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RESEARCH ARTICLE

Changes in tree biomass and soil carbon pools of oak ecosystems along a climate gradient in a Central European region

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Abstract
Background and Aims Climate change has significantly influenced stand density of forest (SDF) and carbon storage in soils and tree biomass, intensifying these effects over the past four decades. To predict future changes in soil organic carbon (SOC) and carbon content of tree biomass (CTB), we conducted a space-for-time substitution study across a climatic gradient in sessile oak forests.
Methods Based on long-term climate data, we studied 33 zonal sessile oak sites in Hungary categorized into three climatic groups (humid, meso, and dry). SOC content, bulk density, CTB and SDF were measured. The vegetation and topographical characteristics of the sites were consistent across sites although precipitation varied among the climate groups.
Results Aboveground CTB accounted for 61% of total organic carbon (TOC) in humid forests, 48% in meso forests, and 37% in dry forests, while SOC represented 18%, 31%, and 44% of TOC, respectively. TOC was similar in humid and dry forests (413 and 420 Mg C·ha^{-1}), but significantly lower in meso forests. Over the last 50 years, average annual temperatures have risen by more than 1.5 °C, and summer temperatures have increased by over 2.2 °C. Along the precipitation gradient, drier climates shifted carbon reserves toward soils, resulting in higher SOC but lower CTB in dry forests compared to humid ones.

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Conclusion Biomass decreases faster than SOC accumulation during the transition from humid to dry forests, and therefore TOC in meso forests is lower than in humid and dry forests. Over longer periods, reduced tree biomass due to drier conditions is offset by increased SOC, demonstrating a balancing effect. Understanding the reciprocal effects of climate, forests, and soils is essential for predicting ecosystem carbon storage responses to climate change.

Keywords Climate change · Forest biomass · Carbon stock · Soil organic matter · Decomposition · Soil biology

Introduction

Forests occupy approximately one third of the terrestrial vegetated surface of the Earth and play a critical role in both local and global carbon (C) and water cycles with feedbacks into the climate system (Reichstein and Carvalhais 2019). Carbon stored in forest biomass accounts for almost 80% of all terrestrial biomass, while the organic C stock of their soils accounts for more than 40% of the total soil C stock of terrestrial ecosystems (Dixon et al. 1994; Gray 2007; Mayer et al. 2020; Wei et al. 2014). Moreover, both carbon content of tree biomass (CTB) and soil organic C (SOC) play a significant role in the long-term sequestration of atmospheric CO_2 (Achat et al. 2015; Kauppi et al. 2020). Climate change could affect these two major C reservoirs in several ways. In some areas, especially in forests with wetter and cooler climates, warming could increase the amount of biomass produced because the length of growing seasons is extended, and excess N deposition and increases in CO_2 levels also stimulate photosynthesis (Cao and Woodward 1998; White et al. 1999). In drier forest areas, climate change-induced water scarcity and temperature stress are expected to inhibit biomass growth and increase tree mortality and this results in a reduction in tree stand densities (Anderegg et al. 2013; Ryan 2011; Schuldt et al. 2020; Uribe et al. 2023).

Dry forests in the wetter margins of drier grasslands (steppes, prairies, pampas, etc.) are also among the climate change losers regarding biomass changes (Mátyás et al. 2018). The inland areas of the Carpathian Basin, which are the westernmost terminus of a band of thousands of kilometers across Ukraine, southern Russia, and Northeast China (Hengeveld et al. 2012; Kempeneers et al. 2011; Tchebakova et al. 2016), are located on the edge of the forested steppes and grassy steppe along xeric limits of forested areas. Long-term meteorological data show that the climate of the Carpathian Basin has become drier and warmer in the last half century (Galos et al. 2009; Ilona et al. 2022); where the impacts of climate change are occurring faster and to a greater extent than the global average (Masson-Delmotte et al. 2021; Mátyás et al.

Table 1 Mean climate parameters of Hungary (the whole country) divided by decade from 1901 to 2020

	FAI	Mean annual temp. (°C)	Mean summer temp. (°C)	Ellenberg index	WB annual (mm)	WB March—August (mm)	Mean annual precipitation (mm)	Mean summer precipitation (mm)
1901–1910	5.96	9.43	19.19	31.00	84.32	–84.64	647.0	208.4
1911–1920	5.57	9.59	18.72	29.45	112.24	–68.50	673.5	220.7
1921–1930	6.70	9.80	19.26	32.40	62.80	–97.65	641.0	204.7
1931–1940	5.72	9.64	19.55	31.46	84.92	–86.85	668.0	216.7
1941–1950	6.86	9.92	19.73	34.51	10.98	–155.05	600.4	185.3
1951–1960	5.72	9.85	19.62	32.29	59.08	–88.11	636.4	232.4
1961–1970	5.90	9.66	19.21	31.74	52.35	–98.08	636.9	218.4
1971–1980	5.59	9.78	18.90	32.36	41.84	–92.92	609.8	220.9
1981–1990	6.58	9.98	19.34	35.43	–18.09	–134.36	577.0	194.0
1991–2000	6.61	10.37	20.23	34.50	7.88	–136.62	609.8	201.7
2001–2010	5.83	10.76	20.71	33.71	25.35	–120.56	656.4	238.9
2011–2020	6.29	11.57	21.49	35.46	–33.11	–176.51	628.2	210.8

2018) (Table 1). During the twentieth century and the first decades of the twenty-first century, the frequency of summer droughts increased, so the summer climate of Hungary shifted towards the Mediterranean climate (Fekete et al. 2021, 2023; Galos et al. 2009). The number of hot days and the frequency and length of dry periods are increasing significantly (Bartholy and Gelybó 2007; Domonkos 2003) and changes in the tree populations of the forests are mainly attributable to the severe water shortage (Szepesi 1997). Our previous studies have shown that the dry oak forests in Hungary have experienced increasing tree mortality and reduced tree biomass due to increased drought (Berki et al. 2009; Fekete et al. 2017; Mátyás et al. 2018). However, there is much less research on how SOC stocks in these forest soils are affected by climate-induced drying and how total ecosystem C stocks are changing. Fekete et al. (2017) showed a 15.5% SOC increase over 40 years in the upper 1 m soil layer in the oak forest of Síkfőkút, an experimental forest in northeastern Hungary, in spite of significant decreases in tree biomass production. That study found that the dendromass of the oaks (*Quercus petraea* (Matt., Liebl) and *Q. cerris* (L.)) in the forest was 19% lower than expected from standard forestry yield tables (Sopp 1974) and if the biomass of tree species (*Acer campestre* (L.), *A. tataricum* (L.), *Prunus avium* (L.)) growing in canopy gaps was included, the dendromass in the area was 13% lower. This increase in SOC was attributed to both the decreasing organic matter decomposition processes due to drought effects on microbial activity as well as the increased amount of organic matter deposited on soils due to tree mortality.

Detecting the impact of climate change on soil parameters is not feasible with real-time series analysis, because there are very few long-term studies that go back 5–6 decades and have an uninterrupted series of data on climate and the changes in the carbon content of forest vegetation and their soils. Thus we conducted a space-for-time substitution (Blois et al. 2013; W. Zhang et al. 2019) study along a humid-dry climatic gradient in sessile oak forests in Hungary to help predict future SOC (Fekete et al. 2021, 2023) and CTB (both above- and belowground) change. This method can be used to investigate changes not only in soils but also in forest stands, using carefully filtered sites under well-designed conditions (Horrocks and Bauch 2020; Móricz et al. 2021; Niu et al. 2019).

In our previous studies (Fekete et al. 2021, 2023), we identified 3 climate groupings along a precipitation gradient (humid, meso, dry) with significant differences in the water balance and species composition among these forest groups (see Materials and Methods). We examined the changes in the SOC concentration of the soil layers in the top 25 cm layer of the soil, the rate of decomposition, the quality of the soil organic matter (SOM) and the age of the soil's organic matter using the C14 isotope method. These studies showed significantly faster decomposition in humid forests'soils than in dry forests'soils. In our current research, we have extended the studies to a depth of 1 m in the soil (divided into 6 depth increments), examining the amount of stored SOC and measuring and comparing the biomass of trees in the three forest climate types. We selected sessile oak forest stands with similar geological and topographical backgrounds to ensure that soils were not influenced by intrazonal microclimatic and edaphic effects but mainly by the macroclimate of the areas.

The study aimed to investigate the effect of a drier climate on the tree biomass of forests and the organic carbon content of their soils. We hypothesize that while a drier climate reduces forest biomass production and thus litter deposition to the forest floor, decomposer activity is reduced even more, so more C accumulates in the soils of dry forests than in humid forests. The increase in soil C content ends when the reduced litter input can compensate for the reduced soil respiration associated with drying. Data obtained from this study of forested areas along a climate gradient in the Carpathian Basin will enable us to predict changes in ecosystem C content over time due to the predicted warming and drying climate and will serve as baseline data for more long-term studies of climate change effects on these terrestrial forests.

Material and method

The description of study sites

We focused on minimizing the confounding factors, because many environmental and ecological factors influence the CTB and the SOC including soil texture, bedrock, and slope aspect (Hassink 1997; Hobley and Wilson 2016; Martin et al. 2011; Six et al. 2002). The sites were selected on gentle slopes at the foot of the mountain regions, hilly areas, as well as on the borders of the plains and mountainous areas in Hungary. Our selected forests are zonal sites with deep soils, meaning that they reside well within the mean conditions for their climate category. The average age of the examined forests (mainly the *Quercetum petraeae-cerris* and *Querco-Carpinetum* community) is 84.9 ± 3.66, and all are older than 60 years (Fig. 1, Table 2.). The sessile oak is autochthonous to all hilly and mid-mountain landscapes of Hungary, but it was the dominant tree species in the hornbeam-sessile oak association (meso sessile oak forest in our category). In the wetter forest areas of the country the beech forest was a natural association, but the foresters has afforested part of the beech trees (*Fagus sylvatica, (L.)*) with pure sessile oak stands (humid sessile oak forest in our category) in the past centuries. Furthermore a warmer and drier climate can reduce the distribution area of beech and growth of beech trees (Bontemps et al. 2012). Sessile oak is expected to adapt better to a warmer and drier climate than European beech, which will therefore modify the competitive relationship between the two species (Maleki et al. 2020; Rubio-Cuadrado et al. 2018). In the dry zonal climate (slightly negative water balance), part of the natural turkey oak-sessile oak association is afforested with pure sessile oak stands also (dry sessile oak forest in our category). So, in our study, the climate categories we use are not differentiated according to the difference in temperature, like the forest formations of the European vegetation map (e.g. boreal, mesophytic, thermophilous), but based on the water supply (humid, meso, dry).

The soil-forming material is loam and loess formed from the fall dust of the Ice Age. In the selected areas, there is no permanent (or long-lasting) water effect in the soils, so anaerobic conditions did not play a role in SOC accumulation. The texture of the topsoil layer was silty clay loam or silty clay, and there was little difference in the clay content between sites. The differences between the soils of the sites (Luvisols, Cambisols, Phaeozems and Chernozems) are explained by macroclimatic factors (Fekete et al. 2021, 2023).

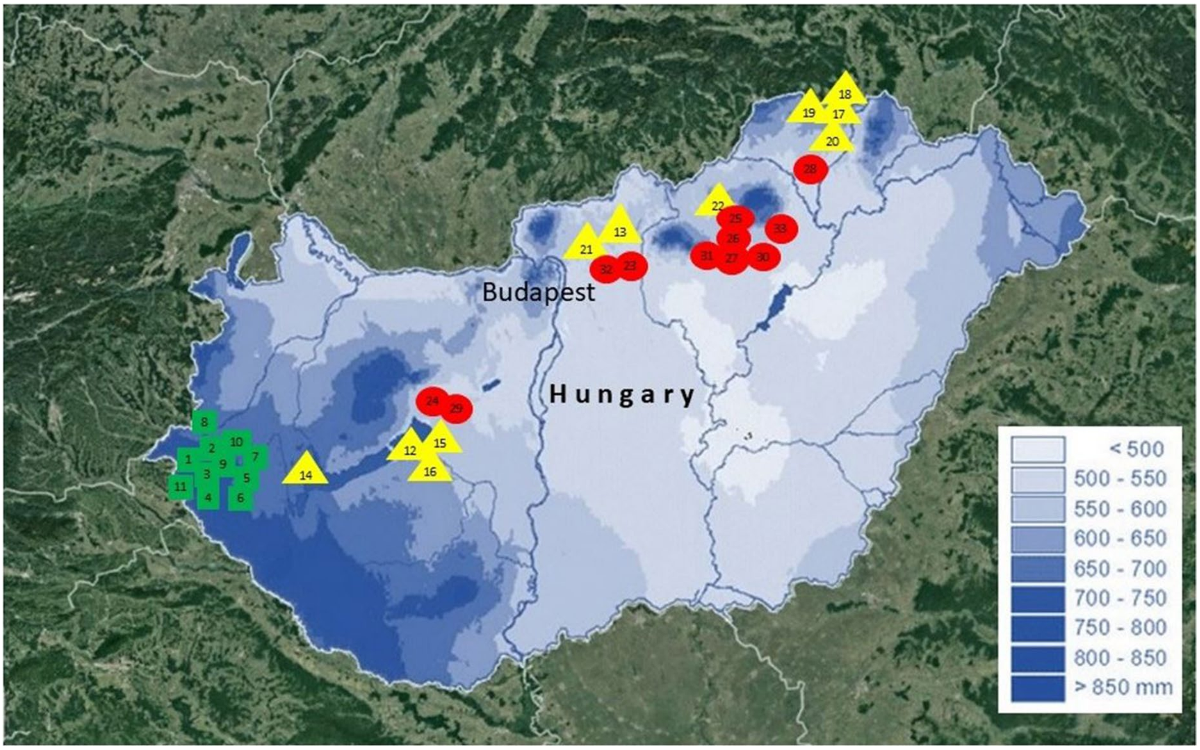

Fig. 1 Location of the forest sites on a precipitation map showing isohyets. Forest types are indicated as follows: Humid forests (H) green square (🟩), meso forests (M): yellow triangle (▲), dry forests (S): red circle (🔴)]

Table 2 The climatic characteristics of the sampling areas (SOC: Soil Organic Carbon, CTB: Carbon content of tree biomass, CTAB: Carbon content of aboveground tree biomass SDF: Stand density of forests, MAT: Mean Annual Temperature, MAP: Mean Annual Precipitation, WB (climatic Water Balance (annual)), FAI: Forest Aridity Index, EQ: Ellenberg index). The climate characteristics refer to the period 1971–2020

Nr	Site Name	Type of Site	N°	E°	Type of Soil	SOC (Mg C*ha^{-1})	CTB Mg C*ha^{-1}	CTAB (Mg C*ha-1)	SDF (%)	MAT (°C)	MAP (mm)	WB (mm)	FAI	EQ
1	**Bajánsenye**	H	46.823	16.402	Luvisols	70.8	301.0	228.3	88	10.2	733	146	5.14	28.6
2	**Ispánk**	H	46.878	16.440	Luvisols	77.0	318.5	245.9	94	9.9	726	157	5.03	28.0
3	**Szilvágy**	H	46.739	16.652	Luvisols	78.5	354.7	267.0	98	10.1	722	138	5.22	28.8
4	**Ortaháza**	H	46.633	16.708	Luvisols	71.4	348.0	260.0	100	10.5	744	144	5.27	28.2
5	**Bak-1**	H	46.755	16.805	Luvisols	67.0	400.7	288.1	112	10.1	716	133	5.53	29.2
6	**Bak-2**	H	46.761	16.812	Luvisols	75.1	373.8	268.7	101	10.1	716	133	5.53	29.2
7	**Bazita (Zalaegerszeg)**	H	46.818	16.814	Luvisols	73.1	286.4	203.7	97	10.3	695	104	5.67	30.3
8	**Felsőmarác**	H	46.933	16.565	Luvisols	81.7	337.3	254.7	94	10.0	710	136	5.18	29.0
9	**Zalalövő**	H	48.358	21.052	Luvisols	69.8	343.5	254.7	98	10.1	702	122	5.31	29.4
10	**Hagyárosbörönd**	H	46.899	16.698	Luvisols	88.2	344.9	246.6	95	10.0	692	114	5.58	30.13
11	**Felsőszenterzsébet**	H	46.750	16.433	Luvisols	75.6	310.2	235.4	95	10.3	742	146	5.14	28.48
12	**Balatonendréd**	M	46.808	17.975	Cambisols	101.9	274.5	186.2	73	10.3	674	81	6.26	31.6
13	**Buják**	M	47.906	19.506	Luvisols	152.7	261.5	177.4	78	8.8	600	73	6.23	33.2
14	**Alsópáhok**	M	46.768	17.158	Cambisols	83.1	281.0	193.2	84	10.9	701	78	6.05	31.2
15	**Lulla-1**	M	46.804	18.051	Cambisols	97.7	315.9	214.3	74	10.3	674	81	6.26	31.6
16	**Lulla-2**	M	46.804	18.051	Cambisols	84.2	315.9	214.3	74	10.3	674	81	6.26	31.6
17	**Fulókércs**	M	48.418	21.117	Luvisols	129.4	232.1	165.1	79	9.0	597	52	5.65	33.9
18	**Szemere**	M	48.492	21.108	Luvisols	120.5	207.4	147.5	75	9.0	597	52	5.65	33.9
19	**Gagyvendégi**	M	48.450	20.998	Luvisols	128.2	243.0	175.6	74	8.9	603	61	5.48	33.6
20	**Fancsal**	M	48.3667	21.051	Cambisols	151.6	275.9	189.7	81	9.7	579	2	6.07	36.4
21	**Püspökszilágy**	M	47.733	19.333	Phaeozems	107.2	209.0	140.5	68	9.7	564	−1	6.41	37.1
22	**Sirok**	M	47.922	20.171	Luvisols	129.7	285.1	196.7	75	9.0	565	25	5.99	35.8
23	**Hévízgyörk**	D	47.617	19.503	Cambisols	139.2	221.5	128.2	69	10.5	556	−55	7.53	39.5
24	**Füle-1**	D	47.076	18.213	Chernozems	195.3	198.8	119.6	75	10.5	579	−30	7.49	38.0
25	**Demjén-Észak**	D	47.830	20.355	Phaeozems	162.3	226.5	154.2	72	10.1	581	−17	6.53	37.3
26	**Demjén-Dél**	D	47.815	20.357	Phaeozems	160.0	247.6	172.1	70	10.1	581	−17	6.53	37.3
27	**Kerecsend**	D	47.792	20.324	Chernozems	157.4	249.9	167.5	65	10.3	570	−44	7.30	39.3
28	**Aszaló**	D	48.228	20.933	Phaeozems	224.5	219.4	131.1	67	9.8	558	−30	6.38	38.6
29	**Füle-3**	D	47.028	18.271	Chernozems	228.6	198.8	126.9	70	10.7	571	−51	7.85	39.1
30	**Füzesabony**	D	47.491	20.270	Chernozems	213.0	273.0	200.7	58	10.4	553	−65	7.44	40.3
31	**Vécs**	D	47.802	20.199	Phaeozems	204.1	204.6	107.3	65	10.1	573	−29	7.04	38.9

Table 2 (continued)

Nr	Site Name	Type of Site	N°	E°	Type of Soil	SOC (Mg C*ha^{-1})	CTB Mg C*ha^{-1}	CTAB (Mg C*ha-1)	SDF (%)	MAT (°C)	MAP (mm)	WB (mm)	FAI	EQ
32	**Bag**	D	47.633	19.450	Cambisols	163.4	285.6	214.4	65	10.1	565	−26	7.63	38.0
33	**Bükkaranyos**	D	48.022	20.763	Phaeozems	164.2	284.8	181.8	73	9.7	567	−21	6.41	38.6

We selected 33 sites (11 humid, 11 meso and 11 dry see Fig. 1 and Table 2) where the slope did not exceed 3–4% to exclude the possibility of erosion or the possibility of deposition from surrounding higher areas.

The interior regions of the Carpathian Basin serve as an excellent sample area for this kind of research. The peculiarity of the nature of the basin is that the amount of annual precipitation decreases in the interior areas as you move towards the interior, away from the surrounding mountains (Alps, Carpathians). At the same time, there are also significant differences in the average annual precipitation between the NW and SE sides of the interior mountains due to the different degrees of oceanic influence. Because oak woodlands are long-lived forests, and thus their biomass is more conservative than is grassland biomass, random annual weather fluctuations have much less influence on biomass and thus they are excellent indicators of decadal climate change. The study area is classified as in the temperate climatic zone and is at the intersection of three macroclimatic regions: Continental, Oceanic, and to a lesser extent Mediterranean (Salamon-Albert et al. 2016). The differences in the selected sites were mainly due to which of the 3 macroclimatic effects dominated each site (Fekete et al. 2021).

Classification of forest climate types

Based on climatic parameters, we classified the 33 forest sites in our sampling area into humid, meso and dry groups based on the last half-century's water balance (WB, precipitation – potential evapotranspiration). The WB results from the difference between the mean annual precipitation and the mean annual potential evapotranspiration. WB can be used well to quantify the aridity of the climate (Zomer et al. 2022). It is important to note that these three categories are to be interpreted based on comparing the sampled areas to each other since the"humid"forests belong to mesophytic forests based on the Map of the Natural Vegetation of Europe (Bohn et al. 2003). In the soils of"humid forests"we studied, which are warmer and drier than in North-West Europe, we found no trace of permanent or lasting water effect in soils. This is indicated by their annual rainfall between 692–744 mm and their relatively high (9.9–10.3 °C) average yearly temperature value.

The average climate values of the three forest types (humid, meso, dry) are well separated, especially with respect to the moisture status of the areas. This is true both in the warming and drying decades starting from 1980 as well as in the period before that. In dry forests the annual mean WB has been negative for the past 50 years, meaning that potential evapotranspiration is greater than precipitation. Meso forests are characterized by slightly positive WB (0–100 mm), while humid forests are characterized by a positive WB exceeding 100 mm. The three categories we use—humid, mesic, and dry forests—reflect the different climates of the sites and mainly represent variations in water availability. Different approaches can be used to group these forests, which give almost exactly the same classification. One alternate approach is a forest ecological approach, which is based on two important tree species that appear as indicators in humid and meso forests. Beech appears in humid forests but is absent in the meso forests. European hornbeam (*Carpinus betulus, (L.))* occurs in meso forests (and humid forests), but is absent in the dry forests (Bölöni et al. 2009). However, in all sites, sessile oak is the dominant species (Fekete et al. 2023). A 3rd approach for forest classification can be defined by the Broken Stick model. Our previous observations proved that there was a strong correlation between the carbon content of the soils and the climate in the zonal forests of the Carpathian Basin. Broken Stick model was created using results of regression analysis between Ellenberg index (EQ) values and SOC content, where breaking points of the EQ were 29.5 and 36.45 (Fekete et al. 2021, 2023). These breaking points marked the border between forest types.

EQ was calculated based on Ellenberg (1963).

$$\mathrm{EQ} = \mathrm{TVII}\ \mathrm{P} - 1 \times 1000$$

where TVII is the average temperature in July (°C), P is the annual precipitation (mm).

Analysis of climate data

The climatic variables used during this study included mean annual temperature, annual precipitation, mean summer temperature, summer precipitation, Forest Aridity Index (FAI), EQ, yearly WB, and growing season WB. For several climate parameters, we also calculated the values for the summer period separately, because more than 80% of organic material is produced from May to August in forests of Hungary (Mátyás et al. 2018).

We used the ODP (Open Data Portal) climate database with a spatial resolution of 10 ×10 km from 1971–2020 (Source: Hungarian Meteorological Service, https://odp.met.hu/) to obtain precipitation and temperature data and to calculate monthly WB (defined as average monthly precipitation – average monthly potential evapotranspiration). Potential evaporation was calculated according to Thornthwaite (1948), which only requires monthly temperature and geographical latitude.

Monthly WB data were summarized both yearly and for the growing season (March-August).

In Hungary, foresters separate forest types into forest climate classes based on Forestry Aridity Index (FAI) values (Führer et al. 2011). The FAI values are a good indication of the climatic characteristics of the growing areas of the forests (Gavrilov et al. 2019; Kis et al. 2023). The FAI value reflects the late spring and summer precipitation values, as well as the temperature of the hottest period, so it carries more important information for vegetation than just annual precipitation values. Oak trees in Hungary typically live in FAI values ranging from 4.75–7.25 (Führer et al. 2011). In the long term, these values indicate these forests' climatic minimum and maximum values. With a lower value (in wetter habitats), we find the forest class of beech trees, while above this, in a drier climate, we find that of forest steppe (Gavrilov et al. 2019; Mátyás et al. 2018). There is an important climate boundary between the closed oak forests and the forest-steppe macroclimate category that dominates most of the Hungarian Great Plain, which was designated along the FAI value of 7.25.

The FAI was calculated based on (Führer et al. (2011):

$$\mathrm{FAI} = \mathrm{Cg} \times \mathrm{TVII} - \mathrm{VIII} \times (\mathrm{PV} - \mathrm{VII} + \mathrm{PVII} - \mathrm{VIII})^{-1}$$

where TVII−VIII is the average temperature in July and August (in °C), PV−VII is the precipitation sum in the period from May to July, PVII−VIII is the precipitation sum in the period from July to August, all in mm, and Cg=100 is constant.

Four forest climate categories are used for forest areas with different climates based on FAI values in Hungary:

- less than 4.75 beech climate.
- 4.75–6.00 hornbeam-oak climate.
- 6.00–7.25 the sessile oak/Turkey oak climate.
- more than 7.25 forest-steppe climate.

The forest types mentioned above can only survive within the indicated FAI values in the long term. Therefore, due to climate change, an area belonging to a specific climate category may shift over time to another climate category, which entails the transformation of the forest vegetation.

The selected database for weather variables has a high resolution give value, but only goes back half a century. Another database, the 0.5° spatial resolution CRUTS (gridded Climatic Research Unit Time-series) Version 4.05, was used to chart change in climate variables over the last 120 years (1901–2020) (Harris et al. 2020). We applied the data through all of Hungary. This database confirms the data of the high-resolution (ODP) database we use and proves the direction and extent of the experienced climate value changes over a longer period of time. Here, we calculated climate variables on the average of 65 pixels (territorial units in this database) in Hungary applying the same methods as for the ODP database. The breakdown of climate data by decade softens the impact of extreme years and shows climate trends, which indicate a significant and continuous increase in temperature over the past half-century. Similarly precipitation values indicate the alternation of shorter drier and wetter periods. Despite the waves, the WB values clearly shows that the climate of the Carpathian Basin is becoming drier. During the growing season (between March and August), there was a water deficit of more than 100 mm in each of the last 4 decades, while there was only one instance of this in the previous 8 decades of measurements.

Relative tree stand densities and analysis of tree biomass

There has been no thinning for at least three decades in the sampled forests and thus trunk loss was caused only by drying-induced mortality. Due to self-thinning, the maximum number of trunks in a tree stand is determined based on the average diameter of the stand (Pretzsch 2009; Reineke 1933). In Hungary, before the current period of warming and drying, the tree yield tables for sessile oak were prepared from measurement data from the 1950 s and 1960 s (Sopp 1974). These tables show the maximum number of trunks per hectare that can be associated with a given average stand diameter. This number read from the table shows the 100% stand density.

In the second half of the 2010's we counted the number of trees in a 50 ×50 m quadrat typical of the forest compartment. After that we measured their diameter at breast height (at 130 cm), so we could determine the actual tree density compared to the maximum possible 100% tree density in the studied stands.

We measured the height of the examined tree stands. Knowing the age of each tree stand, we determined the tree yield class of the sessile oak based on the tree yield tables. Using the tree yield class table, we used the tree volume of each stand at 100 years of age to compare the tree volume of stands of different ages and rate of growth.

The tree volume data in the tree yield tables refer to a 100% tree stand density (full stand density). We reduced the volume of the sampled tree stands according to the relative tree density measured by us for the respective tree stand, since the stand density is less than 100% due to tree decay caused by climate change (relative stand density).

A laser instrument (Tru-Pulse 200; Centennial Co., USA) was used to measure the height of the living trees in the quarter-hectare quadrat.

We calculated the wood volume of the trees per hectare of forest, and afterwards, we calculated the carbon mass per hectare of our forest sites using the volume density and carbon concentration of trees:

$$\mathrm{m} = \mathrm{V} \times \rho \times \mathrm{C}\% \times 10^{-2}$$

where p = density of dried oak (0.714 g/cm^3),

C % = C content of wood (49.2%),

m = carbon mass of tree in one hectare of forest,

V = the wood volume of the trees of one hectare of forest in a site.

Führer et al. (2014) determined the correlation of forest aridity index (FAI) and the ratio of above-ground (without foliage) and belowground carbon stock. Hence the carbon amount in belowground biomass can be estimated based on the stand volume and this climate-dependent ratio. In our research, we used

Table 3 The values marked with an asterisk (*) show the weighted averages of the values of the 0–5, 5–15, 15–30, 30–50, 50–70, 70–100 cm layers. The values marked with two asterisk (**) show the weighted averages of the values of the 0–5, 5–15, 15–30, cm layers. The different letters show significant differences among groups. The letters mean: H: Humid forests; M: Meso forests; S: Dry forests

	SOC% (0–100 cm)*	bulk density (g cm^{-1}) (0–100 cm)*	pH (0–30 cm)**
humid	0.58 ±0.02a	1.5 ±0.04a	4.84 ±0.12a
meso	0.90 ±0.06b	1.45 ±0.04a	5.84 ±0.12b
dry	1.38 ±0.07c	1.46 ±0.05a	5.91 ±0.13b

these results to estimate the belowground dendromass (Führer et al. 2014).

Soil sampling and measurements

We established one randomly located 10 × 10 m plot in every site under complete canopy cover. The soil was sampled in December 2018. Soil cores were collected from the 0–5, 5–15, 15–30, 30–50, 50–70, and 70–100 cm layers in mineral soil with a 20 mm diameter Pürckhauer 1175/1000 mm soil corer (Bürkle GmbH) at three randomly selected locations in each plot. They were combined to form composite samples for each layer. Soil samples were sieved to <2 mm and hand-picked to remove roots and stones. Total C concentrations in ground and homogenized soil samples from all depths were determined using a combustion analyzer. Soil total carbon (STC), soil inorganic carbon (SIC) and SOC content of the soil samples are analysed by Skalar Primacs SNC-100 instrument. TIC is analysed using automatic acidification by phosphoric acid and purging and SOC is calculated from STC—TIC results. Bulk density of soil was measured using undisturbed soil cores (with steel cylinders) after drying in an oven at 105 °C for 24 h. Soil pH was determined potentiometrically in 0.01 M $CaCl_2$ at a soil/solution ratio 1:2.5 (Adwa 1000 desktop digital pH meter) (Table 3).

The mass of SOC in each soil layer was calculated as follows:

SOC mass % value (g SOC in 100 g of dry soil) × Bulk density (g/cm^3) × the depth of the given soil layer in cm.

Statistical analyses

Amounts of SOC, C contents of tree biomass and climate indices among the forest types were compared by one-way ANOVA followed by Tukey's HSD post-hoc test. We applied regression analysis to correlate the SOC and C content of tree biomass to the climate indices. These statistical analyses were conducted using Statistica 8.0. Segmented regression, as implemented in the R package segmented allowed us to model the changes identified by the ANOVAs by fitting piecewise linear regressions. This approach is particularly valuable for capturing non-linearities in climate and ecological data, where abrupt transitions (e.g., tipping points or thresholds) are expected due to climatic extremes or ecosystem responses.

Results

General climatic characteristics of the studied forest areas and their changes due to climate change in recent decades

Although there was no important difference in terms of annual mean temperature between the forest types, the temperature values showed a different seasonal pattern, as the dry forest sites were more continental and thus the winter was colder, and the summer was significantly hotter than in humid forests (Table 4). This different seasonal pattern significantly influences several other climatic parameters, which significantly affected both forest growth and soil decomposition processes. Accordingly, there was a significant difference between the three areas in terms of drought indices (FAI, EQ) and WB (Table 4). The annual precipitation values also differed between the 3 forest types. These differences were also reflected in the differences in SOC and CTB values and soil pH (Tables 3, 5).

Climate indices in the measured forest sites show significant warming and drying over the last 4 decades (Table 4) starting from the 1980 s, similar to global trends. Warming during the summer period was particularly significant (2.20–2.25 °C), which contributed to a drastic decline of the WB especially in the meso and dry forests due to increasing evapotranspiration loss. The same climatic trends are reflected in the time scale from 1901 to 2020 in Hungary as a whole (Table 1). If we compare the means of the first (1901–1910) and the last decades (2011–2020), we see highly significant changes in WB, Ellenberg, and annual temperature values. Climate indices of the three forest climate groups differ significantly (except for temperature values marked with *) (Table 4).

Correlations between the warming and drying climate and the stand density values of the studied oak forests

The drying climate of the last decades has caused significant oak decline in meso and dry forests, reducing the density of forest stands. The extent of this decline well correlated with the climatic parameters of warming and drying (Table 5.). I Stand densities, compared to the potential values

Table 4 Mean climate indices within humid, meso, and dry forests divided by decade. Calculated indices are FA (Forest aridity) index (Führer et al. 2011; Gavrilov et al. 2019), Ellenberg index (Ellenberg 1988), and WB (climatic water balance: precipitation – potential evapotranspiration). Bold highlighting reflects the variables for which we find significant differences among forest types at each decade

	forest climate groups	1971–1980	1981–1990	1991–2000	2001–2010	2011–2020
FA Index	humid	**4.76 ± 0.46a**	**5.05 ± 0.40a**	**5.64 ± 0.73a**	**5.49 ± 0.61a**	**5.69 ± 0.62a**
	meso	**5.39 ± 0.37b**	**6.42 ± 0.49b**	**6.69 ± 0.65b**	**5.56 ± 0.44b**	**6.02 ± 0.43b**
	dry	**6.51 ± 0.49c**	**7.93 ± 0.55c**	**8.33 ± 1.21c**	**6.03 ± 0.58c**	**6.91 ± 0.55c**
Ellenberg Index	humid	**28.1 ± 0.24a**	**28.5 ± 0.28a**	**28 ± 0.22a**	**30.7 ± 0.28a**	**29.7 ± 0.33a**
	meso	**31.6 ± 0.62b**	**34.8 ± 0.91b**	**35.1 ± 1.15b**	**32.8 ± 0.37b**	**34.3 ± 0.46b**
	dry	**35.6 ± 0.44c**	**41.3 ± 0.48c**	**41.4 ± 0.65c**	**35.9 ± 0.46c**	**39.0 ± 0.43c**
Mean annual temp (°C)	humid	9.5 ± 0.1b	9.7 ± 0.1b	10.1 ± 0.1b	10.4 ± 0.05b	11.1 ± 0.05b
	meso	**9.1 ± 0.2a**	**9.2 ± 0.2a**	**9.6 ± 0.2a**	**9.7 ± 0.2a**	**10.6 ± 0.2a**
	dry	9.6 ± 0.1b	9.8 ± 0.1b	10.1 ± 0.1b	10.4 ± 0.1b	11.2 ± 0.1b
Mean summer (Jun–Aug) temp (°C)	humid	18.4 ± 0.06a	18.8 ± 0.06a	19.6 ± 0.06a	19.9 ± 0.05a	20.6 ± 0.05a
	meso	18.2 ± 0.2a	18.6 ± 0.17a	19.5 ± 0.17a	19.7 ± 0.19a	20.5 ± 0.18a
	dry	**19.1 ± 0.26b**	**19.5 ± 0.08b**	**20.5 ± 0.08b**	**20.6 ± 0.09b**	**21.4 ± 0.09b**
Mean winter (Dec–Feb) temp (°C)	humid	**0.68 ± 0.07b**	**−0.09 ± 0.06b**	**0.32 ± 0.05b**	**0.47 ± 0.05b**	**1.59 ± 0.06b**
	meso	−0.25 ± 0.30a	−1.01 ± 0.33a	−0.65 ± 0.33a	−0.61 ± 0.30a	0.5 ± 0.32a
	dry	−0.18 ± 0.15a	−0.96 ± 0.19a	−0.58 ± 0.17a	−0.48 ± 0.15a	0.67 ± 0.17a
Mean annual precipitation (mm)	humid	**699 ± 7c**	**711 ± 6c**	**733 ± 5c**	**707 ± 6c**	**741 ± 8c**
	meso	**629 ± 15b**	**583 ± 20b**	**599 ± 23b**	**661 ± 8b**	**633 ± 13b**
	dry	**575 ± 6a**	**509 ± 6a**	**545 ± 6a**	**634 ± 6a**	**579 ± 4a**
Mean summer precipitation (mm)	humid	**266 ± 3.3c**	**248 ± 4.3c**	**242 ± 2.9c**	**266 ± 3c**	**236 ± 4.6c**
	meso	**229 ± 7.1b**	**195 ± 6.7b**	**201 ± 2.7b**	**248 ± 3.7b**	**214 ± 6.1b**
	dry	**199 ± 4.1a**	**164 ± 4.5a**	**187 ± 4.8a**	**238 ± 6.6a**	**197 ± 4.7a**
WB March-August (mm)	humid	**−9 ± 4c**	**−37 ± 5c**	**−62 ± 4c**	**−62 ± 3c**	**−116 ± 6c**
	meso	**−52 ± 8b**	**−93 ± 8b**	**−123 ± 5b**	**−70 ± 8b**	**−141 ± 9b**
	dry	**−123 ± 9a**	**−174 ± 6a**	**−177 ± 7a**	**−114 ± 10a**	**−198 ± 8a**
WB annual (mm)	humid	**156 ± 5c**	**138 ± 6c**	**155 ± 5c**	**111 ± 5c**	**110 ± 7c**
	meso	**105 ± 11b**	**26 ± 13b**	**31 ± 16b**	**84 ± 8b**	**19 ± 8b**
	dry	**10 ± 8a**	**−82 ± 6a**	**−57 ± 6a**	**23 ± 8a**	**−69 ± 6a**

Table 5 Pairwise correlation (r) among variables. All correlations are significant at $p < 0.01$ (N = 33). Mg (megagram = ton), ** means the mean values,

Climatic parameters/correlation with	stand density 80.5 ± 2.4 (%)**	C content of tree biomass 279.7 ± 9.5 (Mg C*ha^{-1})**	C content of the above-ground biomass of trees 195.7 ± 8.5 (Mg C*ha^{-1})**	SOC 125.1 ± 8.7 (Mg C*ha^{-1})**
1. Average annual precipitation 636 ± 12.1 mm	0.86	0.79	0.82	–0.86
2. WB between March and August (−103 ± 7.9 mm)	0.80	0.67	0.73	–0.81
3. Average annual WB (50.6 ± 12.7) mm)	0.87	0.77	0.81	–0.90
4. FAI index (6.18 ± 0.15)	–0.79	–0.65	–0.70	0.77
5. Ellenberg index (33.7 ± 0.73)	–0.87	–0.77	–0.81	0.90

in the Sopp (1974) yield tables from the 1960s and 70s, declined from 100% to 75.9 ± 1.31% in meso forests and to 68.1 ± 1.43% in dry forests by the years 2010–2020. In contrast, humid forests showed no significant change, maintaining a density of 97.5 ± 1.8% relative to the yield table values. As the forests became drier, a "tipping point" appeared, around which stand density loss accelerated due to the decline of the dominant tree species. The analysis of forest stand density using the "Broken Stick" regression model identified critical thresholds where changes in trends occurred. For annual WB, the breakpoint was approximately 61.3 mm (Figure 2A), marking a shift in the relationship between WB and stand density. Similarly, for the Ellenberg index, a breakpoint was detected at 32.2 (Figure 2B), indicating a change in trend in response to increasing site dryness. These breakpoints highlighted the thresholds where environmental stressors, such as WB deficits and increased aridity, began to significantly influence stand density, particularly in meso and dry forest regions.

The relationship between quantitative parameters of biomass carbon and SOC with different climatic variables

We studied the effect of climate on the CTB and SOC across this climatic gradient. The average annual precipitation, the Ellenberg index and the WB showed

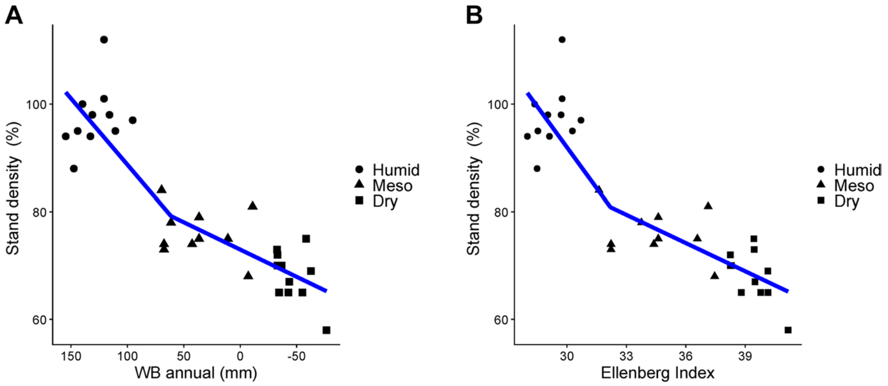

Fig. 2 Relationship between Stand density of forests (%) and (**A**) annual climatic water balance (WB = precipitation – potential evapotranspiration), and (**B**) Ellenberg Index, based on data from 33 forest sites in Hungary. Breakpoints in both WB (psi = 61.31) and Ellenberg Index (psi = 32.22) were identified using segmented regression models. Model performance: WB (Adj. $R^2 = 0.77$; F[29, 3] = 36.46, $p < 0.01$); Ellenberg Index (Adj. $R^2 = 0.78$; F[29, 3] = 38.57, $p < 0.01$)

the highest correlation with the abovementioned values, with an r value of 0.79 or higher (Table 5).

Significant differences were found in the amount of CTB among the three forest types (Fig. 3). The above-ground CTB showed particularly large differences between forest types and the ratio of belowground and above-ground CTB distribution also had significant differences. On the other hand, there was no significant difference among forest types in terms of belowground CTB. The importance of belowground biomass increased with drought, with humid, meso, and dry belowground biomass accounting for 26%, 31%, and 35% of total CTB, respectively.

Significant differences were also found in the amount of SOC and its distribution within soil horizons among the forest types. In dry forests, the amount of SOC in the deeper layers of the soil was also significant. In contrast, SOC was concentrated to the greatest extent in the upper soil layers of humid forests. SOC was 19% in the upper 5 cm layer of the soil, while in the case of meso forests this ratio was 15% and in dry forests 12% compared with the upper 1 m layer (Table 6).

No significant difference was found between the humid and dry forests for CTB + SOC, while the meso forests showed 8 and 10% lower values than the other two types (Fig. 3). However, the ratio of C stored in biomass to C in soil shows a significant difference. For humid forests, the amount of C stored in the biomass of trees is 82% of the total

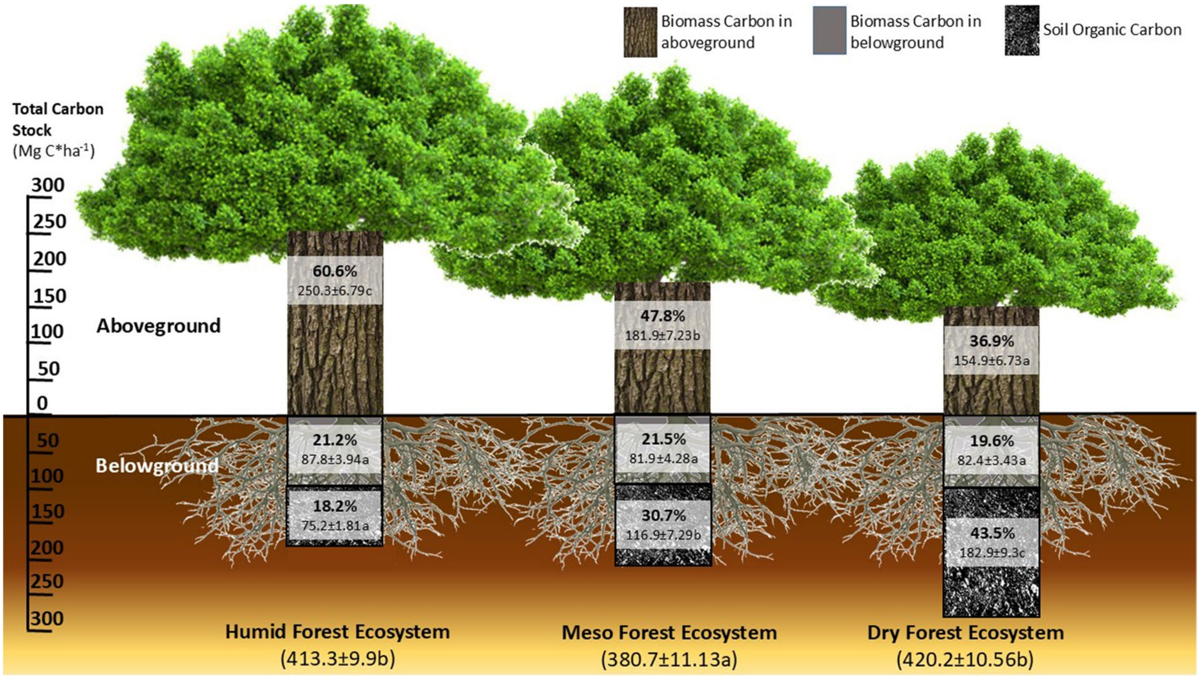

Fig. 3 The size of the carbon stores of the three forest types, the amount of SOC stored in the upper 1 m layer of the soil and the above- and below-surface (roots) parts of the tree stand (in Mg C× ha^{-1}). Different letters indicate significant differences among forest types

Table 6 Quantitative distribution of SOC (in Mg C× ha^{-1}) according to different soil depths in the three forest types. Different letters indicate significant differences among forest types

	0–5 cm	5–15 cm	15–30 cm	30–50 cm	50–70 cm	70–100 cm
humid	14.1 ±0.71a	17.8 ±0.70a	14.3 ±0.54a	10.3 ±0.31a	7.9 ±0.21a	10.9 ±0.27a
meso	17.8 ±0.82b	23.6 ±2.46b	21.6 ±2.03b	20.7 ±1.22b	15.9 ±0.94b	17.3 ±1.48b
dry	22.2 ±0.87c	37.5 ±1.41c	38.7 ±1.97c	36.4 ±3.27c	22.7 ±2.43c	25.6 ±2.5c

amount of carbon (CTB and SOC). In meso forests, this value was 69%, while in dry forests it was 56%. The distribution of C showed an even more significant difference if we compared the belowground (SOC and the C content of the belowground part of the tree biomass) and the C content of the tree biomass above the surface. For humid forests, C below the surface is 65% of that above the surface; for meso and dry forests values were 109% and 171%, respectively (Fig. 3). So, moving towards areas with a drier climate, the C stock of the forest ecosystem accumulated more and more below the surface. This impact was shown by the fact that the total organic carbon stored in dry forests was almost the same as in humid forests (Figs. 3 and 4).

Discussion

The previously presented results are not future projections but serve to show the effects of different climates (humid, meso, dry) in each area and the changes of the past decades. In this research, the carbon pools (SOC and CTB) and relative tree density of forest areas with different average annual precipitation within the Carpathian Basin were compared, and the changes of the most important climate parameters in recent decades were presented. The half-century means of the climatic parameters of the 3 forest types show significant differences and were well correlated with their CTB and SOC values. In our dry forests, the average FAI value in the decade before the warming phase that started in the 1980 s showed a value of 6.51, so these forest sites were located in the optimum zone of the sessile/Turkey oak climate category (6.00–7.25 FAI value (Führer et al. 2011). In the period between 1980 and 2020, the average value was 7.28, but there were two consecutive decades between 1980 and 2000 with values of 7.93 and 8.24. A significant part of the area of dry oak forests has moved into the forest-steppe zone (7.25–8.5 FAI value (Führer et al. 2011) during the last 4 decades, which is

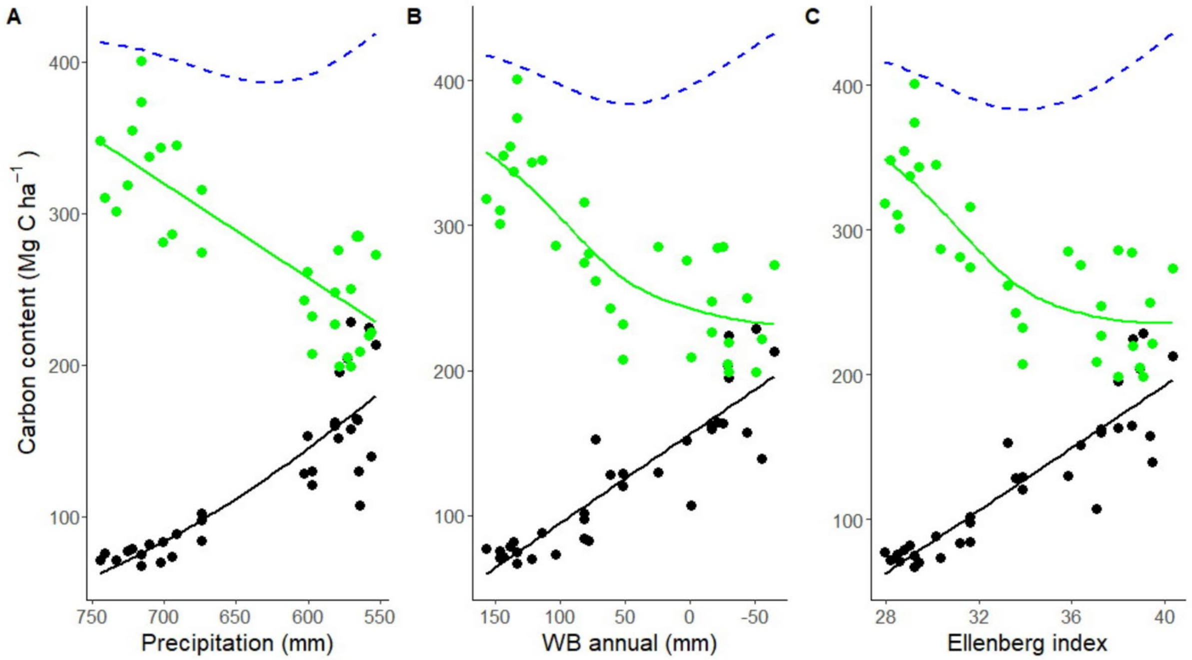

Fig. 4 Changes in SOC (black line), CTB (green line) and the sum of the two (blue dashed line) in forests with different climate parameters (annual average precipitation, EQ, and WB). The equations of the linear regression between SOC vs. precipitation (MAP), annual WB and EQ: SOC =−0.62120 * MAP +520.03163; SOC =−0.61256 * WB +156.05314; SOC =10.8003 * EQ-239.5162 ($p \leq 0.05$). The equations of the linear regression between CTB vs. precipitation (MAP), annual WB and EQ: CTB =0.62307 * MAP −116.46081; CTB =0.57508 * WB +250.60871; CTB =−10.038 * EQ +618.550 ($p \leq 0.05$). We use the smoothing function to draw the lines

indicated by the large-scale destruction of oak trees and the related drying-induced mortality of the stand. The data show that the dry forest populations already live near their xeric limit. The meso forests were located in the optimal range of the hornbeam-oak climate category (4.75–6.00 FAI value (Führer et al. 2011) in the 1970 s. In the following forty years, the average of their FAI values was 6.17, with which the average value of the meso forests already fell into the drier Sessile/Turkey oak climate category. The relative, and in many cases even absolute, drying affected not only the meso and dry forests, but the climatic data also showed this trend in the humid forests. In the period between 1971 and 1980, the humid forests stood on the border between the beech and hornbeam-oak climate classes, which was also indicated by the presence of beech as a mixed species in their stands.

In the last 30 years, however, their FAI values (the average of which was 5.61 during this period) exceeded the average of the meso forests measured in the 1970 s, but they are still in the near-optimal part of the hornbeam-oak climate class. This fact can explain the small decrease in stand density in humid forests, in contrast to meso and dry forests showing a large drying-induced mortality, which have moved out of the previous optimum range of their climate region in recent decades. However, looking into the future, due to the climate becoming even hotter and drier, a decrease in stand density can also be expected in the case of humid forests. For forests growing on deep soils, (Mátyás et al. 2018) found that an FAI value of 5.3–5.5 serves as a limit, above which the drying-induced mortality of oaks begins. Given the average of the last 50 years, the humid forests we studied were already at this limit. Beech forests, which characterize the coolest and wettest areas of the country, reacted similarly to the warming and drying climate, which indicates that the problems provoked by climate change affect most Hungarian forests (Czúcz et al. 2010; Garamszegi and Kern 2014; Rasztovits et al. 2014). The correlations between the decrease in relative tree stand density of sessile oak stands and the drier climate have already been established by previous research (Fekete et al. 2017; Mátyás et al. 2018). Our current study confirmed these findings (Fig. 2). The above results clearly indicate that warming-drying processes cause a significant shift in the areas of the former forest climate zones. The same tendency was observed by (Mátyás et al. 2018) during an extensive study of Hungarian forests. These studies also confirm that the transformation of the forests of the Carpathian Basin has begun as a result of climate change. Similar processes can be observed in many other forests of the Earth, which shows the general spread of the problem of drought stress caused by climate change (Greenwood et al. 2017; Hartmann et al. 2018). The drying-induced mortality of forests directly affects their CTB values, and the climate of the drying vegetation period reduces the decomposition processes in the soils (Fekete et al. 2021, 2023), which predicts a change in the SOC values. Accordingly, a space-for-time substitution study along a climatic gradient can be suitable for predicting the expected changes in the carbon stores of trees and soils in forests, if we know the expected values of the presented climate parameters (precipitation, WB annual, Ellenberg index) (Fig. 4).

Many studies have found that amounts of SOC are positively correlated with precipitation, for example in the zone of steppe and semi-desert areas (Du and Gao 2020; Post et al. 1982; Saljnikov et al. 2009). However, in the seasonally dry tropical forests and in temperate and dry mesophytic forests, as the annual precipitation averages decrease, the SOC content increases due to the slowing decomposition activity (Błońska and Lasota 2017; Campo and Merino 2016; Fekete et al. 2023). In the dry forests we studied, the SOC is almost two and a half times as large as that of the humid forests, despite the fact that their annual litter production is much lower (by 27%) (Fekete et al. 2021). The quantity of C stored in terrestrial soils largely depends upon the magnitude of SOC mineralization (H. Zhang and Zhou 2018). The correlation between the Ellenberg index and SOC content suggests that the dry, hot summer climate plays a particularly important role in the long-term evolution of the soil C content in this habitat type through reduced decomposition of litter (Table 5). Other soil properties may also cause differences in soil C accumulation. Soil pH is significantly lower in humid forests than in meso and dry forests (Table 3.), thus leaching of soil Ca is also much higher in humid forests as calcium carbonate is more soluble at lower pH (Suarez and Rhoades 1982). Accordingly, we measured more as 7 times as much Ca in the soils of the dry forests as in the humid forests (Fekete et al. 2021). Calcium carbonate can play an important role in aggregate stability and thus increase occluded SOC (Rowley et al.

2018). Therefore, the formation of certain types of organo-mineral complexes that significantly influence the organic matter content of soils may occur under more favorable conditions in dry forests, which also increases the SOC content of soils (Fekete et al. 2023). Our previous C^{14} studies showed that the turnover time of organic matter in the soils of dry forests is almost twice as long as in humid forests (Fekete et al. 2021).

We previously found higher fungal biomass and enzyme activity in the soils of humid forests, and a faster decrease in leaf litter mass on the surface of the soils of humid forests than in dry and meso forests (Fekete et al. 2021), supporting our hypothesis that reduced decomposition in dry forests caused the observed increase in soil C. Several previous studies have shown that in a dry soil environment (especially in the warm summer period) the priming effect is much weaker than in soils with higher moisture content and a larger litter input, which are more favorable for decomposer microorganisms (Dijkstra and Cheng 2007; Fontaine et al. 2003). The amount of water needed by trees in dry summer forests can only be provided by a deeper, more extensive root system (Germon et al. 2020), and the amount of organic carbon provided by the root system plays a significant role in the formation of SOC (Rasse et al. 2005). This can also explain the fact that in dry forests, the soil layer that is richer in organic matter extends deeper than in the case of humid forests. Similar observations were made by (Balesdent et al. (2018). We expect that climate in the forests along the gradient that we studied will progressively become warmer and drier. This change in climate will induce changes to soil and forest tree carbon content, but the critical question is the relative timing of these ecosystem carbon changes. In the case of the studied forests, moving towards drier sites, the carbon stored in the biomass continuously decreases. At the same time, the amount of SOC increases in parallel, showing a kind of Balancing Effect. However, the amount of SOC usually changes more slowly than the amount of CTB in natural ecosystems (Hong et al. 2023; Lal 2004). According to our previous observations, the amount of CTB of Hungarian forests is reduced faster by drying due to climate change, than is the increase of carbon in soils due to reduced decomposition (Fekete et al. 2017). This can be explained by the fact that in the case of meso forests, which in a certain sense show an intermediate step in the transformation of humid forests towards dry forests, the decrease in biomass (compared to humid forests) is greater than the increase in soil SOC. As a result, the total carbon stored in the area of meso forests (the amount accumulating above and below the surface) shows a significantly lower value than the amount measured in dry and humid forests. In the shorter term—over a few decades—the amount of carbon stored in Hungarian forest ecosystems (and likely in other forests with similar environmental conditions) is expected to decline due to increasing dryness. This is because forest biomass is projected to decrease more rapidly than the soil organic carbon (SOC) content can increase. At the same time, a significant part of Hungarian forests (as well as European forests) are forest-managed, so the above problems can be partially remedied by careful selection of tree species (or breeding tree species) (Mátyás, 2021). Climate models show that in the coming decades, the climate typical of dry steppes will spread over significant areas in the Carpathian Basin, which will make it extremely difficult to maintain oak forests in drier areas (Gálos et al. 2007; Kis et al. 2023; Mátyás et al. 2018).

Conclusion

In the triple system of climate-vegetation-soil, climate change directly affects vegetation and soil but also affects the latter indirectly through vegetation. These changes cause a direct rearrangement of carbon stores within the ecosystem. The equal carbon storage capacity of humid and dry forests is puzzling.

In the last 40 years, due to the warmer and relatively drier climate, meso forests and dry forests have moved out of the optimum zone of their previous forest climate class, which has resulted in a significant drying-induced mortality of tree stands in these two forest categories, as shown by the significant stand density values decrease. This decrease was not observed in humid forests, as they moved from the extremely humid range to the optimum range within their own forest climate category. Moving from the wetter forests of Western Hungary to the drier interior areas of the country, 2 clearly emerging trends can be observed: moving towards increasingly drier forest sites, the CTB decreases significantly, while the SOC content increases to a similar extent. These trends suggest that a drier climate will result in a similar temporal pattern in drying forests to that observed in the case of spatial differences. The decrease in stand density observed in meso and dry forests over the past 40 years also supports this hypothesis, but our earlier time study covering 40 years within a forest also points in this direction regarding the carbon content of soils (Fekete et al. 2017).

The decline of the forest due to a drying climate can temporarily increase the amount of organic matter from trees entering the soil. The effects of a warmer and drier climate on the C balance of forests in this region will be felt for decades to come as woody litter inputs decay, and forest growth remains impeded. Due to the warmer and drier summer climate, the SOM decomposition processes may slow down, which may explain the permanent increase in the SOC content of the soils, even if the leaf litter production will also decrease due to the drier climate.

Author contributions F. I.: Conceptualization, Writing, review & editing – original draft, Data curation, Supervision; B. I.: Conceptualization; K. L.: Supervision; B. Á.: Investigation; M. N.: Investigation, Data curation; V. G.: Data curation; M. B.: Investigation; H. T.: Investigation, Data curation; J. K.: Investigation, Project administration; K. Zs.: Editing, Supervision, Investigation, Formal Analysis.

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Data availability Data is contained within the article. The datasets generated during and/or analyzed during the current study are available from the corresponding author upon reasonable request.

Declarations

Conflicts of interest The authors declare no conflicts of interest.

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