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

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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.

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 (DaMatta et al., 2010). However, other aspects of predicted climate change are an increase of atmospheric carbon dioxide (CO_2) concentration and of tropospheric ozone (O_3) 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 (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 (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 (Patil et al., 2010; Gavito et al., 2001). 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 CO_2 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 (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).

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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.

Materials and methods

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 (DWD, 2019). In 2016, the annual mean air temperature and precipitation were 10.1 °C and 595.4 mm, respectively (weather station "Hohenheim", 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 (Fig. 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).

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). 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 m × 4 m), one with ambient and one with elevated soil temperature. Soil temperature is elevated by 2.5 °C (T_e) at 4 cm depth and is achieved by heating
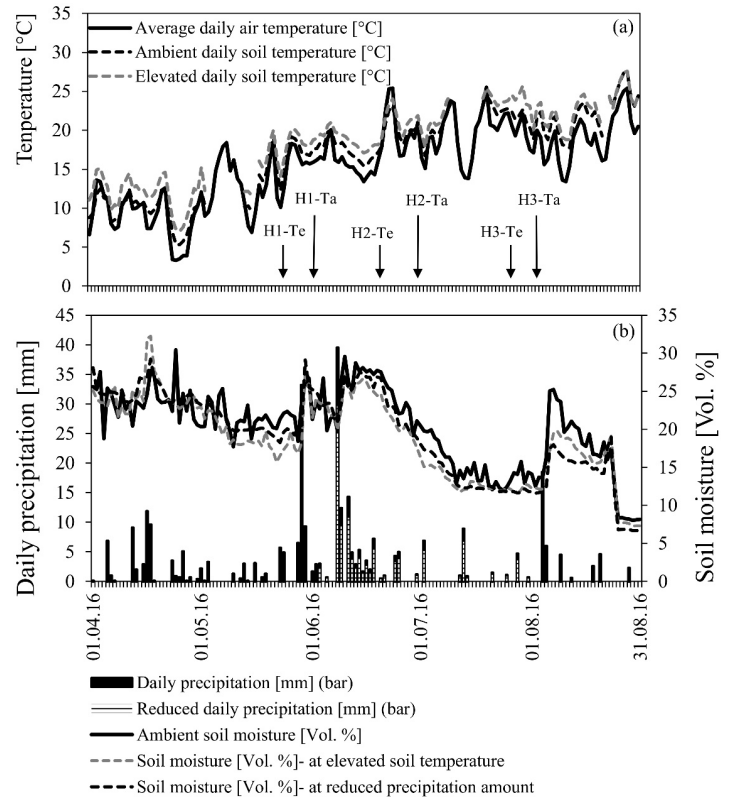

Fig. 1: Average daily air temperature (2 m), ambient and elevated daily soil temperature at the experimental site during the growing season from 01 April until 31 August 2016. Harvest dates are labelled as follows: H1: harvest 1 at stem elongation (DC 31); H2: harvest 2 at flowering (DC 65); H3: harvest 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.

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 m × 1 m subplots, each having a different combination of the two precipitation factors; amount (A) and frequency (F). The surface area of the subplots (1 m × 1 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).

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) (Tab. 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 (Tab. 1). At the final harvest (DC 92), all plants in a square of 0.5 m × 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 (Tab. 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.

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 weather station "Hohenheim" (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.

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 CO_2 (CO_2R) was set to 400 µmol CO_2 mol^{-1} and light intensity in the leaf chamber (ParIn) was set to 1500 µmol m^{-2} s^{-1}. Flow rate to the leaf chamber was adjusted to 400 µmol 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 ± 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 ± 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.

Tab. 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 date	
Harvest	Development stage	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

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".

Results

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 (Tab. 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 (Fig. 1), but not significantly maybe due to variability in the soil moisture measurements.

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 (Tab. 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 (Fig. 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 (Fig. 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.

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% (Fig. 4). A reduction in precipitation amount increased g_s and E by 30% and 20% re-

Tab. 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

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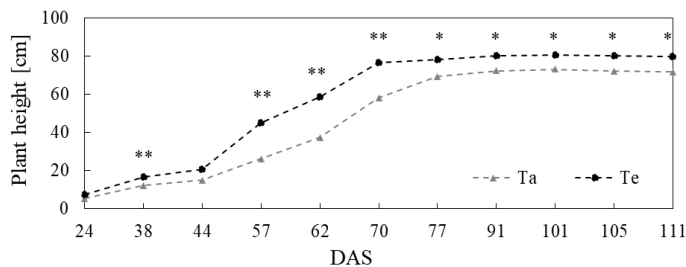
Fig. 2: Plant height measured between 24 DAS and 111 DAS at ambient (T_a) and elevated soil temperature (T_e). Asterisks indicate significant differences between plants under ambient and elevated soil temperatures (*$P \leq 0.05$; **$P \leq 0.01$); n = 4.
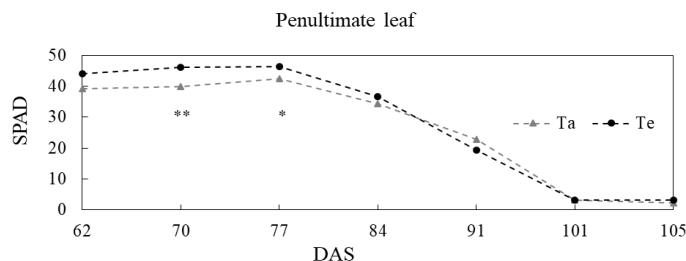

Fig. 3: SPAD values of the penultimate leaf, measured under ambient (T_a) and elevated soil temperature (T_e). SPAD values are averages of five plants of each subplot, used as monitor plants. Asterisks indicate significant differences between plants under ambient and elevated soil temperatures (*$P \leq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

Fig. 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, $P \leq 0.05$).

spectively 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 (Tab. 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 (Fig. 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.

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 (Tab. 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, Tab. 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 (Fig. 5).
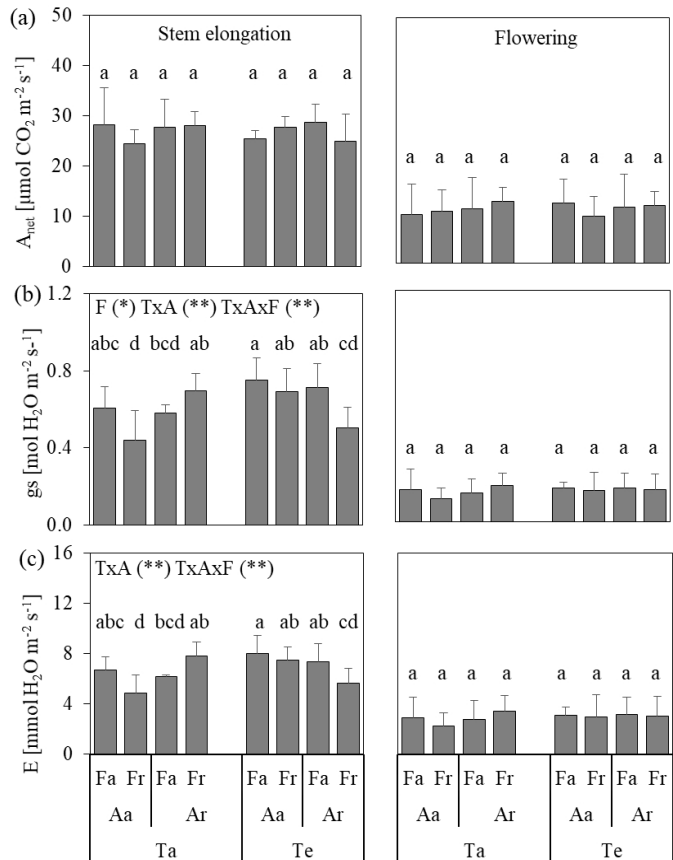
Yield parameter

At maturity, soil warming increased the number of ears per plant by 36% (Fig. 6) and tended to increase the biomass of ears by 51% (P = 0.057, Tab. 3) as well as grain yield by 54% (P = 0.057, Fig. 6). Barley grown under reduced precipitation frequency had 6% less TGW compared to controls (Tab. 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 (Tab. 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).

Discussion

Plant development

Elevated soil temperature accelerated barley development over the entire growing period to maturity, resulting in about one week earlier

Tab. 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 | | | |
	F_a	F_r	F_a	F_r	F_a	F_r	F_a	F_r	T	A	F	T×A	T×F	A×F	T×A×F
Biomass production [g DW plant^{-1}]															
First harvest (stem elongation)															
Aboveground	0.68±0.24a	0.67±0.07a	0.63±0.22a	0.56±0.20a	0.53±0.29a	0.52±0.12ab	0.48±0.17a	0.45±0.05a	ns	ns	ns	ns	ns	ns	ns
Green leaves	0.34±0.13a	0.35±0.05a	0.34±0.11a	0.30±0.10a	0.32±0.16a	0.31±0.09a	0.29±0.05a	0.26±0.04a	ns	ns	ns	ns	ns	ns	ns
Senes. leaves	0.014±0.008ab	0.010±0.006abc	0.013±0.009a	0.010±0.007abc	0.004±0.005c	0.007±0.000bc	0.002±0.000bc	0.010±0.003abc	**0.035**	ns	ns	ns	ns	ns	ns
Stems	0.33±0.11cde	0.31±0.04de	0.28±0.11bcd	0.25±0.11e	0.20±0.13abc	0.20±0.06ab	0.18±0.07ab	0.18±0.01abc	*0.065*	*0.062*	ns	ns	ns	ns	ns
Second harvest (flowering)															
Aboveground	3.84±0.64bcd	3.09±0.54cd	3.94±0.97bcd	2.86±0.12d	4.05±0.12abc	5.07±1.10ab	5.56±1.35a	5.22±1.74ab	**0.014**	ns	ns	ns	**0.010**	ns	ns
Green leaves	0.26±0.07b	0.26±0.06b	0.25±0.12b	0.23±0.04b	0.61±0.12a	0.57±0.16a	0.59±0.17a	0.51±0.16a	**0.003**	ns	ns	ns	ns	ns	ns
Senes. leaves	0.20±0.04a	0.15±0.04abc	0.21±0.06a	0.15±0.04abc	0.09±0.03c	0.14±0.06abc	0.17±0.05ab	0.16±0.06abc	ns	ns	ns	ns	**0.003**	ns	ns
Stems	1.90±0.37bcd	1.68±0.38c	2.17±0.61abc	1.54±0.03d	2.39±0.12ab	2.76±0.20ab	2.89±0.74a	2.50±0.31ab	**0.020**	ns	ns	ns	*0.082*	ns	ns
Ears	1.48±0.30ab	1.01±0.17bc	1.31±0.30bc	0.95±0.11c	0.96±0.09c	1.60±0.53a	1.57±0.30a	1.53±0.54a	ns	ns	ns	ns	**0.010**	ns	ns
Final harvest (maturity)															
Aboveground	2.34±0.38a	2.55±0.61a	2.71±0.46a	2.61±0.50a	3.47±0.75a	4.09±0.79a	3.71±0.94a	3.63±1.19a	*0.062*	*0.089*	ns	ns	ns	ns	ns
Senes. leaves	0.18±0.04c	0.20±0.04bc	0.22±0.05abc	0.19±0.05bc	0.25±0.06abc	0.30±0.05a	0.26±0.06ab	0.27±0.08ab	*0.076*	ns	ns	ns	ns	ns	ns
Stems	0.68±0.18cd	0.76±0.18cd	0.81±0.12bcd	0.74±0.15cd	0.99±0.20ab	1.15±0.19a	1.06±0.21ab	1.08±0.28ab	**0.048**	ns	ns	ns	ns	ns	ns
Ears	1.48±0.21d	1.59±0.39cd	1.68±0.30bcd	1.68±0.31bcd	2.23±0.49abc	2.64±0.56a	2.39±0.6b	2.28±0.83abc	*0.057*	ns	ns	ns	ns	ns	ns
Yield parameters															
Final harvest (maturity)															
Grain size classes [% grains]															
>2.8 mm	52.1±4.6bc	44.8±6.3c	56.6±5.4bc	53.4±10.4bc	65.2±9.9ab	71.2±17.0a	63.9±9.2ab	73.8±12.56a	*0.078*	**0.023**	ns	ns	ns	ns	ns
2.8-2.5 mm	34.0±6.0	36.0±3.9a	30.4±3.6ab	33.3±8.1a	22.9±4.1bc	18.7±7.0c	23.9±2.9bc	20.1±8.1c	**0.030**	**0.035**	ns	ns	ns	ns	ns
2.5-2.2 mm	9.6±1.8ab	13.7±2.9a	8.8±1.3b	9.6±2.1ab	7.2±3.2b	6.1±5.0b	7.5±4.2b	5.3±3.7b	ns	**0.030**	**0.048**	ns	ns	ns	ns
<2.2 mm	4.3±2.3ab	5.5±1.3a	4.2±1.9ab	3.6±1.7ab	4.7±2.7a	1.3±0.2b	4.7±2.9a	3.3±2.3ab	ns	**0.015**	ns	ns	ns	ns	*0.063*
Yield parameters															
Final harvest (maturity)															
Harvest index	0.546±0.02a	0.536±0.03a	0.531±0.03a	0.553±0.02a	0.561±0.01a	0.557±0.02a	0.552±0.04a	0.537±0.04a	ns	ns	ns	ns	ns	ns	ns
TGW [g 1000 grains^{-1}]	47.1±1.7ab	44.4±1.1b	47.5±1.8ab	47.5±2.8ab	48.3±2.1a	48.0±1.9a	50.3±6.2a	50.2±4.4ab	ns	ns	**0.050**	ns	ns	ns	*0.074*
Water-use															
Final harvest (maturity)															
Total water use [l plant^{-1}]	0.8±0.2a	0.8±0.1a	0.8±0.1a	0.7±0.2a	0.7±0.1a	0.7±0.1a	0.7±0.05a	0.7±0.1a	ns	ns	ns	ns	ns	*0.091*	ns
Water use efficiency															
First harvest (stem elongation)															
WUE_P [μmol mmol^{-1}]	4.2±1.1abc	5.2±1.1a	4.5±1.0ab	3.7±0.7bc	3.3±0.7c	4.0±0.8abc	4.0±0.8abc	4.2±0.8ab	ns	ns	ns	**0.020**	ns	ns	ns
Second harvest (flowering)															
WUE_P [μmol mmol^{-1}]	3.2±1.5a	4.8±0.8a	4.0±0.4a	3.8±0.7a	3.0±0.5a	3.2±1.5a	3.5±0.8a	3.3±0.7a	ns	ns	ns	ns	ns	ns	ns
Final harvest (maturity)															
WUE_B [g l^{-1}]	3.0±0.2d	3.1±0.5d	3.4±0.8cd	3.8±1.1bcd	4.8±1.4abc	5.6±1.2a	5.0±0.9abc	5.6±2.3ab	*0.067*	**0.017**	ns	ns	ns	ns	ns
WUE_Y [g l^{-1}]	1.6±0.1c	1.7±0.3c	1.8±0.5bc	2.1±0.7abc	2.7±0.8ab	3.1±0.8ab	2.9±0.5ab	3.1±1.5ab	*0.062*	**0.048**	ns	ns	ns	ns	ns

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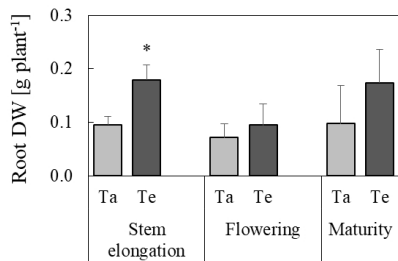
Fig. 5: Effects of elevated temperature (T_e, dark grey) compared to ambient temperature conditions (T_a, light grey) on root dry weight (DW) of barley. Harvests were done at stem elongation, flowering, and plant maturity. Means and SDs are shown, asterisk indicates significance (*$P \leq 0.05$, tested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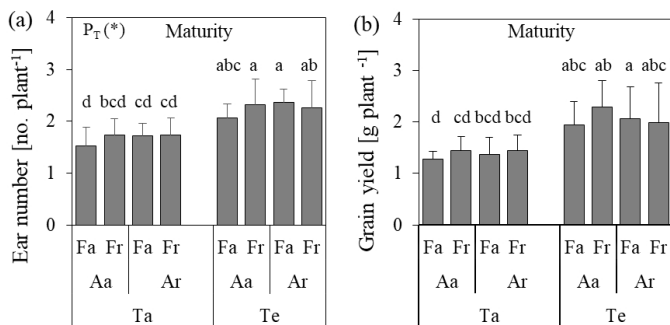

Fig. 6: Effects of soil temperature (T_a, ambient; T_e, elevated), precipitation amount (A_a, ambient; A_r, reduced), and precipitation frequency (F_a, ambient; F_r, reduced) on (a) ear number per plant and (b) grain yield per plant. Measurements were performed at plant maturity. Means and SDs are shown, 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, $P \leq 0.05$).

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.

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 (SCHMID et al., 2016; GONZÁLEZ et al., 2010). 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. (1996) 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.

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.

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). 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 (ALEMAYEHU et al., 2014; SAVIN et al., 1997), 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.

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 CO_2 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 CO_2 enrichment.

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

No potential conflict of interest was reported by the authors.

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