, there are multiple aspects to consider. The nutritional condition of a habitat as a whole, and its inherent shifts, are reflected in the development of different tree compartments (Jiang et al. 2015), promptly and visibly at times (Guan and Wen 2011; Ward et al. 2013; Helm et al. 2023), yet may be latent and obscure as well (Wright et al. 1995; de Vries et al. 2014; Gagen et al. 2019). As such, the woody tissue may hold valuable information on the tree's health and productivity (Helama et al. 2009; Poorter et al. 2010; Gagen et al. 2019; Cherubini et al. 2021), allowing for the provision of growth patterns and prediction models for fitness and mortality, based on tree core characteristics (Baker et al. 2004; Bigler et al. 2004; Cailleret et al. 2017; Liang et al. 2021). Various measures of tree rings have been studied within the reality of climate shifts (Ferretti et al. 2002; Scharnweber et al. 2011; St. George and Ault 2014; Borghetti et al. 2017). In that, wood density has been shown to alter under varying N inputs with divergent responses (Beets et al. 2001; Bucci et al. 2006; Pivovarov et al. 2016), whilst Pretzsch et al. (2018) reported a general declining trend in wood density in Central European forests, alongside an increase in wood volume growth, over the recent century, suggesting a plausible link to rising N deposition rates over the same period.

It is evident that the tree canopy and atmospheric N hold a direct interaction where some canopy interception may occur with a consequent change in the amount and form of deposited N that actually reaches the ground, resulting in a considerable regulation of N distribution within the system (Sparks 2009). It has been demonstrated that as much as 80% of total reactive N descending from the atmosphere may be retained by the canopy before eventually arriving at the forest floor (Klopatek et al. 2006; Lovett and Lindberg 2011; Fenn et al. 2013; Houle et al. 2015), some of which may be immobilized or up-taken by the tree and its associated organisms, as well as being volatilized back as gaseous N (Bryan Dail et al. 2009; Nair et al. 2016). As experimental designs are innately bound by frequent constraints, a major culprit in studying forest ecosystems under increased N deposition, through means of experimental N addition, resides amongst others in the choice of fertilizer, application intervals, and administration method, and may limit favorable examination of hypotheses. While the majority of past studies investigating the effects of experimental N deposition in forests have implemented the traditional ground fertilization methods (Bebber 2021), an apt approach of above tree canopy N application (ACN), which may better mimic the actual deposition pathway than below canopy N application (BCN), has been adopted in more advanced research. In their thorough reviews, Bortolozzi et al. (2021) and Guerrieri et al. (2021b) addressed the matter, accentuating the eminent tree canopy-deposition relationship that is often overlooked, and

presented many of the studies that incorporated the more appropriate approach of above canopy N administration.

Several ACN experiments were previously established in various forests and continents. In subalpine Engelmann spruce growing in Southwestern US, it was shown that N applied from above the tree crown is, similarly to ambient N deposition, mostly retained by the canopy, contributing to increased photosynthetic processes and foliar growth (Sievering et al. 2007; Tomaszewski and Sievering 2007). In a low-elevation red spruce and Eastern hemlock dominated forest in Northeastern US, the significance of the N-canopy interaction was further confirmed through ACN fertilization (Bryan Dail et al. 2009). A large-scale experiment was established in China (Zhang et al. 2015), examining different levels of ACN and BCN treatments in two separate forests dominated by native broadleaved species, where multiple investigations were performed and published since, presenting an array of species and habitat specific responses when measuring stem wood related affects (Yu et al. 2019; Guo et al. 2020; Zhang et al. 2022). An acid mist spray experiment in Scotland compared the effects of N and Sulphur (S) foliar applications in young managed Sitka spruce in Scotland, and detected a positive effect on stem radial growth when combining N + S during four years of treatment, with a minor insignificant negative effect of N alone (Sheppard et al. 2001), which later turned significantly positive after five years (Sheppard et al. 2004). In mature black spruce, growing in a Canadian boreal forest, limited effects of ACN treatment on xylem phenology and anatomy were found after three years (Lupi et al. 2012), which later faded after six years (Dao et al. 2015), to eventually conclude no significant effects. Both these latter spruce studies emphasized the importance of long-term monitoring for more constructive deductions in the context of wood traits, a tree tissue that may lag in immediate and/or obvious response.

The interrelation between N deposition and wood density for both Sessile oak (*Quercus petraea*) and European beech (*Fagus sylvatica*), two of the more ecologically and economically prominent and valuable broadleaved species in Europe (Mölder et al. 2019; Baumbach et al. 2019), has been reported in several observational and modelling studies (Braun et al. 1999, 2010, 2017.; Laubhann et al. 2009; Kint et al. 2012; Vannoppen et al. 2018; Hess et al. 2018). To the best of our knowledge, fewer studies have examined effects of experimental N application on mature oak and beech wood traits (Becker et al. 1996; Elhani et al. 2005; Ponton et al. 2019; Durand et al. 2020). Only one experiment in two Swiss forest sites used actual direct N application to oak (*Q. cerris* and *Q. pubescens*), and beech (*F. sylvatica*) branches, over a short period, and examined photosynthetic efficiency, to find an increase in the oak's foliar

photosynthetic measures, and an indeterminate decrease in beech (Wortman et al. 2012).

With the intention to contribute in filling some of these information voids, we perform an assessment of tree rings in two separate pure and mature Sessile oak and European beech forests. The objective here is to explore intrinsic growth traits in the form of tree ring widths and densities as measures for radial tree expansion and wood production, in forest stands subjected to two different elevated N treatment methods i.e., ACN and BCN. Our main hypotheses in this context are: i) while we expect no significant differences between the untreated experimental units in the period prior to N application, tree ring width and density development may be modified under increased experimental N inputs; ii) the two different N deposition simulation methods, may result in distinct effects on the examined tree ring characteristics; iii) and finally, the entire treatment period trend might reveal separate inferences than that of the single inter-annual rings, which may reflect temporary time point responses.

Methods

Experimental sites

The oak site is located in the temperate forest of Monticolo, South-Tyrol, Italy (46°25'35" N; 11°17'55" E, 530 m elevation), with a mean annual temperature of 11.5 °C and mean annual precipitation of 835 mm. The soil is an acid brown loam, Cambisol (topsoil pH 4.8) overlaying porphyritic quartz rock. The site is dominated by Sessile oak (*Quercus petraea* (Matt.) Liebl.; ~96%), largely even-age averaged at 65 years, with a stand density of 1120 trees ha⁻¹, mean height of 13.3 ± 0.1 m, and mean diameter at breast height (DBH) of 18.2 ± 0.2 cm. Recorded atmospheric bulk N deposition was estimated at ~6.5 kg N ha⁻¹ yr⁻¹ between 1996–1999. Initially managed for thinning, the forest stand has been unmanaged in the past decades and is part of a natural reserve, where no previous experiments were conducted.

The beech site is situated on the periphery of the sub-Alpine plateau of Pian del Cansiglio, Italy (46°3'19" N; 12°22'51" E, 1100 m elevation). With an oceanic climate, the mean annual temperature is 6.2 °C and mean annual precipitation is 2150 mm. The soil is formed on a karst bedrock with a carbonate rock matrix, Haplic Luvisol (topsoil pH 4.3). The site is exclusively dominated by mature European beech (*Fagus sylvatica* L.), even-age averaged at 135 years, with a stand density of 170 trees ha⁻¹, mean height of 29.4 ± 0.1 m and mean DBH of 45.5 ± 1.1 cm. Historical total N deposition averaging around 17.5 kg N ha⁻¹ yr⁻¹. Previously managed as a high forest, it is currently

recognized as a natural reserve. Last intervention of low intensity thinning was performed in early 2000, and no experimental history prior to the current research.

Fertilization treatments

The Monticolo experimental design is detailed and illustrated by Giammarchi et al. (2019). Briefly, the site consists of three treatments: 20 kg N ha⁻¹ yr⁻¹ applied below the tree canopy directly to the forest floor (BCN), 20 kg N ha⁻¹ yr⁻¹ applied above the canopy (ACN), and unfertilized control. Each treatment is replicated in three circular plots (12 m radius), for a total of nine experimental plots, arranged in a completely randomized design with a minimum of 10 m buffer zone to prevent contamination. N fertilizer, as NH₄NO₃ solution (4.3 g N L⁻¹), has been applied five times during the growing season, from May to September, since 2015 and annually thereafter, until this day and ongoing. The BCN treatment is applied through manual spraying, ensuring uniform distribution. For ACN, rotating sprinklers mounted on telescopic masts are utilized, providing a largely uniform spray radius of 12 m above the tree canopy, from the center of the plot. The water supplied with the fertilized treatments (210 L H₂O plot⁻¹ yr⁻¹) is equivalent to a negligible 0.46 mm of precipitation, compared to the region's average annual precipitation. No intervention was performed in the control plots. The conservative application rate of 20 kg ha⁻¹ yr⁻¹, roughly over three times the background atmospheric N deposition, was chosen to simulate feasible future scenarios of N deposition increases.

The Cansiglio experimental design is detailed by Teglia et al. (2022). Briefly, the site contains four treatments: an ACN treatment with 30 kg N ha⁻¹ yr⁻¹, BCN treatment with 30 kg N ha⁻¹ yr⁻¹, a double-dose BCN treatment with 60 kg N ha⁻¹ yr⁻¹ (denoted as BCN60), and unfertilized control. Each treatment was replicated in three plots using a randomized block design, for a total of twelve experimental plots. The control and both below canopy fertilization treatment plots are square (30 × 30 m), while the ACN plots are circular (20 m radius). N has been administered as NH₄NO₃ solution three times annually during the growing season, June to September, since 2015 and annually thereafter. Similarly to the Monticolo site, below canopy fertilization was sprayed manually, while above canopy N was supplied via rotating sprinkler towers from the center of the plots, with a conservative N application rate of two to three times the background atmospheric N deposition.

Tree core sampling and analysis

Due to pre-existing wood sampling of past projects in the sites since 2015, and inclination towards minimizing disturbances of the protected forests, limitations in the current

sampling were enforced. One 5 cm long wood core sample per tree was collected with an increment borer (5 mm diameter) at breast height (~1.3 m) from six trees on average in each plot (in each site) to ensure a minimum of 18 tree repetitions per treatment. The cores from Monticolo were collected in early 2022 and the cores of Cansiglio in the end of the same year. In each site healthy trees with DBH around the stand average were chosen. DBH measurements of the cored trees were obtained accordingly. In the BCN60 treatment of the Cansiglio site two wood cores were damaged during the analysis process, leaving 16 cores instead of 18 for this treatment.

After air drying, the cores were sanded and analyzed for ring width and wood density via the high-frequency densitometry LIGNOSTATION™ method, considered to provide relative density measurements (Schinker et al. 2003; Shchupakivskyy et al. 2014; Koutsianitis and Barboutis 2017). The density analysis is based on the interaction between continuous electromagnetic waves emitted from a transmitter–receiver link of a small electrode system and the dielectric properties of the wood. The instrument simultaneously measures ring width through optically scanning the core path with a high-resolution camera. Analysis with the LIGNOSTATION™ allows for distinguishing between the seasonal sections of the total ring, providing separate early-wood and latewood density and width values.

Data and statistical analyses

The analysis of tree cores was performed on rings dating back two decades up to the year 2000. While the focus of the study was the examination of the N application period (2015 and onward), an additional 15-year period prior to the beginning of the experiment was chosen as a satisfactory time frame baseline for representing the state of the stands prior to any experimental manipulation, for comparing between the two periods of pre- and post-treatment. The most recent ring of each core (2021 for Monticolo and 2022 for Cansiglio) was omitted from the analysis to avoid potentially misreading non-fully consolidated rings. Tree rings were cross-dated with the CDendro software. No age-related trends or other confounding patterns were detected for the analyzed period, thus not warranting for detrending or standardization of the data, and eliminating concerns of potentially losing conceivable N treatment signals. Rather, the entire raw data was used with no manipulation or any removal of data points, and all the presented graphical plots are based on treatment averages of the observed values.

Basal area increment (BAI) was estimated as an extended measure for stem radial expansion and annual tree growth. BAI was computationally reconstructed using the analyzed total ring widths and the coinciding current year DBH measurements. DBH values for past years were back-calculated

using total ring widths under the rough assumption of an even total width around a circular stem area section. Furthermore, to assume the power and necessity of including wood density in tree C storage assessments, an interaction between radial growth and density was to be evaluated. For this purpose, we followed previous studies who used the biomass area increment measure (IAB; Vannoppen et al. 2018; Van Den Berge et al. 2021), or BAIden as it is referred to by Giberti et al. (2022) and referenced here, produced by combining BAI with the annual mean ring density. An overview of the mean values of all the above-mentioned measures and computed response variables is given in Table 1.

A linear mixed effects model was chosen as a robust approach for statistical analysis of the longitudinal tree ring time series. Best model fits were chosen according to the research objectives for the fixed effects and optimization of random effects, while considering the Akaike Information Criterion (AIC) and using Maximum Likelihood (ML) and Restricted Maximum Likelihood (REML) approximations when appropriate. Considering the use of the raw data for analyses, and to address potential temporal dependence and autocorrelation between consecutive tree rings, an autoregressive term of type AR1 for the year variable within the tree was incorporated in all the models, which significantly reduced the AIC:

$$\text{CorrAR1}(\varepsilon_{ij}, \varepsilon_{i'j}) = \rho^{|\text{year}_{ij} - \text{year}_{i'j}|} \varepsilon_{ij} \sim N(0, \sigma^2) \quad (1)$$

The term describes the correlation between the residual errors (ε_{ij} and $\varepsilon_{i'j}$) for two consecutive observations (i and i') within the same tree (j). Where ρ is the autoregressive parameter representing the correlation between the observations in the same tree across different years. σ^2 is the residual variance.

To account for the tree core repeated measurements and between individual variability in each treatment level, the subject unit of ‘tree’ was set as a random effect. The ‘plot’ unit (as the subplot) was included as a random effect in the initial model, yet it was found non-constructive to the model fit and outcome, and therefore was not included in the final model. For potential within individual variability, a random slope was additionally set in the random ‘tree’ term, which further improved the model. For each response variable a different random slope was indicated according to the best model fit.

As an initial approach for distinguishing between the two periods of prior and post the experiment onset a dummy variable named ‘onset’ was defined with two levels: ‘pre_2015’ representing the pre-experiment period of the years 2000 until 2015, and ‘post_2015’ representing the post-experiment period for the years after 2015. ‘treatment’ and ‘onset’ were set as fixed effects with an interaction to investigate the average effects of treatment in each period. ‘tree’ was

Table 1 Mean values of the measured and computed ring data for the sampled *Q. petraea* at the Monticolo site ($n = 18$), and *F. sylvatica* at Cansiglio ($n = 16 - 18$)

Site	Treatment	DBH (cm)	Total Width (100mm ⁻¹)	Earlywood Width (100mm ⁻¹)	Latewood Width (100mm ⁻¹)	Mean Density (kg m ⁻³)	Earlywood Density (kg m ⁻³)	Latewood Density (kg m ⁻³)	BAI (cm ²)	BAI den (g cm ⁻¹)
Monticolo	Control	20.1 (2.4)	96 (44)	45 (23)	51 (29)	920 (174)	783 (184)	1041 (185)	5.3 (2.4)	4.9 (2.4)
	ACN	21.0 (2.6)	103 (43)	51 (28)	52 (28)	929 (201)	795 (195)	1060 (209)	6.2 (3.0)	5.8 (3.1)
	BCN	21.4 (2.7)	91 (35)	41 (18)	49 (26)	875 (165)	729 (185)	995 (170)	5.6 (2.4)	5.0 (2.5)
Cansiglio	Control	46.8 (6.7)	124 (59)	71 (43)	53 (30)	607 (188)	546 (193)	689 (199)	17.2 (9.1)	10.6 (6.7)
	ACN	46.1 (7.3)	114 (63)	59 (39)	55 (36)	637 (202)	567 (203)	711 (206)	15.7 (9.7)	10.4 (7.9)
	BCN	41.2 (5.6)	115 (60)	60 (38)	55 (34)	615 (169)	557 (172)	675 (171)	13.6 (7.4)	8.4 (5.6)
	BCN60	51.9 (5.4)	137 (89)	72 (58)	65 (47)	591 (185)	523 (180)	668 (187)	20.3 (12.1)	12.9 (9.7)

Ring data is averaged for the entire analyzed period per tree. DBH values are for the sampled trees at the time of sampling. Standard deviation in parenthesis

set as a random effect. The best fitted model formula was specified as follows:

$$RT_{ij} = \beta_0 + \beta_1 trtmnt_{ij} + \beta_2 onset_{ij} + \beta_3 (trtmn \times onset)_{ij} + u_{0j} + u_{1j}(onset_{ij} \text{ or } DBH_{ij}) + \epsilon_{ij} \tag{2}$$

where RT_{ij} represents a given ring trait response variable for the i -th observation in the j -th tree. β_0 is the intercept. β_1 , β_2 , and β_3 are the fixed-effect coefficients for the treatment, onset, and the interaction, respectively. u_{0i} and u_{1i} represent the random intercept of the tree and random slope term (either onset or DBH, according to the better fit) for each tree, respectively. ϵ_{ij} is the residual error term.

Next, for a further investigation of potential treatment effects on the ring traits within each individual annual ring, ‘treatment’ and ‘year’ were set as fixed effects with an interaction, where ‘year’ was set as a categorical variable. ‘tree’ was set as a random effect. The best fitted model formula was specified as follows:

$$RT_{ij} = \beta_0 + \beta_1 trtmnt_{ij} + \beta_2 year_{ij} + \beta_2 (trtmn \times year)_{ij} + u_{0j} + u_{1j} year_{ij} + \epsilon_{ij} \tag{3}$$

where RT_{ij} represents a given ring trait response variable for the i -th observation in the j -th tree. β_0 is the intercept. β_1 , β_2 , and β_3 are the fixed-effect coefficients for treatment, year, and the interaction, respectively. u_{0i} and u_{1i} represent the random intercept for the tree and a random slope term of year, respectively. ϵ_{ij} is the residual error term.

Finally, for BAI and BAI den, an evaluation of the overall patterns across the total analyzed periods divided into the two periods of prior and post the experiment was performed, while keeping ‘year’ as a numerical predictor, to produce slope trend values. Here, an addition of ‘DBH’ as a fixed factor proved to improve the models, but not the random slope term. For the pre-treatment period, a general trend for the entire stand was derived for the experimental units combined, while for the post-treatment period the treatments were kept separate as per the previous models:

$$RT_{ij} = \beta_0 + \beta_2 year_{ij} + \beta_4 DBH_{ij} + u_{0i} + \epsilon_{ij} \tag{4}$$

$$RT_{ij} = \beta_0 + \beta_1 trtmnt_{ij} + \beta_2 year_{ij} + \beta_3 (trtmn \times year)_{ij} + \beta_4 DBH_{ij} + u_{0j} + \epsilon_{ij} \tag{5}$$

Equation 4 is for the pre-treatment period, and Eq. 5 is for the post-treatment period. Where RT_{ij} represents either the BAI or BAI den response variables for the i -th observation in the j -th tree. β_0 is the intercept. β_1 , β_2 , β_3 , and β_4 are the fixed-effect coefficients for treatment, year, the interaction of year and treatment, and DBH, respectively. u_{0i} represents the random intercept for the tree. ϵ_{ij} is the residual error term.

After deriving an initial inference from the linear mixed models, particular significance determination was performed for the differences between each treatment pair using the Tukey post-hoc test for multiple pairwise comparisons (Tables S1-S28). A Z-test was performed for determining significant differences between the BAI and BAIDen slope values within the individual treatments (Table S29).

All computation was carried out with R software: BAI reconstruction with the ‘dIpR’ package; linear modeling with the ‘nlme’ package; and post hoc analysis with the ‘emmeans’ package (Bunn 2008; Pinheiro and Bates 2023; Lenth et al. 2023; R Core Team 2023).

Results

Oak ring width and wood density

Ring widths of *Q. petraea* showed marked inter-annual oscillations through the entire analysis period, where total, earlywood, and latewood ring widths all followed a parallel trend (Fig. 1a,b,c). No overall differences were determined between any of the treatments in any of the ring width traits at any point in time by the ‘onset’ model (Table 2). With that said, when testing for differences between the treatments in each individual year (Tables S7-S9), a significant

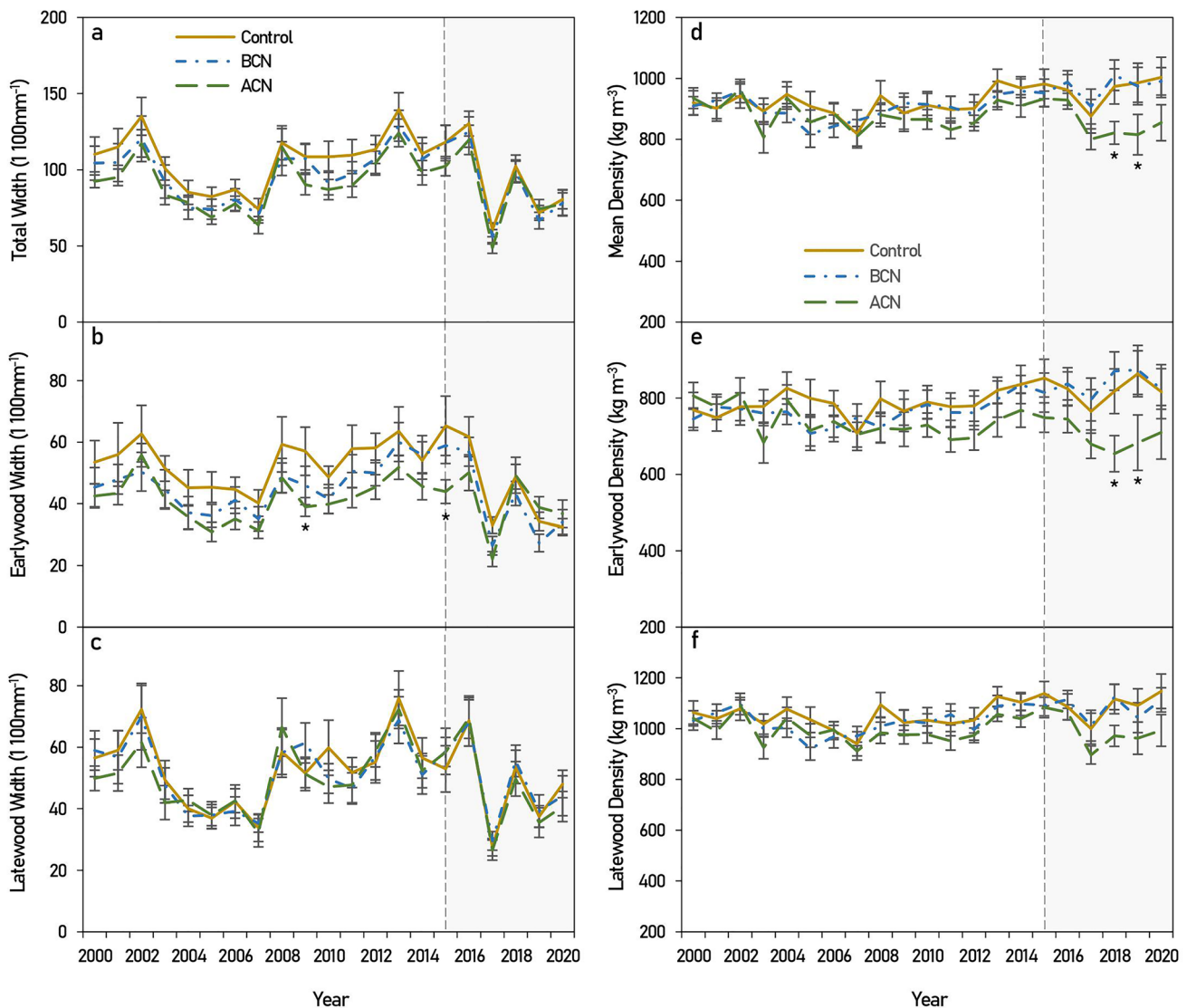


Fig. 1 Monticolo ring data of total (a) earlywood (b), and latewood (c) widths, and mean (d), earlywood (e), and latewood (f) densities, between 2000 and 2020 for *Q. petraea*. General averages for each annual growth ring ($n=18$, SE). Note the y axis for densities is not

set to zero. Dashed line indicates the experiment onset in 2015, with the light gray area thereafter indicating the post-treatment fertilization period. Asterisks indicate significant post-hoc pairwise comparison differences ($p < 0.05$)

Table 2 Linear mixed effects model (upper section) and post-hoc pairwise comparison between the treatments (lower section) of ring traits in the two separated periods of before and after experiment ‘onset’, for *Q. petraea* in Monticcolo

Predictors	Total width	Earlywood width	Latewood width	Mean density	Earlywood density	Latewood density
(Intercept)	112.9 (6.8)	53.8 (3.6)	53.7 (4.1)	921.8 (30.2)	1053.0 (31.6)	792 (31.3)
ACN	-15.5 (9.4)	-11.9 (5.1)	-3.5 (5.7)	-37.2 (42.7)	-51.7 (44.6)	-51.4 (44.3)
BCN	-14.4 (9.9)	-7.1 (5.1)	-3.5 (5.8)	-16.5 (42.7)	-24.3 (44.6)	-24.3 (44.3)
Onset[post_2015]	-15.3 (4.4)	-11.7 (2.6)	-6.4 (3.2)	33.7 (31.0)	32.3 (34.0)	10.8 (26.9)
ACN × Onset[post_2015]	8.6 (6.2)	9.6 (3.7)	-0.2 (4.4)	-67.8 (43.9)	-55.2 (48.1)	-43.5 (38)
BCN × Onset[post_2015]	3.9 (6.3)	2.8 (3.7)	2.7 (4.5)	31.8 (43.9)	20.2 (48.1)	46.2 (38)
Marginal / Conditional R²	0.009 / 0.882	0.078 / NA	0.002 / 0.875	0.028 / 0.563	0.026 / 0.484	0.027 / 0.561
Control—ACN	pre_2015 15.5 (9.4)	0.233 11.9 (5.1)	0.058 3.5 (5.7)	0.817 37.2 (42.7)	0.661 51.4 (44.3)	0.482 51.7 (44.6)
Control—BCN	pre_2015 14.4 (9.9)	0.326 7.1 (5.1)	0.352 3.5 (5.8)	0.822 16.5 (42.7)	0.921 24.3 (44.3)	0.848 24.3 (44.6)
ACN—BCN	pre_2015 -1.2 (9.7)	0.992 -4.8 (5.1)	0.606 0.0 (5.8)	1.000 -20.7 (42.7)	0.879 -27.1 (44.3)	0.814 -27.4 (44.6)
Control—ACN	post_2015 6.9 (9.3)	0.738 2.3 (5.7)	0.916 3.7 (6.4)	0.832 105.0 (61.3)	0.210 94.9 (60.5)	0.268 106.9 (62.9)
Control—BCN	post_2015 10.5 (9.7)	0.529 4.2 (5.7)	0.742 0.8 (6.4)	0.991 -15.3 (61.3)	0.966 -21.9 (60.5)	0.930 4.2 (62.9)
ACN—BCN	post_2015 3.6 (9.6)	0.927 1.9 (5.7)	0.939 -2.9 (6.4)	0.893 -120.3 (61.3)	0.132 -116.8 (60.5)	-102.7 (62.9)

Before experiment onset (pre-treatment period), pre_2015; after experiment onset (post-treatment period), post_2015

Intercept set at—Control × Onset[pre_2015]

Values are for estimates, with the Standard Error in parenthesis, made on 1134 observations (n = 54)

P-values are in Italics with significant differences in bold (p < 0.05)

decrease in the earlywood width of ACN compared to the control was found by the post-hoc analysis, in 2015 (Fig. 1b; Table S8, $p=0.008$), as well as in 2009, prior to the experiment onset (Table S8, $p=0.045$).

Ring wood density exhibited lower inter-annual variability, and similarly to width, mean, earlywood, and latewood ring densities all followed a comparable and similar trend (Fig. 1d,e,f). None of the ring density measures presented an overall effect of any treatment in any period as indicated by the 'onset' model (Table 2). This is despite a possible decreasing trend that was visually suggested in the mean density of the ACN treatment from 2017 (on the third year after the beginning of fertilization) and onwards, while BCN stayed closely uniform with the control (Fig. 1d). Indeed, this seeming decrease became meaningful in 2018 as was indicated by the mixed model results of the individual annual rings (Table S10), and the post-hoc analyses confirmed that ACN had a significantly lower mean density than BCN (Table S10, $p=0.018$), yet not compared with the control (Table S10, $p=0.068$). The difference between ACN and BCN was reduced in 2019 (Table S10, $p=0.062$), while becoming significant between ACN and the control (Table S10, $p=0.043$). In the final analyzed year, the extent of reduction between ACN and the other treatments was further diminished (Table S10, $p=0.097$, $p=0.141$). Earlywood density (Fig. 1e), which appeared visibly more variable than mean density was indeed slightly more impacted by N addition in both 2018 and 2019 (Table S11, $p=0.011$ and $p=0.033$, for ACN vs. BCN in 2018 and 2019, respectively, and $p=0.046$ for ACN vs. control in 2019). For latewood density (Fig. 1f), no significant treatment response was determined (Table S12). None of the density measures were found significantly different in any individual year prior to N application (pre-treatment period). All mixed model and post-hoc results for the treatment effects in each individual annual tree ring, and full onset models, for *Q. petraea* may be found in Online Resource 1.

Beech ring width and wood density

For *F. sylvatica* growing in the Cansiglio forest, all width measures followed a rather unison trend for all treatments (Fig. 2a,b,c), with notable inter-annual fluctuations. Similarly to the case of *Q. petraea*, no treatment effects were found by the 'onset' model for any of the ring width measures in either of the two time periods (Table 3), yet the statistical analysis of the individual annual rings revealed several significant differences by both the mixed model and post-hoc tests (Tables S19-S21), here in each of the ring width traits. For total width, significantly lower in ACN compared to BCN60 in 2016 (Table S19, $p=0.022$) and nearly significant in 2009 (Table S19, $p=0.053$; Fig. 2a). For earlywood

width, significant differences appeared in 2015, lower in ACN compared to BCN (Table S20, $p=0.002$), and compared to BCN60 in 2016 (Table S20, $p=0.04$; Fig. 2b). For latewood width, BCN60 was found significantly higher compared to all other treatments in 2006 (Table S21, $p=0.023$, $p=0.036$, $p=0.042$), and compared to ACN in 2017 (Table S21, $p=0.028$; Fig. 2c).

Ring density of *F. sylvatica* displayed a high intra-annual variability (Fig. 2d,e,f). No significant overall impacts of any treatment were indicated by the 'onset' analysis for any of the density traits, prior nor post N application (Table 3). While, the mixed model test of the individual years suggested some significant differences in each of the three density measures (Tables S22-24), none were reaffirmed by the subsequent post-hoc analysis. All mixed model and post-hoc results for the treatment effects in each individual annual tree ring, and the full onset models, for *F. sylvatica* may be found in Online Resource 2.

BAI and BAIden trends

After establishing no significant differences in total ring widths and mean densities between the treatments prior to the experiment, BAI and BAIden trends for the pre-treatment period were computed for all experimental units combined to present the overall temporal trends in the entire forest stand. The BAI trend for both oak and beech trees was generally negative in the two decades since 2000 (Fig. 3a,c; Table 4), and although extremely minimal when looking at the years prior to the experiments, the downward trend appeared to notably increase in the years after 2015. During the period of N fertilization, the ACN treatment seemed to somewhat attenuate the decline in the negative BAI trend of the two species, as indicated by the milder slopes of ACN compared to the control. While in Monticolo the BCN treatment was well paralleled with the control, in Cansiglio both BCN and BCN60 treatments had the opposite effect of ACN, inducing a greater decline in the BAI trend, which was closely significant for BCN compared to ACN (Table 4, $p=0.052$), but not nearly as much compared to the control ($p=0.385$).

The BAIden trends in the post-treatment period did not display markedly different patterns than that of BAI as a whole, generally slightly decreasing the observed BAI slope (Fig. 3b,d; Table 4). Yet only in the ACN treatment of *Q. petraea*, the incorporation of density in BAI to produce BAIden seemed to somewhat amend the treatment effect that was observed in the BAI trend (Fig. 3a,b), resulting in a larger slope. An outcome that might be expected by the corresponding decreased mean density (Fig. 1d). In *F. sylvatica*, although no concrete effects of N on mean density was concluded, when considering it within the BAIden trend, here the impact of density appeared to be prominent

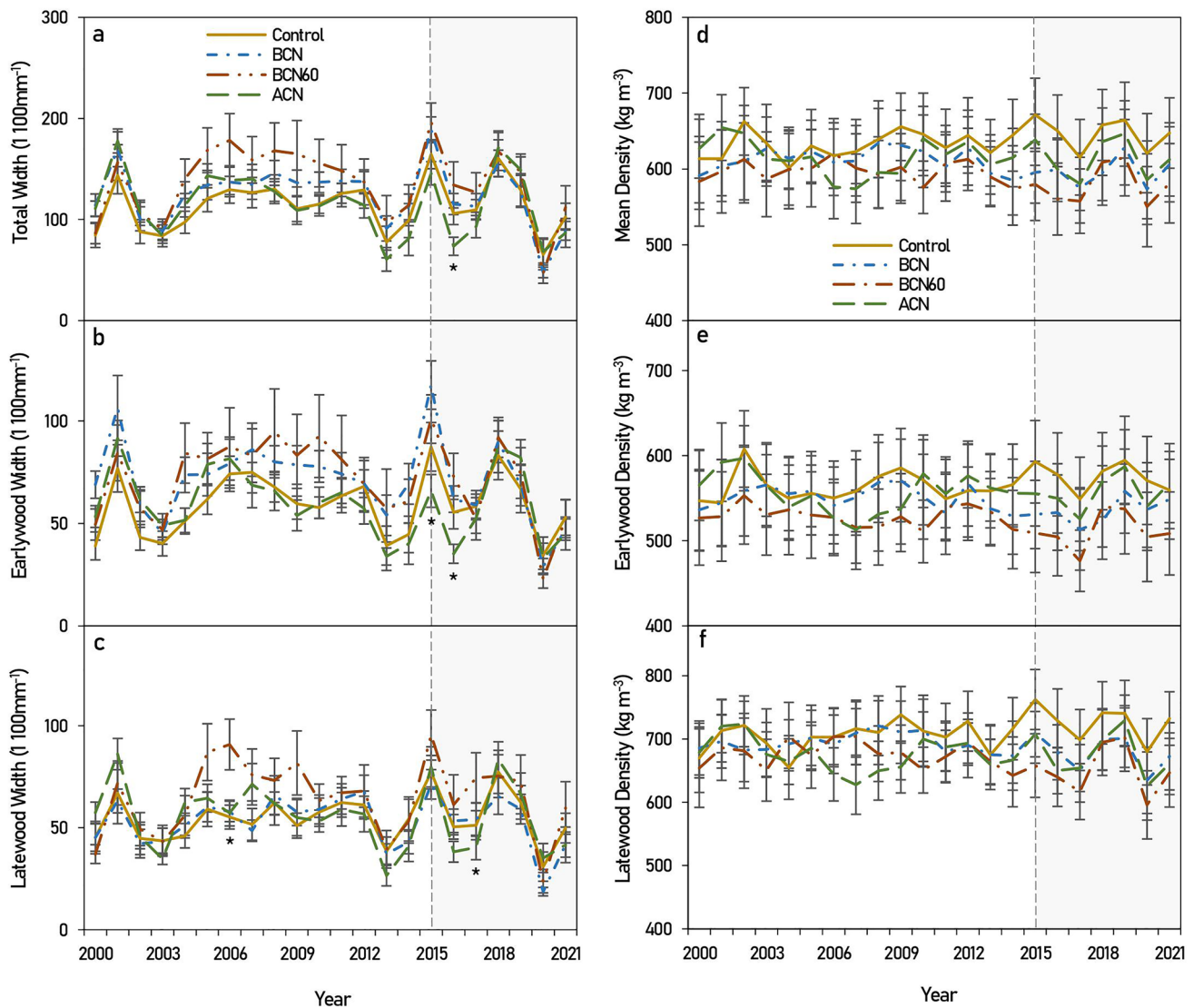


Fig. 2 Cansiglio ring data of total (a) earlywood (b), and latewood (c) widths, and mean (d), earlywood (e), and latewood (f) densities, between 2000 and 2021 for *F. sylvatica*. General averages for each annual growth ring per treatment ($n=16-18$, SE). Note the y axis

for densities is not set to zero. Dashed line indicates the experiment onset in 2015, with the light gray area thereafter indicating the post-treatment fertilization period. Asterisks indicate significant post-hoc pairwise comparison differences ($p < 0.05$)

in both of the below canopy treatments (Fig. 3c,d; Table 4), as the decline that was observed in their BAI trends was significantly contracted for BCN and nearly significant for BCN60 (Table S29, $p=0.027$ and $p=0.059$, respectively). Full mixed model and post-hoc results for BAI and BAIDen of both species may be found in Online Resource 3.

Discussion

It is evident that the majority of existing N application studies in oak species reveal a positive relation between N availability and radial growth (Jennings et al. 2016; Becker et al. 1996). In *Q. petraea* in particular, an increase in ring

width expansion was detected following administration of an excessive $220 \text{ kg N ha}^{-1} \text{ yr}^{-1}$ (along with Ca fertilization) to the forest floor during two consecutive years (Ponton et al. 2019; Durand et al. 2020). The positive effects on radial growth were immediate, yet diminished after five years of monitoring, while no effects on wood density were observed at all. While the effects of N amendment in trees may manifest either promptly or only some years after N application (Sheppard et al. 2001, 2004), in our *Q. petraea*, after six years of consecutive, and moderate, annual N fertilization, neither of the treatments induced changes in ring widths compared to the control.

We observed a general high inter-annual variability in the ring widths of *Q. petraea* in Monticolo, and an overall

Table 3 Linear mixed effects model (upper section) and post-hoc pairwise comparison between the treatments (lower section) of ring traits in the two separated periods of before and after experiment 'onset', for *F. sylvatica* in Cansiglio

Predictors	Total width	Earlywood width	Latewood width	Mean density	Earlywood density	Latewood density
<i>(Intercept)</i>	123.3 (10.9)	<0.001	56.5 (5.5)	645.9 (42.6)	565.8 (42.3)	699.8 (42.2)
<i>ACN</i>	-0.9 (16.2)	0.954	0.8 (8.0)	-16.4 (60.6)	-7.9 (59.8)	-21.3 (59.2)
<i>BCN</i>	15.9 (15.2)	0.297	0.7 (7.6)	-35.0 (60.0)	-18.0 (59.8)	-3.5 (59.7)
<i>BCN60</i>	15.9 (15.2)	0.299	8.3 (7.7)	-55.9 (62.1)	-35.5 (61.7)	-18.6 (62.1)
Onset[post_2015]	-19.6 (8.4)	0.020	0.161	-2.8 (12.0)	-0.7 (12.3)	5.0 (12.7)
<i>ACN × Onset[post_2015]</i>	-8.7 (11.9)	0.465	-1.7 (7.7)	-12.8 (17.0)	-0.3 (17.3)	-24.2 (17.9)
<i>BCN × Onset[post_2015]</i>	-19.7 (11.9)	0.099	-17.3 (7.7)	-3.4 (17.1)	-6.1 (17.3)	-28.5 (17.9)
BCN60 × Onset[post_2015]	-12.0 (12.3)	0.332	-3.4 (6.2)	-14.6 (17.7)	-14.4 (17.9)	-31.6 (18.5)
Marginal/Conditional R²	0.006 / 0.929	0.006 / 0.902	0.002 / 0.893	0.003 / 0.966	0.006 / 0.836	0.007 / 0.771
Control—ACN	pre_2015 0.9 (16.2)	1.000	3.0 (9.9)	1.000	16.4 (60.6)	0.999
Control—BCN	pre_2015 -15.9 (15.2)	0.721	-15.7 (9.3)	1.000	35.0 (60.0)	0.990
Control—BCN60	pre_2015 -15.9 (15.2)	0.722	-10.1 (9.3)	0.701	55.9 (62.1)	0.939
ACN—BCN	pre_2015 -16.9 (15.9)	0.716	-18.6 (9.8)	1.000	18.6 (60.5)	0.998
ACN—BCN60	pre_2015 -16.8 (15.9)	0.718	-13.1 (9.8)	0.778	39.5 (62.5)	0.970
BCN—BCN60	pre_2015 0.1 (14.8)	1.000	5.6 (9.1)	0.747	21.0 (61.9)	0.992
Control—ACN	post_2015 9.6 (17.2)	0.943	4.7 (10.6)	0.962	29.2 (61.2)	0.999
Control—BCN	post_2015 3.8 (16.6)	0.996	1.6 (10.3)	0.984	38.3 (61.1)	0.979
Control—BCN60	post_2015 -3.9 (17.1)	0.996	-0.2 (10.6)	0.941	70.5 (63.6)	0.856
ACN—BCN	post_2015 -5.9 (16.9)	0.985	-3.1 (10.5)	0.999	9.2 (61.0)	0.994
ACN—BCN60	post_2015 -13.5 (17.3)	0.863	-4.9 (10.7)	0.728	41.3 (63.6)	0.910
BCN—BCN60	post_2015 -7.7 (16.8)	0.968	-1.8 (10.4)	0.792	32.1 (63.5)	0.976

Before experiment onset (pre-treatment period), pre_2015; after experiment onset (post-treatment period), post_2015

Intercept set at - Control × Onset[pre_2015]

Values are for estimates, with the Standard Error in parenthesis, made on 1534 observations ($n = 70$)

P-values are in Italics with significant differences in bold ($p < 0.05$)

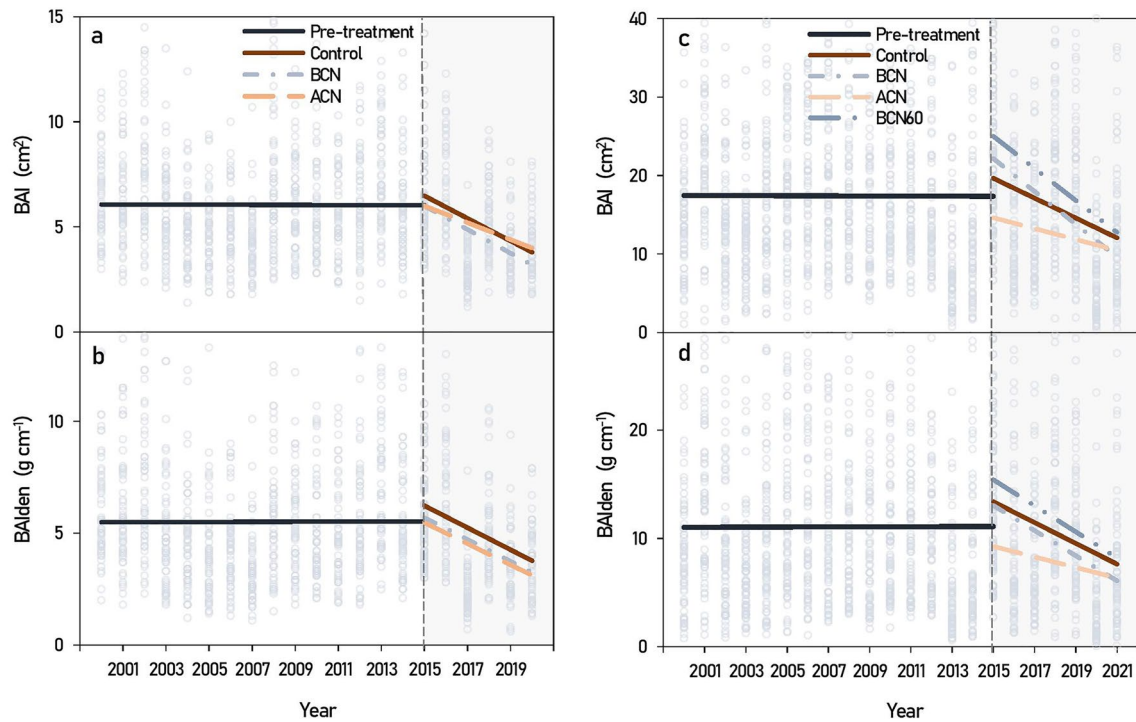


Fig. 3 Basal area increment (BAI) and biomass area increment (BAIden) trends for *Q. petraea* in Monticolo (**a, b**), and *F. Sylvatica* in Cansiglio (**c, d**). General patterns for pre-experiment years ($n=54-60$), and patterns separated by treatment for post treatments years

($n=16-18$). Dashed line indicates the experiment onset in 2015, with the light gray area thereafter indicating the post-treatment fertilization period

Table 4 Basal area increment (BAI) and biomass area increment (BAIden) trends for the two separated periods of before and after experiment onset (upper section) and post-hoc pairwise comparison

between the treatments of the post experiment period (lower section), of *Q. petraea* in Monticolo and *F. sylvatica* in Cansiglio.

Treatments	<i>Q. petraea</i>				<i>F. sylvatica</i>			
	BAI		BAIden		BAI		BAIden	
Pre-treatment	-0.08 (0.02)	<i>0.001</i>	-0.06 (0.02)	<i>0.013</i>	-0.00 (0.07)	<i>0.991</i>	-0.01 (0.05)	<i>0.835</i>
Control	-0.63 (0.08)	<i>0.000</i>	-0.58 (0.08)	<i>0.000</i>	-1.46 (0.36)	<i>0.000</i>	-1.10 (0.26)	<i>0.000</i>
ACN	-0.48 (0.08)	<i>0.000</i>	-0.56 (0.08)	<i>0.000</i>	-0.96 (0.36)	<i>0.008</i>	-0.63 (0.26)	<i>0.010</i>
BCN	-0.66 (0.08)	<i>0.000</i>	-0.58 (0.08)	<i>0.000</i>	-2.27 (0.36)	<i>0.000</i>	-1.29 (0.26)	<i>0.000</i>
BCN60					-2.19 (0.38)	<i>0.000</i>	-1.29 (0.27)	<i>0.000</i>
Control—ACN	-0.15 (0.11)	<i>0.354</i>	-0.03 (0.11)	<i>0.968</i>	-0.50 (0.51)	<i>0.762</i>	-0.43 (0.36)	<i>0.628</i>
Control—BCN	0.02 (0.11)	<i>0.977</i>	0.00 (0.11)	<i>1.000</i>	0.82 (0.51)	<i>0.385</i>	0.19 (0.36)	<i>0.951</i>
ACN—BCN	0.17 (0.11)	<i>0.256</i>	0.03 (0.11)	<i>0.967</i>	1.32 (0.51)	<i>0.052</i>	0.62 (0.36)	<i>0.310</i>
Control—BCN60					0.73 (0.53)	<i>0.514</i>	0.20 (0.37)	<i>0.950</i>
ACN—BCN60					1.23 (0.53)	<i>0.094</i>	0.63 (0.37)	<i>0.326</i>
BCN—BCN60					-0.09 (0.53)	<i>0.998</i>	0.00 (0.37)	<i>1.000</i>

Trend values are for slopes. For the pre-treatment periods (≤ 2015) general averages for the entire stand. For the post-treatment period ($>= 2015$) separated by treatment

Pairwise comparisons are corresponding for the post-treatment years ($>= 2015$)

Values are for estimates of marginal trends, with the Standard Error in parenthesis. *P*-values are in Italics

negative radial growth trend over the past two decades. Inter-annual variability in ring widths of *Q. petraea* was previously linked to various climate variables, where

precipitation frequently enhanced radial growth and temperature had a negative effect (Cedro 2007; Arend et al. 2011; Härdtle et al. 2013; Delpierre et al. 2016), dependant

on the seasonal dynamics, of the current and previous years. Nevertheless, oaks do exhibit high plasticity in their reaction, often displaying marked resilience to environmental stress (Friedrichs et al. 2009; Mérian et al. 2011; Lebourgeois et al. 2013; Trouvé et al. 2017). Although we show a significant decrease in the earlywood of ACN compared to the control in 2015, it is doubtful to conclude that the effect of the N application is involved since the formation of earlywood ends in *Q. petraea* in adjacency to the beginning of the growing season (addressed later), and thus in 2015 ended prior to the very first fertilization event of the experiment. Together with the fact that in 2009 a similar significant difference was found, these results may be rather attributed to incidental divergences stemming from the higher overall variance in earlywood traits and the general susceptibility of ring width towards climatic conditions.

Mean ring wood density of our oaks, in contrast to ring width, seemed to experience a decline already on the third year for the ACN treatment, to become significant in reduction on the fourth year, compared to the BCN treated trees which remained rather consistent with the untreated control. Decrease in wood density is not uncommon in N application experiments (Ross et al. 1979; Hättenschwiler et al. 1996; Beets et al. 2001; Raymond and Muneri 2000; Kostianen et al. 2004), and is possibly related to changes in stem hydraulic architecture and water use efficiency. Wood density has a direct link to transport system performance and vigor of the tree stem, where thicker cell walls are made to endure larger negative water pressure stress, and are consequently more resistant to cell implosion and organ cavitation (Hacke et al. 2001, 2005; Zanne et al. 2010). Lower wood densities on the other hand, have been shown to go in accord with increased stem conductivity (Hacke et al. 2010), while associated with higher foliar N at the same time (Bucci et al. 2006; Pivovarov et al. 2016).

When comparing to reported literature values for *Q. petraea* (Zhang et al. 1993; Bergès et al. 2000, 2008; Cedro 2007; Vavrcik and Gryc 2012), our oaks seem to present general average wood densities on the higher end of the species spectrum, whilst total ring widths being lower. Thus, the relatively prompt apparent response of mean ring density to the direct contact of applied N with the foliage of the ACN treated trees, despite our conservative amount of added N, may be due to a sufficient leeway in the form of robust woody tissue to spare, for a worthwhile compromise towards improved conductivity (Pérez-de-Lis et al. 2018). Once the tree canopy experienced an elevated N supply, a shift could have been triggered in an aim to support the increased essential nutrient inflow. The additional N availability could have promoted growth processes where the decrease in density may allow for a potentially more efficient tree stem transport system.

According to our results of a moderately higher significance in the decrease of earlywood density than that of the mean density in the ACN treatment, in conjunction with no significant effects on latewood density, it is evident that the earlywood might be the more sensitive fraction of the ring and the determining factor in the overall mean ring density of *Q. petraea* (that, in spite of the latewood section having a slightly higher proportion of the total ring). This proposition is contrary to the findings of Pretzsch et al. (2018) who argued the opposite, namely that latewood is the main determinant in the mean ring density. With that said, the role of other environmental variables i.e., CO₂, temperature, and growing season prolongations, where not excluded from their analyses, therefore these may come as a reasoning for the distinction in findings. Pretzsch et al. (2018) did however attribute a century long general decrease in wood density to concomitant N deposition increases in Central European forests, which is in line with the density reduction that we observed.

Earlywood is largely of lower density than latewood and contains a higher percentage of larger transport vessels providing the main pathway for water and nutrient flux during the growing season (Feuillat et al. 1997; Umebayashi et al. 2008). Its' development begins and consolidates rather early in ring-porous species, even prior to full leaf formation (Kitin and Funada 2016), and earlywood to latewood transition in *Q. petraea* in particular may commence as soon as the month of May (Michelot et al. 2012b). At first glance, this might appear counterintuitive when considering our fertilization regimen, beginning right after leaf maturation (around June in the Monticolo forest). Nonetheless, it has been demonstrated that the earlywood often bears an imprint of the previous years' (as well as the pre-growing season) conditions (González and Eckstein 2003; Fonti and García-González 2004; Fonti et al. 2007; González-González et al. 2014). In *Q. petraea*, earlywood and its vessel area composition have been linked to the precipitation rate of the preceding growing seasons in certain environments (Fonti and García-González 2008), while ring density as a whole was impacted by various previous year climate variables (Vanoppen et al. 2018). It has been suggested that earlywood formation originates in the over-wintered cambial cells of the prior growing season (Gričar and Čufar 2008). Further, earlywood development depends on past non-structural C reserves (Barbaroux and Bréda 2002; Kimak and Leuenberger 2015). For both C and N, allocation to different compartments of the tree is spread out along the annum, where N transportation ensues later in the vegetative season, peaking around senescence with leaf N resorption (El Zein et al. 2011a, 2011b; Bazot et al. 2013; Gilson et al. 2014). Therefore, one may assume that increased direct foliage N uptake, during the growing season period, between June–September in our case, might propel an altered forthcoming-season

earlywood production, of presumably wider transport vessels together with a less dense fibrous vicinity, to support likely another anticipated nutrient rich season.

In regard to the BCN treated trees in Monticolo, which did not seem to experience this new nutrient balance, we may suggest that the distinction could arise from the rather conservative amount of ground N fertilization, that might have been initially intercepted by the thick perennial leaf-litter layer in our forest stands prior to even reaching the soil, and possibly up-taken by lower organisms thereafter, and/or being volatilized in part at the same time. Indeed, Da Ros et al. (2023) found a significant difference in the N recovery between the two treatments in our site after a ^{15}N tracer fertilization event during the 2016 growth season in Monticolo, where the vast majority of labeled N in the BCN treatment was retained by the litterfall layer and soil within 4 months post fertilization, twice as much as in the ACN treatment. In contrast, tree N recovery, albeit detected in rather low amounts altogether, was twice as much in ACN than in BCN.

In the case of the beech trees in the Cansiglio forest site, lower earlywood width was found in the ACN treatment compared to both below canopy N treatments in the first two years of the experiment. In the latewood width, the ACN treatment was also shown as significantly lower than that of BCN60 only in 2017, while being significantly higher in BCN60 compared to the rest of the treatments in 2006. At the same time, the total ring width of ACN was significantly lower than in BCN60 only, in 2016. These differences may plausibly imply that above canopy N application may cause a mild decrease in the ring width of *F. sylvatica*, while below canopy fertilization may somewhat increase it, yet when taking into account the entire time series, it does not appear as a consistent tendency considering significant difference determined in the pre-experimental year. Therefore, at this point no definitive statements can be confidently made regarding the effects of any type of N application on the ring width of our beech trees. The contrasting results of the linear mixed model and post-hoc tests for the density traits, ultimately showing no significant effects of any treatment in this regard, reinforce the possibility that the supposed responses seen in the ring widths may essentially be due to a high inter-subject variability of the individual trees, resulting in random signals.

In other studies relating N availability with beech tree ring characteristics, Guerrieri et al. (2021a) found a positive correlation of soil and leaf N to BAI and a negative link with wood density. A similar scale negative effect of N deposition on wood density was reported by Vannoppen et al. (2018). In ~80 old *F. sylvatica* stands fertilized with either N or NPKCa ($100 \text{ kg N h}^{-1} \text{ a yr}^{-1}$ during two consecutive years), radial growth increase was determined for the NPKCa treatment but not for N alone (Elhani et al. 2005). BAI based growth models concerning N deposition

in European forest monitoring plots showed significant positive effects on Scots Pine, Norway Spruce, and oaks, yet for beech significance was only nearly achieved (Laubhann et al. 2009). A three-decade monitoring period of BAI revealed a decline in *F. sylvatica* between 1987–2014, along with an inversive relation with N deposition where a positive effect was observed up to $26 \text{ kg N h}^{-1} \text{ a yr}^{-1}$, and turned negative thereafter (Braun et al. 2017). This was reinforced by the models of Kint et al., (2012), who showed a corresponding inversive trend where the negative effect ensued around $21 \text{ kg N ha}^{-1} \text{ yr}^{-1}$ (and $28 \text{ kg N ha}^{-1} \text{ yr}^{-1}$ for Pedunculate Oak for that matter). Hess et al. (2018), likewise found both favorable and opposing effects on beech ring widths and radial growth with increasing N deposition (of up to $14 \text{ kg N h}^{-1} \text{ a yr}^{-1}$), depending on interactions with temperature, precipitation, and tree age. It is thus apparent that N loads beyond certain thresholds may not act agreeably for overall tree productivity and may farther turn antagonistic (Fleischer et al. 2013; Flechard et al. 2020a, 2020b). The ambient N deposition of $\sim 17.5 \text{ kg N ha}^{-1} \text{ yr}^{-1}$ in the Cansiglio forest surrounds the critical N loads for beech suggested above, and considering the additional supplied amount of $30 \text{ kg N ha}^{-1} \text{ yr}^{-1}$ (more so in the double-dose BCN treatment), exceeds the presumable threshold considerably. While our beech trees seemed to remain supposedly indifferent after seven years of fertilization in terms of the measured ring traits, the BAI results did point to a possible adverse effect of the BCN treatments after all. Indeed, the general declining trend in BAI appeared to be enhanced in both BCN treatments compared to the control, suggesting that a limited undertone response to the added N might have existed nonetheless. The implied opposite effect of ACN on the BAI trend further supports this notion, and at the same time indicates that the mode of N application may in fact matter here as well, and could induce opposing radial growth effects in *F. sylvatica*. For the oak trees in Monticolo, growing under $\sim 6.5 \text{ kg N ha}^{-1} \text{ yr}^{-1}$ of ambient N deposition, total ring width also did not change with any of the added $20 \text{ kg N ha}^{-1} \text{ yr}^{-1}$ treatments, while the declining BAI trend seemed to be similarly mitigated by the ACN treatment, although with no evident impact of BCN in this case.

Climate impacts on beech stem growth and ring development have been studied extensively (Leuschner et al. 2001a; Bouriaud et al. 2004, 2005; Scharnweber et al. 2011; Michelot et al. 2012a). Although beech appears often as the more sensitive to environmental conditions altogether between the two species (Campioli et al. 2012; Michelot et al. 2012a), it was shown to prevail as the dominant one in mixed forests with oak (Leuschner et al. 2001b; Petritan et al. 2012, 2021). It may be argued that the beech in Cansiglio might endure larger N loads than in other habitats, and with a seemingly lower susceptibility than the oak in Monticolo. It is important to note here as well the age difference between the two

species, where the mature beech is at ~135 years while the oaks are at the verge of maturity at ~65, which might contribute to an overall increased resilience towards environmental stresses, and a possibly higher resistance of the beech trees to N overloads in particular.

Contrary to the prevailing findings, where ring width and density alter in parallel under a changing environment, this was not the case in our oaks. Alterations in transport vessel size or area do not always manifest in conjunction with changes in ring width and may be affected by different factors to different extents (Fonti and García-González 2008). A similar lack of accord between external radial expansion and internal wood anatomy variations, was presented in two of the few existing ACN vs. BCN experiments (performed in broadleaf dominated mixed Chinese forests; Jiang et al. 2018; Zhang et al. 2022), emphasizing that wood related phenological shifts may develop beneath the surface, here in the context of varying N availabilities. Stressing yet again the importance of including measures such as wood density when investigating C sequestration. Indeed, further intrinsic wood traits may undergo morphological changes, where inner vessels may contract or expand (Spannl et al. 2016), along with changes in fibrous tissue, while on the macro scale total ring size may not budge. Thus, the differentiation of tree rings to the early and late wood fractions is one step forward in uncovering these phenomena, yet farther discrimination may be required for a deeper grasp of the trees' actual state (Carrer et al. 2015; García-González et al. 2016).

Moreover, changes in wood density, especially when not accompanied with complimenting radial growth, may further take a substantial portion in the C stocks estimations, as suggested by our biomass area increment trends. When considering the density measure with BAI in BAIDen in the ACN treatment of *Q. petraea*, albeit with a subtle effect, the mild upturn of the BAI trend (compared to the control and BCN), was lost, in accordance with the density reductions. Furthermore, even though density did not appear to be altered in *F. sylvatica* as consequence of any N treatment, the decrease that was visible in the BAI trend of both below canopy N treatments, was reduced with the inclusion of wood density when presenting BAIDen. The effect of density here was as such, that there was a significant difference between the BAI and BAIDen slopes of the BCN treatment, and nearly significant for BCN60. It is thus notable that wood functional traits, hereby tree rings and their physiology, are of major importance for both ecological and practical reasons, and considering the possible trade-offs between the ring traits, their significance in deeply understanding the trees' productivity and C storage capacity with relation to its environment calls for a continuous and thorough investigation of as many measures as admissible (Ferretti et al. 2002; Chave et al. 2009; Njana et al. 2016; Giberti et al. 2023).

Conclusions

In the current study we utilized two N application approaches for simulating elevated N deposition in *Q. petraea* and *F. sylvatica*, the conventional ground N fertilization, and the more befitting above canopy N application which mimics closer the interaction of the tree with atmospheric deposition. The ring widths of both species were not conclusively affected by any of the treatments, yet when translating the ring widths to BAI, some patterns emerged where ACN appeared to have a positive effect while BCN had the opposite on the temporal trend. When looking at wood densities on the annual tree ring scale, *Q. petraea* was the more receptive between the two species, exhibiting decreases in mean density under the above canopy N application only, accentuating the established importance of the relationship between the tree canopy and atmospheric N deposition, and emphasizing the significance in choosing the right N application method for experimental research. The earlywood density fraction of *Q. petraea* underwent an additional decrease, while latewood was not affected, pointing to earlywood being the sensitive section of the ring towards N inputs. *F. sylvatica* did not show concrete changes in ring wood density, yet when evaluating biomass area increment (BAIDen) through incorporating density in BAI, the previously observed negative effects of both below canopy N treatments on the BAI patterns were weakened.

Since our outcomes are based on a rather limited number of trees, and cores per tree, it would be encouraged to further substantiate the findings on a larger sample size. In addition, we determined significance of the N application on wood density of *Q. petraea* in middle years of the treatment period but not the last year. Considering past studies that observed reactions in wood traits to experimental treatments only some years down the monitoring periods, or rather responses in early years which diminished thereafter, a repeated analysis of our trees in upcoming years might be advised, as the experiment persists. Finally, in our field experiment, N was the singular factor differentiated in the system. Despite the advantages in focusing on one particular aspect of the environment for a deeper grasp of its role, it is clear that the interaction with other factors is substantial, thus further investigations including additional elements such as climate variables and age-related effects may be valuable.

With our current demonstration of the species-specific reactions to potential anticipated scenarios of increased N deposition rates, we aimed to contribute to a better understanding of possible consequences of increased N availability on the growth and wood formation in *Q. petraea* and *F. sylvatica*, whilst presenting the unique responses to different N application methodologies and utilizing restrained

fertilizer dosages to encourage careful experimental designs with a long-term aptitude in similar prospective studies.

Supplementary Information The online version contains supplementary material available at <https://doi.org/10.1007/s10342-024-01693-x>.

Acknowledgements We thank the Bolzano Province Forest Service for facilitating the study site in the Monticolo Forest. We thank Prof. Federico Magnani and Dr. Rossella Guerrieri from the University of Bologna for facilitating the study site in the Cansiglio Forest. A special gratitude to Ms. Monika Bradatsch for her invaluable assistance in wood core analysis. We thank the ETN Skill-For.Action network and all its' partners for providing a unique professional support system. Finally, we thank all members of the research team at the Analysis and Management of Mountain Ecosystems department, Faculty of Agricultural, Environmental and Food Sciences of the Free University of Bozen-Bolzano, who have been assisting in maintaining the experimental plots in the Monticolo site.

Author contributions Conceptualization: G.T., M.V. and C.W.; Methodology: G.T., M.V. and C.W.; Investigation: D.M.; Data curation and formal analysis: DM; Sample collection and analysis D.M. and D.R.; Supplementary data processing: D.M. and P.J.; Writing – original draft: D.M.; Review, and editing: D.M., C.W. and E.U.; Supervision: C.W. All authors have read and approved the final manuscript.

Funding Open access funding provided by Libera Università di Bolzano within the CRUI-CARE Agreement. The study is supported by the ETN Skill-For.Action project that has received funding from the European Union's HORIZON 2020 research and innovation programme under the Marie Skłodowska Curie grant agreement No. 936355.

Declarations

Conflict of interest The Authors declare no conflicts of interest.

Consent to participate Not applicable.

Consent for publication Not applicable.

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