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CLIMATE CHANGE AND AGRICULTURE PAPER

Growth and yield response of winter wheat to soil warming and rainfall patterns

R. H. PATIL[1,2]*, M. LAEGDSMAND[1], J. E. OLESEN[1] AND J. R. PORTER[2]

[1] *Department of Agroecology and Environment, Faculty of Agricultural Sciences, Aarhus University, 8830 Tjele, Foulum, Denmark*
[2] *Department of Agriculture and Ecology, Faculty of Life Sciences, Copenhagen University, 2630 Taastrup, Denmark*

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SUMMARY

It is predicted that climate change will increase not only seasonal air and soil temperatures in northern Europe but also the variability of rainfall patterns. This may influence temporal soil moisture regimes and the growth and yield of winter wheat. A lysimeter experiment was carried out in 2008/09 with three factors: rainfall amount, rainfall frequency and soil warming (two levels in each factor), on sandy loam soil in Denmark. The soil warming treatment included non-heated as the control and an increase in soil temperature by 5 °C at 100 mm depth as heated. The rainfall treatment included the site mean for 1961–90 as the control and the projected monthly mean change for 2071–2100 under the International Panel on Climate Change (IPCC) A2 scenario for the climate change treatment. Projected monthly mean changes in rainfall compared to the reference period 1961–90 show, on average, 31% increase during winter (November–March) and 24% decrease during summer (July–September) with no changes during spring (April–June). The rainfall frequency treatment included mean monthly rainy days for 1961–90 as the control and a reduced frequency treatment with only half the number of rainy days of the control treatment, without altering the monthly mean rainfall amount. Mobile rain-out shelters, automated irrigation system and insulated heating cables were used to impose the treatments.

Soil warming hastened crop development during early stages (until stem elongation) and shortened the total crop growing season by 12 days without reducing the period taken for later development stages. Soil warming increased green leaf area index (GLAI) and above-ground biomass during early growth, which was accompanied by an increased amount of nitrogen (N) in plants. However, the plant N concentration and its dilution pattern during later developmental stages followed the same pattern in both heated and control plots. Increased soil moisture deficit was observed only during the period when crop growth was significantly enhanced by soil warming. However, soil warming reduced N concentration in above-ground biomass during the entire growing period, except at harvest, by advancing crop development. Soil warming had no effect on the number of tillers, but reduced ear number and increased 1000 grain weight. This did not affect grain yield and total above-ground biomass compared with control. This suggests that genotypes with a longer vegetative period would probably be better adapted to future warmer conditions. The rainfall pattern treatments imposed in the present study did not influence either soil moisture regimes or performance of winter wheat, though the crop receiving future rainfall amount tended to retain more green leaf area. There was no significant interaction between the soil warming and rainfall treatments on crop growth.

* To whom all correspondence should be addressed. Email: Ravi.Patil@agrsci.dk

INTRODUCTION

Global mean air temperature has risen, on average, between 0·6 and 0·8 °C during the 20th century and if current conditions continue, it is projected to rise between 1·1 and 6·4 °C, with local variations, by the end of the 21st century (Solomon *et al.* 2007). With climate change, global atmospheric circulation patterns and hydrological processes are expected to alter inter- and intra-annual variability of precipitation regimes at global (Trenberth *et al.* 2007) and regional scales (Christensen *et al.* 2007).

During the 20th century, precipitation over northern Europe increased by 10–40%, while in parts of southern Europe it decreased by 20% (Klein Tank *et al.* 2002). For the International Panel on Climate Change (IPCC) A2 high emission scenario for 2071–2100, the projected precipitation pattern for northern Europe suggests significant increase in precipitation during winter (October–March) with less change in spring and early summer (April–June), and decreases during late summer and early autumn (July–September) (Christensen & Christensen 2007). For the period 2000–2008, Denmark has witnessed a considerable increase in both average winter (+1·5 °C) and summer (+1·1 °C) temperatures compared with the averages for the period 1961–90. Similarly, recent decades show a trend of increased precipitation during winter, while it has remained unchanged during summer (Kristensen *et al.* in press).

These changes in air temperature, altering seasonal soil temperature as well as leading to increased variability in intra-annual precipitation, can greatly affect the soil moisture variability, soil nitrogen (N) content and availability to plants, and so influence the response of crop production (Hlavinka *et al.* 2009). Increased rainfall during winter under temperate climates, when evapotranspiration is minimal, may cause waterlogging (Vartapetian & Jackson 1997) and has been reported to affect yields of winter wheat by reducing tiller and ear numbers (Cannell *et al.* 1984; Dickin & Wright 2008), but very few studies have reported the impact of greater intra-annual precipitation variability on winter cereals (e.g. Dickin *et al.* 2009) and the implications of extremes in precipitation events have received little attention (Jentsch *et al.* 2007).

The response of a given terrestrial ecosystem to increased variability in precipitation patterns is expected to be different from the response to other climate change factors, including rising air temperature and CO_2 concentrations (Easterling *et al.* 2000; Parmesan 2006). This may also be the case with winter cereals, but few studies have considered this (e.g. Semenov *et al.* 1996).

Low soil temperature is often a constraint in temperate climates during the early stages of crop growth, limiting shoot and root growth, nutrient and water uptake (Bowen 1991) and possibly retarding development. Large changes in plant growth, biomass accumulation and nutrient absorption rates have been reported in response to small increases in soil temperature (Moorby & Nye 1984; Clarkson *et al.* 1992; Engels & Marschner 1992; Gavito *et al.* 2001), which is expected to increase with rising air temperatures. However, relatively little attention has been paid to the effects of soil temperature under changing climates. Only very few *in situ* studies have been carried out elsewhere on the effects of increased soil temperature, e.g. peanut (Awal & Ikeda 2003; Prasad *et al.* 2006), maize (Stone *et al.* 1999) and winter wheat (Gavito *et al.* 2001). This could also be due to the fact that soil temperature is difficult to manipulate (Gavito *et al.* 2001). In the past two decades, many studies have been directed at understanding the effects of projected increases in air temperature and CO_2 concentration on the response of field crops (e.g. Leaky *et al.* 2009), whereas surprisingly little effort has been focused on how anticipated changes in precipitation patterns and elevated soil temperatures might affect winter cereals in temperate climates.

Thus, a lysimeter experiment was carried out in order to study the effects of varying rainfall amounts, number of rainy days and soil warming on temporal soil moisture dynamics, crop phenology, growth and yield of winter wheat.

MATERIALS AND METHODS

Experimental facility

The experiment was carried out in concrete lysimeters at an experimentation facility located at Aarhus University, Faculty of Agricultural Sciences, Foulum, Denmark (56°29′N, 9°34′E). Each lysimeter was 1·5 m^3 (surface area 1 × 1, depth 1·5 m); the bottom 100 mm was filled with coarse gravel to allow free drainage to a collection point for measurement, while the remainder was filled with the local Foulum loamy sand soil (Table 1). All the lysimeters were epoxy concrete coated to prevent seepage through and contamination from the concrete blocks and were built level with the surrounding field. Annual mean temperature at the site (1961–90) was 7·3 °C, with maximum and minimum monthly means of 15·4 °C (July) and −0·5 °C (January and February), respectively, and the site received, on average, 627 mm of rainfall per year. However, during the study period (October 2008–September 2009), the annual mean temperature recorded was 8·6 °C with the maximum and minimum monthly means of 16·1 °C (July–August) and −0·7 °C (January–February).

An automated mobile rain-out shelter covered all the lysimeters only when it rained. A computer-controlled irrigation system allowed an automatic irrigation machine to locate any of the chosen

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Table 1. *Description of physical properties of loamy sand soil used in the study*

Depth (m)	Dry bulk density (tonne/m^3)	Organic matter (g/kg soil)	Clay	Silt	Fine sand (g/kg soil)	Coarse sand
0–0·3	1·5	25	90	110	450	350
0·3–0·6	1·5	5	120	110	450	320
0·6–0·9	1·6	2	140	110	440	310
0·9–1·4	1·6	1	160	110	430	300
1·4–1·5	Filled with small pebbles and gravel for free movement of drainage water					

lysimeters and apply a targeted amount of water at a required intensity to match that of natural rain. The water treatment schedule started on 1 November 2008 and continued until harvest. The irrigation water had a pH of 7·5.

Each lysimeter had eight rows of wheat crop spaced 125 mm apart (details below). In each of the heated plots an insulated heating cable was placed in the crop rows at a depth of 100 mm and connected to a power supply. The heating cable was installed during tillage. Soil in the unheated (control) plots was disturbed in a similar way, but no heating cables were placed in them. A computer-programmed automatic system controlled the soil warming and the soil temperature was monitored using sensors (Campbell Scientific Inc., Germany) placed horizontally between the heating cable rows at a depth of 100 mm in all the plots, and at 50 and 250 mm deep in all the heated plots and in one control plot. Temperature sensors from all the plots and depths were connected to a data logger, which monitored the temperature every 15 s, and a heater maintained the temperature at 100 mm in the heated plots at 5 °C above their respective control plots. The temperature was continuously recorded in 15 min segments, stored and later averaged for each day.

Table 2. *Number and size of rainfall events, and the number and length of dry periods in the various rainfall pattern treatments imposed between 1 November 2008 and 31 July 2009*

	Rainfall pattern treatments			
	Present		Future	
	Normal	Reduced	Normal	Reduced
Rainfall amount/day	Number of rainfall events			
<5 mm	70	28	76	30
5–9 mm	21	12	16	9
10–19 mm	8	12	13	14
>20 mm	1	4	1	6
Length of dry periods	Number of dry periods			
$\leqslant 3$ days	38	23	40	26
4–6 days	7	7	6	9
7–9 days	4	11	6	10
>10 days	3	4	2	3

Experimental design and treatments

The experiment was laid out in a split-split plot design with three factors and two levels in each factor. Factor 1 was number of rainy days (RD) assigned to main plots comprising normal (RD_0) and reduced (RD_1) number of rainy days. Factor 2 was rainfall amount (RF) assigned to sub plots and comprised present (RF_0) and future (RF_1) rainfall amounts. Factor 3 was soil warming (SW) assigned to sub-sub plots and consisted of unheated as control (SW_0) and soil heating (SW_1) at 5 °C above control at 100 mm. The total of eight treatment combinations was replicated four times using 32 lysimeters.

Rainfall data for the period 1961–90 from the Foulum weather station (56°29′N, 9°34′E), located 1200 m away from the lysimeter study site, was considered as reference period for defining the rainfall treatment. A day (0·00–24·00 h) with a minimum of 1 mm rainfall was counted as one rainy day (a rainfall event). When calculating the monthly average number of rainy days for the reference period, rainfall <1 mm on any day was added to the rainfall of its nearest rainy day to derive a scale with smallest unit of 1 mm/day, because the automatic irrigation system was programmed to apply a minimum of 1 mm rainfall (1 litre/m^2) and above. The average monthly number of rainy days for the reference period (1961–90) was regarded as the normal number of rainy days (RD_0) and 50 % fewer rainy days was regarded as a reduced number of rainy days (RD_1). The same actual amount of rain was delivered for both RD_0 and RD_1, but RD_1 represented fewer, heavier rainfall events with longer dry periods in between. The average size of rainfall event in RD_0 and RD_1 treatments was 4 and 7·5 mm/day, respectively, and the majority of dry periods, 0·86 and 0·70 of the total in RD_1 and RD_2 treatments, respectively, were short ($\leqslant 6$ days) (Table 2).

Similarly, the average annual rainfall amount of 627 mm for the reference period (1961–90)

Table 3. *Soil water* (*mm*) *at the start of rainfall pattern treatments and after the crop harvest in top 1 m soil layer, rainfall amount* (*mm*) *applied during winter and spring/summer and the total water lost through drainage* (*mm*) *between 1 November 2008 and 31 July 2009 in the different rainfall treatments*

	Soil water (mm) in 0–1·0 m depth		Rainfall applied (mm)			Drainage water (mm)
Treatments	At start	At harvest	Nov–Mar	Apr–Jul	Total	Nov–Jul
Present rainfall						
Normal rainy days	237	150	200	200	400	150
Reduced rainy days	228	135	202	200	402	161
Future rainfall						
Normal rainy days	235	128	256	194	450	197
Reduced rainy days	235	136	263	193	456	215

was regarded as the present rainfall amount (RF_0). The projection made for Denmark for the period 2071–2100 (658 mm) under the IPCC A2 high emission scenario (Christensen & Christensen 2007) was regarded as future rainfall amount (RF_1). During the study period (November–July), a total of 400 and 450 mm water was applied in RF_0 and RF_1 rainfall amount treatments, respectively (Table 3). The higher rainfall of RF_1 treatment occurred during winter (November–March).

On 23 October 2008, the soil heating system was turned on and the soil temperature in all the heated plots (SW_1) was maintained at 5 °C above the temperature of control plots (SW_0) at 100 mm throughout the study period.

Wheat crop management

Winter wheat (*Triticum aestivum* L. cv. Ambition) seeds were sown at 300 seeds/m² on 10 October 2008 with a row spacing of 125 mm, accommodating eight rows in each plot. Since sowing coincided with a sudden drop in air temperature, the germination of seeds and seedling emergence was severely affected. Gaps due to failed germination were filled in with wheat seedlings raised in soil trays under controlled conditions, which were transplanted at full emergence of the first leaf to obtain a final plant stand of *c.* 150/m². This was in the lower range of that normally found in the field. Inorganic compound fertilizer in granular form, which contained 91 g NO_3-N/kg, 115 g NH_4-N/kg, 26 g P/kg, 96 g K/kg, 36 g S/kg, 11 g Mg/kg and 0·2 g Bo/kg, was applied on the soil surface to supply a total of 170 kg N/ha over the crop cycle. On 27 February and 21 March, 10 kg N/ha was applied, while the remaining 150 kg N/ha was applied in two equal splits on 3 April and 1 May. Lucerne (alfalfa) was grown as the previous crop in all lysimeters during 2008 without applying fertilizers and on 1 October 2008 the above-ground vegetative part, including stubble, was cut and removed from the plots. Major roots from the plough layer were also removed to allow a uniform seed bed and to properly place the heating cables. Tillage was performed manually by turning the top 0·2 m of soil upside down. Disease levels were low during the crop growth period, although powdery mildew (*Blumeria graminis*) was observed in significantly higher levels during early spring in the heated plots compared with unheated plots. A mixture of Flexity (Metratenon) at 0·4 l/ha and Rubric (Epoxiconazol) at 0·4 l/ha fungicides was sprayed on 17 May to control powdery mildew. Pirimor aphicide (Pirimicarb) at 0·25 kg/ha was sprayed for cereal aphids, while weeds were controlled by spraying a mixture of Express (Tribenuron-methyl) at 1·5 kg/ha and Starane XL (Fluroxpyr methyl heptyl ester) at 1·8 l/ha on 4 June.

Measurements

A commercially available cable tester (Campbell Scientific Inc., Germany) connected to a portable battery and time domain reflectometry (TDR) probes were used to measure soil moisture (m³/m³). The TDR probes were installed (1 November 2008) vertically into the soil at the centre of each plot in two replications (16 plots) only, to monitor soil moisture at depths of 0–0·2, 0–0·5 and 0–1·0 m. One pair was installed at each depth and measurements were recorded from 7 November 2008 until the crop was harvested, on average three times a week.

During the present study, soil heating was turned on 13 days after sowing (23 October 2008). Hence, the soil in both heated and control plots had the same soil temperature during seed germination and seedling emergence. The crop phenology during the study period was monitored on the Biologische Bundesanstalt, Bundessortenamt and Chemical industry (BBCH) scale for cereals (Lancashire *et al.* 1991) by recording the dates on which the crop had completed the principal growth stages (GS0–92). For plant and agronomy measurements, destructive above-ground biomass sampling was done on four dates: 28 April, 15 June, 15 July 2009 and at maturity, by cutting the

Table 4. *Average SMD (mm) at 0–0·2, 0–0·5 and 0–1·0 m depths for the period between two above-ground biomass sampling dates starting from sowing and ending at harvest.* S.E.M., *standard error of means;* D.F., *degrees of freedom*

Treatments	Sowing–28 Apr			29 Apr–15 Jun			16 Jun–15 Jul			16 Jul–harvest		
	0–0·2 m	0–0·5 m	0–1·0 m	0–0·2 m	0–0·5 m	0–1·0 m	0–0·2 m	0–0·5 m	0–1·0 m	0–0·2 m	0–0·5 m	0–1·0 m
Rainy days												
Normal (RD_0)	3·6	7·2	9·1	24	55	73	23	66	107	26	70	115
Reduced (RD_1)	3·9	7·1	9·6	25	54	72	24	65	108	27	69	117
S.E.M. (1 D.F.)	0·30	0·12	0·35	0·9	2·0	8·5	1·5	0·8	11·7	1·1	2·4	15·0
Rainfall amount												
Present (RF_0)	3·6	8·3	9·9	23	55	71	23	66	106	25	69	112
Future (RF_1)	3·9	5·9	8·8	26	54	74	24	66	109	28	70	120
S.E.M. (1 D.F.)	0·38	0·22	0·15	0·5	3·9	6·3	0·4	2·8	11·7	0·8	3·6	13·4
Soil warming												
Control (SW_0)	3·5	5·9	7·9	25	47	62	24	62	104	28	66	113
Heated (SW_1)	4·0	8·3	10·9	24	62	82	22	69	111	26	74	119
S.E.M. (3 D.F.)	0·49	0·12	0·75	1·5	0·9	3·2	0·7	1·9	7·6	1·7	2·6	9·5

plants at the soil surface from an area of 0·1 m², from only two replications each time. These samples were used to count shoots on 28 April and ears on 15 June, 15 July and at harvest (number/m²). The total above-ground biomass and its partitioning into green leaf, diseased leaf and stem was recorded on 28 April, while on other sampling dates the plants were partitioned into green leaf, senesced (yellow) leaf, stem, glume (i.e. chaff) and grain (glume + grain = ear; only on 15 June) and dried in an oven (80 °C for 48 h) to obtain weight in g/m².

Before the plant fractions were oven dried, the green leaf area index (GLAI) and diseased leaf area index on 28 April, and GLAI and senesced (yellow) leaf area index (YLAI) on 15 June and 15 July were measured using an LI-3100 Leaf Area Meter (LI-COR, Inc., Lincoln, Nebraska USA). On each biomass sampling date, a representative sample from the partitioned plant parts was ground to a fine powder and analysed for plant N concentration (mg/g) using LECO CNS-1000 Elemental Analyser (LECO Corporation, USA). The N concentration (mg/g) in various plant parts was multiplied with their respective oven dried biomass (g/m²) to derive N amount in various plant parts (g N/m²).

At harvest, in addition to sampling from 0·1 m² area (see above paragraph), the total above-ground biomass and grain yield were also recorded by harvesting the crop at the soil surface (0·4 m² area/plot) from the other two replications, in order to gain a more representative sample from each plot, and the dry matter was expressed in t/ha (referred to as gross plots in Table 8). The grains at harvest from these two replications were recorded for mean grain weight (mg) and number of grains/m². Hence, the observations from 0·1 m² area/plot (Table 7), and those from 0·4 m² area/plot (Table 8) are not identical.

Statistical analyses

Data were subjected to analysis of variance using split–split-plot design with Genstat version 8.1 (Lawes Agricultural Trust, Rothamsted Experimental Station, UK). Where significant, the means of main factor effects and of their interactions were compared using standard error of means. The smallest unit in the ANOVA model was a lysimeter plot that was treated as an independent 'covariate'. Interactions are presented in the tables only when found to be significant ($P \leqslant 0·05$).

RESULTS

Rainfall patterns and soil moisture

Neither number of rainy days (RD) nor rainfall amounts (RF) had any significant effect on average soil moisture deficit (SMD) measured at 0–0·2, 0–0·5 and 0–1·0 m depths for four sampling periods

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Table 5. *Crop growth and development in heated and control plots from sowing to harvest* (*sowing date: 10 October 2008*) *monitored on BBCH scaling from sowing* (*GS0*) *to harvest* (*GS92*) (*Lancashire* et al. *1991*)

Development stages (GS number)	Date of reaching a particular development stage		Duration from sowing to achieve each stage (days)	
	Heated plot	Control plot	Heated plot	Control plot
Nine or more leaves (19)	04 Feb 09	20 Mar 09	117 (107)	161 (151)
End of tillering (29)	22 Apr 09	05 May 09	194 (77)	207 (46)
Flag leaf (39)	15 May 09	26 May 09	217 (23)	228 (21)
First awn visible (49)	27 May 09	04 Jun 09	229 (12)	237 (9)
End of heading (59)	04 Jun 09	13 Jun 09	237 (8)	246 (9)
End of flowering (69)	16 Jun 09	24 Jun 09	249 (12)	257 (11)
Late milk grain filling (77)	30 Jun 09	06 Jul 09	263 (14)	270 (13)
Fully ripe (89)	24 Jul 09	04 Aug 09	287 (24)	299 (29)
Hard grain harvested (92)	27 Jul 09	07 Aug 09	290 (3)	302 (3)

(Table 4). None of the interactions were statistically significant. Soil warming significantly increased the SMD for the period between sowing and 28 April at 0–0·5 m depth ($P<0·001$) and for the period between 29 April and 15 June at 0–0·5 m ($P=0·002$) and at 0–1·0 m ($P=0·022$) depths, compared with the soil in control plots at their respective depths. However, after 15 June no significant effect of soil warming on SMD was recorded across the soil depths (Table 4).

Soil warming system and its effect on crop phenology

The soil warming system in heated plots maintained a mean temperature difference of $5 \pm 0·005$ °C ($n=277$) above control plots at 100 mm depth. The soil in heated plots did not freeze, while the soil temperature in control plots went below zero on several times during several days. In heated plots at 50 and 250 mm depths, the mean temperature difference was *c.* 4·0 and 2·5 °C, respectively, above the corresponding depths in control plots, which indicated that soil warming affected a large part of the soil volume. The mean air temperature of heated plots (measured at 100–150 mm above the soil surface) was 0·19 °C higher than that of control plots, with minimum and maximum mean differences of 0·02 °C (March) and 0·43 °C (July), respectively.

Soil warming greatly affected crop phenology during early stages of crop growth (i.e. until end of tillering). Plants in heated plots reached the nine or more leaf stage (GS19) 44 days earlier than those in control plots (Table 5). However, with the onset of spring and rising air temperature, plant development in the control plots was more rapid and the difference narrowed to 13 days at the end of tillering stage (GS29). Thereafter, this difference ranged from 7 to 12 days until the crop was harvested at maturity (GS92). However, the number of days from beginning of heading to end of grain-filling (GS51–77) was almost the same in heated (34 days) and control (33 days) plots, but the crop in heated plots had completed these stages, on average, 8 days earlier compared with the crop in control plots (Table 5).

Plant stand, above-ground biomass and grain yield

Above-ground biomass was sampled on four specific dates in both heated and control plots, rather than sampling at the same development stages. On the first sampling (28 April), plants in heated and control plots were at the stem elongation (GS31) and tillering (GS27) stages, respectively. On the second sampling (15 June), plants in heated plots had reached the end of flowering (GS68) stage, while the plants in control plots were at the end of heading (GS59) stage. On the third sampling (15 July), plants in heated plots were at the hard dough grain filling (GS86) stage, whereas the plants in control plots were at the soft dough grain filling (GS85) stage. The last biomass sampling was done at crop maturity (GS92); 27 July and 7 August in heated and control plots, respectively.

None of the factors studied had any effect on plant stand and total number of growing shoots per unit area until 15 June sampling and thereafter (Table 6). The growing photoperiod and soil warming from 15 June onwards reduced the number of ears per unit area, significantly in all except the 15 July sampling, although that date followed the same trend. Grains per unit area did not significantly differ between heated and control plots, though the latter had numerically higher number of grains/m^2 (Table 6).

Soil warming significantly increased the above-ground biomass and GLAI only during early stages by hastening the crop development (Table 7; Fig. 4). On 28 April, plants in heated plots had significantly higher GLAI (Fig. 2) and biomass in green leaf ($P=0·002$), stem ($P=0·001$) and the total above-ground biomass ($P<0·001$). However, on 15 June although plants from heated plots had continued to accumulate significantly higher biomass in stem

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Table 6. *Number of plants, shoots, ears and grains per unit area recorded on four sampling dates across crop growth period from sowing to harvest.* S.E.M., *standard error of means;* D.F., *degrees of freedom*

	Plants/m²	Shoots/m²	Ears/m²			Grains/m²
	14 Jan	28 Apr	15 Jun	15 Jul	Harvest	Harvest
Rainy days						
Normal (RD_0)	152	833	471	452	465	21 792
Reduced (RD_1)	152	849	453	475	468	21 410
S.E.M. (1 D.F.)	2·6	39·8	11·5	23·0	16·1	1224·1
Rainfall amount						
Present (RF_0)	152	813	456	470	480	21 878
Future (RF_1)	152	869	468	458	449	21 324
S.E.M. (1 D.F.)	1·7	44·4	3·1	21·4	12·1	104·1
Soil warming						
Control (SW_0)	151	850	481	478	480	22 828
Heated (SW_1)	153	831	443	450	445	20 375
S.E.M. (3 D.F.)	1·6	13·2	4·2	26·3	6·4	754·5

Table 7. *Total above-ground oven dried biomass (g DM/m²) and GLAI recorded on four sampling dates across crop growth period.* S.E.M., *standard error of means;* D.F., *degrees of freedom*

	Total above-ground biomass (g/m²)				GLAI		
Treatments	28 Apr	15 Jun	15 Jul	Harvest	28 Apr	15 Jun	15 Jul
Rainy days							
Normal (RD_0)	141	1138	1561	1578	1·9	4·0	1·1
Reduced (RD_1)	142	1178	1653	1657	1·9	3·9	1·4
S.E.M. (1 D.F.)	5·8	9·7	80·9	63·6	0·12	0·13	0·03
Rainfall amount							
Present (RF_0)	137	1111	1677	1387	1·8	3·8	1·2
Future (RF_1)	147	1205	1535	1578	2·0	4·0	1·2
S.E.M. (1 D.F.)	4·9	31·4	58·0	10·3	0·10	0·02	0·01
Soil warming							
Control (SW_0)	85	1027	1622	1630	1·3	3·9	1·9
Heated (SW_1)	199	1289	1600	1604	2·5	3·9	0·5
S.E.M. (3 D.F.)	5·4	23·8	38·3	37·1	0·09	0·10	0·12
Interactions							
$RD_0 \times RF_0$	ns	ns	ns	ns	ns	ns	0·99
$RD_0 \times RF_1$	ns	ns	ns	ns	ns	ns	1·18
$RD_1 \times RF_0$	ns	ns	ns	ns	ns	ns	1·42
$RD_1 \times RF_1$	ns	ns	ns	ns	ns	ns	1·29
S.E.M. (1 D.F.)	–	–	–	–	–	–	0·021
$RD_0 \times SW_0$	ns	1075	ns	ns	ns	4·3	ns
$RD_0 \times SW_1$	ns	1203	ns	ns	ns	3·7	ns
$RD_1 \times SW_0$	ns	981	ns	ns	ns	3·6	ns
$RD_1 \times SW_1$	ns	1375	ns	ns	ns	4·2	ns
S.E.M. (3 D.F.)	–	29·7	–	–	–	0·15	–

ns, $P > 0·05$.

($P = 0·002$), ear ($P = 0·004$) and total above-ground biomass, GLAI did not differ between the plants in heated and control plots (Figs 1 and 2). On 15 July, when the crop in heated and control plots were at the end and beginning of grain filling stages, respectively, leaves of plants in heated plots were senescing quickly and recorded significantly lower GLAI (Fig. 1); however, total above-ground biomass did not differ

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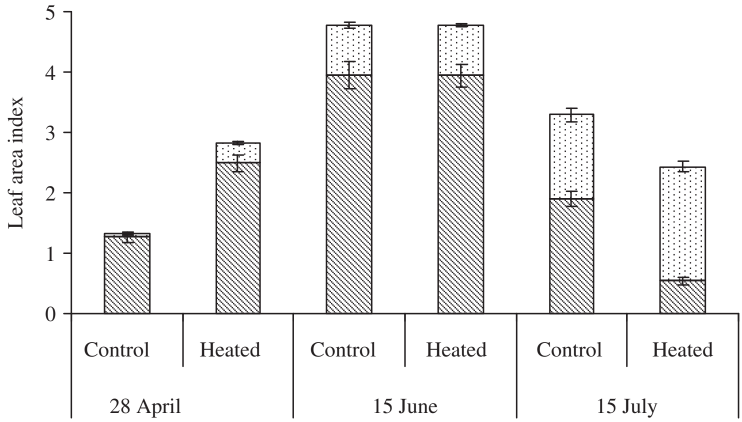

Fig. 1. GLAI and YLAI in control and heated plots across crop growth period on three sampling dates. On 28 April, sampling senesced leaf area represents mildew infected leaf area. Error bars: ±S.E. with $n=8$. ▧, green leaf; ⬚, senesced leaf.

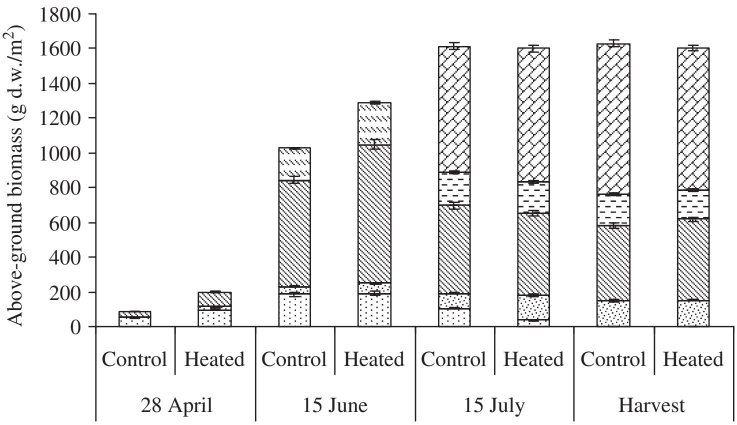

Fig. 2. Above-ground biomass of plant parts (g DM/m^2) in control and heated plots across crop growth period on four sampling dates. Biomass in senesced leaf on 28 April represents biomass of mildew infected leaves. Error bars: ±S.E. with $n=8$. ⬚, green leaf; ⬚, senesced leaf; ▧, stem; ⬚, ear; ⬚, glume; ⬚, grain.

between heated and control plots (Table 7). The plants receiving future rainfall amount had significantly higher GLAI on only 15 July sampling ($P=0{\cdot}044$) compared with those receiving present rainfall amount (Table 7). Among the interactions, significantly lower biomass and GLAI were found for $RD_1 \times SW_0$ on 15 June sampling, whereas significantly higher biomass was found for $RD_1 \times SW_1$ and significantly higher GLAI for $RD_0 \times SW_0$ and $RD_1 \times SW_1$ (Table 7).

Neither rainfall pattern (amount and rainy days) nor soil warming had any significant effect on final grain yield, total above-ground biomass, harvest index (HI) or grain N at harvest (Table 8). However, soil warming significantly increased mean grain weight and there was a significantly higher total above-ground biomass with the $RF_0 \times RD_1$ treatment.

Plant nitrogen

Plants in heated plots had significantly lower N concentration in above-ground biomass throughout the growing season, except at harvest (Table 9). On 28 April sampling, the plants in heated plots had significantly higher amount of N in stem biomass ($P<0{\cdot}001$) and green leaves ($P=0{\cdot}001$), while on 15 July, a significant but opposite trend was recorded as the green leaves from plants grown in control plots had significantly higher amount of N ($P<0{\cdot}001$) than the one from heated plots (Fig. 3).

The effect of number of rainy days on N amount was significant only on 15 July sampling as the green leaves from the plants receiving reduced number of rainy days had significantly higher ($P=0{\cdot}018$) amount of N (1·86 g N/m^2) than those receiving normal

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Table 8. *Grain yield and total above-ground biomass (t DM/ha) and nitrogen amount in grain (kg/ha), HI and 1000 grain weight (g) recorded from gross plots at harvest.* S.E.M., *standard error of means;* D.F., *degrees of freedom*

Treatments	Grain yield (t/ha)	Total biomass (t/ha)	H. I.	Mean grain wt. (mg)	N in grain (kg/ha)
Rainy days					
Normal (RD_0)	8·4	16	0·52	39	169
Reduced (RD_1)	8·8	17	0·52	42	179
S.E.M. (1 D.F.)	0·29	0·6	0·001	1·0	5·3
Rainfall amount					
Present (RF_0)	8·8	17	0·5	40	177
Future (RF_1)	8·5	16	0·5	40	172
S.E.M. (1 D.F.)	0·19	<0·1	0·01	0·7	2·6
Soil warming					
Control (SW_0)	8·9	17	0·53	39	178
Heated (SW_1)	8·4	16	0·51	41	170
S.E.M. (3 D.F.)	0·22	0·3	0·005	0·4	4·2
Interactions					
$RD_0 \times RF_0$	ns	16	ns	ns	ns
$RD_0 \times RF_1$	ns	16	ns	ns	ns
$RD_1 \times RF_0$	ns	18	ns	ns	ns
$RD_1 \times RF_1$	ns	16	ns	ns	ns
S.E.M. (1 D.F.)	–	0·4	–	–	–

ns, $P>0·05$.

number of rainy days (1·52 g N/m²) (data not shown). The interaction between number of rainy days and soil warming was found significant only on 15 June sampling with $RD_1 \times SW_0$ treatment having the highest N amount (21·21 g N/m²) in the total above-ground biomass ($P=0·041$) compared with other combinations of these two treatments. Similarly, significantly higher N uptake by green leaves ($P=0·028$) was recorded with $RD_1 \times SW_1$ treatment compared with $RD_0 \times SW_1$ treatment (data not shown).

DISCUSSION

Soil warming

Soil warming advanced crop development only during vegetative stages and shortened the entire crop growing season by 12 days without significantly affecting grain yield. This suggests that yields of winter cereals in northern Europe could be maintained even under a shorter crop growing season, which is expected with warmer climates, provided that warmer conditions also prevails during winter, where low temperatures are currently limiting the crop growth.

The response of wheat observed in the present study was due only to elevated soil temperature. However, under projected climate change scenarios, increases in both air and soil temperature will occur concurrently, reducing the duration of all growth stages (Craufurd & Wheeler 2009). This effect compounded with an increased frequency of extreme weather events, projected under future climates, during the pre- or post-anthesis periods may create heat and/or moisture stress greatly affecting both grain yield and quality (Semenov & Halford 2009). Hence, this suggests that plant breeding needs to be directed at either screening or developing genotypes which have extended vegetative growth duration during

Table 9. *Average plant N concentration (mg N/g DM) in above-ground biomass analysed on four sampling dates across crop growth period.* S.E.M., *standard error of means;* D.F., *degrees of freedom*

	28 Apr	15 Jun	15 Jul	Harvest
Rainy days				
Normal (RD_0)	53·11	16·12	11·09	13·71
Reduced (RD_1)	55·29	16·63	11·31	13·75
S.E.M. (1 D.F.)	0·002	0·243	0·175	0·064
Rainfall amount				
Present (RF_0)	56	17	11	14
Future (RF_1)	53	16	11	14
S.E.M. (1 D.F.)	1·3	0·3	0·1	0·1
Soil warming				
Control (SW_0)	59	18	12	14
Heated (SW_1)	49	15	11	14
S.E.M. (3 D.F.)	0·5	0·1	0·2	0·1

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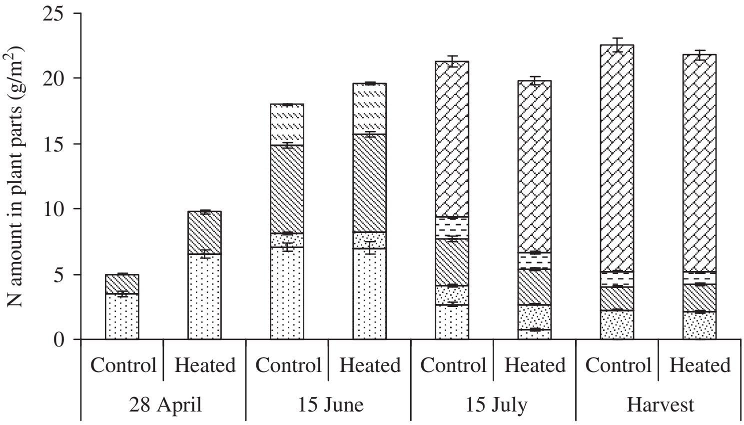

Fig. 3. Nitrogen amount (g N/m²) in above-ground plant parts in control and heated plots across crop growth period on four sampling dates. Error bars: ±S.E. with $n=8$. ▫, green leaf; ▫, senesced (yellow) leaf; ▧, stem; ▫, ear; ▫, glume; ▨, grain.

winter and are tolerant of the temperatures expected under projected future environments.

In the present study, soil warming greatly enhanced wheat crop development until the end of tillering (GS29), but later developmental stages until the end of grain filling (GS77) were not affected (Table 5). Temperature is known to affect the rate of development in plants during their entire growing cycle, generally with higher temperatures increasing developmental rate (Roberts & Summerfield 1987). Crop development in cereals is determined by the temperature effects on the shoot apex, which for winter wheat is located below or around the soil surface until stem elongation (Jamieson *et al.* 1995). Soil temperature is therefore of major importance for crop development, leaf appearance and shoot development during the early stages of cereal development (Vincent & Gregory 1989; McMaster & Wilhelm 1998).

It was also observed that soil warming enhanced increases in GLAI, accumulation of biomass in above-ground plant parts and their N amount during early stages (Table 7; Fig. 3) mainly by hastening crop development. This meant a higher GLAI during spring and thus an earlier start of crop growth, but the faster crop development also advanced the time of flag leaf appearance (GS39) by 11 days, besides advancing later developmental stages. Thus, there was less time available for developing the crop canopy, and this may have resulted in the similarity of the maximum leaf area obtained and in the effective duration of the GLAI between control and heated plots. Further, analysing the total above-ground biomass against crop development stages suggest that the difference in plant biomass in heated and control plots on 28 April and 15 June sampling may also have been due to the crop being in different development stages caused by soil warming (Fig. 4).

Leaf area expansion is regarded to be driven by three main and inter-linked factors; temperature, nitrogen amount and dry matter accumulation (Olesen *et al.* 2002). Soil warming may have affected all of these factors, but the most important one was probably through the direct effect of soil temperature on shoot apex increasing leaf appearance and leaf area expansion rate. Similar effects of soil temperature increasing the rate of leaf appearance have been reported previously for peanut (Awal & Ikeda 2002), and for plant size, shoot phenology (Gavito *et al.* 2001) and the rate of tillering (Brengle & Whitfield 1969) in wheat. The response of above-ground biomass to soil warming followed the same trend as GLAI (Table 7) in line with biomass accumulation, that is, a function of photosynthetically active green leaf area.

Ear number was reduced in heated plots (Table 6), whereas 1000 grain weight was higher (Table 8). This may be due to a lower proportion of growing shoots becoming productive tillers in the heated plots. This may have been partly due to the low plant density, because this puts a higher demand on tillering for producing the necessary reproductive shoots, and in the heated plots there were fewer days available for the production and establishment of reproductive shoots. Increased mean grain weight for the crop in heated plots may have partly compensated for the lower grain number so that grain yield was not significantly affected by soil warming.

Nitrogen amount in the crop from heated plots was more than twice as high as that in the crop from control plots when measured on 28 April (Fig. 3), while there was no significant difference during later sampling dates until harvest, indicating increased sink strength for N (Gavito *et al.* 2001) due to faster crop development and growth during early stages. Whitfield & Smika (1971) attributed increased

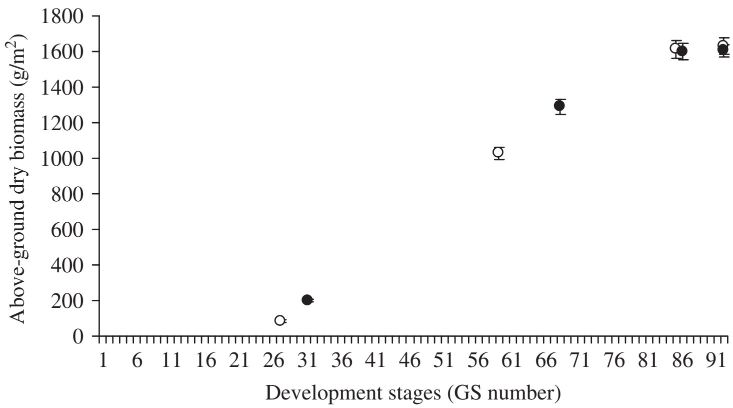

Fig. 4. Total above-ground biomass (g DM/m^2) measured on four dates of sampling during the study period *v.* the crop development stages monitored on BBCH scaling from sowing (GS0) to harvest (GS92) (Lancashire *et al.* 1991). Error bars: ±S.E. with $n=8$. ●, heated; ○, control treatments.

amounts of N in plants to higher biomass accumulation in warmer soil. Increased crop demand for N coincided with the timing of fertilizer applied to the crop in the present study. The first application of N (75 kg N/ha) was applied on 3 April, which may have been more efficiently used by the crop in heated plots because crop demand was much larger at that point. It is argued that the higher amount of N in plant parts during early stages (28 April sampling) grown in heated plots was more due to advanced crop development and a higher crop growth rate increasing the crop N demand than to enhanced supply from the soil. However, during the later developmental stages, neither above-ground biomass nor total N amount in the plant differed between heated and control plots (Fig. 3), despite the top soil (0–0·3 m depth) in heated plots containing significantly higher amounts of mineral N (data not shown). This suggests that the effect of soil warming on crop growth, and accumulation of biomass and N amount in plants, did not continue when the direct effect of air temperature rather than soil temperature on crop growth and development became dominant (Awal & Ikeda 2002).

Soil warming reduced the plant N concentration in the above-ground biomass across sampling dates, except at harvest (Table 9), though both plant biomass and total N amount were much larger during early stages (Table 7; Fig. 3). Plant biomass can be conceived as being composed of two pools (Greenwood *et al.* 1990; Lemaire & Gastal 1997): the 'metabolic' pool with high N concentration directly involved in plant growth processes (green leaf) and the structural pool involved in plant architecture (stem and other storage organs) with low N concentrations (Lemaire *et al.* 2008). It is suggested that the lower plant N concentration in heated plots may have been due to increased structural pool constituents (e.g. stem tissue) with the crop being in advanced development stage compared with the crop in control plots, except at harvest (Table 5), affecting leaf:shoot ratio (Lemaire *et al.* 1992). With advancing plant development and growth, the structural and storage material pool with lower N concentration increased (Greenwood *et al.* 1990) leading to sharp decline in plant N concentration (Lemaire *et al.* 1992) during later development stages, and this decline followed the same pattern in control and heated plots (Fig. 5). Further, plant N dilution curve equations proposed by Greenwood *et al.* (1990) for C_3 plants and Justes *et al.* (1994) for winter wheat were fitted (not calibrated) onto the plant N concentrations measured in this study (Fig. 6). This indicated that the plant N dilution in heated and control plots during later development stages followed the same pattern and were very close to plant critical N (N_{ct}) required for maximum crop growth suggesting that soil N availability was not a limiting factor in heated plots.

Rainfall patterns

Contrary to the initial hypothesis, rainfall treatments (amount and number of rainy days) neither affected plant population during winter nor influenced soil moisture regime (Table 4) or crop performance (Table 8), though future rainfall amount helped the wheat crop to retain higher green leaf area towards the end of grain filling stage. There are three likely reasons for this: (i) almost all the increased rainfall amount with RF_1 treatment occurred during winter and was freely drained down on the loamy sand soil used in the present study (Table 3) and did not cause waterlogging that affected the plant population, (ii) the relatively mild Danish winter conditions may

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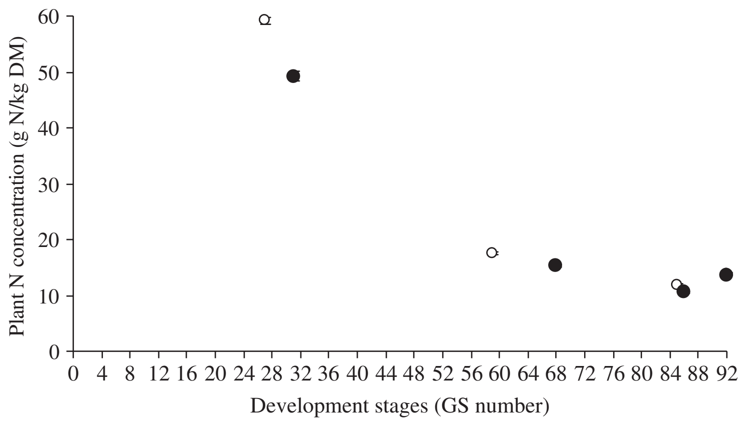

Fig. 5. Average plant N concentration (g N/kg DM) in above-ground biomass measured on four dates of sampling during the study period *v.* the crop development stages monitored on BBCH scaling from sowing (GS0) to harvest (GS92) (Lancashire *et al.* 1991). Error bars: ±S.E. with $n=8$. ●, heated; ○, control treatments.

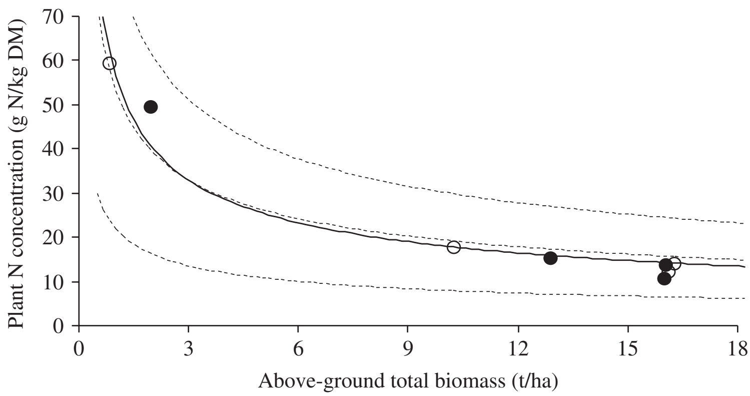

Fig. 6. Average plant N concentration (g N/kg DM) in above-ground biomass *v.* the total above-ground biomass (t DM/ha) measured on four dates of sampling during the study period. The measured points were fitted to the plant critical N (N_{ct}) equation $N_{ct}=5{\cdot}7DM^{-0{\cdot}5}$ (solid line) reported by Greenwood *et al.* (1990). In comparison also $N_{ct}=5{\cdot}35DM^{-0{\cdot}442}$ (dotted middle line), $N_{min}=2{\cdot}2DM^{-0{\cdot}44}$ (dotted lower line) and $N_{max}=8{\cdot}3DM^{-0{\cdot}44}$ (dotted upper line) reported by Justes *et al.* (1994) are presented. The measured critical points are the mean values with $n=8$. ●, heated; ○, control treatments.

have allowed the crop to develop a deep root system, making it more tolerant later in the season (Kristensen *et al.* in press) and (iii) the intra-annual variability of rainfall pattern, in terms of total amount and average size of each rainfall event (Table 2), imposed in the present study was too small to significantly influence on soil moisture regimes.

Temporal soil water regime and its availability to plants are influenced not only by soil characteristics but also by rainfall distribution pattern and environmental factors. In Denmark, the total annual rainfall normally exceeds annual potential evapotranspiration and the surplus winter rainfall helps recharge deeper soil layers to be made available during summer period (Olesen 2001). In the present experiment, this may have enabled the deep-rooted winter wheat crop to extract soil moisture from deeper layers during the later developmental stages and may have resulted in the lack of significant effects of rainfall treatments imposed in the study. This agrees with the findings of Kristensen *et al.* (in press), who found no significant effect of precipitation on wheat yields. Modelling studies by Semenov & Porter (1995) and Semenov *et al.* (1996), while assessing the impact of climate variability on wheat yields, also reported little or no impact of rainfall amount and its variability on wheat yield in northern parts of Europe with relatively wetter and milder weather conditions than in southern parts of Europe, experiencing much drier and warmer conditions.

In conclusion, the rainfall patterns imposed in the present study did not affect growth and yield of wheat. Soil warming accelerated crop growth and development, leading to greater above-ground biomass during vegetative stages. However, soil warming shortened the total crop growing cycle by 12 days without affecting the crop development period during later stages, hence grain yield was not affected by soil warming. This suggests that under future warmer climates yield levels of winter wheat could be maintained even under shorter growing period. To take advantage of this situation to realize higher yields, genotypes that respond to warmer winter temperature by extending their vegetative period without advancing reproductive stages are likely to be better adapted to future warmer conditions.

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