

Effect of two-week heat stress during grain filling on stem reserves, senescence, and grain yield of European winter wheat cultivars

Siegfried Schittenhelm¹  | Tina Langkamp-Wedde^{2,3}  | Martin Kraft² | Lorenz Kottmann¹  | Katja Matschiner⁴

¹Institute for Crop and Soil Science, Julius Kühn-Institut, Braunschweig, Germany

²Institute of Agricultural Technology, Johann Heinrich von Thünen Institute, Braunschweig, Germany

³Institute for Application Techniques in Plant Protection, Julius Kühn-Institut, Braunschweig, Germany

⁴Strube Research, Söllingen, Germany

Correspondence

Siegfried Schittenhelm, Institute for Crop and Soil Science, Julius Kühn-Institut, Braunschweig, Germany.
Email: siegfried.schittenhelm@julius-kuehn.de

Funding information

German Federal Ministry of Food and Agriculture (BMEL) via the Federal Office for Agriculture and Food (BLE) as project management organisation under the innovation support programme. Grant/Award Numbers: 2814600213 (Julius Kühn-Institut), 2814600113 (Johann Heinrich von Thünen Institute), and 2814600313 (Strube Research).

Abstract

To examine the extent to which heat stress during grain filling impacts on the development and yield of winter wheat (*Triticum aestivum* L.), a 3-year field experiment was conducted on a loess soil with high water holding capacity in the North German Plain. Thirty-two mostly European winter wheat cultivars were exposed to heat stress in a mobile foil tunnel with maximum air temperatures of 45.7, 45.4, and 47.2°C in 2015, 2016, and 2017, respectively. The 14-day post-anthesis heat stress treatment caused an average 57.3% grain yield reduction compared to a close-by non-stressed control. The proportion of green crop area after the heat stress phase varied from 7% to 98% in 2016 and from 37% to 94% in 2017. The green crop area percentage did not significantly correlate with grain yield, indicating that the delayed senescence of stay-green phenotypes offers no yield advantage under terminal heat stress. The water soluble carbohydrate (WSC) concentration of the stems at crop maturity varied between 6 and 92 g/kg dry matter, showing that the genotypes differed in their efficiency at using the stem carbohydrate reserves for grain filling under heat stress. The stem WSC concentration correlated positively with the beginning of anthesis ($r = 0.704$; $p < .001$) but negatively with the grain yield ($r = -0.431$; $p < .05$). For heat tolerance breeding, the stem reserve strategy, i. e. the rapid and full exhaustion of the temporary carbohydrate storage therefore seems more promising than the stay-green strategy.

KEYWORDS

chlorophyll degradation, grain weight, post-anthesis heat stress, stay-green, *Triticum aestivum*, wheat breeding

This is an open access article under the terms of the Creative Commons Attribution License, which permits use, distribution and reproduction in any medium, provided the original work is properly cited.

© 2020 The Authors. *Journal of Agronomy and Crop Science* published by Blackwell Verlag GmbH

1 | INTRODUCTION

Ambient air temperature has significantly increased during the last decades and is expected to rise further (IPCC, 2018). The higher air temperature in conjunction with an increase of its variance will lead towards more frequent heat waves and record hot weather (IPCC, 2001; Porter & Semenov, 2005). Wheat is particularly sensitive to high temperatures during anthesis and grain filling (Farooq, Bramley, Palta, & Siddique, 2011; Satorre & Slafer, 1999). While heat stress during anthesis mainly affects the grain number, post-anthesis heat stress reduces the grain yield through a lower grain weight caused by a heat-induced premature leaf senescence and an associated shortened grain filling duration (Bergkamp, Impa, Asebedo, Fritz, & Jagadish, 2018). Heat stress induced yield losses in wheat, which is one of the world's most important food crops poses a serious threat to global food security. Already today, high temperatures are limiting wheat productivity in many countries worldwide (Farooq, Khaliq, & Mahmood, 2015; Narayanan, Prasad, Fritz, Boyle, & Gill, 2015).

It has been estimated that for each 1°C of further temperature increase, grain filling duration of wheat decreases by 2.8 days (Streck, 2005) and, as a consequence, wheat grain yield by about 6% (Asseng et al., 2015). An increase of the average ambient temperature does not only result from a rising maximum temperature, but also from a growing minimum temperature (Vose, Easterling, & Gleason, 2005). Lobell et al. (2005) observed an even stronger dependence of wheat grain yield on the minimum than on the maximum temperature and quantified the yield decrease as 10% for every 1°C rise of the night temperature.

The optimum temperature for grain filling in wheat ranges from 12 to 22°C (Farooq et al., 2011; Porter & Gawith, 1999). The maximum temperature for grain filling above which wheat growth stops is about 35°C and the upper lethal temperature is 47.5°C (Porter & Gawith, 1999). The extent of the heat stress reaction depends on the degree and speed of the temperature increase, as well as the duration of exposure to the high temperature (Wahid, Gelani, Ashraf, & Foolad, 2007). Temperatures of about 45°C represent a critical threshold, because temperatures above this threshold irreversibly damage the photosystem II (PSII), whereas at temperatures below 45°C the PSII functionality is able to recover more or less rapidly depending on the wheat genotype (Haque, Kjaer, Rosenqvist, Sharma, & Ottosen, 2014; Mathur, Jajoo, Mehta, & Bharti, 2011). One of the earliest symptoms of heat-induced premature leaf senescence is the decline in chlorophyll content which becomes apparent in leaf chlorosis caused by the concurrent physiological processes of heat-accelerated chlorophyll degradation and heat inhibition of chlorophyll biosynthesis (Jespersen & Huang, 2014). The carbohydrate depletion resulting from the decrease in photosynthesis and the increase in respiration exhausts the plant's energy reserves that are particularly needed for recovery after long periods of heat stress.

Heat stress in wheat is a particular issue in countries with tropical and sub-tropical climates. However, yield losses and quality deterioration such as small or deformed grains caused by above

optimum temperatures during grain filling are a concern also in temperate climates. Based on long-term phenological and climate data of Germany, Rezaei, Siebert, and Ewert (2015) concluded that despite heat escape through an earlier onset of phenological phases (e. g. 14 days earlier heading), warming might still affect grain yield through a shortened grain filling period. Semenov and Shewry (2011) expect that the increase in frequency and degree of heat stress around anthesis will cause substantial yield losses for the heat-sensitive cultivars that are commonly grown in Northern Europe.

In the present field study, 32 mostly European winter wheat genotypes were exposed to high temperatures for 14 days during grain filling. The study aimed (a) to determine whether there exists genetic variability for terminal heat stress tolerance within the adapted primary gene pool of wheat, which could be used in breeding programmes, and (b) to identify and explain important physiological processes such as the mobilisation of stem carbohydrate reserves, chlorophyll degradation and premature senescence which are involved in the heat tolerance of wheat.

2 | MATERIALS AND METHODS

2.1 | Study site

The experiment was conducted on the experimental fields of the Strube Research wheat breeding station located at Söllingen (52.09°N 10.93°E, elevation 102 m) in the North German Plain. The site is characterised by a long-term mean annual air temperature of 9.0°C and 580 mm rainfall. The soil at the site is a deep loess loam (Luvic Chernozem) with a water holding capacity of 240 mm in the 0–120 cm soil horizon. The field trials were carried out in the 2014/2015, 2015/2016 and 2016/2017 winter wheat growing seasons, referred to as 2015, 2016 and 2017, respectively. Winter wheat was the previous crop in each season.

2.2 | Genetic material

Thirty-two winter wheat (*Triticum aestivum* L.) genotypes, mostly elite cultivars from various European countries, were used in the study. The genotypes were pure-lines with respect to their genetic structure, except for "Hybery," "Hyland" and "Hystar," which were hybrids with a German-French genetic background. The 13 German pure-line cultivars consisted of "Elixer," "Glaucus," "Gordian," "JB Asano," "JB Diego," "Julius," "KWS Milaneco," "Lennox," "Magister," "Memory," "Pegassos," "Rumor" and "Tobak." Another 14 European pure-line cultivars were "Finans" from Sweden, "Mariboss" from Denmark, "Platin" from Poland, "Bernstein" and "Midas" from Austria, "Bohemia" from the Czech Republic, "Apache," "Premio," and "Solehio" from France, "Psenica" from Slovakia, "Viktoriya Odesskaya" from the Ukraine, "MV Lucilla" from Hungary, and "Moskovskaja56" from Russia. "Straw type" and "Extreme dwarf" were experimental lines of Strube Research bred for the joint straw

and grain use and a strongly reduced plant height, respectively. "PS66/13" from China was the most early genotype used in the study. In a parallel study, sixteen of the 32 genotypes named above were also tested for drought tolerance (Schittenhelm, Kottmann, Kraft, Matschiner, & Langkamp-Wedde, 2019).

2.3 | Testing facility and experimental layout

The 32 genotypes were grown under two temperature regimes consisting of a 14-day post-anthesis heat stress treatment and a nearby non-stressed control. Each temperature treatment was laid out as a completely randomised block design with two replicates. The heat stress treatment was conducted in a mobile FILCLAIR 850 foil tunnel (Filclair Serren Industry). The tunnel frame was erected immediately after sowing, but the inflatable duplex polythene foil with about 70% light transmittance was mounted just before the heat stress treatment. The 14-day stress period started on 25 June in 2015 and on 9 June in 2016 and 2017. By that time, all genotypes had completed flowering, corresponding to growth stage 69 on the BBCH-scale (Meier, 2018). The tunnel was 50 m long, 8.5 m wide and had a ridge height of 3.2 m. Four ventilation flaps distributed evenly over the side length of the tunnel allowed for combined side and ridge ventilation. The flaps were opened manually as soon as the temperature in the tunnel approached 40°C. After the heat stress treatment had ended, the tunnel foil was detached so that the environmental conditions were again the same as those in the control.

2.4 | Crop management

The field trials were sown on 1 October 2014, 30 September 2015, and 5 October 2016 with a plot drill (Wintersteiger) at a density of 350 grains/m². The 4.5 m² plots consisted of seven rows with 17.5 cm row spacing. Each year, mineral nitrogen fertiliser in the form of calcium ammonium nitrate was applied at a rate able to close the gap between the available soil mineral N and the target N level of 220 kg/ha. The N fertiliser was provided in split application at the BBCH stages 20, 30 and 47 to support tillering, booting and grain filling, respectively. Herbicides, insecticides, fungicides and growth regulators were applied according to local practice at the rates recommended by the manufacturer.

2.5 | Meteorological measurements

Ambient air temperature, air humidity, global radiation and CO₂ concentration in the foil tunnel and the non-stressed control were recorded every five minutes by an automatic weather station constructed by the Thünen Institute of Agricultural Technology. Air temperature and air humidity were determined by means of 16 EE071 sensors (E + E Elektronik) placed at ear height and equally distributed over the length of the experiment. The EE071 sensors

were equipped with a radiation protection and a solar-powered ventilation. For monitoring the CO₂ concentration, one EE871 sensor each was installed in the centre of the tunnel and in the non-stressed control. The light intensity was determined with a CMP3 pyranometer (Kipp & Zonen). In each year, soil samples from the experimental field were taken in 10-cm intervals for determining the field capacity (FC) and the permanent wilting point (PWP). In the laboratory, the FC was determined in a vacuum chamber at a pF value of 1.8. The PWP was measured at a pF value of 4.2 in a pressure pot. The soil moisture was monitored by means of two Sentek EnviroSCAN sensors (Sentek Sensor Technologies). The sensors were installed between two wheat rows in a centrally situated plot, one sensor in the foil tunnel and one sensor in the control. The moisture readings were taken in 10-cm intervals to a depth of 60 cm. The PWP was used for calculating the plant-available water quantity in the soil (Blume et al., 2016) by subtracting the PWP from the measured soil moisture (mm/dm) and adding up the difference over the 60 cm soil horizon.

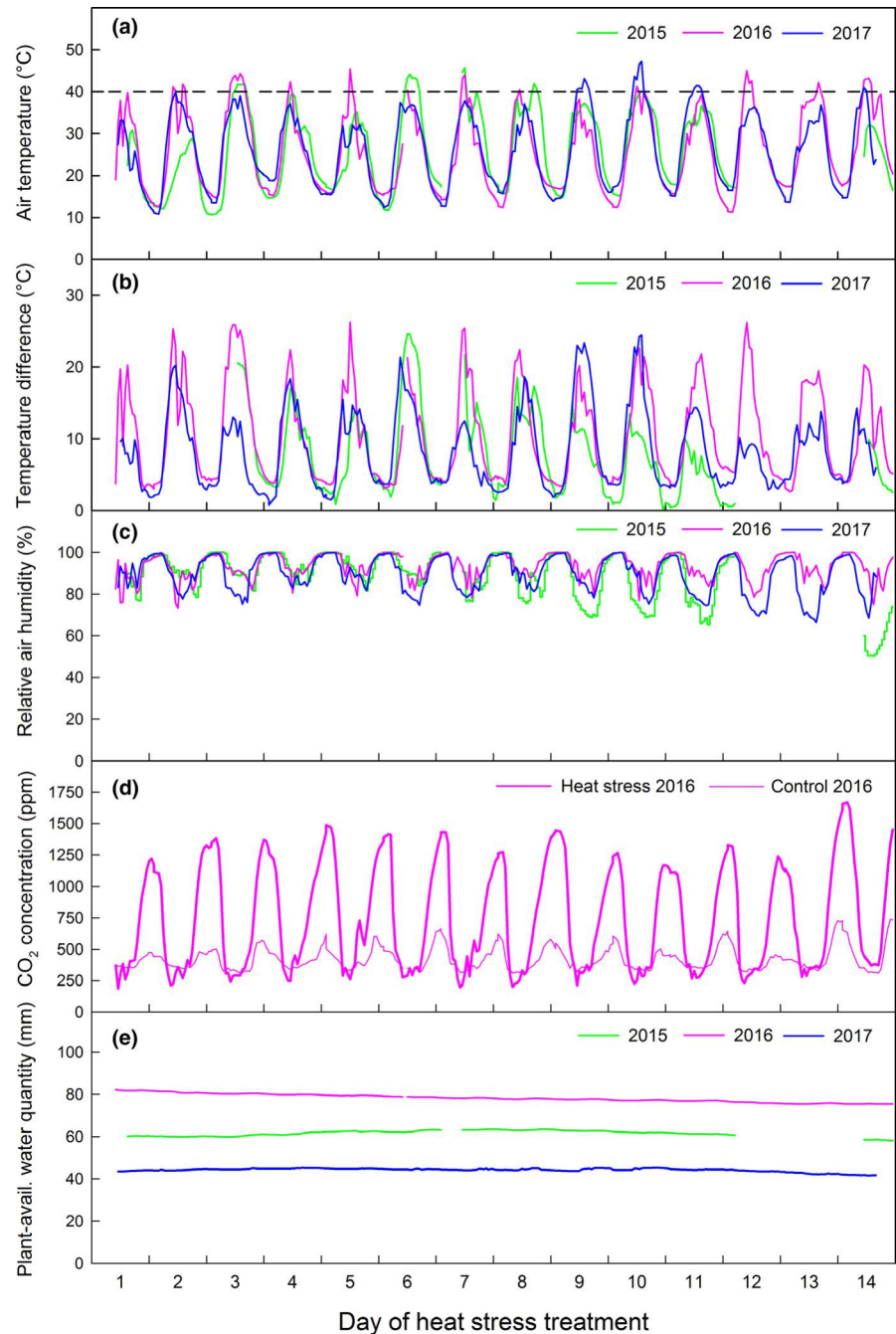
2.6 | Anthesis and grain yield

For each plot, the beginning of anthesis was recorded as the number of days from 1 January to the scoring day when 50% of the plants of a plot had reached BBCH growth stage 61. Each year, the entire experiment was harvested with a plot combine (Wintersteiger). Although the heat-stressed plots always reached maturity prematurely, the plots in both environments were harvested on the same day, that is on 30 July 2015, 22 July 2016 and 17 August 2017. The grain yield is expressed on the basis of 14% water content.

2.7 | Green crop area

For the quantification of heat-induced chlorophyll degradation, digital colour photographs were taken from all experimental plots in the foil tunnel and control. The photographs were taken on three dates in 2016 and on five dates in 2017 during the heat stress treatment and, in both years, on the fourth day after completion of the heat stress treatment. In 2016, the photographs were taken with a Samsung smartphone (model SM-G388F) camera and in 2017 with a Canon EOS 600D camera, using the automatic white balance setting in either case. The photographs were mostly taken with nadir viewing direction and in few cases with oblique viewing angle (about 45° from nadir) and were analysed automatically by means of OpenCV 4 with Python. After conversion to the HIS colour space, very dark pixels (mainly shaded soil and dead lower leaves) as well as extremely light pixels (mostly ears) without reliable colour information were excluded from the analysis. Proper upper and lower limits for hue were chosen to classify and separate the green pixels, representing the photosynthetically active green crop area (Broge & Mortensen, 2002) which is equivalent to the green leaf area but considers all green plant organs including leaves, stems and ears. The green crop area percentage (GCAP) was calculated from the number

FIGURE 1 Daily course for (a) air temperature in the foil tunnel, (b) air temperature difference between foil tunnel and adjacent field control, (c) relative air humidity in the foil tunnel, (d) CO₂ concentration in the foil tunnel and control in 2016, and (e) plant-available water quantity (0–60 cm) in the foil tunnel during the duration of the 14-day post-anthesis heat stress treatments in 2015, 2016 and 2017 at Söilingen, Germany. Breaks in the curves are attributable to sensor failures. The dotted line in (a) indicates 40°C



of green pixels (n_{green}) and the number of non-green pixels (n_{yellow}) as follows:

$$\text{GCAP} = \frac{n_{\text{green}} * 100}{n_{\text{green}} + n_{\text{yellow}}}$$

2.8 | Water soluble carbohydrates

The concentration of water soluble carbohydrates (WSC) of the stems was determined at crop maturity in 2017. Twenty ear-bearing stems were clipped above the ground and stored in a portable cooler until further processing to minimise carbohydrate respiration losses. The ears were cut from the stem at the ear collar.

The samples were dried at 60°C for 72 hr. After removal of leaf blades and leaf sheaths, the stems were ground to 1 mm size using a Brabender mill (Brabender). A 1-g sample of the ground material was extracted using 70-ml demineralised water at 80°C for 30 min in a shaking water bath. The water soluble carbohydrate concentration was determined by means of high-performance liquid chromatography (HPLC) using a Kontron 400 HPLC system (Kontron Instruments) as described in detail by Menge-Hartmann, Soufan, and Greef (2009). In brief, the HPLC was equipped with a Rezex RPM monosaccharide separation column (Phenomenex) and a Shodex RI-71 refractive index detector (Showa Denko America) for identifying the different carbohydrates. The total WSC concentration was calculated as the sum of glucose, fructose, sucrose

and fructans determined by means of peak area comparison with external standards of known concentrations.

2.9 | Statistical analysis

The analyses of variance for all measured traits were carried out for individual years and across years using R (R Core Team, 2018). In these analyses, year, temperature regime and genotype were considered fixed effects. The least significant differences ($p < .05$) were calculated using the function `LSD.test` (package "agricolae") with the Bonferroni correction. SigmaPlot version 13 (Systat Software Inc.) was used for creating the graphs and calculating the linear regression coefficients between different pairs of traits of interest. The relationship between green crop area and water soluble carbohydrate concentration for the heat stress treatment in Figure 1 was described by an exponential curve using the regression procedure of SigmaPlot.

3 | RESULTS

3.1 | Climatic conditions

With the roof foil acting as a light barrier, the radiation intensity in the tunnel was reduced by about 30% compared to that in the adjacent control. The average air temperature in the foil tunnel during the high temperature treatment was quite similar in the three experimental years, averaging 25.8°C in both 2015 and 2016, and 25.9°C in 2017 (Figure 1a). By manually opening the side flaps around midday, temperatures above 40°C, which represent severe heat shock conditions (Wardlaw & Wrigley, 1994), were avoided in most cases. Nevertheless, the tunnel temperature during the 14 days of heat

stress exceeded the 40°C mark for 18 hr in 2015, 29 hr in 2016 and 16 hr in 2017. The maximum measured temperature over a period of more than one hour was 45.7°C in 2015, 45.4°C in 2016 and 47.2°C in 2017. These peak temperatures were only slightly below the 47.5°C lethal maximum temperature for wheat (Porter & Gawith, 1999). The foil tunnel temperature exceeded the non-stressed control by 7.7°C in 2015, 10.5°C in 2016 and 8.3°C in 2017 (Figure 1b). The relative air humidity in the foil tunnel during the 14-day heat treatment was on average 14 percentage points higher than in the field control (Figure 1c). During the nights, the air in the foil tunnel was completely saturated with water vapour. Due to the daytime opening of the side vents, the relative humidity during the day dropped a little but still remained at a high level. The CO₂ concentration also exhibited a sharp increase during the night, but decreased strongly with the onset of the plants' assimilation in the morning and was frequently below the control during the day (Figure 1d). The water available to the plants in the upper 60-cm soil layer averaged 62, 78 and 44 mm in 2015, 2016 and 2017, respectively (Figure 1e), indicating that the heat stress in the tunnel was not superimposed by drought stress as it is often the case in hot environments.

3.2 | Genotype response to heat stress treatment

Averaged across seasons, the 14-day post-anthesis heat stress reduced the grain yield by 57.3% from 10.4 to 4.3 t/ha (Table 1). The thousand grain weight, as the grain yield component most strongly affected by terminal heat stress, decreased by 49% from 47 to 24 g (data not shown). The heat stress treatment caused significant grain yield losses in all genotypes, ranging from 28.7% for "Straw type" in 2015 to 85.9% for "Mariboss" in 2016. Under heat stress conditions, the hybrid cultivars "Hybery" and "Hystar" ranked at places 1 and 4 and even took the two top positions in the non-stressed control.

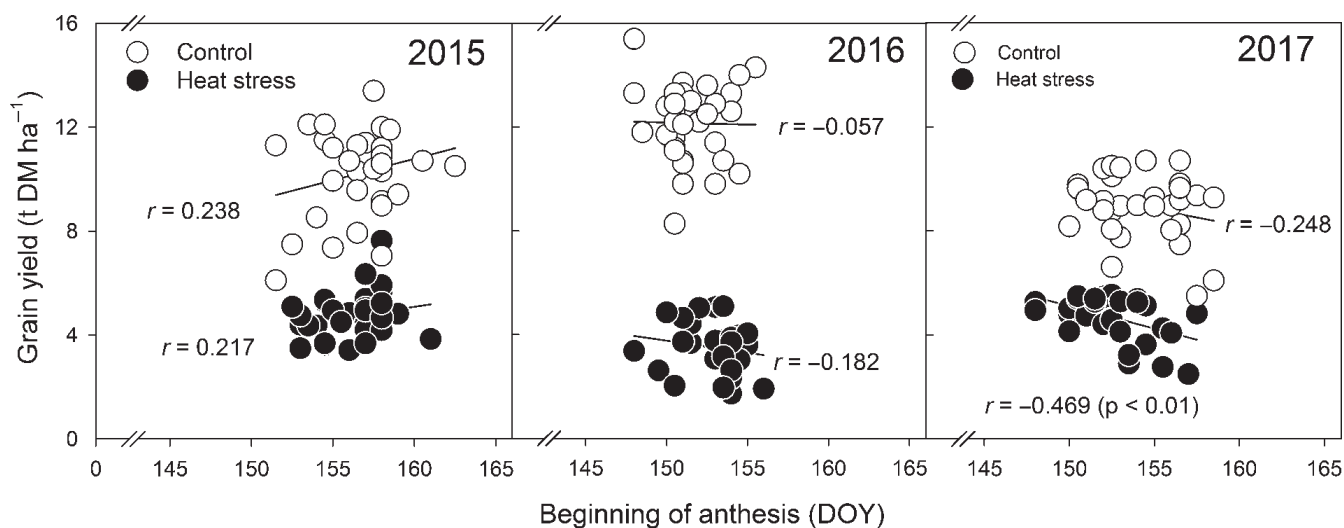


FIGURE 2 Relationships between the beginning of anthesis and grain yield for 32 winter wheat genotypes grown under post-anthesis heat stress and non-stressed control conditions in 2015, 2016 and 2017 at Söllingen, Germany. Each data point represents an average of two replications. DOY, day of year and DM, dry matter

TABLE 1 Grain yield and relative grain yield reduction of 32 winter wheat genotypes grown under non-stressed conditions in an open field control and under 14-day post-anthesis heat stress in a closed foil tunnel during three experimental years at Söllingen, Germany. The genotypes are sorted by ascending mean grain yield under post-anthesis heat stress

Genotype	Grain yield (t/ha)								Relative grain yield reduction (%)			
	Control				Heat stress				2015	2016	2017	Mean
	2015	2016	2017	Mean	2015	2016	2017	Mean				
"Extreme dwarf"	9.4	10.2	5.5	8.4	3.8	2.3	2.5	2.9	59.2	77.5	54.8	63.8
"Moskovskaja56"	7.9	10.6	7.5	8.7	3.4	3.1	3.6	3.4	57.0	71.1	51.7	59.9
"Viktoriya Odesskaya"	6.1	9.8	6.6	7.5	3.5	2.6	4.1	3.4	42.9	73.4	37.7	51.3
"Straw type"	7.1	9.8	6.1	7.7	5.0	2.4	2.8	3.4	28.7	75.3	54.6	52.9
"KWS Milaneco"	9.2	11.4	8.2	9.6	5.7	1.7	2.9	3.4	37.9	84.9	64.9	62.6
"Magister"	10.6	12.1	9.0	10.6	4.7	2.6	3.2	3.5	56.1	78.4	64.0	66.2
"Bohemia"	9.6	10.7	8.1	9.5	3.6	3.0	4.4	3.7	62.3	71.9	45.4	59.9
"Glaucus"	10.7	13.0	9.7	11.1	5.2	2.0	4.1	3.8	51.3	85.0	57.8	64.7
"Finans"	10.4	11.7	9.2	10.4	4.2	2.0	5.5	3.9	60.0	82.7	40.3	61.0
"Pegassos"	10.9	12.5	9.0	10.8	4.5	3.2	4.1	3.9	58.7	74.7	54.3	62.6
"Memory"	11.0	13.3	9.2	11.2	3.8	3.8	4.3	3.9	65.5	71.8	54.0	63.8
"Mariboss"	10.5	13.6	8.8	10.9	4.8	1.9	5.3	4.0	54.2	85.9	40.1	60.1
"Bernstein"	9.0	12.2	8.0	9.7	3.7	3.9	4.6	4.0	59.1	68.2	43.1	56.8
"MV Lucilla"	7.4	10.7	7.8	8.6	4.4	3.4	4.6	4.1	40.8	68.6	40.7	50.0
"JB Asano"	11.3	12.8	9.3	11.1	4.2	3.8	5.0	4.3	62.9	70.6	46.7	60.1
"Premio"	10.7	11.1	10.4	10.7	3.7	4.0	5.3	4.3	65.6	63.6	49.4	59.6
"Platin"	12.0	14.0	9.2	11.7	4.9	3.6	4.7	4.4	59.0	74.3	48.3	60.5
"Midas"	9.9	11.6	8.8	10.1	5.3	3.7	4.8	4.6	46.9	68.0	45.4	53.4
"Julius"	10.3	13.3	9.2	10.9	5.9	3.1	4.8	4.6	42.7	77.1	47.6	55.8
"Hyland"	11.4	13.7	10.1	11.8	4.8	3.8	5.5	4.7	58.5	72.5	45.9	58.9
"Rumor"	11.5	13.3	10.4	11.7	4.8	3.7	5.5	4.7	58.1	72.5	46.5	59.1
"Elixer"	11.2	12.6	10.7	11.5	4.4	4.4	5.2	4.7	60.4	65.1	51.5	59.0
"PS-66/13"	7.5	8.3	9.6	8.5	4.9	3.8	5.4	4.7	34.1	54.5	43.9	44.2
"Gordian"	10.3	11.8	9.0	10.4	5.4	4.0	5.0	4.8	47.6	66.6	44.6	52.9
"Psenica"	8.5	11.2	9.0	9.5	5.4	3.7	5.3	4.8	37.1	66.7	41.3	48.4
"Apache"	11.2	12.6	10.5	11.4	4.4	5.0	5.0	4.8	61.1	60.3	52.1	57.8
"Tobak"	10.9	12.9	9.4	11.0	4.8	4.6	5.1	4.8	56.3	64.0	45.5	55.3
"Solehio"	11.3	12.2	8.2	10.6	4.8	5.1	4.9	4.9	57.8	58.4	39.5	51.9
"Hystar"	12.1	14.3	9.8	12.1	4.4	5.1	5.4	4.9	63.7	64.7	45.1	57.8
"JB Diego"	11.9	13.3	9.8	11.7	6.3	3.7	5.3	5.1	46.7	72.1	46.5	55.1
"Lennox"	12.1	12.9	9.3	11.4	5.1	4.9	5.4	5.1	58.0	62.3	41.9	54.1
"Hybery"	13.4	15.4	10.7	13.2	7.6	3.9	5.4	5.7	43.2	74.4	49.8	55.8
Mean	10.2	12.1	8.9	10.4	4.7	3.5	4.7	4.3	52.9	71.2	48.0	57.3
LSD _{0.05}	2.7	3.6	3.1	2.2	4.6	2.3	2.2	1.7	20.1	19.5	33.1	19.2

The French cultivars "Apache," "Solehio" and "Premio" also recorded above-average grain yields irrespective of the temperature regime. The German pure-line cultivars revealed quite a mixed picture. While "Lennox," "Tobak," "Julius," "Elixer" and "Rumor" in both environments were among the highest yielders, "Pegassos," "Memory," "Glaucus" and "Magister" performed well in the non-stressed control, but only ranked in the lower third when exposed to temporary

heat stress. The experimental lines "Extreme dwarf" and "Straw type" as well as the eastern European cultivars "Moskovskaja56," "Viktoriya Odesskaya" and "Bohemia," produced below-average yields under both stress and non-stressed conditions. The eastern European cultivars "Psenica," "MV Lucilla" and "Viktorya Odesskaya" exhibited a small relative grain yield reduction, but they also only had a low grain yield potential.

3.3 | Days to anthesis and its relation to grain yield

The beginning of anthesis was used as a proxy indicator for earliness. This seems justified because the days to anthesis for 18 of the 32 wheat genotypes mentioned in the descriptive variety list of the German Federal Plant Variety Office (<https://www.bundessortenamt.de/bsa/en/variety-testing/descriptive-variety-lists/>) did closely correlate ($r = 0.753$, $p < .001$) with the maturity score reported there. The beginning of anthesis had a range of 8 days in 2016 and of 11 days each in 2015 and 2017 (Figure 2). In the non-stressed control, the correlation coefficients between the beginning of anthesis and the grain yield were not statistically significant ($p < .05$). Yet in the treatment with temporary heat stress, a significant negative correlation between these two traits was found in 2017 but no significant correlation existed in 2015 and 2016.

3.4 | Stay-green and its relation to maturity, grain yield and assimilate relocation

The heat stress during grain filling had a greatly varying effect on the green crop area retention of the winter wheat genotypes studied in the experiment. The contrasting pattern of chlorophyll degradation during the post-anthesis heat stress treatment is well illustrated when using the German cultivars “JB Asano” and “Julius” as examples. While the senescence of “JB Asano”

proceeded rapidly under high temperature conditions, “Julius” almost completely retained its green colour during the heat stress treatment and beyond (Figure 3). The rapid chlorophyll degradation in 2016 started already after the occurrence of the first extreme temperature with 44.3°C during day 3 of the heat stress treatment (see Figure 1a). In 2017, this transition took place one week later after the first extreme temperature with 47.2°C had occurred on day 10 of the stress treatment. Overall, the green crop area four days after the end of the heat stress phase varied from 7% to 98% in 2016 and from 37% to 94% in 2017. In contrast to that, in the control none of the genotypes in 2016 and only a few genotypes in 2017 showed signs of senescence at that time. The green crop area percentage and the beginning of anthesis were not associated with each other in 2016 (Figure 4). In 2017, however, the later flowering genotypes maintained a significantly larger proportion of green plant parts under heat stress and control conditions. No statistically significant correlation coefficients were found between green crop area percentage and grain yield both under heat stress and control conditions. The green crop area percentage in the heat stress treatment correlated closely and positively with the WSC concentration of the stems, determined at crop maturity in 2017 (Figure 5). The stem WSC concentration was lowest for “JB Asano” (6 g/kg) marked by a low green crop area percentage, but second highest for “Julius” (67 g/kg) with a high green crop area percentage. The “Straw type” (92 g/kg) had the highest WSC concentration at maturity.

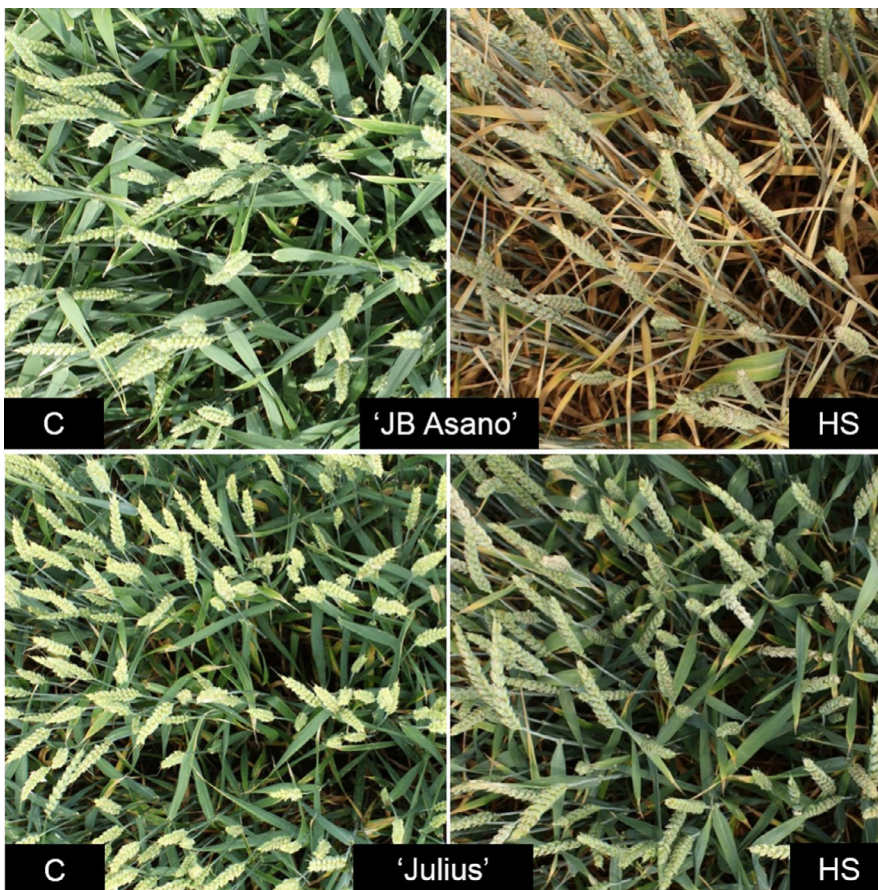
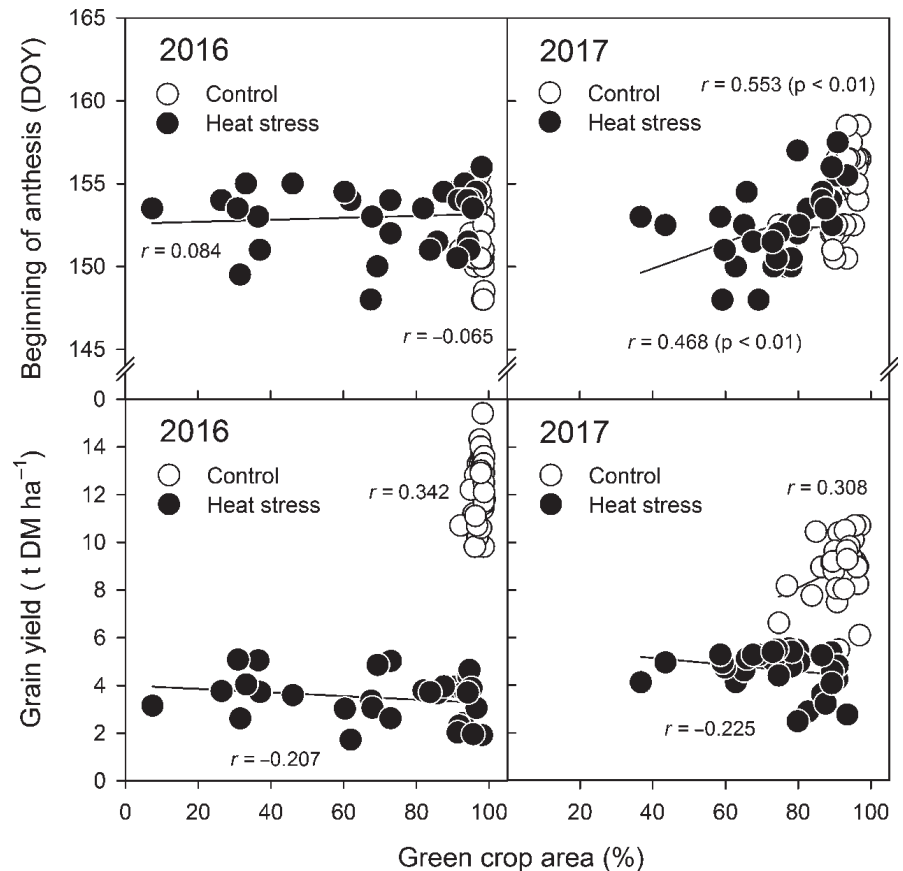


FIGURE 3 Photographs of the German winter wheat cultivars “JB Asano” and “Julius” grown under post-anthesis heat stress (HS) and non-stressed control (C) conditions in 2017 at Söllingen, Germany. The photographs were taken on 26 June 2017, four days after the completion of the 14-day heat stress treatment

FIGURE 4 Relationships of the green crop area percentage with both beginning of anthesis and grain yield for 32 winter wheat genotypes grown under post-anthesis heat stress and non-stressed control conditions in 2016 and 2017 at Söllingen, Germany. The green crop area percentage in 2016 and 2017 was determined 16 and 18 days, respectively, after the initiation of the 14-day post-anthesis heat stress treatment. Each data point represents an average of two replications. DOY, day of year and DM, dry matter



4 | DISCUSSION

4.1 | Drawbacks of foil tunnels for field-based heat tolerance screening

For studying the response of wheat genotypes to high temperatures, different experimental set-ups can be used such as delayed sowing (Kumari, Pudake, Singh, & Joshi, 2013; Nahar, Ahamed, & Fujita, 2010; Trethowan & Mahmood, 2011), growth chambers (Rezaei et al., 2018; Yang, Sears, Gill, & Paulsen, 2002), foil tunnels or foliage greenhouses (Li et al., 2018; Talukder, McDonald, & Gill, 2014), artificially warmed field plots (Kimball et al., 2008), simulation modelling (Asseng, Foster, & Turner, 2011; Semenov & Shewry, 2011), satellite images (Lobell, Sibley, & Ortiz-Monasterio, 2012) and inherently warm environments (Reynolds, Nagarajan, Razzaque, & Ageeb, 2001). Most of the studies aimed at field-based measuring of heat tolerance conducted so far have used controlled environment facilities such as foil tunnels or similar devices (Bergkamp et al., 2018). Foil tunnels enable the simultaneous heat stress screening of numerous genotypes which is particularly important in practical breeding programmes (Wahid et al., 2007). However, though there is the desired effect of an increased air temperature, the microclimate in foil tunnels differs from field conditions particularly with regard to reduced radiation, altered carbon dioxide concentration, and higher air humidity. The possible effects of these environmental artefacts on grain yield will be briefly discussed below.

The decrease of radiation intensity by shading reduces the wheat grain yield (Asana, Parvatikar, & Saxena, 1969; Li, Yu, & Liang, 2005). Xu, Tao, Wang, and Wang (2016) used different numbers of layers of polyethylene screens for achieving varying levels of shading of the wheat canopy from the beginning of anthesis to maturity. The use of two polyethylene layers with 67% light transmittance in their experiment caused an average grain yield reduction of 19.4%. Applied to the present study with a similar light transmittance of 70% and approximately half the shading duration, this corresponds to a roughly 10% grain yield reduction.

As is typical of closed greenhouses, the CO₂ concentration in the foil tunnel through plant respiration and microbial activities increased during the night far beyond the ambient level (Poudel & Dunn, 2017) of currently around 410 ppm. However, after sunrise, the excess CO₂ in the tunnel was completely used up by photosynthesis within a few hours, and often dropped below the ambient level during daytime. It is thus assumed that the CO₂ surplus in the morning and the temporary CO₂ deficit during the day have at least partly offset each other in their effect on grain yield.

The relative humidity of 86% in the foil tunnel during the day was markedly higher than the relative humidity of 66% in the control. The high relative humidity in the tunnel was caused by the good water supply of the deep loess soil which in turn was desirable to avoid mixing up effects of drought stress with those of heat stress. Rawson, Begg, and Woodward (1977) have shown that the relative humidity does not affect photosynthesis of individual leaves in winter wheat and various other crops. Overall, in

comparison to the overwhelming adverse effect of heat stress, it is assumed that the environmental artefacts discussed above had only a minor impact on the grain yield of the genotypes grown in the foil tunnel.

4.2 | heat stress treatment substantially decreased grain yield

The present study showed a decrease in grain yield of 57.3% when a two-week severe heat stress was applied during grain filling (Table 1). Nahar et al. (2010) reported a similarly large grain yield reduction of 53%–73% under late heat stress conditions generated by delayed wheat sowing in Bangladesh. Bergkamp et al. (2018) reported 2%–27% grain yield reduction under post-anthesis heat stress using field based “heat tents” in Kansas, USA. Li et al. (2018) measured the effect of 20-day post-anthesis heat stress in the North China Plain by following the fluctuating field temperature in a temperature-controlled greenhouse on an about 5°C higher level with maximum temperatures of up to 44°C. Under these conditions, the grain yield reduction was 17% on average of the 48 winter wheat cultivars studied. Also in China, Feng et al. (2014) observed a grain yield reduction of 6% and 11% for a low and high heat-sensitive winter wheat genotype, respectively, when heat stress during grain filling was produced by means of white polythene plastic film. Stone and Nicolas (1995) demonstrated in a glasshouse experiment with 75 pot-grown cultivars of wheat (*T. aestivum* L. and *T. turgidum* L.) in Australia that a short 3-day heat phase with maximum temperatures of 40°C during the grain filling significantly reduce the grain yield by 5.4%. Likewise in Australia, Talukder et al. (2014) demonstrated that even a single day with high temperature of 35°C for three hours applied after anthesis in a portable heat chamber, accelerated leaf senescence and caused grain yield reduction of 15%–30%. The results described above are consistent with findings of a simulation study by Asseng et al. (2011) which shows that a single heat event during grain filling has a maximum effect of about 5% on grain yield but can accumulate to a yield reduction of up to 60%.

4.3 | Relationship between earliness and grain yield

In the heat stress treatment of the present study, a significant negative correlation was observed between the beginning of anthesis and the grain yield in one of the three experimental years (Figure 2). These results indicate a tendency towards higher yields of early genotypes if high temperatures are prevailing during grain filling. Tewolde, Fernandez, and Erickson (2006) also observed that, under the high temperature conditions of Southwest Texas, earlier heading cultivars performed better than later heading cultivars. Similarly, Midmore, Cartwright, and Fischer, (1984) reported negative correlations between grain yield and days to anthesis for spring wheat grown along an altitudinal transect in Central Mexico with earliness being most favourable at the warmest, least elevated site. Midmore

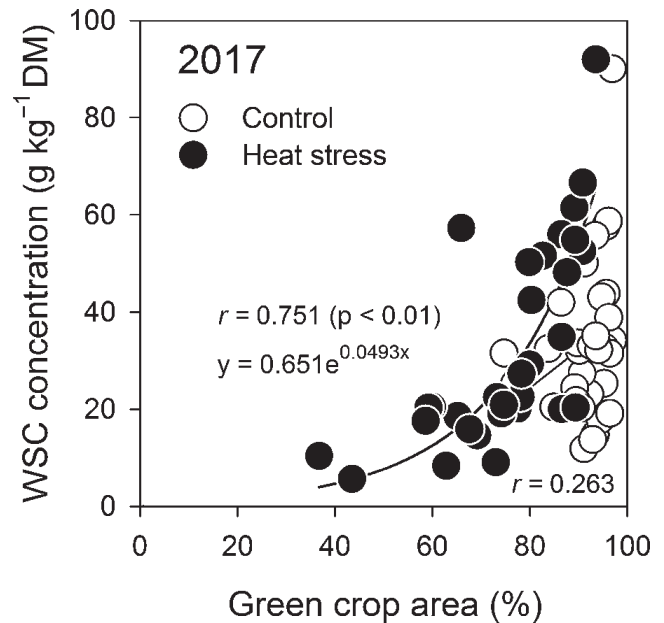


FIGURE 5 Relationship of the green crop area percentage with the water soluble carbohydrate (WSC) concentration of the stem at crop maturity for 32 winter wheat genotypes grown under post-anthesis heat stress and non-stressed control conditions in 2017 at Söllingen, Germany. The green crop area percentage was determined 18 days after the initiation of the heat stress treatment. Each data point represents an average of two replications

et al. (1984) assumed that the lower yields of the later genotypes were attributable to an accelerated senescence and thus a shorter grain filling duration due to the late-season rise in temperature. In contrast to this, Reynolds et al. (2001) reported highly positive genetic correlations of grain yield with both days to anthesis and leaf chlorophyll retention during grain filling in CIMMYT's high temperature mega-environments. It is assumed that differences between the above cited studies with respect to the intensity and duration of heat stress might explain the inconsistent findings.

4.4 | Genotypes do not benefit from stay-green under severe heat stress

The physiological processes involved in yield reduction under heat stress are only poorly understood. Some crop physiologists emphasise the importance of stay-green traits for improving the heat tolerance (Cossani & Reynolds, 2012; Harris et al., 2007; Lopes & Reynolds, 2012). This approach is based on the assumption that the wheat yield under heat stress is source-limited and that extending the green canopy duration by delaying leaf senescence and increasing photosynthesis is the key to improving the biomass and grain yield (Abdelrahman, Burritt, Gupta, Tsujimoto, & Tran, 2019). In the present study, however, the retention of green crop area was not significantly associated with grain yield. Li et al. (2018), too, found in only one of two crop seasons a positive, yet only weak association

between the visually assessed stay-green score and grain yield of winter wheat grown under post-anthesis heat stress.

The transfer of photoassimilates from source to sink is a critical step during wheat grain filling (Abdelrahman et al., 2019). The WSC can become the predominant source of carbohydrates for the developing grain, if the ongoing photosynthesis is severely inhibited by heat stress (Blum, 1998; Talukder, McDonald, & Gill, 2013). While net photosynthesis is declining already at temperatures above 30°C (Wardlaw, 1974) and is irreversibly damaged at temperature > 45°C (Mathur et al., 2011), the relocation of assimilates from the stem reserves to the grains is not affected by high temperatures of up to 50°C (Wardlaw, 1974). It is therefore interesting to note that genotypes with a high concentration of WSC in their stems at maturity showed a higher green crop area percentage under post-anthesis heat stress than those with a low stem WSC concentration (Figure 1). The capacity for photosynthesis lost due to the adverse effect of heat stress was probably compensated for by the transfer of WSCs from the stems into the grains. However, the delayed loss of green colour did not pay off in terms of higher grain yields. Genotypes like “Julius” thus resemble in a way the so-called non-functional (cosmetic) type C stay-green mutants (Thomas & Howarth, 2000; Thomas & Ougham, 2014) which retain chlorophyll but not their photosynthetic capacity. It should be noted, however, that the WSC concentration was only studied in 2017.

The results of the present study do not support the hypothesis that stay-green phenotypes with decreased rates of senescence are a worthwhile goal in breeding for high temperature environments. This result applies at least to conditions of severe and long-lasting post-anthesis heat stress. Blum (1998) proposed to select cultivars with a high capacity for stem reserve storage and utilisation for grain filling. In the present study, the WSC concentration correlated significantly positively with the beginning of anthesis ($r = 0.704$; $p < .001$) but significantly negatively with the grain yield ($r = -0.431$; $p < .05$) (data not shown). This indicates that early genotypes with an efficient remobilisation of the stem carbohydrate reserves are more valuable under late heat stress. For wheat grown under chronic post-anthesis heat stress and heat shock, Yang et al. (2002) obtained high yields regardless of the source of assimilates for grain filling, whether from photosynthesis or stem reserves. Even if both assimilate supply routes were equally effective in terms of grain yield, from the farmers' perspective the use of stem reserves appears preferable because a heat-induced rapid senescence allows an earlier harvest and thus somewhat greater flexibility in the subsequent land use. Furthermore, the earlier harvest preserves the soil water due to lesser evaporation and transpiration losses.

5 | CONCLUSION

In this 3-year field study, 32 mostly European winter wheat genotypes were exposed to severe post-anthesis heat stress, both in terms of stress duration and intensity. The daytime air temperature

during the 14-day heat stress treatment in the foil tunnel frequently exceeded 35°C and repeatedly was just below the lethality threshold of 47.5°C. The genotypes from eastern Europe exhibited a generally small yield reduction relative to the control, but were low yielding under heat stress and control conditions. On the other hand, a number of genotypes from western Europe not only were high yielding in the control but also performed above average under heat stress conditions. The genetic material studied differed markedly in its physiological response to heat stress. While some genotypes tolerated the high temperatures and retained their greenness after the heat treatment, high temperatures in other genotypes triggered a rapid transition to emergency ripening. Earliness was promoting this trigger but was not a precondition. In contrast to stress escape due to earliness, emergency ripening is a physiological response to a stress to which the plant is inescapably exposed. Emergency ripening is characterised by a premature loss of the green canopy, accompanied by the mobilisation of stem carbohydrate reserves and their relocation to the grains. Genotypes exhibiting this kind of heat response might represent a wheat ideotype for environments where extremely high temperatures occur towards the end of the cropping season.

ACKNOWLEDGEMENTS

The authors wish to thank Eugen Diefenbach, Alexander Huf, Fredrik Mühlberger, Sabine Peickert, Martina Schabanoski and Timo Schmidt for their assistance in executing the field experiments. Our thanks also go to Dr. Andreas Jacobi for several stimulating discussions on wheat improvement and to Irene Schäfer for proof-reading the English text.

AUTHOR CONTRIBUTIONS

MK and SS designed the experiments and LK, KM and TL-W monitored their execution. TL-W and SS performed the statistical analyses. MK carried out the image analysis. SS wrote the manuscript with input from the other authors. All authors participated in the critical discussion of the results of the study during the compilation of the manuscript.

ORCID

Siegfried Schittenhelm  <https://orcid.org/0000-0002-2743-0989>

Tina Langkamp-Wedde  <https://orcid.org/0000-0002-3286-8467>

Lorenz Kottmann  <https://orcid.org/0000-0002-9957-1115>

REFERENCES

- Abdelrahman, M., Burritt, D. J., Gupta, A., Tsujimoto, H., & Tran, L. S. P. (2019). Heat stress effects on source-sink relationships and metabolome dynamics in wheat. *Journal of Experimental Botany*, *erz296*, <https://doi.org/10.1093/jxb/erz296>
- Asana, R. D., Parvatikar, S. R., & Saxena, N. P. (1969). Studies in physiological analysis of yield. IX, Effect of light intensity on the development of the wheat grain. *Physiologia Plantarum*, *22*, 915–924. <https://doi.org/10.1111/j.1399-3054.1969.tb07450.x>
- Asseng, S., Ewert, F., Martre, P., Rotter, R. P., Lobell, D. B., Cammarano, D., ... Zhu, A. (2015). Rising temperatures reduce global wheat production. *Nature Climate Change*, *5*, 143–147. <https://doi.org/10.1038/nclimate2470>

- Asseng, S., Foster, I., & Turner, N. C. (2011). The impact of temperature variability on wheat yields. *Global Change Biology*, *17*, 997–1012. <https://doi.org/10.1111/j.1365-2486.2010.02262.x>
- Bergkamp, B., Impa, S. M., Asebedo, A. R., Fritz, A. K., & Jagadish, S. V. K. (2018). Prominent winter wheat varieties response to post-flowering heat stress under controlled chambers and field based heat tents. *Field Crops Research*, *222*, 143–152. <https://doi.org/10.1016/j.fcr.2018.03.009>
- Blum, A. (1998). Improving wheat grain filling under stress by stem reserve mobilisation. *Euphytica*, *100*, 77–83.
- Blume, H.-P., Brümmer, G. W., Fleige, H., Horn, R., Kandeler, E., Kögel-Knabner, I., ...Wilke, B.-M. (2016). Scheffer/Schachtschabel Soil Science. Springer-Verlag GmbH Berlin Heidelberg
- Broge, N. H., & Mortensen, J. V. (2002). Deriving green crop area index and canopy chlorophyll density of winter wheat from spectral reflectance data. *Remote Sensing of Environment*, *81*, 45–57. [https://doi.org/10.1016/S0034-4257\(01\)00332-7](https://doi.org/10.1016/S0034-4257(01)00332-7)
- Cossani, C. M., & Reynolds, M. P. (2012). Physiological traits for improving heat tolerance in wheat. *Plant Physiology*, *160*, 1710–1718. <https://doi.org/10.1104/pp.112.207753>
- Farooq, J., Khaliq, I., & Mahmood, A. (2015). Evaluation of some wheat hybrids under normal and heat stress conditions. *Triticace Genomics and Genetics*, *5*, 1–11. <https://doi.org/10.5376/tgg.2014.05.0002>
- Farooq, M., Bramley, H., Palta, J. A., & Siddique, K. H. M. (2011). Heat stress in wheat during reproductive and grain-filling phases. *Critical Reviews in Plant Sciences*, *30*, 491–507. <https://doi.org/10.1080/07352689.2011.615687>
- Feng, B., Liu, P., Li, G., Dong, S. T., Wang, F. H., Kong, L. A., & Zhang, J. W. (2014). Effect of heat stress on the photosynthetic characteristics in flag leaves at the grain-filling stage of different heat-resistant winter wheat varieties. *Journal of Agronomy and Crop Science*, *200*, 143–155. <https://doi.org/10.1111/jac.12045>
- Haque, M. S., Kjaer, K. H., Rosenqvist, E., Sharma, D. K., & Ottosen, C. O. (2014). Heat stress and recovery of photosystem II efficiency in wheat (*Triticum aestivum* L.) cultivars acclimated to different growth temperatures. *Environmental and Experimental Botany*, *99*, 1–8. <https://doi.org/10.1016/j.envexpbot.2013.10.017>
- Harris, K., Subudhi, P. K., Borrell, A., Jordan, D., Rosenow, D., Nguyen, H., ... Mullet, J. (2007). Sorghum stay-green QTL individually reduce post-flowering drought-induced leaf senescence. *Journal of Experimental Botany*, *58*, 327–338. <https://doi.org/10.1093/jxb/erl225>
- IPCC (2001). Climate change 2001: The scientific basis. In J. T. Houghton, Y. Ding, D. J. Griggs, M. Noguer, P. J. van der Linden, X. Dai, ... C. A. Johnson (Eds.), *Contribution of Working Group I to the Third Assessment Report of the Intergovernmental Panel on Climate Change* (pp. 1038–1039). Cambridge, UK and New York, NY: Cambridge University Press.
- IPCC (2018). Summary for Policymakers. In V. Masson-Delmotte, P. Zhai, H. O. Pörtner, D. Roberts, J. Skea, P. R. Shukla, A. Pirani, Moufouma-Okia, C. Péan, R. Pidcock, S. Connors, J. B. R. Matthews, Y. Chen, X. Zhou, M. I. Gomis, E. Lonnoy, T. Maycock, M. Tignor, & T. Waterfield (Eds.), *Global Warming of 1.5°C. An IPCC Special Report on the impacts of global warming of 1.5°C above pre-industrial levels and related global greenhouse gas emission pathways, in the context of strengthening the global response to the threat of climate change, sustainable development, and efforts to eradicate poverty* (32 pp.). Geneva, Switzerland: World Meteorological Organization.
- Jespersen, D., & Huang, B. (2014). Physiological and biochemical mechanisms of plant tolerance to heat stress. In M. Pessarakli (Ed.), *Handbook of plant and crop physiology* (pp. 389–404). Boca Raton: CRC Press.
- Kimball, B. A., Conley, M. M., Wang, S., Lin, X., Luo, C., Morgan, J., & Smith, D. (2008). Infrared heater arrays for warming ecosystem field plots. *Global Change Biology*, *14*, 309–320. <https://doi.org/10.1111/j.1365-2486.2007.01486.x>
- Kumari, M., Pudake, R. N., Singh, V. P., & Joshi, A. K. (2013). Association of staygreen trait with canopy temperature depression and yield traits under terminal heat stress in wheat (*Triticum aestivum* L.). *Euphytica*, *190*, 87–97. <https://doi.org/10.1007/s10681-012-0780-3>
- Li, Q., Wang, Z. R., Li, D., Wei, J. W., Qiao, W. C., Meng, X. H., ... Zhao, F. W. (2018). Evaluation of a new method for quantification of heat tolerance in different wheat cultivars. *Journal of Integrative Agriculture*, *17*, 786–795. [https://doi.org/10.1016/s2095-3119\(17\)61716-7](https://doi.org/10.1016/s2095-3119(17)61716-7)
- Li, Y., Yu, Z. W., & Liang, X. F. (2005). Response of wheat yields and quality to low light intensity at different grain filling stages. *Acta Phytocologica Sinica*, *29*, 807–813.
- Lobell, D. B., Ortiz-Monasterio, J. I., Asner, G. P., Matson, P. A., Naylor, R. L., & Falcon, W. P. (2005). Analysis of wheat yield and climatic trends in Mexico. *Field Crops Research*, *94*, 250–256. <https://doi.org/10.1016/j.fcr.2005.01.007>
- Lobell, D. B., Sibley, A., & Ortiz-Monasterio, J. I. (2012). Extreme heat effects on wheat senescence in India. *Nature Climate Change*, *2*, 186–189. <https://doi.org/10.1038/nclimate1356>
- Lopes, M. S., & Reynolds, M. P. (2012). Stay-green in spring wheat can be determined by spectral reflectance measurements (normalized difference vegetation index) independently from phenology. *Journal of Experimental Botany*, *63*, 3789–3798. <https://doi.org/10.1093/jxb/ers071>
- Mathur, S., Jajoo, A., Mehta, P., & Bharti, S. (2011). Analysis of elevated temperature-induced inhibition of photosystem II using chlorophyll a fluorescence induction kinetics in wheat leaves (*Triticum aestivum*). *Plant Biology*, *13*, 1–6. <https://doi.org/10.1111/j.1438-8677.2009.00319.x>
- Meier, U. (2018). Growth stages of mono- and dicotyledonous plants: BBCH Monograph. Open Agrar Repository, Quedlinburg. <https://doi.org/10.5073/20180906-074619>
- Menge-Hartmann, U., Soufan, W., & Greef, J. M. (2009). The influence of plant development stage and N fertilization on the content of water-soluble carbohydrates and fructans in different varieties of *Lolium perenne*. *Journal für Kulturpflanzen*, *61*, 365–374 (in German). <https://doi.org/10.5073/JfK.2009.10.01>
- Midmore, D. J., Cartwright, P. M., & Fischer, R. A. (1984). Wheat in tropical environments. II. Crop growth and grain yield. *Field Crops Research*, *8*, 207–227. [https://doi.org/10.1016/0378-4290\(84\)90064-9](https://doi.org/10.1016/0378-4290(84)90064-9)
- Nahar, K., Ahamed, K. U., & Fujita, M. (2010). Phenological variation and its relation with yield in several wheat (*Triticum aestivum* L.) cultivars under normal and late sowing mediated heat stress condition. *Notulae Scientia Biologicae*, *2*, 51–56. <https://doi.org/10.15835/nsb234723>
- Narayanan, S., Prasad, P. V. V., Fritz, A. K., Boyle, D. L., & Gill, B. S. (2015). Impact of high night-time and high daytime temperature stress on winter wheat. *Journal of Agronomy and Crop Science*, *201*, 206–218. <https://doi.org/10.1111/jac.12101>
- Porter, J. R., & Gawith, M. (1999). Temperatures and the growth and development of wheat: A review. *European Journal of Agronomy*, *10*, 23–36. [https://doi.org/10.1016/S1161-0301\(98\)00047-1](https://doi.org/10.1016/S1161-0301(98)00047-1)
- Porter, J. R., & Semenov, M. A. (2005). Crop responses to climatic variation. *Philosophical Transactions of the Royal Society B: Biological Sciences*, *360*, 2021–2035. <https://doi.org/10.1098/rstb.2005.1752>
- Poudel, M., & Dunn, B. (2017). Greenhouse carbon dioxide supplementation. Oklahoma Cooperative Extension Service Fact Sheet HLA-6723. Oklahoma State University, Stillwater, OK, SA. Retrieved from https://www.researchgate.net/publication/316463509_Greenhouse_Carbon_Dioxide_Supplementation
- R Core Team (2018). R: A Language and Environment for Statistical Computing. R Foundation for Statistical Computing, Vienna, Austria.
- Rawson, H. M., Begg, J. E., & Woodward, R. G. (1977). The effect of atmospheric humidity on photosynthesis, transpiration and water

- use efficiency of leaves of several plant species. *Planta*, 134, 5–10. <https://doi.org/10.1007/BF00390086>
- Reynolds, M. P., Nagarajan, S., Razzaque, M. A., & Ageeb, O. A. A. (2001). Heat tolerance. In M. P. Reynolds, J. I. Ortiz-Monasterio & A. McNab (Eds.), *Application of physiology in wheat breeding* (pp. 2–10). Mexico, D.F.: CIMMYT.
- Rezaei, E. E., Siebert, S., Manderscheid, R., Müller, J., Mahrookashani, A., Ehrenpfordt, B., ... Ewert, F. (2018). Quantifying the response of wheat yields to heat stress: The role of the experimental setup. *Field Crops Research*, 217, 93–103. <https://doi.org/10.1016/j.fcr.2017.12.015>
- Rezaei, E. E., Siebert, S., & Ewert, F. (2015). Intensity of heat stress in winter wheat - phenology compensates for the adverse effect of global warming. *Environmental Research Letters*, 10. <https://doi.org/10.1088/1748-9326/10/2/024012>
- Satorre, E. H., & Slafer, G. A. (1999). *Wheat: Ecology and physiology of yield determination*. New York: Food Products Press.
- Schittenhelm, S., Kottmann, L., Kraft, M., Matschiner, K., & Langkamp-Wedde, T. (2019). Agronomic performance of winter wheat grown under highly divergent soil moisture conditions in rainfed and water-managed environments. *Journal of Agronomy and Crop Science*, 205, 283–294. <https://doi.org/10.1111/jac.12322>
- Semenov, M. A., & Shewry, P. R. (2011). Modelling predicts that heat stress, not drought, will increase vulnerability of wheat in Europe. *Scientific Reports*, 1, 66. <https://doi.org/10.1038/srep00066>
- Stone, P. J., & Nicolas, M. E. (1995). A survey of the effects of high temperature during grain filling on yield and quality of 75 wheat cultivars. *Australian Journal of Agricultural Research*, 46, 475–492. <https://doi.org/10.1071/AR9950475>
- Streck, N. A. (2005). Climate change and agroecosystems: The effect of elevated CO₂ and temperature on crop growth, development, and yield. *Ciência Rural*, 35, 730–740. <https://doi.org/10.1590/S0103-84782005000300041>
- Talukder, A. S. M. H. M., McDonald, G. K., & Gill, G. S. (2013). Effect of short-term heat stress prior to flowering and at early grain set on the utilization of water-soluble carbohydrate by wheat genotypes. *Field Crops Research*, 147, 1–11. <https://doi.org/10.1016/j.fcr.2013.03.013>
- Talukder, A. S. M. H. M., McDonald, G. K., & Gill, G. S. (2014). Effect of short-term heat stress prior to flowering and early grain set on the grain yield of wheat. *Field Crops Research*, 160, 54–63. <https://doi.org/10.1016/j.fcr.2014.01.013>
- Tewolde, H., Fernandez, C. J., & Erickson, C. A. (2006). Wheat cultivars adapted to post-heading high temperature stress. *Journal of Agronomy and Crop Science*, 192, 111–120. <https://doi.org/10.1111/j.1439-037X.2006.00189.x>
- Thomas, H., & Howarth, C. J. (2000). Five ways to stay green. *Journal of Experimental Botany*, 51, 329–337. https://doi.org/10.1093/jexbot/51.suppl_1.329
- Thomas, H., & Ougham, H. (2014). The stay-green trait. *Journal of Experimental Botany*, 65, 3889–3900. <https://doi.org/10.1093/jxb/eru037>
- Trethowan, R. M., & Mahmood, T. (2011). Genetics options for improving the productivity of wheat in water-limited and temperature-stressed environments. In S. S. Yadav, R. J. Redden, J. L. Hatfield, H. Lotze-Campen, & A. E. Hall (Eds.), *Crop adaptation to climate change*, 1st ed. (pp. 218–237). Chichester: Wiley-Blackwell.
- Vose, R. S., Easterling, D. R., & Gleason, B. (2005). Maximum and minimum temperature trends for the globe: An update through 2004. *Geophysical Research Letters*, 32, n/a-n/a. <https://doi.org/10.1029/2005GL024379>
- Wahid, A., Gelani, S., Ashraf, M., & Foolad, M. R. (2007). Heat tolerance in plants: An overview. *Environmental and Experimental Botany*, 61, 199–223. <https://doi.org/10.1016/j.envexpbot.2007.05.011>
- Wardlaw, I. F. (1974). Temperature control of translocation. In R. L. Bielske, A. R. Ferguson, & M. M. Cresswell (Eds.), *Mechanism of Regulation of Plant Growth* (pp. 533–538). Bulletin 12, Wellington, Royal Society of New Zealand.
- Wardlaw, I. F., & Wrigley, C. W. (1994). Heat tolerance in temperate cereals: An overview. *Australian Journal of Plant Physiology*, 21, 695–703. <https://doi.org/10.1071/PP9940695>
- Xu, C. L., Tao, H. B., Wang, P., & Wang, Z. L. (2016). Slight shading after anthesis increases photosynthetic productivity and grain yield of winter wheat (*Triticum aestivum* L.) due to the delaying of leaf senescence. *Journal of Integrative Agriculture*, 15, 63–75. [https://doi.org/10.1016/S2095-3119\(15\)61047-4](https://doi.org/10.1016/S2095-3119(15)61047-4)
- Yang, J., Sears, R. G., Gill, B. S., & Paulsen, G. M. (2002). Genotypic differences in utilization of assimilate sources during maturation of wheat under chronic heat and heat shock stresses. *Euphytica*, 125, 179–188. <https://doi.org/10.1023/A:1015882825112>

How to cite this article: Schittenhelm S, Langkamp-Wedde T, Kraft M, Kottmann L, Matschiner K. Effect of two-week heat stress during grain filling on stem reserves, senescence, and grain yield of European winter wheat cultivars. *J Agro Crop Sci*. 2020;206:722–733. <https://doi.org/10.1111/jac.12410>