Experimental drought and soil amendments affect grassland above- and belowground vegetation but not soil carbon stocks

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Abstract

Soils are the largest terrestrial carbon (C) pool on the planet, and targeted grassland management has the potential to increase grassland C sequestration. Appropriate land management strategies, such as organic matter additions, can increase soil C stocks and increase grassland resilience to drought by improving soil water retention and infiltration. However, soil carbon dynamics are closely tied to vegetation responses to management and climate changes, affecting roots and shoots differently. This study presents findings from a three-year field experiment on two Swedish grasslands that assessed the impact of compost amendment and experimental drought on plant biomass and on soil C to a depth of 45 cm. Aboveground biomass and soil C content (% C) increased compared to untreated controls in compost-amended plots, but because bulk density decreased, there was no significant effect on soil C stocks. Experimental drought did not significantly reduce plant biomass compared to control plots, but stunted the increase in aboveground biomass in compost-treated plots and led to changes in root traits. These results highlight the complexity of ecosystem C dynamics and the importance of considering multiple biotic and abiotic factors across spatial scales when developing land management strategies to enhance C sequestration.

Introduction

Soil management has been receiving increasing attention in the past years, with growing awareness that soils provide vital ecosystem services and can act as carbon (C) sinks (Minasny et al. 2017, European Commission, Directorate-General for Health and Food Safety, 2020). The soil-plant system is integral to this process, as plants capture atmospheric carbon dioxide through photosynthesis and transfer C to the soil via root exudates and decaying above- and belowground plant necromass. Concerns about soil erosion and historic soil C depletion in agricultural and grassland soils

28 (Sanderman et al. 2017, Bai and Cotrufo, 2022) have motivated the development of sustainable land

29 management strategies, generally named "carbon farming" (Paul et al. 2023) and promoted by

30 initiatives aimed at increasing the C stored in soils, such as the "4 per 1000" initiative (Minasny et al.

31 2017). These strategies also contribute to mitigating anthropogenic greenhouse gas (GHG) emissions

32 by restoring soil organic carbon (SOC) stocks. SOC restoration can be achieved by decreasing tillage,

33 adopting cover crops, and by using soil C amendments like compost, biochar, and manure on

34 croplands or grasslands (Ryals and Silver 2013; Ryals et al. 2015; Keesstra et al. 2016; Fischer et al.

35 2019; Garbowski et al. 2023). Soil C management via compost amendments, as in Ryals and Silver

36 (2013), aims to facilitate accumulation of plant-derived C SOC, where it can be retained over long

37 time scales – i.e. decades to centuries (Shi et al. 2020). If the total C inputs and accumulation in the

38 soil exceed the total losses, C amendments can lead to C sequestration (Don et al. 2024, Moinet et al.

39 2023).

40 Since C sequestration potential is uncertain and context dependent (Paltineanu et al. 2024), it is

41 important to investigate the effects of C amendments across a range of climatic and management

42 conditions. Grasslands, including croplands converted to grasslands, can store considerable amounts

43 of soil C (Johansson et al. 2023) and are therefore ideal systems to apply C amendments. They can

44 act as C sinks with improved management (Conant et al. 2001), and can have higher root biomass C

45 compared to agricultural lands, usually cultivated with annual crops (Beniston et al. 2014). Several

46 studies have investigated the effects of organic amendments on aboveground biomass (Ryals et al.

47 2016), crop yields (Luo et al. 2018; Ahmad et al. 2009), and on roots in farming systems (Hirte et al.

48 2021), but fewer focus on non-cultivated grasslands.

49 C amendments add C to the soil in two ways: directly, by moving plant biomass from one location to

50 another, and indirectly, by promoting plant growth (Ryals et al. 2016). Compost is rich in organic

51 matter, which serves as a substrate for soil microorganisms. As microbes decompose this organic

52 matter, they release nutrients in forms that plants can readily absorb (Malik et al. 2013). In turn, higher

53 vegetation growth can increase the natural rate of C input and thus potentially SOC stocks (Ryals et

54 al. 2013). Indeed, model predictions suggest that compost additions on grasslands can lead to soil C

55 sequestration through an increase in plant biomass (DeLonge et al. 2013). By improving soil structure

56 and reducing compaction, compost additions may also reduce soil bulk density (Brown & Cotton,

2011). As SOC stocks are calculated by multiplying C concentration by the bulk density, improved management may also lead to net zero effects on C stock despite increased soil C contents. Considering these indirect effects requires an ecosystem-level perspective on the C sequestration potential of soils that accounts for both below- and above-ground vegetation contributions to soil C stocks, as well as the soil depth at which management effects are detectable. Here we adopt this broad perspective and assess changes in C stocks in both soil and vegetation after C amendments.

Compost amendments can impact both above- and belowground plant biomass, but these plant components contribute differently to SOC storage. Root biomass and root exudates are critical to soil C formation and retention (Jackson et al., 2017), as roots are more recalcitrant to decomposition compared to shoots (Rasse et al. 2005, Gaudinski et al. 2000). However, aboveground plant biomass also impacts soil C stocks, and potential trade-offs in above- vs. belowground C allocation within the vegetation pool should be included in ecosystem C balance assessments (Hayes et al. 2017). Above- and belowground biomass may also respond differently to soil amendments (Garbowski et al. 2020). This variation is expected, as roots and shoots respond differently to changes in nutrient (Hayes et al. 2017). Therefore, an approach that accounts for above- and belowground interactions is essential to understand the proportion of plant litter contributing to SOM formation and stabilization (Cotrufo et al., 2015), and to achieve a comprehensive understanding of ecosystem C dynamics (Heimann and Reichstein, 2008).

Soil organic amendments can also help mitigate the negative effects of drought on vegetation and soil microbial communities by increasing soil water-retention (Fischer et al. 2019; Haque et al. 2021). Future climate projections indicate an increase in extreme weather events, including longer and more frequent droughts (IPCC, 2021). These conditions may decrease vegetation growth both above- and belowground (Guasconi et al., 2023) and decrease plant carbon (C) allocation to aboveground organs (Hasibeder et al., 2015), leading to lower C inputs to the soil and potentially decreased soil C stocks (Deng et al., 2021). The effects of organic amendments on water retention are modulated by soil texture, by the quantity and quality of soil organic matter (Rawls et al. 2003; Yang et al. 2014; Franco-Andreu et al. 2017; Sarker et al. 2022) and by its chemical composition (Franco-Andreu et al. 2017). Increased water retention can also indirectly benefit the ecosystem C balance by partly compensating the drought-induced loss of plant biomass (Kallenbach et al. 2019; Ali et al. 2017). These expected

positive effects of organic amendments are not always observed, as soil and plant communities exhibit large variability in response to both drought (Guasconi et al. 2023; Canarini et al. 2017) and soil amendments (Gebhardt et al. 2017). This variability derives partly from the different physical properties of the soil. However, it can also be influenced by factors such as land use history and both small- and large-scale topography (Wang et al. 2020). These complexities highlight the need for more field-based data collections—in particular under experimental conditions that combine soil amendments and drought.

Here, we present the results of a field experiment designed to assess the effects of compost and of experimental drought on both soil and plant biomass after three growing seasons. The changes were observed along the soil profile to a depth of 45 cm, in two grasslands, and at two catenary positions, i.e. at the top and at the bottom of a slope. We tested the hypotheses that:

1) compost amendment increases soil C content and plant growth (both having positive effects on C stocks), while decreasing soil bulk density (having a negative effect on C stocks); we expect that these mechanisms have counteracting effects on net soil C storage;

2) drought has a weak negative or non-detectable effect on SOC by decreasing both productivity (organic C input) and respiration (microbial decomposition of SOM);

3) compost amendment mitigates the loss of soil moisture under drought which may alleviate plant growth reductions under drought.

Methods

Site description and experimental setup

The experimental site was established in summer 2019 in the proximity of Tovetorp Research Station south of Stockholm, Sweden, and consists of two former arable fields (hereafter called "Tovetorp" and "Ämtvik"), each with an upper and a lower catenary position (hereafter called "high" and "low"). Today, the land management consists of cow grazing and hay production (see Roth et al. 2023). Soil in all locations is rich in clay and ranges from silty clay to silty loam (table S1).

In each of these four locations, four treatments were applied in three replicates, resulting in 12 plots per location and 48 plots in total: compost, drought, drought-compost, control (ambient precipitation, no compost treatment). Each plot measured 2x2 m. Because the effects of already partly decomposed

organic amendments can be expected to be longer-lasting than those of easily decomposable ones (Sarker et al. 2022), we applied a one-time compost treatment combined with a growing season drought and investigated the effects on the soil C stocks after three full growing seasons. The compost was made of *Zea mays* and had a C:N ratio of 9.8 and δ^{13}C value of about -15.39‰. After the seasonal corn harvest (August 2019) the green parts of the plants were collected in an open field. The piled material was regularly stirred to promote the composting process, and the resulting compost was collected and applied in mid-February 2020 as a thin surface layer of ca. 11 kg per m^2 (wet weight), similar to the procedure described in Ryals and Silver (2013). The total amount of C added is on average ~0.54 kg C m^{-2}. The δ^{13}C isotope ratio of the compost is higher than that of bulk soil (-15.39 and -27.25, respectively), which means that the δ^{13}C isotope ratios of different treatments can be used to assess if and where in the soil the compost material is retained after the three years of treatment. The drought treatment followed the guidelines of the Drought-Net Research Coordination Network (Knapp et al. 2017; Yahdjian and Sala, 2002), and consisted of 12 rainout shelters (3 per location) with roofs made out of evenly-placed v-shaped polycarbonate strips designed to exclude 60% of the precipitation during the entire growing season (in place from beginning of July to end of October in 2019, and from beginning of April to end of October in 2020, 2021 and 2022). This precipitation reduction corresponds to the 1st quantile of the local 100-year precipitation record (Swedish Meteorological and Hydrological Institute, 2021). Each shelter covered two plots, one for the drought treatment and one for the combined drought-compost treatment. A rubber sheet, approximately 40 cm in depth, was inserted in the soil around each shelter to isolate the study plots from the ambient soil moisture. Pictures and sketches of the sites and of the experimental design are presented in Roth et al. (2023). Total annual precipitation during the study years was retrieved from the records of Tovetorp Research Station (table S2). We note that while the precipitation in the growing seasons 2019 and 2022 (April through August) was roughly the same (157 mm and 156 mm, respectively), the 2019 sampling followed an extremely dry summer in 2018, when the study area received only 77 mm of precipitation, about half of the precipitation compared to the average 1961-1990 (historical data from SMHI, 2021). Conversely, the 2022 sampling followed the very wet 2021, when the area received almost 140% of the normal precipitation over the same time period (250 mm).

Soil and vegetation sampling and analyses

Soil and root samples were collected in three replicates from each of the four sites and treatments (one sampling per plot) at the end of the first growing season in 2019 (August - September), and again at the end of the experiment in 2022 (August and October). Samples for soil bulk density were collected with a large fixed volume root auger with a sharpened cutting edge (8 cm diameter and 15 cm in length; Eijkelkamp, The Netherlands). Three 15 cm segments were collected sequentially using the same hole, reaching a total depth of 45 cm. Upon extraction, the cores were cut into 5 cm segments, and the bulk density was determined after drying the samples at 105 °C. After drying, a subsample from the same core was used to calculate the soil organic matter (SOM) content through loss on ignition at 550 °C for 4 h. A subset was further burned at 960 °C for 2 h in order to determine the presence of inorganic C, which was low (0.5 %), indicating that the total C can be considered equal to organic C (OC). Samples for total C and N and δ^{13}C were taken to a depth of 1 m with a Pürckhauer soil corer (2.5 cm diameter; Eijkelkamp, The Netherlands) in 5 cm increments. The analyses for total C and N contents, and for δ^{13}C were carried out on a subset of the samples by the Stable Isotope Facility at UC Davis (California). A subset of these samples was sent to a commercial lab and used for pH measurements (measured in a commercial lab using distilled water with a Mantech Automax 73, Guelph, ON., Canada) and nutrient content analyses (P, Ca, Mg and K; Avio 500 ICP Optical Emission Spectrometer, Perkin Elmer, Waltham, MA; USA) (Table S3). Soil moisture was measured every three weeks throughout the growing season (2019 through 2022) from one access tube (1 m long) permanently installed in each plot, using a PR2 profile probe (Delta-T Devices Ltd, Cambridge, UK). The values used in the analyses are growing season averages of volumetric soil water content (%) in the first 30 cm in each plot.

Root biomass was collected in September 2019 and in August 2022 with one soil core sampled with a root auger (8 cm diameter; Eijkelkamp, The Netherlands) by placing the auger on top of the plants, but living aboveground plant biomass and fresh litter were removed and not included in the soil samples. Samples were taken to a depth of 30 cm in all plots and to a depth of 45 cm in a subsample of 16 plots (used as control for maximum rooting depth), with soil cores divided into 5 cm segments. The roots were rinsed with water on a 0.5 mm mesh sieve to remove soil, then placed on a transparent tray, covered with water and scanned with a flatbed scanner (Epson Expression 10000XL, Epson Europe Electronics GmbH, Germany) at 600 dpi (grey scale), followed by drying at 60 °C for 48 h to

174   obtain the dry weight. The scanned images were analyzed with WinRhizo (Regent Instruments,

175   Québec, CA) to obtain root volume, length and diameter, used to calculate root mass density (g roots

176   cm^{-3} soil), specific root length (cm g^{-1} roots) and root tissue density (g roots cm^{-3} roots). Aboveground

177   biomass was harvested from one quarter (1 m^2) of each plot every year in mid-July, by cutting at

178   ground level (including moss and dead biomass, table S4). More details of the sampling design are

179   presented in the Supplements (table S5).

Data analyses and statistics

181   Because of the sensitivity of vegetation to natural variability in precipitation (Liu et al. 2020) and

182   potential effects of landscape heterogeneity on both soil C dynamics and plant growth (Sharma et al.

183   2022; Guo et al. 2018), the analyses include testing for differences in the control plots between the

184   start and the end of the experiment, as well quantifying the variability given by grassland and catenary

185   position, which we expect might lead to variations in all C pools. The measured soil organic C

186   contents (mass of C per unit mass of soil) at different depths within the soil profile were used to

187   calculate soil C stocks (C content $\times$ bulk density $\times$ layer thickness). The soil C stocks were then

188   normalized by soil sample thickness (kg m^{-3}) to allow comparisons among soil layers with different

189   thickness. Because C contents were not measured in all samples, a regression was performed to

190   calculate SOC from SOM data (which was available for all samples) and thus obtain a complete

191   dataset,

192    $$SOC = 0.328 \times SOM + 0.217, \tag{1}$$

193   where SOC and SOM are expressed in kg/m^2 (Fig. S1).

194   The fraction F of compost-derived C detected in the soil in year 2022 was calculated with a two end-

195   member mixing model, as in Poeplau et al. (2023),

196    $$F = \frac{\delta^{13}C_{compost\ treatment} - \delta^{13}C_{control}}{\delta^{13}C_{compost} - \delta^{13}C_{control}}, \tag{2}$$

197   where $\delta^{13}C$ was measured in both compost-amended (compost or compost-drought) and control (no

198   compost or drought-no compost, respectively) plots.

199   All the results and statistical analyses are limited to the depth range of 0-45 cm. This is because this

200   soil depth contains the majority of the root biomass (95% within the first 30 cm, mean ~17 cm), and

201   no effect of treatments could be detected below this range (data not shown).

202 All analyses were made in R (version 3.3.3; R core Team 2017), and statistical models were designed

203 with the lmer function (package: lme4). Pairwise comparisons between categorical variables were

204 made with lsmeans (package: emmeans) and p-values ($\alpha = 0.05$) were obtained with the ANOVA

205 function and the lmerTest package. Residuals from the models were checked graphically. Effect sizes

206 were obtained by calculating Cohen's d, with the formula

207 $$d = \frac{\overline{x}_1 - \overline{x}_2}{S},$$ (3)

208 where $\overline{x}_1$ and $\overline{x}_2$ are mean values for the two groups for which the effect size is calculated, and S is

209 the standard deviation.

210 The effect of the treatments was tested on all plots from the 2022 dataset. Values for root biomass

211 and root traits were log-transformed first. The model included compost (categorical variable), drought

212 (categorical variable) and sampling depth (continuous variable) as fixed factors and plot (nested

213 within site) as random factor. Cohen's d was calculated using the standard deviation of the control

214 group. The effect of the compost amendment on the $\delta^{13}C$ ratio was tested with a mixed linear model

215 that included compost and depth as fixed factors, and plot (nested within site) as random factor.

216 Changes in soil C, bulk density and C stocks were also tested with a model using depth as categorical

217 variable, to assess if changes occurred at specific depths. The variability in plant biomass and soil

218 properties across locations was tested on all data collected in 2019 and from the control plots in 2022.

219 The model included grassland site, catenary position and sampling depth (continuous variable) as

220 fixed factors and year and plot as random factors. Cohen's d was calculated using the standard

221 deviation pooled from all groups. Temporal changes during the experiment not caused by the

222 treatments were tested using data obtained in 2019 and 2022 from the control plots. The model

223 included year and sampling depth (continuous variable) as fixed factors and plot (nested within site)

224 as random factor. Cohen's d was calculated using the standard deviation of the 2019 dataset. The

225 variable depth was not included in the models for aboveground biomass.

226

Results

228 The drought treatment decreased soil moisture by 16% in the upper 0-30 cm during the growing

229 season (Fig. S2). The effect of drought was consistent over sites, years and seasons, and there were

230 no statistically significant differences in the drought-driven soil moisture loss between locations,

231 years, or between spring (April-May), summer (June-July-August) or growing season (April through

232 August). There was also no significant difference in soil moisture decrease between drought plots and

233 drought-compost plots (Fig. S3). Additionally, the compost addition did not have any significant

234 effect on soil pH or on soil P, Ca, Mg and K. The compost addition did, however, raise the value of

235 $\delta^{13}C$ in the treated plots (mean control plots = -27.44‰, mean compost plots = -27.10‰, P < 0.01),

236 and the difference was significant in the 0-5 cm, 30-35 cm and 40-45 cm layers. The mixing model

237 (Eq. 2) indicated that after three growing seasons, the percentage of compost-derived C in the compost

238 plots was 3.43 % in the 0-5 cm layer, 4.88 % in the 30-35 cm layer and 5.51 % in the 40-45 cm layer.

239 In the compost × drought plots, the percentage of compost-derived C was 4.55 % in the 0-5 cm layer,

240 6.52 % in the 30-35 cm layer and 2.96 % in the 40-45 cm layer.

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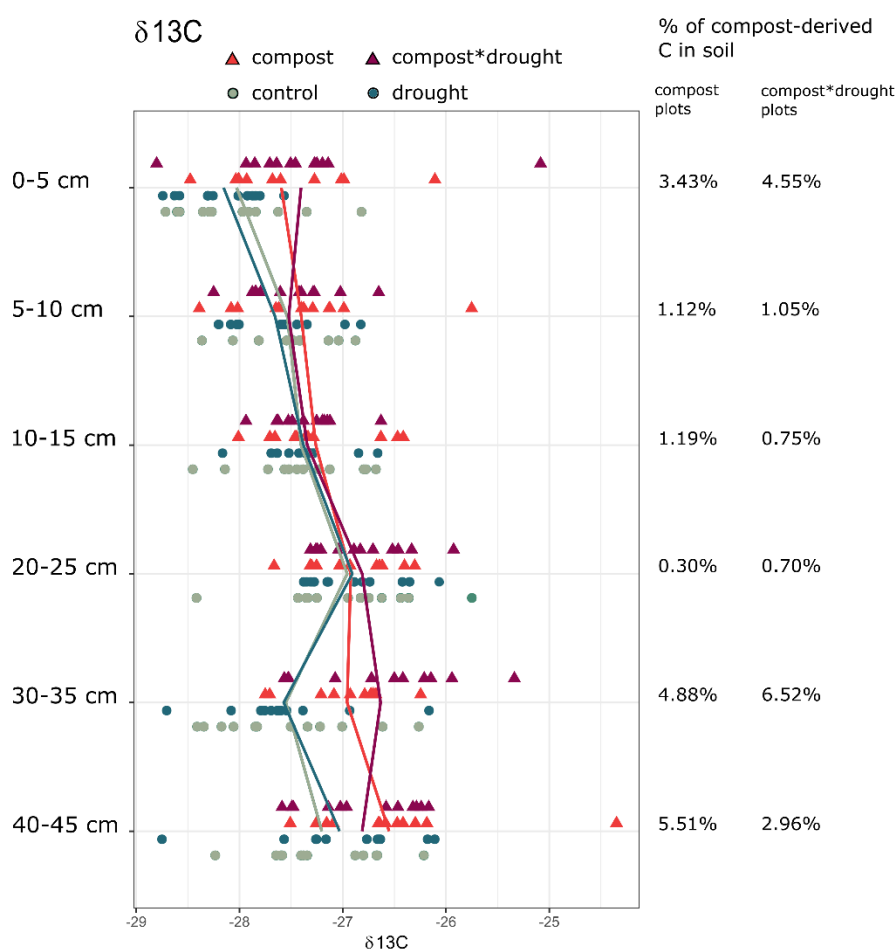
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243 *Fig 1. Values of $\delta^{13}C$ in the soil in compost-treated (triangles) and untreated (control, green dots) plots under drought*
244 *(dark red, dark blue) and at ambient precipitation (orange, light green) in 2022, at different depths. The percentage of*
245 *compost-derived C in the soil was calculated with the isotope mixing model in Eq. 2.*

Compost and drought effects

Total soil C content ($P = 0.04$) and aboveground biomass ($P = 0.04$) increased in the compost-treated plots. The latter increased by 23% (mean control plots = 642 g m^2, SD = 129.23, mean compost plots = 788 g m^2, SD = 221.7). The effect on soil C was significant only in the top 5 cm layer (Fig. 2), where soil C content increased by 18% (mean control plots C content = 29.9 mg/g, SD = 1.03, mean compost plots = 35.3 mg/g, SD = 0.75). Also soil nitrogen (N) was higher in the top 5 cm layer in the compost-treated plots (mean control plots = 2.44 mg/g, SD = 0.06, mean compost plots = 2.88 mg/g, SD = 0.06; $p < 0.05$), but the treatment did not significantly affect the C:N ratio. The compost treatment also decreased bulk density by 9% ($P = 0.03$) in the first 10 cm of soil (mean control plots = 1.34 g cm^3, SD = 0.18, mean compost plots = 1.22 g cm^3, SD = 0.17), but did not affect any other variable. The increase in the soil C content under compost addition in the topsoil was offset by the reduced bulk density, so that there was no statistically significant change to soil C stocks. However, we note that mean soil C stocks in the compost-treated (ambient precipitation) plots were 6% higher in the first 15 cm, though this increase was not statistically significant. This increase is slightly higher than the percentage of compost-derived C found in that layer (mean control plots = 4.02 kg m^2, SD = 0.92, mean compost plots = 4.26 kg m^2, SD = 0.59).

Experimental drought had no significant overall effect on aboveground biomass. Although biomass decreased by nearly 4% under the rainout shelters (mean control plots = 642 g m^2, SD = 129.23, mean drought plots = 617 g m^2, SD = 180.25), this reduction was only statistically significant in the compost-treated plots ($P = 0.02$). Further, there was no significant difference in plant biomass between the drought-treated plots with and without compost addition.

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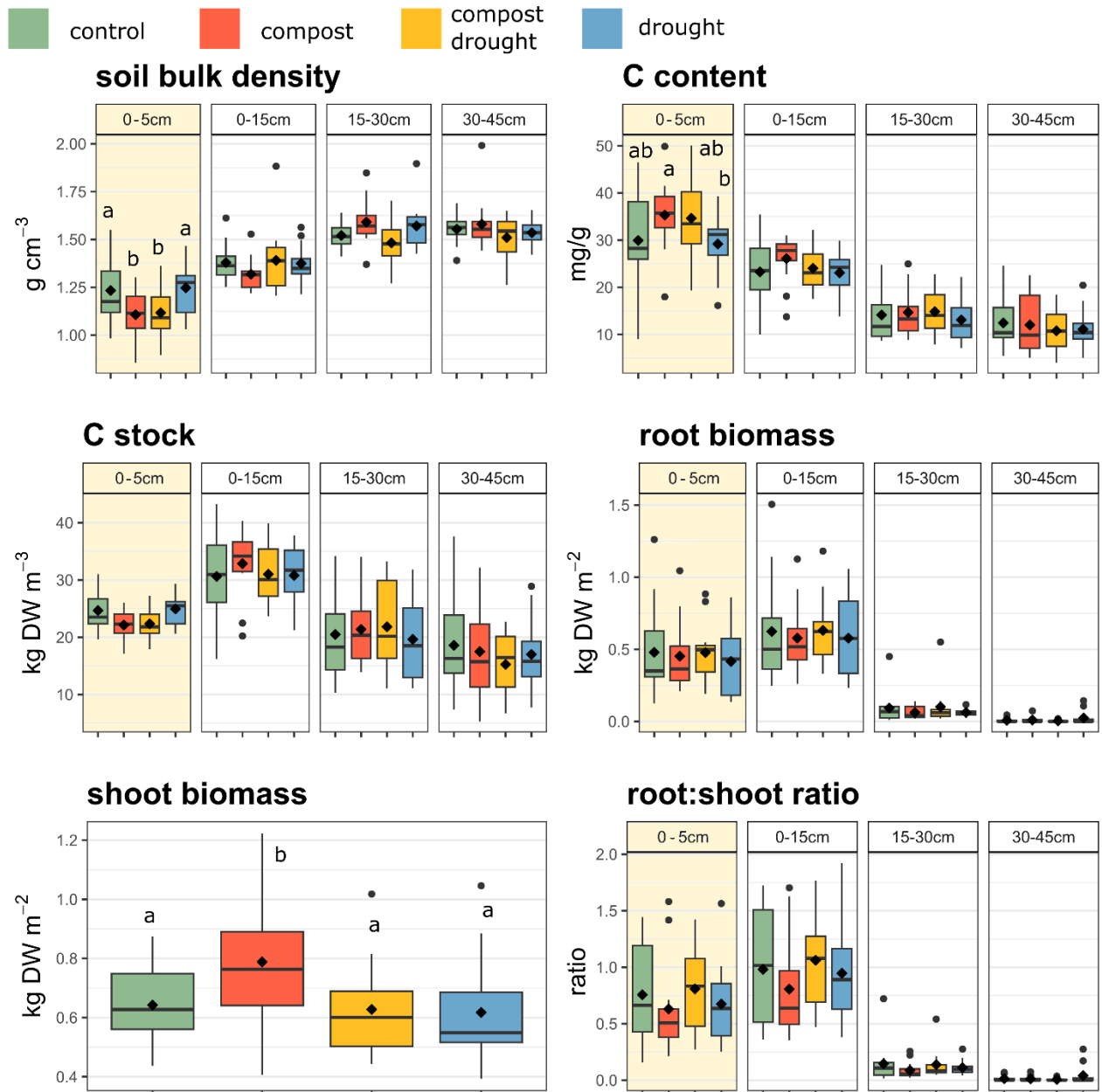
Fig. 2. Values of soil bulk density, soil carbon (C) contents, soil C stocks, root biomass, shoot biomass and root-shoot ratio, at different sampling depths in 2022 (n = 12). Values are averages of all sites. Green = control, red = compost, yellow = compost×drought, blue = drought. Boxes show mean (diamond inside the box), median (horizontal line) and interquantile range (IQR, colored box); whiskers extend to 1.5×IQR; dots in the graph are outliers. Different letters indicate statistically significant differences between means (P < 0.05). The yellow squares indicate the top layer (0-5 cm).

Root traits

In all drought-treated plots we observed an increase in root tissue density (P = 0.048), in specific root length of fine roots (P = 0.049), and in average root diameter (P = 0.045). If only roots in the top layer

276 (0-5 cm) were considered, in addition to these patterns, specific root length of coarse roots decreased

277 under drought (P = 0.04). In contrast, after compost addition root tissue density (P = 0.02) and specific

278 root length of all roots increased (P = 0.01).

279

280 In all control plots, soil C and root biomass were positively correlated both in the top 5-15 cm (5-10

281 cm, r = 0.42, P = 0.04; 10-15 cm, r = 0.5, P = 0.01) and in the whole 0-30 cm layer (0-30 cm, r = 0.63,

282 P < 0.01). Soil C content was also positively correlated to the root:shoot ratio (5-10 cm, r = 0.44, P =

283 0.03; 10-15 cm, r = 0.4, P = 0.052; 0-30 cm, r = 0.43, P = 0.04). In the compost-treated plots, the only

284 significant correlation was between soil C and root biomass when considering the whole 0-30 cm

285 layer (0-30 cm, r = 0.55, P < 0.01). The strength of the correlation did not differ between control and

286 compost-treated plots (r = 0.22, P < 0.01 in control and compost-treated plots).

287

288 **Spatial variability at the landscape scale**

289 Soil C contents, total C stocks, bulk density, root biomass and root:shoot ratio showed significant (P

290 < 0.05) differences between catenary positions and depths, with lower C stocks at low catenary

291 positions in the top 15cm of soil, and soil C content and bulk density also differed significantly

292 between grasslands (Fig. 3, table S8). Grassland identity and the interaction between grasslands and

293 catenary positions were the only significant predictors of aboveground biomass (Fig. 3).

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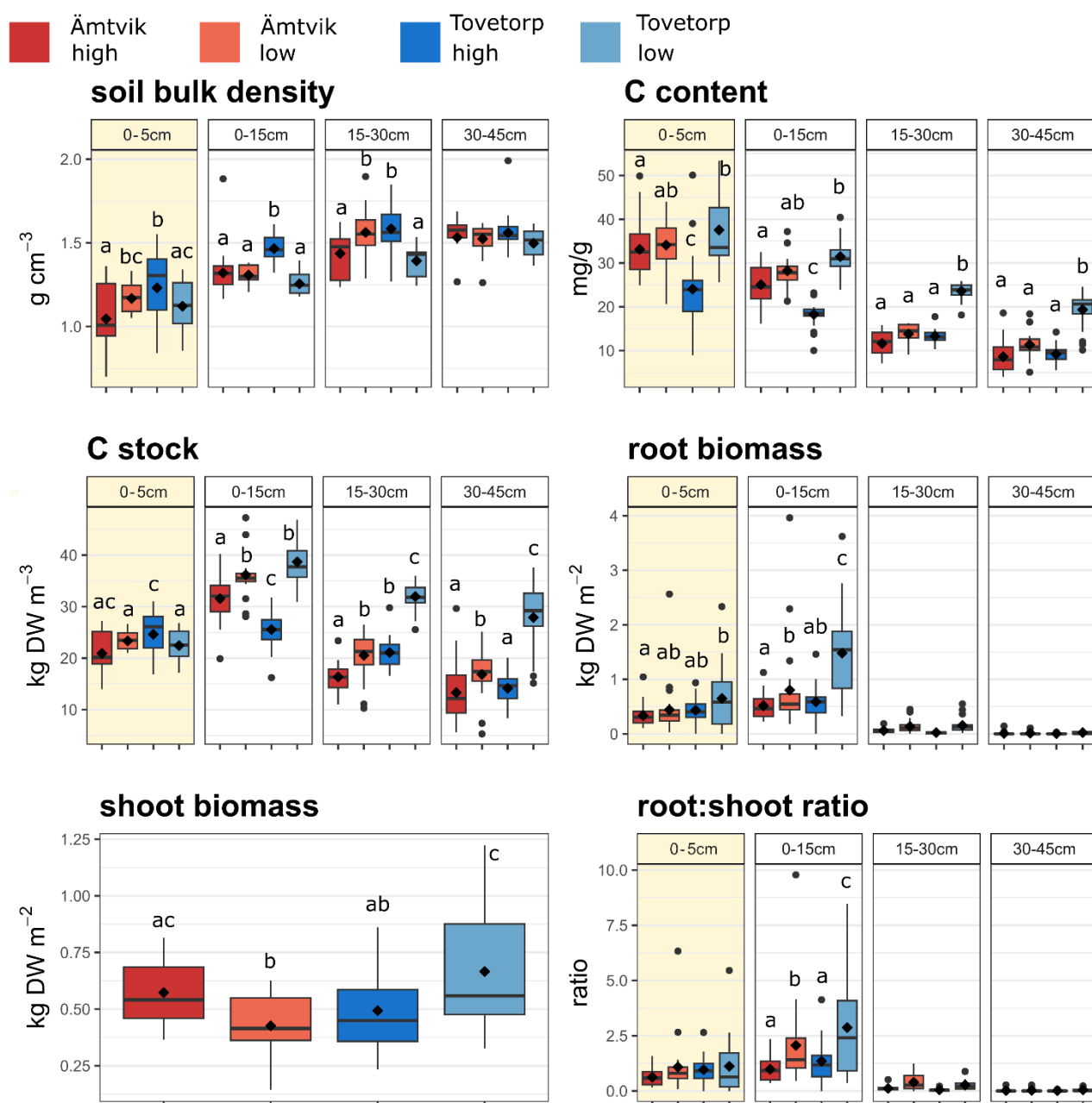
Fig. 3. Values of soil bulk density, soil carbon (C) content, soil C stocks, root biomass, shoot biomass and root-shoot ratio, at different sampling depths at the four sites, excluding treatments. The data consists of average values from 2019 (all plots, n = 48) and 2022 (only control plots, n = 12). Red = Amtvik High catenary position, orange = Ämtvik Low catenary position, blue = Tovetorp High catenary position, light blue = Tovetorp Low catenary position. Boxes show mean (diamond inside the box), median (horizontal line) and interquantile range (IQR, colored box); whiskers extend to 1.5×IQR; dots in the graph are outliers. Different letters indicate statistically significant differences between means (P < 0.05). The yellow squares indicate the top layer (0-5 cm).

Temporal changes during the 2019-2022 period

Aboveground biomass, root biomass and soil C also differed significantly between sampling years (P < 0.05, Fig. 4, table S9). The largest change was observed in aboveground biomass, which was 53% higher in 2022 compared to 2019 (from 419.68 g m^{-2}, SD = 137.45 to 642.23 g m^{-2}, SD = 129.23). Conversely, total soil C contents and root biomass in the first 15 cm decreased by 21.5% (from 29.7 mg/g, SD = 0.73 to 23.3 mg/g, SD = 0.71) and 38.7% (from 1017.95 g m^{-2}, SD = 955.16 to 623.65 g m^{-2}, SD = 65.19), respectively.

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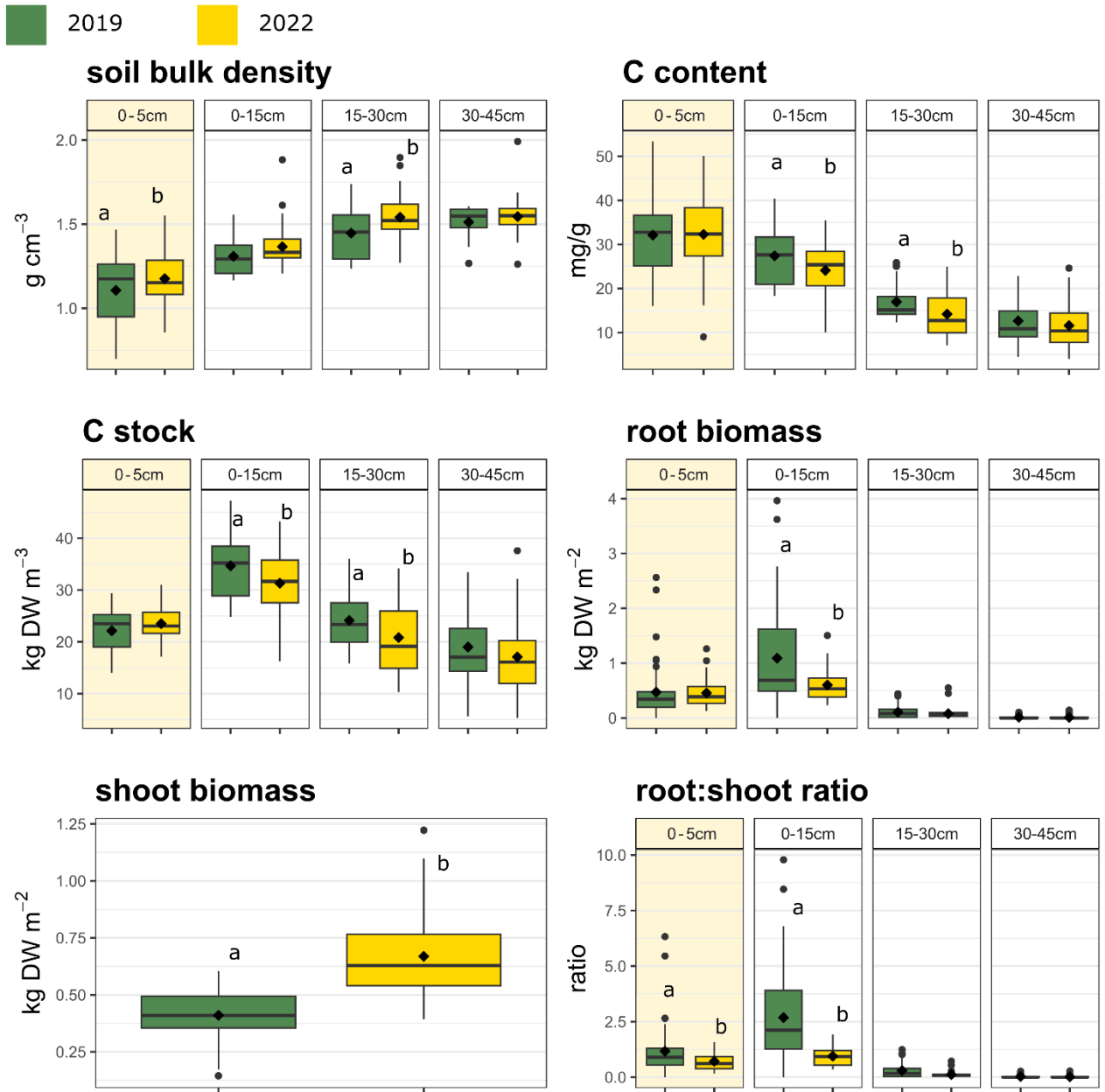
Fig. 4. Values of soil bulk density, soil carbon (C) contents, soil C stocks, root biomass, shoot biomass and root-shoot ratio, at different sampling depths in 2019 and 2022 (control plots, n = 12). Values are means for all plots. Green = 2019, yellow = 2022. Boxes show mean (diamond inside the box), median (horizontal line) and interquantile range (IQR, colored box); whiskers extend to 1.5×IQR; dots in the graph are outliers. Different letters indicate statistically significant differences between means (P < 0.05). The yellow squares indicate the top layer (0-5 cm).

Discussion

Compost effects on soil C and plant growth

Total soil C contents increased after compost application, but because bulk density was also reduced, there was no significant increase in soil C stocks (partly confirming our first hypothesis), despite higher mean soil C stocks in the compost treated plots in the first 15 cm of soil. This difference was lower than the C addition (~0.54 kg C m^{-2}) because of respiration. Compost is partly decomposed organic matter, and thus more chemically recalcitrant than fresh grass residues. As a result, its effects on SOC accrual can be persistent over several years (Sarker et al. 2022) even after a single application (Ryals et al. 2013). Despite evidence that compost amendments can lead to SOC accumulation already within two years after application (Gravuer et al. 2023), it is likely that the effect of our treatment on soil properties and soil C will persist beyond the 2022 sampling. This is also supported by the isotope tracing (Fig. 1), indicating that at least a fraction of the compost-derived C is still present in the soil after three growing seasons. The significant increase in aboveground biomass three years after the compost application could partly be explained by the persistence of favorable plant growing conditions promoted by the compost amendment, such as increased plant-available N in the soil. This mechanism was invoked by Oladeji et al (2020), and may interact with precipitation-related interannual variability in plant growth (Sala et al. 2012). Our results suggest that compost treatments might benefit the ecosystem C balance indirectly through increased biomass production, while others argued that compost can also extend the growing season (Fenster et al. 2023). These interactions between land management, vegetation growth and plant-derived C inputs also underline the importance of including vegetation dynamics when assessing the effectiveness of C management. Our compost addition treatment did not lead to a significant increase in soil C stocks, but resulted in a lower net C loss from the grassland mediated by an increase in plant biomass. In fact, there was a tendency for higher SOC stock (though not statistically significant) and the magnitude of such changes was higher than the amount of compost -derived C remaining in that layer. This suggests that the increase in soil C is not only derived from the amendment itself, but also from increased plant C inputs. However, longer-term studies are necessary to understand whether SOC saturation limits the effectiveness of compost amendments in sustaining these gains over time (Moinet et al. 2023), as well as to account for loss of C elsewhere, where compost is produced.

Compost enhanced aboveground biomass growth, but not root growth, possibly in response to the increased nutrient supply (Bloom et al. 1985; Poorter and Nagel 2000), thereby only partly confirming our first hypothesis. In broader terms, this suggests that the compost treatment led plants to preferentially allocate to aboveground organs the resources that would otherwise be allocated to nutrient acquisition belowground (Cleland et al. 2017). Nevertheless, increased root tissue density and specific root length in the top 5 cm layer suggest that root response to organic amendments is manifested in more subtle changes in root traits related to nutrient acquisition (Bardgett et al. 2014), rather than in net root biomass production.

Microbial activity and microbial biomass can be higher after compost addition (Sarker et al. 2022; Gravuer et al. 2019). Here, the limited effects of the compost treatment on soil C stocks suggest that the potential C accrual brought by the increased plant productivity might have been offset by increased microbial respiration (promoted by either compost or enhanced rhizodeposition of more productive plants) (Borken et al. 2002; Janzen 2006). Finally, the significant spatial and temporal variability in both soil C and vegetation biomass observed in the control dataset suggests that treatment effects might be site-specific (Garbowsi et al. 2020), and management plans seeking to increase C accrual should consider the potentially interactive effects of several biotic and abiotic factors, such as plant community composition, soil type and climate. For instance, C stocks are typically higher at lower catenary positions (Johansson et al. 2023; Fig. 3), and in our experiment aboveground biomass increase was highest at the site with the greatest abundance of grasses (table S4).

Drought effects on soil moisture, soil C and plant growth

Drought treatments reduced soil moisture and aboveground plant biomass, but did not significantly decrease root biomass (table S7), indicating preferential biomass allocation and resource investment to belowground organs under experimental drought. Plant growth is very sensitive to yearly fluctuations and even intra-annual distribution of precipitation (Knapp and Smith 2001, Porporato et al. 2006). Because our analyses are based on only two temporal datapoints (2019 and 2022), it is difficult to assess whether drought reduced plant turnover, defined as the ratio of standing biomass to net primary productivity (NPP). As there was some natural variability in the annual precipitation (see methods section), it is possible that a legacy effect of this variability may have affected plant growth

375 (Sala et al. 2012) particularly aboveground (Fig. 4), where growth is more sensitive than root biomass

376 to yearly fluctuations in water availability (Zhang et al. 2021). In particular, legacy effects of the 2018

377 drought could have hampered growth in 2019, as aboveground vegetation in the control plots

378 increased by more than 50% between 2019 and 2022. Conversely, the high summer precipitation in

379 2021 could have buffered the effects of the experimental drought in 2022, leading to overall weak

380 drought effects (Sala et al. 2012).

381 The drought treatment had a relatively small impact on plant biomass and on roots in particular (Fig.

382 2). Because we do not know which plant species the sampled roots belong to, we cannot make any

383 conclusions related to belowground drought responses of different plant functional groups (Zhang et

384 al. 2017; Mackie et al. 2019; Zhong et al. 2019). However, we note that the magnitude of the drought

385 did not differ between locations and soil physical properties were similar across sites, but drought

386 effects differed across locations (Fig. S4). Therefore, we can hypothesize that differences in the plant

387 communities account for at least some of the spatial heterogeneity observed in our study, as was

388 observed by Garbowski et al. (2020). Also, while drought effects on root biomass were marginal, the

389 drought treatment did increase both root tissue density and average root diameter. Climate is a strong

390 predictor of root trait variation (Freschet et al. 2017), and higher root tissue density is correlated with

391 resource-conservative acquisition strategies (Bardgett et al. 2014) and longer root life span (Ryser,

392 1996), suggesting some degree of drought adaptation in our plant communities.

393 Adopting a standardized drought experimental design improves comparability, but partial rainout

394 shelters will still allow for a substantial amount of precipitation to pass through, potentially raising

395 soil moisture above the wilting point. Experimental droughts also fail to account for reduced air

396 humidity, which may underestimate negative responses of plant biomass to drought in field

397 experiments (Kröel-Dulay et al. 2022), and for increased temperatures, which often occur in

398 combination with natural droughts. These methodological limitations might explain why we observed

399 minor drought effects on vegetation. To understand the ecosystem-level implications of drought, soil

400 C changes need to be considered as well. Dry conditions likely decrease heterotrophic respiration

401 because microbial activity is inhibited due to both physiological mechanisms, such as osmoregulation

402 diverting efforts from resource acquisition to survival, and physical mechanisms, like the slower

403 transport of substrates in dry soils (as the water films around soil particles shrink and pore

404 connectivity is lost) (Moyano et al. 2013; Schimel 2018). However, heterotrophic respiration
405 increases again after soil rewetting, leading to disproportionally large C emissions during the short
406 post-rewetting period (Canarini et al. 2017; Barnard et al. 2020). Because the drought plots with
407 added compost had a higher fraction of compost-labelled isotopes compared to the non-drought plots
408 in the topsoil (Fig. 1), this would imply that any soil C emission pulses at rewetting were not sufficient
409 to compensate for the possibly lowered microbial activity during the soil moisture dry-downs. As a
410 result, in our experiment drought had no effects on soil C contents and stocks, as per our second
411 hypothesis, although it slightly reduced soil bulk density (in a pre-treatment vs post-treatment
412 comparison, data not shown), possibly in relation to shrinkage in dry soil.

413 **Interactive effects of compost and drought**
414 While previous studies indicated increased soil water retention after soil amendments (Franco-Andreu
415 et al. 2017; Ali et al. 2017), in our study compost-treated drought plots did not have higher soil
416 moisture than the untreated drought plots three years after compost application (Fig. S3), which leads
417 us to reject our third hypothesis. As the negative effects of drought on aboveground biomass were
418 weak, they were not visibly compensated for by the compost addition. On the contrary, the
419 experimental drought eliminated the biomass increase detected in the compost-treated plots under
420 ambient rainfall, overriding the positive effects of the increased C and N provided through the
421 compost. This suggests that the vegetation response in our experiment does not only depend on
422 nutrient addition and interannual variability in precipitation, but likely also on plant physiological
423 processes related to water availability (Bista et al. 2018) and on the ability of soil microbes to render
424 the nutrients available for plant uptake (which also depends on soil water). Interestingly however,
425 while both compost and drought tended to reduce root biomass, there was a tendency for higher
426 root:shoot ratio in the plots with combined compost and drought treatment (Fig. 2). While our results
427 from the compost-treated plots show that plants may reduce their belowground biomass investment
428 relative to aboveground growth when adding organic matter, this mechanism appeared to work
429 differently under drought conditions, when plants may shift C allocation belowground to aid in water
430 acquisition (Eziz et al. 2017; Guswa et al. 2010). This improved capacity for soil water absorption
431 could offset any compost-induced increase in soil water retention capacity. However, since our
432 experiment did not include drought recovery, it is not known if this change would persist after the
433 end of the experimental drought.

Conclusions

We explored how drought and compost amendment affect soil properties and above- and belowground plant biomass within a grassland ecosystem. Compost amendment and drought had distinct effects on plant shoot and root growth, revealing the presence of trade-offs in their responses to environmental change. The compost treatment led to an increase in biomass in shoots but not in roots, and ultimately did not result in an increase in soil C stocks. Drought did not significantly affect plant biomass, but led to changes in root traits and stunted the compost-induced increase in plant growth measured in plots under ambient precipitation. These findings improve our understanding of C dynamics in grasslands by illustrating the different components of plant and soil properties affected by compost amendment. We also observed significant spatial and temporal variability in vegetation and soil C dynamics over the study period, which may be driven by differences in topography, land use and plant community composition, as well as temporal variability in precipitation.

Author contributions

Conceptualization and methodology: SC, DG, GH, SM, NR; Field investigation and lab work: DG, NR; Statistical analysis: DG; Writing – original draft: DG; Writing – review & editing: DG, SC, GH, SM, NR.

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