

University of Hohenheim
Institute of Landscape and Plant Ecology
Department of Plant Ecology
apl. Prof. Dr. rer. nat. Petra Högy

**Impacts of Temperature Increase and Change in Precipitation
Pattern on Ecophysiology, Biomass Allocation and Yield Quality
of selected Crops**

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Ireen Drebenstedt

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Examination Committee

Supervisor and Reviewer:	apl. Prof. Dr. Petra Högy
Co-reviewer:	Prof. Dr. Håkan Pleijel
Additional examiner:	Prof. Dr. Ellen Kandeler
Head of Committee:	Prof. Dr. Martin Hasselmann
Dean of the Faculty of Agricultural Sciences:	Prof. Dr. Ralf Vögele

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1 Summary

Climate change poses a challenge for the production of crops in the twenty-first century due to alterations in environmental conditions. In Central Europe, temperature will be increased and precipitation pattern will be altered, thereby influencing soil moisture content, physiological plant processes and crop development in agricultural areas, with impacts on crop yield and the chemical composition of seeds. Warming and drought often occur simultaneously. The combination of multiple abiotic stresses can be synergistic, leading to additive negative effects on crop productivity. To date, little information is available from multi-factor experiments analyzing interactive effects of warming and reduced precipitation in an arable field. In addition, one major issue of studying climate change effects on crop development in the long-term is that weather conditions can vary strongly between years, e.g., with hot and dry summers in comparison to cool and wet ones, which directly affects soil moisture content and indirectly affects crop development. Thus, considering yearly weather conditions seems to be important for the analyses of climate change effects on aboveground biomass and harvestable yield of crops.

The aim of the present work was to identify single and combined effects of soil warming (+2.5 °C), reduced summer precipitation amount (-25%), and precipitation frequency (-50%) on crop development, ecophysiology, aboveground biomass and yield as well as on yield quality of wheat, barley, and oilseed rape grown in the Hohenheim Climate Change (HoCC) field experiment. These crops are commonly grown in a typical crop rotation in southwest Germany and are used as food or feed, for malting properties or as bioenergy crop for the production of biodiesel. Furthermore, this thesis presents novel results from the HoCC experiment in the long-term perspective. Thus, aboveground biomass and yield data (2009-2018) of the three crops were analyzed with regard to their inter-annual variability, including annual fluctuations in weather conditions.

This thesis consists of three publications. In the first and second publication a field experiment within the scope of the HoCC experiment was conducted with spring barley (*Hordeum vulgare* L. cv. RGT Planet) and winter oilseed rape (*Brassica napus* L. cv. Mercedes) in 2016 and 2017. The objective was to investigate the impacts of soil warming, altered precipitation pattern and their interactions on biomass production and crop yield. In addition, it was examined, whether the simulated climate changes affecting barley photosynthesis and the seed quality compounds of oilseed rape. In the third publication, long-term plant productivity data of wheat, barley, and

oilseed rape were evaluated, including aboveground biomass and yield data from the field experiment in 2018 with winter wheat (*Triticum aestivum* L. cv. Rebell).

In the first publication, leaf gas exchange during stem elongation of spring barley was either increased under reduced precipitation amount alone or decreased under reduced precipitation amount combined with soil warming. In contrast, aboveground biomass and yield were more affected under soil warming alone. Accordingly, soil warming positively affected the number of ears and the grain yield, although elevated soil temperatures led to higher rates of evapotranspiration. It was suggested that the water availability during the growing period was sufficient because of high ambient precipitation amounts during spring and June 2016 combined with an optimal water storage capacity of the studied loess soil. Therefore, negative effects of high evapotranspiration on the plant and soil water budget in the soil warming treatment were mitigated.

As shown in the second publication, soil warming did not affect the seed yield of winter oilseed rape, which was assumed being a result of the wet conditions during summer 2017, which maintained a sufficient water availability in the heated treatments. Reduced precipitation amount had no effect on the seed protein and oil concentration. Most likely because the applied precipitation in this study was based on relatively high ambient precipitation amounts during the growing period. Altogether, the results of the first and second publication underlined the need for long-term studies, including a range of weather conditions during the vegetation period of different years, which enable to analyze their effects on crop development and productivity.

In the third publication annual weather conditions were used to explain inter-annual variability in the long-term crop productivity data (2009-2018) under soil warming. It was found that under high cumulative ambient precipitation and high mean soil moisture, soil warming increased aboveground biomass and yield of barley and wheat, whereas under low cumulative ambient precipitation and low soil moisture no effect occurred. Therefore, inter-annual variability in cumulative ambient precipitation seemed to determine the effect of soil warming on cereal productivity.

Overall, the results presented in this thesis showed that aboveground biomass and yield production of spring wheat, winter wheat and spring barley were stronger affected by increasing soil temperature than by reduced precipitation amount or reduced precipitation frequency. Thus, wheat and barley aboveground biomass and yield increased under soil warming in those years which included high ambient precipitation events during the vegetation period. In contrast,

altered precipitation pattern had minor effects on biomass and no effects on yield of the three crops, since in spring wheat a reduced precipitation amount decreased aboveground biomass tendentially only in 2009, whereas in winter oilseed rape an increase in aboveground biomass was only observed in the vegetation period 2010/2011. Most likely, the reduced precipitation amount and –frequency during summer in combination with the good water holding capacity of the investigated Luvisol with high loess proportion was too small to induce drought stress conditions on crop development. Moreover, it was revealed that yearly weather conditions seem to be a key control on plant productivity in cereal crops under global warming. Since biomass production and yield are influenced strongly by the plant available water, which varies greatly under different precipitation amounts and –frequencies and is additionally reduced by soil warming and the associated increase in evapotranspiration. This underlined the need for long-term studies, including a range of weather conditions during the vegetation period of crops. Furthermore, it would be important to determine the effects of the studied climate change factors at further locations in soils with less optimal water holding capacity. For the future it can be assumed that the positive effects of soil warming on cereal biomass and yield, which were found in moist years under high cumulative ambient precipitation and high soil moisture, will decrease as consequences of lower average yearly precipitation amounts.

2 Zusammenfassung

Der Klimawandel stellt aufgrund veränderter Umweltbedingungen eine Herausforderung für den Anbau von landwirtschaftlichen Nutzpflanzen im 21. Jahrhundert dar. In Mitteleuropa steigt die Temperatur an und die Niederschlagsmuster verändern sich, wodurch die Bodenfeuchte, die physiologischen Pflanzenprozesse und die Pflanzenentwicklung in landwirtschaftlichen Gebieten beeinflusst werden. Dies wirkt sich auf den Ernteertrag und die chemische Zusammensetzung der Erträge aus. Häufig treten Erwärmung und Trockenheit gleichzeitig auf. Dabei kann sich das Vorkommen mehrerer abiotischer Stressoren synergistisch auswirken und zu additiv negativen Effekten auf die Pflanzenproduktivität führen. Bisher liegen nur wenige Informationen aus multifaktoriellen Experimenten vor, welche die Wechselwirkungen von Erwärmung und Trockenheit in einem landwirtschaftlichen Feld untersuchen. Darüber hinaus ist es wichtig die Auswirkungen des Klimawandels auf die Entwicklung von Nutzpflanzen in Langzeitstudien zu untersuchen, da die Wetterbedingungen zwischen den Jahren stark variieren können, z. B. mit heißen und trockenen Sommern im Vergleich zu kühlen und nassen, mit direkter Auswirkung auf die Bodenfeuchte und indirekter Wirkung auf die Entwicklung der Pflanzen. Demzufolge scheint eine Berücksichtigung der jährlichen Wetterbedingungen wichtig zu sein, wenn die Folgen des Klimawandels auf die oberirdische Biomasse und den Ernteertrag von landwirtschaftlichen Nutzpflanzen abgeschätzt werden.

Das Ziel der vorliegenden Arbeit war es im Rahmen des Hohenheim Climate Change (HoCC) Feld-Experimentes die Folgen der drei Faktoren Bodenerwärmung (+2,5°C), reduzierter Sommer Niederschlagsmenge (-25 %) und Niederschlagshäufigkeit (-50 %) einzeln oder in Kombination auf die Parameter Pflanzenentwicklung, Ökophysiologie, oberirdische Biomasse, Ertrag und Ertragsqualität von Weizen, Gerste und Raps zu untersuchen. Diese Nutzpflanzen stellen in Südwestdeutschland eine typische Fruchtfolge dar und werden als Nahrungs- oder Futtermittel, für die Malzbereitung oder als Bioenergiepflanze für die Herstellung von Biodiesel angebaut. Weiterhin werden in dieser Arbeit neue Ergebnisse aus dem Langzeit - HoCC-Experiment präsentiert. Dazu wurden Daten von 2009-2018 zu oberirdischer Biomasse und Ertrag der drei Kulturen hinsichtlich ihrer zwischenjährlichen Variabilität analysiert und jährliche Schwankungen in den Witterungsbedingungen berücksichtigt.

Die Dissertation besteht aus drei Publikationen. In der ersten und zweiten Veröffentlichung wurde im Rahmen des HoCC Experimentes in den Jahren 2016 und 2017 ein Feldversuch mit den Nutzpflanzen Sommergerste (*Hordeum vulgare* L. cv. RGT Planet) und Winterraps

(*Brassica napus* L. cv. Mercedes) durchgeführt. Ziel war es, die Auswirkungen einer Bodenerwärmung, veränderten Niederschlagsmustern und deren Wechselwirkungen auf die Biomasseproduktion und den Ernteertrag zu untersuchen. Darüber hinaus wurde untersucht, ob sich die simulierten Klimaänderungen auf die Photosynthese von Gerste sowie auf die Inhaltsstoffe von Rapssamen auswirken. In der dritten Veröffentlichung wurden Langzeit - Produktivitätsdaten von Weizen, Gerste, und Raps ausgewertet, darunter oberirdische Biomasse und Ertragsdaten aus dem HoCC Feldversuch von 2018 mit Winterweizen (*Triticum aestivum* L. cv. Rebell).

Ein Ergebnis aus der ersten Veröffentlichung war, dass einerseits eine Verringerung der Niederschlagsmenge allein zu einer Erhöhung des Blattgasaustausches von Sommergerste während des Schossens führte, andererseits in Kombination mit einer Bodenerwärmung der Blattgasaustausch jedoch reduziert wurde. Im Gegensatz dazu hatte die Bodenerwärmung als einzelner Faktor einen stärkeren Einfluss auf die oberirdische Biomasse und den Ertrag. Demzufolge wirkte sich die Bodenerwärmung trotz einer höheren Verdunstungsrate positiv auf die Anzahl der Ähren und den Getreideertrag aus. Wahrscheinlich war die Wasserverfügbarkeit während der Vegetationsperiode der Sommergerste ausreichend, da sowohl hohe Niederschlagsmengen im Frühjahr und Juni 2016 gefallen waren, als auch die Wasserspeicherkapazität des untersuchten Lössbodens optimal war. Dadurch wurden negative Auswirkungen der hohen Evapotranspiration auf den Pflanzen- und Bodenwasserhaushalt unter Bodenerwärmung abgemildert.

In der zweiten Veröffentlichung wurde aufgezeigt, dass eine Bodenerwärmung keinen Einfluss auf den Samenertrag von Winterraps hatte. Ursächlich hierfür waren sehr wahrscheinlich die nassen Bedingungen im Sommer 2017, welche zu einer ausreichenden Wasserverfügbarkeit in den beheizten Behandlungen führte. Darüber hinaus hatte eine verringerte Niederschlagsmenge keine Auswirkung auf die Protein- und Ölkonzentration in den Samen. Höchstwahrscheinlich, da die applizierten Niederschläge in dieser Studie auf relativ hohen Umgebungsniederschlagsmengen während der Wachstumsperiode basierten. Die Ergebnisse der ersten und zweiten Publikation verdeutlichen die Notwendigkeit von Langzeitstudien, die es ermöglichen eine große Bandbreite von Witterungsbedingungen während der Vegetationsperiode verschiedener Jahre abzubilden und deren Effekte auf die Entwicklung und die Produktivität der untersuchten Nutzpflanzen zu untersuchen.

In der dritten Veröffentlichung konnten jährliche Witterungsbedingungen zur Erklärung der zwischenjährigen Variabilität in den langfristigen Daten zur Pflanzenproduktivität

(2009 - 2018) unter Bodenerwärmung beitragen. Es wurde aufgezeigt, dass unter hohen kumulativen Umgebungsniederschlägen und hoher mittlerer Bodenfeuchte die Bodenerwärmung die oberirdische Biomasse und den Ertrag von Gerste und Weizen erhöhte; wohingegen diese unter niedrigen kumulativen Umgebungsniederschlägen und niedriger Bodenfeuchte nicht verändert wurden. Die Wirkung der Bodenerwärmung auf die Produktivität von Getreide wurde demnach von der Variabilität der kumulativen Umgebungsniederschläge zwischen den Jahren beeinflusst.

Insgesamt wurde die oberirdische Biomasse und die Ertragsproduktion von Sommerweizen, Winterweizen und Sommergerste stärker durch eine Erhöhung der Bodentemperatur beeinflusst als durch eine reduzierte Niederschlagsmenge oder eine reduzierte Niederschlagshäufigkeit. Demnach gab es unter Bodenerwärmung einen Anstieg der oberirdischen Biomasse und des Ertrages von Weizen und Gerste in den Jahren, in denen es hohe Umgebungsniederschläge während der Vegetationsperiode gab. Im Gegensatz dazu hatten veränderte Niederschlagsmuster kaum einen Effekt auf die Biomasse und keinen Effekt auf den Ertrag der drei Nutzpflanzen, da eine reduzierte Niederschlagsmenge bei Sommerweizen nur in 2009 tendentiell zu einem Rückgang der oberirdischen Biomasse führte, wohingegen bei Winterraps eine Zunahme der oberirdischen Biomasse nur in der Vegetationsperiode 2010/2011 beobachtet wurde. Möglicherweise war die reduzierte Niederschlagsmenge und –frequenz in den Sommermonaten durch die gute Wasserspeicherkapazität des untersuchten Luvisol mit hohem Loess Anteil zu gering, um Trockenstressbedingungen für die Pflanzenentwicklung zu induzieren. Darüber hinaus wurde gezeigt, dass jährliche Witterungsbedingungen eine Schlüsselrolle für die Produktivität von Getreide unter globaler Erwärmung einzunehmen scheinen. Denn Biomasse Produktion und Ertrag werden stark vom pflanzenverfügbaren Wasser beeinflusst, welches je nach Niederschlagsmenge und Niederschlagshäufigkeit stark variiert und zusätzlich durch eine Bodenerwärmung und die damit einhergehende erhöhte Evapotranspiration reduziert wird. Insgesamt unterstreichen die Ergebnisse die Notwendigkeit von Langzeitstudien, welche die Witterungsbedingungen verschiedener Vegetationsperioden von Nutzpflanzen miteinschließen. Weiterhin ist es wichtig, die Wirkungen der hier untersuchten klimaverändernden Faktoren an weiteren Standorten in Böden mit weniger optimaler Wasserhaltekapazität zu untersuchen. Für die Zukunft ist davon auszugehen, dass die positiven Effekte der Bodenerwärmung auf Getreidebiomasse und -ertrag, die bei hohen kumulativen Umgebungsniederschlägen und hoher Bodenfeuchte beobachtet wurden, infolge geringerer durchschnittlicher Jahresniederschlagsmengen abnehmen werden.

3 General introduction

3.1 Global warming and changes in precipitation pattern

The global natural greenhouse effect is critically strengthened by increasing global atmospheric concentrations of carbon dioxide (CO₂), methane (CH₄) and nitrous oxide (N₂O) since 1750 (IPCC 2007; Oreskes 2004), resulting in global warming. During the 21st century, global warming of 1.5 °C to 2.0 °C will likely be exceeded unless great reductions in CO₂ and other greenhouse gas emissions will be managed (IPCC 2021b). At the same time, a higher variability in precipitation pattern is expected in Europe, including a decrease in precipitation during summer and an increase in agricultural droughts (IPCC 2021a).

3.2 Climate change predictions for Germany

As a result of global warming, climate scenarios predict an increase by 1.2–5.3 °C of the mean air temperature in Germany until 2100 compared to 1971–2000 (DWD 2017). Accompanied by increased air temperatures are elevated soil temperatures (Zheng et al. 1993). Soil temperature, in contrast to air temperature, is known for its low variability and directly affects the water and nutrient absorption by plant roots (Körner 2012; Zhang et al. 2016; Xue et al. 2020). It is complex to predict the effects of increasing soil temperatures on agricultural production, because unlike air temperature, soil temperature is additionally influenced by soil moisture and texture or vegetation (Gray and Brady 2016). Warming of soil temperatures will be a permanent effect. In Central and Northern Europe, a decrease in precipitation is predicted by climate scenarios during summer months (IPCC 2021a). The average precipitation amount during summer months is forecasted to decrease by up to 9% until 2071–2100 compared to the long-term period 1971–2000 (DWD 2017).

3.3 Typical field crops in the study area of southwest Germany

In the region of Stuttgart, wheat, barley and oilseed rape are often grown in crop rotations as important field crops. Wheat is highly adaptable to different soil and climatic conditions. Wheat is highly important worldwide in terms of productivity and food security and one of the largest growing areas for wheat is within the European Union. In Germany, the harvested yield of wheat in 2020 was 78.2 dt ha⁻¹ (FAOSTAT 2022), whereby mainly soft wheat (*Triticum aestivum* L.) is grown as summer or winter variety (Lütke Entrup and Schäfer 2011). Winter wheat is usually sown in autumn and harvested in summer, and therefore includes periods

during the growing season, that are particularly affected by climate warming (Wang et al. 2016). The second crop barley (*Hordeum vulgare* L.) is relatively drought tolerant and is predicted to gain more importance under future climate in terms of food security because it can help to mitigate malnutrition (Richardson et al. 2009; Högy et al. 2013). It is used mainly as source for feed and food or for malting properties, being one of the most widely adapted cereal crops with production areas in extreme climates including high temperatures and water stress (Baik and Ullrich 2008). In Germany, the harvested yield of barley was 64.6 dt ha⁻¹ in 2018 and thus lower as compared to wheat yield (FAOSTAT 2022). Primary, winter oilseed rape (*Brassica napus* L.) is cultivated in Central Europe because of higher yields as compared to spring varieties, and it is used as seed oil in human consumption, as protein source for animal feed or is used for the biodiesel production (Walker and Booth 2001; He et al. 2017). Economically, oilseed rape has to compete with cereal crops, which achieve comparable higher yields (Weymann et al. 2015). In Germany, the harvested yield of oilseed rape was 36.8 dt ha⁻¹ in 2018 (FAOSTAT 2022). Nevertheless, oilseed rape is a preferred pre- crop for cereals due to its deep rooting system which opens up the soil. Cereals also benefit from nutrients left by residues of oilseed rape after harvest (Walker and Booth 2001).

3.4 Research gap – Multi-factorial experiment with climate change parameters in an arable field

Warming is expected to shorten the grain filling stage, resulting in reduced starch accumulation and therefore reduced grain weight and crop yield (Barnabás et al. 2008). In addition, soil warming and a reduction in soil moisture can alter the bio-physical nature of soils in agricultural ecosystems in Europe. For example warming increases the decomposition rate of organic material, which results in a reduction in soil organic carbon stocks and in a higher release of CO₂ in the atmosphere (Jones et al. 2009). However, field experiments which focus on effects of increased soil temperature on crop development or productivity aspects have been rarely conducted so far. For example, field experiments using heating cables were conducted in winter wheat to simulate soil warming of, e.g., 3.0 °C in 0.02 m depth (Hantschel et al. 1995; Kamp et al. 1998), four levels of soil warming (0.6-2.2 °C) on the soil surface (Xiao et al. 2010) and 5.0 °C elevated soil temperature in 0.1 m depth in lysimeters (Patil et al. 2010). Other field experiments with heating cables on the soil surface simulated soil warming of 2.5 °C in spring wheat, spring barley and winter oilseed rape (Högy et al. 2013; Poll et al. 2013). Further soil warming experiments were conducted in climate chambers with winter wheat under 5.0 °C soil temperature increase (Gavito et al. 2001), in plastic containers located in an unheated

greenhouse studying soil temperature increases of 2.0 and 4.0 °C in winter oilseed rape (Siebold and Tiedemann 2012) or in a glasshouse where pots with spring wheat were placed on heating cables to warm the soil by 3.0 °C (Weldearegay et al. 2016). Another field experiment was conducted in maize using surface layers of polythene to warm the soil (Stone et al. 1999). Beside increasing temperatures, drought is a climate factor which highly impacts crop growth and yield due to stomatal closure, inhibition of photosynthesis and reduced carbohydrate synthesis (Barnabás et al. 2008). Moreover changes in precipitation pattern (e.g. reduced precipitation amount or –frequency) affecting the soil-water-plant system due to water available to roots with effects on evapotranspiration and plant growth (Jones et al. 2009). In winter wheat, the effects of reduced precipitation was studied under field conditions by Zhao et al. (2020). The effect of drought achieved by withholding of irrigation until complete soil water transpiration in pots placed in a glasshouse was studied in spring wheat (Weldearegay et al. 2012; Weldearegay et al. 2016). Field experiments focusing on the effects of reduced precipitation on grassland species have been done using rainout-shelters to reduce average summer-moisture by 50% (English et al. 2005) or using open top chambers covered by rainout shelters to simulate a 50% reduction of the long-term mean weekly precipitation (Dermody et al. 2007). Often increasing temperatures and drought occur simultaneously in the field (Shah and Paulsen 2003) and they can act synergistic with more adverse and stressful effects on the development of crops (Barnabás et al. 2008; Gray and Brady 2016). Multi-factor climate change experiments are necessary for predictions about their interactive effects on crop performance. Until now, only less information is available from multi-factor experiments on the combined effects of permanent soil warming and drought on aboveground biomass and yield production or ecophysiology of crops (Patil et al. 2010; Weldearegay et al. 2012; Weldearegay et al. 2016). Thus, for the production of high-quality food and feed in the future, and with regard to food security, it is necessary to gain data about single- and multi-factorial impacts of soil warming and reduced precipitation amount and –frequency on plant development, biomass and yield production of important crops grown under field conditions.

3.5 Effects of soil warming and altered precipitation pattern on soil processes, performance and productivity of wheat, barley and oilseed rape

It is known, that the agricultural production of food and feed is highly susceptible to temperature increase and changes in precipitation pattern (IPCC 2018). Moreover, water availability can be seen as a limiting factor for the production of agricultural crops. Both, soil warming and reduced

precipitation amount and frequency are affecting the water availability of soils in agroecosystems. Changes in temperature and precipitation can result either in positive or negative impacts on crop development and physiological plant processes, with effects on crop yield and the chemical composition of seeds (DaMatta et al. 2010). The state of the art regarding effects of soil warming, reduced precipitation amount and –frequency on plant and soil parameters, which are examined in this thesis, is exposed in the following sections. Most of the observations were made under controlled environmental conditions in growth chambers and greenhouses, or plants were grown outside, but were planted in pots or lysimeters and not in arable soils.

3.5.1 Soil processes

Soil characteristics are affected by increased soil temperature as well as by reduced soil water input as a consequence of both less precipitation amount or frequency. In an agricultural field heating cables were used to increase soil temperature by 3.0 °C, leading to an increase in evaporation which reduced soil moisture (Hantschel et al. 1995; Kamp et al. 1998). This was also shown for grassland, where the soil was warmed by 2.0 °C and 2.6 °C due to the use of infrared radiators (Luo et al. 2001; Norby and Luo 2004; English et al. 2005; Dermody et al. 2007). Thus, soil warming induced changes in the soil water content, which have an indirect effect on soil respiration, net nitrogen mineralization and plant productivity (Shaver et al. 2000; Weltzin et al. 2003). Moreover, an alteration in plant–microbe interactions have been observed under increased soil temperatures, with impacts on the availability and allocation of nutrients in the rhizosphere (Singh et al. 2019). Generally, the uptake of water and nutrients is accelerated in warmer soils (Bowen 1991). Under controlled environmental conditions, soil warming stimulated the root growth of crops such as winter wheat and oilseed rape (Moorby and Nye 1984; Gavito et al. 2001). Furthermore, soil warming indirectly reduces the water use efficiency of crops due to higher evapotranspiration (Fatima et al. 2020). A good water use efficiency is desired for crops to cope well under future climate conditions and this parameter is closely related to root structure, which is affected by the temperature in the soil (Nagel et al. 2009).

Timing and amount of precipitation inputs as well as transpiration influence soil evaporation, and therefore, these variables affect the soil moisture content (Weltzin et al. 2003). Accordingly, if effects of altered precipitation amount and frequency on crop performance are of interest, soil moisture should be analyzed as well because of the direct link between precipitation and ecological systems (Weltzin et al. 2003). An earlier study within the Hohenheim Climate Change experiment demonstrated soil warming to increase

evapotranspiration and to reduce soil moisture and aboveground biomass of spring wheat, whereas no consistent effects of reduced precipitation amount and frequency were observed (Poll et al. 2013). For a better statement about possible effects of precipitation changes on soil moisture and on agricultural crop production, data from several years, which differ in ambient precipitation, have to be analyzed as well.

3.5.2 Plant development

Elevated soil temperatures of 2.2 °C above ambient have been reported to accelerate crop development and to increase crop growth of winter wheat, if plants were grown under field conditions (Xiao et al. 2010). This was also shown for winter wheat grown either in plant growth chambers or in lysimeters with 5.0 °C soil warming (Power et al. 1970; Gavito et al. 2001; Patil et al. 2010). Accordingly, earlier flowering times in winter wheat have been observed under soil warming by 5.0 °C (Gavito et al. 2001; Patil et al. 2010). In addition, winter oilseed rape, grown in plastic containers in an unheated greenhouse, reached flowering (BBCH 60) and full flowering (BBCH 65) stages seven days earlier under 2.0 °C and 14 days earlier under 4.0 °C soil warming using heating cables (Siebold and Tiedemann 2012). In accordance, crop development was shown to be restricted under low soil temperatures since shoot growth was limited during early growth stages in temperate climate (Bowen 1991). For barley, the impacts on growth were not homogeneous under increased soil temperature. Growth of barley was accelerated due to soil warming by 6.5 °C under controlled conditions in growth chambers (Power et al. 1967). In contrast, growth depression was observed under soil warming by 5.0 °C and 10.0 °C in a glasshouse, which was assumed to be a result of temperature stress (Baon et al. 1994). Also growth rates of barley were decreased under elevated soil temperatures by 6.5 °C in growth chambers (Power et al. 1970).

Besides warming, the water availability affects plant development as well. Thus, low precipitation amounts are known to decrease crop growth and development of wheat and sorghum (Blum 1996). Since barley is vulnerable during flowering and ear formation to water shortage, reduced water availability shortens the grain filling period, with negative impacts on the development of ears (Sánchez-Díaz et al. 2002; González et al. 2007; Samarah et al. 2009). In contrast, plant development of winter wheat remained unaffected under -24% summer precipitation in lysimeters (Patil et al. 2010). Most likely in that study, high winter precipitation affected the soil moisture regime by recharging deeper soil layers with water, which was available for the deep-rooted winter wheat during the summer period.

3.5.3 Leaf gas exchange

Although effects of increasing air temperatures on plant physiological processes like photosynthesis are well examined in cereals, resulting in decreasing plant productivity and crop yield (Conroy et al. 1994; Barnabás et al. 2008; Fang et al. 2013), soil warming effects on photosynthesis were often studied in tree species (Bergh and Linder 1999; Strand et al. 2002; Reich et al. 2018) or in forest-floor plants (Ishioka et al. 2013) and in tundra plants (Starr et al. 2008). But information on effects of increased soil temperature on the photosynthesis of cereals and oilseed rape is scarce. However, Weldearegay et al. (2016) found that soil warming of 3.0 °C hardly affected net photosynthesis or stomatal conductance during flowering in spring wheat, using heating cables in a greenhouse. In contrast to studies with soil warming, more knowledge has been gained about the effects of water limitation on leaf gas exchange of cereals and oilseed rape. As consequences of metabolic impairment, photosynthesis decreases under limited water availability predominantly through a reduction in stomatal conductance or due to lower CO₂ assimilation (Flexas and Medrano 2002). In accordance, photosynthesis and stomatal conductance were either decreased in spring wheat by water limitation from stem elongation until maturity grown in open-top chambers (Schütz 2002) or decreased in spring barley by reduced water supply by 33%, starting 16 days after sowing until maturity grown in growth chambers (Schmid et al. 2016). Similarly, Jensen et al. (1996a) suggested limited photosynthesis in field-grown spring oilseed rape due to stomatal closure as consequence of a single drought event, which was finished when all plant-available soil water had been used. In addition, a reduction in water supply between 25% and 50% resulted in an increase in photosynthetic water-use efficiency in spring wheat and spring barley (Schmid et al. 2016; Tatar et al. 2016), which might be an advantage for the biomass production of crops under future water scarcity.

3.5.4 Biomass and yield production

Prolonged soil warming by 5.0 °C was found to increase decomposition and also nutrient availability for plants, thereby leading to enhanced vegetation productivity in nutrient limited ecosystems (IPCC 2021b; Melillo et al. 2011). In a field study, grain yield was increased due to 2.2 °C elevated soil temperature in winter wheat (Xiao et al. 2010). Aboveground biomass and grain yield of winter wheat were not affected if plants were grown in chambers or in lysimeters with 5.0 °C soil temperature elevation. In the same studies, number of ears and thousand grain weight were decreased, whereas root growth was increased (Gavito et al. 2001; Patil et al. 2010).

Moreover, Moorby and Nye (1984) reported that root growth was increased by soil warming in oilseed rape grown in pots under controlled environmental conditions. The seed yield of oilseed rape is highly variable and depends on temperature conditions during the seed filling period in Central Europe (Weymann et al. 2015; Brown et al. 2019). Accordingly, decreasing yields of winter oilseed rape were observed under rising mean temperatures, meaning the yield stability of winter oilseed rape will be a major challenge under changing climatic conditions in the next decades (Brown et al. 2019). Nowadays, only few studies focused on soil warming effects on barley grain yield, showing grain yield was either not affected or tendentially increased (Högy et al. 2013; Drebenstedt et al. 2020b). However, several studies with elevated air temperatures up to 5.0 °C above ambient air temperatures reported a decrease in barley grain yield (Savin et al. 1997; Alemayehu et al. 2014; Ingvordsen et al. 2018).

Regarding the other variable of interest, a reduction in water availability can negatively affect the harvestable crop yield in agroecosystems (Istanbulluoglu et al. 2010; Bodner et al. 2015), resulting in a major limitation of food production (Barnabás et al. 2008). Grain yield was marginally decreased by reduced precipitation amount (-33%) at stem elongation in winter wheat grown under field conditions (Zhao et al. 2020). This was associated with the formation of less, but bigger grains, which was reflected in a decreased kernel number and an increased thousand grain weight. At the same time, the water use efficiency of yield was improved under reduced precipitation amount (Zhao et al. 2020). In a previous study of these research group, Xu et al. (2016) reported an increased root growth of winter wheat to deeper soil layers, which improved the water uptake, which was assumed to improve the water use efficiency as well. Resilient aboveground biomass and grain yield of winter wheat were observed by Patil et al. (2010), both, under 24% reduced precipitation amount and under 50% reduced precipitation frequency. Winter oilseed rape showed declined seed yield under water shortage occurring from flowering to the end of seed set, grown in pots in a controlled environment (Champolivier and Merrien 1996). In contrast, the grain yield of six barley cultivars was not affected due to terminal water stress simulated in rain shelters under field conditions when the crops reached the flag-leaf stage (González et al. 2007). Although several experiments analyzed biomass and yield performance of wheat, barley and oilseed rape under water stress conditions (e.g., reduced water availability and drought), only in a few studies crops were exposed to terminal water scarcity during the summer month in the end of the vegetation period. Therefore, effects of declining summer precipitation amount and frequency on the productivity of crops are not well understood at the moment.

3.5.5 Yield quality of oilseed rape

In this thesis, the effects of soil warming and altered precipitation pattern on seed quality characteristics of winter oilseed rape were analyzed. Important quality parameters of seeds of oilseed rape are the concentrations of oil and protein, because the seeds are used as food and feed, e.g., as vegetable oil or as protein meal for livestock (Walker and Booth 2001; Högy et al. 2010). Data about soil warming effects on seed quality of oilseed rape from other experiments are missing to date. However, increasing air temperature of 5.0 °C was reported to decrease the seed oil concentration in oilseed rape and especially the content of fatty acids such as linoleic acid (C18:2), linolenic acid (C18:3) and oleic acid (C18:1) were decreased due to warming (Namazkar et al. 2016). Reduced water availability was shown to decrease seed oil concentration, whereas the protein concentration increased, in both, spring and winter oilseed rape (Bouchereau et al. 1996; Champolivier and Merrien 1996). In accordance, the concentration of oil in seeds was decreased due to a late drought period during the pod filling stage in spring oilseed rape grown in lysimeters (Jensen et al. 1996b). Furthermore, the concentration of glucosinolates increased under water scarcity (Bouchereau et al. 1996). A high concentration of glucosinolate has the potential to harm animals, e.g., leading to a reduction in milk or egg production of dairy cows and laying hens (Mawson et al. 1994; Alexander et al. 2008). Therefore the concentration of glucosinolates in rapeseeds used for protein meal is restricted (Jensen et al. 1996b).

3.6 Research questions and hypotheses asked within the scope of the Hohenheim Climate Change experiment

The Hohenheim Climate Change (HoCC) experiment was setup in 2008 at the Heidfeldhof (48°43'N, 9°13'E, 401 m a.s.l.), which is an experimental station of the University of Hohenheim in Stuttgart. Annual mean air temperature and precipitation at the site (1981–2010) were 9.4 °C and 718 mm, respectively (DWD 2020). Soil type is a loess-derived stagnic Luvisol. The pH is 7.0 with an organic carbon content of 12.1 g kg⁻¹ (Poll et al. 2013). Within the HoCC experiment, crops were exposed to several climate change factors in an arable field in the growing seasons 2016 (spring barley), 2016/2017 (winter oilseed rape) and 2017/2018 (winter wheat), in order to analyze their single or combined effects on parameters with regard to soil properties, photosynthesis, crop development and productivity as well as yield and yield quality. As climate change parameters, elevated soil temperature (+2.5 °C), reduced summer precipitation amount (-25%) and reduced summer precipitation frequency (-50%) were applied.

The first two manuscripts deal with research questions and hypotheses in the subject areas crop development, biomass production, yield, yield quality and photosynthesis and refer to the growing seasons 2016 (spring barley) and 2016/2017 (winter oilseed rape):

- (i) Soil warming accelerates crop development only during spring but not afterwards.
- (ii) A simultaneous occurrence of soil warming, decreased precipitation amount and precipitation frequency will have additive negative effects on plant ecophysiology.
- (iii) Soil warming will affect photosynthesis more than altered precipitation amount and frequency, because this physiological process is highly sensitive to temperature changes.
- (iv) Under soil warming, the water availability in soils is decreased, which will reduce the duration of the seed- and grain-filling period with negative impacts on crop yield.
- (v) Reduced precipitation amount or frequency during summer will decrease biomass production and crop yield.
- (vi) Less summer precipitation amounts will increase the protein and reduce the oil concentration in seeds of winter oilseed rape.

In the third manuscript, long-term data from ten growing seasons (2009-2018) of aboveground biomass, harvestable yield and climate conditions (air temperatures, precipitation, soil moisture) were analyzed, including the data from the season 2017/2018 on winter wheat. Thus, from 2009 to 2018, wheat, barley and oilseed rape were grown in a typical crop rotation on the experimental area of the HoCC experiment. The research questions were as follows:

- (vii) Are there universal effects of elevated soil temperature and altered precipitation pattern on aboveground biomass and crop yield across years and are these effects similar for all crops?
- (viii) And if not, do specific annual environmental conditions (e.g., wet or dry year) explain observed inter-annual variability in the responses of specific crops?

4 Effects of soil warming and altered precipitation patterns on photosynthesis, biomass production and yield of barley

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Ireen Drebenstedt^{1*}, Iris Schmid^{1,2}, Christian Poll³, Sven Marhan³, Robert Kahle³, Ellen Kandeler³, Petra Högy¹

¹*Institute of Landscape and Plant Ecology, University of Hohenheim, Stuttgart, Germany*

²*Institute of Crop Science, University of Hohenheim, Stuttgart, Germany*

³*Institute of Soil Science and Land Evaluation, University of Hohenheim, Stuttgart, Germany*

*Corresponding author

Summary

Crop productivity and plant physiology are affected by rising temperatures and altered precipitation patterns due to climate change. We studied the impacts of an increase in soil temperature of 2.5 °C, a decrease in summer precipitation amount of 25%, a reduction in summer precipitation frequency of 50%, and their interactions on photosynthesis, biomass production, and yield of spring barley (*Hordeum vulgare* L. cv. RGT Planet) in a temperate agricultural ecosystem near Stuttgart (Germany). Leaf gas exchange of barley appeared to be affected mainly by drought in the form of reduced precipitation frequency or by a combination of changes in soil temperature and precipitation patterns. In contrast, biomass production and yield parameters were more affected under soil warming alone. In addition, biomass of roots increased under soil warming at stem elongation. Stable grain yield was observed under reduced precipitation amount and also under increased evaporation through soil warming. These findings provide additional evidence that barley is relatively drought tolerant, which should be taken into consideration in the context of appropriate crop selection under climate change.

Keywords: soil warming; altered precipitation patterns; climate change; barley

4.1 Introduction

Temperature and precipitation are two important climate factors controlling crop production (Richardson et al. 2009; Hatfield et al. 2011). An increase in temperature and change in precipitation patterns can negatively affect crop development and crop yield (Barnabás et al. 2008; DaMatta et al. 2010). However, other aspects of predicted climate change are an increase of atmospheric carbon dioxide (CO₂) concentration and of tropospheric ozone (O₃) concentration, which can occur simultaneously with changes in temperature and precipitation during crop growth (DaMatta et al., 2010).

In Germany, average air temperature increased by 1.4 °C from 1881 to 2016 (DWD 2017). According to climate predictions, mean air temperature will continue to increase by 1.2 – 5.3 °C until 2100, as compared to 1971-2000 (Umweltbundesamt 2006; DWD 2017). Closely related to a rise in air temperature is an increase in soil temperature (Zheng et al. 1993). In addition, precipitation is expected to change as precipitation events become less frequent. During summer months, average precipitation amount is expected to decrease up to 9% until 2100, with few regional differences, compared to 1961-1990 (Umweltbundesamt 2006; Jacob et al. 2008; DWD 2017).

Predicting effects of elevated soil temperature due to global warming is more complex than corresponding changes in air temperature because soil temperature is additionally influenced by other factors such as soil moisture and texture, vegetation, or season (Gray and Brady, 2016). It is known that crop growth and development are stimulated by an increase in soil temperature, especially during early growth stages, resulting in earlier flowering times (Gavito et al. 2001; Patil et al. 2010). In addition, uptake of water and nutrients is accelerated under warmer soil temperatures in temperate climates (Bowen 1991). An increase in soil temperature directly affects root development (Gray and Brady 2016), which can lead to an increase in root biomass (Clark and Reinhard 1991). Understanding reactions of root growth in crops under global warming is crucial due to the essential role of root systems in water and nutrient uptake. Accordingly, traits such as abiotic stress tolerance or water use efficiency (WUE; biomass produced per unit of transpiration), which are linked to crop performance under future climate conditions, are closely related to root structure in the soil (Nagel et al. 2009). It is known that rising air temperatures can impact plant physiological processes, including photosynthesis, which can lead to shortened life cycle, reduced plant productivity, and reduced crop yield

(Conroy et al. 1994). However, impacts of elevated soil temperature on cereal physiology are not well understood.

Warm periods often occur in combination with reduced water availability. Under elevated temperatures plant water status is critical, because only well-watered plants tend to maintain stable tissue water status (Machado and Paulsen 2001; Wahid et al. 2007). Low water availability is known to decrease plant growth and to delay plant development. It can also result in crop yield reduction by limiting plant organ growth and final size (Blum 1996). The magnitude of agricultural yield losses is tightly linked to the developmental stage at which crops experience water stress (Gray and Brady 2016). Physiological processes such as photosynthesis are also limited by water limitation, mainly due to reduced stomatal conductance (g_s), or by metabolic impairment, leading to lower CO₂ assimilation (Flexas and Medrano 2002).

Often warming and drought occur in the field simultaneously, but their effects on crop performance are often analysed separately (Shah and Paulsen, 2003; Gray and Brady, 2016). However, the combination of multiple abiotic stresses can result in climate change effects that differ strongly from those observed in single-factor experiments (Gray and Brady 2016) and often result in more adverse impacts on plant development and crop yield than under a single stressor (Barnabás et al. 2008). To date, little data is available from climate manipulation experiments done in agricultural ecosystems.

The cultivation of barley (*Hordeum vulgare* L.) is expected to increase in the future due to its relative drought tolerance, which is an important trait with respect to food security (Richardson et al. 2009; Högy et al. 2013). However, barley is vulnerable to reduced water availability during flowering and ear formation, because water shortage can shorten the grain filling period and therefore have negative impacts on barley grain weight and size (Savin and Nicolas 1999; Sánchez-Díaz et al. 2002; González et al. 2007; Samarah et al. 2009). Spring barley is used as feedstock for animal feed and malt production. With regard to the effect of air temperature increase on barley grain yield, previous studies have shown a reduction in yield (Savin et al. 1997; Alemayehu et al. 2014; Ingvorsen et al. 2018).

The aim of the present study was to investigate the interactive effects of soil warming and altered precipitation amount and frequency on photosynthesis, crop development, and yield of spring barley in an arable field near Stuttgart (Germany). We hypothesized (i) that soil warming accelerates barley development during spring but not during later developmental stages, when the soil is dryer due to higher air temperatures and less precipitation in comparison to the period

of spring. Thus, an elevation in soil temperatures during later growth stages would decrease soil water amount additionally, which limits plant growth. Furthermore, (ii) we expected a greater influence on photosynthesis from elevated soil temperature than from altered precipitation amount and frequency, because this physiological process is well known to be highly sensitive to temperature changes. We hypothesized further (iii) that reduced precipitation amount or frequency during summer months will decrease biomass production and grain yield. Finally, (iv) we expected an additive negative effect of the three climate factors - soil warming, reduced precipitation amount, and reduced precipitation frequency - on ecophysiology of barley. To test these hypotheses, we used the Hohenheim Climate Change (HoCC) experiment where since 2008 an increase in soil warming (+ 2.5 °C) and during summer a reduction in precipitation amount (-25%) and frequency (-50%) is simulated under field conditions. We collected data on plant physiological responses and plant performance. Photosynthesis was measured at stem elongation and flowering. Plant development was monitored over the entire growing period. Biomass and yield data were collected at stem elongation, flowering, and maturity.

4.2 Materials and methods

4.2.1 Site description

The Hohenheim Climate Change (HoCC) experiment is located at the research station Heidfeldhof at the University of Hohenheim (Stuttgart) (48°43'N, 9°13'E, 401 m a.s.l.), and was established in 2008. The soil is a loess-derived stagnic Luvisol with pH 7.0, organic carbon content of 12.1 g kg⁻¹, and texture of 9.4% sand, 68.1% silt, and 22.6% clay. Annual mean air temperature and precipitation at the site (1961–1990) were 8.7 °C and 679 mm, respectively (Deutscher Wetterdienst 2019). In 2016, the annual mean air temperature and precipitation were 10.1 °C and 595.4 mm, respectively (Agricultural Technology Centre (LTZ) Augustenberg 2018). During the growing season of spring barley, from April until August 2016, average air temperature was 15.7 °C and total precipitation was 312 mm (Figure 4. 1), which is in the range of the long term average air temperature and total precipitation of 15.6 °C and 377.4 mm, respectively (1961 – 1990, Agricultural Technology Centre (LTZ) Augustenberg, 2018).

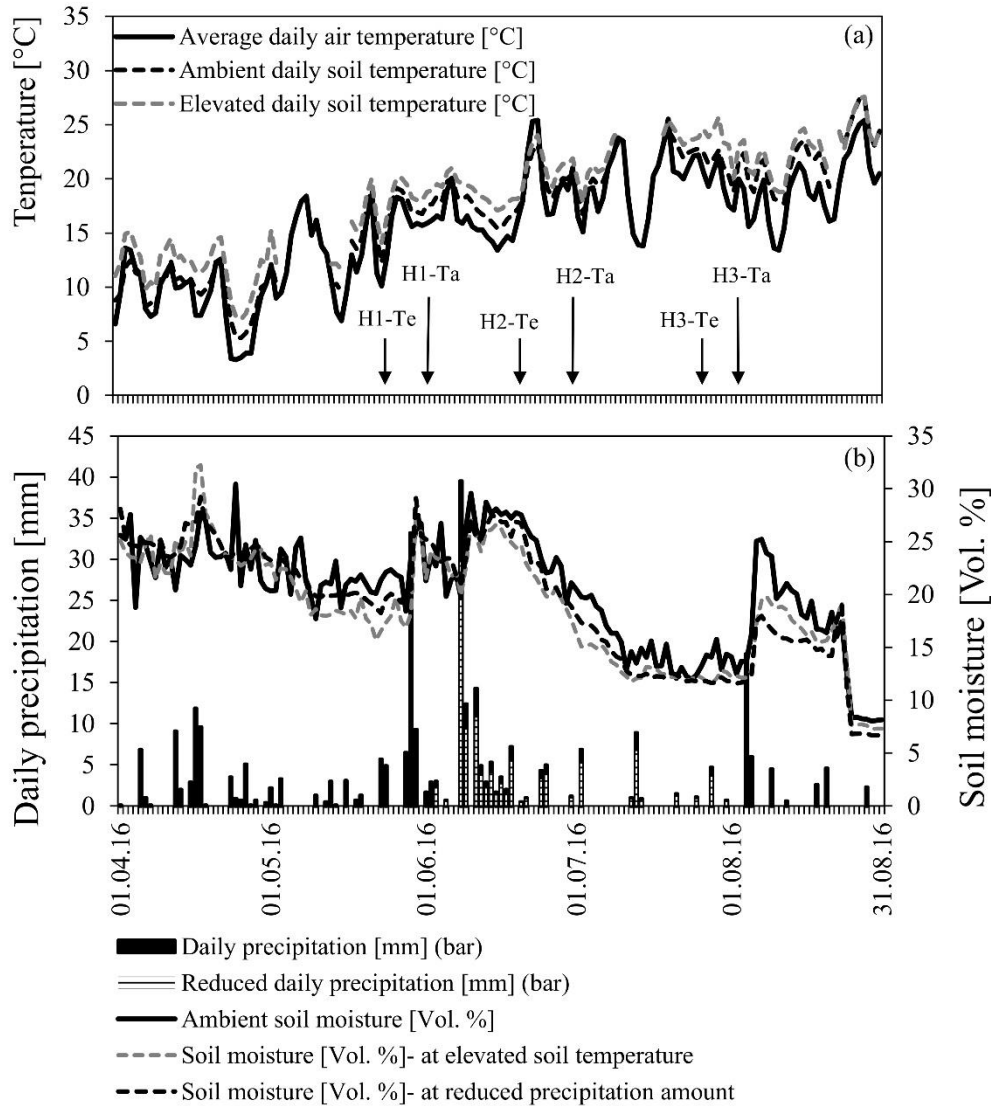


Figure 4. 1: Average daily air temperature (2 m), ambient and elevated daily soil temperature at the experimental site during the growing season from 01 April until 31 August 2016. Harvest dates are labelled as follows: H1: harvest 1 at stem elongation (DC 31); H2: harvest 2 at flowering (DC 65); H3: harvest 3 at maturity (DC 92); T_a: ambient temperature; T_e: elevated temperature. The harvest of plants grown under ambient soil temperature was about one week after plants grown under elevated soil temperature. Harvests dates: H1-T_a at 02 June 2016; H1-T_e at 25 May 2016; H2-T_a at 01 July 2016; H2-T_e at 23 June 2016; H3-T_a at 02 August 2016; H3-T_e at 27 July 2016 (see Tab. 1) (a). Daily precipitation and the amount of daily precipitation reduced by 25 % (named as reduced daily precipitation) as well as soil moisture measured in different treatments (ambient; at 2.5°C elevated soil temperature over the whole growing period; at -25 % reduced precipitation amount from 04 June 2016 until final harvest) (b). Temperature and precipitation data are from the weather station “Hohenheim” of the Agricultural Technology Centre (LTZ) Augustenberg, Germany. Soil moisture data are from TDR probes installed in 0–15 cm depth at every subplot at the HoCC experiment.

4.2.2 Experimental design

Within the HoCC experiment, future climate conditions, i.e., soil temperature (T), precipitation amount (A), and frequency (F) were simulated based on climate change predictions to 2100 for southwest Germany (Umweltbundesamt 2006; DWD 2017). Since 2008, soil temperature has been manipulated during the entire year and precipitation patterns have been manipulated

during summer months (June to August). In 2016, precipitation manipulation began on 04 June 2016 and was conducted until the final harvest of barley: in the ambient soil temperature treatments this date was 02 August 2016 while in the elevated soil temperature treatment harvest date was 27 July 2016. Treatments are set up in a split-plot-design replicated in four blocks. Each block consists of two plots (each $1\text{ m} \times 4\text{ m}$), one with ambient and one with elevated soil temperature. Soil temperature is elevated by $2.5\text{ }^{\circ}\text{C}$ (T_e) at 4 cm depth and is achieved by heating cables installed on the soil surface (RS 611-7918, RS Components GmbH). Dummy cables on ambient soil temperature plots (T_a) account for effects of the presence of heating cables on the soil, such as retention of water from precipitation. Each plot consists of four $1\text{ m} \times 1\text{ m}$ subplots, each having a different combination of the two precipitation factors; amount (A) and frequency (F). The surface area of the subplots ($1\text{ m} \times 1\text{ m}$) is lower than that normally used in field experiments, but was considered suitable as the plant density was comparable to other field experiments studying effects of soil warming or low water availability on cereals (González et al., 2010; Patil et al., 2010) and allowed a high number of treatment replicates. Roofs are used to protect the plots from precipitation (Folitec UV 5 foil, folitec Agrarfolien-Vertriebs GmbH). The height of the roofs is between 2 and 2.4 m at the lowest and highest point, respectively. Precipitation is collected in rain barrels and subplots are manually watered, making it possible to precisely control precipitation amount on the plots. In the manipulated plots precipitation amount was reduced by 25% (A_r) compared to ambient precipitation (A_a). Precipitation frequency simulated longer dry periods by reducing the number of rainy days by 50% (F_r), i.e. the cumulative precipitation amount of two events was delivered as one event compared to ambient precipitation frequencies (F_a). PVC barriers around each subplot impede lateral water movement. In addition to the roofed plots (R_r), each block includes two subplots without roofs (roof-control: R_c) to control for any roof effect on plant development. Precipitation patterns are not manipulated in the roof-control subplots. In every subplot, soil temperature is recorded using temperature probes at 4 cm depth and soil moisture is measured in a range of 0–15 cm depth using TDR probes (CS630/CS635, Campbell Scientific Ltd.). Additional information about the experimental setup is given in Poll et al. (2013).

4.2.3 Plant cultivation and biomass harvest

Since 2008, within the HoCC experiment, wheat, barley, and oilseed rape have been cultivated in a crop rotation. This study deals with spring barley (*Hordeum vulgare* L. cv. RGT Planet, Rubin® TT stained), which was sown on 05 April 2016 (0 days after sowing, 0 DAS) at a density of 400 plants m⁻² and adjusted to a final density of 290 plants m⁻² on 06 May 2016. Plants were fertilised with 60 kg N ha⁻¹ using calcium ammonium nitrate (29 April 2016). On 06 June 2016, 2.5 l ha⁻¹ fungicide Osiris was applied. Three harvests were made at specific plant developmental stages. The first harvest took place at the beginning of stem elongation (DC 31; BBCH Code (Meier 2001), while the second harvest was at full flowering (DC 65) (Table 4. 1). At the first and second harvests, two representative plants per subplot were cut one cm above the soil surface. The numbers of green and senescent leaves, stems, and ears were counted and fresh weight was determined. As plants cultivated on subplots with elevated soil temperature grew faster and reached the specific DC stage earlier than plants on subplots with ambient soil temperature, plants on heated subplots were harvested approximately one week before the non-heated plants (Table 4. 1). At the final harvest (DC 92), all plants in a square of 0.5 m x 0.5 m in the centre of each subplot were cut one cm above the soil surface and treated identically to the plants taken at the first and second harvests. Leaves and stems were dried at 60 °C and ears at 30 °C to constant weight. Ears were threshed to separate grains. Grain yield was measured and thousand grain weight (TGW) was determined using a seed counter (Condator “E”, Pfeuffer, Germany). Grains were then separated into grain size classes (GSC: >2.8 mm; 2.8 – 2.5 mm; 2.5 – 2.2 mm; <2.2 mm) using a Sortimat (Type K, Pfeuffer, Germany). Biomass of roots were sampled with a cylinder (20 cm length, 4.5 cm Ø), taking a soil core containing roots of two barley plants on 01 June 2016 (DAS 57, DC 31), 27 June 2016 (DAS 83, DC 65) and 19 July 2016 (DAS 105, DC 92), which were near the three harvest dates of the aboveground biomass (Table 4. 1). Because of the severe soil disturbance, sampling of barley roots was not possible in all subplots and was done only at roof-control subplots with ambient and elevated soil temperature, meaning that no effects of changes in precipitation patterns on biomass of roots could be tested. Roots were washed over a sieve (mesh size 1 mm) and dried at 40 °C for 2 days to determine the root dry weight per plant.

Table 4. 1: Harvest dates of the aboveground biomass. Plants on plots with ambient and elevated soil temperature were sown on the same day (05 April 2016) but harvested on different dates (T_a : 02 August 2016 and T_e : 27 July 2016).

Harvest	Development stage	Harvest date	
		Ambient soil temperature	Elevated soil temperature
First	DC 31, stem elongation	02 June 2016	25 May 2016
Second	DC 65, full flowering	01 July 2016	23 June 2016
Final	DC 92, maturity	02 August 2016	27 July 2016

4.2.4 Measurement of plant-related parameters

Five plants in the center of each subplot were labelled with rings around the stems. These plants were monitored for all crop development parameters. Plant phenology was measured weekly using the BBCH decimal codes (Meier 2001). Greenness index of the penultimate leaf was measured from 62 DAS onwards using a SPAD meter (Konica Minolta Optics Inc., Japan) to detect possible differences in leaf senescence during the growing period between all treatments. The SPAD measurements were performed at three different positions at the central part of the leaf. From these three values a mean value was calculated. Water use efficiency of the biomass (WUE_B) was calculated by dividing total aboveground biomass per plant by total water use per plant until final harvest. Additionally, the ratio between grain yield per plant and total water use per plant until final harvest was calculated for the water use efficiency of grain yield (WUE_Y). Total water use per plant was calculated by dividing precipitation amount per m^2 (from sowing until final harvest) by the number of plants per m^2 of each subplot. Precipitation amount data were taken by the (Agricultural Technology Centre (LTZ) Augustenberg 2018). Precipitation amount per m^2 was higher in subplots with ambient than elevated soil temperature, because final harvest of barley under ambient soil temperature conditions was approximately one week later.

4.2.5 Leaf gas exchange

On each subplot one plant was labelled and used only for gas exchange measurements. The youngest fully expanded leaf was chosen for the measurement, resulting in a total of one measurement per plant at each measurement date. Gas exchange was measured during two different time periods: (1) one week before and one week after the first harvest (stem elongation) and (2) one week before and one week after the second harvest (flowering) with a LI-COR open photosynthesis system (LI-6400). Measurements during stem elongation were taken on 20 May, 01 June, and 07 June 2016; those during flowering were taken on 22 June, 27

June, and 04 July 2016 between 09:30 and 13:30 each. Before each measurement, the SPAD value of the leaf used for gas exchange measurement was measured three times to calculate an average SPAD value. Then the leaf was fixed in the chamber head and the in-chamber leaf area was calculated using a ruler. Afterwards, the in-chamber conditions were adjusted and the leaf adapted for 10 minutes to the conditions inside the chamber. In-chamber conditions were as follows: reference CO₂ (CO₂R) was set to 400 $\mu\text{mol CO}_2 \text{ mol}^{-1}$ and light intensity in the leaf chamber (ParIn) was set to 1500 $\mu\text{mol m}^{-2} \text{ s}^{-1}$. Flow rate to the leaf chamber was adjusted to 400 $\mu\text{mol s}^{-1}$. Also, relative humidity (RH) in the leaf chamber, leaf temperature (T_{leaf}), and vapour pressure deficit at the leaf surface (VPD_L) were controlled: leaf temperature reflected the mean midday temperatures of each time period. For time period 1, RH was adjusted to $57.8 \pm 4.7\%$, T_{leaf} was set to 21.2 ± 3.1 °C, and VPD_L was 1.2 ± 0.2 . T_{air} outside the leaf chamber was on average 19.7 ± 3.6 °C. During time period 2, the parameters were as follows: RH $52.2 \pm 9.0\%$, T_{leaf} 30.0 ± 0.03 °C, VPD_L 1.9 ± 0.3 , and T_{air} 30.8 ± 1.6 °C. The means of each gas exchange parameter for time periods 1 and 2 were then calculated. Net photosynthesis (A_{net}), stomatal conductance (g_s), and transpiration (E) were derived from the gas exchange measurements. Instantaneous water use efficiency of photosynthesis (WUE_P) was calculated using the formula A_{net}/E .

4.2.6 Statistical tests

Each variable was analysed by a linear mixed-effects model. Fixed factors were “soil temperature” (T_a and T_e), “precipitation amount” (A_a and A_r), and “precipitation frequency” (F_a and F_r). Random factors were block, plot and subplot. Data were analysed separately for each measurement date and were checked for outliers using the Grubb’s Test (Grubbs 1950). Outliers were eliminated from the data set. An analysis of variance (ANOVA) was applied to the model to detect significant main and interaction effects of the fixed factors soil temperature (T), precipitation amount (A), and precipitation frequency (F) on each variable (e.g., plant height). Data were \ln transformed prior to analysis if heterogeneity of variance was identified by Levene’s Test. A level of probability of $P \leq 0.05$ was set as statistically significant. Least significant difference (LSD) post-hoc tests were performed.

The data were analysed with the statistical software R (version 3.4.2 for Windows, R Foundation for Statistical Computing, Vienna, AT). The lme function of the R 3.4.0 nlme package provided the linear mixed-effects model. For the Grubb’s Test the R package “outliers” was applied and the Levene’s Test was done with the leveneTest function of the R package “car”. The LSD test was done with the R package “agricolae”.

4.3 Results

4.3.1 Environmental conditions

Warming increased soil temperature in 4 cm depth over the entire growing period by on average 1.51 ± 0.49 °C in roofed plots and 1.94 ± 0.35 °C in roof-control plots. Plants grown under ambient soil temperature developed more slowly than those in the elevated soil temperature treatment and therefore were finally harvested six days later than plants under soil warming (Table 4. 1). As a consequence, the precipitation amount and the number of rain events varied between subplots with ambient and elevated soil temperature. In ambient soil temperature plots, precipitation amount was 139.7 mm in the control and 104.8 mm in the reduced treatment, meaning a reduction in precipitation amount by 25% (34.9 mm). Under soil warming, the precipitation amount was reduced by 25% (33.6 mm) from 134.3 mm in the control to 100.7 mm in the reduced treatment. The number of rainy days was decreased by 50% from 26 to 13 and from 24 to 12 days, for ambient and elevated soil temperature subplots, respectively. Soil warming and a reduction in precipitation amount decreased soil moisture compared to control subplots (Figure 4. 1), but not significantly maybe due to variability in the soil moisture measurements.

4.3.2 Plant development

Plants under soil warming developed faster with the beginning of stem elongation, which led to accelerated formation of the first node (DC 31) by seven days (Table 4. 2). Accordingly, the first harvest at stem elongation had to be conducted earlier on elevated soil temperature subplots than on ambient soil temperature subplots. Under soil warming conditions, plants also reached full flowering (DC 65) and fully ripe (DC 89) stages seven and five days earlier, respectively. The final harvest of hard grains (DC 92) of barley grown under elevated soil temperature was six days before that grown under ambient soil temperature conditions.

From the beginning of plant development measurements (24 DAS) until the last measurement date (111 DAS), elevated soil temperature increased plant height (Figure 4. 2). Roof effects on barley height were limited to DAS 38 and were less pronounced under ambient (+8%) than under elevated soil temperature (+30%) (data not shown).

SPAD values of the penultimate leaf, measured on five monitored plants per subplot, were increased due to elevated soil temperature on average from 38.9 to 46.0 at 70 DAS and from 42.8 to 46.9 at 77 DAS (Figure 4. 3). After plants under elevated soil temperature reached full flowering stage (DC 65) at DAS 84, SPAD values at the warmed plots approximated the values

at the control plots. A reduction in precipitation amount and frequency had no significant effect on SPAD values over the entire vegetation period.

Table 4. 2: Duration of growth stages from sowing until final harvest of spring barley. Decimal code (DC) was used to quantify the growth stages (Meier 2001). Sowing date: 05 April 2016. Final harvest of plants grown under ambient and elevated soil temperature were on 02 August 2016 and 27 July 2016, respectively.

Development stage (DC stadiums)	Date of reaching a specific development stage		Duration from sowing to achieve each stage (days)	
	Ambient soil temperature	Elevated soil temperature	Ambient soil temperature	Elevated soil temperature
First leaf unfolded (11)	29 April 2016	29 April 2016	24	24
First tiller detectable (21)	14 May 2016	14 May 2016	39	39
First node at least 1 cm above tillering node (31)	01 June 2016	25 May 2016	57	50
Flag leaf unrolled, ligule just visible (39)	09 June 2016	03 June 2016	65	59
First awn visible (49)	14 June 2016	06 June 2016	70	62
End of heading (59) ¹	03 July 2016	23 June 2016	89	79
Full flowering: 50% of anthers mature (65)	28 June 2016	21 June 2016	84	77
Late milk (77)	14 July 2016	03 July 2016	100	89
Fully ripe (89)	22 July 2016	17 July 2016	108	103
Hard grain harvest (92)	02 August 2016	27 July 2016	119	113

¹A high number of plants entered the full flowering stage (DC 65) before all plants completed the BBCH stage end of heading (DC 59). Therefore, the DC 59 stage was completed on ambient and elevated soil temperature subplots after the DC 65 stage was finished.

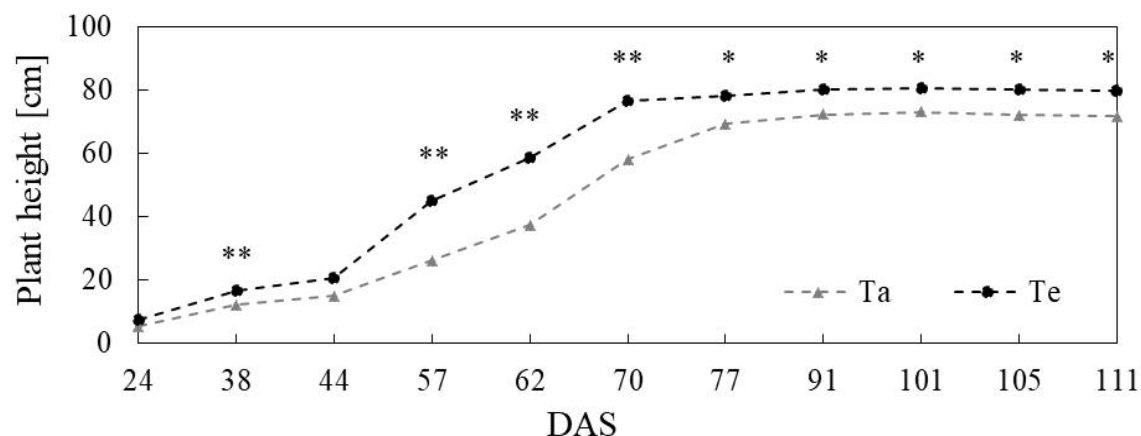


Figure 4. 2: Plant height measured between 24 DAS and 111 DAS at ambient (T_a) and elevated soil temperature (T_e). Asterisks indicate significant differences between plants under ambient and elevated soil temperatures (* $P \leq 0.05$; ** $P \leq 0.01$); $n = 4$.

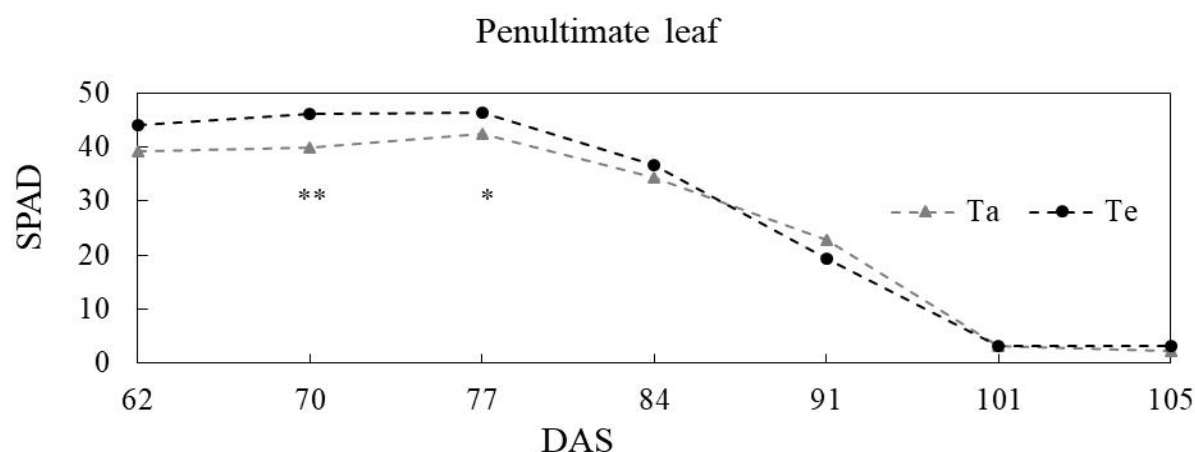


Figure 4. 3: SPAD values of the penultimate leaf, measured under ambient (T_a) and elevated soil temperature (T_e). SPAD values are averages of five plants of each subplot, used as monitor plants. Asterisks indicate significant differences between plants under ambient and elevated soil temperatures (* $P \leq 0.05$; ** $P \leq 0.01$); $n = 4$.

4.3.3 Leaf gas exchange

During stem elongation, leaf gas exchange was measured on leaves of plants with similar SPAD values (between 40.3 and 43.1) over all treatments (data not shown). Thus, differences in g_s and E were not due to differences in SPAD values. During flowering, the youngest fully expanded leaf showed no differences between SPAD values over all treatments. However, SPAD values at flowering were lower than at stem elongation, falling between 30.0 and 39.6.

During stem elongation, longer dry periods as consequence of reduced precipitation frequency reduced g_s by 33% (Figure 4. 4). A reduction in precipitation amount increased g_s and E by 30% and 20% respectively under ambient soil temperature. However, this effect was opposite

that under elevated soil temperature, where reduced precipitation amount decreased g_s and E by 20% and 16%, respectively. WUE_P of barley was reduced by 13% under reduced precipitation amount among plants grown under ambient soil temperature (Table 4. 3). But under elevated soil temperature, the WUE_P increased by 16% if the precipitation amount was reduced.

At flowering, the SPAD values of plant leaves used for leaf gas exchange measurements were similar (between 30.0 and 39.6) for all treatments (data not shown). The gas exchange parameters A_{net} , g_s and E were not significantly affected by any of the three climate factors (Figure 4. 4). However, values of g_s and E were considerably lower at flowering than at stem elongation, resulting in lower rates of A_{net} in all treatments. No treatment effect on WUE_P could be detected at flowering.

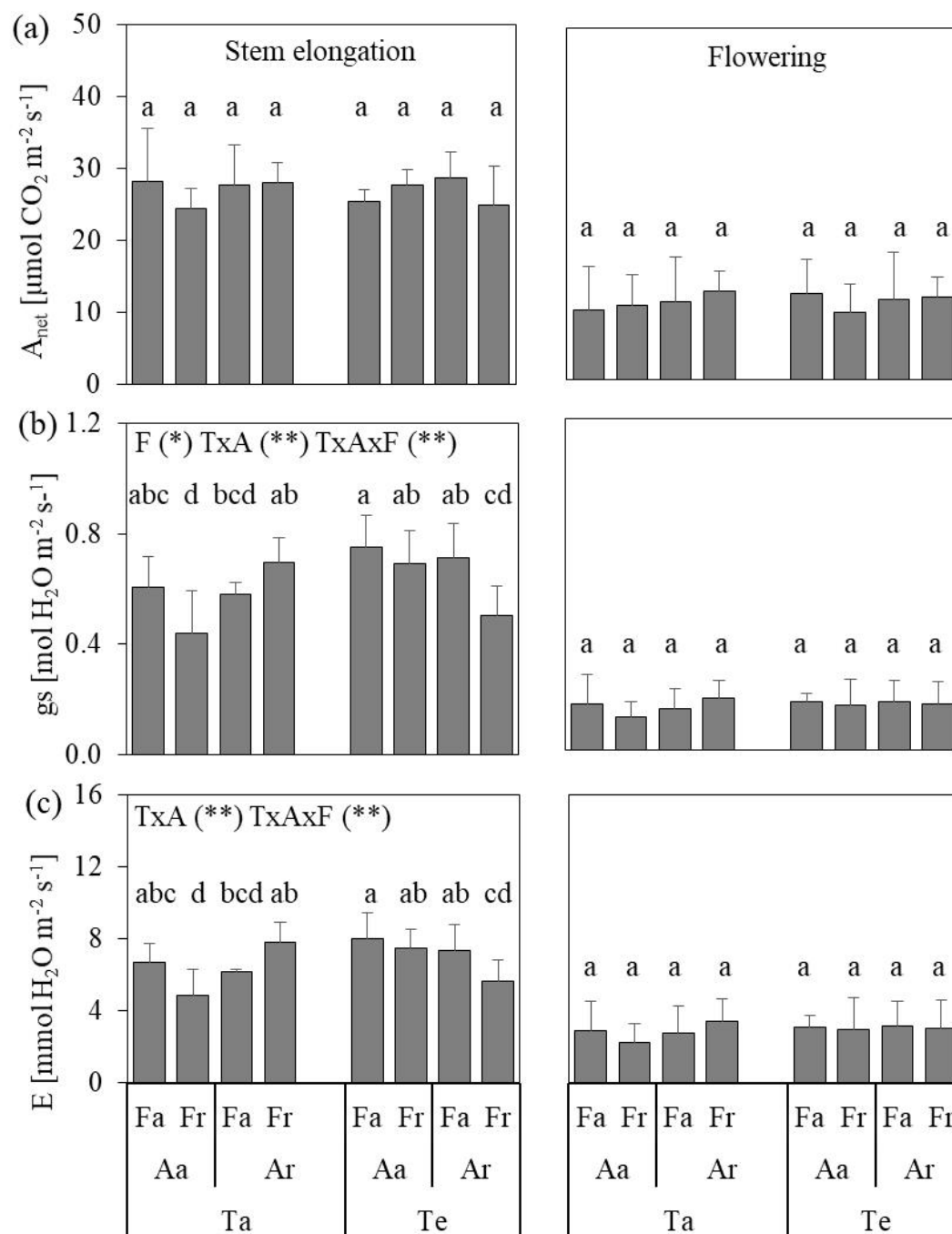


Figure 4. 4: Reactions of net photosynthesis (A_{net}) (a), stomatal conductance (g_s) (b), and transpiration (E) (c) to changes in soil temperature (T_a , ambient; T_e , elevated), precipitation amount (A_a , ambient; A_r , reduced) and precipitation frequency (F_a , ambient; F_r , reduced). Measurements were performed at stem elongation and flowering. Means and SDs are shown, asterisks indicate significance (* $P \leq 0.05$, ** $P \leq 0.01$) tested by three-way ANOVA applied to a mixed-effects model; $n = 3$. Different letters indicate significant differences between treatments (LSD test, $P \leq 0.05$).

4.3.4 Biomass production

At stem elongation, biomass of senescent leaves was 71% higher under ambient than elevated soil temperature, whereas biomass of green leaves and total aboveground biomass remained unaffected (Table 4. 3). At flowering, soil warming increased aboveground biomass production by 6% and increased biomass of green leaves and stems by 135% respective 26%. If soil warming and reduced precipitation frequency occurred at the same time, there was an increase in aboveground biomass (+18%), biomass of senescent leaves (+35%), and ears (+21%). At maturity, biomass of stems increased by 46% due to soil warming. Barley had a 13% higher WUE_B under reduced precipitation amount. Moreover, WUE_B increased tendentially by 60% under elevated soil temperature ($P = 0.067$, Table 4. 3). Root biomass increased by 80% under elevated soil temperature at stem elongation, whereas at flowering or maturity no effects on root biomass could be detected (Figure 4. 5).

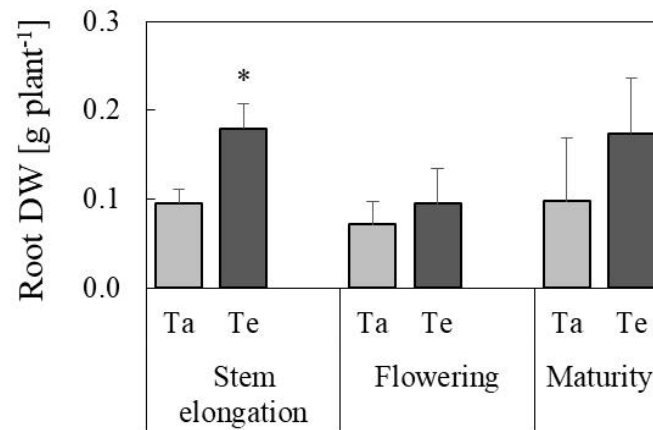


Figure 4. 5: Effects of elevated temperature (T_e , dark grey) compared to ambient temperature conditions (T_a , light grey) on root dry weight (DW) of barley. Harvests were done at stem elongation, flowering, and plant maturity. Means and SDs are shown, asterisk indicates significance ($*P \leq 0.05$, tested by a mixed-effects model); $n = 4$.

4.3.5 Yield parameter

At maturity, soil warming increased the number of ears per plant by 36% (Figure 4. 6) and tended to increase the biomass of ears by 51% ($P = 0.057$, Table 4. 3) as well as grain yield by 54% ($P = 0.057$, Figure 4. 6). Barley grown under reduced precipitation frequency had 6% less TGW compared to controls (Table 4. 3). Harvest index was not significantly affected by the climate factors soil warming, precipitation amount, and precipitation frequency. The WUE_Y of barley increased by 13% under reduced precipitation amount.

All grain size classes (GSC) were affected by reduction in precipitation amount (Table 4. 3). Thus, reduced precipitation amount led to a 9% increase in grains >2.8 mm, whereas GSC 2.8 – 2.5 mm, GSC 2.5 – 2.2 mm, and GSC <2.2 mm decreased by 11%, 8%, and 2%, respectively. A reduction in precipitation frequency increased GSC 2.5 – 2.2 mm by 43%. Barley tended to produce 1% more grains >2.5 mm under reduced precipitation amount ($P = 0.053$, data not shown). Roofing increased GSC >2.8 mm by 19%, and decreased GSC 2.8 – 2.5 mm by 19% (data not shown).

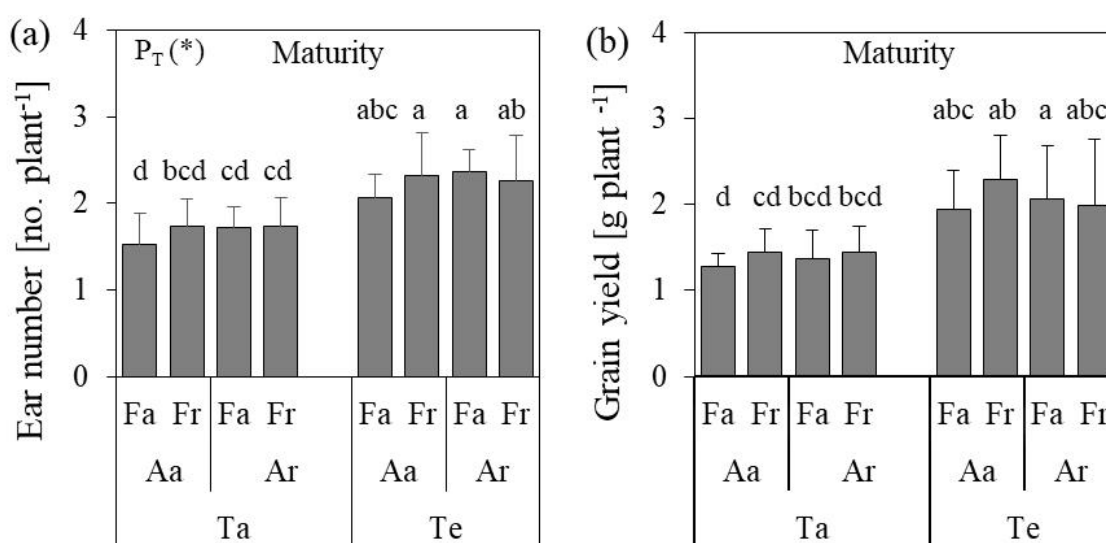


Figure 4. 6: Effects of soil temperature (T_a , ambient; T_e , elevated), precipitation amount (A_a , ambient; A_r , reduced), and precipitation frequency (F_a , ambient; F_r , reduced) on (a) ear number per plant and (b) grain yield per plant. Measurements were performed at plant maturity. Means and SDs are shown, asterisk indicates significance ($*P \leq 0.05$, tested by three-way ANOVA applied to a mixed-effects model); $n = 4$. Different letters indicate significant differences between treatments (LSD test, $P \leq 0.05$).

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Table 4. 3: Biomass production, yield parameters, and water use efficiency of barley. Plants were grown under ambient (T_a) or elevated (T_e) soil temperature in combination with the following precipitation patterns: ambient (A_a) or reduced (A_r) precipitation amount and ambient (F_a) or reduced (F_r) precipitation frequency.^a

	T _a				T _e				Three-way ANOVA ^b						
	A _a		A _r		A _a		A _r		Main effects			Interactions			
												T _x		T _x	
	F _a	F _r	F _a	F _r	F _a	F _r	F _a	F _r	T	A	F	A	F	F	F
Biomass production [g DW plant ⁻¹]															
<i>First harvest (stem elongation)</i>															
Aboveground	0.68 ± 0.24 ^a	0.67 ± 0.07 ^a	0.63 ± 0.22 ^a	0.56 ± 0.20 ^a	0.53 ± 0.29 ^a	0.48 ± 0.17 ^a	0.52 ± 0.12 ^a	0.45 ± 0.05 ^a	ns	ns	ns	ns	ns	ns	ns
Green leaves	0.34 ± 0.13 ^a	0.35 ± 0.05 ^a	0.34 ± 0.11 ^a	0.30 ± 0.10 ^a	0.32 ± 0.16 ^a	0.29 ± 0.10 ^a	0.31 ± 0.05 ^a	0.26 ± 0.04 ^a	ns	ns	ns	ns	ns	ns	ns
Senes. leaves	0.014±0.008 ^{ab}	0.010±0.006 ^{abc}	0.013±0.009 ^a	0.010±0.007 ^{abc}	0.004±0.005 ^c	0.002±0.000 ^{ab}	0.007±0.000 ^{bc}	0.010±0.003 ^{abc}	0.035	0.062	ns	ns	ns	ns	ns
Stems	0.33 ± 0.11 ^{cde}	0.31 ± 0.04 ^{de}	0.28 ± 0.11 ^{bcd}	0.25 ± 0.11 ^e	0.20 ± 0.13 ^{abc}	0.18 ± 0.07 ^a	0.20 ± 0.06 ^{ab}	0.18 ± 0.01 ^{abc}	0.065	ns	ns	ns	ns	ns	ns
<i>Second harvest (flowering)</i>															
Aboveground	3.84±0.64 ^{bcd}	3.09±0.54 ^{cd}	3.94±0.97 ^{bcd}	2.86±0.12 ^d	4.05±0.12 ^{abc}	5.56±1.35 ^a	5.07±1.10 ^{ab}	5.22±1.74 ^{ab}	0.014	ns	ns	ns	0.010	ns	ns
Green leaves	0.26 ± 0.07 ^b	0.26 ± 0.06 ^b	0.25 ± 0.12 ^b	0.23 ± 0.04 ^b	0.61 ± 0.12 ^a	0.59 ± 0.17 ^a	0.57 ± 0.16 ^a	0.51 ± 0.16 ^a	0.003	ns	ns	ns	ns	ns	ns
Senes. leaves	0.20±0.04 ^{ab}	0.15±0.04 ^{abc}	0.21±0.06 ^a	0.15±0.04 ^{abc}	0.09±0.03 ^c	0.17±0.05 ^{ab}	0.14±0.05 ^{bc}	0.16±0.06 ^{abc}	ns	ns	ns	ns	0.003	ns	ns
Stems	1.90±0.37 ^{bcd}	1.68±0.38 ^{cd}	2.17±0.61 ^{abc}	1.54±0.05 ^d	2.39±0.12 ^{ab}	2.89±0.74 ^a	2.76±0.49 ^a	2.50±0.31 ^{ab}	0.020	ns	ns	ns	0.082	ns	ns
Ears	1.48±0.30 ^{ab}	1.01±0.17 ^{bc}	1.31±0.30 ^{abc}	0.95±0.11 ^c	0.96±0.09 ^c	1.57±0.30 ^a	1.60±0.53 ^a	1.53±0.54 ^a	ns	ns	ns	ns	0.010	ns	ns
<i>Final harvest (maturity)</i>															
Aboveground	2.34 ± 0.38 ^a	2.55 ± 0.61 ^a	2.71 ± 0.46 ^a	2.61 ± 0.50 ^a	3.47 ± 0.75 ^a	3.71 ± 0.94 ^a	4.09 ± 0.79 ^a	3.63 ± 1.19 ^a	0.062	ns	ns	ns	ns	ns	ns
Senes. leaves	0.18 ± 0.04 ^c	0.20 ± 0.04 ^{bc}	0.22 ± 0.05 ^{abc}	0.19 ± 0.05 ^{bc}	0.25 ± 0.06 ^{abc}	0.26 ± 0.06 ^{ab}	0.30 ± 0.05 ^a	0.27 ± 0.08 ^{ab}	0.076	0.089	ns	ns	ns	ns	ns
Stems	0.68±0.13 ^d	0.76±0.18 ^{cd}	0.81±0.12 ^{bcd}	0.74±0.15 ^{cd}	0.99±0.20 ^{abc}	1.06±0.21 ^{ab}	1.15±0.19 ^a	1.08±0.28 ^{ab}	0.048	ns	ns	ns	ns	ns	ns
Ears	1.48±0.21 ^d	1.59±0.39 ^{cd}	1.68±0.30 ^{bcd}	1.68±0.31 ^{bcd}	2.23±0.49 ^{abc}	2.39±0.6 ^{ab}	2.64±0.56 ^a	2.28±0.83 ^{abc}	0.057	ns	ns	ns	ns	ns	ns
Yield parameters															
<i>Final harvest (maturity)</i>															
<i>Grain size classes [% grains]</i>															
>2.8 mm	52.1 ± 4.6 ^{bc}	44.8 ± 6.3 ^c	56.6 ± 3.4 ^{bc}	53.4 ± 10.4 ^{bc}	65.2 ± 9.9 ^{ab}	63.9 ± 9.2 ^{ab}	71.2 ± 17.0 ^a	73.8 ± 12.56 ^a	0.078	0.023	ns	ns	ns	ns	ns
2.8-2.5 mm	34.0 ± 6.0 ^a	36.0 ± 3.9 ^a	30.4 ± 3.6 ^{ab}	33.3 ± 8.1 ^a	22.9 ± 4.1 ^{bc}	23.9 ± 2.9 ^{bc}	18.7 ± 7.0 ^c	20.1 ± 8.1 ^c	0.030	0.035	ns	ns	ns	ns	ns
2.5-2.2 mm	9.6 ± 1.8 ^{ab}	13.7 ± 2.9 ^a	8.8 ± 1.3 ^b	9.6 ± 2.1 ^{ab}	7.2 ± 3.2 ^b	7.5 ± 4.2 ^b	6.1 ± 5.0 ^b	5.3 ± 3.7 ^b	ns	0.030	0.048	ns	ns	ns	ns
<2.2 mm	4.3 ± 2.3 ^{ab}	5.5 ± 1.3 ^a	4.2 ± 1.9 ^{ab}	3.6 ± 1.7 ^{ab}	4.7 ± 2.7 ^a	4.7 ± 2.9 ^a	1.3± 0.2 ^b	3.3± 2.3 ^{ab}	ns	0.015	ns	ns	ns	ns	0.063

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Table 4. 3: Continued.

	T_a		T_e		Three-way ANOVA^b											
	A_a		A_r		A_a		A_r		Main effects			Interactions				T_x
	F_a	F_r	F_a	F_r	F_a	F_r	F_a	F_r	T	A	F	T_x A	T_x F	A_x F	A_x F	A_x F
Yield parameters																
<i>Final harvest (maturity)</i>																
Harvest index	0.546±0.02 ^a	0.536 ±0.03 ^a	0.531 ±0.03 ^a	0.553 ±0.02 ^a	0.561±0.01 ^a	0.552 ±0.04 ^a	0.557 ±0.02 ^a	0.537 ±0.04 ^a	ns	ns	ns	ns	ns	ns	ns	ns
TGW [g 1000 grains ⁻¹]	47.1 ± 1.7 ^{ab}	44.4 ± 1.1 ^b	47.5 ± 1.8 ^{ab}	47.5 ± 2.8 ^{ab}	48.3 ± 2.1 ^a	48.0 ± 1.9 ^a	50.3 ± 6.2 ^a	50.2 ± 4.4 ^{ab}	ns	ns	0.050	ns	ns	ns	ns	<i>0.074</i>
Water-use																
<i>Final harvest (maturity)</i>																
Total water use [l plant ⁻¹]	0.8 ± 0.2 ^a	0.8 ± 0.1 ^a	0.8 ± 0.1 ^a	0.7 ± 0.2 ^a	0.7 ± 0.1 ^a	0.8 ± 0.0 ^a	0.7 ± 0.05 ^a	0.7 ± 0.1 ^a	ns	ns	ns	ns	ns	<i>0.091</i>	ns	
Water use efficiency																
<i>First harvest (stem elongation)</i>																
WUE _P [μmol mmol ⁻¹]	4.2 ± 1.1 ^{abc}	5.2 ± 1.1 ^a	4.5 ± 1.0 ^{ab}	3.7 ± 0.7 ^{bc}	3.3 ± 0.7 ^c	3.8 ± 0.6 ^{bc}	4.0 ± 0.8 ^{abc}	4.2 ± 0.8 ^{ab}	ns	ns	ns	0.020	ns	ns	ns	ns
<i>Second harvest (flowering)</i>																
WUE _P [μmol mmol ⁻¹]	3.2 ± 1.5 ^a	4.8 ± 0.8 ^a	4.0 ± 0.4 ^a	3.8 ± 0.7 ^a	3.0 ± 0.5 ^a	3.5 ± 0.8 ^a	3.2 ± 1.5 ^a	3.3 ± 0.7 ^a	ns	ns	ns	ns	ns	ns	ns	ns
<i>Final harvest (maturity)</i>																
WUE _B [g l ⁻¹]	3.0 ± 0.2 ^d	3.1 ± 0.5 ^d	3.4 ± 0.8 ^{cd}	3.8 ± 1.1 ^{bcd}	4.8 ± 1.4 ^{abc}	5.0 ± 0.9 ^{abc}	5.6 ± 1.2 ^a	5.6 ± 2.3 ^{ab}	<i>0.067</i>	0.017	ns	ns	ns	ns	ns	ns
WUE _Y [g l ⁻¹]	1.6 ± 0.1 ^c	1.7 ± 0.3 ^c	1.8 ± 0.5 ^{bc}	2.1 ± 0.7 ^{abc}	2.7 ± 0.8 ^{ab}	2.9 ± 0.5 ^{ab}	3.1 ± 0.8 ^a	3.1 ± 1.5 ^{ab}	<i>0.062</i>	0.048	ns	ns	ns	ns	ns	ns

^aData are means ± standard deviations across four replicates (n = 4) and were tested by three-way ANOVA for main effects or interaction effects of the fixed factors T, A, and F. LSD post-hoc results indicate statistically significant differences at P < 0.05 level of probability and are labelled by different letters above the standard deviations. ^bns = not significant (P > 0.05); bold numbers indicate significant main or interaction effects of T, A, F (*P ≤ 0.05, **P ≤ 0.01) and numbers in italics indicate trend (0.1 ≥ P > 0.05). Abbreviations: Senes. Leaves = senescent leaves; DW = dry weight; TGW = thousand grain weight; WUE = water use efficiency.

4.4 Discussion

4.4.1 Plant development

Elevated soil temperature accelerated barley development over the entire growing period to maturity, resulting in about one week earlier flowering and final harvest. Similarly, the rate of peanut development was also accelerated under elevated soil temperature in a greenhouse experiment (Prasad et al. 2006). In contrast, plant development of winter wheat, which was also more rapid under elevated soil temperature, declined after stem elongation (Patil et al. 2010). In the present study, the height of barley was significantly higher under elevated soil temperature over the entire growing period. This effect on canopy height was also reported for winter rapeseed grown under elevated soil temperature within the HoCC experiment in 2014 (Bamminger et al. 2016).

Our hypothesis, that elevated soil temperature accelerated plant development during spring was supported by these results. In plots with soil warming the evaporation rate was most likely increased, but the soil was still moist due to continuous precipitation events during spring 2016. In accordance, during spring there was no water scarcity and barley growth seemed to be stimulated due to soil warming.

However, in contrast to our hypothesis we also found a more rapid plant development during later growth stages and at maturity. These findings are supported by a relatively wet summer with high precipitation amounts in the end of May and during June 2016. Thus, different than expected, the soil was relatively wet after spring and an additional evaporation due to soil warming was most likely not strong enough to limit plant growth. In addition, also the WUE_B tended to increase in plots with soil warming. This can be an indication that barley did not experience water stress after spring under elevated soil temperature despite less total water use per plant due to higher evaporation compared to control group.

4.4.2 Leaf gas exchange

Photosynthesis is known as one of the most vulnerable physiological processes to warming in crops. In the present study, an increase in soil temperature showed no significant impact at stem elongation on A_{net} , g_s , or E , suggesting (1) crop photosynthesis reacts differently to changes in air and soil temperature, which has also been reported for grain yield in many studies (Stone et al. 1999; Gavito et al. 2001; Patil et al. 2010) and (2) the soil temperature increase in this study may have been too small to prompt physiological changes. This is in agreement with findings

of Gavito et al. (2001) in winter wheat, who increased soil temperature by 5°C in chambers with a separate control of air and soil temperature, and who detected no effect of elevated soil temperature on A_{net} . However, the effect of a reduction in precipitation amount on g_s and E seemed to depend on soil temperature: g_s and E increased under ambient and decreased under elevated soil temperature if precipitation amount was reduced. These findings support observations from other studies, demonstrating that multiple factor experiments can identify new and more adverse effects of climate change on plant physiology than single factor experiments can do. This also confirmed our hypothesis that the simultaneous occurrence of multiple climate factors results in an additive negative effect on barley ecophysiology.

In addition, longer dry periods as consequence of reduced precipitation frequency decreased g_s at stem elongation, but E and A_{net} were unaffected. In former studies with barley grown in growth chambers, g_s decreased as a consequence of reduced water amount (González et al. 2010; Schmid et al. 2016). A simultaneous occurrence of reduced precipitation amount and soil warming decreased WUE_p , which is in agreement with the observed reactions of drought- and temperature-stressed wheat plants grown in a greenhouse (Shah and Paulsen 2003).

At flowering, the youngest fully developed plant leaves were still green, with SPAD values above 30 during gas exchange measurements. Values of A_{net} , g_s , and E were lower than at stem elongation but without significant effects due to the three climate factors. Similarly, Jensen et al. (1996a) measured gas exchange in oilseed rape at T_{leaf} of 23 – 30 °C and also detected higher g_s (and A_{net}) values before flowering and a decrease in those parameters during and after flowering. It has also been reported for wheat that A_{net} and g_s in 16 genotypes were on average higher during stem elongation than during flowering (Reynolds et al. 2000).

Overall, we hypothesized a greater impact of elevated soil temperature than of changes in precipitation patterns on photosynthesis, given that photosynthesis is a temperature sensitive process. This hypothesis could not be confirmed, since reduced precipitation frequency surrounding the stem elongation period significantly affected gas exchange by reducing g_s . Soil warming had a significant impact on g_s and E only when it simultaneously occurred in combination with reduced precipitation amount. This was perhaps due to the fact that the effects of air and soil temperature on crop photosynthesis are different: an increase in air temperature directly affects leaf gas exchange, whereas elevated soil temperature indirectly affects crop physiology through effects on root growth and plant water and nutrient availability.

4.4.3 Biomass production

At the early developmental stage (stem elongation), barley leaves senesced more under ambient than elevated soil temperature conditions. Other studies have reported that biomass of senescent leaves typically increased under warming, as this is a symptom of heat stress (Bita and Gerats 2013), but we could not detect this in the present study. In contrast to the study of Patil et al. (2010) of winter wheat, aboveground biomass of barley did not increase under soil warming; it remained unaffected. But we observed an increase in root biomass under soil warming, possibly because root growth is stimulated up to a species-specific temperature optimum (Gray and Brady, 2016). This could have led to an increase in the nutritive value of barley or have mitigated negative impacts of water loss through transpiration under elevated soil temperature on barley biomass production.

At flowering, plants grown under soil warming conditions produced greater biomass of green leaves and stems, leading to an increase in aboveground biomass. Gavito et al. (2001) also observed an increase in leaf and stem biomass under elevated soil temperature in climate chamber grown winter wheat which was harvested one week after the beginning of flowering. An increase in aboveground biomass of winter wheat was also reported by Patil et al. (2010) under elevated soil temperature. In our experiment, a combination of warming and reduced precipitation frequency increased aboveground biomass and biomass of ears. This is similar to a study of winter wheat in which a higher total aboveground biomass also occurred at flowering under the condition of soil warming and reduced precipitation frequency interaction (Patil et al. 2010). No effect of soil warming on root biomass was observed in our study at this stage. This was likely due to the completion of root growth before the beginning of flowering, providing the plant with more energy for the grain filling period. This may also explain our result that at maturity no soil warming effect was detected in root biomass.

At maturity, elevated soil temperature increased biomass of stems. Similarly, the aboveground biomass of field-grown maize in a cool-temperate climate increased under elevated soil temperature (Stone et al. 1999). However, a former study at the same experimental area (HoCC experiment) in 2010 found no significant effect of elevated soil temperature on aboveground biomass of spring barley (*H. vulgare* cv. Quench) (Högy et al. 2013).

We hypothesized that we would detect a decrease in biomass production through reduced precipitation amount and frequency during summer months. We cannot confirm this by the results of the present study, as changes in precipitation patterns from the beginning of June to

beginning of August did not appear to adversely affect biomass production of spring barley. Some possible explanations for this result are: (1) barley is relatively tolerant to water scarcity and therefore the simulated precipitation changes were too moderate to harm biomass production, or (2) the relatively wet conditions during June 2016 mitigated negative effects of reduced precipitation amount and frequency on biomass production.

4.4.4 Yield components

The final harvest of barley grown under elevated soil temperature occurred one week before plants under ambient soil temperature, however, no yield losses were detected in all treatments. Under elevated soil temperature, barley experienced a two-day longer grain filling period compared to plants under ambient soil temperature, but this period occurred earlier than that of those grown under ambient conditions. Under soil warming plants needed in total 26 days from full flowering (DAS 77) to full ripeness (DAS 103), whereas control plants needed 24 days. A lengthening in grain filling duration under soil warming is in contrast to a previous study with wheat and elevated air temperature, where a decrease in the length of the grain filling period was observed (Sofield et al. 1977; Chowdhury and Wardlaw 1978). In our study, these additional two days could explain the observed tendency toward grain yield increase under soil warming, meaning plants had more time to acquire carbohydrates for grain growth. These results are hard to compare with literature values, since only a few experiments with cereals grown under manipulated moderate soil warming in an arable field have been conducted to date. However, in a similar study at the same experimental site, no effect on spring barley grain yield was observed by Högy et al. (2013) and also in a lysimeter experiment with winter wheat, soil warming of 5°C showed no effect on grain yield (Patil et al., (2010). In studies in which air temperature was increased, inducing heat stress on cereals, reductions in grain yield under warming have been reported (Savin et al. 1997; Alemayehu et al. 2014; Ingvordsen et al. 2018), whereas in our experiment a soil temperature increase of about 2°C did not exceed the temperature optimum of barley and therefore grain yield was resilient and tended to increase. This may have been due to (1) sufficient water availability during the growing period as a consequence of moderate and relatively high ambient precipitation amounts during spring and June 2016, or to (2) stimulated root growth at stem elongation through an enhanced supply of water and nutrients.

Contrary to our hypothesis, changes in precipitation patterns had no effect on grain yield, possibly due to an increase in WUE_Y under reduced precipitation amount. Because the barley cultivar RGT Planet is preferred as malting barley, their grain size is important for brewers and

malt houses because it positively correlates with the amount of malt extract that can be obtained (Schwarz and Li 2011). In our study, soil warming led to the formation of more ears per plant, but had only a minor impact on grain size: only the second biggest GSC, 2.8 – 2.5 mm, decreased under elevated soil temperature, as Högy et al. (2013) found in the same experiment with spring barley in 2010. Mostly reduced precipitation amount affected grain size due to shifting grain size patterns: barley produced more grains >2.8 mm and fewer grains smaller than 2.8 mm. Therefore, grains >2.5 mm, which are relevant for the brewing industry, tended to increase under reduced precipitation amount. We also found that a reduction in precipitation frequency, unlike our observations under reduced precipitation amount, induced barley to produce more grains of smaller size, 2.5 – 2.2 mm, which was reflected by a reduction in TGW.

Overall, spring barley was shown to be tolerant of an absolute water shortage resulting from lower precipitation amount: grain yield was shown to be stable due to a shift in grain size patterns by the formation of more bigger grains and fewer smaller grains. In addition, the increase in biomass of roots at stem elongation under soil warming possibly mitigated negative impacts of reduced water availability on aboveground biomass and grain yield.

4.5 Conclusions

The results of the present study indicate that with constant soil warming and a reduction in precipitation amount and frequency during summer months, barley produces stable biomass and yield with changes in ear number, grain size classes and biomass of roots. Overall, barley development and biomass production were more strongly affected by elevation in soil temperature than by altered precipitation patterns. Knowledge about climate change effects on barley production can help farmers to select appropriate crop varieties under future climate conditions. However, a further interaction with an increasing atmospheric CO₂ concentration have to be investigated as well under field conditions, since effects of elevated soil temperature and altered precipitation patterns on barley ecophysiology, growth and yield can be different under atmospheric CO₂ enrichment.

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Author contributions

CP, PH and EK designed the study. IS, CP, SM, EK, PH provided critical feedback of the manuscript. Root biomass data originate from RK. ID performed the experiments and wrote the manuscript. All authors read and approved the final manuscript.

Conflict of interest

The authors declare that they have no conflict of interest.

5 Do soil warming and changes in precipitation patterns affect seed yield and seed quality of field-grown winter oilseed rape?

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Ireen Drebenstedt^{1,*}, Leonie Hart^{2,3}, Christian Poll⁴, Sven Marhan⁴, Ellen Kandeler⁴,
Christoph Böttcher⁵, Torsten Meiners⁵, Jens Hartung⁶ and Petra Högy¹

¹*Institute of Landscape and Plant Ecology, University of Hohenheim, Ökologiezentrum 2,
August-von-Hartmann Str. 3, D-70599 Stuttgart, Germany*

²*Institute of Agricultural Sciences in the Tropics, University of Hohenheim, Fruwirthstr. 31,
D-70599 Stuttgart, Germany*

³*Competitiveness and System Evaluation, Agroscope, Tänikon 1, CH-8356 Ettenhausen,
Switzerland*

⁴*Institute of Soil Science and Land Evaluation, University of Hohenheim, Emil-Wolff-Str. 27,
D-70599 Stuttgart, Germany*

⁵*Institute for Ecological Chemistry, Julius Kühn-Institute, Königin-Luise-Str. 19, D-14195
Berlin, Germany*

⁶*Institute of Crop Science, University of Hohenheim, Fruwirthstr. 23, D-70599 Stuttgart,
Germany*

*Corresponding author

Abstract

Increasing air and soil temperatures and changes in precipitation patterns as consequences of climate change will affect crop production in agricultural ecosystems. The combined effects of soil warming and altered precipitation on the productivity and product quality of oil crops are not yet well studied. Winter oilseed rape (OSR) (*Brassica napus* L., cv. Mercedes) was field-grown under elevated soil temperature (+2.5 °C), reduced precipitation amount (−25%), reduced precipitation frequency (−50%) both separately and in combination in order to investigate effects on crop development, seed yield, and seed quality. Soil warming accelerated crop development during early plant growth and during spring. At maturity, however, plants in all treatments were similar in quantitative (aboveground biomass, seed yield) and qualitative (protein and oil content, amino acids, fatty acids) parameters. We observed the long-term effects of the precipitation manipulation on leaf size, leaf senescence and biomass allocation. Seed yield was not affected by the altered climatic factors, perhaps due to adaptation of soil microorganisms to permanent soil warming and to relatively wet conditions during the seed-filling period. Overall, OSR performed well under moderate changes in soil temperature and precipitation patterns; thus, we observed stable seed yield without negative impacts on nutritive seed quality.

Keywords: climate change; altered precipitation patterns; soil warming; seed yield; seed quality; oilseed rape

5.1 Introduction

Climate change poses a challenge for crop production in the twenty-first century. Changes in temperature and precipitation patterns can result in either positive or negative effects on crop development and physiological plant processes, with impacts on crop yield and the chemical composition of seeds (DaMatta et al. 2010). Under global warming, the mean air temperature in Germany is predicted to increase by 1.2–5.3 °C by 2100 compared to 1971–2000 (DWD 2017). Elevated air temperature will lead to an increase in soil temperature (Zheng et al. 1993), affecting soil moisture content and crop development in agroecosystems (Patil et al. 2010). In temperate climates it has been observed that the shoot growth of crops is limited by low soil temperature during early development stages (Bowen 1991). Accordingly, even a small increase in soil temperature can accelerate crop growth and promote the development of crops (Gavito et al. 2001; Patil et al. 2010). Also, the uptake of water and nutrients from the soil and most likely the overall development of crops is accelerated due to elevated soil temperature (Bowen 1991).

Besides changes in soil temperature, amount and frequency of precipitation are also expected to be altered within coming decades in Germany (DWD 2017). Thus, water availability in agricultural areas will be affected, reflected by changes in soil moisture content. In agroecosystems, a reduction in water availability of crops can negatively affect harvestable yield (Istanbulluoglu et al. 2010; Bodner et al. 2015), resulting in a major limitation to food production (Barnabás et al. 2008).

In Central Europe, *Brassica napus* L. is used both as an oil and a protein crop, with the winter variety most frequently cultivated due to its higher yields in comparison to summer varieties (Walker and Booth 2001). Winter oilseed rape (OSR) is predominantly cultivated in France and Germany (Weymann et al. 2015) and is a preferred pre-crop for cereals due to its deep rooting system, which improves soil structure. The yield of oilseed rape is known to be highly variable, depending on temperature and precipitation conditions during the growing period. For instance, yield losses of winter oilseed rape appear to be correlated with rising mean temperatures (Brown et al. 2019). Also, a deficiency in water availability occurring in the period from flowering to the end of seed set was found to reduce the seed yield of oilseed rape (Champolivier and Merrien 1996). Thus, yield stability of oilseed rape will be a major challenge under changing climatic conditions in coming decades (Brown et al. 2019).

The seed quality of OSR is represented by the concentrations of oil, protein, and glucosinolates, all of which are expected to change under elevated temperature and water shortage (DaMatta et al. 2010). In pot experiments with OSR, water stress induced by withholding of irrigation at different crop developmental stages (Bouchereau et al. 1996) and reduction in water amount (Champolivier and Merrien 1996) increased the concentration of protein in seeds, but decreased oil concentration. Similar results were observed under elevated air temperature in soybean (Piper and Boote 1999; Pipolo et al. 2004). Under a water shortage, OSR accumulated secondary metabolites such as glucosinolates in mature seeds (Jensen et al. 1996b). The utilization of OSR meal, which is a byproduct of oil extraction and a protein source for livestock, can be compromised by high glucosinolate content, due to the potential of glucosinolates to harm animals, e.g., leading to a reduction in milk production or to impaired reproductive activity (Alexander et al. 2008)

Crops in agricultural landscapes will likely be exposed to several climate change factors at the same time. Hence, we investigated in the Hohenheim Climate Change (HoCC) experiment the interactive effects of soil warming and altered precipitation patterns on the yield and yield quality traits of OSR. In this temperate agroecosystem, an increase in soil temperature by 2.5 °C and, during summer months, a reduction in precipitation amount (−25%) and frequency (−50%) were simulated. Crop development was measured over the entire growing period. Seed yield data from three specific time points (stem elongation, flowering, maturity) and quality components of mature seeds were analyzed. The hypotheses were as follows: (i) soil warming will accelerate crop development only during spring but not afterwards; (ii) a reduction in precipitation amount during summer months will increase the protein concentration of the seeds, but reduce oil concentration; (iii) a reduction in precipitation frequency during summer will increase periods of reduced water availability, which will reduce the seed-filling period and thus decrease seed yield; and (iv) a simultaneous occurrence of soil warming, reduced precipitation amount, and precipitation frequency will have additive negative effects on seed yield.

5.2 Materials and methods

5.2.1 Site description

This study was conducted at the HoCC experimental research station (University of Hohenheim, Stuttgart, Germany), which was established in 2008 in order to investigate climate change effects on agroecosystems. The HoCC experiment is located at the Heidfeldhof research

station (48°43' N, 9°13' E, 401 m a.s.l.). From 1961 to 1990, annual mean air temperature was 8.7 °C and annual precipitation was 679 mm (Deutscher Wetterdienst). In 2016 and 2017, when OSR was grown at the experimental site, the mean annual air temperature was 10.1 °C and 10.2 °C and annual precipitation was 595.4 mm and 830.9 mm, respectively (weather station “Hohenheim”, (Agricultural Technology Centre (LTZ) Augustenberg 2019)) (Figure 5. 1). The soil at the field site is a loess-derived stagnic Luvisol of a pH 6.9, organic carbon content of 12.1 g kg⁻¹, and soil texture of 9.4% sand, 68.1% silt, and 22.6% clay (Poll et al. 2013).

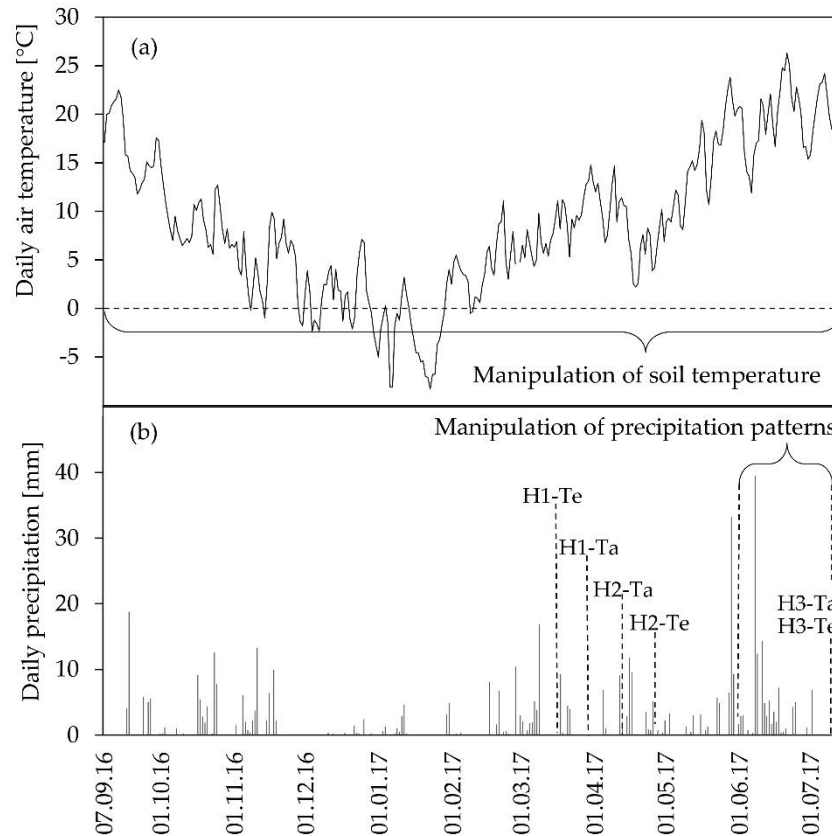


Figure 5. 1: (a) Average daily air temperature at 2 m height and (b) daily precipitation at the experimental site during the growing season of winter oilseed rape (OSR) from 7 September 2016 to 11 July 2017. In total, three harvests were made: harvest 1 (H1) at stem elongation, harvest 2 (H2) at full flowering and harvest 3 (H3) at maturity. At the first and second harvests, plants grown under elevated soil temperature (Te) were harvested about two weeks earlier than plants grown under ambient soil temperature (Ta). Harvest dates: H1-Te, 15 March 2017; H1-Ta, 27 March 2017; H2-Te, 10 April 2017; H2-Ta, 24 April 2017. At maturity, plants grown under Ta and Te were similarly developed and harvested on the same day: H3-Te and H3-Ta, 11 July 2017. Data are from the weather station “Hohenheim” of the Agricultural Technology Centre (LTZ) Augustenberg, Germany. The manipulation of the precipitation patterns (–25% precipitation amount, –50% precipitation frequency) started on 6 June 2017, when plants had developed to between the middle of fruit development (development stage DC 76) and the beginning of ripening (DC 80) stage (Meier 2001). OSR was watered until plant maturity (H3).

5.2.2 Experimental setup

Since 2008, soil temperature (T) as well as precipitation amount (A) and frequency (F) have been manipulated within the HoCC experiment, based on climate change predictions until 2100 for southwest Germany (Umweltbundesamt 2006). The treatments are replicated in four blocks in a split-plot design. Treatments are specified in Table 5. 1. Each block is separated into two mainplots each with two 1 m × 4 m plots. Each plot is further split into four 1 m x 1 m subplots. Soil warming is simulated in one of the mainplots per block using heating cables located on the soil surface (RS 611-7918, RS Components GmbH). Soil temperature is elevated by 2.5 °C (Te) at 4 cm depth. Dummy cables on ambient temperature mainplots (Ta) are installed to account for side effects of the presence of heating cables, such as retention of water from precipitation. In one plot within each mainplot, a roof is used to manipulate precipitation (Folitec UV 5 foil, folitec Agrarfolien-Vertriebs GmbH, Westerburg, Germany). To manipulate subplots individually, each subplot is surrounded by a polyvinyl chloride (PVC) barrier to prevent lateral water movement. The 32 roof-covered subplots are watered manually with rainwater collected in rain barrels. During the period of the precipitation treatment, from June to August, the ambient precipitation amount (Aa) is reduced by 25% (Ar). Precipitation frequency simulates longer dry periods by reduction in the number of rainy days by 50% (Fr) as compared to ambient precipitation frequency (Fa) (i.e., the cumulative precipitation of two ambient rain events is delivered as one event). In the study period, alterations in precipitation patterns were simulated during the summer months from 6 June 2017 until plant maturity (11 July 2017). Soil temperature is recorded using temperature probes at 4 cm depth. TDR (time-domain reflectometry) probes (CS630/CS635, Campbell Scientific Ltd., Loughborough, UK) installed at 0–15 cm depth are used to measure soil moisture content. The combination of ambient soil temperature, ambient precipitation amount, and ambient precipitation frequency simulated under the roofs was taken as control conditions. The subplots are covered by roofs (roofed: R1), except that two subplots in each block have no roofs (roof-control: R0) in order to identify possible roof effects. Precipitation patterns are not manipulated in the roof-control plots. Additional information about the experimental setup can be found in Poll et al. (Poll et al. 2013).

Table 5. 1: Treatment combinations of the experiment: ambient (Ta) or elevated (Te) soil temperature in combination with the following precipitation patterns: ambient (Aa) or reduced (Ar) precipitation amount and ambient (Fa) or reduced (Fr) precipitation frequency. In treatments 1–8 oilseed rape (OSR) was grown under roofs (R1) to enable the manipulation of precipitation patterns. OSR in treatments 9 and 10 was not covered by roofs (R0), to check for a roofing effect. Abbreviations: AMB = ambient; ELE = elevated; RED = reduced; temp. = temperature; prec. = precipitation.

Treatment Number	Roof	Treatment Description	Treatment Short Form
1	Yes	AMB soil temp. × AMB prec. amount × AMB prec. frequency	TaAaFa
2	Yes	AMB soil temp. × AMB prec. amount × RED prec. frequency	TaAaFr
3	Yes	AMB soil temp. × RED prec. amount × AMB prec. frequency	TaArFa
4	Yes	AMB soil temp. × RED prec. amount × RED prec. frequency	TaArFr
5	Yes	ELE soil temp. × AMB prec. amount × AMB prec. frequency	TeAaFa
6	Yes	ELE soil temp. × AMB prec. amount × RED prec. frequency	TeAaFr
7	Yes	ELE soil temp. × RED prec. amount × AMB prec. frequency	TeArFa
8	Yes	ELE soil temp. × RED prec. amount × RED prec. frequency	TaArFr
9	No	AMB soil temp. × AMB prec. amount × AMB prec. frequency	TaAaFa
10	No	ELE soil temp. × AMB prec. amount × AMB prec. frequency	TeAaFa

5.2.3 Plant cultivation, crop development measurement, biomass harvests and seed quality analyses

Winter OSR (*Brassica napus* cv. Mercedes) was cultivated from 7 September 2016 to 11 July 2017. In total, 85 plants m⁻² were sown and adjusted to a final density of 60 plants m⁻². Pre-crop was spring barley (*Hordeum vulgare* cv. RGT Planet). Plants were fertilized with 50, 60 and 40 kg N ha⁻¹ calcium ammonium saltpeter on 28 September 2016, 7 March 2017, and 14 March 2017, respectively. OSR was weeded regularly to keep weed pressure low, snail granule was scattered when plants were small and insecticides were applied for chemical disease control (Supplement, Table S5. 1). In the center of each subplot, five plants were labelled and used to measure crop development parameters, which were measured weekly by using the BBCH decimal code (DC) (Meier 2001).

Three harvests were performed at fixed crop developmental stages: (1) at the beginning of stem elongation (DC 31), (2) at full flowering (DC 65), and (3) at maturity (DC 99) (Table 5. 2). At harvests 1 and 2, two representative plants per subplot were cut 1 cm above the soil surface and separated into green and senescent leaves, stems and flowers. Fresh and dry weights were

determined. Green leaf area was determined with a leaf area meter (LI3000, Li-Cor, Lincoln, NE, USA) and specific leaf area (SLA) was calculated (green leaf area divided by green leaf dry weight). Leaves and stems were dried at 60 °C to constant weight, while flowers were dried at 30 °C. At harvest 3, all plants in a center 0.5 m × 0.5 m of each subplot were cut and separated into straw (stems and leaves) and pods. Pods were manually threshed in order to separate seeds and seed yield was measured. For the calculation of the harvest index (HI), seed yield per plant was divided by total aboveground biomass per plant (straw and seeds). Thousand seed weight was determined using a seed counter (Condator “E”, Pfeuffer, Germany) (Högy et al. 2013). Before quality assessment, seeds were milled into fine powder with a Brabender Quadrumat Junior mill. Total protein concentration was determined by the Kjeldahl method (European Commission Regulation (EC) No 152/2009 III C 2009) and total oil concentration was analyzed by method H of the same regulation (European Commission Regulation (EC) No 152/2009 III H 2009). The composition of amino acids was analyzed using the European Commission Regulation (EC) No 152/2009 III F (European Commission Regulation (EC) No 152/2009 III F 2009), whereas tryptophan was analyzed separately according to European Commission Regulation (EC) No 152/2009 III G (2009). For analysis of the fatty acids, seed samples were treated with trimethylsulphonium hydroxide (TMSH) to extant fatty acid methyl esters (FAMES). FAMES were analyzed using capillary gas chromatography and flame ionization detection (GC-FID) (DIN EN ISO 12966-1:2015-03; Högy et al. 2010). To analyze the glucosinolate concentrations, homogenized seed material was extracted and desulfated following the method described in DIN EN ISO 9167-1: 2013-12 [DIN EN ISO 9167-1: 2013-12]. The identity of individual desulfoglucosinolates was determined by high-performance liquid chromatography/electrospray-ionisation quadrupole time-of-flight tandem mass spectrometry (HPLC/ESI-QTOFMS) in positive ion mode. For this purpose, an Infinity 1290 Series UHPLC system interfaced via a dual Agilent jet stream electrospray ion source to an iFunnel Q-TOF mass spectrometer (G6550A, Agilent Technologies, Santa Clara, CA, USA) was used. For further instrument settings see Böttcher et al. (2017).

Table 5. 2: Harvest dates of OSR depended on the development stage of plants. Harvest 1 and harvest 2 of OSR plants grown under ambient soil temperature were performed about two weeks later than under elevated soil temperature. OSR was sown on 7 September 2016. The development stage is expressed as BBCH decimal code (DC) (Meier 2001).

Harvests	Development Stage	Harvest Date Ambient Soil Temperature	Harvest Date Elevated Soil Temperature
Harvest 1	DC 31, stem elongation	27 March 2017	15 March 2017
Harvest 2	DC 65, full flowering	24 April 2017	10 April 2017
Harvest 3	DC 99, maturity	11 July 2017	11 July 2017

5.2.4 Statistical analyses

Treatment effects on canopy height, aboveground biomass, specific leaf area, seed yield and seed quality of OSR were analyzed with linear mixed-effects models fitted by maximum likelihood (lme function of the R 3.4.2 nlme package). The model was as follows:

$$y_{hijklmn} = \mu + b_h + m_{hi} + p_{hij} + \tau_k + o_l + \vartheta_{ml} + \theta_{nl} + (\tau o)_{kl} + (\tau \vartheta)_{kml} + (\tau \theta)_{knl} + (\vartheta \theta)_{nml} + (\tau \vartheta \theta)_{kmnl} + e_{hijklmn}$$

where b_h , m_{hi} and p_{hij} are the random effect of the h^{th} block, i^{th} mainplot within h^{th} block and the j^{th} plot nested within the hi^{th} mainplot, respectively. τ_k , o_l , ϑ_{ml} , and θ_{nl} are the main effects of the k^{th} temperature, l^{th} roof, m^{th} precipitation frequency and n^{th} precipitation amount, respectively. Note that the latter two effects were applied under a roof only, thus the main effects are confounded with the corresponding interaction effects with roof and only one of both terms can be estimated. To account for this, we included arbitrarily the main effects into the model, but added the index l for all these effects. Interaction effects were denoted by parenthesis around the corresponding main effects. $e_{hijklmn}$ is the subplot error of observation $y_{hijklmn}$. It was assumed, that all random effects (block, mainplot, plot and subplot error) were independent and identically distributed with homogeneous variances σ_b^2 , σ_m^2 , σ_p^2 , and σ_e^2 , respectively. For the biomass of flowers we assumed a variance proportional to the number of flowers using the inverse of this number as weight. Residuals were graphically checked for homogeneous error variance and normal distribution using residuals-versus-fitted value plots and QQ (quantil-quantil) plots (Kozak and Piepho 2018). In case of extreme residuals, the corresponding data points were checked for plausibility. In total, two outliers were eliminated due to a lack of plausibility. After finding significant differences via global F test at $\alpha = 0.05$, Fishers least significant difference (LSD) test was used to find differences between means (again with

$\alpha = 0.05$) and was performed with R package “agricolae”. Ratios of means were calculated for presentation purpose only. Non-significant effects and differences with p -values between 0.05 and 0.1 were denoted as trend or tendency.

5.3 Results

5.3.1 Environmental conditions and biomass harvests

Soil temperature increased by on average 1.7 ± 0.4 °C and 2.2 ± 0.4 °C in roofed and roof-control plots, respectively, during the entire growing period (7 September 2016 to 11 July 2017; Table 5. 2). Precipitation patterns were manipulated from the beginning of summer to maturity (6 June 2017 to 11 July 2017). During that time period, the number of rainy days was ten days in control subplots. Consequently, in subplots where the precipitation frequency was reduced by 50%, the number of rainy days was five days. The ambient precipitation amount was 106 mm (control) in comparison to 79.8 mm in the reduced treatment (reduction of precipitation amount by 25%). Soil moisture in the 0–15 cm depth was not affected due to the water shortage or soil warming in comparison to control treatments.

5.3.2 Crop development

Canopy height increased due to soil warming from the end of March 2017 (21 March 2017) to the beginning of May 2017 (2 May 2017) (Figure 5. 2, Figure 5. 3). Thus, the soil warming effect started when the inflorescence of OSR emerged (DC 50) and lasted until full flowering, at which time 50% of the flowers on the main racemes were open (DC 65). During this time period, the largest differences in canopy height were observed in April 2017: plants in the soil warming treatment were up to 40 cm higher than under ambient soil temperature. After flowering, plants under ambient soil temperature approximated the height of plants under elevated soil temperature.

Crop development of OSR was at first accelerated due to soil warming at the end of October 2016, when plants were quite young. Thus, plants under elevated soil temperature entered the development stage DC 15 (five leaves unfolded) seven days earlier than plants under ambient soil temperature ($p = 0.05$). Later, soil warming accelerated OSR development during spring: the stages indicating the end of flowering (DC 69, $p = 0.017$) and the beginning of fruit development (DC 71, $p = 0.013$) were entered seven and five days earlier than under ambient soil temperature. However, these differences in crop development between plants under

ambient and elevated soil temperature disappeared by maturity (DC 99) and the final harvest (harvest 3) of all treatments took place on the same day (Table 5. 2).

When the precipitation manipulation was started on 6 June 2017, crop development was between the stages of the middle of fruit development (DC 76) and beginning of ripening (DC 80). Overall, changes in precipitation patterns did not alter the phenology of the crop in all treatments. However, plants which grew under reduced precipitation amount and frequency tended to enter the end of the flowering stage (DC 69) on average one day after plants under ambient precipitation amount and frequency ($p = 0.069$).

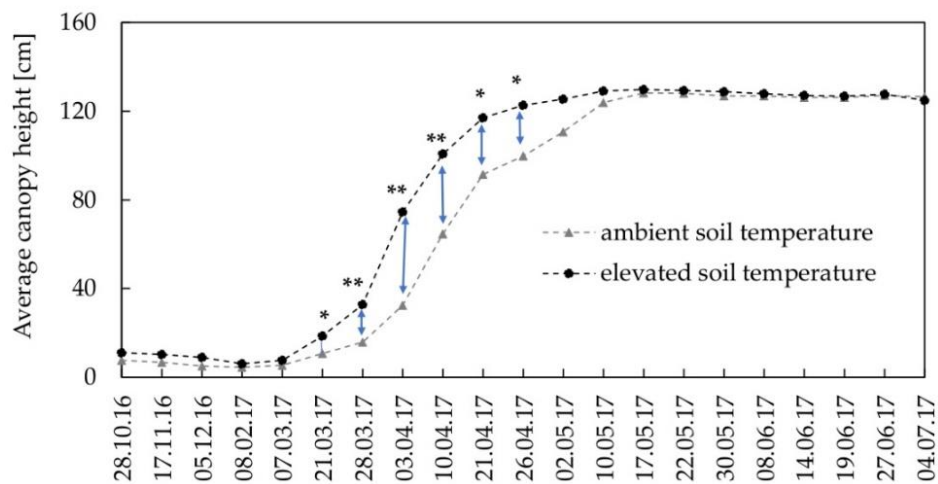


Figure 5. 2: Canopy height measured between 28 October 2016 and 4 July 2017 at ambient and elevated soil temperature. Asterisks indicate significant differences (** $p \leq 0.01$, * $p \leq 0.05$) between plants grown under ambient and elevated soil temperatures; $n = 4$. Differences in average canopy height between treatments are labeled with blue arrows.

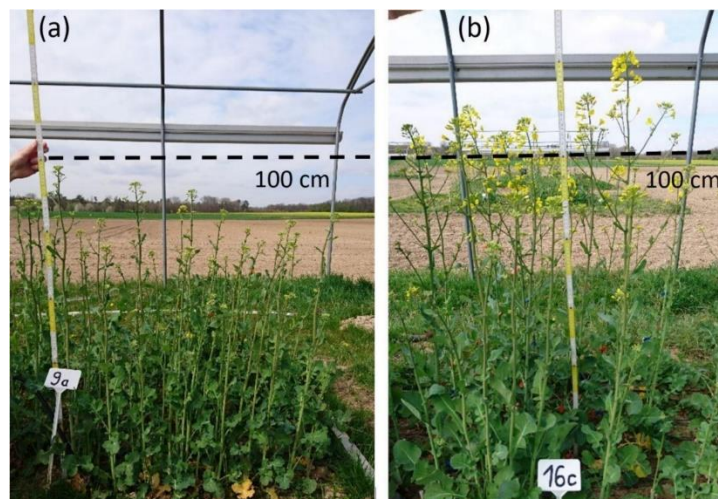


Figure 5. 3: Differences in canopy height and crop development of OSR (oilseed rape) on 11 April 2017. Plants were grown either (a) under ambient soil temperature or (b) under soil warming. In (a) under control conditions, canopy height was up to 100 cm and plants were in development stage DC 59–DC 60. OSR under soil warming (b) was up to 120 cm high and in development stage DC 60–DC 65. The BBCH decimal code (DC) is used to define the development stages of the plants (Meier 2001).

5.3.3 Biomass allocation and seed yield

At stem elongation, aboveground biomass of OSR was not affected due to soil warming or changes in precipitation patterns (Figure 5. 4). In contrast, soil warming tended to increase biomass of flowers by 138% ($p = 0.058$). In addition, a reduction in precipitation frequency increased biomass of flowers by 23% under ambient soil temperature, whereas the opposite was observed under elevated soil temperature (-19%) (Supplement, Table S5. 2). When precipitation amount was reduced, biomass of senescent leaves tended to increase by 60% ($p = 0.076$). SLA decreased by 11% if precipitation frequency was decreased under ambient soil temperature (Figure 5. 5). In contrast, a reduction in precipitation frequency increased SLA by 14% under elevated soil temperature.

At flowering, SLA decreased by 5% under reduced precipitation frequency (Figure 5. 5). Moreover, SLA increased by 18% due to a reduction in precipitation amount under ambient soil temperature. A decrease in SLA was observed under reduced precipitation amount in combination with elevated soil temperature (-17%). Roofing decreased SLA by 5% (data not shown).

At maturity, aboveground biomass, straw, and seed yield did not differ between treatments (Figure 5. 4). Nevertheless, TSW increased by 7% under soil warming (Supplement, Table S5. 2). HI was increased under roofs at ambient (7%) and at elevated soil temperature (45%) as compared to non-roof-control plots (data not shown).

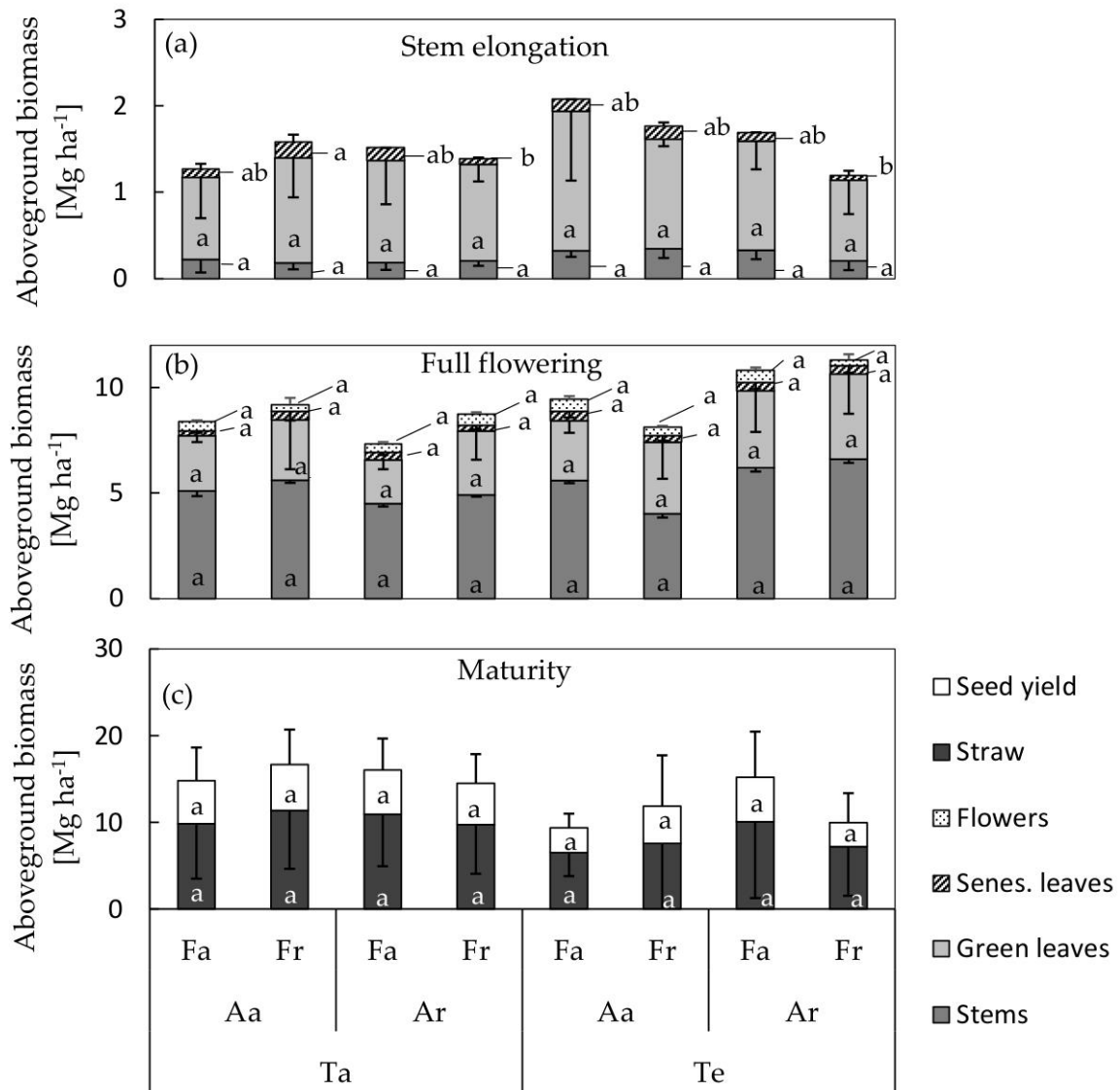


Figure 5. 4: Aboveground biomass of OSR grown under ambient (Ta) or elevated (Te) soil temperature in combination with the following precipitation patterns: ambient (Aa) or reduced (Ar) precipitation amount and ambient (Fa) or reduced (Fr) precipitation frequency. Three harvests were performed: harvest 1 at stem elongation (DC 31) (a), harvest 2 at full flowering (DC 65) (b), and harvest 3 at maturity (DC 99) (c). The aboveground biomass fractions are shown as dry weight. Data are means \pm standard deviations across four replicates ($n = 4$). Means with the same letter indicate a non-significant difference between these means based on Fishers least significant difference (LSD) test. Straw contains stem and senescent leaf biomass. The data originate from OSR covered by roofs. The roofs had no effects on aboveground biomass of the three harvest dates. Abbreviation: Mg = megagram; ha = hectare; senes. = senescent.

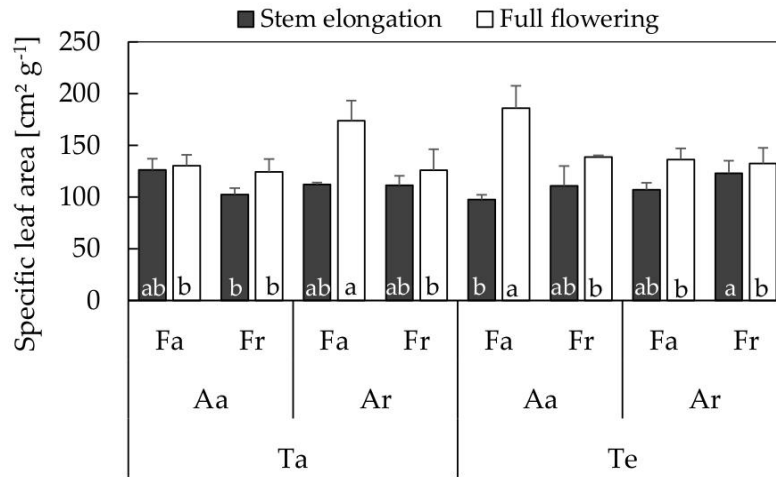


Figure 5. 5: Specific leaf area (SLA) of OSR measured at stem elongation and full flowering. Data are means \pm standard deviations across four replicates ($n = 4$). Means with the same letter indicate a non-significant difference between these means based on Fishers LSD test. The data originate from OSR covered by roofs. Effects of the roofing are mentioned in the text and therefore data of OSR planted under roofs are compared with OSR planted without roofs.

5.3.4 Seed quality

The total protein content in seeds of OSR, as well as the concentrations of total amino acids on a per protein basis, remained unaffected under soil warming or changes in precipitation patterns (Supplement, Table S5. 3). Only the individual concentrations of essential and semi-essential amino acids [% protein] changed slightly under climate change conditions (Table 5. 3): under reduced precipitation amount phenylalanine decreased (-1%), while isoleucine increased by 1% in response to reduced precipitation frequency. Additionally, interaction effects of the climate factors were observed: less precipitation amount at ambient soil temperature increased lysine by 1% . In contrast, lower precipitation amount at elevated soil temperature decreased concentration of lysine (-1%). Individual amino acids essential for children and semi-essential based on protein did not vary under the simulated climatic changes (Supplement, Table S5. 4). Roof effects on amino acid concentration were limited to a reduction of aspartic acid under ambient (-4%) and elevated (-1%) soil temperature (data not shown). The total and individual concentration of amino acids per unit dry weight did not vary between treatments (Supplement, Table S5. 5, Table S5. 6).

The total oil content in mature seeds, as well as the total concentration of fatty acids on a per oil basis, did not vary between all treatments (Supplement, Table S5. 7). Correspondingly, the composition of fatty acids on a per oil basis remained more or less unaffected. However, the concentration of some saturated fatty acids changed in seeds of OSR (Table 5. 3): the concentration of capric acid increased by 40% under ambient soil temperature and reduced

precipitation amount. In contrast, 26% less capric acid was produced under elevated soil temperature and reduced precipitation amount. Moreover, reduced precipitation frequency decreased the lignoceric acid concentration at ambient precipitation amount (−3%) and increased it at reduced precipitation amount (+23%). Similar effects were found for saturated fatty acids on a per dry weight basis (Supplement, Table S5. 8). The concentrations of unsaturated fatty acids, e.g., of oleic acid, linoleic acid and linolenic acid per oil or dry weight basis, remained unaffected in all treatments (Supplement, Table S5. 9). Roofing affected the concentration of essential fatty acids: linoleic acid and linolenic acid decreased by 3% both under ambient and under elevated soil temperatures (data not shown).

Total glucosinolate concentration in OSR seeds was $10.9 \pm 1.2 \mu\text{mol g}^{-1}$ DW (dry weight) in the control treatment (Supplement, Table S5. 10). Soil warming increased the total glucosinolate content by 26% to $13.8 \pm 2.9 \mu\text{mol g}^{-1}$ DW in seeds. Looking at the concentration of individual glucosinolates, soil warming increased progoitrin, gluconapin and gluconapoleiferin by 29%, 24%, and 109%, respectively (Supplement, Table S5. 10). In contrast, a reduction in precipitation frequency decreased Gluconasturtiin by 14%. In roofed OSR, gluconasturtiin concentration was reduced by 9% and 38% under ambient and elevated soil temperatures (data not shown).

Table 5. 3: Overall statistical analyses of impacts of soil warming (T), precipitation amount (A), precipitation frequency (F) as well as their interactions, on amino acid concentration (% protein) and fatty acid concentration (% oil) of mature OSR seeds.¹ Only parameters are presented that yielded significant effects of, or interactions between, treatments.²

Response Variable	T	A	F	T × A	T × F	A × F	T × A × F
Amino acid concentration [% protein]							
Essential [% protein]							
Isoleucine	ns	ns	0.040	0.048	ns	ns	ns
Phenylalanine	ns	0.041	ns	<i>0.086</i>	ns	ns	ns
Lysine	ns	ns	ns	0.015	ns	ns	0.015
Non-essential [% protein]							
Asparagine/aspartic acid	ns	ns	<i>0.077</i>	ns	ns	ns	ns
Glutamine/glutamic acid	<i>0.086</i>	ns	<i>0.070</i>	ns	ns	ns	ns
Proline	ns	<i>0.082</i>	ns	ns	ns	ns	ns
Alanine	ns	ns	ns	ns	<i>0.090</i>	ns	ns
Fatty acids concentration [% oil]							
Saturated fatty acids [% oil]							
Capric acid	ns	ns	ns	0.023	ns	ns	ns
Myristic acid	ns	ns	ns	ns	ns	ns	0.047
Lignoceric acid	ns	ns	ns	ns	ns	0.048	ns

¹ Data were tested by three-way analysis of variance (ANOVA) for main effects or interaction effects of the fixed factors T, A and F across four replicates ($n = 4$). Bold numbers indicate significant main or interaction effects of T, A, F ($p < 0.05$), numbers in italics indicate trend ($0.1 \geq p \geq 0.05$), ns = not significant ($p > 0.05$). Lipid numbers of the fatty acids: capric acid = C10:0; myristic acid = C14:0; lignoceric acid = C24:0. ² Means and standard deviations of all determined amino and fatty acid concentrations are given in the supplement, Table S5. 4 and Table S5. 7.

5.4 Discussion

5.4.1 Crop development and crop yield parameters

Soil warming accelerated OSR development during early crop growth and during spring, which was similar to what we expected. It is known that in temperate climates an elevation in soil temperature can stimulate crop development (Bowen 1991), which has also been shown for winter wheat (Patil et al. 2010). In the present study, OSR grown under elevated soil temperature was taller compared to ambient soil temperature from early growth stages to the beginning of May 2017 (DC 65). Afterwards, the soil warming effect on canopy height vanished, possibly due to a reduction in soil moisture due to higher air temperatures and less precipitation during summer compared to the period of spring. This is similar to an OSR field study in 2014, which was also performed within the HoCC experiment (Bamminger et al. 2016). Accordingly, OSR was taller under soil warming until April and afterwards the huge difference in canopy height diminished until final harvest. Therefore, the effect of soil warming on canopy height appeared to decrease with increasing ambient temperatures in air and soil. In addition, soil warming resulted in a greater impact on smaller than on taller plants.

In our study, no change in total aboveground biomass was observed under soil warming at maturity, which was in agreement with a study using winter wheat (Patil et al. 2010). In contrast, Bamminger et al. (2016) found higher OSR aboveground biomass under soil warming at maturity. Increasing ambient air temperatures result in soil warming, which can alter plant–microbe interactions with impacts on the allocation of nutrients belowground in the rhizosphere (Singh et al. 2019). It is possible that the higher mean air (+1 °C) and soil temperatures (+0.4 °C) in the study of Bamminger et al. (2016) in 2014 compared to 2017 changed the nutrient availability for the plants and therefore promoted plant biomass production.

We observed stable seed yield under soil warming as well as under reduced precipitation amount and frequency. The achieved seed yield of OSR planted under control conditions (ambient soil temperature and precipitation) either under roofs or without roofs was 5.0 Mg ha⁻¹ and 4.3 Mg ha⁻¹, respectively. Hence, seed yield of the control treatment correspond to the average winter OSR seed yield of 3.8 Mg ha⁻¹ in the region Stuttgart in 2017. The average OSR seed yield in Stuttgart was achieved under normal agricultural practice (Statistisches Landesamt Baden-Württemberg 2017).

To date, only a few studies investigating soil warming effects have been conducted on crop yield, e.g., of winter wheat (Gavito et al. 2001; Patil et al. 2010) or maize (Stone et al. 1999) in

temperate climates. However, elevated soil temperature can differ in their impacts on crop yield as compared to elevated air temperature. On the one hand, elevated air temperature can shorten the period of grain filling (Yadav et al. 2019). In low latitudes, elevation of air temperatures during the grain filling period are associated with a decrease in crop yield as a consequence of a reduction in plant photosynthesis, degradation of thylakoid components, and lower carbon exchange rate per unit of leaf area (Hatfield 2019). On the other hand, it has been observed that soil warming can affect the diversity and abundance of soil microorganisms (Aamir et al. 2019). Thus, alterations in plant–microbe interactions can occur due to impacts on the nutrient supply from the microbiome to the crop. Soil warming can stimulate the activity of soil microorganisms for a short time, but the microbial community seems to acclimatize to soil warming after a long exposure time (Kannoja et al. 2019). This corresponds to the observations in the present study. Under permanent soil warming, we have observed stable seed yields of OSR. Thus, our results suggest an adaptation of soil microorganisms to permanent soil warming, assuming fewer alterations in plant–microbe interactions and no or minor impacts on the nutrition supply from the microbiome to the crop.

However, other explanations should also be considered. The detected stable OSR seed yield under soil warming in our study may have been due to sufficient water availability during the seed-filling period from beginning of April 2017 (DC 60) until end of June 2017 (DC 89), which mitigated evaporation consequences resulting from elevated soil temperature. This period included a wet April 2017 and high ambient precipitation amounts at the end of May 2017. Another explanation could be that soil warming by about 2 °C was too low to result in changes in factors such as the activity of soil microorganisms and the distribution of nutrients from the rhizosphere to the crop. In another soil warming experiment, crop yield of winter wheat remained unaffected at 5 °C elevated soil temperature to 100 mm depth (Patil et al. 2010).

In contrast, decreased OSR and cereal yields were observed in several studies with elevated air temperature (Savin et al. 1997; Faraji et al. 2009; Kutcher et al. 2010; Alemayehu et al. 2014; Ingvordsen et al. 2018). Therefore, stable crop yields of OSR observed in our study under soil warming seemed to be a further indication that elevated temperatures in soil or air can result in different impacts on crop yield.

Besides elevated temperature, water scarcity also impacts seed yield. The time in plant life at which water scarcity appears is associated with effects on seed yield: reduced water amount during the periods of seed set or seed-filling can result in a decrease in seed yield (Singer et al. 2016). Furthermore, Champolivier and Merrien (Champolivier and Merrien 1996) observed a

reduction in seed yield in winter OSR after a period of water shortage which persisted from flowering until maturity. Our study did not detect reduced crop yields in OSR grown under reduced precipitation amount, presumably due to relatively wet conditions in the summer of 2017. Moreover, we hypothesized that seed yield of OSR decreases under reduced precipitation frequency. Accordingly, longer drought periods reduced the seed-filling period in OSR, as demonstrated by Hlavinka et al. (2009) and Istandbulluoglu et al. (2010). In contrast, we found stable seed yield in OSR under reduced precipitation frequency and no change in seed-filling period, most likely due to high precipitation amounts during this period. Furthermore, our hypothesis that a simultaneous occurrence of soil warming, reduced precipitation amount, and reduced precipitation frequency have additive negative effects on seed yield of OSR could not be confirmed. This was perhaps due to moderate air temperatures below 30 °C from June to August 2017, resulting in moderate mean soil temperatures (24.6 °C) and sufficient water supply during the growing period. In addition, we observed relatively heavy rainfall events of between 20 and 30 mm at the beginning and end of June 2017. They appeared to mitigate negative effects of evapotranspiration and of a dry period in mid-June 2017 on soil water availability.

The SLA of crops is known to decline under elevated temperatures coupled with water shortage by a decrease in final leaf size (Morison and Lawlor 1999). Similarly, the SLA of OSR in the present study decreased under soil warming in combination with reduced precipitation amount.

Significant main effects and their interactions between amount and frequency of precipitation were detected in biomass allocation before the precipitation manipulation in 2017 began. Thus, biomass of flowers and senescent leaves increased, whereas SLA decreased, most likely as a result of plants producing smaller leaves under conditions of limited water availability. These are long-term effects of the precipitation manipulation, which is conducted every year during summer (always from June until August) in the same way at the same subplots since 2008. With regard to other long-term studies, which have been conducted mainly in grasslands, forests, and shrublands, variability in precipitation patterns over several years can lead to changes in, for example, soil respiration, as a consequence of alterations in soil structure or in the composition of the soil microbial community (Sowerby et al. 2008; Beier et al. 2012). In our study, long-term changes in amount and frequency of precipitation may have resulted in an altered composition of the soil microbial community, which in turn affects availability of nutrients for the crops, and in the end, leaf size, leaf senescence, and biomass allocation of OSR.

5.4.2 Seed quality

Alterations in seed yield, resulting from environmental stresses (e.g., temperature and precipitation patterns) can stimulate changes in the quantity of the seed oil produced (Singer et al. 2016). Since seed yield did not vary under changes in soil temperature and precipitation in the present study, it appears that the total seed oil content remained unaffected in all treatments. By contrast with what is hypothesized, a reduction in precipitation amount neither increased the protein nor decreased the oil concentration, as had been found previously in OSR seeds when water scarcity was applied during the ripening period (Mailer and Pratley 1990; Bouchereau et al. 1996; Champolivier and Merrien 1996). These contrasting results could be due to the fact that the reduced precipitation amount in this study was based on relatively high ambient precipitation amounts during the growing period of OSR. Thus, the simulated decrease in precipitation amount was too small to effect shifts in protein and oil concentrations.

In the present study, the observed changes in the essential amino acids phenylalanine, isoleucine, and lysine, when exposed to altered precipitation patterns alone or in combination with soil warming, seem to be negligible. In a previous study, an increase in those amino acids in leaves of OSR by 10% to more than 300% after two-day and four-day drought events was found (Good and Zaplachinski 1994).

The lipid biosynthesis of oil producing crops can be affected due to global warming, because an elevation in temperature can result in less desirable fatty acid profiles of vegetable oils (Singer et al. 2016). Water availability is a second factor, one which can alter the composition of oilseeds since crops are prone to close their stomata under reduced water supply. This reduces carbon dioxide assimilation as well as sugar uptake by embryos (Singer et al. 2016). Similarly, in the present study, minor changes in the fatty acid composition of OSR seeds were observed. Capric acid concentration decreased under elevated soil temperature combined with reduced precipitation amount and lignoceric acid increased if precipitation amount and precipitation frequency were reduced both. As far as we know, the function of saturated fatty acids in the metabolism of OSR is currently not fully understood. Capric acid, as a medium-chain fatty acid, is a valuable ingredient in OSR seed oil and used as feedstock in the production of biodiesel, cosmetics, lubricants, and surfactants (Dyer et al. 2008). Thus, a decrease in capric acid concentration could be unfavorable for the industrial usage of OSR seeds.

OSR is used for the production of edible oil or as a protein source for livestock so, for quality reasons, the concentrations of glucosinolates in mature seeds is restricted to $18 \mu\text{mol g}^{-1}$ (Jensen et al. 1996b), which was adhered to in all treatments. In this study soil warming increased

glucosinolates in seeds. A positive correlation between increasing temperatures and glucosinolates was also shown in *Brassica oleracea* seeds (Del Carmen Martínez-Ballesta et al. 2013). Since glucosinolates are part of the plant defense reaction in the Brassicales order (Wittstock and Burow 2010), water shortage during late growth stages can increase the glucosinolate concentration of OSR seeds at maturity (Jensen et al. 1996b). In the present study, no effects of reduced amount and frequency of precipitation on the total glucosinolate concentration were observed. Several studies have reported that lower water availability will lead to a reduction in the number of seeds per plant, with glucosinolates distributed to fewer seeds, resulting in increased concentrations of glucosinolates in seeds (De March et al. 1989; Champolivier and Merrien 1996). In the present study, however, a stable seed yield was observed, which constitutes a stable sink capacity for glucosinolates. Most likely for that reason, total glucosinolate concentration did not change under water scarcity. A second explanation for why the precipitation treatments showed no effects on total glucosinolate concentration is that the growing period of OSR was relatively wet in 2017. Thus, the reduction in amount and frequency of precipitation was too mild to significantly increase the production of glucosinolates. Similarly, in a former field study with OSR grown in lysimeters, the glucosinolate concentration in seeds was not affected under mild drought stress conditions during the late developmental stage (pod filling stage) (Jensen et al. 1996b). When determining the environmental effects on the quality of OSR grown across Victoria, Pritchard et al. (2000) reported that the impact of cultivar on the glucosinolate content was greater than environmental impacts such as air temperature and rainfall amount.

5.5 Conclusions

In the present study, the interactive effects of soil warming and altered precipitation patterns on crop performance of winter oilseed rape were analyzed in a field experiment. At final harvest, crop development was similar in all treatments and no differences in aboveground biomass and seed yield were detected, suggesting that no adaptation to the date of sowing or harvest would be necessary under future climate change. Presumably, stable seed yield under soil warming was caused due to (1) an adaptation of soil microorganisms to permanent soil warming, due to (2) a sufficient water availability during the seed-filling period, which mitigated evaporation caused by elevated soil temperature, or (3) the soil warming by about 2 °C was too low to change the activity of the soil microorganisms and the distribution of nutrients from the rhizosphere to the crop. Furthermore, it is possible that seed yield did not change under reduced precipitation amount or frequency due to wet conditions during summer 2017. This underlines

the need for long-term studies including a range of weather conditions during the vegetation period of oilseed rape. The mild environmental changes as simulated in the HoCC experiment, i.e., without pronounced periods of water shortage or drought, slightly changed the concentration of some amino acids, fatty acids, and glucosinolates. Therefore, irrigation of oilseed rape seems unnecessary to fulfil quality standards for seed marketing. It may be assumed that effects on seed yield and on the chemical composition of seeds will be more pronounced under a climate scenario with stronger increases in soil temperature and longer drought periods during summer months.

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5.6 Supplementary material

Table S5. 1: Agricultural practices during the growing period.^a

DAS	Date	Measures
0	07.09.2016	Sowing of winter oilseed rape (cultivar „Mercedes“ from Rapool), each subplot contains 5 rows with 12-15 seeds each, Scattering snail granules
12	19.09.2016	Weeding, Spraying against flea beetle using Syngentas `Karate Zeon`, agent Lambda-Cyhalothrin
14	21.09.2016	Weeding and scattering snail granules
16	23.09.2016	Weeding, Spraying against flea beetle using Syngentas `Karate Zeon`, agent Lambda-Cyhalothrin
21	28.09.2016	Fertilisation of 50 kg N ha ⁻¹ (about 5 g N m ⁻²) as calcium ammonium nitrate, Weeding and scattering snail granules
29	06.10.2016	Thinning or partial seeding on subplots with less than 40 plants
40	17.10.2016	Weeding
42	19.10.2016	Scattering snail granules
44	21.10.2016	Scattering mice poison
51	28.10.2016	Scattering snail granules
57 58	03.11.2016, 04.11.2016	Weeding
75	21.11.2016	Weeding
155	09.02.2017	Weeding
181	07.03.2017	Fertilisation of 60 kg N ha ⁻¹ as calcium ammonium nitrate
188	14.03.2017	Fertilisation of 40 kg N ha ⁻¹ as calcium ammonium nitrate, Spraying 150 g ha ⁻¹ Trafo from Syngenta against stem weevil, repeated one week later
197	23.03.2017	Weeding
205 210	31.03.2017, 05.04.2017	Spraying against pollen beetle, 200 g ha ⁻¹ `Mospilan` in 300 L ha ⁻¹ water, agent Acetamiprid (against imagines and larvea, time of treatment: crop development stage DC 51 (beginning of bud formation) to 69 (end of blooming)
237	02.05.2017	Weeding
244	09.05.2017	Weeding
246	11.05.2017	Weeding
268	02.06.2017	Taking up nets against bird damage
272	06.06.2017	Taking up roofs (start of precipitation manipulation)
301	05.07.2017	Weeding
307	11.07.2017	Final harvest

^aAbbreviation: DAS=days after sowing.

Table S5. 2: Biomass of flowers at stem elongation, as well as thousand seed weight (TSW) and Harvest Index (HI) at maturity.^a

	T_a		T_e					
	A_a	A_r	A_a	A_r	A_a	A_r	A_a	A_r
	F_a	F_r	F_a	F_r	F_a	F_r	F_a	F_r
<i>Stem elongation (Harvest 1)</i>								
Flowers [g DW plant ⁻¹]	0.006 (0.004)	0.008 (0.005)	0.007 (0.003)	0.008 (0.003)	0.014 (0.005)	0.014 (0.012)	0.012 (0.001)	0.007 (0.005)
<i>Maturity (Harvest 3)</i>								
TSW [g 1000 seeds ⁻¹]	4.11 (0.14)	3.79 (0.15)	3.99 (0.48)	3.83 (0.20)	4.38 (0.18)	4.23 (0.39)	4.19 (0.14)	4.19 (0.42)
HI.	0.31 (0.01)	0.30 (0.15)	0.29 (0.02)	0.30 (0.01)	0.31 (0.01)	0.29 (0.05)	0.28 (0.04)	0.26 (0.01)

^aValues are means of four replicates, numbers in parentheses give the standard deviation. Ta: ambient soil temperature, Te: elevated soil temperature, Aa: ambient precipitation amount, Ar: reduced precipitation amount, Fa: ambient precipitation frequency, Fr: reduced precipitation frequency.

Table S5. 3: Total protein content (% dry weight), total amino acid concentration (% protein) and total concentration of amino acid types (% protein) in mature OSR seeds.^a

	T_a		T_e					
	A_a	A_r	A_a	A_r	A_a	A_r	A_a	A_r
	F_a	F_r	F_a	F_r	F_a	F_r	F_a	F_r
Total protein content [% DW]	13.325 (0.866)	12.875 (0.287)	13.400 (1.225)	12.775 (0.395)	13.767 (0.815)	13.233 (0.751)	13.567 (0.569)	13.867 (0.351)
Total amino acids [% protein]	92.331 (1.515)	92.213 (2.297)	92.159 (0.947)	93.359 (1.279)	93.031 (3.129)	94.949 (0.482)	94.091 (1.339)	91.985 (1.774)
<i>Total concentration of amino acids [% protein]</i>								
Essential a.a.	35.099 (0.711)	34.724 (1.517)	35.091 (0.570)	35.589 (0.733)	34.016 (2.656)	35.901 (0.321)	35.251 (0.386)	34.241 (1.055)
Essential for children a.a.	4.559 (1.129)	5.104 (0.176)	5.058 (0.091)	5.069 (0.040)	5.134 (0.028)	5.140 (0.080)	5.133 (0.088)	4.999 (0.110)
Sem-essential a.a.	8.463 (0.090)	8.408 (0.077)	8.358 (0.055)	8.474 (0.073)	8.450 (0.219)	8.634 (0.153)	8.571 (0.141)	8.457 (0.277)
Non-essential a.a.	44.211 (0.690)	43.976 (0.902)	43.652 (0.497)	44.226 (0.622)	45.432 (0.423)	45.274 (0.419)	45.136 (0.869)	44.288 (1.101)

^aValues are means of four replicates, numbers in parentheses give the standard deviation. Ta: ambient soil temperature, Te: elevated soil temperature, Aa: ambient precipitation amount, Ar: reduced precipitation amount, Fa: ambient precipitation frequency, Fr: reduced precipitation frequency. Abbreviation: a.a.=amino acid.

Table S5. 4: Individual amino acid concentration (% protein) in mature seeds.^a

	Ta		Te					
	Aa	Ar	Aa	Ar				
	Fa	Fr	Fa	Fr	Fa	Fr	Fa	Fr
<i>Essential [% protein]</i>								
Valine	5.357 (0.216)	5.517 (0.134)	5.393 (0.150)	5.542 (0.202)	5.441 (0.182)	5.539 (0.088)	5.406 (0.101)	5.289 (0.041)
Isoleucine	4.094 (0.090)	4.118 (0.111)	4.090 (0.071)	4.209 (0.115)	4.063 (0.138)	4.206 (0.058)	4.053 (0.073)	4.038 (0.043)
Leucine	7.020 (0.088)	6.992 (0.105)	7.059 (0.243)	7.086 (0.153)	7.138 (0.124)	7.180 (0.032)	7.073 (0.119)	7.066 (0.090)
Phe	3.997 (0.051)	4.002 (0.116)	3.960 (0.092)	3.993 (0.098)	4.082 (0.095)	4.107 (0.049)	4.028 (0.058)	3.965 (0.098)
Lysine	6.551 (0.087)	6.564 (0.095)	6.556 (0.138)	6.655 (0.050)	6.561 (0.059)	6.702 (0.052)	6.585 (0.50)	6.490 (0.054)
Methionine	2.008 (0.029)	2.016 (0.042)	2.014 (0.026)	2.035 (0.036)	2.033 (0.060)	2.064 (0.061)	2.039 (0.023)	2.007 (0.010)
Threonine	4.902 (0.172)	4.856 (0.093)	4.862 (0.178)	4.894 (0.100)	4.873 (0.160)	4.945 (0.208)	4.913 (0.024)	4.830 (0.188)
Tryptophan	1.170 (0.142)	1.164 (0.109)	1.157 (0.113)	1.174 (0.039)	1.185 (0.057)	1.158 (0.048)	1.153 (0.073)	1.225 (0.041)
<i>Essential for children [% protein]</i>								
Tyrosine	2.816 (0.080)	2.815 (0.055)	2.803 (0.102)	2.800 (0.060)	2.812 (0.082)	2.876 (0.140)	2.824 (0.070)	2.800 (0.060)
Cysteine	2.324 (0.064)	2.289 (0.135)	2.255 (0.065)	2.270 (0.032)	2.322 (0.055)	2.263 (0.080)	2.309 (0.017)	2.188 (0.066)
<i>Semi-essential [% protein]</i>								
Histidine	2.739 (0.019)	2.738 (0.023)	2.722 (0.038)	2.760 (0.014)	2.760 (0.064)	2.820 (0.032)	2.775 (0.037)	2.739 (0.075)
Arginine	5.724 (0.074)	5.670 (0.069)	5.636 (0.051)	5.715 (0.061)	5.690 (0.157)	5.718 (0.205)	5.796 (0.104)	5.718 (0.205)
<i>Non-essential [% protein]</i>								
Asx	7.455 (0.141)	7.555 (0.118)	7.454 (0.172)	7.596 (0.200)	7.552 (0.081)	7.713 (0.079)	7.517 (0.180)	7.499 (0.185)
Serine	4.504 (0.197)	4.447 (0.033)	4.392 (0.128)	4.443 (0.021)	4.536 (0.221)	4.517 (0.219)	4.568 (0.073)	4.469 (0.230)
Glx	16.15 (0.51)	15.81 (0.32)	15.90 (0.34)	15.97 (0.24)	16.74 (0.39)	16.40 (0.37)	16.53 (0.40)	16.24 (0.47)
Proline	6.152 (0.429)	6.121 (0.352)	6.020 (0.237)	6.101 (0.270)	6.506 (0.233)	6.393 (0.155)	6.356 (0.290)	6.151 (0.206)
Glycine	5.350 (0.065)	5.361 (0.134)	5.307 (0.143)	5.423 (0.159)	5.423 (0.044)	5.490 (0.046)	5.454 (0.037)	5.336 (0.070)
Alanine	4.601 (0.100)	4.681 (0.115)	4.579 (0.122)	4.698 (0.031)	4.673 (0.040)	4.759 (0.035)	4.716 (0.067)	4.791 (0.058) ^b

^aValues are means of four replicates, numbers in parentheses give the standard deviation. Ta: ambient soil temperature, Te: elevated soil temperature, Aa: ambient precipitation amount, Ar: reduced precipitation amount, Fa: ambient precipitation frequency, Fr: reduced precipitation frequency. Abbreviations: asx=asparagine/aspartic acid; glx=glutamine/glutamic acid; phe=phenylalanine.

Table S5. 5: Total amino acid concentration (% dry weight) and total concentration of amino acid types (% dry weight) in mature OSR seeds.^a

	Ta		Te					
	Aa	Ar	Aa	Ar	Aa	Ar	Aa	Ar
	Fa	Fr	Fa	Fr	Fa	Fr	Fa	Fr
Total amino acids [% DW]	12.368 (0.803)	11.940 (0.108)	12.138 (0.638)	11.925 (0.335)	12.737 (0.399)	12.567 (0.760)	12.770 (0.717)	12.847 (0.552)
<i>Total concentration of amino acids [% DW]</i>								
Essential a.a.	3.738 (0.159)	3.640 (0.045)	3.548 (0.136)	3.640 (0.080)	3.627 (0.225)	3.800 (0.197)	3.823 (0.180)	3.857 (0.131)
Essential for children a.a.	0.673 (0.057)	0.658 (0.036)	0.678 (0.059)	0.697 (0.040)	0.707 (0.038)	0.680 (0.036)	0.697 (0.040)	0.693 (0.029)
Sem-essential a.a.	1.128 (0.069)	1.083 (0.021)	1.120 (0.102)	1.083 (0.031)	1.163 (0.078)	1.143 (0.085)	1.163 (0.068)	1.173 (0.067)
Non-essential a.a.	5.895 (0.450)	5.660 (0.022)	5.848 (0.507)	5.650 (0.195)	6.257 (0.429)	5.993 (0.396)	6.127 (0.376)	6.143 (0.291)

^aValues are means of four replicates, numbers in parentheses give the standard deviation. Ta: ambient soil temperature, Te: elevated soil temperature, Aa: ambient precipitation amount, Ar: reduced precipitation amount, Fa: ambient precipitation frequency, Fr: reduced precipitation frequency. Abbreviations: DW=dry weight; a.a.=amino acid.

Table S5. 6: Individual amino acid concentration (% dry weight) in mature seeds.^a

	Ta		Te					
	Aa	Ar	Aa	Ar				
	Fa	Fr	Fa	Fr	Fa	Fr	Fa	Fr
<i>Essential [% protein]</i>								
Valine	0.713 (0.022)	0.710 (0.008)	0.690 (0.017)	0.708 (0.017)	0.710 (0.000)	0.725 (0.044)	0.733 (0.031)	0.733 (0.015)
Isoleucine	0.545 (0.025)	0.530 (0.008)	0.548 (0.042)	0.538 (0.012)	0.560 (0.052)	0.557 (0.028)	0.557 (0.030)	0.560 (0.020)
Leucine	0.935 (0.052)	0.900 (0.008)	0.945 (0.076)	0.905 (0.024)	0.983 (0.076)	0.950 (0.050)	0.960 (0.056)	0.980 (0.036)
Phe	0.533 (0.034)	0.515 (0.006)	0.530 (0.040)	0.510 (0.014)	0.577 (0.042)	0.543 (0.025)	0.547 (0.031)	0.550 (0.026)
Lysine	0.873 (0.048)	0.845 (0.013)	0.878 (0.065)	0.850 (0.020)	0.903 (0.058)	0.887 (0.035)	0.893 (0.035)	0.900 (0.030)
Methionine	0.268 (0.015)	0.265 (0.017)	0.270 (0.027)	0.260 (0.012)	0.280 (0.020)	0.273 (0.021)	0.277 (0.012)	0.273 (0.006)
Threonine	0.663 (0.031)	0.627 (0.006)	0.663 (0.032)	0.623 (0.012)	0.670 (0.017)	0.653 (0.015)	0.667 (0.031)	0.670 (0.036)
Tryptophan	0.155 (0.010)	0.150 (0.016)	0.155 (0.021)	0.150 (0.008)	0.163 (0.015)	0.153 (0.012)	0.157 (0.015)	0.170 (0.010)
<i>Essential for children [% protein]</i>								
Tyrosine	0.375 (0.021)	0.363 (0.013)	0.375 (0.026)	0.358 (0.005)	0.387 (0.012)	0.380 (0.010)	0.383 (0.025)	0.390 (0.026)
Cysteine	0.298 (0.041)	0.295 (0.024)	0.303 (0.034)	0.290 (0.012)	0.320 (0.027)	0.300 (0.030)	0.313 (0.015)	0.303 (0.006)
<i>Semi-essential [% protein]</i>								
Histidine	0.365 (0.024)	0.353 (0.005)	0.365 (0.037)	0.353 (0.010)	0.380 (0.026)	0.373 (0.025)	0.377 (0.021)	0.380 (0.020)
Arginine	0.763 (0.046)	0.730 (0.016)	0.755 (0.066)	0.730 (0.022)	0.783 (0.051)	0.770 (0.060)	0.787 (0.047)	0.793 (0.047)
<i>Non-essential [% protein]</i>								
Asx	0.993 (0.047)	0.973 (0.015)	0.998 (0.072)	0.970 (0.021)	1.040 (0.069)	1.020 (0.028)	1.020 (0.056)	1.040 (0.044)
Serine	0.600 (0.044)	0.573 (0.013)	0.588 (0.039)	0.568 (0.015)	0.605 (0.012)	0.597 (0.006)	0.620 (0.036)	0.620 (0.044)
Glx	2.155 (0.209)	2.035 (0.013)	2.133 (0.225)	2.040 (0.086)	2.307 (0.189)	2.173 (0.200)	2.243 (0.145)	2.253 (0.119)
Proline	0.823 (0.113)	0.788 (0.034)	0.808 (0.090)	0.780 (0.054)	0.897 (0.081)	0.847 (0.067)	0.863 (0.076)	0.853 (0.046)
Glycine	0.713 (0.039)	0.690 (0.008)	0.710 (0.048)	0.693 (0.017)	0.747 (0.046)	0.727 (0.035)	0.740 (0.036)	0.740 (0.026)
Alanine	0.613 (0.026)	0.603 (0.005)	0.613 (0.039)	0.600 (0.016)	0.643 (0.040)	0.630 (0.040)	0.640 (0.036)	0.637 (0.021)

^a Values are means of four replicates, numbers in parentheses give the standard deviation. Ta: ambient soil temperature, Te: elevated soil temperature, Aa: ambient precipitation amount, Ar: reduced precipitation amount, Fa: ambient precipitation frequency, Fr: reduced precipitation frequency. Abbreviations: asx=asparagine/aspartic acid; glx=glutamine/glutamic acid; phe=phenylalanine.

Table S5. 7: Total oil content (% dry weight), total fatty acid concentration (% oil) and the concentration of individual saturated fatty acids (% oil) in mature OSR seeds.^a

	Ta		Te					
	Aa	Ar	Aa	Ar				
	Fa	Fr	Fa	Fr	Fa	Fr	Fa	Fr
Total oil content [% DW]	52.850 (0.810)	52.675 (0.846)	52.250 (1.179)	53.125 (0.645)	52.100 (1.039)	52.133 (0.896)	51.767 (0.493)	51.133 (0.945)
Total fatty acids [% oil]	100.01 (0.01)	100.01 (0.01)	100.00 (0.02)	100.00 (0.00)	100.00 (0.01)	100.01 (0.01)	100.00 (0.01)	99.99 (0.02)
<i>Saturated fatty acids [% oil]</i>								
Capric a.	0.010 (0.000)	0.010 (0.000)	0.013 (0.005)	0.015 (0.006)	0.010 (0.000)	0.017 (0.006)	0.010 (0.000)	0.010 (0.000)
Lauric a.	0.013 (0.006)	0.010 (0.000)	0.015 (0.006)	0.018 (0.010)	0.013 (0.006)	0.017 (0.012)	0.020 (0.010)	0.010 (0.000)
Myristic a.	0.053 (0.005)	0.053 (0.005)	0.050 (0.008)	0.055 (0.006)	0.053 (0.006)	0.060 (0.010)	0.053 (0.006)	0.047 (0.006)
Pentadecyclic a.	0.025 (0.006)	0.028 (0.005)	0.025 (0.006)	0.023 (0.005)	0.030 (0.000)	0.027 (0.006)	0.030 (0.000)	0.027 (0.006)
Palmitic a.	4.370 (0.463)	4.623 (0.169)	4.423 (0.473)	4.817 (0.133)	4.727 (0.250)	4.503 (0.445)	4.420 (0.544)	4.510 (0.433)
Margaric a.	0.045 (0.010)	0.043 (0.005)	0.048 (0.010)	0.045 (0.010)	0.047 (0.006)	0.043 (0.006)	0.050 (0.010)	0.047 (0.006)
Stearic a.	2.085 (0.053)	2.115 (0.119)	2.020 (0.226)	2.153 (0.125)	2.160 (0.101)	2.047 (0.185)	1.873 (0.097)	2.023 (0.212)
Arachidic a.	0.583 (0.031)	0.570 (0.022)	0.580 (0.008)	0.570 (0.020)	0.577 (0.021)	0.570 (0.022)	0.590 (0.040)	0.610 (0.000)
Behenic a.	0.273 (0.013)	0.263 (0.006)	0.275 (0.017)	0.275 (0.017)	0.280 (0.026)	0.263 (0.006)	0.287 (0.006)	0.287 (0.006)
Lignoceric a.	0.118 (0.010)	0.108 (0.010)	0.100 (0.014)	0.108 (0.019)	0.103 (0.012)	0.108 (0.010)	0.100 (0.014)	0.130 (0.014)

^aValues are means of four replicates, numbers in parentheses give the standard deviation. Ta: ambient soil temperature, Te: elevated soil temperature, Aa: ambient precipitation amount, Ar: reduced precipitation amount, Fa: ambient precipitation frequency, Fr: reduced precipitation frequency. Abbreviations: DW=dry weight; a.=acid. Lipid numbers of the fatty acids: capric acid=C10:0; lauric acid=C12:0; myristic acid=C14:0; pentadecyclic acid=C15:0; palmitic acid=C16:0; margaric acid=C17:0; stearic acid=C18:0; arachidic acid=C20:0; behenic acid=C22:0; lignoceric acid=C24:0.

Table S5. 8: Total and saturated fatty acid concentration (% dry weight) in mature OSR seeds.^a

	Ta		Te					
	Aa	Ar	Aa	Ar				
	Fa	Fr	Fa	Fr	Fa	Fr	Fa	Fr
Total fatty acids	52.844	52.628	52.127	52.701	52.098	52.100	51.758	51.127
[% DW]	(0.825)	(0.774)	(1.414)	(1.234)	(1.033)	(0.866)	(0.480)	(0.948)
<i>Saturated fatty acids [% DW]</i>								
Capric a.	0.005	0.005	0.007	0.008	0.004	0.009	0.004	0.004
	(0.000)	(0.000)	(0.003)	(0.003)	(0.003)	(0.003)	(0.003)	(0.000)
Lauric a.	0.005	0.005	0.008	0.009	0.007	0.009	0.010	0.005
	(0.004)	(0.000)	(0.003)	(0.005)	(0.004)	(0.006)	(0.005)	(0.000)
Myristic a.	0.028	0.028	0.026	0.029	0.028	0.031	0.028	0.024
	(0.003)	(0.003)	(0.005)	(0.003)	(0.003)	(0.006)	(0.003)	(0.003)
Pentade-cyclic a.	0.013	0.015	0.013	0.012	0.016	0.014	0.016	0.014
	(0.003)	(0.003)	(0.003)	(0.003)	(0.000)	(0.003)	(0.000)	(0.003)
Palmitic a.	2.311	2.435	2.314	1.924	2.463	2.349	2.290	2.307
	(0.269)	(0.112)	(0.283)	(1.284)	(0.139)	(0.250)	(0.299)	(0.237)
Margaric a.	0.024	0.022	0.025	0.024	0.024	0.023	0.026	0.024
	(0.006)	(0.003)	(0.005)	(0.005)	(0.003)	(0.003)	(0.005)	(0.003)
Stearic a.	1.102	1.114	1.057	1.143	1.126	1.068	0.969	1.034
	(0.040)	(0.056)	(0.136)	(0.053)	(0.071)	(0.112)	(0.041)	(0.103)
Arachidic a.	0.308	0.300	0.303	0.303	0.300	0.308	0.305	0.312
	(0.019)	(0.009)	(0.009)	(0.010)	(0.014)	(0.010)	(0.021)	(0.006)
Behenic a.	0.144	0.103	0.144	0.146	0.146	0.095	0.148	0.147
	(0.007)	(0.069)	(0.010)	(0.009)	(0.016)	(0.083)	(0.003)	(0.005)
Lignoceric a.	0.062	0.057	0.052	0.057	0.054	0.056	0.040	0.067
	(0.028)	(0.004)	(0.006)	(0.010)	(0.006)	(0.004)	(0.034)	(0.009)

^aValues are means of four replicates, numbers in parentheses give the standard deviation. Ta: ambient soil temperature, Te: elevated soil temperature, Aa: ambient precipitation amount, Ar: reduced precipitation amount, Fa: ambient precipitation frequency, Fr: reduced precipitation frequency. Abbreviations: DW=dry weight; a.=acid. Lipid numbers of the fatty acids: capric acid=C10:0; lauric acid=C12:0; myristic acid=C14:0; pentadecyclic acid=C15:0; palmitic acid=C16:0; margaric acid=C17:0; stearic acid=C18:0; arachidic acid=C20:0; behenic acid=C22:0; lignoceric acid=C24:0.

Table S5. 9: Concentration of the unsaturated fatty acids: oleic acid, linoleic acid and linolenic acid (in % oil and in % dry weight) in mature OSR seeds.^a

	T_a		T_e					
	A_a	A_r	A_a	A_r	A_a	A_r	A_a	A_r
	F_a	F_r	F_a	F_r	F_a	F_r	F_a	F_r
<i>Unsaturated fatty acids [% oil]</i>								
Oleic a.	65.933 (0.671)	65.550 (0.436)	65.673 (0.243)	65.788 (0.465)	65.407 (0.621)	65.873 (0.244)	65.943 (0.398)	65.887 (0.0757)
Linoleic a.	17.545 (0.081)	17.755 (0.185)	17.915 (0.468)	17.663 (0.301)	17.650 (0.599)	17.690 (0.478)	17.720 (0.330)	17.570 (0.321)
Linolenic a.	7.960 (0.256)	7.615 (0.168)	7.613 (0.282)	7.648 (0.258)	7.710 (0.159)	7.557 (0.241)	7.680 (0.184)	7.633 (0.270)
<i>Unsaturated fatty acids [% DW]</i>								
Oleic a.	34.843 (0.419)	34.526 (0.366)	34.316 (0.884)	34.950 (0.551)	34.081 (0.999)	34.343 (0.684)	34.136 (0.345)	33.690 (0.646)
Linoleic a.	9.273 (0.165)	9.354 (0.241)	9.357 (0.087)	9.382 (0.108)	9.192 (0.126)	9.220 (0.166)	9.173 (0.163)	8.983 (0.135)
Linolenic a.	4.065 (0.161)	4.012 (0.151)	3.976 (0.093)	4.062 (0.130)	4.016 (0.069)	3.939 (0.113)	3.975 (0.075)	3.904 (0.169)

^aValues are means of four replicates, numbers in parentheses give the standard deviation. Ta: ambient soil temperature, Te: elevated soil temperature, Aa: ambient precipitation amount, Ar: reduced precipitation amount, Fa: ambient precipitation frequency, Fr: reduced precipitation frequency. Abbreviations: DW=dry weight; a.=acid. Lipid numbers of the fatty acids: oleic acid=C18:1n9c; linoleic acid=C18:2n6c; linolenic acid=C18:3n3.

Table S5. 10: Concentration of total and individual glucosinolates in mature OSR seeds.^a

	T_a		T_e		T_a		T_e	
	A_a	A_r	A_a	A_r	A_a	A_r	A_a	A_r
	F_a	F_r	F_a	F_r	F_a	F_r	F_a	F_r
Total glucosinolates	10.904 (1.212)	10.188 (0.679)	11.323 (2.475)	10.798 (0.965)	13.770 (2.924)	12.114 (3.421)	11.674 (1.952)	13.013 (2.447)
<i>[μmol g⁻¹ DW]</i>								
<i>Individual glucosinolates [μmol g⁻¹ DW]</i>								
Gluconasturtiin	0.069 (0.006)	0.060 (0.005)	0.080 (0.014)	0.075 (0.009)	0.059 (0.014)	0.044 (0.020)	0.049 (0.026)	0.064 (0.012)
Glucobrerooin	0.038 (0.009)	0.037 (0.005)	0.048 (0.010)	0.043 (0.007)	0.036 (0.010)	0.030 (0.009)	0.030 (0.009)	0.038 (0.012)
Glucorucin	0.081 (0.024)	0.080 (0.026)	0.078 (0.035)	0.076 (0.029)	0.101 (0.011)	0.099 (0.002)	0.075 (0.014)	0.105 (0.009)
Progoitrin	3.534 (0.280)	3.154 (0.269)	3.748 (1.029)	3.456 (0.278)	4.567 (1.184)	3.973 (1.409)	4.002 (1.138)	4.422 (1.298)
Epiprogoitrin	0.071 (0.005)	0.064 (0.005)	0.076 (0.019)	0.070 (0.006)	0.082 (0.018)	0.074 (0.020)	0.078 (0.018)	0.083 (0.020)
Gluconapoleiferin	0.301 (0.124)	0.316 (0.093)	0.354 (0.109)	0.337 (0.127)	0.630 (0.294)	0.565 (0.331)	0.435 (0.222)	0.578 (0.238)
Glucolysin	0.137 (0.046)	0.119 (0.014)	0.148 (0.093)	0.123 (0.017)	0.135 (0.046)	0.136 (0.072)	0.104 (0.037)	0.142 (0.045)
Gluconapin	2.103 (0.202)	1.841 (0.104)	2.103 (0.665)	2.037 (0.348)	2.616 (0.683)	2.116 (0.593)	2.116 (0.347)	2.479 (0.589)
4-Hydroxygluco-brassicin	3.569 (0.432)	3.575 (0.109)	3.682 (0.281)	3.604 (0.117)	3.631 (0.243)	3.386 (0.250)	3.752 (0.308)	3.703 (0.376)
Glucobrassicin	0.701 (0.290)	0.641 (0.176)	0.659 (0.228)	0.701 (0.222)	1.456 (0.744)	1.411 (1.184)	0.736 (0.467)	1.023 (0.527)
Glucobrassicin	0.101 (0.029)	0.098 (0.035)	0.099 (0.033)	0.082 (0.029)	0.150 (0.041)	0.081 (0.003)	0.128 (0.037)	0.115 (0.014)
4-Methoxygluco-brassicin	0.015 (0.007)	0.011 (0.010)	0.011 (0.010)	0.011 (0.009)	(/)	(/)	(/)	0.018 (0.005)
1-Methoxygluco-Brassicin	0.136 (0.033)	0.145 (0.037)	0.130 (0.017)	0.134 (0.042)	0.151 (0.052)	0.136 (0.015)	0.112 (0.070)	0.121 (0.014)

^aValues are means of four replicates, numbers in parentheses give the standard deviation. The “/” indicates that no standard deviation is calculated because only one value is available after outlier elimination (Grubb’s Test). Ta: ambient soil temperature, Te: elevated soil temperature, Aa: ambient precipitation amount, Ar: reduced precipitation amount, Fa: ambient precipitation frequency, Fr: reduced precipitation frequency. Abbreviation: DW=dry weight.

6 Annual cumulative ambient precipitation determines the effects of climate change on biomass and yield of three important field crops

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Ireen Drebenstedt^{1,*}, Sven Marhan², Christian Poll², Ellen Kandeler², Petra Högy¹

¹*Institute of Landscape and Plant Ecology (320), Plant Ecology Section, University of Hohenheim, Otilie-Zeller-Weg 2, 70599 Stuttgart, Germany*

²*Institute of Soil Science and Land Evaluation (310), Soil Biology Section, University of Hohenheim, Emil-Wolff-Str. 27, 70599 Stuttgart, Germany*

*Corresponding author

Abstract

Climate change is affecting agricultural crop production, but there is little information to date from climate change experiments on agricultural ecosystems over the long-term. Data from a ten-year experimental arable field using several climate change factors and their interactions were analyzed with respect to their impacts on crop biomass and harvestable yield production. From 2009-2018, a crop rotation of wheat, barley, and oilseed rape was exposed to increased soil temperature (+2.5°C), reduced summer precipitation amount (-25%), and frequency (- 50%) in a multifactorial design. Depending on the growing period, aboveground biomass and crop yield of spring wheat, winter wheat, and spring barley were either increased or unaffected under soil warming. In moist years with high cumulative ambient precipitation, cereal productivity was enhanced due to soil warming, whereas no effect was visible in dry years. Experimental reductions in summer precipitation amount had only minor effects on aboveground biomass and yield of wheat, barley, or oilseed rape, possibly due to an increase in those crops' water use efficiency under water scarcity. However, a reduction in summer precipitation frequency had no effects on aboveground biomass and yield of the selected crops. The results illustrate that effects of climate change on plant development and yield also depend on the immediate weather conditions during the growing period. This underscores the need for long-term climate change experiments under field conditions where, in addition to manipulated experimental treatments, annual variations in precipitation and temperature can be studied.

Keywords: Climate change; crop production; yield; cereals; oilseed rape

6.1 Introduction

Consequences of climate change are increasing air temperatures and alterations in precipitation patterns, with impacts on agricultural crop production (DaMatta et al. 2010). Global warming is predicted to increase the mean air temperature to 2100 in Germany by 1.2–5.3°C compared to 1971–2000 (DWD 2017), resulting as well in elevated soil temperatures (Zheng et al. 1993). Projecting the effects of elevated soil temperature on crop biomass production and harvestable yield is more complex than predicting effects of elevated air temperatures, because soil temperature is additionally affected by soil moisture, soil texture, vegetation, and season (Gray und Brady 2016). In addition to increases in air and soil temperatures, precipitation events will also change in the future, including an increase in droughts.

In temperate climates, low soil temperatures are a limiting factor for shoot growth of crops in early stages of development (Bowen 1991). Accordingly, even a small increase in soil temperature can accelerate crop growth and promote development of crops (Gavito et al. 2001; Patil et al. 2010). Elevated soil temperature can also stimulate root growth, e.g., of winter wheat and oilseed rape (Gavito et al. 2001; Moorby and Nye 1984) and accelerated uptake of water and nutrients from the soil in temperate climates (Bowen 1991). Moreover, elevated temperatures have been shown to increase evaporation from soils (Luo et al. 2001), with direct negative effects on soil water content and indirect effects on soil respiration, net nitrogen mineralization and plant productivity (Weltzin et al. 2003; Shaver et al. 2000). Besides changes in soil water content, soil warming can alter plant–microbe interactions, with impacts on the availability and allocation of nutrients in the rhizosphere. In addition, soil warming was shown to increase the relative abundance of soil-borne potential fungal plant pathogens (Delgado-Baquerizo et al. 2020) and is expected to alter host-pathogen interactions by increasing pathogen reproduction, and promote plant diseases by changing host modulation (e.g. tissue size) (Singh et al. 2019). This soil warming induced changes at both plant and soil levels can also influence crop production. In southwest Germany wheat, barley, and oilseed rape are often grown in crop rotation as three important field crops; used as food or feed, for malting properties or as bioenergy crop for the production of biodiesel. For example, previous studies under soil warming of +5.0°C found that winter wheat grown in chambers or in lysimeters had increased aboveground biomass and root growth in their early growth stages (Gavito et al. 2001), whereas at maturity aboveground biomass and grain yield was not affected (Patil et al. 2010). Maintaining yield stability of winter oilseed rape will be a major challenge under changing climatic conditions in the next decades, because the seed yield of oilseed rape depends on

temperature conditions during the growing period and decreasing yields have been observed in the field under rising mean temperatures (Brown et al. 2019). In contrast, under controlled growing conditions in an unheated greenhouse, soil warming of +4.0°C accelerated development and growth of winter oilseed rape, which was most notable during flowering (Siebold and Tiedemann 2012). Similar to the findings on winter wheat and winter oilseed rape, barley growth accelerated under controlled conditions in growth chambers by application of +6.5°C soil warming (Power et al. 1967). Effects of soil warming on barley grain yield are not yet clear, however, although previous studies under elevated air temperatures with +3.0-5.0°C or max. 40°C for 6 hours day⁻¹ have been shown to reduce yield (Savin et al. 1997; Alemayehu et al. 2014; Ingvordsen et al. 2018).

Most experiments focusing on soil warming effects have been made under controlled conditions, but responses of plants grown under field conditions can be different, highlighting the need for field experiments under more realistic conditions, including annual fluctuations in weather conditions.

Besides changes in temperature, climate models predict a decrease in precipitation during summer in Central and Northern Europe (IPCC 2021a). In Germany, average precipitation during summer months is expected to decrease by up to 9% from 2071-2100 compared to the long-term period 1971-2000 (DWD 2017). Reduction in water availability can delay plant development and decrease plant growth and harvestable yields by limiting plant organ growth and final size (Blum 1996). For example, decreased precipitation amount resulted in reductions of grain yield in winter wheat (Zhao et al. 2020). Less water availability decreased the grain filling period of barley and reduced its grain weight and size (Sánchez-Díaz et al. 2002; González et al. 2007; Samarah et al. 2009). The seed yield of winter oilseed rape also declined under water shortage that occurred from flowering to the end of seed set (Champolivier and Merrien 1996). Effects of water reduction on plant morphology also depend on whether a spring or winter crop was investigated, because their development differs at specific time points. Hence, the responses of spring and winter crops to water shortage might differ.

Global warming and reductions in precipitation amount or frequency often occur simultaneously; multi-factor experiments under realistic field conditions are therefore necessary to predict their interactive effects on crop performance. One major issue in studying climate change effects on crop growth is the annual variability in weather conditions, e.g., with hot, dry summers or cool, wet ones. Thus, yearly weather conditions must be considered in evaluating climate change effects on aboveground biomass and yield. We aimed to answer the following questions: (1) Are there universal effects of elevated soil temperature and altered

precipitation patterns on aboveground biomass and crop yield across years and are these effects similar for all crops? And if not, (2) do specific annual environmental conditions (e.g., wet or dry year) explain observed inter-annual variability in the responses of specific crops? To address these questions, we analyzed long-term (2009-2018) aboveground biomass and yield data of wheat, barley, and oilseed rape grown in a typical crop rotation at the Hohenheim Climate Change (HoCC) field experiment in southwest Germany. Crops were exposed to soil warming and reduced precipitation amount and frequency, both as single factors and in combination.

6.2 Materials and methods

6.2.1 Location, climate and soil characteristics

The Hohenheim Climate Change (HoCC) experiment (Figure 6. 1) was setup at the Heidfeldhof (48°43'N, 9°13'E, 401 m a.s.l.) in Stuttgart, an experimental site of the University of Hohenheim, in August 2008. Soil type is a Luvisol with a silty loamy texture. The pH is 7.0 with a soil organic carbon content of 12.1 g kg⁻¹. Annual mean air temperature and precipitation at the site (1981–2010) were 9.4°C and 718 mm, respectively (DWD 2020). Information about climatic conditions at the experimental site are given in Table 1.

Daily sums of air temperature and precipitation, as well as growing degree days (>5°C) originated from the weather station “Hohenheim”, located at the Heidfeldhof, approx. 500 m southeast of the field experiment (Landwirtschaftliches Technologiezentrum (LTZ) Augustenberg 2022).



Figure 6. 1: Experimental site of the Hohenheim Climate Change (HoCC) experiment (Heidfeldhof, University of Hohenheim). For precipitation manipulation, roofs covered the plots from June to August. The picture was taken on 03.06.2016, showing spring barley.

6.2.2 Soil warming and precipitation treatments

Comprehensive information about the experimental setup are given by Poll et al. (2013) and Drebenstedt et al. (2020a). In brief, at an arable field, the climate factors soil temperature (T), precipitation amount (A) and precipitation frequency (F) were manipulated to simulate future conditions based on climate change predictions for southwest Germany until 2100 (IPCC 2021a; Jacob et al. 2008). In principle, soil temperature has been elevated since 2008 during the entire year, whereas precipitation was manipulated only during summer (June to August). The field experiment is split into four blocks. Each block is separated into two main plots, each with two $1\text{ m} \times 4\text{ m}$ plots. In one main plot per block, soil temperature was elevated by the use of heating cables (RS 611-7918, RS Components GmbH) (Figure 6. 2) to a target temperature difference of $+2.5^\circ\text{C}$ (T_e) at 4 cm depth in comparison to the ambient temperature main plot. Dummy cables at 4 cm depth on ambient soil temperature main plots (T_a) are installed to account for side effects of the presence of heating cables in the plots, such as retention of water from precipitation. Each main plot is split into four subplots ($1\text{ m} \times 1\text{ m}$) and each of these subplots has a different combination of the two precipitation factors. To prevent lateral water movement for example to a non-irrigated subplot, each subplot is surrounded by a PVC barrier to a depth of 0.5 m. Precipitation is manipulated by the use of roofs (more specifically rainout shelters) covering the main plots (R_r). The roofs are made of UV 5 foil (Folitec Agrarfolien-Vertriebs GmbH), which is a plastic canopy. The light quality reaching the crops grown under the roofs is very similar to the light quality in roof-control plots, because approx. 90 % of the

light spectrum reaches the crops under the roofs. There is a roof overhang of 1 m on each side of a main plot to prevent natural rainfall from falling onto the subplots. The sides of the roofs are open to minimize the effect of the shelters on microclimatic conditions. Rainfall is collected in rain barrels and the subplots are watered manually. Precipitation amount is reduced by 25% (A_r) in manipulated subplots compared to ambient precipitation amount (A_a). Precipitation frequency is manipulated to simulate longer dry periods by reducing the number of rainy days by 50% (F_r) as compared to ambient precipitation frequencies (F_a), i.e., the cumulative precipitation of two ambient rain events is delivered in one application after the second rain event. The classification of precipitation amounts and the lengths of the dry periods were based on a study of Patil et al. (2010). Each treatment is replicated four times and consists of a combination of three factors: soil warming (T_a or T_e), precipitation amount (A_a or A_r), and precipitation frequency (F_a or F_r). Every block has additionally two roof-control subplots (ambient and elevated soil temperature) without roofs (R_c) where precipitation patterns are not manipulated to account for any roof effect on plant development. Over the entire period, temperature probes at 4 cm depth in each subplot recorded soil temperature every minute. Soil volumetric water content (VWC) was monitored in each subplot every 20 minutes with time domain reflectometry (TDR) probes in 0-15 cm depth.

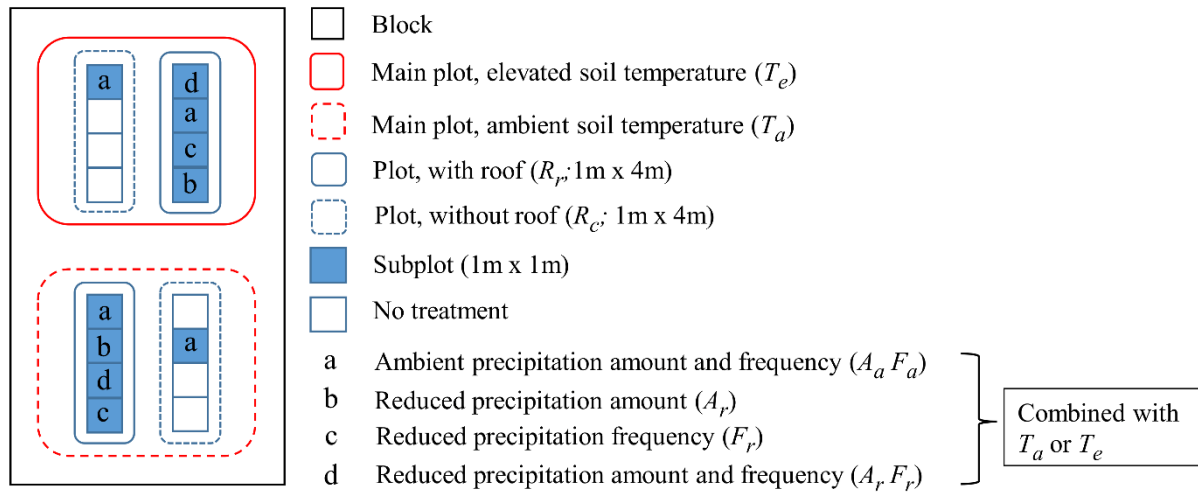


Figure 6. 2: Example of one of the four blocks of the Hohenheim Climate Change (HoCC) experiment, including the treatment combinations.

6.2.3 Plant cultivation and plant harvests

During the ten growing periods (2009-2018), spring wheat, spring barley, winter oilseed rape and winter wheat were cultivated in crop rotation. Dates of sowing and harvest as well as plant density can be found in Table 6. 1. Before each growing period, subplots were ploughed manually. For wheat and barley, each subplot contained nine rows with 45-50 seeds each,

leading to a row spacing of ~120 mm. For oilseed rape each subplot contained five rows with 15 seeds each and a row spacing of 200 mm. The seeding was done manually. During early plant growth, thinning of plants was done to aim a specific plant density (Table 6. 1). Subplots were weeded by hand regularly to keep weed pressure low, especially at the beginning of each growing period. The application of fertilizers and plant protection were done according to local practice based on best agricultural practice rules. For further information on fertilizer application please see supplement (**Table S6. 1**). Snail granule was scattered when oilseed rape plants were small and insecticides were applied for chemical disease control. Plants in the centre of each subplot (0.5 m x 0.5 m) were harvested at maturity by hand, cutting them 1 cm above soil surface. The centre plants were used to gain data on aboveground biomass and grain or seed yield. By the use of the centre plants for measurement purposes border effects were reduced. All plants around each subplot centre were also harvested, but not included into the data set. About 80-120 g of plant residues were returned to each of the subplots.

Root biomass data were collected in the growing period 2016 with spring barley (Drebenstedt et al. 2020b). Further information on growth parameters, grain quality, microbial biomass carbon and CO₂ fluxes studied since the HoCC experiment was established in 2008, is presented elsewhere (Högy et al. 2013; Poll et al. 2013; Bamminger et al. 2016; Drebenstedt et al. 2020a; Drebenstedt et al. 2020b).

Table 6. 1: Overview of crop species, sowing and harvest dates, plant density, duration of experimental and climatic conditions from ten growing periods (2009–2018) at the experimental site. Soil moisture is taken from control subplots covered by roofs (Rr) with ambient temperature and precipitation amount and –frequency.

Growing period	Crop ¹	Sowing date	Harvest date	Plant density (n m ⁻²)	Duration days	Mean air temperature (°C) ²	Long-term mean air temperature (°C, 1981-2010) ³	Growing degree days (>5.0°C)	Cumulative ambient precipitation (mm) ²	Mean long-term cumulative ambient precipitation (mm, 1981-2010) ³	Mean soil moisture (Vol.%)
2009	Spring wheat	02.04.09	11.08.09	200	131	16.2	15.3	1468	381	377	21
2010	Spring barley	30.03.10	05.08.10	290	128	15.2	13.6	1276	262	425	19
2010/2011	Winter OSR	26.08.10	15.07.11	40	322	8.7	9.4	1697	506	718	22
2011/2012	Winter wheat	20.10.11	20.07.12	200	274	8.2	8.0	1296	397	592	16
2013	Spring barley	04.04.13	06.08.13	290	124	15.6	15.3	1313	341	377	27
2013/2014	Winter OSR	02.09.13	17.07.14	40	318	9.7	8.6	1711	519	649	25
2015	Spring wheat	19.03.15	31.08.15	200	165	16.1	13.6	1766	243	425	15
2016	Spring barley	05.04.16	02.08.16	290	119	15.0	15.3	1185	270	377	21
2016/2017	Winter OSR	07.09.16	11.07.17	40	307	8.6	8.6	1571	515	649	20
2017/2018	Winter wheat	24.10.17	19.07.18	200	268	8.8	8.0	1410	534	592	28

¹Abbreviation: OSR=oilseed rape.²The values refer to the growing period of each crop from sowing to harvest measured at the weather station “Hohenheim” (Landwirtschaftliches Technologiezentrum (LTZ) Augustenberg 2022). ³The values refer to the long-term period (1981-2010) and are monthly averages from sowing to harvest measured at the weather station “Stuttgart-Ech. (Flugwewa)”, 2 km south of the experimental field (DWD 2020).

6.2.4 Statistical analysis

Daily averages of air and soil temperatures, precipitation amount, and soil moisture were used for the statistical analysis. Data of aboveground biomass, crop yield and soil moisture were first analyzed as time series over all growing periods (2009-2018). Time series were analyzed using a first-order autoregressive correlation between residuals of repeated measurements from the same subplot. For this, the fixed factor ‘year’ was integrated into the model. Note that year means the period from sowing to the final harvest of a crop at maturity, which is synonymous with a growing period.

In a second step, treatment effects on aboveground biomass, crop yield, and soil moisture were analyzed for each growing period separately with linear mixed-effects models fitted by maximum likelihood (lme function of the R 3.4.2 nlme package). For each growing period, raw data with four replicates per treatment were used. Furthermore, for each crop species (spring wheat, spring barley, winter oilseed rape, winter wheat) group average values were calculated over all growing periods in which the crop was planted. The model was as follows:

$$\begin{aligned} y_{hijklmnp} = & \mu + b_h + m_{hi} + p_{hij} + \gamma_k + \tau_l + o_m + \vartheta_{nm} + \theta_{pm} + (\gamma\tau)_{kl} + (\gamma\vartheta)_{knm} \\ & + (\gamma\theta)_{kpm} + (\tau o)_{lm} + (\tau\vartheta)_{lnm} + (\tau\theta)_{lpm} + (\vartheta\theta)_{nmp} + (\tau\vartheta\theta)_{lnmp} \\ & + (\gamma\tau\vartheta)_{klm} + (\gamma\tau\theta)_{klpm} + (\gamma\vartheta\theta)_{knmp} + (\gamma\tau\vartheta\theta)_{klmnp} + e_{hijklmnp} \end{aligned}$$

where b_h , m_{hi} and p_{hij} are the random effect of the h^{th} block, i^{th} mainplot within h^{th} block and the j^{th} plot nested within the hi^{th} mainplot, respectively. γ_k , τ_l , o_m , ϑ_{nm} , and θ_{pm} are the main effects of the k^{th} year, l^{th} temperature, m^{th} roof, n^{th} precipitation frequency and p^{th} precipitation amount, respectively. The two effects precipitation frequency and precipitation amount were applied under roofs only, thus the main effects are confounded with the corresponding interaction effects with roof so only one of those terms can be estimated. To account for this, we included arbitrary main effects into the model, but added the index m for all these effects. Interaction effects were denoted by parentheses around the corresponding main effects. The term $e_{hijklmnp}$ is the subplot error of observation $y_{hijklmnp}$. It was assumed that all random effects (block, mainplot, plot, and subplot error) were independent and identically distributed with homogeneous variances σ_b^2 , σ_m^2 , σ_p^2 , and σ_e^2 , respectively. Residuals were graphically checked for homogeneous error variance and normal distribution using residuals-versus-fitted value plots and QQ plots (Kozak and Piepho 2018). In case of extreme residuals, the corresponding data points were checked for plausibility. In total, three outliers were eliminated due to a lack of plausibility. After finding significant differences via global F test at $\alpha=0.05$, Fishers LSD test was used to find differences between means ($\alpha=0.05$) and was performed with

R package “agricolae”. Ratios of means were calculated for presentation purposes only. Non-significant effects and differences with p-values between 0.05 and 0.1 were denoted as trend or tendency.

Changes in aboveground biomass and yield [%] of heated compared to unheated subplots with crops (wheat, barley, oilseed rape) were correlated with the relative difference [%] in cumulative ambient precipitation during the growing period from the long-term average (1981-2010). Cumulative ambient precipitation refers to the growing period of each crop from sowing to harvest measured at the weather station “Hohenheim” (Landwirtschaftliches Technologiezentrum (LTZ) Augustenberg 2022). Heated crops were grown under elevated soil temperature during the entire growing period. Pearson’s correlation analyzes were done in Excel (Sheppard 2019). Therefore, Pearson’s correlation coefficient (r) was calculated using the CORREL function. Afterwards, a t -value was calculated using r and n as the number of growing periods of a crop which were correlated with each other:

$t = \frac{r\sqrt{n-2}}{\sqrt{1-r^2}}$. For the P-value the function “T.VERT.2S(ABS(x);degrees of freedom)” was used and x was replaced by the t -value. The degrees of freedom were $n-2$. A level of probability of $P \leq 0.05$ was set as statistically significant.

6.3 Results

6.3.1 Environmental conditions from 2009-2018

Air temperature

The years 2014 and 2018 were on average more than 1.5°C warmer than the long-term period (1981-2010) (Table 6. 2). Only in 2010 the mean air temperature was cooler than in the long-term period (- 0.5°C). Beginning in 2014, monthly air temperatures >1.5°C warmer than the long-term average for the respective months were observed more frequently. Particularly warm springs with air temperatures >1.5-3.5°C above the monthly long-term averages were observed in the years 2009, 2011, 2012, 2014 and 2018. In contrast, spring 2013 was cooler than the long-term average. Summer was warmer in 2015 and 2018 than the long-term average.

In addition, the experimental soil heating had only minor effect on air temperature at canopy level (30 cm aboveground) under the roofs (supplement, Figure S6. 1).

Table 6. 2: Temperature difference [°C] of the average monthly air temperature from the long-term average (1981-2010). Temperature differences $>+1.5^{\circ}\text{C}$ and $<-1.5^{\circ}\text{C}$ are color-coded. Warmer than the long-term average: >1.5 to 2.5°C ; >2.5 to 3.5°C ; $>3.5^{\circ}\text{C}$. Colder than the long-term average: -1.5 to -2.5°C ; -2.5 to -3.5°C ; $<-3.5^{\circ}\text{C}$. Ø: difference between the yearly average air temperature compared to the long-term period (1981-2010). Temperature was measured at 2 m height. Data from 2009-2018 originate from the weather station “Hohenheim”, which is 0.5 km southeast of the field site (DWD 2020; Landwirtschaftliches Technologiezentrum (LTZ) Augustenberg 2022). The long-term data originate from the weather station “Stuttgart-Ech. (Flugwewa)” 2 km south of the experiment (DWD 2020).

	Year of experiment									
Month	2009	2010	2011	2012	2013	2014	2015	2016	2017	2018
Jan	-2.4	-2.5	0.8	2.0	0.8	3.1	2.1	2.2	-3.2	4.5
Feb	-0.5	-0.1	1.3	-3.7	-2.0	3.3	-1.0	3.0	3.0	-2.5
Mar	-0.5	-0.2	1.7	3.1	-2.8	2.9	1.1	-0.6	3.1	-1.1
Apr	3.5	1.1	3.6	0.2	0.5	2.7	0.9	-0.2	-0.6	4.8
May	1.7	-2.0	1.6	1.9	-1.9	-0.6	0.4	-0.1	1.1	2.7
Jun	0.0	1.1	0.8	0.7	0.2	0.9	0.8	0.6	2.9	1.7
Jul	0.0	2.1	-2.0	-0.4	2.4	0.4	2.9	1.0	0.5	1.8
Aug	1.2	-0.8	1.0	1.8	0.3	-1.9	2.6	0.7	0.7	2.0
Sep	1.4	-1.3	2.3	0.4	0.4	1.0	-0.5	3.0	-1.3	1.6
Oct	-0.7	-1.4	0.1	-0.3	1.5	2.6	-0.5	-0.8	1.5	1.3
Nov	2.6	1.0	0.2	1.3	0.2	2.4	3.3	0.0	0.5	0.9
Dec	-0.2	-3.3	2.7	0.9	1.6	2.1	4.8	-0.2	0.7	2.3
Ø	0.5	-0.5	1.2	0.7	0.1	1.6	1.4	0.7	0.7	1.7

Soil temperature

Soil temperature was continuously measured in roofed and in roof-control plots from 2009-2018. Heating cables increased soil temperature during the vegetation period of spring crops (2009, 2010, 2013, 2015, 2016) on average by $1.9 \pm 0.3^{\circ}\text{C}$ and $1.9 \pm 0.2^{\circ}\text{C}$ in the roofed and in the roof-control plots, respectively Figure 6. 3). For winter crops (2010/2011, 2011/2012, 2013/2014, 2016/2017, 2017/2018), the soil temperature increase was on average $1.9 \pm 0.2^{\circ}\text{C}$ under the roofs and $2.1 \pm 0.3^{\circ}\text{C}$ in the roof-control plots.

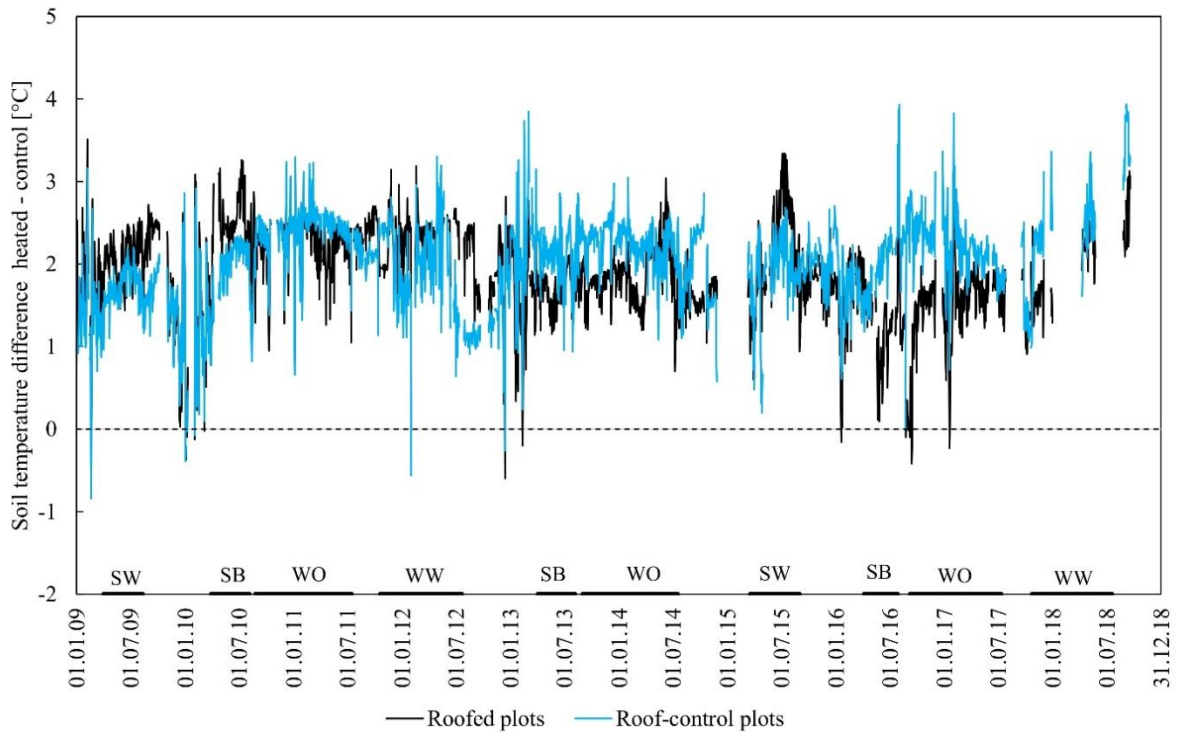


Figure 6. 3: Soil temperature difference between heated (elevated soil temperature) and control (ambient soil temperature) plots at 4 cm depth. Abbreviations: SW: spring wheat; SB: spring barley; WO: winter oilseed rape; WW: winter wheat. Data gaps were due to failure of temperature loggers.

Precipitation

In eight of the ten years, average yearly precipitation amount was lower than the long-term average (1981-2010) (Table 6. 3). Average yearly precipitation amount was above the long-term average by 10.0% and 14.5% only in 2013 and 2017, respectively. During spring of several years, ambient precipitation amount was 25% to 100% lower than in the long-term period 1981-2010. Particularly dry springs were observed from 2010 to 2012, in 2014, and 2018. For example, in six of ten years (2010 to 2014 and 2018), the precipitation amount in March was lower by more than 50% compared to the long-term average. The summer months were very dry in 2015. In contrast, compared to the long-term period, 25-50% more rainfall was achieved in June or July 2009, 2011, 2016 and 2017; and >50% more rainfall was achieved in August 2014. A particular dry year was 2015, although in January and November the rainfall amount

was >50% and >25% higher than in the long-term period. Absolute differences [mm] of the ambient average monthly precipitation amounts from the long-term average (1981-2010) are given in the supplement (Table S6. 2).

Table 6. 3: Relative difference [%] of the ambient average monthly precipitation amount from the long-term average (1981-2010). Color-coded are differences in precipitation which were more or less than 25% than the long-term average: relative difference of 25 to 50%; >50 to 100%; >100% more precipitation than in the long-term average; relative difference of 25 to 50% or >50 to 100% less precipitation than in the long-term average. Ø: difference between the yearly averages of precipitation amount compared to the long-term period (1981-2010). Data from 2009-2018 originate from the weather station “Hohenheim”, which is 0.5 km southeast of the field site (DWD 2020; Landwirtschaftliches Technologiezentrum (LTZ) Augustenberg 2022). The long-term data originate from the weather station “Stuttgart-Ech. (Flugwewa)” 2 km south of the experiment (DWD 2020).

	Year of experiment									
Month	2009	2010	2011	2012	2013	2014	2015	2016	2017	2018
Jan	-60.5	-54.6	-12.2	52.2	-62.9	3.9	75.9	-9.5	-52.4	139.3
Feb	0.0	-27.8	-80.6	-75.0	28.3	-10.0	-57.2	49.7	-18.3	-44.4
Mar	45.0	-56.7	-57.5	-78.3	-50.8	-80.2	-13.1	-20.4	11.9	-58.3
Apr	-41.6	-81.6	-54.3	-17.1	-0.4	-38.0	-44.3	12.4	-11.2	-66.3
May	32.3	-15.1	-74.0	-71.4	47.7	-49.8	-19.0	-12.6	-0.1	-14.3
Jun	-22.1	-21.6	-5.5	8.0	-18.6	-48.2	-33.2	31.8	37.5	56.0
Jul	49.5	4.0	30.0	-20.2	9.8	10.6	-82.4	-68.7	41.0	-61.0
Aug	-16.5	19.7	-3.8	-38.3	13.9	62.8	-32.9	-41.9	-9.6	-28.7
Sep	-70.9	-11.6	-45.6	-23.5	-7.4	-11.2	-51.9	-12.6	60.2	8.4
Oct	-13.6	-42.7	-20.3	-13.6	100.5	-18.8	-69.8	-19.5	-5.4	-42.7
Nov	28.4	46.0	-96.0	156.8	47.6	-17.4	40.8	1.8	81.6	-61.0
Dec	14.4	54.8	104.4	10.8	-18.8	-46.6	-43.2	-88.0	-1.6	70.8
Ø	-1.5	-13.2	-23.2	-12.0	10.0	-19.6	-31.8	-17.1	14.5	-9.9

During summer (June, July, August), both precipitation amount and frequency were experimentally manipulated.

Under ambient precipitation, from 2009-2018, 55% of the precipitation events were small, 0.5-5.9 mm day⁻¹, whereas 14% of the events were >20 mm day⁻¹ (supplement, Table S6. 3). In contrast, in treatments where ambient precipitation was reduced by 25%, small precipitation events of 0.5-5.9 mm day⁻¹ occurred more frequently by +9%, in 2009-2018. At the same time, events with high precipitation amounts occurred less frequently, by -3% (10-19.9 mm day⁻¹) and -4% (>20 mm day⁻¹).

At ambient precipitation frequency, the growing periods 2009-2018 mainly varied in the length of shorter dry periods, which were ≤3 days or 4–6 days long (supplement, Table S6. 4). In our study, the growing periods 2009, 2010 and 2016 had the shortest dry periods. At reduced precipitation frequency, there was an increase in the length of dry periods compared to ambient

conditions. Thus, dry periods of 7–9 days or >10 days in duration occurred 15% and 7% more frequently compared to ambient conditions, whereas shorter dry periods of ≤ 3 days or 4–6 days became less frequent by -7% and -15%, respectively.

Soil moisture

Overall, soil moisture fluctuated between 10 Vol.% and 40 Vol.% in the roof-control plots during the growing period (Figure 6. 4). Soil warming reduced soil moisture in nine of ten growing periods (exception: 2016/2017). Greatest reductions in soil moisture under soil warming were observed in the growing periods 2009 (-33%, $P<0.001$), 2010 (-23%, $P<0.001$), 2010/2011 (-25%, $P<0.001$) and 2013 (-45%, $P<0.001$). A reduction in precipitation amount reduced soil moisture except in the years 2011/2012 and 2016. Reduction in precipitation frequency had no consistent effect on soil moisture. The combination of soil warming, reduced precipitation amount, and reduced precipitation frequency led to consistently lower soil moisture, except for the growing periods 2010/2011, 2011/2012, and 2017/2018. Roofing decreased mean soil moisture for the roofed period; for example in 2009 from 23 Vol.% to 19 Vol.% ($P<0.001$), in 2015 from 15 Vol.% to 11 Vol.% ($P<0.001$), and in 2017 from 18 Vol.% to 14 Vol.% ($P<0.001$). Only in 2013 and 2016, roofing had no effect on average soil moisture (data not shown).

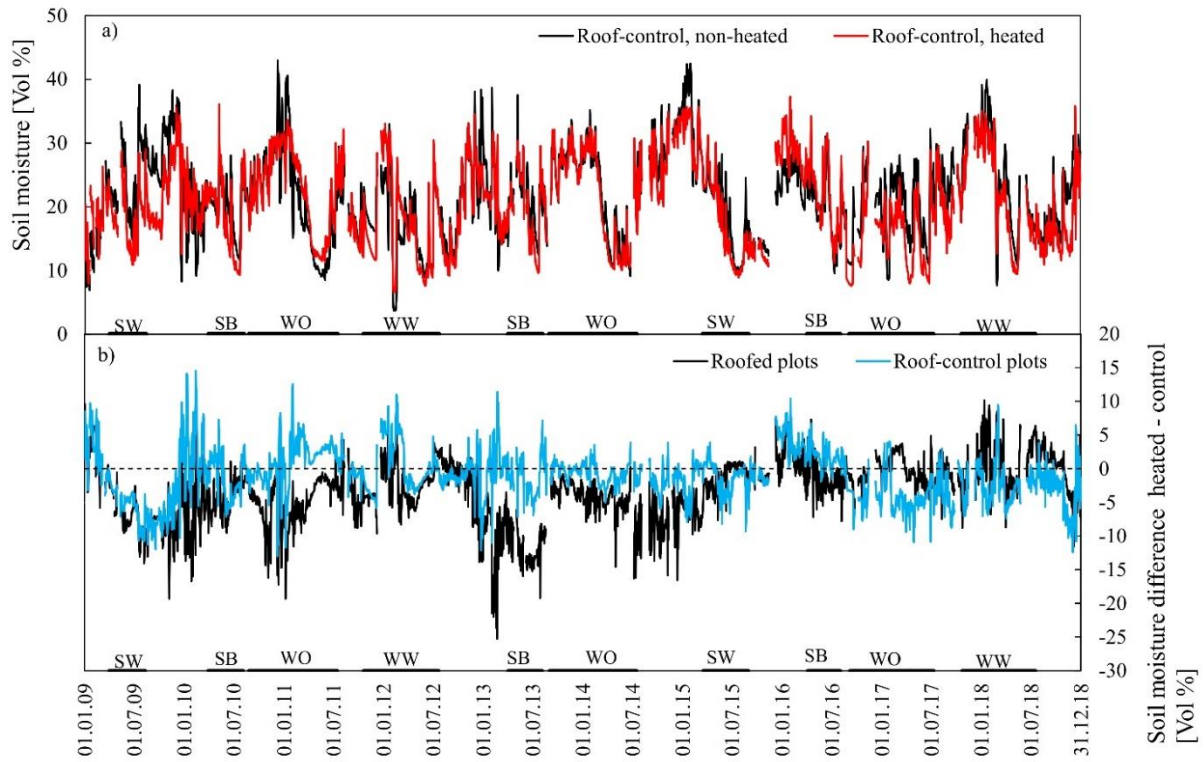


Figure 6. 4: Soil moisture conditions in the roof-control plots (a). Soil moisture difference between heated (+2.5 °C) and control (ambient soil temperature) plots in 0-15 cm depth (b). We focus on the effect of soil warming due to the small effects of altered precipitation. Ten growing periods from 2009-2018 are denoted by abbreviations of the planted crops: SW: spring wheat; SB: spring barley; WO: winter oilseed rape; WW: winter wheat.

6.3.2 Aboveground biomass

The response of aboveground biomass to soil warming depended on the growing period, in which a crop was planted (year x warming, $P < 0.001$). In the growing period 2009, spring wheat increased in aboveground biomass from 630 g DW (dry weight) m^{-2} under ambient to 737 g DW m^{-2} (+17%, $P < 0.05$) under elevated soil temperature (Figure 6. 5). In contrast, aboveground biomass of spring wheat grown in the much drier year 2015 was not affected by warming. Soil warming had no effect on winter wheat in the growing period 2011/2012, which was dry during spring and summer of 2012. In contrast, autumn and winter of 2017 were moist during the growing period 2017/2018 of winter wheat, and soil warming increased aboveground biomass from 402 g DW m^{-2} to 672 g DW m^{-2} (+67%, $P < 0.05$). In 2010, the spring was dry and soil warming did not affect aboveground biomass of spring barley, whereas it increased by 43% ($P < 0.05$) and 48% ($P = 0.052$) in 2013 and 2016, respectively, under wetter spring conditions. Aboveground biomass of winter oilseed rape remained unaffected by elevated soil temperature. A reduction in precipitation amount tended to decrease aboveground biomass of spring wheat in 2009 from 630 g DW m^{-2} to 516 g DW m^{-2} (-18%, $P = 0.066$) (supplement, Table S6. 5). In

contrast, aboveground biomass of winter oilseed rape increased from 1677 g DW m⁻² to 1834 g DW m⁻² in 2010/2011 (+10%, $P < 0.05$) under reduced precipitation amount.

Aboveground biomass of spring wheat, winter wheat, spring barley or winter oilseed rape did not respond to the longer dry periods caused by a reduction in precipitation frequency in any of the ten growing periods (supplement, Table S6. 5).

A combined effect of the three climate factors soil warming, reduced precipitation amount, and frequency were only observed in two growing periods. First in 2010, the aboveground biomass of spring barley decreased from 1182 g DW m⁻² to 1051 g DW m⁻² (- 11%, $P < 0.05$). Second in 2013/2014, an increase in oilseed rape aboveground biomass from 1062 g DW m⁻² to 1228 g DW m⁻² was observed. (+16%, $P = 0.081$; supplement, Table S6. 5).

In general, there were no consistent significant effects of the roof on aboveground biomass. Roofing increased spring barley aboveground biomass by 21% ($P = 0.052$) in 2010. In winter oilseed rape, the roofs had an effect in 2010/2011 (+33%, $P = 0.087$) and 2013/2014 (+7%, $P = 0.075$). For a comparison of aboveground biomass data of crops grown under the roofs compared to no roofs (roof-control plots) see supplement (Figure S6. 2).

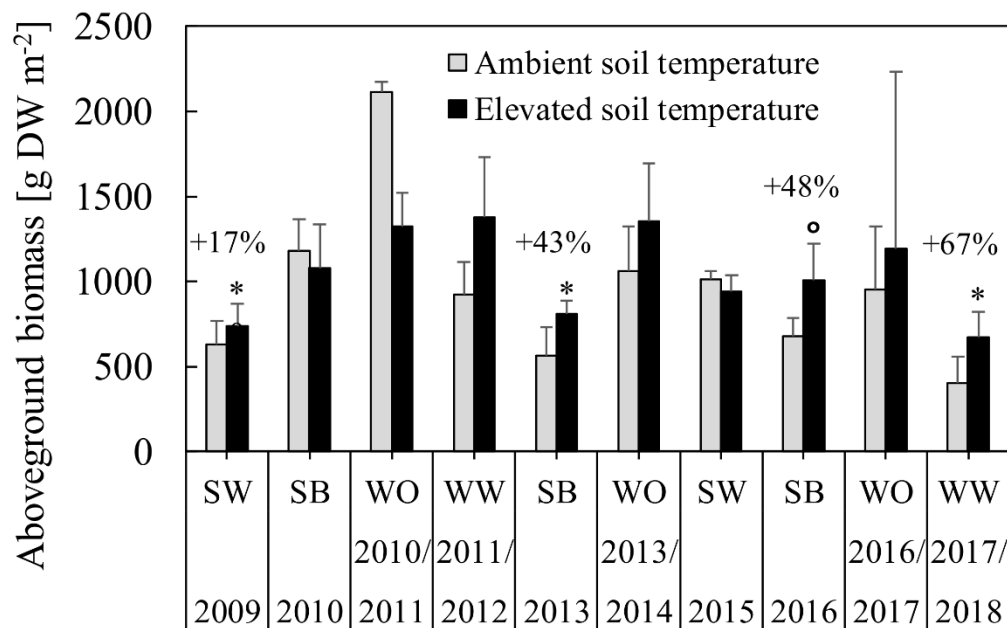


Figure 6. 5: Effects of elevated soil temperature on aboveground biomass of crops grown in crop rotation between 2009 and 2018. Percent values show the relative change between ambient and elevated soil temperature of plots covered by roofs. Asterisks (*) indicate statistically significant effects of elevated soil temperature ($P \leq 0.05$), whereas the degree sign (°) indicate trend ($0.1 \geq P > 0.05$). Error bars show standard deviation ($n = 16$; mixed-effects model fitted with maximum likelihood). Abbreviations: DW: dry weight; SW: spring wheat; SB: spring barley; WO: winter oilseed rape; WW: winter wheat.

6.3.3 Yield

The yields of winter oilseed rape and spring barley (only in 2010), which we achieved under ambient conditions in the field experiment, were similar to the long-term average seed or grain yields for those crops in Baden-Wuerttemberg (1989-2018) (Figure 6. 6).

The effect of soil warming on grain or seed yield depended on the growing period (year x warming, $P < 0.001$). Overall, soil warming had either a positive or no effect on yields of the different crops, similar to its effect on aboveground biomass. For example, spring wheat grain yield increased by 28% in 2009 ($P < 0.05$) but remained unaffected in the much drier year 2015 (Figure 6. 6; supplement, Table S6. 5). Grain yield of winter wheat was not affected by soil warming in 2011/2012 but tended to increase by 51% (from 211 g m⁻² to 319 g m⁻², $P = 0.067$) in the wetter growing period 2017/2018. Spring barley grain yield increased due to soil warming from 296 g m⁻² to 458 g m⁻² (+55%, $P < 0.05$) in 2013 and from 370 g m⁻² to 566 g m⁻² (+53%, $P = 0.064$, trend) in 2016, whereas it was similar under soil warming and ambient conditions in 2010, which had a much drier spring. The seed yield of winter oilseed rape did not respond to elevated soil temperature in 2010/2011, 2013/2014, or 2016/2017.

In all years, reduced precipitation amount and frequency had no effect on grain or seed yield of spring wheat, winter wheat, spring barley or winter oilseed rape (supplement, Table S6. 5).

Interaction effects of the three climate factors were only observed for spring barley in 2010. That year was quite dry until the beginning of the precipitation manipulation in June 2010 and the combination of soil warming, reduced precipitation amount and frequency decreased grain yield from 663 g DW m⁻² to 585 g DW m⁻² (-12%, $P < 0.05$; supplement, Table S6. 5).

Roofing of the plots tended to increase the yield of spring barley in 2010 (+21%, $P = 0.082$) and the yield of winter oilseed rape (+12%, $P = 0.053$) in 2013/2014. Figure S6. 3 (supplement) shows yield data from roof-control plots compared to roofed plots.

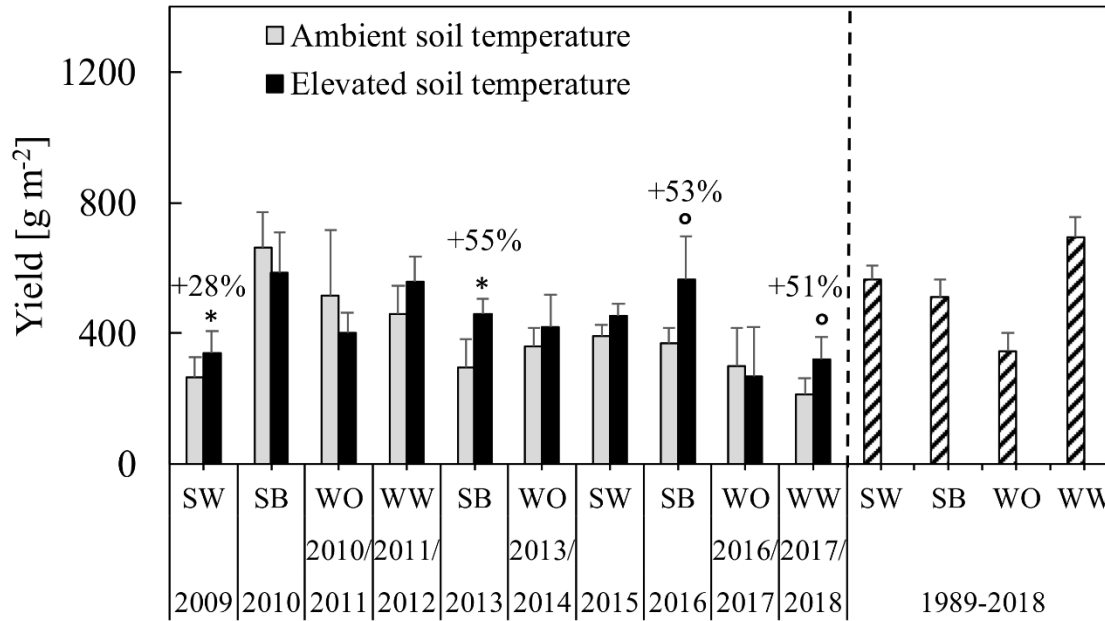


Figure 6. 6: Effects of elevated soil temperature on grain or seed yield of different crops in growing periods 2009 to 2018. Grey and black bars show average yield of roof covered plots with ambient and elevated soil temperature, respectively (n=16). Striped bars show the long-term average grain or seed yield in Baden-Wuerttemberg (1989-2018; n=30) (Statistisches Landesamt Baden-Württemberg 1989-2018), which is comparable to the ambient soil temperature treatment. Error bars show standard deviations. We focus on effects of soil warming due to small effects of altered precipitation. Asterisks (*) indicate statistically significant effects of elevated soil temperature ($*P \leq 0.05$), whereas degree signs (°) indicate trends ($0.1 \geq P > 0.05$). Percent values show the relative change between ambient and elevated soil temperature for significant interactions or trends. We used a mixed-effects model fitted with maximum likelihood. Abbreviations: SW: spring wheat; SB: spring barley; WO: winter oilseed rape; WW: winter wheat.

6.3.4 Effects of annual precipitation on aboveground biomass and yield

Soil warming induced changes in biomass and yield of wheat, barley, and oilseed rape were positively correlated with the cumulative ambient precipitation during the growing periods, leading to pronounced increases in crop productivity due to soil warming in moist years. Cumulative ambient precipitation contributed to the inter-annual variability in crop productivity. Looking at the control treatment ($A_d F_d$), the soil warming-induced increase in wheat aboveground biomass (by 15-65%) occurred when the relative differences in cumulative ambient precipitation were 5 -10% from the long-term average (1981-2010) during the growing periods (Figure 6. 7). In addition, the soil warming-induced increase in wheat yield correlated positively with 5-10% higher cumulative ambient precipitation compared to long-term, meaning 30-50% more yield. Similarly, barley produced approximately 40% and 50% more aboveground biomass and yield under soil warming, respectively, when cumulative ambient precipitation increased by 10%. The aboveground biomasses and yields of wheat and barley were observed to increase until the cumulative ambient precipitation was 30% and 20% lower

than the long-term. In oilseed rape, the positive effect of soil warming on aboveground biomass under high cumulative ambient precipitation compared to long-term was lower than for cereal crops and the yield was barely affected (supplement, Figure S6. 4, Figure S6. 5).

Correlations of soil moisture averages during the growing periods with soil warming effects on aboveground biomass or yield were worse than with ambient precipitation amounts (supplement, Figure S6. 6, Figure S6. 7), possibly because some of the precipitation evaporated on the soil surface, thus soil moisture did not noticeably increase, or because the TDR sensors did not work well on very dry soils.

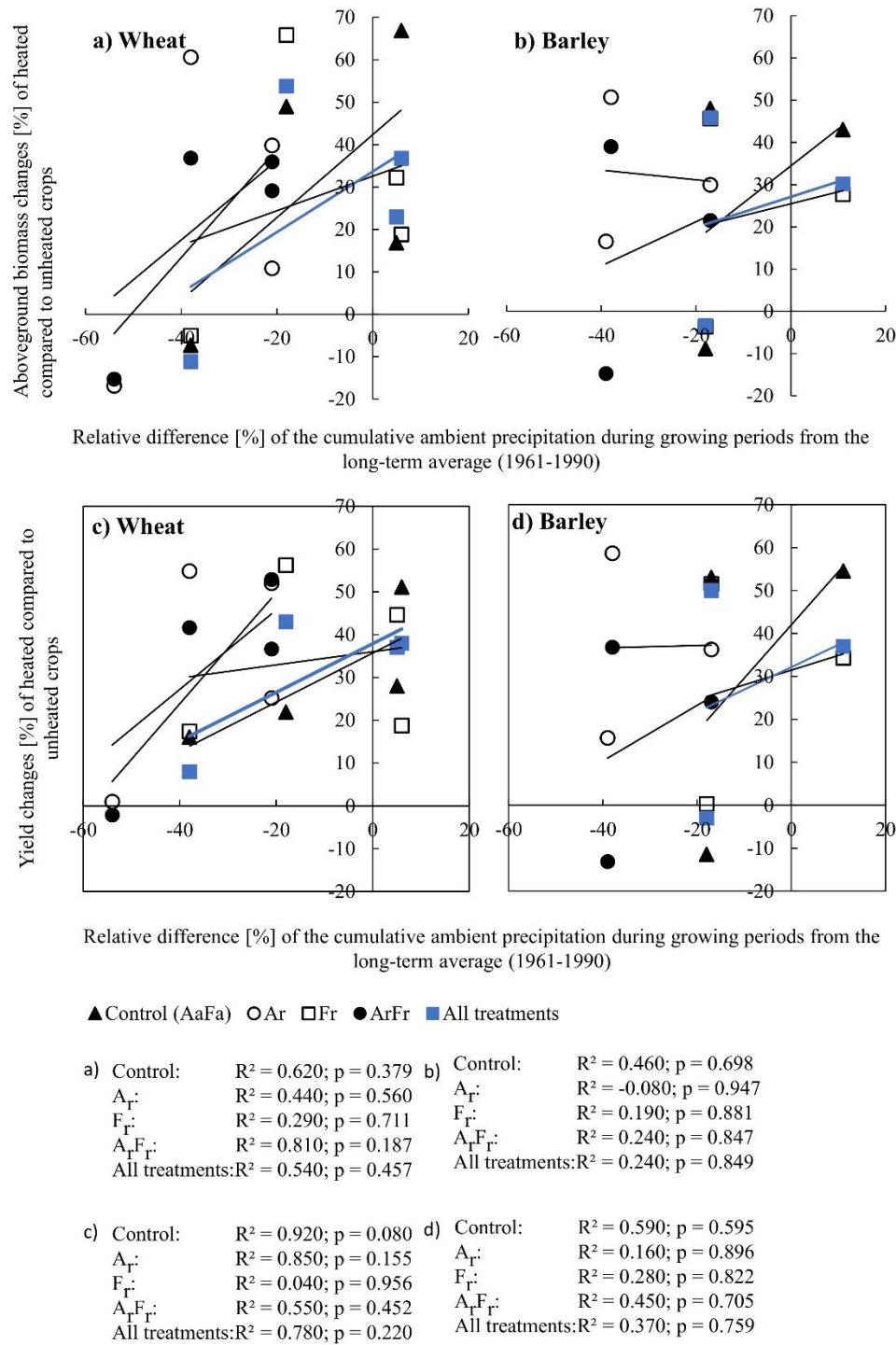


Figure 6. 7: Changes in aboveground biomass and yield [%] under elevated compared to ambient soil temperature are correlated with the relative difference [%] of the cumulative ambient precipitation during the growing periods from the long-term average (1981-2010). Data for wheat (a, c) and barley (b, d) are analyzed by a Pearson's correlation analysis. Wheat growing periods: 2009 and 2015 spring wheat, 2011/2012 and 2017/2018 winter wheat (n=4). Barley growing periods: 2010, 2013 and 2016 spring barley (n=3). Treatments: triangle: ambient precipitation amount (A_a) and –frequency (F_a); unfilled circle: reduced precipitation amount (A_r); unfilled square: reduced precipitation frequency (F_r); filled circle: reduced precipitation amount (A_r) and –frequency (F_r). The trendlines “all treatments” compare all ambient soil temperature treatments ($T_a A_a F_a$, $T_a A_r F_a$, $T_a A_a F_r$, $T_a A_r F_r$; n=16) with all elevated soil temperature treatments ($T_e A_a F_a$, $T_e A_r F_a$, $T_e A_a F_r$, $T_e A_r F_r$; n=16). Only roofed plots are included.

6.4 Discussion

6.4.1 Crop responses to soil warming

We analyzed data from ten growing seasons (2009-2018) to determine the impact of climate change manipulations on biomass production and yield of a typical crop rotation in the temperate region of southwest Germany. Across these ten growing periods, inter-annual variability in cumulative ambient precipitation and in soil moisture conditions influenced the effect of soil warming on aboveground biomass and yield of cereal crops (spring barley, spring wheat, winter wheat). Mean soil moisture during the growing periods varied strongly from 15 to 28 Vol.% between years. Under low cumulative ambient precipitation and low mean soil moisture, soil warming did not affect crop biomass and yield, while greater precipitation and higher soil moisture were linked to an increase in aboveground biomass and harvestable yield of cereals in warmed plots. Therefore, yearly weather conditions seem to be a key control on plant growth in cereal crops under global warming. For example, aboveground biomass of spring wheat, spring barley, and winter wheat increased by 23%, 30-46%, and 37%, respectively, in moist years, whereas no increase was detected in dry years. This was similar for yield, in which increases of 37%, 37-50%, and 38% in spring wheat, spring barley and winter wheat, respectively, occurred in moist years.

In accordance with these observations, Hartley et al. (2007) observed no changes in aboveground biomass and yield of spring wheat under soil warming of +3.0°C and low soil moisture content during the growing period. Since they observed no biomass or yield losses despite the dry soil conditions, they suggested that soil warming did not cause drought stress. In another study, aboveground biomass and yield of winter wheat were not affected at maturity under the conditions of soil warming (+5.0°C) and greater soil moisture deficit as compared to unheated conditions (Patil et al. 2010).

Increased crop productivity under soil warming and high soil moisture could have been due to increased root growth. In general, elevated soil temperatures led to reduced soil moisture content in our study. This was also shown in field experiments conducted in grasslands (Liu et al. 2009) and boreal forests (Shaver et al. 2000). However, in addition to soil temperature, precipitation also affects soil moisture content. Thus, whenever ambient precipitation was sufficient in our experiment to maintain rather high soil moisture conditions, water losses caused by higher evapotranspiration rates under elevated soil temperature were less important, which possibly enabled increased root growth. As shown by Gray and Brady (2016), root development can be stimulated by soil warming; therefore, the uptake of water and nutrients is

accelerated under warmer soil temperatures, as observed previously in temperate climates (Bowen 1991). For example, root biomass of spring barley was increased due to soil warming grown in the Hohenheim Climate Change (HoCC) experiment in 2016 (Drebenstedt et al. 2020b). Similarly, Gavito et al. (2001) observed that root growth and nutrient uptake increased in winter wheat grown under +5.0°C elevated soil temperature, resulting in increased aboveground biomass production.

In the present study, the growing period 2017/2018 was especially interesting because the year 2018 was a warm year with less frequent precipitation events. We observed that mean air temperatures were higher by +4.5°C and +4.8°C in January and April 2018, respectively, and air temperature increased by >1.5°C in spring and summer compared to the reference period (1981-2010). High air temperatures increase evapotranspiration rates, influencing ecosystem water budgets, in turn negatively affecting plant productivity and soil respiration (Shaver et al. 2000). That raises the question: Why was soil warming able to promote crop growth of winter wheat under such high air temperatures? On the one hand, plants were grown in an arable soil with good water holding capacity, which likely mitigated consequences of prolonged dry periods. On the other hand, the growing period 2017/2018 was variable in terms of precipitation. We observed a wet autumn and winter with precipitation amounts 60-140% above the monthly long-term values. Although the spring was dry, in June 2018 precipitation was +56% above the long-term period. In confirmation of our observations, Kannoja et al. (2019) mentioned increased soil microbial activity during a wet season or when soils regained their moisture through wet conditions. This can result in increased mineralization rates of nitrogen and phosphorus, which are beneficial for plant nutrition and biomass production. Therefore, observed high mean soil moisture values during winter 2017/2018 as a result of high ambient precipitation, in combination with a soil capable of storing great volumes of water and also possibly higher soil microbial activity, positively affected crop growth under elevated soil temperature. In regions where soils have high water holding capacity like in our experiment, heavy rain events during autumn or winter can compensate for water scarcity caused by longer dry periods in spring and summer (Wang et al. 2009; He et al. 2021).

In contrast to the positive effects of soil warming on aboveground biomass and yield of cereals, the response of winter oilseed rape to higher soil temperatures was much less pronounced in the present study. Winter oilseed rape prefers cooler temperatures, especially during early winter, when slightly elevated mean air temperatures of only 1.0°C have been shown to induce yield instability and yield losses (Brown et al. 2019). Since higher air temperatures are linked

with higher soil temperatures, it seems reasonable to conclude soil warming had no stimulating effect on yield of winter oilseed rape especially when winter crop plants were young and small. We suggest that cumulative ambient precipitation was the factor regulating the response of plant growth of cereal crops to soil warming. We assume that sufficient ambient mean soil moisture as a result of high ambient precipitation amounts is necessary for soil warming to enhance crop biomass and yield. In contrast, if soil moisture is not sufficient, the effect of soil warming might be countered by water limitation even in semi-humid regions and in soils with almost optimal water storage capacity, such as the investigated loess soil.

6.4.2 Crop response to altered precipitation

During summer, precipitation amount and frequency were reduced by 25% and 50% respectively, based on actual precipitation conditions in the field. The applied precipitation treatments were, therefore, representative, and natural fluctuations in precipitation and soil moisture were major drivers of the observed plant responses to climate change manipulations, as discussed above with respect to soil warming. A reduction in summer precipitation amount by 25% resulted in only minor effects on aboveground biomass of the investigated crops, with a tendency toward reduced aboveground biomass of spring wheat in 2009 and increased aboveground biomass of winter oilseed rape in 2010/2011. The increased biomass production of winter oilseed rape under reduced precipitation amount contrasts with some of the literature (Raza et al. 2017). However, it is possible that the simulated water scarcity during summer resulted in mild drought conditions instead of severe drought stress. Mild drought was shown to increase root growth in oilseed rape (Raza et al. 2017), which could explain the ability of winter oilseed rape to increase its aboveground biomass in our study.

Additionally, in the present study, summer precipitation frequency was reduced by 50% to simulate longer dry periods. However, no effects on aboveground biomass of the tested crops were observed. An explanation could be that even though the length of dry periods was doubled, the difference was not very high between the ambient and reduced treatment. Hence, under ambient and reduced precipitation frequency, the length of dry periods were on average four and five days, respectively. Another possible explanation is the timing of reduced precipitation frequency with respect to crop developmental stage. Here, it lasted from the beginning of June to the end of August, when the production of yield-forming leaves, stems and ears had already occurred. Thus, aboveground biomass production was likely finished before the simulation of longer dry periods began. Overall, the overriding trend in precipitation (especially the amount) during summer appeared to dominate, while changes in precipitation frequency did not play a

major role on that relatively short time scale. Additionally, the minor effects of the altered precipitation (amount and frequency reduction) were most likely linked with the soil type of the arable field where the experiment is established. Loess-derived arable soils (Luvisol) are well known for their high water holding capacity, helping the plants to cope with water shortage during dry periods.

Harvestable yields of all tested crops did not change under reduced summer precipitation amount or under reduced summer precipitation frequency. In accordance with our observations, Patil et al. (2010) observed stable yields of winter wheat grown under reduced precipitation amount (-24%) and frequency (-50%) during summer. Additionally, in our study, increased water use efficiency of the crops under this condition of water scarcity could have accounted for the failure to observe lower yields under less precipitation amount. We found evidence for this in spring barley in 2016 (Drebenstedt et al. 2020b). It is known that the water use efficiency of plants can increase under dry conditions, i.e., in semiarid regions (Bhattacharya 2019). In cereals, greater water use efficiency under water scarcity is linked with yield improvements (Barnabás et al. 2008). Under future climate conditions, improved water use efficiency of a certain crop type or variety could be advantageous to prevent yield losses as consequence of water scarcity.

A three-factor interaction between soil warming, precipitation amount and frequency appeared only in 2010, contrary to our expectations, with an additive negative effect on spring barley yield. Nevertheless, we observed an interaction between the climate factors soil warming and soil moisture. We suggest that variations in cumulative ambient precipitation between the different years, i.e., the dry year 2015 and the wet year 2009, had greater impacts on the productivity of cereal crops than a temporary reduction in ambient precipitation amount by -25%, as simulated in our study.

6.4.3 Future perspectives based on the environmental conditions during the growing periods 2009-2018

A trend for declining precipitation amounts since 2010 was observed in the precipitation data at the experimental site of the HoCC experiment. In several years, especially during spring and summer, a reduction in precipitation was observed, but a trend toward an increase in precipitation during winter was visible as compared to 1981-2010. These findings are partly supported by climate simulations for the period 2071-2100 in Germany with precipitation increases during spring and winter, and a precipitation reduction during summer months (DWD 2017). During spring, conditions of water scarcity usually occur simultaneously with the early

developmental stages of crops. Water shortages during early growth stages induce changes in crop morphology (Bodner et al. 2015), such as a reduction in number of leaves and tillers (Lütke Entrup and Schäfer 2011). In late spring, drought affects booting, inflorescence or flowering stage, which impacts cereals by reducing the number of ears, grains or grain weight (Lütke Entrup and Schäfer 2011; Barnabás et al. 2008). In oilseed rape, drought in late spring reduces pod number per plant, seed weight, and seed oil concentration (Champolivier and Merrien 1996). Consequently, water shortages during spring can have an impact on future crop productivity, negatively impacting growth and yield.

Based on our observations, we assume that the positive effects of elevated soil temperature on biomass production and yield of cereals, which were observed under high cumulative ambient precipitation and high soil moisture, will decrease in the future due to decreasing precipitation amounts linked with lower soil moisture content throughout the growing periods. Under future projections for global warming, each incremental change will lead to greater changes in regional mean temperature, precipitation, and soil moisture (IPCC 2021b). With regard to the region of Western and Central Europe, at 2.0°C global warming, mean temperature and precipitation during summer are predicted to increase by +1.0 to 2.0°C and decrease by -10%, respectively (IPCC 2021a). In combination with more frequent drought periods (IPCC 2021b), this might pose a major threat to future productivity of cereals in southwest Germany.

6.5 Conclusions

Our data highlight the key role cumulative ambient precipitation seems to have in determining responses of crop development to soil warming. Under low cumulative ambient precipitation during a growing period, crop biomass and yields of wheat, barley and oilseed rape were not increased by elevated soil temperatures, whereas higher cumulative ambient precipitation was linked to an increase in aboveground biomass and harvestable yield, especially for cereals. The studied loess soil has optimal water storage capacity, which is an important property driving the responses of plant growth to reduced precipitation. For the prediction of future food production, it would therefore be important to study the responses of biomass and yield production to predicted climate change in soils with less optimal water holding capacity.

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Author contributions

PH, EK, CP and SM conceived the project; ID, CP and SM undertook fieldwork; ID collected and analyzed the data and wrote the manuscript; all authors read and approved the final manuscript.

Conflicts of interest

The authors declare that they have no conflicts of interest. The funders had no role in the design of the study; in the collection, analyzes, or interpretation of data; in the writing of the manuscript, or in the decision to publish the results.

6.6 Supplementary material

Table S6. 1: Fertilizer application during the ten growing periods.

Growing periods	Crop	Date of fertilizer application	Fertilizer
2009	Spring wheat	29.04.	Calcium ammonium nitrate, 50 kg N ha ⁻¹
		16.06.	Calcium ammonium nitrate, 26 kg N ha ⁻¹
2010	Spring barley	29.04.	Calcium ammonium nitrate, 60 kg N ha ⁻¹
2010/2011	Winter oilseed rape	11.03.	Calcium ammonium nitrate, 70 kg N ha ⁻¹
		31.03.	Ammonium thiosulfate, 110 l ha ⁻¹ (that implies 17.2 kg N ha ⁻¹ and 37.2 kg S ha ⁻¹)
		15.04.	Urea ammonium nitrate, 60 l ha ⁻¹ (that implies 21.6 kg N ha ⁻¹)
2011/2012	Winter wheat	23.03.	Calcium ammonium nitrate, 67.5 kg N ha ⁻¹
		27.04.	Calcium ammonium nitrate, 27 kg N ha ⁻¹
		31.05.	Calcium ammonium nitrate, 40.5 kg N ha ⁻¹
2013	Spring barley	10.05.	Calcium ammonium nitrate, 60 kg N ha ⁻¹
2013/2014	Winter oilseed rape	13.03.	Calcium ammonium nitrate, 70 kg N ha ⁻¹
		31.03.	Ammonium thiosulfate, 110 l ha ⁻¹ (that implies 17.2 kg N ha ⁻¹ and 37.2 kg S ha ⁻¹)
2015	Spring wheat	07.05.	Calcium ammonium nitrate, 60 kg N ha ⁻¹
		03.06.	Calcium ammonium nitrate, 80 kg N ha ⁻¹
2016	Spring barley	29.04.	Calcium ammonium nitrate, 60 kg N ha ⁻¹
2016/2017	Winter oilseed rape	07.03.	Calcium ammonium nitrate, 60 kg N ha ⁻¹
		14.03.	Calcium ammonium nitrate, 40 kg N ha ⁻¹
2017/2015	Winter wheat	23.03.	Calcium ammonium nitrate, 60 kg N ha ⁻¹

Table S6. 2: Absolute difference [mm] of the ambient average monthly precipitation amount [mm] from the long-term average (1981-2010). Ø: difference between the yearly averages of precipitation amount compared to the long-term period (1981-2010). Data from 2009-2018 originate from the weather station “Hohenheim”, which is 0.5 km southeast of the field site. The long-term data originate from the weather station “Stuttgart-Ech. (Flugwewa)” 2 km south of the experiment (Agricultural Technology Centre (LTZ) Augustenberg 2020; DWD 2020).

	Year of experiment									
Month	2009	2010	2011	2012	2013	2014	2015	2016	2017	2018
Jan	-24.8	-22.4	-5	21.4	-25.8	1.6	31.1	-3.9	-21.5	57.1
Feb	0	-10	-29	-27	10.2	-3.6	-20.6	17.9	-6.6	-16
Mar	21.6	-27.2	-27.6	-37.6	-24.4	-38.5	-6.3	-9.8	5.7	-28
Apr	-20.4	-40	-26.6	-8.4	-0.2	-18.6	-21.7	6.1	-5.5	-32.5
May	27.8	-13	-63.6	-61.4	41	-42.8	-16.3	-10.8	-0.1	-12.3
Jun	-19.2	-18.8	-4.8	7	-16.2	-41.9	-28.9	27.7	32.6	48.7
Jul	42.6	3.4	25.8	-17.4	8.4	9.1	-70.9	-59.1	35.3	-52.5
Aug	-11.4	13.6	-2.6	-26.4	9.6	43.3	-22.7	-28.9	-6.6	-19.8
Sep	-40.4	-6.6	-26	-13.4	-4.2	-6.4	-29.6	-7.2	34.3	4.8
Oct	-8	-25.2	-12	-8	59.3	-11.1	-41.2	-11.5	-3.2	-25.2
Noc	14.2	23	-48	78.4	23.8	-8.7	20.4	0.9	40.8	-30.5
Dec	7.2	27.4	52.2	5.4	-9.4	-23.3	-21.6	-44	-0.8	35.4
Ø	-0.9	-7.9	-13.9	-7.2	6	-11.7	-19	-10.2	8.7	-5.9

Table S6. 3: Given is the number of precipitation events, at which daily precipitation amounts were achieved in a range of 0.5 to >20 mm/day from 2009–2018. The precipitation manipulation lasted from 01 June until final harvest in every year. Data are splitted into ambient precipitation amount/day (control treatment) and reduced precipitation amount/day (25% reduction in daily rainfall amount).

		Number of precipitation events with							
		Ambient precipitation amount/day [mm]				Reduced precipitation amount/day [mm]			
Growing season	Crop¹	0.5–5.9	6–9.9	10–19.9	>20	0.5–5.9	6–9.9	10–19.9	>20
2009	Spring wheat	13	4	5	4	16	4	5	0
2010	Spring barley	15	4	2	2	17	2	2	2
2010/2011	Winter OSR	6	6	5	1	10	6	1	1
2011/2012	Winter wheat	19	5	3	1	22	3	3	0
2013	Spring barley	6	5	3	3	8	5	2	2
2013/2014	Winter OSR	12	4	1	3	12	2	2	1
2015	Spring wheat	12	4	3	1	14	5	0	1
2016	Spring barley	19	4	2	1	19	3	1	1
2016/2017	Winter OSR	5	1	1	3	6	1	1	2
2017/2018	Winter wheat	5	0	2	3	3	0	2	3

¹Abbreviation: OSR=oilseed rape.

Table S6. 4: Number of dry periods with specific lengths between ≤ 3 and >10 days from 2009–2018. The precipitation manipulation lasted from 01 June until final harvest in every year. The length of dry periods was measured at ambient precipitation frequency (control treatment) and reduced precipitation frequency (50% reduction in precipitation frequency, meaning 50% longer dry periods).

		Number of dry periods							
		Length of dry periods [days] at ambient precipitation frequency				Length of dry periods [days] at reduced precipitation frequency			
Growing season	Crop ¹	≤ 3	4–6	7–9	>10	≤ 3	4–6	7–9	>10
2009	Spring wheat	9	4	0	0	6	2	3	0
2010	Spring barley	10	1	1	1	8	2	1	1
2010/2011	Winter OSR	8	2	1	0	5	1	2	1
2011/2012	Winter wheat	7	2	0	0	9	4	0	0
2013	Spring barley	5	1	1	1	3	0	1	2
2013/2014	Winter OSR	4	4	0	0	5	1	0	2
2015	Spring wheat	3	9	1	1	1	2	4	1
2016	Spring barley	9	2	1	1	7	1	2	1
2016/2017	Winter OSR	2	1	0	1	1	0	1	1
2017/2018	Winter wheat	1	2	0	1	2	1	1	1

¹Abbreviation: OSR=oilseed rape.

Table S6. 5: Aboveground biomass production and grain/seed yield of spring wheat, winter wheat, spring barley and winter oilseed rape grown at the Hohenheim Climate Change Experiment 2009-2018. Plants were grown under ambient (T_a) or elevated (T_e) soil temperature in combination with the following precipitation patterns: ambient (A_a) or reduced (A_r) precipitation amount and ambient (F_a) or reduced (F_r) precipitation frequency.^a

	T_a				T_e				Three-way ANOVA ^b							
	A_a		A_r		A_a		A_r		Main effects				Interactions			
	F_a	F_r	F_a	F_r	F_a	F_r	F_a	F_r	T	A	F		T_x A	T_x F	A_x F	T_x A_x F
Spring wheat																
a) Aboveground biomass production at plant maturity [g DW m⁻²]																
2009	630.2 ± 135.6 ^{abc}	508.7 ± 42.4 ^c	515.6 ± 56.9 ^c	494.1 ± 44.5 ^c	736.6 ± 134.2 ^a	672.8 ± 131.1 ^{ab}	571.6 ± 122.8 ^{bc}	671.9 ± 47.2 ^{ab}	0.027	0.066	ns		ns	ns	0.068	ns
2015	1014.0 ± 44.9 ^a	991.8 ± 225.6 ^a	1055.7 ± 210.5 ^a	978.1 ± 201.9 ^a	940.1 ± 96.9 ^a	942.3 ± 79.4 ^a	877.6 ± 202.1 ^a	828.9 ± 75.5 ^a	ns	ns	ns		ns	ns	ns	ns
b) Yield at plant maturity [g m⁻²]																
2009	265.6 ± 60.1 ^{bc}	212.6 ± 16.9 ^c	209.7 ± 25.7 ^c	204.0 ± 19.6 ^c	339.8 ± 66.3 ^a	307.4 ± 66.4 ^{ab}	262.5 ± 57.8 ^{bc}	311.9 ± 23.8 ^{ab}	0.011	ns	ns		ns	ns	0.059	ns
2015	390.4 ± 34.1 ^a	388.9 ± 91.3 ^a	421.1 ± 79.1 ^a	396.5 ± 51.6 ^a	453.3 ± 36.8 ^a	456.7 ± 20.5 ^a	425.1 ± 83.8 ^a	387.9 ± 32.5 ^a	ns	ns	ns		ns	ns	ns	ns
Winter wheat																
a) Aboveground biomass production at plant maturity [g DW m⁻²]																
2011/2012	923.5 ± 190.0 ^{bc}	786.9 ± 60.4 ^c	905.2 ± 255.8 ^{bc}	952.4 ± 154.1 ^{abc}	1375.9 ± 354.5 ^{ab}	1305.2 ± 543.7 ^{abc}	1454.0 ± 572.1 ^a	1353.3 ± 419.3 ^{ab}	ns	ns	ns		ns	ns	ns	ns
2017/2018	402.4 ± 156.1 ^d	550.2 ± 124.3 ^{abcd}	502.6 ± 62.4 ^{bcd}	490.3 ± 67.8 ^{cd}	671.5 ± 152.5 ^{ab}	653.9 ± 69.2 ^{abc}	702.9 ± 102.9 ^a	633.2 ± 95.6 ^{abc}	0.041	ns	ns		ns	ns	ns	ns
b) Yield at plant maturity [g m⁻²]																
2011/2012	458.7 ± 85.7 ^{abc}	383.3 ± 35.8 ^c	440.9 ± 116.9 ^{bc}	465.7 ± 78.7 ^{abc}	559.0 ± 75.2 ^{abc}	598.9 ± 268.9 ^{abc}	562.7 ± 44.6 ^a	659.5 ± 196.3 ^{ab}	ns	ns	ns		ns	ns	ns	ns
2017/2018	211.2 ± 50.2 ^b	251.8 ± 67.7 ^{ab}	218.8 ± 32.9 ^b	224.2 ± 43.1 ^b	319.2 ± 69.9 ^a	298.9 ± 35.5 ^{ab}	332.6 ± 65.3 ^a	306.3 ± 54.0 ^{ab}	0.067	ns	ns		ns	ns	ns	ns
Spring barley																
a) Aboveground biomass production at plant maturity [g DW m⁻²]																
2010	1181.6 ± 182.2 ^a	1114.4 ± 192.5 ^a	1048.2 ± 120.0 ^a	1232.1 ± 236.4 ^a	1077.2 ± 259.9 ^a	1073.6 ± 159.2 ^a	1222.2 ± 44.2 ^a	1050.9 ± 25.8 ^a	ns	ns	ns		ns	ns	ns	0.045
2013	564.5 ± 166.7 ^c	613.2 ± 178.5 ^{bc}	579.4 ± 149.0 ^c	650.5 ± 151.1 ^{abc}	807.7 ± 81.1 ^a	783.2 ± 92.9 ^{ab}	753.3 ± 90.9 ^{abc}	790.7 ± 79.2 ^{ab}	0.022	ns	ns		ns	ns	ns	ns
2016	679.6 ± 108.8 ^d	738.9 ± 175.8 ^{bcd}	785.9 ± 133.9 ^{cd}	757.9 ± 145.8 ^{cd}	1006.2 ± 216.1 ^{abc}	1076.4 ± 271.4 ^{ab}	1184.7 ± 228.5 ^a	1053.4 ± 343.8 ^{abc}	0.052	ns	ns		ns	ns	ns	ns
b) Yield at plant maturity [g m⁻²]																
2010	663.1 ± 109.5 ^a	590.8 ± 88.9 ^a	587.5 ± 82.1 ^a	672.8 ± 142.6 ^a	587.3 ± 121.6 ^a	592.6 ± 71.9 ^a	679.7 ± 13.9 ^a	584.5 ± 32.1 ^a	ns	ns	ns		ns	ns	ns	0.021
2013	296.2 ± 86.7 ^d	322.9 ± 100.7 ^{cd}	312.6 ± 86.2 ^d	346.8 ± 87.7 ^{bcd}	457.8 ± 48.9 ^a	433.8 ± 48.3 ^{ab}	426.1 ± 49.9 ^{abc}	430.3 ± 38.1 ^{ab}	0.014	ns	ns		ns	ns	ns	ns
2016	369.7 ± 46.7 ^d	396.9 ± 91.3 ^{cd}	418.2 ± 81.9 ^{bcd}	420.1 ± 87.4 ^{bcd}	565.8 ± 130.7 ^{abcd}	600.7 ± 179.0 ^{ab}	663.6 ± 149.2 ^a	574.7 ± 224.2 ^{abc}	0.064	ns	ns		ns	ns	ns	ns

Table S6.5: Continued.

	T _a				T _e				Three-way ANOVA ^b							
	A _a		A _r		A _a		A _r		Main effects				Interactions			
	F _a	F _r	F _a	F _r	F _a	F _r	F _a	F _r	T	A	F	T _x A	T _x F	A _x F	A _x F	T _x A _x F
Winter oilseed rape																
a) Aboveground biomass production at plant maturity [g DW m⁻²]																
2010/2011	1677.3 ± 755.3 ^{abc}	1694.8 ± 240.7 ^{abc}	1833.9 ± 246.5 ^{ab}	2117.1 ± 306.9 ^a	1324.3 ± 195.0 ^c	1306.3 ± 180.9 ^c	1632.9 ± 253.8 ^{bc}	1564.7 ± 208.9 ^{bc}	ns	0.016	ns	ns	ns	ns	ns	ns
2013/2014	1061.8 ± 260.2 ^a	1336.4 ± 304.2 ^a	1209.1 ± 358.8 ^a	1057.0 ± 318.6 ^a	1352.5 ± 345.3 ^a	1297.7 ± 219.5 ^a	1096.8 ± 177.5 ^a	1227.6 ± 477.3 ^a	ns	ns	ns	ns	ns	ns	ns	<i>0.081</i>
2016/2017	953.4 ± 372.5 ^a	1087.0 ± 402.1 ^a	1028.9 ± 337.9 ^a	936.0 ± 335.3 ^a	1190.1 ± 1044.8 ^a	922.1 ± 406.5 ^a	1321.1 ± 175.2 ^a	1331.4 ± 1308.9 ^a	ns	ns	ns	ns	ns	ns	ns	ns
b) Yield at plant maturity [g m⁻²]																
2010/2011	514.9 ± 199.2 ^{abc}	476.1 ± 84.8 ^{abc}	602.3 ± 124.8 ^{ab}	623.8 ± 110.3 ^a	401.1 ± 61.1 ^c	389.6 ± 65.6 ^c	476.9 ± 83.7 ^{abc}	462.2 ± 70.2 ^{bc}	ns	ns	ns	ns	ns	ns	ns	ns
2013/2014	360.8 ± 54.5 ^a	474.9 ± 99.4 ^a	426.4 ± 138.2 ^a	378.9 ± 122.1 ^a	419.5 ± 96.9 ^a	426.7 ± 49.7 ^a	371.2 ± 58.4 ^a	395.3 ± 134.1 ^a	ns	ns	ns	ns	ns	ns	ns	ns
2016/2017	297.2 ± 118.9 ^a	329.8 ± 132.8 ^a	298.9 ± 99.5 ^a	287.8 ± 110.1 ^a	268.4 ± 150.2 ^a	279.8 ± 167.4 ^a	373.1 ± 66.9 ^a	290.5 ± 250.6 ^a	ns	ns	ns	ns	ns	ns	ns	ns

^aData are means ± standard deviations across four replicates (n = 4) and were tested by three-way ANOVA for main effects or interaction effects of the fixed factors T, A, and F. Fishers least significance difference (LSD) test results indicate statistically significant differences at P < 0.05 level of probability and are labelled by different letters above the standard deviations. ^bns = not significant (P > 0.05); bold numbers indicate significant main or interaction effects of T, A, F (P ≤ 0.05) and numbers in italics indicate trend (0.1 ≥ P > 0.05). Abbreviation: DW = dry weight.

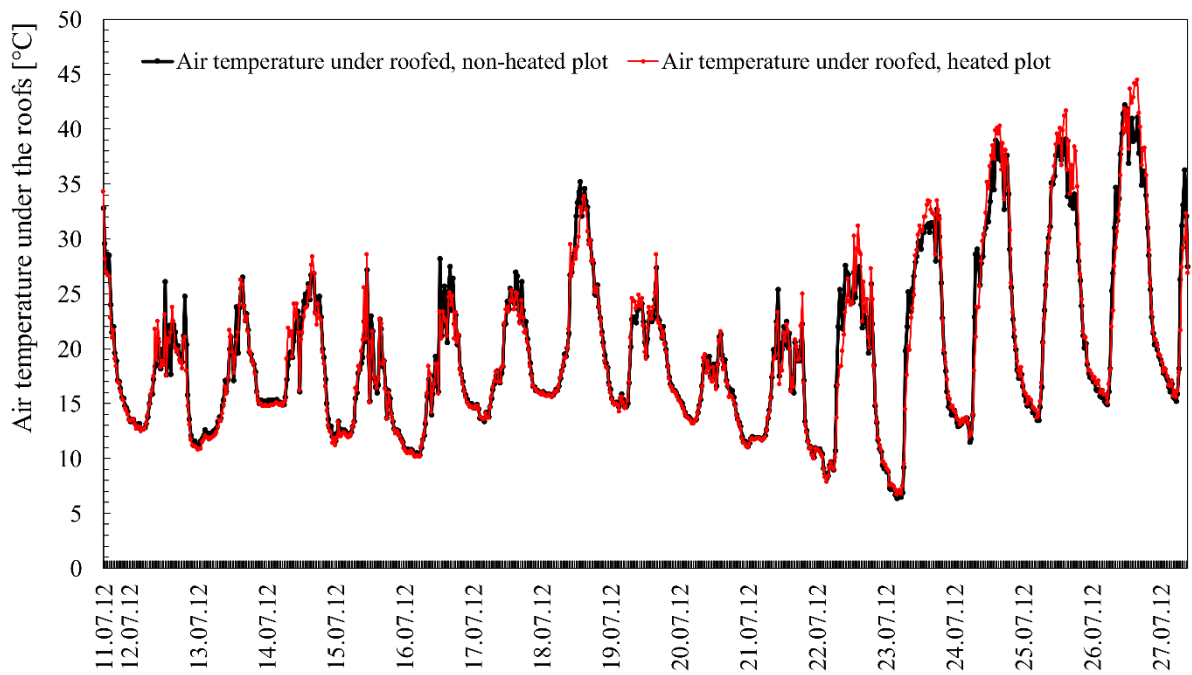


Figure S6. 1: Air temperature measured in 0.3 m height under the roofs. The measurement was done in two randomly selected roofed subplots in winter wheat: subplot number 10 with elevated soil temperature and subplot number 6 with ambient soil temperature. Data logger were used for the measurement.

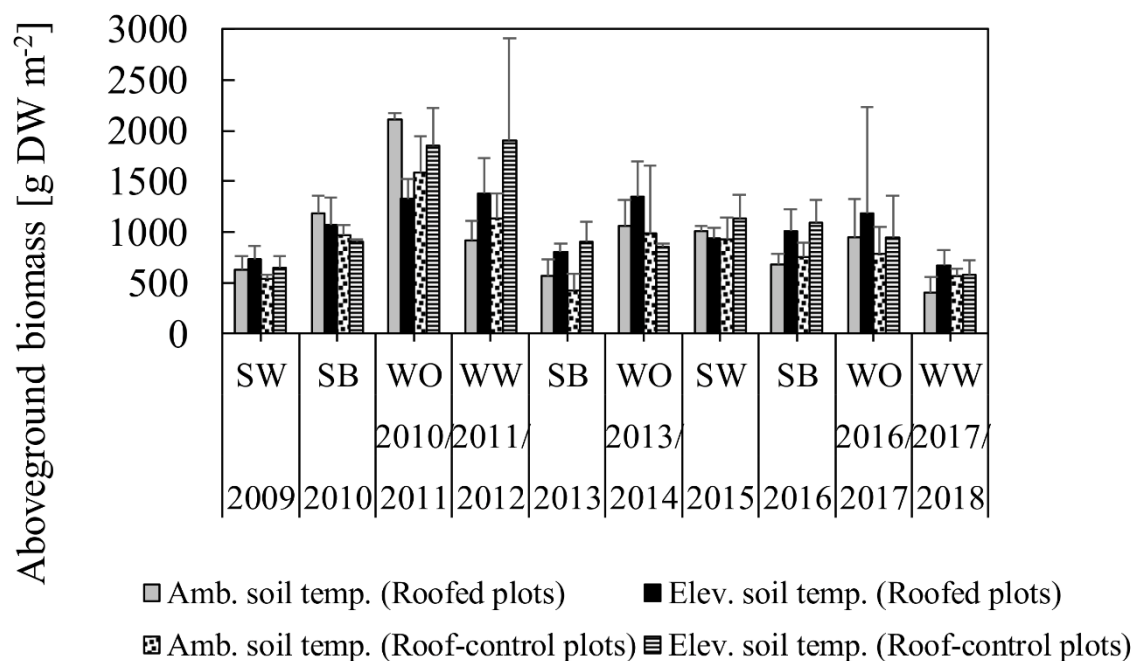


Figure S6. 2: Aboveground biomass of crops grown in crop rotation between 2009 and 2018 either in roofed plots (n=4) or in roof-control plots (n=4). Error bars show standard deviation (n=4). Abbreviations: DW: dry weight; SW: spring wheat; SB: spring barley; WO: winter oilseed rape; WW: winter wheat; Amb.: ambient; Elev.: elevated.

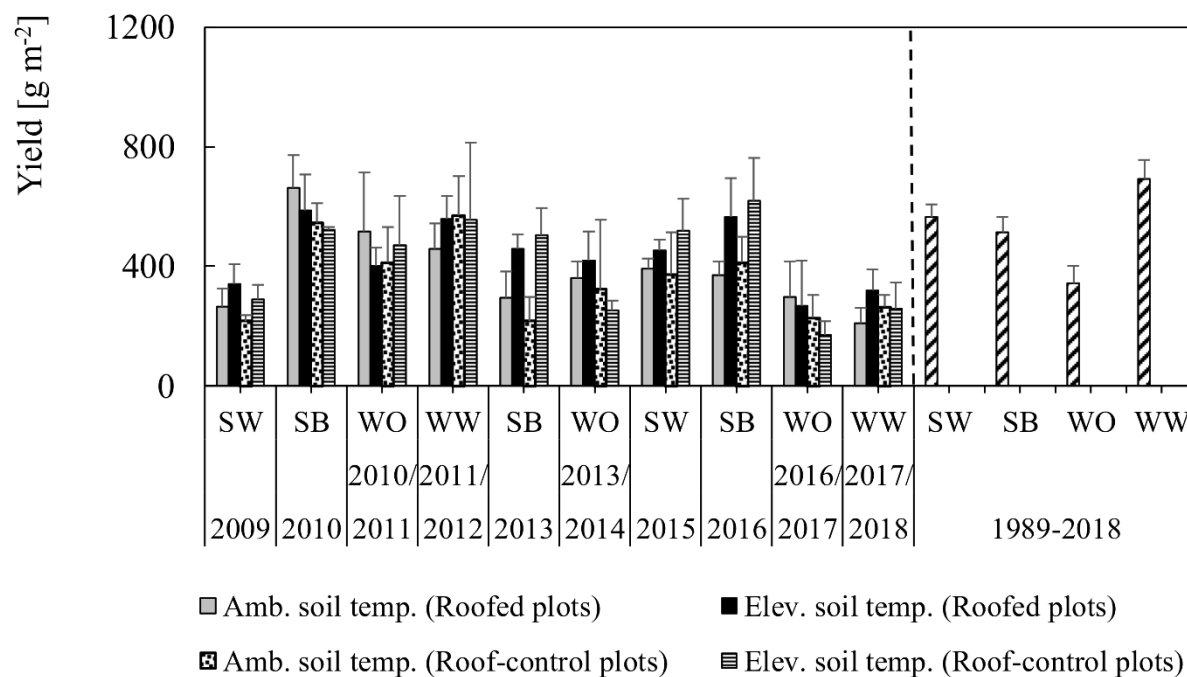


Figure S6. 3: Yield of crops grown in crop rotation between 2009 and 2018 either in roofed plots ($n=4$) or in roof-control plots ($n=4$). Striped bars show the long-term average grain or seed yield in Baden-Wuerttemberg (1989-2018; $n=30$) (Statistisches Landesamt Baden-Württemberg 1989-2018), which is comparable to the ambient soil temperature treatment. Error bars show standard deviation. Abbreviations: DW: dry weight; SW: spring wheat; SB: spring barley; WO: winter oilseed rape; WW: winter wheat; Amb.: ambient; Elev.: elevated.

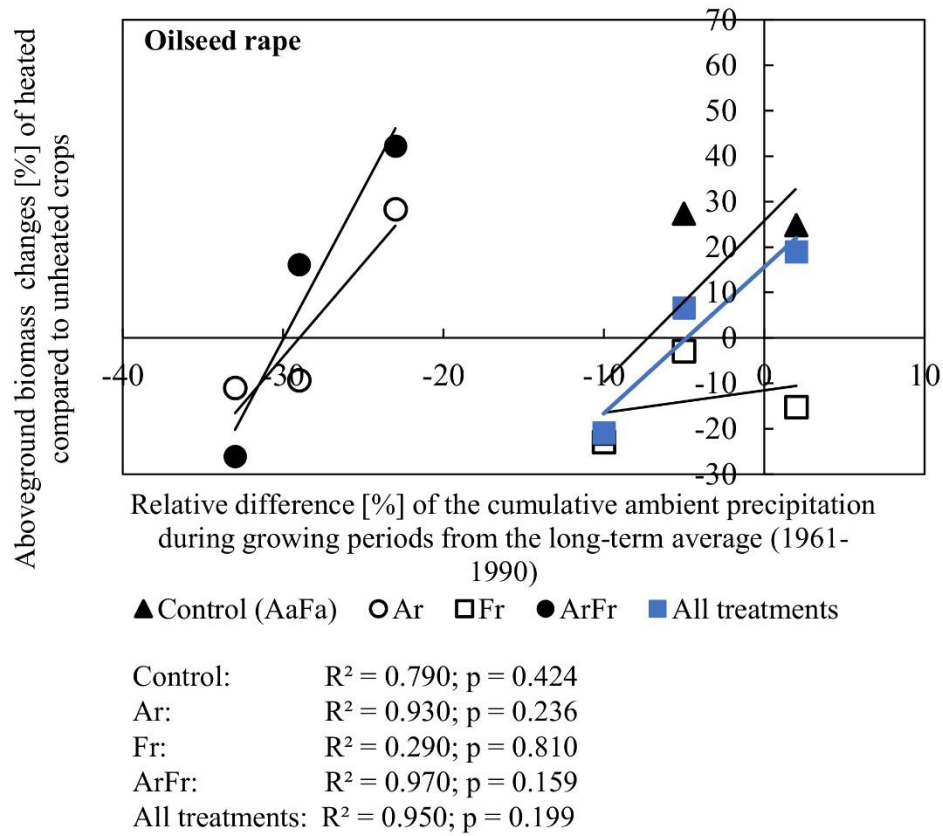


Figure S6. 4: Aboveground biomass changes (%) of oilseed rape under elevated compared to ambient soil temperature if grown under different cumulative ambient precipitation (mm) during the growing periods. Oilseed rape growing periods: 2010/2011, 2013/2014 and 2016/2017 winter oilseed rape (n=3). Treatments: triangle: ambient precipitation amount (Aa) and –frequency (Fa); unfilled circle: reduced precipitation amount (Ar); unfilled square: reduced precipitation frequency (Fr); filled circle: reduced precipitation amount (Ar) and –frequency (Fr). The trendline “all treatments” compares all ambient soil temperature treatments (TaAaFa, TaArFa, TaAaFr, TaArFr; n=16) with all elevated soil temperature treatments (TeAaFa, TeArFa, TeAaFr, TeArFr; n=16). Only roofed plots are included. Data are analysed by a correlation analysis.

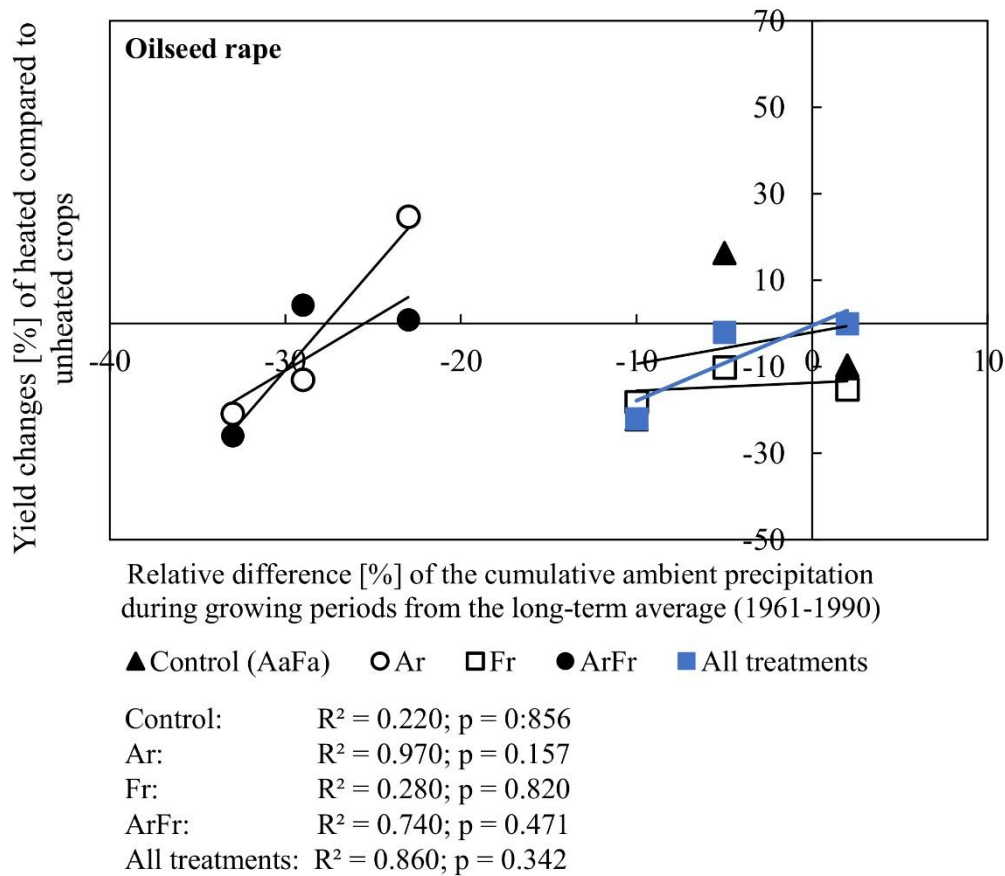


Figure S6. 5: Yield changes (%) oilseed rape under elevated compared to ambient soil temperature if grown under different cumulative ambient precipitation (mm) during the growing periods. Oilseed rape growing periods: 2010/2011, 2013/2014 and 2016/2017 winter oilseed rape ($n=3$). Treatments: triangle: ambient precipitation amount (Aa) and –frequency (Fa); unfilled circle: reduced precipitation amount (Ar); unfilled square: reduced precipitation frequency (Fr); filled circle: reduced precipitation amount (Ar) and –frequency (Fr). The trendline “all treatments” compares all ambient soil temperature treatments (TaAaFa, TaArFa, TaAaFr, TaArFr; $n=16$) with all elevated soil temperature treatments (TeAaFa, TeArFa, TeAaFr, TeArFr; $n=16$). Only roofed plots are included. Data are analysed by a correlation analysis.

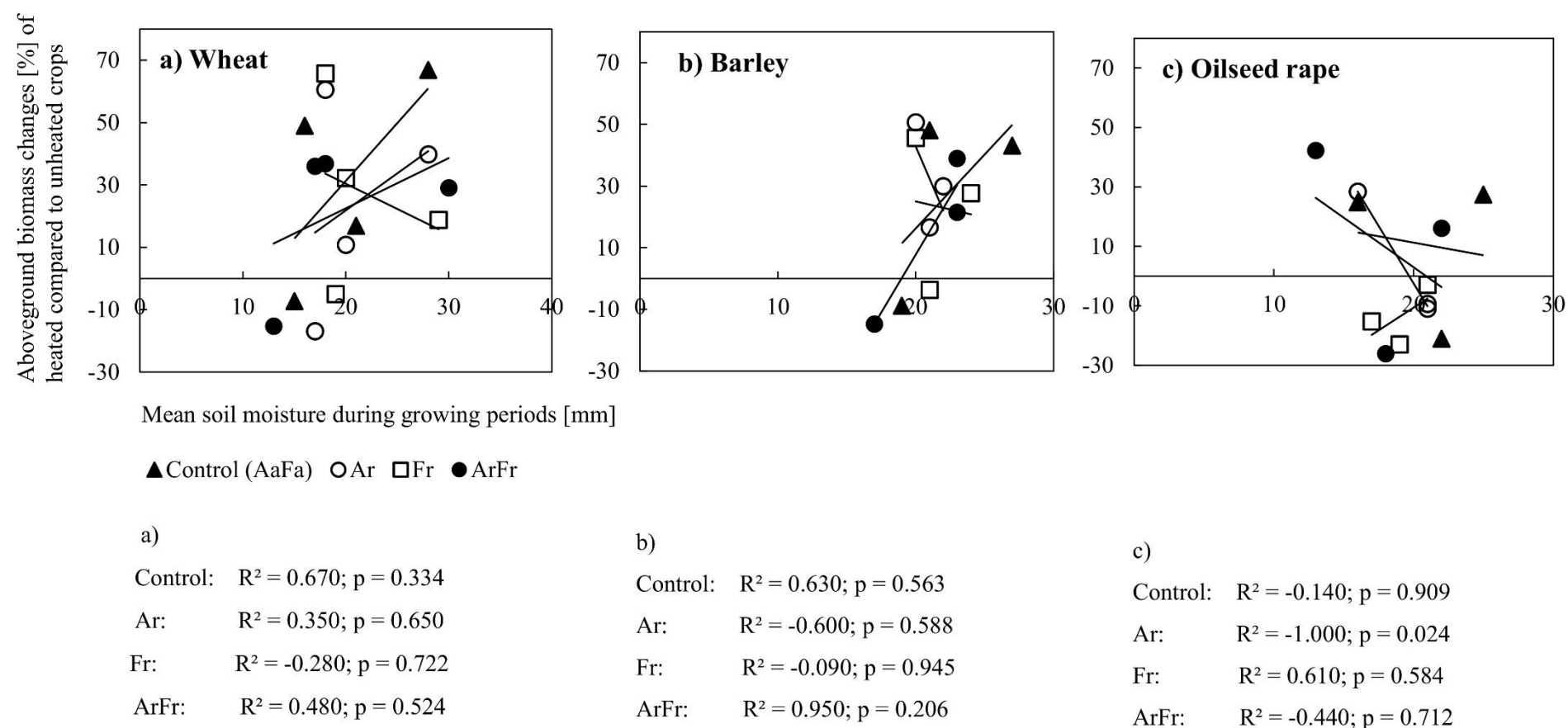


Figure S6. 6: Changes of aboveground biomass [%] under elevated compared to ambient soil temperature are correlated with the mean soil moisture during growing periods [mm]. Data of wheat (a), barley (b) and oilseed rape (c) are analyzed by a Pearson's correlation analysis. Wheat growing periods: 2009 and 2015 spring wheat, 2011/2012 and 2017/2018 winter wheat (n=4). Barley growing periods: 2010, 2013 and 2016 spring barley (n=3). Oilseed rape growing periods: 2010/2011, 2013/2014 and 2016/2017 winter oilseed rape (n=3). Treatments: triangle: ambient precipitation amount (Aa) and –frequency (Fa); unfilled circle: reduced precipitation amount (Ar); unfilled square: reduced precipitation frequency (Fr); filled circle: reduced precipitation amount (Ar) and –frequency (Fr).

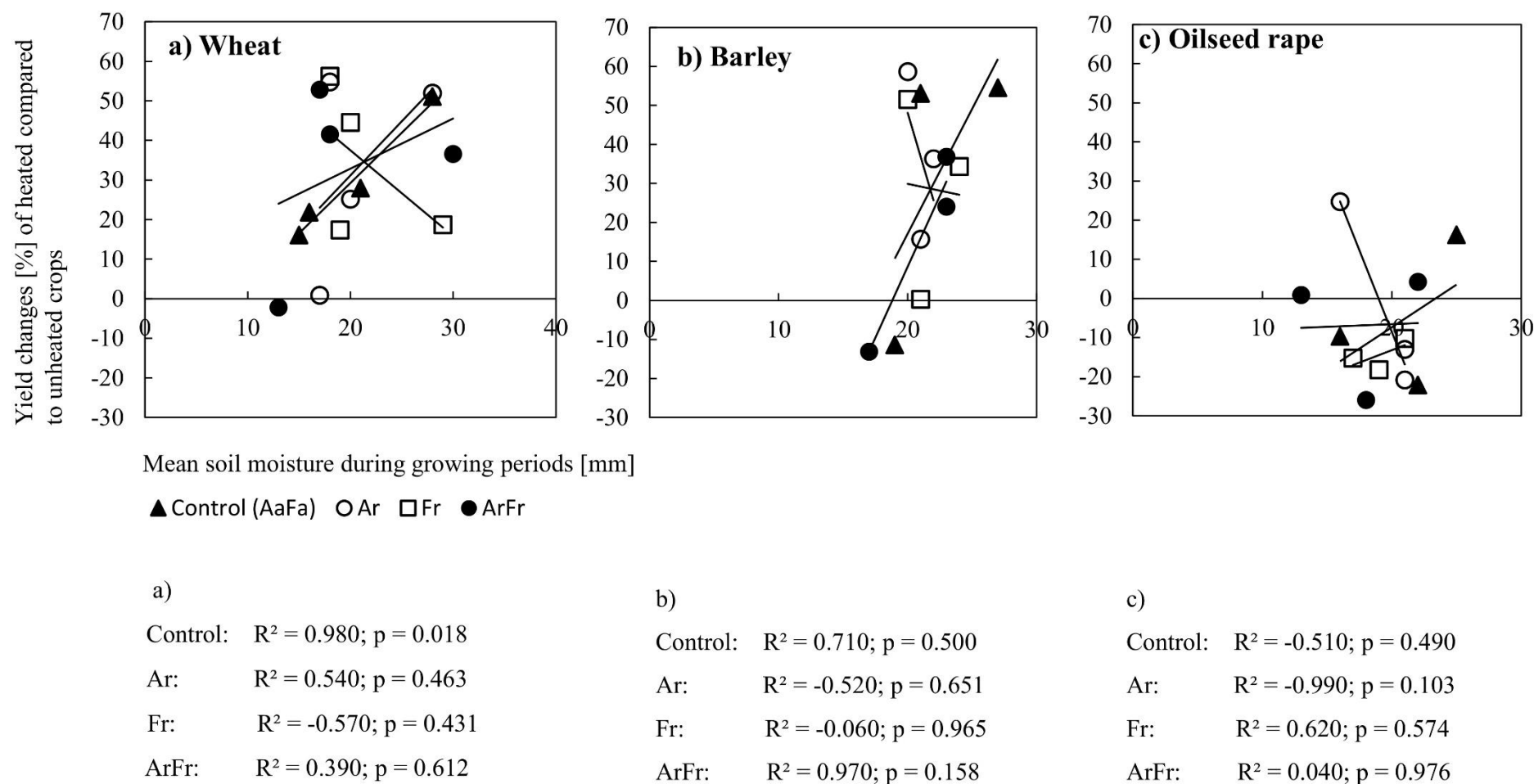


Figure S6. 7: Changes of yield [%] under elevated compared to ambient soil temperature are correlated with the mean soil moisture during growing periods [mm]. Data of wheat (a), barley (b) and oilseed rape (c) are analyzed by a Pearson's correlation analysis. Wheat growing periods: 2009 and 2015 spring wheat, 2011/2012 and 2017/2018 winter wheat (n=4). Barley growing periods: 2010, 2013 and 2016 spring barley (n=3). Oilseed rape growing periods: 2010/2011, 2013/2014 and 2016/2017 winter oilseed rape (n=3). Treatments: triangle: ambient precipitation amount (Aa) and –frequency (Fa); unfilled circle: reduced precipitation amount (Ar); unfilled square: reduced precipitation frequency (Fr); filled circle: reduced precipitation amount (Ar) and –frequency (Fr).

7 General discussion

Within the scope of this thesis, winter wheat, spring barley and winter oilseed rape were grown in crop rotation from 2016-2018 at a temperate agricultural ecosystem to analyze single and combined effects of elevated soil temperature (+2.5 °C), reduced summer precipitation amount (-25%), and reduced summer precipitation frequency (-50%) on crop development, leaf gas exchange, biomass production, harvestable yield and yield quality. In addition, possible impacts of individual weather conditions during each growing seasons on the effects of the climate changes factors were investigated.

In general, experimental warming in the HoCC experiment was quite stable across the ten growing seasons (2009-2018), meaning on average an increase in soil temperature in the roofed plots by 1.9 ± 0.3 °C during the vegetation period of spring crops (2009, 2010, 2013, 2015, 2016) and by 1.9 ± 0.2 °C for winter crops (2010/2011, 2011/2012, 2013/2014, 2016/2017, 2017/2018). Mean soil moisture varied strongly between 15-28 Vol% across the years. In addition, elevated soil temperature reduced the soil moisture content in our study, which was most likely a consequence of increasing soil evaporation. This resulted in a decrease in water availability in the soil, which was in agreement with hypothesis (iv). A soil moisture reduction under elevated soil temperature was also shown before in the HoCC experiment (Högy et al. 2013; Poll et al. 2013) and in field experiments conducted in grassland with infrared radiators (Liu et al. 2009) or heating cables (Ineson et al. 1998; Shaver et al. 2000).

7.1 Plant development

Soil waring effects on the development of spring barley and winter oilseed rape were studied in Chapter 4 and 5, since an accelerated crop development was supposed only during spring but not afterwards (hypothesis (i)). It is known that in temperate climates an increase in soil temperature can stimulate plant development (Bowen 1991). In accordance, Patil et al. (2010) reported for winter wheat grown under 5.0 °C soil warming in lysimeters a faster development during early plant life. Similarly, the rate of early peanut development was accelerated under elevated soil temperature by 4.5 °C in a greenhouse experiment (Prasad et al. 2006). As expected, the development of spring barley and winter oilseed rape under increased soil temperature in the present study was accelerated during the moist period of spring in the growing periods 2016 and 2016/2017 (Chapter 4 and 5). Although the evaporation rate was higher in plots with soil warming, sufficient soil moisture conditions during early growth stages were observed as a result of frequent precipitation events during spring 2016 and rather high

precipitation amounts during spring 2017. In accordance, crops experienced no water scarcity during spring and soil warming accelerated plant development. However, in contrast to the hypothesis (i) posed in this thesis, spring barley showed also an accelerated plant development during later growth stages and at maturity in 2016. This differed was in contrast to observations made in winter wheat, because after stem elongation the faster development under soil warming declined (Patil et al. 2010). This resulted in about one week earlier flowering and final harvest. These findings can be explained by a relatively wet summer with high precipitation amounts end of May and during June 2016. Thus, different than expected, the soil was relatively moist after spring and an additional evaporation due to soil warming during summer was not strong enough to limit plant development. In addition, the water use efficiencies of biomass and yield tended to increase by 60% and 69% in plots with soil warming, respectively ($P=0.067$ and $P=0.062$). This seems to be an indication that spring barley did not experienced water stress after spring in the soil warming treatment.

Beside a faster development in warmed plots, also increased canopy heights of spring barley and winter oilseed rape were observed in 2016 and 2016/2017. Whereas spring barley was taller under increased soil temperature over the entire growing period, the canopy height of winter oilseed rape was only taller from early growth stages to full flowering (Chapter 4 and 5). Afterwards, the soil warming effect on canopy height of winter oilseed rape vanished. A likely explanation for different soil warming effects on canopy height of both crops after spring is, that the weather conditions during summer in 2016 (barley) and in 2017 (winter oilseed rape) differed. In summer 2017, higher air temperatures and less precipitation were recorded, which reduced soil moisture in a higher degree than in summer 2016. Similarly to the results for barley in 2016, Bamminger et al. (2016) reported increased canopy heights during the entire growing period of winter oilseed rape in 2014 within the HoCC experiment, most likely due to wet summer conditions with high precipitation from May until final harvest in July in 2014. Appropriate high soil moisture values were measured in 2014 at the HoCC field site (Chapter 6). In contrast, Siebold and Tiedemann (2012) found the plant lengths of winter oilseed rape was not significantly effected by 4.0 °C soil warming during the entire growing period.

The results indicate that the development of spring barley and winter oilseed rape under soil warming was directly linked to soil moisture, which in turn was related to individual weather conditions during the growing period.

7.2 Leaf gas exchange

In 2016 we studied the effects of soil warming, reduced summer precipitation amount, and – frequency on leaf gas exchange (A_{net} , g_s , E) of spring barley at stem elongation and flowering (Chapter 4). At both development stages, soil warming did not affect net photosynthesis (A_{net}), stomatal conductance (g_s) and transpiration (E), which was different than hypothesized (iii). Only when combined with reduced precipitation amount, soil warming reduced g_s and E . However, these findings were partly supported by observations of Weldearegay et al. (2016), who exposed three spring wheat cultivars in pots placed in a glasshouse during anthesis to soil warming (+3.0 °C), longer dry periods (withholding of irrigation for approximately two weeks) and a combination of both. Similarly they found that soil warming did not affect A_{net} . Contrary, soil warming alone was able to decrease g_s , but only in the beginning of anthesis. And A_{net} and g_s were reduced by soil warming combined with longer dry periods, which we did not observe in spring barley.

Photosynthesis of higher plant species is known to be affected by elevated temperatures (Berry and Bjorkman 1980; Paulsen 1994). However, there are differences in the response of photosynthesis to changes in air and soil temperatures. The effects of air temperatures on crop photosynthesis are direct, since increased air temperatures until a temperature optimum can alter leaf gas exchange due to an increasing stomatal conductance (Berry and Bjorkman 1980). In contrast, elevated soil temperatures indirectly affect crop physiology through effects on the root system (Hantschel et al. 1995). Soil warming of 2.5 °C in this thesis were supposed to be too small to prompt physiological changes in barley.

Similar to soil warming, altered precipitation pattern have also an indirect effect on leaf gas exchange. A lower precipitation amount or -frequency reduce water availability for plants in the soil, which can lead to the production of abscisic acid which is transported to the leaves and resulting in stomatal closure (Feller and Vaseva 2014).

Interestingly, interacting effects of precipitation amount and soil temperature were observed (Chapter 4). A simultaneous occurrence of reduced precipitation amount and soil warming decreased water use efficiency of photosynthesis, which was in agreement with the observed reactions of drought- and temperature-stressed wheat plants grown in a greenhouse (Shah and Paulsen 2003) and underlined the hypothesis (ii) that the simultaneous occurrence of multiple climate factors results in an additive negative effect on barley ecophysiology.

Reduced summer precipitation amount was shown to increase g_s and E of barley in this thesis (Chapter 4), whereas both parameters were reduced in barley grown under 33% less water amount in growth chambers (Schmid et al. 2016). With regard to the effects of longer dry

periods as consequence of reduced precipitation frequency in our study, a decrease in g_s at stem elongation of spring barley occurred (Chapter 4), which was similar observed by Weldearegay et al. (2016) in spring wheat at anthesis. In our study, g_s was the leaf gas exchange parameter which was most sensitive to water scarcity (reduced precipitation amount and –frequency). This was in agreement to observations in barley either exposed to longer dry periods (withholding of irrigation for approximately 50 days depending on the genotype) in rain shelters (González et al. 2010) or to 33% reduced water amount in growth chambers (Schmid et al. 2016). It can be supposed, that a reduction in precipitation stronger reduced soil water content than higher evaporation rates due to soil warming. Therefore leaf gas exchange of spring barley was more affected by altered precipitation patterns than by soil warming in this thesis.

In general, spring barley showed higher values of A_{net} , g_s , and E at stem elongation than at full flowering, which was independent from the climate manipulations (Chapter 4). This could be linked with different ambient weather conditions at both physiological stages in 2016. Plants reached the stem elongation stage during spring, when soil moisture was higher and air temperatures lower than during the flowering stage in the beginning of summer time. The temperature optimum for barley net photosynthesis is between 15.0-20.0 °C for vegetative and reproductive growth (Todd 1982). Therefore, lower air temperatures during spring in our study seemed to enable barley to reach higher photosynthesis rates at stem elongation than at flowering. In agreement, Jensen et al. (1996a) measured leaf gas exchange in oilseed rape and also detected higher A_{net} and g_s values before flowering and a decrease in those parameters during and after flowering. Similarly, it has been reported that A_{net} and g_s were higher during stem elongation than during flowering in 16 wheat genotypes (Reynolds et al. 2000).

7.3 Biomass and yield

7.3.1 Biomass and yield responses to soil warming

Around flowering, soil warming was observed to stimulate the production of green leaves and stems of spring barley in the growing season 2016 (Chapter 4). As a consequence, the total aboveground biomass was higher under elevated soil temperature as compared to ambient soil temperatures. Also Gavito et al. (2001) observed an increase in leaf and stem biomass of winter wheat around flowering under elevated soil temperature of 5.0 °C. Increased crop productivity under soil warming was maybe an effect of increased root growth, because soil warming enhanced root biomass by 80% at stem elongation in 2016 (Chapter 4). This is in accordance with earlier observations, showing a stimulated root growth rate under soil warming (Gray and

Brady 2016). Thus more roots leading to an accelerated uptake of water and nutrients in warmer soils, which was found in temperate climates (Bowen 1991). Similarly, Gavito et al. (2001) observed elevated root growth as well as enhanced nutrient uptake under soil warming by 5.0 °C, assuming them being the reason for a stimulation effect on aboveground biomass production of winter wheat.

Yield of wheat, barley and oilseed rape was not decreased under soil warming in the present studies. In 2016, the length of the grain filling period was increased due to soil warming in spring barley (Chapter 4). Therefore, plants had more time to acquire carbohydrates for grain growth. This tended to increase the grain yield of barley by 54% ($P=0.057$) since the number of ears was increased by 36%. This result is in contradiction to hypothesis (iv) and hard to compare with literature, since only a few experiments with cereals grown under soil warming in an arable field have been conducted until now (Hantschel et al. 1995; Kamp et al. 1998; Xiao et al. 2010). However, Patil et al. (2010) found in a lysimeter experiment no effects of soil warming (+5.0 °C) on grain filling period and grain yield of winter wheat. Similarly, the grain filling period of wheat did not change under soil warming by 2.4 °C (Li et al. 2016). Impacts of elevated soil temperature on crop yield can differ as compared to effects due to elevated air temperature. Elevated air temperature can shorten the period of grain filling (Yadav et al. 2019). In low latitudes, increase of air temperatures during the grain filling period is associated with a decrease in crop yield as a consequence of a reduction in plant photosynthesis, degradation of thylakoid components, and lower carbon exchange rate per unit of leaf area (Hatfield 2019). Accordingly, the length of the grain filling period of wheat and barley was reduced in studies with elevated air temperature to simulate heat stress (Sofield et al. 1977; Chowdhury and Wardlaw 1978; Ingvordsen et al. 2018), and grain yield reductions in barley have been reported as well under air temperature increases (Savin et al. 1997; Alemayehu et al. 2014; Ingvordsen et al. 2018). Most likely, soil warming was able to stimulate root growth due to sufficient ambient precipitation in 2016 in the present study, resulting in enhanced uptake of water and nutrients. According to that, the lack of negative impacts of soil warming on the grain filling period and crop yield seemed to be an indication that elevated temperatures in soil or air can differ in their impacts on crop physiology.

An explanation for missing soil warming effects on aboveground biomass and seed yield of winter oilseed rape in our study (Chapter 5 and 6) could be since it prefers cooler temperatures, especially during early winter, when slightly elevated mean air temperatures of only 1.0 °C have been shown to induce yield instability and yield losses (Brown et al. 2019). Since higher

air temperatures are linked with higher soil temperatures, it seems reasonable that soil warming had no stimulating effect on yield of winter oilseed rape.

Long-term aboveground biomass and yield data (2009-2018) of wheat, barley and oilseed rape were analyzed with regard to universal effects of elevated soil temperature and altered precipitation pattern on those parameters (Chapter 6). In order to explain the inter-annual variability in biomass and yield responses of these three crops, specific annual environmental conditions (cumulative ambient precipitation, soil moisture, air temperature) were analyzed for each of the growing seasons. While biomass and yield of spring wheat remained unaffected due to soil warming of about 2.0 °C under dry growing conditions in 2015, spring wheat biomass was increased in the moist growing season 2009 due to sufficient precipitation in spring. In accordance to our results in 2015, Hartley et al. (2007) observed that aboveground biomass and yield of spring wheat remained unaffected under soil warming of 3.0 °C and low soil moisture content during the growing season. Since no biomass or yield losses were observed in wheat, they suggested that soil warming did not cause drought stress despite the soil was rather dry. In another soil warming study with +5.0 °C above ambient soil temperature, Patil et al. (2010) found winter wheat to increase aboveground biomass at early plant development, whereas aboveground biomass was not affected at maturity. They supposed that higher soil temperatures accelerate plant growth during early development. However, in later growth stages, this soil warming effect decreased because the effect of increasing air temperatures became dominant (Awal and Ikeda 2002; Patil et al. 2010). With regard to our observations, no universal effects of elevated soil temperature on aboveground biomass and yield of wheat, barley and oilseed rape over the ten growing seasons (2009-2018) were found (see hypothesis (vii)). Since in some of the growing seasons aboveground biomass of cereals were stable under soil warming at maturity, it increased in others. Therefore it can be concluded, that the acceleration effect on plant biomass production due to soil warming did not solely depend on air temperatures. It was likely, that another factor have to be involved, which also has an impact on plant growth and is present during later growth stages. Accordingly, a stimulating effect of soil warming on aboveground biomass and yield production of spring barley in 2013 and 2016 was detected. During both growing seasons, air temperatures were moderate, but soil moisture was at a high level. It can be suggested that the high soil moisture content was the factor which promoted plant growth of spring barley. Similarly, the aboveground biomass of winter wheat was increased in the wet growing season 2017/2018, but not in the dry season 2011/2012. The growing season 2017/2018 had 137 mm more mean ambient precipitation and 28 Vol.% instead of 16 Vol.% mean soil moisture compared to 2011/2012.

The most interesting finding from the comparison of the ten-year data was, that cumulative ambient precipitation and annual soil moisture conditions determined the effects of elevated soil temperature. Accordingly, under low cumulative ambient precipitation and low mean soil moisture, stable crop biomasses and yields were observed, whereas greater cumulative ambient precipitation and higher soil moisture were linked to an increase in aboveground biomass and harvestable yield of cereals. Therefore, yearly weather conditions seem to be a key control for enhanced plant growth in cereal crops under global warming. Moreover, specific annual environmental conditions (e.g., wet or dry year) can explain the observed inter-annual variability in the responses of aboveground biomasses and yields of the specific crops (see hypothesis (viii)).

Another interesting result was that soil warming was able to promote crop growth of winter wheat in the growing period 2017/2018, as air temperature was noticeable high. Both 2017 and 2018 belonged to the five warmest years ever recorded in Germany since 1881 (Umweltbundesamt 2020). Therefore, the air temperature was >1.5 °C higher in spring and summer at the HoCC experimental area compared to the long-term period (1981-2010). Rising air temperatures are known to increase evaporation rates, which reduce ecosystem water budgets and can negatively affect plant productivity and soil respiration (Shaver et al. 2000). However, high mean soil moisture values during winter 2017/2018 as a result of high ambient precipitation were observed. Kannoja et al. (2019) reported that the activity of soil microorganisms increase during a wet season or when soils regained their moisture through wet conditions. A higher microorganism activity in soils elevates the mineralization of nitrogen and phosphorus, which can explain the enhanced crop growth of winter wheat. Also soil warming of 2.0 and 4.0 °C was observed to stimulate the soil microbial activities (Chen et al. 2020; Wu et al. 2020). Moreover the soil in this study was capable of storing great volumes of water. According to that it was observed in other regions, where soils have high water holding capacity, that high precipitation during autumn or winter can compensate for water scarcity caused by dry conditions in spring and summer (Wang et al. 2009; He et al. 2021).

7.3.2 Biomass and yield responses to altered precipitation pattern

With regard to long-term data 2009-2018, decreasing summer precipitation amounts by 25% showed only marginal effects on aboveground biomass and yield of wheat, barley and oilseed rape (Chapter 6). In agreement with our hypothesis (v), a tendentially reduction in the aboveground biomass of spring wheat due to reduced precipitation amount was observed in 2009. In contrast to hypothesis (v), aboveground biomass of winter oilseed rape was increased

in the growing season 2010/2011 under less precipitation amount, which seems to be in disagreement to the literature (Kang et al. 2009; Hatfield 2019). Most likely because the simulated water scarcity during summer was not enough to induce drought stress conditions in the present study. Moreover, the grain and seed yield was not changed under reduced precipitation amount in all crops.

Furthermore, a reduction in precipitation frequency by 50% did not change aboveground biomass and yield of wheat, barley and oilseed rape were. An explanation could be, that the length of dry periods was not notable enhanced compared to ambient precipitation frequency (Chapter 6). Another explanation could be the time in the crop life when the precipitation frequency was reduced. Terminal water scarcity was simulated in the HoCC experiment from beginning of June until end of August and in this crop development phase the formation of leaves, stems and ears was already finished and plants started with grain filling and ripening. Thus, the production of aboveground biomass was likely finished before the simulation of longer dry periods started.

Similarly, Patil et al. (2010) simulated terminal water scarcity during summer months by reducing precipitation amount (-24%) and -frequency (-50%) in winter wheat. They also observed that grain yield remained unaffected. Furthermore, grain yields of six barley cultivars were not affected due to terminal water stress under rain shelters in a field experiment (González et al. 2007). Another explanation for missing yield changes in cereal crops under less precipitation amount could be an increased water use efficiency under water scarcity, which was observed in spring barley in 2016 (Chapter 4). Also Bhattacharya (2019) reported that plants can increase their water use efficiency under dry conditions, i.e., in semiarid regions. Beside a higher water use efficiency of yield, a shift in grain size patterns of spring barley was observed in 2016. Thus, the biggest grain size class (GSC) >2.8 mm increased only marginal under less precipitation amount, whereas grains smaller >2.8 mm decreased markedly, resulting in grain yield which was not affected under reduced precipitation amount.

The explanation for missing effects on the seed yield of oilseed rape under water scarcity seems to be different than that for cereals. Champolivier and Merrien (1996) reported that a terminal water reduction from flowering until maturity resulted in reduced seed yield of winter oilseed rape. Also Singer et al. (2016) demonstrated that reduced water amount during the periods of seed set or seed-filling can result in a decrease in seed yield. Therefore, terminal water shortage was most likely not the reason for stable seed yield of winter oilseed rape observed in this thesis. However, observed were relatively wet conditions during the three growing seasons of winter

oilseed rape (2010/2011, 2013/2014, 2016/2017) as result of high cumulative ambient precipitation amounts (> 500 mm) during the growing periods (Chapter 6). Possibly, negative effects of water shortage in the precipitation treatments were mitigated though high ambient precipitation amounts and rather high soil moisture during the growing seasons. Therefore, seed yield of oilseed rape did not decrease because crops did not experienced water stress.

Interestingly, long-term effects of the precipitation manipulation in the growing season 2016/2017 of winter oilseed rape were found (Chapter 5). The HoCC experiment simulates since 2008 alterations in precipitation patterns every year during summer (always from June until August) in the same way at the same subplots. In 2017, before the precipitation manipulation began, significant main effects and their interactions between amount and frequency of precipitation on biomass allocation of winter oilseed rape were detected. Thus, biomass of flowers and senescent leaves increased, whereas specific leaf area decreased, most likely as a result of plants producing smaller leaves under conditions of limited water availability. With regard to other long-term studies, which have been conducted mainly in grasslands, forests, and shrublands, a variability in precipitation pattern over several years can alter soil respiration, soil structure or the composition of the soil microbial community (Sowerby et al. 2008; Beier et al. 2012). Thus, long-term changes in amount and frequency of precipitation may have resulted in an altered composition of the soil microbial community in our field experiment. This in turn affects the availability of nutrients for the crops through higher rates of mineralization, which was accompanied by changes in leaf size, leaf senescence, and biomass allocation of winter oilseed rape.

7.4 Yield quality of oilseed rape

Soil warming and altered precipitation pattern had only minor effects on the composition of seeds in winter oilseed rape. Total amino acid or total fatty acid concentration on a per protein or oil basis were unaffected. However, interaction effects of the climate factors which resulted in slightly shifts in the composition of some amino and fatty acids were observed. For example, lysine, which is an essential amino acid, increased under less precipitation amount at ambient soil temperature. In contrast, lower precipitation amount at elevated soil temperature decreased concentration of lysine, however, both of these changes were quite small.

Global warming can affect the lipid biosynthesis of oil producing crops, because an increase in temperature can result in less desirable fatty acid profiles of vegetable oils (Singer et al. 2016). Water availability is a second important factor, which can alter the composition of oilseeds,

because crops are prone to close their stomata under reduced water supply. This reduces CO₂ assimilation as well as sugar uptake by embryos (Singer et al. 2016). Similarly, in the present study, interactions of elevated soil temperature with reduced precipitation amount or frequency resulted in changes in the concentration of some saturated fatty acids. Capric acid concentration decreased under elevated soil temperature combined with reduced precipitation amount, and lignoceric acid increased if precipitation amount and precipitation frequency were reduced both. To date, the function of saturated fatty acids in the metabolism of oilseed rape is not fully understood. Capric acid, as a medium-chain fatty acid, is a valuable ingredient in oilseed rape seed oil and used as feedstock in the production of biodiesel, cosmetics, lubricants, and surfactants (Dyer et al. 2008). Thus, a decrease in capric acid concentration could be unfavorable for the industrial usage of oilseed rape seeds.

Differently than hypothesized (vi), a reduction in summer precipitation amount alone neither increased the protein nor decreased the oil concentration, as it had been found previously in oilseed rape seeds when water scarcity was applied during the ripening period (Mailer and Pratley 1990; Bouchereau et al. 1996; Champolivier and Merrien 1996). Possibly, the missing effect of reduced precipitation amount in this study on total protein and oil content in seeds was based on relatively high ambient precipitation amounts during the growing period 2016/2017. Thus, the simulated decrease in precipitation amount was too small to effect shifts in protein and oil concentrations.

7.5 Future perspectives based on the environmental conditions during the growing periods (2009-2018)

In the future, rising soil and air temperatures as well as decreasing precipitation amounts during the growing periods of wheat, barley and oilseed rape are predicted (Zheng et al. 1993; DWD 2017; IPCC 2021a; IPCC 2021b). With regard to the long-term data from the ten consecutive growing periods (2009-2018), a trend for increasing mean air temperature and decreasing ambient precipitation amounts compared to the long-term period 1981-2010 at the experimental site of the HoCC experiment was noticed (Chapter 6). It is predicted that at 2.0 °C global warming, mean temperature will increase by 1.0 to 2.0 °C in the region of Western and Central Europe (IPCC 2021a). This is in agreement with observations made on the experimental site of the HoCC experiment (Chapter 6). In the growing-periods 2009, 2010, 2013/2014 and 2015, the mean air temperature at the field site were 1.0 °C above the values of the long-term period (1981-2010). Only in 2010/2011, the mean air temperature was colder than in the long-term period (-0.7 °C). In accordance, the years 2014, 2015, 2016, 2017 and 2018 belong to the ten

warmest years ever recorded in Germany since 1881 (DWD 2017; Umweltbundesamt 2020). Looking at the precipitation at the experimental site, a trend for declining precipitation amounts since 2010 was visible. Accordingly, in nine out of ten years, the precipitation during the growing periods was between 36 mm in 2013 and 212 mm in 2010/2011 lower than in the long-term period 1981-2010. In several years, especially low precipitation was observed during spring and summer, but also a trend for an increase in precipitation during winter was visible as compared to 1981-2010. These findings are partly supported by climate simulations for the period 2071-2100 in Germany. Thus, an increase in winter precipitation was projected, but in contrast to observations at the present study site, forecasted was also an increase in spring precipitation (DWD 2017). Possibly, spring precipitation differed from climate projections because the predictions are average values for the whole area of Germany. The amount of precipitation may be spacial or temporal (in single years) lower or higher than predicted.

Based on these observations it can be assumed, that the positive effects of elevated soil temperature on biomass production and yield of cereals, which were found under high cumulative ambient precipitation and high soil moisture, will decrease in the future due to decreasing precipitation amounts leading to lower soil moisture contents throughout the growing period. Furthermore, as predicted for global warming of 2.0 °C in Western and Central Europe, a mean temperature elevation of 1.0 to 2.0 °C (IPCC 2021a) and a decrease in precipitation by 10% during summer, combined with more frequent drought periods (IPCC 2021b), might pose a major threat to future biomass and yield productivity of wheat, barley and oilseed rape in southwest Germany.

8 Final conclusions and outlook

The results of the experimental studies demonstrated that soil warming induced an increase in aboveground biomass and grain yield of wheat and barley in moist years, whereas no changes were detected in dry years. Moreover, it was found that aboveground biomass and seed yield were unaffected due to soil warming in all growing periods of oilseed rape (2010/2011, 2013/2014, 2016/2017). The roots of wheat and barley are known to be colonized by arbuscular mycorrhizal fungi (AMF), providing phosphorus (P) (Karandashov et al. 2004) and nitrogen (N) (Hodge and Storer 2015) to the plants, which enhance crop productivity and promote plant health (Al-Karaki et al. 2004; Kempel et al. 2010; Mäder et al. 2011; Zhang et al. 2019; Wahdan et al. 2021), in exchange for carbohydrates from the host plant (Koide 1991; Heinemeyer et al. 2003). The impacts of climate change on the symbiosis between higher plants such as wheat and AMF has gained increasing attention, e.g., recent studies focused on the effects of temperature increase and altered precipitation pattern on AMF communities in agroecosystems and unmanaged ecosystems (Bennett and Classen 2020; Wahdan et al. 2021). In general, elevated temperatures and higher amounts in precipitation can alter the microbial community in the rhizosphere directly due to an elevated carbon (C) allocation (Gorissen et al. 2004; Wahdan et al. 2021) or indirectly due to alterations of their host plant (e.g., elevated plant growth) (Cotton 2018; Wahdan et al. 2021). A meta-analysis with the focus on unmanaged ecosystems found that soil warming either increased, unaffected or decreased the root colonization rate of AMF (Bennett and Classen 2020). An increase in precipitation was shown to increase C availability in the root zone (Gorissen et al. 2004) and alter AMF community composition (Gao et al. 2016; Wahdan et al. 2021). In our study, a combination of soil warming and comparable moist soil due to higher ambient precipitation in the growing periods 2009, 2013, 2016 and 2017/2018 (Chapter 6) may have promoted the colonization of plant roots with AMF, resulting in an improved nutrient availability, which in the end enhanced crop productivity (biomass, yield) in wheat and barley. The plant-soil-microbe network in agroecosystems needs to be further studied, since cereals can benefit due to enhanced AMF colonization under soil warming and the impacts of soil warming on AMF communities are highly variable and not fully understood right now. In contrast to cereals, oilseed rape as *Brassicacea* do not host AMF (Vierheilig et al. 2000) and could not benefit from possible higher AMF colonization rates under conditions of soil warming and adequate soil moisture in our study, which was reflected by a lack of increasing rates of aboveground biomass and yield (Chapters 5 and 6).

In addition, a stimulation effect of soil warming on root growth may have enhanced cereal aboveground biomass and grain yield production in moist years in our study (Chapter 6). In agreement with Campbell et al. (1977) on stubble land in lysimeters, root growth was increased in spring wheat with elevated soil moisture. Moreover, winter wheat grown in growth chambers showed an increased root growth under soil warming of 5.0 °C and adequate soil moisture (Gavito et al. 2001). In our study, root biomass was increased in spring barley due to 2.5 °C soil warming and wet spring conditions in 2016 (Chapter 4). It is well known that roots are essential for the supply of crops with water and nutrients (Farrar and Jones 2000; Nagel et al. 2009). Most likely, spring barley tended to produce more aboveground biomass and grain yield under soil warming compared to ambient soil temperature because the enhanced root biomass improved its nutritive value or mitigated water loss through elevated evapotranspiration in warmed plots. For the future, getting root biomass data for each growing period is time-consuming but may answer the question if root growth is increased under soil warming in those years with increased aboveground biomass and yield. Moreover, root biomass data from oilseed rape would give a hint why aboveground biomass and yield of that crop did not respond to soil warming.

Most likely, a mineralization effect under soil warming stimulated biomass and grain yield production of wheat and barley in this study (Chapter 4 und 6). Ineson et al. (1998) found increasing plant biomass under soil warming of 3.0 °C using heating cables in an upland grassland. Soil warming of 3.0 °C was shown to stimulate the mineralization of organic matter in grassland, which resulted in an increased availability of N, resulting in improved plant growth (Shaver et al. 2000). In tundra, low tundra, grassland and forest it was reported that soil warming in the range of 0.3-6.0 °C can increase N mineralization rates in soils, leading to an increase of the plant primary production in that ecosystems (Rustad et al. 2001; Schmidt et al. 2004; Andresen et al. 2010). A higher rate of N mineralization under soil warming may be a hint for an increased microorganisms activity (Kannoja et al. 2019). The activity of soil microorganisms is affected by soil warming and soil moisture (Allison and Treseder 2008; Bamminger et al. 2016). During a wet season, Kannoja et al. (2019) reported an increased soil microbial activity. Maybe the enhanced biomass and yield production of wheat and barley under elevated soil temperature in moist years in our study (Chapters 4 and 6) was an effect of increased N supply as result of higher microorganism activity. Accordingly, Poll et al. (2013) reported from the Hohenheim Climate Change (HoCC) experiment with spring wheat during moist conditions in spring 2009 an increase in microbial activity under 2.5 °C elevated soil temperature. To gain more information about the possible link in this experiment between

higher crop production and higher microorganisms activity under elevated compared to ambient soil temperature in moist years, it would be interesting to examine microbial biomass data from all ten growing seasons (2009-2018) regarding from the HoCC experiment. Possibly, this could give a hint for the missing effects of soil warming on biomass and yield of oilseed rape.

It must be taken into account, that oilseed rape is an essential pre-crop in crop rotation with cereals, because with its deep rooting tap it aerates the soil and improves soil fertility due to high amounts of straw residues, which were incorporated after harvest into the soil, providing subsequent crops with nutrients (N, P) (Walker and Booth 2001). This fertilization effect of oilseed rape may be another explanation for increased cereal biomass and yields observed in this thesis (Chapters 5 and 6). This illustrates how many parameters could have an impact on crop productivity, because interaction between crops and their environment (soil properties, nutrient availability, air and soil temperatures, precipitation, microorganisms) are complex and therefore challenging to study. Although research of climate impacts aims to simulate future climate conditions as realistic as possible to investigate their effects on important agronomic parameters, e.g., biomass and yield, it has to be considered, that with each additional parameter the evaluation of possible interaction effects increase in complexity.

Effects of a reduced summer precipitation amount (-25%) on aboveground biomass production were limited, whereas harvestable yields of wheat, barley and oilseed rape remained unaffected (Chapter 6). Furthermore, longer dry periods during summer as result of a reduced precipitation frequency (-50%) had no effects on biomass and yield of the three crops (Chapter 6). The minor effects of the simulated water scarcity in the studied agroecosystem may be a result of the experimental site. According to Chapter 4, the soil is a loess-derived stagnic Luvisol, which is well-used in farming due to its high water holding capacity (Glina et al. 2014). Moreover, high precipitation events during winter months were measured at the field site in several years (2010-2012, 2015, 2018; Chapter 6), which are in accordance to future climate predictions for Germany for the periods 2041-2060 (IPCC 2021a) and 2071-2100 (DWD 2017). The high cumulative ambient precipitation amounts in several years (Chapter 6) may explain the minor impacts of altered precipitation pattern on aboveground biomass and harvestable yield since crops did not experienced water stress and the reduction in precipitation amount and –frequency may have induced only mild drought. Interestingly, Raza et al. (2017) reported an increased root growth of oilseed rape due to a mild drought. In the growing season 2010/2011, aboveground biomass was increased in winter oilseed rape under reduced precipitation amount (Chapter 6), and maybe root growth was increased as well because rape experienced only a

mild drought. In addition, Xu et al. (2016) observed an increased root growth of winter wheat into deeper soil layers under limited irrigation, therefore plants enhanced their water uptake, which was assumed to improve the water use efficiency. An increased water use efficiency was also observed by Zhao et al. (2020) in winter wheat grown under limited irrigation. In the growing season 2016 with spring barley, a higher water use efficiency under reduced precipitation amount was observed (Chapter 4). Barnabás et al. (2008) reported for cereal crops that an increased water use efficiency was linked with yield improvements under water scarcity. In our study, an increase in root growth and water use efficiency under mild drought conditions could have accounted for the observed stable yields under less precipitation amount and – frequency in moist years.

In the HoCC experiment, heating cables were used to simulate increasing soil temperatures. Heating cables are a valuable method to warm soils, because they can constantly elevate the soil temperature of huge experimental plots and they can cope well with vegetation cover (Hantschel et al. 1995; Siebold and Tiedemann 2012). This offers a valuable possibility to analyze soil warming effects on belowground parameter, e.g., soil moisture, soil respiration, microbial biomass or root growth. In this thesis it was observed that belowground changes (soil moisture reduction, root biomass increase) due to soil warming most likely altered the development of aboveground plant parts (aboveground biomass production and grain yields; Chapter 4 and 6). However, under global warming, plants are not only affected due to soil warming but also due to increasing air temperatures. As the heating cables lay very close to the top soil, also a thin air layer above the ground was heated in this experiment. Accordingly, crops were exposed to increased air temperatures during the beginning of plant growth as a result of elevated soil temperatures. Thus, the accelerated crop development during early growth stages under soil warming may have resulted from elevated air temperatures (Chapters 4 and 5). However, it can be supposed that this effect vanished with increasing crop growth and canopy height since less parts of the crops were exposed to elevated air temperatures. To sum up, it is important to analyze the effects of soil warming on aboveground biomass and yield production of crops, however, elevated air temperatures have to be considered in future experiments as well as done in the Global Change Experimental Facility (Schädler et al. 2019).

Overall, the experimental results from ten year HoCC experiment (Chapter 6) revealed that long-term studies are necessary to get a more comprehensive understanding about the variability of crop productivity (biomass, yield) between different growing seasons. Especially annual environmental conditions (e.g., wet or dry year) should be considered when studying

climate change effects (warming, drought) on crop productivity. In that context, soil moisture is one of the key parameter, which illustrated differences in weather conditions between years, since it is strongly affected by the climate change factors such as elevated temperature and drought periods.

9 References

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List of publications

Drebenstedt, Ireen; Schmid, Iris; Poll, Christian; Marhan, Sven; Kahle, Robert; Kandeler, Ellen; Högy, Petra (2020): Effects of soil warming and altered precipitation patterns on photosynthesis, biomass production and yield of barley. In: *Journal of Applied Botany and Food Quality* 93: 44–53. DOI: 10.5073/JABFQ.2020.093.006.

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Eidesstattliche Versicherung über die eigenständig erbrachte Leistung

gemäß § 18 Absatz 3 Satz 5 der Promotionsordnung der Universität Hohenheim für die Fakultäten Agrar-, Natur- sowie Wirtschafts- und Sozialwissenschaften

1. Bei der eingereichten Dissertation zum Thema

Impacts of Temperature Increase and Changes in Precipitation Pattern on Ecophysiology, Biomass Allocation and Yield Quality of selected Crops

handelt es sich um meine eigenständig erbrachte Leistung.

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