Experimental drought and soil amendments affect grassland
 above- and belowground vegetation but not soil carbon stocks
 Spatial and temporal variability in soil and vegetation carbon
 dynamics under experimental drought and soil amendments

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9 Abstract

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10 Soils are the largest terrestrial carbon (C) pool on the planet, and targeted grassland management has the potential to increase grassland C sequestrationand grassland soils have a particularly large C 11 12 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 13 improving soil moisture retention water retention and infiltration. However, soil carbon dynamics are 14 15 closely tied to vegetation responses to management and climate changes, affecting both-roots and shoots differently. However, soil C dynamics are deeply linked to vegetation response to changes in 16 both management and climate, which may also be manifested differently in roots and shoots. This 17 18 study presents findings from a three-year field experiment on two Swedish grasslands that assessed the impact of a-compost amendment and of-reduced precipitation on plant biomass and on soil C at 19 various soil depthssoil and vegetation C pools. Aboveground biomass and soil C content (% C) 20 21 increased compared to controls in compost-amended plotsCompost addition increased aboveground 22 biomass and soil C content (%C), but because bulk density decreased, there was no significant effect 23 on soil C stocks. Experimental drought did not significantly reduce plant biomass compared to control 24 plots, but stunted the increase in aboveground biomass in compost-treated plots and led to changes in 25 root traits. 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 26 27 belowground organs. We also observed significant spatial and temporal variability in vegetation 28 biomass and soil C over the study period. These results highlight the complexity of ecosystem C

29 dynamics and the importance of considering the need to consider multiple biotic and abiotic factors

30 driving ecosystem C dynamics across spatial scales when developing land management strategies to

31 <u>enhance C sequestration</u> when upscaling results from field trials.

32 Introduction

33 Management of soil health and soil carbon (C) stocks Soil management has been receiving increasing 34 attention in the past years, with growing awareness that soils provide vital ecosystem services and 35 can act as C sinks (Minasny et al. 2017, European Commission, Directorate-General for Health and 36 Food Safety, 2020). The soil-plant system is integral to this process, as plants capture atmospheric 37 carbon dioxide through photosynthesis and transfer it to the soil via roots and organic matter. 38 Concerns about soil erosion and historic soil C depletion in agricultural and grassland soils 39 (Sanderman et al. 2017, Bai and Cotrufo, 2022) have motivated the development of sustainable land 40 management strategies, sometimes generally named "carbon farming" (Paul et al. 2023) and 41 promoted by the "4 per 1000" initiative (Minasny et al. 2017). These approaches include mitigating soil organic carbon (SOC) loss in specific sites resulting from agricultural activities such as tilling, 42 43 which can be achieved with One such strategy is the use of soil C amendments (Ryals and Silver 2013; 44 Rvals et al. 2015; Keesstra et al. 2016; Fischer et al. 2019; Garbowski et al. 2023), including like 45 compost, biochar, and various types of manure on croplands or grasslands (Ryals and Silver 2013; 46 Ryals et al. 2015; Keesstra et al. 2016; Fischer et al. 2019; Garbowski et al. 2023)- These treatments 47 can be applied on croplands or rangelands, in single or multiple applications, and can increase soil 48 aggregation (Sarker et al. 2022) Soil C management via compost -amendments aims at transferring 49 plant derived organic matter to facilitate C accumulation of plant-derived C in the soil C pool-in 50 specific locations, where it can be retained over long time scales – i.e. decades to centuries (Shi et al. 51 2020). If the total C inputs and accumulation in the soil exceed the total losses, C amendments can lead to C sequestration (Don et al. 2024, Moinet et al. 2023). - and mitigate soil organic carbon (SOC) 52 53 loss resulting from human activities such as tilling. In some cases, C amendments have even been proposed as means to actively sequester C in soils, with initiatives like the "4 per 1000" (Minasny et 54 al. 2017) have been promoting their implementation as a climate change mitigation strategy. 55 Consequently, soil C management methods aim to shift the ecosystem C balance by facilitating the 56 57 movement of C from the atmosphere into vegetation and subsequently, into the soil C pool, where it

58 can be retained over long time scales.

Since SOC accrual and C sequestration potential are uncertain and context dependent (Moinet et al. 59 2023), it is important to investigate the effects of C amendments across a range of climatic and 60 management conditions. Grasslands and croplands converted to grasslands can store considerable 61 62 amounts of soil C and are therefore ideal systems to apply C amendments. They can act as C sinks if managed appropriately (Conant et al. 2001), and can have higher root biomass C compared to 63 64 agricultural lands, usually cultivated with annual crops (Beniston et al. 2014). ManySeveral studies 65 have investigated the effects of organic amendments on aboveground biomass (Ryals et al. 2016), on crop yields (Luo et al. 2018; Ahmad et al. 2009), and ofn roots in farming systems (Hirte et al. 2021), 66 67 but fewer focus on non-cultivated grasslands. -i C amendments add C to the soil in two ways: directly, by moving plant biomass from one location to 68 another, and indirectly, by promoting plant growth (Ryals et al. 2016). Compost is rich in organic 69 70 matter, which serves as a substrate food source for soil microorganisms. As microbes decompose this 71 organic matter, they release nutrients in forms that plants can readily absorb (Malik et al. 2013). In 72 turn, the increased vegetation growth can increase the natural rate of C input and thus potentially SOC 73 stocks (Ryals et al. 2013). Indeed, and-model predictions suggest that compost additions on grasslands 74 can lead to soil C sequestration (DeLonge et al. 2013). By improving soil structure and reducing 75 compaction, compost additions may also reduce soil bulk density. As SOC stocks are calculated by 76 multiplying C concentration by the bulk density, improved management may also lead to net zero

79 ecosystems natural ability to sequester C via indirect effects. If C amendments promote plant growth, 80 they also increase the natural rate of C input to the soil and thus potentially SOC stocks if the 81 additional C input is stabilized and does not promote mineralization of native SOC. Considering these 82 indirect effects requires an ecosystem-level perspective on the potential C soil C sociec - sequestration 83 potential of potential in soils that accounts for both below- and above-ground vegetation contributions 84 to soil C stocks, as well as the soil depth at which management effects are detectable. To this end, the 85 use of isotope-labelled compost can improve our understanding of soil C dynamics.

effects on C stock despite increased soil C contentsAdding C to soils in the form of amendments

directly increases the standing stock of SOC, but C amendments may also act as a primer to an

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<u>Land management practices—including Ccompost amendments—can significantly impact both</u>
 <u>above- and belowground plant biomass, which contribute differently to SOC storage.</u> Root biomass;

88 belowground plant organs - and root exudates are an integral part of soil C formation and retention 89 (Jackson et al., 2017). In fact, roots are more recalcitrant to decomposition compared to shoots (Rasse 90 et al. 2005, Gaudinski et al. 2000), and play a central role in C sequestration efforts. However, 91 aboveground plant biomass should also be included in these assessments to identify potential tradeoffs in above- vs.and belowground C allocation within the vegetation pool, and to determine whether 92 93 there are changes in plant biomass vegetation C pools which may affect the soil C pool (Hayes et al. 94 2017). It is especially important to determine the proportion of plant litter that contributes to soil 95 organic matter (SOM) formation and stabilization (Cotrufo et al. 2015). Above- and belowground 96 biomass may also respond differently to soil amendments (Garbowski et al. 2020). This variation is 97 expected, as roots and shoots respond differently to changes in nutrient (Hayes et al. 2017) and water 98 availability (Wilcox et al. 2017; Guasconi et al. 2023). Therefore, an approach that accounts for 99 above- and belowground interactions is essential to understand the proportion of plant litter 100 contributing to SOM formation and stabilization (Cotrufo et al., 2015), and to get-achieve a 101 comprehensive understanding of ecosystem C dynamics (Heimann and Reichstein, 2008).

102 Land management practices, whether through conventional or regenerative methods, can significantly 103 impact soil C and plant biomass both above and belowground. For instance, historic land use has 104 depleted the soil of C (Sanderman et al. 2017), and agricultural lands have lower root biomass C 105 compared to managed grasslands (Beniston et al. 2014). Organic amendments affect different 106 properties and mechanisms in soils, including soil aggregation and structure, soil microbial 107 communities, and plant roots, and the interactions between these elements (Sarker et al. 2022, Liu et 108 al. 2016). Amendments provide nutrients that can stimulate microbial activity and plant growth 109 (Hammerschmiedt et al. 2021), and increase crop yields (Luo et al. 2018). Another promising 110 application of soil organic amendments -is their use to mitigate the negative effects of drought on 111 vegetation and soil microbial communities, as has been observed with biochar (Fischer et al. 2019) 112 (Fischer et al. 2019). Future climate projections indicate an increase in extreme weather events, 113 including longer and more frequent droughts (IPCC, 2021). These conditions may decrease 114 vegetation growth both above- and belowground (Guasconi et al., 2023) and modify plant carbon (C) 115 allocation (Hasibeder et al., 2015), leading to lower C inputs to the soil and potentially decreased soil 116 C stocks (Deng et al., 2021)., which may decrease the soil C sequestration capacity of grasslands by 117 altering plant community composition, plant C allocation and microbial processes (Bai and Cotrufo,

2022). Organic soil amendments can enhance resilience to drought by increasing soil's water-holding capacity to retain soil moisture (Fischer et al. 2019; Haque et al. 2021). These effects of soil amendments on water retention capacity-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 theits chemical composition of the compost (Franco-Andreu et al. 2017). ThisThe 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).

125 Many studies have investigated the effects of organic amendments on aboveground biomass (Ryals 126 et al. 2016) and on crop yield (Luo et al. 2018; Ahmad et al. 2009, Hirte et al. 2021), but fewer focused 127 on roots and on non cultivated grasslands. Garbowski et al. (2020) observed that soil amendments can have an effect only on aboveground biomass or only on belowground biomass, which may be 128 129 expected since roots and shoots respond differently to changes in nutrient (Hayes et al. 2017) and water availability (Wilcox et al. 2017; Guasconi et al. 2023). Furthermore, Ssoil and plant 130 131 communities can show great variability in response to both drought (Guasconi et al. 2023; Canarini 132 et al. 2017) and soil amendments (Gebhardt et al. 2017). This variability derives partly from the 133 variable physical properties of soil, but can also depend on land use history or on small- and large-134 scale topography (Wang et al. 2020)-, and highlights the need for more field-based data collections-135 in particular under experimental conditions that combine soil amendments and drought. This may 136 partly explain why results from field vs. lab experiments can differ considerably (Canarini et al. 137 2017), and highlights the need for more field based data collections in particular under experimental 138 conditions that combine soil amendments and drought.

139 Here, we present the results of a field experiment designed to assess the effects of a soil 140 amendmentcompost and of reduced precipitation on both soil and plant biomass after three growing 141 seasons, vegetation C pools, where we observed changes The changes were observed at various soil 142 depths, in two grasslands, and at two catenary positions, i.e. at the top and at the bottom of a slope. 143 Because the effects of already partly decomposed organic amendments can be expected to be longer-144 lasting than those of easily decomposable ones (Sarker et al. 2022), we applied a one time compost 145 treatment coupled to a yearly growing season drought and investigated their effect on the soil C stocks 146 after three full growing seasons. We measured soil organic C contents (mass of C per unit mass of

147	soil) and soil C stocks (calculated as C content × bulk density × layer thickness) at different depths
148	within the soil profile, and vegetation biomass (encompassing both root biomass and aboveground
149	biomass, including plant litter). We tested the hypotheses that:
150	1) compost amendment increases soil C content and plant growth (both having positive effects on C
151	stocks), while decreasing soil bulk density (having a negative effect on C stocks); we expect that these
152	mechanisms have counteracting effects on net soil C storage;
153	2) dDrought will have a weak negative or non-detectable effect on SOC by decreasing both
154	productivity (organic C input) and respiration (microbial decomposition of SOM)by decreasing both
155	productivity (organic C input) and respiration (microbial decomposition of SOM), drought will have
156	a weak or non-detectable effect on SOC;
157	3) compost amendment mitigates the loss of soil moisture under drought which may alleviate loss of
158	plant growth under drought.
159	Because of the sensitivity of vegetation to natural variability in precipitation (Liu et al. 2020) and
160	potential effects of landscape heterogeneity on both soil C dynamics and plant growth (Sharma et al.
161	2022; Guo et al. 2018), the analyses include testing for differences in the control plots between the
162	start and the end of the experiment, as well quantifying the variability given by grassland and eatenary
163	position, which we expect might lead to variations in all C pools.
164	
165	Methods
166	Site description and experimental setup
167	The experimental site was established in summer 2019 in the proximity of Tovetorp Research Station
168	south of Stockholm, Sweden, and consists of two former arable fields (hereafter called "Tovetorp"
169	and "Ämtvik"), each with an upper and a lower catenary position (hereafter called "high" and "low").
170	Today, the land management consists of cow grazing and hay production (see Roth et al. 2023)the
171	fields are managed for grazing and haymaking. Soil in all locations is rich in clay and ranges from

172 <u>silty clay to silty loam (table S1)</u>.

- 173 In each of these four locations, four treatments (compost, drought, drought compost, control) were
- applied in three replicates, resulting in 12 plots per location and 48 plots in total: compost, drought,
- 175 <u>drought-compost, control (ambient precipitation, no compost treatment)</u>. Each plot measured 2x2 m.
- 176 Soil in all locations is rich in clay and ranges from silty clay to silty loam. Because the effects of

177 already partly decomposed organic amendments can be expected to be longer-lasting than those of 178 easily decomposable ones (Sarker et al. 2022), we applied a one-time compost treatment 179 coupled combined with to a yearly growing season drought and investigated the effects on the soil C 180 stocks after three full growing seasons. The compost was made of Zea mays with a C:N ratio of 9.8 181 and δ^{13} C value of about -15.39‰.-After the seasonal corn harvest (summer 2019) the green parts of 182 the plants were collected in an open field. The piled material was regularly stirred to promote the 183 composting process, and the resulting compost was collected and and was applied in mid-February 184 2020 as a thin surface layer of ca. 11 kg per m² (wet weight), similar to the procedure described in 185 Ryals and Silver (2013). The total amount of C added is estimated to be average ~0.54 kg C m⁻². 186 The δ^{13} C isotope ratio of the compost is higher than that of bulk soil (-15.39 and -27.25, respectively), 187 which means that the δ^{13} C isotope ratios of different treatments can be used to assess if and where in 188 the soil the compost material is retained after the three years of treatment. 189 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) 190 191 with roofs made out of evenly-placed v-shaped polycarbonate strips designed to exclude 60% of the 192 precipitation during the entire growing season (in place from beginning of July to end of October in 193 2019, and from beginning of April to end of October in 2020, 2021 and 2022). This precipitation 194 reduction corresponds to the 1st quantile of the local 100-year precipitation record (Swedish 195 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 40 196 197 cm in depth, was inserted in the soil around each shelter to isolate the study plots from the ambient 198 soil moisture. Pictures and sketches of the sites and of the experimental design are presented in Roth 199 et al. (2023). Total annual precipitation during the study years was retrieved from the records of 200 Tovetorp Research Station (table S2). We note that while the precipitation in the growing seasons 201 2019 and 2022 (April through August) was roughly the same (157 mm and 156 mm, respectively), 202 the 2019 sampling followed an extremely dry summer in 2018, when the study area received only 77 203 mm of precipitation, about half of the precipitation compared to the average 1961-1990 (historical 204 data from SMHI, 2021). Conversely, the 2022 sampling followed the very wet 2021, when the area 205 received almost 140% of the normal precipitation over the same time period (250 mm). 206

207 Soil and vegetation sampling and analyses

208 Soil and root samples were collected in three replicates from each of the four sites and treatments 209 (one sampling per plot) at the end of the first growing season in 2019 (August - September), and again 210 at the end of the experiment in 2022 (August and October). Soil and root samples were collected in 211 all plots at the end of the first growing season in 2019 (August September), and again at the end of 212 the experiment in 2022 (August and October). Samples for soil bulk density were collected to a depth 213 of 45 cm with a large fixed volume root auger with a sharpened cutting edge (8 cm diameter; 214 Eijkelkamp, The Netherlands). Samples for soil bulk density were collected with a large fixed volume 215 root auger with a sharpened cutting edge (8 cm diameter and 15 cm in length; Eijkelkamp, The 216 Netherlands). Three 15 cm segments were collected sequentially using the same hole, reaching a total 217 depth of 45 cm. Upon extraction, the cores were cut into 5 cm segments, and the bulk density was 218 determined after drying the samples at 105 °CThe cores were taken incrementally every 15 cm and 219 then divided in 5 cm segments, and the bulk density was determined after drying the samples at 105 220 ℃. After drying, a subsample from the same core was used to calculate the soil organic matter (SOM) 221 content through loss on ignition at 550 °C for 4 h. A subset was further burned at 960 °C in order to 222 determine the presence of inorganic C, which was $\frac{1}{2} \log (0.5 \%)$, indicating that the total C can be 223 considered equal to organic C (OC). Samples for total C and N and δ^{13} C were taken to a depth of 1 224 m with a Pürckhauer soil corer (2.5 cm diameter; Eijkelkamp, The Netherlands) in 5 cm increments. 225 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 226 227 commercial lab and used for pH measurements (measured in a commercial lab using distilled water 228 with a Mantech Automax 73, Guelph, ON., Canada) and nutrient content analyses (P, Ca, Mg and K; 229 Avio 500 ICP Optical Emission Spectrometer, Perkin Elmer, Waltham, MA; USA) (Table S3). Soil 230 moisture was measured every three weeks throughout the growing season (2019 through 2022) from 231 one access tube (1 m long) permanently installed in each plot, using a PR2 profile probe (Delta-T 232 Devices Ltd, Cambridge, UK). The values used in the analyses are growing season averages of 233 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) <u>by placing the auger on top of the plants</u>, <u>but living aboveground plant biomass and fresh litter were removed and not included in the soil</u>

237 samples. Samples were taken to a depth of 30 cm in all plots and to a depth of 45 cm in a subsample 238 of 16 plots (used as control for maximum rooting depth), with soil cores divided into 5 cm segments. 239 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 at 600 dpi (grey scale), followed by 240 241 drying at 60 °C for 48 h to obtain the dry weight. The scanned images were analyzed with WinRhizo 242 (Regent Instruments, Québec, CA) to obtain root volume, length and diameter, used to calculate root 243 mass density (g roots cm⁻³ soil), specific root length (cm g⁻¹ roots) and root tissue density (g roots cm⁻³ 244 3 roots). The roots were rinsed with water on a 0.5 mm mesh sieve to remove soil and then scanned, 245 followed by drying at 60 °C for 48 h to obtain the dry weight. The scanned images were analyzed 246 with WinRhizo (Regent Instruments, Québec, CA) to obtain root volume, length and diameter, used 247 to calculate root mass density (groots cm-3 soil), specific root length (cm g-1 roots) and root tissue density 248 $(\frac{1}{2})$ Aboveground biomass was harvested from one quarter (1 m²) of each plot every year 249 in mid-July, by cutting at ground level (including moss and dead biomass, table S4). More details of 250 the sampling design are presented in the Supplements (Table table T1S5).

251 Statistical analyses

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Because of the sensitivity of vegetation to natural variability in precipitation (Liu et al. 2020) and potential effects of landscape heterogeneity on both soil C dynamics and plant growth (Sharma et al. 2022; Guo et al. 2018), the analyses include testing for differences in the control plots between the start and the end of the experiment, as well quantifying the variability given by grassland and catenary position, which we expect might lead to variations in all C pools.

258 The measured soil organic C contents (mass of C per unit mass of soil) at different depths within the 259 soil profile were used to calculate and soil C stocks (ealculated as C content × bulk density × layer 260 thickness) at different depths within the soil profile, and vegetation biomass (encompassing both root 261 biomass and aboveground biomass, including plant litter). Total C content was calculated for all 48 262 plots as % of total mass, and C stocks were calculated using total C content, bulk density and SOM 263 dataTotal C content (as % of total soil mass) and soil C stocks normalized by soil sample thickness 264 (kg/m³) were calculated for all 48 plots using the total C content data (available for a subset of the 265 samples) and the bulk density and SOM data (available for a complementary subset of the samples). The soil C stocks - These-were then normalized by soil sample thickness (kg /m⁻³) to allow 266

267 comparisons among soil layers with different thickness. Because C contents were not measured in all 268 samples, A-a regression was performed to calculate SOC from SOM data (which was available for 269 all samples) and thus obtain a complete dataset, 270 $SOC = 0.328 \times SOM + 0.217$, (1)271 where SOC and SOM are expressed in kg/m² (Fig. S1). The fraction F of compost-derived C detected in the soil in year 2022 was calculated with a two end-272 273 member mixing model, as in Poeplau et al. (2023), $F = \frac{\delta^{13} C_{compost treatment} - \delta^{13} C_{control}}{\delta^{13} C_{compost} - \delta^{13} C_{control}},$ 274 (2)

where δ^{13} C was measured in both compost-amended (compost or compost-drought) and control (no compost or drought-no compost, respectively) plots.

All the results and statistical analyses are limited to the depth range of 0-45 cm. This is because this soil depth contains the majority of the root biomass (95% within the first 30_cm, mean ~17 cm) and of the microbiological activity, and no effect of treatments could be detected below this range (data not shown).

All analyses were made in R (version 3.3.3; R core Team 2017), and statistical models were designed with the lmer function (package: lme4). Pairwise comparisons between categorical variables were made with lsmeans (package: emmeans) and p-values ($\alpha = 0.05$) were obtained with the ANOVA function and the lmerTest package. Residuals from the models were checked graphically. Effect sizes were obtained by calculating Cohen's d, with the formula

$$286 d = \frac{\overline{x}_1 - \overline{x}_2}{s}, (3)$$

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 the standard deviation.

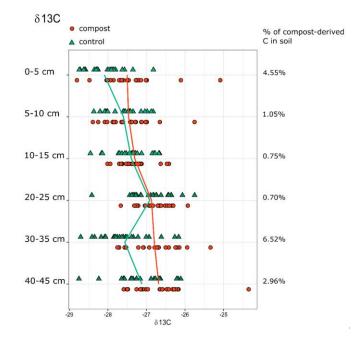
The effect of the treatments was tested on all plots from the 2022 dataset., including Values for root biomass and root traits, for which the values were log-transformed first. The model included compost (categorical variable), drought (categorical variable) and sampling depth (continuous variable) as fixed factors and plot (nested within site) as random factor. Cohen's d was calculated using the standard deviation of the control group. The effect of the compost amendment on the <u> $\delta^{13}CC$ isotopie</u> ratio was tested with a <u>mixed linear</u> model that included compost and depth as fixed factors, and plot (nested within site) as random factor. Changes in soil C, bulk density and C stocks were also tested

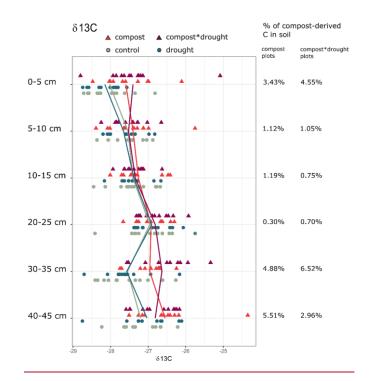
with a model using depth as categorical variable, to assess if changes occurred at specific depths. The 296 297 landscape variability in plant biomass and soil properties across locations was tested on all data 298 collected in 2019 and from the control plots in 2022. The model included grassland site, catenary 299 position and sampling depth (continuous variable) as fixed factors and year and plot as random factors. Cohen's d was calculated using the standard deviation pooled from all groups. Temporal 300 changes during the experiment not caused by the treatments were tested using data obtained in 2019 301 302 and 2022 from the control plots. The model included year and sampling depth (continuous variable) 303 as fixed factors and plot (nested within site) as random factor. Cohen's d was calculated using the standard deviation of the 2019 dataset. The variable depth was not included in the models for 304 305 aboveground biomass.

307 Results

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308 The dDrought treatment decreased soil moisture by 16% in the upper 0-30 cm during the growing 309 season (Fig. S2). The effect of drought was consistent over sites, years and seasons, and there were 310 no statistically significant differences in the drought-driven soil moisture loss between locations, 311 years, or between spring (April-May), summer (June-July-August) or growing season (April through 312 August). There was also no significant difference in soil moisture decrease between drought plots and 313 drought-compost plots (Fig. S3). Additionally, the compost addition did not have any significant 314 effect on soil pH or on soil P, Ca, Mg and K. The compost addition did, however, raise the value of 315 δ^{13} C in the treated plots (mean control plots = -27.44‰, mean compost plots = -27.10‰, P < 0.01), 316 and the difference was significant at 0-5 cm, 30-35 cm and 40-45 cm. The mixing model (Eq. 2) 317 indicated that after three growing seasons, the percentage of compost-derived C in the compost plots 318 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 319 compost plots. In the compost x drought plots, and and the percentage of compost-derived C was 4.55 320 % in the 0-5 cm layer, 6.52 % in the 30-35 cm layer and 2.96 % in the 40-45 cm layer of the compost 321 x drought plots.





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Fig 1. Values of δ¹³C in the soil in compost-treated (red dotstriangles) and untreated (control, green trianglesdots) 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 isotopea mixing model in (Eq. 2).

327 Compost and drought effects

328 The compost treatment increased tT otal soil C content (P = 0.04) and above ground biomass (P \equiv 329 0.04<0.01) increased in the compost-treated plots. The latter increased by 23% (mean control plots 330 = 642 g m². SD = \pm 129.23, mean compost plots = 788 g m² \pm , SD = 221.7). The effect on soil C was 331 significant only in the top 5 cm layertopsoil (0.5 cm, Fig. 2), where the relative increase of soil C 332 content was-increased by 18% (mean control plots C content = 2-9.9% mg/g \pm , SD = 1.03, mean 333 compost plots = 3.5.3 mg/g + , SD = -0.75). Soil nitrogen (N) was higher in the topsoil top 5 cm 334 <u>layer</u> in the compost-treated plots (mean control plots = $\frac{0.242.44\%}{Mg/g}$ mg/g \pm , SD = 0.06, mean compost 335 plots = $\frac{0.28\%2.88 \text{ mg/g} \pm \text{, SD} = 0.06; \text{ p} < 0.05}{\text{, p} < 0.05}$, 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 336

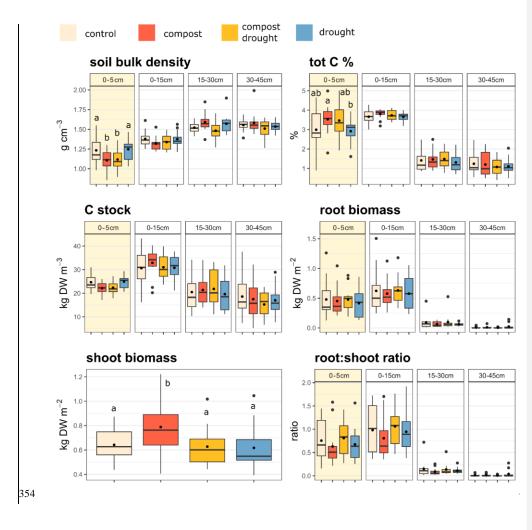
337	soil (mean control plots = 1.34 g cm ³⁺ \pm , <u>SD</u> = 0.18, mean compost plots = 1.22 g cm ³⁺ \pm , <u>SD</u> = 0.17).
338	The compost , but did not correlate affect with any other variable did not have any statistically
339	significant effect on other variables
340	Experimental dDrought only had an effect on aboveground biomass, which decreased by almost 4%
341	under the rainout shelters (mean control plots = $642 \text{ g m}^2 \pm \frac{129.23}{129.23}$, mean drought plots = 617
342	$g \text{ m}^2 \pm \underline{SD} = 180.25$). The increase in the soil C content under compost addition was offset by the
343	lower-reduced bulk density, so that there was no statistically significant change to soil C stocks.
344	However, we note that, albeit non-statistically significant, mean soil C stocks were 6% higher in the
345	compost-treated (ambient precipitation) plots in the first 15 cm, slightly higher than the percentage
346	of compost-derived C found in that layer (mean control plots = $4.02 \text{ kg m}^2 \pm \text{SD} = 0.92$, mean
347	compost plots = 4.26 kg m ² \pm , SD = 0.59).
348	Experimental drought had only an effect on aboveground biomass, which decreased by almost 4%

Experimental drought had only an effect on aboveground biomass, which decreased by almost 4%
 under the rainout shelters (mean control plots = 642 g m², SD = 129.23, mean drought plots = 617 g

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

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

biomass between the drought-treated plots with and without compost addition.



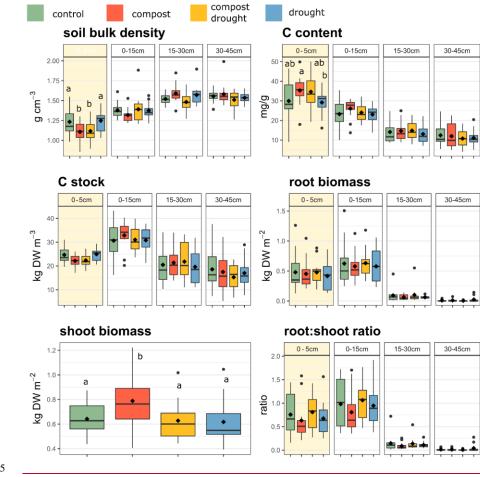


Fig. 2. Values of soil bulk density, total-soil <u>carbon (C)</u> contents, soil C stocks, root biomass, shoot biomass and rootshoot ratio, at different sampling depths in 2022 (n = 12). Values are averages of all sites. White-Green = control, red = compost, yellow = compost×drought, blue = drought. Bars-Boxes show mean (dot diamond inside the barbox), median (horizontal line) and interquantile range (IQR, colored barbox); whiskers extend to $1.5 \times IQR$; 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).



Brought led to 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 topsoil-top layer (0-5 cm) were considered, in addition to these patterns-above, specific root length of coarse roots decreased under drought (P = 0.04), while root tissue density (P = 0.02) and specific root length of all roots increased after compost addition (P = 0.01).

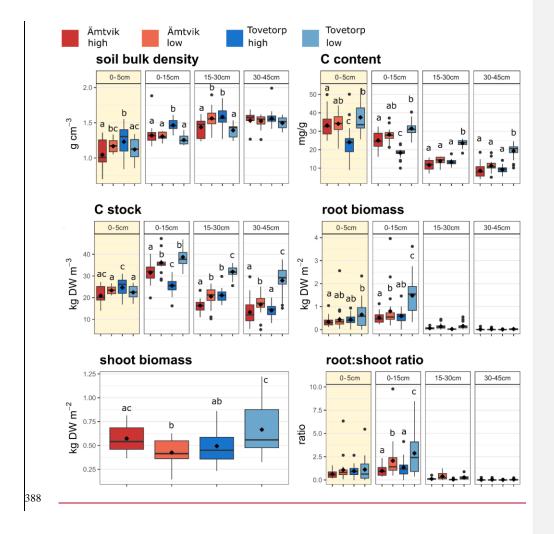
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369 In all control plots, soil C and root biomass was positively correlated both in the topsoil top 5-15 cm 370 (5-10 cm, r = 0.42, P = 0.04; 10-15 cm, r = 0.5, P = 0.01) and in the <u>whole</u> 0-30 cm layer (0-30 cm, r = 0.42, P = 0.04; 10-15 cm, r = 0.42, P = 0.04; 10-15 cm, r = 0.42, P = 0.01) 371 = 0.63, P < 0.01). Soil C content was also positively correlated to the root:shoot ratio (5-10 cm, r = 372 0.44, P = 0.03; 10-15 cm, r = 0.4, P = 0.052; 0-30 cm, r = 0.43, P = 0.04). In the compost_-treated 373 plots, the only significant correlation was between soil C and root biomass when considering the 374 whole 0-30 cm layer (0-30 cm, r = 0.55, P < 0.01). The strength of the correlation did not differ 375 between control and compost-treated plots The correlation between soil C and aboveground biomass 376 remained constant in both control and compost treated plots (r = 0.22, P < 0.01 in control and 377 compost-treated plotsboth groups). This indicates that the compost treatments affected soil C in the 378 topsoil and aboveground biomass more than they affected roots and deeper soil.

379

380 Landscape Sepatial variability at the landscape scale

Soil C contents, total C stocks, bulk density, root biomass and root:shoot ratio all-showed statistically significant (P < 0.05) differences between catenary positions and depths, and soil C content and bulk density also differed significantly between grasslands (Fig. 3, Table T3table S8). Grassland identity and the interaction between grasslands and catenary positions were the only significant predictors of aboveground biomass (Fig. 3), suggesting this variable is most likely related to land use history and plant community composition.



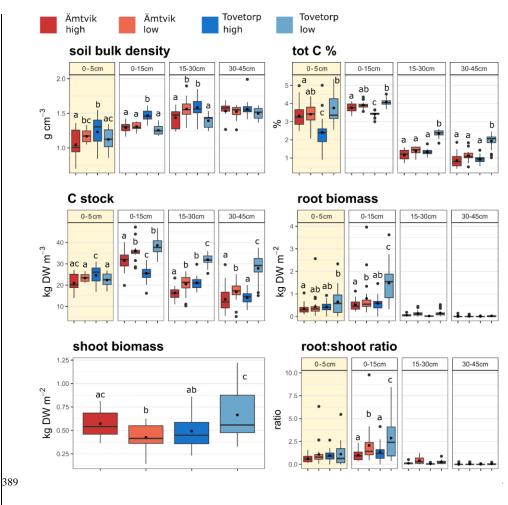
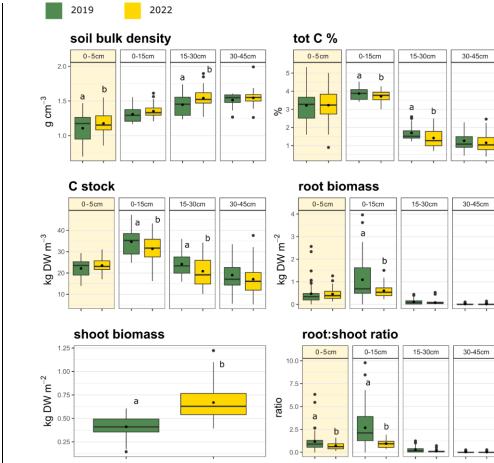


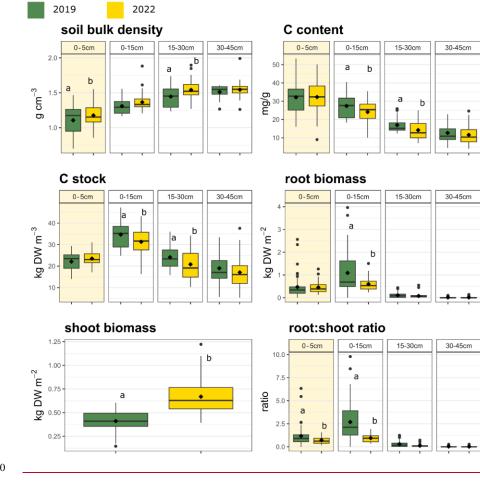
Fig. 3. Values of soil bulk density, total soil carbon (C) content, soil C stocks, root biomass, shoot biomass and root-shoot
ratio, at different sampling depths at the four sites, excluding treatments. The data consists of average values from 2019
(all plots, n = 48) and 2022 (only control plots, n = 12). Red = Amtvik High catenary position, orange = Ämtvik Low
catenary position, blue = Tovetorp High catenary position, light blue = Tovetorp Low catenary position.
show mean (dot diamond inside the barbox), median (horizontal line) and interquantile range (IQR, colored barbox);
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).

397 Natural changes during the 2019-2022 period

- 398 From 2019 to 2022, we observed large changes in soil C and plant biomass in the control plots. Soil
- 399 C-contents, total C stocks, bulk density, root biomass and root:shoot ratio all showed statistically
- 400 significant (P < 0.05) differences between 2019 and 2022 and between depths (Fig. 4, Table T4).
- 401 Aboveground biomass also differed significantly between sampling years. Between 2019 and 2022
- 402 (Fig. 4, table S9) total soil C contents and root biomass in the first 5 cm of the control plots decreased
- 403 by 10.7% (from 3-3.5% mg/g \pm , SD = 1.05 to 2-99% mg/g \pm , SD = 1.03) and 8.4% (from 522.96 g
- 404 $m^2 \pm , SD = 626.48$ to 479.25 g $m^2 \pm , SD = 320.75$), respectively. In the first 15 cm, , in the first 5
- 405 cm, and they decreased by $\frac{27.121.5}{}$ % (from $2\frac{.779.7}{mg/g} \pm .5D = 0.78-73$ to $2\frac{.023.3}{mg/g} \pm .25$
- 406 SD = 0.6171) and 67.438.7% (from 477.261017.95 g m⁻² \pm , SD = 252.49955.16 to 155.81623.65 g
- 407 m⁻² \pm , <u>SD</u> = <u>51.62</u>65.19), respectively, in the first 15 cm. Aboveground biomass instead increased
- 408 by 53% (from 419.68 g m⁻² \pm , <u>SD</u> = 137.45 to 642.23 g m⁻² \pm , <u>SD</u> = 129.23).



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Fig. 4. Values of soil bulk density, total-soil <u>carbon (C)</u> contents, soil C stocks, root biomass, shoot biomass and rootshoot ratio, at different sampling depths in 2019 and 2022 (<u>excluding treatment control</u> plots, n = 12). Values are means for all plots. Green = 2019, yellow = 2022. <u>Bars Boxes</u> show mean (<u>dot diamond</u> inside the <u>barbox</u>), median (horizontal line) and interquantile range (IQR, colored <u>barbox</u>); whiskers extend to $1.5 \times IQR$; dots in the graph are outliers. Different letters indicate statistically significant differences between means (P < 0.05). <u>The yellow squares indicate the top layer</u> (<u>0-5 cm</u>). 417 Table 1. Effect sizes (Cohen's d) of the differences between sites, years and treatments for each soil

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

419 Discussion

420 Compost effects on soil C and plant growth

421 Total soil C contents increased after compost application, but because bulk density was also reduced, 422 there was no significant increase in soil C stocks (partly confirming our first hypothesis), despite 423 higher mean values of soil C per m²stocks in the compost treated plots in the first 15 cm of soil. This 424 difference was lower than the estimated-C addition (~0.54 kg C m⁻²) and thus lower than expected, 425 but is, likely due to respiration loss. Compost is partly decomposed organic matter, and thus more 426 chemically recalcitrant than fresh grass residues. As a result, its Compost can be considered a 427 recalcitrant type of organic amendment, effects on SOC accrual can be persistent over several years 428 with initially slow but persistent effects expected to be observed years after the first application 429 (Sarker et al. 2022) even after a single application (Ryals et al. 2013). Therefore Despite there being 430 evidence that compost amendments can lead to SOC accumulation already within two years after 431 application (Gravuer et al. 2023), it is unlikely that an-the effect of the our treatment on soil properties 432 and soil C had occurred before our will persist beyond the 2022 sampling, and that such an effect was 433 somewhat transient and undetectable at the time of the sampling. This conclusion is also supported 434 by the isotope tracing (Fig. 1), indicating that at least a fraction of the compost-derived C is still 435 present in the soil after three growing seasons. TIn addition, he significant increase in aboveground 436 biomass three years after the compost application could partly be explained by the persistence of 437 favorable plant growing conditions, such as increased N in the soil. This mechanism was invoked by 438 Oladeji et al (2020), and may interact with precipitation-related interannual variability in plant growth 439 (Sala et al. 2012)the significant increase in aboveground biomass three years after the compost 440application indicate the persistence of favorable plant growing conditions, such as increased N in the 441 soil. Our results suggest that compost treatments might benefit the ecosystem C balance indirectly 442 through increased biomass production, such as in this case, or by extending the growing season, such 443 as in Fenster et al. (2023). These results are in accordance with Fenster et al. (2023), who found that 444 the benefits of compost treatments on the ecosystem C balance of grasslands one year after application 445 were manifested as extended growing season, and thus potentially higher plant productivity, rather 446 than as an increase in net soil C. Thiese interactions between land management, vegetation growth 447 and plant-derived C inputs also stresses-underline the importance of including vegetation dynamics when assessing the effectiveness of C management. Our compost addition treatment did not lead to 448 449 an increase in soil C accumulation, but resulted however-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 450 451 layer. This suggests that the increase in soil C is not only derived from the amendment itself, but also 452 from increased plant C inputs. However, longer-term studies are necessary to understand whether 453 SOC saturation limits the effectiveness of compost amendments in sustaining these gains over time 454 (Moinet et al. 2023). 455 Compost enhanced aboveground biomass growth, but not root growth, thereby only partly confirming 456 our first hypothesis, possibly in response to the increased nutrient supply (Bloom et al. 1985; Poorter 457 and Nagel 2000), thereby only partly confirming our first hypothesis. and suggesting the presence of

458 a tradeoff between root and shoot investment. This was already observed in Garbowski et al. (2020) 459 and is in line with the expectation that plants in nutrient rich environments can allocate to 460 aboveground tissue growth the resources that would otherwise be allocated to nutrient acquisition belowground (Bloom et al. 1985; Poorter and Nagel 2000). In broader terms, this suggests that the 461 462 compost treatment led plants to preferentially allocate to aboveground organs the resources that would 463 otherwise be allocated to nutrient acquisition belowground (Cleland et al. 2017)this suggests that the compost treatment shifted the C balance between soil pool and vegetation pool, and moved the plant 464 465 C allocation from belowground to aboveground organs. Nevertheless, increased root tissue density 466 and specific root length in the topsoil top 5 cm layer suggest that root response to organic amendments 467 is manifested in more subtle changes in root traits related to nutrient acquisition (Bardgett et al. 2014), 468 rather than in net root biomass production.

469

Microbial activity and microbial biomass can be higher after<u>as a result of compost addition (Sarker</u>
 et al. 2022; Gravuer et al. 2019). Here, the limited effects Our experimental setup did not allow us to
 test whether microbial activity and microbial biomass increased as a result of compost addition, as
 was reported by previous studies (Sarker et al. 2022; Gravuer et al. 2019). However, the limited
 effects of the compost treatment on soil C stocks suggest that the potential C accrual brought by the
 increased plant productivity the C sequestration benefits in the form of increased plant growth might

476 have been offset by increased microbial respiration (promoted by either compost or enhanced 477 rhizodeposition of more productive plants) (Borken et al. 2002). Finally, the significant spatial and 478 temporal variability in both soil C and vegetation biomass observed in the control dataset suggests 479 that treatment effects might be site-specific (Garbowsi et al. 2020), and management plans seeking 480 to optimize soil C sequestration increase C accrual should consider the potentially interactive effects 481 of several biotic and abiotic factors, such as plant community composition, soil type and climate. For 482 instance, in our experiment, aboveground biomass increase was highest at the site with the greatest 483 abundance of grasses (table S4)the increase in aboveground plant biomass after compost application 484 was mostly driven by the grass-rich plots in the Tovetorp grassland (Roth, 2023), suggesting that 485 plant community composition might be important in determining the effects of soil amendments on 486 grasslands.

487 Drought effects on soil moisture, soil C and plant growth

488 Drought treatments reduced soil moisture and aboveground plant biomass, but did not significantly 489 decrease root biomass (Table table T2S7), indicating preferential biomass allocation and resource 490 investment to belowground organs under precipitation reductiona tradeoff between above and 491 belowground biomass investment. Plant growth is very sensitive to yearly fluctuations and even intra-492 annual distribution of precipitation (Knapp and Smith 2001, Porporato et al. 2006). Because our 493 analyses are based on only two temporal datapoints (2019 and 2022), it is difficult to assess whether 494 drought reduced plant turnover, defined as the ratio of standing biomass to net primary productivity 495 (NPP). Because plant growth is very sensitive to yearly fluctuations and even intra-annual distribution 496 of precipitation (Knapp and Smith 2001, Porporato et al. 2006), and because our analyses are based on only two temporal datapoints (2019 and 2022), it is difficult to assess whether drought reduced 497 498 plant turnover, defined as the ratio of standing biomass to net primary productivity (NPP). We note 499 that while the precipitation in the growing seasons 2019 and 2022 (April through August) was roughly 500 the same (157 mm and 156 mm, respectively), the 2019 sampling followed an extremely dry summer 501 in 2018, when the study area received only 77 mm of precipitation, about half of the precipitation 502 compared to the average 1961-1990 (historical data from SMHI, 2021). Conversely, the 2022 503 sampling followed the very wet 2021, when the area received almost 140% of the normal precipitation 504 over the same time period (250 mm). As there was some natural variability in the annual precipitation 505 (see methods section), It is possible that a legacy effect of these two precipitation extremesthis variability may have affected plant growth <u>(Sala et al. 2012)</u>, particularly aboveground (Fig. 4), where
growth is more sensitive than root biomass to yearly fluctuations in water availability (Zhang et al.
2021). <u>In particular, IL</u>egacy 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 2021 could have buffered the effects of the experimental
drought in 2022, leading to overall weak drought effects <u>(Sala et al. 2012)</u>.

512 The drought treatment had a relatively small impact on plant biomass and on r(Fig. 2). In addition to 513 potential effects of interannual precipitation variation, this may be due to adaptation in the plant 514 community during the treatment years (Basu et al. 2016), or that the drought was not intense enough. 515 Roots in particular where not significantly affected by drought (Fig. 2)., but while we monitored the 516 relative proportions of annuals and perennials, grasses and forbs in each plot, we do not know which 517 plant species the sampled roots belong to. Therefore,). Because we do not know which plant species the sampled roots belong to, we cannot make any conclusions related to belowground drought 518 519 responses of different plant functional groups the ecology of these plant groups, all of which can be 520 expected to respond differently to drought (Zhang et al. 2017; Mackie et al. 2019; Zhong et al. 2019). 521 However, since we note that-the magnitude of the drought did not differ between locations and since 522 soil physical properties were similar across sites, whilebut drought effects differed across locations 523 (Fig. S4). Therefore, we can hypothesize that differences in the plant communities account for at least 524 some of the spatial heterogeneity observed in our study, as was observed in-by Garbowski et al. 525 (2020). Also, while drought effects on root biomass were marginal, the drought treatment did increase 526 both root tissue density and average root diameter. Climate is a strong predictor of root trait variation 527 (Freschet et al. 2017), and higher root tissue density is correlated with resource-conservative 528 acquisition strategies (Bardgett et al. 2014) and longer root life span (Ryser, 1996), suggesting 529 adaptation of root traitssome degree of drought adaptation in these our plant communities.

Adopting a standardized approach for the drought experimental design makes our findings easier to compare with othersimproves comparability, but partial rainout shelters will still allow for a substantial amount of precipitation to pass through, potentially raising soil moisture above the wilting point the roof sheets. If there is enough precipitation, even the small percentage of rain that reaches the ground might bring the soil moisture over the threshold of the permanent wilting point. It is also 535 possible that soil water retained in the soil from snowmelt or winter/spring precipitation could have 536 sustained vegetation growth in the drought treatments. Experimental droughts also fail to account 537 Finally, experimental droughts do not control for reduced air humidity, which may underestimate negative responses of plant biomass to drought in field experiments (Kröel-Dulay et al. 2022), and 538 539 for increased temperatures, which often occur in combination with natural droughts. Drier and 540 warmer air increases evaporative demand, causing stomatal closure and thus lower productivity for a 541 given soil moisture level (Zhang et al. 2019). These methodological limitations might explain why we 542 observed minor drought effects on vegetation.

543 To understand the ecosystem-level implications of drought, soil C changes need to be considered as 544 well. Dry conditions decrease heterotrophic respiration because microbial activity is inhibited due to both physiological mechanisms, such as osmoregulation diverting efforts from resource acquisition 545 to survival, and physical mechanisms, like the slower transport of substrates in dry soils (as the water 546 547 films around soil particles shrink and pore connectivity is lost) (Moyano et al. 2013; Schimel 2018). 548 However, heterotrophic respiration increases again after soil rewetting, leading to disproportionally large C emissions during the short post-rewetting period (Canarini et al. 2017; Barnard et al. 2020). 549 550 Because the drought plots with added compost had a higher fraction of compost-labelled isotopes 551 compared to the non-drought plots in the topsoil (Fig. 1), this would imply that any soil C emission 552 pulses at rewetting were not sufficient to compensate for the possibly lowered microbial activity 553 during the soil moisture dry-downs. As a result, in our experiment drought had no effects on soil C 554 contents and stocks, as per our second hypothesis, although it slightly reduced soil bulk density (in a 555 pre-treatment vs post-treatment comparison, data not shown), possibly in relation to shrinkage in dry 556 soil.In our experiment, drought had no effects on soil C contents and stocks, as per our second 557 hypothesis, but it slightly reduced soil bulk density (in a pre-treatment vs post-treatment comparison, 558 data not shown), possibly in relation to shrinkage in dry soil. Because drought reduced plant 559 productivity (and thus C inputs to soil), the lack of drought effect on soil C stocks can be explained 560 by a reduction of microbial activity approximately of the same magnitude as the reduction in plant 561 productivity. This is supported by the fact that in the topsoil, the drought plots with added compost 562 had a higher fraction of compost-labelled isotopes compared to the non-drought plots. Therefore, any 563 soil C emission pulses at rewetting were not sufficient to compensate for the lowered microbial 564 activity during the soil moisture dry-downs.

565 Interactive effects of compost and drought

566 The effects of soil amendments on water retention capacity are modulated by quantity and quality of soil organic matter (Rawls et al. 2003; Yang et al. 2014; Franco Andreu et al 567 2022) and by the chemical composi-568 2017: Sarker et al. 569 2017). While previous studies indicated increased soil water retention after soil amendments In our 570 study, soil moisture did not differ between the drought plots and the ones with drought and compost, 571 which indicates that the soil amendment did not increase soil moisture, in contrast with previous 572 findings (Franco-Andreu et al. 2017; Ali et al. 2017), in our study compost-treated drought plots did 573 not have higher soil moisture than the untreated drought plots three3 years after compost application 574 (Fig. S3), which leads us to reject our third hypothesisand leads us to reject our third hypothesis. As 575 the negative effects of drought on aboveground biomass were weak, they were not visibly 576 compensated for by the compost addition. On the contrary, the experimental precipitation reduction 577 obliterated the biomass increase detected in the compost-treated plots in ambient rainfall, overriding 578 the positive effects of the increased C and N provided through the compost. This suggests that the 579 vegetation response in our experiment does not only depend on nutrient addition and interannual 580 variability in precipitation, but likely also on plant physiological processes related to water 581 availability (Bista et al. 2018) and on the ability of soil microbes to render the nutrients available for 582 plant uptake. Interestingly however, while both compost and drought slightly reduced tended to reduce 583 root biomass, there was a tendency for higher root:shoot ratio in the plots with combined compost 584 and drought treatment the compost applied on the drought plots led to an increase in root:shoot ratio 585 (Fig. 42). While our results from the compost-treated plots show that plants may reduce their 586 belowground biomass investment relative to aboveground growth when adding organic matter, this 587 mechanism appears appeared to work differently under drought conditions, when plants may and the 588 observed shift in-C allocation belowground may serve to aid in water acquisition (Eziz et al. 2017; Guswa et al. 2010). This, in turn, could lead to increased evapotranspiration, and this improved 589 590 capacity for soil water absorption could potentially offset any compost-induced increase in soil water 591 retention capacitymask any increase in soil water retention capacity in the compost x drought plots. 592 However, since our experiment did not include drought recovery, it is not known if this change would 593 persist after the end of the experimental drought.

594 Conclusions

The goal of this study was to We explored how drought and compost amendment affect-provide an 595 596 overview of the changes in soil properties and, above- and belowground plant biomass vegetation C 597 content and biomass within a grassland ecosystem, through a multifactorial drought and compost 598 amendment field trial. Compost amendment and drought had distinct effects on plant shoot and root 599 growth, revealing the presence of trade-offs in their responses to environmental change. The compost 600 treatment led to an increase in biomass in shoots but not in roots, and ultimately did not result in an 601 increase in soil C stocks. Drought did not significantly affect plant biomass, but led to changes in root 602 traits and stunted the compost-induced increase in plant growth measured in plots under ambient 603 precipitation. The compost treatment revealed contrasting responses of shoots and roots, but it 604 ultimately did ultimately not result in an increase in soil C stocks. Drought decreased aboveground 605 biomass, but root response was limited to shifts in root traits. Compost amendment and drought had 606 distinct effects on plant C allocation, revealing the presence of trade-offs in their responses to 607 environmental change. These findings improve our understanding of C dynamics in grasslands by 608 illustrating the different components of plants and soil properties affected by theland managementoffering potential contributions to ecosystem C modelling. We also observed significant spatial and 609 610 temporal variability in vegetation and soil C dynamics over the study period, which may be driven 611 by differences in topography, land use and plant community composition, as well as temporal 612 variability in precipitation. This suggests that ecosystem C dynamics can be influenced by multiple 613 biotic and abiotic factors, which can be revealed by field observations and multifactorial experiments.

614 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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