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Response of Soil Microarthropods to Drought in Arable Fields

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Svenja Meyer

from Sulingen

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Thesis Committee

Stefan Scheu, Animal Ecology, Universität Göttingen

Klaus Birkhofer, Ecology, Universität Cottbus

Martin Potthoff, Centre of Biodiversity and Sustainable Land Use, Universität Göttingen

Members of the Examination Board

Reviewer: Stefan Scheu, Animal Ecology, University Göttingen

Second Reviewer: Klaus Birkhofer, Ecology, University Cottbus

Further Members of the Examination Board

Mark Maraun, Animal Ecology, University Göttingen

Christoph Bleidorn, Animal Evolution and Biodiversity, University Göttingen

Klaus Hövemeyer, Animal Ecology, University Göttingen

Catrin Westphal, Functional Agrobiodiversity, University Göttingen

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“From the freedom to explore comes the joy of learning. From knowledge acquired by personal initiative arises the desire for more knowledge. And from mastery of the novel and beautiful world awaiting every child comes self-confidence. The growth of a naturalist is like the growth of a musician or athlete: excellence for the talented, lifelong enjoyment for the rest, benefit for humanity.”

— Edward O. Wilson

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SUMMARY

In the face of current as well as projected increased frequencies and severities of droughts the interest in responses of the belowground system to such profound changes in environmental conditions has risen. The heavily disturbed soils of agricultural fields deserve special attention since they seem especially vulnerable and are of crucial importance for future crop production. Soil organisms mediate a number of functions in soil, hence, in order to develop strategies for mitigating detrimental drought effects on agricultural systems, it is essential to better understand their response to drought and how this may be modulated by interactive factors.

In Chapter 2 we present the methodological basis of the drought experiments conducted in this thesis. We describe in great detail an adapted roof design that is suitable for experiments in agricultural context and includes the concept of a roof control in order to deal with potential unintended artifacts. We evaluated potential artifacts on microclimate by including three drought treatments: (I) A roof that intercepts precipitation, (II) a roof similar to the previous one, but without rain interception and (III) an ambient control without any manipulation. Artifacts were generally small, but soil and air temperature were little increased under high ambient temperature. The roof intercepted 64.9% of the precipitation, which is very close to the a priori calculated exclusion of 65.1%, indicating a precise prediction of experimental rain exclusion is possible with this roof design. The roofs further proofed to sustain under heavy weather in an open landscape and were suited for the use in agricultural fields where management operation require regular removal. We hope to promote this roof design for future drought simulation experiments by providing detailed technical drawings, a complete parts list and an assembly instruction.

In the study presented in Chapter 3 we investigated the effects of simulated drought on the abundance and community composition of soil microarthropods in winter wheat fields under long-term conventional and organic farming in the DOK trial, Switzerland. Drought decreased the abundance of Collembola and Oribatida more consistently in conventionally compared to organically managed fields. The abundance of Collembola as well as Meso-, Pro- and Astigmata, but not the abundance of Oribatida, increased in deeper soil layers due to simulated drought, suggesting vertical migration as drought avoidance strategy in these taxa. The species composition of Oribatida communities, but not of Collembola communities, differed significantly between drought treatments as well as between farming systems with soil carbon content being among the factors structuring Oribatida communities.

The indication, that soil organic carbon (SOC) has the potential to mitigate drought effects led to the study presented in Chapter 5, where we conducted a drought manipulation experiment in fields with high and low SOC content. Further, we extended the scope of the climate

manipulation to the question if natural differences in climate influence the effect of simulated drought by establishing the same experiment at sites with temperate (Sweden and Germany) and Mediterranean climate (Spain). Of the studied microarthropod groups only Oribatida were significantly affected by drought with the direction of these effects being different in high and low SOC fields and among countries. Drought decreased abundances of Oribatida in low SOC fields and increased them in high SOC field. Negative drought effects occurred only in Sweden driven by strong negative effects in low SOC fields, where soil water content was extremely low (below 7%), indicating a threshold of soil water content below which negative drought effects prevail irrespective of the SOC content. Oribatida at the Spanish sites were only little affected indicating that communities from dry climates are adapted to drought, e.g. by living in deeper soil.

In the study presented in Chapter 4 we investigated, in addition to changes in abundances, drought induced shifts in trophic niches of Collembola and Oribatida as indicated by stable isotope analysis (^{13}C and ^{15}N). The study was conducted in the same fields as the first two studies (Chapter 2 and 3) under long-term conventional and organic farming in the DOK trial. Stable isotope values suggested that plant litter and root exudates were the most important resources for Collembola (*Isotoma caerulea*, *Isotomurus maculatus* and *Orchesella villosa*) and older plant material and microorganisms for Oribatida (*Scheloribates laevigatus* and *Tectocepheus sarekensis*). Drought treatment and farming system did not affect abundances of the studied species. However, isotope values of some species increased in organically managed fields indicating a higher proportion of microorganisms in their diet. Trophic niche size, a measure of both isotope values combined, decreased with drought and under organic farming in some species presumably due to favored use of plants as basal resource instead of algae and microorganisms.

Overall, the results from Chapter 3 and 5 indicate that the vulnerability of soil microarthropods against drought is high in soils with low SOC content and at very low soil moisture. On the other hand, in soils with high SOC content they may profit from drought, suggesting that increasing SOC levels in agricultural soils may be a useful tool to mitigate or even reverse negative drought effects. High SOC contents modulated drought effects presumably by buffering the decrease in soil moisture and providing a more complex soil structure that allowed vertical migration to deeper soil as drought avoidance strategy. Responses of soil microarthropods to simulated drought were only small at sites with Mediterranean climate, suggesting communities from dry climates being generally better adapted to drought. The results of Chapter 4 further suggest that the flexible usage of resources may buffer effects of drought and management practices on the abundance of microarthropods in agricultural systems and may be one reason for neutral responses in abundances in drought experiments. Altogether, this thesis contributes to a better understanding of the response of soil microarthropods to droughts in arable fields by identifying determinants for the direction of these responses and potential mechanisms of adaptation to drought by the different taxa.

1 GENERAL INTRODUCTION

1.1 CLIMATE CHANGE

Droughts are the result of several forces that are altered by global climate change. During the last decades temperature increased and precipitation became more variable, hence, it is no surprise that droughts have become more frequent and intensive (IPCC 2021). In the future, even under conservative scenarios for climate change, drought is predicted to further increase in frequency and severity within the current century. For Europe models using differently weighted indices consistently project increasing duration, frequency and affected area of drought (Samaniego et al. 2018). However, the magnitude of this increase is spatially and temporally different. Generally, extreme dry, but also extreme wet years are projected to become more frequent with more pronounced dry years in Southern Europe and more pronounced wet years in Northern Europe (Russo et al. 2013; Spinoni et al. 2015). Yet, drought is predicted to increase in spring and summer all over Europe under a moderate climate change scenario (Spinoni et al. 2018). Drought is still not uniquely defined; thus, different modelling approaches focus on different indicators. For belowground systems soil moisture is likely to be the most crucial measure, which is projected to decrease in all seasons in Southern Europe, in summer in Western and Central Europe and in spring in Northern Europe (Ruosteenoja et al. 2018). Generally, episodes with anomalously low moisture are expected to become more frequent in all regions of Europe. Such, in part, profound effects on environmental conditions in the belowground systems are likely to also affect soil organisms with potential differences between different regions of Europe.

1.2 DROUGHT EXPERIMENTS

A consortium of soil ecologists identified the effects of global change on soil organisms as one of the most important future priorities for research in soil ecology (Eisenhauer et al. 2017). Among the many aspects encompassed by the term global change, climate change is one of the most rapidly ongoing processes affecting ecosystems around the globe. For soil organisms alterations in the precipitation regime were shown to have the greatest impact of all the different measures of climate change (Blankinship et al. 2011).

1.2.1 Laboratory experiments

Responses of soil organisms to different soil water contents were first investigated in controlled laboratory experiments. Such experiments allow to precisely manipulate water availability and investigate responses at species level. Results indicate that some species are vulnerable to drought, but many can survive even severe reductions in soil water potential (Siepel 1996; Waagner et al. 2011; Slotsbo et al. 2017). Although conclusions on the responses of whole communities under field conditions cannot be drawn from such experiments, they do reveal possible mechanisms which enable soil animals to cope with drought conditions, thus giving valuable hints for the interpretation of responses of different taxa in the field. A number of general morphological and physiological drought adaptations of animals have been identified early on and subsequently experimentally tested in different soil animals (Marx et al. 2012). Some taxa, including heavily sclerotized Oribatida, reduce water loss by a thick cuticula which is covered with water proofing carbohydrates (Benoit et al. 2008; Slotsbo et al. 2017). Additional physiological adaptations to drought include the increase in osmolarity of body fluids by which water vapor can be absorbed even against a water-vapor pressure gradient from the surrounding air. This mechanism has been shown for Collembola as well as for Oribatida (Holmstrup et al. 2015; Slotsbo et al. 2017). Further, the most extreme physiological adaptation to drought, anhydrobiosis, i.e. the tolerance of dehydration of the majority of the body tissue, has been found for the Collembola species *Folsomia angularis* (Crowe et al. 1992; Marx et al. 2012). Hence, laboratory experiments indicate that soil arthropods are principally equipped with different drought adaptations, with Oribatida being generally well adapted by their thick cuticula, while Collembola rather respond to drought with physiological changes.

1.2.2 Field experiments

Results obtained from laboratory experiments may not necessarily be transferred to the situation in the field, because they usually exclude many of the interactions between the organisms and their biotic and abiotic environment. Consequently, a number of experiments have been established to address effects of climate change on soil organisms under field conditions (Beier et al. 2004; Mikkelsen et al. 2008; Schädler et al. 2019). However, the construction of such drought experiments in the field is accompanied by several challenges (Beier et al. 2012). One is to achieve a predictable amount of rain exclusion. This has been approached by using either permanent or automatically closing roofs. Permanent roofs with complete or partial coverage of a predefined area can principally be adjusted according to the intended amount of rain interception. However, in reality this did not always give satisfying results (Yahdjian and Sala 2002; Gimbel et al. 2015; Canarini et al. 2016). Roofs that close automatically during rain events usually reliably intercept close to 100% of the ambient precipitation. In some experiments part of the precipitation is redirected onto the plot in order to simulate a more realistic drought scenario, with the intercepted amount of rain precisely controlled (Mikkelsen et al. 2008; Parra et al. 2012). This approach is, however, expensive and labor intensive because an electricity source and regular maintenance are needed, making such constructions not suitable for many field experiments. Besides the reliable amount of rain exclusion, the main advantage of roofs that are only closed in times when there is precipitation is the reduction of unintended artifacts caused by the roof construction itself. Such artifacts include passive warming, increased humidity and reduced photosynthetically active radiation (PAR) and were reported from several studies using permanent roof constructions (Svejcar et al. 1999; Vogel et al. 2013). When using permanent roofs it is therefore necessary to either minimize these artifacts or account for them. Yahdjian and Sala (2002) have proposed using V-shaped acrylic glass bands with free space in between to increase air flow under the roofs and thereby reduce effects on other environmental variables except precipitation. They did, however, detect shelter artifacts on radiation, air and soil temperature. Nonetheless, this roof design had many advantages including the low costs and the flexible amount of interception by a variable number of acrylic glass bands. We therefore developed this design further first by using PAR-transparent acrylic glass in order to reduce alteration of radiation and second by including a control roof construction that did not exclude rain, but affected other environmental variables in the same way as the original roof construction did (Kundel et al. 2018). We thereby reduced unintended alterations of environmental conditions under the roof and accounted for inevitable artifacts.

1.3 DROUGHT AND SOIL ANIMALS

A meta-analysis by Blankinship et al. (2011), including only results from field experiments, indicated a general positive correlation between soil moisture and the abundance of soil organisms. However, results on drought effects from field experiments are not consistent with some showing negative, but with others reporting also neutral or even positive effects on soil organisms making general conclusions uncertain (Petersen 2011; Eisenhauer et al. 2012; Holmstrup et al. 2013; Vestergård et al. 2015; Flórián et al. 2019; Homet et al. 2021). Several authors suggested that interactive effects with other parameters, such as soil characteristics, taxonomic group or local climate, may modulate the effect of drought and, hence, should be considered in future drought experiments (Blankinship and Hungate 2007; Wu et al. 2011; Beier et al. 2012).

1.3.1 Soil characteristics

Soil organic carbon (SOC) content is a soil parameter that has the potential to interact with drought, as it increases soil structure and thereby soil water holding capacity (WHC) (Shepherd et al. 2002; Manns and Martin 2018). Higher SOC content and subsequently high WHC may thereby mitigate drought effects on soil water content and soil organisms. Further, soils with high SOC content comprise more soil organic matter and associated microorganisms (Fließbach et al. 2007), a major food resource for many soil organisms, such as Collembola and Oribatida (Schneider et al. 2004; Chahartaghi et al. 2005). Hence, shortages in food resources caused by negative drought effects on e.g., microorganisms may be smaller by a generally higher abundance of these resources in soils with high SOC content. Further, SOC content can be actively manipulated by management practices and therefore be one of several tools for adaptation to future climate change in agricultural systems (Iglesias and Garrote 2015).

1.3.2 Local climate

Local climate is an important determinant for soil animal communities in different geographic regions (Nielsen et al. 2010; Ponge and Salmon 2013). Hence, the vulnerability of such communities to drought might differ depending on the conditions they are adapted to with species from arid climates generally being better adapted to drought than species from humid climates. Studies from arid and semiarid climates indeed found no or only minor effects of drought on soil organisms (Liu et al. 2017; Flórián et al. 2019). Such neutral responses under arid climate might be either explained by communities consisting of generally more drought-tolerant species, or, by individual acclimatization. Sjursen et al. (2001) showed for the Collembola species *Folsomia candida* that desiccation-tolerance during severe droughts is higher when there was a preceding mild drought. Similarly, for the Oribatida *Phauloppia* spp. specimens collected during summer were more drought tolerant than specimens collected during winter (Sjursen and Sømme 2000) suggesting seasonal short-term adaptations within a population. In the face of projected severe droughts especially for Southern Europe, it is crucial to better understand such interactions of drought effects and ambient climatic conditions.

1.3.3 Vertical distribution

Most studies on drought effects on soil organisms use changes in abundance as measures of responses to drought. However, animals may additionally or solely respond with changes in behavior. Usually, the abundance of soil animals is higher in upper soil layers, where resources such as soil organic matter and associated microorganisms are most abundant (Perdue and Crossley 1990; Frouz et al. 2004; Bell et al. 2012). One behavioral response to drought is the vertical migration to deeper soil layers, which are usually less affected by drought than upper soil layers (Petersen 2011; Fraser et al. 2012). Such movement through the soil is facilitated in more structured soils that comprise larger and a higher quantity of pores and tunnels (Erktan et al. 2020). Thus, vertical migration as a drought avoidance strategy is more likely in soils with high amounts of soil organic matter, structuring the soil. Moreover, the vertical distribution within the soil profile may be a permanent adaptation to dry conditions, as shown in a study by Petersen (2011), where the abundance of Collembola in deeper soil increased from Northern to Southern Europe.

1.3.4 Trophic niche

Within the soil food web every species is connected with other species via links of different strength (Brose and Scheu 2014; Hines et al. 2015; Potapov et al. 2019). These links have been shown to change in response to changes in environmental conditions (Haubert et al. 2009; MacFadyen et al. 2009; Birkhofer et al. 2011). Drought may thus not only affect individual species by challenging their capability to keep homeostasis, but also by affecting components of the food web with which this species is linked (Verhoef and Witteveen 1980; Bear et al. 2013). Generally, the diet of microarthropods comprises organic matter, microorganisms, fresh plant-based resources such as roots, leaves or roots exudates and other animals (Schneider et al. 2004; Potapov et al. 2016; Li et al. 2020). From the perspective of microarthropods, some of these trophic links to potential food resources might be especially vulnerable against drought (Kaneda and Kaneko 2011) as they are strictly water dependent. Taxa like bacteria and nematodes need a water film inside the soil matrix for being able to move and feed (Erktan et al. 2020). Other links may be affected less drastically. Reduced plant growth under drought might be accompanied by a decrease in plant root growth and the provisioning of rhizodeposits to the soil food web, both comprising important resources for microarthropods, especially in agricultural systems (Jaleel et al. 2009; Scheunemann et al. 2015). Drought is therefore likely to alter the availability of food resources and consumers might respond either by starvation and eventually reduced abundances, or, by a switch in food resources. Such a change in number of realized links to food resources would alter the size of the trophic niche of a species. Generally, niche sizes are predicted to become smaller in stable habitats due to advanced specialization (Giller 1996) and in accordance with this were shown to be smaller in undisturbed compared to disturbed habitats (Korotkevich et al. 2018). Drought is by definition an extraordinary event and must, therefore, be considered as a disturbance that potentially broadens the trophic niches of species.

1.4 ARABLE FIELDS

Most drought experiments have been done in forest and grassland ecosystems, whereas arable fields have received little attention (Beier et al. 2012). However, crop production has suffered from drought in the recent past in Central Europe and is predicted to be even more detrimentally affected by drought in the future (Olesen and Bindi 2002; Falloon and Betts 2010; Olesen et al. 2011). Arable systems may be especially vulnerable against drought because they usually lack a litter layer and permanent vegetation cover that could buffer drought effects on the soil. Hence, plants will not only suffer from deficits in their own water demand but may additionally face changes in ecosystem functions that are provided by the soil system (Wardle et al. 2004; Kaneda and Kaneko 2011; Nielsen et al. 2011).

1.4.1 The role of soil microarthropods

Many of these ecosystem functions are mediated by soil organisms, including nutrient cycling, soil structuring and pest control (Bardgett and Van Der Putten 2014). Collembola and Acari, and here in particular Oribatida, are the most abundant arthropods living in agricultural soils (Behan-Pelletier 2003) and, though principally classified as detritivores, feeding on a wide array of resources such as plant litter and roots, bacteria, fungi, algae and other soil animals (Schneider et al. 2004; Chahartaghi et al. 2005; Heidemann et al. 2011). By these many links to other components of the belowground system they influence major processes and ecosystem functions. One is the cycling of nutrients which is modulated by microarthropods mainly by their manifold interactions with microorganisms (Eisenhauer et al. 2010). Microarthropods modulate abundances and species compositions of microorganisms directly by feeding on them and indirectly by dispersing them internally via their digestive system as well as externally on their body surface (Behan-Pelletier 2003; Crowther et al. 2011). In addition, fragmentation and pre-digestion of litter by microarthropods, which increases the surface-to-volume ratio, facilitates further decomposition by microorganisms. Crop production might further benefit from pest control by microarthropods (Schütz et al. 2008; Neher and Barbercheck 2019). This includes direct feeding on e.g., nematode pest species as well as indirect promotion of pest control by fueling populations of predatory antagonists during times of low abundances of pest species. Moreover, soil microarthropods contribute to the formation of soil physical structure. Despite microarthropods are not able to actively create pore space, their feces contribute to soil aggregate formation thereby enhancing soil structure complexity (Maaß et al. 2015; Erktan et al. 2020). Most of these effects of soil microarthropods on belowground processes have indirect effects on crop plants, however, laboratory experiments have shown, that plants indeed profit from the presence of microarthropods (Scheu et al. 1999; Winck et al. 2020). Hence, promoting soil biodiversity including the ecosystem services they enhance is received as a crucial part of sustainable agricultural management.

1.4.2 Management practices

Current decisions on management practices in agriculture face the trade-off between short-term demands of high productivity and maintaining the capacity of food production and the provisioning of ecosystem function in the long-term. Concepts for long-term sustainability are nowadays additionally challenged by stressors caused by climate change which needs to be considered in actions taken to ensure future soil health. Agricultural systems are generally highly disturbed ecosystems, with conventional systems facing the greatest physical and chemical disturbances that include next to regular ploughing and biomass removal also nutrient cycles that are driven by synthetic rather than organic fertilizer inputs (Crossley et al. 1992). Different management regimes, such as organic and conventional farming, can thereby result in profoundly different soil characteristics. Organically managed fields only receive organic fertilizers, such as compost, manure or slurry. Consequently, organically managed fields have higher amounts of soil organic matter accompanied by more complex soil structure and higher WHC compared to conventionally managed fields (Shepherd et al. 2002; Lotter et al. 2003; Gattinger et al. 2012), and, thus, provide soil characteristics that potentially mitigate drought effects. One of the few studies investigating this interaction suggested that climate effects on soil fauna vary little with land-use intensity (Yin et al. 2019). Generally, however, the combined effect between management practices and drought has received only little attention and more evidence is needed to consolidate such indications.

1.5 METHODOLOGY

This dissertation originated within the framework of the project “SoilClim”, a joint project as part of the 2015–2016 BiodivERsA COFUND call for research proposals with partners from Lund University (Sweden), the Research Institute of Organic Agriculture (Switzerland), the Spanish National Research Council (Spain), University of Tartu (Estonia) and University Göttingen (Germany) (ERA-NET 2016). We conducted two drought experiments in winter wheat fields (*Triticum aestivum*). In the first experiment we simulated drought in organically and conventionally managed fields of a long-term agricultural field experiment (DOK-trial; Switzerland; Krause et al. 2020). In the second experiment we established the same roof set-up to establish drought experiments in fields with high and low SOC content along a natural climatic gradient in Europe.

For the drought simulation we developed a new roof design based on the roofs presented by Yahdjian and Sala (2002). We used V-shaped acrylic glass bands to channel rain away from the plot. The design principally allows to adjust the amount of intercepted rain and in our experiments, we intercepted 65% of the ambient precipitation. In a first study we evaluated artifacts of the roof by including two kinds of controls: a second roof construction that included the same metal pipes and acrylic glass bands (turned upside down) as in the drought-simulating roof, but did not intercept rain, and an ambient control without any manipulation. Artifacts were small but present, so we used the two different roof constructions, one intercepting rain, one accounting for roof artifacts, in all other studies. The roofs had a size of 2.5 × 2.5 × 1.2–1.7 m covering an area of 6.25 m². This relatively small steel pipe frame is screwed to impact sleeves in the soil making the construction stable and at the same time giving flexibility for regular removal to allow agricultural management. Roof effects on soil moisture indicated an edge effect of about 75 cm leaving an area of 1 × 1 m for sampling in the center of each plot. A description and evaluation of the roof construction, including a parts list, an assembly instruction and detailed technical drawings are presented in the second chapter of this thesis.

The first drought experiment was conducted in 2017 on the long-term agricultural field experiment, the DOK-trial (Therwil, Switzerland) with a mean annual temperature of 10.5°C and mean annual precipitation of 842 mm (Krause et al. 2020). The soil is a Haplic Luvisol on deposits of alluvial loess. On the DOK-trial different conventional and organic management practices are compared since 1978. We used eight experimental fields (each 5 × 20 m²) that were arranged in four blocks, each including one conventionally and one organically managed field (corresponding to the "CONMIN" and "BIODYN" treatment of the DOK-trial). The organically managed fields received only organic fertilizers, i.e. farmyard manure, compost and slurry, whereas the conventionally managed fields received only mineral fertilizer. Weeds were controlled mechanically in organically managed fields and treated with herbicides in conventionally managed fields. Additionally, pesticides and plant growth regulators were applied in the conventional system. We conducted four sampling campaigns during the growing season of winter wheat, starting in March, before the roofs have been established to measure soil characteristics, and in April, May, and June to sample soil animals.

In the second experiment we established the same roofs at sites in Germany, Sweden, and Spain, representing a natural gradient in precipitation from high to low. Generally, the sites in Germany and Sweden had a temperate, and the sites in Spain a Mediterranean climate. Five field pairs in every country, each comprising one field with high and one with low SOC content, resulted in a complete randomized block design. All plots were established in a 5 × 10 m stripe where no pesticides were applied during the time of the experiment and had a minimum distance to the field edge of 20 m. We conducted three sampling campaigns from March to May (Germany), April to June (Sweden) and February to May (Spain).

Besides responses of abundances, we further analyzed changes of trophic niches of Collembola and Oribatida using stable isotope analysis. The ratio of the stable isotopes of nitrogen allows insight into the trophic level of consumers due to enrichment in ^{15}N in higher trophic levels, whereas the ratio of carbon stable isotopes reflects the basal resources used (Post 2002; Potapov et al. 2019). So far, stable isotope analyses have mainly been used to characterize the trophic structure of soil animal communities of different habitats and to generally clarify the usage of basal resources of certain taxonomic groups (Scheu and Falca 2000; Potapov et al. 2019). Here we apply it in a field experiment with controlled manipulation of environmental factors, allowing to identify changes in trophic niches induced by drought and by different agricultural management. We first compared mean values of isotope ratios in order to detect changes in trophic level and shift of basal resources. Further, we calculated niche sizes, a combined measure of both isotope values of ^{13}C and ^{15}N (Bearhop et al. 2004). As theory suggests that niche sizes are smaller in stable, deterministic environments due to specialization (Giller 1996), we expected trophic niches to be larger under drought and in conventionally managed fields where soil animals face highest levels of disturbance.

1.6 SCOPE OF THE DISSERTATION

This dissertation aims to improve the understanding of drought effects on abundances and trophic behavior of microarthropods in arable crop systems and, further, to identify potential determinants of such responses to drought.

We examined the following main hypotheses:

(1) Drought effects on soil microarthropods are mitigated by organic farming and by high SOC content.

(2) Drought effects are smaller in Mediterranean compared to temperate climate.

(3) Adaptations of microarthropods to drought include migration to deeper soil layers and the broadening of trophic niches.

1.6.1 Chapter overview

In **Chapter 2** we present and evaluate a new roof design that we developed in order to meet all needs of drought simulation experiments in agricultural fields. We provide a detailed description of the roof construction including computer-aided design (CAD) drawings, a complete parts list and an assembly instruction. We further quantified potential artifacts caused by the roof construction by using two types of controls, one ambient control without manipulation and one “control roof” that did not intercept rain. Artifacts were generally small, only under high ambient temperature, soil temperature was slightly increased by the roof. The roof excluded 64.9% of the ambient precipitation, which is very close to the a priori calculated exclusion of 65.1%, indicating a precise prediction of experimental rain exclusion is possible with this roof design. The roofs further proved to sustain under heavy weather in an open landscape and were suited to be used in agricultural fields where management operation require regular removal of the roof.

In the study presented in **Chapter 3** we investigated the effects of simulated drought on the abundance and community composition of soil microarthropods in winter wheat fields under long-term conventional and organic farming in the DOK trial, Switzerland. The abundance of Collembola and Oribatida declined more consistently in conventionally compared to organically managed fields under simulated drought. The abundance of Collembola as well as Meso-, Pro- and Astigmata, but not the abundance of Oribatida, increased in deeper soil layers due to simulated drought, suggesting vertical migration as drought avoidance strategy. The species composition of Oribatida communities, but not of Collembola communities, differed significantly between drought treatments as well as between farming systems and soil carbon content was a major factor structuring Oribatida communities. The results suggest that organic farming buffers negative effects of drought on soil microarthropods, presumably due to higher soil carbon content, and associated higher soil moisture and improved soil structure.

The study presented in **Chapter 4** was based on the same field experiment, but in addition to responses in abundances, we investigated shifts in trophic niches of Collembola and Oribatida as indicated by stable isotope analysis (^{13}C and ^{15}N). Stable isotope values suggested that plant litter and root exudates were the most important resources for Collembola (*Isotoma caerulea*, *Isotomurus maculatus* and *Orchesella villosa*) and older plant material and microorganisms for Oribatida (*Scheloribates laevigatus* and *Tectocepheus sarekensis*). Drought treatment and farming systems did not affect abundances of the studied species. However, isotope values of some species increased in organically managed fields indicating a higher proportion of microorganisms in their diet. Trophic niche size, a measure of both isotope values combined, decreased with drought and under organic farming in some species presumably due to favored use of plants as basal resource instead of algae and microorganisms. Overall, the results suggest that the flexible usage of resources may buffer effects of drought and management practices on the abundance of microarthropods in agricultural systems.

As indicated in chapter 3, SOC has the potential to mitigate drought effects. In the study presented in **Chapter 5**, we therefore conducted a drought manipulation experiment in fields with high and low SOC content. Further, we extended the scope of the climate manipulation to the question if natural differences in climate influence the effect of simulated drought by establishing the same experiment at sites with temperate (Sweden and Germany) and Mediterranean climate (Spain). Of the studied microarthropod groups only Oribatida were significantly affected by drought with the direction of these effects being different in high and low SOC fields and among countries. Drought decreased abundances of Oribatida in low SOC fields and increased them in high SOC field. Negative drought effects occurred only in Sweden driven by strong negative effects in low SOC fields, where soil water content was extremely low (below 7%). Oribatida at the Spanish sites were only little affected indicating that communities from dry climates are adapted to drought, e.g. by living in deeper soil. Overall, the results suggest that drought effects on Oribatida are strongest under temperate climate conditions and that increasing SOC levels in agricultural soils may be a useful tool to mitigate or even reverse negative drought effects.

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2 DESIGN AND MANUAL TO CONSTRUCT RAINOUT-SHELTERS FOR CLIMATE CHANGE EXPERIMENTS IN AGROECOSYSTEMS

Rainout-shelter in winter wheat field in March

Peer-reviewed article:

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ABSTRACT

Climate change models predict reduced summer precipitations for most European countries, including more frequent and extreme summer droughts. Rainout-shelters which intercept part of the natural precipitation provide an effective tool to investigate effects of different precipitation levels on biodiversity and ecosystem functioning. In this study, we evaluate and describe in detail a fixed-location rainout-shelter (2.5 × 2.5 m) with partial interception of natural rainfall. We provide a complete parts list, a construction manual and detailed CAD drawings allowing to rebuild and use these shelters for rainfall manipulation studies. In addition, we describe a rainout-shelter control treatment giving the possibility to quantify and account for potential shelter artefacts. To test the rainout-shelters, we established the following three treatments each in eight winter wheat plots of the agricultural long-term farming system comparison trial DOK in Therwil (Switzerland): (1) A rainout-shelter with 65% interception of rainfall, (2) a rainout-shelter control without interception of rainfall and (3) an ambient control. The rainout-shelter effectively excluded 64.9% of the ambient rainfall, which is very close to the a priori calculated exclusion of 65.1%. In comparison to the ambient control plots, gravimetric soil moisture decreased under the rainout-shelter by a maximum of 11.1 percentage points. Air temperature under the rainout-shelter differed little from the ambient control (-0.55°C in 1.2 m height and +0.19°C in 0.1 m height), whereas soil temperatures were slightly higher in periods of high ambient temperature (+1.02°C) but remained basically unaffected in periods of low ambient temperature (+0.14°C). A maximum edge effect of 0.75 m defined a sampling area of 1 × 1 m under the rainout-shelter. The rainout-shelters presented here, proved to sustain under heavy weather and they were well suited to be used in agricultural fields where management operations require the removal of the rainout-shelters for management operations. Overall, the results confirmed the good performance of the presented rainout-shelters regarding rainout-shelter artefacts, predictable rain exclusion, and feasibility for experimental studies in agricultural fields.

2.1 INTRODUCTION

Climate change models predict a future increase in temperature and altered precipitation regimes for Central Europe (Russo et al. 2013; Spinoni, Naumann, and Vogt 2015; EEA 2017) as well as on a global scale (IPCC 2014). For Switzerland, average annual precipitation is predicted to decrease by 21-28% by the end of the century, accompanied by more frequent drought events in summer (CH2011 2011). Temperature and water availability are key drivers of ecosystem functioning and effects of these changing conditions are expected on biotic and abiotic system components (Porporato, Daly, and Rodriguez-Iturbe 2004). Effects of altered precipitation are primarily documented from forest and grassland ecosystems (Blankinship, Niklaus, and Hungate 2011), with far fewer studies from agroecosystems (Wu et al. 2011; Beier et al. 2012). Models for agricultural systems predict an increased risk of crop yield loss due to higher seasonal variation in precipitation and more frequent water shortages during the growing season (Olesen and Bindi 2002; Falloon and Betts 2010; Trnka et al. 2011; EEA 2017). In order to understand how climate change affects biotic and abiotic components in agroecosystems, it is crucial to simulate such precipitation regimes under field conditions.

Field studies that experimentally alter rainfall primarily use rainout-shelters to exclude ambient precipitation from a pre-defined experimental area. One group of shelter types provides a complete or almost complete exclusion of precipitation by permanently closed roofs (Svejcar, Angell, and Miller 1999; Fay et al. 2000; Poll et al. 2013; Prechsl et al. 2015) or by roofs that are closing automatically during rain events (Mikkelsen et al. 2008; Parra et al. 2012). Roofs that only close during rain events minimize unintended shelter effects on the microclimate, as they are only closed for short periods of time (closed for < 5% of daytime, Mikkelsen et al. 2008). Yet, these roofs do not operate during strong wind, which often coincides with rainfall events and therefore do not exclude 100% of precipitation. The need for a motor and an electricity source for each roof makes this rainout-shelter type very costly for experimental designs with replicated sites and time consuming in terms of maintenance. Fixed rainout-shelters with permanently closed roofs, on the other hand, are often suitable for long-term studies. However, a complete exclusion of precipitation by a permanent roof inevitably has effects on the microclimate, such as alterations of air temperature and photosynthetic active radiation (PAR) (Beier et al. 2012). Further, in long-term studies, complete roofs necessarily need extra irrigation systems, otherwise they do not reflect realistic conditions under climate change as predicted for the next 50-100 years in most regions of Europe.

Major problems of permanent roofs relevant for biota and ecosystem processes include in particular passive warming (Svejcar, Angell, and Miller 1999; Fay et al. 2000; Vogel et al. 2013) and reduced PAR (Svejcar, Angell, and Miller 1999; Vogel et al. 2013). Reduced air circulation under complete exclusion roofs may lower the vapour-pressure deficit (VPD) and thereby reduce evapotranspiration, which in turn lowers the water demand of plants. The combination of complete exclusion roofs with irrigation systems that recirculate the intercepted rain water back onto the plots allows for flexible control of the amount of excluded precipitation (Svejcar, Angell and Miller, 1999; Fay et al., 2003; Castro et al., 2010), but holds the risk of changes in water chemistry (Beier et al. 2012). Again, such systems cannot be installed without access to electricity. Side-effects due to reduced air circulation and changes in water chemistry are limited by using roofs that only partially exclude rain (Yahdjian and Sala 2002; Gimbel et al. 2015; Canarini et al. 2016). These roofs can further be designed to exclude pre-defined amounts of precipitation (e.g. according to predicted climate scenarios) during long-term experiments (Yahdjian and Sala 2002). These authors used V-shaped acrylic bands (**Figure 2.1 C**), which function as gullies to lead the water away and can have varying spacing in between to exclude pre-defined amounts of rain while minimizing effects on other environmental variables.

Here, we propose a revised design of the rainout-shelters by Yahdjian and Sala (2002) for the use in arable crop fields. We inspected potential side-effects of our design and provide a parts list, a construction manual and detailed CAD drawings (computer-aided design) to allow construction of such rainout-shelters. The type of acrylic glass used for our rainout-shelters is highly UV-transparent, which is a major improvement over previously used shelter designs. We tested the effect of these rainout-shelters on basic abiotic conditions in cereal fields in an agricultural long-term experiment in Switzerland (DOK Trial, Mäder et al. 2002). To disentangle intended effects of the manipulated precipitation regime from unintended artefacts of the rainout-shelters, we further established two sets of control plots. Besides undisturbed plots that received ambient precipitation, we installed a replicated set of rainout-shelters that were identical to our original rainout-shelters, but allowed all natural precipitation to reach the area under the rainout-shelter (V-bands were turned over to become Λ-bands). The partial reduction of rainfall simulated by our rainout-shelters reflects predictions of future precipitation changes during the crop growing season in Central Europe (Russo et al. 2013; Spinoni, Naumann, and Vogt 2015; EEA 2017). Our rainout-shelters are suitable for studies in a wide range of ecosystems, including agricultural systems, as they are both stable enough to endure extreme weather events in open land and are removable to allow for management activities. It is further possible to adapt the amount of excluded rainfall according to the needs of a study by adjusting the distance between the V-bands. In this manuscript, we provide a detailed description and evaluation of the proposed rainout-shelter design and discuss the performance of rainout-shelters considering intended and unintended effects on microclimate, soil moisture and edge effects.

2.2 MATERIAL AND METHODS

2.2.1 Site description and design of drought manipulation experiment

We established rainout-shelters in the ‘DOK’ farming system trial (bio**D**ynamic, bio**O**rganic, **K**onventionell, Mäder et al. 2002). The DOK trial has been established in 1978 by the Swiss Federal Research Station for Agroecology and Agriculture (Zürich-Reckenholz, Switzerland) and the Research Institute of Organic Agriculture (Frick, Switzerland) to compare the production levels of arable crops under different organic and conventional farming systems (Fliessbach et al. 2007). The trial site is located in the Leimen valley near Basel, Switzerland (47°30'09.3"N 7°32'21.5"E, 300 a.s.l.) and has a slope of 3-5% in S-N-direction. Mean annual temperature at the site is 9.5°C and mean annual precipitation is 785 mm. The soil (15% clay, 70% silt, 15% sand, Fliessbach et al. 2007) at the site is a haplic luvisol on deposits of alluvial loess (Mäder et al. 2002). Soils in plots where the roofs were installed contained on average 11.9 mg organic carbon per gram of soil.

The rainout-shelter design we present here was developed in the ERA-Net Biodiversa project ‘SOILCLIM’ (http://www.biodiversa.org/976). The main aim of SOILCLIM is to investigate links between soil biodiversity and ecosystem functioning along natural and simulated precipitation gradients and different soil organic matter (SOM) levels.

We established three treatments in four replicated winter wheat (*Triticum aestivum* L. cv. ‘Wiwa’) plots (5 × 20 m) of two farming systems, resulting in 24 subplots. As the aim of the current study was to evaluate the general performance of the rainout-shelter, we did not differentiate between the two farming systems but treated the plots of the two systems as independent replicates (n=8 plots). The three treatments were (i) a precipitation reduction treatment with rainout-shelters (R) (ii) a rainout-shelter control treatment with a modified rainout-shelter that allowed for ambient precipitation levels to assess rainout-shelter artefacts (RC) and (iii) an untreated ambient control without any rainout-shelter (C). Treatments were established in a row, both at the near and the far end of each plot. In order to prevent mutual interference of rainout-shelter and rainout-shelter control treatments, these were never located side by side (**Supplementary Figure 2.1**). Instead, rainout-shelter and rainout-shelter control treatments were always located next to the ambient control treatment or had no adjacent treatment. Positions of treatments were randomised across the eight plots within these limitations, whereas every treatment combination occurred twice across the DOK trial. We maintained a distance between treatments as well as between treatments and field edges of at least 0.5 m. To avoid potential confounding edge effects such as lateral inflow of precipitation on our measurements, we determined all abiotic conditions only in the center of each plot (1.5 × 1 m) Approximately two months after rainout-shelter establishment, we quantified this edge effect by measuring gradients in soil humidity (see 2.3 *Data collection* for details).

2.2.2 Rainout-shelter design

The rainout-shelters consist of a tubular steel frame (2.5 × 2.5 × 1.2-1.7 m, 6.25 m^2; **Figure 2.1 A**) supporting 12 V-shaped clear and UV transparent acrylic glass bands (PLEXIGLAS SUNACTIVE® GS 2458, Evonik Perfomances Materials GmbH, Darmstadt, Germany). Each band had a length of 2500 mm, an inner flange leg length of 96 mm, an angle of 90° and a thickness of 3 mm. According to **Equation 1**, 12 acrylic bands should exclude 65% of the ambient precipitation.

$$Equation\ 1{:}\ Intercepted\ precipitation\ [\%] = \frac{N * Width\ of\ band}{Shelter\ width} * 100\%$$

Equation 1 Amount of precipitation intercepted [%] by number of bands (N). For the current design: N= number of bands (here 12), width of the bands: 135.8 mm, shelter width: 2500 mm.

The amount of intercepted precipitation can easily be adjusted by changing the number of bands (see also Yahdjian and Sala, 2002).

In order to alter natural light conditions as little as possible, we chose a roof band material that is as permeable for the full range of PAR and transparent for most wavelengths of UV-a and -b radiation (Transmission: 380-780 nm ≥ 90%, 315 nm ≥80%), but is still resistant against weathering and possible damage under field conditions [for details see http://www.plexiglas.de/sites/lists/PM/DocumentsAP/222-6-PLEXIGLAS-GS-UV-durchlaessig-de.pdf (in German)]. The acrylic bands were fixed to the steel frame by custom-made holders (**Figure 2.1 B**) on the front steel pipe and an additional central parallel steel pipe (**Figure 2.1 C**). The rainout-shelters have a maximum height of 1.7 m and a minimum height of 1.2 m, resulting in an incline of 13°, which guarantees water run-off, but the incline can be adjusted if required. The horizontal roof parts rest on four supporting steel pipes anchored in the soil using commercially available metal drive-in sleeves (**Figure 2.1 A**).

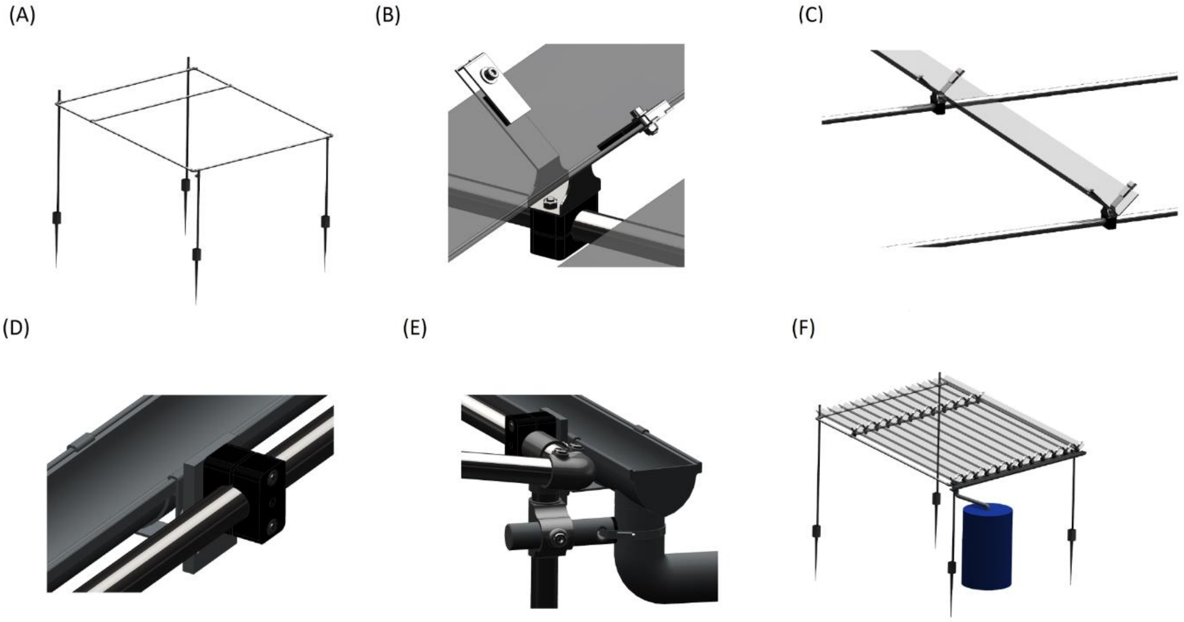

Figure 2.1 A A metal frame (2,5 x 2,5 m) serves as the basic rainout-shelter construction, the shelter is anchored in the soil using drive-in sleeves **B** Acrylic glass bands are fixed to the steel frame by specially designed holders **C** The metal frame supports V-shaped clear acrylic glass bands in which rainfall is collected **D** Rain gutter holder consisting of pipe clamp, adapter plate and gutter bracket (view from the rear) **E** A T-pipe connector with adaptor piece holds the drain pipe in place **F** the final rainout-shelter with partial rainfall interception and precipitation collection.

This construction allows to temporarily remove the rainout-shelter during management actions without much effort. Shelters were located with the lower side facing west, as this is the prevailing wind direction at the study site. Water that was collected by the acrylic bands was channeled via rain gutters (**Figure 2.1 D, E**) at the lower side of the steel frame into 310 L rain barrels (**Figure 2.1 F**). This prevented a reflux of water onto the experimental plot under the roof and allowed to measure the amount of intercepted precipitation. As mentioned above, we established a rainout-shelter control treatment that was identical to the rainout-shelter except that the 12 V-shaped acrylic glass panels were turned over allowing the precipitation to fall onto the plot under the rainout-shelter control. This treatment made it possible to quantify potential artefacts. More details on the parts and the assembly of the rainout-shelters are given in **Supplementary Table 2.1** and **2.2**. A blank-free cutting plan for the pipes, the distances between band holders and details on the adaptor plates for the rain-gutter brackets, the holders for the acrylic glass bands and the clamping claws are shown in **Supplementary Figure 2.7- .11**. One rainout-shelter as we present it in this study costs 730€ (630€ for a control shelter).

2.2.3 Data collection

To assess the actual percentage of precipitation intercepted by the rainout-shelters, we used the precipitation data from a close-by weather station in Therwil, Switzerland (http://www.bodenmessnetz.ch/messwerte/datenabfrage) as well as data from the on-field meteorological station (Campbell-CR1000) and regularly measured the amount of intercepted precipitation in the rain barrels. We then subtracted the average amount of precipitation collected in the rain barrels from the amount of rain that fell on the ambient control plot (6.25 m^2) to calculate the actual percentage of precipitation that was intercepted by the rainout-shelters.

From April to June 2017, we took weekly measurements at three randomly chosen locations within the centre of all 24 subplots to assess volumetric soil water content in 0-6 cm depth (in approx. 75 cm^3 soil) using a handheld Time Domain Reflectometry (TDR)-device (ML-2x ThetaProbe, Delta-T). Each month, we sampled soil in the centre of all experimental plots (0-20 cm depth), oven-dried the soil sample to constant weight and calculated the soil water content [% water, based on g H_2O/g dry weight]. In May 2017, we assessed the extent of lateral water movement ("edge effect") under the rainout-shelter and the rainout-shelter control in a subset of 2 plots, each along transects from north to south and from west to east (see also Yahdjian and Sala (2002)). Along each transect, we measured the volumetric water content using the TDR device in 0-6 cm depth in triplicates at 13 measurement positions (25 cm apart from each other, see **Supplementary Figure 2.2**). For each transect, rainout-shelter type and plot, we performed a one-way ANOVA to assess the effect of the measurement position (distance from shelter edge) on the soil water content, followed by a Tukey's honestly significance post hoc test. We confirmed the fit of the models by visual inspection of the residual plots, which did not reveal any obvious deviations from homoscedasticity or normality.

We assessed possible shelter effects on the microclimate using iButtons temperature loggers (DS1922L/T/E/S; accuracy: 0.0625 °C, 1 record/hour) by constantly measuring air temperature at a height of 0.1 m in the centre of each plot (total N = 3 subplots, each one iButton in a rainout-shelter treatment, a rainout-shelter control treatment and an ambient control treatment), and 1.2 m (total N = 6 subplots, each one iButton per treatment in 2 plots) as well as on soil temperature at 0.1 m depth (total N = 6 subplots, each one iButton per treatment, 2 plots). For each of the three temperature datasets, we calculated a daily mean temperature to determine the day with the highest and lowest temperature, respectively. We then averaged the individual hourly temperature readings of the highest temperature day, the respective previous and following day for each of the three treatments to calculate mean differences and standard deviations between rainout-shelter treatments and ambient control plots. We used this information to describe potential shelter artefacts under the two most extreme environmental scenarios. In the same way, we also proceeded with the lowest temperature day. In cases the lowest/highest day was the first/last day of the recording period, we used the two following or preceding days, respectively. We harvested aboveground biomass of the wheat plants four, eight and 13 weeks after rainout-shelter establishment from subplots (20 cm x 50 cm, 2 wheat rows), each subplot located in the core area of the experimental plots (see **Figure 2.3**). The analysis of all data and drawing of all figures (excluding the CAD drawings) were done using R (R Core Team 2016) and the package *ggplot2* (Wickham 2009). CAD drawings were created with Siemens NX.

2.3 RESULTS

2.3.1 Precipitation interception, soil moisture and edge effect

In total, precipitation under the rainout-shelters was 70.6 mm (19th of April - 06th of June 2017) corresponding to a precipitation reduction of 64.9% as compared to the ambient precipitation (201.1 mm) at the study site.

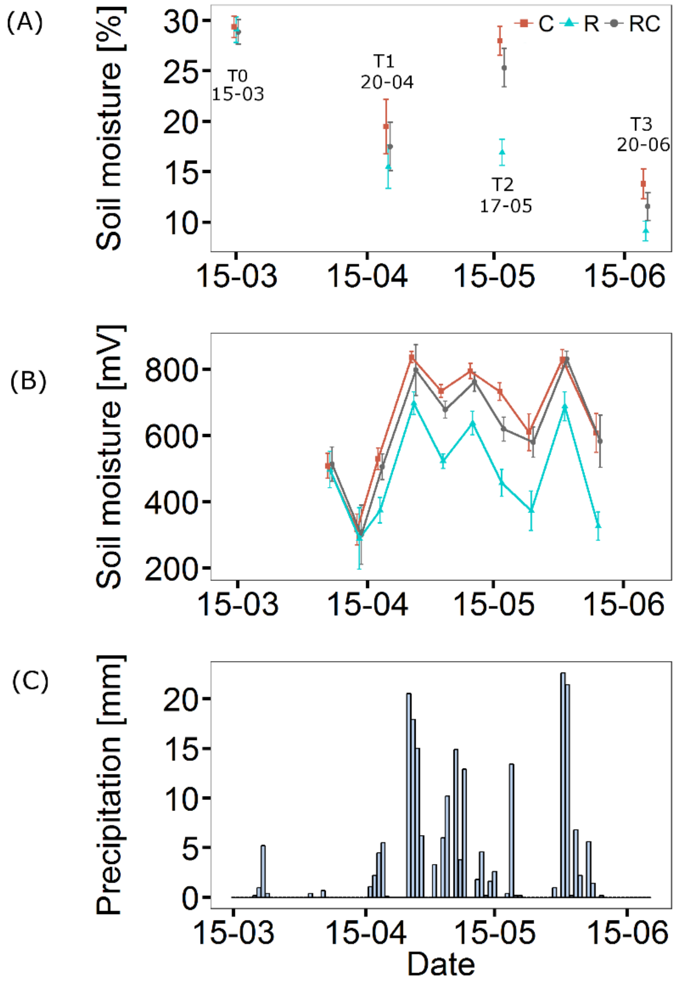

Figure 2.2 **A** Rainout-shelter effect on soil water content [% water, based on g H_2O/g soil dry weight] as assessed in the top 20 cm (means ± standard deviation, n= 8) on March 15, 2017 (baseline assessment; T0), April 20, 2017 (first assessment; T1), May 17, 2017 (second assessment; T2) and June 20, 2017 (third assessment; T3) **B** Rainout-shelter effects on volumetric soil water content measured with a TDR device (ML-2x ThetaProbe, Delta-T) in 0-6 cm depth. Data points represent means ± standard deviation, n=8 **C** Precipitation [mm in 24 hours] during the rainfall manipulation experiment. Data between April 5 to May 8, 2017, derived from the online database http://www.bodenmessnetz.ch (station in Therwil), all other data was recorded by the on-site weather station (Campbell-CR1000).

This observed value is almost identical to the expected precipitation exclusion values based on a priori calculations for a shelter with 12 bands (-65.2%, **Equation 1**). In the week prior to rainout-shelter establishment (baseline assessment; T0), all treatment plots had comparable soil water contents (ambient control (C): 29.37% ± 1.07% (Mean ±SD), rainout-shelter control (RC): 28.87% ± 1.21%, rainout-shelter (R): 29.10% ± 1.27%; **Figure 2.2 A**). There was little precipitation between T0 and the first assessment (T1; 21.2 mm in 36 days, **Figure 2.2 C**). Soil water content under both shelter types therefore differed only slightly from the ambient control plots (R: -4.0 percentage points (pp) ± 1.54 pp, n = 8, RC: -1.98 pp ± 1.50 pp, n = 8) at T1 (35 days after rainout-shelter establishment). The amount of precipitation increased between T1 and the second assessment (T2; 121.6 mm in 27 days; **Figure 2.2 C**) and we recorded more pronounced differences in the soil water content between the rainout-shelter treatment plots and the ambient control plots (R: -11.06 pp ± 0.71 pp, n = 8). In contrast, the soil water content in the rainout-shelter control treatment plots was only weakly lower as compared to the ambient control plot (RC: -2.66 pp ± 1.27 pp, n = 8). Between T2 and the third assessment (T3), precipitation was low again (75.6 mm in 35 days; **Figure 2.2 C**), and differences between the two rainout-shelters and ambient control decreased (R: -4.68 pp ± 1.65 pp, RC: -2.24 pp ± 1.39 pp).

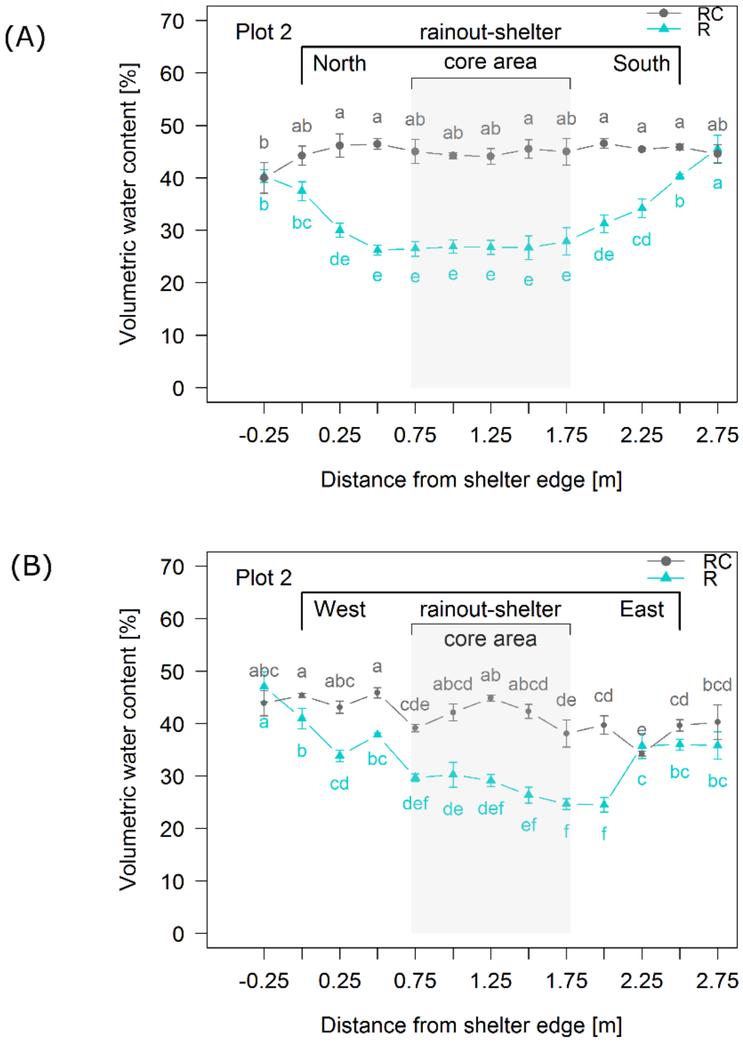

Figure 2.3 **A** Assessment of the soil water content under the rainout-shelter (R) and the rainout-shelter control (RC) using a handheld TDR device (ML-2x ThetaProbe, Delta-T) in the top 6 cm of soil. Data points represent means ± standard deviation, n=3. We measured along transects located **A** North–South and **B** West-East in two of the eight experimental plots (see also **Supplementary Figure 2.3**) on May 15, 2017. Data was analyzed by a one-way ANOVA followed by a Tukey's honestly signi-ficance post hoc test. Means within treatments not sharing the same letter are significantly different (Tukey HSD, $P < 0.05$). Rainout-shelters were located with the lower side facing west as this is the prevailing wind direction at the study site.

Data from weekly soil moisture measurements as determined with the TDR device in the top 6 cm of soil also revealed only minor deviations in soil water content between the rainout-shelter control treatment and the ambient control. The data further confirmed that soil moisture content in the rainout-shelter treatment was considerably lower already 1 month after rainout-shelter establishment as compared to the ambient control treatment (Figure 2B). Edge effects on soil moisture were only detectable up to 75 cm under shelter the area (Figures 3A, B, Supplementary Figures 3A, B).

2.3.2 Shelter Effect on Microclimate

Our rainout-shelters had slight impacts on air temperature at 1.2 m height (06th of April - 20th of June 2017; **Supplementary Figure 2.4**) in comparison to ambient control plots (R: -0.55°C ± 2.76 °C, n = 3648; RC: -0.59 °C ± 2.58 °C, n = 3648). During the period with high ambient temperatures (18th -20th of June 2017), we recorded reduced temperatures up to 1.0 °C in the two rainout-shelter treatments as compared to the ambient control plot (rainout-shelter; R: -0.92 °C ± 3.46 °C, n = 144; rainout-shelter control; RC: -0.94 °C ± 3.3 °C, n = 144; **Figure 2.4 A**). During the period with rather low temperatures (26th - 28th of April 2017) air temperature was only marginally lower under both rainout-shelter types (R: -0.11 °C ± 1.27 °C, n = 144; RC: -0.23 °C ± 1.28 °C, n = 144) as compared to the ambient control plots (**Figure 2.4 B**).

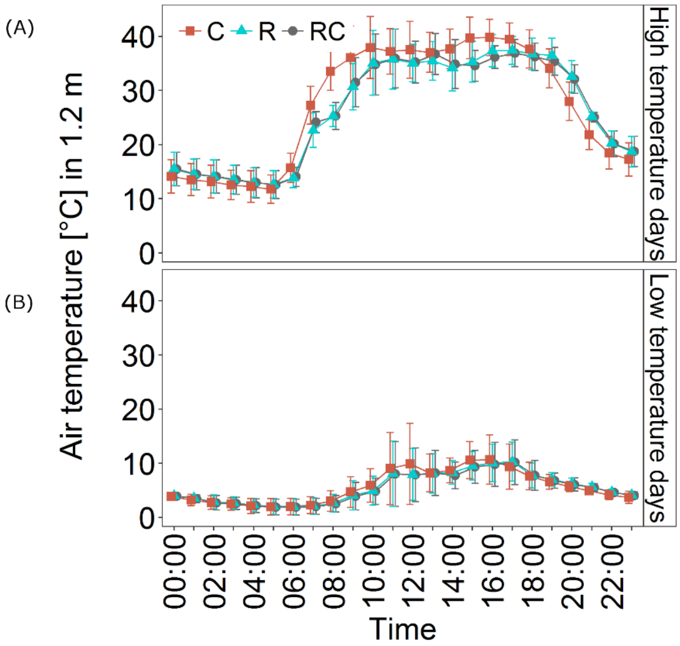

Figure 2.4 Air temperature [°C] as measured in 1.2 height using iButton temperature loggers under the rainout-shelter (R), the rainout-shelter control treatment (RC) and the ambient control plots (C). Data points represent hourly temperature measurements (means ± standard deviation) of two plots and three days during **A** a high temperature phase (June 18-20, 2017) and **B** a low temperature phase (April 26-28, 2017).

The rainout-shelters had very little impact on air temperature at 10 cm above soil surface (07th of April-05th of June 2017; **Supplementary Figure 2.5**) as compared to ambient control plots (R: +0.19°C ± 1.25°C, n = 1440; RC: +0.19°C ± 1.06°C, n = 1440). Deviations from ambient temperature readings were low during the high (R: +0.11°C ± 1.06°C, n = 72; RC: +0.19°C ± 0.88°C, n = 72; **Figure 2.5 A**) and low (R: +0.17°C ± 1.56°C, n = 72; RC: -0.15°C ± 1.36°C, n = 72; **Figure 2.5 B**) temperature period.

Similarly, the two rainout-shelter types had little impact on soil temperature (07th of April - 05th of June 2017; **Supplementary Figure 2.6**) in comparison to ambient control plots (R: +0.64 °C ± 0.53 °C, n = 6076; RC: +0.39 °C ± 0.33 °C, n = 6076). Deviations from ambient temperature readings were low during the high (R: +1.02 °C ± 0.46 °C, n = 828; RC: +0.63 °C ± 0.31 °C, n = 828; **Figure 2.6 A**) and low (R: +0.14 °C ± 0.52 °C, n = 828; RC: +0.20 °C ± 0.41 °C, n = 828; **Figure 2.6 B**) temperature phase.

2.3.3 Shelter effect on shoot biomass production

Shoot biomass production was not significantly affected by the rain exclusion treatment, neither four, eight or 13 weeks after rainout-shelter establishment (data not shown).

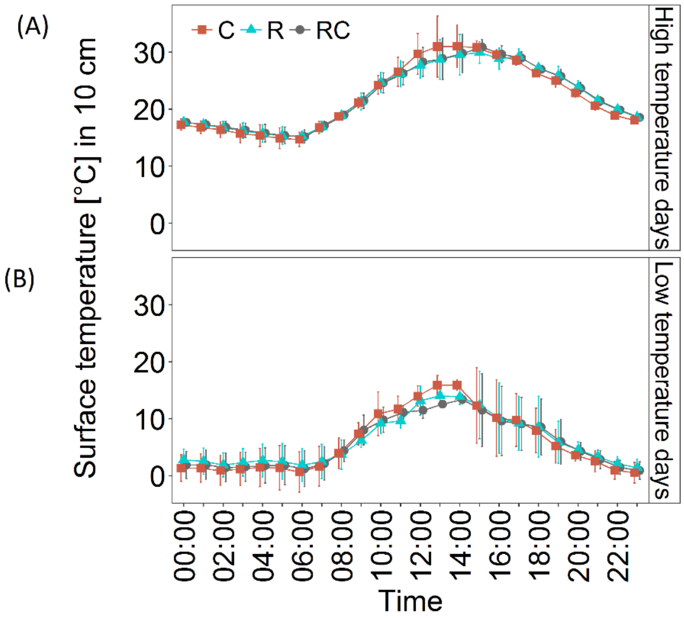

Figure 2.5 Surface temperature [°C] as measured in 0.1 m height using iButton temperature loggers under the rainout-shelter (R), the rainout-shelter control treatment (RC) and the ambient control plots (C). Data points represent hourly temperature measurements (means ± standard deviation) of one plots and three days during **A** a high temperature phase (May 28-30, 2017) and **B** a low temperature phase (April 18-20, 2017).

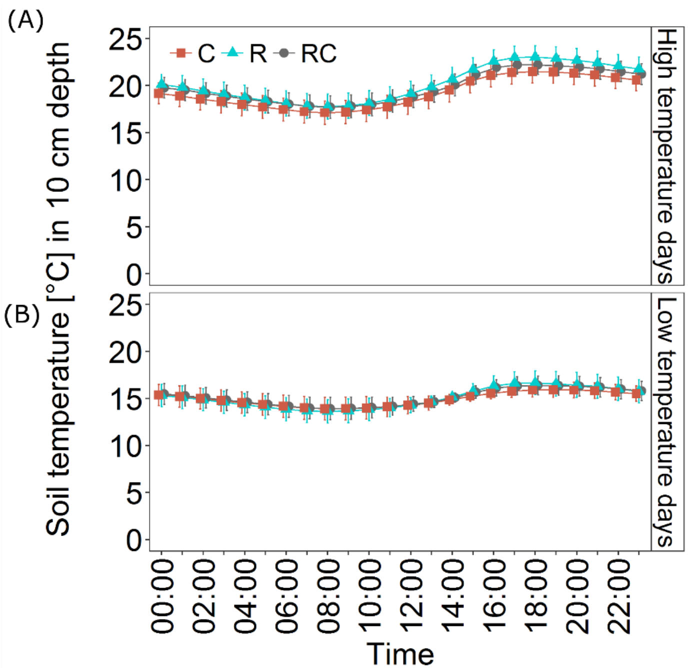

Figure 2.6 Soil temperature [°C] as measured in 10 cm depth using iButton temperature loggers under the rainout-shelter (R), the rainout-shelter control treatment (RC) and the ambient control plots (C). Data points represent hourly temperature measurements (means ± standard deviation) of two plots and three days during (A) a high temperature phase (June 18-20, 2017) and (B) a low temperature phase (June 6-8, 2017).

2.4 DISCUSSION

Previous designs of rainout-shelters revealed several methodological challenges. Rainout-shelters should allow for a predictable alteration of the precipitation amount, minimize artefacts on microclimatic conditions under the shelter, allow for replication across larger spatial scales and be stable enough to persist under field conditions. The rainout-shelter design described here fulfils all these requirements.

2.4.1 Rainout-shelter performance

The rainout-shelters effectively excluded 64.9% of the ambient precipitation, very close to the a priori calculated rain exclusion of 65.2%. A precise prediction of the amount of excluded water depending on the number of acrylic bands in the roof construction is thereby possible and provides a crucial tool for the planning of field experiments.

In addition to measurements of rain drainage and natural precipitation levels, soil water content is an important parameter for the evaluation of the performance of rainout-shelters. Soil water content was very similar in the rainout-shelter control and the ambient control treatment during the whole sampling campaign, and lowest in the rainout-shelter treatment for most of the study period. After an initial phase with similar soil water content in each of the three treatments, soil water content was constantly lower under the rainout-shelter as compared to the ambient control and the rainout-shelter control plots. The soil water content in the experimental treatments started to differ after the first heavy rain events supporting results of previous studies (Mikkelsen et al. 2008; Vogel et al. 2013). Although the early summer 2017 was characterized by several short drought-like periods, the developed rainout-shelters still resulted in differences in soil water content, making the design also suitable for regions with drier climatic conditions.

The spatial extent of an edge effect defines the size of the suitable sampling area under a rainout-shelter. However, only few studies determined edge effects by measurements in the field (Yahdjian and Sala, 2002; Beier et al., 2004). In this study, the maximum edge effect was 0.75 m beyond the edges of the 2.5 x 2.5 m roof area, resulting in a 1.00 x 1.00 m core area receiving full treatment effect and thereby being available for measurements. The assessment of edge effects was conducted after a period of rain events, so that the edge effect of 0.75 m can be considered as the maximum edge effect. The chosen dimensions of the rainout-shelters (2.5 x 2.5 x 1.2 to 1.7 m), which mainly determine the size of the edge effect, result in a reasonable balance between available sampling area, handling and material costs.

The performance of the rainout-shelter material in terms of stability and practicability was excellent. The construction was not damaged by heavy hailstorms or rain events as well as temperatures below 0 and above 30°C, and the UV bands did not show any signs of weathering over the study period. The plastic rain gutters slightly deformed during hot summer days and should be replaced by metal rain gutters, especially at field sites with higher maximum temperatures. The specific requirements of field studies in agricultural areas, i.e. the need to remove the shelters for management activities, were successfully met by our removable rainout-shelter construction (note that at least 4 people are needed to move the rainout-shelter). The workload for maintenance was limited to the drainage of the water barrels which took place every one to two weeks, depending on precipitation events. This limited workload for maintenance allows managing several replicated rainout-shelters even if in use for longer periods of time.

2.4.2 Microclimate

Rainout-shelters may cause lower air temperature due to the interception of radiation (Yahdjian and Sala 2002), on the one hand, on the other hand a greenhouse effect, enhanced by reduced air flow under shelters, may cause higher temperature (Svejcar, Angell, and Miller 1999; Vogel et al. 2013). Both artefacts may bias the results of rainout-shelter experiments.

In this study, air temperature at 1.2 and 0.1 m height above ground was little affected by the rainout-shelter, especially during periods of low ambient temperature. This suggests that the spacing of the acrylic bands allowed sufficient airflow to prevent greenhouse effects under the rainout-shelters. A setup with more acrylic bands and subsequently a narrower spacing between bands, however, may have stronger impact on the temperature regimes. The facilitation of air movement is especially crucial in systems with high and dense plant growth such as cereal crops. In the current study, winter wheat plants in their final growth stages almost reached the height of the rainout-shelter, but temperature measurements still did not indicate greenhouse effects (**Figure 2.4 A**). However, differences in air temperatures of up to 1 °C during periods of high ambient temperature confirm the need of a rainout-shelter control treatment. Our data showed virtually identical temperature under the two rainout-shelter types (**Figure 2.4** and **2.5**, **Supplementary Figure 2.4** and **2.5**), thereby supporting the suitability of a rainout-shelter control, especially under constantly warm conditions.

Soil temperature was slightly higher under the rainout-shelter as compared to the ambient control, but only during periods of high ambient temperature and differences to the control plot were more pronounced under the rainout-shelter than under the rainout-shelter control (**Figure 2.6**). This might be caused by lower soil moisture under the rainout-shelter and consequently lower total water content that buffer heating of the soil by solar radiation. Accordingly, the soil temperature was highest in the rainout-shelter treatment in which soil moisture contents were lowest and only slightly increased in the rainout-shelter control treatment which had intermediate soil moisture contents. This artefact cannot be avoided because lower soil moisture is the goal of the rainout-shelter.

The interception of radiation was minimized by the use of highly UV-permeable acrylic glass bands as roof material (transmission at 315 nm ≥80, transmission 380 - 780 nm ≥ 90%). The use of this material guaranteed natural PAR levels under the rainout shelters.

2.4.3 Conclusions

The rainout-shelter design presented here is well suited for experimental manipulations of precipitation in open land ecosystems and agricultural fields in particular. Microclimatic conditions under the rainout-shelter were largely unaffected and the intended alteration of soil moisture followed our a-priori calculations. Slightly lower under-shelter air temperatures during high ambient temperature phases were the only unintended artefacts we measured. These artefacts were reflected by the rainout-shelter control treatment allowing to account for them. Soil moisture differences between the different treatments established after the first rain events and remained present throughout the experiment. Animated 3-D drawings of the rainout-shelter design (note that the PDF reader needs to be able to show animated PDFs), detailed descriptions of shelter construction, manuals for their setup and a list of material allow future users to apply the developed design in their studies. With this study, the authors hope to promote the use of rainout-shelters to simulate and investigate climate change effects on agricultural systems, which is crucial given the risk of crop yield losses under altered future precipitation regimes.

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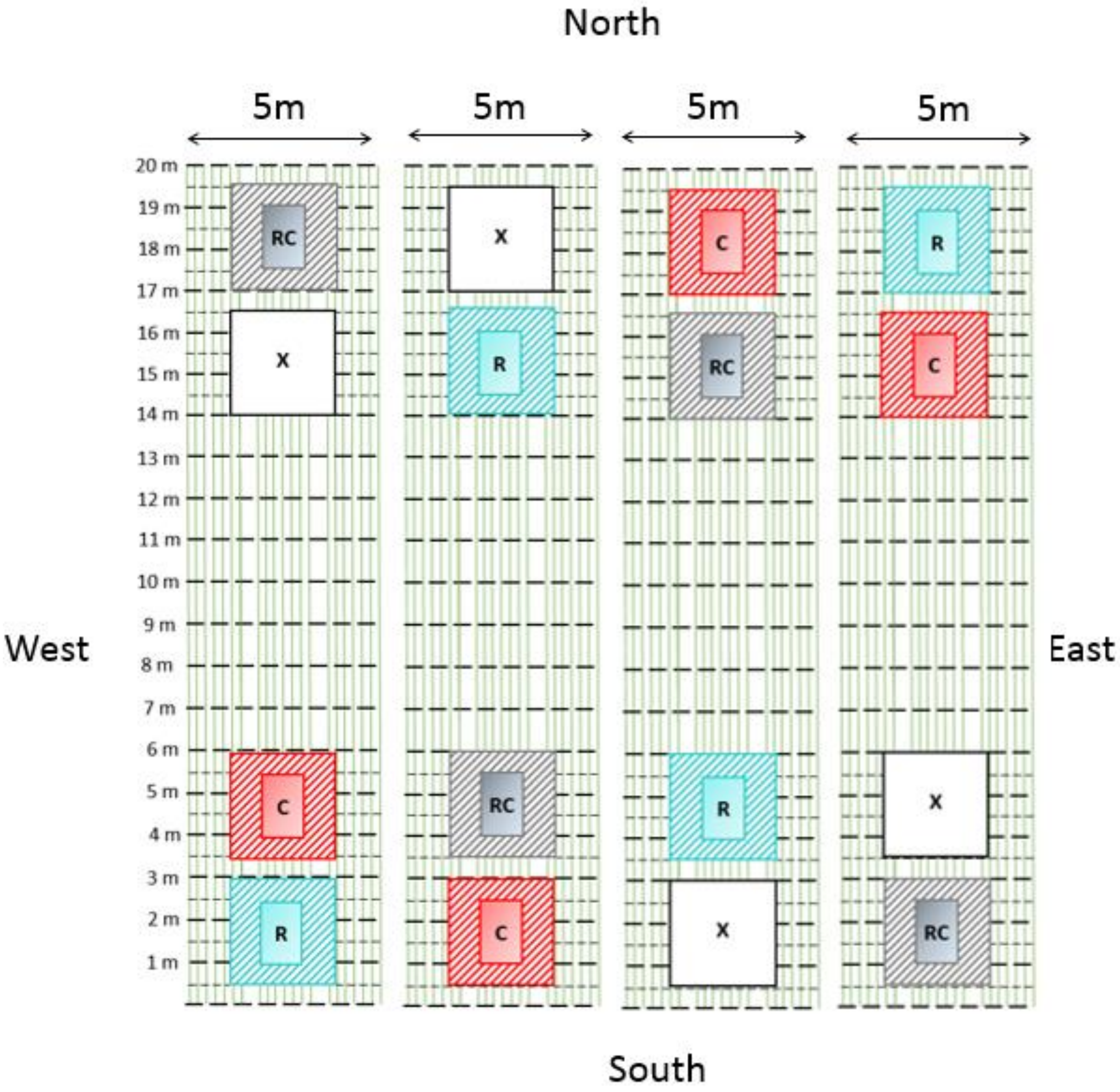
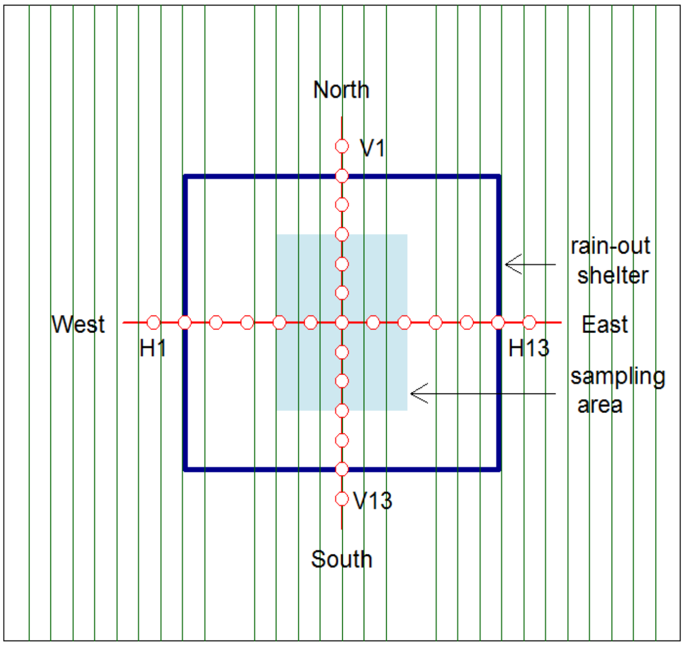
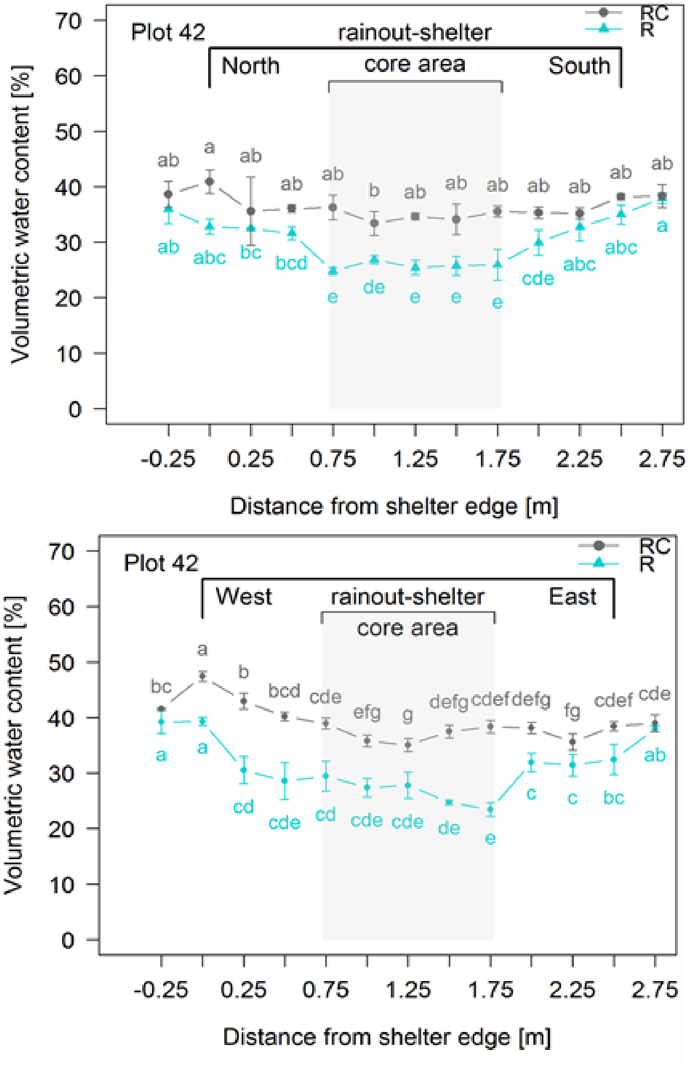
APPENDIX



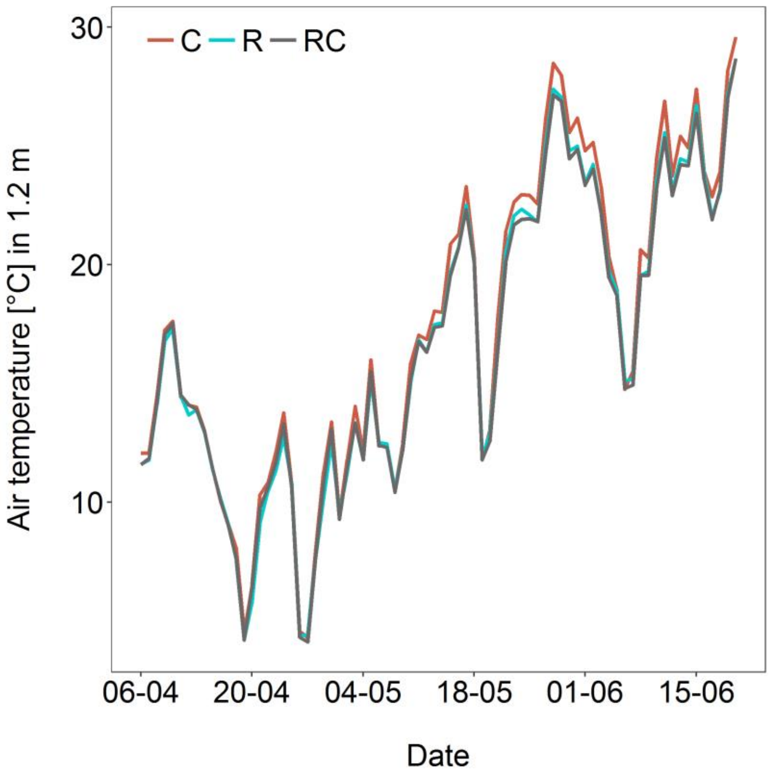
Supplementary Figure 2.1 We established three treatments in each of eight replicated plots (5 × 20 m) as shown (note that only four of the eight plots are shown here, because the remaining four plots are arranged in exactly the same way), resulting in 24 total experimental subplots. R = rainout-shelter, RC = rainout-shelter control treatment, C = ambient control, X = empty position, not used in the experiment. Treatments were established in a row, both at the near and the far end of each plot. We maintained a distance between treatments or treatments and field edges of at least 0.5 m.



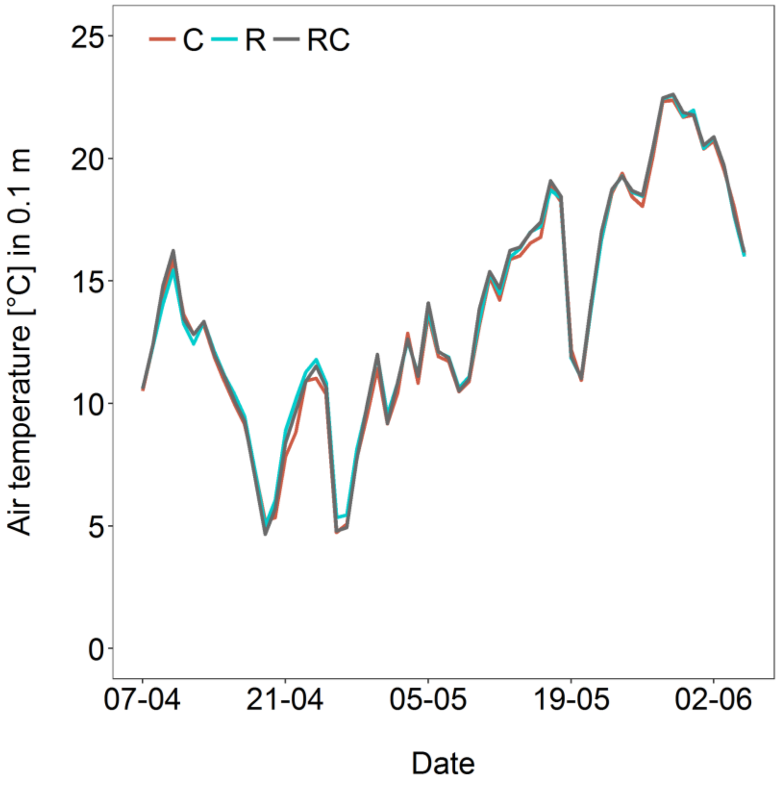
Supplementary Figure 2.2 Assessment of the “edge effect” (extent of lateral water movements into the area under the rainout-shelter) along transect from North to South and from West to East. Along each transect, volumetric water content in 0-6 cm depth was measured in triplicates at 13 measurement positions (H1: (horizontal) W-E measurement position 1-H13: (horizontal) W-E measurement position 13 and V1-V13 for the (vertical) N-S transect, respectively) using a TDR device (ML-2x ThetaProbe, Delta-T). Measurement positions were 25 cm apart. Green lines indicate rows of winter wheat. Design adapted from Yahdjian & Sala (2002).



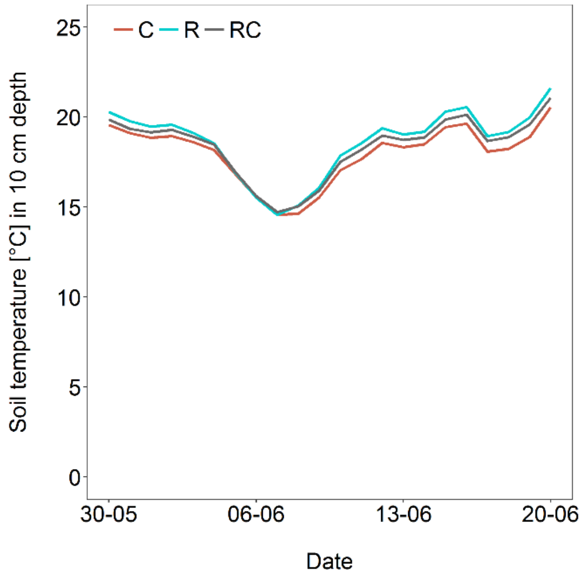
Supplementary Figure 2.3 Assessment of the soil water content under the rainout-shelter (R) and the rainout-shelter control (RC) using a handheld TDR device (ML-2x ThetaProbe, Delta-T) in the top 6 cm of soil. Data points represent mean volumetric water contents [%] ± standard deviation, n=3. We measured along transects located (upper panel) North–South and (lower panel) West-East in two of the eight experimental plots (Plot 42, see also **Figure 2.3**) on May 15th 2017. Data was analyzed by a one-way Anova followed by a Tukey’s honestly significance post hoc test. Means within treatments not sharing the same letter are significantly different (Tukey HSD, $P < 0.05$). Rainout-shelters were located with the lower side facing west as this is the prevailing wind direction at the study site.



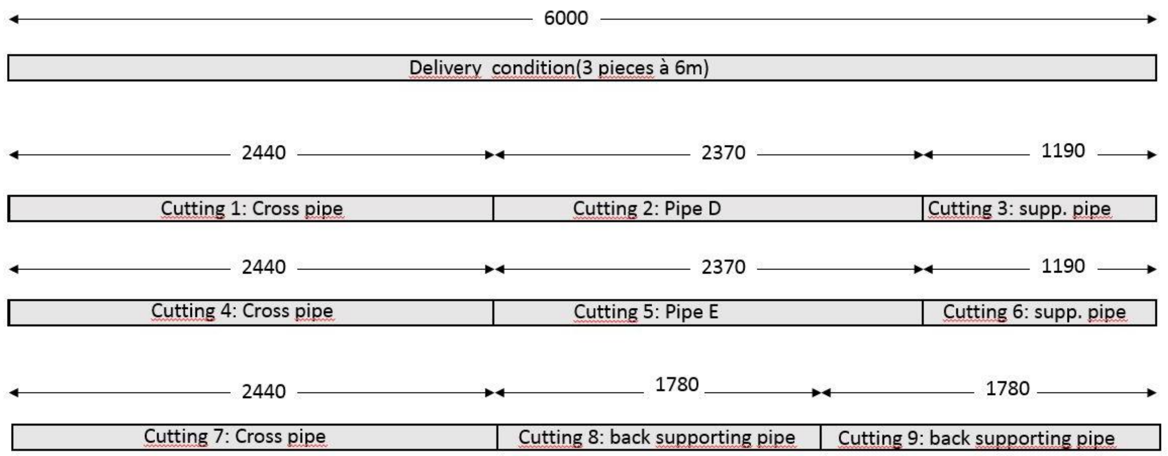
Supplementary Figure 2.4 Average daily temperature readings [°C, two subplots per treatment, 1.2 m height] as calculated from hourly records using iButton temperature loggers. R: rainout-shelter, RC: rainout-shelter control, C: ambient control plot. Temperature was recorded from April 6-June 20, 2017.



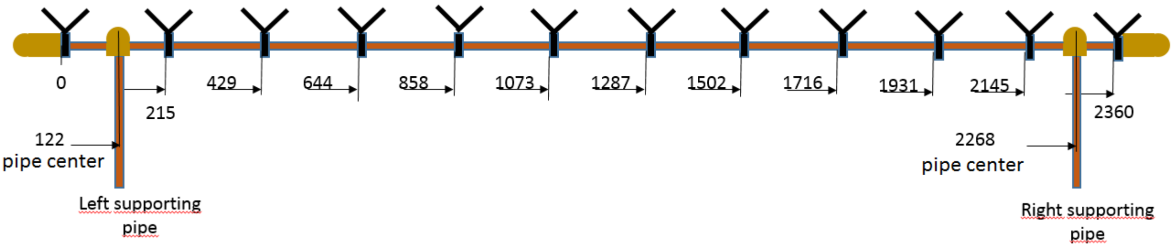
Supplementary Figure 2.5 Average daily temperature readings [°C, one subplot per treatment, 0.1 m height] as calculated from hourly records using iButton temperature loggers. R: rainout-shelter, RC: rainout-shelter control, C: ambient control plot. Temperature was recorded from April 7 - June 5, 2017.



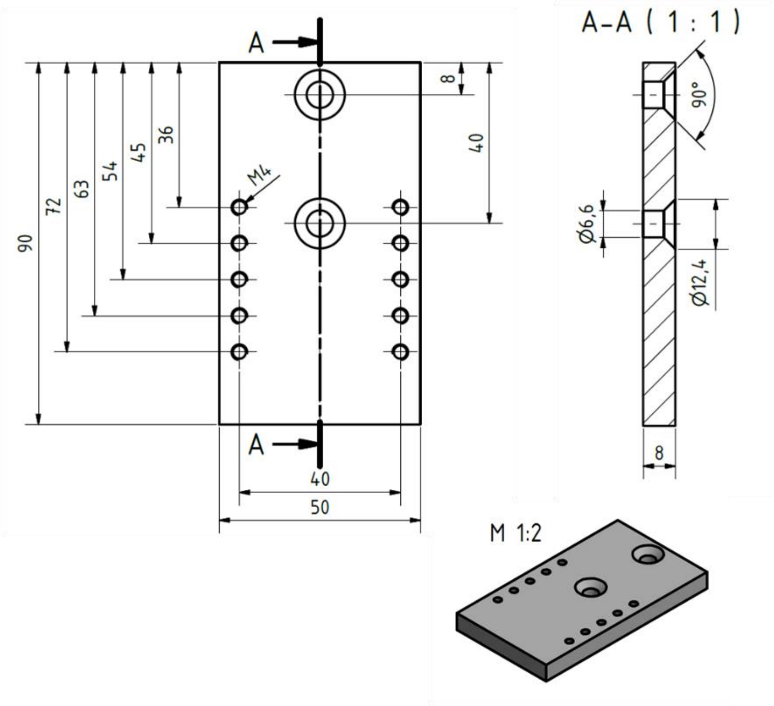
Supplementary Figure 2.6 Average daily soil temperature readings [°C, two subplots per treatment, 0.1 m depth] as calculated from hourly records using iButton temperature loggers. R: rainout-shelter, RC: rainout-shelter control, C: ambient control plot. Temperature was recorded from May 30 - June 20, 2017.



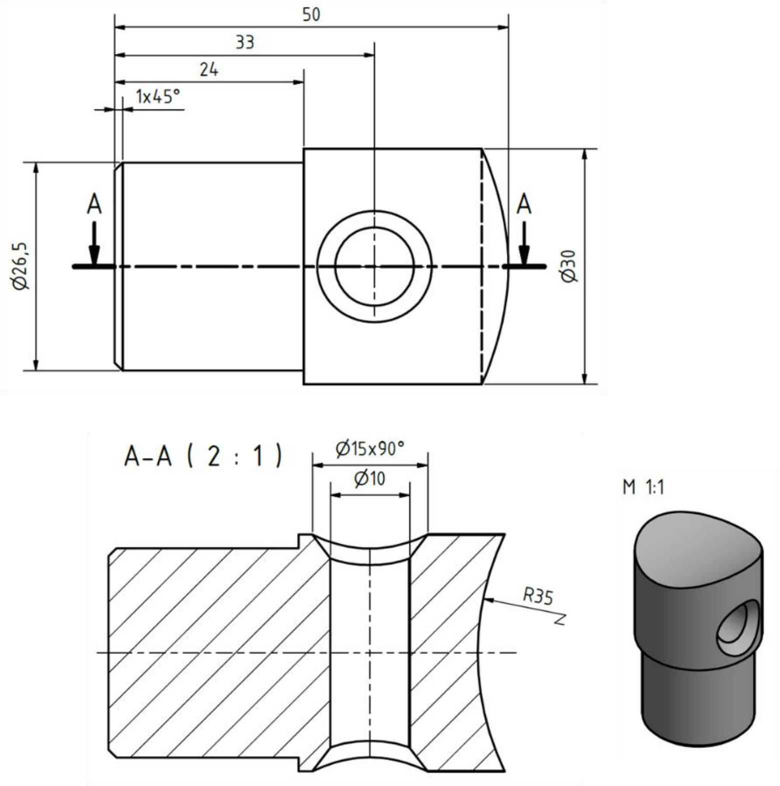
Supplementary Figure 2.7 Blank-free cutting plan for pipes d= 26.9 mm for the rainout-shelter and rainout-shelter control tubular frames. All 4 supporting pipes have 2 cross holes (d=7 mm) at one end for screw connections to attach them to the drive-in sleeves. All dimensions in millimeters.



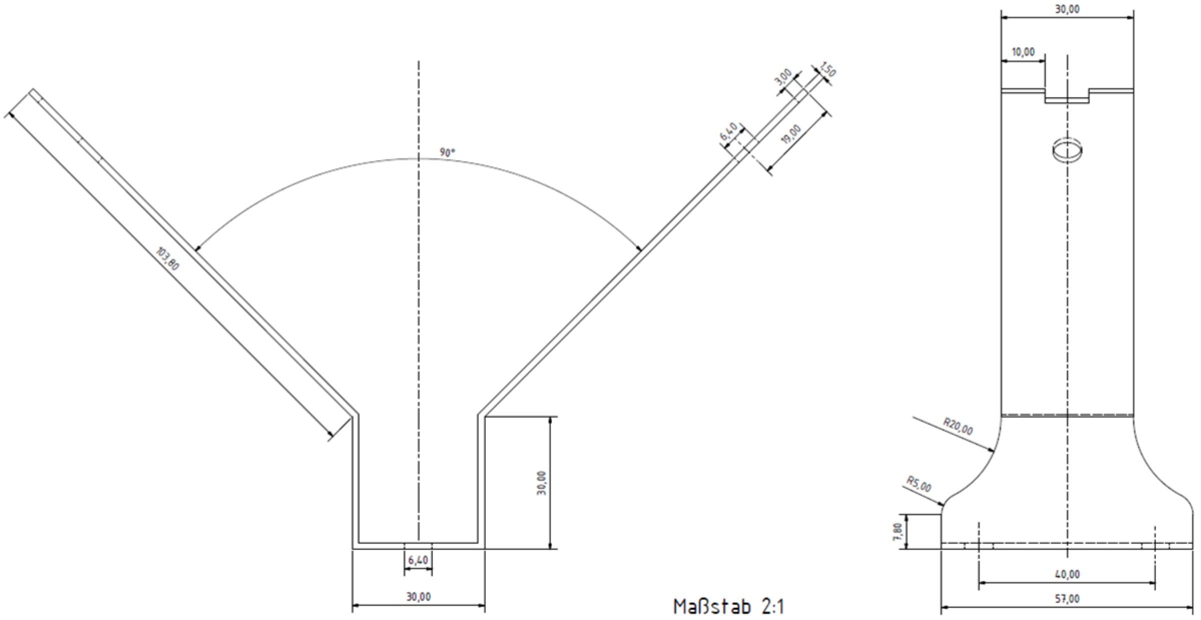
Supplementary Figure 2.8 Distance between acrylic glass band holder positions for a rainout-shelter/rainout-shelter control with 12 bands. It is recommended to mark the distances between holders with felt-tip pen on the 2 cross pipes before mounting the tubular frame as this facilitates the alignment of the pipe clamps/holders afterwards (see supplementary **Figure 2.7** and **Supplementary Table 2.2** for a clarification of the naming of the different pipes). All dimensions in millimetres.



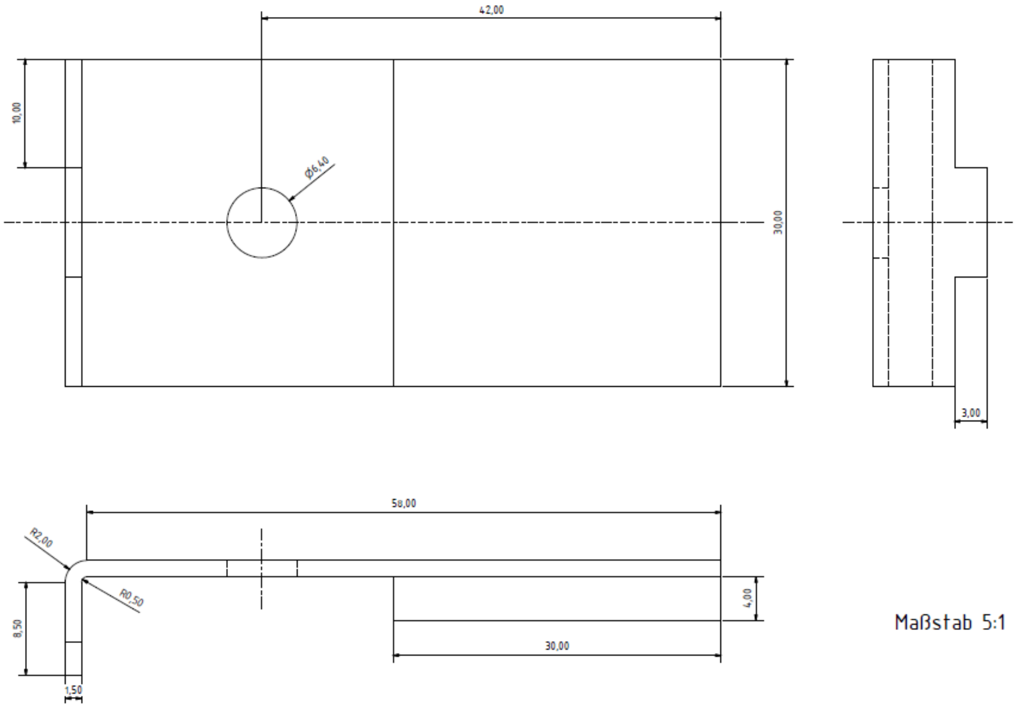
Supplementary Figure 2.9 Adapter plate for mounting of rain gutter. All dimensions in millimeters.



Supplementary Figure 2.10 Connecting part (custom-made from PVC) to connect the outlet cone of the rain gutter to the pipe steel frame of the rainout-shelter. View below: Connecting part rotated by 90°. All dimensions in millimeters.



Supplementary Figure 2.11 Single piece laser-cut holders for acrylic glass bands, sheet thickness 1.5 mm**;** arm-length of the holder 103.8 mm. All dimensions in millimeters.



Supplementary Figure 2.12 Clamping claw to fix the acrylic glass band in the holder, punched d = 6.4 mm; width 30 mm Flange-length 60 x 7/8 mm after bending; all parts in stainless steel 1.4301. All dimensions in millimeters.

Supplementary Table 2.1 Parts list for a rainout-shelter and a rainout-shelter control (= without rainfall collection system). Each shelter with 12 acrylic bands à 2 band holders, complete frame with a central cross-pipe, roof pitch can be adjusted from 0 to 13 degrees.

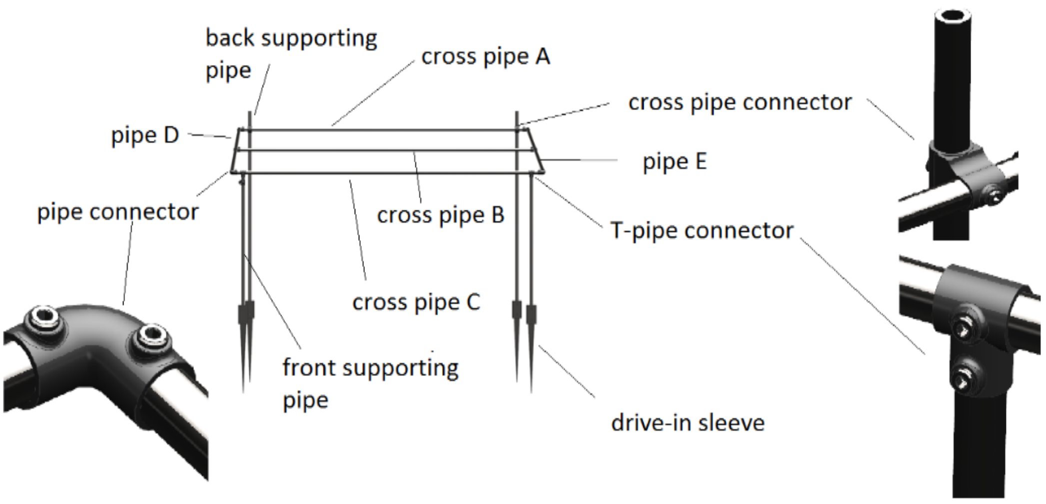
Part No.	Part	Specification	Material	Number of parts	
				for 1 experimental shelter	for 1 control shelter
1	Cross pipe A, B & C	26.9 (R3/4“) x 2440 mm length	V2A (stainless steel 1.4301), pipes welded but not sanded	3	3
2	Pipe D & E	26.9 (R3/4“) x 2370 mm length	V2A (stainless steel 1.4301), pipes welded but not sanded	2	2
3	Front supporting pipe*	26.9 (R3/4“) x 1190 mm length	V2A (stainless steel 1.4301), pipes welded but not sanded	2	2
4	Back supporting pipe*	26.9 (R3/4“) x 1780 mm length	V2A (stainless steel 1.4301), pipes welded but not sanded	2	2
5	T-pipe connector	Type 2B; 26.9 mm (3/4“)	Grey cast iron, galvanized	4	4
6	Elbow pipe connector (90º)	Type 6B; 26.9 mm (3/4“)	Grey cast iron, galvanized	4	4
7	Cross pipe connector	Typ 288; 26.9 mm (3/4“)	Grey cast iron, galvanized	3	3
8	V-shaped acrylic glass band	Length=2500 mm, flange length before bending 193 mm, flange length bended 96 mm (inside), opening angle 90º, thickness 3 mm (‘UV-transparent and UV-stabilized’)	Acrylic glass GS 2458	12	12
9	Adapter plate for gutter	See **Supplementary Figure 2.9**	Polyvinyl chloride	3	0
*Rework pipes: 6 cutting sections in the 6 m pipes according to **Supplementary Figure 2.7**, **2.4** supporting pipes with 2 holes each (d=6.4 mm; distance of the holes according to the holes in the drive-in sleeves)					

10	Connecting part for gutter	See **Supplementary Figure 2.10**	Polyvinyl chloride	1	0
11	Holder acrylic glass band	Single piece laser-cut part, sheet thickness 1.5 mm (see **Supplementary Figure 2.11**)	Stainless steel 1.4301	24	24
12	Clamp for acrylic glass band	Sheet thickness 1.5 mm, punched d=6.4 mm; width 30 mm Flange-length 60 x 7/8 mm after bending (see **Supplementary Figure 2.12**)	Stainless steel 1.4301	48	48
13	Drive-in sleeve	Drive-in sleeve 71 x 71 x 750 mm	Steel galvanized	4	4
14	Pipe clamps**	Pipe clamps, light series – plastic, pipe outer diameter 26.9 (¾“) mm, size 4	Polypro-pylene	33 (Holder acrylic-band: 24, gutter: 3, drive-in sleeves: 4 (8 half pieces), safety-stop on back supporting pipes: 2)	30 (Holder acrylic-band: 24, drive-in sleeves: 4 (8 half pieces), safety-stop on back supporting pipes: 2)
15	Hose clamp (for gutter)	Worm thread clamp - 1.4301 W4 - clamping range 80 – 75 mm - belt width 9 mm; DIN 3017	V2A (stainless steel 1.4301)	1	0
16	Rain gutter	Nominal diameter 75 mm, length 3.00 m	Polyvinyl chloride	1	0
17	Gutter end part	Nominal diameter 75 mm	Polyvinyl chloride	2	0
18	Rain gutter outlet cone	Rain gutter outlet cone, 75/50 mm	Polyvinyl chloride	1	0
**Rework pipe clamps: Central hole d = 7 mm; 4 (8 half-pieces) for 1 rainout-shelter, 4 (8 half-pieces) for 1 rainout-shelter control					

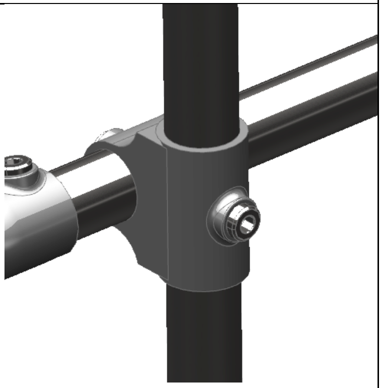
19	Gutter bracket	Nominal diameter 75 mm	Polyvinyl chloride	3	0
20	Angular pipe (gutter)	Angular pipe, nominal diameter 75 mm, 87 degree, grey	Polyvinyl chloride	2	0
22	PVC-glue (for rain gutter)	PVC-glue 100 g		As required	0
23	Socket head cap screw	DIN 912 Socket head cap screw, stainless steel, A2 M6x45	V2A	60 (Holder acrylic-band: 48, drive-in sleeves: 8, safety-stop: 4)	60 (Holder acrylic-band: 48, drive-in sleeves: 8, safety-stop: 4)
24	Socket head cap screw	DIN 912 Socket head cap screw, stainless steel, A2; M6x20	V2A	48 (Clamp for acrylic-band: 48)	48 (Clamp for acrylic-band: 48)
25	Washer	DIN 125-A grade A washers; washer without chamfer, size: 6.4 x 12 x 1.6 mm	V2A	54 (Holder acrylic-band: 48, pipe clamp for gutter bracket: 6)	54 (Holder acrylic-band: 48, pipe clamp for gutter bracket: 6)
26	Large diameter washer	DIN 9021 A2 large diameter washer, size 6.4 x 18 x 1.6 mm	V2A	56 (Holder acrylic band: 48, drive-in sleeves: 8)	56 (Holder acrylic band: 48, drive-in sleeves: 8)
27	Hexagon nut	ISO 4032 A2 Hexagon-nut, ISO-Type 1, size M6	V2A	62 (Holder acrylic band: 48, drive-in sleeves: 8, Gutter mounting: 6)	62 (Holder acrylic band: 48, drive-in sleeves: 8, Gutter mounting: 6)

28	Self-locking nut	DIN 985 A2 self-locking nut, size M6	V2A	48 (Clamp for acrylic band: 48)	48 (Clamp for acrylic band: 48)
29	Counter-sunk screw	DIN 965 A2 -H Countersunk screw with Phillips-crosshead H, size M6x50 -H	V2A	6 (Gutter adapter plate: 6)	0
30	Large diameter washer	DIN 9021 A2 large diameter washer, size: 5.3 x 15 x 1.2 mm	V2A	15 (Gutter mounting:15)	0
31	Self-tapping screw	DIN 7981 self-tapping screw, form C, stainless steel, A2 4.8x 13, DIN 7981	V2A	15 (Gutter mounting: 15)	0
32	Neoprene base	NBR Cellular rubber – 4 mm thickness, one-sided self-adhesive, 10 m roll, width 30 mm	Neoprene	48 pieces, length 30 mm = 1,440 m (=0,144 x length of roll of 10 m; 10 m roll sufficient for 6,95 roofs)	48 pieces, length 30 mm = 1,440 m (=0,144 x length of roll of 10 m; 10 m roll sufficient for 6,95 roofs)
33	Rain barrel	Rain barrel (appr. 300 litre)	Plastic	1	0

Supplementary Table 2.2 Assembly instruction to build the rainout-shelter and the rainout-shelter control, respectively. All items needed are listed in the material list (**Supplementary Table 2.1**).

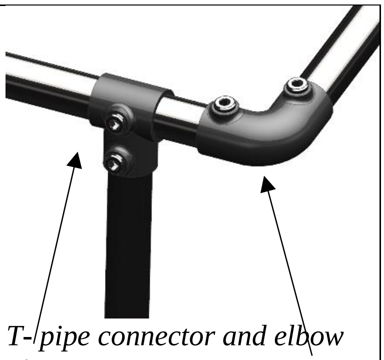
<table>
<tr><td colspan="3">

Naming and positions of rainout-shelter parts</td></tr>
<tr><th>Step</th><th>Material/Description</th><th>Illustration/Comment</th></tr>
<tr><td>Required tools</td><td>• Sledgehammer for driving in the impact sleeves
• Square timber (70mm x 70mm x >150mm)
• Hexagonal key (S4, S5, S ¼“)
• Ring spanner M6 – Size 10
• Slot screwdriver (small and medium size)
• Phillips screwdriver (medium)
• 4 assembly trestle for the pre-assembly of the shelter roof
• Crowbar or long iron bar (ca. 1 m) to pre-drill holes into the ground for later insertion of the drive-in sleeves
• Spirit level
• Iron saw (for cutting the plastic roof gutter to length)
• Nitro-dilution or alcohol
• Fine sandpaper
• Compass saw (d=50mm) to insert a hole for the rain gutter outlet cone
• Cordless screwdriver</td><td></td></tr>
</table>

Reworking of the delivered parts	If not done already by the steel pipe supplier, the following work on the pipes in delivery condition (6m length) is necessary: • Cutting the steel pipes to length according to the cutting plan (**Supplementary Figure 2.7**). • Insertion of drill holes (d=7mm) into the lower end of front and back supporting pipe; distance of drill holes according to spacing of holes in the drive-in sleeves. • Insertion of 1 central bore hole (d=7mm) into 8 halves (per roof) of the pipe clamps (black plastic) to provide a passage of the connecting screws (M6x45) between supporting pipes and drive-in sleeves. • Cut strips of neoprene tape (30mm wide) of approx. 30mm length and glue them on the inside of the clamping claws which will later hold the acrylic bands. Clean the adhesive surface on the clamping claw beforehand with thinner/alcohol. Attention: Drill hole must remain open to be able to insert screws. • The rain gutter must be shortened and a hole (d = 50 mm) must be drilled for the rain gutter outlet cone. This and the gluing of the rain gutter parts is described when adjusting the rain gutter.	 *One pair of pipe clamps*
Further preparation	• Prepare all parts and tools needed. • Check that all parts are present (compare with item list, **Supplementary Table 2.1**). • Mark all steel pipe ends of the steel frame (felt marker line 25mm away from the pipe end). The elbow pipe connectors are only pushed up to this mark during assembly.	
Pre-assembly of the steel frame **Pre-assembly of the steel frame** *(continued)*	• Place the pipe D and E (length 2370mm) parallel on the 4 assembly trestles. Slide a T-pipe connector onto each of the pipe ends (in about 2/3 of the pipe length) and lightly tighten it with the screws (all screw holes point upwards); all pipe connectors are fixed with hexagon socket head cap screws. Since the screws have an inch-thread, an Allen wrench with the width S ¼“ is required! • At the ends of each pipe D and E, slide one elbow pipe connector up to the mark (all screws point upwards) and tighten the screws. • Insert the cross pipe B (length 2440mm) into the T-pieces of the pipe D and E up to the markings and screw tight.	 *Cross pipe connectors.*

- Slide 2 T-pipe connector onto cross pipe C (length 2440mm) and 2 cross pipe connectors onto the cross pipe A.
- Insert cross pipe A and B into the elbow pipe connector of pipes D and E up to the markings and screw tight.
- Now lightly tighten the T-pipe connectors and cross-pipe connectors on cross pipe A and B with a distance of 122mm from the inner edge of the elbow pipe connector (see **Supplementary Figure 2.8**) so that the vertical hole points upwards and the connectors can still be turned by hand.
- Turn the frame upside-down (180°) so that the screw holes point downwards (then no water or dirt will get in).

→ **The frame is now completely pre-assembled**



T-pipe connector and elbow pipe connector.

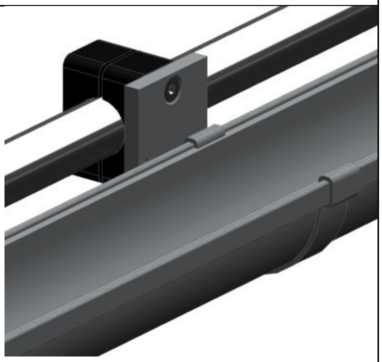
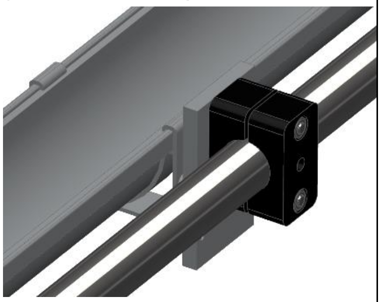
Insertion of the drive-in sleeves

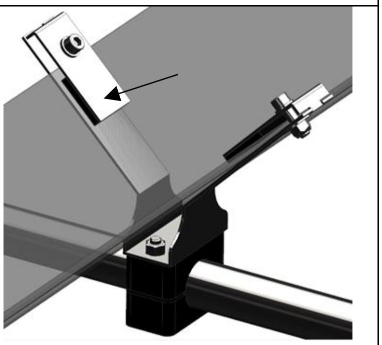
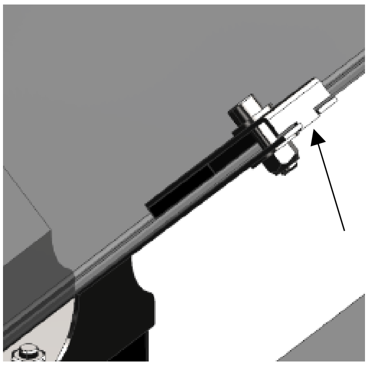
- Now place the frame on the final spot and align it.
- Mark the positions of the T- and cross pipe connectors pointing vertically downwards in a clearly visible way (e.g. with a screwdriver) in order to mark the spot where the drive-in sleeves have to be inserted.
- Raise the frame and lay it aside.
- Adjust the two markings for the high side of the roof (roof opening) inwards into the test field according to the intended roof pitch (see table below).

Roof pitch [°]	2	4	6	8	10	12
Offset marking (mm)	0	8	15	25	40	55

Insertion of the drive-in sleeves *(continued)*

- Deepen the final 4 markings (using a crowbar or a long iron rod).
- Align the drive-in sleeves one after the other so that their cross bores all point in the same direction.
- To insert the drive-in sleeves into the ground, put the square timber into the sleeve and drive it in with a sledge hammer. Do not hit the drive-in sleeves directly! Use a spirit level to check that the drive-in sleeves are driven in vertically.
- Place the pipe frame on the sleeves. Check with a spirit level whether all pipes are horizontal. If not => Correction of the impact sleeves’ depth.

	• Put the metal frame back onto the assembly trestles. **→ The drive-in sleeves are now aligned and firmly anchored in the ground.**	
Rain gutter holders	• The gutter should be installed before installing the acrylic glass bands. So the ends of the acrylic glass bands can be adjusted in a way that rain from the bands runs smoothly into the gutter. • Mount the 3 adapter plates for the rain gutter. Therefore, slide one pipe clamp onto cross pipe C and tighten with 2 M6x50 (DIN 965) countersunk screws each. The holders should be positioned one in the middle and two as far outwards as possible. Screw one gutter bracket (PVC grey) each to the adapter plate with 4 M6x50 (DIN 7981) slotted screws. Attention! Align the height of the holder so that water flows towards the discharge funnel. Select the appropriate tapped holes for this purpose. In the holder there is a Phillips-head screw so that the height, distance and inclination of the channel can also be adjusted.	 *Rain gutter holder consists of pipe clamp, adapter plate and gutter bracket (frontal view).*  *Rain gutter holder consisst of pipe clamp, adapter plate and gutter bracket (view from the rear).*
Installation of the gutter	• Move the gutter outlet cone over one end of the gutter. • Insert and align the gutter into the gutter brackets and mark the required length with a marker. • Move the gutter outlet cone to the correct position and mark it on the rain gutter. • Remove the rain gutter and saw it off at the marking. • Drill the hole (d=50mm) for the rain gutter outlet at the marking with compass saw into the rain gutter. • Slightly sand the parts at the contact areas for bonding, clean it with thinner or alcohol and glue the discharge funnel to the position on the gutter. • Subsequently, the 87grd elbow piece of the gutter is glued to the rain gutter outlet cone. • Then sand paper is used to roughen the ends of the gutter. Clean with thinner/alcohol and glue the end pieces to the gutter with PVC adhesive. • Lay the gutter aside.	 *A hole is drilled into the rain gutter after the rain gutter outlet cone is moved over the gutter to the correct position.*

Mounting the band holders	• Mark the required distances according to the **Supplementary Figure 2.8** with a felt marker on cross pipe B and C. The outer right band holder is located on the far right of the elbow pipe connector, the outer left band holder is located on the far left of the elbow pipe connector. • Attach the black plastic pipe clamp to the marking on the pipes, insert 2 M 6x45 hexagon socket head screws (DIN 912) with a washer (DIN 125-A) from below, insert the band holder and tighten it lightly with 2 nuts (DIN 985). Holders must still be able to be turned by hand on pipe. • Mount all band holders one after the other on cross pipe B and C. → **All required band holders are now mounted on cross pipe B and C**	
Installation of the acrylic glass bands	Install the acrylic glass bands: • Remove protective foil on both sides of the band. • Place the band on the holders. • If necessary, turn the holder in such a way that the band rests on the whole surface. Do not tilt! • Now tighten 2 screws (M6x45, DIN 912) on the holder. • Align the acrylic glass band lengthwise so that water from the band later runs smoothly into the gutter. For this purpose the rain gutter can be put back into place. • Place the clamping claws with the neoprene rubber glued to the holder/band in such a way that the nose of the clamping claws engages in the recess of the holder (anti-twist device); from above push the hexagon socket head screw (M6x20, DIN 912) with large diameter washer through the hole in the clamping claw and the holder and tighten it from below with the stop nut (DIN 985). Attention: Tighten only so far that neoprene rubber is pressed lightly together and the acrylic glass band rests completely on the holder. Never tighten so much that the underside of the clamping claw is resting on the holder or the clamping claw is deformed. → **Acrylic bands are now aligned and securely fixed.**	 *Clamping claw*  *Nose of the clamping claw engages in the recess of the holder*

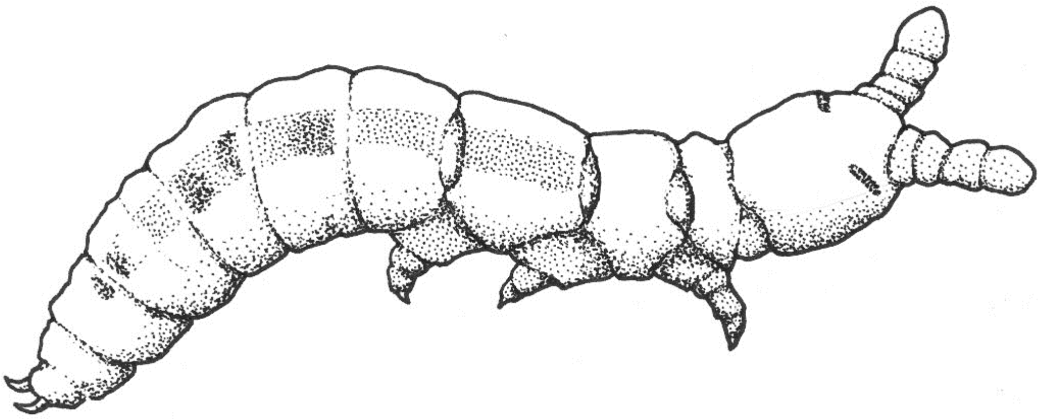
Installation of the 4 supporting pipes	- Place supporting pipes in front of the drive-in sleeves. Front supporting pipes (short) where the gutter is installed, back supporting pipes (long) where the roof should be high. - Insert supporting pipes one after the other into the drive-in sleeves and screw tight. For this purpose, each supporting pipe is provided with two predrilled pipe clamp halves and M6 x 45 hexagon socket screws (DIN 912) at the bottom, the pipe ends are inserted with the screws and pipe clamp halves into the sleeve and the screws should be pushed through the holes in the drive-in sleeves from the inside. - Place the large diameter washers (DIN 9021) on the screws and tighten with M6 nuts (ISO 4032). Check the vertical position of the supporting pipes with a spirit level. - Slide a T-piece onto the front supporting pipe on which the rain drain is to be mounted and fix it lightly (required for rain drain). → **The supporting pipes are now aligned on the field**	 *Supporting pipe are provided with two predrilled pipe clamp halves*  *The pipe ends are inserted with screws and pipe clamp halves into the sleeve. The screws are pushed through the holes in the drive-in sleeves from the inside*
Installation of the tubular frame and rain gutter **Installation of the tubular frame and rain gutter *(continued)***	- Put on each of the back supporting pipes (long) one pipe clamp about 600mm below the upper end of the pipes as a safety-stop and fix it. - Lift the pipe-frame up and place it on the supporting pipes with the T-pipe connectors or the cross pipe connectors. - Tighten the screws on the two T-pipe connectors (front supporting pipe). - Adjust the height on the cross-pipe connectors so that the desired roof pitch is obtained. Tighten the screws. - Adjust the 2 safety-stop pipe clamps up to the two T-pipe connectors and fix them. - Check the pipe-frame completely (level, general inspection). - Tighten all pipe connector screws firmly. - The pipe-frame is now aligned on the field. - Put the rain gutter back in its holder. - Align the holders with the cross-head screw on the side of the holder. → **The gutter is now mounted**	

Installation of the rain drain	- Insert the drain pipe into the 87grd elbow piece. Attach the elbow piece on the gutter outlet cone. - Mark and cut off the length of the drainpipe / drain hose suitable for entry into the rain barrel. - At this end glue the second pipe elbow piece (=inlet into rain barrel). - Align one T-pipe connector with adapter piece in the appropriate position so that 87grd pipe elbow piece fits to it. - Attach the pipe elbow piece with a hose clamp through the bore hole to the adapter to support the drain pipe. - Insert the drain pipe into the fixed elbow piece and glue it in place. → **The rain drain is now mounted.**	 *Align one T-pipe connector with adapter piece in the appropriate position so that 87grd pipe elbow piece fits to it.*
Inspecting the rainout-shelter	- Visual inspection and manual test of stability - Is the tubular frame securely fixed? Jogging - Are the acrylic glass bands well aligned and securely fixed? - Does the water run beautifully from the bands into the gutter? - Is the rain gutter held and cannot slide apart?	 *The final rainout-shelter with partial rainfall interception and precipitation collection*

<table>
<tr><td colspan="3">Comments on the rainout-shelter control
Follow the instruction for the rainout shelter described above, yet, no rainfall collection system is needed, so all steps in the manual above dealing with the installation of the rainfall collection system can be omitted (Check the parts list, to see which parts are needed).

An important difference between the two shelter types is the orientation of the bands, they are mounted as described for the rainout-shelter but then the frame with the acrylic glass bands is turned around and the V-shaped profiles become Λ bands.</td></tr>
<tr><td>Installation of the tubular frame</td><td>• Carefully turn around by 180 ° the frame with the acrylic glass bands. This requires at least 3 (better 4) persons! The acrylic glass bands now face downwards.
• Lift the tubular frame up and place it on the supporting tubes with the T-pipe connectors or the cross pipe connectors.
• Tighten the screws on the two T-pieces on the front supporting tube.
• Adjust the height on the cross pipe connectors so that the desired roof pitch is obtained. Tighten the screws.
• Check the tubular frame completely (level, inspection).
• Tighten all pipe connector screws firmly.</td><td></td></tr>
</table>

3 SOIL MICROARTHROPODS RESPOND DIFFERENTLY TO SIMULATED DROUGHT IN ORGANIC AND CONVENTIONAL FARMING SYSTEMS



The endogeic Collembola *Mesaphorura* sp.

Peer-reviewed article:

Meyer S, Kundel D, Birkhofer K, Fliessbach A, Scheu S (2021) Soil microarthropods respond differently to simulated drought in organic and conventional farming systems. Ecol Evol 10369–10380.

ABSTRACT

In Central Europe summer droughts are increasing in frequency which threatens production and biodiversity in agroecosystems. The potential of different farming systems to mitigate detrimental drought effects on soil animals is largely unknown. We investigated the effects of simulated drought on the abundance and community composition of soil microarthropods (Collembola, Oribatida, Meso-, Pro- and Astigmata) in winter wheat fields under long-term conventional and organic farming in the DOK trial, Switzerland. We simulated drought by excluding 65% of the ambient precipitation during the wheat growing season from March to June 2017. The abundance of Collembola and Oribatida declined more consistently in conventionally compared to organically managed fields under simulated drought. The abundance of Collembola as well as Meso-, Pro- and Astigmata, but not the abundance of Oribatida, increased in deeper soil layers due to simulated drought, suggesting vertical migration as drought avoidance strategy. The species composition of Oribatida communities, but not of Collembola communities, differed significantly between drought treatments as well as between farming systems. Soil carbon content was a major factor structuring Oribatida communities. Our results suggest that organic farming buffers negative effects of drought on soil microarthropods, presumably due to higher soil carbon content, and associated higher soil moisture and improved soil structure. This potential of organic farming systems to mitigate consequences of future droughts on soil biodiversity is promising and needs further exploration across larger climatic and spatial scales and should be extended to other groups of soil biota.

3.1 INTRODUCTION

Agriculture in Europe has experienced an intensification of management practices in the past decades and agroecosystems are likely to be sensitive to the changing climate. Central Europe is facing changes in temperature as well as precipitation and the magnitude of these changes is predicted to increase in the 21st century (EEA 2017). Rising temperatures and a shift in precipitation towards the winter months increases the risk of summer droughts (Russo et al. 2013; Spinoni et al. 2015). Under these conditions, soil animals are likely to be more frequently exposed to reduced soil water content, which alters the availability of food resources (Bear et al. 2013) and the capacity to maintain homeostasis (Verhoef and Witteveen 1980). Hence, crop plants will not only suffer from direct consequences of higher water stress in drought periods, but will also have to cope with changes in ecosystem functions that are provided by soil organisms (Kaneda and Kaneko 2011; Yin et al. 2019a). Negative effects of drought conditions on soil organisms and crop plants might be mitigated by agricultural management practices that increase soil water-holding capacity and provide additional resources. However, recent studies suggested that climate effects on soil fauna taxa vary little with land-use intensity (Schädler et al. 2019; Yin et al. 2019b), but in particular, the abundance of Collembola may decrease under future climate conditions in organically, but not in conventionally managed fields (Yin et al. 2019c). Generally, however, combined effects of simulated drought and management practices on soil microarthropods in agroecosystems received little attention.

Soil microarthropods are adapted to more constant environmental conditions compared to aboveground arthropods. However, climate change also alters belowground conditions including temperature, CO_2 levels and water availability, with changes in precipitation presumably most severely affecting soil biota (Blankinship et al. 2011). Many soil organisms, from soft-bodied springtails (Collembola) to heavily sclerotized Oribatida, are known to be vulnerable to desiccation. Field experiments suggested that soil animals respond negatively to simulated drought (Blankinship et al. 2011; Petersen 2011; Vestergård et al. 2015), but other studies did not report such effects (Taylor et al. 2004; Kardol et al. 2011; Krab et al. 2014). Yet, the majority of drought experiments has been performed in forests, which are more buffered against changes in abiotic conditions than open habitats, such as grasslands or arable fields. Soils in open habitats are generally more exposed to climatic conditions and agricultural soils, in particular, are not well protected against extreme conditions during most parts of the year, and therefore undergo pronounced annual fluctuations in soil moisture. These conditions may filter for species in agricultural soil animal communities that are generally adapted to drought conditions. However, these species may already live at the edge of their ecological niche in terms of climatic conditions and may not be able to tolerate even harsher conditions predicted for the future. Responses of soil animals to drought are likely to be taxon-specific as there are variations in the individual drought tolerance and resilience of taxonomic groups (Lindberg and Bengtsson 2005). Filtering of more drought-tolerant species, therefore, would likely result in different and less diverse communities compared to less severe climatic conditions (Pflug and Wolters 2001; Kardol et al. 2011; Makkonen et al. 2011; Petersen 2011). An improved understanding of these filtering effects at species-level provides the opportunity to identify indicator species for drought stress in soil communities.

Differences in biological and physico-chemical soil properties between agricultural fields, even across geographical regions, are mainly driven by different management practices. In conventional farming systems chemical pesticides and inorganic fertilizers are applied, whereas organic farming omits conventional pesticides and exclusively uses organic fertilizers, such as manure, compost or slurry. The resulting higher levels of soil organic matter in organic farming systems (Gattinger et al. 2012) provide additional resources for decomposers, reflected in higher abundance of soil organisms in organically managed fields (Bengtsson et al. 2005; Birkhofer et al. 2008, 2012). High levels of organic matter cause structurally more complex soils and increase soil water-holding capacity (Lotter et al. 2003) potentially mitigating negative effects of drought on soil animals. For a comprehensive understanding of future drought effects on biota in agroecosystems it is therefore crucial to consider different farming systems and their potential to buffer against drought conditions.

The present study investigates the interactive effect of simulated drought and different long-term farming systems on soil microarthropod communities. We compared microarthropod communities in conventionally and organically managed winter wheat fields in an agricultural long-term experiment in Switzerland (DOK trial; Krause et al. 2020). Additionally, we experimentally manipulated soil moisture by establishing roofs that excluded 65% of the ambient precipitation. We hypothesized that (1) simulated drought reduces microarthropod abundances with these effects (2) being more pronounced under conventional compared to organic management. We further hypothesized that (3) microarthropods migrate into deeper soil under simulated drought and that (4) individual species show specific responses to simulated drought resulting in different compositions of Collembola and Oribatida communities.

3.2 METHODS

3.2.1 Study site

The DOK trial is a long-term experiment comparing organic and conventional agricultural management since 1978. It is located in Therwil in the Leimen Valley close to Basel, Switzerland (47°30’09.3’’N, 7°32’21.5’’E). Mean annual temperature is 10.5 °C and mean annual precipitation is 842 mm (Krause et al. 2020). The soil is a Haplic Luvisol (16% clay, 72% silt, 12% sand) on deposits of alluvial loess. For this study we used winter wheat fields (*Triticum aestivum* L. cv. “Wiwa”). Eight experimental fields (each 5 x 20 m^2) were located in four blocks each including one organically (biodynamic) and one conventionally managed field (BIODYN and CONMIN treatments of the DOK trial, respectively; **Figure 3.1**). In each field we established two types of roofs: one roof that excluded 65% of the ambient precipitation and a modified “control roof” that did not intercept rain, but controlled for potential artifacts caused by the roof construction itself. This results in a total number of eight replicates for the factors drought and farming system, respectively, and four replicates for the drought x farming system interaction for each sampling date. For details on the design of the experimental roofs see Kundel et al. (2018). The roofs had a minimum distance from the field edges of 0.5 m. The organic farming system received only organic fertilizers (farmyard manure, compost and slurry) and weeds were controlled mechanically. Further, biodynamic preparations were applied to soils, plants and organic fertilizers (Krause et al. 2020; Kundel et al. 2020). In the organic farming system twice during the experiment (March and April) 20 m³/ha slurry was applied. Fields in the conventional farming system received mineral fertilizer (40 – 60 kg N/ha in March, April and May). Plant protection in the conventional farming system was carried out with insecticides, herbicides and fungicides, according to threshold values as recommended by the producer (see **Supplementary Table 3.1** for details on pesticide products, amount of applied active ingredients and application dates).

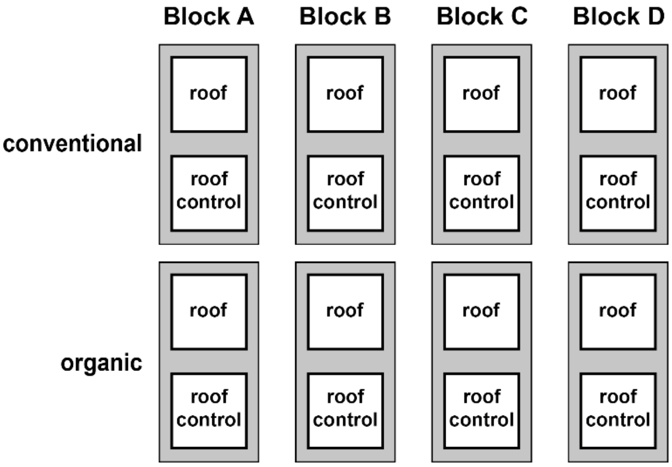


Figure 3.1 Scheme of the experimental design with four blocks (A– D) each containing one organic and one conventional field and each field with one control (roof control) and one drought treatment (roof)

Pesticides were applied with a knapsack-sprayer with multiple nozzles. Additionally, plant growth regulators (1.5 l/ha Cycocel extra, Omya, in March) were applied in the conventional farming system. The experiment was established in March 2017 and lasted until shortly before harvesting in the end of June 2017. We sampled at four sampling dates: T0 in March before the roofs were established and T1-T3 in April, May and June, respectively.

3.2.2 Soil and plant properties

Soil samples were taken using a soil corer in the center of the plots to a depth of 20 cm and the following soil properties were determined: water holding capacity, bulk density, pH, and concentrations of total phosphorus, phosphate, total organic carbon and total nitrogen (all at T0), and gravimetric soil water content (T0, T1, T2, T3) and mineral nitrogen (at T2). Additionally, plant properties (root dry weight, wheat biomass, wheat height, grain yield, weed cover, and concentrations of nitrogen and carbon of shoots and roots) and microbial activity (soil respiration) were measured (all at T2, except grain yield at T3). Further, data on the microbial community composition were obtained by measuring phospholipid fatty acids (PLFAs) and neutral lipid fatty acids (NLFAs) from soil samples at T2 (Kundel et al. 2020). We used the NLFA 16:1ω5 as measure of the amount of arbuscular mycorrhizal fungi (AMF) and converted it into biomass carbon using the following conversion factor: 1.047 nmol NLFA = 1 µg AMF biomass carbon (Olsson et al. 1995). For measuring the relative importance of non-mycorrhizal fungi and bacteria we used the proportions of respective marker PLFAs to the total amount of PLFAs. The PLFAs i15:0, a15:0, 15:0, i16:0, 16:1ω9, i17:0, a17:0, cy17:0, 18:1ω7 and cy19:0 were used as markers for bacteria (Frostegård and Bååth 1996) and the PLFA 18:2ω6 as marker for saprotrophic fungi (Olsson et al. 1995).

3.2.3 Soil animals

We took two soil cores, one of 5 and one of 20 cm diameter, under every roof at T1-T3 covering a sampled area of 20 and 314 cm², respectively, at each sampling time. Soil cores were taken to a depth of 10 cm and separated into upper (0-5 cm) and lower layer (5-10 cm). Animals were extracted by heat; temperature was gradually increased from 25 to 55 °C over ten days, for the large soil cores in steps of 5 °C and for the small soil cores in steps of 2.5 °C until 30 °C and in steps of 5 °C from 30 to 55 °C per day (Macfadyen 1961; Kempson et al. 1963). Animals were collected into a glycol - water solution (1:1), filtered and stored in 70% ethanol. Animals were sorted to order level under a dissecting microscope (Stemi 2000; Zeiss, Jena, Germany). Additionally, we identified Collembola and Oribatida from the small soil cores of the second sampling campaign to species level using a microscope (Axioplan; Zeiss) and keys by Hopkin (2007), Fjellberg (1998, 2007) and Weigmann (2006). In addition, large Collembola (> 1.5 mm) and Oribatida were identified from the large cores. We chose the second sampling campaign for species identification because differences in soil moisture were greatest at this sampling (see **Figure 3.2**).

3.2.4 Statistical analysis

Data were analyzed in R (R Development Core Team 2020) using mixed-effects models including field nested in block and drought nested in field (to account for multiple sampling dates) as random factors, and farming system and sampling date as fixed factors. The abundances of total Collembola, epigeic Collembola, Oribatida, Meso-, Pro- and Astigmata were analyzed using generalized linear mixed-effects models (GLMMs) with a Poisson distribution using the R package *lme4* (Bates et al. 2015). The model for Meso-, Pro- and Astigmata accounted for zero-inflation by using the R package *glmmTMB* (Brooks et al. 2017). The model for Oribatida accounted for overdispersion using a negative binomial distribution. In the model for Collembola we excluded data from the third sampling date due to excess zero-count data. We analyzed differences in the depth distribution with linear mixed-effects models (LMMs) using the same random effect structure as in the models for the abundance data. The depth distribution was expressed as the proportion of total individuals in the upper 0-5 cm of each sample; prior to the analyses, the data were arcsin square root transformed. Afterwards we run Wald chi-square tests to inspect significances of the fixed effects. We only analyzed differences in depth distribution at the second sampling date when differences in soil moisture were most pronounced (**Figure 3.2**). We tested the fit of all GLMMs and LMMs with the function *testResiduals()* from the DHARMa package (Hartig 2017).

Species richness of Collembola, epigeic Collembola and Oribatida was analyzed using LMMs with field nested in block as random factors, and drought and farming system as fixed factors.

For the statistical analyses of taxonomic composition all abundance data were log(x+1) transformed to weigh down the importance of abundant species and a dummy variable (1) was added as recommended by Anderson et al. (2008). A Bray-Curtis resemblance matrix based on these data was then tested with permutational analyses of variance (PERMANOVA) with farming system and drought as fixed factors and 9999 permutations of residuals under a reduced model. For significant model terms, similarity percentage analyses (SIMPER) were used to identify the most discriminating species (>25% individual contribution to Bray-Curtis dissimilarities). Non-metric multidimensional scaling (NMDS) based in the same Bray-Curtis resemblance matrix was used to visualize the data. The PERMANOVA and SIMPER analysis were performed using the software PRIMER version 7.0.13 and the PERMANOVA add-on (PRIMER-e, Quest Research Limited, Auckland, New Zealand). Additionally, we used redundancy analysis (RDA) to evaluate interrelationships between the measured soil, plant and microbial parameters, and the community composition of total Collembola, epigeic Collembola and Oribatida. All constraining factors were standardized to a range between 0 and 1 to account for different scales of the variables included. We used the function *ordistep()* for model selection with a stepwise addition of constrains to the null model based on the AIC selection criteria using permutation tests. From the full set of the measured variables, weed cover, water holding capacity and carbon content of the roots were identified as the most relevant factors. We then added variables related to drought and farming system (TOC, water content) as well as potential resources for Oribatida and Collembola (AMF, proportion of bacterial and fungal PLFAs, and root dry weight) as explanatory variables to the model. From this model we excluded AMF biomass because it was highly correlated with TOC. We assessed the significance of these factors by ANOVA-like permutation tests using the function *anova.cca()*. For the RDA we used the vegan package in R (Oksanen et al. 2019). See **Supplementary Table 3.2** for all predictor variables included in the RDA.

3.3 RESULTS

3.3.1 Soil water content

Soil water content was consistently lower in the drought than in the control treatment (**Figure 3.2**).

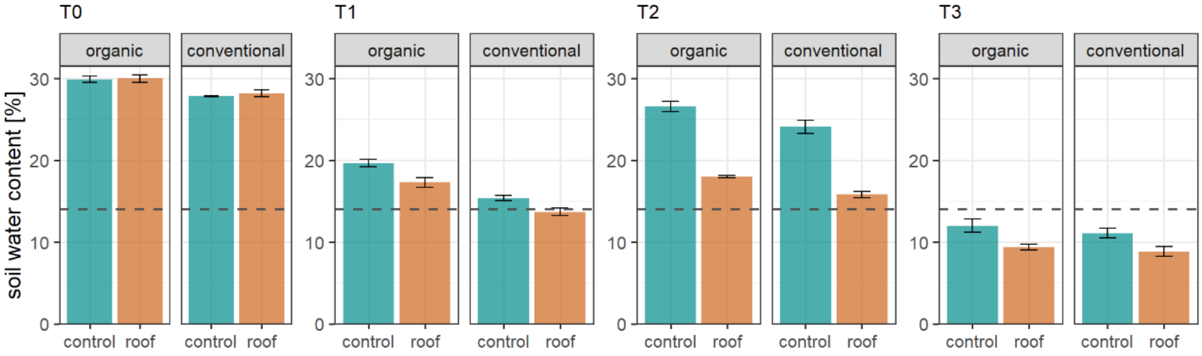


Figure 3.2 Gravimetric soil water content (0-20 cm depth) in control and drought treatments (roof) in wheat fields under organic and conventional management in March (T0, before roof establishment), April (T1), May (T2) and June (T3); dashed line, estimated wilting point; means ± SE.

Table 3.1 GLMM on the effect of drought, farming system and sampling date on the abundance of total Collembola, epigeic Collembola, Oribatida, and Meso-, Pro- and Astigmata. Significant P-values are given in bold

	Total Collembola				**Epigeic Collembola**				**Oribatida**				**Meso-, Pro- and Astigmata**			
	Estimate	Std. error	*z*-value	*P*-value	Estimate	Std. error	*z*-value	*P*-value	Estimate	Std. error	*z*-value	*P*-value	Estimate	Std. error	*z*-value	*P*-value
Intercept	3.024	0.547	5.530	< **0.001**	2.333	0.262	8.917	< **0.001**	4.751	0.272	17.485	< **0.001**	2.781	0.267	10.399	< **0.001**
Drought	-0.162	0.469	-0.345	0.73	-0.481	0.274	-1.756	0.079	-0.438	0.367	-1.195	0.232	0.078	0.385	0.203	0.839
Farming system	-1.547	0.513	-3.019	**0.003**	-1.101	0.326	-3.384	< **0.001**	-1.986	0.4	-4.962	< **0.001**	-0.307	0.385	-0.798	0.425
Sampling date	0.514	0.113	4.560	< **0.001**	-	-	-	-	-	-	-	-	-	-	-	-
Sampling date T1 x T2	-	-	-	-	0.333	0.199	1.674	0.094	-1.010	0.373	-2.705	**0.007**	0.278	0.171	1.623	0.105
Sampling date T1 x T3	-	-	-	-	-1.197	0.315	-3.797	< **0.001**	-0.08	0.361	-0.221	0.825	-0.813	0.284	-2.865	**0.004**
Drought x Farming system	1.788	0.696	2.570	**0.01**	1.397	0.428	3.262	**0.001**	1.413	0.529	2.669	**0.008**	-0.699	0.56	-1.248	0.212
Drought x Sampling date	-0.374	0.181	-2.070	**0.039**	-	-	-	-	-	-	-	-	-	-	-	-
Drought x Sampling date T1 x T2	-	-	-	-	1.008	0.29	3.471	< **0.001**	0.912	0.518	1.761	0.078	-0.776	0.27	-2.879	**0.004**
Drought x Sampling date x T3	-	-	-	-	1.502	0.401	3.745	< **0.001**	0.303	0.511	0.593	0.553	-0.377	0.519	-0.727	0.467
Farming system x Sampling date	-0.652	0.284	-2.300	**0.022**	-	-	-	-	-	-	-	-	-	-	-	-
Farming system x Sampling date T1 x T2	-	-	-	-	1.366	0.343	3.980	< **0.001**	1.744	0.54	3.229	**0.001**	-0.277	0.262	-1.060	0.289
Farming system x Sampling date T1 x T3	-	-	-	-	1.667	0.455	3.666	< **0.001**	1.330	0.524	2.540	**0.011**	-0.387	0.422	-0.918	0.359
Drought x Farming system x Sampling date	-0.271	0.348	-0.778	0.436	-	-	-	-	-	-	-	-	-	-	-	-
Drought x Farming system x Sampling date T1 x T2	-	-	-	-	-1.822	0.447	-4.081	< **0.001**	-1.313	0.746	-1.760	0.078	1.933	0.399	4.849	< **0.001**
Drought x Farming system x Sampling date T1 x T3	-	-	-	-	-2.314	0.575	-4.021	< **0.001**	-0.61	0.74	-0.824	0.41	1.973	0.702	2.809	**0.005**

However, the effect of simulated drought varied with time and was most pronounced at T2 (significant drought × sampling date interaction; Chisq = 224.1, P < 0.001). Moreover, soil water content was higher in organically than in conventionally managed fields at all sampling dates except for T3. At T3 the soil water content generally was very low irrespective of the farming system with < 10% in the drought and < 13% in the control treatments, both being below the estimated wilting point of 14%.

3.3.2 Abundance of soil animals

The effect of simulated drought on mesofauna abundances differed between the two farming systems and this interaction differed among animal groups (**Figure 3.3, Table 3.1**). Drought reduced the abundance of Collembola and Oribatida in conventionally, but not in organically managed fields. On the contrary, drought reduced the abundance of epigeic Collembola in organically, but not in conventionally managed fields at T2 and T3. By contrast, drought increased the abundance of Meso-, Pro- and Astigmata at T1 in both farming systems, whereas at T2 it was higher under drought in organically but lower in conventionally managed fields.

3.3.3 Depth distribution of soil animals

Collembola as well as Meso-, Pro- and Astigmata migrated to deeper soil (5 - 10 cm) in the drought treatment, whereas epigeic Collembola were not affected and Oribatida even showed the opposite pattern (**Figure 3.4**). In Collembola, however, movement into deeper soil was restricted to the organically managed fields (marginally significant drought × farming system interaction, Chisq = 2.7, P = 0.098). In Meso-, Pro- and Astigmata movement into deeper soil was consistent in both farming systems (Meso-, Pro- and Astigmata: Chisq = 24.1, P < 0.001). On the contrary, Oribatida moved into the upper soil layer (0 - 5 cm) in the drought treatment in both farming systems (Chisq = 5.7, P = 0.017).

3.3.4 Species composition

Species richness of Oribatida was significantly higher in organically than in conventionally managed fields (F1,3 = 12.78, P = 0.037), but did not differ between the drought treatments. Species richness of Collembola was reduced by simulated drought in organically managed fields (drought x farming system interaction; F1,6 = 7.71, P = 0.032). Species richness of epigeic Collembola did not differ significantly between the farming systems and between the drought treatments. The NMDS ordination (stress = 0.057) separated Oribatida communities in the drought treatment from communities in the control (**Figure 3.5**). Also, the NMDS ordination separated the Oribatida communities of the two farming systems (**Figure 3.6**). Supporting these separations, drought (F1,12 = 2.40, P = 0.046) and farming system (F1,12 = 11.20, P = 0.002) were significant in the respective model, with no significant interaction term. The significant differences between farming systems were mainly due to *Oppiella subpectinata* (SIMPER: 29.2% contribution to dissimilarity between farming systems) and *Zygoribatula excavata* (26.2%) being exclusively present in the organically but missing from the conventionally managed fields. No single Oribatida species contributed more than 25% to the dissimilarity between drought treatments. Contrary to Oribatida, neither drought nor farming system

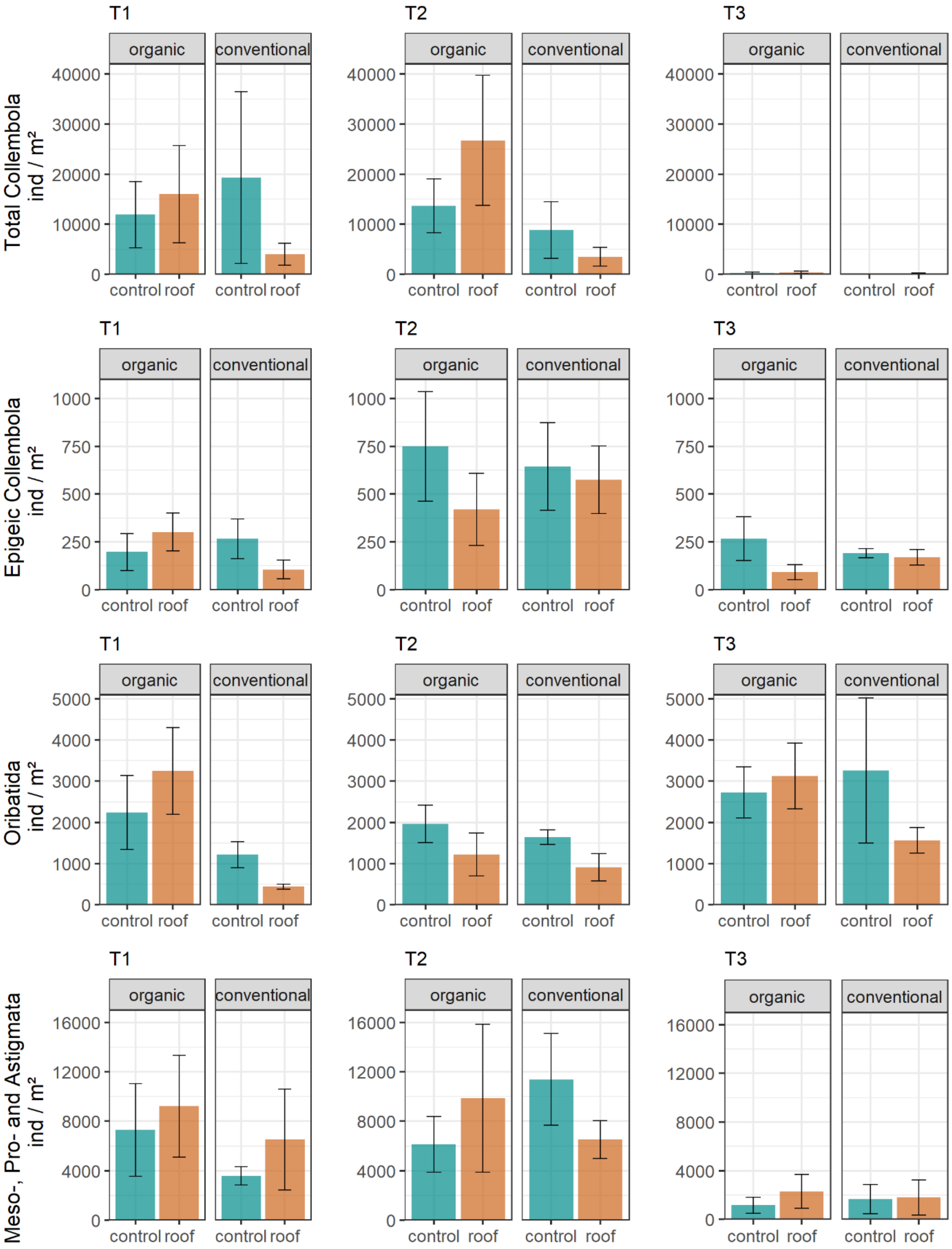


Figure 3.3 Abundance of total Collembola, epigeic Collembola, Oribatida, and Meso-, Pro- and Astigmata in control and drought treatments (roof) under organic and conventional management in April (T1), May (T2) and June (T3). Abundances are given in individuals per square meter; means ± SE; for statistical analyses see **Table 3.1**.

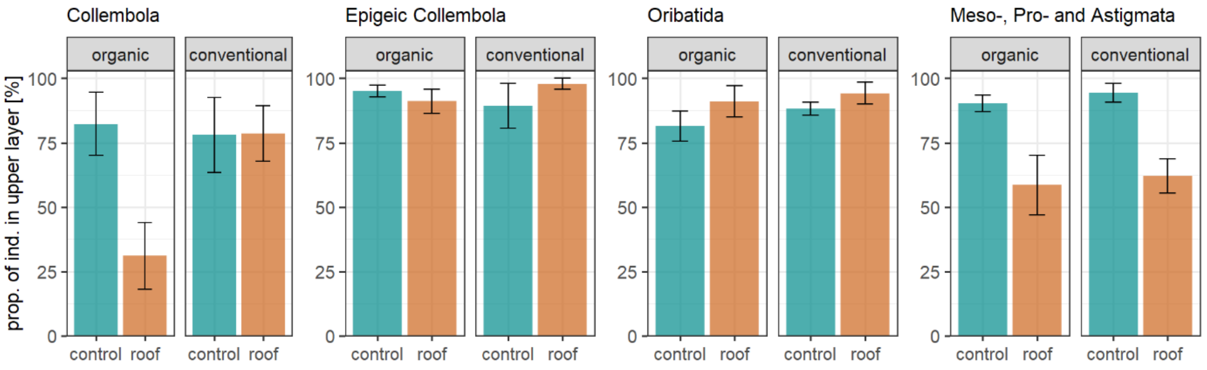


Figure 3.4 Depth distribution of Collembola, epigeic Collembola, Oribatida, and Meso-, Pro- and Astigmata in control and drought treatments (roof) under organic and conventional management as proportion of individuals (of total) in the upper layer (0-5 cm); means ± SE.

significantly affected the community composition of epigeic and total Collembola. Species-environment relationships were only significant in Oribatida with the first and second axes explaining 12.2 and 10% of the variation in species composition, respectively (adjusted R² = 0.331; **Figure 3.7**). Significant predictors were total organic carbon ($F_{1,7}$ = 2.37, P = 0.011), proportion of fungal PLFAs ($F_{1,7}$ = 2.63, P = 0.007) and carbon content of roots ($F_{1,7}$ = 4.14, P = 0.005), with total organic carbon being closely related to the organic farming system. In line with the NMDS results, the species *Zygoribatula excavata* and *Oppiella subpectinata*, but also *Phthiracarus compressus* were associated with the organic system.

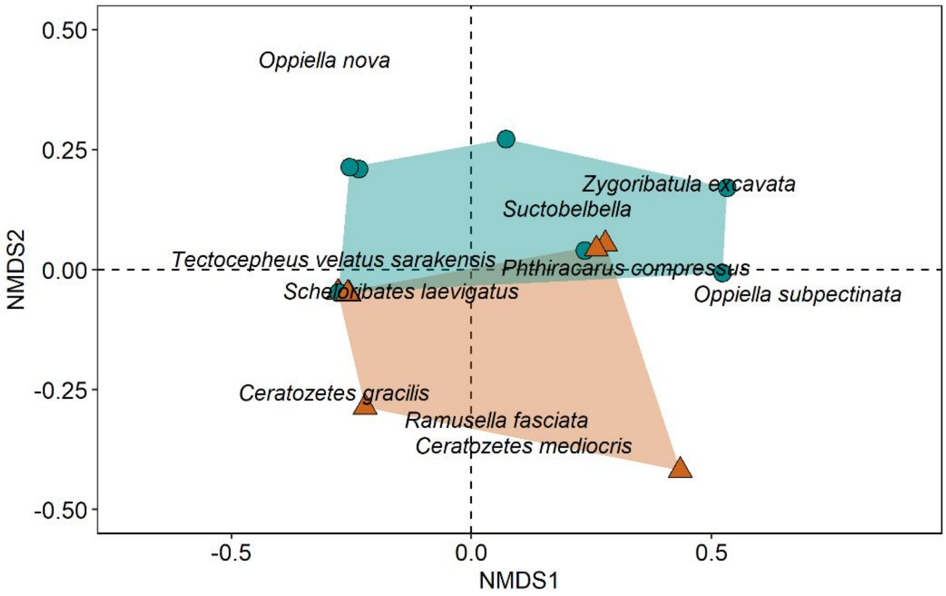


Figure 3.5 NMDS ordination based on the Oribatida community composition in control and drought treatments as reflected by the first and second NMDS dimensions. Colored polygons frame sites of the control (turquoise; circle) and drought treatment (orange; triangle).

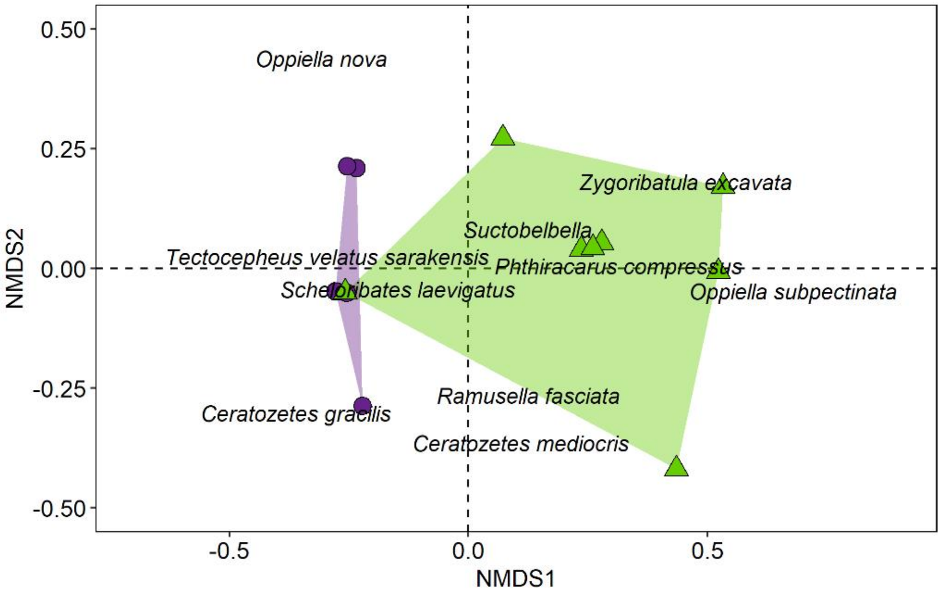


Figure 3.5 Oribatida community composition in organic and conventional farming as reflected by the first and second NMDS dimensions. Colored polygons frame sites of organic (green; triangle) and conventional farming (violet; circle).

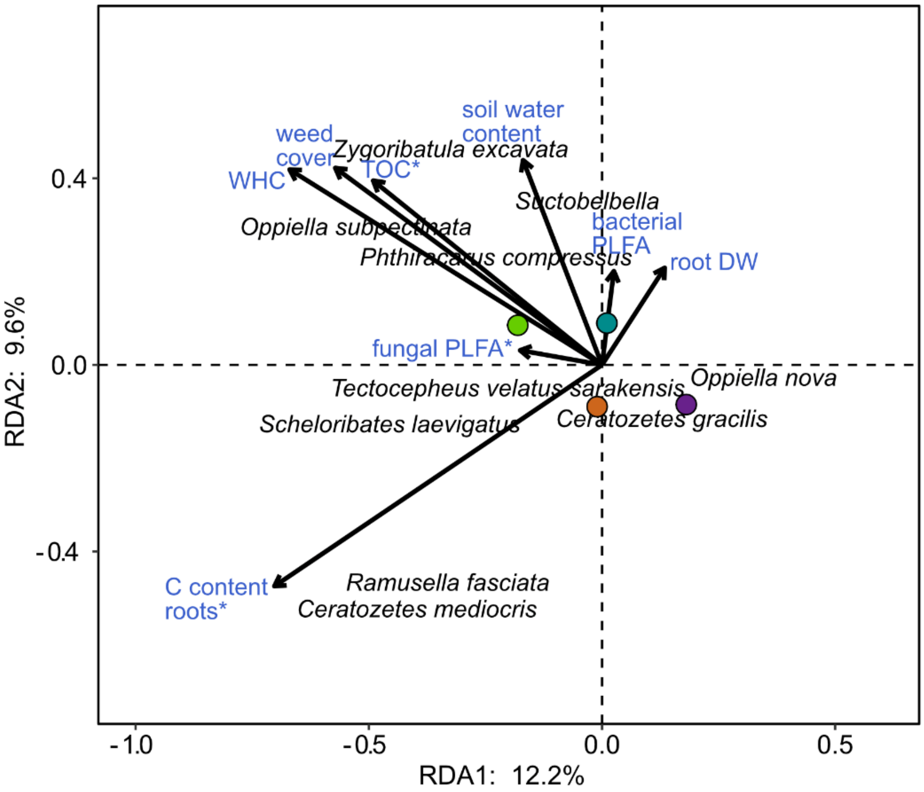


Figure 3.7 Species – environment relationships of Oribatida in two farming systems (organic, green, and conventional, purple) and two drought treatments (roof control, turquoise and roof, orange) as indicated by RDA ordination. Environmental variables included carbon (C) content of roots, weed cover, water holding capacity (WHC), total organic carbon (TOC), soil water content, proportion of bacterial and fungal phospholipid fatty acids (PLFA) and root dry weight (DW). Significant environmental variables are marked with asterisks.

3.4 DISCUSSION

3.4.1 Abundance

Collembola and Oribatida were most sensitive to drought, but as hypothesized, the decline in abundance was more severe in conventionally than in organically managed fields. This indicates that negative effects of drought are mitigated by conditions in the organic farming system. A major difference between the two farming systems is the fertilization with compost, manure and slurry in the organic system and synthetic, inorganic NPK fertilizer in the conventional system. This difference results in a higher concentration of soil organic matter in the organic system which is positively correlated with water holding capacity of soils (Shepherd et al. 2002). Indeed, soil water content was generally higher in organically compared to conventionally managed fields when soil moisture was above the estimated wilting point.

Organic farming systems further are known to have higher microbial biomass and activity compared to conventional systems (Birkhofer et al. 2012). For the current field experiment, Kundel et al. (2020) reported higher fungal and bacterial abundances and microbial respiration in the organically compared to the conventionally managed fields. Microbes serve as important food resource for many soil microarthropods (Schneider et al. 2004; Chahartaghi et al. 2005) and their availability may alter effects of simulated drought on microarthropod abundances. At our field site, drought increased Collembola abundances in organically and decreased them in conventionally managed fields. Though microbial biomass was higher in the organically managed fields, microorganisms might be in part inaccessible for Collembola when soil moisture is too high. Microarthropods move in air filled spaces through the soil and movement might be hindered when soil pores are filled with water (Schimel 2018). Under simulated drought lower soil moisture therefore may have increased the accessibility of microorganisms as food and thereby resulted in increased abundance of Collembola in organically managed fields. These effects on Collembola may have cascaded up to higher trophic levels as Meso-, Pro- and Astigmata partly followed the abundance responses of Collembola, which are potential prey for Meso- and Prostigmata (Koehler 1999). Oribatida abundance also decreased under simulated drought in the conventional system at all sampling dates. However, the abundance of Oribatida did not increase under simulated drought in the organically managed fields suggesting that, in contrast to Collembola, Oribatida did not benefit from higher resource availability. Contrasting to our second hypothesis, the abundance of epigeic Collembola decreased with drought mainly in organically managed fields. Epigeic Collembola may have benefitted from the presence of a herb layer, which was absent in the conventionally managed fields. Herbaceous plants may provide both habitat and food resources for epigeic Collembola (Potapov et al. 2016) and negative effects of drought on herbs thereby may have detrimentally affected epigeic Collembola. Though simulated drought did not affect the percentage cover of herbs in organically managed fields, plant water stress may have detrimentally affected epigeic Collembola as shown for herbivores (Huberty and Denno 2004).

3.4.2 Vertical distribution

Drought effects on soil microarthropods might be mitigated by improved soil structure with larger pores in organically managed fields allowing vertical movement to avoid drier upper soil layers. Supporting our third hypothesis, drought increased Collembola abundance in deeper soil layers, but only in organically managed fields, where high amounts of organic matter may support a more structured soil (Shepherd et al. 2002). In fact, in the DOK-trial Mäder et al. (2002) found soil aggregate stability to be 10 to 60% higher in organically compared to conventionally managed fields. Parallel to the higher abundance of Collembola in deeper soil layers, total Collembola abundance was higher under drought only in organically managed fields at the second sampling date. Exploitation of additional resources in deeper soil layers may have contributed to this abundance pattern. In contrast to total Collembola, epigeic Collembola, mainly colonizing the soil surface, were not found in the deeper soil layers under simulated drought and consistent with this, their abundance also declined in the well-structured soil of the organically managed fields at T2 and T3.

In contrast to our third hypothesis, Oribatida did not move into deeper soil layers under simulated drought, indicating that, compared to Collembola, they did not benefit from the improved soil structure in the organic farming system. Consequently, their abundance decreased under drought simulation in both farming systems. Similar to our study, Perdue and Crossley (1990) also found that most mites did not migrate to deeper soil layers, even when abundances declined dramatically during periods of low soil moisture in agricultural fields. However, in our study Meso-, Pro- and Astigmata followed in part the depth distribution of Collembola. Their relative abundance in the upper soil layer decreased under drought, although less strongly than in Collembola. However, in contrast to Collembola, Meso-, Pro- and Astigmata migrated to deeper soil in both organically and conventionally managed fields suggesting that these taxonomic groups can better cope with the less structured soils in the conventional system.

3.4.3 Temporal changes

Towards the end of the experiment, ambient drought conditions decreased soil water content dramatically to an average of 10.3% of dry weight, i.e. below the estimated wilting point of 14%. At this very low level, the small remaining differences in soil water content between the drought and control treatment probably were of little relevance for soil microarthropod communities. The generally very low abundance of soil mesofauna at the last sampling date, therefore, presumably was due to an overall low soil moisture overriding roof effects of the previous sampling dates. The changes in abundance during the three sampling dates suggest different population dynamics for each microarthropod group as response to naturally occurring changes in soil moisture. While the abundance of total Collembola, epigeic Collembola and Meso-, Pro- and Astigmata peaked at T1 and T2, and decreased severely at T3, the abundance of Oribatida peaked at T3. Highest abundance of Oribatida at T3 indicates that they are not only able to survive, but even to thrive under low moisture conditions in arable fields, probably due to low metabolic rates and slow development (Norton 1994). However, simulated drought reduced the abundance increase of Oribatida from T2 to T3 in the conventionally managed fields, indicating that low abundances early in the season (T1 and T2) could not be compensated towards T3.

Collembola, on the other hand, reproduce fast allowing the buildup of high population densities early in the season (T1 and T2), which then dramatically collapsed at T3 when soil moisture levels were very low. This suggests that Collembola are generally more sensitive to drought than Oribatida. However, fast reproduction also enables fast recolonization and this likely contributes to the fast recovery of Collembola populations after disturbances in agricultural fields. In fact, Alvarez et al. (1999) found that watering of arable fields after a 4-month drought period provoked immediate hatching from eggs in several Collembola species. Furthermore, Collembola are known to recolonize previously hostile habitats faster than Oribatida by wind drift and active locomotion (Dunger et al. 2002; Lehmitz et al. 2011). The abundance dynamics of Meso-, Pro- and Astigmata at the three sampling dates resembled that of Collembola again indicating that Meso- and Prostigmata were trophically linked to Collembola. The similar response of Collembola and Astigmata may be due to the fact that both taxa are little sclerotized (contrasting to Oribatida), rendering similar sensitivity to drought.

3.4.4 Community composition

Overall, species richness of Collembola and Oribatida was rather low; however, in Oribatida it was generally higher in organically than conventionally managed fields irrespective of simulated drought, whereas in Collembola total species richness was reduced by simulated drought but only in organically managed fields. Again, this suggests higher sensitivity of Collembola than Oribatida to drought. By contrast, the species structure of Oribatida, but not that of Collembola communities reflected the drought treatments. Previous studies on drought effects from other non-forest, open habitats (mainly grasslands) reported changes (Pflug and Wolters 2001; Lindberg et al. 2002; Kardol et al. 2011; Yin et al. 2019c) or no changes (Holmstrup et al. 2013; Krab et al. 2014) of Collembola community composition, but rarely included Oribatida. Generally, Oribatida are perceived as being poor bioindicators, because they only respond slowly to changes in environmental conditions due to their long life cycles (Behan-Pelletier 1999). Contrasting this assumption and our fourth hypothesis, Oribatida communities differed significantly between the drought and control treatments, although no individual species was characteristic for a specific treatment and Oribatida communities were relatively species-poor. Notably, effects already occurred three months after the start of drought simulation.

Oribatida community composition also differed between the two farming systems, whereas again, this was not the case for Collembola communities. Differences in the community structure of Oribatida between the farming systems were mainly due to *Zygoribatula excavata* and *Oppiella subpectinata*, which were significantly more abundant in organically compared to conventionally managed fields. Both species are known from forest and grassland habitats with high amounts of soil organic matter (Weigmann 2006). Our study suggests that these species also colonize agricultural fields, in particular farming systems with high levels of soil carbon. Soil carbon content was an important driver for Oribatida communities in our study sites favouring *Z. excavata* and *O. subpectinata*. A significant effect of soil carbon on mite communities also has been found in previous studies (Scheu and Schulz 1996; Minor and

Norton 2004; Wissuwa et al. 2013). The relative abundance of fungi also affected Oribatida community composition in our study. Fungi form a major part of the diet of Oribatida, including species of the family Oribatulidae and Scheloribatidae, such as *Z. excavata* and *Scheloribates laevigatus* (Schneider et al. 2004), abundant at our study sites. Moreover, the carbon content of roots significantly affected the species composition of Oribatida possibly via rhizodeposition, feeding on dead roots or root-associated fungi (Pollierer et al. 2007).

Although the different farming systems in the DOK trial have been established more than 40 years ago, Collembola communities did not differ significantly between the systems, which is consistent with previous studies (Alvarez et al. 1999; Birkhofer et al. 2008). Our results showed that the abundance of Collembola may dramatically decrease in cereal fields at the end of the growing season and this likely increases the risk of extinction of local populations. It needs to be studied if these responses are associated to drought conditions and if they are aggravated by water uptake of crop plants. Agricultural practices such as tillage, but in particular drought events, may prevent the establishment of stable Collembola communities in future agroecosystems.

3.4.5 Conclusions

Our findings show that the vulnerability of soil microarthropods against drought in agricultural fields depends on the farming system with more severe negative impacts of drought in long-term conventional compared to organic farming systems. The results suggest that soil carbon content is among the most important factors driving differences between farming systems and indicate that soils with high carbon content may buffer detrimental effects of future drought conditions on soil animal communities. The observed beneficial effects of high soil carbon content in this study likely were driven by higher soil moisture and improved soil structure under organic farming. Improved soil structure may promote the ability of soil microarthropods to migrate vertically, thereby allowing them to avoid most severe drought conditions in the upper soil layers. Community responses to simulated drought as well as community differences between the farming systems were found for Oribatida but not for Collembola. This indicates that Oribatida communities respond to both short-term (drought) and long-term (farming system) changes in environmental conditions. The community composition of Oribatida, rather than that Collembola, therefore may serve as indicators for effects of drought and management on soil biota.

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APPENDIX

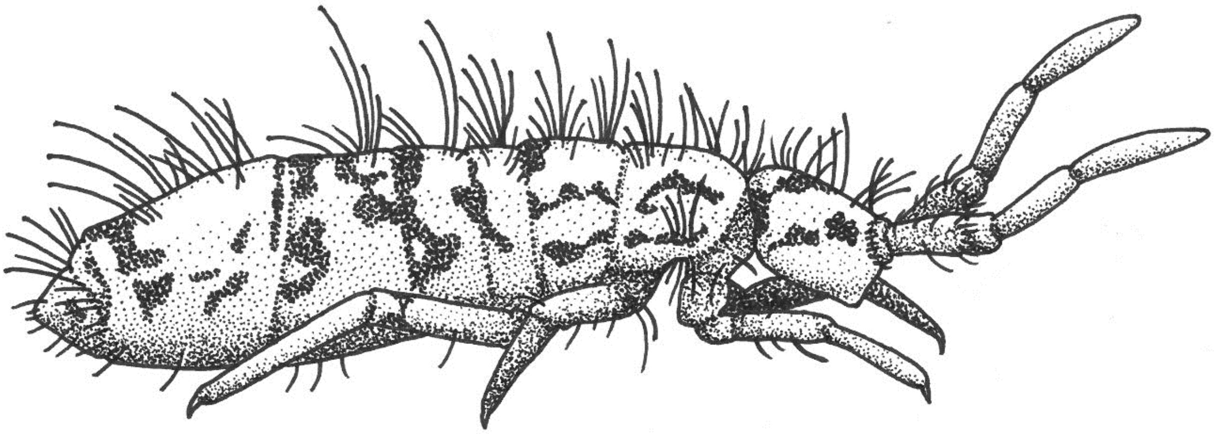
Supplementary Table 3.1 Pesticide application performed in the conventional farming system.

Date of application	Type of pesticide	Product	Manufacturer	Active ingredients	Applied product (l/ha)	Applied active ingredients (g/ha)
March, 20	herbicide	HusarOD (Bayer, Zollighofen)	Bayer (Zollighofen)	Iodosulfuron-methyl-natrium	0.1	10
				Mefenpyr-diethyl (Safener)		30
March, 20	herbicide	Mondera	Syngenta (Switzerland)	Diflufenican	1	33.3
				MCPP-P		500
April, 11	fungicide	Pronto plus	Bayer (Zollighofen)	Sprioxamin	1.5	375
				Tebuconazol		200
May, 30	fungicide	Aviator Xpro	Bayer (Zollighofen)	Bixafen	1	75
				Prothioconazol		150
May, 30	fungicide	Miros FL	Bayer (Zollighofen)	Chlorothalonil	1	500
May, 30	insecticide	Audienz	Omya (Oftringen)	Spinosad	0.1	48

Supplementary Table 3.2 Soil (water holding capacity, total organic carbon, water content), plant (root dry weight, carbon content of roots, weed cover) and microbial parameters (proportion of fungal and bacterial PLFAs) in the different farming systems (conventional, organic) and drought treatments (control, roof) used in the RDA (see **Figure 3.6**).

Farming system	Drought	Water holding capacity (%)	Total organic carbon (%)	Soil water content (%)	Root dry weight (g/l of soil)	Total weed cover (%)	Root carbon content (%)	Proportion of fungal PLFAs (%)	Proportion of bacterial PLFAs (%)
Conventional	Control	41.93	1.45	26.27	0.63	0.00	39.78	1.37	44.22
		38.50	1.12	23.03	0.60	0.00	41.41	1.49	46.10
		38.86	1.25	24.47	0.65	0.00	40.30	1.36	43.41
		34.41	1.29	22.59	0.70	0.00	38.06	1.32	47.37
	Roof	42.48	1.44	15.66	0.76	0.00	39.20	1.53	43.63
		39.52	1.11	14.89	1.12	0.00	37.33	1.72	45.20
		39.76	1.21	16.67	0.78	0.00	37.63	1.63	44.99
		37.81	1.25	16.07	0.85	0.00	38.73	1.41	45.92
Organic	Control	45.55	1.63	28.22	0.64	15.00	40.43	1.51	45.26
		39.81	1.50	26.46	0.91	70.00	42.04	1.30	47.24
		46.47	1.59	26.36	0.90	35.00	40.48	1.61	45.33
		38.11	1.67	25.15	0.59	30.00	42.94	1.36	46.75
	Roof	46.08	1.64	17.59	0.45	55.00	41.22	1.44	43.99
		41.61	1.66	18.39	0.72	15.00	38.89	1.52	46.07
		39.86	1.45	17.98	0.61	35.00	50.54	1.41	45.51
		38.71	1.68	18.09	0.69	40.00	40.45	1.44	44.36

4 TROPHIC NICHE BUT NOT ABUNDANCE OF COLLEMBOLA AND ORIBATIDA CHANGES WITH DROUGHT AND FARMING SYSTEM



The epigeic Collembola *Orchesella villosa*

Peer-reviewed article:

Meyer S, Kundel D, Birkhofer K, Fliessbach A, Scheu S (2022) Trophic niche but not abundance of Collembola and Oribatida changes with drought and farming system. PeerJ 10:e12777.

ABSTRACT

Higher frequencies of summer droughts are predicted to change soil conditions in the future affecting soil fauna communities and their biotic interactions. In agroecosystems drought effects on soil biota may be modulated by different management practices that alter the availability of different food resources. Recent studies on the effect of drought on soil microarthropods focused on measures of abundance and diversity. We here additionally investigated shifts in trophic niches of Collembola and Oribatida as indicated by stable isotope analysis (^{13}C and ^{15}N). We simulated short-term summer drought by excluding 65% of the ambient precipitation in conventionally and organically managed winter wheat fields on the DOK trial in Switzerland. Stable isotope values suggest that plant litter and root exudates were the most important resources for Collembola (*Isotoma caerulea*, *Isotomurus maculatus* and *Orchesella villosa*) and older plant material and microorganisms for Oribatida (*Scheloribates laevigatus* and *Tectocepheus sarekensis*). Drought treatment and farming systems did not affect abundances of the studied species. However, isotope values of some species increased in organically managed fields indicating a higher proportion of microorganisms in their diet. Trophic niche size, a measure of both isotope values combined, decreased with drought and under organic farming in some species presumably due to favored use of plants as basal resource instead of algae and microorganisms. Overall, our results suggest that the flexible usage of resources may buffer effects of drought and management practices on the abundance of microarthropods in agricultural systems.

4.1 INTRODUCTION

Soils in agricultural systems are not well buffered against changes in climate and therefore are likely to undergo profound transformations in face of future climate change. For Central Europe, the predicted climate changes include reduced precipitation during summer with consequent higher frequency of summer droughts (EEA 2017; Samaniego et al. 2018). The resulting lower soil moisture levels are not only relevant for the water supply of crops, but also for soil biota and associated ecosystem functions, such as nutrient cycling and soil aggregate formation (Geng et al. 2015; Spinoni et al. 2015; Zhang et al. 2018). Studies on the effect of drought on soil microarthropods have focused on measures of diversity and abundance and indicate either a negative (Frampton et al. 2000; Blankinship et al. 2011; Karbol et al. 2011; Vestergård et al. 2015) or no response (Holmstrup et al. 2013; Krab et al. 2014).

One way to better understand the response of soil microarthropods to increased drought conditions and to further connect them to processes such as nutrient cycling is to investigate changes in their feeding behavior. Soil organisms interact with each other in a food web with links of different strengths between the individual components (Scheu 1998; Hines et al. 2015; Potapov et al. 2019). From the perspective of soil microarthropods, some of these links may be particularly vulnerable to a decrease in soil moisture (Barreto et al. 2021). Bacteria and nematodes, for example, need water films between soil particles to move, grow and survive (Erktan et al. 2020), and thus are only available as a food resource for microarthropods at sufficiently high soil moisture levels. Further, drought may reduce plant biomass and thereby major basal resources of soil food webs such as leaf litter, roots and rhizodeposits (Jaleel et al. 2009; Scheunemann et al. 2015). Negative effects on these basal resources of soil food webs may cascade up to higher trophic levels resulting in decreased abundance and changes in trophic niches towards more drought-resistant resources like soil organic matter.

In agricultural systems trophic links are likely to vary with soil characteristics and management practices. The availability of resources for microarthropods, such as soil organic matter and microorganisms, differs substantially between management systems receiving organic or mineral fertilizers (Mäder et al. 2002; Birkhofer et al. 2008). Organically managed fields are characterized by higher abundances of microorganisms with a larger proportion of fungi compared to systems receiving only mineral fertilizer (Haubert et al. 2009). These form an important food resource for Collembola and Oribatida (Schneider et al. 2004; Chahartaghi et al. 2005; Pollierer and Scheu 2021). Such differences in resource availability are likely to change the feeding behavior of microarthropods, which has been shown for several other compartments of soil food webs before (Haubert et al. 2009; MacFadyen et al. 2009; Birkhofer et al. 2011). However, the few studies that include Collembola and Oribatida species only documented subtle or no niche shifts with changes in environmental conditions (Korotkevich et al. 2018; Krause et al. 2019).

In this study we use stable isotope analysis to characterize trophic niches of abundant species of Collembola and Oribatida in replicated plots of long-term conventional and organic farming systems. The ratio of the stable isotopes of nitrogen allows insight into the trophic level of consumers due to enrichment in ^{15}N in higher trophic levels, whereas the ratio of carbon stable isotopes reflects the utilization of basal resources (Post 2002; Potapov et al. 2019). In previous studies, stable isotope analysis has mainly been used to characterize the trophic structure of soil animal communities of different habitats and to generally clarify the usage of basal resources by certain taxonomic groups (Scheu and Falca 2000; Potapov et al. 2019). Only few studies employed stable isotope analysis to investigate the response of the trophic structure of soil food webs to different experimental treatments such as different farming systems (Haubert et al. 2009; Birkhofer et al. 2011; Susanti et al. 2021) or track changes in trophic niches induced by changes in environmental conditions (Birkhofer et al. 2016; Korotkevich et al. 2018; Krause et al. 2019). Dry conditions were shown to increase δ^{15}N values of Oribatida in forests possibly due to trophic shifts resulting from changes in microbial activity and community composition (Melguizo-Ruiz et al. 2017). Further, drought is likely to increase periods of starvation due to lower availability of resources that depend on high soil moisture. Starvation has been shown to increase δ^{13}C and δ^{15}N values of the body tissue of animals in part as a result of metabolizing lipids, which are depleted in ^{13}C (Adams and Sterner 2000; Oelbermann and Scheu 2002; Haubert et al. 2009). Effects of drought on stable isotope ratios of microarthropods are likely to differ between different farming systems which comprise differently structured soil food webs (Birkhofer et al. 2011). Additionally, a reduction in soil moisture can be buffered in organically managed fields due to high soil organic carbon contents that result in more structured soils with a higher water holding capacity (Lotter et al. 2003; Kundel et al. 2020). However, the interactive effects of experimental drought and farming systems on the trophic behavior of microarthropods, to the best of our knowledge, have not been investigated before.

Besides looking into mean values of stable isotope ratios of carbon and nitrogen separately, we further include estimates of trophic niche sizes combining measurements of both isotopes in a two-dimensional space (Bearhop et al. 2004; Jackson et al. 2011). Niche sizes are proposed to become narrower in stable, deterministic environments due to more specialization (Giller 1996). In line with this assumption empirical studies on trophic niches of soil animals suggest that trophic niche sizes are smaller in undisturbed compared to disturbed habitats (Korotkevich et al. 2018). We, therefore, expected disturbances such as drought to enlarge the trophic niche of Collembola and Oribatida. Likewise, regarding farming systems, we assumed that a conventional system based on the input of mineral fertilizer without organic fertilizers to represent a more disturbed system compared to an organically managed system receiving manure. Conditions in the conventional system should hence force consumers to enlarge their trophic niche.

Here, we investigated the trophic niches of individual species of Collembola and Oribatida as affected by experimental drought and conventional versus organic farming. We hypothesized (1) trophic niches to vary among species indicating the occupation of different trophic levels and the utilization of different basal resources with intraspecific differences between the conventional and the organic farming system. Further, we hypothesized (2) drought to change the trophic ecology of the studied microarthropod species expressed by increased δ^{13}C and δ^{15}N values of individual species with this being more pronounced in conventionally compared to organically managed fields. We further hypothesized that (3) trophic niche sizes are larger in the experimental drought treatments and the conventional farming system as more severely disturbed systems.

4.2 METHODS

4.2.1 Study site

The study was performed in 2017 in the DOK trial, an agricultural long-term field experiment established in 1978 comparing different organic and conventional farming systems. The DOK trial is located in Therwil, Switzerland, at 300 m above sea level on a Haplic Luvisol on deep deposits of alluvial loess (Fließbach et al. 2007). The mean annual temperature over the last five years was 10.5 °C and the mean annual precipitation was 842 mm (Krause et al. 2020). For this study we used winter wheat fields with soybean as the previous crop. The experimental fields were organized in four blocks each comprising a conventionally and an organically managed field (factor farming system, CONMIN and BIODYN systems of the DOK trial, respectively). Conventionally managed fields received mineral fertilizer (40 – 60 kg N/ha in March, April and May), herbicides (0.1 l/ha of Husar OD, Bayer, Zollikofen, Switzerland, and 1 l/ha of Mondera, Switzerland, once in March), insecticides (0.1 l/ha of Audienz, Omya, Oftringen, Switzerland, in May) and fungicides (1.5 l/ha Pronto Plus in April and 1 l/ha AviatorXpro and Miros FL in May; all Bayer) as well as plant growth regulators (1.5 l/ha Cycocel extra, Omya, in March). Organically managed fields received only organic fertilizers (farmyard manure, compost and slurry), biodynamic preparations and mechanical weed control (Krause et al. 2020; Kundel et al. 2020). All fields were ploughed up to a depth of 20 cm and seedbed preparation was done with a tooth harrow to a depth of 10 cm. In both systems 415 grains/m² were sown. All fields followed the same 7-year crop rotation with soybean as the preceding crop. On each field one drought treatment and one control plot were established (factor drought). We simulated drought by using experimental rainout-shelters that excluded 65% of the precipitation (for details on the shelter construction see Kundel et al. 2018). On the control plots, we established a similar shelter construction with the difference, that it did not reduce precipitation entering the plot. Thereby, we accounted for possible side effects caused by the roof construction itself (Kundel et al. 2018).

4.2.2 Sampling

Samples were taken in May, eight weeks after the establishment of the experiment, with soil cores of 5 and 20 cm diameter to a depth of 10 cm in the center of the plots (n = 16). Microarthropods with high densities, in our case the Collembola *Mesaphorura* sp. and Oribatida, were taken from the 5 cm cores. For the other Collembola, i.e. *Isotoma caerulea, Isotomurus maculatus* and *Orchesella villosa*, abundances in the small cores were too low to obtain enough material for stable isotope measurements, so we took them from the large soil cores that were initially taken to extract macrofauna. Soil animals were extracted from intact soil cores by gradually increasing the temperature from 25 to 55 °C over ten days (Macfadyen 1961; Kempson et al. 1963), collected into a glycol-water solution (1:1) in canisters underneath the soil coresand stored in 70% ethanol. We first sorted the extracted animals to order level under a stereomicroscope (Stemi 2000; Zeiss). Thereafter, Collembola and Oribatida were identified to species or genus level under the microscope (Axioplan; Zeiss). As slide-mounting medium we used 70% ethanol, because other commonly used solutions like lactic acid may change stable isotope compositions. We used keys by Hopkin (2007), Fjellberg (1998, 2007) and Weigmann (2006).

4.2.3 Stable isotope analysis

The four most abundant Collembola taxa (*I. caerulea*, *I. maculatus*, *O. villosa* and *Mesaphorura* sp.) and the two most abundant Oribatida species (*Scheloribates laevigatus* and *Tectocepheus sarekensis*) were chosen for stable isotope analysis. To achieve at least 10 µg of animal dry weight per sample we used 1 - 14 individuals per sample. To have at least three values for every species x drought x farming system combination we included pseudoreplicates in plots with many individuals (**Table 4.1**).

Table 4.1 Number of replicates for stable isotope measurements per farming system (conventional, conv; organic, org) and drought treatment (control, roof).

Species	Farming system	Drought	number of replicates	
			$\delta^{13}C$	$\delta^{15}N$
Isotoma caerulea	conv	control	5	5
		roof	4	3
	org	control	6	6
		roof	4	3
Isotomurus maculatus	conv	control	4	5
		roof	4	4
	org	control	5	5
		roof	4	3
Orchesella villosa	conv	control	6	7
		roof	7	7
	org	control	6	6
		roof	5	6
Scheloribates laevigatus	conv	control	4	4
		roof	6	6
	org	control	7	6
		roof	7	7
Tectocepheus sarekensis	conv	control	6	6
		roof	6	5
	org	control	5	5
		roof	4	4

Animals were weighed into tin capsules and dried at 60°C for 24 h. Wheat from every plot was dried, milled and weighed into tin capsules (ca. 1 mg per sample). Stable isotope analysis of animals was done with a coupled setup of an elemental analyzer (Eurovector, Milano, Italy) and a mass spectrometer (Delta Vplus, Thermo Fisher Scientific, Bremen, Germany) adjusted for small sample sizes (Langel and Dyckmans 2014). Stable isotope analysis of wheat was done with another set of elemental analyzer and mass spectrometer (Flash 2000 elemental analyser coupled to a DELTA Plus XP continuous-flow IRMS via a ConFlo IV interface, Thermo Fisher Scientific, Bremen, Germany). Variations in stable isotope ratios including baseline correction were expressed using the delta notation with $\Delta X = (R_{SAMPLE} / R_{STANDARD}) / R_{STANDARD} \times 1000$ with X representing the target isotope (^{13}C, ^{15}N), and R_{SAMPLE} and $R_{STANDARD}$ the ratios of the heavy to the light isotope ($^{13}C/^{12}C$, $^{15}N/^{14}N$) of the sample and the standard, respectively. As standard for ^{13}C PeeDee Belemnite and for ^{15}N atmospheric air was used (Coplen et al. 2002). Acetanilide was used for internal calibration.

4.2.4 Statistical analyses

All statistical analyses were done in R version 4.0.2 (R Development Core Team 2020).

We calculated mean abundances for each species. Abundance data were analyzed with linear mixed effects models (LMMs) for individual species with farming system and drought as fixed factors, and field as random factor using the package nlme (Pinheiro et al. 2021).

Stable isotope data were baseline corrected using wheat stable isotope values of the respective plot and analyzed with a LMM with farming system and drought as fixed factors, and plot as random factor to account for differences in sample size. Because the interaction species x drought as well as species x farming system was significant (**Table 4.2**), we ran individual LMMs for each species to detect species-specific effects of drought and farming system. In these models we again included drought and farming system and their interaction as fixed factors, and plot as random factor.

The size of the isotopic niches of each species in the two farming systems and in the two drought treatments was calculated and visualized with the R package SIBER (Jackson et al. 2011). Standard ellipse areas with a correction for small sample sizes (SEAc) based on maximum likelihood were estimated and used to visualize isotopic niches of all species in the two farming systems and drought treatments. To compare isotopic niche widths between farming systems and drought treatments within species, Bayesian multivariate normal distributions were fitted to the two levels of the factor farming system and drought, with prior settings of length, number and iterations of sampling chains, and distribution parameters as recommended by Jackson (2019). Based on these probability distributions Bayesian standard ellipse areas were calculated and plotted using the function siberDensityPlot() including 50%, 75% and 95% credible intervals. For statistical comparison of isotopic niche sizes of the farming systems and the drought treatments for individual species, we compared probability distributions from the Bayesian standard ellipses with 95% credible intervals.

4.3 RESULTS

4.3.1 Soil characteristics

Water holding capacity, pH and total carbon were higher in organically compared to conventionally managed fields (**Supplementary Table 4.1**). Total carbon at our study site is equivalent to total organic carbon, because the soil is free of carbonates. Soil water content was decreased by experimental drought by 4.23% and was generally higher in organically compared to conventionally managed fields (**Supplementary Figure 4.1**; see Meyer et al. 2021).

4.3.2 Abundance

Based on their mean abundance the six mesofauna taxa could be separated into two groups of high and low abundance with abundances of the former being 23 to 73 times higher than that of the latter. Highly abundant taxa included *S. laevigatus*, *T. sarekensis* and *Mesaphorura* sp. (overall average of 7648 ± 1528, 7392 ± 1286 and 5312 ± 1734 ind. m^{-2}, respectively; mean ± SE). Species with low abundances included *I. caerulea, I. maculatus* and *O. villosa* (106.8 ± 32.7, 105.0 ± 29.3 and 227.5 ± 49.8 ind. m^{-2}, resepectively). Generally, abundances of individual species did not change significantly with drought treatment or farming system (**Table 4.3**, **Supplementary Figure 4.2**).

Table 4.2 Results of LMM on the effects of drought, farming system and species identity on Δ^{13}C and Δ^{15}N values of the studied mesofauna species; significant effects ($P < 0.05$) are given in bold.

	Δ^{15}N			**Δ^{13}C**		
	df	***F***	***P***	**df**	***F***	***P***
Drought (D)	1,12	2.74	0.124	1,12	3.09	0.104
Farming system (F)	**1,12**	**13.84**	**0.003**	1,12	3.02	0.108
Species (S)	**4,71**	**32.56**	**<0.001**	**5,83**	**43.02**	**<0.001**
D x F	1,12	2.19	0.164	1,12	0.04	0.844
D x S	4,71	0.72	0.58	**5,83**	**2.92**	**0.018**
F x S	**4,71**	**10.11**	**<0.001**	**5,83**	**4.30**	**0.002**
D x F x S	4,71	2.39	0.059	5,83	1.49	0.203

Table 4.3 Results of LMMs on the effects of drought and farming system on the abundance, Δ^{13}C and Δ^{15}N values of abundant species of the mesofauna; significant effects are given in bold.

	Scheloribates laevigatus			***Tectocepheus sarekensis***			***Isotoma caerulea***			***Isotomurus maculatus***			***Orchesella villosa***			***Mesaphorura* sp.**		
	df	***F***	***P***	**df**	***F***	***P***	**df**	***F***	***P***	**df**	***F***	***P***	**df**	***F***	***P***	**df**	***F***	***P***
Abundance																		
Drought (D)	1,6	0.01	0.943	1,6	2.68	0.153	1,6	0.88	0.384	1,6	3.06	0.131	1,6	1.05	0.344	1,6	0.53	0.495
Farming system (F)	1,6	1.80	0.228	1,6	0.01	0.910	1,6	0.83	0.396	1,6	0.13	0.728	1,6	1.63	0.249	1,6	1.79	0.229
D x F	1,6	0.84	0.394	1,6	0.42	0.540	1,6	1.51	0.266	1,6	0.49	0.510	1,6	0.09	0.779	1,6	4.56	0.077
d13C																		
Drought (D)	**1,6**	**17.08**	**0.001**	1,6	1.16	0.310	1,6	0.54	0.485	1,6	2.51	0.157	1,6	0.01	0.922	1,6	0.10	0.766
Farming system (F)	1,6	<0.01	0.960	**1,6**	**14.11**	**0.005**	1,6	1.16	0.312	1,6	0.88	0.379	1,6	0.36	0.562	1,6	0.43	0.536
D x F	1,6	0.07	0.798	1,6	0.04	0.851	1,6	0.19	0.676	1,6	2.68	0.145	1,6	0.13	0.726	1,6	0.75	0.419
d15N																		
Drought (D)	1,6	0.03	0.867	1,6	0.04	0.845	1,6	0.10	0.759	1,6	0.21	0.663	1,6	1.44	0.261	-	-	-
Farming system (F)	1,6	4.30	0.062	1,6	2.82	0.132	**1,6**	**15.47**	**0.008**	1,6	2.69	0.145	**1,6**	**15.90**	**0.003**	-	-	-
D x F	1,6	0.09	0.771	1,6	0.22	0.649	1,6	3.92	0.095	1,6	2.22	0.180	1,6	0.04	0.855	-	-	-

4.3.3 Isotope values

Mean stable isotope values were significantly different between species, spanning over two δ units for ^{13}C and over four δ units for ^{15}N (**Figure 4.1**, **Table 4.2**). The Δ^{13}C values of the two Oribatida species were three to four δ units higher than those of the three Collembola species. Mean Δ^{15}N values spanned over four δ units with the values of *S. laevigatus* exceeding those of the other species by three to four δ units.

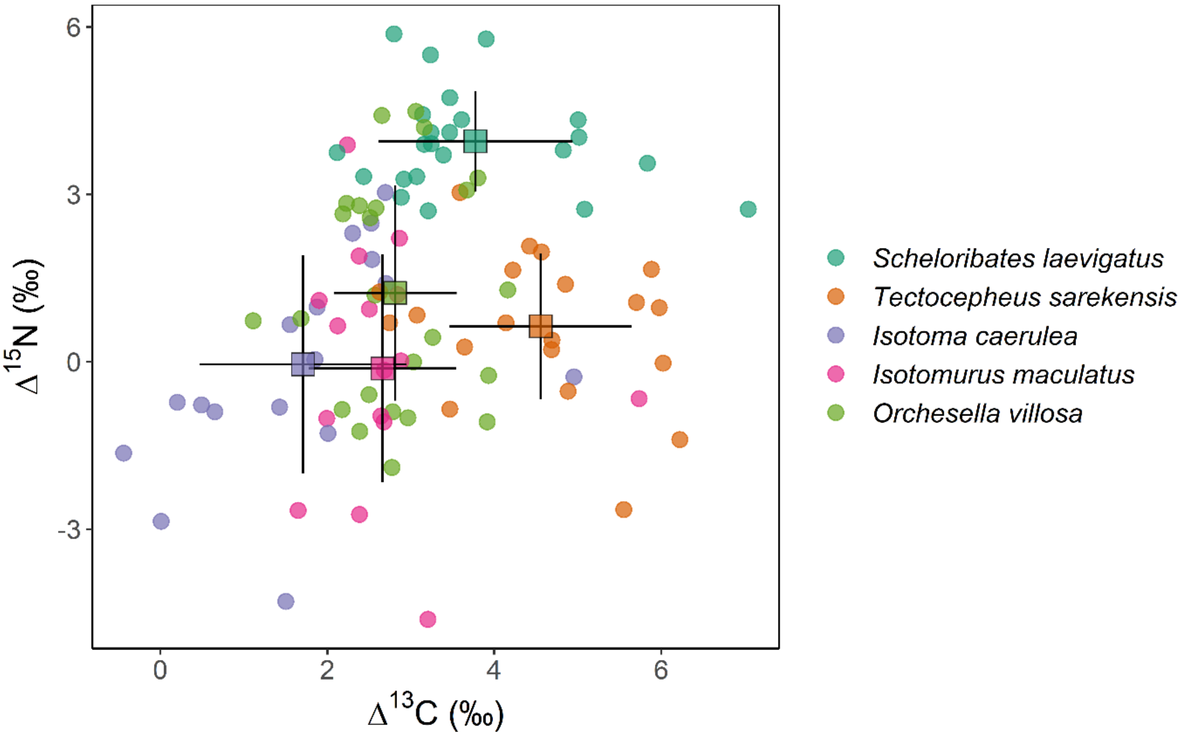


Figure 4.1 Mean (± standard deviation) Δ^{13}C and Δ^{15}N values of two species of Oribatida (*Scheloribates laevigatus*, *Tectocepheus sarekensis*) and three species of Collembola (*Isotoma viridis*, *Isotomurus maculatus*, *Orchesella villosa*); data are calibrated against stable isotope values of wheat in the respective plot.

The Δ^{13}C but not Δ^{15}N values differed significantly among the studied mesofauna species between the drought treatments (**Table 4.2**), with this pattern being driven by a significant reduction in the Δ^{13}C values of *S. laevigatus* under drought; Δ^{13}C values of the other species were not significantly affected by drought (**Figure 4.2**, **Table 4.3**). By contrast, both Δ^{13}C and Δ^{15}N values of mesofauna species varied significantly with farming system (significant species × farming system interaction; **Table 4.2**). In organically managed fields the Δ^{13}C value of *T. sarekensis* and the Δ^{15}N values of *I. caerulea* and *O. villosa* significantly exceeded those in conventionally managed fields (**Figure 4.3**, **Table 4.3**).

Drought significantly reduced the isotopic niche width of *S. laevigatus* ($P = 0.016$), *I. caerulea* ($P = 0.003$) and *I. maculatus* ($P = 0.032$) (**Figure 4.4**), with isotopic niches of *S. laevigatus* partly overlapping between the two drought treatments, whereas in *I. caerulea* and *I. maculatus* they overlapped in full (**Figure 4.5**). Further, the isotopic niche space of *I. caerulea* and *I.*

maculatus was significantly smaller in organically compared to conventionally managed fields, with isotopic niches of *I. caerulea* partly overlapping between the two farming systems, whereas those of *I. maculatus* overlapped in full (**Figure 4.6**).

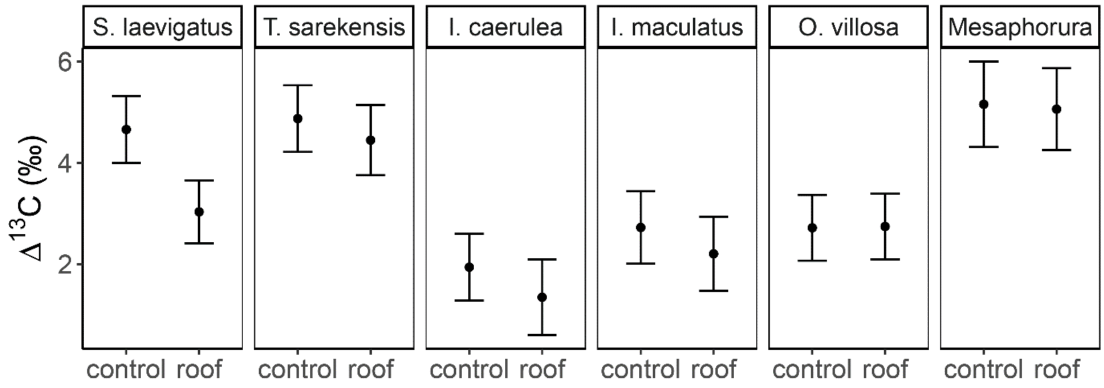


Figure 4.2 Mean (± 95% confidence interval) $\Delta^{13}C$ values in control and drought treatments (roof) for two species of Oribatida (*Scheloribates laevigatus*, *Tectocepheus sarekensis*) and four Collembola taxa (*Isotoma caerulea, Isotomurus maculatus, Orchesella villosa*, *Mesaphorura* sp.); for statistical analysis see **Table 4.3**.

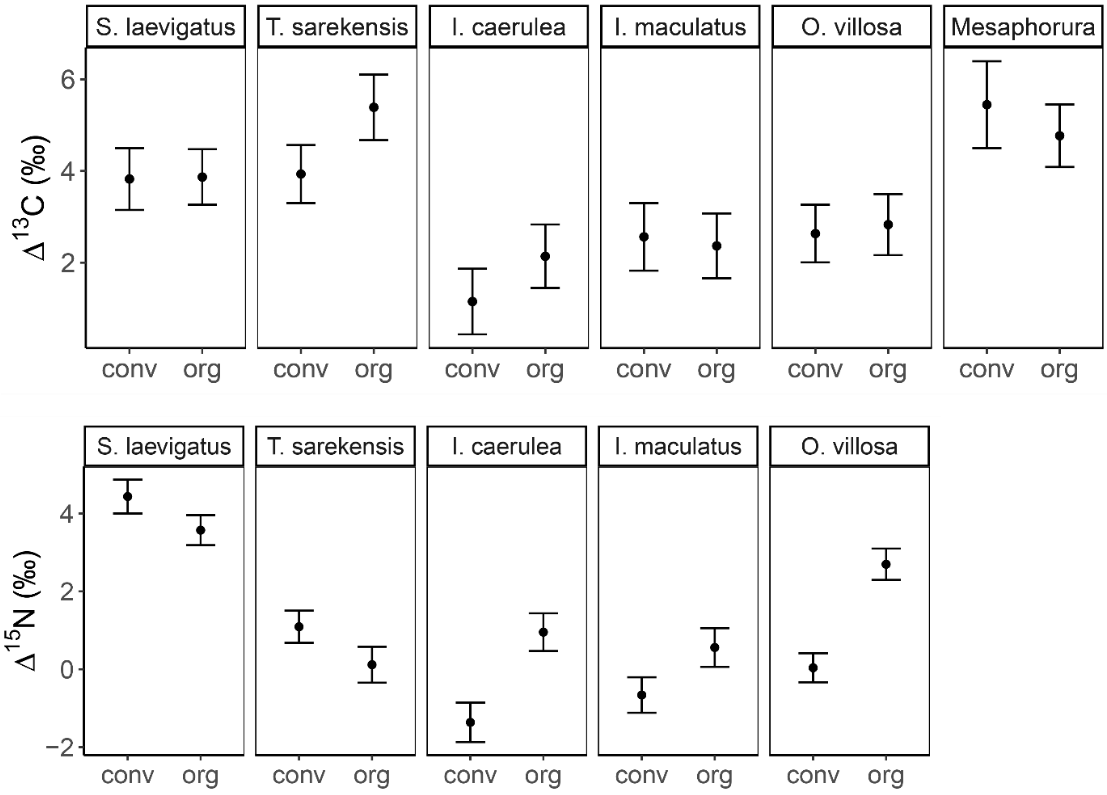


Figure 4.3 Mean (± 95% confidence interval) $\Delta^{13}C$ (upper panel) and $\Delta^{15}N$ values (lower panel) of two Oribatida (*Scheloribates laevigatus*, *Tectocepheus sarekensis*) and four Collembola species (*Isotoma caerulea*, *Isotomurus maculatus*, *Orchesella villosa*, *Mesaphorura* sp.) in conventional (conv) and organic (org) farming systems; note that for *Mesaphorura* sp. only $\Delta^{13}C$ values are shown. For statistical analysis see **Table 4.3**.

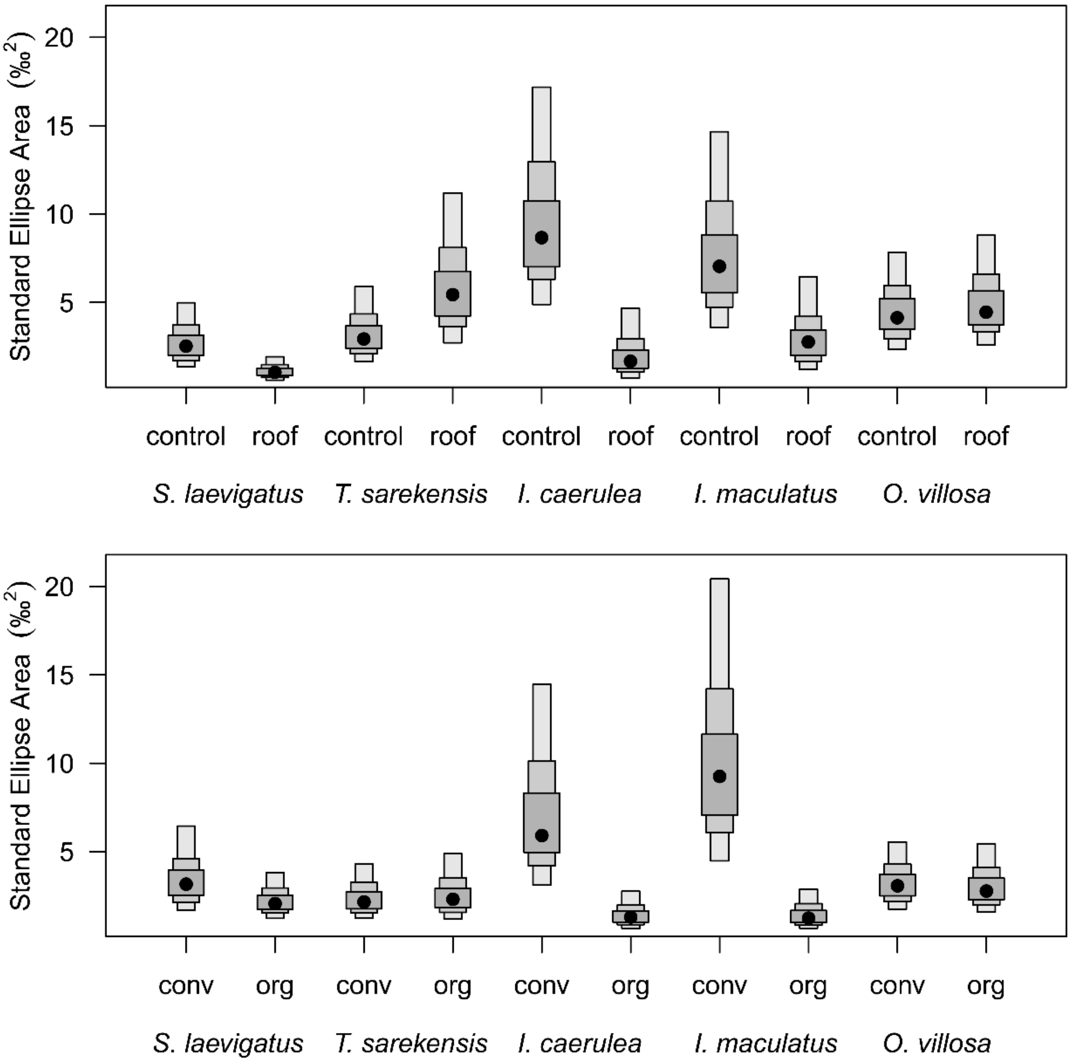


Figure 4.4 Probability distribution of the sizes of isotopic niches of five microarthropod species (*Scheloribates laevigatus, Tectocepheus sarekensis, Isotoma caerulea, Isotomurus maculatus, Orchesella villosa*) in the drought (roof) and the control treatment (upper panel), and in conventional (conv) and organic (org) farming systems (lower panel). Points show posterior estimates of the Bayesian standard ellipse area with 50%, 75% and 95% credible intervals (from dark to light gray).

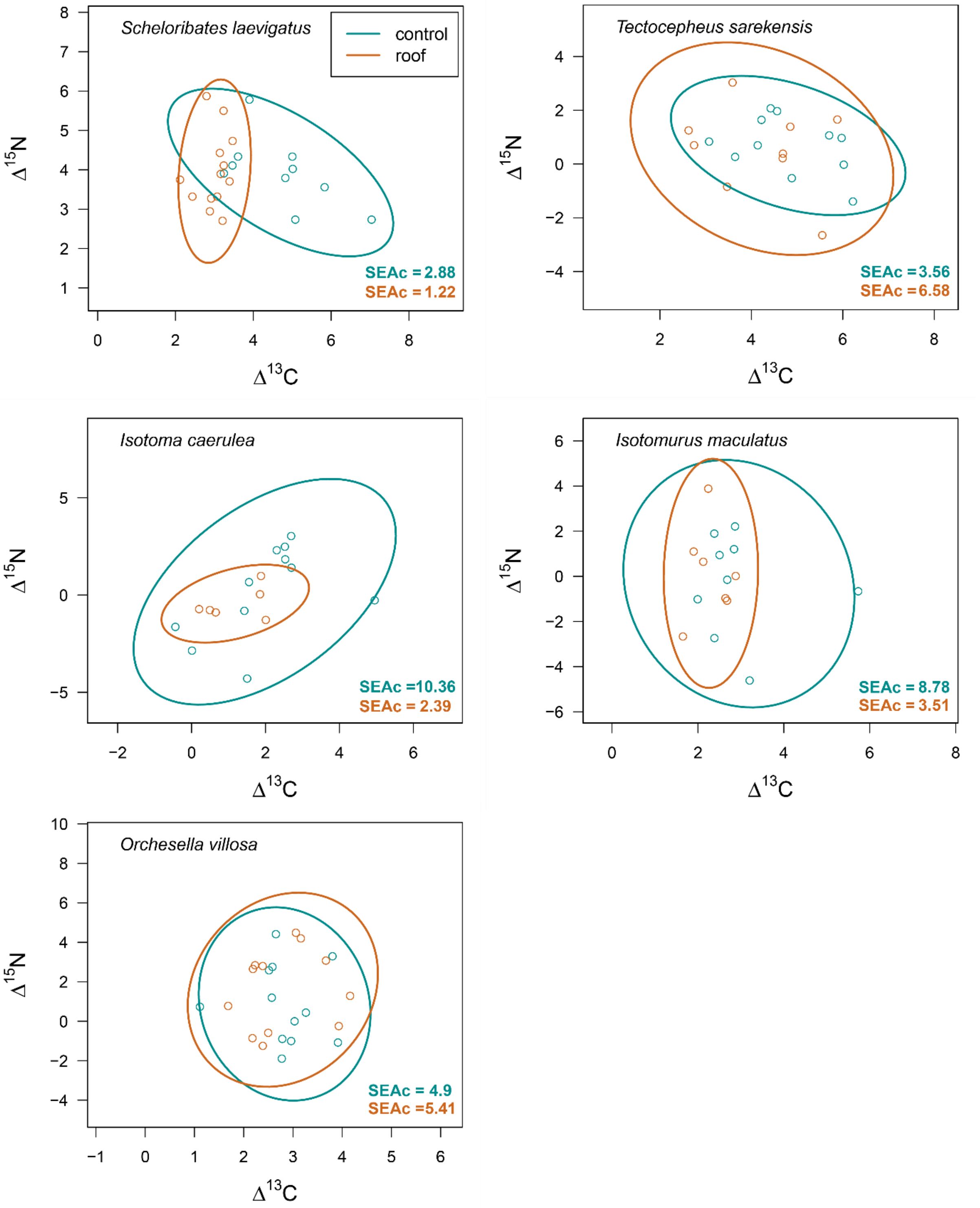


Figure 4.5 Isotopic niche space of two Oribatida (*Scheloribates laevigatus*, *Tectocepheus sarekensis*) and three Collembola species (*Isotoma caerulea*, *Isotomurus maculatus*, *Orchesella villosa*) in the drought (roof, orange) and the control (turquoise) treatment. Standardized ellipses (SEAc) account for different sample sizes between taxa and small sample sizes per taxon and encompass approximately 95% of the data; see Methods.

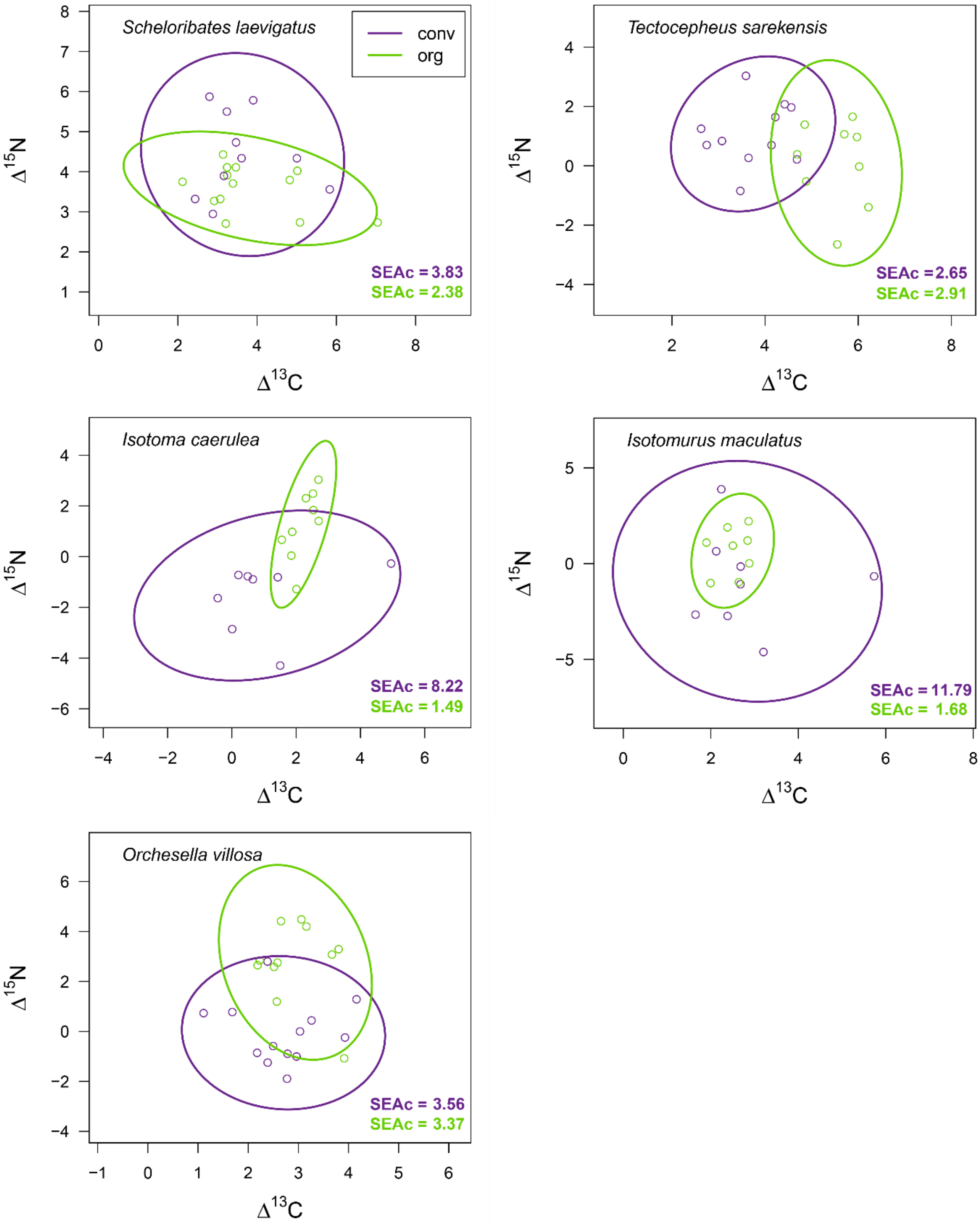


Figure 4.6 Isotopic niche space of two Oribatida (*Scheloribates laevigatus*, *Tectocepheus sarekensis*) and three Collembola species (*Isotoma caerulea*, *Isotomurus maculatus*, *Orchesella villosa*) in conventionally (conv, purple) and organically (org, green) managed fields. Standardized ellipses (SEAc) account for different sample sizes between taxa and small sample sizes per taxon and encompass approximately 95% of the data; see Methods.

4.4 DISCUSSION

The species studied were selected based on two criteria: sufficiently high abundance combined with sufficiently high biomass for stable isotope analyses, and therefore can be considered as the most important Collembola and Oribatida species of the system regarding energy flux and functioning. Interestingly, the farming system and the experimental drought did not affect the abundances of the studied species significantly, but affected their trophic niches as indicated by stable isotope analyses.

4.4.1 Trophic positions

Overall, stable isotope values of the studied microarthropods spanned two δ units in ^{13}C and four δ units in ^{15}N, indicating the utilization of different C resources and the representation of at least two trophic levels, assuming an enrichment of about 3 δ units per trophic level (Post 2002). Based on the Δ^{13}C and Δ^{15}N values of the individual species, the studied taxa can be separated into three groups, the three Collembola species, the Oribatida species *T. sarekensis* and the Oribatida species *S. laevigatus.*

The three Collembola species *I. caerulea*, *I. maculatus* and *O. villosa* had Δ^{15}N values close to zero, indicating they are closely linked to wheat plants and suggesting that they live as primary decomposers that are little enriched in ^{15}N (-0.05 ‰, -0.12 ‰, 1.23 ‰, respectively). Earlier studies also found large epi- and hemiedaphic Collembola species, such as the ones we studied, to predominantly feed on plant-derived resources in both agroecosystems and forests (Pollierer et al. 2009; Birkhofer et al. 2016; Potapov et al. 2016). Ngosong et al. (2009) further found plant rather than fungal resources to be incorporated by Collembola in agricultural systems, and results of the study of Li et al. (2020) suggest that root-derived carbon is a major resource.

Isotope values of ^{13}C of both Oribatida species exceeded those of the three Collembola species by one to two δ units, indicating that both are linked to resources enriched in ^{13}C. However, their Δ^{15}N values indicated that they occupy different trophic levels with *T. sarekensis* living as primary decomposer and *S. laevigatus* as secondary decomposer or predator, similar to what has been previously suggested (Schneider et al. 2004; Haynert et al. 2017). The average δ^{13}C value of *T. sarekensis* being 4.55 ‰ higher than plant litter indicates that *T. sarekensis* is linked to older carbon resources, probably soil organic matter in deeper soil layers (Potapov et al. 2019). The average δ^{15}N value of *S. laevigatus* being 3.77 ‰ higher than that of plant litter indicates a mixed diet consisting of mainly microorganisms, but in part also microbial feeders such as nematodes.

4.4.2 Farming system

Our second hypothesis was partly supported by the significantly higher isotope values of *T. sarekensis*, *I. caerulea* and *O. villosa* in the organic compared to the conventional farming system. However, we did not find differences for the other taxa, which is in line with earlier studies comparing different agricultural systems (Haubert et al. 2009; Birkhofer et al. 2011; Lagerlöf et al. 2017). The higher isotope values of *T. sarekensis, I. caerulea* and *O. villosa* in the organic farming system likely are related to the higher soil organic carbon content that was found in this system. The higher Δ^{13}C values of *T. sarekensis* in organically compared to conventionally managed fields indicate that they more intensively feed on old carbon resources in the organic system, which is richer in soil organic matter due to long-term input of farmyard manure and compost (Mäder et al. 2002). In *I. caerulea* and *O. villosa* $\Delta^{15}N$ values were higher in organically compared to conventionally managed fields, pointing to a higher proportion of microorganisms in their diet in the organic system. In fact, previous studies conducted in the same long-term experiment as the present study found higher microbial biomass in the organically than the conventionally managed fields indicating a higher availability of microbes as food resource (Esperschütz et al. 2007; Fließbach et al. 2007). This is likely to be a consequence of higher soil water content and soil organic carbon in the organically managed fields. This effect might further be enhanced by higher $\delta^{15}N$ values of the organic fertilizer (farmyard manure) compared to the inorganic fertilizer in the conventional system (Birkhofer et al. 2011). Higher stable isotope values in the organic system may additionally be caused by stable isotope enrichment of soil organic matter due to stronger internal nutrient cycling (Vervaet et al. 2002; Hobbie and Ouimette 2009).

Besides the comparison of mean stable isotope values, additional information on trophic shifts of species can be obtained by comparing trophic niche width and trophic niche space (Behan-Pelletier 1999; Bearhop et al. 2004). Our hypothesis on changes in trophic niche width with farming system was based on the assumption that in less disturbed habitats consumers would have a greater range of potentially available food resources, from which species could select according to their preferences. By contrast, in more severely disturbed systems, preferred resources may not be available, forcing consumers to feed on a wider range of resources resulting in broader trophic niches. Our data support this hypothesis only partly for the two farming systems and, interestingly, in some species showed the opposite pattern for the drought treatment (see below). Variations in $\Delta^{13}C$ values in *I. caerulea* and *I. maculatus* were small in the organic farming system indicating a diet consisting of fresh litter or root exudates, whereas in the conventional farming system diets varied more widely. This suggests the utilization of a wider range of resources including old litter and microorganisms resulting in increased $\delta^{13}C$ values (Potapov et al. 2019) or algae resulting in decreased $\delta^{13}C$ values (Tozer et al. 2005). In the conventional system, the amount of litter input is low and limited to plant residues from the crop plant, i.e., mainly roots, whereas in the organic system plant residues in the organic fertilizer provide additional food resources. Further, the amount of rhizodeposits in the conventional system is likely to be lower than in the organic system, thereby providing fewer resources to the belowground food web (Jones et al. 2001; Li et al. 2016; Wang et al. 2016). The lower availability of preferred food resources in the conventional compared to the organic farming system may force soil invertebrates to broaden their trophic niche. Further, in the conventional farming system more algae may be present due to the scarcity of weeds (Meyer et al. 2021) providing additional food resources that are not equally available in organic farming systems.

4.4.3 Drought

Drought significantly decreased soil moisture in both farming systems. However, contradicting our second hypothesis, drought did not affect stable isotope values of most taxa and there was no significant interaction with farming system. Only *S. laevigatus* had lower $\Delta^{13}C$ and constantly high $\Delta^{15}N$ values in the drought treatment indicating prey switching. Assuming that *S. laevigatus,* at least in part, feeds on nematodes, this might represent a switch from microbial-feeding to plant-feeding nematodes, due to microbial-feeding nematodes being heavily stressed under dry conditions due to reduced microbial activity (Kundel et al. 2020). In contrast to conventional farming and contrasting our second hypothesis, drought decreased the trophic niche width in some species (*S. laevigatus, I. caerulea* and *I. maculatus*). For *S. laevigatus* this was caused by lower $\Delta^{13}C$ values in the drought treatment, probably due to prey switching (see above). In the two Collembola species the decreased trophic niche width was due to decreased variation in $\Delta^{13}C$ values, but not lower mean $\Delta^{13}C$ values, indicating more restricted consumption of plant-derived resources rather than algae and microorganisms. Accessibility of algae and microorganisms is likely to decrease at low soil moisture, whereas the availability of (higher) plant-derived resources may be less affected. In fact, plant-related variables, including root biomass, shoot biomass and grain yield, did not differ between the drought treatments in this experiment (Kundel et al. 2020). For *I. caerulea*, additionally, the smaller variation in $\Delta^{15}N$ values, but no changes in mean $\Delta^{15}N$ values, in the drought treatment supports the conclusion of narrower trophic niches due to more pronounced feeding on plant material.

4.4.4 Conclusions

Drought did not significantly affect mean stable isotope values of most of the studied mesofauna species, but trophic niche width and space changed significantly, highlighting the relevance of these trophic niche characteristics for tracking effects of changes in environmental factors on soil food webs. Our results provide further evidence that in agricultural fields both plant litter and root-derived carbon play an important role as food resource for soil microarthropods. Overall, our data indicate that short-term drought as well as organic farming reduces the diversity of the resources used by soil microarthropods and favors the use of plants as basal resource for Collembola and Oribatida instead of microorganisms and algae. At the same time, the abundances of Collembola and Oribatida were not affected, suggesting that a flexible usage of resources may buffer negative effects of drought conditions on microarthropod communities in agricultural fields.

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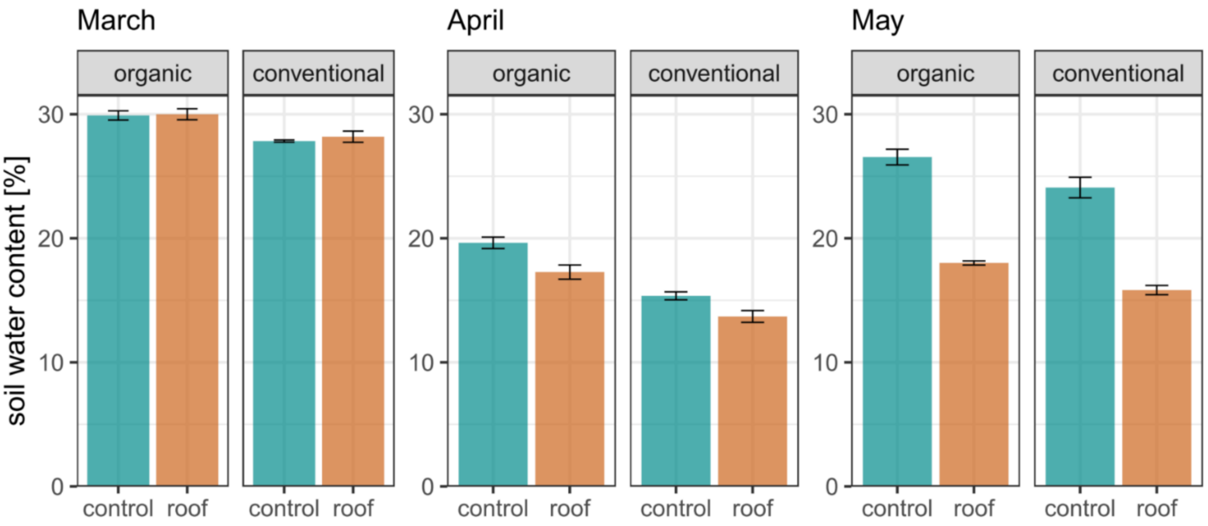
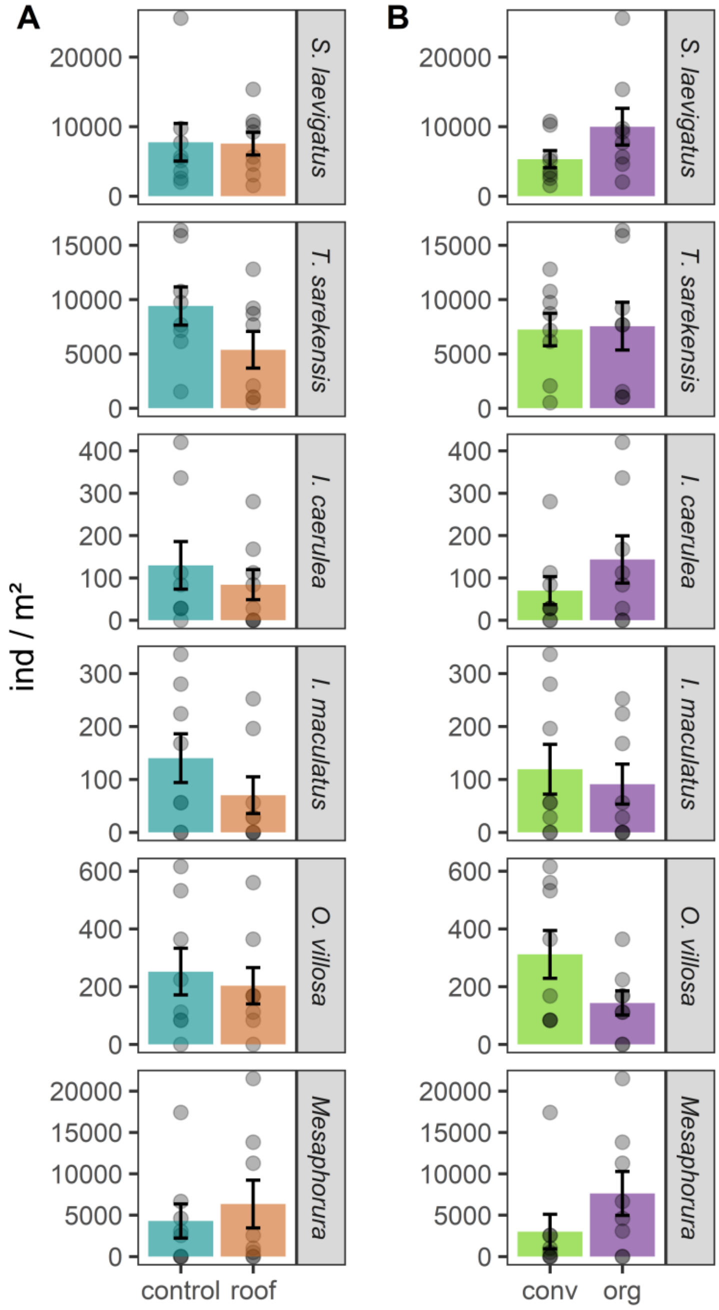
APPENDIX

Supplementary Table 4.1 Soil characteristics in the conventional ("ConMin" of the DOK-trial) and the organic ("BioDyn") farming system. Mean ± SE.

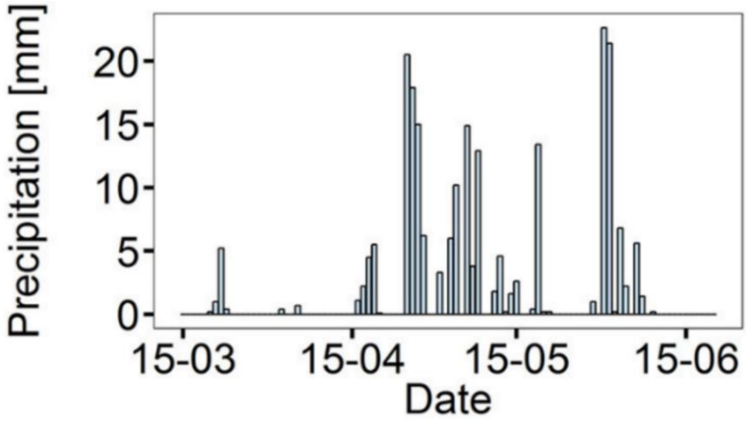
	Farming system	
	conventional	**organic**
pH (in water)	6.03 ± 0.1	6.63 ± 0.04
WHC (0-10 cm) [%]	39.16 ± 0.89	42.03 ± 1.23
bulk density (0-10 cm) [g/cm³]	1.21 ± 0.02	1.17 ± 0.03
C_{tot} [%]	1.27 ± 0.05	1.60 ± 0.03
N_{tot} [%]	0.13 ± 0	0.17 ± 0
PO4-P [µg/g DW]	0.00104 ± 0.00005	0.001 ± 0.00005
P [mg/g DW]	0.827 ± 0.014	0.801 ± 0.024



Supplementary Figure 4.1 Gravimetric soil water content (0– 20 cm depth) in control and drought treatments (roof) in wheat fields under organic and conventional management in March (before roof establishment), April and May (sampling of soil animals); means ± SE based on four replicates; modified from Meyer et al. 2021.

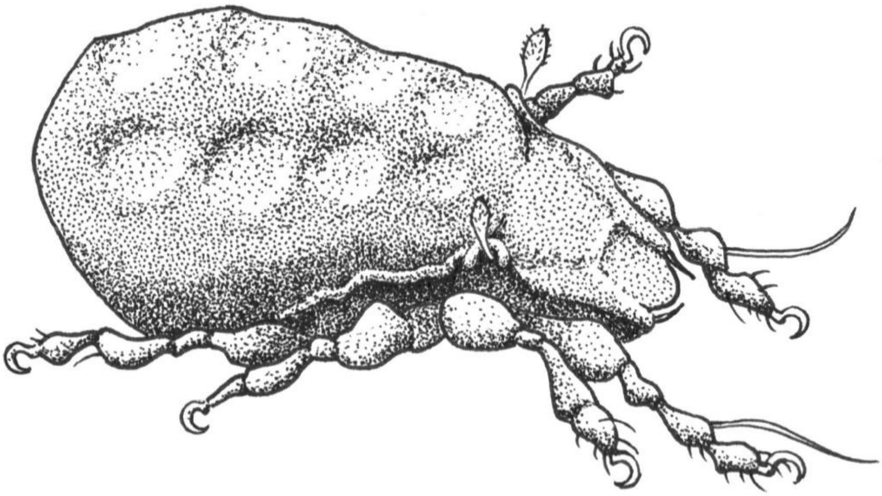


Supplementary Figure S 4.2 Abundance (mean ± standard error) of two Oribatida (*Scheloribates laevigatus*, *Tectocepheus sarekensis*) and four Collembola species (*Isotoma caerulea*, *Isotomurus maculatus*, *Orchesella villosa*, *Mesaphorura* sp.) in **A** control and drought treatments (roof) and **B** under conventional (conv) and organic (org) management.



Supplementary Figure 4.3 Precipitation (mm in 24h) during the time of the experiment; data between April 5 to May 8, 2017 derived from the online database http://www. bodenmessnetz.ch (station in Therwil), all other data was recorded by the on-site weather station (Campbell-CR1000); modified from Kundel et al. 2018.

5 SOIL CARBON CONTENT AND LOCAL CLIMATE DETERMINE DROUGHT EFFECTS ON ORIBATIDA



The oribatid mite *Tectocepheus sarekensis*

Meyer S, Birkhofer K, Scheu S. Soil organic carbon content and local climate determine drought effects on Oribatida. *in prep.* (2022).

ABSTRACT

Droughts will become more frequent and more severe in Europe under future climate change. Soil animals were shown to react differently to drought with negative, neutral, and positive responses being reported from field experiments. To better understand these different responses, we conducted a drought manipulation experiment that included additional factors that might modulate the response of microarthropods (Acari and Collembola) to drought: Soil organic carbon (SOC) content and country, e.g. local climate. We established roofs in winter wheat fields (*Triticum aestivum*) with high and low SOC content at sites with temperate (Sweden and Germany) and Mediterranean climate (Spain). Of the studied microarthropod groups only Oribatida were significantly affected by drought with the direction of these effects being different in high and low SOC fields and among countries. Drought decreased abundances of Oribatida in low SOC fields and increased them in high SOC field. Negative drought effects occurred only in Sweden driven by strong negative effects in low SOC fields, where soil water content was extremely low (below 7%). Oribatida at the Spanish sites were only little affected indicating that communities from dry climates are adapted to drought, e.g. by living in deeper soil. Overall, the results suggest that drought effects on Oribatida are strongest under temperate climate conditions and that increasing SOC levels in agricultural soils may be a useful tool to mitigate or even reverse negative drought effects.

5.1 INTRODUCTION

With future climate change the intensity and frequency of summer droughts are predicted to increase in Europe (Spinoni et al. 2018). Such droughts are accompanied by reduced soil water content and thereby likely will affect soil fauna (Samaniego et al. 2018; Ruosteenoja et al. 2018). Consequently, a number of experiments have been established to better understand how such drought effects act on different compartments of the soil system (Beier et al. 2004; Mikkelsen et al. 2008; Schädler et al. 2019). Most of the studies that included soil organisms focused on forests and grasslands, whereas studies in agricultural cropping systems are rare.

In the face of future food production, the potential vulnerability of agricultural systems to climate change is of great importance and their response is likely to be different than that of forest and grassland ecosystems. Agricultural fields are often only little protected by vegetation cover or a litter layer that might buffer effects of reduced precipitation and increased air temperature. Additionally, the soil is heavily disturbed by management practices such as ploughing and frequent biomass removal. Such harsh conditions may result in a community comprising few robust species that are resistant against periodic drought and possibly not heavily affected by a further increase in drought severity and frequency. On the other side, conditions in agricultural fields may already represent the limits of the ecological niche of species and a further increase in stress may critically affect them. Results of field studies point towards both of these scenarios reporting negative as well as neutral and positive effects of drought on soil organisms (Petersen 2011; Vestergård et al. 2015; Holmstrup et al. 2017; Flórián et al. 2019; Homet et al. 2021). Hence, despite negative effects of drought appear to be more likely, as Blankinship et al. (2011) summarized in a meta-analysis, general conclusions are still uncertain. A number of authors therefore advocated for adopting a broader perspective considering a wider range of factors, such as taxonomic group, soil characteristics and local climate, to better understand the different responses of soil biota to increased drought (Blankinship et al. 2011; Wu et al. 2011; Beier et al. 2012).

We conducted a drought manipulation experiment across arable fields varying in soil organic carbon (SOC) content and local climate conditions as additional variables. High SOC content increases water holding capacity by enhancing soil structure and thereby may buffer negative effects of drought on soil animals (Shepherd et al. 2002; Manns and Martin 2018; Meyer et al. 2021). In addition, SOC content can be manipulated by management practices thereby providing a tool to mitigate potential negative effects of drought (Iglesias and Garrote 2015). Communities of soil organisms are known to vary with local climatic conditions and this likely also applies to their vulnerability to drought (Nielsen et al. 2010; Ponge and Salmon 2013). Studies from semiarid and arid climates did not find effects of drought on soil microarthropods (Liu et al. 2017; Flórián et al. 2019), suggesting that local species are adapted to dry soil conditions. However, only few studies on drought effects on soil organisms included replicated experiments along a natural climatic gradient and to the best of our knowledge none were conducted in agricultural fields (Petersen 2011; Peguero et al. 2019).

Periods of drought do not uniformly affect the water content across the soil profile, rather upper layers are drying up faster than deeper layers. This may induce vertical migration to deeper soil as response to drought as shown for Collembola and earthworms (Petersen 2011; Fraser et al. 2012). Such vertical migration might further be facilitated by a more structured soil high in SOC content (Meyer et al. 2021). Additionally, Petersen (2011) reported the fraction of Collembola (of total) colonizing upper soil layers to decrease from North to South Europe, suggesting that the vertical distribution of soil animals within the soil profile may be an adaptation to drought with soil animal communities in more dry regions colonizing deeper soil layers.

In the present study we experimentally simulated short-term drought during the growing season of winter wheat (*Triticum aestivum*) at sites with different local climate. Two sites had a temperate climate (Sweden and Germany), and one site had a Mediterranean climate. Further, we included fields with high and low SOC content and two different soil layers (0-5 and 5-10cm depth). We hypothesized that (1) microarthropods are negatively affected by experimental drought with this (2) being more pronounced in fields with low than in fields with high SOC content. We further hypothesized that (3) effects of experimental drought are larger in Sweden and Germany compared to Spain due to communities in Spain being better adapted to drought. Finally, we hypothesized (4) microarthropods to migrate into deeper soil layers under drought to escape dry soil conditions in the upper soil.

5.2 METHODS

5.2.1 Experimental design

In 2018 drought experiments were established in winter wheat fields (*T. aestivum*) in Germany, Sweden and Spain representing a natural gradient in precipitation from high to low (**Figure 5.1**, **Table 5.1**).

Data on the 30 year means of temperature and precipitation were obtained from the E-OBS daily data set at a horizontal resolution of about 10 km (https://www.ecad.eu/download/ensembles/download.php, Cornes et al. 2018). The experiment was established in a complete randomized block design with five field pairs in every country each comprising one field with low and one with high SOC content (**Figure 5.2**). To select field pairs SOC was measured before the experiment started. Measurements during the experiment, however, showed that in one Spanish and two German field pairs "high SOC" fields had lower SOC than the low SOC fields. Nonetheless, differences between high and low SOC fields were significant in all countries (Germany: $F_{1,24} = 9.53$, $p = 0.005$; Sweden: $F_{1,24} = 33.92$, $p = < 0.001$; Spain: $F_{1,24} = 5.03$, $p = 0.035$). The differences between the two fields within one field pair were generally largest in Sweden (**Table 5.1**).

All experimental plots had a minimum distance to the field edge of 20 m and were in a 5 to 10 m stripe where no pesticides were applied during the experiment (February to July). In February (Spain), March (Germany) and April (Sweden) we established two drought

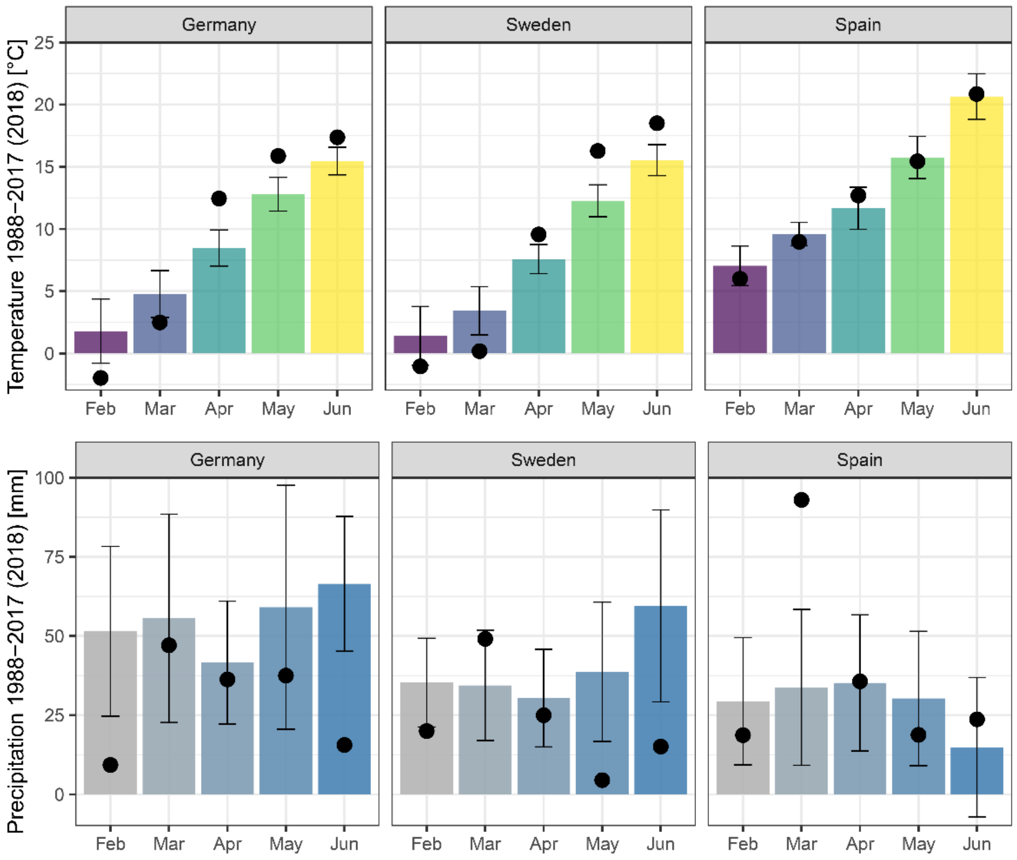


Figure 5.1 Temperature and precipitation for the months February to June from a 30-year period (1988-2017) (bars; means ± standard deviation) and from 2018 (black dots) as means over all study sites in Germany, Sweden and Spain, respectively; data were obtained from the E-OBS daily data set at a horizontal resolution of about 10 km (https://www.ecad.eu/download/ensembles/download.php, Cornes et al. 2018).

Table 5.1 Site characteristics of all field pairs in Germany, Sweden, and Spain; data on temperature and precipitation are based on interpolated datasets drawn from E-OBS (Cornes et al. 2018); Temperature (T), pH and SOC are means over all plots within one field pair (n = 4); precipitation is the sum of the precipitation during the main growing season of winter wheat (February to May for Spain and March to June for Germany and o); data on the 30 year means of temperature and precipitation were obtained from the E-OBS daily data set at a horizontal resolution of about 10 km (https://www.ecad.eu/download/ensembles/download.php, Cornes et al. 2018).

	Germany					Sweden					Spain				
Field pair	1	2	3	4	5	1	2	3	4	5	1	2	3	4	5
T growing season [°C]	12.1	11.7	11.8	11.8	11.1	11.2	10.9	11.4	10.8	10.5	12.1	12.1	12.9	12.9	12.9
precipitation growing season [mm]	301	296	301	294	329	254	264	224	248	246	149	149	144	144	144
pH	8.1	8.3	7.4	8.1	7.4	6.8	6.1	7.5	7.2	6.4	8.5	8.3	8.7	8.6	8.7
SOC [%]	1.81	2.05	1.52	1.48	1.45	1.79	2	2.63	2.25	1.63	0.57	0.4	0.43	0.65	0.86
difference high SOC - low SOC field	1.03	-0.07	-0.05	0.07	0.2	0.69	0.46	2.41	0.64	0.48	0.22	0.09	-0.18	0.18	0.15

treatments in each field, one roof that excluded 65% of the ambient precipitation and one control roof, that did not exclude any precipitation but accounted for possible side effects of the roofs. For details on the design and the performance of the roofs see Kundel et al. (2018).

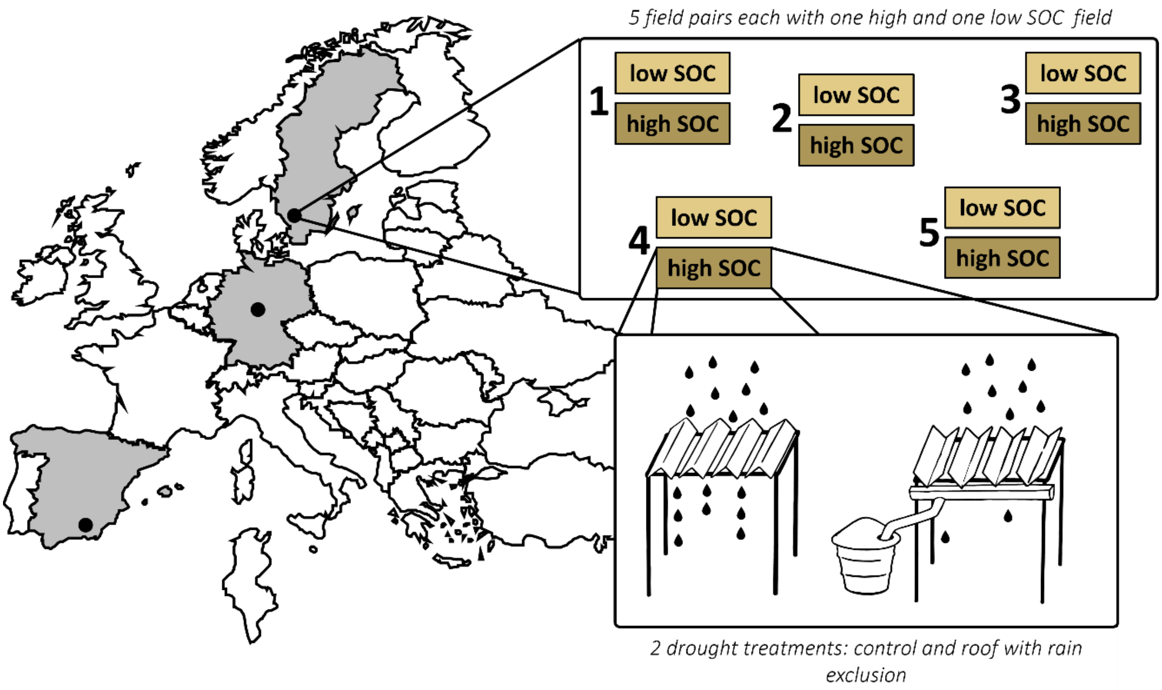


Figure 5.2 Experimental split plot design: 3 countries (Sweden, Germany and Spain) each with 5 field pairs comprising one field with high and one with low SOC content; on every field there were two drought treatments (control and roof) (total n = 30).

5.2.2 Sampling and extraction of soil animals

During the establishment of the experiment in February and March 10-12 soil cores of a diameter of 3 cm were taken to a depth of 20 cm on each plot, pooled and homogenized to determine total soil organic carbon (SOC), pH and soil water content (**Table 5.1**). A second sampling campaign was done 9 to 13 weeks after the experiment was established. Bulk soil samples were taken in the same way as initially and soil water content was determined. Additionally, soil cores of 5 cm diameter were taken to a depth of 10 cm and separated into an upper (0-5 cm depth) and lower layer (5-10 cm depth). Soil animals were extracted by heat by gradually increasing the temperature from 25 to 55 °C in steps of 2.5 °C per day up to 30 °C and in steps of 5 °C up to 55 °C (Macfadyen 1961; Kempson et al. 1963). Animals were collected into a 1:1 water-glycol solution, and then transferred and stored in 70% ethanol. Animals were sorted into Collembola, Oribatida, Mesostigmata, Prostigmata and Astigmata under a stereomicroscope (Axioplan; Zeiss, Jena, Germany).

5.2.3 Statistical analyses

Data were analyzed in R (R Development Core Team 2020) using the *lme4* package for performing linear mixed-effects models (LMMs). We used drought treatment (“Drought”:

roof, control), SOC ("Carbon": high SOC, low SOC) and country ("Country": Germany, Sweden, Spain) as fixed factor and field pair nested in country as random factor to account for the paired design of the experiment. Differences in SOC content between high and low SOC fields were analyzed for every country individually. The abundances of Collembola, Oribatida, and Meso-, Pro- and Astigmata were analyzed separately in three individual models. The depth distribution of animals was expressed as the difference between the number of animals in the upper layer and the number of animals in the lower layer. We analyzed effects on depth distributions using LMMs with the same structure of fixed and random factors as in the models for the overall abundances, but additionally included a random term for soil core. All abundance data was log(x+1) transformed to meet the assumptions of normality of residuals and homogeneity of variance.

5.3 RESULTS

5.3.1 SOC, soil water content and weather

SOC content was generally higher in Sweden (2.06 ± 0.16%) and Germany (1.66 ± 0.08%) than in Spain (0.58 ± 0.05%). Accordingly, differences between the high and low SOC fields were largest in Sweden (0.94 ± 0.37%) and small in Germany (0.24 ± 0.2%) and Spain (0.09 ± 0.07%).

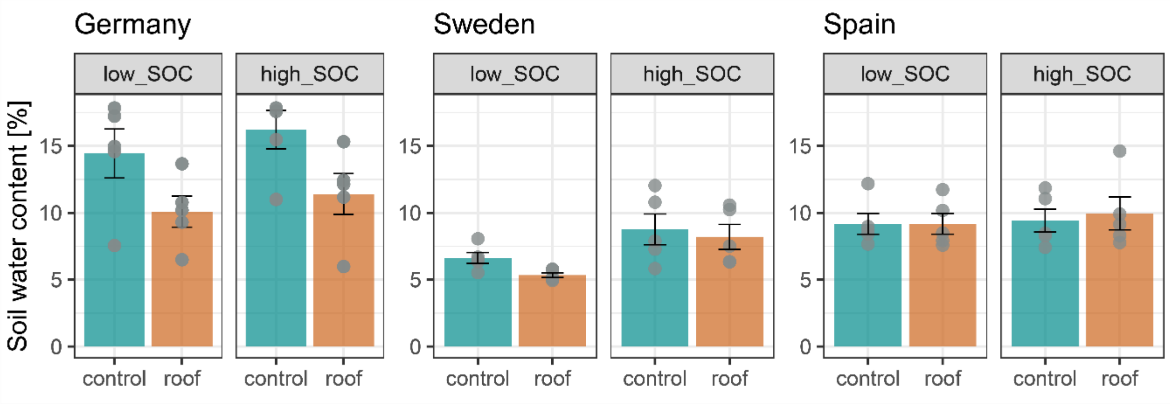


Figure 5.3 Gravimetric soil water content (0-20 cm depth) in control and drought treatments (roof) in fields with low and high SOC content in Germany, Sweden and Spain; means ± SE.

Likewise, soil water content differed strongly between countries both in overall means and between the drought treatments (**Figure 5.3**, **Supplementary Table 5.1**).

Germany generally had a higher gravimetric soil water content (13.04 ± 0.89%) than Sweden and Spain (7.23 ± 0.47% and 9.43 ± 0.43%, respectively). In Germany the drought treatment reduced soil water content considerably without being affected by the SOC content (low SOC: 4.35%, high SOC 4.82%). In Sweden drought reduced soil water content less than in Germany, but generally more in low SOC fields (1.28%) than in high SOC fields (0.56%).

In Spain soil water content was neither affected by the drought treatment nor by differences in SOC content. Temperatures from April to June were higher compared to the average over the previous 30 years in Sweden and Germany. In Spain temperature was close to the long-term average, i.e. was within the standard deviation of the previous 30-year period. Likewise, precipitation was lower than the long-term average in January and June in Germany and January, May, and June in Sweden. Spain had extraordinarily high precipitation in March due to few heavy rain events. The expected gradient in decreasing precipitation from Germany to Sweden to Spain therefore was not present during the time of this experiment.

5.3.2 Abundance of soil animals

Abundances of Oribatida, but not of Collembola, and Meso-, Pro- and Astigmata, were affected by experimental drought and differences in SOC content (**Figure 5.4**, **Table 5.2**).

Table 5.2 Results of the LMMs on the effect of drought, soil organic carbon content, and country on the abundance of Collembola, Oribatida and Meso-, Pro-, and Astigmata.

	Collembola			**Oribatida**			**Meso-, Pro- and Astigmata**		
	df	*F*-value	*P*-value	*df*	*F*-value	*P*-value	*df*	*F*-value	*P*-value
Drought (D)	1,36	2.02	0.164	1,36	0	0.986	1,36	0.01	0.919
Soil organic carbon (C)	1,36	0.88	0.355	1,36	0.01	0.938	1,36	0.07	0.800
Country (Co)	2,12	2.43	0.130	2,12	1.79	0.209	2,12	0.77	0.485
D x C	1,36	0.65	0.425	1,36	6.05	**0.019**	1,36	1.41	0.243
D x Co	2,36	1.38	0.265	2,36	4.87	**0.013**	2,36	2.54	0.093
C x Co	2,36	0.64	0.533	2,36	0.87	0.428	2,36	1.19	0.316
D x C x Co	2,36	0.42	0.658	2,36	2.5	0.096	2,36	0.62	0.542

Note: Significant p- values are given in bold.

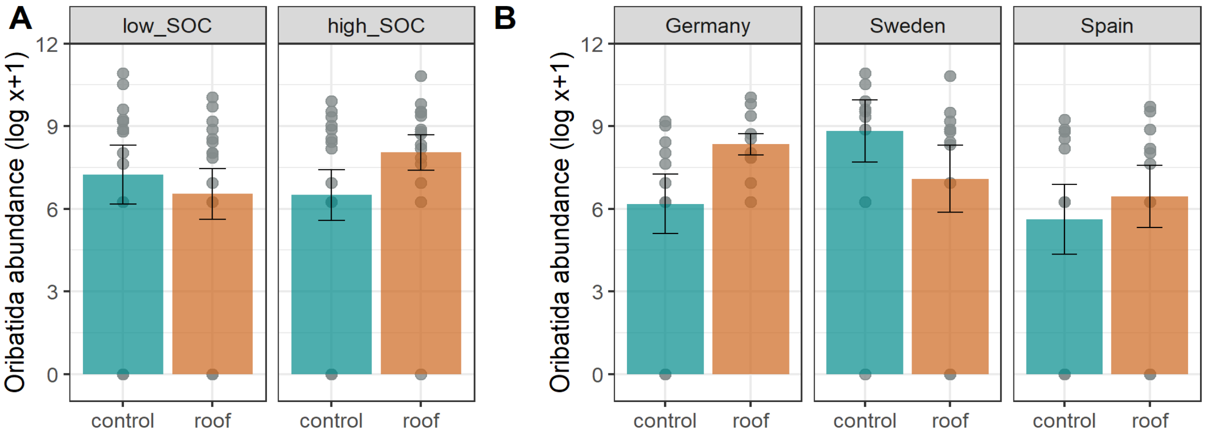


Figure 5.4 Abundance of Oribatida in control and drought treatments (roof) in (A) fields with low and high SOC content and (B) in Germany, Sweden and Spain. Abundances are log (x+1) transformed; means ± SE; for statistical analyses, see **Table 5.2**.

Experimental drought reduced the abundance of Oribatida in fields with low SOC content and increased their abundance in fields with high SOC content. Additionally, drought effects on Oribatida abundances differed between the countries with a negative drought effect in Sweden and a positive drought effect in Germany and Spain.

5.3.3 Depth distribution of soil animals

The depth distribution of Oribatida differed between the drought treatments with opposing effects in the different countries (**Figure 5.5**, **Table 5.3**). The relative number of individuals in the upper layer was lower in the roof treatment in Sweden, but higher in Germany.

Table 5.3 Results of the LMMs on the effect of drought, soil organic carbon content, and country on the depth distribution of Collembola, Oribatida and Meso-, Pro-, and Astigmata.

	Collembola			**Oribatida**			**Meso-, Pro- and Astigmata**		
	df	*F*-value	*P*-value	*df*	*F*-value	*P*-value	*df*	*F*-value	*P*-value
Drought (D)	1,36	0.35	0.559	1,36	1.69	0.202	1,36	1.81	0.187
Soil organic carbon (C)	1,36	0.44	0.512	1,36	0.12	0.736	1,36	0.35	0.556
Country (Co)	2,12	3.54	0.062	2,12	3.67	0.057	2,12	0.06	0.939
D x C	1,36	0.05	0.833	1,36	0.23	0.637	1,36	1.05	0.311
D x Co	2,36	0.38	0.686	2,36	4.77	**0.014**	2,36	1.47	0.242
C x Co	2,36	2.23	0.122	2,36	1.44	0.251	2,36	4.41	**0.019**
D x C x Co	2,36	0.04	0.961	2,36	0.23	0.796	2,36	1.05	0.362

Note: Significant p- values are given in bold.

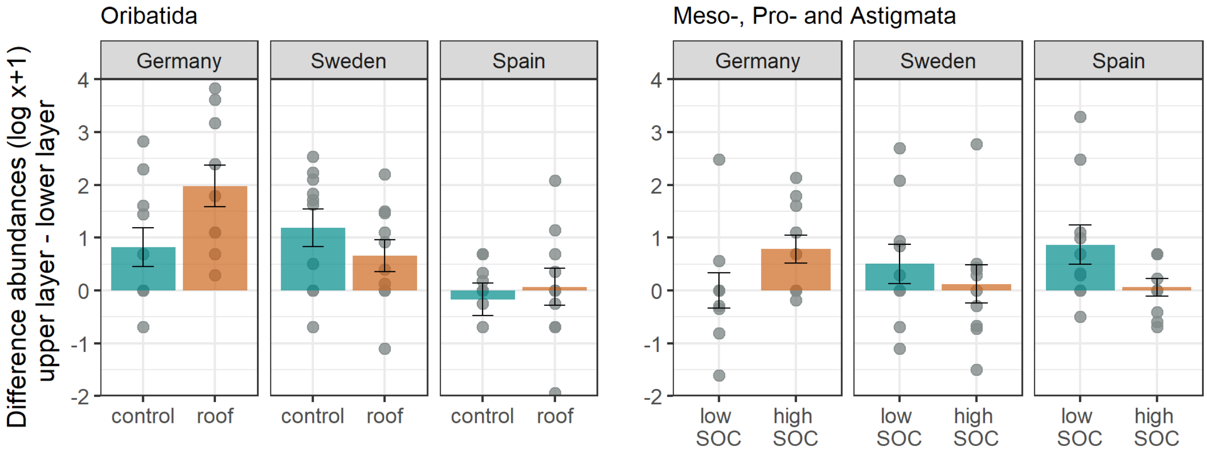


Figure 5.5 Depth distribution of Oribatida in control and drought treatments (roof) and depth distribution of Meso-, Pro-, and Astigmata in fields with low and high SOC content. Depth distribution is shown as difference in log (x+1) transformed abundance in upper layer (0-5 cm) minus lower layer (5-10 cm); means ± SE; for statistical analyses, see **Table 5.3**.

Generally, the relative number of individuals in the upper soil layer was much lower in Spain than in Germany and Sweden and was not affected by the drought treatment. The depth distribution of Meso-, Pro- and Astigmata was affected by the SOC content, and the direction of this effect differed between the countries. In Sweden and Spain relative abundances in the upper soil layer were higher in fields with low SOC content, whereas in Germany relative abundances in the upper layer where higher in fields with high SOC content.

5.4 DISCUSSION

Contrary to our first hypothesis experimental drought per se did not negatively affect microarthropods. Only Oribatida, but not Collembola and Meso-, Pro- and Astigmata, differed significantly in experimental drought plots with the direction of these effects differing with SOC content and among the countries. Such inconsistency of drought effects was reported before, both, between different and within single studies (Blankinship et al. 2011; Vries et al. 2012; Holmstrup et al. 2013). In order to better understand determinants of such in part opposing effects we investigated the influence of SOC content and country, i.e., ambient climatic conditions, in this study.

5.4.1 SOC content

Drought effects on soil water content were mitigated by high SOC content only in Sweden, probably because Sweden had the greatest differences in SOC content between high and low SOC fields. Partly in line with our second hypothesis drought decreased abundances of Oribatida in low SOC fields but increased them in high SOC fields. Since Oribatida were shown to cope well with severe desiccation (Sjursen and Sømme 2000; Benoit et al. 2008; Slotsbo et al. 2017), it is likely that positive drought effects act via availability of resources such as food and habitat space. Generally, Oribatida profit from soils with higher SOC that comprise more soil organic matter and associated microorganisms, a major food resource of Oribatida (Schneider et al. 2004). However, part of these food resources might not be accessible when soil pores are saturated with water. Hence, Oribatida may profit from a decrease in soil water content by gaining access to additional food resources. In fact, Turnbull and Lindo (2015) found for Collembola that increased precipitation may decrease abundances and suggested saturation of air-filled pore space being among the reasons for the decrease. The second difference between high and low SOC soils affecting soil organisms is the soil structure. Soils with high amounts of soil organic matter are better structured providing more habitat space for soil organisms that are not able to construct their own pores and tunnels (Shepherd et al. 2002; Erktan et al. 2020). Nielsen et al. (2008) showed that mite abundances (Oribatida and Mesostigmata) are positively correlated with relatively large soil pores of 60 to 300 μm suggesting that mite abundances are limited by the amount of pore space in which they are able to move. In soils with low SOC content a combination of less habitat space, limited mobility and fewer food resources may result in greater vulnerability against drought. Our results therefore suggest that SOC content can act as a modulator of drought effects, resulting in positive drought effects in high SOC fields and negative drought effects in low SOC fields.

5.4.2 Country

In accordance with our third hypothesis drought had a smaller effect at the Mediterranean sites in Spain compared to the sites with temperate climate in Sweden and Germany. Such small or even positive effects of reduced soil water content on soil microarthropods were reported before for arid or semiarid systems (Liu et al. 2017; Flórián et al. 2019) and might be explained by local microarthropod communities being generally well adapted to dry conditions. However, in Spain the manipulation of precipitation by the experimental roofs only little affected soil water content and also the soil fauna. At the sites in the temperate region, surprisingly, the response of Oribatida to drought was opposite, with drought decreasing abundances in Sweden and increasing them in Germany. In Germany, drought may have increased abundances of Oribatida by opening up formerly water filled pores, as discussed before, but this did not apply for Sweden. At sites in both countries, weather conditions were extraordinary warm and dry during the time of the experiment resulting in very low soil water contents. However, in Sweden soil water content was extremely low with less than 9% in high SOC fields and less than 7% in low SOC fields. Possibly, positive effects of reduced soil water content on soil mesofauna only occur up to a certain threshold at which negative effects prevail. Detrimental effects may be due to reduced availability of soil microorganisms serving as food for Oribatida (Schneider et al. 2004). In accordance with this, Jensen et al. (2003) reported that drought reduced microbial activity only at dry sites, whereas it increased it at wet sites. Although differences between soil water content in Sweden and Germany were small, our results on Oribatida abundances resemble this pattern suggesting a possible limitation by food resources under very dry conditions. Notably, the negative drought effect in Sweden was most pronounced in low SOC fields, whereas Oribatida abundances in high SOC fields were little affected (**Supplementary Figure 5.1**). Although this interaction was not significant over all countries, it indicates that negative drought effects on Oribatida are more pronounced in soils with low SOC content.

5.4.3 Vertical distribution

Drought effects on the vertical distribution of Oribatida generally resembled the pattern of overall abundances for the three countries. In Germany drought resulted in an increased number of individuals in the upper soil layer, while in Sweden and Spain the vertical distribution of Oribatida was not affected by drought. Hence, contrary to our fourth hypothesis, in Germany Oribatida did not migrate to lower, but to upper soil layers under drought. Generally abundances of soil animals are higher in upper soil layers due to higher amount of resources such as soil organic matter and associated microorganisms (Perdue and Crossley 1990; Frouz et al. 2004; Bell et al. 2012). However, some of these resources might be concealed in water filled soil pores and thereby inaccessible for most soil microarthropods (Erktan et al. 2020). Reduced soil water content potentially unlocks part of the food resources in the upper soil and induces a vertical migration. Independent of the experimental treatments, the proportion of animals in the upper layer was lower in Spain compared to Sweden and Germany, suggesting the vertical distribution within the soil profile being among the adaptations of the Spanish communities to the dry climate.

The vertical distribution of Meso-, Pro- and Astigmata was not affected by drought, but by SOC content and this differed between the countries. In Spain the number of individuals in the lower layer was higher in high SOC fields, possibly due to more structured soil in high SOC fields facilitating vertical movement (Shepherd et al. 2002). However, in Germany the number of individuals in the lower layer was higher in low than in high SOC fields and in Sweden the vertical distribution was not affected suggesting that the factors driving vertical movement of Meso-, Pro- and Astigmata differ among the countries.

5.4.4 Differences between taxa

Lab experiments suggested that Collembola are sensitive to varying levels of soil water content (Kaneda and Kaneko 2011), however, there is evidence from fields studies that this might not be the case under natural conditions (Taylor and Wolters 2005; Kardol et al. 2011; Krab et al. 2014), which is in line with the results of this study. Marx et al. (2012) suggested several mechanisms by which Collembola cope with periodically low soil moisture levels including short life cycles and colonization of remaining small refuges. Small soil pores, that either serve as refuge against desiccation or provide resources, are accessible for small and slender Tullbergiidae (Collembola) that make up a large proportion of the total number of Collembola in agricultural fields, and this might not be the case for the typically larger species of Oribatida in agricultural fields such as *Scheloribates laevigatus* (Meyer et al. 2021). Further, the capability to quickly recolonize habitats after drought as shown for Collembola in agricultural fields (Alvarez et al. 1999; Waagner et al. 2011) may be a major ecological difference between Collembola and Oribatida as pointed out for forests by Lindberg and Bengtsson (2005).

5.4.5 Conclusions

Our results confirm previous studies showing effects of experimental drought on microarthropods being negative, neutral or positive, but, beyond that, identify determinants for the direction of these effects. Of the studied taxa only Oribatida responded to experimental drought suggesting them being among the most sensitive arthropod groups in agricultural soils. Specifically, our data indicate SOC content, soil moisture and local climate being among the factors modulating drought effects on Oribatida. The results suggest that the vulnerability of Oribatida against drought is high in soils with low SOC content and at very low soil moisture. On the other hand, in soils with high SOC content Oribatida may profit from drought especially if soil water content is above 10%. Such interactive effects of drought and SOC content were observed at the two sites with temperate climate, but not at the Mediterranean site, suggesting communities from dry climates being adapted to drought, e.g. by living in deeper soil. Overall, the results indicate that drought effects on Oribatida are strongest under temperate climate conditions and that increasing SOC levels in agricultural soils may be a useful tool to mitigate or even reverse negative drought effects.

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Appendix

Supplementary Table 5.1 Soil water content and coordinates of all individual plots from the experiment.

Country	Field pair	Carbon	Drought	Latitude	Longitude	Soil water content [%]
Germany	1	high SOC	roof	51.6146	9.9278	15.32
Germany	1	high SOC	control	51.6148	9.9278	19.24
Germany	1	low SOC	roof	51.6138	9.9332	9.3
Germany	1	low SOC	control	51.6139	9.9332	14.96
Germany	2	high SOC	roof	51.5833	9.9704	12.14
Germany	2	high SOC	control	51.5833	9.9706	17.59
Germany	2	low SOC	roof	51.5830	9.9704	10.78
Germany	2	low SOC	control	51.5831	9.9707	17.23
Germany	3	high SOC	roof	51.5567	9.8978	12.43
Germany	3	high SOC	control	51.5567	9.8979	17.85
Germany	3	low SOC	roof	51.5559	9.9003	13.67
Germany	3	low SOC	control	51.5559	9.9001	17.85
Germany	4	high SOC	roof	51.5084	9.9173	11.17
Germany	4	high SOC	control	51.5084	9.9174	15.48
Germany	4	low SOC	roof	51.4958	9.9226	10.2
Germany	4	low SOC	control	51.4958	9.9223	14.59
Germany	5	high SOC	roof	51.7700	9.6929	5.98
Germany	5	high SOC	control	51.7701	9.6929	11
Germany	5	low SOC	roof	51.7762	9.6943	6.49
Germany	5	low SOC	control	51.7761	9.6940	7.55
Sweden	1	high SOC	roof	55.8763	13.2276	7.51
Sweden	1	high SOC	control	55.8763	13.2279	5.83
Sweden	1	low SOC	roof	55.8772	13.2352	5.03
Sweden	1	low SOC	control	55.8773	13.2352	6.5
Sweden	2	high SOC	roof	55.8563	13.4241	6.33
Sweden	2	high SOC	control	55.8563	13.4238	7.28
Sweden	2	low SOC	roof	55.8556	13.4322	4.94
Sweden	2	low SOC	control	55.8557	13.4317	6.35
Sweden	3	high SOC	roof	55.6518	13.0825	10.58
Sweden	3	high SOC	control	55.6520	13.0825	10.79
Sweden	3	low SOC	roof	55.6565	13.0872	5.78
Sweden	3	low SOC	control	55.6565	13.0870	6.68
Sweden	4	high SOC	roof	55.6781	13.6383	6.34
Sweden	4	high SOC	control	55.6781	13.6385	7.88

Sweden	4	low SOC	roof	55.6807	13.6432	5.77
Sweden	4	low SOC	control	55.6808	13.6427	8.06
Sweden	5	high SOC	roof	55.4940	13.4333	10.24
Sweden	5	high SOC	control	55.4941	13.4331	12.04
Sweden	5	low SOC	roof	55.4930	13.4355	5.17
Sweden	5	low SOC	control	55.4930	13.4352	5.52
Spain	1	high SOC	roof	37.5768	-2.3182	9.91
Spain	1	high SOC	control	37.5766	-2.3183	8.47
Spain	1	low SOC	roof	37.5757	-2.3177	10.18
Spain	1	low SOC	control	37.5759	-2.3175	12.18
Spain	2	high SOC	roof	37.5740	-2.3157	14.62
Spain	2	high SOC	control	37.5742	-2.3155	11.86
Spain	2	low SOC	roof	37.5748	-2.3158	11.73
Spain	2	low SOC	control	37.5745	-2.3161	8.69
Spain	3	high SOC	roof	37.7292	-2.3192	8.31
Spain	3	high SOC	control	37.7294	-2.3192	7.42
Spain	3	low SOC	roof	37.7308	-2.3193	7.58
Spain	3	low SOC	control	37.7306	-2.3189	8.97
Spain	4	high SOC	roof	37.7270	-2.3168	7.77
Spain	4	high SOC	control	37.7266	-2.3171	8.28
Spain	4	low SOC	roof	37.7259	-2.3176	8.49
Spain	4	low SOC	control	37.7261	-2.3175	8.41
Spain	5	high SOC	roof	37.7270	-2.3087	9.14
Spain	5	high SOC	control	37.7269	-2.3085	11.06
Spain	5	low SOC	roof	37.7264	-2.3093	7.93
Spain	5	low SOC	control	37.7265	-2.3095	7.66

6 GENERAL DISCUSSION

Soil organisms in agricultural systems are under pressure by a changing climate including more frequent and severe summer droughts. However, the magnitude and direction of the effect of drought on soil organisms may not be uniform but depend on interacting factors. The studies presented in this dissertation were conducted as part of the SoilClim project, which aims to investigate interactive effects of drought and agricultural management practices, soil characteristics and the local climate on above- and belowground compartments of wheat fields. This thesis focuses on the response of soil microarthropods to drought. In Chapter 2 I provided a detailed description and evaluation of an adapted roof design optimized for drought experiments in agricultural fields. We found responses of microarthropods being negative, neutral or positive with this depending on certain environmental conditions, in particular the farming system (Chapter 3), SOC content and local climate (Chapter 5). Adaptations to drought included vertical migration to deeper soil (Chapter 3) and trophic niche shifts (Chapter 4). Temporal dynamics of responses to drought differed considerably between taxa with Oribatida, though being sensitive to medium drought, thriving under an increasingly severe natural drought when Collembola populations were collapsing. Overall, the studies presented in this dissertation contribute to a better understanding of drivers that shape responses of microarthropods to drought and suggest that adaptations to drought are taxon-specific.

6.1 ADDRESSING THE CHALLENGES OF DROUGHT EXPERIMENTS

Laboratory experiments exclude most interactive factors in order to single out the effect of one or few factors on the response variable. This comes at the cost of results often being uselessly unrealistic and not allowing general conclusions or even practical applications (Diamond 1983). Thus, being close to natural conditions is perceived as the major advantage of field experiments where only one or few variables are manipulated. This, however, introduces new challenges, primarily, the presence of a number of uncontrolled variables that may correlate with the response variable, and which, in an ideal experiment, should be excluded. In reality, violations of this excludability assumption can hardly be avoided in field experiments, because not all confounding variables are known, or, they cannot be avoided or measured in order to be incorporated in statistical models (Kimmel 2021). In drought simulation experiments main sources for such unintended variation are artifacts on microclimate caused by the roof construction itself (Beier et al. 2012). With our adapted roof design presented and evaluated in Chapter 2 we addressed the problem of excludability violation by (I) reducing the artifacts that we are aware of to a minimum and (II) accounting for unpreventable or unknown artifacts by including a control roof (**Figure 6.1**). In detail, the evaluation of roof artifacts indicated that soil and air temperature are unaffected by the roof construction in periods with low ambient temperature but are increased in periods of high ambient temperature, confirming the need of a roof control treatment.

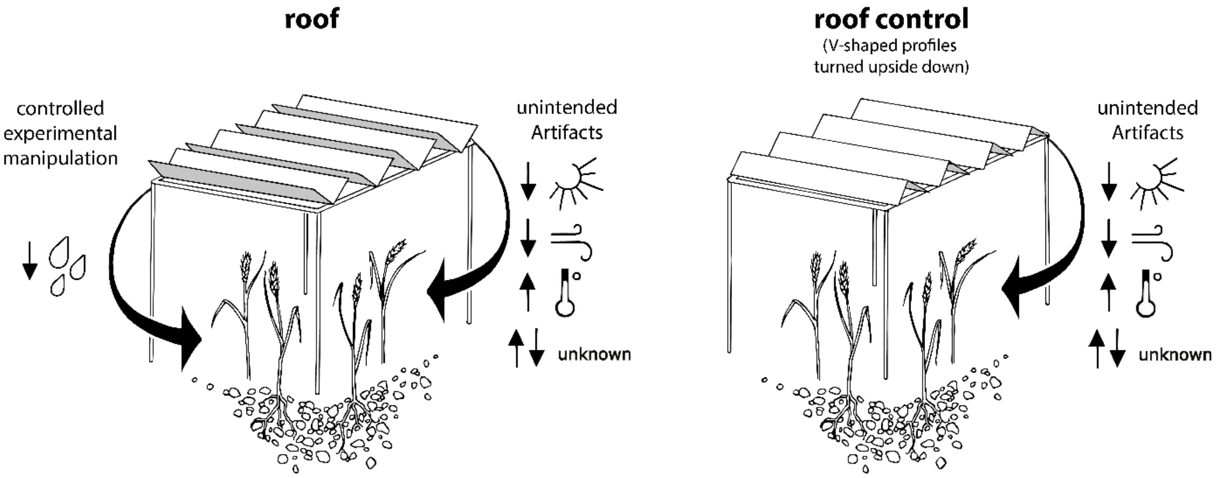

Figure 6.1 Concept of a roof control as a control treatment in drought simulation experiments; effects of the roof on the plot are: controlled reduction in precipitation (V-shaped profiles channeling precipitation away from the plot) and unintended artifacts including decreased radiation and airflow, increased temperature and potentially additional unknown effects; effects of the roof control include the same artifacts, but no reduction in precipitation (V-shaped profiles turned upside down); modified from Kimmel et al. (2021).

Besides accounting for potential artifacts, our roof design proofed to meet practical needs, i.e. a predictable amount of intercepted precipitation accompanied by a significant reduction in soil water content, the feasibility to be used in an agricultural context by the option of flexible removal allowing management activities and a reasonable prize to allow sufficient replication. Moreover, only few previous studies measured edge effects, which can considerably affect the suitable sampling area especially under small roofs (Yahdjian and Sala 2002). For the here presented roof the maximum edge effect was 0.75 m within a roof area of 2.5 × 2.5 m leaving a core area of 1 × 1 m that received the full treatment effect and is subsequently used as sampling area. Overall, we demonstrated that the presented roof design is well suited for drought experiments in agricultural fields and that a roof control is needed to account for unintended artifacts. We subsequently used the roof control as the control treatment in all following studies (Chapter 3-5).

6.2 WHAT SHAPES THE RESPONSE OF SOIL MICROARTHROPODS TO DROUGHT?

In previous studies responses of soil microarthropods to drought were, though for the most part negative, not consistent (Blankinship et al. 2011). Besides negative, also neutral and positive responses were reported. Hence, authors suggested that interacting factors may modulate drought effects on soil microarthropods and need to be integrated in future experiments (Blankinship et al. 2011; Wu et al. 2011; Beier et al. 2012). Within the framework of the SoilClim project, we therefore established experiments that included interactions of drought with agricultural management regime, SOC content and local climate. Importantly, the general trend that drought affects microarthropods negatively is not supported by the results presented in this thesis. Drought effects on microarthropods rather depended on the environmental setting and, in line with our first hypothesis, in part were mitigated towards neutral or even reversed to positive responses under organic farming and in high SOC fields.

Soil organic carbon

Results presented in Chapter 3 showed that the abundance of microarthropods mostly decreased in conventionally managed fields, whereas responses in organically managed fields were more consistently neutral or positive. Such an opposing response is most likely caused by profoundly different soil characteristics in the two farming systems and here foremost the difference in soil organic matter resulting from different fertilization regimes. Only the organically managed fields received organic fertilizers such as manure and compost resulting in a higher amount of SOC (Mäder et al. 2002). The potential importance of soil organic matter as modulator of drought effects is further indicated in the Europe-wide study presented in Chapter 5, where abundances of Oribatida increased in fields with high and decreased in fields with low SOC content. SOC has been suggested to principally enhance the soil's resilience to disturbances such as climate change, but to the best of my knowledge the interactive effect with drought on microarthropods has not been tested before in field experiments (Iglesias et al. 2009; Manns and Martin 2018; Droste et al. 2020). Based on the results presented in this thesis, we suggest three mechanisms by which high SOC content modulates the effect of drought on microarthropod abundances: (I) by increasing water holding capacity and thereby buffering drought effects on soil water content, (II) by providing additional food resources and habitat space, and (III) by facilitating vertical migration to deeper soil layers as drought avoidance strategy.

The basis of these mechanisms is the correlation between SOC and soil structure with high SOC content increasing soil aggregations and thereby leading to a more complex soil structure (Mäder et al. 2002; Bronick and Lal 2005). This is accompanied by an increase in the water holding capacity that attenuates the decrease in soil water content caused by drought (Shepherd et al. 2002; Manns and Martin 2018). Indeed, in our studies, negative drought effects on soil water content were smaller in organically compared to conventionally managed fields (Chapter 3) and in high compared to low SOC fields in Sweden, where differences in SOC content were most pronounced (Chapter 5). This is likely to indirectly also mitigate the effect of drought on microarthropods.

A more direct effect of high SOC content on soil microarthropods is the provisioning of additional resources in the form of soil organic matter and associated microorganisms (Fließbach et al. 2007). Part of these resources may, however, be inaccessibly locked in water-filled soil pores and a reduction of soil water content may provide formerly inaccessible food resources, thereby being beneficial for soil microarthropods (Erktan et al. 2020). Indeed, we found positive drought effects on Collembola in organically managed fields (Chapter 3) and on Oribatida in high SOC fields. In line with this reasoning, Turnbull and Lindo (2015) found increased precipitation to decrease abundances of Collembola and suggested saturation of former air-filled soil pores being among the reasons for the decrease. Hence, the physical niche that determines the availability of food resources for soil microarthropods must be perceived as a highly dynamic space that may change rapidly in soils with varying soil water content (**Figure 6.2**). However, in our studies, this positive drought effect in high SOC fields was mainly due to a strong effect in Germany, whereas in Sweden Oribatida decreased under drought irrespective of the SOC content (Chapter 5). Due to a natural drought in 2018 when the study was conducted, soil water content was extraordinarily low in Germany and Sweden. However, Sweden had extremely low soil moisture levels of less than 9% in high SOC fields and less than 7% in low SOC fields. This may indicate that positive drought effects in soils with high SOC content only occur above a certain threshold of soil water content, whereas below this threshold negative effects, such as hostile microclimatic conditions, prevail (**Figure 6.2**). Additionally, food accessibility may not further increase below very low soil moisture levels when main food resources such as microorganisms are locked in the smallest pores that are inaccessible for microarthropods irrespective of the soil water content.

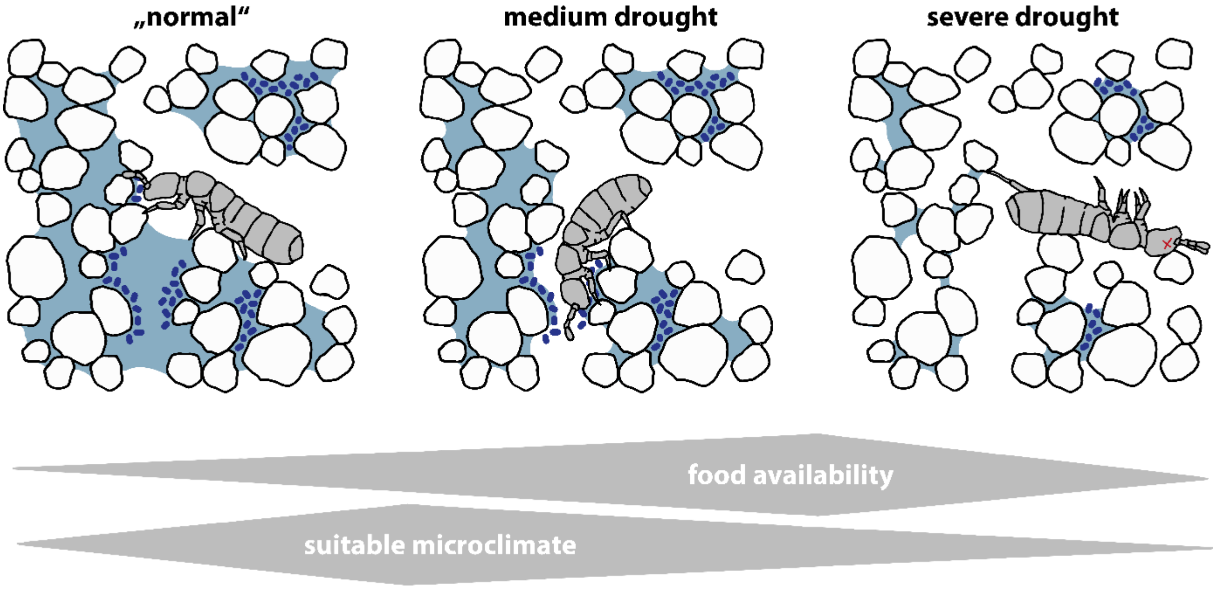

Figure 6.2 Concept illustrating potential positive drought effects on microarthropods (here Collembola); a decrease in soil water content may increase the availability of food resources by making food resources in former water filled pores accessible (medium drought); at very low soil water content food availability decreases again with e.g., microorganisms (as major food resource) being restricted to the few remaining small water filled pores, and the microclimate becoming unsuitable for microarthropod survival (severe drought); modified from Erktan et al. (2020).

For active movement through the soil matrix soil arthropods rely on existing pores and tunnels as they are not able to create their own pore space (Nielsen et al. 2008; Erktan et al. 2020). Hence, the more complex soil structure in high SOC fields, comprising a larger soil pore volume and a greater connectivity of pores, may considerably enhance their mobility including the migration to deeper soil layers less affected by drought. In fact, drought increased Collembola abundances in deeper soil only in organically managed fields (Chapter 3), suggesting vertical migration as a drought avoidance strategy depending on the complexity of the soil structure and accompanied increased mobility.

Local climate

A repeatedly mentioned gap in drought experiments is the expansion to a wider geographical range in order to represent different natural climatic conditions (Wu et al. 2011; Beier et al. 2012; Hoover et al. 2018). We addressed this gap by establishing drought experiments in three European countries covering a climatic range from temperate (Sweden and Germany) to Mediterranean climate (Spain) (Chapter 5). In contrast to the clear drought effects (positive and negative) in Sweden and Germany, abundances of Oribatida were only little affected by the reduction in precipitation in Spain, suggesting the local community to be better adapted to dry conditions than in temperate regions and confirming results of previous studies from arid or semiarid habitats (Liu et al. 2017; Flórián et al. 2019). However, the drought simulation at Spanish sites resulted only in small differences in soil moisture. Yet, results on the vertical distribution may reflect an adaptation of Oribatida at Mediterranean sites, where the proportion of individuals in deeper soil was higher than in Sweden and Germany.

6.3 BEYOND NUMERICAL RESPONSES: DROUGHT INDUCED CHANGES IN TROPHIC NICHES

Most approaches investigating the response of microarthropods to drought focused on measuring abundance and diversity. Studying trophic responses, however, may be equally fruitful for a number of reasons. First, trophic links in the soil food web are associated with soil functions such as nutrient cycling and pest control, and may change irrespective of responses in abundances (De Vries et al. 2013). Second, shifts in trophic niches may be a key component in explaining the variability in responses of abundances found in different studies as most detrimental effects on microarthropods are likely caused by shortages in food resources. This is supported by results presented in Chapter 3 and 5 indicating that different responses at least in part are due to differences in the availability of food resources such as soil organic matter and associated microorganisms. In Chapter 4 we therefore studied the trophic responses to drought in organically and conventionally managed fields as indicated by stable isotope analysis.

The general characterization of trophic niches revealed that the three Collembola species, *I. caerulea*, *I. maculatus* and *O. villosa*, are closely linked to wheat plants, whereas the Oribatida *T. sarekensis* and *S. laevigatus* live as primary and secondary decomposer, respectively, which is in line with results from previous studies (Schneider et al. 2004; Ngosong et al. 2009; Pollierer et al. 2009). However, comparisons between the two drought treatments and the two farming systems revealed a plasticity of this trophic niches with, at the same time, abundances of these most abundant species of the system being unaffected. Based on the assumption that in stable, deterministic environments trophic niches are small due to specialization and that under disturbance niches would broaden, because preferred resources may not be available (Giller 1996; Korotkevich et al. 2018), we hypothesized a niche broadening with drought and under conventional management. We did find the expected larger trophic niches for some species in conventionally managed fields, whereas under drought, contrary to our hypothesis, trophic niches were smaller. In detail, smaller trophic niches in the organic farming system were accompanied by higher mean $\Delta^{13}C$ (*T. sarekensis*) and $\Delta^{15}N$ values (*I. caerulea* and *O. villosa*), indicating a general increase in microorganisms in their diet, while other resources, such as litter and algae, were used to a lesser extent. This reflects the general higher abundance of microorganisms in the organically managed fields and suggests microorganisms being the preferred resource of these species (Kundel et al. 2020).

The differences in niche sizes between the drought treatments were not related to changes in mean values of stable isotopes, emphasizing the value of niche size measures to detect changes in trophic behavior. Instead, the variation in Δ^{13}C (*S. laevigatus*, *I. caerulea* and *I. maculatus*) and Δ^{15}N values (*I. caerulea*) decreased, suggesting a more restricted consumption of plant-derived resources rather than algae and microorganisms, which may have been detrimentally affected by drought. From these results a number of conclusions may be drawn: (I) even though agricultural fields principally undergo harsh disturbances, long-term organic farming allows trophic specialization; (II) generally, having a plastic trophic niche, hence, being a "choosy generalist" might prevent detrimental effects of conventional farming and drought on abundances of soil microarthropods; and (III) drought reduces the complexity of the food web by reducing the number of realized trophic links, thereby possibly decreasing its stability.

6.4 DIFFERENCES BETWEEN TAXA

All microarthropod taxa included in our studies were affected by drought, however, the consistency and temporal dynamics of such effects differed between the taxa studied. Generally, simulated drought affected abundances of Oribatida more consistently (Chapter 3 and 5) than abundances of Collembola (partly in Chapter 3). In both taxa, differences in abundances between the drought treatments were driven by relatively rare species as indicated by the neutral response of the most common species presented in Chapter 4. This resulted in drought induced differences in community composition in Oribatida, but not in Collembola. However, no particular species could be identified as being responsible for changes in community composition, i.e. as being especially vulnerable to drought. Yet, our results suggest that Oribatida better indicate medium drought than Collembola, at both the level of community density as well as in community composition, challenging the commonly advocated role of Collembola as bioindicators in respect to future climate change.

The results presented in this thesis further indicate a number of drought coping strategies, which partly differed between taxa. While we found a change in trophic behavior as response to drought both in Oribatida and Collembola, migration to deeper soil layers as drought avoidance strategy was only observed in Collembola (Chapter 3). In line with this result, Perdue and Crossley (1990) found that most mites did not migrate to deeper soil layers under drought even when abundances dramatically declined. In the relatively compact soil of agricultural fields movement through the soil matrix might generally be more restricted for Oribatida than for Collembola due to their different body shape. The body width of the Oribatida species in our study had an estimated range between 150 and 500 µm, whereas the most common Collembola species found (*Mesaphorura* spp.) have an estimated body width of 100 µm (Weigmann 2006; Hopkin 2007). Furthermore, a natural drought occurring during the first experiment (Chapter 3) allows the interpretation of temporal population dynamics in response to drought, which profoundly differed between Collembola and Oribatida. The abundance of Collembola peaked two months after establishment of the experiment in May and declined close to local extinction at the last sampling date in June, when soil moisture was extremely low. By contrast, overall abundances of Oribatida peaked at the last sampling date, despite the very low soil moisture. Oribatida with their thick cuticle are morphologically better equipped to sustain drought than the soft bodied Collembola and presumably still reproduce successfully even at dry conditions (Norton 1994). Collembola, on the other hand, might rather respond with circles of local extinction and recolonization to disturbances such as drought. Alvarez et al. (2001) reported that Collembola in arable fields survived periods of drought as eggs and rapidly hatched after conditions had improved. Collembola further were shown to recolonize previously hostile habitats by wind drift and active locomotion much faster than Oribatida (Lehmitz et al. 2011). Hence, differences in morphology and life-history traits may lead to taxon-specific responses to drought suggesting that studies need to include different taxa in order to identify the vulnerability of decomposers to drought.

6.5 CONCLUDING REMARKS AND IMPLICATIONS OF THE RESULTS

The methodological basis of drought experiments in the field is a roof that reduces ambient precipitation. With the roof design presented in Chapter 2 we intended to promote and facilitate the use of drought simulation experiments in agricultural fields by providing a detailed construction manual of a rain excluding roof that proofed to be applicable in an agricultural context. The evaluation of roof artifacts revealed that a complete prevention of unintended artifacts is unfeasible but can be addressed by including a roof control. We applied this roof design in two drought experiments and the results suggest that high SOC content mitigates or even reverses detrimental drought effects on microarthropods. This opens up the potential to actively counteract the impact of drought on agricultural systems by adapting management practices resulting in an enrichment in SOC content. However, positive effects of high SOC content vanished at extremely low soil moisture levels indicating a threshold of soil water content below which negative drought effects prevail. In face of drought effects switching from positive to negative, quantifying such thresholds seems crucial and might be addressed by simulating gradients of drought intensity, i.e. soil water content instead of having a two level treatment design. Results obtained from our Europe-wide drought experiment suggest that microarthropods from sites with an arid Mediterranean climate are less vulnerable against drought than those from temperate climates, indicating that communities from dry climates are better adapted to drought, e.g. by living in deeper soil. However, sites with arid climate in Southern Europe are predicted to be confronted with the most severe increase in drought events within Europe, hence, responses of soil microarthropods should be reevaluated under extreme drought simulation scenarios. Our data indicate that microarthropods adapt to drought conditions by changes in behavior, such as vertical migration to deeper soil and shift in trophic niches. Under drought trophic niche size of some species became smaller by the favored use of plants instead of microorganisms and algae as food resource. At the same time abundances were unaffected, suggesting that a flexible usage of resources may buffer negative drought effects on microarthropods in agricultural fields. However, such a reduction in trophic links between species in a species poor system might reduce its stability. The temporal dynamics of responses to drought differed between microarthropod taxa reflecting their profoundly different morphology and life-history. While Oribatida thrived even at very low soil moisture conditions, Collembola abundances collapsed at extremely low soil moisture levels. Hence, future studies investigating drought responses on microarthropods should consider different taxa and include several sampling dates in order to measure drought effects on decomposers. Long-term experiments spanning over several seasons and even years would further elucidate the potential of resilience, which is potentially high in fast reproducing taxa like Collembola but may vanish under long lasting drought conditions.

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LIST OF PUBLICATIONS

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THESIS DECLARATIONS

Declaration of the author's own contribution to manuscripts with multiple authors

Chapter 2: Design and manual to construct rainout-shelters for climate change experiments in agroecosystems

Dominika Kundel, Svenja Meyer, Herbert Birkhofer, Andreas Fliessbach, Paul Mäder, Stefan Scheu, Mark van Kleunen, Klaus Birkhofer

Together with Dominika Kundel I am the first author of this paper. I was involved in rainout-shelter set-up, collecting, and analyzing the data as well as writing the manuscript. Dominika Kundel, Herbert Birkhofer, Andreas Fliessbach, Paul Mäder, Stefan Scheu and Klaus Birkhofer were involved in the conception of the rainout-shelter. Stefan Scheu, Klaus Birkhofer and Mark van Kleunen contributed to finalizing the manuscript.

Chapter 3: Soil microarthropods respond differently to simulated drought in organic and conventional farming systems

Svenja Meyer, Dominika Kundel, Klaus Birkhofer, Andreas Fliessbach, Stefan Scheu

I am the first author of the paper. I collected and analyzed the data and wrote the manuscript. Dominika Kundel contributed to data collection. Klaus Birkhofer and Stefan Scheu contributed to data analysis. All co-authors were involved in conceptualization of the experiment and finalizing the manuscript.

Chapter 4: Trophic niche but not abundance of Collembola and Oribatida changes with drought and farming system

Svenja Meyer, Dominika Kundel, Klaus Birkhofer, Andreas Fliessbach, Stefan Scheu

I am the first author of the paper. I collected and analyzed the data and wrote the manuscript. Dominika Kundel contributed to data collection. Klaus Birkhofer and Stefan Scheu contributed to data analysis. All co-authors were involved in conceptualization of the experiment and finalizing the manuscript.

Chapter 5: Soil organic carbon content and local climate determine drought effects on Oribatida

Svenja Meyer, Klaus Birkhofer, Stefan Scheu

I am the first author of the paper. I collected and analyzed the data and wrote the manuscript. Klaus Birkhofer and Stefan Scheu contributed to conceptualization of the experiment, data analysis and finalizing the manuscript.

Plagiarism declaration

I declare that I have written this doctoral thesis independently. All persons contributing to the manuscripts have been named so. All sentences or passages quoted from other people's work have been specifically acknowledged by clear cross-referencing. I have not submitted this thesis in any form for another degree at any university or institution.

Svenja Meyer

Göttingen, January 2022