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 reduced precipitation on plant biomass and on soil C at various soil depths. Aboveground biomass and soil C content (% C) increased compared to 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 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 it to the soil via roots and organic matter. Concerns about soil erosion and historic soil C depletion in agricultural and grassland soils (Sanderman et al. 2017, Bai and Cotrufo, 2022) have motivated the

28 development of sustainable land management strategies, generally named "carbon farming" (Paul et
29 al. 2023) and promoted by the "4 per 1000" initiative (Minasny et al. 2017). These approaches include
30 mitigating soil organic carbon (SOC) loss in specific sites resulting from agricultural activities such
31 as tilling, which can be achieved with the use of soil C amendments like compost, biochar, and manure
32 on croplands or grasslands (Ryals and Silver 2013; Ryals et al. 2015; Keesstra et al. 2016; Fischer et
33 al. 2019; Garbowski et al. 2023). Soil C management via compost amendments aims to facilitate
34 accumulation of plant-derived C in the soil C pool, where it can be retained over long time scales –
35 i.e. decades to centuries (Shi et al. 2020). If the total C inputs and accumulation in the soil exceed the
36 total losses, C amendments can lead to C sequestration (Don et al. 2024, Moinet et al. 2023).

37 Since SOC accrual and C sequestration potential are uncertain and context dependent (Moinet et al.
38 2023), it is important to investigate the effects of C amendments across a range of climatic and
39 management conditions. Grasslands and croplands converted to grasslands can store considerable
40 amounts of soil C and are therefore ideal systems to apply C amendments. They can act as C sinks if
41 managed appropriately (Conant et al. 2001), and can have higher root biomass C compared to
42 agricultural lands, usually cultivated with annual crops (Beniston et al. 2014). Several studies have
43 investigated the effects of organic amendments on aboveground biomass (Ryals et al. 2016), crop
44 yields (Luo et al. 2018; Ahmad et al. 2009), and on roots in farming systems (Hirte et al. 2021), but
45 fewer focus on non-cultivated grasslands.

46 C amendments add C to the soil in two ways: directly, by moving plant biomass from one location to
47 another, and indirectly, by promoting plant growth (Ryals et al. 2016). Compost is rich in organic
48 matter, which serves as a substrate for soil microorganisms. As microbes decompose this organic
49 matter, they release nutrients in forms that plants can readily absorb (Malik et al. 2013). In turn, the
50 increased vegetation growth can increase the natural rate of C input and thus potentially SOC stocks
51 (Ryals et al. 2013). Indeed, model predictions suggest that compost additions on grasslands can lead
52 to soil C sequestration (DeLonge et al. 2013). By improving soil structure and reducing compaction,
53 compost additions may also reduce soil bulk density. As SOC stocks are calculated by multiplying C
54 concentration by the bulk density, improved management may also lead to net zero effects on C stock
55 despite increased soil C contents. Considering these indirect effects requires an ecosystem-level
56 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. To this end, the use of isotope-labelled compost can improve our understanding of soil C dynamics.

Land management practices—including compost amendments—can significantly impact both above- and belowground plant biomass, which contribute differently to SOC storage. Root biomass and root exudates are an integral part of soil C formation and retention (Jackson et al., 2017). In fact, roots are more recalcitrant to decomposition compared to shoots (Rasse et al. 2005, Gaudinski et al. 2000), and play a central role in C sequestration efforts. However, aboveground plant biomass should also be included in these assessments to identify potential trade-offs in above- vs. belowground C allocation within the vegetation pool, and to determine whether changes in plant biomass affect the soil C pool (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) and water availability (Wilcox et al. 2017; Guasconi et al. 2023). 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).

Another promising application of soil organic amendments is their use to mitigate the negative effects of drought on vegetation and soil microbial communities, as has been observed with biochar (Fischer et al. 2019). 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 modify plant carbon (C) allocation (Hasibeder et al., 2015), leading to lower C inputs to the soil and potentially decreased soil C stocks (Deng et al., 2021). Organic soil amendments can enhance resilience to drought by increasing soil's water-holding capacity (Fischer et al. 2019; Haque et al. 2021). These effects 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). The increased moisture 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).

Soil and plant communities can show great 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 variable physical properties of soil, but can also depend on land use history or on small- and large-scale topography (Wang et al. 2020), and highlights 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 reduced precipitation on both soil and plant biomass after three growing seasons. The changes were observed at various soil depths, 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 will have 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 loss of plant growth 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* with a C:N ratio of 9.8 and $\delta^{13}C$ value of about -15.39‰. After the seasonal corn harvest (summer 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 $\delta^{13}C$ isotope ratio of the compost is higher than that of bulk soil (-15.39 and -27.25, respectively), which means that the $\delta^{13}C$ 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

146   collected with a large fixed volume root auger with a sharpened cutting edge (8 cm diameter and 15

147   cm in length; Eijkelkamp, The Netherlands). Three 15 cm segments were collected sequentially using

148   the same hole, reaching a total depth of 45 cm. Upon extraction, the cores were cut into 5 cm

149   segments, and the bulk density was determined after drying the samples at 105 °C. After drying, a

150   subsample from the same core was used to calculate the soil organic matter (SOM) content through

151   loss on ignition at 550 °C for 4 h. A subset was further burned at 960 °C in order to determine the

152   presence of inorganic C, which was low (0.5 %), indicating that the total C can be considered equal

153   to organic C (OC). Samples for total C and N and $\delta^{13}C$ were taken to a depth of 1 m with a Pürckhauer

154   soil corer (2.5 cm diameter; Eijkelkamp, The Netherlands) in 5 cm increments. The analyses for total

155   C and N contents, and for $\delta^{13}C$ were carried out on a subset of the samples by the Stable Isotope

156   Facility at UC Davis (California). A subset of these samples was sent to a commercial lab and used

157   for pH measurements (measured in a commercial lab using distilled water with a Mantech Automax

158   73, Guelph, ON., Canada) and nutrient content analyses (P, Ca, Mg and K; Avio 500 ICP Optical

159   Emission Spectrometer, Perkin Elmer, Waltham, MA; USA) (Table S3). Soil moisture was measured

160   every three weeks throughout the growing season (2019 through 2022) from one access tube (1 m

161   long) permanently installed in each plot, using a PR2 profile probe (Delta-T Devices Ltd, Cambridge,

162   UK). The values used in the analyses are growing season averages of volumetric soil water content

163   (%) in the first 30 cm in each plot.

164   Root biomass was collected in September 2019 and in August 2022 with one soil core sampled with

165   a root auger (8 cm diameter; Eijkelkamp, The Netherlands) by placing the auger on top of the plants,

166   but living aboveground plant biomass and fresh litter were removed and not included in the soil

167   samples. Samples were taken to a depth of 30 cm in all plots and to a depth of 45 cm in a subsample

168   of 16 plots (used as control for maximum rooting depth), with soil cores divided into 5 cm segments.

169   The roots were rinsed with water on a 0.5 mm mesh sieve to remove soil, then placed on a transparent

170   tray, covered with water and scanned with a flatbed scanner at 600 dpi (grey scale), followed by

171   drying at 60 °C for 48 h to obtain the dry weight. The scanned images were analyzed with WinRhizo

172   (Regent Instruments, Québec, CA) to obtain root volume, length and diameter, used to calculate root

173   mass density (g roots cm^{-3} soil), specific root length (cm g^{-1} roots) and root tissue density (g roots cm^{-3}

174   ^{3} roots). Aboveground biomass was harvested from one quarter (1 m^2) of each plot every year in mid-

175 July, by cutting at ground level (including moss and dead biomass, table S4). More details of the

176 sampling design are presented in the Supplements (table S5).

Statistical analyses

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

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

180 2022; Guo et al. 2018), the analyses include testing for differences in the control plots between the

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

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

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

184 calculate soil C stocks (C content × bulk density × layer thickness). The soil C stocks were then

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

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

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

188 dataset,

189 $$SOC = 0.328 \times SOM + 0.217, \tag{1}$$

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

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

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

193 $$F = \frac{\delta^{13}C_{compost\ treatment} - \delta^{13}C_{control}}{\delta^{13}C_{compost} - \delta^{13}C_{control}}, \tag{2}$$

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

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

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

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

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

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

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

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

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

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

204 $$d = \frac{\overline{x}_1 - \overline{x}_2}{S},\tag{3}$$

205 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

206 the standard deviation.

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

223

Results

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

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

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

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

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

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

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

232 $\delta^{13}C$ in the treated plots (mean control plots = -27.44‰, mean compost plots = -27.10‰, P < 0.01),

233 and the difference was significant at 0-5 cm, 30-35 cm and 40-45 cm. The mixing model (Eq. 2)

indicated that after three growing seasons, the percentage of compost-derived C in the compost 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. In the compost x drought plots, the percentage of compost-derived C was 4.55 % in the 0-5 cm layer, 6.52 % in the 30-35 cm layer and 2.96 % in the 40-45 cm layer.
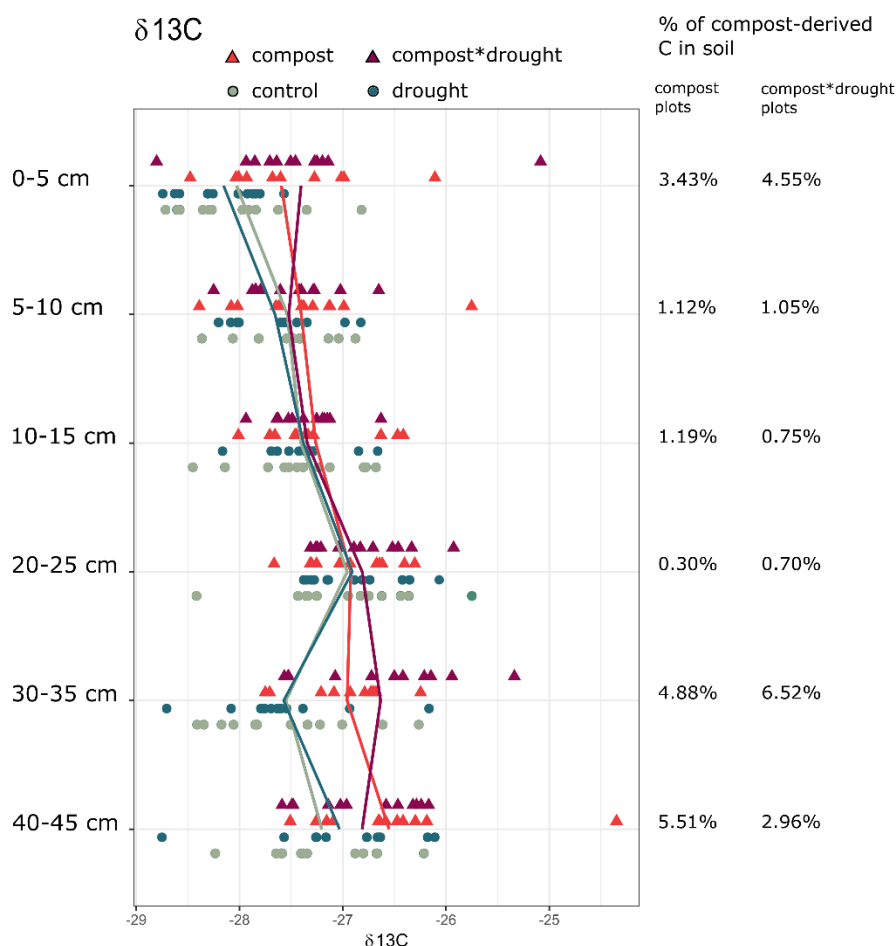
Fig 1. Values of $\delta^{13}C$ in the soil in compost-treated (triangles) and untreated (control, green dots) plots under drought (dark red, dark blue) and at ambient precipitation (orange, light green) in 2022, at different depths. The percentage of compost-derived C in the soil was calculated with 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

248   compost plots = 35.3 mg/g, SD = 0.75). Soil nitrogen (N) was higher in the top 5 cm layer in the

249   compost-treated plots (mean control plots = 2.44 mg/g, SD = 0.06, mean compost plots = 2.88 mg/g,

250   SD = 0.06; $p < 0.05$), but the treatment did not significantly affect the C:N ratio. The compost

251   treatment also decreased bulk density by 9% (P = 0.03) in the first 10 cm of soil (mean control plots

252   = 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

253   variable. The increase in the soil C content under compost addition was offset by the reduced bulk

254   density, so that there was no statistically significant change to soil C stocks. However, we note that,

255   albeit non-statistically significant, mean soil C stocks were 6% higher in the compost-treated (ambient

256   precipitation) plots in the first 15 cm, slightly higher than the percentage of compost-derived C found

257   in that layer (mean control plots = 4.02 kg m^2, SD = 0.92, mean compost plots = 4.26 kg m^2, SD =

258   0.59).

259   Experimental drought had only an effect on aboveground biomass, which decreased by almost 4%

260   under the rainout shelters (mean control plots = 642 g m^2, SD = 129.23, mean drought plots = 617 g

261   m^2, SD = 180.25). However, this effect was significant only relatively to the compost-treated plots (P

262   = 0.02), but not relatively to untreated control. Further, there was no significant difference in plant

263   biomass between the drought-treated plots with and without compost addition.
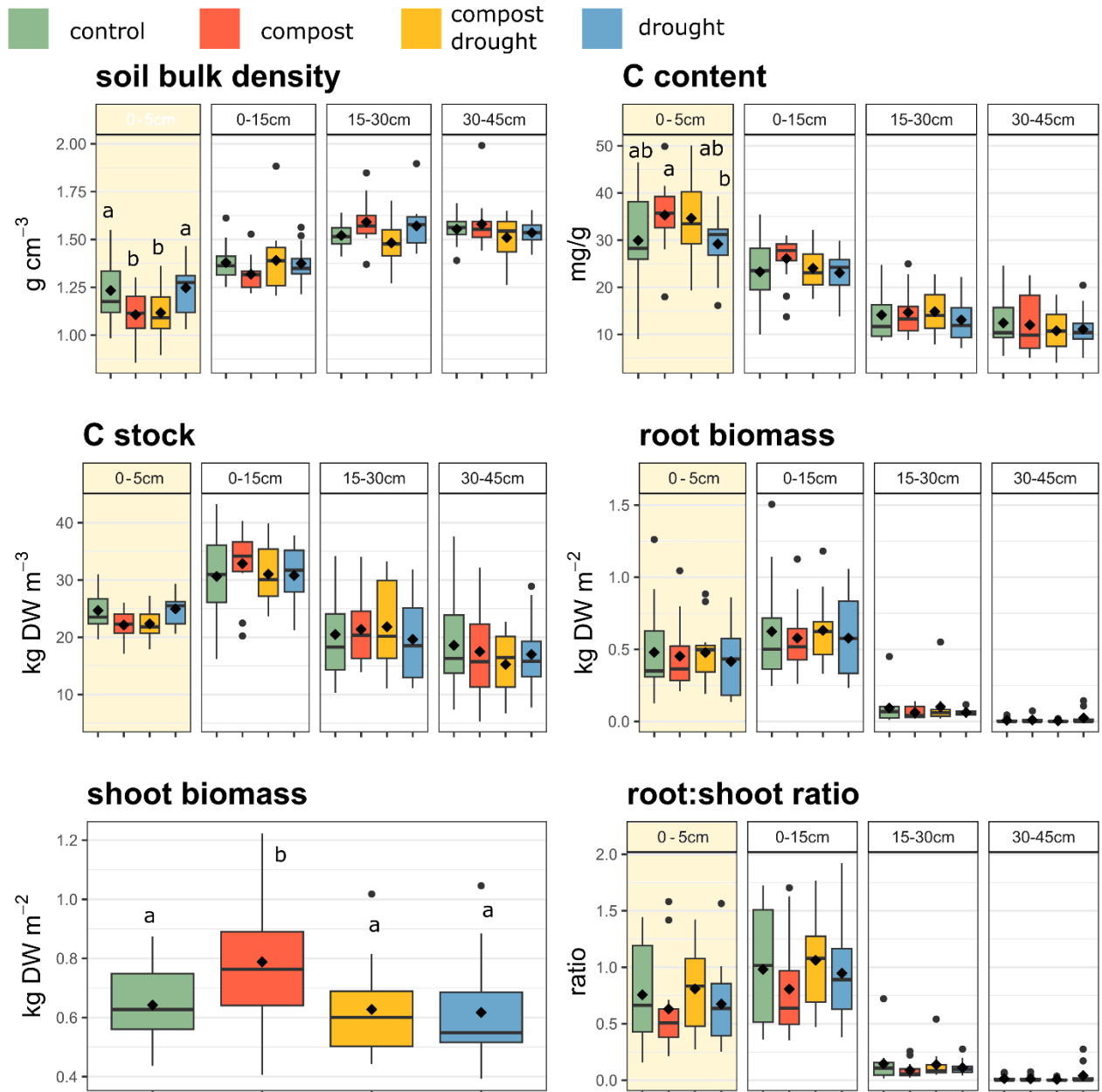
Fig. 2. Values of soil bulk density, soil carbon (C) contents, soil C stocks, root biomass, shoot biomass and root-shoot ratio, at different sampling depths in 2022 (n = 12). Values are averages of all sites. Green = control, red = compost, yellow = compost×drought, blue = drought. Boxes show mean (diamond 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

273   (0-5 cm) were considered, in addition to these patterns, specific root length of coarse roots decreased

274   under drought (P = 0.04), while root tissue density (P = 0.02) and specific root length of all roots

275   increased after compost addition (P = 0.01).

276

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

278   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,

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

280   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

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

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

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

284

285   **Spatial variability at the landscape scale**

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

287   < 0.05) differences between catenary positions and depths, and soil C content and bulk density also

288   differed significantly between grasslands (Fig. 3, table S8). Grassland identity and the interaction

289   between grasslands and catenary positions were the only significant predictors of aboveground

290   biomass (Fig. 3).

291

292
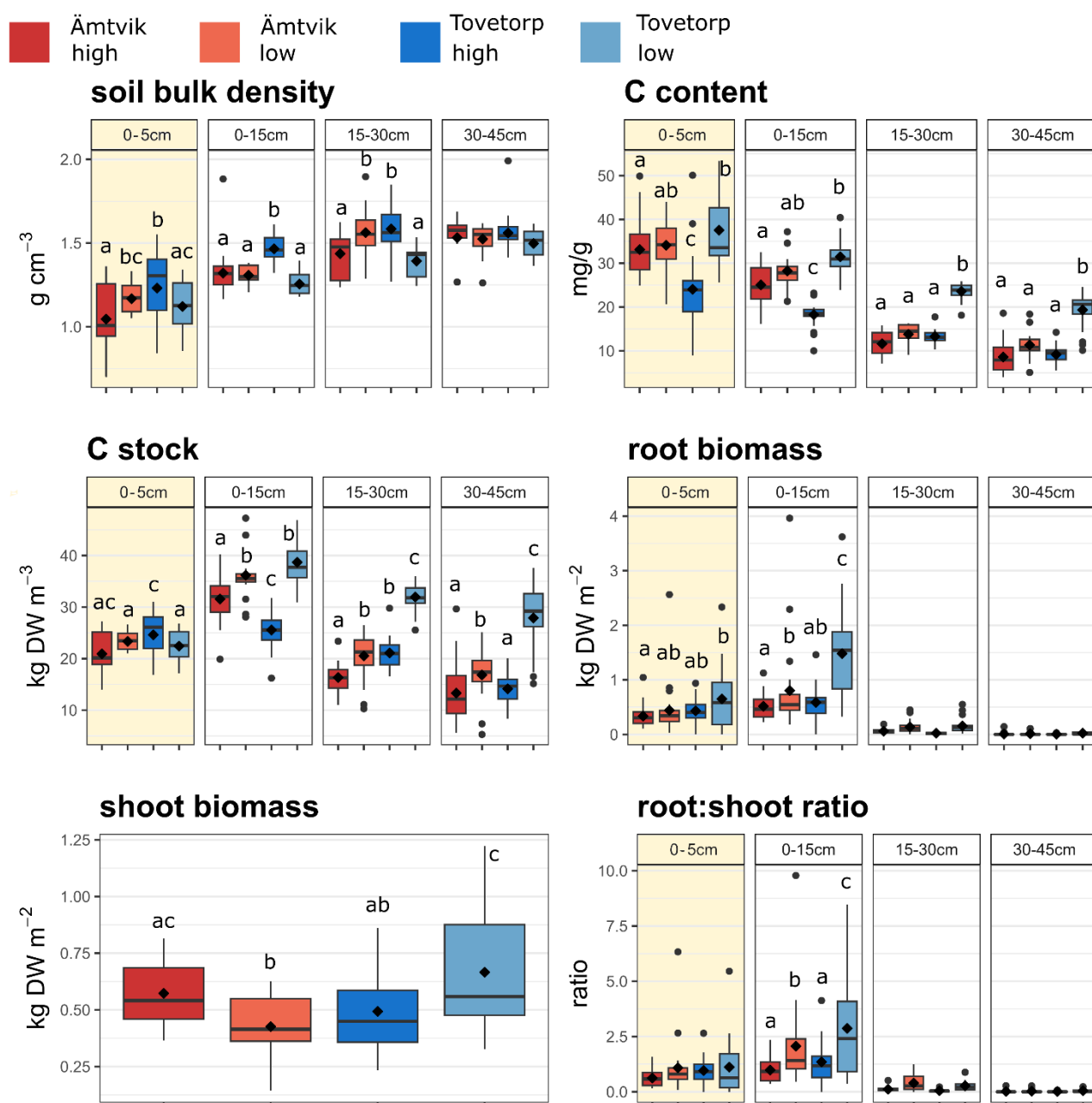
Fig. 3. Values of soil bulk density, soil carbon (C) content, soil C stocks, root biomass, shoot biomass and root-shoot ratio, at different sampling depths at the four sites, excluding treatments. The data consists of average values from 2019 (all plots, n = 48) and 2022 (only control plots, n = 12). 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).

Natural changes during the 2019-2022 period

Aboveground biomass also differed significantly between sampling years. Between 2019 and 2022 (Fig. 4, table S9) total soil C contents and root biomass in the first 5 cm of the control plots decreased by 10.7% (from 33.5 mg/g, SD = 1.05 to 2.99 mg/g, SD = 1.03) and 8.4% (from 522.96 g m^{-2}, SD = 626.48 to 479.25 g m^{-2}, SD = 320.75), respectively. In the first 15 cm, they 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. Aboveground biomass instead increased by 53% (from 419.68 g m^{-2}, SD = 137.45 to 642.23 g m^{-2}, SD = 129.23).

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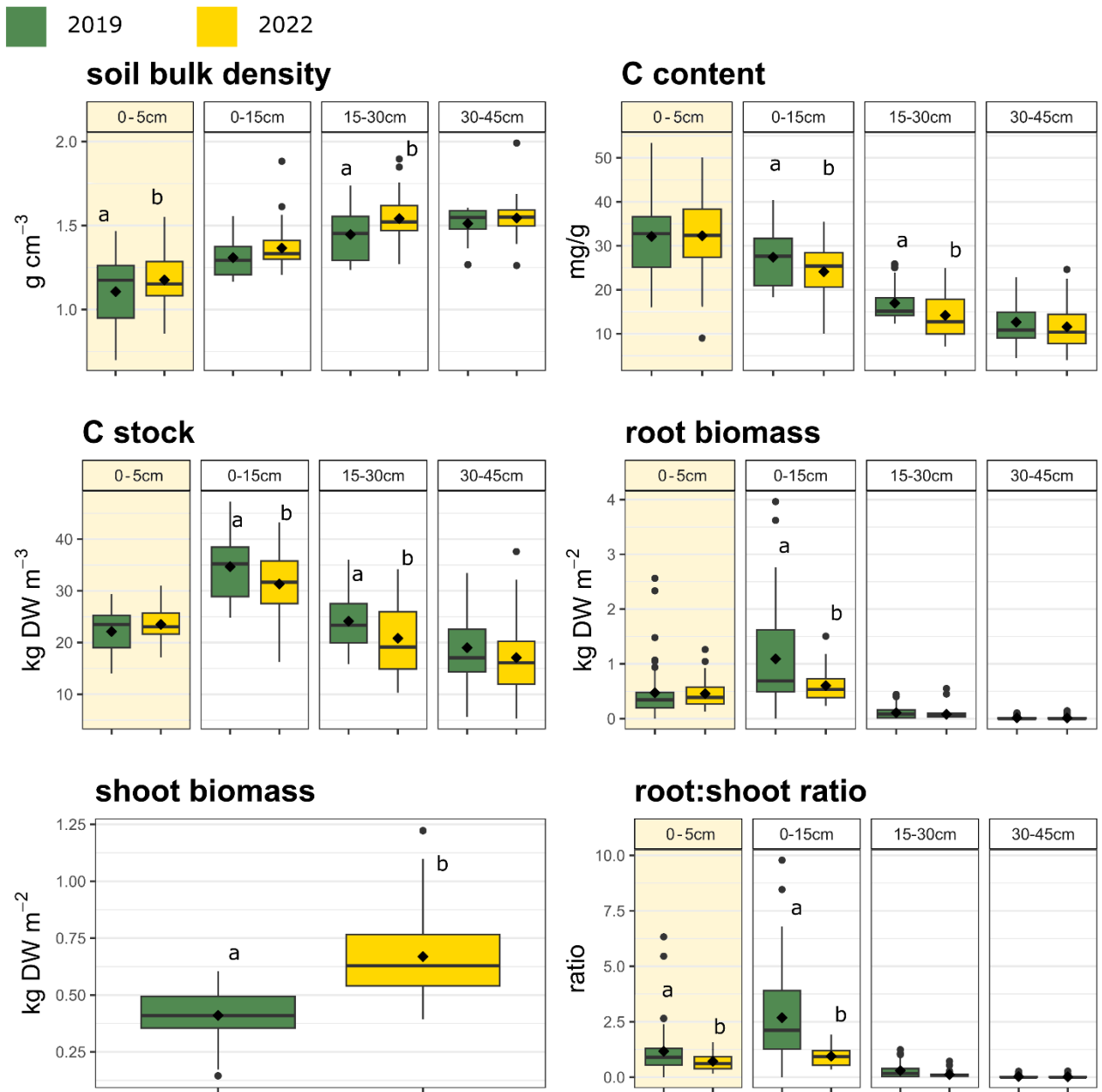
Fig. 4. Values of soil bulk density, soil carbon (C) contents, soil C stocks, root biomass, shoot biomass and root-shoot ratio, at different sampling depths in 2019 and 2022 (control plots, n = 12). Values are means for all plots. Green = 2019, yellow = 2022. Boxes show mean (diamond inside the box), 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}) and thus lower than expected, but is likely due to respiration loss. 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, such as increased 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, such as in this case, or by extending the growing season, such as in 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 an increase in soil C accumulation, but resulted in a lower net C loss from the grassland. In fact, soil C in a given layer increased more 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).

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). 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, 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 precipitation reduction. 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 (Sala et al. 2012) particularly aboveground (Fig. 4), where growth is more sensitive than root biomass to yearly fluctuations in water availability (Zhang et al. 2021). In particular, legacy effects of the 2018 drought could have hampered growth in 2019, as aboveground vegetation in the control plots increased by more than 50% between 2019 and 2022. Conversely, the high summer precipitation in

373   2021 could have buffered the effects of the experimental drought in 2022, leading to overall weak

374   drought effects (Sala et al. 2012).

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

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

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

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

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

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

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

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

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

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

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

386   1996), suggesting some degree of drought adaptation in our plant communities.

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

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

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

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

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

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

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

394   C changes need to be considered as well. Dry conditions decrease heterotrophic respiration because

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

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

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

398   connectivity is lost) (Moyano et al. 2013; Schimel 2018). However, heterotrophic respiration

399   increases again after soil rewetting, leading to disproportionally large C emissions during the short

400   post-rewetting period (Canarini et al. 2017; Barnard et al. 2020). Because the drought plots with

401   added compost had a higher fraction of compost-labelled isotopes compared to the non-drought plots

402 in the topsoil (Fig. 1), this would imply that any soil C emission pulses at rewetting were not sufficient
403 to compensate for the possibly lowered microbial activity during the soil moisture dry-downs. As a
404 result, in our experiment drought had no effects on soil C contents and stocks, as per our second
405 hypothesis, although it slightly reduced soil bulk density (in a pre-treatment vs post-treatment
406 comparison, data not shown), possibly in relation to shrinkage in dry soil.

Interactive effects of compost and drought

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

Conclusions

429 We explored how drought and compost amendment affect soil properties and above- and
430 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 plants and soil properties affected by land management. 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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