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Temperate agroforestry systems take up more CO_2 compared to conventional crop- or grassland, without consuming more water

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Abstract. Ecosystem-atmosphere interactions remain poorly quantified in temperate agroforestry systems despite their potential as nature-based solutions against climate change. In this study, we present CO_2 and H_2O balances measured with eddy covariance over four pairs of agroforestry with open cropland or grassland systems in northern Germany from 2019 to 2024. Annual sums of net ecosystem CO_2 uptake were generally 1.2- to 4-fold larger at agroforestry sites (average of -113.9 g C m^{-2} yr^{-1}) compared to open cropland or grassland (average of 20.4 g C m^{-2} yr^{-1}), while differences in evapotranspiration between systems were comparatively small (averages of 473.7 mm yr^{-1} and 423.5 mm yr^{-1}, respectively). Water-use efficiency was thus generally higher at agroforestry, driven primarily by enhanced photosynthetic activity. Site-years with winter crops showed stronger carbon uptake, mostly due to reduced soil emissions in winter. Overall, the inclusion of trees resulted in an extended growing season and reduced sensitivity of these agroecosystems to high air temperature and low soil moisture. Furthermore, although net biome production was positive for most of the site-years, indicating a net carbon release, its magnitude was two or three times higher at open croplands and grassland than agroforestry, indicating stronger carbon losses from the reference systems that always showed a positive balance. These results reveal the potential of agroforestry systems as nature-based solution for climate change mitigation in agriculture, without compromising water availability.

1 Introduction

The agricultural sector is one of the main contributors to greenhouse gas (GHG) emissions from land systems and, consequently, to anthropogenic climate change (Calvin et al., 2023). Direct contribution from the agricultural sector at the farm level

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to the GHG emissions including CO_2, CH_4 and N_2O, accounts to 9 to 14 % worldwide, while indirect contributions associated with land use, land-use change and supply chain activities contribute an additional 10 to 24 % (Calvin et al., 2023). Croplands alone are expected to contribute around 5 % of global GHG emissions (Carlson et al., 2017).

At the same time, agricultural systems are particularly vulnerable to climate change: they are critically impacted by increasing aridity, rapidly increasing temperatures, and changing precipitation patterns, with more frequent and intense droughts or floods (Calvin et al., 2023). As a consequence of these impacts, soil fertility is reduced (Eekhout and De Vente, 2022; Mandal and Roy, 2024), and crops are directly damaged by extreme weather events (Lesk et al., 2022). Paradoxically, conventional agricultural practices, such as open cropland (OC) or open grassland (OG) systems, further exacerbate this challenge, as they generally produce larger environmental impacts than traditional and nature-based management systems (Abdo et al., 2025), and are also more sensitive to climate change impacts (Calvin et al., 2023).

Agroforestry (AF) has emerged as a promising land-use strategy to simultaneously reduce GHG emissions and increase the resilience of agricultural systems to climate change (Kay et al., 2019). AF was a broadly and traditionally extended practice in the temperate region, and it comprises any agricultural system combining trees with crops, perennial grasses, or livestock (Nair, 1985). AF was demonstrated to provide environmental benefits in terms of ecosystem services or functioning (Kay et al., 2019), which explains the increased interest in AF in recent years (Gupta et al., 2020). A particular type of AF, short rotation alley cropping (hereinafter also referred to as AF) combines rows of trees that are harvested in cycles of 3 to 6 years with rows of annual crops or grasslands (Markwitz et al., 2020). These systems can provide woody biomass as a renewable energy source while maintaining crop or grassland yields and enhancing the overall productivity and sustainability of the production system (Böhm et al., 2014; Veldkamp et al., 2023).

Quantifying ecosystem-scale carbon and water fluxes of AF systems is essential for evaluating the potential of agroforestry systems to mitigate climate change while improving the resilience of agricultural production. The eddy covariance (EC) technique provides direct measurements of net ecosystem CO_2 exchange (NEE), H_2O,and energy exchanges between terrestrial ecosystems and the atmosphere (Baldocchi, 2020). From these fluxes, ecosystem water use efficiency (WUE) can be derived, which is defined as the amount of carbon assimilated per unit of water lost through evapotranspiration and provides an integrative indicator of the coupling between carbon uptake and water use. (Hatfield and Dold, 2019). Quantifying WUE can provide valuable information on whether a change in management (open cropland or grassland to agroforestry) leads to a more sustainable water use while maintaining high yields.

We hypothesize that AF systems exhibit higher WUE than adjacent OC or OG systems, allowing higher carbon uptake without a proportional increase in water consumption. To test this hypothesis, in this study we analyzed a multiyear dataset of EC and meteorological measurements at four pairs of AF and reference OC or OG systems, published in Callejas-Rodelas et al. (2026). Specifically, we address four objectives: (i) quantify differences in annual and multi-annual balances of NEE and ET over the studied AF and OC or OG systems; (ii) analyze the dynamics of WUE over the studied sites; (iii) identify the biophysical drivers of NEE and ET; and (iv) quantify the net ecosystem carbon balance by integrating NEE with carbon exports through harvest.

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2 Methods

2.1 Site description

The study sites were located in Northern Germany in four different regions (Fig. 1): Dornburg (51.015 °N, 11.64 °E, Thuringia), Forst (51.79 °N, 14.63 °E, Brandenburg), Mariensee (52.565 °N, 9.464 °E, Lower Saxony) and Wendhausen (52.33 °N, 10.632 °E, Lower Saxony). Each study site included an AF as well as an adjacent OC or OG plot (Fig. 1). The AF plot consisted of strips of fast-growing tree species (poplar *Populus nigra x Populus maximowiczii* in Dornburg and Wendhausen, willow - *Salix schwerinii x S. viminalis* - in Mariensee, and poplar and black locust - *Robinia pseudoacacia* in Forst), which were intercalated by crops, for Dornburg, Forst and Wendhausen; or by perennial grassland, for Mariensee. Each site covered several hectares. The management of crops or grass at both OC or OG and AF was similar. Crops were subject to a yearly rotation scheme, while trees were typically harvested in cycles of three to four years. A high-yield grass cut was done once per year in Mariensee in June, and a low-yield harvest was done in October. Tree harvest took place in February 2021 at Forst, Mariensee and Wendhausen. Table B1 shows crop sowing- and tree and crop harvest dates.

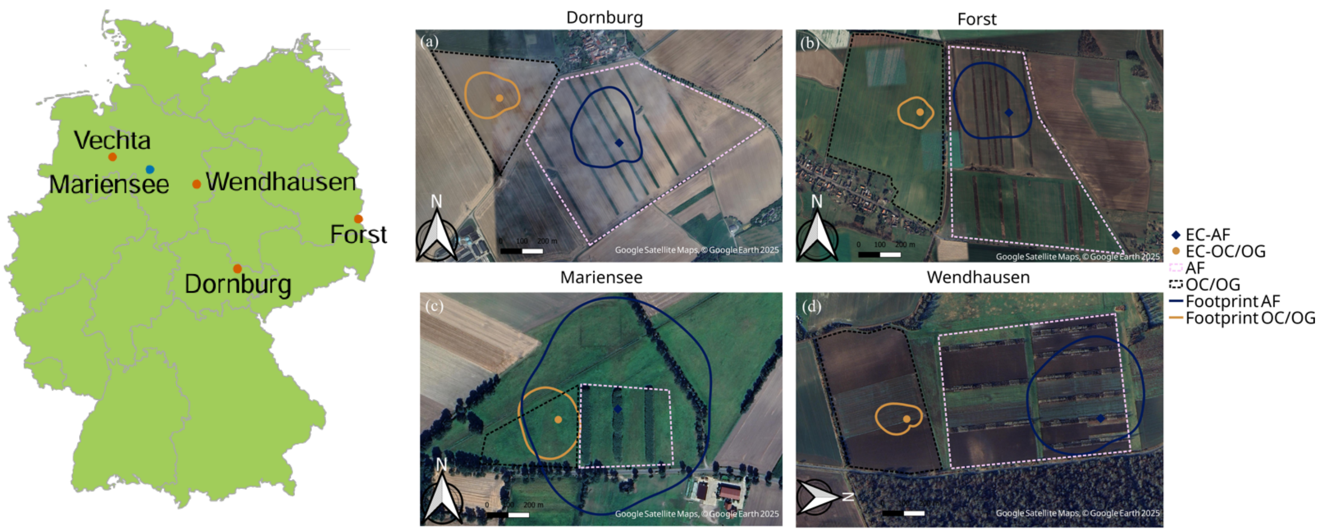

Figure 1. (Left) Map of site location within Germany. Blue dot represents the grassland agroforestry (Mariensee) and red dots represent the cropland agroforestry sites (Dornburg, Forst and Wendhausen). (Right) Satellite view of the pairs AF-OC/OG systems (a-Dornburg, b-Forst, c-Mariensee, d-Wendhausen), including the distribution of the agroforestry (AF, pink dotted line) and the open cropland or grassland (OC/OG, black dotted line) areas, the location of the eddy covariance stations (dark blue diamond for AF and orange circle for OC/OG). Dark-blue and orange solid lines represent the 80%-contribution area to the footprint climatology (calculated after Kljun et al., 2015). Details about footprint calculation and original figures were published in Callejas-Rodelas et al. (2026). Figures were created with QGIS v. 3.22.11 and Google Satellite Maps. © Google 2025.

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2.2 Eddy covariance and meteorological measurements

2.2.1 Instrumentation

Two EC towers were installed at each region, one at the AF plot and one at the OC/OG plot. The towers at the AF were 10 m tall and located within the tree strips. The OC/OG towers were 3 m (Forst and Mariensee) or 3.5 m (Dornburg and Wendhausen) tall, and located approximately at the center of the OC/OG plots. The measurement period comprised mid/early 2019 to fall 2024, except in Mariensee where measurements stopped at the end of 2021.

At each tower, CO_2 molar density, relative humidity (RH), three-dimensional wind speed, and sonic air temperature were measured using lower-cost EC setups (LC-EC) described and validated in Callejas-Rodelas et al. (2024) and van Ramshorst et al. (2024). Ancillary meteorological parameters were measured at each station. A list of measured variables is provided in Table S1.

2.2.2 Data processing

Initially, CO_2 and H_2O mole fractions were calculated from the raw CO_2 molar density and relative humidity (RH), respectively. Later, the CO_2 flux (FC), latent heat flux (LE) and sensible heat flux (H) were calculated using the EddyUH EC processing software (Mammarella et al., 2016). The storage of CO_2 (SC) was added to FC to get net ecosystem CO_2 exchange (NEE): NEE = FC + SC. SC was calculated using single point concentration measurements, as a vertical profile was non existent (Callejas-Rodelas et al., 2026; Pastorello et al., 2020).

NEE, LE and H were filtered for outliers, using the median absolute deviation (MAD) filter (Mauder et al., 2013); for quality flags, selecting flags of 1 to 6 and rejecting 7 to 9 (Foken et al., 2005); and for non-turbulent conditions by applying a friction velocity (USTAR) threshold (Papale et al., 2006; Reichstein et al., 2005). Following FLUXNET (Pastorello et al., 2020), 40 different USTAR thresholds were applied, based on the 2.5 % to 97.5 % percentiles in steps of 2.5 % of the USTAR distribution. This generated 40 different time series for each variable (NEE, LE and H). For the analyses here, the 2.5, 50 and 97.5 % percentiles were selected.

Filtered EC data were gap-filled by combining REddyProc (Wutzler et al., 2018), based on the marginal distribution sampling technique (MDS; Reichstein et al., 2005) for short gaps; and extreme gradient boosting (XGBoost, adapted from Vekuri et al., 2023), for longer gaps. Subsequently, NEE was partitioned into gross primary production (GPP) and ecosystem respiration (RECO), based on both daytime (Lasslop et al., 2010) and nighttime approaches (Reichstein et al., 2005). Finally, evapotranspiration (ET) was calculated from LE such as $\mathrm{ET(mm)} = \mathrm{LE(Wm^{-2})} \cdot 1800\mathrm{(s)} \cdot [\lambda(\mathrm{Jkg^{-1}})]^{-1}$, with λ the latent heat of vaporization, $\lambda = (2.501 - 0.00237 \cdot \mathrm{TA}) \cdot 10^6$.

Meteorological data were first aggregated to 30-min periods and cleaned for outliers. Gaps were then filled using a four-step routine: 1) linear interpolation for gaps $\leq$ 2 h; 2) linear models using a nearby station as a reference, whenever data was available; 3) linear models using ERA5-Land re-analysis data (Muñoz-Sabater et al., 2021) as a reference; and 4) using XGBoost for variables not available in the ERA5-Land dataset. More details on instrumentation and all steps of data processing, filling and partitioning are given in Callejas-Rodelas et al. (2026, 2024).

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2.3 Calculation of Water Use Efficiency

To compare crops within one site, between AF and OC/OG, and between sites, the ecosystem-scale WUE was calculated as cumulative GPP divided by cumulative ET (WUE=GPP/ET) on weekly, monthly, annual and whole-measurement-period scales. The periods from 1 November until 15 February the following year were excluded to reduce noise due to very low ET sums in winter. At each time step, six WUE values were calculated, based on the three daytime and three nighttime GPP time series, corresponding to the three different USTAR percentiles. WUE was then calculated as the average across all six values, with its error as the standard deviation across the six values.

2.4 Response of NEE, ET and WUE to environmental drivers

The alternating conditional expectation method (ACE; Breiman and Friedman, 1985) was applied to study the relation between environmental drivers and NEE or ET, following Baldocchi and Arias Ortiz (2024) who first applied this method to EC data. We used a modified version in Python (v. 3.11) of the original code by Voss and Kurths (1997). ACE analysis builds optimal functions that explain the response of a certain variable to a set of predictors (Eq. 1):

$$\theta^*(Y) = \sum_{i=1}^{n} \phi_i^*(X_i) + \epsilon^* \qquad (1)$$

where $\theta^*(Y)$ is the optimal transformation of the response (NEE or ET), ϕ is the optimal function of predictor X, and ϵ is the error term (Baldocchi and Arias Ortiz, 2024).

The ACE method was applied to 30-min values of NEE_U50 and ET_U50 using only measured values, with the objective of avoiding bias related to gap-filling, and for the growing season of each crop, which is defined as the time from crop sowing to harvest. We chose four predictors explaining the highest variance in NEE and ET: global radiation (R_G), TA, vapor pressure deficit (VPD) and USTAR. Section 3 only shows NEE and ET response to R_G, TA and VPD. Polynomial 2^{nd}-degree curves were fit to the data to better visualize patterns. An assessment of the applied transformations is provided in the supplement.

A generalized additive mixed model (GAMM, Baayen and Linke, 2020) was employed to analyze the influence of the standardized precipitation and evapotranspiration index (SPEI) (Vicente-Serrano et al., 2010) and soil moisture (SM; depth 0-25 cm) on NEE, ET and WUE. SPEI and SM were provided by Felix Pohl (Helmholtz-Centre for Environmental Research, internal communication) and calculated based on Pohl et al. (2023). The model was fitted on weekly sums of NEE_U50 and ET_U50, as well as weekly WUE. To this end, GPP_U50 was averaged from daytime and nighttime models.

The GAMM was represented by Equation 2

$$y_i = \beta_0 + f_1(\mathrm{SPEI}_i) + f_2(\mathrm{SM}_i) + \beta_1\,\mathrm{treatment}_i + \beta_2\,\mathrm{Tair}_i + \beta_3\,\mathrm{VPD}_i + \beta_4\,\mathrm{Rg}_i + b_{\mathrm{year}(i)} + \varepsilon_i \qquad (2)$$

where y_i is the response for observation i (ith-week of the time series), β_0 is the intercept or baseline level of the response, and $f_1(\mathrm{SPEI}_i)$ and $f_2(\mathrm{SM}_i)$ the spline capturing nonlinear effects of SPEI and SM. The term $\beta_1\mathrm{treatment}_i$ represents the fixed effect of AF or OC/OG. The terms $\beta_2\,\mathrm{Tair}_i$, $\beta_3\,\mathrm{VPD}_i$, and $\beta_4\,\mathrm{Rg}_i$ are linear effects of TA, VPD and Rg, included as covariates; $b_{\mathrm{year}(i)}$ is the random intercept for year, capturing interannual variability not explained by fixed effects. Finally,

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ε_i is the residual error term, representing the remaining unexplained variation. This model resulted in a similar non-linear response of NEE, ET and WUE to SPEI and SM for AF and OC/OG, with the two systems differing only by a constant shift in the ordinate across the predictor range, which represents a mean difference between treatments. This choice was based on the premise that we aimed to obtain an average response, assuming a similar shape, for both treatments, without complicating the model's capacity to produce accurate predictions by introducing other effects. This model's validation is provided in the Supplement.

2.5 Estimates of carbon balance and uncertainties in eddy covariance data

Estimates of Net Biome carbon Production (NBP) were obtained by combining annual NEE and carbon export through harvest. Woody biomass was estimated following the method described in Lamerre et al. (2015). The yield of crops (Choe et al., 2025) and grasslands (Langhof and Swieter 2024) was determined by biomass harvesting and dry matter measurements. Straw remained in the field; therefore, the biomass carbon content was quantified only for grain. If no carbon data was available, carbon content was calculated based on other years' estimates for similar crops, or on literature values for winter rapeseed in Dornburg and Wendhausen (Poyda et al., 2019) and for grasses in Mariensee Banowetz et al. (2009). For AF, although carbon removal from trees only occurred after tree harvest, annual carbon growth was considered in the yearly balance, instead of at the end of the growing cycle. Processes like manure application, leaching or soil erosion were considered negligible. Soil organic carbon (SOC) was measured once along the project duration (Choe et al., 2025) and considered stable. There were no major disturbances apart from harvest events.

The uncertainty in annual or multi-annual sums of NEE or ET was calculated based on Richardson and Hollinger (2007), with slight modifications (described in section C). The uncertainty in NBP was estimated annually adding in quadrature the errors from NEE and C yield (see section 3).

3 Results

3.1 Annual and multi-annual sums of NEE and ET

All AF sites were stronger CO_2 sinks than their corresponding OC or OG reference systems, with mean annual NEE of -113.9 g C m^{-2} yr^{-1} (AF) versus 20.4 g C m^{-2} yr^{-1} (OC/OG), though effects varied by site and year (Fig. 2). Cumulative NEE exhibited a pronounced seasonal cycle, characterized by net CO_2 emissions (negative NEE) during senescence and winter dormancy, and net CO_2 uptake (positive NEE) during the growing season. In Dornburg and Forst (Fig. 2a-d), AF had consistently greater CO_2 uptake than their adjacent OC: in Dornburg, multi-annual NEE sum was -569.6 g C m^{-2} yr^{-1} at AF and -322.3 g C m^{-2} yr^{-1} at OC, while in Forst, it was -1142 g C m^{-2} yr^{-1} at AF and -400.4 g C m^{-2} yr^{-1} at OC. The contrast was stronger at Forst, where AF shifted from a weaker sink than OC to a stronger sink after tree harvest in 2021. At these sites, winter crops (winter wheat or barley, winter rapeseed) were more frequent and extended the growing season, partially compensating for winter respiration with earlier CO_2 uptake. Crop ripening reduced CO_2 uptake less strongly at AF than OC; AF generally

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maintained an uptake until crop harvest or beyond. At Mariensee (Fig. 2e and f), AF was a CO_2 sink, whereas OG was a source from the start of the measurements (long-term sums of -350.4 g C m^{-2} yr^{-1} and 773.9 g C m^{-2} yr^{-1}, respectively), because OG growing-season uptake was insufficient to offset winter emissions, while uptake at AF did. Grass cutting further suppressed OG uptake and increased emissions. At Wendhausen (Fig. 2g and h), AF was a weak CO_2 sink and OC, a moderate source (long-term sums of -48.6 and 209.3 g C m^{-2} yr^{-1}, respectively), but the uncertainty at AF was high and precluded a robust sink classification. AF's negative NEE sum was driven by a strong initial uptake in 2019, however, dominant summer crops (summer barley or maize), with shorter growing seasons and larger dormant-season emissions, progressively weakened the sink strength in both systems. Crop-ripening effects were stronger in OC than AF in 2019 and 2021, but similar thereafter.

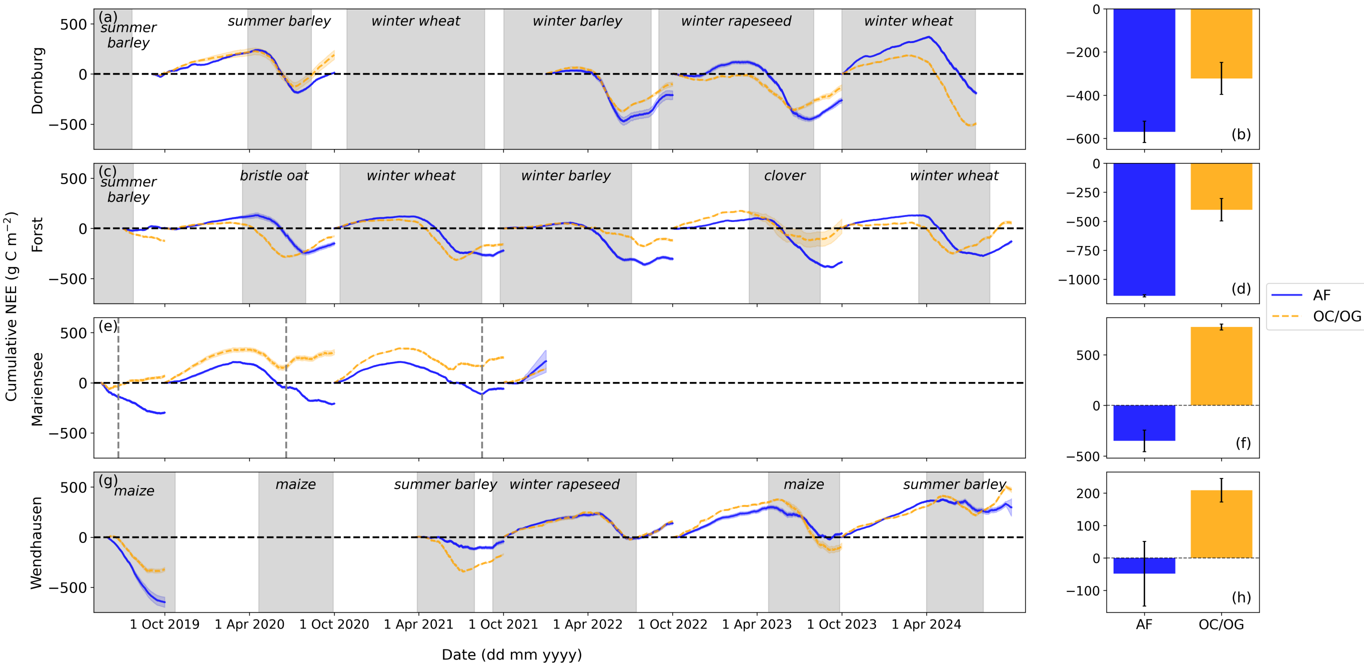

Figure 2. Cumulative sums of net ecosystem CO_2 exchange (NEE) along the measured period for single years (left) and multi-annual (right, bar plots), for Dornburg (a, b), Forst (c, d), Mariensee (e, f), and Wendhausen (g, h), for AF (blue) and OC or OG (orange). Years were considered from 1 October until 30 September of the following year. 2019 was only partially covered, and 2021 for Wendhausen. Sums were calculated only for overlapping periods across the pairs AF-OC/OG, within each site. Bold lines indicate the mean across NEE_U2.5, NEE_U50 and NEE_U97.5. Shaded areas around the yearly sums and lines at the bar plots represent NEE standard deviation. In Dornburg, Forst and Wendhausen, grey shading corresponds to crops' growing season from sowing to harvest, whereas in Mariensee the vertical dashed lines indicate the major grass cuts. The horizontal dashed line indicates a zero NEE.

Multi-annual and yearly ET sums were larger at AF (average of 473.7 mm yr^{-1}) than OC/OG (average of 423.5 mm yr^{-1}) except in Wendhausen, although the relative differences between systems were smaller than for NEE, but with also evident seasonal dynamics (Fig. 3). The largest ET rates occurred during a relatively short period during the growing season, while

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it remained very low during senescence. At Dornburg, AF showed a higher annual ET than OC during all years, particularly in 2023 and 2024 (Fig. 3a), with long-term sums of 2560 and 2012 mm, respectively. At Forst, ET was slightly higher at AF than OC (Fig. 3c) with long-term sums of 2793 and 2640, respectively. Mariensee showed higher annual ET at AF than OG during all years (Fig. 3e); long-term sums were 1488 and 1345 mm, respectively. Wendhausen exhibited higher annual ET at OC than AF except in 2023 (Fig. 3g), with long-term sums of 2286 mm at AF and 2643 mm at OC. Generally, increases in ET were dampened by crop or grass ripening and harvest. Finally, annual ET sums appeared to increase progressively over the measurement period, regardless of crop type, a pattern not observed for NEE.

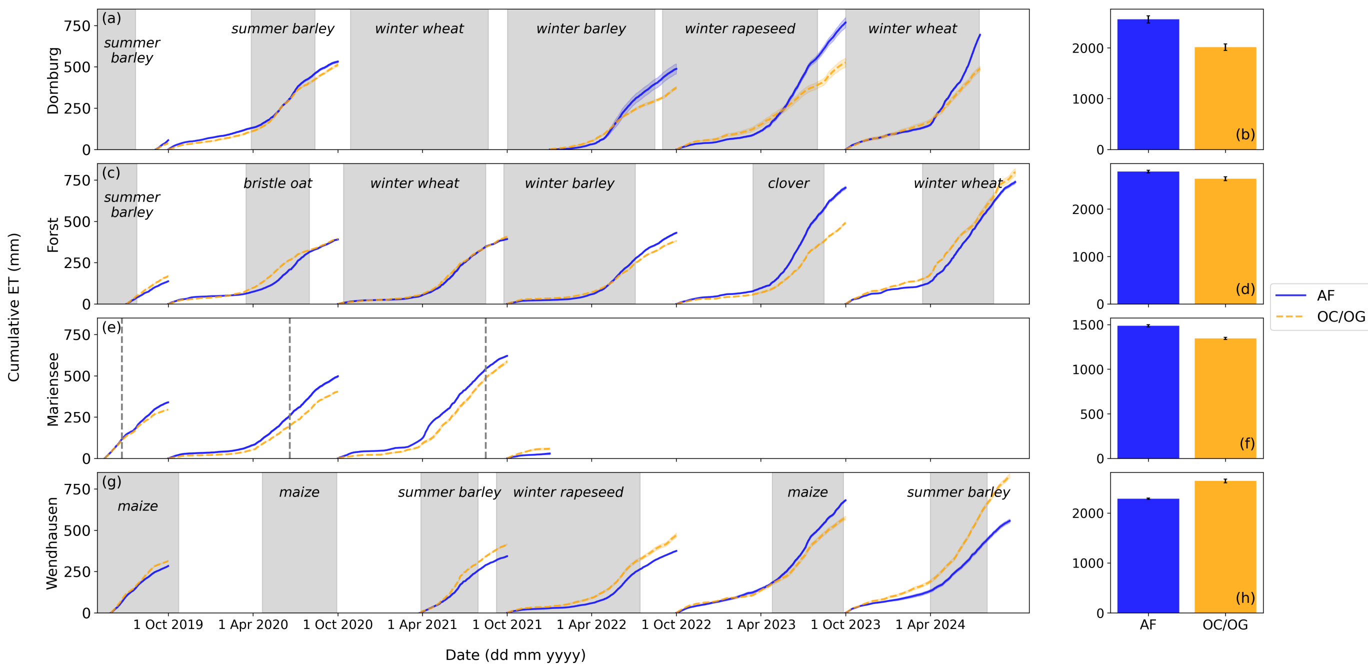

Figure 3. Cumulative sums of evapotranspiration (ET) along the measured period for single years (left) and multi-annual (right, bar plots), for Dornburg (a, b), Forst (c, d), Mariensee (e, f) and Wendhausen (g, h), for AF (blue) and OC or OG (orange). Years were considered from 1 October until 30 September of the following year. 2019 was only partially covered, and 2021 for Wendhausen. Sums were calculated only for overlapping periods across the pairs AF-OC/OG, within each site. Bold lines indicate the mean across ET_U2.5, ET_U50 and ET_U97.5. Shaded areas around the yearly sums and lines at the bar plots represent ET standard deviation. In Dornburg, Forst and Wendhausen, grey shading corresponds to crops' growing season from sowing to harvest, whereas in Mariensee the vertical dashed lines indicate the major grass cuts.

3.2 Weekly and monthly WUE

Multi-annual WUE was higher at AF in Dornburg, Forst and Wendhausen, and higher at the OG in Mariensee (Table 1). The dynamics of WUE differed between years (Fig. 4), but some patterns were consistent between sites and similar crops. Site-years with summer barley (2020 in Dornburg and 2021 and 2024 in Wendhausen) had on average 48 % higher WUE at AF

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than OC (Table 1). For winter wheat, WUE was 50 % higher at OC than AF in Dornburg in 2024, but 3 and 53 % higher at AF than OC in Forst in 2021 and 2024, respectively. For winter barley, WUE was 7 and 31 % higher at AF than OC in both Dornburg and Forst, respectively, in 2022. For winter rapeseed, WUE was similar between AF and OC in Dornburg in 2023, but 35 % higher at AF than OC in Wendhausen in 2022. When maize was cultivated (2019 and 2023 in Wendhausen), WUE was on average 21 % higher at OC than AF. In Forst, WUE was 6 % higher at OC than AF in 2020 with bristle oat, and 15 % lower in 2023 with clover, although clover did not grow well that year. Overall, summer crops (summer barley, maize and bristle oat) exhibited a higher WUE at OC than AF, whereas winter crops (winter wheat, barley or rapeseed) tended to show higher WUE at AF than OC. At Mariensee, WUE was higher at OG in 2020 and 2021 and similar between AF and OG in 2019. Furthermore, both OC and OG were more affected by crop or grass ripening and harvest (Fig. 4), with WUE rapidly declining, whereas WUE at AF declined less strongly afterwards.

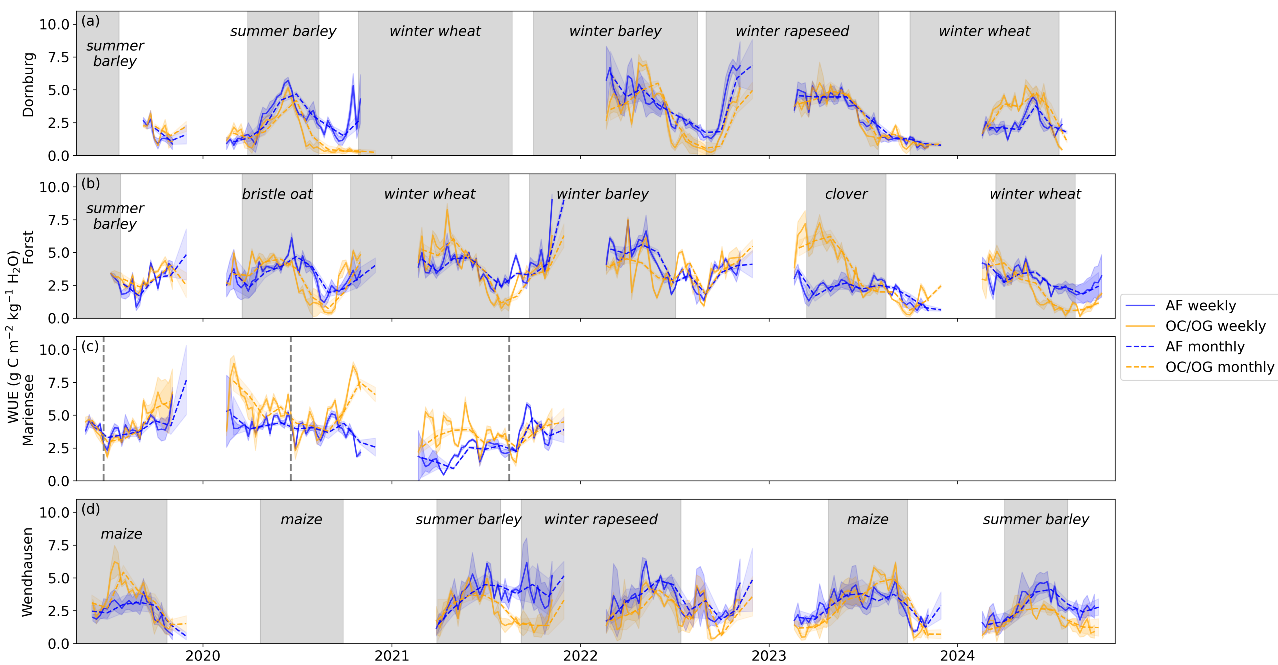

Figure 4. Water Use Efficiency (WUE) at weekly (solid lines) and monthly (dashed lines) scales, for Dornburg (a), Forst (b), Mariensee (c) and Wendhausen (d), for AF (blue) and OC or OG (orange), across the measurement period. The period 1 November to 15 February was removed every year to avoid noise related to small ET in winter. 2019 was only partially covered, and 2021 for Wendhausen. Shaded areas around the sums represent WUE standard deviation (section 2.3). In Dornburg, Forst and Wendhausen, grey shading corresponds to the growing season of crops from sowing to harvest, whereas in Mariensee the vertical dashed lines indicate the major grass cuts.

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Table 1. Water Use Efficiency (WUE; g C $kg^{-1}_{H_2O}$) at annual and multi-annual scales for AF and OC/OG. The period 1 November to 15 February was removed every year to avoid noise related to small ET in winter. Values and errors correspond to means and standard deviations of WUE calculated for the six GPP time series (day- and nighttime, and the three USTAR scenarios).

Site	2019	2020	2021	2022	2023	2024	Multi-annual
Dornburg AF	1.7 ± 0.1	3.2 ± 0.2	3.7 ± 0.1	3.3 ± 0.2	2.8 ± 0.1	2.4 ± 0.1	2.8 ± 0.1
Dornburg MC	1.9 ± 0.1	2.0 ± 0.1	-	3.1 ± 0.2	2.8 ± 0.1	3.6 ± 0.2	2.7 ± 0.1
Forst AF	2.5 ± 0.1	3.5 ± 0.1	3.6 ± 0.1	3.7 ± 0.1	2.2 ± 0.1	2.6 ± 0.2	3.0 ± 0.0
Forst MC	2.9 ± 0.1	3.3 ± 0.1	3.5 ± 0.0	3.4 ± 0.1	2.6 ± 0.1	1.7 ± 0.2	2.8 ± 0.1
Mariensee AF	3.8 ± 0.1	4.0 ± 0.2	2.3 ± 0.1	-	-	-	3.3 ± 0.1
Mariensee MC	3.8 ± 0.2	4.8 ± 0.2	3.4 ± 0.1	-	-	-	4.0 ± 0.2
Wendhausen AF	2.7 ± 0.5	3.7 ± 0.5	3.8 ± 0.6	3.5 ± 0.4	3.1 ± 0.5	3.1 ± 0.5	3.2 ± 0.3
Wendhausen MC	3.6 ± 0.1	-	2.8 ± 0.3	2.6 ± 0.4	3.4 ± 0.3	2.0 ± 0.3	2.7 ± 0.2

3.3 Response of NEE, ET and WUE to environmental drivers

Responses of NEE and ET differed by system (AF and OC/OG) and between winter and summer crops (Fig. 5), being stronger for NEE than ET. Overall, AF responded more dynamically to high energy or atmospheric water demand than OC/OG. y-axes values do not represent actual NEE or ET values; rather, they denote the expected contribution of the predictor (x-axis) to their variability. Consequently, a negative value of NEE with respect to a predictor indicates that NEE responds by reducing its value by that magnitude with respect to a certain predictor value.

NEE became more negative with increasing R_G until around 500-600 W m^{-2}, then slightly less negative, while ET increased until saturation or a slight decline above 600 W m^{-2}. AF winter crops' contributions to NEE were more negative than OC/OG in Dornburg and Forst and similar between systems in Wendhausen, while summer crops' contributions were similar between systems at all sites. AF winter crops or AF grassland exhibited the highest ET contributions. Generally, NEE became more negative at TA $>$ 15-20 °C for AF summer crops and Mariensee AF, while for both AF and OC winter crops and Mariensee OG, NEE became more negative for TA $<$ 15 °C and more positive for TA $>$ 20, indicating a stronger sensitivity to high TA at OC/OG than AF. ET generally shifted from slightly negative to positive contributions with rising TA, showing the strongest increase at high TA ($>$ 20 °) for AF summer crops or for Mariensee OG. With increasing VPD, NEE contributions progressively became more positive above 1-1.5 kPa, except for OC winter crops in Forst. Contributions were larger for summer crops in Dornburg and Forst, larger for AF than OG in Mariensee, and larger for OC winter crops in Wendhausen. ET usually increased at low VPD and declined at higher VPD ($>$ 1.5 kPa), with the strongest reductions for AF summer crops in Dornburg and Forst, followed by OC winter crops, while Mariensee showed similar behavior in AF and OG, and Wendhausen showed small difference among crop types and AF/OC.

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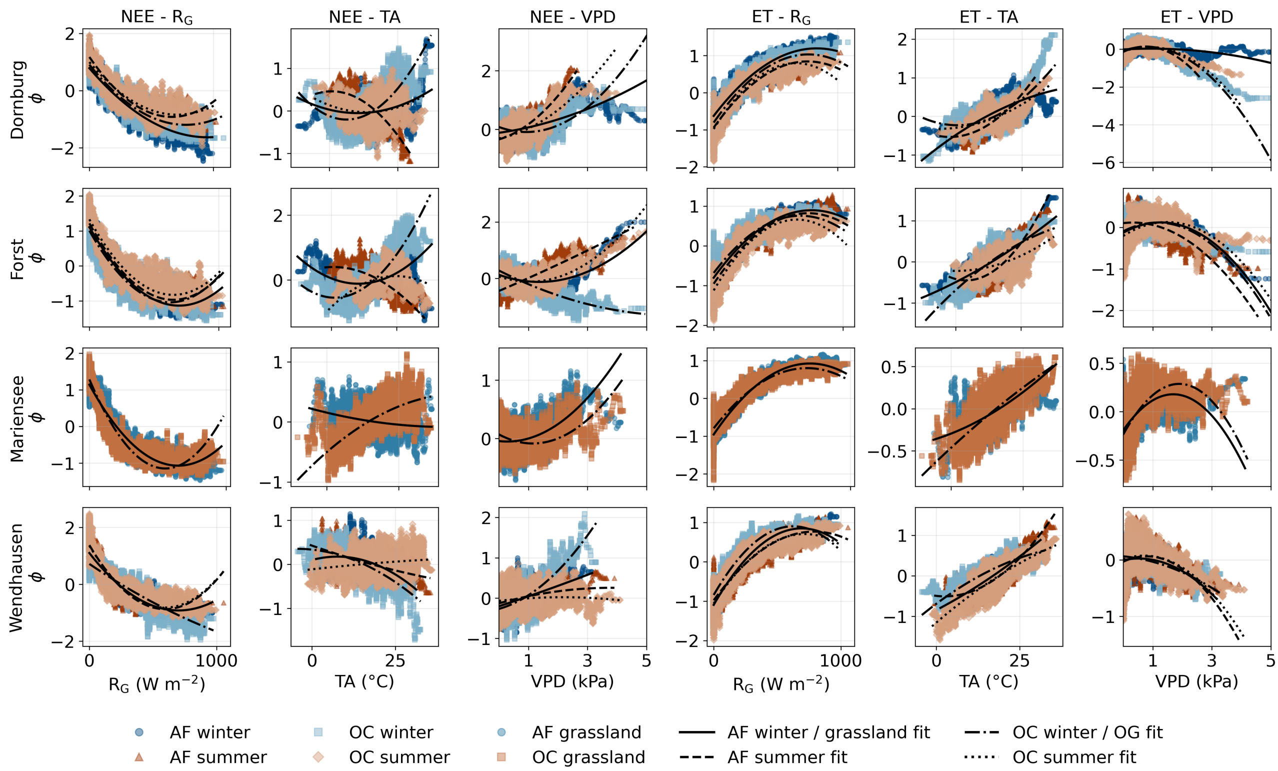

Figure 5. Shape of the optimized transformations, ϕ, as a function of the input predictors for Dornburg (first row), Forst (second row), Mariensee (third row) and Wendhausen (fourth row). Data were divided in winter or summer crops, for the AF and OC sites. For Mariensee, no distinction was made. Black lines show the polynomial fit to the shape of ϕ, solid lines for winter crops at AF and full year at Mariensee; dashed lines for summer crops at AF; dash-dotted lines for winter crops at OC and OG at Mariensee; dotted lines for summer crops at OC. The first three columns correspond to NEE and the last three to ET; columns are ordered by predictor: global radiation (Rg), air temperature (TA) and vapor pressure deficit (VPD). The growing season was defined from crop sowing to harvest. Note the different y-axis scales, chosen to better show small differences between AF-OC/OG.

The modeled responses of GAMM to SPEI and SM remained similar between AF and OC/OG, with just a small vertical shift (Fig. 6), which represents the treatment contribution to the responses (section 2.4). NEE response to SPEI was positive at Dornburg and was approximately constant. At Forst, it was initially negative and increased with increasing SPEI. At Mariensee, NEE declined across the SPEI range. At Wendhausen NEE shifted from positive to negative at low SPEI ($\approx$-1.5) and was near zero at high positive SPEI ($>$ 1.5). NEE became more negative with increasing SM in Dornburg and Forst, while in Mariensee NEE response increased from slightly negative to slightly positive values along the SM range. In Wendhausen, NEE remained mostly positive and weakly variable, decreasing only at very high SM (0.7). ET showed higher values at AF than OC/OG at all sites except Wendhausen. ET response to SPEI decreased steadily along the SPEI range, increasing again in Forst at very high SPEI ($>$ 1.5). In Mariensee and Wendhausen, ET increased with increasing SPEI. ET increased with SM in all sites and dropped at very high SM ($>$ 0.9), except in Mariensee where it was highest for moderate SM ($\approx$0.5) and then declined. WUE

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reduced with increasing SPEI at all sites except Dornburg, where it increased until a decline at very high SPEI (1.5). WUE increased with SM in all sites, but showed an initial decline at low SM (< 0.2).

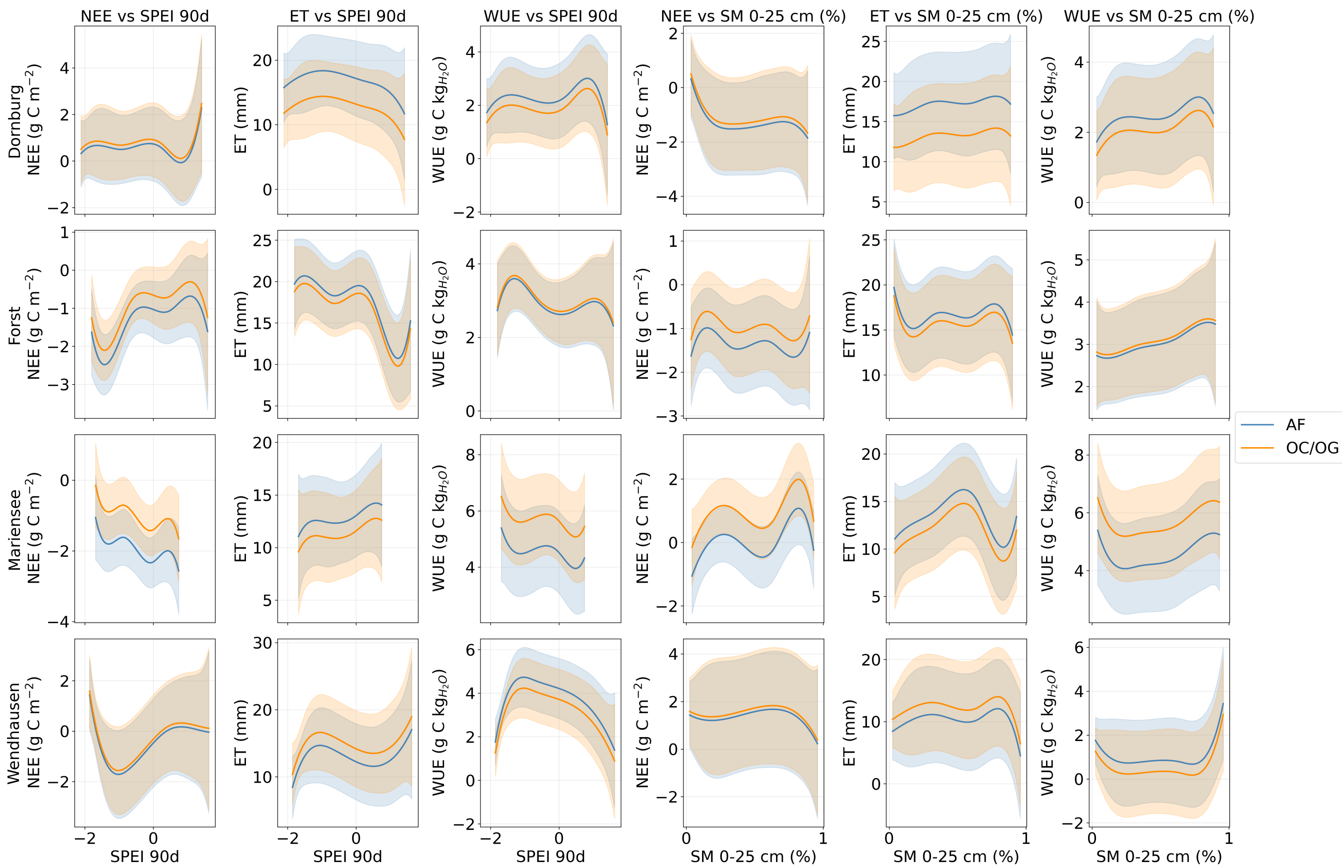

Figure 6. Response curves obtained from the main-effect Generalized Additive Mixed Model (GAMM) fitted to the relation between NEE, ET and WUE to SPEI and SM, for AF (blue) and OC/OG (orange). Lines indicate the fitted mean response curves from the model, by holding all predictors fixed at their median values and varying the one of interest (SPEI or SM). Shaded areas are uncertainty bands, calculated as 1.96 times the fitted mean. More details on GAMMs preparation is available in section 2.4. Positive SPEI indicates wet conditions and negative SPEI indicates dry conditions.

3.4 Carbon balance over the measurement sites

Annual NBP was mostly positive for both AF and OC/OG, indicating a C release from these agroecosystems, with values larger at OC/OG (202.4 g C m^{-2} y^{-1} on average) than AF (107.4 g C m^{-2} y^{-1} on average). In Dornburg, the average NBP at OC was 98.9 g C m^{-2} y^{-1}, and at AF, 65 g C m^{-2} y^{-1}, with only two years, 2023 for AF (-37.9 g C m^{-2} y^{-1}) and 2024 for OC (-193.1 g C m^{-2} y^{-1}) with negative NBP. In Forst, all years except 2024 indicated a net uptake at the AF with NBP of -14 g C m^{-2} y^{-1} on average, and a net release with 107.3 g C m^{-2} y^{-1} on average at the OC. In Mariensee, the OG had a large

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NBP of 366.2 g C m^{-2} y^{-1} on average, while the AF presented a negative NBP in 2020 (-126.7 g C m^{-2} y^{-1}) and positive in 2021 (54.4 g C m^{-2} y^{-1}). In Wendhausen, all years indicated a C release with NBP of 342.9 g C m^{-2} y^{-1} for AF and 319.1 g C m^{-2} y^{-1} for OC.

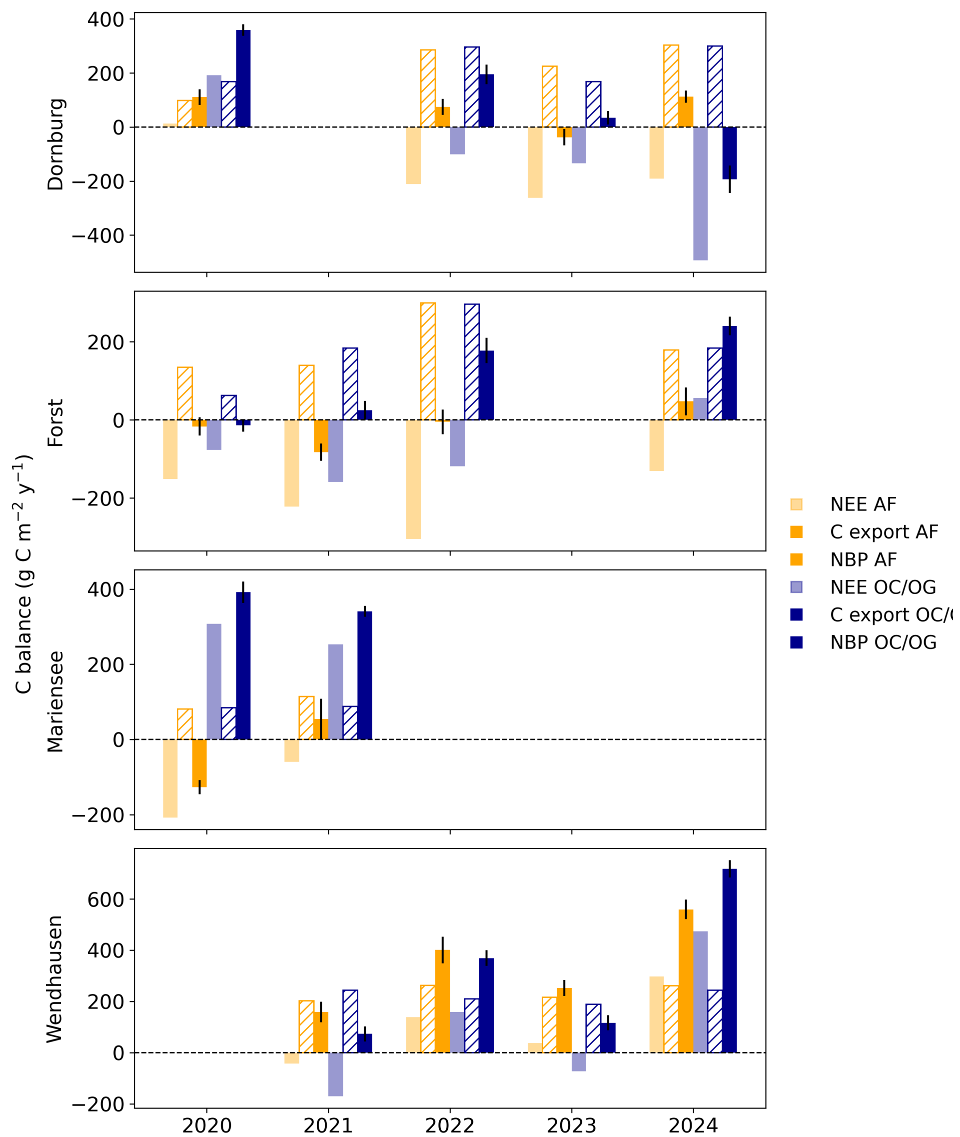

Figure 7. Annual C export, NEE and NBP, in g C m^{-2}, for all sites. Years were considered from 1 October until 30 September of the following year. 2019 was only partially covered, therefore it was not included herein. C yield from AF was calculated as the average between C yield of crop at AF and C yield of trees, each weighted by the corresponding area they cover at the site. NBP was the sum of NEE (negative if there was a net C uptake or positive if there was a net C emission) and C yield (positive). Uncertainties in C yield and EC fluxes were estimates as explained in section C

4 Discussion

In this study we tested the hypothesis whether AF systems have a higher WUE than the reference OC or OG systems, which indicates they exhibit a higher carbon uptake without a similar increase in water consumption. We examine this hypothesis in view of the objectives presented in the introduction.

4.1 Annual and multi-annual NEE and ET of AF and MC systems

Stronger CO_2 uptake by AF, mostly concentrated in summer, and larger ET at annual scale was caused by plant physiological activity, enhanced for trees that keep a extended growing season in comparison to crops, and have access to deeper water reservoirs. Furthermore, the differences in NEE were larger than for ET, indicating that AF kept a stronger carbon uptake without a proportional increase in water consumption, which validated our initial hypothesis.

Nevertheless, the discrepancies in fluxes between AF and OC/OG were not constant throughout the growing season. During winter, CO_2 exchange was dominated by ecosystem respiration, with low ET due to plants being in the dormant phase. The higher winter respiration at the AF in Dornburg and Forst was consistent with a higher biomass content due to the additional trees, agreeing with Shao et al. (2025). The higher respiration at the OG in Mariensee could be due to a very large SOC content (Table A1), soil water level, previous management, and the low intensity management (Baah-Acheamfour et al., 2016). Similar respiration between AF and OC in Wendhausen may reflect a balance between the greater input of organic matter to the soil from maize straw, which would affect OC more strongly, and the compensatory effect of tree cover at the AF.

This generally larger winter respiration at AF was compensated in summer depending on whether there were more frequent winter crops, with an extended growing period, that reinforced the AF CO_2 uptake (Dornburg and Forst), or summer crops. These, more abundant in Wendhausen, have a shorter growing period and despite having a strong uptake they are not sufficient to compensate for winter emissions. Therefore, the choice of winter crops determined the long-term CO_2 sink behavior at Dornburg and Forst, which was stronger at AF, while in Wendhausen the AF was a weak sink and the OC a weak source, with large uncertainty (Fig. 2). In Mariensee, the difference in long-term CO_2 balance, with AF as a sink and the OG as a source, could be due to the low management activity at the OG and a large SOC content; therefore, summer uptake from grasses was not sufficient to compensate the large respiration during winter.

There were smaller differences in ET between AF and OC/OG, as also found in Ward et al. (2012) over a similar agroforestry system. This may indicate a larger WUE of trees, that contributed to an improved NEE uptake of AF (van Ramshorst et al., 2025) to a greater extent than to ET increase. Some studies measured a lower ET at short rotation poplar plantations (Fischer et al., 2018; Bloemen et al., 2017) compared to reference grasses or crops, combined with a larger CO_2 uptake from trees, which suggest that increasing the proportion of trees in relation to grass/crop area might be beneficial in alley cropping systems.

Regarding harvest events, fluxes at the AF were less affected by crop/grass ripening and harvest than at OC/OG, as the trees kept photosynthesizing and transpiring after the crops or grasses had been harvested. Tree cut appeared to have an effect in Forst AF, enhancing CO_2 uptake and slightly increasing ET, perhaps due to the combination of a less strong CO_2 uptake by

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winter barley in 2022 and clover in 2023, together with young, re-sprouting trees at the AF. Nevertheless, in Mariensee and Wendhausen, tree cut did not seem to alter fluxes.

4.2 Annual and multi-annual WUE of AF and MC systems

The larger WUE at AF for the cropland sites (Dornburg, Forst and Wendhausen; Table 1) could be attributed to the trees, which increased significantly photosynthetic uptake and contributed to only a small increase in ET. This validates the hypothesis underlined in the study. Nevertheless, in Mariensee, the higher WUE at OG than AF could be attributed to differences in photosynthetic uptake, very high at the OG, while ET was not very different between systems, probably due to a balance at the AF between earlier grass development but low tree transpiration, and earlier grass ripening while trees still transpired in summer.

We observed a high inter-annual variability in WUE, which can be referred to differences in crop type and management, and meteorological conditions. The driest years (2020 and 2022) consistently showed a larger WUE at AF for the cropland sites, attributed to a deeper root system of trees and longer growing season, which copes better with dry soils (Fahad et al., 2022); this effect may have been particularly pronounced at Forst, which had a low SOC and a high sand content. This suggest that AF may particularly benefit agricultural systems that are prone to soil degradation and are poor in organic matter, improving microclimatic conditions for crop growth (Kanzler et al., 2019).

Summer crops present more adapted strategies to cope with higher atmospheric water demand than winter crops (Mbava et al., 2020), which could explain a smaller WUE at AF than OC for these crops. Correspondingly, a larger WUE at AF than OC when winter crops were grown could be due to tree-crop interactions. Tree shading reduces both crop area and ET next to the tree strips, and the start of the growing season of trees is later than for crops, hence also keeping a longer growing season but not contributing largely to ET. A higher multi-annual WUE at Dornburg OC could be explained by the old trees at the AF, compared to typical alley cropping systems in which trees are harvested after 3 to 5 years (Böhm et al., 2014). More biomass contributed to a larger ET difference between AF and OC, particularly in 2023 and 2024, compared to the observed differences in Forst and Wendhausen; besides, the replacement of winter wheat by summer barley in 2024, did not compensate very large emissions due to snail infestation. The stronger decline in WUE at OC/OG than AF after crop or grass ripening and harvest (Fig. 4) was a result of biomass removal, while trees at AF maintained high photosynthesis rates.

In conclusion, interactions between different crops and tree species are complex. Finding the optimal AF design in the context of water conservation and CO_2 sequestration requires more investigation (Tsonkova et al., 2012; Wu et al., 2017), as well as partitioning the contribution of different ecosystem components within AF systems (crops/grasses, soil and trees, respectively) to NEE and ET (Bastos Campos et al., 2025; Cui et al., 2024). The divergence in WUE between AF and OC/OG is expected to increase with increasing heat and drought stress conditions and aridity (Mbava et al., 2020).

4.3 Drivers of NEE, ET and WUE

NEE was more noisy than ET and showed a greater sensitivity to all drivers studied (Fig. 5). For cropland sites, winter crops at both AF and OC showed more negative contributions to NEE representing CO_2 uptake, and more positive contributions to ET

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representing H_2O release, compared to summer crops due to the longer growing season. Winter crops showed a decline in CO_2 uptake at lower TA values, corresponding to an earlier ripening, compared to summer crops (Béziat et al., 2009). AF winter crops' larger CO_2 uptake and H_2O release compared to OC at high R_G could be explained by the fact that trees were reaching their maximum leaf development and physiological activity during the time of stronger radiation (mid June) while crops had started to ripe. AF was equally sensitive to R_G as OC for summer crops due to the decline in physiological activity of both. We also observed less sensitivity of AF to TA both for winter and summer crops than for OC or OG. This can be explained by the capability of AF systems to maintain CO_2 uptake and H_2O release even during warm conditions due to the tree deeper root system (Allen et al., 2004). However, in the case of summer crops for AF, a higher sensitivity to VPD shades doubt on the capability of AF to keep normal functioning under high atmospheric evaporative demand, in comparison to winter crops. This could be due to the fact that winter crops may also have a deeper, more developed root system (Thorup-Kristensen et al., 2020), which illustrates a positive tree-crop interaction effect for these crops.

The responses of NEE to SPEI and SM (Fig. 6) were generally consistent between sites and AF-OC/OG. At Mariensee, at the OG respiration was increased with increasing soil moisture, which lead to higher microbial activity in the soil (Zeng et al., 2025), and was compensated at the AF by the trees lowering soil moisture content. At the other sites, generally higher soil water content increased CO_2 uptake and ET due to the activation of crops, with more intense physiological activity than grasses (Lloyd et al., 2025), but at high or very high SPEI or SM the responses were site-specific due to the balance with other factors like increased soil respiration, potentially larger at AF (Ngaba et al., 2024) and during leaf-out periods. Nevertheless, WUE declined with SPEI, but increased with SM. Low-to-moderate SPEI could induce a water-saving strategy of trees and crops (Chaves et al., 2011), while high SPEI could be dominant in winter or transition periods, promoting soil respiration which offsets plants' CO_2 uptake. Nevertheless, SPEI does not reflect the soil humidity conditions, but the difference between atmospheric demand and water availability; besides, WUE could be larger for periods with low ET (late-winter, early spring) which correspond usually to larger SM, therefore this does not necessarily reflect an enhanced photosynthesis. Studying more specifically plant-water relations during those periods could shed light on this difference.

4.4 Carbon balance over AF and OC/OG systems

A positive NBP most of the site-years was a result of the large carbon exports through harvest, enough to compensate a negative NEE. Importantly, AF systems generally loss less carbon as evidenced by a lower NBP than OC/OG (Fig. 7), which is consistent with the general evidence that AF contributes to improve carbon sequestration, and should be considered in the context of promoting its potential for climate change mitigation (Cardinael et al., 2021). This is a matter of global relevance and may be beneficial at diverse agricultural regions worldwide.

Our findings agree with many studies quantifying the carbon balance of agroecosystems. Béziat et al. (2009) reported a cropland close to a neutral balance, with rapeseed, winter wheat and sunflower, and another cropland with a positive NBP of 100 g C m^{-2}, similar to our systems. Anthoni et al. (2004) reported that winter wheat was a significant carbon source, similar to our systems, but at Forst its impact was attenuated at the AF, showing a negative NBP in 2020 and a much lower NBP than OC in 2024 (Fig. 7); higher values, indicating stronger export, were reported by Li et al. (2006) and Schmidt et al.

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(2012). For summer barley or maize, different studies reported a NBP indicating small carbon sinks (Hollinger et al., 2005), or either small (Grant et al., 2007) or significant (Niu et al., 2022) carbon sources. Furthermore, crops with longer growing season (winter crops) generally showed lower NBP, that is, less carbon exports from the system, as a result of a balance between a more negative NEE and a comparable C yield to summer crops (Ceschia et al., 2010). This was also observed in our data, except for winter rapeseed in Wendhausen 2022, but this may have been an effect of both a positive annual NEE and a C yield estimate according to literature and not based on measured field values. The extensively managed OG at Mariensee was a source of carbon, in agreement with Hussain et al. (2011); nevertheless, it lost more carbon than croplands in our study, in disagreement with Lloyd et al. (2025). The potential of OG as a carbon sink could be limited by a high SOC content (increasing soil respiration) and factors like management or species combination.

These results imply an important role of trees in reducing CO_2 emissions, while maintaining substantial yield production over the crop- or grassland systems (Choe et al., 2025; Veldkamp et al., 2023). Generally, perennial plants (trees, grasses) contribute to increase SOC content (Ledo et al., 2020). Nevertheless, it is key to climate change mitigation that CO_2 stays in soils in the long term (Mayer et al., 2022). In alley cropping systems, this balance ultimately depends on management, harvest frequency or use of wood (Cardinael et al., 2021; Horemans et al., 2019), and other ecosystem biophysical characteristics like changes in albedo due to land-surface change (Zenone et al., 2015). Since respiration affects largely annual carbon budgets (Ward et al., 2012), management measures like cover crops or reduced tillage could be implemented to reduce emissions (Mangalassery et al., 2015; Seitz et al., 2023). Cover crops, for instance, should be adapted to site-specific climate conditions, considering that soil characteristics directly impact its respiration and indirectly vegetation development (Lohila et al., 2004). Besides, some effects of AF, such as reducing wind or drought damage, are beneficial for yields and carbon uptake of crops as they are more stable in comparison to OC (Liu et al., 2019), especially considering the likely increase of weather extremes in many regions worldwide (Coumou and Rahmstorf, 2012; Tang et al., 2025).

Nevertheless, these NBP estimates should be considered cautiously, as they did not considered manure or inorganic fertilizer applications, and some years were either not quantified (2024) or not available (Forst from 2022 to 2024) and had to be estimated. Furthermore, external carbon inputs (e.g. manure) might modify the relative differences in NBP between AF and OC/OG, as nutrient leaching is different among these systems (Choe et al., 2026). A life-cycle assessment is recommended in this content to better characterize the impact of AF vs. OC/OG (Coelho et al., 2025).

4.5 Limitations of the study and outlook

The data presented in this study and the full dataset in Callejas-Rodelas et al. (2026) could be used as input to models that quantify the long term carbon and water cycles of AF and OC/OG systems, including tree-crop interactions, biomass dynamics, and lateral input or output of carbon, nitrogen or other elements. Carbon cycling in this study was only considered between atmospheric uptake and harvest export: other processes (manure application, leaching, etc.) should be addressed in the balance, for which modeling/other measurements would be needed (Laubach et al., 2023). Furthermore, future climate change mitigation potential assessments could analyze the radiative forcing of AF vs. OC/OG based on surface energy balance, combining modeling (Graf et al., 2023) and measurements of other GHGs (Shao et al., 2025).

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ACE and GAMM provided insight into how NEE, ET and WUE responded to the main meteorological drivers and should be considered as a driver sensitivity analysis. ACE focused on measured data and gave an indication of actual meteorological forcing on differences in the response of AF vs. OC/OG. GAMM focused on weekly gap-filled data and provided relative differences in the response to SPEI or SM. Both were limited by their parameterization, but could be the basis for developing ecosystem-level models and, together with a longer measurement period and more repetitions of crop-site combinations, to understand phenomena such as the legacy effects after a disturbance or the impact of compound extreme weather events (heat waves with flash droughts) on AF-OC/OG carbon and water balances (Zhao et al., 2025).

Gap-filling inherently smooths statistical distributions of measured data (Chen and Guestrin, 2016) and, although there is some guarantee that it adequately reproduced the temporal behavior of fluxes (Callejas-Rodelas et al., 2026), it may have contributed to reduce differences AF-OC/OG. This would potentially bias the conclusions from our analyses. Furthermore, the inclusion of non-target areas in the footprint could also affect the results' interpretation, which could be solved by applying a footprint-based flux attribution and filtering, as e.g. in Fang et al. (2024). Additionally, it remains unclear how uncertainty in NEE or ET propagates to modeled GPP and WUE. Therefore, the uncertainty estimates (Callejas-Rodelas et al., 2026; Richardson and Hollinger, 2007) should not be considered definitive and this method could be extended to include other effects.

5 Conclusions

This study provides one of the first multiyear ecosystem-scale comparisons of CO_2 and H_2O ecosystem-atmosphere exchanges between temperate agroforestry and adjacent open cropland or grassland systems using standardized eddy covariance measurements in four sites in northern Germany. In general, agroforestry consistently improved net CO_2 uptake relative to the corresponding reference system without increasing evapotranspiration at a similar rate. This was explained by the longer growing season of the trees and their increased physiological activity with respect to crops or grasses. The magnitude of these differences depended strongly on crop type and management. Although winter crops strengthened the carbon sink of both agroforestry and open cropland, the effect was larger at the agroforestry sites. WUE was variable between systems and depended on crop type and year, but it was generally larger for winter crops at agroforestry and for summer crops at open croplands.

The analysis of meteorological controls further demonstrated that agroforestry modifies ecosystem responses to environmental variability. In particular, agroforestry reduced the sensitivity of carbon uptake to high temperatures and drought conditions, indicating an increased resilience of ecosystem functioning under climate stress. However, these advantages were only partly reflected in ecosystem WUE, which remained strongly dependent on crop type and interannual climatic variability.

Despite the improved carbon balance of AF relative to adjacent open systems, net biome production showed that most site-years resulted in a carbon release after accounting for harvest. Only the Forst site functioned as a persistent carbon sink during the observation period. These findings demonstrate that tree integration improves carbon balance but is not sufficient to guaranty long-term carbon sequestration. Instead, the climate mitigation potential of temperate agroforestry emerges from the interaction between trees, crop rotation, and management practices.

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Although this study identifies robust patterns across multiple sites representing temperate agroforestry vs. open cropland or grassland systems, several processes remain insufficiently constrained. Future research should integrate ecosystem-scale flux measurements with footprint analysis and additional carbon inputs and outputs to obtain a more complete ecosystem carbon budget. This integrated assessment will be essential for accurately quantifying the contribution of agroforestry to mitigation and adaptation to climate change under future climatic conditions.

Code and data availability. The code necessary to perform the described analysis and generate the presented figures is publicly available in the repository https://github.com/jangelcrgot/nee_et_wue_agroforestry.git. Data corresponding to this article are available in the repository https://10.5281/zenodo.21353133. The complete dataset corresponding to the SIGNAL project was published in https://doi.org/10.25625/A2Z8T8 (Callejas-Rodelas et al., 2025).

Appendix A: Site characteristics

Table A1. Site location, climatological averages and standard deviations of annual air temperature (*TA*) and annual sum of precipitation (*P*) for the reference period 1981-2010 (DWD, 2024), elevation above sea level and soil characteristics, for all the project sites. Soil type and organic carbon content are based on Shao et al. (2025), Veldkamp et al. (2023) and Schmidt et al. (2021), while soil bulk density is based on Shao et al. (2025) and Markwitz et al. (2020).

	Dornburg	Forst	Mariensee	Wendhausen
Location	51°00’50" N 11°38’38" E	51°47’20" N 14°37’57" E	52°33’51" N 09°27’51" E	52°19’59" N 10°37’53" E”
Mean *TA* (°C)	9.9 ± 0.8	9.6 ± 0.8	9.6 ± 0.8	9.6 ± 0.9
Mean *P* (mm)	608 ± 117	568 ± 117	661 ± 109	637 ± 125
Elevation a.s.l (m)	289	66	42	82
Soil type	Calcaric Phaeozem	Gleyc Cambisol	Anthrosol	Vertic Cambisol
Soil organic carbon (kg C m^{-2})	4.64	3.48	22.5	6.16
Soil bulk density (Mg m^{-3})	1.19	1.28	1.28	0.89

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Appendix B: Management information

Table B1. Sowing and harvest dates of crops, harvest dates of trees, and cutting dates for the grassland in Mariensee, throughout the project duration. In 2023, clover did not grow well in Forst due to the very wet winter conditions, therefore no harvest took place. In 2024, part of the winter wheat in Dornburg was infested by snails and it was replaced in March by summer barley. Harvest of both crops took place on the same day. In Wendhausen, there were three crops, typically summer barley, corn and winter rapeseed, rotating each year across the site. In the table, only the crop located in the main footprint area of the EC station is written down.

Type	Year	Dornburg	Forst	Mariensee	Wendhausen
Crop / sowing-harvest date	2019	Summer barley 5 March - 22 July	Summer barley 25 March - 25 July	Grass 4 June	Silo maize 24 April - 23 October
	2020	Summer barley 28 March - 12 August	Bristle oat 17 March - 31 July	Grass 15 June	Silo maize 21 April - 28 September
	2021	Winter wheat 28 October 2020 - 21 August	Winter wheat 13 October 2020 - 15 August	Grass 14 June	Summer barley 22 March - 30 July
	2022	Winter barley 2 October 2021 - 15 August	Winter barley 24 September 2021 - 4 July	-	Winter rapeseed 8 September 2021 - 14 July
	2023	Winter rapeseed October 2022 - 11 August	Clover Bad growth	-	Silo maize 26 April - 26 September
	2024	Winter wheat October 2023 - 13 August Summer barley March 2024 - 13 August	Winter wheat 30 October 2023 - 17 July	-	Summer barley 10 April - 5 August
Tree harvest	–	-	February 2021	February 2021	February 2021

Appendix C: Uncertainty estimation of annual NEE, ET and NBP

The error in annual or multi-annual sums of NEE or ET was based on Richardson and Hollinger (2007). For this evaluation, we used the time series corresponding to the USTAR 2.5, 50 and 97.5 % percentile scenario. The method consisted of two distinct steps. First, the uncertainty due to noise in the data was calculated as the standard deviation across the cumulative sums for 50 different scenarios in which random noise was added to the measured data. Second, the uncertainty due to random gaps (covering 30 % of the dataset, in addition to the originally existing gaps) and systematic gaps (of duration from 1 to 60 days, in steps of 3 days, from day 1 until the last day of measurements), was evaluated by calculating the relationship between length of gaps and the period (month of the year) in which gaps occurred; then, this relationship was applied to determine the standard deviation of the sum across the short, random gap, and the long gap scenarios. All scenarios from steps 1 and 2 underwent the same gap-filling routine as applied to the original data (section 2.2.2). ET was calculated from filled LE time series as mentioned in section 2.2.2. Finally, both the uncertainty related to noise in the measurements, and the uncertainty due to the long gaps, were added in quadrature to obtain total uncertainty of the sum of NEE or ET. The procedure was applied to all available periods for all stations, but the uncertainty was calculated separately for single years or for multi-annual balances, by just determining the standard deviation across scenarios in steps 1 and 2 for the specific period. A detailed explanation was provided in section 2.3.4 in Callejas-Rodelas et al. (2026). The main change with respect to that method was that, for the

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long-gap scenarios evaluation, the full measured period was considered, not only 1 year, and gap length extended from 1 day until 60 days, instead of 28 days.

Errors in C yield were calculated based on the standard deviation of the measured C across the different samples; they were roughly 10 % of the total C estimates. Therefore, for years when C yield was estimated (based on similar years and/or crops or on literature), its error was calculated as 10 % of the estimated C value. To determine uncertainty in NBP, we first calculated the uncertainty in NEE_U2.5, NEE_U50 and NEE_U97.5 using the method described above. Then, NEE uncertainty from each of the time series was added in quadrature to get a combined uncertainty in NEE (Fig. 7). Finally, errors in NEE and in C yield were added in quadrature to get the uncertainty in NBP.

Author contributions. JACR, JvR and CM performed field measurements and data analysis during phases III, II, and I of the SIGNAL project, respectively. JACR compiled and processed the longer term dataset, performed the analyzes presented in this text, and wrote the manuscript. JvR contributed to data processing and manuscript writing. AK and CM wrote the project proposal and contributed to data processing and manuscript writing. SC and ML provided data on biomass and yield carbon content and contributed to manuscript writing.

Competing interests. The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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