Spatial and temporal variability in soil and vegetation carbon dynamics under experimental drought and soil amendments

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Abstract

Soils are the largest carbon (C) pool on the planet, and grassland soils have a particularly large C sequestration potential. Appropriate land management strategies, such as organic matter additions, can improve soil health, increase soil C stocks, and increase grassland resilience to drought by improving soil moisture retention. However, soil C dynamics are deeply linked to vegetation response to changes in both management and climate, which may also be manifested differently in roots and shoots. This study presents findings from a three-year experiment that assessed the impact of a compost amendment and of reduced precipitation on soil and vegetation C pools. Compost addition increased aboveground biomass and soil C content (%C), but because bulk density decreased, there was no significant effect on soil C stocks. Drought decreased aboveground biomass, but did not significantly affect root biomass. Overall, the soil amendment shifted C allocation to aboveground plant organs, and drought to belowground organs. We also observed significant spatial and temporal variability in vegetation biomass and soil C over the study period. These results highlight the need to consider multiple biotic and abiotic factors driving ecosystem C dynamics across spatial scales when upscaling results from field trials.

Introduction

Management of soil health and soil carbon (C) stocks has been receiving increasing attention in the past years, with growing awareness that soils provide vital ecosystem services and act as C sinks. 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 development of sustainable land management strategies, sometimes named "carbon farming". One such strategy is the use of soil C amendments (Ryals and Silver 2013; Ryals et al. 2015; Keesstra et al. 2016; Fischer et al. 2019;

29   Garbowski et al. 2023), including compost, biochar, and various types of manure. These treatments

30   can be applied on croplands or rangelands, in single or multiple applications, and can increase soil

31   aggregation (Sarker et al. 2022) and mitigate soil organic carbon (SOC) loss resulting from human

32   activities such as tilling. In some cases, C amendments have even been proposed as means to actively

33   sequester C in soils, with initiatives like the "4 per 1000" (Minasny et al. 2017) promoting their

34   implementation as a climate change mitigation strategy. Consequently, soil C management methods

35   aim to shift the ecosystem C balance by facilitating the movement of C from the atmosphere into

36   vegetation and subsequently, into the soil C pool, where it can be retained over long time scales.

37   Adding C to soils in the form of amendments directly increases the standing stock of SOC, but C

38   amendments may also act as a primer to an ecosystems natural ability to sequester C via indirect

39   effects. If C amendments promote plant growth, they also increase the natural rate of C input to the

40   soil and thus potentially SOC stocks if the additional C input is stabilized and does not promote

41   mineralization of native SOC. Considering these indirect effects requires an ecosystem-level

42   perspective on soil C sequestration potential that accounts for both below- and above-ground

43   vegetation contributions. Root biomass, belowground plant organs and root exudates are an integral

44   part of soil C formation and retention (Jackson et al., 2017). However, aboveground plant biomass

45   should also be included in these assessments to identify potential trade-offs in above-and

46   belowground C allocation within the vegetation pool, and to determine whether there are changes in

47   vegetation C pools which may affect the soil C pool. It is especially important to determine the

48   proportion of plant litter that contributes to soil organic matter (SOM) formation and stabilization

49   (Cotrufo et al. 2015). It has been argued that an approach that accounts for above- and belowground

50   interactions is essential to get a comprehensive understanding of ecosystem C dynamics (Heimann

51   and Reichstein, 2008).

52   Land management practices, whether through conventional or regenerative methods, can significantly

53   impact soil C and plant biomass both above- and belowground. For instance, historic land use has

54   depleted the soil of C (Sanderman et al. 2017), and agricultural lands have lower root biomass C

55   compared to managed grasslands (Beniston et al. 2014). Organic amendments affect different

56   properties and mechanisms in soils, including soil aggregation and structure, soil microbial

57   communities, and plant roots, and the interactions between these elements (Sarker et al. 2022, Liu et

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58   al. 2016). Amendments provide nutrients that can stimulate microbial activity and plant growth
59   (Hammerschmiedt et al. 2021), and increase crop yields (Luo et al. 2018). Another promising
60   application of soil organic amendments is their use to mitigate the negative effects of drought on
61   vegetation and soil microbial communities (Fischer et al. 2019). Future climate projections indicate
62   an increase in extreme weather events, including longer and more frequent droughts (IPCC, 2021),
63   which may decrease the soil C sequestration capacity of grasslands by altering plant community
64   composition, plant C allocation and microbial processes (Bai and Cotrufo, 2022). Organic soil
65   amendments can enhance resilience to drought by increasing soil capacity to retain soil moisture
66   (Fischer et al. 2019; Haque et al. 2021). This can also indirectly benefit the ecosystem C balance by
67   partly compensating the drought-induced loss of plant biomass (Kallenbach et al. 2019; Ali et al.
68   2017).

69   Many studies have investigated the effects of organic amendments on aboveground biomass (Ryals
70   et al. 2016) and on crop yield (Luo et al. 2018; Ahmad et al. 2009, Hirte et al. 2021), but fewer focused
71   on roots and on non-cultivated grasslands. Garbowski et al. (2020) observed that soil amendments
72   can have an effect only on aboveground biomass or only on belowground biomass, which may be
73   expected since roots and shoots respond differently to changes in nutrient (Hayes et al. 2017) and
74   water availability (Wilcox et al. 2017; Guasconi et al. 2023). Furthermore, soil and plant communities
75   can show great variability in response to both drought (Guasconi et al. 2023; Canarini et al. 2017)
76   and soil amendments (Gebhardt et al. 2017). This variability derives partly from the variable physical
77   properties of soil, but can also depend on land use history or on small- and large-scale topography
78   (Wang et al. 2020). This may partly explain why results from field vs. lab experiments can differ
79   considerably (Canarini et al. 2017), and highlights the need for more field-based data collections—in
80   particular under experimental conditions that combine soil amendments and drought.

81   Here, we present the results of a field experiment designed to assess the effects of a soil amendment
82   and of reduced precipitation on both soil and vegetation C pools, where we observed changes at
83   various soil depths, in two grasslands, and at two catenary positions. Because the effects of already
84   partly decomposed organic amendments can be expected to be longer-lasting than those of easily
85   decomposable ones (Sarker et al. 2022), we applied a one-time compost treatment coupled to a yearly
86   growing season drought and investigated their effect on the soil C stocks after three full growing

87   seasons. We measured soil organic C contents (mass of C per unit mass of soil) and soil C stocks

88   (calculated as C content × bulk density × layer thickness) at different depths within the soil profile,

89   and vegetation biomass (encompassing both root biomass and aboveground biomass, including plant

90   litter). We tested the hypotheses that:

91   1) compost amendment increases soil C content and plant growth (both having positive effects on C

92   stocks), while decreasing soil bulk density (having a negative effect on C stocks); we expect that these

93   mechanisms have counteracting effects on net soil C storage;

94   2) by decreasing both productivity (organic C input) and respiration (microbial decomposition of

95   SOM), drought will have a weak or non-detectable effect on SOC;

96   3) compost amendment mitigates the loss of soil moisture under drought which may alleviate loss of

97   plant growth under drought.

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

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

100   2022; Guo et al. 2018), the analyses include testing for differences in the control plots between the

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

102   position, which we expect might lead to variations in all C pools.

103

Methods

Site description and experimental setup

106   The experimental site was established in summer 2019 in the proximity of Tovetorp Research Station

107   south of Stockholm, Sweden, and consists of two former arable fields (hereafter called "Tovetorp"

108   and "Ämtvik"), each with an upper and a lower catenary position. Today the fields are managed for

109   grazing and haymaking. In each of these four locations, four treatments (compost, drought, drought-

110   compost, control) were applied in three replicates, resulting in 12 plots per location and 48 plots in

111   total. Each plot measured 2x2 m. Soil in all locations is rich in clay and ranges from silty clay to silty

112   loam. The compost was made of *Zea mays* with a C:N ratio of 9.8 and $\delta^{13}C$ value of about -15.39‰

113   and was applied in mid-February 2020 as a thin surface layer of ca. 11 kg per m^2 (wet weight), similar

114   to the procedure described in Ryals and Silver (2013). The total amount of C added is estimated to be

115   ~0.54 kg C m^{-2}. The $\delta^{13}C$ isotope ratio of the compost is higher than that of bulk soil, which means

116   that the $\delta^{13}C$ isotope ratios of different treatments can be used to assess if and where in the soil the

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117   compost material is retained after the three years of treatment. The drought treatment followed the
118   guidelines of the Drought-Net Research Coordination Network (Knapp et al. 2017; Yahdjian and
119   Sala, 2002), and consisted of 12 rainout shelters (3 per location) with roofs made out of evenly-placed
120   v-shaped polycarbonate strips designed to exclude 60% of the precipitation during the entire growing
121   season (in place from beginning of July to end of October in 2019, and from beginning of April to
122   end of October in 2020, 2021 and 2022). This precipitation reduction corresponds to the 1st quantile
123   of the local 100-year precipitation record (Swedish Meteorological and Hydrological Institute, 2021).
124   Each shelter covered two plots, one for the drought treatment and one for the combined drought-
125   compost treatment. A rubber sheet, approximately 40 cm in depth, was inserted in the soil around
126   each shelter to isolate the study plots from the ambient soil moisture. Pictures and sketches of the
127   sites and of the experimental design are presented in Roth et al. (2023).

128   **Soil and vegetation sampling and analyses**
129   Soil and root samples were collected in all plots at the end of the first growing season in 2019 (August-
130   September), and again at the end of the experiment in 2022 (August and October). Samples for soil
131   bulk density were collected to a depth of 45 cm with a large fixed volume root auger with a sharpened
132   cutting edge (8 cm diameter; Eijkelkamp, The Netherlands). The cores were taken incrementally
133   every 15 cm and then divided in 5 cm segments, and the bulk density was determined after drying the
134   samples at 105 °C. After drying, a subsample from the same core was used to calculate the soil organic
135   matter (SOM) content through loss on ignition at 550 °C. A subset was further burned at 960 °C in
136   order to determine the presence of inorganic C, which was very low (0.5 %), indicating that the total
137   C can be considered equal to organic C (OC). Samples for total C and N and δ^{13}C were taken to a
138   depth of 1 m with a Pürckhauer soil corer (2.5 cm diameter; Eijkelkamp, The Netherlands). The
139   analyses for total C and N and δ^{13}C were carried out by the Stable Isotope Facility at UC Davis
140   (California). A subset of these samples was sent to a commercial lab and used for pH measurements
141   (Mantech Automax 73, Guelph, ON., Canada) and nutrient content analyses (P, Ca, Mg and K; Avio
142   500 ICP Optical Emission Spectrometer, Perkin Elmer, Waltham, MA; USA). Soil moisture was
143   measured every three weeks throughout the growing season (2019 through 2022) from one access
144   tube (1 m long) permanently installed in each plot, using a PR2 profile probe (Delta-T Devices Ltd,
145   Cambridge, UK). The values used in the analyses are growing season averages of volumetric soil
146   water content (%) in the first 30 cm in each plot. Root biomass was collected in September 2019 and

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147   in August 2022 with one soil core sampled with a root auger (8 cm diameter; Eijkelkamp, The

148   Netherlands) to a depth of 30 cm in all plots and to a depth of 45 cm in a subsample of 16 plots, with

149   soil cores divided into 5 cm segments. The roots were rinsed with water on a 0.5 mm mesh sieve to

150   remove soil and then scanned, followed by drying at 60 °C for 48 h to obtain the dry weight. The

151   scanned images were analyzed with WinRhizo (Regent Instruments, Québec, CA) to obtain root

152   volume, length and diameter, used to calculate root mass density (g_{roots} cm^{-3}_{soil}), specific root length

153   (cm g^{-1}_{roots}) and root tissue density (g_{roots} cm^{-3}_{roots}). Aboveground biomass was harvested from one

154   quarter (1 m^2) of each plot every year in mid-July, by cutting at ground level (including moss and

155   dead biomass). More details of the sampling design are presented in the Supplements (Table T1).

Statistical analyses

157   Total C content (as % of total soil mass) and soil C stocks normalized by soil sample thickness (kg/m^3)

158   were calculated for all 48 plots using the total C content data (available for a subset of the samples)

159   and the bulk density and SOM data (available for a complementary subset of the samples). A

160   regression was performed to calculate SOC from SOM data and thus obtain a complete dataset,

161    $$SOC = 0.328 \times SOM + 0.217,$$ (1)

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

163   The fraction F of compost-derived C remaining in the soil in year 2022 was calculated with a two

164   end-member mixing model, as in Poeplau et al. (2023),

165    $$F = \frac{\delta^{13}C_{compost\ treatment} - \delta^{13}C_{control}}{\delta^{13}C_{compost} - \delta^{13}C_{control}},$$ (2)

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

167   compost or drought-no compost) plots.

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

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

170   of the microbiological activity, and no effect of treatments could be detected below this range (data

171   not shown).

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

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

174   made with lsmeans (package: emmeans) and p-values were obtained with the ANOVA function and

175 the lmerTest package. Residuals from the models were checked graphically. Effect sizes were

176 obtained by calculating Cohen's d, with the formula

177 $d = \frac{\overline{x_1} - \overline{x_2}}{s},$ (3)

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

179 the standard deviation.

180 The effect of the treatments was tested on all plots from the 2022 dataset, including root biomass and

181 root traits, for which the values were log-transformed first. The model included compost (categorical

182 variable), drought (categorical variable) and sampling depth (continuous variable) as fixed factors

183 and plot (nested within site) as random factor. Cohen's d was calculated using the standard deviation

184 of the control group. The effect of the compost amendment on the C isotopic ratio was tested with a

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

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

187 variable, to assess if changes occurred at specific depths. The landscape variability was tested on all

188 data collected in 2019 and from the control plots in 2022. The model included grassland site, catenary

189 position and sampling depth (continuous variable) as fixed factors and year and plot as random

190 factors. Cohen's d was calculated using the standard deviation pooled from all groups. Temporal

191 changes during the experiment not caused by the treatments were tested using data obtained in 2019

192 and 2022 from the control plots. The model included year and sampling depth (continuous variable)

193 as fixed factors and plot (nested within site) as random factor. Cohen's d was calculated using the

194 standard deviation of the 2019 dataset. The variable depth was not included in the models for

195 aboveground biomass.

196

197 ## Results

198 Drought decreased soil moisture by 16% in the upper 0-30 cm. The effect of drought was consistent

199 over sites, years and seasons, and there were no statistically significant differences in the drought-

200 driven soil moisture loss between locations, years, or between spring, summer or growing season.

201 There was also no significant difference in soil moisture decrease between drought plots and drought-

202 compost plots. Additionally, the compost addition did not have any significant effect on soil pH or

203 on soil P, Ca, Mg and K. The compost addition did, however, raise the value of $\delta^{13}C$ in the treated

204 plots (mean control plots = -27.44‰, mean compost plots = -27.10‰, P < 0.01), and the difference

205   was significant at 0-5 cm, 30-35 cm and 40-45 cm. The mixing model (Eq. 2) indicated that after

206   three growing seasons, the percentage of compost-derived C was 3.43 % in the 0-5 cm layer, 4.88 %

207   in the 30-35 cm layer and 5.51 % in the 40-45 cm layer in the compost plots, and 4.55 % in the 0-5

208   cm layer, 6.52 % in the 30-35 cm layer and 2.96 % in the 40-45 cm layer of the compost x drought

209   plots.

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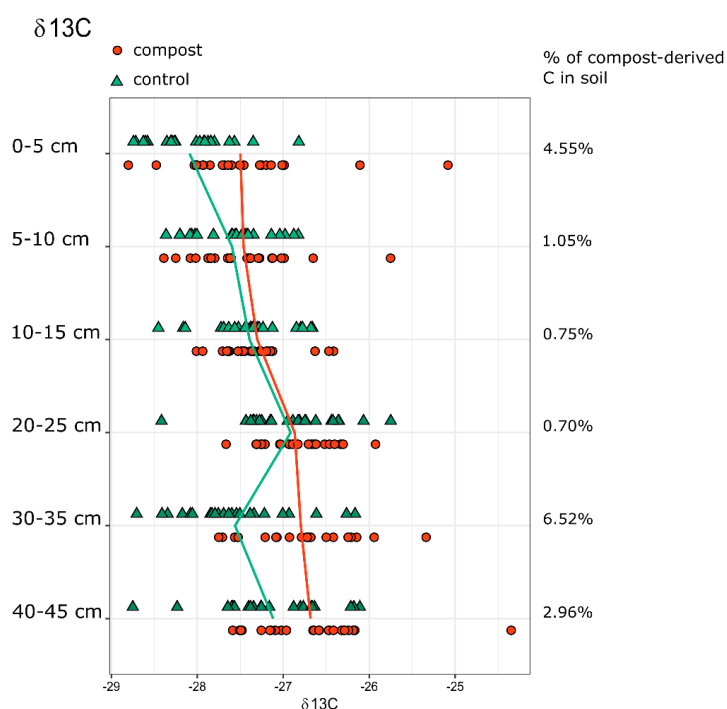
Fig 1. Values of δ^{13}C in the soil in compost-treated (red dots) and untreated (control, green triangles) plots in 2022, at
different depths. The % of compost-derived C in the soil was calculated with a mixing model (Eq. 2).

Compost and drought effects

214   The compost treatment increased total soil C content (P = 0.04) and aboveground biomass (P < 0.01).

215   The latter increased by 23% (mean control plots = 642 g m^2 ± 129.23, mean compost plots = 788 g

216   m^2 ± 221.7). The effect on soil C was significant only in the topsoil (0-5 cm, Fig. 2), where the relative

217   increase of soil C content was 18% (mean control plots C content = 2.99% ± 1.03, mean compost

218   plots = 3.53% ± 0.75). Soil nitrogen (N) was higher in the topsoil in the compost-treated plots (mean

219   control plots = 0.24% ± 0.06, mean compost plots = 0.28% ± 0.06), but the treatment did not affect

220   the C:N ratio. The compost treatment also decreased bulk density by 9% (P = 0.03) in the first 10 cm

221   of soil (mean control plots = 1.34 g cm^3 ± 0.18, mean compost plots = 1.22 g cm^3 ± 0.17). The compost

222   did not have any statistically significant effect on other variables.

223   Drought only had an effect on aboveground biomass, which decreased by almost 4% under the rainout

224   shelters (mean control plots = 642 g m^2 ± 129.23, mean drought plots = 617 g m^2 ± 180.25). The

225   increase in the soil C content under compost addition was offset by the lower bulk density, so that

226   there was no statistically significant change to soil C stocks. However, we note that mean soil C

227   stocks were 6% higher in the compost-treated plots in the first 15 cm, slightly higher than the

228   percentage of compost-derived C found in that layer (mean control plots = 4.02 kg m^2 ± 0.92, mean

229   compost plots = 4.26 kg m^2 ± 0.59).

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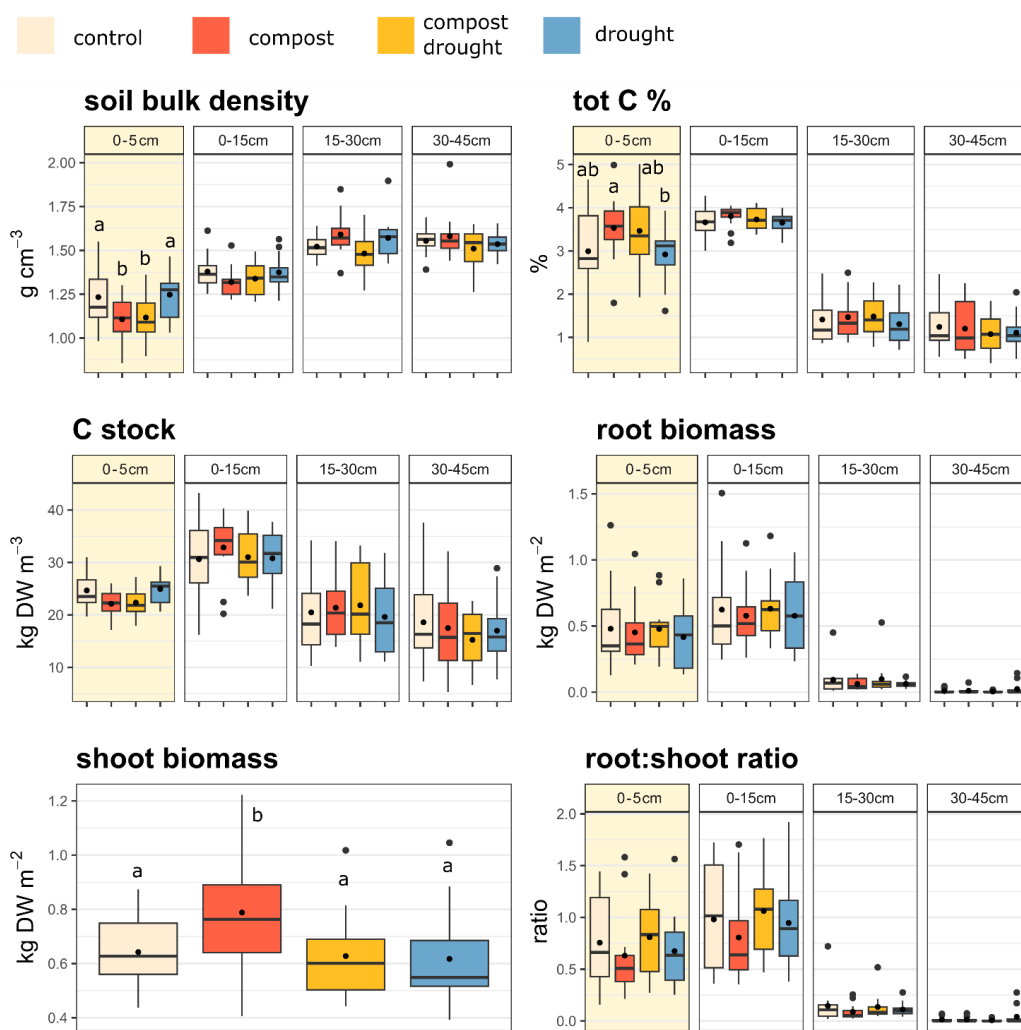
Fig. 2. Values of soil bulk density, total soil C contents, soil C stocks, root biomass, shoot biomass and root-shoot ratio, at different sampling depths in 2022. White = control, red = compost, yellow = compost×drought, blue = drought. Bars show mean (dot inside the bar), median (horizontal line) and interquantile range (IQR, colored bar); whiskers extend to 1.5×IQR; dots in the graph are outliers. Different letters indicate statistically significant differences between means (P < 0.05).

Root traits

Drought led to 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 topsoil (0-5 cm) were considered,

240   in addition to the patterns above, specific root length of coarse roots decreased under drought (P =
241   0.04), while root tissue density (P = 0.02) and specific root length of all roots increased after compost
242   addition (P = 0.01).

243

244   In all control plots, soil C and root biomass was correlated both in the topsoil (5-10 cm, r = 0.42, P =
245   0.04; 10-15 cm, r = 0.5, P = 0.01) and in the 0-30 cm layer (0-30 cm, r = 0.63, P < 0.01). Soil C
246   content was also correlated to the root:shoot ratio (5-10 cm, r = 0.44, P = 0.03; 10-15 cm, r = 0.4, P
247   = 0.052; 0-30 cm, r = 0.43, P = 0.04). In the compost treated plots, the only significant correlation
248   was between soil C and root biomass when considering the whole 0-30 cm layer (0-30 cm, r = 0.55,
249   P < 0.01). The correlation between soil C and aboveground biomass remained constant in both control
250   and compost-treated plots (r = 0.22, P < 0.01 in both groups). This indicates that the compost
251   treatments affected soil C in the topsoil and aboveground biomass more than they affected roots and
252   deeper soil.

253

254   **Landscape spatial variability**
255   Soil C contents, total C stocks, bulk density, root biomass and root:shoot ratio all showed statistically
256   significant (P < 0.05) differences between catenary positions and depths, and soil C content and bulk
257   density also differed significantly between grasslands (Fig. 3, Table T3). Grassland identity and the
258   interaction between grasslands and catenary positions were the only significant predictors of
259   aboveground biomass, suggesting this variable is most likely related to land-use history and plant
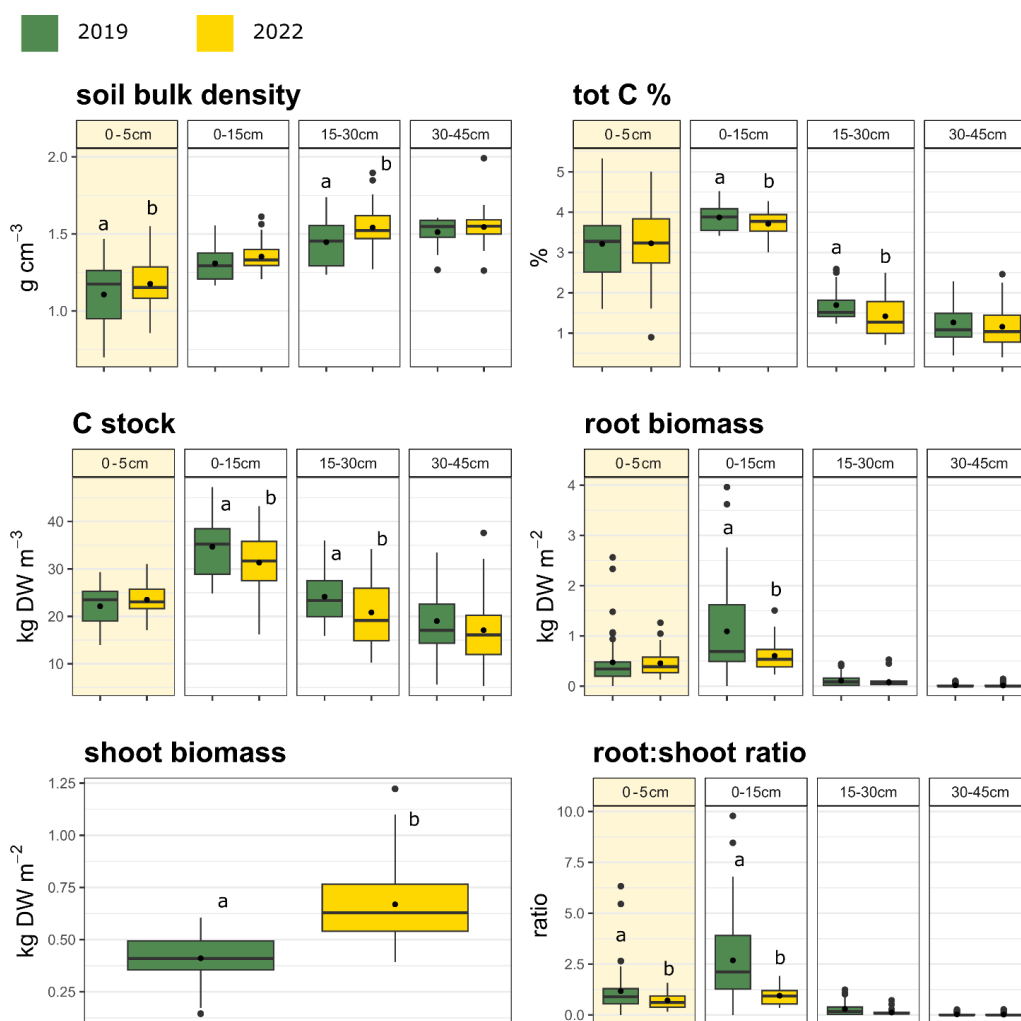260   community composition.

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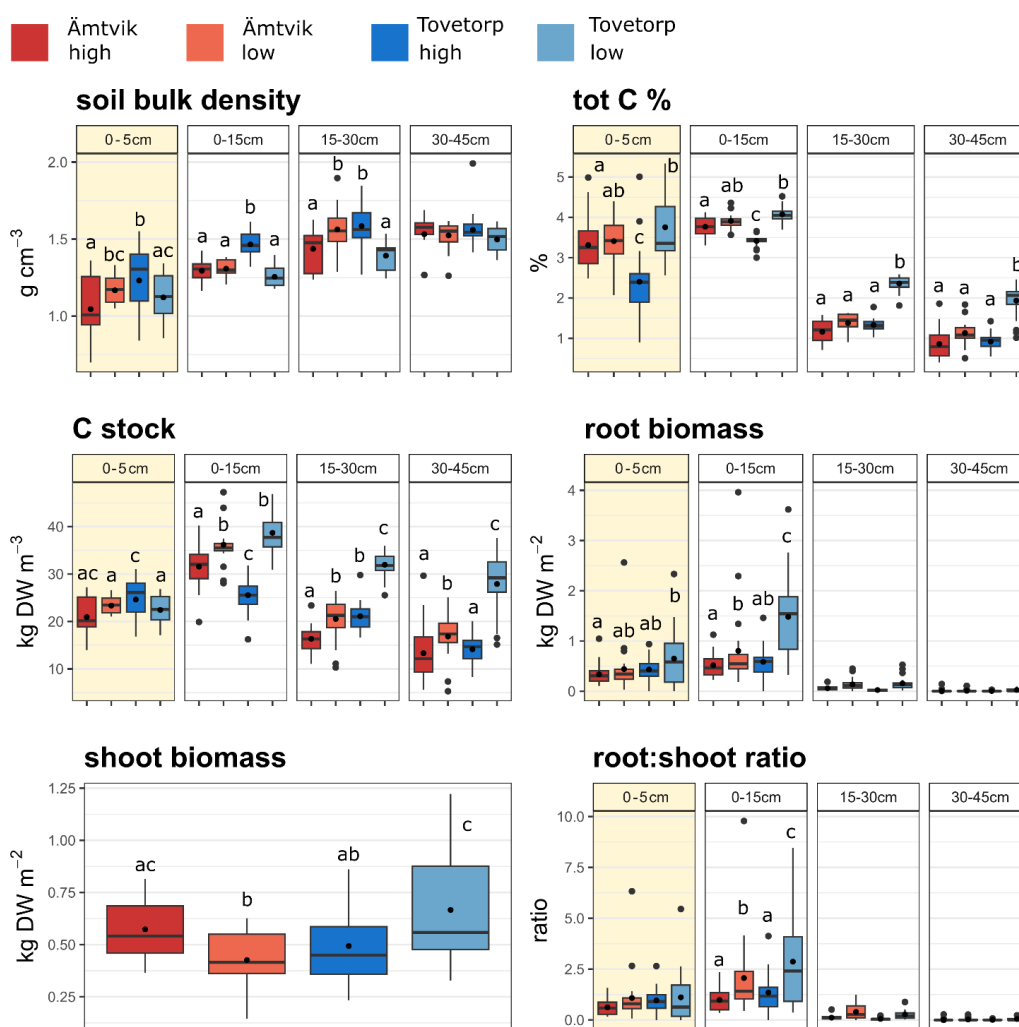
Fig. 3. *Values of soil bulk density, total soil C content, soil C stocks, root biomass, shoot biomass and root-shoot ratio, at different sampling depths at the four sites, excluding treatments. The data consists of average values from 2019 (all plots) and 2022 (only control plots). Red = Ämtvik High, orange = Ämtvik Low, blue = Tovetorp High, light blue = Tovetorp Low. Bars show mean (dot inside the bar), median (horizontal line) and interquantile range (IQR, colored bar); whiskers extend to 1.5×IQR; dots in the graph are outliers. Different letters indicate statistically significant differences between means (P < 0.05).*

269 **Natural changes during the 2019-2022 period**

270　From 2019 to 2022, we observed large changes in soil C and plant biomass in the control plots. Soil

271　C contents, total C stocks, bulk density, root biomass and root:shoot ratio all showed statistically

272　significant ($P < 0.05$) differences between 2019 and 2022 and between depths (Fig. 4, Table T4).

273　Aboveground biomass also differed significantly between sampling years. Between 2019 and 2022

274　total soil C contents and root biomass in the control plots decreased by 10.7% (from 3.35% ± 1.05 to

275　2.99% ± 1.03) and 8.4% (from 522.96 g m^{-2} ± 626.48 to 479.25 g m^{-2} ± 320.75), respectively, in the

276　first 5 cm, and by 27.1% (from 2.77% ± 0.78 to 2.02% ± 0.61) and 67.4% (from 477.26 g m^{-2} ±

277　252.49 to 155.81 g m^{-2} ± 51.62), respectively, in the first 15 cm. Aboveground biomass instead

278　increased by 53% (from 419.68 g m^{-2} ± 137.45 to 642.23 g m^{-2} ± 129.23).

Fig. 4. Values of soil bulk density, total soil C contents, soil C stocks, root biomass, shoot biomass and root-shoot ratio, at different sampling depths in 2019 and 2022 (excluding treatment plots). Values are means for all plots. Green = 2019, yellow = 2022. Bars show mean (dot inside the bar), median (horizontal line) and interquantile range (IQR, colored bar); whiskers extend to 1.5×IQR; dots in the graph are outliers. Different letters indicate statistically significant differences between means (P < 0.05).

285 Table 1. Effect sizes (Cohen's d) of the differences between sites, years and treatments for each soil

286 depth. Effect sizes can be regarded as small (absolute value <0.2, black), medium (0.2-0.8, orange)

287 or large (> 0.8, red).

depth	factor	Tot C	C stock	Bulk density	Root biomass	Aboveground biomass
0–5 cm	grassland	0.21	0.10	-0.40	-0.32	
0–15 cm	grassland	0.64	0.58	-0.36	-0.24	-0.17
15–30 cm	grassland	-0.67	-0.89	-0.01	1.00	
30–45 cm	grassland	-0.53	-0.51	0.53	0.28	
0–5 cm	catenary position	-1.03	-1.12	-0.06	-0.44	
0–15 cm	catenary position	-0.61	-0.47	1.09	-0.86	0.14
15–30 cm	catenary position	-0.48	-0.46	-0.68	-0.64	
30–45 cm	catenary position	-0.96	-0.99	0.62	0.27	
0–5 cm	year	0.34	-0.08	-0.81	0.07	
0–15 cm	year	0.96	1.25	0.06	1.27	-1.62
15–30 cm	year	0.21	0.23	-0.19	0.49	
30–45 cm	year	0.30	0.13	-1.41	0.87	
0–5 cm	compost	0.52	0.26	-0.79	-0.08	
0–15 cm	compost	-0.02	0.26	0.40	0.14	1.13
15–30 cm	compost	-0.13	-0.18	0.50	-0.33	
30–45 cm	compost	-0.49	-0.33	1.25	1.82	
0–5 cm	drought	-0.07	0.01	0.09	-0.20	
0–15 cm	drought	-0.29	-0.22	-0.12	0.95	-0.19
15–30 cm	drought	-0.33	0.09	0.93	-0.49	
30–45 cm	drought	-0.39	-0.63	-1.03	0.24	

288

Discussion

289

Compost effects on soil C and plant growth

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291 Total soil C contents increased after compost application, but because bulk density was also reduced,

292 there was no significant increase in soil C stocks (confirming our first hypothesis), despite higher

293   mean values of soil C per m^2 in the compost treated plots in the first 15 cm of soil. This difference

294   was lower than the estimated C addition (~0.54 kg C m^{-2}), likely due to respiration loss. Compost can

295   be considered a recalcitrant type of organic amendment, with initially slow but persistent effects

296   expected to be observed years after the first application (Sarker et al. 2022). Therefore, it is unlikely

297   that an effect of the treatment on soil properties and soil C had occurred before our 2022 sampling,

298   and that such an effect was somewhat transient and undetectable at the time of the sampling. This

299   conclusion is also supported by the isotope tracing, indicating that at least a fraction of the compost-

300   derived C is still present in the soil after three growing seasons. In addition, the significant increase

301   in aboveground biomass three years after the compost application indicate the persistence of favorable

302   plant growing conditions, such as increased N in the soil. These results are in accordance with Fenster

303   et al. (2023), who found that the benefits of compost treatments on the ecosystem C balance of

304   grasslands one year after application were manifested as extended growing season, and thus

305   potentially higher plant productivity, rather than as an increase in net soil C. This also stresses the

306   importance of including vegetation dynamics when assessing the effectiveness of C management.

307   Compost enhanced aboveground biomass growth, but not root growth, thereby only partly confirming

308   our first hypothesis, and suggesting the presence of a tradeoff between root and shoot investment.

309   This was already observed in Garbowski et al. (2020) and is in line with the expectation that plants

310   in nutrient-rich environments can allocate to aboveground tissue growth the resources that would

311   otherwise be allocated to nutrient acquisition belowground (Bloom et al. 1985; Poorter and Nagel

312   2000). In broader terms, this suggests that the compost treatment shifted the C balance between soil

313   pool and vegetation pool, and moved the plant C allocation from belowground- to aboveground

314   organs. Nevertheless, increased root tissue density and specific root length in the topsoil suggest that

315   root response to organic amendments is manifested in more subtle changes in root traits, rather than

316   in net root biomass production.

317

318   Our experimental setup did not allow us to test whether microbial activity and microbial biomass

319   increased as a result of compost addition, as was reported by previous studies (Sarker et al. 2022;

320   Gravuer et al. 2019). However, the limited effects of the compost treatment on soil C stocks suggest

321   that the C sequestration benefits in the form of increased plant growth might have been offset by

322   increased microbial respiration (promoted by either compost or enhanced rhizodeposition of more

323   productive plants). Finally, the significant spatial and temporal variability in both soil C and

324   vegetation biomass observed in the control dataset suggests that treatment effects might be site-

325   specific (Garbowsi et al. 2020), and management plans seeking to optimize soil C sequestration

326   should consider the potentially interactive effects of several biotic and abiotic factors. For instance,

327   the increase in aboveground plant biomass after compost application was mostly driven by the grass-

328   rich plots in the Tovetorp grassland (Roth, 2023), suggesting that plant community composition might

329   be important in determining the effects of soil amendments on grasslands.

Drought effects on soil moisture, soil C and plant growth

331   Drought treatments reduced soil moisture and aboveground plant biomass but did not significantly

332   decrease root biomass (Table T2), indicating a tradeoff between above- and belowground biomass

333   investment. Because plant growth is very sensitive to yearly fluctuations and even intra-annual

334   distribution of precipitation (Knapp and Smith 2001, Porporato et al. 2006), and because our analyses

335   are based on only two temporal datapoints (2019 and 2022), it is difficult to assess whether drought

336   reduced plant turnover, defined as the ratio of standing biomass to net primary productivity (NPP).

337   We note that while the precipitation in the growing seasons 2019 and 2022 (April through August)

338   was roughly the same (157 mm and 156 mm, respectively), the 2019 sampling followed an extremely

339   dry summer in 2018, when the study area received only 77 mm of precipitation, about half of the

340   precipitation compared to the average 1961-1990 (historical data from SMHI, 2021). Conversely, the

341   2022 sampling followed the very wet 2021, when the area received almost 140% of the normal

342   precipitation over the same time period (250 mm). It is possible that a legacy effect of these two

343   precipitation extremes may have affected plant growth, particularly aboveground (Fig. 4), where

344   growth is more sensitive than root biomass to yearly fluctuations in water availability (Zhang et al.

345   2021). Legacy effects of the 2018 drought could have hampered growth in 2019, as aboveground

346   vegetation in the control plots increased by more than 50% between 2019 and 2022. Conversely, the

347   high summer precipitation in 2021 could have buffered the effects of the experimental drought in

348   2022, leading to overall weak drought effects.

349   The drought treatment had a relatively small impact on plant biomass (Fig. 2). In addition to potential

350   effects of interannual precipitation variation, this may be due to adaptation in the plant community

351   during the treatment years (Basu et al. 2016), or that the drought was not intense enough. Roots in

352 particular where not significantly affected by drought (Fig. 2), but while we monitored the relative

353 proportions of annuals and perennials, grasses and forbs in each plot, we do not know which plant

354 species the sampled roots belong to. Therefore, we cannot make any conclusions related to the

355 ecology of these plant groups, all of which can be expected to respond differently to drought (Zhang

356 et al. 2017; Mackie et al. 2019; Zhong et al. 2019). However, since the magnitude of the drought did

357 not differ between locations and since soil physical properties were similar across sites, we can

358 hypothesize that differences in the plant communities account for at least some of the spatial

359 heterogeneity observed in our study, as was observed in Garbowski et al. (2020). Also, while drought

360 effects on root biomass were marginal, the drought treatment did increase both root tissue density and

361 average root diameter, suggesting adaptation of root traits in these plant communities.

362 Adopting a standardized approach for the drought experimental design makes our findings easier to

363 compare with others, but partial rainout shelters will still allow for a substantial amount of

364 precipitation to pass through the roof sheets. If there is enough precipitation, even the small

365 percentage of rain that reaches the ground might bring the soil moisture over the threshold of the

366 permanent wilting point. It is also possible that soil water retained in the soil from snowmelt or

367 winter/spring precipitation could have sustained vegetation growth in the drought treatments. Finally,

368 experimental droughts do not control for reduced air humidity, which may underestimate negative

369 responses of plant biomass to drought in field experiments (Kröel-Dulay et al. 2022), and for

370 increased temperatures, which often occur in combination with natural droughts. Drier and warmer

371 air increases evaporative demand, causing stomatal closure and thus lower productivity for a given

372 soil moisture level (Zhang et al. 2019).

373 To understand the ecosystem-level implications of drought, soil C changes need to be considered as

374 well. Dry conditions decrease heterotrophic respiration because microbial activity is inhibited due to

375 both physiological mechanisms, such as osmoregulation diverting efforts from resource acquisition

376 to survival, and physical mechanisms, like the slower transport of substrates in dry soils (as the water

377 films around soil particles shrink and pore connectivity is lost) (Moyano et al. 2013; Schimel 2018).

378 However, heterotrophic respiration increases again after soil rewetting, leading to disproportionally

379 large C emissions during the short post-rewetting period (Canarini et al. 2017; Barnard et al. 2020).

380 In our experiment, drought had no effects on soil C contents and stocks, as per our second hypothesis,

381   but it slightly reduced soil bulk density (in a pre-treatment vs post-treatment comparison, data not

382   shown), possibly in relation to shrinkage in dry soil. Because drought reduced plant productivity (and

383   thus C inputs to soil), the lack of drought effect on soil C stocks can be explained by a reduction of

384   microbial activity approximately of the same magnitude as the reduction in plant productivity. This

385   is supported by the fact that in the topsoil, the drought plots with added compost had a higher fraction

386   of compost-labelled isotopes compared to the non-drought plots. Therefore, any soil C emission

387   pulses at rewetting were not sufficient to compensate for the lowered microbial activity during the

388   soil moisture dry-downs.

389   **Interactive effects of compost and drought**

390   The effects of soil amendments on water retention capacity are modulated by soil texture, by the

391   quantity and quality of soil organic matter (Rawls et al. 2003; Yang et al. 2014; Franco-Andreu et al.

392   2017; Sarker et al. 2022) and by the chemical composition of the compost (Franco-Andreu et al.

393   2017). In our study, soil moisture did not differ between the drought plots and the ones with drought

394   and compost, which indicates that the soil amendment did not increase soil moisture, in contrast with

395   previous findings (Franco-Andreu et al. 2017; Ali et al. 2017), and leads us to reject our third

396   hypothesis. Interestingly however, while both compost and drought slightly reduced root biomass,

397   the compost applied on the drought plots led to an increase in root:shoot ratio (Fig. 4). While plants

398   may reduce their belowground biomass investment when adding organic matter, this mechanism

399   appears to work differently under drought, and the observed shift in C allocation belowground may

400   serve to aid in water acquisition. This, in turn, could lead to increased evapotranspiration, and this

401   improved capacity for soil water absorption could mask any increase in soil water retention capacity

402   in the compost x drought plots. However, since our experiment did not include drought recovery, it

403   is not known if this change would persist after the end of the experimental drought.

Conclusions

405   The goal of this study was to provide an overview of the changes in soil, above- and belowground

406   vegetation C content and biomass within a grassland ecosystem, through a multifactorial drought and

407   compost amendment field trial. The compost treatment revealed contrasting responses of shoots and

408   roots, but it did ultimately not result in an increase in soil C stocks. Drought decreased aboveground

409   biomass, but root response was limited to shifts in root traits. Compost amendment and drought had

410 distinct effects on plant C allocation, revealing the presence of trade-offs in their responses to
411 environmental change. These findings improve our understanding of C dynamics in grasslands,
412 offering potential contributions to ecosystem C modelling. We also observed significant spatial and
413 temporal variability in vegetation and soil C dynamics over the study period, which may be driven
414 by differences in topography, land use and plant community composition. This suggests that
415 ecosystem C dynamics can be influenced by multiple biotic and abiotic factors, which can be revealed
416 by field observations and multifactorial experiments.

Author contributions

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

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