



TUM School of Life Sciences

Phenotyping Complex Traits of Drought and Heat Tolerance for Future Climate-resilient German Wheat

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Vollständiger Abdruck der von der TUM School of Life Sciences der Technischen Universität München zur Erlangung des akademischen Grades einer

Doktorin der Agrarwissenschaften (Dr. agr.)

genehmigten Dissertation.

Vorsitzender: Prof. Dr. Gerd Patrick Bienert

Prüfende der Dissertation:

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Die Dissertation wurde am 24.06.2021 bei der Technischen Universität München eingereicht und durch die TUM School of Life Sciences am 16.11.2021 angenommen.

Glücklich, wer ohne zerbrechliche Instrumente reist

Alexander von Humboldt

Table of contents

I. List of abbreviations	IV
II. List of figures	V
III. List of tables	VI
Zusammenfassung	9
Summary	11
1. Introduction	13
1.1. <i>Climate change – a challenge for maintaining wheat quality and ensuring yield stability</i>	13
1.1.1. Climate change.....	13
1.1.2. Genetic background.....	14
1.2. <i>Relevant traits reflecting drought and heat tolerance</i>	15
1.2.1. Effects of drought on plant physiology.....	15
1.2.2. Effects of heat on plant physiology.....	17
1.2.3. Tolerance mechanisms.....	18
1.2.4. Physiological traits.....	19
1.2.5. Agronomical traits.....	21
1.3. <i>Importance of platforms to simulate climate change for the evaluation of wheat varieties</i>	23
1.4. <i>Using high-throughput phenotyping technology to identify the key traits of plant drought and heat tolerance</i>	25
2. Objectives	28
3. Materials and Methods	29
3.1. <i>Field trial set up</i>	29
3.2. <i>Measurements</i>	34
3.2.1. Spectral reflectance measurements.....	34
3.2.2. Thermal measurements.....	35

3.3. <i>Plant samples</i>	35
3.4. <i>Statistical analysis</i>	37
4. Results	38
4.1. <i>Growth and development of wheat under abiotic stress</i>	38
4.1.1. Growth stages (Zadoks).....	38
4.1.2. Duration of grain filling.....	39
4.1.3. Harvest parameters and nitrogen traits	41
4.1.4. Correlations between harvest parameters	53
4.1.5. Rank sum of grain yield and grain N uptake	56
4.1.6. Heritability of agronomical traits.....	58
4.2. <i>Impact of heat and drought on carbon isotope discrimination and leaf water content</i>	60
4.2.1. Carbon Isotope Discrimination.....	60
4.2.2. Rank sum of CID	63
4.2.3. Relative Leaf Water Content	64
4.2.4. Heritability of physiological traits	66
4.3. <i>Use of high-throughput phenotyping for identification of stress tolerant varieties</i>	67
4.3.1. Spectral indices and canopy temperature measurements	67
4.3.2. Comparison of measurements: Origin and irrigation.....	72
4.3.3. Comparison of measurements: Drone vs. handheld	75
4.3.4. Correlation of harvest parameters and spectral / thermal measurements	79
4.3.5. Rank sum of canopy temperature.....	85
4.3.6. Comparison of rank sums.....	87
4.3.7. Heritability of spectral indices and canopy temperature	88
5. Discussion	90
5.1. <i>Growth and development of wheat under abiotic stress</i>	90
5.1.1. Influence of heat and drought on wheat phenology	90
5.1.2. Agronomical parameters and biomass growth under heat and drought stress	92

5.1.3. Nitrogen traits under heat and drought.....	95
5.2. <i>Impact of heat and drought on relative leaf water content, canopy temperature, and carbon isotope discrimination.....</i>	97
5.3. <i>Use of terrestrial and aerial high-throughput phenotyping for identification of stress tolerant varieties.....</i>	102
5.3.1. Relation between vegetation indices and canopy temperature.....	102
5.3.2. Assessment of agronomical parameters with high-throughput phenotyping.....	104
5.3.3. Detection of stress with aerial and terrestrial devices under drought and irrigation.....	107
5.3.4. Advantages and disadvantages of drones for high-throughput phenotyping.....	110
5.4. <i>Identification of drought and heat stress tolerant varieties</i>	111
5.4.1. Identification of different strategies against abiotic stress.....	113
6. Conclusion	115
6.1. <i>Growth and development of wheat under abiotic stress.....</i>	115
6.2. <i>Impact of heat and drought on relative leaf water content, canopy temperature, and carbon isotope discrimination.....</i>	116
6.3. <i>Use of terrestrial and aerial high-throughput phenotyping for identification of stress tolerant varieties.....</i>	116
6.4. <i>Identification of drought and heat stress tolerant varieties</i>	117
7. Literature	118
8. Appendix	135
9. Acknowledgement	152

I. List of abbreviations

ABA	Abscisic acid
CID	Carbon isotope discrimination
CT	Canopy temperature
GDD	Growing degree-days
h^2	Heritability
HI	Harvest index
HS	HandySpec
LAI	Leaf area index
N	Nitrogen
NDVI	Normalized difference vegetation index
NIR	Near-infrared spectral region
NWI	Normalized water index
REIP	Red-edge inflection point
RLWC	Relative leaf water content
ROS	Reactive oxygen species
SR	Single ratio
TGW	Thousand grain weight
VIS	Visible spectral region
WI	Water index

II. List of figures

Figure 1 Climate diagram of Bălți, Moldova	31
Figure 2 Sum of temperature and precipitation in Bălți, Moldova, from April 1 until harvest	32
Figure 3 Growth stages of winter wheat.	39
Figure 4 Yield parameters per experimental year	45
Figure 5 Proportion of Tillers and Ears m ⁻² of each experimental year and of each origin.	47
Figure 6 Grain size distribution	48
Figure 7 Nitrogen content and uptake at three sampling times per experimental year	50
Figure 8 Comparison of protein content and grain yield for Eastern European varieties and for each quality group of German varieties	51
Figure 9 Comparison of nitrogen uptake and grain yield for Eastern European varieties and per quality group for German varieties.....	52
Figure 10 Carbon isotope discrimination of winter wheat leaves at three growth stages and grains of all experimental years	61
Figure 11 Relative leaf water content (RLWC) of all experimental years at growth stage Z71 (T1) and Z79 (T2).....	64
Figure 12 Time shift of NDVI measurements (HandySpec) between May and July of all experimental years.....	68
Figure 13 Time shift of WI measurements (HandySpec) between May and July of all experimental years.....	69
Figure 14 Time shift of REIP measurements (HandySpec) between May and July of all experimental years.....	70
Figure 15 Time shift of the canopy temperature measured with the handheld thermal camera between May and July of all experimental years.....	72
Figure 16 NDVI (A), WI (B) and REIP (C) calculated from HandySpec data and canopy temperature (D) from the handheld thermal camera of 2019, comparing the drought stressed and the irrigated plots	74
Figure 17 Comparison of handheld (Fluke/HandySpec) and aerial (DuetT/Sequoia) measurements of canopy temperature (A) and NDVI (B).....	76

Figure 18 Time shift of correlation between handheld and aerial measurements of canopy temperature (A) and NDVI (B) from May to July 2019	77
Figure 19 Correlation between the rank sum of grain yield and rank sums of grain N uptake (A), CID (B), and canopy temperature (C).....	87
Figure 20 Days until beginning of grain filling (Z70).....	137
Figure 21 Duration of grain filling (Z70-Z83)	137
Figure 22 Temperature sum during grain filling (Z70-Z83).....	138
Figure 23 Mean temperature during grain filling (Z70-83).....	138
Figure 24 Precipitation sum during grain filling (Z70-83).....	138

III. List of tables

Table 1 Varieties of winter wheat grown in the field trial and the country of origin	29
Table 2 Comparison of site conditions in Bălți, Moldova, and Freising, Germany.....	30
Table 3 Mean temperature, temperature sum and precipitation sum of all experimental years from October 1 and April 1 until harvest.....	33
Table 4 Ratio of precipitation sum and mean temperature of the given period (mm/°C) for all experimental years.	33
Table 5 Indices calculated from spectral reflectance measurements with HandySpec and Sequoia sensors.	35
Table 6 Days to the beginning of grain filling (Z70).....	40
Table 7 Duration, temperature sum, mean temperature and precipitation sum during grain filling in all experimental years, across all varieties.....	40
Table 8 Duration, temperature sum, mean temperature and precipitation sum during grain filling for all varieties, across all trials.....	40
Table 9 Correlation of DAS to reach Z70, resp. Z83, duration of grain filling, temperature and precipitation sum and mean temperature with grain yield, TGW, and HI, across all trials and varieties.....	41
Table 10 Number of ears per tiller.	47
Table 11 Protein content, grain yield and nitrogen uptake per quality class of German varieties and for Eastern European lines across all years.....	52

Table 12 Correlation between harvest parameters for 2017 and 2018, and both trials 2019.....	54
Table 13 Rank sum across all years of grain yield per variety.	57
Table 14 Rank sum across all years of grain N uptake of all varieties. Sorted from highest to lowest N uptake within the groups of origin.....	58
Table 15 Heritability of grain yield, TGW, HI, grain N uptake and protein content.....	59
Table 16 Heritability of grain yield, TGW, HI, grain N uptake, and protein content within drought stress plots only, across all years.	59
Table 17 Correlation between carbon isotope discrimination and grain yield.....	62
Table 18 Rank sum across all years of CID in grains per variety.....	63
Table 19 Correlation of RLWC with WI and canopy temperature, and CID with sum of WI and sum of canopy temperature for each experimental year at EC 71 (above) and EC 79 (below).	65
Table 20 Heritability of RLWC and CID.	66
Table 21 Heritability of RLWC and CID within drought stress plots only, across all years.	66
Table 22 Correlation canopy temperature, single ratio indices and NDVI between handheld and aerial measurements in drought stress and irrigated plots 2019....	78
Table 23 Correlation of spectral indices and canopy temperature with harvest parameters, and with dry weight, N content and N uptake at anthesis and milk ripeness.	80
Table 24 Rank sum across all years of canopy temperature (CT) per variety.....	86
Table 25 Rank sums of grain yield, grain N uptake, CID, and canopy temperature, and average grain yield of each variety	87
Table 26 Heritability of canopy temperature and spectral indices.	89
Table 27 Heritability of canopy temperature and spectral indices within drought stress plots only, across all years.	89
Table 28 Zadoks growth stages per group of origin and within all trials.	135
Table 29 Days to the beginning of grain filling.	136
Table 30 Duration, temperature sum, mean temperature and precipitation sum during grain filling.....	137

Table 31 Significant differences of the grain size distribution for three groups of varieties and each year.	139
Table 32 Protein content, grain yield and N uptake of all winter wheat varieties, separated for each quality class and individual years.....	139
Table 33 NDVI values of each variety group in all trials.....	140
Table 34 WI values of each variety group in all trials.....	142
Table 35 REIP values of each variety group in all trials.....	144
Table 36 Canopy temperature (Fluke) of all variety groups in all trials.....	146
Table 37 Differences of NDVI, WI, REIP, and canopy temperature values between irrigated and drought stress plots 2018/2019.....	147
Table 38 Differences in canopy temperature and NDVI of irrigated and drought stress plots between terrestrial (Fluke/HandySpec) and airborne (DuetT/Sequoia) measurements.	149

Zusammenfassung

Der fortschreitende Klimawandel gefährdet die Weizenproduktion weltweit. Auch unter unterschiedlichen Klimabedingungen sind hohe Erträge wichtig, um die weltweite Nahrungsmittelversorgung sicher zu stellen. Die Kombination hoher Temperaturen mit geringen Niederschlägen kann die Weizenerträge drastisch reduzieren. Extreme Wetterbedingungen werden in den kommenden Jahrzehnten voraussichtlich häufiger auftreten. Eine wachsende Weltbevölkerung und der Verlust landwirtschaftlich nutzbarer Flächen verstärken den Bedarf an Weizensorten, welche ein hohes Ertragspotential haben und diesen Bedingungen widerstehen können. Um gut angepasste Sorten zu selektieren, die für weitere Züchtungsschritte verwendet werden können, werden genaue Informationen über den Einfluss von abiotischem Stress auf agronomische und physiologische Parameter benötigt. Die Durchführung von Feldversuchen hilft, die Pflanzenentwicklung unter Bedingungen zu beurteilen, die der landwirtschaftlichen Praxis ähnlich sind. Dadurch lassen sich die Ergebnisse oft besser auf die Praxis übertragen als von Versuchen unter kontrollierten Bedingungen, z.B. Gewächshäusern. Für diese Studie wurde ein dreijähriger Feldversuch im Norden der Republik Moldau durchgeführt, wo Weizensorten aus Osteuropa und Deutschland angebaut wurden. In allen drei Jahren wuchsen die Pflanzen unter natürlichen Stressbedingungen; im dritten Jahr wurde zusätzlich ein bewässerter Teilversuch angelegt. Die osteuropäischen Sorten zeichneten sich dadurch aus, dass sie genetisch an eine kürzere Vegetationsperiode und kontinentale Klimabedingungen angepasst sind. Spektrale und thermale Messungen zur Hochdurchsatz-Phänotypisierung wurden mit händischen und drohnenbasierten Sensoren durchgeführt. Diese können helfen, mehrere Pflanzenparameter gleichzeitig, rasch und nicht-destruktiv zu erfassen. Zusätzlich wurden von Mai bis Juli Wachstumsstadien bonitiert und Pflanzenproben geschnitten, um die Daten der Sensoren zu referenzieren. Im ersten Teil der Arbeit wurden die Pflanzenentwicklung und agronomische Parameter analysiert. Während osteuropäische Weizensorten ihr Ertragspotential nahezu ausschöpfen konnten, erbrachten deutsche Sorten einen geringeren Kornertrag, sowohl im Vergleich zu den osteuropäischen Linien, und insbesondere verglichen mit dem Anbau unter gemäßigten Bedingungen in Deutschland. Da die deutschen Sorten an die in Moldau vorherrschenden Klimabedingungen nicht angepasst waren, wurden wichtige Ertragsparameter, wie die Anzahl der Triebe und Körner, die Korngröße und der Harvest Index stark reduziert. Die Stickstoffaufnahme war geringer, der Proteingehalt in Körnern höher als bei osteuropäischen Sorten. Letzterer war jedoch häufig mit Ertragsreduktionen verbunden. Die bewässerten Parzellen zeigten in allen agronomischen Parametern bessere Resultate.

Zusätzlich wurden mit der Kohlenstoffisotopendiskriminierung und dem relativen Blattwassergehalt auch physiologische Parameter gemessen. Als Folge der besseren Anpassung zeigten die osteuropäischen Sorten auch unter Stress eine signifikant stärkere Isotopendiskriminierung. Die Diskriminierung nahm über die Vegetationsperiode hinweg ab und war in den Körnern am geringsten. Der Blattwassergehalt zeigte keine signifikanten Unterschiede zwischen den einzelnen Sortengruppen aber zwischen den Probezeitpunkten. Auch er nahm zum Ende der Vegetationsperiode hin ab.

Der dritte Teil der Studie vergleicht die Messungen der händischen und drohnenbasierten Sensoren und zeigt auf, wie damit Stresssymptome bzw. -toleranz erfasst werden können. Die Zeitverläufe der berechneten Vegetationsindizes und der Bestandestemperatur waren in allen Versuchsjahren vergleichbar. Indizes, die den Chlorophyllgehalt der Pflanzen abbilden (NDVI, REIP) zeigten bei osteuropäischen Weizensorten eine frühere Abnahme, was auf eine Anpassung an kurze Vegetationsperioden hinweist. Die deutschen Sorten zeigten zu späteren Messzeitpunkten noch höhere NDVI- und REIP-Werte, jedoch kurz vor der Ernte einen plötzlichen starken Abfall. Dies deutet auf sehr starken finalen Stress hin, wodurch die deutschen Sorten zur Notreife gezwungen wurden und Ertragsverluste entstanden. Obwohl normalerweise eine geringere Bestandestemperatur mit höheren Erträgen verbunden ist, wurde bei osteuropäischen Sorten eine höhere Temperatur gemessen als bei deutschen. Die Korrelationen zwischen Vegetationsindizes, Temperatur und Biomasse- bzw. Ernteparametern waren in den Versuchsjahren unterschiedlich stark, abhängig vom Zeitpunkt und der Intensität des eintretenden Stresses. In allen Jahren zeigten jedoch jeweils die gleichen Indizes einen Zusammenhang mit den Pflanzenparametern. Die Korrelationen waren jeweils zur Milchreife stärker als zur Blüte. Der Unterschied zwischen bewässerten und nicht-bewässerten Parzellen war nicht nur im Kornertrag, sondern auch in den thermalen und spektralen Sensormessungen ersichtlich. So zeigten die bewässerten Parzellen eine geringere Bestandestemperatur und höhere NDVI- bzw. REIP-Werte, was auf ein geringeres Stresslevel hindeutet. Die drohngestützten Messungen zeigten geringere absolute Messwerte als die händischen. Die Daten wiesen jedoch einen ähnlichen Zeitverlauf und sehr hohe Korrelationen auf, sodass von einer vergleichbaren Messgenauigkeit der Sensoren ausgegangen werden kann. Der Vorteil der Drohnen lag in der geringeren Messdauer, wodurch sich Verfälschungen durch Umwelteinflüsse verringern ließen. Abschließend konnten mithilfe von Heritabilität und Rangsummen einzelne besonders stabile Sorten und deren Toleranzmechanismen gegen Hitze und Trockenheit identifiziert werden.

Summary

As one of the most important cereal crops globally, wheat production is highly threatened by a changing climate. Stable yields, despite varying climatic conditions, are a crucial part of ensuring global food security. The combination of high temperature and decreased rainfall can reduce wheat yield drastically. Such extreme conditions are expected to happen more often in the coming decades. A growing global population and decreasing area of arable land reinforce the need for wheat varieties, which have high yield potential and can withstand such conditions. Selecting well-adapted varieties, which can be used for further breeding efforts, requires precise information about the impact of abiotic stress on their agronomical and physiological traits. Screening in field trials helps to assess the plants' performance under conditions similar to farming practice, and results are often easier to transfer as obtained from greenhouse experiments. For this study, a field trial was conducted for three years in the Northern part of the Republic of Moldova, with wheat varieties of Eastern European and German origin. In all three years, plots were grown under natural stress conditions; in the third year, an irrigated experiment was conducted as well. The Eastern European lines were characterized by genetic adaptation to a shorter vegetation period and continental climate conditions. Spectral and thermal sensors for high-throughput phenotyping approaches were used, including both handheld and drone-based sensors. These can help to assess multiple parameters simultaneously in a quick and non-destructive way. Additionally, growth stages were scored, and plant samples were cut between May and July to corroborate the findings of the sensors. In the first part of the study, the plants' development and agronomical parameters were analyzed. While Eastern European varieties could almost fully exploit their yield potential, varieties from Germany showed significantly lower grain yield, compared to both Eastern European lines under stress conditions and German lines under moderate conditions. Important harvest parameters, such as the number of tillers and grains, the grain size, and harvest index were strongly reduced due to the climatic conditions, to which the German varieties were not adapted. While the nitrogen uptake was lower than in Eastern European varieties, the protein content of grains was higher, however often accompanied by yield reductions. All agronomical parameters showed the benefit of additional water in irrigated plots. Further, physiological parameters – carbon isotope discrimination and relative leaf water content – were assessed. Due to better adaptation, the Eastern European varieties showed a significantly higher degree of carbon isotope discrimination, even under abiotic stress conditions. The discrimination rate decreased during the growing seasons and was lowest in the grains. In measurements of the leaf water content, no difference between the varieties was detected. However, the water content decreased significantly

across the growing season. The third part of the study compares terrestrial and aerial sensor systems and their ability to detect stress symptoms and stress tolerance, respectively. The time course of the vegetation indices and the canopy temperature was similar across the years. The vegetation indices describing the chlorophyll content (NDVI, REIP) decreased earlier in plots of Eastern European lines, indicating an adaptation to shorter vegetation periods. The German varieties, in contrast, showed higher levels of the NDVI and REIP, followed by a more sudden and steeper decrease, indicating intense stress towards the end of the growing season and a premature ripening process, causing yield reductions. While usually cooler canopy temperature is associated with higher grain yield, the Eastern European lines showed higher canopy temperature than the German varieties. This suggests using different mechanisms to cope with heat and drought stress in the two groups of origin. Correlations between vegetation indices, canopy temperature, and biomass and harvest parameters were of varying strength across the years, depending on the timing and intensity of the stress. However, across all years, the same indices resulted in meaningful correlations. Correlations at milk ripeness were stronger than at anthesis. Irrigated plots did not only show higher grain yield than non-irrigated, but the difference and the reduced stress level were also detectable with thermal and spectral sensors. The canopy temperature was reduced, and the NDVI- and REIP-values were higher compared to non-irrigated plots. The data provided from drone-based sensors resulted in lower absolute values, both for the spectral and the thermal data, than for handheld devices. Nevertheless, the data of both sensor systems was highly correlated and showed the same time course across the vegetation period. The advantage of the drone was the faster acquisition of the data, which led to less change of conditions while the measurements were taken. Heritability and rank sums were calculated from the assessed data to identify stress-tolerant varieties and to determine the strategies and mechanisms that the plants use to withstand heat and drought stress.

1. Introduction

1.1. Climate change – a challenge for maintaining wheat quality and ensuring yield stability

1.1.1. Climate change

Wheat is an important crop all over the world, cultivated on more than 220 million ha every year (Shiferaw et al., 2013). Within the European Union, 46% of cereal grain produced in 2017 was wheat (Eurostat, 2018), making it a crucial food security component in many regions. The global population is expected to reach 9.7 billion by the year 2050 and 11.2 billion by 2100 (FAO, 2017). To secure food safety, an increase in agricultural production of ca. 50% in 2050 compared to 2012 is needed (FAO, 2017).

The intergovernmental panel on climate change (IPCC) established several climate change scenarios based on different long-term assumptions of greenhouse gas emissions. These scenarios are used to understand driving forces and the consequences of climate change (Nakicenovic et al., 2000). The scenario labeled *A1B* is seen as particularly likely to occur (Herbst and Frühauf, 2018). The main characteristics of this scenario are rapid economic growth, an increase in global population until mid-century, accompanied by the rapid development of new technology, and balanced use of energy from fossil and non-fossil sources (Nakicenovic et al., 2000).

The frequency of extreme weather events is likely to increase in the future (IPCC, 2007), and droughts are expected to become more severe in large parts of Europe, North and Central America, and southern Africa (IPCC, 2012). These factors both will impact the survival of plants and play a crucial role in the decrease of plant productivity (De Micco and Aronne, 2012, Bacelar et al., 2012). According to Araus et al. (2002), drought is one of the main limiting factors to grain yield. Due to higher CO₂ concentrations and breeding progress, grain yields increased since the industrial revolution. However, this development is limited, and a further rise of CO₂ concentrations can only increase yield levels if enough water is available for the plants (Araus et al., 2002). Increasing temperatures of 2°C above the level of the end of the 20th century will negatively affect crop production in temperate and tropical regions (Porter et al., 2014). The risk of yield reduction due to drought events is likely to increase by 30% in Europe (Trnka et al., 2014) as a consequence of climate change – which leads to an increasing number of dry days between June and August (Trnka et al., 2011) when wheat plants are in the developmental stage of grain filling.

Hulme et al. (1999) found that the negative impact of human-induced climate change would be highest in southern Europe compared to central Europe. However, Herbst and Frühauf (2018) also report a higher frequency of early-season drought in Germany in the recent past. According to Doleschel and Frahm (2014), the average temperature in Germany will increase by ca. 2.3°C until the end of the 21st century. During summer, precipitation will be reduced by ca. 20% in most parts of Germany, whereas during winter, it will increase by ca. 30% on average. In all regions, extreme weather events will happen more frequently (Doleschel and Frahm, 2014).

The combination of heat and drought stress impairs several physiological processes and hinders photosynthesis (Prasad et al., 2008), leading to an expected decrease of wheat grain yield by 6% per 1°C of temperature increase (Asseng et al., 2014). However, in crop breeding, it must be considered that drought events do not happen regularly in cropping areas. Therefore, it is necessary to screen for and develop genotypes that show good and stable yields in both drought and optimal environments.

1.1.2. Genetic background

Numerous studies have shown that the tolerance towards heat and drought stress is genetically determined, and therefore largely depends on the origin and breeding history of wheat varieties (Barlow et al., 2015; Cao et al., 2015; Gutierrez et al., 2010; Mäkinen et al., 2018; Manda and Săulescu, 2018; Ratajczak and Górny, 2012; Schittenhelm et al., 2019). Dodig et al. (2012) showed that landraces are highly adapted to local soil and weather conditions of their region of origin and are still widely used in Eastern Europe and the Balkans. They show a more diverse reaction to water stress, not necessarily in the form of yield reductions (Abu-Zaitoun et al., 2018). However, their potential grain yield is significantly lower than that of modern cultivars (Abu-Zaitoun et al., 2018; Dodig et al., 2012). The latter are well adapted to favorable growing conditions (Blum, 1996; Ceccarelli et al., 1991) and can develop high grain yields, yet also show substantial decreases in yield under environmental stress (Abu-Zaitoun et al., 2018; Dodig et al., 2012; Mäkinen et al., 2018). Wheat genotypes originating from semi-arid areas can be beneficial for breeding programs in Western Europe, as they already show traits for abiotic stress tolerance (Schittenhelm et al., 2019) and can enhance the genetic range of modern wheat varieties (Abu-Zaitoun et al., 2018). Landraces help improve the stress tolerance of high-yielding varieties (Yadav, 2008) and new cultivars by enriching their diversity (Dodig et al., 2012).

A study by Mäkinen et al. (2018) showed that modern varieties are also adapted to their origin's conditions. Cultivars from nine European countries were compared concerning their sensitivity to climate extremes. It was found that varieties from Northern and Central

Europe were more sensitive to high temperatures than those from Southern European countries regarding plant development and yield productivity (Mäkinen et al., 2018).

Genotypes and the environmental conditions have a strong impact on the plants' growth and performance. Manda and Săulescu (2018) showed that the same varieties grown in England and Romania, developed differently. In Southern Romania, the same varieties had smaller and lighter grains than in England, most likely due to higher summer temperatures compared to England.

Another important aspect is the difference between breeds. Schittenhelm et al. (2019) compared German wheat lines and hybrids with lines from Southern and Eastern Europe growing in rainout shelters in Germany. They found that the varieties from foreign countries started anthesis earlier than hybrids. German lines were last. The same order was observed for the end of flowering and grain ripening. The duration of grain filling was shorter for foreign varieties. This suggests that the foreign varieties are better adapted to late-season drought than German varieties, escaping drought through earlier maturity (Schittenhelm et al., 2019).

The heterosis effect of hybrid varieties leads to a higher yield potential compared to line varieties (Longin et al., 2012). This advantage was found in favorable environments (Bruns and Peterson, 1997; Schittenhelm et al., 2019) and under water-limited conditions, indicating that hybrid varieties possibly can endure increased drought and heat stress better than lines (Schittenhelm et al., 2019). Additionally, hybrid varieties often show higher yield stability, suggesting that they might be grown in a broader range of environments compared to lines (Mühleisen et al., 2014). Varieties with comparable performance across different environments are considered yield stable (Becker and Leon, 1988). High yield stability shows an advantage for increased abiotic stress tolerance (Mühleisen et al., 2014) and a higher degree of uniform plant establishment (Gupta et al., 2019).

1.2. Relevant traits reflecting drought and heat tolerance

1.2.1. Effects of drought on plant physiology

Water plays an important role in physiological processes in plants (Lambers and Oliveira, 2019). Therefore, drought is the most detrimental stress that has several negative consequences on the plants' growth and development (Farooq et al., 2012). Reduced possibility of water uptake leads to a water deficit in plant tissue (Vilagrosa et al., 2012) and a limited nutrient uptake from the soil (Farooq et al., 2012). Water shortage in the cells causes a decrease of the relative leaf water content (RLWC) (Farooq et al., 2012)

and loss of turgor, which – amongst other factors – leads to decreased leaf area (Farooq et al., 2010). Drought triggers an increased biosynthesis of abscisic acid (ABA), which is highly involved in the plant stress response (Xiong et al., 2002; Yamaguchi-Shinozaki and Shinozaki, 2006). It leads to an upregulation of stress-responsive genes (Xiong et al., 2002). ABA stimulates the closure of stomata (Jacob et al., 1999; Yamaguchi-Shinozaki and Shinozaki, 2006; Zhu, 2002), leading to reduced transpirational water loss (Farooq et al., 2012). That, in turn, limits the uptake of CO₂ and photosynthesis (Reddy et al., 2004). Additionally, a lower transpiration rate leads to a decreased water uptake by the roots and, therefore, a decreased uptake of dissolved nutrients (Turner et al., 2001 in Rouphael et al., 2012, Taiz et al., 2015).

Drought stress can cause a reduction in leaf number (Farooq et al., 2010; Prasad et al., 2008) and leaf size (Farooq et al., 2012; Li et al., 2009; Prasad et al., 2008) due to a reduced rate of cell division and expansion (Kiani et al., 2007). Under severe stress, leaf senescence is accelerated (De Souza et al., 1997), leading to the premature death of leaves and leaf drop, whilst the initiation of new leaves is decreased (Prasad et al., 2008). Together, these factors result in a lower total leaf area, which can be advantageous to restricted water use (Sinclair and Muchow, 2001). However, a smaller leaf area also means a smaller photosynthetically active surface, which, combined with reduced CO₂ uptake, is often associated with reduced yield in cereal crops (Fischer and Kohn, 1966; Sinclair and Muchow, 2001).

Photosynthesis under drought is not only limited through decreased CO₂-influx but also due to a decline of enzyme activity of the Calvin cycle (Dias and Bruggemann, 2010), a decreased rubisco activity (Castrillo et al., 2001), and a reduced electron transport chain in chloroplasts and thylakoid membranes (Dias and Bruggemann, 2010).

Depending on the growth stage of crops, drought has different effects on growth and grain development. During germination, imbibition of the seeds can be delayed, leading to a decreased and uneven germination rate (Prasad et al., 2008). During flowering, drought decreases photosynthetic activity and, therefore, the amount of photosynthates allocated in floral organs (Raper and Kramer, 1987 in Prasad et al., 2008), and affects early stages of embryo development (Westgate and Peterson, 1993), both increasing the rate of abortion (Prasad et al., 2008). The seed-set of cereal crops is also limited due to impaired pollen viability (Bokshi et al., 2021; Prasad et al., 2008). Drought stress at later growth stages negatively impacts grain size (Prasad et al., 2008). It shortens the total developmental cycle of crops, and physiological maturity is triggered early (McMaster and Wilhelm, 2003). As the duration of growth is accelerated, the duration of single growth phases, such as grain filling, is also decreased (Vignjevic et al., 2015), causing smaller and lighter grains (Prasad et al., 2008).

1.2.2. Effects of heat on plant physiology

Depending on the growth stage, the average optimum temperature for wheat is between 20.3°C (shoot growth) and 21.0°C (anthesis). Temperatures above 31°C at anthesis and above 35°C for grain filling were found to affect plant development negatively. However, these values depend on environmental conditions, such as the water availability, the duration and intensity of extreme temperatures (Porter and Gawith, 1999), and the origin and the genetic background of the wheat varieties (Dodig et al., 2012).

To avoid any physiological damage through heat, plants use transpiration to control leaf temperature (Araus et al., 2002). Reduced transpiration rates will lead to high temperatures in the plant, causing thermal damage to the plant (Taiz et al., 2015). As the thylakoid membranes of the chloroplasts react very sensitively to high temperature, photosynthesis is one of the first processes to be affected by heat (Al-Khatib and Paulsen, 1990; Erice et al., 2012). High temperatures decrease the chlorophyll content (Morales et al., 2003; Todorov et al., 2003), damage the Calvin cycle enzymes (Erice et al., 2012), and decrease net photosynthetic rate and stomatal conductance (Morales et al., 2003). Most crop species' photosynthetic processes are stable at temperatures of up to 30-35°C (Edwards and Walker, 1983 in Wahid et al., 2012; Prasad et al., 2008). Temperatures >40°C affect photosynthesis negatively (Prasad et al., 2008) and can lead to permanent damage of the entire photosynthetic system (Wahid et al., 2012).

Most abiotic stresses, including heat, induce the formation of reactive oxygen species (ROS), highly reactive forms of oxygen. They react with many cell components, such as proteins, lipids, or DNA (Taiz et al., 2015). That can lead to the destruction of pigments, modification of membrane functions (Xu et al., 2006 in Wahid et al., 2012), and the degradation of membranes or cell organelles (Taiz et al., 2015). On the other hand, ROS accumulation triggers acclimation mechanisms, helping plants tolerate abiotic stress and the ROS accumulation itself (Taiz et al., 2015). These mechanisms include the synthesis of different antioxidant systems (Apel and Hirt, 2004). Under high temperatures, the amount of antioxidants needs to be increased to enhance heat tolerance (Wahid et al., 2012).

Heat stress restricts growth by causing rapid water loss and tissue dehydration (Wahid et al., 2012). The translocation of water, ions, and solutes within the plant is decreased (Wahid et al., 2012), leading to lower biomass compared to plants grown at a cooler temperature (Kim et al., 2007) and to decreased dry weight and growth of above-ground biomass (Wahid, 2007).

The reproductive growth stages are more severely affected by heat stress than vegetative growth (Wahid et al., 2012). High temperatures during flowering and

pollination can lead to pollen sterility and decreased seed-set (Moriondo et al., 2011; Porter et al., 2014; Prasad et al., 2008; Saini et al., 1983; Wahid et al., 2012). High temperatures shorten the life cycle of cereal crops, and senescence is triggered early (Prasad et al., 2008; Wahid et al., 2012). Lower numbers of grains combined with decreased grain filling rates and duration, thus smaller grains, have a strong negative influence on total grain yield (Prasad et al., 2008; Wahid et al., 2012).

A synergistic effect of heat and drought stress can be observed (Barnabás et al., 2008; Prasad et al., 2008). High temperatures combined with drought during vegetative growth will lead to a higher level of stress and higher yield losses (Semenov et al., 2009 and Gobin, 2018 in Mäkinen et al., 2018).

1.2.3. Tolerance mechanisms

The classification of different mechanisms of plants to withstand stress is not described uniformly in literature. Farooq et al. (2009a) distinguished two main morphological resistance mechanisms against drought, *escape* and *avoidance*. Ludlow and Muchow (1990) described drought *escape* and *resistance*, of which resistance can be divided into dehydration *tolerance* and dehydration *avoidance*.

Escape is defined as a shortening of the life cycle so that plants can fully develop and reproduce before the drought hits a critical intensity. This is particularly helpful in areas with a high chance of terminal drought, where plants with a shorter life cycle can escape drought better than those with a longer life cycle (Meyre et al., 2001). However, it has to be taken into account, that those varieties and genotypes showing pronounced drought escape mechanisms are limited in their yield potential (Turner et al., 2001 in Farooq et al., 2012). *Avoidance* includes mechanism, which maintain a high plant water status and therefore avoid the plant tissue to be exposed to stress (Blum, 2005). Helpful are the reduction of water loss through control of stomatal opening, (Farooq et al., 2009a), and an extensive root system to extract water from deeper soil layers (Blum, 2005; Turner et al., 2001). One advantage in drought environments for plants can be smaller leaves, which reduces transpirational losses but often causes lower yield in crops, varying widely between genotypes (Sinclair and Muchow, 2001). The third resistance mechanism, *tolerance*, enables the plant to endure the stress factor without serious damage (Schopfer and Brennicke, 2010). These strategies are not mutually exclusive; they can arise simultaneously in the same plant (Ludlow, 1989 in De Micco and Aronne, 2012).

1.2.4. Physiological traits

Crops often experience drought and heat stress simultaneously (Prasad et al., 2008). For winter wheat, heat episodes typically occur during its reproductive growth stages. Thus, mechanisms for heat and drought tolerance involve a complex interaction among various traits. Physiological traits related to heat and drought stress reveal that combining those two stresses has several unique impacts on the plant. These include the simultaneous occurrence of high respiration, low photosynthesis, closed stomata, high leaf temperature, and decreased leaf chlorophyll content, relative leaf water content, and leaf water potential (Farooq et al., 2011; Mittler, 2006).

1.2.4.1. *Stay green*

Consequently, drought and heat stress increase senescence and shorten the grain filling period, resulting in reduced productivity. Maintenance of leaf chlorophyll and photosynthetic capacity at grain filling, called *stay-green*, is considered an indicator of combined stress tolerance (Adu et al., 2011; Farooq et al., 2011). Some modern wheat varieties show stay-green traits, characterized by delaying leaf senescence, decreasing chlorophyll degradation, and thereby extending the time to carry out photosynthesis (Borrell et al., 2001; Park et al., 2007; Prasad et al., 2008; Thomas and Howarth, 2000), even under droughty conditions (Nawaz et al., 2013). A prolonged period of photosynthesis leads to a higher N uptake during grain filling (Kipp et al., 2014), increased grain weight (Verma et al., 2004), and higher yield (Bogard et al., 2011; Christopher et al., 2008; Nawaz et al., 2013; Pask et al., 2012). Few studies showed a negative relation between stay-green traits and grain yield (Derkx et al., 2012; Jiang et al., 2004; Kichey et al., 2007).

Nawaz et al. (2013) mention that this positive correlation with grain yield may also be advantageous under water-limited conditions. Several studies showed that stay-green traits are associated with heat stress tolerance (Cao et al., 2015; Kumari et al., 2013; Lopes and Reynolds, 2012; Naruoka et al., 2012), as well as drought tolerance (Rivero et al., 2007).

1.2.4.2. *Carbon isotope discrimination*

During photosynthesis, plants take up CO₂ through the stomata. The atmosphere contains CO₂ with either ¹²C or ¹³C isotopes, whereby the lighter ¹²C is much more abundant (98.9%) than ¹³C (1.1%) (Farquhar et al., 1989). Due to its lower molecular weight, more ¹²CO₂ than ¹³CO₂ diffuses through the stomata (Condon, 2004). Additionally, the carboxylation enzyme rubisco discriminates against ¹³C due to its lower reactivity compared to ¹²C (Melander and Saunders, 1979 in Farquhar et al., 1982).

Under non-stress conditions, a high stomatal conductance allows high selectivity of rubisco, and thus strong discrimination against $^{13}\text{CO}_2$ (Treydte, 2003), leading to a disequilibrium between the atmosphere and plant tissue (Farquhar et al., 1982). As a reference value determining carbon isotope ratios, a fossil from the Pee Dee Formation (Pee Dee Belemnite, PDB) is used. The atmosphere contains ca. 8‰ less $^{13}\text{CO}_2$ than the PDB (Farquhar et al., 1989), C3 plants ca. 24-34‰ less (Schopfer and Brennicke, 2010).

Open stomata are the pathway for CO_2 uptake and water loss, e.g. transpiration. In case of water shortage, plants will close the stomata to avoid further water loss (Farooq et al., 2009a). As the uptake of CO_2 is limited, the relative abundance of $^{13}\text{CO}_2$ inside the leaf tissue increases, and the carbon isotope discrimination (CID) decreases (Farquhar et al., 1989). Overall, the discrimination of rubisco has a stronger effect on total CID than the unequal diffusion rate (Farquhar et al., 1989).

In plants exposed to drought stress, more ^{13}C can be found in the biomass. The rate of CID can be used as a measure of stress intensity (Condon et al., 1990; Schopfer and Brennicke, 2010), stomatal conductance (Condon et al., 2002), water use efficiency (Tambussi et al., 2007), and as a selection criterion for grain yield under drought stress conditions (Becker and Schmidhalter, 2017; Condon, 2004). High heritability (Becker and Schmidhalter, 2017; Merah et al., 2001) makes CID an important breeding target to improve plant water use efficiency and yield under drought stress.

1.2.4.3. Canopy temperature

As plants close their stomata under drought (Farooq et al., 2009a), transpiration is minimized, leading to increased temperature in the plant tissue (Patel et al., 2001). Therefore, the canopy temperature (CT) is closely related to the plant water status (Hackl et al., 2012; Rischbeck et al., 2017; Schädler et al., 2019). Amani et al. (1996) used the CT to select for yield under the hot and irrigated environment in Mexico and found strong relations between grain yield and cooler canopy temperature. Becker and Schmidhalter (2017) reported that the CT could indicate and differentiate the rooting depth of different wheat varieties. These findings assume that CT can be used as a selection criterion for better growth and higher yield under drought.

1.2.5. Agronomical traits

The influence of any abiotic stress condition alters the duration to maturity of all crops (Nahar et al., 2010). Water stress (Angus and Moncur, 1977) and higher mean temperatures during the growing season (Rezaei et al., 2015) affect the phasic development of crops and accelerate growth. The intensity and timing of the stress can influence the effects on plant growth. Ihsan et al. (2016) observed a reduction in time to complete phenological growth stages under drought stress, whereas Angus and Moncur (1977) showed that mild water stress led to hastening of the maturing process, while severe stress delayed the development of wheat. These results indicate different physiological mechanisms, depending on the stress severity (Angus and Moncur, 1977). The occurrence of stress throughout the entire plant development exerts a negative effect on all growth stages (Ihsan et al., 2016). Early stress at germination can lead to lower plant density and abortion of initial tillers and acceleration of tillering (Prasad et al., 2008). In a field trial, Ihsan et al. (2016) found an average reduction of 20-31 days until complete tillering under drought compared to irrigated plots. Days to complete 50% heading and physiological crop maturity were reduced by 31-72%, making these the most susceptible growth stages (Ihsan et al., 2016). Due to changing climate, for most regions in Germany date of heading was shifted from late June in 1951-1975 to late May and mid-June in 1976-2009. This development went parallel with the increase in air temperature in spring (Rezaei et al., 2015). With an expected increase of mean temperature in the near future, simulations indicate further acceleration of crop development across Europe (Rezaei et al., 2015).

Heat and drought stress negatively affect crop growth, particularly dry matter accumulation and crop growth rate (Ihsan et al., 2016). The growth rate is an accurate indicator of net photosynthesis and a good measure of radiation use efficiency (Reynolds et al., 2016). Heat and drought stress leads to a reduction of organ size under drought and heat stress, leading to fewer and smaller leaves, tillers, and spikes (Hossain et al., 2013).

Besides vegetative growth, all generative growth stages and phases are also affected by abiotic stresses. Grain filling is one of the most sensitive growth stages to heat (Porter and Gawith, 1999). During the phase of grain filling, early stress is more detrimental than heat applied later throughout the growth stage (Stone and Nicolas, 1995). High temperature after anthesis shortens the duration of the grain filling period, which is the major cause for the reduction in kernel weight at maturity (Nahar et al., 2010; Stone and Nicolas, 1995; Wiegand and Cuellar, 1981). The strength of this effect depends strongly on the variety and the timing of the stress (Stone and Nicolas, 1995). Under heat stress, with sufficient water supply, Dias and Lidon (2009) observed an average decrease in

grain filling duration of 16% in a greenhouse trial with four wheat and durum wheat varieties. Plants exposed to the strongest environmental stress show the shortest grain filling duration (Ihsan et al., 2016), which leads to decreased grain size, promotes grain shrinking and causes a reduction of individual grain weight (Dias and Lidon, 2009), and results in a low grain yield per area (Ihsan et al., 2016; Nahar et al., 2010). The yield reduction through a shorter grain filling duration can be compensated by a higher grain filling rate, which is genotype-dependent (Dias and Lidon, 2009). Wardlaw and Moncur (1995) showed that cultivars with a high grain filling rate were more tolerant of high temperature during the grain filling period.

Breeding programs can use the knowledge about phenological growth stages in different wheat varieties under drought and heat stress. Varieties with higher tillering capacity, stay green traits, longer reproductive growth, more extended grain filling period, and higher grain filling rate seem to have an advantage in arid environments with hot and dry grain filling periods (Dias and Lidon, 2009; Ihsan et al., 2016; Nahar et al., 2010).

1.2.5.1. Nitrogen traits

Plants need nitrogen (N) in high amounts for their development and growth. In general, ca. 1-5% of the plant dry matter consists of nitrogen. It is essential to form proteins, chlorophyll, phytohormones, and other important molecules in plants (Hawkesford et al., 2012). In wheat grain, the protein content varies between 7-22% (Shewry, 2007 in Hawkesford et al., 2012), accounting for the high N requirements. The large variation is mainly driven by non-genetic factors, i.e. by the environment in which the plants grow (Hawkesford et al., 2012). In dry environments, the uptake and the N-concentration in the plant are limited by several factors: Firstly, the N-mineralization in the soil can be reduced, causing a decreased N availability (Bloem et al., 1992 in Rouphael et al., 2012). Secondly, nutrient movement, in general, is determined by the soil water content, leading to a lower nutrient diffusion rate at decreased soil water availability (Marschner and Rengel, 2012; Singh and Singh, 2004). Finally, the plants' active nutrient uptake is limited under drought conditions, as the limited soil water content decreases the diffusion rate of nutrients between the soil matrix and the plant root surface (Farooq et al., 2009b in Farooq et al., 2012). Under such conditions, the stomatal closure in the leaves causes reduced transpiration, leading to a reduction of water flow in the plant and reducing nutrient uptake (Tanguilig et al., 1987 in Rouphael et al., 2012).

In cases of insufficient N supply or limited uptake, plants rapidly show symptoms of N deficiency. Depending on the intensity and duration of the N shortage, the plants will have light green or yellow leaves, develop chlorosis and show early signs of senescence (Hawkesford et al., 2012), which can be associated with a breakdown of nucleic acids

and proteins in the leaves (Hörtensteiner and Feller, 2002). Furthermore, the plants will grow shorter under limited N conditions (Hawkesford et al., 2012; Taiz et al., 2015) and have lower protein content in their grains (Fischer et al., 1993).

German wheat varieties are classified into four groups, according to their baking quality and usage. A distinction is made between “*elite varieties*” (E), “*quality wheat*” (A), “*bread wheat*” (B), and “*other wheat*” (C). Varieties used for baking purposes are ranked in quality groups E, A, and B. Fodder wheat is ranked as B and C (Doleschel and Frahm, 2014). The most important criterion for quality classification is the raw protein content, which is calculated from the N content. Wheat protein contains 17.5% nitrogen. Hence, the protein content can be calculated by multiplication of the N content by the factor 5.7 (Doleschel and Frahm, 2014; McCance and Widdowson, 2014).

1.3. Importance of platforms to simulate climate change for the evaluation of wheat varieties

Many plant physiological experiments are carried out in controlled environments, such as greenhouses or growth chambers, where the plants are grown in pots or containers (Hackl et al., 2014; Wu et al., 2011). That enables control of environmental parameters, easy application of treatments, and repeatability of the trials (Passioura, 2006; Wu et al., 2011). However, due to the smaller available soil volume in pots, the rooting environment differs considerably from field trials. This mainly concerns soil temperature, water availability, uniformity of moisture content, rooting volume, and nutrient availability (Townend and Dickinson, 1995; Wu et al., 2011). The limitations in rooting volume exert adverse effects on the physiological processes, growth, and size of many plant organs, and are very likely to alter the plant’s phenotypic appearance (Dambreville et al., 2016). This effect becomes stronger with time as the plants’ root system expands (Poorter et al., 2012). Pot size also influences the timing of plant development, which seems decelerated in small pots (Dambreville et al., 2016).

The simulation of drought stress in controlled environments can lead to results, which are influenced by the pot size, and are not necessarily a consequence of the plants’ reaction to drought itself (Dambreville et al., 2016). The limited soil volume in pots can lead to much faster consumption of the available water, leading to a water deficiency within several days (Passioura, 2012). A slower and gradual imposition of drought stress leads to a better osmotic adjustment and enables the plants to better tolerate stress (Wang et al., 2017). Additionally, the soil temperature in pots can be influenced by

cooling down or heating up from the pots' edges, and the soil structure often does not correspond to field conditions (Hackl et al., 2014; Passioura, 2006).

Many studies indicate that pot size has a substantial effect on plant growth (Blum, 2014; Bourgault et al., 2017; Hackl et al., 2014; Poorter et al., 2012; Ray and Sinclair, 1998) and the response to water deficit (Dambreville et al., 2016). Small pots can decrease root and shoot biomass (Dambreville et al., 2016), whereas tubes allow the roots to grow deeper and reduce the risk of hypoxia (Bourgault et al., 2017; Poorter et al., 2012). Pennypacker et al. (1990) found that the use of containers is advantageous compared to pots since the volume and height of the containers allow the plant to develop an extensive root system, both horizontally and vertically, and the slower progression of dehydration of the soil rather corresponds to that in the field. Under controlled environmental conditions, only a limited number of cultivars can be tested, the experimental costs are high, and it can be challenging to transfer the results to field conditions (Passioura, 2012). Trait expression often is very different from field values (Bourgault et al., 2017), and limited root growth in pots significantly affects yield reduction (Wang et al., 2017). It is crucial to consider the effects of the experimental set-up (Bourgault et al., 2017) since ignoring the interaction between pot size and environmental stress can lead to misleading conclusions in research practices (Dambreville et al., 2016). Drought stress can be simulated with soil conditions similar to field trials by using rain-out shelters, which are moving glasshouses. Crops can grow under natural conditions, but while it rains the shelter closes and prevents irrigation of the plants (Rischbeck et al., 2017). These shelters represent an intermediate platform between controlled environment pot trials and the field. However, they are expensive, and do not cover a large area, so that only a small number of varieties can be screened. While drought can be simulated well in such shelters, the artificial generation of heat stress, e.g. with infrared heaters, is more difficult (Kimball et al., 2008).

In contrast, field trials under real stress conditions provide unambiguous findings on stress tolerance and yield performance of a genotype. A large number of varieties can be tested simultaneously by using high-throughput phenotyping approaches. Under the assumption that findings from model species would easily be transferable to cereal crops, much has been invested in controlled environment facilities (Cooper et al., 2014), while less attention has been put on field phenotyping facilities in international research (Reynolds et al., 2016). Consequently, there is a lack of studies investigating climate change effects of crops in realistic land-use scenarios, including management strategies such as fertilization and crop rotations (Schädler et al., 2019). Limited association between results from controlled environments and crop performance in the field has led

to a renewed awareness of the need for high-quality field experiments supporting crop improvement for heat and drought stress (Reynolds et al., 2016).

In order to provide reliable information about traits, which have been identified under controlled environments, a comprehensive and careful field evaluation of the performance of commercial German wheat varieties in the future growing conditions was urgently needed. To simulate anticipated climate conditions in Germany, the experiments were carried out under natural field conditions, in the continental climate of the Republic of Moldova. The present-day conditions in northern Moldova, with hot and dry periods during summer, are expected to resemble future climate scenarios in Germany. Furthermore, genetic sources of drought and heat tolerance already present in plant material from Eastern European countries are highly interesting.

1.4. Using high-throughput phenotyping technology to identify the key traits of plant drought and heat tolerance

Spectral sensors help to assess plant characteristics in a non-destructive way. They measure the reflection in the visible (VIS; ca. 400-700 nm) and near infrared (NIR; ca. 700-2500 nm) spectrum from single plants or crop canopies. A distinction is drawn between active and passive sensors. Active sensors are provided with a source of electromagnetic radiation in one or several specific wavelengths. Therefore, they are independent of surrounding conditions but limited to these specific wavelengths. Passive sensors, however, measure the reflection of the sunlight, whereby they can utilize the entire spectrum, are more flexible, and offer a broader range of applications (Erdle et al., 2011).

By putting two or more wavelengths in relation to each other, vegetation indices can be calculated. These can provide information about several physiological characteristics, such as chlorophyll content and canopy greenness (Araus et al., 2002), plant water status (Peñuelas et al., 1997; Rischbeck et al., 2014), or biomass (Gracia-Romero et al., 2019; Tucker, 1979). Using such indices, it is possible to simultaneously determine several traits, while other methods are more time-consuming (Araus et al., 2002). Indices including more than two wavelengths and other spectral ranges besides red and near infrared, show a higher correlation to plant parameters (Hasituya et al., 2020; Li et al., 2014; Lilienthal, 2014). Shaver et al. (2010) found that the NIR reflectance is positively correlated with biomass and nitrogen content of leaves, whereas VIS reflectance is negatively correlated to leaf N content.

Ground-based sensors can be limited by the non-simultaneous measurement of different plots, and vibrations arising from uneven field surfaces, which both might influence and bias the data (Hu et al., 2020). Some of these challenges can be addressed using high-resolution aerial platforms, such as small unmanned aerial vehicles (UAVs) (Sankaran et al., 2015). In recent years, drones and other UAVs have been of growing importance in agricultural land monitoring and precision farming (Urbahs and Jonaite, 2013). Possible implementations are e.g. crop health management, and identification of crop damage, irrigation monitoring, fertilizer management and weed monitoring (Grenzdörffer et al., 2008; Natu and Kulkarni, 2016; Urbahs and Jonaite, 2013). The use of drones enables precise crop management, saving farmers time and resources by being repeatable and relatively easy to operate (Urbahs and Jonaite, 2013). The vehicles can be equipped with different multi- and hyperspectral sensors, as well as thermal and RGB-cameras (Gracia-Romero et al., 2019; Matese and Di Gennaro, 2015; Puri et al., 2017). Using UAVs has many advantages, such as the measurement of large areas and many trial plots in a short amount of time, which helps to reduce the variation of sensor data through environmental or meteorological influences (Araus and Cairns, 2014; Gracia-Romero et al., 2019; Hu et al., 2020). UAVs are easy to install and operate and can be used anytime to monitor the field throughout the growing season (Stehr, 2015; Urbahs and Jonaite, 2013). Flight planning can be automated and geo-referenced, allowing an exact mapping and allocation of the data (Urbahs and Jonaite, 2013).

Compared with remote sensing satellites, the use of UAVs is more flexible in time, and data is immediately available. Additionally, UAVs fly lower, which brings the advantage that measurements are not interfered by cloud coverage (Stehr, 2015). The area, where measurements are performed is smaller than with satellites, however, data can be recorded with a higher resolution (Matese and Di Gennaro, 2015; Stehr, 2015; Urbahs and Jonaite, 2013).

The most significant drawbacks of drones are the limited payload weight for sensors and batteries and flight time, which reduces the area that can be covered within one operated flight (Marinello et al., 2016; Matese and Di Gennaro, 2015; Urbahs and Jonaite, 2013). Furthermore, flights cannot be carried out at intense rainfalls or winds (Urbahs and Jonaite, 2013). Barriers are also found in the high initial costs of the UAVs, the sensor accuracy, and the processing of a large amount of data (Natu and Kulkarni, 2016).

Spectral reflectance, digital imaging, and thermography represent possibilities of high-throughput phenotyping of biomass-related parameters in the field (Babar et al., 2006a; Rischbeck et al., 2016), which can replace the time-consuming direct measurement through growth analysis. They can also help detect the plant water status, nitrogen status, leaf senescence, and stay green traits (Araus and Cairns, 2014; Mistele and

Schmidhalter, 2008; Peñuelas et al., 1993; Rischbeck et al., 2016). Hence, the effects of drought and heat on plant physiology and development can be assessed in a non-destructive way.

Since the distance between the sensor and crop surface is larger using UAVs than ground-based sensor platforms, the resolution of the measured data needs to be much higher. Consequently, there still is a need to compare aerial and terrestrial phenotyping tools for the acquisition of physiological and agronomical traits in wheat.

2. Objectives

This thesis aims to answer the following hypotheses:

- I. The performance of representative commercial German wheat varieties under heat and drought must be assessed under realistic field conditions to meet the challenges of climate change and develop strategies for climate resilience improvement.
A comprehensive and careful field evaluation under “future” growing conditions is urgently needed to provide reliable information about heat and drought tolerance traits in wheat. Such a realistic evaluation is possible under present-day continental climate conditions in northern Moldova.
- II. Identifying new genetic sources from existing Eastern European wheat cultivars will be necessary for the future adaptation of German wheat varieties to drought and heat stress.
- III. Establishing drought-stressed and irrigated treatments allows an assessment of the effects of the stressor on plant development. It will be possible to separate traits related to either heat, drought, or combined stress tolerance.
- IV. Algorithms, indices, and traits, which allow the interference of enhanced heat and drought tolerance, need to be validated and proved under realistic conditions. That includes data from hyperspectral, multispectral and thermal sensors, and measurement of the relative water content and carbon isotope discrimination of leaves and grain.
Water indices, red-edge-based vegetation indices and thermal phenotyping are expected to deliver relevant information about heat and drought stress tolerance.
- V. In order to establish the use of UAVs for phenotyping and the detection of abiotic stress tolerance traits, terrestrial and aerial sensing technologies need to be applied at the same time, and their performance must be compared. This will help to develop further and enhance high-throughput phenotyping techniques.

3. Materials and Methods

3.1. Field trial set up

A three-year field trial was performed from 2016-2019 at the Selectia Research Institute of Field Crops in Bălți, Republic of Moldova (47° 46' N, 27° 56' E). The location is at 85 m above sea level. 40 varieties of winter wheat (*Triticum aestivum* L.) were grown, including 20 lines from Eastern European countries (Romania, Ukraine, Bulgaria and Moldova), as well as 16 lines and 4 hybrids from Germany. A list of all varieties and their origin and breed is given in Table 1. In 2018/2019, *Hylux* replaced the variety *Hystar* used in 2016/2017 and 2017/2018. The classification according to grain quality is only common for German varieties.

Table 1 Varieties of winter wheat grown in the field trial and the country of origin (BG: Bulgaria, MD: Moldova, RO: Romania, UA: Ukraine, DE: Germany).

Variety	Country	Breed	Variety	Country	Breed	Quality
Acord	MD	Line	Akteur	DE	Line	E
Amor	MD	Line	Anapolis	DE	Line	C
Clasic	MD	Line	Apertus	DE	Line	A
FGmut 293	RO	Line	Colonia	DE	Line	B
Kuialnik	UA	Line	Discus	DE	Line	A
Meleag	MD	Line	Elixer	DE	Line	C
Numitor	MD	Line	Genius	DE	Line	E
Pajura	RO	Line	Hybery	DE	Hybrid	B
Rowina	RO	Line	Hybred	DE	Hybrid	B
Savant	MD	Line	Hyfi	DE	Hybrid	B
Semnal	RO	Line	Hystar	DE	Hybrid	B
Slava	BG	Line	Hylux	DE	Hybrid	B
Talisman	MD	Line	Impression	DE	Line	A
Transitor	RO	Line	JB Asano	DE	Line	A
Ujinoc	UA	Line	Kerubino	DE	Line	E
Unitar	RO	Line	Kometus	DE	Line	A
Ursita	RO	Line	Manager	DE	Line	B
Zagrava	UA	Line	Mulan	DE	Line	B
Zisk	UA	Line	Patras	DE	Line	A
Zolotocolosa	UA	Line	Rumor	DE	Line	B
			Tobak	DE	Line	B

The trial was conducted as a complete block design with three replicates. In order to avoid shading from taller growing Eastern European on German varieties, the varieties were grown in blocks depending on their origin. The plots were 5 m x 1 m with 12 cm row distance, resulting in seven rows per plot. The experimental site was integrated into a crop rotation with winter wheat, sugar beet, corn and three years of alfalfa. Preceding

crop to the experiment in all years was alfalfa (*Medicago sativa* L.). The sowing was done with 500 grains/m² on October 7, 2016, October 3, 2017, and October 8, 2018. Harvest was on July 11, 2017, July 2, 2018, and July 7, 2019, respectively.

In the growing season 2018/2019, the trial was sown twice, directly neighboring. One part was left without irrigation as in previous years; the other block was irrigated 60 liters per square meter, directly after sowing (October 10, 2018). Afterwards, due to sufficient rainfall irrigation was not required.

Table 2 shows the average climatic conditions (Climate-Data, 2020a, 2020b), amongst other location factors of Bălți, and of Freising, Germany, the location of the agricultural experimental station of the Technical University of Munich. This comparison was drawn due to the similar degree of latitude of the two locations. The location of Freising in central Europe is stronger influenced by maritime climate conditions than Bălți. In the Republic of Moldova, continental climate is predominant. According to the classification of Köppen and Geiger (1928) it is described as *Dfb* (Kottek et al., 2006; Petrick, 2008), characterized by strong annual variation, with cold winters and hot summers (Malberg, 2002). On long term average, areas with *Dfb* climate classification are described as cold snowy forest climate, characterized as humid in all seasons (i.e. neither dry winter nor summer) with warm summer (Kottek et al., 2006; Müller et al., 1996). However, in the three years of the field trials, dry periods were observed (cf. Figure 1).

Table 2 Comparison of site conditions in Bălți, Moldova, and Freising, Germany.

	Bălți	Freising
Latitude	47°46'N	48°24'N
Longitude	27°56'E	11°44'E
Soil texture	Clay loam	Silt loam
Soil type	Chernozem (Boincean and Dent, 2019)	Dystric eutrochrept and fine- loam typical udifluent (VDLUFA, 2021)
Average annual sum precipitation	587 mm	833 mm
Average annual temperature	9.2°C	7.9°C
Average sum of precipitation April-July	289 mm	363 mm
Average air temperature April-July	16.3°C	13.15°C

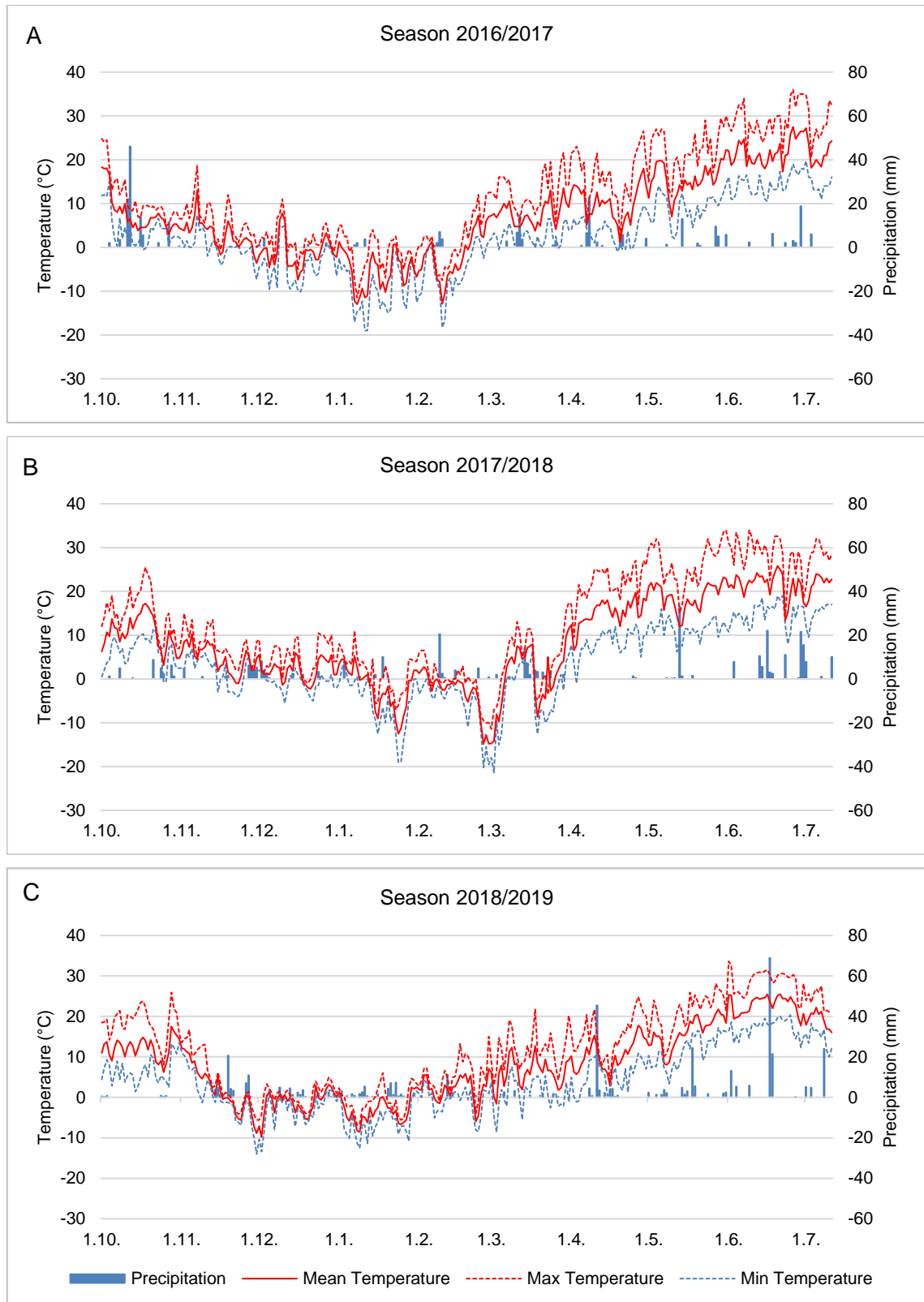


Figure 1 Climate diagram of Bălți, Moldova, during the growing seasons 2016/2017 (A), 2017/2018 (B), and 2018/2019 (C).

In the seasons of 2016/2017 and 2017/2018 no irrigation was applied. As visible in Figure 1A from April until harvest (July 11 2017) there was only little precipitation (77.25 mm), with an average temperature of 19.1°C. In the same period in 2018 (May

until July 2) (Figure 1B) precipitation was much higher (144.5 mm), whereas the average temperature was not significantly higher (20.1°C). However, in April 2018 an early period of drought occurred.

In the season 2018/2019, precipitation was evenly distributed (see Figure 1C), except for June 17 and 18, when a sum of 90.3 mm was recorded. Strong drought appeared in October and November 2018, leading to uneven emergence. Plants in irrigated plots emerged in autumn 2018, whilst plants in non-irrigated plots emerged only in February 2019.

Figure 2 and Table 3 show the sum of the mean daily temperature and precipitation of all three experimental years between April and the final harvest, during which period all morphological and phenological measurements were taken. It clearly shows increasing severity of drought in 2017 starting mid-May (Figure 2A). In 2018 (Figure 2B) April and early May were characterized by drought but during the following months a higher amount of precipitation was observed, leading to a higher precipitation in total in 2018 than in 2017. During the vegetation period in 2019 (Figure 2C) total precipitation was not only distributed across all months but also much higher than in the previous years (2017: 125.00 mm, 2018: 146.25 mm, 2019: 245.40 mm), so that drought was not as severe as in 2017 and 2018.

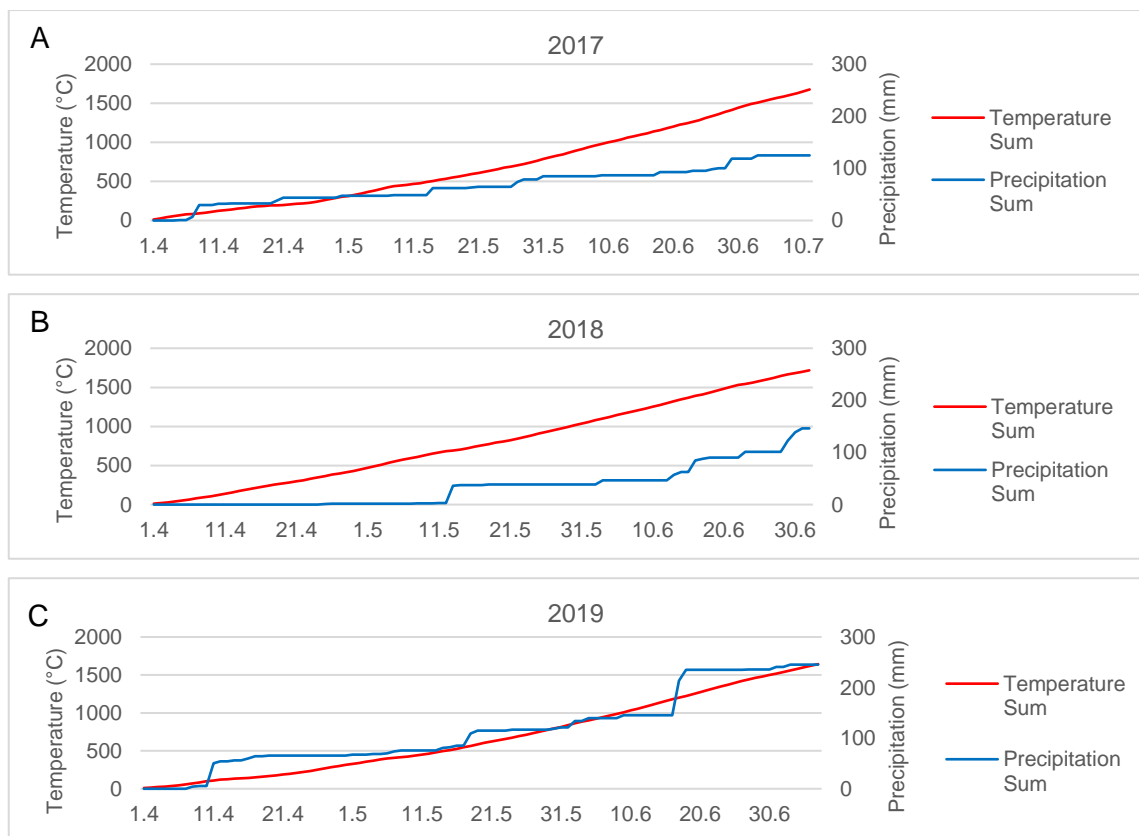


Figure 2 Sum of temperature and precipitation in Bălți, Moldova, from April 1 until harvest in 2017 (A), 2018 (B) and 2019 (C).

Table 3 Mean temperature, temperature sum and precipitation sum of all experimental years from October 1 and April 1 until harvest. T_{Mean} : Mean Temperature, T_{Sum} : Temperature sum, Prec: Precipitation sum.

	October 1 - Harvest			April 1 - Harvest		
	T_{Mean} (°C)	T_{Sum} (°C)	Prec (mm)	T_{Mean} (°C)	T_{Sum} (°C)	Prec (mm)
2016/2017	6.97	1980.00	294.75	16.44	1676.55	125.00
2017/2018	7.72	2122.00	326.50	18.47	1717.60	146.25
2018/2019	7.82	2188.53	402.40	16.76	1642.48	245.40

In order to find a measure to compare drought intensity across the three experimental years, the ratio of precipitation sum and mean temperature was calculated (Table 4). The results are shown for each month, for the entire growth period (sowing to harvest), and for the period of April until harvest, when plants go through the most sensitive developmental stages. As the scales of climate diagrams (cf. Figure 1) are based on the assumption of a relation between precipitation and temperature-dependent evaporation (Malberg, 2002), a higher ratio between precipitation and temperature indicates a higher amount of plant-available water, and thereby a lower degree of drought stress. In Table 4 it is clearly visible that the average intensity of drought stress in the growing seasons 2016/2017 (43.05 mm/°C, 7.60 mm/°C) and 2017/2018 (42.29 mm/°C, 7.92 mm/°C) was similar but the distribution over the year was very different. In the first year, the drought intensity was much stronger in June, while the second year had dry periods already in April and May. The season 2018/2019 was characterized by the least drought stress, both from sowing until harvest (52.00 mm/°C), and across spring and summer (14.64 mm/°C), however the ratio in October was very low, indicating strong drought stress for the seedlings.

Table 4 Ratio of precipitation sum and mean temperature of the given period (mm/°C) for all experimental years.

	2016/2017	2017/2018	2018/2019
October, after sowing	17.76	2.77	0.15
November	0.00	6.45	26.96
December	8.04	11.85	20.54
January	1.22	10.24	13.00
February	7.33	11.27	7.92
March	4.27	89.65	1.51
April	4.73	0.12	6.26
May	2.37	1.95	3.45
June	1.57	4.62	5.01
July, until harvest	0.28	0.45	0.48
Sowing to harvest	43.05	42.29	52.00
April 1 to harvest	7.60	7.92	14.64

3.2. Measurements

Spectral and thermal measurements were performed in all three years from May until final harvest in the beginning of July. All measurements were taken during the time of strongest heat stress, between 11 a.m. until 2 p.m.. In order to corroborate the non-destructive findings, plant samples were taken and analyzed.

3.2.1. Spectral reflectance measurements

To measure the spectral reflection of the plant surface, the HandySpec Field (tec5 AG, Oberursel, Germany) was used. During the data acquisition, the spectrometer was held ca. 120 cm above ground. It records reflectance between 302-1148 nm. These data can be used to calculate vegetation indices that can provide information about the plants' physiological status, e.g. nutrient or water content. As the HandySpec is a passive spectrometer, which also measures the current radiation of the sun to calculate the relative reflectance, these measurements were independent from cloud cover and could be used at all days as long as the plants' surface was dry.

In the third year of the field trial, a drone (UAV) was used for reflectance measurements, additionally to the handheld device. Here, the eBee Classic drone (senseFly, Lausanne, Switzerland) was equipped with a Sequoia sensor (Parrot Drones SAS, Paris, France). The sensor records reflection of the near infrared (NIR, 790nm \pm 40nm), red-edge (735nm \pm 10nm), red (660nm \pm 40nm) and green (550nm \pm 40nm) bands. Pictures were taken with 80% longitudinal and lateral overlap. After stitching the single pictures to one orthophoto with the Pix4D software (version 3.1.23), the mean values per plot could be calculated for each band using the ArcGIS software (version 10.5).

Table 5 shows all indices used in this study. The NIR-based single ratios (SR) (Erdle et al., 2011; Jasper et al., 2009; Mistele et al., 2004; Takebe et al., 1990) were compared to the corresponding ratios of drone bands. The remaining single ratios (Green/Red, Red edge/Green, Red edge/Red) were calculated with the data of the HandySpec for the sake of completeness, in order to have all bands of the Sequoia sensor plotted against each other.

Table 5 Indices calculated from spectral reflectance measurements with HandySpec and Sequoia sensors.

Index	HandySpec	Sequoia		Literature
	Formula	Bands	Formula	
NDVI	$(R_{780}-R_{670})/(R_{780}+R_{670})$	(NIR-Red)/ (NIR+Red)	$(R_{790}-R_{660})/$ $(R_{790}+R_{660})$	Rouse Jr et al. (1974)
WI	R_{900}/R_{970}			Peñuelas et al. (1997)
Normalized Water Index (NWI) 1	$(R_{970}-R_{900})/(R_{970}+R_{900})$			Babar et al. (2006)
NWI 2	$(R_{970}-R_{850})/(R_{970}+R_{850})$			Babar et al. (2006)
NWI 3	$(R_{970}-R_{920})/(R_{970}+R_{920})$			Prasad et al. (2007)
NWI 4	$(R_{970}-R_{880})/(R_{970}+R_{880})$			Prasad et al. (2007)
REIP	$700 + 40 * \frac{(R_{670} + R_{780})}{2} - R_{700}$ $R_{740} - R_{700}$			Guyot et al. (1988)
R760_R670	R_{760}/R_{670}	NIR/Red	R_{790}/R_{660}	Erdle et al. (2011)
R780_R740	R_{780}/R_{740}	NIR/Red edge	R_{790}/R_{735}	Mistele et al. (2004)
R760_R730	R_{760}/R_{730}			Jasper et al. (2009)
R780_R550	R_{780}/R_{550}	NIR/Green	R_{790}/R_{550}	Takebe et al. (1990)
Green - Red	R_{550}/R_{660}	Green/Red	R_{550}/R_{660}	
Red edge - Green	R_{735}/R_{550}	Red edge/Green	R_{735}/R_{550}	
Red edge - Red	R_{735}/R_{660}	Red edge/Red	R_{735}/R_{660}	

3.2.2. Thermal measurements

The surface temperature of the plants was measured with the hand held thermal camera Fluke Ti400 (Fluke Deutschland GmbH, Glottertal, Germany) with a resolution of 320 x 240 pixels. For the measurements, the camera was held ca. 120 cm above ground in a nadir position. As clouds easily bias the plant surface temperature, the thermal pictures were only taken at days without any cloud cover. For analysis, soil and plant pixels were separated using the software LabView Fluke (National Instrument v.12.0f3) and only the temperature of the plants was calculated as mean value for the plot.

The drone used in 2019 could be equipped with a DuetT thermal camera (senseFly). It has a resolution of 640 x 512 pixel. As for the spectral sensor, the same flight settings were used and the same procedure as described above was applied to calculate mean temperature values per plot. Thermal measurements with the drone were only taken at cloudless days.

3.3. Plant samples

During the time, when measurements were taken, the growth stage after (Zadoks et al., 1974) was determined regularly in all plots.

Plant samples of the entire wheat plants to determine the above ground biomass and the nitrogen uptake of all varieties, were taken twice. Per plot, 50 cm of one row was cut

directly above the soil surface, once at anthesis (June 16, 2017 (252 DAS), June 1, 2018 (241 DAS), June 5, 2019 (240 DAS, irrigated plots) and June 11, 2019 (246 DAS, drought stress plots)) and again at milk ripeness (June 27, 2017 (263 DAS), and June 20, 2018 (260 DAS)). In 2019, sampling was only possible at anthesis. The tillers were counted and dried at 60°C for at least 24 hours until they reached a constant weight. The samples were ground and analyzed for their N content in a mass spectrometer (Europe Scientific, Crewe, UK).

At harvest (July 11, 2017 (277 DAS), July 2, 2018 (272 DAS), July 7, 2019 (272 DAS, irrigated plots) and July 10, 2019 (275 DAS, drought stress plots)), two rows of 50 cm were cut per plot. After drying and weighing, the tillers and ears were counted. The ears were threshed and the grain number, thousand grain weight (TGW), and grain size distribution were determined. The grains were then ground and analyzed in the mass spectrometer, not only for N content but also for their rate of ¹³C-discrimination. Due to a severe infection with *Tilletia caries* in 2019 the yield data and all related results were excluded for the varieties *Slava*, *Ujinoc*, *Akteur*, *Apertus*, *JB Asano*, *Kometus*, *Rumor* and *Tobak*. To keep data comparable, the plant dry weight and straw weight at harvest were divided by two. Thus, all data of plant dry weight refers to a sample of 50 cm.

From the results for N content of the mass spectrometer, the protein content of biomass and grains was calculated by multiplying the N content (%) x 5.7 (McCance and Widdowson, 2014).

Three times per year single leaf samples were taken. The first and second sampling were used to determine the relative leaf water content (RLWC). The procedure corresponded to that of Mullan and Pietragalla (2012): From five plants per plot, the penultimate leaf was cut to a length of ca. 8 cm, and immediately put into a closed plastic tube, to avoid transpirational water losses. The fresh weight of the samples (FW) was determined. Afterwards, distilled water was filled into the plastic tubes until the base of the plants was ca. 1 cm deep in the water. The tubes were left in a dark place at ca. 8°C for about 24 h. After reaching full turgor, the leaves were taken out of the tubes, quickly blot dried with a paper towel and turgid weight (TW) was determined. Subsequently, the leaves were dried at 60°C for 24 hours and weighed again to obtain the dry weight (DW). The RLWC could then be calculated as $RLWC = ((FW-DW) / (TW-DW)) \times 100$ (Mullan and Pietragalla, 2012).

After being dried, the leaves were ground and analyzed for ¹³C-discrimination in the mass spectrometer. The third set of penultimate leaves was used only for mass spectrometry. The mass spectrometer measures the deviation of carbon isotope composition from the isotopic composition of the PDB-standard (Farquhar et al., 1989):

$$\delta [‰] = \frac{R_p - R_s}{R_s}$$

whereas R_p is the isotopic abundance in the plant, R_s the abundance ratio $^{13}\text{C}/^{12}\text{C}$ of the standard (Farquhar et al., 1989).

The carbon isotope discrimination of the plant (Δ) can then be calculated as:

$$\Delta [‰] = \frac{\delta_a - \delta_p}{1 + \delta_p} * 1000$$

where δ_a is the isotopic composition of the atmosphere (ca. -8‰) and δ_p is the isotopic composition of the plant sample (Farquhar et al., 1989).

3.4. Statistical analysis

R studio (version 1.2.5019, RStudio Inc., Boston, MA, USA) was used for statistical evaluations. The residuals of all data were tested for normal distribution with the Kolmogorov-Smirnov test. In order to find differences between varieties, groups of origin, or irrigation treatments, analyses of variance (ANOVA) were performed. If significant differences were indicated ($p < 0.05$), a Tukey's HSD test was calculated, to identify the groups and means. Pearson correlation coefficient (r) was calculated with significance levels at $\alpha = 0.05$ and $\alpha = 0.01$. Scatter plots indicating the coefficient of determination (R^2) were calculated with Microsoft Excel 2016 (Microsoft Corporation, Redmond, WA, USA).

Rank sums were calculated for grain yield, nitrogen uptake, canopy temperature and CID according to Gad (2010). For each year separately, the data was listed in decreasing (grain yield, N uptake, CID), respectively increasing (canopy temperature) order, using mean values per variety. Each variety received a rank in each year, which were then summed up, to calculate the rank sum across all years and irrigation treatments. Due to the severe infestation with *Tilletia caries* in 2019, all rank sums were calculated without the varieties *Slava*, *Ujinoc*, *Akteur*, *Apertus*, *JB Asano*, *Kometus*, *Rumor* and *Tobak*.

Heritability was calculated in R Studio, using the lme4 package (Bates et al., 2015). All factors were considered as random. Heritability within one year was calculated as $h^2 = V_g / (V_g + V_r / r)$, where V_g is the genotypic variance component, V_r is the residual variance component, and r is the number of replicates per environment (Holland et al., 2003). Heritability across years was calculated as $h^2 = V_g / [V_g + V_{ge} / e + V_r / (r * e)]$, where V_g is the genetic variance component, V_{ge} is the genotype x environment interaction variance component, e is the number of environments, V_r is the residual variance component, and r is the number of replicates per environment (Holland et al., 2003).

4. Results

4.1. Growth and development of wheat under abiotic stress

4.1.1. Growth stages (Zadoks)

Figure 3A-F show the development of the wheat plants in Zadoks growth stages for the period during which the measurements were taken. In all years, it is clearly visible that the Eastern European varieties reached later Zadoks stages earlier, i.e. they developed faster than the German varieties.

In the year 2017 (Figure 3C) and 2018 (Figure 3D) the German hybrids developed quicker until about Zadoks stage of 65, later on growth was comparable. Values of the Eastern European lines were well above the German varieties; only at harvest, they were comparable. In 2019, Eastern European varieties of the plants in non-irrigated plots (Figure 3E) were developing considerably slower and later than those in the irrigated part of the trial (Figure 3F). 220 days after sowing (DAS), when Zadoks stage was recorded for the first time, the plots under drought stress were on average at Z43 (mid-booting stage), whilst irrigated plots were at Z48 (booting, first awns visible). German varieties showed even earlier development stages at that time. As in the previous years, the Eastern European varieties showed later Zadoks stages through the entire period of observation. German hybrids show further developed stages than German lines until ca. 240 DAS (244 in drought stress plots) afterwards they run parallel at a very similar level.

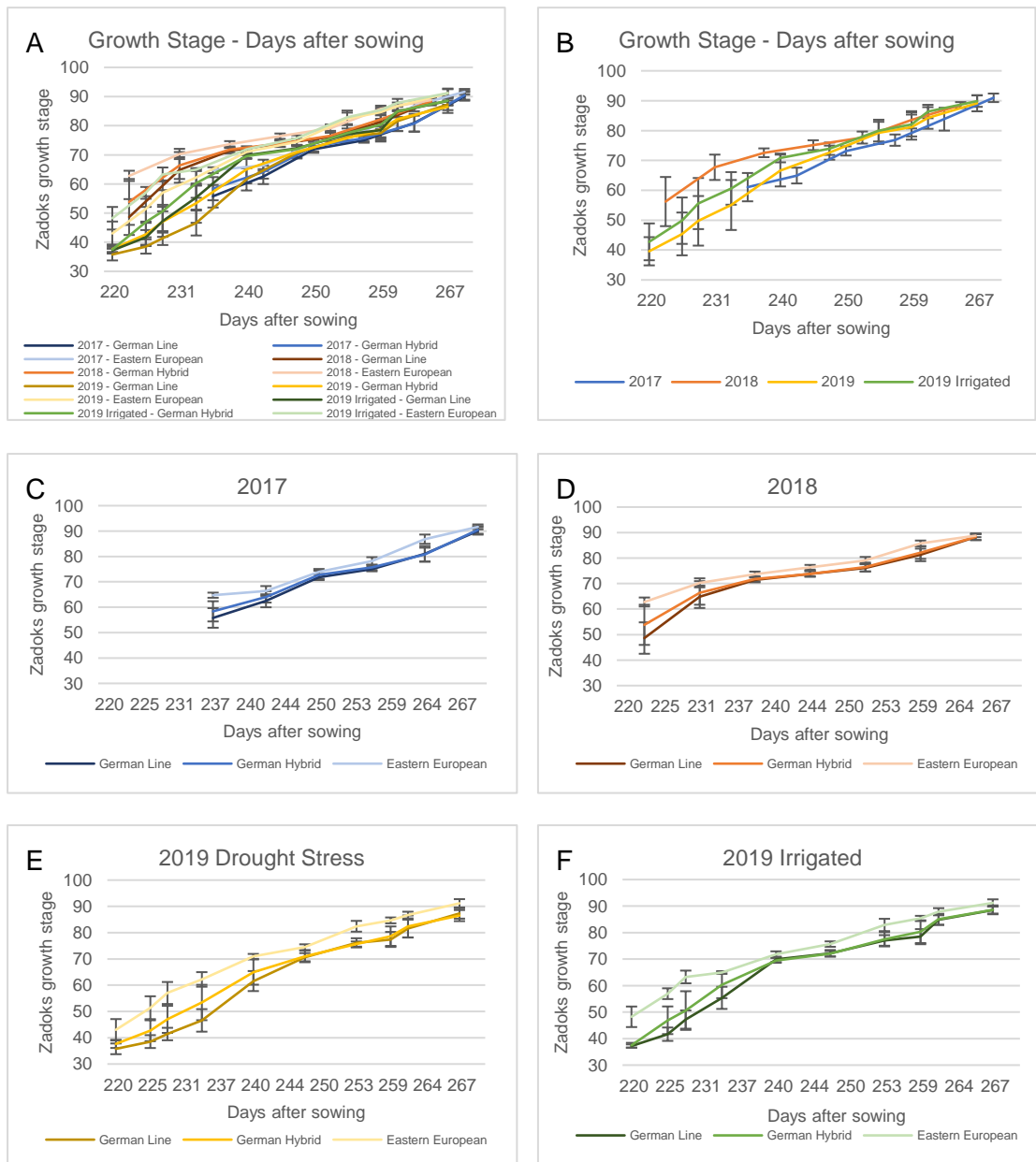


Figure 3 Growth stages of winter wheat.

4.1.2. Duration of grain filling

The number of days after sowing to the beginning of grain filling (Table 6) and the duration of grain filling, between Zadoks stage Z70 and Z83, differed significantly between years (Table 7) and varieties (Table 8). Across all years, the Eastern European varieties (238.75 DAS) reached grain filling significantly earlier than German varieties (hybrids: 241.32 DAS, lines: 242.21 DAS). Comparing the years, the duration to grain filling in average for all varieties was shortest in 2018 (233.43 DAS) and longest in 2017 (246.75 DAS). Across all varieties, the plants needed the longest time to reach Z83 in 2018 (25.31 days), which also leads to the highest temperature sum (581.35 °C).

However, mean temperature and precipitation sum were in the middle range of all years. In 2017, the plants were exposed to the lowest temperature sum (373.14 °C) and mean temperature (21.35 °C), but also received the least precipitation (16.48 mm) during grain filling. In 2019, the duration of grain filling in drought stress plots (16.57 days) was slightly longer than in irrigated plots (16.49 days), leading to a higher temperature sum, mean temperature and precipitation sum in drought stress plots.

Table 6 Days to the beginning of grain filling (Z70).

	Days to the beginning of grain filling						
	mean DAS			mean DAS			
	mean	sd	sig		mean	sd	sig
EE	238.75	± 5.50	b	2017	246.75	± 1.55	a
Ger Hy	241.32	± 4.73	a	2018	233.43	± 3.33	d
Ger Li	242.21	± 5.13	a	2019	241.44	± 2.49	b
				2019 irrigated	239.53	± 1.34	c

EE: Eastern European varieties, Ger Hy: German hybrids, Ger Li: German lines, mean DAS: mean values (days after sowing) per group, sd: standard deviation, sig: significant differences across all varieties, and years resp.

Table 7 Duration, temperature sum, mean temperature and precipitation sum during grain filling in all experimental years, across all varieties.

	Duration (days)			Temperature sum (°C)			Mean temperature (°C)			Precipitation sum (mm)		
	mean	sd	sig	mean	sd	sig	mean	sd	sig	mean	sd	sig
2017	16.53	± 2.21	b	373.14	± 61.51	c	21.35	± 0.81	d	16.48	± 9.77	d
2018	25.31	± 2.37	a	581.35	± 43.81	a	21.87	± 0.31	c	49.28	± 9.29	c
2019	16.57	± 3.12	b	409.29	± 77.01	b	23.25	± 0.44	a	93.19	± 18.07	a
2019 Irrigated	16.49	± 3.83	b	403.26	± 95.39	b	22.97	± 0.50	b	84.12	± 33.00	b

mean: mean values per group of varieties, sd: standard deviation, sig: significant differences within one factor across all years and varieties.

Table 8 Duration, temperature sum, mean temperature and precipitation sum during grain filling for all varieties, across all trials.

	Duration (days)			Temperature sum (°C)			Mean temperature (°C)			Precipitation sum (mm)		
	mean	sd	sig	mean	sd	sig	mean	sd	sig	mean	sd	sig
EE	17.52	± 5.39	b	402.44	± 116.75	b	21.93	± 0.92	b	53.81	± 39.29	b
Ger Hy	20.53	± 3.84	a	486.99	± 82.71	a	22.66	± 0.89	a	67.74	± 32.59	a
Ger Li	20.54	± 3.57	a	488.08	± 79.12	a	22.67	± 0.81	a	60.33	± 30.86	ab

EE: Eastern European lines, Ger Hy: German hybrids, Ger Li: German Lines, mean: mean values per group of varieties, sd: standard deviation, sig: significant differences within one factor across all years and varieties.

In average across all years, the varieties from Eastern Europe showed a significantly shorter grain filling period (17.52 days) than German hybrids (20.53 days) and German lines (20.54 days). Therefore, also the temperature sum (402.44 °C), the mean temperature (21.93 °C), and the precipitation sum (53.81 mm) were significantly lower than for German varieties. For all four parameters, no significant difference was found

between German hybrids and German lines. Detailed values for each group of origin within the individual years can be found in the Tables 29-30, and Figures 20-24 in the appendix.

Table 9 shows the correlations between grain yield, TGW, and HI with the grain filling parameters mentioned above. The number of days between sowing and the start (Z70) and the end (Z83) of grain filling showed strong negative correlation with all three harvest parameters. The duration of the grain filling was positively correlated to grain yield and HI. The temperature sum was not correlated to any of the three harvest parameters. Mean temperature and precipitation sum showed significant negative correlation to TGW and HI. The correlation between precipitation sum and grain yield was significantly positive.

Table 9 Correlation of DAS to reach Z70, resp. Z83, duration of grain filling, temperature and precipitation sum and mean temperature with grain yield, TGW, and HI, across all trials and varieties.

	Grain yield		TGW		HI	
	r	p	r	p	r	p
DAS Z70	-0.59	**	-0.44	**	-0.52	**
DAS Z83	-0.58	**	-0.51	**	-0.45	**
Duration	0.11	*	0.01		0.16	**
Temperature sum	0.09		-0.07		0.062	
Mean temperature	-0.06		-0.36	**	-0.46	**
Precipitation sum	0.14	**	-0.11	*	-0.22	**

r: Pearson correlation coefficient
 Statistical significance as indicated by p-value: * p < 0.05, ** p < 0.01.

4.1.3. Harvest parameters and nitrogen traits

Yield parameters, vegetative plant parameters, and nitrogen traits were assessed for each plot. The graphs in the Figures 4 and 7 show mean values for each group of origin (Eastern European lines, German hybrids and German lines) per year and, for 2019, per experiment. Capital letters indicate significant differences between the years; lowercase letters indicate significant differences between the origins.

In the years 2017 and 2019 under drought stress, and in 2018 and 2019 with irrigation, a similar grain yield level was reached (Figure 4A). As the environmental conditions were different across the three years, grain yield also varied considerably. Eastern European lines reached 5.36 t/ha (2017) to 7.20 t/ha (2019 irrigated), German hybrids 4.90 t/ha (2017) to 6.94 t/ha (2019 irrigated), and German lines 4.46 t/ha (2019 drought stress) to 6.35 t/ha (2018). Within three trials, a significant difference between Eastern European and German lines was found. In 2017, German hybrid varieties were align with German

lines, and in the irrigated plots in 2019, they were grouped together with the Eastern European lines. In drought stress plots in 2019, no significant difference to either one of the line groups could be determined. In 2018, no difference between varieties was found.

A more consistent picture was obtained for the thousand-grain weight (TGW) (Figure 4B). The average over all varieties only showed significantly higher values in 2018 compared to the other trials. In all years and trials, Eastern European lines were significantly higher in TGW than the German varieties, both hybrids and lines. 2018 was the only year in which German lines showed a considerably higher TGW than hybrids, however being not significant. The German varieties showed higher values for 2018 than for 2017 and for irrigated plots in 2019 compared to drought stress plots. The Eastern European varieties did so for 2018 compared to 2017, however the difference between drought and irrigated plots in 2019 was marginal.

The number of grains per ear (Figure 4C) differed markedly between years, but less between the three groups of varieties. In 2017, 2018, and irrigated plots 2019, no significance was found between Eastern European and German varieties. In drought stress plots in 2019, the German lines showed a significantly lower grain number than the other two groups. In the year 2019, hybrids showed a higher number of grains per ear than the lines, both for Eastern European and German ones. Other than the results for grain yield and TGW, in 2018 the number of grains per ear was lower than in 2017.

The harvest Index (HI) (Figure 4D) showed a similar picture like the TGW: 2018 was the only year with significantly higher HI (0.45-0.50) than in the other years; within years, varieties from Eastern European countries were significantly higher in HI (0.43-0.50) than the German varieties (0.33-0.45) and showed smaller variation between years than the German ones. In the drought stress trial in 2019, German lines had a significantly lower HI than German hybrids. In all other trials, lines and hybrids were not significantly different.

The number of tillers (Figure 4E) and ears (Figure 4F) per square meter was quite similar within each year. In average over all varieties, the trials in 2018 (tillers: 612.89-639.72, ears: 581.87-613.33) and 2019 with irrigation (tillers: 607.56-625.56, ears: 568.57-594.44) depicted a significantly higher number of both, tillers and ears, than 2019 without irrigation (tillers: 481.22-568.06, ears: 468.11-540.97), and 2017 (tillers: 440.89-464.72, ears: 418.89-427.8). Within the years, no significant difference was found between Eastern European and German varieties in 2017 and 2018. In 2019, the drought stress experiment showed the same ranking for tillers and ears per square meter, with German lines being significantly higher than Eastern European lines. An intermediate level, with no significance to either one of the lines was observed for the German hybrids. Irrigated

plots showed the same ranking for tillers, but no significant difference between origins for ears per square meter was detected.

The number of grains per square meter showed significant differences between the years, however not between the three groups of varieties (Figure 4G). In 2017, Eastern European varieties had the highest number of grains, followed by German hybrids and lines. In 2018 and 2019 (drought stress), the number of grains of hybrids was highest, followed by German lines. In both years, Eastern European varieties showed the lowest number of grains per square meter.

In 2017 and 2018, Eastern European varieties were significantly taller than German lines, while German hybrids did not differ significantly from either one of the line groups (Figure 4H). In 2019, the plants were significantly taller than in the previous years, with plants in irrigated plots being taller than those in the drought stress trial area. Other than in the first two years, German varieties were taller than the Eastern European ones, but in case of the irrigated plots, this difference was not significant.

The dry weight of wheat plants at anthesis (Figure 4I) was significantly higher in the irrigated plots in 2019 and in 2018, than in 2017. In the irrigated plots, German hybrids (107.96 g) had a significantly higher dry weight than Eastern European lines (85.50 g). They also showed the biggest increase in dry weight in irrigated plots, compared to drought stress trials. In all other trials, Eastern European varieties tended to have a higher dry weight, however being not significant.

Dry weight at milk ripeness could only be determined in the first two years of the field trials (Figure 4J). The groups do not differ within one year; however, in 2018 (96.84 g-106.28 g) the dry weight was significantly higher than in 2017 (81.05 g-89.81 g). The increase in dry weight from anthesis to milk ripeness was strongest for German lines in both years (2017: +13.09 g, 2018: +15.95 g). German hybrids gained 4.72 g in 2017 and 5.11 g in 2018, leading to a comparable increase for all German varieties in both years. Eastern European lines, however, showed a very different picture in the two years, gaining 2.03 g in 2017 and 12.36 g in 2018, respectively.

For the dry weight of entire plants at harvest, significant differences were found between all years (Figure 4K). Within the individual years, significance was found between the Eastern European and the German varieties (2017), respectively the lines and hybrids (2018). In 2019, there was no significant difference between the three groups of varieties, in either the irrigated or the drought stress trial. In the last year (2019), it is remarkable that the hybrids had a higher dry weight than the line varieties, while the contrary was the case in 2017 and 2018.

The annual average of straw weight (Figure 4L) differed significantly between both trials in 2019, whereas 2017 and 2018 ranked comparable. In 2019, the Eastern European varieties had significantly lower straw weight (drought stress: 36.26 g, irrigated: 47.23 g) than both the German hybrids (drought stress: 49.77 g, irrigated: 58.56 g) and the German lines (drought stress: 51.67 g, irrigated: 59.65 g). In 2017, Eastern European lines (28.12 g) were significantly lower in straw weight than German lines (32.15 g), but hybrids (30.22 g) were intermediate; whereas in 2018, Eastern European lines (31.28 g) and German hybrids (32.49 g) grouped together and were significantly lower in straw weight than German lines (36.07 g).

Post anthesis dry matter assimilation (Figure 4M) was calculated as *plant dry weight at harvest - plant dry weight at anthesis* (Dordas and Sioulas, 2009). In the drought plots in 2019, a significant difference between German hybrids and Eastern European lines was found. In other years, the results showed no significance between groups of varieties. The results of 2017 and 2018 did not differ significantly, whereas in 2019 both trials showed significantly higher assimilation than previous years. In 2017 and 2018, the average post anthesis dry matter assimilation was negative in all groups of origin, i.e. the dry weight at harvest was lower than at anthesis. In 2019, all groups showed positive values in average. However, high standard deviations indicated negative post anthesis dry matter assimilation for some varieties.

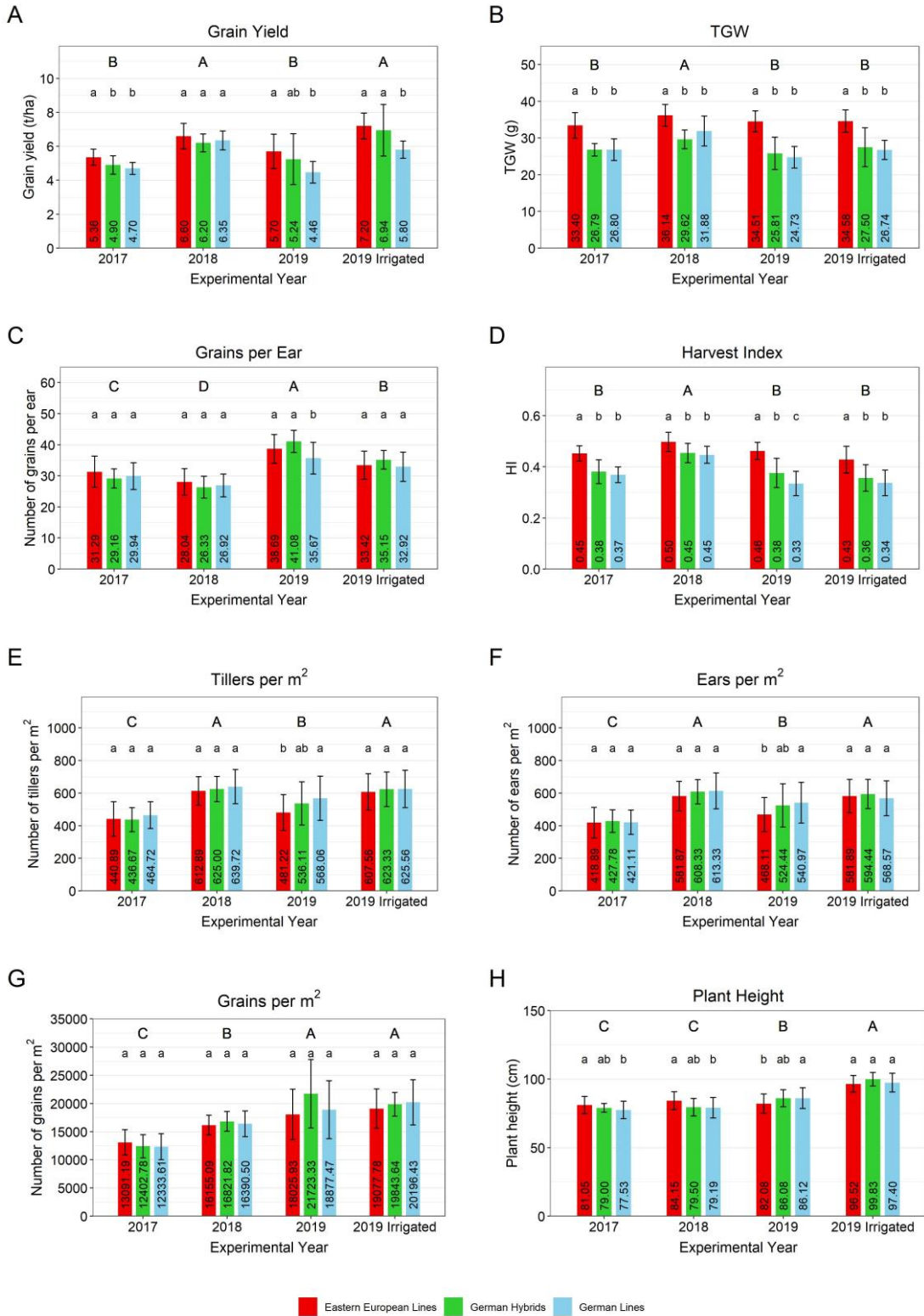


Figure 4 Yield parameters per experimental year. Capital letters show significance between the years, lowercase letters show significance between origins within one year.

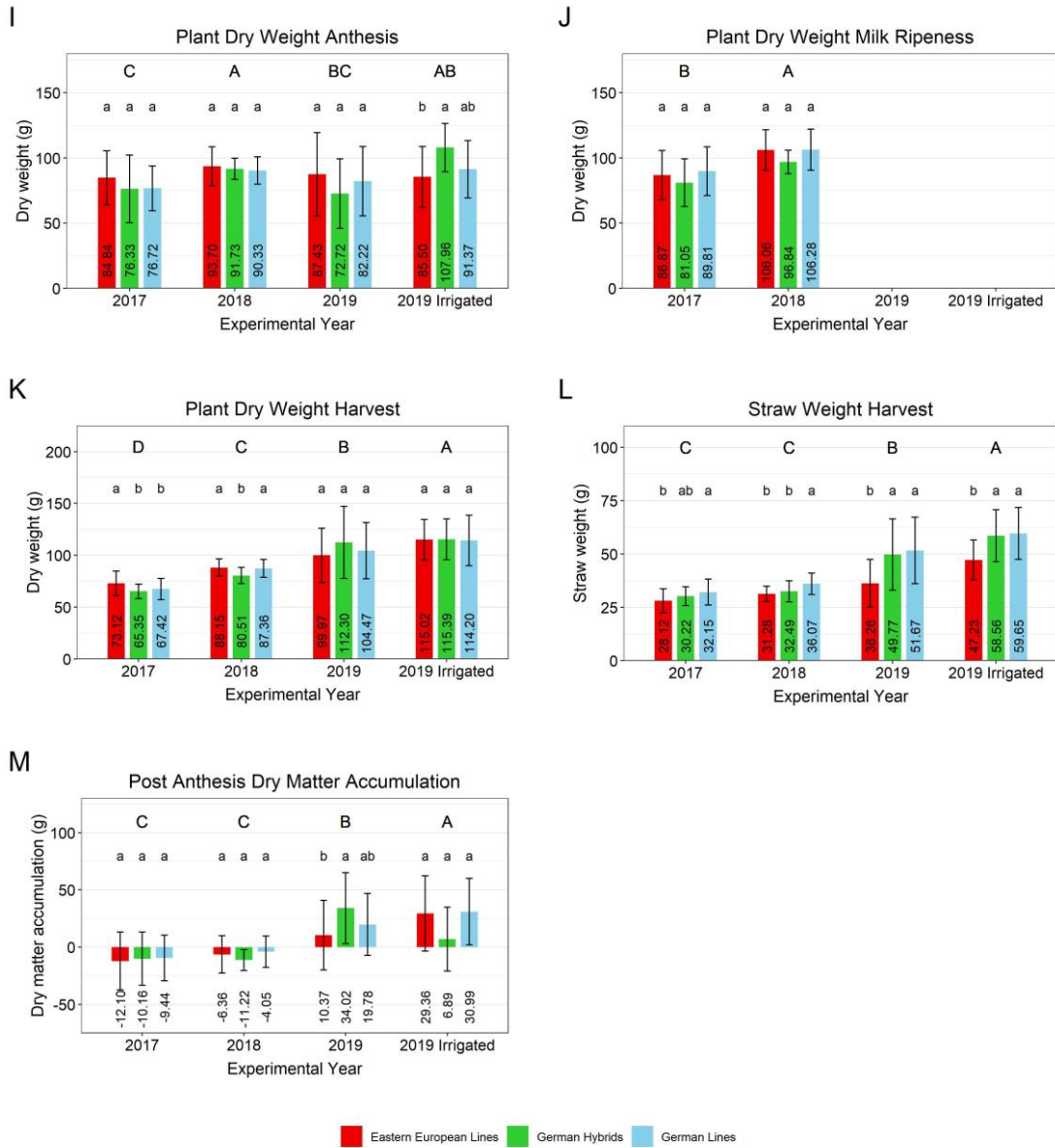


Figure 4 (continued) Yield parameters per experimental year. Capital letters show significance between the years, lowercase letters show significance between origins within one year.

The proportion of tillers and ears per square meter was close to one in all years and trials (Figure 5 and Table 10). The lowest value was found for German lines in 2017 (0.84 ears per tiller). Figure 5A shows the data per year averaged over all varieties. The trials in 2017 (blue) and 2019 (drought stress, yellow) showed a lower number of both tillers and ears per square meter. The trial in 2018 (orange) and the irrigated plots in 2019 indicated a higher number of tillers and ears. Averaged over all years (Figure 5B) shows that Eastern European lines (red) tended to have a lower number of tillers and ears than the German lines (blue), whilst German hybrids (green) were intermediate.

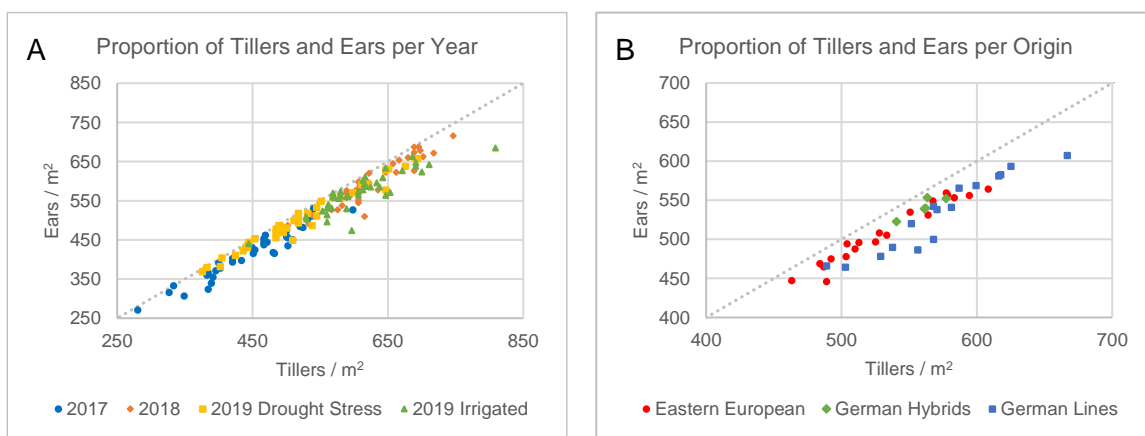


Figure 5 Proportion of Tillers and Ears m⁻² of each experimental year and of each origin.

Table 10 Number of ears per tiller.

	Ears per Tiller			
	2017	2018	2019	2019 Irrigated
Eastern European Lines	0.86-1.00	0.91-1.00	0.94-1.00	0.90-1.00
German Hybrids	0.94-0.98	0.96-0.99	0.97-0.99	0.93-0.98
German Lines	0.84-0.97	0.90-1.00	0.94-1.00	0.87-0.96

The grain size distribution is shown in Figure 6. Detailed numeric data can be found in Table 31 (appendix). In all years, the difference for each size was significant between Eastern European and German varieties. The only exception was the percentage of the grain size 0-2.2 mm in 2018. In none of the trials and no grain size category, a significant difference between German lines and hybrids was observed.

In 2017, the Eastern European lines had the highest percentage of large grains. 25.23% of grains were larger than 2.8 mm, 42.72% belonged to the size 2.5-2.8 mm. Only 30.07% of the grains were smaller than 2.5 mm. The share of this size was much larger for German varieties (hybrids: 57.01%, lines: 58.91%). The amount of grains >2.8 mm reached only 5.61% (hybrids) and 5.35% (lines), respectively. Within the year 2017,

significant differences between German and Eastern European varieties were found for all grain sizes. No significance was observed between German lines and hybrids.

In 2018, the percentage of large grains (>2.8 mm) was significantly higher than in 2017 and 2019 for all three groups of origin (Eastern European lines: 52.21%, German hybrids: 25.01%, German lines: 23.66%). The amount of small grains (0-2.2 mm and 2.2-2.5 mm) was lower in 2018 than in 2017 and 2019. Eastern European lines only had 2.43% of grains smaller than 2.2 mm, German hybrids 4.12% and German lines 3.62%. Grains between 2.2-2.5 mm accounted for 11.22% (Eastern European lines), 22.91% (German hybrids) and 22.64% (German lines), respectively. Hence, the share of grains, both from 0-2.2 mm and 2.2-2.5 mm, was significantly smaller in 2018 than in the other years.

Eastern European varieties showed significant differences compared to German varieties in all size categories in 2019; however, German lines and hybrids were not statistically different. In the drought stress plots, the share of grains was highest for the grain size 2.5-2.8 mm for Eastern European lines (40.90%), whereas for German varieties this was the case for the grain size 2.2-2.5 mm (hybrids: 44.14%, lines: 49.68%). German varieties had a much higher percentage of small grains (hybrids: 18.66%, lines: 19.51%) than Eastern European lines (5.80%). In the irrigated plots, the share of small grains (<2.2 mm) was lower (Eastern European lines: 5.79%, German hybrids: 14.71%, German lines: 14.38%) and the share of larger grains was higher (Eastern European lines: 31.85%, German hybrids: 10.77%, German lines: 7.36%). However, the difference between drought stress and irrigation was not significant.

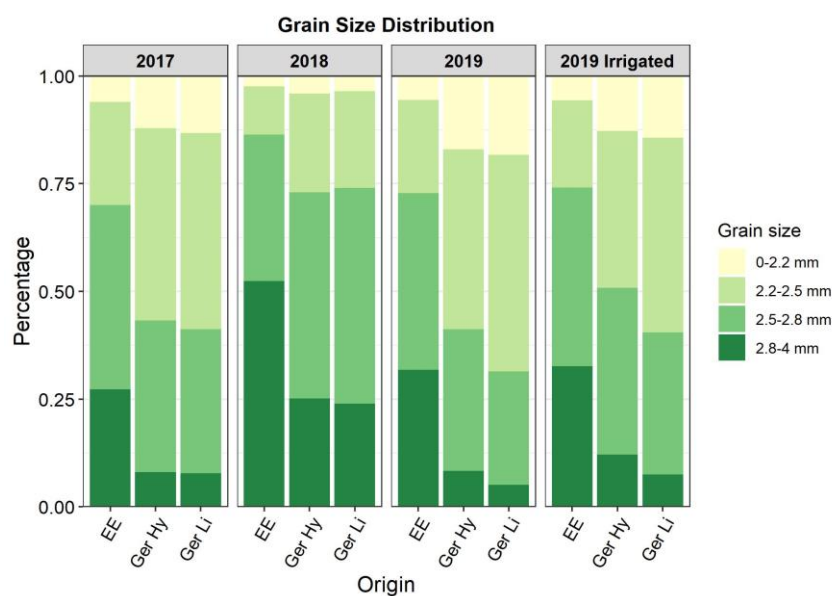


Figure 6 Grain size distribution. EE: Eastern European lines, Ger Hy: German hybrids, Ger Li: German lines.

In Figure 7, the results of the plant nitrogen (N) content and N uptake are shown at anthesis, milk ripeness and harvest. At anthesis and milk ripeness, the entire plant was analyzed, at harvest only the grain.

N content at anthesis (Figure 7A) differed significantly between the years but not between the drought stress and the irrigated plots in 2019. In 2017 and 2019, Eastern European lines had a significantly lower nitrogen content than German lines and – except irrigated plots – also German hybrids. In 2018, no significant difference between the groups of origin was found. N uptake at anthesis (Figure 7B), which was calculated as the *N content multiplied by the dry weight of the biomass*, was highest for the irrigated plots in 2019, being significantly higher than in drought stress plots in 2019 and in the first two years, which were comparable. Within the individual years, only irrigated plots showed distinct differences between varieties. German lines and hybrids showed a significantly higher N uptake than Eastern European lines in the irrigated trial. This was the only trial where a higher N uptake for hybrids than German lines was observed. In the other years, no difference between the groups of origin was evident, but German varieties seemed to have a tendency for higher N uptake than Eastern European lines.

At milk ripeness, sampling could only be done in 2017 and 2018; hence, no data to compare drought stress and irrigation in 2019 are available. Whilst the average N content (Figure 7C) was significantly higher in 2018 than in 2017, this difference was not detectable for N uptake (Figure 7D). Within the years, comparing the groups of origin, no significant difference was found, for neither N content nor N uptake.

The average N content of grains (Figure 7E) was highest in 2017 (2.51-2.80%) and lowest in 2018 (2.11-2.22%). In 2018, no difference was found between the groups of origin. In all other trials, Eastern European lines had a significantly lower nitrogen content than German lines. In 2017 and in the drought stress plots of 2019, German hybrid varieties were comparable to German lines. In the irrigated trial of 2019, they were intermediate between the lines. Grain N uptake was significantly different between years averaged across all varieties (Figure 7F). Within the individual years, Eastern European lines were always characterized by the highest N uptake. In 2017 and 2018, the nitrogen uptake was significantly higher than for the German varieties, in 2019 (drought stress) significantly higher than for the German lines. In the irrigated plots of 2019, no significance was found between the three groups.

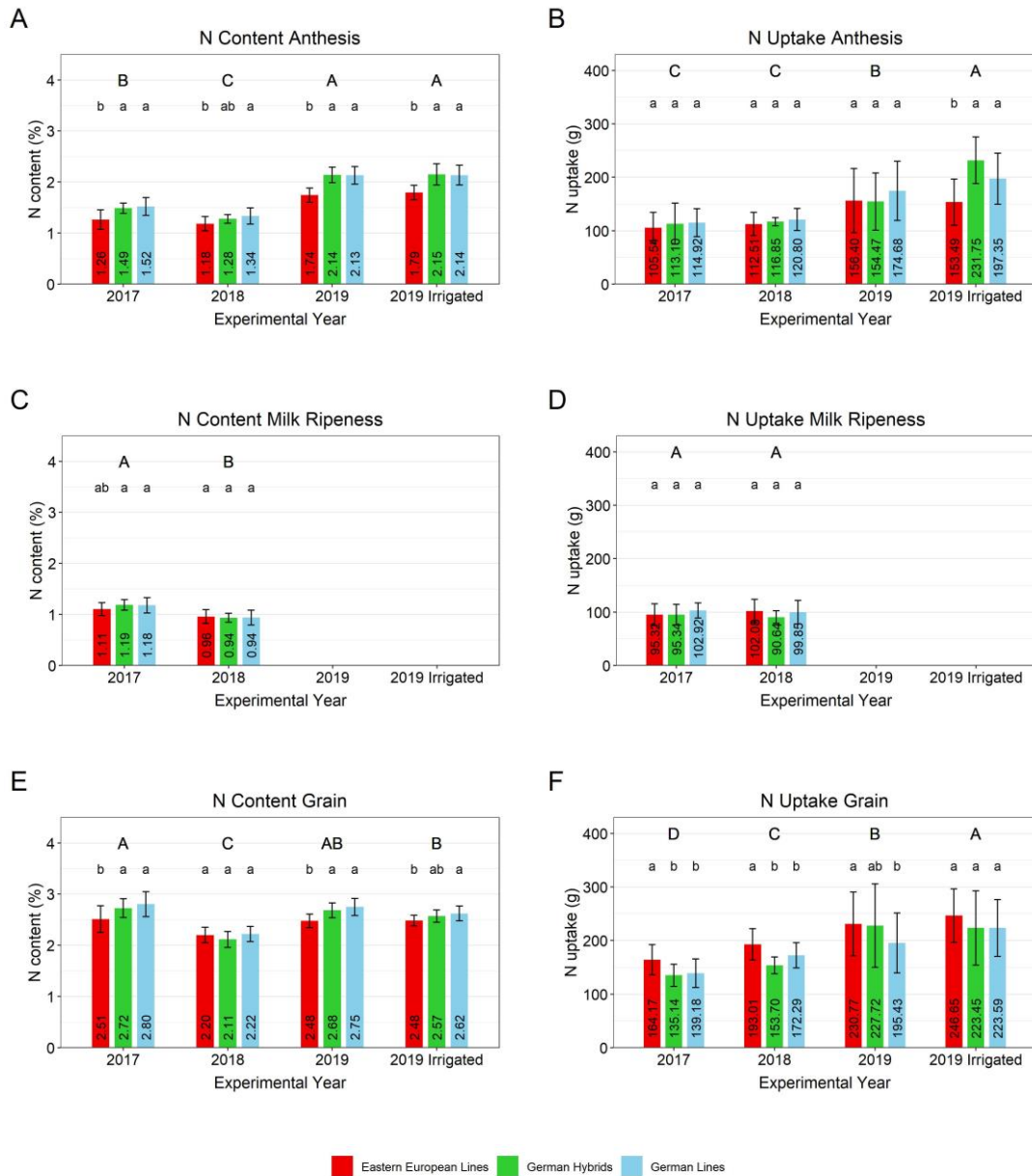


Figure 7 Nitrogen content and uptake at three sampling times per experimental year. At anthesis and milk ripeness, the entire plant was analyzed, at harvest only the grain. Capital letters show significance between the years, lowercase letters show significance between origins within one year.

Protein content (blue) and the grain yield (orange) are depicted in Figure 8. Detailed numeric data of protein content, grain N uptake and grain yield can be found in Table 32 in the appendix. In all years, Eastern European varieties had the highest grain yield and, except 2018, the lowest protein content. In 2018, German hybrids had a slightly lower protein content, however the difference was not significant.

In 2017, the protein content of Eastern European lines (14.32%) was significantly lower than for the German lines of the quality groups A, B, and E. German lines of group C and hybrids did not differ from the other varieties. Varieties of group E had the lowest grain

yield (4.57 t/ha) but a high protein content (16.06%). In 2018, all varieties showed a higher grain yield (6.09-6.60 t/ha) and lower protein content (12.05-13.50%) than in the previous year. The German lines of group E had a significantly higher protein content than the German varieties of the groups B and C, and than Eastern European lines. German lines of the quality group A did not differ significantly from the other groups. Grain yield was not significantly different between varieties, but a tendency was visible for a lower yield going along with a higher protein content. In 2019, the drought stress plots showed similar results as in 2017. German lines of the quality groups A, B, and C had a lower grain yield than in 2017, but a comparable protein content. The difference in yield was higher than in protein. Irrigation in 2019 led to a strong increase of grain yield for Eastern European lines (7.2 t/ha) and German hybrids (6.94 t/ha). However this was associated with a lower protein content (Eastern European lines: 14.22%, German hybrids: 14.66%) compared to German lines. German lines showed an average yield of 5.8 t/ha, but a significantly higher protein content than Eastern European lines (15.27%). The average protein content across all years and trials showed a significant lower protein content for the Eastern European lines (13.78%) than for the German varieties of all quality groups (14.52-15.18%), whilst the grain yield was significantly higher for Eastern European lines (6.2 t/ha) compared to German varieties (5.31-5.61 t/ha) (Table 11).

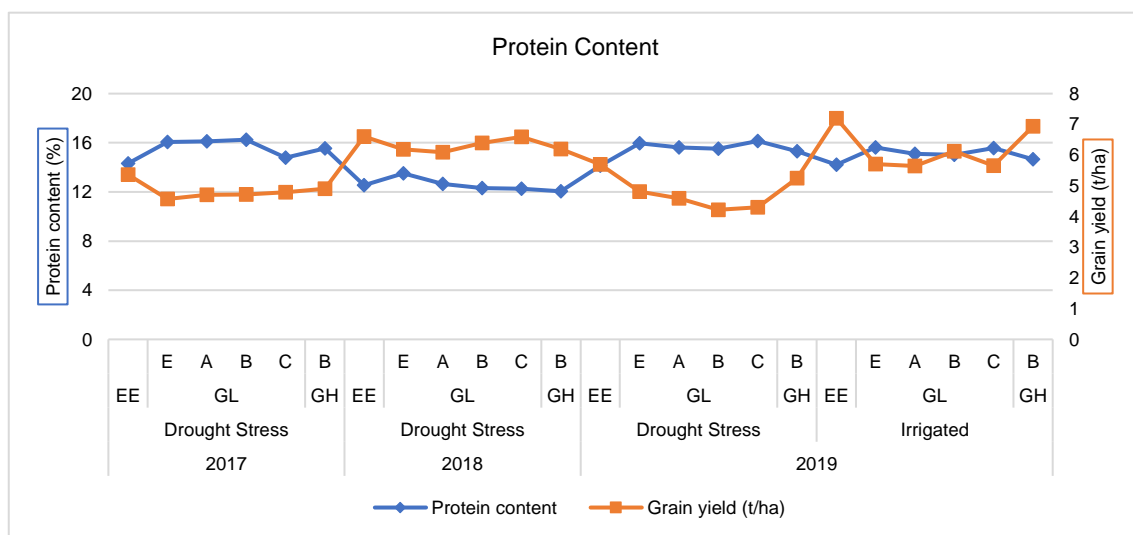


Figure 8 Comparison of protein content and grain yield for Eastern European varieties and for each quality group of German varieties. EE: Eastern European lines, GL: German lines, GH: German hybrids, A-E: Quality ranking of German varieties.

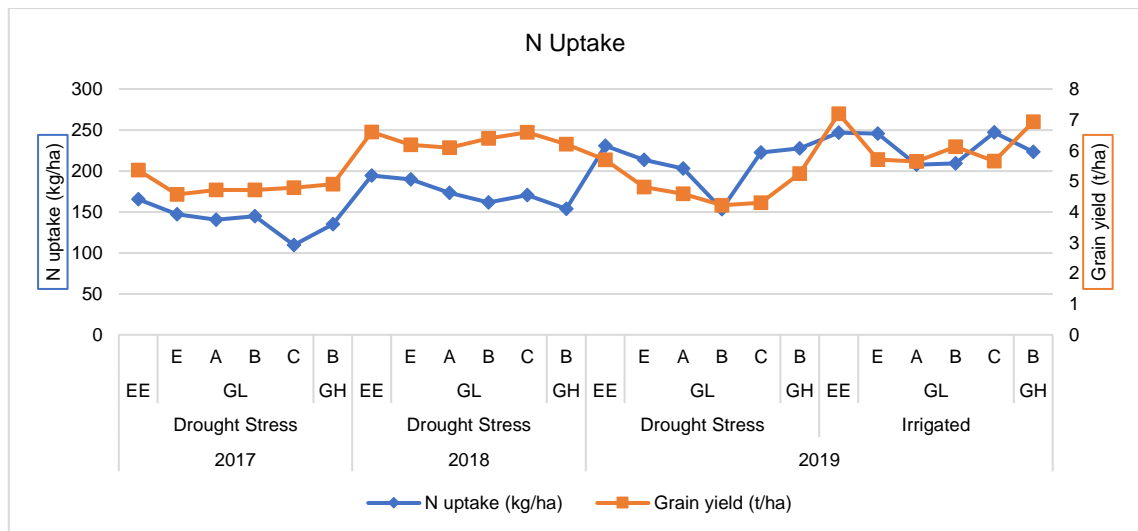


Figure 9 Comparison of nitrogen uptake and grain yield for Eastern European varieties and per quality group for German varieties. EE: Eastern European lines, GL: German lines, GH: German hybrids, A-E: Quality ranking of German varieties.

Contrary to the protein content, the N uptake (Figure 9) showed a similar development like the grain yield when looking at the different quality groups. In most trials, Eastern European lines had the highest grain yield in combination with the highest N uptake of all varieties. Only in the irrigated plots in 2019, German lines of the quality group C were slightly higher (246.98 g, Eastern European: 246.65 g); however, the difference was not significant. German hybrids showed a lower N uptake compared to the average of the German lines, except in the drought stress trial in 2019. Within each year, the N uptake of German lines differed more than grain yields, which was relatively steady amongst all quality groups. The average of the quality groups across all years showed a significant difference between Eastern European lines (207.73 g) and German lines of quality group A (172.97 g) and B (163.88 g) (Table 11).

Table 11 Protein content, grain yield and nitrogen uptake per quality class of German varieties and for Eastern European lines across all years.

		Protein content (%)			Grain yield (t/ha)			N uptake		
		mean	std	sig	mean	std	sig	mean	std	sig
German varieties	E	15.18	± 1.61	a	5.33	± 0.84	b	192.89	± 54.45	ab
	A	14.71	± 1.83	a	5.31	± 0.87	b	172.97	± 41.86	b
	B lines	14.65	± 1.85	ab	5.41	± 1.06	b	163.88	± 38.01	b
	B hybrids	14.38	± 1.63	ab	5.81	± 1.38	ab	185.00	± 66.54	ab
	C	14.68	± 2.07	a	5.33	± 1.03	b	187.34	± 68.64	ab
Eastern European lines		13.78	± 1.25	b	6.20	± 1.05	a	207.73	± 53.80	a

mean: mean values per group of varieties, sd: standard deviation, sig: significant differences within one parameter across all varieties.

4.1.4. Correlations between harvest parameters

Table 12 shows correlations between the harvest parameters presented in the Figures 4 and 7. The correlations were calculated across all varieties of all origins. The grain yield showed a rather close positive correlation with TGW ($r=0.42-0.68$), HI ($r=0.55-0.66$), and grain N uptake ($r=0.30-0.50$) in all trials. For all three parameters, this correlation was strongest in the trials of 2019. Consistent negative significant correlation with grain yield was found for the N content at anthesis in 2017 and 2019, and for the N content of the grains and the protein content in all years. In contrast to N content, the correlation of grain yield with N uptake at anthesis and at milk ripeness did not show regularities between the years.

In most cases, the number of tillers and ears per square meter, as well as the plant height were not significantly correlated to grain yield. An exception was found for plant height in 2017. The number of grains per ear and per square meter were significantly correlated to yield in 2017 and drought stress plots in 2019, grains/ear also in 2018. The correlation between grain yield and biomass dry weight at anthesis, milk ripeness and harvest was significantly positive for most measurements. Exceptions were the dry weight at anthesis 2019 in both trials, milk ripeness in 2017, and at harvest in irrigated plots 2019. In the other trials, correlations were found between $r=0.23-0.29$. Straw weight and post-anthesis dry matter assimilation never showed a strong correlation to grain yield.

As TGW and grain yield were strongly correlated, the correlations of TGW to other parameters were similar to those of the yield. However, the numbers of tillers and ears per square meter showed significant negative correlations to TGW in 2017 and 2018. In 2019, the correlations were also negative, but not significant. A similar result was found for the correlation of tillers and ears per square meter with the number of grains per ear, where drought stress plots in 2019 were the only ones depicting no significant negative correlation.

Plant height was significantly negatively correlated to N content at anthesis and milk ripeness in the years 2017 and 2018. In 2019, the correlation with N content at anthesis was positive, but very weak. N content at milk ripeness was not determined in 2019. Strong negative correlations were also found between HI and N content at anthesis and in grains, respectively.

In all trials, the N content at anthesis was negatively correlated to N uptake in grains ($r=-0.18$ to $r=-0.35$). Most other correlations between the N content at anthesis and the other N parameters in all years were significantly positive.

Table 12 Correlation between harvest parameters for 2017 and 2018, and both trials 2019.

	2017																																																		
	Grain Yield		TGW		Grains/Ear		HI		Tillers/m ²		Ears/m ²		Grains/m ²		Plant height		Drywt Anth		Drywt MR		Drywt H		Straw weight		PA Dry Matter		N Cont Anth		N Cont MR		N / Prot Cont Gr		N Up Anth		N Up MR		N Up Gr														
	r	p	r	p	r	p	r	p	r	p	r	p	r	p	r	p	r	p	r	p	r	p	r	p	r	p	r	p	r	p	r	p	r	p	r	p	r	p													
Grain Yield			0.51	**	0.20	*	0.56	**	0.00		0.09		0.21	*	0.23	*	0.29	**	-0.09		0.26	**	-0.15		-0.13		-0.59	**	-0.25	**	-0.47	**	-0.07		-0.22	*	0.31	**													
TGW	0.42	**			0.06		0.75	**	-0.27	**	-0.21	*	-0.13		0.13		0.14		-0.01		0.18		-0.31	**	-0.05		-0.44	**	-0.22	*	-0.66	**	-0.12		-0.14		0.23	*													
Grains/Ear	0.24	*	0.17				0.43	**	-0.57	**	-0.56	**	0.17		-0.10		0.25	**	-0.09		-0.14		-0.39	**	-0.26	**	-0.04		0.01		-0.09		0.27	**	-0.07		0.11														
HI	0.55	**	0.62	**	0.51	**			-0.35	**	-0.22	*	0.21	*	0.03		0.16		-0.05		0.14		-0.55	**	-0.09		-0.37	**	-0.17		-0.66	**	-0.06		-0.11		0.37	**													
Tillers/m ²	-0.12		-0.37	**	-0.64	**	-0.38	**			0.94	**	0.51	**	0.18		-0.10		0.23	*	0.67	**	0.75	**	0.34	**	-0.09		-0.19	*	0.22	*	-0.22	*	0.12		0.45	**													
Ears/m ²	-0.11		-0.42	**	-0.63	**	-0.34	**	0.96	**			0.61	**	0.24	**	-0.10		0.21	*	0.73	**	0.72	**	0.36	**	-0.15		-0.23	**	0.13		-0.25	**	0.08		0.53	**													
Grains/m ²	0.15		-0.36	**	0.27	**	0.16		0.38	**	0.46	**			0.16		0.00		0.15		0.78	**	0.45	**	0.29	**	-0.17		-0.27	**	0.05		-0.14		0.01		0.78	**													
Plant height	0.00		0.18		-0.19	*	-0.15		0.02		-0.04		-0.29	**			0.05		0.18				0.05		0.18		0.31	**	0.28	**	0.09		-0.50	**	-0.50	**	-0.13		-0.21	*	-0.10		0.22	*							
Drywt Anth	0.28	**	0.04		0.16		0.03		-0.09		-0.07		-0.02		0.18				-0.26	**	0.02		-0.09		-0.87	**	-0.30	**	-0.05		-0.03		0.81	**	-0.31	**	0.12														
Drywt MR	0.29	**	0.11		-0.07		-0.03		0.03		0.05		-0.03		0.19	*	0.36	**			0.17		0.22	*	0.23	*	-0.06		-0.46	**	0.09		-0.28	**	0.82	**	0.16														
Drywt H	0.23	*	0.27	**	0.09		0.13		0.41	**	0.37	**	0.56	**	0.03		-0.03		0.11				0.73	**	0.38	**	-0.28	**	-0.36	**	-0.02		-0.20	*	-0.06		0.87	**													
Straw weight	-0.11		-0.27	**	-0.28	**	-0.63	**	0.53	**	0.47	**	0.26	**	0.13		-0.01		0.17		0.60	**			0.37	**	0.02		-0.23		0.41	**	-0.10		0.03		0.45	**													
PA Dry Matter	-0.09		0.07		-0.06		0.05		0.27	**	0.25	**	0.33	**	-0.18	*	-0.82	**	-0.22	*	0.52	**	0.34	**			0.12		-0.11		0.03		-0.80	**	0.17		0.24	*													
N Cont Anth	-0.05		-0.31	**	0.03		-0.27	**	0.01		0.03		0.08		-0.35	**	-0.04		0.10		-0.12		0.10		-0.02				0.54	**	0.29	**	0.29	**	0.21	*	-0.35	**													
N Cont MR	-0.04		-0.24	**	0.11		-0.01		0.01		0.03		0.16		-0.24	**	0.06		0.11		-0.11		-0.16		-0.10		-0.10		0.42	**			0.01		0.27	**	0.09		-0.42	**											
N Cont Gr	-0.27	**	0.17		0.12		-0.02		-0.11		-0.16		-0.08		0.02		-0.08		-0.07		0.12		0.07		0.08		0.10		-0.06				0.11		0.07		0.11														
N Up Anth	0.22	*	-0.17		0.17		-0.08		-0.10		-0.09		0.08		-0.12		0.69	**	0.34	**	-0.09		0.02		-0.60	**	0.65	**	0.36	**	-0.04				-0.18		-0.14														
N Up MR	0.18	*	-0.07		0.02		0.00		0.03		0.06		0.09		-0.05		0.27	**	0.75	**	0.01		0.00		-0.20	*	0.34	**	0.74	**	-0.09		0.46	**			-0.09														
N Up Gr	0.30	**	0.57	**	0.37	**	0.62	**	0.03		0.01		0.42	**	-0.06		-0.04		0.00		0.70	**	0.02		0.35	**	-0.18		-0.07		0.46	**	-0.12		-0.03																

2018

HI: Harvest Index, Drywt Anth: Dry weight at anthesis, Drywt MR: Dry weight at milk ripeness, Drywt H: Dry weight at harvest, N Cont Anth: N content at anthesis, N Cont MR: N content at milk ripeness, N / Prot Cont Gr: N and protein content of grains, N Up Anth: N uptake at anthesis, N Up MR: N uptake at milk ripeness, N Up Gr: N uptake of grains, Protein: Protein content of grains

r: Pearson correlation coefficient

Statistical significance as indicated by p-value: * p < 0.05, ** p < 0.01.

Table 12 (continued) Correlation between harvest parameters for 2017 and 2018, and both trials 2019.

	2019 Drought stress																																	
	Grain Yield		TGW		Grains/ Ear		HI		Tillers/m2		Ears/m2		Grains/ m2		Plant height		Drywt Anth		Drywt H		Straw weight		PA Dry Matter		N Cont Anth		N / Prot Cont Gr		N Up Anth		N Up Gr			
	r	p	r	p	r	p	r	p	r	p	r	p	r	p	r	p	r	p	r	p	r	p	r	p	r	p	r	p	r	p	r	p		
Grain Yield			0.68	**	0.35	**	0.66	**	0.02	0.01	0.21	*	0.06	0.16	0.24	*	-0.02	-0.03	-0.47	**	-0.47	**	0.00	0.50	**									
TGW	0.64	**			0.20		0.89	**	-0.18	-0.18	-0.07		-0.14	0.16	0.04		-0.32	**	-0.17		-0.75	**	-0.61	**	-0.05	0.41	**							
Grains/ Ear	0.16		0.02				0.46	**	-0.12	-0.12	0.39	**	-0.05	-0.03	0.20		0.01	0.06	-0.08		-0.17		-0.04	0.41	**									
HI	0.61	**	0.86	**	0.32	**			-0.31	**	-0.31	**	-0.02	-0.20	*	0.09		-0.09		-0.47	*	-0.23	*	-0.65	**	-0.62	**	-0.11	0.37	**				
Tillers/ m2	0.01		-0.07		-0.34	**	-0.16				0.99	**	0.83	**	0.35	**	0.34	**	0.85	**	0.88	**	0.35	**	0.15	0.06	0.41	**	0.66	**				
Ears/ m2	0.12		0.01		-0.31	**	-0.05		0.95	**			0.84	**	0.31	**	0.33	**	0.87	**	0.86	**	0.35	**	0.13	0.08	0.40	**	0.67	**				
Grains/ m2	0.14		-0.06		0.31	**	0.14		0.59	**	0.68	**			0.33	**	0.28	**	0.93	**	0.81	**	0.35	**	0.04	-0.07	0.31	**	0.85	**				
Plant height	-0.06		-0.18		-0.40	**	-0.40	**	0.24	**	0.17		-0.05				0.19	*	0.35	**	0.49	**	0.15	0.03	0.04	0.20	*	0.20						
Drywt Anth	0.04		-0.22	*	-0.16		-0.20		0.08	0.07	0.01		0.20	*					0.37	**	0.30	**	-0.63	**	-0.24	**	-0.22	*	0.93	**	0.32	**		
Drywt H	0.10		-0.06		0.02		-0.08		0.63	**	0.69	**	0.87	**	0.21	*	-0.02				0.86	**	0.37	**	-0.08	-0.06	0.37	**	0.87	**				
Straw weight	-0.18		-0.46	**	-0.09		-0.49	**	0.65	**	0.59	**	0.59	**	0.42	**	0.15		0.74	**			0.40	**	0.26	**	0.22	*	0.41	**	0.59	**		
PA Dry Matter	0.07		0.12		0.17		0.11		0.38	**	0.38	**	0.54	**	-0.05		-0.74	**	0.67	**	0.43	**		0.22	*	0.16	-0.59	**	0.23	*				
N Cont Anth	-0.35	**	-0.52	**	-0.02		-0.47	**	-0.01		-0.10		0.03		0.00		0.13		-0.03		0.35	**	-0.06			0.59	**	0.07	-0.27	**				
N Cont Gr	-0.42	**	-0.56	**	-0.12		-0.60	**	0.08		0.06		0.07		0.21	*	0.23	*	0.11		0.31	**	-0.12		0.36	**		0.01	-0.19					
N Up Anth	-0.13		-0.42	**	-0.13		-0.38	**	0.06		0.02		0.01		0.18	*	0.89	**	-0.05		0.28	**	-0.66	**	0.52	**	0.35	**		0.28	**			
N Up Gr	0.45	**	0.42	**	0.26	*	0.51	**	0.39	**	0.48	**	0.77	**	-0.12		-0.14		0.78	**	0.38	**	0.64	**	-0.18	-0.15	-0.21	*						

2019 Irrigated

HI: Harvest Index, Drywt Anth: Dry weight at anthesis, Drywt MR: Dry weight at milk ripeness, Drywt H: Dry weight at harvest, N Cont Anth: N content at anthesis, N Cont MR: N content at milk ripeness, N / Prot Cont Gr: N content of grains, N Up Anth: N uptake at anthesis, N Up MR: N uptake at milk ripeness, N Up Gr: N uptake of grains, Protein: Protein content of grains
r: Pearson correlation coefficient
Statistical significance as indicated by p-value: * p < 0.05, ** p < 0.01.

4.1.5. Rank sum of grain yield and grain N uptake

Grain yield (Table 13) was ranked from highest to lowest yield. The results are shown sorted by origin of the varieties. It is visible that three varieties from Eastern Europe (*Ursita*, *Pajura* and *Zřsk*) ranked higher than the best yielding German variety (*Hyfi*). Seven German wheat varieties ranked lower than the lowest Eastern European line. The two best yielding German varieties were two hybrids. However between the first and second rank of the German varieties was a huge gap. The best German variety (*Hyfi*) ranked 4th in total (rank sum of 35), the second German variety (*Hybery*, rank sum of 59) ranked 14th across all varieties. Best German lines were *Mulan* (rank sum of 65) and *Elixer* (rank sum of 67). The Eastern European lines with lowest rank sum, i.e. high grain yield, were *Ursita* (rank sum of 23) and *Pajura* (rank sum of 25). Remarkably, *Ursita* was the variety with the highest yield in 2018 and drought plots of 2019, but only in the 16th place in 2017. *Pajura* showed its highest yield in 2019 (irrigated). *Hyfi* performed best in irrigated plots, *Hybery* in drought plots in 2019. *Mulan* and *Elixer* ranked highest in 2018.

Table 14 shows the ranking of grain N uptake, also sorted by origin of the varieties and from highest to lowest N uptake. Eight Eastern European lines showed better ranking than the best German variety (*Genius*). Seven German varieties ranked lower than the lowest line from Eastern Europe. The best-classified line *Pajura* ranked in the 1st and 2nd place in 2017, 2018 and in the irrigated plots of 2019. *Rowina*, second overall, ranked better in 2018 and under drought stress in 2019, however was ranked 16th in 2017. The two best German varieties, *Genius* and *Hyfi*, both ranked well in the irrigated plots in 2019, but lower in the non-irrigated trials.

Table 13 Rank sum across all years of grain yield per variety. Sorted highest to lowest yield within the groups of origin.

Variety	Origin	Breed	Rank Sum of Grain Yield (t/ha)								Rank sum
			Grain yield 2017	Rank 2017	Grain yield 2018	Rank 2018	Grain yield 2019 Drought stress	Rank 2019 Drought stress	Grain yield 2019 Irrigated	Rank 2019 Irrigated	
Ursita	EE	Line	5.14	16	7.39	1	7.93	1	7.99	5	23
Pajura	EE	Line	5.42	9	7.06	7	6.32	6	8.32	3	25
Získ	EE	Line	6.01	1	6.80	12	6.68	5	7.75	7	25
Meleag	EE	Line	5.80	3	6.56	19	5.96	8	7.70	8	38
Rowina	EE	Line	5.85	2	6.33	21	6.14	7	7.41	10	40
Zolotocolosa	EE	Line	5.52	7	7.37	2	4.83	20	7.05	12	41
Amor	EE	Line	5.67	5	7.03	8	5.45	12	6.64	16	41
Unitar	EE	Line	4.33	31	7.26	3	6.82	4	7.90	6	44
Semnal	EE	Line	4.60	27	6.72	15	7.24	3	8.38	2	47
Transitor	EE	Line	5.80	4	6.76	13	5.32	13	6.46	19	49
Kuialnik	EE	Line	4.93	19	7.13	5	5.15	17	7.41	9	50
FGmut 293	EE	Line	5.54	6	6.58	18	5.18	15	6.91	14	53
Acord	EE	Line	5.31	12	7.07	6	4.34	27	7.33	11	56
Clasic	EE	Line	5.19	15	6.35	20	5.77	10	6.87	15	60
Numitor	EE	Line	5.33	11	6.72	14	4.39	26	6.95	13	64
Talisman	EE	Line	5.39	10	6.17	25	4.69	21	6.50	18	74
Savant	EE	Line	5.00	18	6.22	24	5.69	11	5.89	25	78
Zagrava	EE	Line	5.27	13	5.36	31	4.66	22	6.10	22	88
Hyfi	Ger	Hybrid	5.44	8	6.68	17	5.92	9	8.39	1	35
Hybery	Ger	Hybrid	4.69	25	6.07	28	7.25	2	8.31	4	59
Mulan	Ger	Line	4.86	21	6.84	10	5.22	14	6.43	20	65
Elixer	Ger	Line	5.09	17	6.96	9	5.03	18	6.00	23	67
Discus	Ger	Line	4.50	28	7.25	4	4.42	25	5.92	24	81
Colonia	Ger	Line	4.76	23	6.82	11	3.61	31	6.50	17	82
Genius	Ger	Line	4.71	24	6.09	26	5.15	16	6.28	21	87
Kerubino	Ger	Line	4.85	22	6.70	16	4.47	24	5.14	32	94
Patras	Ger	Line	4.89	20	5.96	29	4.85	19	5.64	27	95
Hystar	Ger	Hybrid	5.19	14	4.44	32	4.08	28	5.78	26	100
Impression	Ger	Line	4.64	26	6.28	22	4.50	23	5.36	29	100
Manager	Ger	Line	4.48	30	6.07	27	3.83	29	5.43	28	114
Anapolis	Ger	Line	4.48	29	6.22	23	3.57	32	5.30	30	114
Hybred	Ger	Hybrid	4.28	32	5.54	30	3.72	30	5.27	31	123

EE: Eastern European varieties, Ger: German varieties.

Table 14 Rank sum across all years of grain N uptake of all varieties. Sorted from highest to lowest N uptake within the groups of origin

Variety	Origin	Breed	Rank sum of grain N uptake								
			Grain N uptake 2017	Rank 2017	Grain N uptake 2018	Rank 2018	Grain N uptake 2019 Drought stress	Rank 2019 Drought stress	Grain N uptake 2019 Irrigated	Rank 2019 Irrigated	Rank sum all years
Pajura	EE	Line	183.76	1	232.94	2	239.74	10	295.75	2	15
Rowina	EE	Line	161.85	16	239.59	1	268.36	4	265.19	7	28
Semnal	EE	Line	168.64	11	212.42	5	233.79	13	284.80	3	32
Amor	EE	Line	170.84	7	188.11	14	246.56	7	282.56	4	32
FGmut 293	EE	Line	179.26	2	196.95	10	244.76	8	247.86	12	32
Zisk	EE	Line	162.91	15	203.42	8	289.99	2	255.17	10	35
Ursita	EE	Line	175.36	3	209.91	6	249.34	6	228.51	20	35
Unitar	EE	Line	168.56	12	220.02	4	233.30	14	263.56	9	39
Numitor	EE	Line	171.69	6	208.09	7	202.73	22	236.36	17	52
Kuialnik	EE	Line	163.59	14	199.38	9	213.85	19	244.50	14	56
Acord	EE	Line	139.57	24	222.04	3	223.12	17	247.29	13	57
Meleag	EE	Line	172.43	5	167.19	24	216.85	18	238.42	16	63
Savant	EE	Line	163.95	13	172.63	22	254.89	5	213.61	25	65
Talisman	EE	Line	161.29	17	182.40	18	224.33	16	240.73	15	66
Clasic	EE	Line	150.18	21	172.17	23	234.63	12	249.18	11	67
Transitor	EE	Line	169.44	9	184.29	17	206.68	21	219.03	21	68
Zolotocolosa	EE	Line	158.11	19	175.45	20	198.91	23	235.68	18	80
Zagrava	EE	Line	169.26	10	185.86	16	172.01	28	191.43	30	84
Genius	Ger	Line	143.83	22	189.80	13	239.25	11	296.22	1	47
Hyfi	Ger	Hybrid	140.20	23	154.29	29	243.47	9	275.59	5	66
Hybery	Ger	Hybrid	125.52	28	147.52	31	304.65	1	269.95	6	66
Mulan	Ger	Line	173.05	4	186.87	15	163.68	31	217.68	23	73
Elixer	Ger	Line	120.26	30	166.85	25	270.25	3	229.72	19	77
Kerubino	Ger	Line	169.86	8	181.18	19	187.68	25	195.22	27	79
Patras	Ger	Line	128.18	26	194.80	11	206.84	20	210.23	26	83
Discus	Ger	Line	136.28	25	193.54	12	173.74	27	218.10	22	86
Anapolis	Ger	Line	98.96	32	174.05	21	174.42	26	264.23	8	87
Impression	Ger	Line	160.99	18	154.96	28	228.47	15	194.58	28	89
Colonia	Ger	Line	127.86	27	165.24	26	119.89	32	215.75	24	109
Hystar	Ger	Hybrid	157.61	20	152.09	30	165.91	29	169.94	32	111
Hybred	Ger	Hybrid	117.23	31	160.92	27	196.87	24	178.31	31	113
Manager	Ger	Line	122.49	29	144.70	32	164.88	30	194.15	29	120

EE: Eastern European varieties, Ger: German varieties.

4.1.6. Heritability of agronomical traits

Heritability was calculated for each trial, separately for each group of varieties and additionally for all varieties within one trial. Table 15 shows the heritability (h^2) for agronomical traits. Grain yield, TGW and HI showed high heritability in all years. Lowest values were obtained for TGW of Eastern European lines in 2017 ($h^2=0.37$) and for German lines in irrigated plots of 2019 ($h^2=0.43$). The nitrogen uptake of grains showed moderate to high heritability in all years. The protein content of grains showed lowest heritability in 2017 ($h^2=0.06-0.35$), but considerably higher values in 2018 and 2019 ($h^2=0.51-0.96$). Altogether, German hybrids often showed the highest heritability

compared to other varieties within one year. Calculating heritability across all years, TGW and HI showed a heritability of $h^2 > 0.5$.

Table 15 Heritability of grain yield, TGW, HI, grain N uptake and protein content.

		Heritability					
		Yield	TGW	HI	Gr N up	Protein	
		h^2	h^2	h^2	h^2	h^2	
2017	EE	0.87	0.37	0.88	0.00	0.35	
	Ger Hy	0.91	0.90	0.95	0.74	0.14	
	Ger Li	0.64	0.62	0.54	0.61	0.06	
	All var	0.88	0.76	0.93	0.45	0.52	
2018	EE	0.85	0.88	0.79	0.74	0.73	
	Ger Hy	0.95	0.75	0.97	0.00	0.70	
	Ger Li	0.94	0.95	0.89	0.67	0.85	
	All var	0.89	0.94	0.90	0.79	0.78	
2019	Drought stress	EE	0.98	0.82	0.92	0.05	0.77
		Ger Hy	0.99	0.99	0.81	0.91	0.96
		Ger Li	0.94	0.91	0.90	0.66	0.75
		All var	0.98	0.97	0.97	0.49	0.89
	Irrigated	EE	0.94	0.57	0.66	0.00	0.51
		Ger Hy	0.98	0.99	0.97	0.72	0.91
		Ger Li	0.94	0.43	0.88	0.61	0.58
		All var	0.97	0.90	0.92	0.44	0.69
Both trials	All var	0.76	0.93	0.92	0.55	0.82	
All years	All var	0.49	0.88	0.85	0.34	0.44	

h^2 : Heritability, EE: Eastern European varieties, Ger Hy: German hybrid varieties, Ger Li: German Line varieties, All var: All varieties
Yield: Grain yield, TGW: Thousand grain weight, HI: Harvest index; Gr N up: N uptake of grains, Protein: Protein content of grains

Table 16 Heritability of grain yield, TGW, HI, grain N uptake, and protein content within drought stress plots only, across all years.

		Heritability				
		Yield	TGW	HI	Gr N up	Protein
		h^2	h^2	h^2	h^2	h^2
All years drought stress	EE	0.01	0.69	0.75	0.46	0.53
	Ger Hy	0.42	0.42	0.63	0.00	0.74
	Ger Li	0.30	0.61	0.67	0.04	0.00
	All var	0.43	0.87	0.85	0.50	0.45

h^2 : Heritability, EE: Eastern European varieties, Ger Hy: German hybrid varieties, Ger Li: German Line varieties, All var: All varieties
Yield: Grain yield, TGW: Thousand grain weight, HI: Harvest index; Gr N up: N uptake of grains, Protein: Protein content of grains

The heritability values in Table 16 were calculated using only data from drought stress plots. The heritability across all varieties decreased to $h^2=0.43$, hence is a bit lower than when including irrigated plots. Heritability of TGW ($h^2=0.87$) and HI ($h^2=0.85$) remained on a very high level. Grain N uptake and protein content also showed higher heritability than grain yield itself. However, considering the groups of origin separately, only the Eastern European lines showed promising heritability in all traits. The heritability

of grain N uptake was at or close to zero for both German hybrids and lines; the heritability of protein content of German lines was also zero. TGW and HI showed good heritability in all groups of origin.

4.2. Impact of heat and drought on carbon isotope discrimination and leaf water content

4.2.1. Carbon Isotope Discrimination

The rate of carbon isotope discrimination (CID) in different years, sampling times and varieties is shown in Figure 10. Each graph shows the CID of leaf and grain samples of one year, differentiated between Eastern European lines, German lines and German hybrids. Over the years, leaf samples were taken at comparable growth stages whenever possible. On average plants were at Z71 (sampling time (T) 1), Z79 (T2) and Z87-89 (T3). The CID of grains was determined after harvest. In 2017 (Figure 10A), at the first sampling time of leaves no difference between the varieties could be detected. From T1 to T2, the CID of Eastern European lines increased, whereas for German varieties it decreased. At T2, the difference between all three groups of varieties was significant. Between T2 and T3 CID of all varieties decreased to different degrees, leading to a significant difference between Eastern European lines and German lines. German hybrids were not significantly different to either one of the lines. The grains of 2017 showed the lowest CID-values, even compared to other years. Significant difference could be found between Eastern European lines and German varieties, but not between German hybrids and German lines. In 2018 (Figure 10B), the CID rate was higher than 2017 at all measuring times. At T1 in 2018, no significant difference was found between the three groups of varieties. As in the previous year, the CID of Eastern European lines increased slightly and for German varieties decreased, leading to a significant difference between German and Eastern European lines, with hybrids being intermediate. At leaf sampling T3 and the grain sampling, the CID decreased further for all varieties. At these sampling times, German hybrids showed a significantly higher CID than German lines, while Eastern European lines did not differ significantly. In both trials of 2019 (Figure 10C and D), the CID was considerably higher than in 2017 and 2018. Also in both trials, German hybrids showed the highest CID for all leaf samples and Eastern European lines for grain samples. In the plots under drought stress, the hybrids had significantly higher CID than German lines at all sampling times. At T1 and T3, Eastern European lines were comparable to German lines; at T2 and in grains, they were comparable to German hybrids. In the irrigated plots, the Eastern European lines had the lowest CID at the first

sampling time T1. The CID of German hybrids and lines was significantly higher. At T2, all varieties showed significant differences from each other. This difference became smaller in T3, where hybrids were significantly higher than both line groups. The CID of grains was similar for Eastern European lines and German hybrids, but significantly lower in German lines, resulting in a similar pattern as in the drought stress plots. Across all years, it is clearly visible that the difference in CID between T1 and grains was smallest for Eastern European lines in most cases (2017: 3.03 ‰, 2019 drought stress: 1.71 ‰, 2019 irrigated: 1.3 ‰). Only in 2018, German hybrids showed a smaller difference between the first and last sampling time (2.24 ‰). The difference between 2017 and 2018 was higher than between drought stress and irrigated plots in 2019.

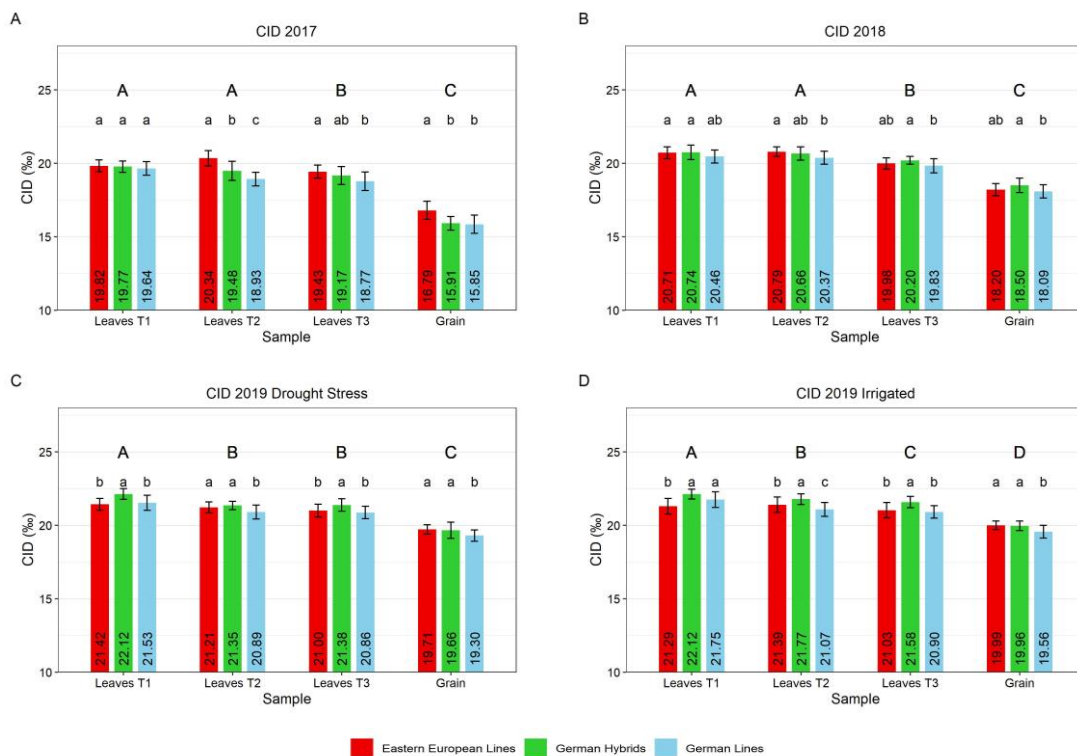


Figure 10 Carbon isotope discrimination of winter wheat leaves at three growth stages and grains of all experimental years. Capital letters show significance between the years, lowercase letters show significance between origins within each year.

Table 17 Correlation between carbon isotope discrimination and grain yield in leaf samples (T1-T3) and grains.

Correlation of CID and Grain Yield										
			Eastern European Lines		German Hybrids		German Lines		All varieties	
			r	p	r	p	r	p	r	p
2017	Leaves	T1	-0.07		-0.46		0.03		0.07	
		T2	0.14		0.52		0.45	**	0.61	**
		T3	-0.02		0.70	*	0.63	**	0.52	**
	Grain		0.06		0.59	*	0.20		0.46	**
2018	Leaves	T1	0.06		0.10		0.10		0.13	
		T2	0.07		0.30		0.18		0.22	*
		T3	0.05		0.10		-0.03		0.04	
	Grain		0.06		0.68	*	0.10		0.12	
2019	Drought stress	T1	0.06		-0.15		-0.16		-0.05	
		T2	0.21		0.16		0.01		0.30	**
		T3	0.33	*	0.38		0.08		0.30	**
	Grain		0.01		0.84	**	0.30	*	0.46	**
	Irrigated	T1	-0.05		0.06		0.05		-0.18	*
		T2	-0.10		-0.17		-0.08		0.17	
T3		-0.05		0.34		0.26		0.22	*	
Grain		0.28	*	0.82	**	0.32	*	0.57	**	

r: Pearson correlation coefficient
 Statistical significance as indicated by p-value: * p < 0.05, ** p < 0.01

Table 17 shows the correlation between the rate of carbon isotope discrimination and grain yield. It was calculated for each sample at each trial, separately for the three groups of varieties and additionally over all varieties within one year (last column). Comparing the years and single groups of varieties, most significant correlations were found in 2017; however, none of them was obtained for Eastern European lines and none for the first sampling of leaves. In 2018, only the CID of grains of hybrid varieties was significantly correlated with yield. In 2019, in both trials significant correlations were found for T3 leaf samples (Eastern European lines, drought stress) and for grains of all other varieties. Comparing the three groups of varieties during all years, best correlations could be found for German hybrids, followed by German lines. When the data of all varieties was used to calculate the correlation, more significances were found; however, again in the year 2018 the lowest number of significant correlations were observed. It is obvious that higher correlations can be found at later growth stages of the leaves and with the grains. Only in the irrigated plots of 2019, a significant correlation with grain yield was found in T1 leaf samples.

4.2.2. Rank sum of CID

Table 18 shows the rank sum of CID in grains. Ranking was done from highest to lowest CID, since a high discrimination rate is an indicator for lower stress level in the plants. Across all trials, two Eastern European lines (*Ursita*, *Talisman*) ranked higher than the best-ranked German line *Elixer. Pajura*, the lowest ranked Eastern European line, performed better than eight German varieties, leading to only six German varieties that showed a similar stress level as Eastern European lines. Amongst the three best performing German varieties were two of the hybrids (*Hybery*, *Hyfi*).

Table 18 Rank sum across all years of CID in grains per variety. Sorted from highest to lowest discrimination within the groups of origin.

Rank Sum of CID											
Variety	Origin	Breed	CID Grain 2017	Rank 2017	CID Grain 2018	Rank 2018	CID Grain 2019 Drought stress	Rank 2019 Drought stress	CID Grain 2019 Irrigated	Rank 2019 Irrigated	Rank sum CID
Ursita	EE	Line	17.21	1	18.45	7	20.03	4	20.35	1	13
Talisman	EE	Line	16.77	12	18.80	3	19.92	6	20.25	4	25
Unitar	EE	Line	17.20	2	18.55	5	19.50	21	20.16	7	35
Zolotocolosa	EE	Line	16.95	7	18.52	6	19.75	11	20.09	11	35
Numitor	EE	Line	16.94	8	18.29	14	19.78	10	20.04	14	46
Acord	EE	Line	16.92	10	18.24	18	19.88	7	19.95	16	51
FGmut 293	EE	Line	17.04	3	18.34	11	19.68	16	19.83	21	51
Meleag	EE	Line	16.41	18	17.88	25	19.86	8	20.32	2	53
Clasic	EE	Line	16.24	20	18.25	15	19.73	12	20.22	6	53
Savant	EE	Line	16.48	16	18.13	20	19.99	5	20.08	13	54
Amor	EE	Line	16.19	21	18.07	22	20.06	3	20.14	10	56
Transitor	EE	Line	17.03	5	18.24	16	19.62	17	19.91	18	56
Zagrava	EE	Line	17.04	4	18.24	17	19.68	13	19.79	22	56
Rowina	EE	Line	16.51	15	18.10	21	19.81	9	19.92	17	62
Kuialnik	EE	Line	16.86	11	18.37	9	19.54	20	19.77	23	63
Zisk	EE	Line	16.92	9	18.22	19	19.47	22	20.03	15	65
Semnal	EE	Line	16.57	14	17.60	30	19.27	25	20.08	12	81
Pajura	EE	Line	16.68	13	17.70	29	19.59	18	19.64	25	85
Elixer	Ger	Line	16.25	19	18.59	4	20.10	2	20.14	8	33
Hybery	Ger	Hybrid	15.81	25	18.39	8	20.36	1	20.30	3	37
Hyfi	Ger	Hybrid	16.04	22	18.86	2	19.68	15	20.14	9	48
Anapolis	Ger	Line	16.96	6	18.35	10	19.57	19	19.90	19	54
Hystar	Ger	Hybrid	16.43	17	18.87	1	19.44	23	19.86	20	61
Mulan	Ger	Line	15.80	26	17.95	23	19.68	14	20.24	5	68
Colonia	Ger	Line	15.79	27	18.32	13	19.23	26	19.68	24	90
Discus	Ger	Line	15.62	28	18.34	12	19.21	28	19.51	29	97
Impression	Ger	Line	14.96	32	17.94	24	19.30	24	19.54	27	107
Patras	Ger	Line	15.97	23	17.76	27	19.13	30	19.45	30	110
Hybred	Ger	Hybrid	15.36	30	17.88	26	19.14	29	19.53	28	113
Manager	Ger	Line	15.49	29	17.54	32	19.21	27	19.60	26	114
Genius	Ger	Line	15.91	24	17.70	28	18.98	31	19.26	31	114
Kerubino	Ger	Line	15.19	31	17.55	31	18.97	32	19.24	32	126

EE: Eastern European varieties, Ger: German varieties.

4.2.3. Relative Leaf Water Content

The first two leaf samples T1 (Z71) and T2 (Z79) were used to determine the relative leaf water content (RLWC). In all years, it was significantly lower in the second sampling than in the first (Figure 11). In 2017 (Figure 11A) and the drought stress trial of 2019 (Figure 11C), Eastern European lines had a significantly lower RLWC at anthesis than German lines. Hybrids were not different from either one of the lines in 2017, and grouped with German lines in 2019, respectively. At all other sampling times of all years, no difference between the three groups of varieties was detected. Although not significant, the German lines and hybrids had a lower RLWC at T2 than Eastern European lines in all drought stress trials. The only exception was found for hybrids in 2019 (Figure 11C and D), being slightly higher than Eastern European lines.

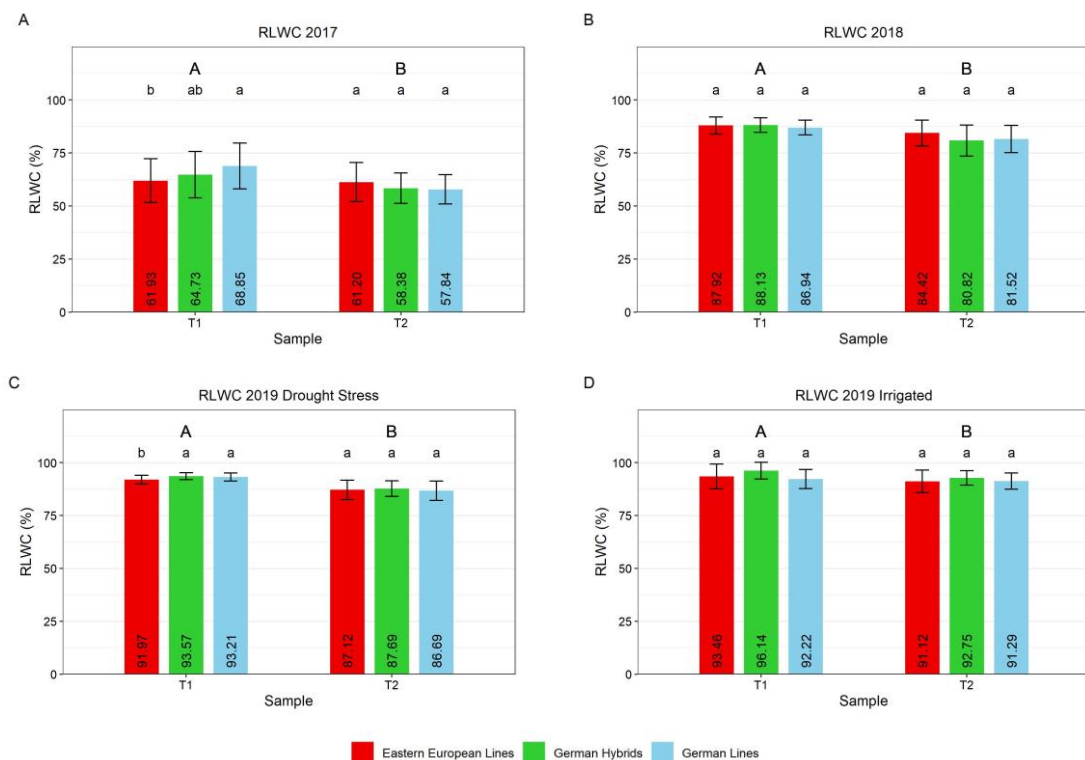


Figure 11 Relative leaf water content (RLWC) of all experimental years at growth stage Z71 (T1) and Z79 (T2).

WI, canopy temperature and RLWC are measures strongly influenced by daily temperature and quickly alter under changing weather conditions, whereas CID values integrate over time. Therefore, RLWC was correlated with WI and canopy temperature measured at the same day. CID, however, was correlated with the sum of canopy temperature and WI, summing up until the day when leaf samples were taken. Results are shown in Table 19. At Z71, the correlations with WI were only significant in 2019 in

the drought stress plots. Most correlations with temperature or temperature sum were significant. Except for 2017, all significant correlations with temperature data were negative. Higher temperature was therefore related to lower carbon isotope discrimination and to lower leaf water content. Comparing the years, most correlations were found in the drought stress and irrigated plots in 2019.

At the second sampling (Z79), strong negative correlations between the sum of WI and the CID were found for drought stress trials in all years. In drought stressed plots of 2019, almost all correlations including temperature were significant, whereas in irrigated plots only drone derived temperature was correlated to RLWC and CID.

Table 19 Correlation of RLWC with WI and canopy temperature, and CID with sum of WI and sum of canopy temperature for each experimental year at EC 71 (above) and EC 79 (below). Aerial measurements (DuetT) were only taken in 2019.

		Correlation of CID and Drought Related Parameters Z71											
		WI		Sum WI		Temp Fluke		Sum Temp Fluke		Temp DuetT		Sum Temp DuetT	
		r	p	r	p	r	p	r	p	r	p	r	p
2017	RLWC	0.08				0.21	*						
	CID			-0.11				-0.03					
2018	RLWC	-0.06				-0.16							
	CID			-0.03				-0.26	**				
2019	Drought stress	RLWC	0.33	**			0.05			-0.27	**		
		CID			0.24	**			-0.28	**		-0.36	**
	Irrigated	RLWC	0.13				-0.20	*			-0.07		
		CID			0.13				-0.18	*		-0.34	**

WI: Water Index, Sum WI: Sum of Water Index, Temp Fluke: Canopy temperature obtained with the handheld thermal camera, Sum of canopy temperature obtained with the handheld thermal camera, Temp DuetT: canopy temperature obtained with the thermal sensor of the drone, Sum Temp DuetT: Sum of canopy temperature obtained with the thermal sensor of the drone.

r: Pearson correlation coefficient

Statistical significance as indicated by p-value: * p < 0.05, ** p < 0.01

		Correlation of CID and Drought Related Parameters Z79											
		WI		Sum WI		Temp Fluke		Sum Temp Fluke		Temp DuetT		Sum Temp DuetT	
		r	p	r	p	r	p	r	p	r	p	r	p
2017	RLWC	0.18				0.14							
	CID			-0.55	**			-0.16					
2018	RLWC	-0.05				-0.42	**						
	CID			-0.32	*			-0.12					
2019	Drought stress	RLWC	0.05				-0.27	**		-0.07			
		CID			0.24	**			-0.32	**		-0.16	
	Irrigated	RLWC	0.22	*			-0.09				-0.28	**	
		CID			0.18				-0.09			-0.20	*

WI: Water Index, Sum WI: Sum of Water Index, Temp Fluke: Canopy temperature obtained with the handheld thermal camera, Sum of canopy temperature obtained with the handheld thermal camera, Temp DuetT: canopy temperature obtained with the thermal sensor of the drone, Sum Temp DuetT: Sum of canopy temperature obtained with the thermal sensor of the drone.

r: Pearson correlation coefficient

Statistical significance as indicated by p-value: * p < 0.05, ** p < 0.01

4.2.4. Heritability of physiological traits

The RLWC showed moderate to high heritability in all years (Table 20). CID of leaves and grain was higher for German varieties than for Eastern European varieties in most trials. Only in drought stress plots in 2019, the genetic variance was estimated to be zero, thus no heritability could be calculated. Most calculated h^2 were higher for CID than for RLWC. Across all years, CID of leaves and grain showed a heritability of $h^2 > 0.5$. Heritability of RLWC and CID within drought plots only is shown in Table 21. The heritability of RLWC was lower than of CID within the individual groups of origin ($h^2 = 0.08-0.54$), as well as across all varieties ($h^2 = 0.22$). The CID showed higher heritability in leaves than in grains, and higher heritability for German lines and hybrids than Eastern European lines.

Table 20 Heritability of RLWC and CID.

			Heritability		
			RLWC	CID Leaves	CID Grain
			h^2	h^2	h^2
2017	Drought stress	EE	0.63	0.46	0.37
		Ger Hy	0.59	0.96	0.90
		Ger Li	0.00	0.79	0.62
		All var	0.43	0.89	0.76
2018	Drought stress	EE	0.48	0.80	0.64
		Ger Hy	0.44	0.91	0.95
		Ger Li	0.54	0.91	0.88
		All var	0.53	0.89	0.82
2019	Drought stress	EE	0.67	0.80	0.39
		Ger Hy	0.00	0.00	0.86
		Ger Li	0.56	0.84	0.71
	Irrigated	All var	0.59	0.82	0.76
		EE	0.73	0.79	0.65
		Ger Hy	0.09	0.94	0.95
		Ger Li	0.63	0.90	0.88
Both trials	All var	0.61	0.87	0.88	
	All var	0.49	0.83	0.78	
All years	All var	0.37	0.69	0.64	

h^2 : Heritability, EE: Eastern European varieties, Ger Hy: German hybrid varieties, Ger Li: German Line varieties, All var: All varieties
 RLWC: Relative leaf water content, CID Leaves: Carbon isotope discrimination in leaves;
 CID Grain: Carbon isotope discrimination in grains

Table 21 Heritability of RLWC and CID within drought stress plots only, across all years.

			Heritability		
			RLWC	CID Leaves	CID Grain
			h^2	h^2	h^2
All years drought stress	EE	0.35	0.60	0.41	
	Ger Hy	0.54	0.73	0.68	
	Ger Li	0.08	0.86	0.72	
	All var	0.22	0.74	0.65	

h^2 : Heritability, EE: Eastern European varieties, Ger Hy: German hybrid varieties, Ger Li: German Line varieties, All var: All varieties

4.3. Use of high-throughput phenotyping for identification of stress tolerant varieties

4.3.1. Spectral indices and canopy temperature measurements

In all years and trials, the development of the NDVI throughout the vegetation period was comparable (Figure 12). From the start of measurements until 240 DAS, no difference between the three groups of varieties could be detected. In 2017 and 2018, a slight decrease was visible from 230-240 DAS, which was not observed in the two trials of 2019. In 2017, German lines showed the highest NDVI values during senescence, while Eastern lines were depicted the lowest ones. German hybrid varieties were ranked in between. In the other years, the hybrids ranked highest. The NDVI of German lines was interjacent, the one of Eastern European lines lowest. The order of varieties remained the same until harvest. In the irrigated plots of 2019, it is visible that the difference between the three groups of origin was larger than in plots under drought stress. In summary, German varieties showed higher NDVI values for a longer time than Eastern European lines and started senescing later.

Figure 13 shows the development of the WI over time. In 2017, a continuous decrease of WI was detectable throughout the vegetation period. German lines had the highest WI, German hybrids and Eastern European lines were at the same level. In 2018, the WI started at a similar level as in 2017, showing a slight increase from 225 DAS to 240 DAS. Towards the end of the vegetation period, the WI was on a much lower level, yet still slightly higher than in the previous year. The order of varieties was the same with German lines having the highest WI and Eastern European lines the lowest. The measurements of 2019 started with higher WI values than in the past years. At the beginning of measurements until 230 DAS, Eastern European lines had higher WI in the irrigated plots. After 230 DAS, German hybrids showed highest WI in both, the irrigated and the drought stress trial.

The biggest differences in 2019 contrasting with 2017 and 2018 were two peaks of WI, visible in (Figure 13E-F). From 244-247 DAS (June 9-12, 2019) the irrigated plots showed an increase of WI, whilst the plots under drought stress did not. After a fast decrease of the irrigated plots, WI was on the same level for all plots on 249 DAS (June 14, 2019). The second peak was measured on 253 DAS (June 18, 2019). Thereby all plots showed an increase in WI. After these events, the WI of irrigated plots was below the drought stress plots at most measurement days.

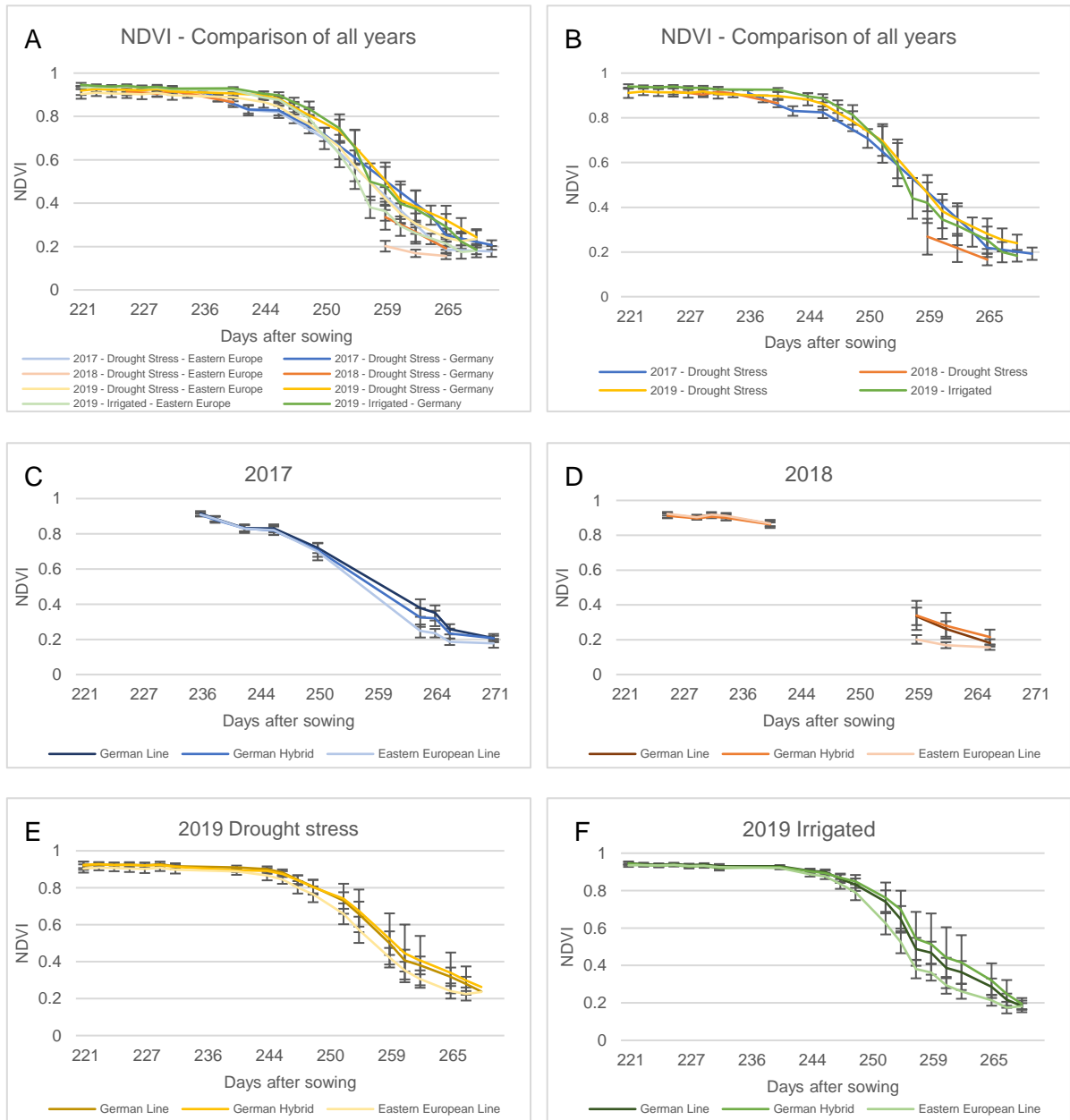


Figure 12 Time shift of NDVI measurements (HandySpec) between May and July of all experimental years.

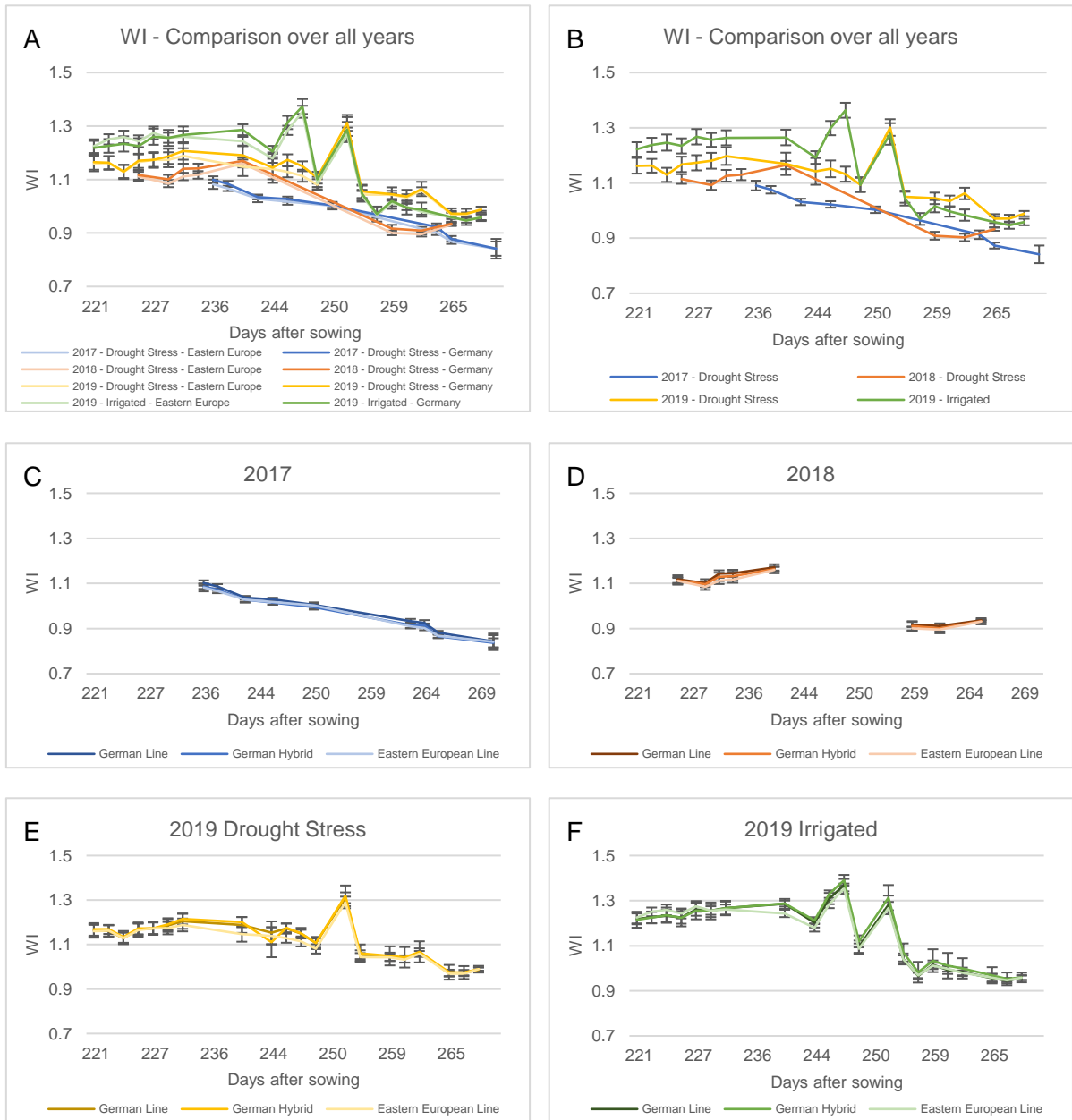


Figure 13 Time shift of WI measurements (HandySpec) between May and July of all experimental years.

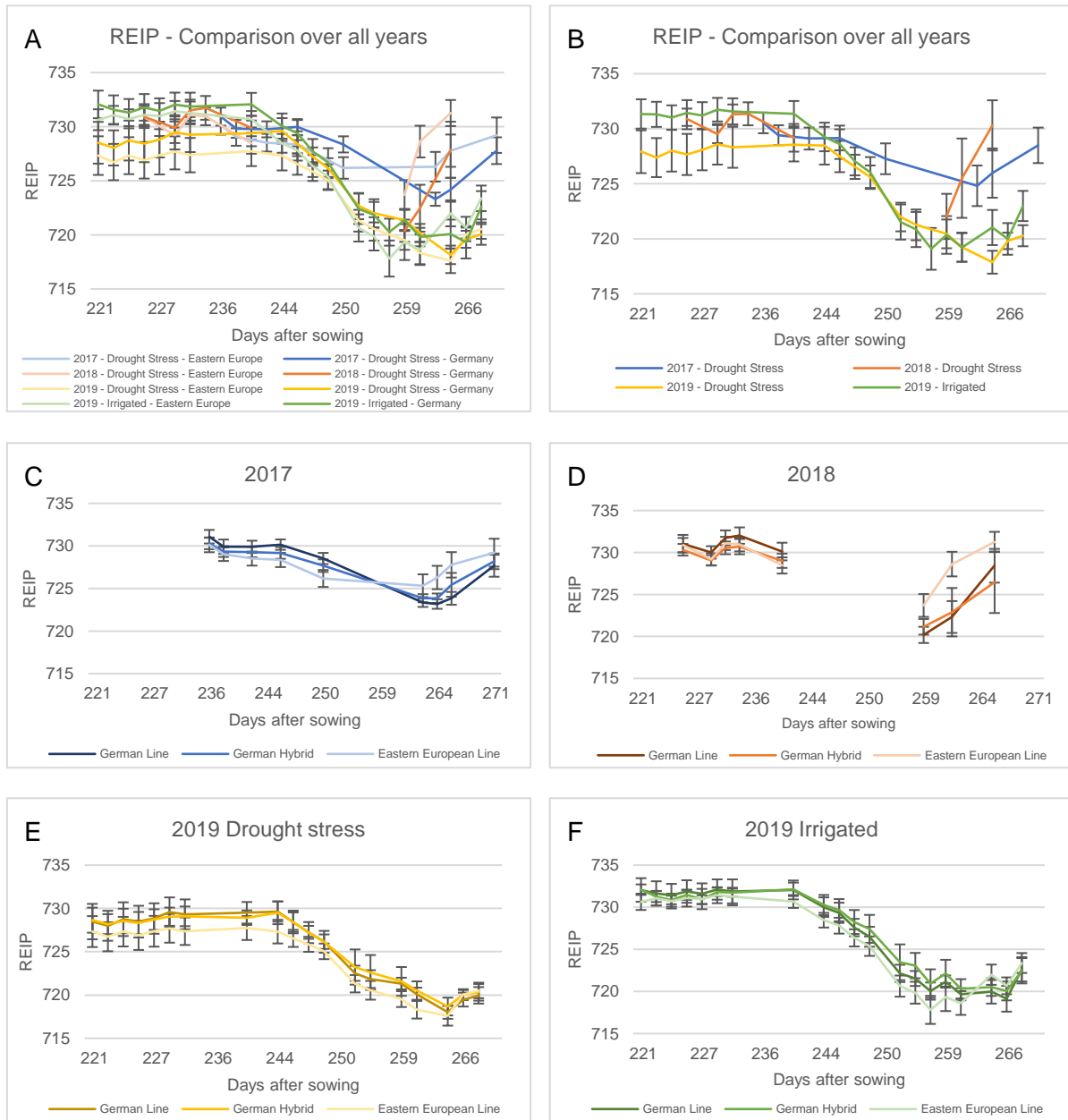


Figure 14 Time shift of REIP measurements (HandySpec) between May and July of all experimental years.

In Figure 14, it is visible that the REIP index stayed stable until 240 DAS in all years. At the beginning of the measurements, the highest values were found for German lines, followed by hybrids and Eastern European lines. After ca. 240-244 DAS, the REIP values started to decrease. In both trials of 2019, the hybrids then had higher values than all line varieties. In 2017 and 2018, German lines tended to have a higher REIP index, however due to only little available data, these findings should be considered with caution. The difference between German and Eastern European varieties was biggest in the drought stress plots of 2019, with Eastern European having significantly lower REIP than German varieties at most of the measuring days. In the irrigated plots, the

difference between origins was smaller but the order was the same as observed for the drought stressed plots.

Figure 15 shows the canopy temperature across time. It is clearly visible that the canopy temperature increased during the vegetation period but was sensitive to short-term changes due to precipitation or lower air temperature. In all years, the three groups of origin were very similar in temperature. In 2017, at all days of measurement the German lines tended to have the highest canopy temperature, whereas the Eastern European lines were lowest. The same trend was found in 2018 until ca. 246 DAS. Towards the end of the vegetation period, the Eastern European varieties showed a higher canopy temperature. The most striking difference between the two trials in 2019 was a strong increase in temperature of the drought stressed plots at 251 DAS, followed by a decrease towards 255 DAS. This change was found for all varieties. In irrigated plots, the German lines did not show such changes at all, they indicated a constant increase in temperature during these days. The temperature of Eastern European varieties increased more at 251 DAS, the growth flattened towards 255 DAS. However, the temperature did not decrease, as it was the case for non-irrigated plots.

Detailed data, corresponding to the Figures 12-15, can be found in the Tables 33-36 (Appendix).

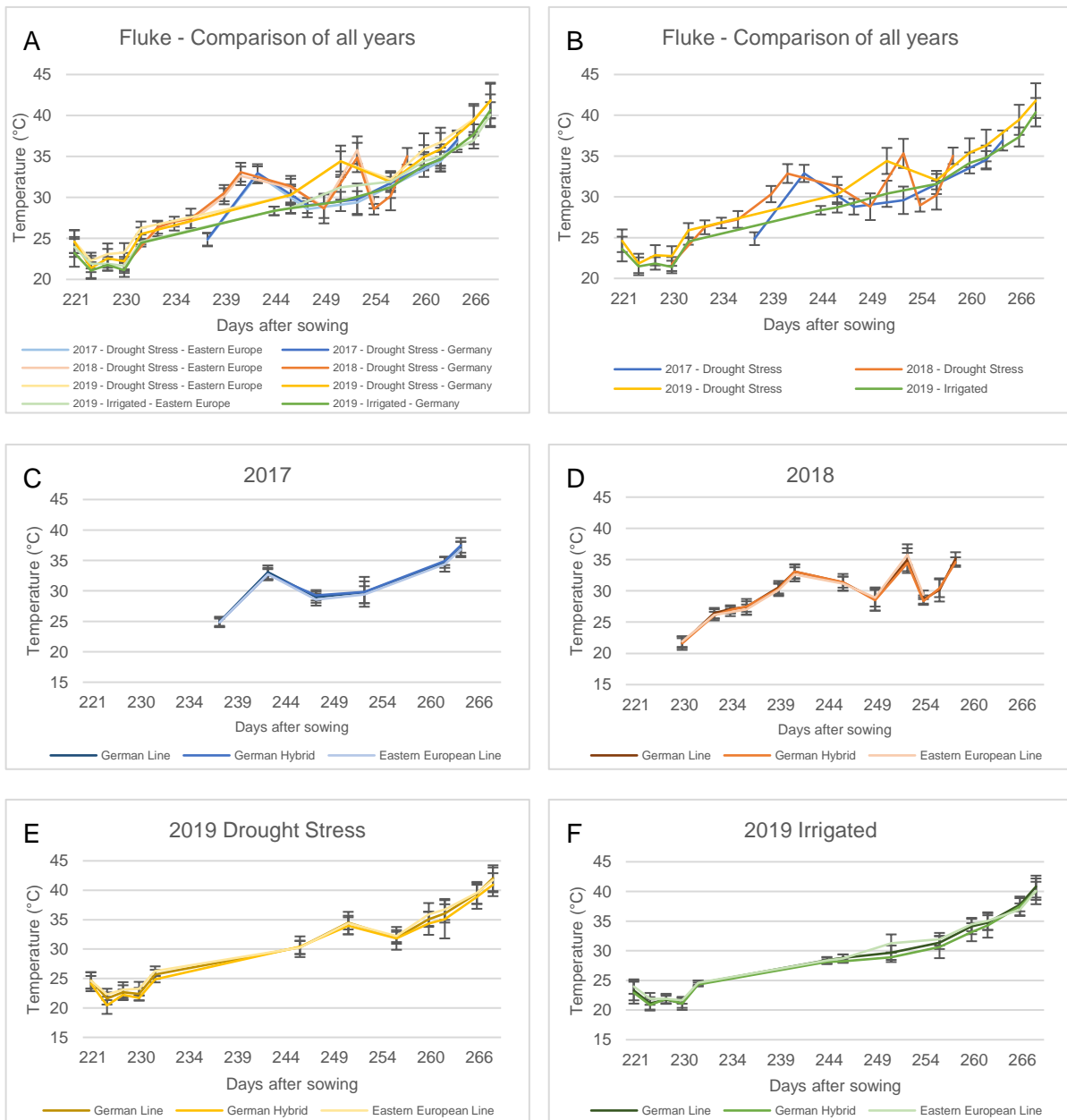


Figure 15 Time shift of the canopy temperature measured with the handheld thermal camera between May and July of all experimental years.

4.3.2. Comparison of measurements: Origin and irrigation

Figure 16 shows the chronological sequences of the spectral indices NDVI, WI and REIP and the temperature derived from the handheld Fluke camera in the year 2019 in order to point out differences between the varieties depending on origin and irrigation. All numeric data can be found in Table 37 (Appendix).

The NDVI (Figure 16A) showed only small differences until mid-June. It is visible that German varieties with irrigation (yellow) tended to have higher NDVI's, whereas Eastern

European lines under drought (blue) showed the lowest NDVI values. After 249 DAS (June 14 2019), the NDVI decreased in all plots. Until 267 DAS (July 2 2019), German varieties showed higher NDVI's than Eastern European ones. From 249-259 DAS (June 14 to 24), irrigated plots had a higher NDVI than drought stress plots. After 259 DAS (June 24), German varieties under drought (grey) showed the highest NDVI values of all plots. The values of Eastern European lines decreased earlier and faster, i.e. they became senescent earlier than German varieties. At most days the irrigated plots with Eastern European lines (orange) showed lowest the NDVI values of all plots. Towards the end of the vegetation period, the difference between German and Eastern European varieties and between irrigated and drought stress treatments became smaller.

Differences in the spectral index WI were much more distinct between drought stress and irrigated plots than between the groups of origin (Figure 16B). Between 221-247 DAS (May 17-June 12, 2019), the irrigated plots showed a significantly higher WI than plots under drought stress. The difference between origins was not at all days significant. After the two peaks of WI-values, following precipitation events as mentioned above (Figure 13), the drought stressed plots maintained higher WI-values than irrigated plots, while the difference between the irrigation treatments became smaller. Over all, it is noticeable that the WI in irrigated plots showed a higher variability between the start of the measurements and harvest than in non-irrigated plots.

Figure 16C shows the temporal development of the REIP. Until 240 DAS (June 5, 2019), the irrigated plots had higher REIP values than plots under drought. In both treatments, German varieties showed higher REIP than Eastern European lines. After 244 DAS (June 9, 2019), the highest REIP values were measured for German varieties, both in irrigated and under drought stressed treatments. In the beginning of the measurements, the difference was detectable between irrigated and non-irrigated plots, whereas towards the end of the vegetation period, the difference arose from the origin of varieties.

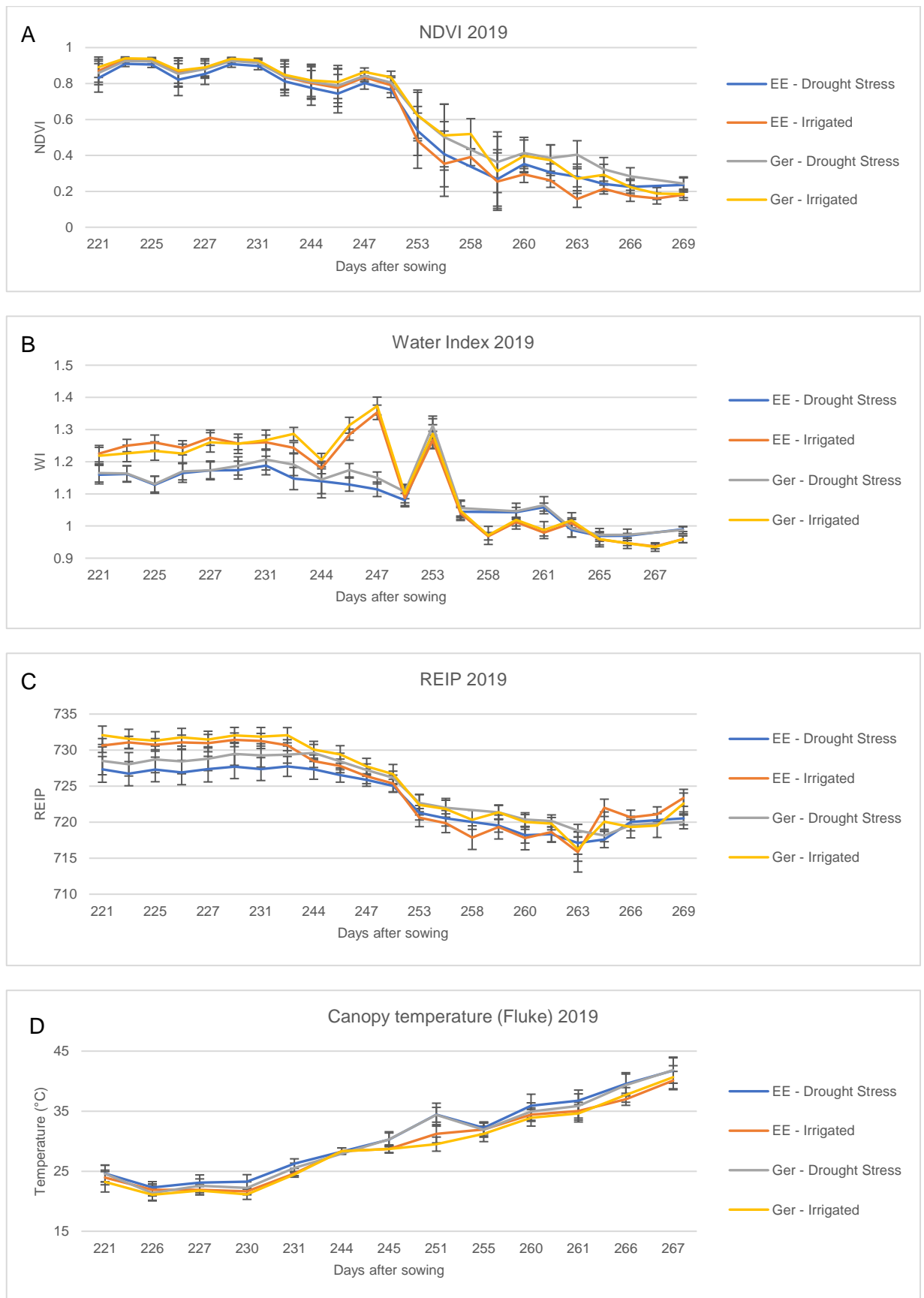


Figure 16 NDVI (A), WI (B) and REIP (C) calculated from HandySpec data and canopy temperature (D) from the handheld thermal camera of 2019, comparing the drought stressed and the irrigated plots. EE: Eastern European varieties, Ger: German varieties.

The canopy temperature (CT) of drought stress plots was always high than of irrigated plots (Figure 16D). From 221 DAS (May 17, 2019) to 230 DAS (May 26, 2019), the temperature of all plots remained at a similar level. Afterwards, CT of all plots started to increase. Drought stressed plots showed a strong increase in CT between 245 and 251 DAS, leading to the biggest difference between irrigated and non-irrigated plots at 251 DAS (June 16, 2019). Thereafter, the temperature in drought stress plots decreased to a similar level as in irrigated plots (255 DAS, June 20, 2019). From this day until harvest, the temperature in all plots increased steadily, while irrigated plots showed significantly lower CT than plots under drought stress. The difference between the two groups of origin (varieties from Germany or from Eastern European countries, respectively) was not at all days significant (cf. Table 37, appendix) but in most cases the Eastern European lines showed higher CT than German varieties. Towards the end of growing season after 266 DAS, German varieties showed higher CT than Eastern European lines.

4.3.3. Comparison of measurements: Drone vs. handheld

In Figure 17, the comparison between handheld and airborne measurements is shown. Detailed data is provided in Table 38 (appendix). The graphs include average data of all plots of 2019, separated by irrigation. Temperature and NDVI measurements showed lower values for the drone. The temperature data Figure 17A was very similar for both sensors and both trials until 241 DAS (June 6, 2019). From 241 to 244 DAS (June 6-9, 2019), the data of the drone based DuetT thermal camera decreased in the irrigated and non-irrigated plots. This change was not visible in the data of the handheld camera Fluke. After June 9 (244 DAS), the sensors showed a similar development of the canopy temperature, however on a different level. The lines in Figure 17A run almost parallel with the drone data being significantly lower at all measuring days. In addition, the irrigated plots showed lower canopy temperature than plots under drought stress. On 251 DAS (June 16, 2019), no data was collected with the drone, hence the increase in drought stressed plots recorded with the Fluke camera was not found with the DuetT sensor.

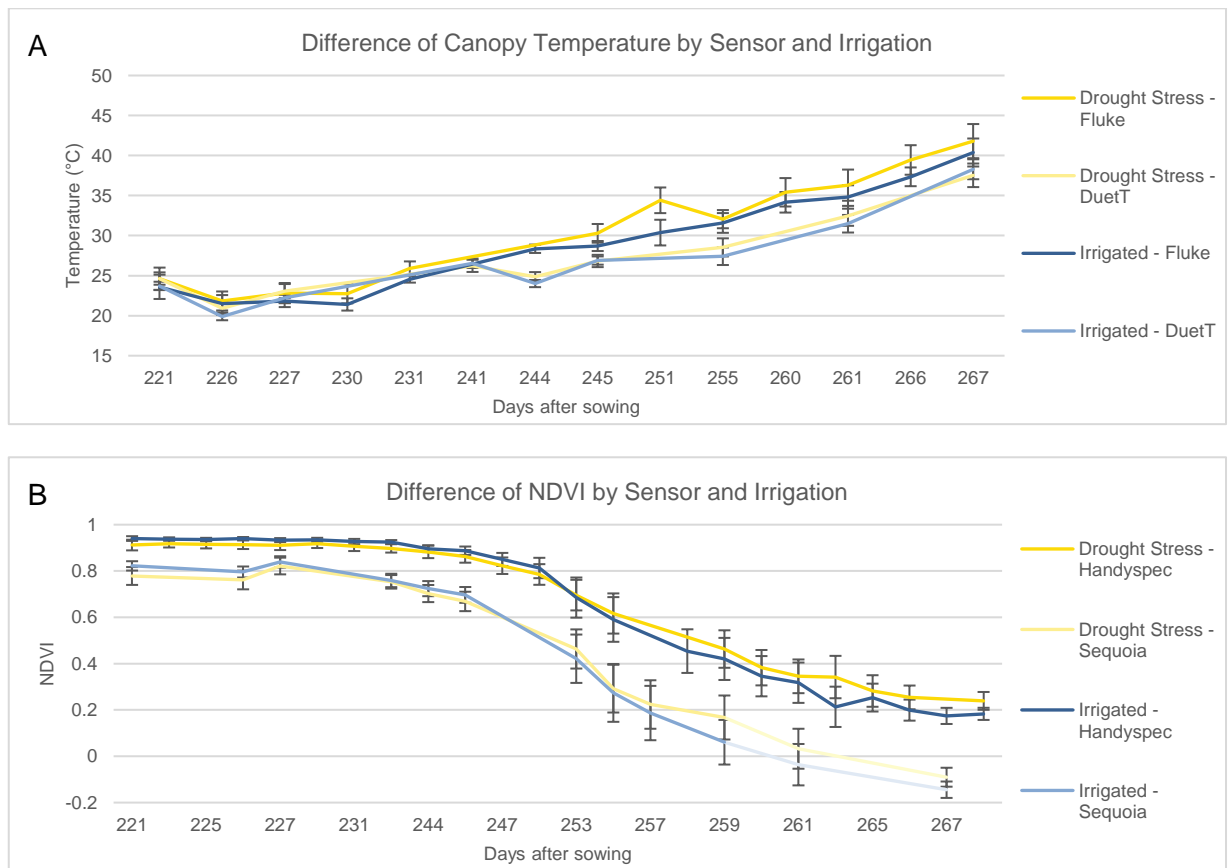


Figure 17 Comparison of handheld (Fluke/HandySpec) and aerial (DuetT/Sequoia) measurements of canopy temperature (A) and NDVI (B).

The NDVI (Figure 17B) of the drone obtained with Sequoia sensor was lower than the NDVI calculated from the HandySpec data at all measuring days. The data of the HandySpec was taken into account until the final harvest, as it did not show negative values, and decreased constantly until the end of the vegetation period. The drone data was only taken into account until 259 DAS (June 24, 2019), as later measurements resulted in negative NDVI values. Despite the negative values, the temporal course of the drone-derived data was similar to the one of terrestrial measurements (cf. Figure 17, pale yellow and blue lines after 259 DAS). For both sensors, the irrigated plots showed higher NDVI values until mid-June. After 253 DAS (June 18), both the Sequoia and HandySpec recorded higher NDVI's for plants under drought stress.

Although the absolute values of the data were found to differ between the sensors (cf. Figure 17), the correlation between airborne and handheld sensors was good throughout most of the vegetation period (Figure 18). The thermal cameras Fluke and DuetT showed only weak correlation values in May for the Eastern European lines under drought ($r=0.08$), German lines irrigated ($r=0.09$), and Eastern European lines irrigated ($r=0.13$). The correlation values increased quickly and reached the maximum in mid-

June for German hybrids under drought ($r=0.94$). The correlation of NDVI determined with HandySpec and Sequoia sensor was higher already at the beginning of the measurements in May. The difference between the three groups of varieties and between the irrigated and non-irrigated plots was much smaller than for the temperature correlations. On 227 DAS (May 23 2019), all correlations were between $r=0.66$ (German lines, irrigated) and $r=0.74$ (German hybrids, drought stress). They increased towards harvest and reached values between $r=0.84$ (Eastern European lines, irrigated) and $r=0.97$ (German hybrids, drought stress) at 255 DAS (June 20, 2019).

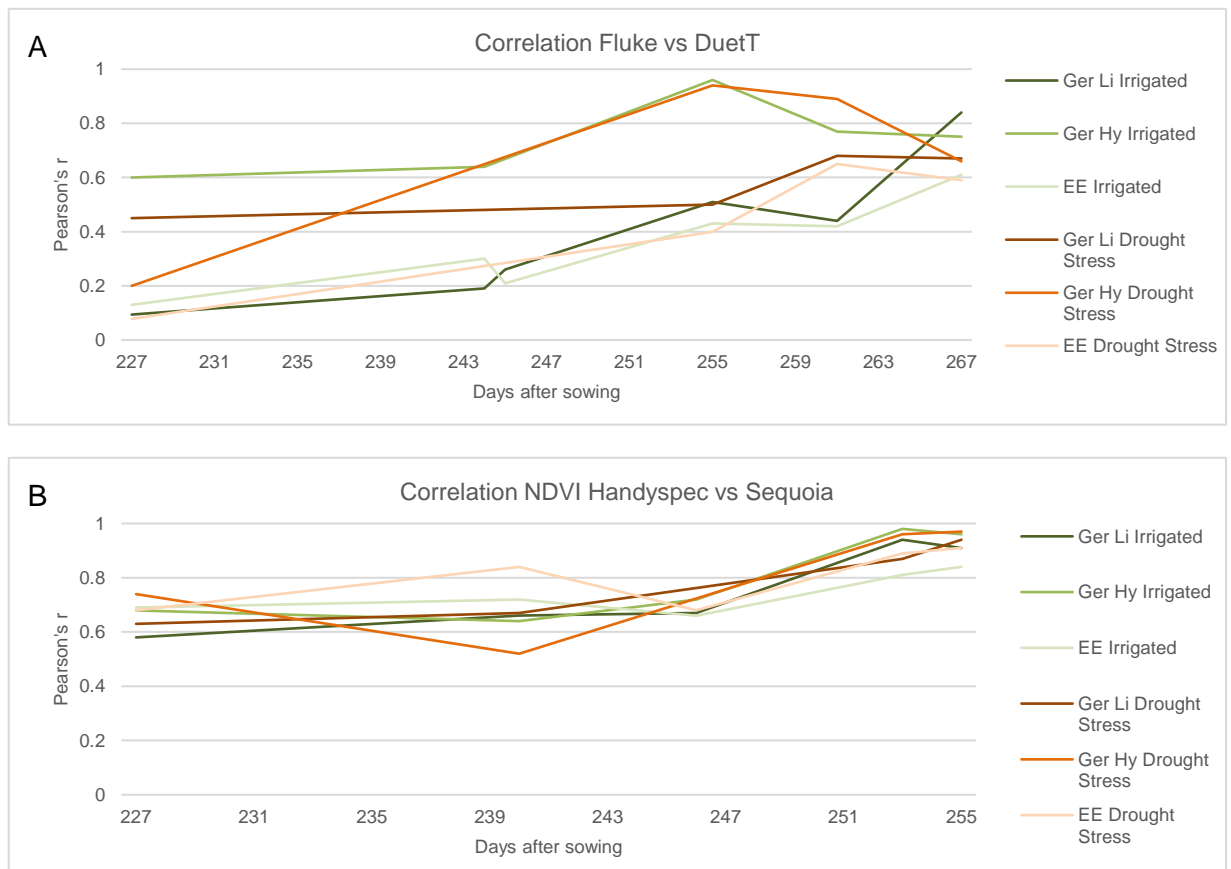
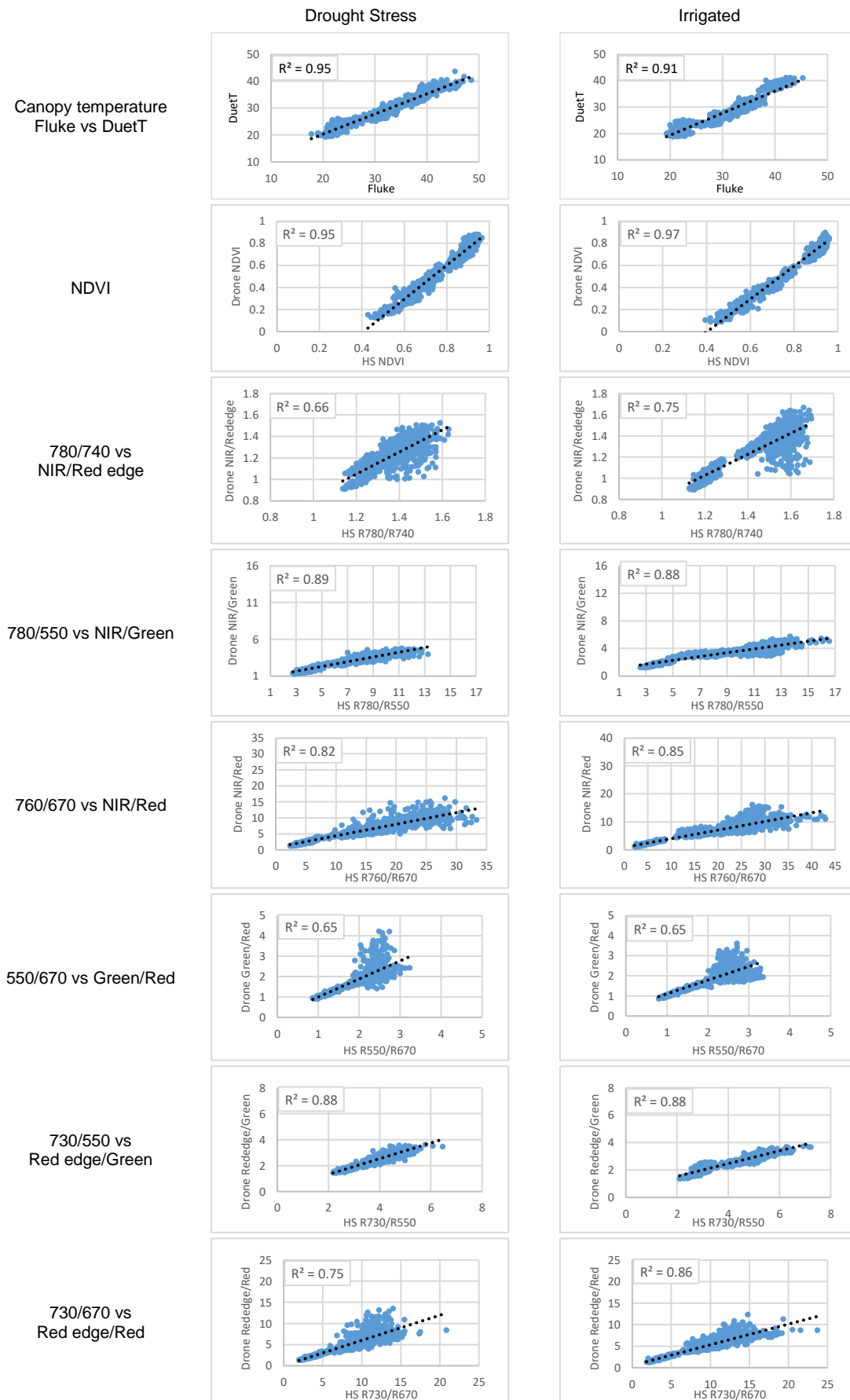


Figure 18 Time shift of correlation between handheld and aerial measurements of canopy temperature (A) and NDVI (B) from May to July 2019. Ger Li: German line varieties; Ger Hy: German hybrid varieties; EE: Eastern European varieties.

Table 22 Correlation canopy temperature, single ratio indices and NDVI between handheld and aerial measurements in drought stress and irrigated plots 2019.



The correlation between drone-based and equivalent terrestrial NDVI, single ratio indices, and canopy temperature are shown in Table 22. All varieties and all measuring days were included to determine the correlation, separated by irrigation treatment. All correlations were strong, ranging from $R^2=0.65$ (R_{550}/R_{670} vs Green/Red, drought stress) to $R^2=0.97$ (NDVI, irrigated).

4.3.4. Correlation of harvest parameters and spectral / thermal measurements

Correlations between thermal and spectral measurements and plant parameters at anthesis and milk ripeness are indicated in Table 23. For each year and trial, the correlations were calculated including all varieties. Spectral and thermal information was correlated with the harvest parameters, as well as the N content and N uptake of each specific plant sample. Dry weight, N content and N uptake were obtained for the total aboveground biomass at anthesis and milk ripeness. The plant samples at anthesis were taken on June 16, 2017 (252 DAS), June 1, 2018 (241 DAS), June 5, 2019 (240 DAS) in irrigated plots, and June 11, 2019 (246 DAS) in drought stress plots. Plant samples at milk ripeness were taken on June 27, 2017 (263 DAS), and June 20, 2018 (260 DAS). Correlations at milk ripeness in 2019 were calculated based on the data of Zadoks growth stages. Although no plant samples could have been cut, spectral and thermal data measured at respective days was correlated with the harvest parameters.

At anthesis, the correlations differed a lot between years. In 2017, grain yield, TGW, and HI showed significant negative correlation with the REIP index and three single-ratio indices (SR) calculated from the HandySpec data. The NWI 2 and 3 were significantly correlated with TGW. The thermal data from the Fluke handheld camera was not correlated with the harvest parameters. In 2018, WI and NWI 1-4 were highly correlated to yield. Correlations with other indices were not significant. TGW did not show significant correlation with any of the spectral and thermal data, whereas HI was correlated to REIP and two of the SR. In the drought stress trial of 2019, only thermal data from the handheld camera Fluke was significantly correlated to grain yield. Neither thermal data from the drone, nor any of the spectral indices showed any correlation. The grain yield of irrigated plots was significantly correlated to most of the indices of both, HandySpec and drone, but not to any thermal data. All indices were significantly correlated with TGW and HI of the drought stress trial in 2019, whereas thermal data was not. In the irrigated trial, significant correlation could be found for all data from the HandySpec, but only for a few indices of the drone. Thermal data from the drone was correlated with HI, other than the Fluke, which did not show significant coherence. For both trials in 2019, all significant correlations of yield, TGW and HI with NDVI, REIP, WI, and single ratios were negative,

whereas correlations with NWI 1-4 were always found to be positive. The number of grains per ear was only significantly correlated to NDVI (HandySpec) and few single ratios (SR) in the irrigated plots of 2019. Neither the drought stress trial, nor the previous years pointed out any correlation to spectral or thermal data. The number of tillers and ears per square meter was correlated to the NDVI and some SR's in 2017. No correlation was found in 2018. In 2019 however, all spectral and thermal measurements were significantly correlated in the drought stress plots. The irrigated plots showed correlation between the number of tillers and the NDVI and some SR's or the HandySpec. Whereas the number of ears was correlated to SR of the drone. Correlations with dry weight were found for NDVI and SR (HandySpec) in 2017, thermal data (Fluke) in 2019 in the drought stress plots, and REIP and SR (HandySpec) in the irrigated plots of 2019.

In 2017, the nitrogen content was significantly correlated to most of the spectral indices, but not to thermal data. N uptake was only correlated to REIP and the R_{780}/R_{740} -SR. In 2018, REIP, SR and Fluke were positively correlated to both, N content and uptake. Plots under drought stress of 2019 showed significant correlation between N content and all indices. N uptake was correlated to most HandySpec data, except to the water indices and to some of the drone-derived SR. In the irrigated plots, all indices from the HandySpec data were significantly correlated to both N content and N uptake. However, none of the drone SR's were found to be significant. Thermal measurements in 2019 were only significant for Fluke and N uptake (drought stress), and DuetT and N content (irrigated).

Table 23 Correlation of spectral indices and canopy temperature with harvest parameters, and with dry weight, N content and N uptake at anthesis and milk ripeness.

	Anthesis 2017																	
	Grain yield		TGW		HI		Grains per Ear		Tillers/m ²		Ears/m ²		DW anthesis		N content anthesis		N uptake anthesis	
	r	p	r	p	r	p	r	p	r	p	r	p	r	p	r	p	r	p
NDVI HS	-0.17		0.04		-0.02		0.08		-0.21	*	-0.21	*	-0.21	*	0.52	**	0.05	
REIP	-0.51	**	-0.52	**	-0.56	**	0.00		-0.07		-0.17		-0.21	*	0.71	**	0.21	*
WI	0.04		0.13		0.04		0.06		-0.09		-0.09		-0.03		0.26	**	0.04	
NWI 1	-0.04		-0.13		-0.04		-0.05		0.09		0.09		0.03		-0.26	**	-0.04	
NWI 2	-0.06		-0.23	*	-0.13		-0.08		0.13		0.11		0.04		-0.17		0.02	
NWI 3	-0.07		-0.19	*	-0.09		-0.06		0.09		0.08		0.02		-0.16		0.01	
NWI 4	0.00		-0.07		0.01		-0.04		0.07		0.08		0.04		-0.31	**	-0.06	
R760_R670	-0.13		0.10		0.05		0.11		-0.21	*	-0.21	*	-0.21	*	0.49	**	0.02	
R780_R740	-0.45	**	-0.44	**	-0.49	**	0.01		-0.09		-0.18	*	-0.22	*	0.73	**	0.19	*
R760_R730	-0.43	**	-0.31	**	-0.37	**	0.04		-0.15		-0.22	*	-0.26	**	0.72	**	0.14	
R780_R550	-0.31	**	-0.20	*	-0.22	*	0.06		-0.13		-0.17		-0.23	*	0.62	**	0.1	
Fluke	0.04		-0.03		-0.03		0.11		-0.10		-0.11		-0.04		0.13		0.06	

TGW: Thousand-grain weight, HI: Harvest Index, DW anthesis: Dry weight of above ground biomass at anthesis, N content anthesis: Nitrogen content of above ground biomass at anthesis, N uptake anthesis: Nitrogen uptake of above ground biomass at anthesis. All indices calculated from HandySpec data. Fluke: Canopy temperature from the Fluke camera.

r: Pearson correlation coefficient

Statistical significance as indicated by p-value: * p < 0.05, ** p < 0.01.

Table 23 (continued) Correlation of spectral indices and canopy temperature with harvest parameters, and with dry weight, N content and N uptake at anthesis and milk ripeness.

Anthesis 2018																		
	Grain yield		TGW		HI		Grains per Ear		Tillers/m ²		Ears/m ²		DW anthesis		N content anthesis		N uptake anthesis	
	r	p	r	p	r	p	r	p	r	p	r	p	r	p	r	p	r	p
NDVI HS	0.16		0.16		0.00		-0.08		-0.01		0.01		0.02		-0.1		-0.07	
REIP	0.12		-0.1		-0.25	**	0.02		-0.04		0.01		-0.00		0.54	**	0.37	**
WI	0.26	**	0.07		-0.15		-0.1		0.03		0.06		0.01		0.19	*	0.13	
NWI 1	-0.26	**	-0.07		0.15		0.10		-0.03		-0.06		-0.01		-0.19	*	-0.13	
NWI 2	-0.30	**	-0.15		0.10		0.10		-0.02		-0.04		-0.04		-0.11		-0.09	
NWI 3	-0.23	*	-0.04		0.17		0.10		-0.03		-0.07		-0.00		-0.21	*	-0.14	
NWI 4	-0.29	**	-0.11		0.13		0.11		-0.03		-0.06		-0.04		-0.15		-0.12	
R760_R670	0.14		0.15		-0.02		-0.09		-0.01		0.01		0.04		-0.11		-0.06	
R780_R740	0.15		-0.06		-0.22	*	0.02		-0.05		0.00		0.01		0.49	**	0.34	**
R760_R730	0.14		-0.03		-0.21	*	0.01		-0.05		-0.01		-0.00		0.43	**	0.29	**
R780_R550	0.12		0.08		-0.12		-0.06		-0.02		0.01		-0.03		0.1		0.04	
Fluke	0.05		-0.16		0.00		-0.03		0.09		0.13		-0.02		0.42	**	0.27	**

TGW: Thousand-grain weight, HI: Harvest Index, DW anthesis: Dry weight of above ground biomass at anthesis, N content anthesis: Nitrogen content of above ground biomass at anthesis, N uptake anthesis: Nitrogen uptake of above ground biomass at anthesis. All indices calculated from HandySpec data. Fluke: Canopy temperature from the Fluke camera.
r: Pearson correlation coefficient
Statistical significance as indicated by p-value: * p < 0.05, ** p < 0.01

Anthesis 2019 Drought Stress																		
	Grain yield		TGW		HI		Grains per Ear		Tillers/m ²		Ears/m ²		DW anthesis		N content anthesis		N uptake anthesis	
	r	p	r	p	r	p	r	p	r	p	r	p	r	p	r	p	r	p
NDVI HS	-0.03		-0.41	**	-0.43	**	0.04		0.31	**	0.30	**	0.06		0.49	**	0.27	**
REIP	-0.02		-0.42	**	-0.46	**	0.03		0.31	**	0.29	**	0.06		0.53	**	0.26	**
WI	-0.05		-0.53	**	-0.51	**	0.02		0.29	**	0.28	**	-0.01		0.58	**	0.18	
NWI 1	0.05		0.53	**	0.51	**	-0.02		-0.29	**	-0.28	**	0.01		-0.58	**	-0.18	
NWI 2	0.03		0.51	**	0.49	**	-0.01		-0.26	**	-0.26	**	0.03		-0.55	**	-0.14	
NWI 3	0.06		0.54	**	0.51	**	-0.03		-0.30	**	-0.29	**	0.00		-0.59	**	-0.19	*
NWI 4	0.03		0.51	**	0.50	**	-0.02		-0.29	**	-0.27	**	0.02		-0.56	**	-0.16	
R760_R670	-0.10		-0.44	**	-0.46	**	0.00		0.30	**	0.28	**	0.05		0.53	**	0.27	**
R780_R740	-0.01		-0.42	**	-0.45	**	0.04		0.32	**	0.31	**	0.08		0.52	**	0.28	**
R760_R730	-0.04		-0.42	**	-0.46	**	0.01		0.29	**	0.28	**	0.04		0.53	**	0.25	**
R780_R550	-0.06		-0.36	**	-0.40	**	0.01		0.27	**	0.26	**	0.07		0.47	**	0.27	**
NDVI eBee	-0.05		-0.5	**	-0.51	**	-0.02		0.31	**	0.30	**	0.00		0.46	**	0.16	
Green - red	-0.14		-0.52	**	-0.52	**	-0.07		0.25	**	0.25	**	-0.10		0.45	**	0.06	
Red edge -green	-0.05		-0.39	**	-0.40	**	-0.02		0.25	**	0.25	**	0.05		0.31	**	0.16	
NIR - green	-0.03		-0.48	**	-0.49	**	-0.01		0.32	**	0.31	**	0.06		0.44	**	0.20	*
Red edge - red	-0.10		-0.47	**	-0.48	**	-0.05		0.26	**	0.26	**	-0.03		0.40	**	0.12	
NIR - red	-0.08		-0.51	**	-0.52	**	-0.04		0.30	**	0.29	**	0.00		0.47	**	0.15	
NIR - red edge	0.01		-0.50	**	-0.52	**	0.01		0.34	**	0.33	**	0.06		0.53	**	0.21	*
Fluke	-0.29	*	-0.12		-0.07		-0.01		-0.20	*	-0.21	*	-0.24	*	0.11		-0.25	*
DuetT	-0.11		0.13		0.12		-0.08		-0.19	*	-0.21	*	-0.09		-0.09		-0.13	

TGW: Thousand-grain weight, HI: Harvest Index, DW anthesis: Dry weight of above ground biomass at anthesis, N content anthesis: Nitrogen content of above ground biomass at anthesis, N uptake anthesis: Nitrogen uptake of above ground biomass at anthesis. NDVI HS - R780_R550: Indices from HandySpec data. NDVI eBee - NIR-red edge: Indices derived from Sequoia data. Fluke: Canopy temperature from the Fluke camera, DuetT: Canopy temperature from the DuetT camera.
r: Pearson correlation coefficient
Statistical significance as indicated by p-value: * p < 0.05, ** p < 0.01

Table 23 (continued) Correlation of spectral indices and canopy temperature with harvest parameters, and with dry weight, N content and N uptake at anthesis and milk ripeness.

Anthesis 2019 Irrigated																		
	Grain yield		TGW		HI		Grains per Ear		Tillers/ m ²		Ears/ m ²		DW anthesis		N content anthesis		N uptake anthesis	
	r	p	r	p	r	p	r	p	r	p	r	p	r	p	r	p	r	p
NDVI HS	-0.33	**	-0.45	**	-0.50	**	-0.23	*	0.29	**	0.16		0.13		0.42	**	0.29	**
REIP	-0.22	*	-0.47	**	-0.51	**	-0.12		0.18		0.10		0.23	*	0.51	**	0.42	**
WI	-0.33	**	-0.55	**	-0.57	**	-0.02		0.13		0.05		0.16		0.56	**	0.40	**
NWI 1	0.33	**	0.55	**	0.57	**	0.02		-0.14		-0.05		-0.16		-0.56	**	-0.40	**
NWI 2	0.33	**	0.53	**	0.56	**	0.03		-0.14		-0.05		-0.16		-0.54	**	-0.39	**
NWI 3	0.32	**	0.56	**	0.57	**	0.02		-0.14		-0.06		-0.17		-0.56	**	-0.40	**
NWI 4	0.32	**	0.54	**	0.56	**	0.03		-0.14		-0.06		-0.17		-0.54	**	-0.39	**
R760_R670	-0.32	**	-0.42	**	-0.46	**	-0.21	*	0.27	**	0.14		0.11		0.43	**	0.27	**
R780_R740	-0.23	*	-0.48	**	-0.52	**	-0.12	*	0.19	*	0.11		0.23	*	0.51	**	0.42	**
R760_R730	-0.24	*	-0.45	**	-0.49	**	-0.15		0.19	*	0.11		0.21	*	0.49	**	0.40	**
R780_R550	-0.20	*	-0.34	**	-0.39	**	-0.20		0.20	*	0.12		0.19	*	0.36	**	0.34	**
NDVI eBee	-0.40	**	-0.14	*	-0.21	*	-0.20		0.17		0.18		-0.08		-0.01		-0.07	
Green - red	-0.32	**	-0.17	*	-0.20		-0.03		0.01		-0.05		-0.03		0.14		0.04	
Red edge -green	-0.03		0.09		0.04		-0.03		0.13		0.10		-0.06		0.01		-0.05	
NIR - green	-0.18		-0.02		-0.05		-0.22	*	0.18		0.23	*	-0.08		-0.13		-0.13	
Red edge - red	-0.29	**	-0.10		-0.14		-0.04		0.06		0.00		-0.06		0.12		0.00	
NIR - red	-0.39	**	-0.12	*	-0.19		-0.21	*	0.17		0.17		-0.09		-0.01		-0.08	
NIR - red edge	-0.20		-0.03		-0.08		-0.23	*	0.14		0.22	*	-0.07		-0.15		-0.12	
Fluke	-0.02		-0.06		0.12		0.12		-0.14		-0.18		-0.09		0.05		-0.05	
DuetT	0.08		0.17		0.27	**	0.15		-0.12		-0.11		-0.04		-0.25	**	-0.16	

TGW: Thousand-grain weight, HI: Harvest Index, DW anthesis: Dry weight of above ground biomass at anthesis, N content anthesis: Nitrogen content of above ground biomass at anthesis, N uptake anthesis: Nitrogen uptake of above ground biomass at anthesis. NDVI HS - R780_R550: Indices from HandySpec data. NDVI eBee - NIR-red edge: Indices derived from Sequoia data. Fluke: Canopy temperature from the Fluke camera, DuetT: Canopy temperature from the DuetT camera. r: Pearson correlation coefficient

Statistical significance as indicated by p-value: * p < 0.05, ** p < 0.01

Milk ripeness 2017																		
	Grain yield		TGW		HI		Grains per Ear		Tillers/ m ²		Ears/ m ²		DW milk ripe		N content milk ripe		N uptake milk ripe	
	r	p	r	p	r	p	r	p	r	p	r	p	r	p	r	p	r	p
NDVI HS	-0.66	**	-0.42	**	-0.60	**	-0.20	*	-0.08		-0.20	*	-0.01		0.50	**	0.26	*
REIP	0.56	**	0.33	**	0.33	**	-0.07		0.23	*	0.27	**	-0.02		-0.33	**	-0.20	*
WI	-0.55	**	-0.32	**	-0.50	**	-0.14		-0.08		-0.21	*	-0.03		0.40	**	0.18	
NWI 1	0.55	**	0.32	**	0.50	**	0.13		0.08		0.21	*	0.03		-0.40	**	-0.18	
NWI 2	0.55	**	0.26	**	0.45	**	0.11		0.10		0.22	*	0.03		-0.37	**	-0.17	
NWI 3	0.53	**	0.28	**	0.47	**	0.12		0.08		0.21	*	0.03		-0.37	**	-0.16	
NWI 4	0.56	**	0.34	**	0.51	**	0.15		0.08		0.21	*	0.02		-0.40	**	-0.20	*
R760_R670	-0.64	**	-0.39	**	-0.58	**	-0.22	*	-0.08		-0.20	*	-0.01		0.50	**	0.26	*
R780_R740	-0.57	**	-0.41	**	-0.65	**	-0.31	**	0.00		-0.13		-0.02		0.47	**	0.23	*
R760_R730	-0.62	**	-0.39	**	-0.60	**	-0.25	*	-0.05		-0.18		-0.02		0.50	**	0.25	*
R780_R550	-0.46	**	-0.32	**	-0.58	**	-0.32	**	0.02		-0.08		-0.01		0.36	**	0.18	
Fluke	-0.11	**	0.03		0.10		0.14		-0.26	**	-0.28	**	-0.07		0.39	**	0.16	

TGW: Thousand-grain weight, HI: Harvest Index, DW milk ripe: Dry weight of above ground biomass at milk ripeness, N content milk ripe: Nitrogen content of above ground biomass at milk ripeness, N uptake milk ripe: Nitrogen uptake of above ground biomass at milk ripeness. All indices calculated from HandySpec data. Fluke: Canopy temperature from the Fluke camera.

r: Pearson correlation coefficient

Statistical significance as indicated by p-value: * p < 0.05, ** p < 0.01

Table 23 (continued) Correlation of spectral indices and canopy temperature with harvest parameters, and with dry weight, N content and N uptake at anthesis and milk ripeness.

Milk ripeness 2018																		
	Grain yield		TGW		HI		Grains per Ear		Tillers/m ²		Ears/m ²		DW milk ripe		N content milk ripe		N uptake milk ripe	
	r	p	r	p	r	p	r	p	r	p	r	p	r	p	r	p	r	p
NDVI HS	-0.38	**	-0.43	**	-0.64	**	-0.15		0.09		0.09		-0.13		-0.14		-0.18	*
REIP	0.30	**	0.39	**	0.55	**	0.16		-0.11		-0.11		0.09		0.06		0.09	
WI	-0.37	**	-0.27	**	-0.61	**	-0.17		0.02		-0.02		-0.13		-0.07		-0.13	
NWI 1	0.36	**	0.27	**	0.61	**	0.17		-0.03		0.02		0.13		0.07		0.13	
NWI 2	0.35	**	0.22	*	0.54	**	0.14		0.00		0.06		0.12		0.02		0.1	
NWI 3	0.36	**	0.29	**	0.62	**	0.19	*	-0.04		-0.01		0.13		0.08		0.14	
NWI 4	0.35	**	0.24	**	0.58	**	0.17		-0.01		0.04		0.11		0.05		0.11	
R760_R670	-0.4	**	-0.42	**	-0.64	**	-0.15		0.07		0.07		-0.13		-0.13		-0.18	*
R780_R740	-0.27	**	-0.35	**	-0.56	**	-0.15		0.08		0.10		-0.08		-0.2	*	-0.19	*
R760_R730	-0.37	**	-0.40	**	-0.62	**	-0.14		0.07		0.07		-0.14		-0.15		-0.2	*
R780_R550	-0.31	**	-0.38	**	-0.6	**	-0.17		0.10		0.11		-0.07		-0.23	*	-0.18	*
Fluke	0.10		0.37	**	0.34	**	0.00		-0.01		-0.05		-0.14		-0.1		-0.14	

TGW: Thousand-grain weight, HI: Harvest Index, DW milk ripe: Dry weight of above ground biomass at milk ripeness, N content milk ripe: Nitrogen content of above ground biomass at milk ripeness, N uptake milk ripe: Nitrogen uptake of above ground biomass at milk ripeness. All indices calculated from HandySpec data. Fluke: Canopy temperature from the Fluke camera.

r: Pearson correlation coefficient

Statistical significance as indicated by p-value: * p < 0.05, ** p < 0.01

Milk ripeness 2019 Drought Stress												
	Yield		TGW		HI		Grains per Ear		Tillers/m ²		Ears/m ²	
	r	p	r	p	r	p	r	p	r	p	r	p
NDVI HS	0.04		-0.26	*	-0.33	**	0.01		0.07		0.08	
REIP	-0.07		-0.44	**	-0.50	**	-0.02		0.21	*	0.18	*
WI	0.37	**	0.26	*	0.20		0.07		-0.08		-0.07	
NWI 1	-0.37	**	-0.27	*	-0.20		-0.07		0.08		0.07	
NWI 2	-0.45	**	-0.41	**	-0.36	**	-0.10		0.10		0.10	
NWI 3	-0.43	**	-0.35	**	-0.28	**	-0.09		0.05		0.05	
NWI 4	-0.30	**	-0.15		-0.08		-0.04		0.06		0.05	
R760_R670	-0.20		-0.34	**	-0.39	**	-0.12		0.10		0.09	
R780_R740	0.05		-0.34	**	-0.42	**	0.02		0.19	*	0.18	*
R760_R730	0.10		-0.28	**	-0.35	**	0.04		0.13		0.13	
R780_R550	0.13		-0.21	*	-0.29	**	0.06		0.12		0.12	
NDVI eBee	0.04		-0.34	**	-0.37	**	0.02		0.09		0.10	
Green - red	0.05		-0.23	*	-0.26	**	0.01		0.03		0.03	
Red edge - green	0.03		-0.21	*	-0.27	**	0.00		0.06		0.07	
NIR -green	0.02		-0.31	**	-0.38	**	0.01		0.13		0.14	
Red edge-red	0.08		-0.23	*	-0.29	**	0.03		0.06		0.06	
NIR -red	0.08		-0.27	**	-0.33	**	0.04		0.10		0.10	
NIR-red edge	-0.04		-0.46	**	-0.51	**	-0.02		0.23	*	0.22	*
Fluke	-0.33	**	0.04		0.15		-0.14		-0.36	**	-0.35	**
DuetT	-0.27	**	0.13		0.20		-0.13		-0.37	**	-0.37	**

TGW: Thousand-grain weight, HI: Harvest Index. NDVI HS - R780_R550: Indices from HandySpec data. NDVI eBee - NIR-red edge: Indices derived from Sequoia data. Fluke: Canopy temperature from the Fluke camera, DuetT: Canopy temperature from the DuetT camera.

r: Pearson correlation coefficient

Statistical significance as indicated by p-value: * p < 0.05, ** p < 0.01

Table 23 (continued) Correlation of spectral indices and canopy temperature with harvest parameters, and with dry weight, N content and N uptake at anthesis and milk ripeness.

	Milk ripeness 2019 Irrigated											
	Yield		TGW		HI		Grains per Ear		Tillers/m ²		Ears/m ²	
	r	p	r	p	r	p	r	p	r	p	r	p
NDVI HS	-0.14		-0.34	**	-0.34	**	0.02		0.15		0.10	
REIP	-0.15		-0.34	**	-0.26	*	0.11		0.08		0.02	
WI	0.28	**	0.02		-0.02		0.00		0.15		0.20	*
NWI 1	-0.14		0.02		0.01		0.05		-0.17		-0.22	*
NWI 2	-0.37	**	-0.20		-0.14		0.06		-0.17		-0.25	**
NWI 3	-0.26	*	-0.14		-0.12		0.06		-0.18	*	-0.26	**
NWI 4	-0.08		0.09		0.06		0.03		-0.16		-0.20	*
R760_R670	-0.42	**	-0.52	**	-0.46	**	-0.02		0.14		0.07	
R780_R740	-0.44	**	-0.52	**	-0.44	**	0.01		0.19	*	0.11	
R760_R730	-0.45	**	-0.55	**	-0.47	**	0.00		0.18		0.09	
R780_R550	-0.39	**	-0.41	**	-0.36	**	0.04		0.14		0.08	
NDVI eBee	-0.20		-0.45	**	-0.41	**	0.06		0.14		0.10	
Green - red	-0.31	**	-0.35	**	-0.39	**	-0.06		-0.18		-0.22	*
Red edge - green	-0.06		-0.24	*	-0.18		0.05		0.30	**	0.29	**
NIR-green	-0.21	*	-0.38	**	-0.28	**	0.04		0.34	**	0.30	**
Red edge-red	-0.44	**	-0.49	**	-0.44	**	-0.03		0.12		0.07	
NIR-red	-0.46	**	-0.54	**	-0.46	**	-0.01		0.15		0.10	
NIR-red edge	-0.14		-0.38	**	-0.32	**	0.07		0.21	*	0.16	
Fluke	0.02		0.15		0.22	*	-0.02		0.01		0.04	
DuetT	-0.14		-0.06		-0.02		-0.15		0.00		-0.03	

TGW: Thousand-grain weight, HI: Harvest Index. NDVI HS - R780_R550: Indices from HandySpec data. NDVI eBee - NIR-red edge: Indices derived from Sequoia data. Fluke: Canopy temperature from the Fluke camera, DuetT: Canopy temperature from the DuetT camera.

r: Pearson correlation coefficient

Statistical significance as indicated by p-value: * p < 0.05, ** p < 0.01

At milk ripeness, the data of 2017 and 2018 showed similar results, in general. For grain yield, TGW, and HI, a significant negative correlation with NDVI (HandySpec), WI and all SR of HandySpec was found. REIP and NWI 1-4 were significantly positive correlated to all three harvest parameters. The only exception was the correlation between NWI 2 and TGW, which was positive but not significant. Thermal measurements with the handheld Fluke camera were significantly negatively correlated to grain yield in 2017 and positively to TGW and HI in 2018. The numbers of grains per ear, tillers and ears per square meter and dry weight showed only a few significant correlations with the spectral indices, whereas in 2018 were even less found than in 2017. Tillers and ears per square meter were significantly negatively correlated with canopy temperature in 2017. In 2017, all spectral and thermal measurements were significantly correlated with the N content. The pattern of positive and negative correlation was opposite to the correlations between grain yield and remote measurements. NDVI, WI, SR of HandySpec and temperature (Fluke) were positively, REIP and NWI 1-4 were negatively correlated. N uptake of 2017 showed the same pattern as N content; however, fewer correlations were significant. In 2018, N content was correlated significantly only to two SR. Nitrogen uptake had significant correlations to the NDVI and some SR's.

The correlation of spectral and thermal data at milk ripeness to harvest parameters in 2019 was different from the previous years. In most cases, the correlation was weaker. Regarding spectral data, in both trials, the correlation between grain yield and NDVI or REIP, respectively, was not significant, whereas WI and grain yield showed a significant positive correlation. Drought stressed plots had no significant correlation of any SR with the grain yield, while in irrigated plots, most of the SR showed significant negative correlation. TGW and HI showed a similar pattern of correlations in both trials, whereas the correlations in the drought stress plots tended to be stronger. No significant relation with any spectral index was found for the number of grains per ear. Most correlations between tillers and ears per square meter and the indices were not significant. In irrigated plots, negative correlations were found for NWI 1-4 (HandySpec) and the Green-Red SR (drone) with tillers and ears per square meter, some of which were significant. Significant positive relation was detected between tillers and ears per square meter and the Red edge-green, and NIR-green SR. Thermal measurements were significantly negative correlated with grain yield, tillers and ears per square meter in drought stressed, but not in irrigated plots.

4.3.5. Rank sum of canopy temperature

The rank sum of the canopy temperature (Table 24) was calculated from data of the handheld Fluke, which was used in all years of the field trial. The ranking was done from coolest to highest temperature. The two lowest values of rank sum, i.e. coolest canopy temperature, were found for the German varieties *Hybery* (17) and *Impression* (20). Only one German lines (*Anapolis*) were ranked with a higher rank sum than the worst performing Eastern European lines (*Numitor*, *Semnal*). The difference of rank sum between Eastern European and German varieties is therefore much smaller than as indicated in the previous rank sum tables (cf. Tables 13, 14 and 18).

Table 24 Rank sum across all years of canopy temperature (CT) per variety. Sorted lowest to highest temperature within the groups of origin.

Rank Sum of Temperature Sum (Fluke)											
Variety	Origin	Breed	CT sum 2017	Rank 2017	CT sum 2018	Rank 2018	CT sum 2019 Drought stress	Rank 2019 Drought stress	CT sum 2019 Irrigated	Rank 2019 Irrigated	Rank sum CT
Meleag	EE	Line	207.84	2	283.68	4	335.27	14	313.40	2	22
Amor	EE	Line	207.77	1	286.52	8	330.59	6	316.43	7	22
Clasic	EE	Line	208.60	3	283.94	5	332.65	8	322.35	15	31
Talisman	EE	Line	212.48	11	284.95	6	340.60	22	319.56	13	52
Savant	EE	Line	210.43	6	288.19	12	331.30	7	327.49	30	55
Zisk	EE	Line	211.43	9	286.30	7	335.08	12	326.60	28	56
Kuialnik	EE	Line	213.04	12	289.62	17	335.23	13	322.47	16	58
FGmut 293	EE	Line	215.69	18	289.49	14	339.51	20	322.65	17	69
Ursita	EE	Line	214.71	16	289.64	19	338.20	18	323.57	20	73
Zagrava	EE	Line	214.00	15	288.60	13	340.60	21	325.56	25	74
Pajura	EE	Line	217.01	21	292.49	26	336.27	15	324.67	23	85
Acord	EE	Line	221.01	29	289.53	15	341.19	23	325.57	26	93
Zolotocolosa	EE	Line	215.99	19	292.07	24	346.21	30	323.69	21	94
Transitor	EE	Line	213.29	13	290.73	21	346.02	29	328.35	32	95
Rowina	EE	Line	218.84	27	294.32	30	337.03	17	323.84	22	96
Unitar	EE	Line	222.10	30	292.80	27	344.22	27	323.25	19	103
Numitor	EE	Line	218.49	26	291.13	22	349.97	32	326.13	27	107
Semnal	EE	Line	217.56	23	299.35	31	342.12	24	326.60	29	107
Hybery	Ger	Hybrid	213.38	14	282.04	1	314.64	1	304.35	1	17
Impression	Ger	Line	211.43	10	282.44	2	328.23	4	315.75	4	20
Discus	Ger	Line	210.64	7	287.05	10	326.89	3	317.58	10	30
Kerubino	Ger	Line	208.83	4	282.91	3	336.57	16	316.85	9	32
Mulan	Ger	Line	211.01	8	292.21	25	332.68	9	314.52	3	45
Hybred	Ger	Hybrid	216.75	20	289.64	18	325.92	2	315.91	5	45
Hyfi	Ger	Hybrid	214.95	17	289.60	16	329.58	5	316.64	8	46
Manager	Ger	Line	210.23	5	290.12	20	339.49	19	315.99	6	50
Elixer	Ger	Line	218.90	28	286.94	9	333.50	11	318.42	11	59
Genius	Ger	Line	217.14	22	293.99	29	333.12	10	318.57	12	73
Colonia	Ger	Line	217.97	24	288.02	11	346.46	31	320.27	14	80
Patras	Ger	Line	218.40	25	299.49	32	343.17	25	322.87	18	100
Hystar	Ger	Hybrid	222.71	31	292.00	23	343.68	26	325.16	24	104
Anapolis	Ger	Line	224.94	32	293.15	28	344.89	28	327.98	31	119

EE: Eastern European varieties, Ger: German varieties.

4.3.6. Comparison of rank sums

Table 25 Rank sums of grain yield, grain N uptake, CID, and canopy temperature, and average grain yield of each variety, sorted by the rank of grain yield.

Comparison of rank sums and average grain yield							
Variety	Origin	Breed	Rank sum Grain yield	Rank sum Grain N uptake	Rank sum CID	Rank sum Temperature sum	Average grain yield (t/ha) across three years
Ursita	EE	Line	23	35	13	73	7.11
Pajura	EE	Line	25	15	85	85	6.78
Zisk	EE	Line	25	35	65	56	6.81
Hyfi	Ger	Hybrid	35	66	48	46	6.61
Meleag	EE	Line	38	63	53	22	6.50
Rowina	EE	Line	40	28	62	96	6.43
Amor	EE	Line	41	32	56	22	6.20
Zolotocolosa	EE	Line	41	80	35	94	6.19
Unitar	EE	Line	44	39	35	103	6.58
Semnal	EE	Line	47	32	81	107	6.74
Transitor	EE	Line	49	68	56	95	6.09
Kuialnik	EE	Line	50	56	63	58	6.15
FGmut 293	EE	Line	53	32	51	69	6.05
Acord	EE	Line	56	57	51	93	6.01
Hybery	Ger	Hybrid	59	66	37	17	6.58
Clasic	EE	Line	60	67	53	31	6.05
Numitor	EE	Line	64	52	46	107	5.85
Mulan	Ger	Line	65	73	68	45	5.84
Elixer	Ger	Line	67	77	33	59	5.77
Talisman	EE	Line	74	66	25	52	5.69
Savant	EE	Line	78	65	54	55	5.70
Discus	Ger	Line	81	86	97	30	5.52
Colonia	Ger	Line	82	109	90	80	5.42
Genius	Ger	Line	87	47	114	73	5.56
Zagrava	EE	Line	88	84	56	74	5.35
Kerubino	Ger	Line	94	79	126	32	5.29
Patras	Ger	Line	95	83	110	100	5.34
Impression	Ger	Line	100	89	107	20	5.20
Hystar	Ger	Hybrid	100	111	61	104	5.32
Anapolis	Ger	Line	114	87	54	119	4.89
Manager	Ger	Line	114	120	114	50	4.95
Hybred	Ger	Hybrid	123	113	113	45	4.70

EE: Eastern European varieties, Ger: German varieties.

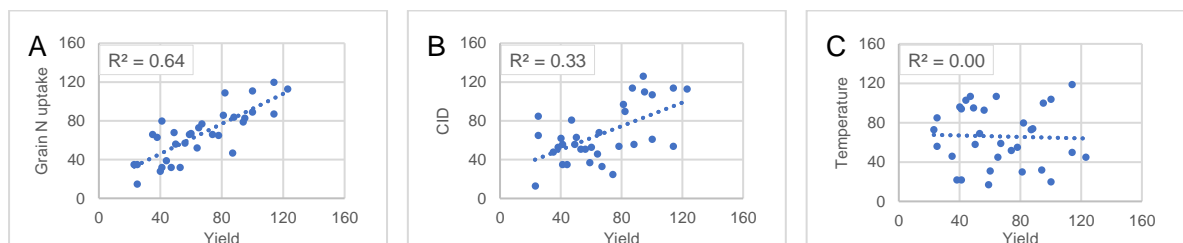


Figure 19 Correlation between the rank sum of grain yield and rank sums of grain N uptake (A), CID (B), and canopy temperature (C).

In Table 25, it is visible that rankings of grain N uptake and – to a lower extent – of CID were similar to the one of grain yield. The order of average grain yield was similar to the one of the rank sum of grain yield, with only a few exceptions, such as *Amor*, *Zolotocolosa* and *Hybery*. A high grain yield (low rank sum) was therefore often associated with a high grain N uptake and a high rate of CID. This can also be seen in the high coefficient of determination in Figure 19A and B for the correlation of rank sum of grain yield and grain N uptake ($R^2=0.64$), and grain CID ($R^2=0.33$), respectively. A strong relation between grain yield and canopy temperature could not be found. The pattern in Table 25 is very different for canopy temperature, the weak correlation in Figure 19C ($R^2=0.00$) underlines this result.

4.3.7. Heritability of spectral indices and canopy temperature

Heritability of canopy temperature and spectral indices is shown in Table 26. The canopy temperature, measured with the Fluke camera, resulted in higher heritability for German varieties than Eastern European lines in 2017 and 2018. In both trials of 2019, German hybrids showed a high heritability of canopy temperature, whereas German and Eastern European lines only showed low to moderate heritability (drought stress: $h^2=0.27-0.30$, irrigated: $h^2=0.66$). The same pattern was found for canopy temperature derived from the drone. However, heritability of the line varieties was higher than as calculated with the data of the Fluke camera (drought stress: $h^2=0.55-0.70$, irrigated: $h^2=0.59-0.88$). Heritability of spectral data was consistently high in irrigated plots of 2019 for all indices and all varieties – drought stress plots had slightly lower heritability for WI and REIP ($h^2=0.76-0.92$). In 2017 and 2018, no regularity could be found between the different groups of varieties. NDVI of HandySpec showed lower heritability in 2017 and 2018 than in both trials of 2019. The heritability of WI in Eastern European lines in 2018 ($h^2=0.13$) and of REIP in German hybrids 2017 ($h^2=0.07$) was low. Other varieties were considerably higher ($h^2=0.55-0.97$). Across all trials, canopy temperature, NDVI and WI showed a heritability of $h^2>0.5$.

Table 26 Heritability of canopy temperature and spectral indices.

			Heritability					
			Fluke	DuetT	NDVI HS	NDVI drone	WI	REIP
			h ²	h ²	h ²	h ²	h ²	h ²
2017	Drought stress	EE	0.85	-	0.63	-	0.55	0.89
		Ger Hy	0.97	-	0.76	-	0.77	0.07
		Ger Li	0.94	-	0.86	-	0.75	0.92
		All var	0.83	-	0.79	-	0.88	0.90
2018	Drought stress	EE	0.53	-	0.00	-	0.13	0.55
		Ger Hy	0.84	-	0.99	-	0.97	0.66
		Ger Li	0.94	-	0.33	-	0.64	0.91
		All var	0.80	-	0.43	-	0.69	0.89
2019	Drought stress	EE	0.30	0.70	0.89	0.95	0.82	0.66
		Ger Hy	0.90	0.90	1.00	0.99	0.92	0.76
		Ger Li	0.27	0.55	0.93	0.96	0.76	0.69
		All var	0.56	0.75	0.97	0.97	0.85	0.83
	Irrigated	EE	0.66	0.59	0.85	0.96	0.93	0.93
		Ger Hy	0.98	0.98	1.00	1.00	1.00	0.95
		Ger Li	0.66	0.88	0.97	0.96	0.95	0.96
		All var	0.84	0.76	0.97	0.98	0.95	0.96
Both trials	All var	0.31	0.56	0.84	0.96	0.50	0.44	
All years	All var	0.65	-	0.69	-	0.67	0.00	

h²: Heritability, EE: Eastern European varieties, Ger Hy: German hybrid varieties, Ger Li: German Line varieties, All var: All varieties

Fluke: Canopy temperature measured with handheld Fluke camera; DuetT: canopy temperature measured with drone-based DuetT camera; NDVI HS: NDVI calculated from HandySpec data; NDVI eBee: NDVI calculated from drone-based Sequoia sensor data; WI: Water index from HandySpec data; REIP: REIP index from HandySpec data

Table 27 shows the heritability of canopy temperature, NDVI, WI, and REIP for drought plots only. For canopy temperature and NDVI, the calculation of the heritability was only possible for terrestrial (i.e. handheld) measurements, as the drone was not used in the first and second year of field trial. Across all varieties, the temperature, NDVI, and WI showed very high heritability ($h^2=0.71-0.85$). Within the individual groups of origin, the German hybrids had the highest heritability for these three traits ($h^2=0.80-0.89$). The heritability of NDVI and WI were considerably lower for Eastern European and German lines ($h^2=0.42-0.52$). The heritability for REIP could only be calculated for German lines and showed a good result with $h^2=0.64$.

Table 27 Heritability of canopy temperature and spectral indices within drought stress plots only, across all years.

		Heritability			
		Fluke	NDVI HS	WI	REIP
		h ²	h ²	h ²	h ²
All years drought stress	EE	0.78	0.42	0.52	0.00
	Ger Hy	0.89	0.85	0.80	0.00
	Ger Li	0.75	0.46	0.44	0.64
	All var	0.71	0.85	0.75	0.00

Heritability, EE: Eastern European varieties, Ger Hy: German hybrid varieties, Ger Li: German Line varieties, All var: All varieties

Fluke: Canopy temperature measured with handheld Fluke camera; DuetT: canopy temperature measured with drone-based DuetT camera; NDVI HS: NDVI calculated from HandySpec data; NDVI eBee: NDVI calculated from drone-based Sequoia sensor

5. Discussion

5.1. Growth and development of wheat under abiotic stress

5.1.1. Influence of heat and drought on wheat phenology

Abiotic stress conditions reduce the duration of crop growth to maturity (Nahar et al., 2010). The three experimental years of this study differed substantially in timing and intensity of heat and drought stress. In the season of 2016/2017, the mean temperature and temperature sum from sowing until harvest were the lowest of all three experimental years (Table 3), indicating a lower degree of heat stress for the plants than in 2017/2018 and 2018/2019, when the average temperature and temperature sum were higher. The ratio between the precipitation sum and the mean temperature (Table 4) was highest in October, which is advantageous for an even germination of the seeds. From February through July, the ratio decreased significantly, showing an increasing level of drought stress during generative development. The timely development of growth stages (Figure 3C) showed a steeper course for German wheat varieties than for Eastern European lines. German varieties experienced a higher degree of heat stress, which led to a reduction of the length of the growth stages. In the spring of 2018, the ratio between precipitation and temperature was very low in April and May (Table 4). This led to an early drought stress, resulting in an early shift from vegetative to generative development, as observed by Desclaux and Roumet (1996). In Figure 3D this can be seen, as the growth stage of anthesis (>Z61) was already reached at 220 DAS by Eastern European lines and ca. 231 DAS by German varieties, considerably earlier than in 2017 (ca. 243 DAS).

In the period from October and from April to harvest, respectively (Table 3), the amount of precipitation in 2018/2019 was considerably higher than in the previous years, suggesting a lower degree of drought stress (Table 4). Particularly striking was the difference in the precipitation sum and mean temperature from April to harvest between the second and third season with 100 mm higher precipitation in the spring and summer of 2019, while the average temperature in the same period was 1.7°C cooler than in the previous year, resulting in a lower stress level. However, it is clearly visible that the degree of drought stress in October was very high (0.15 mm/°C), resulting in an uneven and incomplete germination in non-irrigated plots. Many of those plots only germinated in early spring of 2019 and therefore were delayed in many developmental stages compared to irrigated plots (cf. Figure 3E and F).

In all years, Eastern European varieties showed an earlier increase in Zadoks growth stages, since they are bred for and adapted to a shorter vegetation period than the German varieties. This helps the Eastern European varieties to escape the fierce heat in summer, to complete the grain formation and grain filling earlier, and to keep yield losses due to abiotic stress as low as possible (Shavrukov et al., 2017). During periods of intense stress, the growth curve of the German varieties became steeper (Figure 3), as the impact of drought and heat stress caused a shorter duration of developmental stages (Farooq et al., 2012; Ihsan et al., 2016; McMaster and Wilhelm, 2003; Nahar et al., 2010; Prasad et al., 2008).

Grain filling is one of the most sensitive growth stages to drought stress (Barnabás et al., 2008; Ihsan et al., 2016) due to strong influence rather on the grain filling duration, than on the grain filling rate (Nahar et al., 2010; Wardlaw, 2002; Wiegand and Cuellar, 1981). A shorter duration of the grain filling leads to smaller and lighter grains and results in yield reduction (Prasad et al., 2008). The results showed significant differences in the starting date of grain filling (Table 6) and in grain filling duration (Tables 7 and 8) between all trials and between Eastern European and German varieties. Due to their breeding history, Eastern European varieties started the grain filling phase earlier (238.75 DAS) than German hybrids (241.32 DAS) and German lines (242.21 DAS). A shorter duration between sowing and grain filling was shown to be strongly correlated with higher yields and TGW (Table 9). In addition, the phase of grain filling lasted shorter (Eastern European lines: 17.52 days, German hybrids: 20.53 days, German lines: 20.54 days). Consequently, they are exposed to a lower temperature sum during this growth stage (Eastern European lines: 402.44°C, German hybrids: 486.99°C, German lines: 488.08°C). In 2018, drought conditions occurred early in spring, accelerating the phasic development and led to the earliest start of grain filling observed in the trials (233.43 DAS). Precipitation thereafter led to a deceleration of the phasic development, so that the duration of grain filling in 2018 was the longest of all trials (25.31 days). The difference between drought stress (241.44 DAS) and irrigated (239.53 DAS) plots in 2019 is most likely explained by the delayed emergence of the drought stress plots. These findings are consistent with several studies observing a shortened grain filling duration under drought (Ihsan et al., 2016; Mäkinen et al., 2018; Prasad et al., 2008). The earlier beginning and shorter duration of grain filling of Eastern European varieties suggests a higher grain filling rate. In environments with heat and drought events during grain filling of wheat, a high grain filling rate can be advantageous (Whan et al., 1996), as it allows the plants to complete their life cycle earlier (Nahar et al., 2010). Therefore, it can be considered a helpful breeding aim to ensure high grain weights and stable yield (Dias and Lidon, 2009; Whan et al., 1996). While Ihsan et al. (2016) suggested that a

long grain filling period might be an advantageous breeding goal under arid conditions, Dias and Lidon (2009) found that selection for a high grain filling rate may be more helpful as that is influenced rather from the genotype than from the environmental conditions.

5.1.2. Agronomical parameters and biomass growth under heat and drought stress

The influence of the timing and intensity of stress on the plant development is clearly visible in the yield data and harvest parameters (Figure 4). Numerous previous studies found a negative effect of insufficient time to maturity on grain yield (Farooq et al., 2012; McMaster and Wilhelm, 2003; Wahid et al., 2012), as it was the case for German varieties (Figure 4A).

The different timing of stress across the years led to different causes for yield reduction. In 2017, drought at the beginning of the season caused low numbers of tillers and ears per square meter (Figure 4E and F). It was also strong towards the end of the season, causing a reduced number of grains per ear (Figure 4C), and a high proportion of small grains (Figure 6), resulting in low grain yield (4.70-5.36 t/ha). These findings are in accordance with Dias and Lidon (2009) and Prasad et al. (2008), who mentioned that high temperatures restrict grain filling and thereby negatively influence yield. Evenly distributed rainfall in the autumn of 2017 resulted in a higher number of tillers and ears per square meter in the following trial. In 2018, early drought before anthesis triggered generative growth early and had a negative effect on the grain number (Bokshi et al., 2021; Cattivelli et al., 2008; Innes and Blackwell, 1981; Moriondo et al., 2011; Prasad et al., 2008). The high number of ears per square meter could not make up for the low number of grains per ear, leading to a low number of grains per square meter (Figure 4G). However, sufficient precipitation after anthesis ensured larger grains and higher grain weight, resulting in a high total grain yield (6.20-6.60 t/ha).

Drought in autumn 2018 caused delayed imbibition and decreased germination (Prasad et al., 2008; Wahid et al., 2012), which was compensated for in irrigated plots but had a strong negative impact on the number of tillers and ears in the drought stress plots. Due to the delayed germination in drought stress plots, the plants reached anthesis only in June of 2019, in irrigated plots already in May. The ratio between precipitation sum and mean temperature was higher in June, which was advantageous for the number of grains per ear in drought stress plots. However, due to the significantly lower number of ears and grains per square meter and slightly lower TGW, the grain yield in drought plots (4.46-5.70 t/ha) was strongly reduced compared to irrigated plots 5.80-7.20 t/ha).

Denčić et al. (2000) found that a high kernel weight can be advantageous under droughty conditions and an increased number of grains can result in increased grain yield. From the above-mentioned results, however, larger grains and a higher TGW seem to be more crucial for a high grain yield than the number of grains. This is corroborated by the correlations between the harvest parameters (Table 12), which showed closer correlations between TGW and grain yield ($r=0.41-0.68$) than between grain yield and the number of grains per ear ($r=0.09-0.37$), or per square meter ($r=0.14-0.21$), respectively.

Biomass accumulation strongly depends on the availability of water and on temperature (Ihsan et al., 2016). High temperatures accelerate the development and increase the rate of leaf appearance (Prasad et al., 2008) but decrease the total dry matter accumulation (Wahid et al., 2012). Plants grown under high temperature therefore show lower biomass compared to optimum conditions (Kim et al., 2007). Drought decreases the leaf size (Farooq et al., 2012) and dry matter accumulation (Ihsan et al., 2016). These results were also found in the field trials of this study. Small leaf area can be an advantage to reduce water use but also limits the productivity of the crop (Sinclair and Muchow, 2001).

As germination was decreased in autumn 2018, the difference between drought stress and irrigated plots was visible for the dry weight at anthesis, at harvest, and for the straw weight in 2019 (Figure 4I-L). In 2017 and in drought stress plots in 2019, the dry weight at anthesis (Figure 4I) was lower than in the other two trials. In 2017, it can be referred to smaller plant height (Figure 4H) due to droughty conditions throughout the season, in 2019 rather to the reduced germination and smaller number of tillers per square meter due to drought in autumn. The germination rate most likely is also the reason why the standard deviations were much higher than in other years, as within each group of origin some varieties showed uneven germination, while others were not as strongly affected. With sufficient precipitation (2018) or irrigation (2019), the plant dry weight was higher and the standard deviations were smaller. The difference between 2017 and 2018 is also visible at milk ripeness (Figure 4J). In 2019, no plant samples were taken at milk ripeness, but the comparison of the other plots allows the conclusion that there also was a clear difference between irrigated and non-irrigated plots.

While there was a significant difference in plant dry weight at harvest between 2017 and 2018, no difference was found for straw weight. This can be explained by the higher grain weight and a higher number of grains per square meter in 2018, resulting in a higher HI.

The difference between plant dry weight at harvest and straw weight was largest in both trials of 2019. Comparing the trials, straw weight was highest in the irrigated plots of 2019, but those did not show a significantly higher HI than the non-irrigated plots of the same year although grain yield was found to be higher in the irrigated plots. The high straw weight most likely resulted from a higher plant density and taller plant height (Figure 4H) and therefore reduced the HI.

The post-anthesis dry matter accumulation was extremely variable across varieties (Figure 4M). Negative results indicate dry matter loss from anthesis to harvest, which occurs through the dropping of old and mature leaves - a consequence of continuous drought stress (Prasad et al., 2008). Prey et al. (2019) reported that the major fraction of traits contributing to grain yield is formed post-anthesis; however, it is also influenced by remobilization of N from pre-anthesis uptake (Dupont and Altenbach, 2003; Kichey et al., 2007). The results indicate that in 2017 and 2018 after anthesis, not enough biomass was newly produced to compensate biomass loss due to leaf drop. Only translocation seems to have played a role. In 2019, the amount of precipitation after anthesis was much higher than in previous years, which allowed the plant to still accumulate and produce more biomass in addition to translocation from the shoots. As the grain yield in the irrigated plots was higher than in 2018, the findings indicate that the translocation contributed substantially to grain yield. However, as mentioned by Užík and Žofajová (2006), the contribution of assimilates stored in the plant organs to grain yield varies a lot dependent on the precipitation pattern, temperature and genotype, which makes a final conclusion difficult in the given experimental setup. Prey et al. (2020) found close relations between grain yield and post-anthesis dry matter accumulation. In this study, the correlations were much weaker (cf. Table 12), most likely due to the high variability of the dry matter accumulation.

The main agronomical goal of wheat breeding is a high grain yield. However, wheat shows high genotype x environment interaction and low heritability for grain yield (Araus et al., 2002). Therefore, grain yield itself is often not a helpful selection criterion, except in multiannual and multisite field trials (Passioura, 2012; Rebetzke et al., 2013). This challenge can partly be overcome by choosing secondary traits with high genetic correlation to grain yield and a higher heritability than grain yield itself as selection criterion (Araus et al., 2002; Jackson et al., 1996). In this study, heritability was calculated for three trials under drought stress, and for all four trials including the irrigated plots. Since abiotic stress conditions do not occur every year at the same intensity, it is desirable to target high heritability in a broad range of environments, under stress and under optimum conditions (Farooq et al., 2012). Compared to other agronomical

parameters, the results of TGW and HI (Figure 4B and D) showed lower variation across years, and between the groups of origin within each trial. From these results, a high heritability could be suspected. The calculation of the heritability supported these findings. The TGW ($h^2=0.87-0.88$) and HI ($h^2=0.85$) showed a considerably higher heritability than grain yield ($h^2=0.43-0.49$) across all trials and across drought stress trials, respectively (Tables 15 and 16).

5.1.3. Nitrogen traits under heat and drought

Nutrient availability and movement is dependent on soil water content (Marschner and Rengel, 2012). Drought reduces N mineralization in the soil (Bloem et al., 1992) and lowers the diffusion rate of plant nutrients (Singh and Singh, 2004). As a consequence, the nutrient uptake by plant roots decreases (Farooq et al., 2009b; Mäkinen et al., 2018; Roupael et al., 2012) as well as the transport within the plant (Farooq et al., 2012). The N content (Figure 7A) and N uptake (Figure 7B) of above ground dry matter at anthesis in 2017 and 2018 was significantly lower than in both trials of 2019, which can be attributed to the dry conditions until anthesis in both years. In 2019, a difference between irrigated and non-irrigated plots was only found for the N uptake, caused by the higher dry weight of the plants. The N content at milk ripeness was lower than at anthesis, which indicates a dilution effect due to increasing biomass.

The N content in grains showed the opposite pattern to grain yield, i.e. trials with lower yield (2017 and 2019 under drought stress) had higher grain N content than those with high grain yield (2018 and 2019 irrigated). Also, within the years, the results showed an opposite pattern than for grain yield, with German lines having the highest grain N content but the lowest grain yield in all years, except in 2018. As seen in previous results, German hybrids behaved intermediate. Grain N uptake was highest for Eastern European lines, which arose from the higher total grain weight of the samples. It showed a similar pattern across years, as did the grain yield (cf. Figure 9). In 2019, the N content was comparable for both trials; however, the N uptake of the irrigated plots was significantly higher.

The protein content of wheat ranges between 7-22% (Hawkesford et al., 2012). As the protein content is a factor of N content, the contrary development to grain yield is the same for protein (Figure 8). Higher yield usually comes along with lower protein content in the grain (Terman et al., 1969), which was observed for the trials of 2017 and 2018. Differentiated by quality group, the German lines showed a ranking as expected, with E-varieties having the highest protein content but lowest yield, decreasing protein content in A- and B-varieties and lowest protein content in C-varieties, whilst showing highest

grain yield. Drought plots of 2019 showed strongly reduced yield, which was a consequence of combined uneven germination, delayed development and drought during the entire development. Irrigated plots in 2019 showed the advantage of irrigation by only slight decrease of protein content, compared to drought stress of 2019, but significantly higher grain yield.

Correlations of the harvest parameters and the nitrogen traits among each other showed a consistent picture across all years (Table 12). The strongest positive correlations with grain yield were found for TGW, HI, and grain N uptake, whereas the protein content showed a strong negative correlation in all trials. As yield is closer correlated with the number of grains per ear than with the number of tillers per square meter, that trait seems to be a useful breeding goal under both drought and irrigated conditions. Similar results were found by Shpiler and Blum (1990). The number of tillers and ears per square meter showed a significant negative correlation to the number of grains per ear, showing that the plant invested only in one of the traits, i.e. a reduced number of grains per ear compensated for a high number of tillers per square meter. The dilution effect of nitrogen content was visible in the negative correlation between plant height and N content at both, anthesis and milk ripeness. The positive correlation of dry weight and N uptake arose due to the calculation formula for N uptake and was not affected by plant characteristics. In 2017, the correlation between N uptake at anthesis and dry weight at milk ripeness was negative, however positive in 2018, which most likely was due to the different precipitation patterns of the years. In 2017, the soil became gradually drier during the vegetation period, making it increasingly difficult for the plants to take up water and nutrients. In 2018 however, the amount of precipitation increased after anthesis, enabling the plants to further take up nutrients and increase additional biomass.

Comparing the variability between groups of origin within the trials, and the overall variability across all trials, it is clearly visible that the N content of grains (protein content, respectively) (Figure 7E) seemed less influenced by environmental conditions than the grain N uptake (Figure 7F). The former showed a much more regular pattern across years and was rather congruent to grain yield than the latter. While the heritability of the protein content ($h^2=0.44$) was higher than of the grain N uptake ($h^2=0.34$), they were both lower than the heritability of grain yield ($h^2=0.43$) across all trials (Table 15). Across the drought stress plots (Table 16), the heritability of grain N uptake ($h^2=0.50$) was higher than both protein content ($h^2=0.45$) and grain yield ($h^2=0.43$). This inconsistency does not suggest either grain N content/protein content or grain N uptake as a secondary trait for breeding targeted on grain yield.

5.2. Impact of heat and drought on relative leaf water content, canopy temperature, and carbon isotope discrimination

The relative leaf water content (RLWC) was determined twice, at Z71 and Z79 and showed significant differences between the two sampling times in all trials (Figure 11). The difference between the RLWC in 2017 and in the other years was particularly striking. These results are congruent with the much lower precipitation that was recorded in the first year. In 2018, spring was characterized by drought, but the increased precipitation after anthesis led to a higher RLWC. As the RLWC is highly sensitive to the soil water content, the samples were taken at days with no precipitation on the previous days. High precipitation (2018) or water storage from irrigation (2019, irrigated plots) decreased the difference between varieties in the first sampling time T1. Drought negatively affects RLWC in many field crops (Farooq et al., 2012). It leads to water deficit in the plant tissue, affecting many physiological processes (Vilagrosa et al., 2012) damaging leaf tissue and the chloroplasts (Grigorova et al., 2012). Thereof reduced nutrient uptake, biomass accumulation, and early triggered senescence of leaves can lead to decreased grain yield. Araus et al. (2002) mentioned that increased water use efficiency (WUE) can be advantageous and can improve grain yield potential if water availability is limited during plant growth. Not only is the RLWC directly affected by drought (i.e. low water availability) but also through heat, which increases the transpiration rate and the water loss from the plant surface, causing tissue dehydration and growth restrictions (Wahid et al., 2012).

When growing under high temperature, plants regulate the leaf temperature through transpirational cooling. Tissue dehydration due to insufficient water availability leads to stomatal closure, a decrease of transpiration, and in turn to an increase in canopy temperature. Measuring the surface temperature of the plants can show the degree of drought stress during growth (Araus and Cairns, 2014). The combination of heat and drought stress increases the damage within the plant tissue and the chloroplasts, reduces the photosynthetic capacity, and lowers CO₂ uptake, biomass accumulation and grain yield. Numerous studies showed an association between cooler canopy temperature and higher grain yield under water-limited conditions (Olivares-Villegas et al., 2007; Rashid et al., 1999) and under hot irrigated conditions (Amani et al., 1996; Ayeneh et al., 2002; Lopes and Reynolds, 2010; Reynolds et al., 1994). The varieties used for the field trial in Moldova had a different genetic background, which makes it difficult to transfer the findings from other studies one-to-one. In 2017, German lines showed the highest canopy temperature at most measuring days, and provided the lowest grain yield at harvest, which is in accordance with the above-mentioned studies.

However, in the following years, at most measuring days, the Eastern European lines had a higher canopy temperature and still higher grain yields. Comparing only the temperature and yield data, these findings would lead to the conclusion that a higher leaf temperature is associated with higher grain yield, which contradicts the aforementioned physiological principles. In this case, it has to be taken into account that the Eastern European varieties are much better adapted to the climate in northern Moldova than the German varieties. In order to find a possible relation between canopy temperature and grain yield, the varieties should be compared with each other within one group of origin, rather than across the origins. Such a comparison will be drawn in chapter 5.4.

The increase in measured temperature towards the end of the vegetation period was made up from multiple factors: The average air temperature increased towards the summer, heating up the leaf surface of the plants. The plants themselves were affected more and more by drought stress, which made it more difficult to cool down the leaf temperature through transpiration. Towards the end of the growing season, the plants started to become senescent and transpirational cooling was not possible any more. With progressing senescence, the plant surface became less dense, leading to a possible bias due to the high surface temperature of the soil. The same applied for the plots with poor plant density in the drought stress trial of 2018/2019. Although for the calculation of the average temperature, only pixels of plant surface were used, it is likely that the dark soil heated up, radiated heat, and increased the temperature of the plant surface, additionally to direct solar radiation from above (Deery et al., 2016; Rischbeck et al., 2017). Another difficulty was that the color differentiation between plant surface and soil pixels became more and more challenging with senescence, which can easily lead to biased results.

On a molecular level, the degree of drought stress can be determined with the help of ^{13}C isotopes (Condon et al., 1990; Schopfer and Brennicke, 2010). As under drought plants close the stomata to reduce transpirational water loss, the CO_2 uptake is also limited (Farooq et al., 2012; Medrano, 2002), leading to an increasing $^{13}\text{C}:^{12}\text{C}$ ratio and a reduction of carbon isotope discrimination (Farquhar et al., 1989). In 2017, the discrimination values of leaves and grains were lowest compared to the other years, indicating the highest level of stress for the plants (Figure 10). Between 2018 and both trials of 2019, the difference was much smaller. These results go together with the recorded meteorological data, where the season of 2016/2017 had the lowest total precipitation (Table 3) and the lowest ratio between precipitation and mean temperature (Table 4). In all years, the CID decreased from the first sample towards the grain. It is generally known that the carbohydrates stored in the upper leaf levels contribute to the

grain filling to a large extent (Lupton, 1966). However, the difference between CID of the third leaf sample (Z87-89) and CID of the grains was significant in all trials. This might arise because carbohydrates, which are exported to the grains, have a different isotopic composition than those remaining in the leaves, or because the grains accumulate carbon not only from the leaves but also from other source organs, such as the stem (Merah et al., 1999a).

In 2017 and 2018, the Eastern European lines showed a higher rate of CID than German varieties for most samples. In 2019, the CID of German hybrids was comparable or higher than of the Eastern European lines. Based on the meteorological data, these results indicate that the Eastern European lines could withstand a higher stress level in 2017 and 2018 better than the German varieties. That could imply either a closure of stomata to reduce water loss while tolerating increased tissue temperature, or the ability to keep stomata open and tolerate a lower water potential. As Eastern European varieties had a slightly higher canopy temperature (Figure 15) than German varieties, they seem to close the stomata. However, it is very likely that both strategies are used to a certain level.

In 2019, the stress level was lower than in the previous years, more precipitation could be stored in the soil, resulting in higher CID values. Due to the relatively high amount of precipitation during the growing season, the difference between drought stressed and irrigated plots was not as large. Also, the difference between the third leaf sample and the grains was smaller than in previous years. The largest difference between the three years was the increased CID of German hybrid varieties in 2019. A high degree of CID indicates the ability of the plants to keep the stomata open and have a higher stomatal conductance (Farooq et al., 2012). Although, the differences were not significant at all times, it can be concluded that the hybrids were able to maintain a higher photosynthetic activity in 2019, compared to the two groups of line varieties. These assumptions are supported by the high plant dry weight at anthesis and harvest, plant height, and the grain size distribution. The grain yield of hybrids was comparable to the Eastern European lines and significantly higher than the German lines in the irrigated plots.

Hybrid varieties are often able to tolerate abiotic stress better than line varieties (Schittenhelm et al., 2019). Considering the CID, this was also the case in the trial of 2018/2019, but it has to be kept in mind that the level of stress was lower than in the first and second year.

Previous studies have found a positive correlation between CID and grain yield (Becker and Schmidhalter, 2017; Condon, 2004). The results in Table 17 depict low correlations for Eastern European varieties. German hybrids and lines showed more significant

correlations, particularly for the grains. Only in 2017, significant correlations between leaf CID and grain yield were found. The stronger the stress in the trial was, the more likely significant correlations could be found, since the varieties within one group of origin reacted more variably and the data showed more scattering. With higher precipitation or irrigation (2017/2018 and 2018/2019), the differences between the varieties became smaller and a possible correlation was more difficult to detect. Eastern European varieties showed lower variability in reaction to stress due to the higher degree of adaptation. Therefore, the correlation decreased. The same effect could be observed, when the correlation was calculated across all varieties. The difference between the varieties led to a larger scattering of the data and therefore to a higher correlation, even in leaf samples. Comparable results were found by Merah et al. (1999b) who reported that the CID of grain showed good correlations with grain yield, whereas the CID of leaves correlated only when the plants were grown under water limitation. Since CID tends to be lower under less favorable environmental conditions, the correlation with grain yield was found to be stronger in plant organs that expand later during the growing period, such as the flag leaf, peduncle or grain (Condon et al., 2002).

The correlations of CID and drought related parameters (Table 19) were calculated based on the idea that RLWC, WI and the canopy temperature are values, which are very sensitive to prevailing environmental conditions and change quickly. The CID, however, integrates over time and is not comparable to daily values. Therefore, the sum of WI and the sum of canopy temperature were used to detect possible relations between these data. Canopy temperature, WI and RLWC were measured on the same day if possible, or at least with the smallest possible interval. Still, the variability of the data was high, since all three methods are highly susceptible even to small environmental changes. RLWC sampling always runs the risk of being falsified by water loss during the handling or weighing processes. The canopy temperature was very sensitive to cloud cover and the intensity of sunshine. Although, thermal pictures were only taken on cloudless days, the radiation intensity might have varied across the days and the duration of the measurement is still fairly long (ca. 40 min per 120 plots), so that the conditions are not exactly equal for all images. These difficulties need to be taken into consideration when judging the results. Integrated values are less affected by day-to-day variation and therefore might have more explanatory power and show stronger correlations.

The correlation of RLWC and WI was not significant for most samples, very likely due to the error-prone sampling. Correlating the accumulated WI with the CID, the relations were much stronger, especially at growth stage Z79. As the WI indicates the water content of the plant tissue and reacts sensitively to senescence, this strong increase in

correlation may be due to the different senescence levels, leading to a strong scatter of the data, which in turn increases the correlation coefficient.

The correlation between RLWC and canopy temperature, obtained with both handheld and aerial thermography, was significant for half of the measurements, whereas the correlation between temperature sum and CID was significant for most measurements at Z71. These correlations indicate that a lower canopy temperature, i.e. higher water content in the plant tissue, is related to a higher degree of CID, as the rate of evaporation is related to the stomatal conductance (Araus et al., 2002; Farooq et al., 2012; Taiz et al., 2015). For the temperature sum, the progressing senescence led to a decrease in correlation towards the second sampling in Z79. Senescent plants are not able to control their canopy temperature any longer. The temperature increases with higher air temperature and longer sun shine periods, leading to a bias in temperature data. The consistently significant correlations of temperature sum from the drone-based camera indicate a higher accuracy compared to terrestrial measurements, due to the much faster data acquisition (ca. 4 min per 120 plots).

Beside the relation of physiological traits to grain yield, their heritability is also an important measure. The RLWC ($h^2=0.22-0.37$) showed lower heritability than grain yield ($h^2=0.43-0.49$) across all years (Tables 20 and 21) and is therefore not recommended as a useful secondary trait for selection. The heritability of CID of leaves ($h^2=0.69-0.74$) and grain ($h^2=0.64-0.65$) (Tables 20 and 21), and of the canopy temperature (Fluke; $h^2=0.65-0.71$) (Tables 26 and 27) was strong, as reported previously by Becker and Schmidhalter (2017) and Merah et al. (2001). Considering the individual years, heritability was stronger for German varieties than for Eastern European lines, most of the time. The heritability of CID of leaves was even higher than of grains; however, the differences were marginal in many cases. The canopy temperature (Fluke) showed a level of heritability comparable to the CID, indicating that CT as well could be used as secondary trait in selection processes. This supports the findings of Amani et al. (1996), Becker and Schmidhalter (2017) and Deery et al. (2016).

5.3. Use of terrestrial and aerial high-throughput phenotyping for identification of stress tolerant varieties

5.3.1. Relation between vegetation indices and canopy temperature

Spectral data can help gather information about physiological conditions of plants without the need to cut and analyze samples. Often, this method is quicker and less labor-intensive than destructive measurements (Prasad et al., 2007). The vegetation indices, which can be calculated from reflectance data of certain wavelengths, are often related to one another as well as to the canopy temperature (Babar et al., 2006b; Peñuelas et al., 1997). As visible in the Figures 15 and 16, high values of NDVI, WI, and REIP go along with lower canopy temperature in most cases, as it was already described by Babar et al. (2006b). When the NDVI decreased, so did the WI, and the canopy temperature increased. The NDVI is a good indicator for the vitality of the plant tissue and the senescence, respectively. Progressing senescence goes along with lower water content (i.e. decreasing WI) and lower transpiration rate, leading to higher canopy temperature. Young leaves reflect high amounts of NIR radiation while absorbing more photosynthetically active radiation (Babar et al., 2006b). Old leaves, in which the chlorophyll concentration decreases, reflect more of the visible wavelengths and less NIR radiation. The NDVI, based on wavelengths of the red and NIR spectrum, is higher in early growth stages and decreases with advancing senescence (Aparicio et al., 2000; Babar et al., 2006b). High mean temperatures accelerate the crop development (Rezaei et al., 2015) and senescence is triggered early (Cao et al., 2015). Under favorable growing conditions, plants, which maintain a high NDVI for a longer time, so-called 'stay-green' varieties, are believed to have a higher productivity due to a longer period of photosynthetic activity (Adu et al., 2011) resulting in higher grain yield (Adu et al., 2011; Gregersen et al., 2008; Kipp et al., 2014; Pinto et al., 2010).

As visible in Figure 12, the German varieties had higher NDVI values than the Eastern European lines for an extended period. In 2018 and 2019, the German hybrids had even higher values than the German lines. These results indicate a stay-green trait in German varieties, which is even more pronounced in German hybrids than in the lines. The adaptation to a shorter vegetation period causes the Eastern European lines to show an earlier senescence.

The time shift of the WI (Figure 13) was similar to the one of NDVI, as increasing senescence led to decreased water content. The WI reacted very sensitively to precipitation, which is clearly visible in the graphs of 2019 (Figure 13E and F), when the precipitation events of June 9, 2019 (244 DAS) and June 17 and 18, 2019

(252/253 DAS) increased the soil water content considerably (cf. Figure 1C). In drought stress plots, the first precipitation event (5.7 mm) only gave a very small increase in WI values. It is very likely that the soil surface in these plots was very dry and encrusted, only little water could infiltrate, and most of the precipitation drained at the surface or has seeped through drought cracks into deeper soil layers. Therefore, the roots could not take it up. In irrigated plots, the soil was less dried out and could take up water. This led to the peak at 246/247 DAS in Figure 13F. The next precipitation event was much stronger. On June 17 and 18, 2019, rainfall amounted to 90.3 mm over ca. 7 hours, leading to a very strong increase in the WI signal in all plots the following day.

During growth, Eastern European varieties showed lowest WI values at most days. Low WI indicates low water content, which causes a decreased transpiration rate and therefore higher canopy temperature. That goes along with the findings of the temperature measured with the infrared Fluke camera (Figure 15) and was also shown in previous studies, whereby relations got stronger with later growth stages of the plants (Babar et al., 2006b; Gutiérrez-Rodríguez et al., 2004; Peñuelas et al., 1997). At most measurements, the temperature of the Eastern European varieties was higher than of the German varieties. In 2019, it is clearly visible that the non-irrigated plots showed an earlier and stronger increase in canopy temperature, with a strong temperature depression after precipitation after 249 DAS. In irrigated plots, the effect of the precipitation is less marked, since the soil stored water from irrigation and the canopy temperature had not risen as far as in the drought stressed plots. Towards the end of the growing season of all years, the WI of German varieties became higher than of Eastern European varieties, which is due to the longer growth period of German varieties, while Eastern European varieties were already senescing.

The differences in NDVI and WI between German and Eastern European varieties towards the end of the growing season can be explained by the breeding history and the adaptation of Eastern European varieties to a shorter vegetation period. During the time before senescence started (until ca. 240 DAS) the differences between the varieties are caused by the different strategies and varying degree of tolerance against abiotic stress.

The effect of irrigation in the experimental year of 2018/2019 is difficult to interpret, as non-irrigated plots emerged only in spring 2019, instead of autumn 2018. This caused a delay in plant development and the later decrease of NDVI compared to irrigated plots. The level of WI was generally lower in drought stress plots, but the difference between the beginning and the end of the measurements was more distinct in the irrigated plots. Towards the end of the season, German hybrids showed the highest WI in the irrigated plots, which might be an indicator for a high degree of the stay-green characteristics.

5.3.2. Assessment of agronomical parameters with high-throughput phenotyping

Besides physiological parameters, also harvest traits can be assessed with spectral reflectance data. Previous studies showed relations between canopy temperature, different vegetation indices, and agronomical parameters, such as grain yield, TGW, biomass, and N-status, under drought stress and irrigated conditions (Babar et al., 2006a; Cao et al., 2015; Fischer et al., 1998; Lopes and Reynolds, 2010; Mistele and Schmidhalter, 2010; Mistele et al., 2004; Reynolds et al., 1994)

Previous studies showed that stay-green is a valuable trait associated with increased yield (Hafsi et al., 2007; Xu et al., 2000) and resistance against premature senescence under drought stress (Xu et al., 2000). Within the set of German varieties, these findings could be verified, with hybrids having higher grain yield than German lines (cf. Figure 4). However, Eastern European lines showed decreasing NDVI values earlier, i.e. had a shorter period of photosynthetic activity, but still had the highest grain yield in all trials. That implies that in environments with severe abiotic stress conditions, without further adaptation through breeding progress the use of only the stay-green trait is limited. In the irrigated plots of 2019, the advantage of pronounced stay-green trait was visible for the hybrids. They showed a grain yield level comparable to Eastern European lines. In combined heat and drought stress, the advantage was smaller. It can be postulated that stay-green under severe heat and drought stress (e.g. in 2017) can even be disadvantageous, as the plants transpire over a longer period, increasing the water loss and therefore the risk of premature ripening and small grains. These observations are in accordance with Kamal et al. (2019) who reported a positive relation between grain yield and late senescence under heat, but a negative relation under combined heat and drought stress.

In order to reliably predict physiological and agronomical parameters under heat and drought stress with non-destructive methods, the relation between spectral information and respective traits must be assessed. Calculating correlations several times throughout the season also helps to find out, which growth stages have the highest explanatory power for grain yield and quality prediction. Mistele et al. (2004) and Mistele and Schmidhalter (2010) described an increasing strength of correlations towards the end of the growing period. In this study, those findings could be confirmed in 2017 and 2018, but not in the trials of 2019.

Correlations between spectral vegetation indices and grain yield, TGW, and HI differed at anthesis 2017 and 2018. However, at milk ripeness both years showed very similar correlations. Especially striking was the change from a negative correlation between the REIP and the three harvest parameters at anthesis to a significant positive one at milk ripeness. The same applied for all four NWI. NWI 1 and 2 were developed for spring wheat (Babar et al., 2006b), whereas NWI 3 and 4 were found to be more predictive for winter wheat (Prasad et al., 2007), but in this study, no difference in usability between the indices was found, they all showed a comparable level of correlation. The same was found by Becker and Schmidhalter (2017). The results of 2019 were different from the previous years. In the drought stress plots, no correlation between spectral data and grain yield could be found, which can be ascribed to the low germination in autumn. The uneven development of the plants could have reduced the explanatory power of the spectral reflectance. As many plots had gaps, the reflectance of soil could have biased the measurements and altered the correlations. This assumption is supported by the correlations found in irrigated plots. However, they showed the opposite patterns compared to 2017 and 2018, with positive correlations between yield parameters and NWI 1-4, whilst all others were significantly negative. Correlations with TGW and HI were often not significant in previous years as they were in both, irrigated and non-irrigated plots of 2019. In drought stress plots all SR showed significant correlation with TGW and HI, whereas in irrigated plots most of the drone-based SR did not. At milk ripeness in 2019, the WI was positively, other indices were negatively correlated with TGW and HI. Correlations with grain yield were significant for NWI 1-4 (negative) and WI (positive), which is in accordance with Babar et al. (2006a), who also found a strong association between WI and wheat yield. Stronger correlations in drought stress than in the irrigated plots arose from the different susceptibility of the varieties to drought and heat stress.

The NDVI is one of the most commonly used vegetation indices (Wall et al., 2008). The ability to maintain high levels of chlorophyll content in the leaves indicates a low degree of photoinhibition (Cao et al., 2015) and damage to thylakoid membranes (Erice et al., 2012) and has been proven to be associated with TGW (Cao et al., 2015), biomass, and grain yield (Govaerts et al., 2007). In a study of Cao et al. (2015) it was found that heat tolerant wheat varieties maintained the chlorophyll content when exposed to stress, whereas more susceptible lines became senescent. However, all varieties used in that study were released in the same region. The present study showed different results with either insignificant or significantly negative correlations between NDVI and grain yield. As described by Kamal et al. (2019), the stay green trait might be a disadvantage when heat and drought stress appear in combination during late growth stages. It increases the risk of premature ripening and a shorter period for grain filling, and therefore reduced

the grain size and led to a low grain yield, in plants, which maintain green leaves for a longer period. The high grain yield of Eastern European varieties with an early starting senescence, and low grain yield of German varieties with higher NDVI values led to negative correlations.

The number of tillers and ears per square meter was significantly correlated to all indices in drought stress plots of 2019. The extreme drought in autumn 2018 led to large differences in emergence and tiller number between varieties. Strong scatter of data resulted in high correlations. Compared with the other trials, however, indicates that the differences between varieties are not strong enough to be detected, when the normal rate of emergence is ensured by either autumn precipitation or irrigation.

Although many previous studies found a relation between biomass and vegetation indices (NDVI (Govaerts et al., 2007; Mistele et al., 2004), NIR/Red (Mistele et al., 2004), WI (Royo et al., 2003)), this was not the case in the present trials. The number of grains per ear did also not show consistent correlation to any vegetation index across the years.

The correlations between indices and N content, and N uptake respectively, showed a relatively uniform picture across all trials. Only at milk ripeness in 2018 the relation was weaker, as well as for N uptake at anthesis in 2017. In the other trials, the relations with WI and the SR (HandySpec and drone) were positive; with the NWI 1-4 were negative. The NDVI and REIP were significantly positively correlated, except the NDVI at anthesis in 2018, and the REIP at milk ripeness in 2017. Both these irregularities occurred when the stress was exceptionally strong. Lilienthal (2014) pointed out that most indices mainly respond to biomass and the leaf area index (LAI), only weakly to the chlorophyll content and not to the nitrogen content of the vegetation. A direct assessment of N content would not be possible with current available sensor systems (Lilienthal, 2014). However, previous studies found a strong relation between total aerial N and REIP, and R_{780}/R_{740} , N content and REIP, N content and NIR/NIR, and N uptake and REIP (Mistele and Schmidhalter, 2008, 2010; Mistele et al., 2004). The R_{760}/R_{730} index was found to also assess the N status of wheat and to be more resistant to saturation than REIP at high N levels (Erdle et al., 2011). Shaver et al. (2010) mentioned that the leaf N content is positively correlated to the reflectance of the NIR spectrum, negatively to the VIS reflectance. Other authors found that the correlation to plant parameters increases with increasing spectral ranges and the number of wavelengths (Hasituya et al., 2020; Li et al., 2014; Lilienthal, 2014). This supports the results of a good correlation between the REIP and the plant parameters, as the REIP includes four different wavelengths, whereas the NDVI, WI, NWI, and SR are calculated from only two wavelengths.

The correlations between plant parameters and temperature measurements were very similar for the terrestrial and the aerial thermal measurements. However, most correlations were not close. Significant correlations were mostly positive with nitrogen traits, and negative with grain yield. High N content (high protein content) is usually combined with a lower grain yield (cf. Figure 8), which was the case for the German varieties. As they were more affected by the abiotic stress, they showed a higher canopy temperature due to a lower water content (cf. Figure 11), leading to a negative relation between high temperature and low grain yield. These findings are supported by the results of many other studies under drought as well as irrigated conditions (e.g. Amani et al., 1996; Ayeneh et al., 2002; Deery et al., 2016; Fischer et al., 1998; Lopes and Reynolds, 2010; Olivares-Villegas et al., 2007; Rashid et al., 1999; Reynolds et al., 1994), suggesting that canopy temperature can be used as a selection tool for breeders (Deery et al., 2016; Prashar and Jones, 2014). However, it has to be considered that the leaf and canopy temperature react very sensitively to cloud cover, precipitation, and daily air temperature. The data is subject to strong fluctuations and depends strongly on the time of the day, when the measurements are taken. Therefore, predictions based on daily temperature are challenging, and might be more stable when averaged or summarized over a specific period.

At anthesis and milk ripeness, significant correlations were found between thermal data and the number of tillers and ears per square meter, which is most likely attributable to the uneven and low rate of emergence. The less plants were growing in a certain area, the more the soil temperature likely influences the measurement. The Chernozem soil in Moldova is of very dark color and heats up stronger than the plant tissue. The possible bias in thermal pictures of exposed dry soil and poor plant establishment was also described by Deery et al. (2016) and Rischbeck et al. (2017), who mention a great need of enhanced image analysis techniques to counteract these challenges.

5.3.3. Detection of stress with aerial and terrestrial devices under drought and irrigation

In order to detect the effects of irrigation on the development of the plants and the harvest parameters, the trial was grown twice in 2019. One part was left to natural conditions as in the previous years; the other part was irrigated to ensure sufficient water availability. Growing the two trials simultaneously ensured the same environmental conditions and increased the comparability.

In Figure 16, the difference between origins and irrigation treatments was clearly visible. Eastern European varieties are well adapted to a shorter vegetation period and therefore showed an earlier decrease of the NDVI, earlier senescence, than German varieties. Towards the end of the growing season, the irrigated plots showed a lower NDVI than the drought stress plots. As the NDVI is an indicator of vitality and greenness of the plants and drought triggers early senescence, this cannot be explained only by the growing conditions. Rather the later emergence of the plants in non-irrigated plots, and therefore the delayed development caused a delay in senescence.

The difference between irrigated and drought stress plots was not as distinct for the NDVI as it was for the WI. The WI of plants in drought stress plots was significantly lower than in the irrigated plots, for both Eastern European and German varieties, until ca 253 DAS, when heavy rain increased the soil water content and therefore the water uptake of plants (cf. Figure 1). Contrastingly, after this precipitation event, the WI values of wheat in the irrigated plots were significantly lower than in non-irrigated plots. This is in line with the higher NDVI values in drought stress plots and was caused by the delayed germination and development.

As the WI was lower in drought stressed plots, the canopy temperature was significantly higher than in the irrigated plots most days. The difference between Eastern European and German varieties was visibly smaller than for the indices and not always significant. However, whilst the WI was at a higher level in the drought stressed plots due to late development of the plants, the canopy temperature was thereby not lower. Although the plants in the drought stressed plots were in an earlier growth stage (cf. Figure 3) and showed higher values in NDVI and WI, they were not able to cool down more than plants in irrigated plots, which had a lower WI at that time. Canopy temperature is strongly influenced by the daily weather and more susceptible to short-term changes than the indices. Measurements of the canopy temperature were always done at cloudless days around noon, when the sunshine was strongest. Therefore, the high canopy temperature might have been caused by high air temperature and direct solar radiation during the measurement and would be lower, and matching the results of the vegetation indices, when averaged over the entire day.

The REIP index showed a similar course as the NDVI; however, the separation between origins and irrigation was more distinct, especially at the beginning of the measurements. The REIP is a good estimate of the chlorophyll content and the LAI (Broge et al., 2003), as well as the vegetative N uptake (Prey and Schmidhalter, 2019). During grain filling, as the nitrogen is translocated from the leaves to the ear, the nitrogen was not as easily detectable with the sensor any more, leading to a decrease in REIP after ca 235-

240 DAS (cf. Figure 3E-F), which was enhanced through progressing senescence and decreasing chlorophyll content of the leaves.

As the leaf area index decreases in later growth stages (Kumari et al., 2009), more reflectance data of the soil is recorded. The high reflectance values of dry soil in the range of the NIR spectrum (Short, 1982 in Mohamed et al., 2018) might cause the increasing REIP signal towards the end of the growing season. Consistent with the aforementioned influence of delayed development in drought stressed plots, this increase of the REIP index was visible earlier for the irrigated plots than for plots under drought stress.

Comparing terrestrial (Fluke/HandySpec) and aerial (DuetT/Sequoia) sensor systems, both showed similar results for the thermal and spectral measurements (Figures 17 and 18). Both canopy temperature and NDVI were found significantly lower when recorded with the drone-based sensors. The NDVI throughout the entire period of measurements, the canopy temperature after a precipitation event at 244 DAS. Tattaris et al. (2016) described similar findings for the canopy temperature and assumed that the distance between the sensor and the plant canopy, as well as environmental factors, such as time of day, temperature, and especially wind speed might influence the comparison of the two systems. Besides these differences, both aerial and terrestrial sensor systems showed a comparable temporal course: The canopy temperature was measured lower in irrigated plots than in drought stress plots. The NDVI was high in irrigated plots at the beginning of the measurements, as the plant establishment was earlier than in drought plots, whereas towards the end the delayed development caused higher NDVI values in drought stress plots. The only problem with the aerial NDVI-measurements occurred after 259 DAS, when negative NDVI values were assessed in some plots. The time course was still comparable to the terrestrial HandySpec measurements, however negative NDVI values usually indicate water surface or bare soil with no vegetation cover (Choubin et al., 2019). As plants rolled and shed their leaves due to the drought, and became senescent, a larger area of bare soil was exposed. In combination with the resolution of the sensor and the distance between sensor and crop canopy, this might have influenced the NDVI-measurements and resulted in negative values.

Comparable high correlations between aerial and terrestrial measurements were found for all SR indices across all measurements and all varieties (Table 22). Most SRs can be calculated from drone-derived or terrestrial sensors with comparable precision. The correlations of NIR/Green vs. R_{780}/R_{550} , Red edge/Green vs. R_{730}/R_{550} , and NIR/Red vs. R_{760}/R_{670} showed a coefficient of determination of $R^2 > 0.8$ in both drought stressed and irrigated plots. It is visible that the correlations are higher than those in Figure 18, as they

were calculated with all available data points and it has to be kept in mind that the data scattering, which is visible in some of the graphs (Table 22), had stronger influence if values of individual days would have been analyzed. The level of the canopy temperature and some indices was not exactly the same when recorded with aerial or terrestrial sensors, respectively. While the actual temperature or reflectance differed and it is not possible to know, which sensor was 'right', it is important to see, that the validity and the explanatory power of both systems are comparable.

5.3.4. Advantages and disadvantages of drones for high-throughput phenotyping

Given the comparability and high correlation between data of terrestrial handheld and of aerial drone-based sensor systems, it is important to see the advantages and disadvantages of the relatively new approach using UAVs compared to established ground-based methods.

Changing weather conditions during the measurements can strongly influence the measurements and increase bias of the data. Gathering clouds, for example, can decrease the canopy temperature in the plants within seconds. Therefore, the time spent for data collection is a crucial aspect concerning data accuracy and reliability, especially for temperature measurements. To measure the 240 plots in this study, the flight duration of the UAV was ca. 7-8 minutes with the thermal camera, and 5 minutes with the multispectral sensor. Terrestrial measurements took 70-80 min for thermal pictures and about 30 min with the HandySpec sensor. This large time difference influences especially the temperature data, which is more sensitive to quick changes in the environmental conditions and also increases noticeably under strong solar radiation. Comparable results were found by Deery et al. (2016), even within 30 min of measurement. It can be assumed, that even small changes in local weather cause a lower heritability of temperature data when acquired with ground-based compared to aerial sensors (Deery et al., 2016). The same was observed in this study in most trial sections with the handheld Fluke showing a heritability of $h^2=0.27-0.98$ and the aerial DuetT showing $h^2=0.55-0.98$ (Table 26). The heritability of the NDVI from the HandySpec measurements in 2019 was exceptionally high, compared to the previous years. Therefore, the advantage of an increased heritability in airborne measurements was also found for NDVI values, albeit to a lesser extent (HandySpec: $h^2=0.84-1.00$, Sequoia: $0.95-1.00$).

Another important aspect of the measurements is the resolution of the sensor. The Fluke camera was held ca. 120 cm above ground, thus it was possible to separate soil and plant pixels and analyze only the temperature of the plant surface. The reflectance of heat from the dry and hot soil could still play a role, indirectly heating up the plants additionally to the solar radiation from above (Rischbeck et al., 2017), but leaving out soil pixels in the analysis can decrease the risk of data bias. Due to the distance, a separation of soil and plant pixels was not possible in the drone data. The flight height of the UAV depends on the latitudinal and longitudinal overlap of the single picture needed to create an orthophoto. However, in this given case, the resolution was not high enough to distinguish leaves from surrounding soil surface, leading to mixed pixels containing information about both soil and plant temperature. These mixed pixels are very likely to bias the temperature measurement, especially in plots with areas of exposed soil or uneven plant establishment (Deery et al., 2016; Jones and Sirault, 2014). As in this study the temperature of the aerial sensor was lower than terrestrial data, it seems that the influence of the environmental conditions and the distance between plant surface and the drone (Tattaris et al., 2016) was stronger than the influence of the mixed pixels.

The strongest limitation to UAVs are the small payload for cameras and sensors, battery endurance, and the susceptibility to environmental conditions, such as wind and rain and the computing power needed to assemble and analyze the orthophotos (Deery et al., 2016). However, the short duration of measurements, easy repeatability and high heritability of the data promote UAVs as a possible tool for breeders' decisions in field trials (Deery et al., 2016).

5.4. Identification of drought and heat stress tolerant varieties

Calculating the rank sum of certain traits for each variety across multiple years, helps to identify varieties performing well under different environmental conditions. As abiotic stress conditions do not occur every year or in regular intervals, it is an important trait for crops to show high grain and high yield stability yield in a wide range of environments, under stress and favorable conditions (Dodig et al., 2012; Farooq et al., 2012). As visible in Table 13, a low rank sum indicated a high grain yield across years, which in this study was mainly shown by Eastern European varieties. In the top 50% of rank sums (16 varieties) only two German varieties can be found, both hybrids (*Hyfi*, *Hybery*). The highest ranked German line (*Mulan*) came in on 18th. Zörb et al. (2017) found that hybrids showed less yield reduction under drought compared to line varieties, comparing drought stressed plots in a rainout shelter with open field conditions. Schittenhelm et al. (2019)

reported an average yield advantage of 7.9% of hybrids over lines in a trial comparing drought stress plots in a rain out shelter and irrigated field plots. The average yield of hybrids in this study was higher than of German lines in 2017 and 2019 (cf. Figure 4A) but the differences between the four hybrid varieties were large. While *Hyfi* and *Hybery* showed an average yield of more than 6.5 t/ha across all years and a medium rank sum (Table 25), *Hystar* (5.32 t/ha, rank sum 100) and *Hybred* (4.70 t/ha, rank sum 123) were amongst the worst performing varieties. Regarding *Hyfi* and *Hystar*, the results are in accordance with Buczek (2020 and Guță and Marin (2020) who also detected higher average grain yield in *Hyfi* (7.68 t/ha (Buczek, 2020); 7.02 t/ha (Guță and Marin, 2020)) than in *Hystar* (7.15 t/ha (Buczek, 2020); 6.8 t/ha (Guță and Marin, 2020)). Both did not report any irrigation of the trials. On the other hand Gupta et al. (2019) and Schittenhelm et al. (2019) reported of good results from *Hystar* with high and stable yields under drought conditions, as it is also mentioned by the breeder (<https://www.saaten-union.com/index.cfm/action/varieties/cul/296/v/1501.html>, accessed May, 24, 2021). Literature mentioning average yield data of the German varieties is scarce. However, the Food and Agriculture Organization of the United Nations (FAO) reported an average yield of 6.67-7.64 t/ha of winter wheat in Germany between 2017 and 2019 (<http://www.fao.org/faostat/en/#data/QC>, accessed May 24, 2021). The national variety trials in the Tertiary Hill Country in Southern Bavaria included eight of the varieties used in this study (*Elixer*, *Genius*, *JB Asano*, *Kerubino*, *Kometus*, *Patras*, *Rumor* and *Tobak*) and showed an average yield of 7.9-11.0 t/ha, depending on variety and year (<https://www.lfl.bayern.de/ipz/getreide/019108/index.php#>, accessed May 24, 2021). Under severe drought stress (2017 and non-irrigated plots in 2019), all varieties showed considerably lower grain yield in the field trial in Moldova than the average yield in Germany, considering both databases the FAO and the national variety trials. In 2018, six varieties (*Hyfi*, *Mulan*, *Elixer*, *Discus*, *Colonia*, and *Kerubino*) showed higher yields than averaged in Germany; in irrigated plots, it was *Hyfi* and *Hybery* (Table 13).

Comparing the effects of combined heat and drought stress to heat stress only, was only possible in 2019 with the irrigated part of the trial. However, as visible in Table 13, also in irrigated plots the rank number of German varieties was higher than of Eastern European varieties, indicating lower grain yield. Again, *Hyfi* and *Hybery* showed good grain yield under irrigation, whereas the other hybrids and most of the line varieties did not take big advantage from the irrigation. The advantage through irrigation was very different between the varieties. The ranking of *Acord*, *Colonia*, *Hyfi*, *Kuialnik*, *Numitor*, and *Zolotocolosa* was considerably better (≥ 5 ranks) under irrigation than under drought stress, whereas *Clasic*, *Elixer*, *Genius*, *Impression*, *Kerubino*, *Mulan*, *Patras*, *Savant*, and *Transitor* had a higher rank number (≥ 5 ranks) under irrigation. Seeing that the

majority of these varieties were from Germany indicates that the irrigation was beneficial for plant establishment and growth. However, as the NDVI values of irrigated plots were at a higher level for a long period (cf. Figure 16), a delayed start of the grain filling process, resulting in small and light grains and a reduced grain yield, is suggested. All wheat varieties had a higher absolute grain yield in irrigated than in drought stress plots. The fact that the aforementioned came on a higher rank number, showed that the varieties benefitted from irrigation to different extents.

This can also be transferred to the rank sum across multiple years. A high rank sum despite high average grain yield (e.g. *Hybery*, Table 25) indicates that the variety has good yield, but others are better under stress conditions. In this case, many Eastern European varieties showed a lower rank sum. On the other hand, low average yield can occur in the combination with a low rank sum, leading to a position high up in the ranking, and suggests a high yield stability. Although the yield level might not be very high, the respective variety can withstand stress better than others can and does not show too much yield reduction in non-optimal environmental conditions.

The high correlations between the rank sums of grain yield and other parameters (Figure 19) showed that the grain N uptake and CID were closely positively related to grain yield and show similar reactions to heat or combined heat and drought. The canopy temperature seemed not to be such a closely related selection option, not even within one group of origin.

5.4.1. Identification of different strategies against abiotic stress

From the results of this study, a tendency is visible how the varieties from different origins cope with abiotic stress. The Eastern European varieties often showed a higher CID (Figure 10) and canopy temperature (Figure 16D) than German varieties, especially lines, whilst maintaining a comparable level of RLWC (Figure 11). These findings suggest two possible strategies: The first one is that the Eastern European transpired less water because they had a higher tolerance towards heat, therefore had a lower water loss than German varieties, could keep their stomata open and show a high CID. The second possibility is the formation of a larger and deeper root system than German varieties, allowing them to reach into deeper soil levels and gain access to more water supplies (Blum, 2005; Turner et al., 2001). It is very likely that both mechanisms contribute to a certain extent (Ludlow, 1989 in De Micco and Aronne, 2012). The heat could be tolerated as long as sufficient water is available. Towards the end of the growing

period, the stress can become too intense, causing a decrease in CID. However, it was still less pronounced than in German varieties.

Eastern European varieties were bred for a shorter vegetation period and therefore have a genetic predisposition for an *escape* strategy from severe heat and drought stress. In combination with the *tolerance* strategy against heat stress, they were able to produce a higher grain yield than German varieties. Similar results were found by Mäkinen et al. (2018) who reported a better tolerance to high temperatures in cultivars from southern Europe compared to cultivars from central Europe. The German varieties are adapted to a longer vegetation period and moderate climate conditions. They showed an *avoidance* strategy against water loss and closed their stomata and an *escape* strategy with premature senescence, a shortened grain filling period and severe yield reduction. However, no *tolerance* of heat stress was observed. For both groups of origin, the additional water supply through irrigation in 2019 brought considerable advantage for the formation of grain yield (Figure 4A) and helped to withstand high temperatures.

One of the main goals in wheat research in Germany is to breed and establish varieties for a changing climate. Landraces often show a high degree of adaptation to the local conditions of their origin (Dodig et al., 2012). Using genetic material of landraces from regions, where weather conditions today are similar to those predicted for Western Europe and Germany can help to prepare the wheat cultivation for the future (Adu et al., 2011; Ceccarelli et al., 1991; Trnka et al., 2014). The potential of this genetic resource should be taken into consideration, as heat stress during sensitive growth stage, such as anthesis and grain filling, is very likely to occur more often due to climate change (Mäkinen et al., 2018; Semenov and Shewry, 2011). However, Mäkinen et al. (2018) points out that the average yield under drought can be reduced by up to 50%, even if adapted varieties are grown. In a simulation including spring and winter wheat cultivars, Asseng et al. (2014) predicted a grain yield reduction of 6% per degree increase in global mean temperature. Considering an average grain yield of winter wheat in Germany of 7.49 t/ha between 2000-2019 (<http://www.fao.org/faostat/en/#data/QC>, accessed May 24, 2021), those findings can be transferred to the results of this study. While the annual average temperature in Bălți is only 1.3 °C higher than in Freising (Climate-Data, 2020a, 2020b), the long-term average temperature during the growing season, from April through July, is 3.15°C higher (Table 2). Such a strong temperature increase during the most susceptible growth phases could reduce grain yield in Germany by ca. 18.9% (ca. 1.42 t/ha) to an average yield of ca. 6.08 t/ha. In the three years of field trials, the temperature difference was 2.48°C, which would result in a reduction of ca. 14.9% (1.1 t/ha) to ca. 6.38 t/ha. The average yield of German varieties across all trials in this

study was even lower (5.50 t/ha), most likely due the combination of heat with drought stress.

A highly desirable combination of traits for future wheat varieties would be a high grain yield potential with a high heat tolerance (Semenov and Shewry, 2011), a short growth period and early maturity (Trnka et al., 2014) in order to start grain filling earlier (Porter and Gawith, 1999), and a high grain filling rate, making the cultivars more tolerant to high temperatures (Wardlaw and Moncur, 1995), and compensating a shorter grain filling duration (Dias and Lidon, 2009).

6. Conclusion

6.1. Growth and development of wheat under abiotic stress

The heat and drought stress during the field trial affected all parts of the plants' physiology and all stages of growth and development. Compared to conditions in Germany, the growth period for wheat is shorter in the Republic of Moldova, due to high temperatures and drought in the summer months, to which German varieties are not adapted. Under these conditions, they do not have sufficient time to complete their grain filling stages, since they start the grain filling later. This leads to light and small grains, less grains per ear and subsequently to yield reduction. The beginning and the duration of grain filling was highly variable between the different groups of origins, and dependent on the weather conditions of each year, i.e. the timing of the abiotic stress. In the variety set of Eastern European lines, German hybrids and German lines, yield reductions were strongest for German lines. The hybrids are known to be more stress tolerant and showed higher yields in this study. The stay green trait of German varieties seemed to be only of limited advantage and is surpassed by physiological adaptation, as seen in Eastern European lines. Higher precipitation and irrigation, respectively, increased the number of tillers and ears per square meter, the TGW and percentage of large grains, the N uptake of grains and the total grain yield per hectare. The positive effect was clearly visible in the protein content of 2019, when in irrigated plots high protein content was found in combination with higher grain yield than in drought stressed plots. Across all years, the Eastern European lines showed higher yield but lower protein content than most German varieties. The correlation of grain yield with TGW was higher than with the number of grains per ear and per square meter. This indicates that sufficient grain filling is important for the yield. Also, a high heritability for TGW and HI was found, which makes

them useful as secondary traits for selection. The availability and uptake of nitrogen are reduced under drought. Across years, the N content of grains – and therefore the protein content – showed a contrary picture to the grain yield. High N content most often came along with reduced yield. Especially the German lines had a higher N content, but low yield in drought stressed plots. Eastern European lines tended to have higher grain yield with lower N/protein content. The N uptake was higher in Eastern European lines, due to the higher weight of the grain samples. This was also visible in the correlations.

6.2. Impact of heat and drought on relative leaf water content, canopy temperature, and carbon isotope discrimination

The RLWC, CID and canopy temperature are closely linked through the control of stomata opening and transpiration. The CID of all varieties decreased during the growing period in all years, with German varieties showing lower CID than Eastern European lines in most samples. The higher level of CID in Eastern European lines indicated a higher tolerance against abiotic stress. Correlations between CID and grain yield were found to be meaningful only across all varieties, not within single groups of origin. The canopy temperature was shown to increase in plants that are not well adapted to drought stress. They reduced transpirational water to avoid drought damage to the tissue and closed their stomata, which led to a higher temperature and fits with the results of a reduced CID due to a reduced CO₂ uptake. Even in well-adapted varieties, the RLWC of the leaves decreased with progressing growth in droughty conditions. However, it is an error-prone and time-consuming method so that the environmental conditions can change during the sampling. Therefore, a distinct difference between the varieties was not detectable. These challenges were also reflected in the heritability, where the RLWC showed much lower h²-values than the CID. The heritability of CID was comparable for leaves and grains.

6.3. Use of terrestrial and aerial high-throughput phenotyping for identification of stress tolerant varieties

The time course of the vegetation indices and the canopy temperature was similar across the years. It varied slightly due to different precipitation and temperature patterns. The ranking of index values, and temperature, respectively, for the three groups of origin was comparable across all years. The WI and canopy temperature were more susceptible for daily temperature change of single precipitation events, than the NDVI and REIP were.

The correlations of the vegetation indices and harvest and biomass parameters also differed across years, but delivered a similar picture and were found to be stronger at milk ripeness than at anthesis. The strongest correlations were found for the grain yield, TGW, and HI with NDVI, REIP, WI and NWI 1-4, whereas the number of grains per ear and tillers or ears per square meter could not reliably be assessed with a spectrometer or thermal camera. Correlations with the N content and N uptake were found with data from the HandySpec but not from the drone. Correlations with thermal data were inconsistent and rather incidental.

In general, the data of the terrestrial (HandySpec/Fluke) and aerial (Sequoia/DuetT) sensors were comparable. The single ratios, NDVI and canopy temperature showed a very good correlation between the sensors. Using a drone is associated with high acquisition costs and needs a higher computational power to analyze the measurements, but it also brings the advantage of much faster data acquisition and less change of conditions during the measurement.

6.4. Identification of drought and heat stress tolerant varieties

The combination of averaged yield data and the calculation of rank sums can help to identify varieties that are more tolerant to abiotic stress conditions. From this study, it is visible that the varieties showed different strategies to cope with the stress conditions. They varied depending on the environmental conditions where the varieties originated. Landraces are an important and diverse genetic resource pool to be used in wheat breeding and to prepare wheat for the conditions in a changing climate. Highly desirable is a high production potential in combination with good tolerance against heat and drought, such as the adaptation to a shorter vegetation period, early maturity and a high grain filling rate to ensure high grain yield.

7. Literature

Abu-Zaitoun, S., Chandrasekhar, K., Assili, S., Shtaya, M., Jamous, R., Mallah, O., Nashef, K., Sela, H., Distelfeld, A., Alhajaj, N., et al. (2018). Unlocking the Genetic Diversity within a Middle-East Panel of Durum Wheat Landraces for Adaptation to Semi-arid Climate. *Agronomy* 8, 233.

Adu, M.O., Sparkes, D.L., Parmar, A., and Yawson, D.O. (2011). Stay green in wheat: Comparative study of modern bread wheat and ancient wheat cultivars. 6, 10.

Al-Khatib, K., and Paulsen, G.M. (1990). Photosynthesis and Productivity during High-Temperature Stress of Wheat Genotypes from Major World Regions. *Crop Sci.* 30, 1127.

Amani, I., Fischer, R.A., and Reynolds, M.P. (1996). Canopy Temperature Depression Association with Yield of Irrigated Spring Wheat Cultivars in a Hot Climate. *J. Agron. Crop Sci.* 176, 119–129.

Angus, J., and Moncur, M. (1977). Water stress and phenology in wheat. *Aust. J. Agric. Res.* 28, 177.

Aparicio, N., Villegas, D., Casadesus, J., Araus, J.L., and Royo, C. (2000). Spectral vegetation indices as nondestructive tools for determining durum wheat yield. *Agron. J.* 92, 83–91.

Apel, K., and Hirt, H. (2004). Reactive Oxygen Species: Metabolism, Oxidative Stress, and Signal Transduction. *Annu. Rev. Plant Biol.* 55, 373–399.

Araus, J.L., and Cairns, J.E. (2014). Field high-throughput phenotyping: the new crop breeding frontier. *Trends Plant Sci.* 19, 52–61.

Araus, J., Slafer, G., Reynolds, M., and Royo, C. (2002). Plant breeding and drought in C3 cereals: what should we breed for? *Ann. Bot.* 89, 925–940.

Asseng, S., Ewert, F., Martre, P., Rötter, R.P., Lobell, D.B., Cammarano, D., Kimball, B.A., Ottman, M.J., Wall, G.W., White, J.W., et al. (2014). Rising temperatures reduce global wheat production. *Nat. Clim. Change* 5, 143.

Ayeneh, A., van Ginkel, M., Reynolds, M.P., and Ammar, K. (2002). Comparison of leaf, spike, peduncle and canopy temperature depression in wheat under heat stress. *Field Crops Res.* 79, 173–184.

Babar, M.A., Reynolds, M.P., van Ginkel, M., Klatt, A.R., Raun, W.R., and Stone, M.L. (2006a). Spectral Reflectance Indices as a Potential Indirect Selection Criteria for Wheat Yield under Irrigation. *Crop Sci.* 46, 578.

Babar, M.A., Reynolds, M.P., van Ginkel, M., Klatt, A.R., Raun, W.R., and Stone, M.L. (2006b). Spectral Reflectance to Estimate Genetic Variation for In-Season Biomass, Leaf Chlorophyll, and Canopy Temperature in Wheat. *Crop Sci.* 46, 1046.

Bacelar, E.L.V.A., Moutinho-Pereira, J.M., Gonçalves, B.M.C., Brito, C.V.Q., Gomes-Laranjo, J., Ferreira, H.M.F., and Correia, C.M. (2012). Water Use Strategies of Plants Under Drought Conditions. In *Plant Responses to Drought Stress: From Morphological to Molecular Features*, R. Aroca, ed. (Berlin, Heidelberg: Springer Berlin Heidelberg), pp. 145–170.

- Barlow, K.M., Christy, B.P., O'Leary, G.J., Riffkin, P.A., and Nuttall, J.G. (2015). Simulating the impact of extreme heat and frost events on wheat crop production: A review. *Field Crops Res.* *171*, 109–119.
- Barnabás, B., Jäger, K., and Fehér, A. (2008). The effect of drought and heat stress on reproductive processes in cereals. *Plant Cell Environ.* *31*, 11–38.
- Bates, D., Mächler, M., Bolker, B., and Walker, S. (2015). Fitting Linear Mixed-Effects Models Using **lme4**. *J. Stat. Softw.* *67*.
- Becker, E., and Schmidhalter, U. (2017). Evaluation of Yield and Drought Using Active and Passive Spectral Sensing Systems at the Reproductive Stage in Wheat. *Front. Plant Sci.* *8*.
- Becker, H.C., and Leon, J. (1988). Stability Analysis in Plant Breeding. *Plant Breed.* *101*, 1–23.
- Bloem, J., de Ruiter, P.C., Koopman, G.J., Lebbink, G., and Brussaard, L. (1992). Microbial numbers and activity in dried and rewetted arable soil under integrated and conventional management. *Soil Biol. Biochem.* *24*, 655–665.
- Blum, A. (1996). Yield potential and drought resistance: are they mutually exclusive? In *Increasing Yield Potential in Wheat: Breaking the Barriers*, (Mexico DF CIMMYT), pp. 90–100.
- Blum, A. (2005). Drought resistance, water-use efficiency, and yield potential—are they compatible, dissonant, or mutually exclusive? *Aust. J. Agric. Res.* *56*, 1159.
- Blum, A. (2014). Genomics for drought resistance – getting down to earth. *Funct. Plant Biol.* *41*, 1191.
- Bogard, M., Jourdan, M., Allard, V., Martre, P., Perretant, M.R., Ravel, C., Heumez, E., Orford, S., Snape, J., Griffiths, S., et al. (2011). Anthesis date mainly explained correlations between post-anthesis leaf senescence, grain yield, and grain protein concentration in a winter wheat population segregating for flowering time QTLs. *J. Exp. Bot.* *62*, 3621–3636.
- Boincean, B., and Dent, D. (2019). *Farming the Black Earth: Sustainable and Climate-Smart Management of Chernozem Soils* (Cham: Springer International Publishing).
- Bokshi, A.I., Tan, D.K.Y., Thistlethwaite, R.J., Trethowan, R., and Kunz, K. (2021). Impact of elevated CO₂ and heat stress on wheat pollen viability and grain production. *Funct. Plant Biol.*
- Borrell, A., Hammer, G., and Oosterom, E. (2001). Stay-green: A consequence of the balance between supply and demand for nitrogen during grain filling? *Ann. Appl. Biol.* *138*, 91–95.
- Bourgault, M., James, A.T., and Dreccer, M.F. (2017). Pot size matters revisited: does container size affect the response to elevated CO₂ and our ability to detect genotypic variability in this response in wheat? *Funct. Plant Biol.* *44*, 52.
- Broge, N., Thomsen, A., and Andersen, P. (2003). Comparison of selected vegetation indices as indicators of crop status. *Geoinformation Eur.-Wide Integr.* 591–596.

- Bruns, R., and Peterson, C.J. (1997). Yield and stability factors associated with hybrid wheat. In *Wheat: Prospects for Global Improvement*, H.-J. Braun, F. Altay, W.E. Kronstad, S.P.S. Beniwal, and A. McNab, eds. (Dordrecht: Springer Netherlands), pp. 23–27.
- Buczek, J. (2020). Quality and productivity of hybrid wheat depending on the tillage practices. *Plant Soil Environ.* 66, 415–420.
- Cao, X., Mondal, S., Cheng, D., Wang, C., Liu, A., Song, J., Li, H., Zhao, Z., and Liu, J. (2015). Evaluation of agronomic and physiological traits associated with high temperature stress tolerance in the winter wheat cultivars. *Acta Physiol. Plant.* 37.
- Castrillo, M., Fernandez, D., Calcagno, A.M., Trujillo, I., and Guenni, L. (2001). Responses of Ribulose-1,5-Bisphosphate Carboxylase, Protein Content, and Stomatal Conductance to Water Deficit in Maize, Tomato, and Bean. *Photosynthetica* 39, 221–226.
- Cattivelli, L., Rizza, F., Badeck, F.-W., Mazzucotelli, E., Mastrangelo, A.M., Francia, E., Marè, C., Tondelli, A., and Stanca, A.M. (2008). Drought tolerance improvement in crop plants: An integrated view from breeding to genomics. *Field Crops Res.* 105, 1–14.
- Ceccarelli, S., Acevedo, E., and Grando, S. (1991). Breeding for yield stability in unpredictable environments: single traits, interaction between traits, and architecture of genotypes. *Euphytica* 56, 169–185.
- Choubin, B., Soleimani, F., Pirnia, A., Sajedi-Hosseini, F., Alilou, H., Rahmati, O., Melesse, A.M., Singh, V.P., and Shahabi, H. (2019). Effects of drought on vegetative cover changes: Investigating spatiotemporal patterns. In *Extreme Hydrology and Climate Variability*, (Elsevier), pp. 213–222.
- Christopher, J.T., Manschadi, A.M., Hammer, G.L., and Borrell, A.K. (2008). Developmental and physiological traits associated with high yield and stay-green phenotype in wheat. *Aust. J. Agric. Res.* 59, 354.
- Climate-Data (2020a). Bălți climate: Average Temperature, weather by month, Bălți weather averages, accessed 20 October 2020. <https://en.climate-data.org/europe/moldova/balti/balti-3309>.
- Climate-Data (2020b). Freising climate: Average Temperature, weather by month, Freising weather averages, accessed 20 October 2020. <https://en.climate-data.org/europe/germany/free-state-of-bavaria/freising-7579>.
- Condon, A.G. (2004). Breeding for high water-use efficiency. *J. Exp. Bot.* 55, 2447–2460.
- Condon, A., Farquhar, G., and Richards, R. (1990). Genotypic Variation in Carbon Isotope Discrimination and Transpiration Efficiency in Wheat. *Leaf Gas Exchange and Whole Plant Studies. Funct. Plant Biol.* 17, 9.
- Condon, A.G., Richards, R.A., Rebetzke, G.J., and Farquhar, G.D. (2002). Improving intrinsic water-use efficiency and crop yield. *Crop Sci.* 42, 122–131.
- Cooper, M., Gho, C., Leafgren, R., Tang, T., and Messina, C. (2014). Breeding drought-tolerant maize hybrids for the US corn-belt: discovery to product. *J. Exp. Bot.* 65, 6191–6204.

- Dambreville, A., Griolet, M., Rolland, G., Dauzat, M., Bédiée, A., Balsera, C., Muller, B., Vile, D., and Granier, C. (2016). Phenotyping oilseed rape growth-related traits and their responses to water deficit: the disturbing pot size effect. 11.
- De Micco, V., and Aronne, G. (2012). Morpho-Anatomical Traits for Plant Adaptation to Drought. In *Plant Responses to Drought Stress: From Morphological to Molecular Features*, R. Aroca, ed. (Berlin, Heidelberg: Springer Berlin Heidelberg), pp. 37–61.
- De Souza, P.I., Egli, D.B., and Bruening, W.P. (1997). Water Stress during Seed Filling and Leaf Senescence in Soybean. *Agron. J.* 89, 807–812.
- Deery, D.M., Rebetzke, G.J., Jimenez-Berni, J.A., James, R.A., Condon, A.G., Bovill, W.D., Hutchinson, P., Scarrow, J., Davy, R., and Furbank, R.T. (2016). Methodology for High-Throughput Field Phenotyping of Canopy Temperature Using Airborne Thermography. *Front. Plant Sci.* 7.
- Denčić, S., Kastori, R., Kobiljski, B., and Duggan, B. (2000). Evaluation of grain yield and its components in wheat cultivars and landraces under near optimal and drought conditions. 10.
- Derkx, A.P., Orford, S., Griffiths, S., Foulkes, M.J., and Hawkesford, M.J. (2012). Identification of Differentially Senescing Mutants of Wheat and Impacts on Yield, Biomass and Nitrogen Partitioning. *J. Integr. Plant Biol.* 54, 555–566.
- Desclaux, D., and Roumet, P. (1996). Impact of drought stress on the phenology of two soybean (*Glycine max* L. Merr) cultivars. *Field Crops Res.* 10.
- Dias, A.S., and Lidon, F.C. (2009). Evaluation of Grain Filling Rate and Duration in Bread and Durum Wheat, under Heat Stress after Anthesis. *J. Agron. Crop Sci.* 195, 137–147.
- Dias, M.C., and Bruggemann, W. (2010). Limitations of photosynthesis in *Phaseolus vulgaris* under drought stress: gas exchange, chlorophyll fluorescence and Calvin cycle enzymes. *Photosynthetica* 48, 96–102.
- Dodig, D., Zorić, M., Kandić, V., Perović, D., and Šurlan-Momirović, G. (2012). Comparison of responses to drought stress of 100 wheat accessions and landraces to identify opportunities for improving wheat drought resistance: Wheat genotypes response to drought stress. *Plant Breed.* 131, 369–379.
- Doleschel, P., and Frahm, J. (2014). *Landwirtschaftlicher Pflanzenbau: Grundlagen des Acker- und Pflanzenbaus, der guten fachlichen Praxis und der Verfahrenstechnik sowie der Agrarmeteorologie und des Klimawandels, Produktions- und Verfahrenstechnik der Kulturpflanzen, Dauergrünland - Sonderkulturen, Nachwachsende Rohstoffe, Ökologischer Landbau, Naturschutz und Landschaftspflege, Feldversuchswesen, Waldbewirtschaftung* (BLV Buchverlag).
- Dordas, C.A., and Sioulas, C. (2009). Dry matter and nitrogen accumulation, partitioning, and retranslocation in safflower (*Carthamus tinctorius* L.) as affected by nitrogen fertilization. *Field Crops Res.* 110, 35–43.
- Dupont, F.M., and Altenbach, S.B. (2003). Molecular and biochemical impacts of environmental factors on wheat grain development and protein synthesis. *J. Cereal Sci.* 38, 133–146.

- Edwards, G.E., and Walker, D. (1983). C3, C4: Mechanisms and cellular and environmental regulation of photosynthesis (University of California Press, Berkeley, CA).
- Erdle, K., Mistele, B., and Schmidhalter, U. (2011). Comparison of active and passive spectral sensors in discriminating biomass parameters and nitrogen status in wheat cultivars. *Field Crops Res.* 124, 74–84.
- Erice, G., Sanz-Sáez, A., Aranjuelo, I., Irigoyen, J.J., and Sánchez-Díaz, M. (2012). Future environmental conditions will limit yield in N₂ fixing alfalfa. In *Plant Responses to Drought Stress*, (Springer), pp. 363–382.
- Eurostat (2018). *Agriculture, forestry and fishery statistics - 2018 edition*.
- FAO (2017). *The future of food and agriculture: trends and challenges* (Rome: Food and Agriculture Organization of the United Nations).
- Farooq, M., Wahid, A., Kobayashi, N., Fujita, D., and Basra, S.M.A. (2009a). Plant drought stress: effects, mechanisms and management. *Agron. Sustain. Dev.* 29, 185–212.
- Farooq, M., Basra, S.M.A., Wahid, A., Ahmad, N., and Saleem, B.A. (2009b). Improving the Drought Tolerance in Rice (*Oryza sativa* L.) by Exogenous Application of Salicylic Acid. *J. Agron. Crop Sci.* 195, 237–246.
- Farooq, M., Kobayashi, N., Ito, O., Wahid, A., and Serraj, R. (2010). Broader leaves result in better performance of indica rice under drought stress. *J. Plant Physiol.* 167, 1066–1075.
- Farooq, M., Bramley, H., Palta, J.A., and Siddique, K.H.M. (2011). Heat Stress in Wheat during Reproductive and Grain-Filling Phases. *Crit. Rev. Plant Sci.* 30, 491–507.
- Farooq, M., Hussain, M., Wahid, A., and Siddique, K.H.M. (2012). Drought Stress in Plants: An Overview. In *Plant Responses to Drought Stress: From Morphological to Molecular Features*, R. Aroca, ed. (Berlin, Heidelberg: Springer Berlin Heidelberg), pp. 1–33.
- Farquhar, G., O'Leary, M., and Berry, J. (1982). On the Relationship Between Carbon Isotope Discrimination and the Intercellular Carbon Dioxide Concentration in Leaves. *Funct. Plant Biol.* 9, 121.
- Farquhar, G.D., Ehleringer, J.R., and Hubick, K.T. (1989). Carbon isotope discrimination and photosynthesis. *Annu. Rev. Plant Biol.* 40, 503–537.
- Fischer, R., and Kohn, G. (1966). The relationship of grain yield to vegetative growth and post-flowering leaf area in the wheat crop under conditions of limited soil moisture. *Aust. J. Agric. Res.* 17, 281.
- Fischer, R.A., Howe, G.N., and Ibrahim, Z. (1993). Irrigated spring wheat and timing and amount of nitrogen fertilizer. I. Grain yield and protein content. *Field Crops Res.* 33, 37–56.
- Fischer, R.A., Rees, D., Sayre, K.D., Lu, Z.-M., Condon, A.G., and Saavedra, A.L. (1998). Wheat Yield Progress Associated with Higher Stomatal Conductance and Photosynthetic Rate, and Cooler Canopies. *Crop Sci.* 38, 1467.

- Gad, S.C. (2010). 3.13 - Statistical Methods in Toxicology. In *Comprehensive Toxicology (Second Edition)*, C.A. McQueen, ed. (Oxford: Elsevier), pp. 183–197.
- Gobin, A. (2018). Weather related risks in Belgian arable agriculture. *Agric. Syst.* 159, 225–236.
- Govaerts, B., Verhulst, N., Sayre, K.D., De Corte, P., Goudeseune, B., Lichter, K., Crossa, J., Deckers, J., and Dendooven, L. (2007). Evaluating spatial within plot crop variability for different management practices with an optical sensor? *Plant Soil* 299, 29–42.
- Gracia-Romero, A., Kefauver, S.C., Fernandez-Gallego, J.A., Vergara-Díaz, O., Nieto-Taladriz, M.T., and Araus, J.L. (2019). UAV and Ground Image-Based Phenotyping: A Proof of Concept with Durum Wheat. *Remote Sens.* 11, 1244.
- Gregersen, P.L., Holm, P.B., and Krupinska, K. (2008). Leaf senescence and nutrient remobilisation in barley and wheat. *Plant Biol.* 13.
- Grenzdörffer, G.J., Engel, A., and Teichert, B. (2008). The photogrammetric potential of low-cost UAVs in forestry and agriculture. *Int. Arch. Photogramm. Remote Sens. Spat. Inf. Sci.* 31, 1207–1214.
- Grigorova, B., Vassileva, V., Klimchuk, D., Vaseva, I., Demirevska, K., and Feller, U. (2012). Drought, high temperature, and their combination affect ultrastructure of chloroplasts and mitochondria in wheat (*Triticum aestivum* L.) leaves. *J. Plant Interact.* 7, 204–213.
- Gupta, P.K., Balyan, H.S., Gahlaut, V., Saripalli, G., Pal, B., Basnet, B.R., and Joshi, A.K. (2019). Hybrid wheat: past, present and future. *Theor. Appl. Genet.* 132, 2463–2483.
- Guță, B.A., and Marin, D.I. (2020). Grain yield and yield components on an assortment of winter wheat (*Triticum aestivum* L.) genotypes cultivated under conditions of A.R.D.S. Teleorman. *AAB Bioflux* 12, 45–51.
- Gutierrez, M., Reynolds, M.P., and Klatt, A.R. (2010). Association of water spectral indices with plant and soil water relations in contrasting wheat genotypes. *J. Exp. Bot.* 61, 3291–3303.
- Gutiérrez-Rodríguez, M., Reynolds, M.P., Escalante-Estrada, J.A., and Rodríguez-González, M.T. (2004). Association between canopy reflectance indices and yield and physiological traits in bread wheat under drought and well-irrigated conditions. *Crop Pasture Sci.* 55, 1139–1147.
- Guyot, G., Baret, F., and Major, D. (1988). High spectral resolution: Determination of spectral shifts between the red and the near infrared. *Int. Arch. Photogramm. Remote Sens.* 11.
- Hackl, H., Baresel, J.P., Mistele, B., Hu, Y., and Schmidhalter, U. (2012). A Comparison of Plant Temperatures as Measured by Thermal Imaging and Infrared Thermometry: Thermal Imaging and IR Thermometry. *J. Agron. Crop Sci.* 198, 415–429.
- Hackl, H., Hu, Y., and Schmidhalter, U. (2014). Evaluating growth platforms and stress scenarios to assess the salt tolerance of wheat plants. *Funct. Plant Biol.* 41, 860.

- Hafsi, M., Akhter, J., and Monneveux, P. (2007). Leaf Senescence and Carbon Isotope Discrimination in Durum Wheat (*Triticum durum* Desf.) Under Severe Drought Conditions. *Cereal Res. Commun.* 10.
- Hasituya, Li, F., Elsayed, S., Hu, Y., and Schmidhalter, U. (2020). Passive reflectance sensing using optimized two- and three-band spectral indices for quantifying the total nitrogen yield of maize. *Comput. Electron. Agric.* 173, 105403.
- Hawkesford, M., Horst, W., Kichey, T., Lambers, H., Schjoerring, J., Møller, I.S., and White, P. (2012). Functions of Macronutrients. In *Marschner's Mineral Nutrition of Higher Plants (Third Edition)*, P. Marschner, ed. (San Diego: Academic Press), pp. 135–189.
- Herbst, M., and Frühauf, C. (2018). Wird das Wasser knapp? Wasserbedarf und -verfügbarkeit heute und in Zukunft. In *Bewässerung in Der Landwirtschaft*, (Braunschweig: Thünen-Institute), pp. 1–9.
- Holland, J.B., Nyquist, W.E., and Cervantes-Martínez, C.T. (2003). Estimating and interpreting heritability for plant breeding: an update. *Plant Breed. Rev.* 22, 9–112.
- Hörtensteiner, S., and Feller, U. (2002). Nitrogen metabolism and remobilization during senescence. *J. Exp. Bot.* 53, 927–937.
- Hossain, A., Sarker, M., Hakim, M., Lozovskaya, M., and Zvolinsky, V. (2013). Effect of Temperature on Yield and Some Agronomic Characters of Spring Wheat (*Triticum aestivum* L.) Genotypes. *Int. J. Agric. Res. Innov. Technol.* 1, 44–54.
- Hu, Y., Knapp, S., and Schmidhalter, U. (2020). Advancing High-Throughput Phenotyping of Wheat in Early Selection Cycles. *Remote Sens.* 12, 574.
- Hulme, M., Barrow, E.M., Arnell, N.W., Harrison, P.A., Johns, T.C., and Downing, T.E. (1999). Relative impacts of human-induced climate change and natural climate variability. *Nature* 397, 688–691.
- Ihsan, M.Z., El-Nakhawy, F.S., Ismail, S.M., Fahad, S., and daur, I. (2016). Wheat Phenological Development and Growth Studies As Affected by Drought and Late Season High Temperature Stress under Arid Environment. *Front. Plant Sci.* 7.
- Innes, P., and Blackwell, R.D. (1981). The effect of drought on the water use and yield of two spring wheat genotypes. *J. Agric. Sci.* 96, 603–610.
- IPCC (2007). *Climate change 2007: the physical science basis* (Cambridge ; New York: Cambridge University Press).
- IPCC (2012). *Managing the Risks of Extreme Events and Disasters to Advance Climate Change Adaptation: Special Report of the Intergovernmental Panel on Climate Change* (Cambridge: Cambridge University Press).
- Jackson, P., Robertson, M., Cooper, M., and Hammer, G. (1996). The role of physiological understanding in plant breeding; from a breeding perspective. *Field Crops Res.* 49, 11–37.
- Jacob, T., Ritchie, S., Assmann, S.M., and Gilroy, S. (1999). Abscisic acid signal transduction in guard cells is mediated by phospholipase D activity. *Proc. Natl. Acad. Sci.* 96, 12192–12197.

- Jasper, J., Reusch, S., and Link, A. (2009). Active sensing of the N status of wheat using optimized wavelength combination: impact of seed rate, variety and growth stage. *Precis. Agric.* *9*, 23–30.
- Jiang, G.H., He, Y.Q., Xu, C.G., Li, X.H., and Zhang, Q. (2004). The genetic basis of stay-green in rice analyzed in a population of doubled haploid lines derived from an indica by japonica cross. *Theor. Appl. Genet.* *108*, 688–698.
- Jones, H.G., and Sirault, X.R.R. (2014). Scaling of Thermal Images at Different Spatial Resolution: The Mixed Pixel Problem. *17*.
- Kamal, Alnor Gorafi, Abdelrahman, Abdellatef, and Tsujimoto (2019). Stay-Green Trait: A Prospective Approach for Yield Potential, and Drought and Heat Stress Adaptation in Globally Important Cereals. *Int. J. Mol. Sci.* *20*, 5837.
- Kiani, S.P., Talia, P., Maury, P., Grieu, P., Heinz, R., Perrault, A., Nishinakamasu, V., Hopp, E., Gentzbittel, L., Paniego, N., et al. (2007). Genetic analysis of plant water status and osmotic adjustment in recombinant inbred lines of sunflower under two water treatments. *Plant Sci.* *172*, 773–787.
- Kichey, T., Hirel, B., Heumez, E., Dubois, F., and Le Gouis, J. (2007). In winter wheat (*Triticum aestivum* L.), post-anthesis nitrogen uptake and remobilisation to the grain correlates with agronomic traits and nitrogen physiological markers. *Field Crops Res.* *102*, 22–32.
- Kim, S., Gitz, D., Sicher, R., Baker, J., Timlin, D., and Reddy, V. (2007). Temperature dependence of growth, development, and photosynthesis in maize under elevated CO₂. *Environ. Exp. Bot.* *61*, 224–236.
- Kimball, B.A., Conley, M.M., Wang, S., Lin, X., Luo, C., Morgan, J., and Smith, D. (2008). Infrared heater arrays for warming ecosystem field plots. *Glob. Change Biol.* *14*, 309–320.
- Kipp, S., Mistele, B., and Schmidhalter, U. (2014). Identification of stay-green and early senescence phenotypes in high-yielding winter wheat, and their relationship to grain yield and grain protein concentration using high-throughput phenotyping techniques. *Funct. Plant Biol.* *41*, 227.
- Köppen, W., and Geiger, R. (1928). *Klimakarte der Erde*.
- Kottek, M., Grieser, J., Beck, C., Rudolf, B., and Rubel, F. (2006). World Map of the Köppen-Geiger climate classification updated. *Meteorol. Z.* *15*, 259–263.
- Kumari, M., Pudake, R.N., Singh, V.P., and 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.
- Kumari, P., Wadood, A., Singh, R., and Kumar, R. (2009). Response of wheat crop to different thermal regimes under the agroclimatic conditions of Jharkhand. *J. Agrometeorol.* *11*, 85–88.
- Lambers, H., and Oliveira, R.S. (2019). *Plant Physiological Ecology* (Cham: Springer International Publishing).

- Li, F., Mistele, B., Hu, Y., Chen, X., and Schmidhalter, U. (2014). Reflectance estimation of canopy nitrogen content in winter wheat using optimised hyperspectral spectral indices and partial least squares regression. *Eur. J. Agron. 52, Part B*, 198–209.
- Li, Y., Ye, W., Wang, M., and Yan, X. (2009). Climate change and drought: a risk assessment of crop-yield impacts. *Clim. Res.* 39, 31–46.
- Lilienthal, H. (2014). Optische Sensoren in der Landwirtschaft: Grundlagen und Konzepte. *J. Für Kult.* 66, 34–41.
- Longin, C.F.H., Mühleisen, J., Maurer, H.P., Zhang, H., Gowda, M., and Reif, J.C. (2012). Hybrid breeding in autogamous cereals. *Theor. Appl. Genet.* 125, 1087–1096.
- Lopes, M.S., and Reynolds, M.P. (2010). Partitioning of assimilates to deeper roots is associated with cooler canopies and increased yield under drought in wheat. *Funct. Plant Biol.* 37, 147.
- Lopes, M.S., and Reynolds, M.P. (2012). Stay-green in spring wheat can be determined by spectral reflectance measurements (normalized difference vegetation index) independently from phenology. *J. Exp. Bot.* 63, 3789–3798.
- Ludlow, M.M. (1989). Strategies of response to water stress. In *Structural and Functional Responses to Environmental Stresses: Water Shortage*, K. Kreeb, H. Richter, and T. Hinckley, eds. (SPB Academic Publishers), pp. 269–281.
- Ludlow, M.M., and Muchow, R.C. (1990). A Critical Evaluation of Traits for Improving Crop Yields in Water-Limited Environments. In *Advances in Agronomy*, (Elsevier), pp. 107–153.
- Lupton, F.G.H. (1966). Translocation of photosynthetic assimilates in wheat. *Ann. Appl. Biol.* 57, 355–364.
- Mäkinen, H., Kaseva, J., Trnka, M., Balek, J., Kersebaum, K.C., Nendel, C., Gobin, A., Olesen, J.E., Bindi, M., Ferrise, R., et al. (2018). Sensitivity of European wheat to extreme weather. *Field Crops Res.* 222, 209–217.
- Malberg, H. (2002). *Meteorologie und Klimatologie: eine Einführung* (Berlin: Springer).
- Mandea, V., and Säulescu, N.N. (2018). Wheat grain size and dimensions in contrasting environments of Eastern and Western Europe. *Romanian Agric. Res.* 35, 45–48.
- Marinello, F., Pezzuolo, A., Chiumenti, A., and Sartori, L. (2016). Technical Analysis of Unmanned Aerial Vehicles (Drones) for Agricultural Applications. *Eng. Rural Dev.* 6.
- Marschner, P., and Rengel, Z. (2012). Nutrient availability in soils. In *Marschner's Mineral Nutrition of Higher Plants (Third Edition)*, (Elsevier), pp. 315–330.
- Matese, A., and Di Gennaro, S.F. (2015). Technology in precision viticulture: a state of the art review. *Int. J. Wine Res.* 69.
- McCance, R.A., and Widdowson, E.M. (2014). *McCance and Widdowson's the Composition of Foods* (Royal Society of Chemistry).
- McMaster, G.S., and Wilhelm, W.W. (2003). Phenological responses of wheat and barley to water and temperature: improving simulation models. *J. Agric. Sci.* 141, 129–147.

- Medrano, H. (2002). Regulation of Photosynthesis of C3 Plants in Response to Progressive Drought: Stomatal Conductance as a Reference Parameter. *Ann. Bot.* *89*, 895–905.
- Melander, L.C., and Saunders, W.H. (1979). Reaction rates of isotopic molecules (John Wiley & Sons).
- Merah, O., Monneveux, P., Nachit, M., and Deléens, E. (1999a). La composition isotopique du carbone, critère intégrateur du fonctionnement photosynthétique: application à l'amélioration génétique du blé dur en conditions méditerranéennes. *Cah. Agric.* *8*, 37–47.
- Merah, O., Deleens, E., and Monneveux, P. (1999b). Grain yield, carbon isotope discrimination, mineral and silicon content in durum wheat under different precipitation regimes. *Physiol. Plant.* *107*, 387–394.
- Merah, O., Deleens, E., Al Hakimi, A., and Monneveux, P. (2001). Carbon Isotope Discrimination and Grain Yield Variations among Tetraploid Wheat Species Cultivated under Contrasting Precipitation Regimes. *J. Agron. Crop Sci.* *186*, 129–134.
- Meyre, D., Leonardi, A., Brisson, G., and Vartanian, N. (2001). Drought-adaptive mechanisms involved in the escape/tolerance strategies of *Arabidopsis Landsberg erecta* and Columbia ecotypes and their F1 reciprocal progeny. *J. Plant Physiol.* *158*, 1145–1152.
- Mistele, B., and Schmidhalter, U. (2008). Estimating the nitrogen nutrition index using spectral canopy reflectance measurements. *Eur. J. Agron.* *29*, 184–190.
- Mistele, B., and Schmidhalter, U. (2010). Tractor-Based Quadrilateral Spectral Reflectance Measurements to Detect Biomass and Total Aerial Nitrogen in Winter Wheat. *Agron. J.* *102*, 499.
- Mistele, B., Gutser, R., and Schmidhalter, U. (2004). Validation of field-scaled spectral measurements of the nitrogen status in winter wheat. pp. 1187–1195.
- Mittler, R. (2006). Abiotic stress, the field environment and stress combination. *Trends Plant Sci.* *11*, 15–19.
- Mohamed, E.S., Saleh, A.M., Belal, A.B., and Gad, A. (2018). Application of near-infrared reflectance for quantitative assessment of soil properties. *Egypt. J. Remote Sens. Space Sci.* *21*, 1–14.
- Morales, D., Rodriguez, P., Dell'Amico, J., Nicolas, E., Torrecillas, A., and Sanchez-Blanco, M.J. (2003). High-Temperature Preconditioning and Thermal Shock Imposition Affects Water Relations, Gas Exchange and Root Hydraulic Conductivity in Tomato. *Biol. Plant.* *46*, 203–208.
- Moriondo, M., Giannakopoulos, C., and Bindi, M. (2011). Climate change impact assessment: the role of climate extremes in crop yield simulation. *Clim. Change* *104*, 679–701.
- Mühleisen, J., Piepho, H.-P., Maurer, H.P., Longin, C.F.H., and Reif, J.C. (2014). Yield stability of hybrids versus lines in wheat, barley, and triticale. *Theor. Appl. Genet.* *127*, 309–316.

- Mullan, D., and Pietragalla, J. (2012). Leaf relative water content. *Physiol. Breed. II Field Guide Wheat Phenotyping Mex. CIMMYT* 25–27.
- Müller, M.J., Baltés, K., Werle, D., Lutz, E., Renschler, C., and Richter, G. (1996). *Handbuch ausgewählter Klimastationen der Erde* (Univ. Trier).
- Nahar, K., Ahamed, K.U., and 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. *Not. Sci. Biol.* 2, 51–56.
- Nakicenovic, N., Alcamo, J., Grubler, A., Riahi, K., Roehrl, R., Rogner, H.-H., and Victor, N. (2000). Special report on emissions scenarios (SRES), a special report of Working Group III of the intergovernmental panel on climate change (Cambridge University Press).
- Naruoka, Y., Sherman, J.D., Lanning, S.P., Blake, N.K., Martin, J.M., and Talbert, L.E. (2012). Genetic Analysis of Green Leaf Duration in Spring Wheat. *Crop Sci.* 52, 99–109.
- Natu, A.S., and Kulkarni, S.C. (2016). Adoption and Utilization of Drones for Advanced Precision Farming: A Review. *Int. J. Recent Innov. Trends Comput. Commun.* 4, 3.
- Nawaz, A., Farooq, M., Cheema, S.A., Yasmeen, A., and Wahid, A. (2013). Stay Green Character at Grain Filling Ensures Resistance against Terminal Drought in Wheat. *Int J Agric Biol* 15, 5.
- Olivares-Villegas, J.J., Reynolds, M.P., and McDonald, G.K. (2007). Drought-adaptive attributes in the Seri/Babax hexaploid wheat population. *Funct. Plant Biol.* 34, 189.
- Park, S.-Y., Yu, J.-W., Park, J.-S., Li, J., Yoo, S.-C., Lee, N.-Y., Lee, S.-K., Jeong, S.-W., Seo, H.S., Koh, H.-J., et al. (2007). The Senescence-Induced Staygreen Protein Regulates Chlorophyll Degradation. *Plant Cell* 19, 1649–1664.
- Pask, A.J.D., Pietragalla, J., Mullan, D.M., and Reynolds, M.P. (2012). Physiological breeding II: a field guide to wheat phenotyping (CIMMYT).
- Passioura, J.B. (2006). The perils of pot experiments. *Funct. Plant Biol.* 33, 1075.
- Passioura, J.B. (2012). Phenotyping for drought tolerance in grain crops: when is it useful to breeders? *Funct. Plant Biol.* 39, 851.
- Patel, N.R., Mehta, A.N., and Shekh, A.M. (2001). Canopy temperature and water stress quantification in rainfed pigeonpea (*Cajanus cajan* (L.) Millsp.). *Agric. For. Meteorol.* 109, 223–232.
- Pennypacker, B.W., Leath, K.T., Stout, W.L., and Hill, R.R. (1990). Technique for Simulating Field Drought Stress in the Greenhouse. *Agron. J.* 82, 951–957.
- Peñuelas, J., Filella, I., Biel, C., Serrano, L., and Savé, R. (1993). The reflectance at the 950–970 nm region as an indicator of plant water status. *Int. J. Remote Sens.* 14, 1887–1905.
- Peñuelas, J., Pinol, J., Ogaya, R., and Filella, I. (1997). Estimation of plant water concentration by the reflectance water index WI (R900/R970). *Int. J. Remote Sens.* 18, 2869–2875.

- Petrick, M. (2008). *Landwirtschaft in Moldova*, Discussion Paper, No.117. Leibniz Inst. Agric. Dev. Cent. East. Eur. IAMO Halle Saale 1–38.
- Pinto, R.S., Reynolds, M.P., Mathews, K.L., McIntyre, C.L., Olivares-Villegas, J.-J., and Chapman, S.C. (2010). Heat and drought adaptive QTL in a wheat population designed to minimize confounding agronomic effects. *Theor. Appl. Genet.* 121, 1001–1021.
- Poorter, H., Bühler, J., van Dusschoten, D., Climent, J., and Postma, J.A. (2012). Pot size matters: a meta-analysis of the effects of rooting volume on plant growth. *Funct. Plant Biol.* 39, 839.
- Porter, J.R., and Gawith, M. (1999). Temperatures and the growth and development of wheat: a review. *Eur. J. Agron.* 10, 23–36.
- Porter, J.R., Xie, L., Challinor, A.J., Cochrane, K., Howden, S.M., Iqbal, M.M., Lobell, D.B., and Travasso, M.I. (2014). Food security and food production systems. In *Climate Change 2014: Impacts, Adaptation, and Vulnerability. Part A: Global and Sectoral Aspects. Contribution of Working Group II to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change*, C.B. Field, V.R. Barros, D.J. Dokken, K.J. Mach, M.D. Mastrandrea, T.E. Bilir, M. Chatterjee, K.L. Ebi, Y.O. Estrada, R.C. Genova, et al., eds. (Cambridge University Press, Cambridge, United Kingdom and New York, NY, USA: Cambridge University Press), pp. 485–533.
- Prasad, B., Carver, B.F., Stone, M.L., Babar, M.A., Raun, W.R., and Klatt, A.R. (2007). Potential Use of Spectral Reflectance Indices as a Selection Tool for Grain Yield in Winter Wheat under Great Plains Conditions. *Crop Sci.* 47, 1426.
- Prasad, P.V.V., Staggenborg, S.A., and Ristic, Z. (2008). Impacts of drought and/or heat stress on physiological, developmental, growth, and yield processes of crop plants. *Response Crops Ltd. Water Underst. Model. Water Stress Eff. Plant Growth Process.* 301–355.
- Prashar, A., and Jones, H. (2014). Infra-Red Thermography as a High-Throughput Tool for Field Phenotyping. *Agronomy* 4, 397–417.
- Prey, L., and Schmidhalter, U. (2019). Sensitivity of Vegetation Indices for Estimating Vegetative N Status in Winter Wheat. *Sensors* 19, 3712.
- Prey, L., Hu, Y., and Schmidhalter, U. (2019). Temporal Dynamics and the Contribution of Plant Organs in a Phenotypically Diverse Population of High-Yielding Winter Wheat: Evaluating Concepts for Disentangling Yield Formation and Nitrogen Use Efficiency. *Front. Plant Sci.* 10, 1295.
- Prey, L., Hu, Y., and Schmidhalter, U. (2020). High-Throughput Field Phenotyping Traits of Grain Yield Formation and Nitrogen Use Efficiency: Optimizing the Selection of Vegetation Indices and Growth Stages. *Front. Plant Sci.* 10, 1672.
- Puri, V., Nayyar, A., and Raja, L. (2017). Agriculture drones: A modern breakthrough in precision agriculture. *J. Stat. Manag. Syst.* 20, 507–518.
- Raper, C.D., and Kramer, P.J. (1987). Stress Physiology. In *Soybeans: Improvement, Production and Uses*, 2nd Ed, J.R. Wilcox, ed. (ASA, Madison, WI), pp. 589–641.
- Rashid, A., Stark, J.C., Tanveer, A., and Mustafa, T. (1999). Use of Canopy Temperature Measurements as a Screening Tool for Drought Tolerance in Spring Wheat. *J. Agron. Crop Sci.* 182, 231–238.

- Ratajczak, D., and Górný, A.G. (2012). Water- and nitrogen-dependent alterations in the inheritance mode of transpiration efficiency in winter wheat at the leaf and whole-plant level. *J. Appl. Genet.* *53*, 377–388.
- Ray, J.D., and Sinclair, T.R. (1998). The effect of pot size on growth and transpiration of maize and soybean during water deficit stress. *6*.
- Rebetzke, G.J., Chenu, K., Biddulph, B., Moeller, C., Deery, D.M., Rattey, A.R., Bennett, D., Barrett-Lennard, E.G., and Mayer, J.E. (2013). A multisite managed environment facility for targeted trait and germplasm phenotyping. *Funct. Plant Biol.* *40*, 1.
- Reddy, A.R., Chaitanya, K.V., and Vivekanandan, M. (2004). Drought-induced responses of photosynthesis and antioxidant metabolism in higher plants. *J. Plant Physiol.* *161*, 1189–1202.
- Reynolds, M., Balota, M., Delgado, M., Amani, I., and Fischer, R. (1994). Physiological and Morphological Traits Associated With Spring Wheat Yield Under Hot, Irrigated Conditions. *Aust. J. Plant Physiol.* *21*, 717.
- Reynolds, M.P., Quilligan, E., Aggarwal, P.K., Bansal, K.C., Cavalieri, A.J., Chapman, S.C., Chapotin, S.M., Datta, S.K., Duveiller, E., Gill, K.S., et al. (2016). An integrated approach to maintaining cereal productivity under climate change. *Glob. Food Secur.* *8*, 9–18.
- Rezaei, E.E., Siebert, S., and Ewert, F. (2015). Intensity of heat stress in winter wheat—phenology compensates for the adverse effect of global warming. *Environ. Res. Lett.* *10*, 024012.
- Rischbeck, P., Baresel, P., Elsayed, S., Mistele, B., and Schmidhalter, U. (2014). Development of a diurnal dehydration index for spring barley phenotyping. *Funct. Plant Biol.* *41*, 1249.
- Rischbeck, P., Elsayed, S., Mistele, B., Barmeier, G., Heil, K., and Schmidhalter, U. (2016). Data fusion of spectral, thermal and canopy height parameters for improved yield prediction of drought stressed spring barley. *Eur. J. Agron.* *78*, 44–59.
- Rischbeck, P., Cardellach, P., Mistele, B., and Schmidhalter, U. (2017). Thermal phenotyping of stomatal sensitivity in spring barley. *J. Agron. Crop Sci.* *203*, 483–493.
- Rivero, R.M., Kojima, M., Gepstein, A., Sakakibara, H., Mittler, R., Gepstein, S., and Blumwald, E. (2007). Delayed leaf senescence induces extreme drought tolerance in a flowering plant. *Proc. Natl. Acad. Sci.* *104*, 19631–19636.
- Rouphael, Y., Cardarelli, M., Schwarz, D., Franken, P., and Colla, G. (2012). Effects of Drought on Nutrient Uptake and Assimilation in Vegetable Crops. In *Plant Responses to Drought Stress: From Morphological to Molecular Features*, R. Aroca, ed. (Berlin, Heidelberg: Springer Berlin Heidelberg), pp. 171–195.
- Rouse Jr, J., Haas, R.H., Schell, J.A., and Deering, D.W. (1974). Monitoring vegetation systems in the Great Plains with ERTS. 309–317.
- Royo, C., Aparicio, N., Villegas, D., Casadesus, J., Monneveux, P., and Araus, J.L. (2003). Usefulness of spectral reflectance indices as durum wheat yield predictors under contrasting Mediterranean conditions. *Int. J. Remote Sens.* *24*, 4403–4419.

- Saini, H., Sedgley, M., and Aspinall, D. (1983). Effect of Heat Stress During Floral Development on Pollen Tube Growth and Ovary Anatomy in Wheat (*Triticum aestivum* L.). *Funct. Plant Biol.* *10*, 137.
- Sankaran, S., Khot, L.R., Sathuvalli, V.R., Vandemark, G.J., Miklas, P.N., Carter, A.H., Pumphrey, M.O., Knowles, N.R., and Pavek, M.J. (2015). Low-altitude, high-resolution aerial imaging systems for row and field crop phenotyping: A review. *12*.
- Schädler, M., Buscot, F., Klotz, S., Reitz, T., Durka, W., Bumberger, J., Merbach, I., Michalski, S.G., Kirsch, K., Remmler, P., et al. (2019). Investigating the consequences of climate change under different land-use regimes: a novel experimental infrastructure. *Ecosphere* *10*, e02635.
- Schittenhelm, S., Kottmann, L., Kraft, M., Matschiner, K., and Langkamp-Wedde, T. (2019). Agronomic performance of winter wheat grown under highly divergent soil moisture conditions in rainfed and water-managed environments. *J. Agron. Crop Sci.* *205*, 283–294.
- Schopfer, P., and Brennicke, A. (2010). *Pflanzenphysiologie* (Heidelberg: Spektrum, Akad. Verl).
- Semenov, M.A., and Shewry, P.R. (2011). Modelling predicts that heat stress, not drought, will increase vulnerability of wheat in Europe. *Sci. Rep.* *1*, 66.
- Semenov, M.A., Martre, P., and Jamieson, P.D. (2009). Quantifying effects of simple wheat traits on yield in water-limited environments using a modelling approach. *Agric. For. Meteorol.* *149*, 1095–1104.
- Shaver, T.M., Khosla, R., and Westfall, D.G. (2010). Evaluation of Two Ground-Based Active Crop Canopy Sensors in Maize: Growth Stage, Row Spacing, and Sensor Movement Speed. *Soil Sci. Soc. Am. J.* *74*, 2101–2108.
- Shavrukov, Y., Kurishbayev, A., Jatayev, S., Shvidchenko, V., Zotova, L., Koekemoer, F., de Groot, S., Soole, K., and Langridge, P. (2017). Early Flowering as a Drought Escape Mechanism in Plants: How Can It Aid Wheat Production? *Front. Plant Sci.* *8*, 1950.
- Shewry, P.R. (2007). Improving the protein content and composition of cereal grain. *J. Cereal Sci.* *46*, 239–250.
- Shiferaw, B., Smale, M., Braun, H.-J., Duveiller, E., Reynolds, M., and Muricho, G. (2013). Crops that feed the world 10. Past successes and future challenges to the role played by wheat in global food security. *Food Secur.* *5*, 291–317.
- Short, N.M. (1982). *The Landsat tutorial workbook: Basics of satellite remote sensing* (National Aeronautics and Space Administration, Scientific and Technical ...).
- Shpiler, L., and Blum, A. (1990). Heat tolerance for yield and its components in different wheat cultivars. *Euphytica* *51*, 257–263.
- Sinclair, T.R., and Muchow, R.C. (2001). System Analysis of Plant Traits to Increase Grain Yield on Limited Water Supplies. *Agron. J.* *93*, 263–270.
- Singh, B., and Singh, G. (2004). Influence of soil water regime on nutrient mobility and uptake by *Dalbergia sissoo* seedlings. *4*.

- Stehr, N.J. (2015). Drones: The Newest Technology for Precision Agriculture. *Nat. Sci. Educ.* *44*, 89–91.
- Stone, P., and Nicolas, M. (1995). Effect of Timing of Heat Stress During Grain Filling on Two Wheat Varieties Differing in Heat Tolerance. I. Grain Growth. *Funct. Plant Biol.* *22*, 927.
- Taiz, L., Zeiger, E., Møller, I.M., and Murphy, A. (2015). *Plant Physiology and Development* (Sinauer Associates, Incorporated).
- Takebe, M., Yoneyama, T., Inada, K., and Murakami, T. (1990). Spectral reflectance ratio of rice canopy for estimating crop nitrogen status. *Plant Soil* *122*, 295–297.
- Tambussi, E.A., Bort, J., and Araus, J.L. (2007). Water use efficiency in C₃ cereals under Mediterranean conditions: a review of physiological aspects. *Ann. Appl. Biol.* *150*, 307–321.
- Tanguilig, V.C., Yambao, E.B., O'toole, J.C., and De Datta, S.K. (1987). Water stress effects on leaf elongation, leaf water potential, transpiration, and nutrient uptake of rice, maize, and soybean. *Plant Soil* *103*, 155–168.
- Tattaris, M., Reynolds, M.P., and Chapman, S.C. (2016). A Direct Comparison of Remote Sensing Approaches for High-Throughput Phenotyping in Plant Breeding. *Front. Plant Sci.* *7*.
- Terman, G.L., Ramig, R.E., Dreier, A.F., and Olson, R.A. (1969). Yield-Protein Relationships in Wheat Grain, as Affected by Nitrogen and Water¹. *Agron. J.* *61*, 755–759.
- Thomas, H., and Howarth, C.J. (2000). Five ways to stay green. *J. Exp. Bot.* *51*, 329–337.
- Todorov, D.T., Karanov, E.N., Smith, A.R., and Hall, M.A. (2003). Chlorophyllase activity and chlorophyll content in wild type and eti 5 mutant of *Arabidopsis thaliana* subjected to low and high temperatures. *4*.
- Townend, J., and Dickinson, A.L. (1995). A comparison of rooting environments in containers of different sizes. *Plant Soil* *175*, 139–146.
- Treydte, K.S. (2003). *Dendro-Isotope und Jahringbreiten als Klimaproxis der letzten 1200 Jahre im Karakorumgebirge/Pakistan* (Jülich: Forschungszentrum Jülich, Zentralbibliothek).
- Trnka, M., Olesen, J.E., Kersebaum, K.C., Skjelvåg, A.O., Eitzinger, J., Seguin, B., Peltonen-Sainio, P., Rötter, R., Iglesias, A., Orlandini, S., et al. (2011). Agroclimatic conditions in Europe under climate change. *Glob. Change Biol.* *17*, 2298–2318.
- Trnka, M., Rötter, R.P., Ruiz-Ramos, M., Kersebaum, K.C., Olesen, J.E., Žalud, Z., and Semenov, M.A. (2014). Adverse weather conditions for European wheat production will become more frequent with climate change. *Nat. Clim. Change* *4*, 637–643.
- Tucker, C.J. (1979). Red and Photographic Infrared Linear Combinations for Monitoring Vegetation. *Remote Sens. Environ.* *8*, 127–150.

- Turner, N.C., Wright, G.C., and Siddique, K.H.M. (2001). Adaptation of grain legumes (pulses) to water-limited environments. In *Advances in Agronomy*, (Elsevier), pp. 193–231.
- Urbahs, A., and Jonaite, I. (2013). Features of the use of unmanned aerial vehicles for agriculture applications. *Aviation* 17, 170–175.
- Užík, M., and Žofajová, A. (2006). Translocation and accumulation of dry matter in winter wheat genotypes. *Cereal Res. Commun.* 34, 1013–1020.
- VDLUFA (2021). Methode C 2.2.1, Texturanalyse des Feinbodens Kombination von Nasssiebung und Pipettmethode nach KÖHN, accessed 07 May 2021. https://www.vdlufa.de/Methodenbuch/index.php?option=com_content&view=article&id=7&Itemid=108&lang=de&lang=en.
- Verma, V., Foulkes, M.J., Worland, A.J., Sylvester-Bradley, R., Caligari, P.D.S., and Snape, J.W. (2004). Mapping quantitative trait loci for flag leaf senescence as a yield determinant in winter wheat under optimal and drought-stressed environments. *Euphytica* 135, 255–263.
- Vignjevic, M., Wang, X., Olesen, J.E., and Wollenweber, B. (2015). Traits in Spring Wheat Cultivars Associated with Yield Loss Caused by a Heat Stress Episode after Anthesis. *J. Agron. Crop Sci.* 201, 32–48.
- Vilagrosa, A., Chirino, E., Peguero-Pina, J.J., Barigah, T.S., Cochard, H., and Gil-Pelegrín, E. (2012). Xylem Cavitation and Embolism in Plants Living in Water-Limited Ecosystems. In *Plant Responses to Drought Stress: From Morphological to Molecular Features*, R. Aroca, ed. (Berlin, Heidelberg: Springer Berlin Heidelberg), pp. 63–109.
- Wahid, A. (2007). Physiological implications of metabolite biosynthesis for net assimilation and heat-stress tolerance of sugarcane (*Saccharum officinarum*) sprouts. *J. Plant Res.* 120, 219–228.
- Wahid, A., Farooq, M., Hussain, I., Rasheed, R., and Galani, S. (2012). Responses and Management of Heat Stress in Plants. In *Environmental Adaptations and Stress Tolerance of Plants in the Era of Climate Change*, P. Ahmad, and M.N.V. Prasad, eds. (New York, NY: Springer New York), pp. 135–157.
- Wall, L., Larocque, D., and Léger, P. (2008). The early explanatory power of NDVI in crop yield modelling. *Int. J. Remote Sens.* 29, 2211–2225.
- Wang, J.-Y., Xiong, Y.-C., Li, F.-M., Siddique, K.H.M., and Turner, N.C. (2017). Effects of Drought Stress on Morphophysiological Traits, Biochemical Characteristics, Yield, and Yield Components in Different Ploidy Wheat. In *Advances in Agronomy*, (Elsevier), pp. 139–173.
- Wardlaw, I.F. (2002). Interaction Between Drought and Chronic High Temperature During Kernel Filling in Wheat in a Controlled Environment. *Ann. Bot.* 90, 469–476.
- Wardlaw, I., and Moncur, L. (1995). The Response of Wheat to High Temperature Following Anthesis. I. The Rate and Duration of Kernel Filling. *Funct. Plant Biol.* 22, 391.
- Westgate, M.E., and Peterson, C.M. (1993). Flower and Pod Development in Water-Deficient Soybeans (*Glycine max* L. Merr.). *J. Exp. Bot.* 44, 109–117.

- Whan, B., Carlton, G., and Anderson, W. (1996). Potential for increasing rate of grain growth in spring wheat. I. Identification of genetic improvements. *Aust. J. Agric. Res.* *47*, 17–31.
- Wiegand, C.L., and Cuellar, J.A. (1981). (1981) Duration of Grain Filling and Kernel Weight of Wheat as Affected by Temperature. *7*.
- Wu, Y., Huang, M., and Warrington, D.N. (2011). Growth and transpiration of maize and winter wheat in response to water deficits in pots and plots. *Environ. Exp. Bot.* *71*, 65–71.
- Xiong, L., Schumaker, K.S., and Zhu, J.-K. (2002). Cell Signaling during Cold, Drought, and Salt Stress. *Plant Cell* *14*, S165–S183.
- Xu, S., Li, J., Zhang, X., Wei, H., and Cui, L. (2006). Effects of heat acclimation pretreatment on changes of membrane lipid peroxidation, antioxidant metabolites, and ultrastructure of chloroplasts in two cool-season turfgrass species under heat stress. *Environ. Exp. Bot.* *56*, 274–285.
- Xu, W., Rosenow, D., and Nguyen, H. (2000). Stay green trait in grain sorghum: relationship between visual rating and leaf chlorophyll concentration. *Plant Breed.* *119*, 365–367.
- Yadav, O.P. (2008). Performance of landraces, exotic elite populations and their crosses in pearl millet (*Pennisetum glaucum*) in drought and non-drought conditions. *Plant Breed.* *127*, 208–210.
- Yamaguchi-Shinozaki, K., and Shinozaki, K. (2006). Transcriptional Regulatory Networks in Cellular Responses and Tolerance to Dehydration and Cold Stresses. *Annu. Rev. Plant Biol.* *57*, 781–803.
- Zadoks, J.C., Chang, T.T., and Konzak, C.F. (1974). A decimal code for the growth stages of cereals. *Weed Res.* *14*, 415–421.
- Zhu, J.-K. (2002). Salt and Drought Stress Signal Transduction in Plants. *Annu. Rev. Plant Biol.* *53*, 247–273.
- Zörb, C., Becker, E., Merkt, N., Kafka, S., Schmidt, S., and Schmidhalter, U. (2017). Shift of grain protein composition in bread wheat under summer drought events. *J. Plant Nutr. Soil Sci.* *180*, 49–55.

Table 28 (continued) Zadoks growth stages per group of origin and within all trials.

DAS	2017			2018			2019 Drought stress			2019 Irrigated		
	mean	sd	sig	mean	sd	sig	mean	sd	sig	mean	sd	sig
259	EE			85.77 ± 1.11	a		84.67 ± 1.11	a		85.33 ± 0.99	a	
	Ger Hy			82.17 ± 2.48	b		78.67 ± 3.70	b		80.33 ± 4.29	b	
	Ger Li			81.25 ± 2.46	b		77.42 ± 2.86	b		78.46 ± 2.85	c	
263	EE						86.70 ± 1.27	a		87.87 ± 1.35	a	
	Ger Hy						82.33 ± 4.21	b		85.00 ± 2.09	b	
	Ger Li						81.58 ± 3.38	b		84.88 ± 1.95	b	
264	EE	86.80 ± 1.83	a									
	Ger Hy	80.73 ± 2.71	b									
	Ger Li	81.00 ± 3.07	b									
265	EE			88.80 ± 0.61	a							
	Ger Hy			88.33 ± 1.30	ab							
	Ger Li			88.29 ± 1.20	b							
267	EE						91.17 ± 1.59	a		91.20 ± 1.34	a	
	Ger Hy						86.50 ± 2.11	b		88.58 ± 1.68	b	
	Ger Li						87.31 ± 1.97	b		88.50 ± 1.32	b	
272	EE	91.65 ± 0.97	a									
	Ger Hy	90.46 ± 1.52	b									
	Ger Li	90.04 ± 1.46	b									

DAS: Days after sowing; EE: Eastern European lines, Ger Hy: German hybrids, Ger Li: German Lines, mean: mean values per group of varieties, sd: standard deviation, sig: significant differences within one trial and DAS

8.2. Beginning and duration of grain filling

Table 29 Days to the beginning of grain filling.

Beginning of grain filling (DAS)				
		mean	sd	sig
2017	EE	245.83 ± 1.15	b	
	Ger Hy	246.17 ± 1.19	b	
	Ger Li	248.04 ± 1.11	a	
2018	EE	231.12 ± 1.80	h	
	Ger Hy	234.64 ± 3.61	g	
	Ger Li	236.04 ± 2.58	g	
2019	Drought stress	EE	239.56 ± 0.74	e
		Ger Hy	242.92 ± 2.35	cd
		Ger Li	244.23 ± 1.25	c
	Irrigated	EE	238.56 ± 0.50	f
		Ger Hy	241.00 ± 1.28	de
		Ger Li	240.70 ± 0.84	e

EE: Eastern European lines, Ger Hy: German hybrids, Ger Li: German Lines, mean: mean values per group of varieties, sd: standard deviation, sig: significant differences within one factor across all years and varieties.

Table 30 Duration, temperature sum, mean temperature and precipitation sum during grain filling.

		Grain filling											
		Duration (days)			Temperature sum (°C)			Mean temperature (°C)			Precipitation sum (mm)		
		mean	sd	sig	mean	sd	sig	mean	sd	sig	mean	sd	sig
2017	EE	15.24 ± 1.39		d	332.36 ± 36.82		e	20.67 ± 0.33		f	9.67 ± 1.73		e
	Ger Hy	18.83 ± 2.17		bc	432.19 ± 55.27		cd	21.75 ± 0.56		e	22.5 ± 9.98		de
	Ger Li	17.50 ± 2.08		c	409.34 ± 53.03		d	22.08 ± 0.53		d	23.48 ± 9.80		d
2018	EE	25.83 ± 2.02		a	589.05 ± 30.79		a	21.66 ± 0.18		e	45.42 ± 11.08		c
	Ger Hy	25.64 ± 3.26		a	593.73 ± 62.80		a	21.93 ± 0.26		de	53.25 ± 4.45		c
	Ger Li	24.58 ± 2.40		a	569.45 ± 50.14		a	22.12 ± 0.26		d	53.20 ± 4.47		c
2019 Drought stress	EE	14.56 ± 2.36		de	357.41 ± 56.91		e	22.95 ± 0.27		b	91.53 ± 23.90		a
	Ger Hy	19.33 ± 1.92		bc	477.00 ± 42.97		bc	23.47 ± 0.26		a	96.52 ± 2.77		a
	Ger Li	19.10 ± 1.75		bc	475.58 ± 36.75		bc	23.68 ± 0.30		a	94.84 ± 3.14		a
2019 Irrigated	EE	13.83 ± 2.31		e	335.28 ± 54.95		e	22.58 ± 0.24		c	74.44 ± 41.62		b
	Ger Hy	18.75 ± 3.05		bc	462.84 ± 74.01		bc	23.42 ± 0.30		a	97.48 ± 2.25		a
	Ger Li	20.37 ± 2.01		b	501.79 ± 45.78		b	23.49 ± 0.15		a	96.18 ± 0.15		a

EE: Eastern European lines, Ger Hy: German hybrids, Ger Li: German Lines, mean: mean values per group of varieties, sd: standard deviation, sig: significant differences within one factor across all years and varieties.

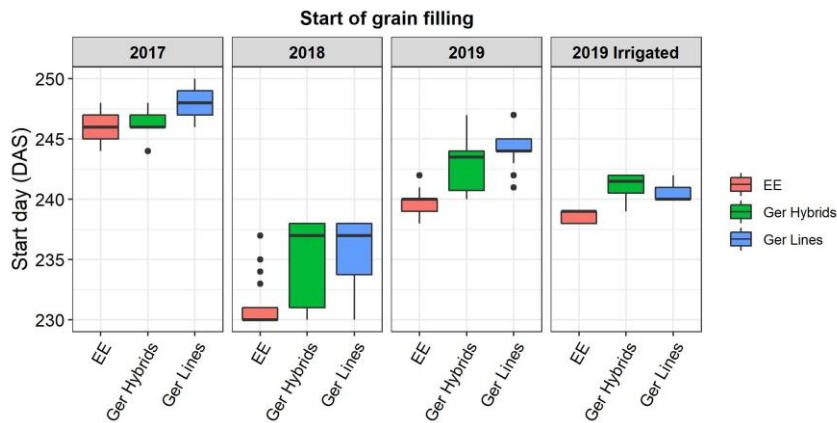


Figure 20 Days until beginning of grain filling (Z70). EE: Eastern European lines, Ger Hybrids: German hybrids, Ger Lines: German Lines.

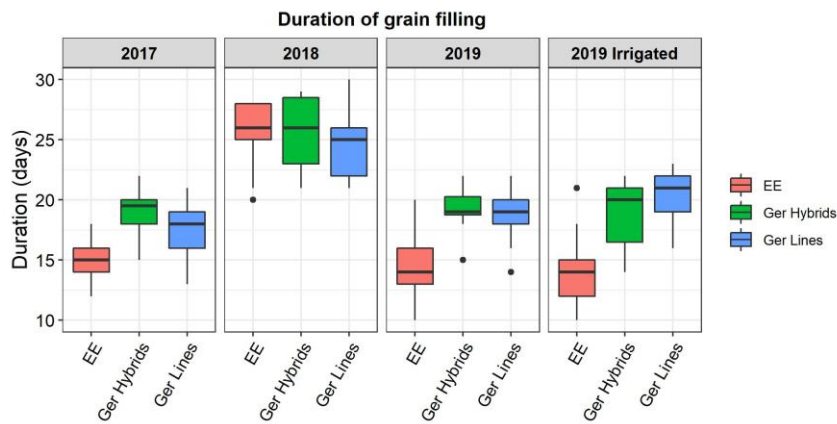


Figure 21 Duration of grain filling (Z70-Z83). EE: Eastern European lines, Ger Hybrids: German hybrids, Ger Lines: German Lines.

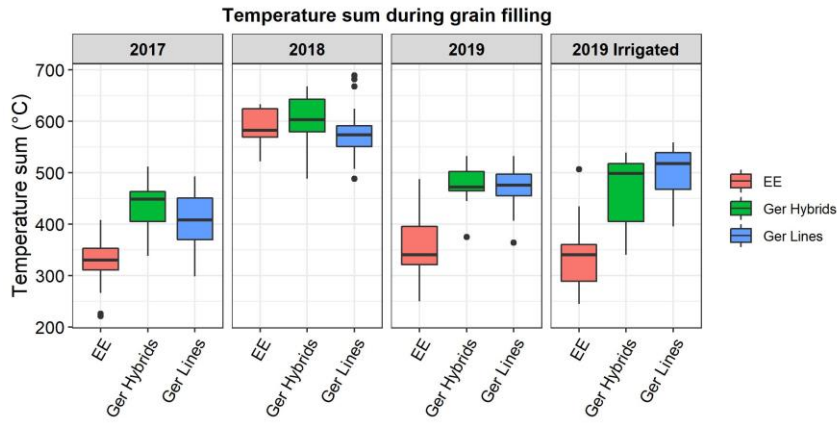


Figure 22 Temperature sum during grain filling (Z70-Z83). EE: Eastern European lines, Ger Hybrids: German hybrids, Ger Lines: German Lines.

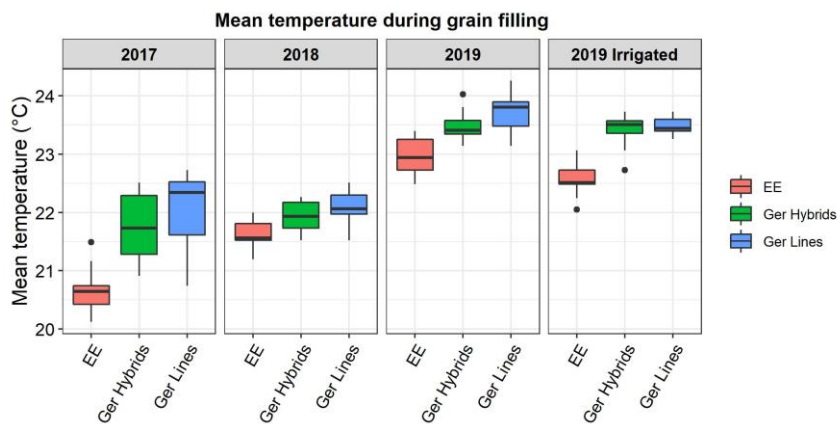


Figure 23 Mean temperature during grain filling (Z70-83). EE: Eastern European lines, Ger Hybrids: German hybrids, Ger Lines: German Lines.

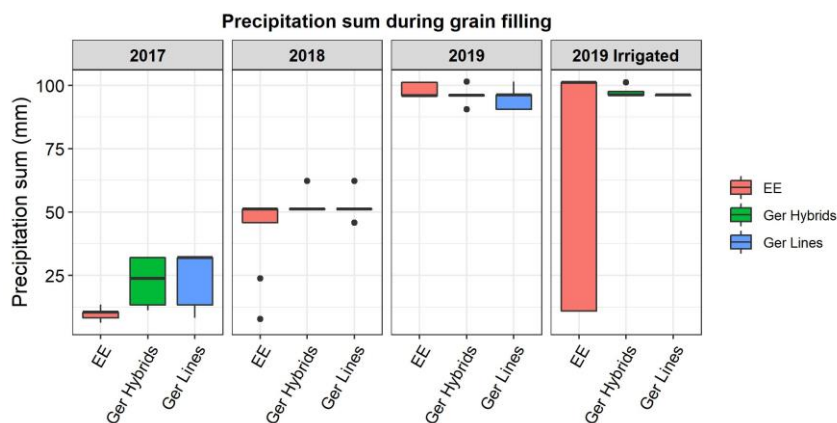


Figure 24 Precipitation sum during grain filling (Z70-83). EE: Eastern European lines, Ger Hybrids: German hybrids, Ger Lines: German Lines.

8.3. Grain size distribution significance table

Table 31 Significant differences of the grain size distribution for three groups of varieties and each year.

		Grain size distribution											
		2017			2018			2019			2019		
								Drought stress			Irrigated		
		mean	sd	sig	mean	sd	sig	mean	sd	sig	mean	sd	sig
Eastern European Lines	0-2.2 mm	6.07	± 3.36	c	2.43	± 3.04	d	5.80	± 2.99	d	5.79	± 4.75	d
	2.2-2.5 mm	24.00	± 9.45	b	11.22	± 3.58	c	22.01	± 6.88	c	20.83	± 20.83	c
	2.5-2.8 mm	42.72	± 6.82	a	34.14	± 7.75	b	40.90	± 5.20	a	41.54	± 6.02	a
	2.8-4 mm	25.23	± 16.47	b	52.21	± 11.98	a	31.30	± 13.04	b	31.85	± 31.85	b
German Hybrids	0-2.2 mm	12.14	± 2.41	c	4.12	± 0.97	c	18.66	± 8.62	bc	14.71	± 8.81	b
	2.2-2.5 mm	44.87	± 4.04	a	22.91	± 4.76	b	44.14	± 10.45	a	39.62	± 14.01	a
	2.5-2.8 mm	35.07	± 4.03	b	47.96	± 2.46	a	29.28	± 13.95	b	34.89	± 16.35	a
German Lines	2.8-4 mm	5.61	± 2.14	d	25.01	± 5.81	b	7.92	± 3.55	c	10.77	± 5.82	b
	0-2.2 mm	13.47	± 7.36	c	3.62	± 2.22	c	19.51	± 7.72	c	14.38	± 5.87	c
	2.2-2.5 mm	45.44	± 9.50	a	22.64	± 10.10	b	49.68	± 5.81	a	45.24	± 8.58	a
	2.5-2.8 mm	33.33	± 11.50	b	50.08	± 6.42	a	25.65	± 8.89	b	33.02	± 8.50	b
	2.8-4 mm	5.35	± 3.52	d	23.66	± 13.96	b	5.17	± 2.11	d	7.36	± 5.45	d

mean: mean values per group of varieties, sd: standard deviation, sig: significant differences within one size, year, and group of varieties.

8.4. Protein content, grain yield, and grain nitrogen uptake per quality class

Table 32 Protein content, grain yield and N uptake of all winter wheat varieties, separated for each quality class and individual years.

		Protein			Grain yield			Grain N uptake		
		mean	sd	sig	mean	sd	sig	mean	sd	sig
2017	E	16.06	± 1.77	a	4.57	± 0.36	b	147.26	± 30.08	ab
	A	16.11	± 1.29	a	4.71	± 0.37	b	140.45	± 22.85	b
	B line	16.25	± 1.09	a	4.72	± 0.37	b	144.63	± 25.56	ab
	B hybrid	15.53	± 1.05	ab	4.90	± 0.54	b	135.14	± 20.85	b
	C	14.78	± 1.55	ab	4.78	± 0.33	b	109.61	± 17.71	b
	EE lines	14.32	± 1.49	b	5.36	± 0.46	a	165.38	± 29.67	a
2018	E	13.50	± 0.88	a	6.18	± 0.50	a	189.56	± 12.81	ab
	A	12.66	± 0.90	ab	6.09	± 0.88	a	173.14	± 25.38	bc
	B line	12.32	± 0.36	b	6.39	± 0.54	a	161.65	± 25.32	bc
	B hybrid	12.05	± 0.89	b	6.20	± 0.53	a	153.70	± 15.51	c
	C	12.25	± 0.77	b	6.59	± 0.48	a	170.45	± 10.05	bc
	EE lines	12.54	± 0.85	b	6.60	± 0.75	a	194.32	± 30.83	a
2019 Drought stress	E	15.96	± 0.57	a	4.81	± 0.51	ab	213.47	± 50.55	a
	A	15.62	± 0.71	a	4.59	± 0.30	b	203.02	± 50.01	a
	B line	15.51	± 1.19	a	4.22	± 0.78	b	153.18	± 41.41	b
	B hybrid	15.30	± 0.82	a	5.24	± 1.50	ab	227.72	± 77.82	ab
	C	16.14	± 1.71	a	4.30	± 0.83	b	222.34	± 65.05	a
	EE lines	14.12	± 0.74	b	5.70	± 1.02	a	230.77	± 59.58	a
2019 Irrigated	E	15.61	± 0.97	a	5.71	± 0.66	bc	245.72	± 72.82	a
	A	15.11	± 1.25	ab	5.64	± 0.26	c	207.64	± 43.36	a
	B line	15.02	± 0.69	ab	6.12	± 0.57	ba	209.19	± 37.59	a
	B hybrid	14.66	± 0.69	ab	6.94	± 1.52	ab	223.45	± 69.31	a
	C	15.56	± 1.80	a	5.65	± 0.42	bc	246.98	± 60.82	a
	EE lines	14.22	± 0.74	b	7.20	± 0.76	a	246.65	± 49.91	a

Protein: Protein content of grains, N uptake: N uptake of grains, A, B line, B hybrid, C, E: Quality groups of German varieties, EE lines: Eastern European lines
mean: mean values per group of varieties, sd: standard deviation, sig: significant differences within one parameter and year across varieties.

8.5. Differences of spectral indices and canopy temperature between the varieties within each trial

8.5.1. NDVI

Table 33 NDVI values of each variety group in all trials.

DAS		NDVI											
		2017			2018			2019 Drought stress			2019 Irrigated		
		mean	sd	sig	mean	sd	sig	mean	sd	sig	mean	sd	sig
221	EE							0.90	± 0.02	b	0.93	± 0.01	b
	Ger Hy							0.92	± 0.02	a	0.95	± 0.01	a
	Ger Li							0.92	± 0.02	a	0.95	± 0.01	a
224	EE							0.91	± 0.02	b	0.94	± 0.01	b
	Ger Hy							0.93	± 0.01	a	0.94	± 0.01	ab
	Ger Li							0.93	± 0.01	a	0.94	± 0.01	a
225	EE							0.91	± 0.02	b	0.93	± 0.01	b
	Ger Hy							0.92	± 0.01	a	0.93	± 0.01	b
	Ger Li							0.92	± 0.01	a	0.94	± 0.01	a
226	EE				0.92	± 0.01	a	0.90	± 0.02	b	0.94	± 0.01	b
	Ger Hy				0.91	± 0.01	b	0.92	± 0.01	a	0.94	± 0.01	b
	Ger Li				0.91	± 0.02	b	0.92	± 0.01	a	0.94	± 0.01	a
227	EE							0.90	± 0.02	b	0.93	± 0.01	b
	Ger Hy							0.92	± 0.01	a	0.93	± 0.01	b
	Ger Li							0.92	± 0.02	a	0.94	± 0.01	a
230	EE				0.90	± 0.01	a	0.91	± 0.02	b	0.93	± 0.01	b
	Ger Hy				0.90	± 0.01	a	0.92	± 0.01	a	0.93	± 0.01	b
	Ger Li				0.91	± 0.01	a	0.93	± 0.01	a	0.94	± 0.01	a
231	EE				0.92	± 0.01	a	0.90	± 0.02	b	0.93	± 0.01	ab
	Ger Hy				0.91	± 0.01	b	0.91	± 0.01	a	0.92	± 0.01	b
	Ger Li				0.92	± 0.02	a	0.92	± 0.02	a	0.93	± 0.01	a
234	EE				0.91	± 0.01	a						
	Ger Hy				0.90	± 0.01	a						
	Ger Li				0.91	± 0.02	a						
236	EE	0.91	± 0.01	b									
	Ger Hy	0.91	± 0.01	b									
	Ger Li	0.92	± 0.01	a									
238	EE	0.88	± 0.02	a									
	Ger Hy	0.88	± 0.02	a									
	Ger Li	0.89	± 0.02	a									
240	EE				0.87	± 0.02	a	0.89	± 0.02	b	0.92	± 0.01	b
	Ger Hy				0.86	± 0.01	a	0.89	± 0.01	a	0.93	± 0.00	ab
	Ger Li				0.87	± 0.02	a	0.91	± 0.01	a	0.93	± 0.01	ab
243	EE	0.83	± 0.02	a									
	Ger Hy	0.83	± 0.02	a									
	Ger Li	0.83	± 0.02	a									
244	EE							0.87	± 0.03	b	0.89	± 0.01	b
	Ger Hy							0.89	± 0.02	a	0.90	± 0.01	a
	Ger Li							0.90	± 0.02	a	0.91	± 0.01	a
246	EE	0.82	± 0.03	a				0.85	± 0.02	b	0.88	± 0.02	b
	Ger Hy	0.82	± 0.02	a				0.87	± 0.02	a	0.89	± 0.01	a
	Ger Li	0.83	± 0.02	a				0.88	± 0.02	a	0.90	± 0.01	a
247	EE							0.80	± 0.03	b	0.84	± 0.03	b
	Ger Hy							0.84	± 0.03	a	0.87	± 0.02	a
	Ger Li							0.84	± 0.02	a	0.86	± 0.02	a
249	EE							0.76	± 0.04	b	0.79	± 0.04	b
	Ger Hy							0.80	± 0.04	a	0.85	± 0.03	a
	Ger Li							0.81	± 0.04	a	0.83	± 0.03	a

Table 33 (continued) NDVI values of each variety group in all trials.

DAS		NDVI											
		2017			2018			2019 Drought stress			2019 Irrigated		
		mean	sd	sig	mean	sd	sig	mean	sd	sig	mean	sd	sig
250	EE	0.70	± 0.05	b									
	Ger Hy	0.71	± 0.04	ab									
	Ger Li	0.72	± 0.03	a									
253	EE						0.66	± 0.06	b	0.63	± 0.06	b	
	Ger Hy						0.74	± 0.08	a	0.76	± 0.08	a	
	Ger Li						0.73	± 0.04	a	0.74	± 0.06	a	
255	EE						0.57	± 0.07	b	0.52	± 0.06	b	
	Ger Hy						0.67	± 0.12	a	0.70	± 0.10	a	
	Ger Li						0.66	± 0.07	a	0.65	± 0.07	a	
259	EE				0.20	± 0.02	b	0.42	± 0.05	b	0.36	± 0.04	b
	Ger Hy				0.34	± 0.08	a	0.52	± 0.14	a	0.51	± 0.16	a
	Ger Li				0.33	± 0.05	a	0.50	± 0.06	a	0.47	± 0.06	a
260	EE						0.35	± 0.05	b	0.29	± 0.04	c	
	Ger Hy						0.44	± 0.16	a	0.44	± 0.16	a	
	Ger Li						0.41	± 0.06	a	0.39	± 0.05	b	
261	EE				0.17	± 0.02	b	0.31	± 0.05	b	0.26	± 0.04	c
	Ger Hy				0.28	± 0.07	a	0.41	± 0.13	a	0.42	± 0.15	a
	Ger Li				0.26	± 0.04	a	0.38	± 0.05	a	0.36	± 0.06	b
263	EE	0.25	± 0.04	c			0.28	± 0.06	b	0.16	± 0.05	b	
	Ger Hy	0.32	± 0.05	b			0.41	± 0.14	a	0.31	± 0.13	a	
	Ger Li	0.38	± 0.05	a			0.40	± 0.05	a	0.26	± 0.06	a	
264	EE	0.24	± 0.02	c									
	Ger Hy	0.32	± 0.04	b									
	Ger Li	0.35	± 0.04	a									
265	EE	0.19	± 0.02	c	0.16	± 0.01	c	0.24	± 0.04	b	0.21	± 0.03	b
	Ger Hy	0.23	± 0.03	b	0.22	± 0.04	a	0.34	± 0.11	a	0.32	± 0.09	a
	Ger Li	0.26	± 0.03	a	0.18	± 0.02	b	0.32	± 0.05	a	0.29	± 0.04	a
266	EE						0.22	± 0.04	b	0.17	± 0.03	c	
	Ger Hy						0.30	± 0.08	a	0.25	± 0.07	a	
	Ger Li						0.28	± 0.04	a	0.22	± 0.03	b	
267	EE									0.16	± 0.03	c	
	Ger Hy									0.21	± 0.05	a	
	Ger Li									0.18	± 0.02	b	
269	EE						0.24	± 0.04	a	0.18	± 0.03	a	
	Ger Hy						0.26	± 0.05	a	0.19	± 0.03	a	
	Ger Li						0.24	± 0.03	a	0.18	± 0.02	a	
271	EE	0.18	0.03	b									
	Ger Hy	0.21	0.01	a									
	Ger Li	0.21	0.02	a									

DAS: Days after sowing; EE: Eastern European lines, Ger Hy: German hybrids, Ger Li: German Lines, mean: mean values per group of varieties, sd: standard deviation, sig: significant differences within one trial and DAS

8.5.2. Water Index

Table 34 WI values of each variety group in all trials.

DAS		WI											
		2017			2018			2019 Drought stress			2019 Irrigated		
		mean	sd	sig	mean	sd	sig	mean	sd	sig	mean	sd	sig
221	EE							1.16 ± 0.03	a		1.22 ± 0.03	a	
	Ger Hy							1.17 ± 0.03	a		1.21 ± 0.03	a	
	Ger Li							1.16 ± 0.03	a		1.22 ± 0.02	a	
224	EE							1.16 ± 0.03	a		1.25 ± 0.02	a	
	Ger Hy							1.17 ± 0.02	a		1.22 ± 0.03	b	
	Ger Li							1.16 ± 0.03	a		1.23 ± 0.03	b	
225	EE							1.13 ± 0.03	a		1.26 ± 0.02	a	
	Ger Hy							1.13 ± 0.03	a		1.24 ± 0.03	b	
	Ger Li							1.13 ± 0.02	a		1.23 ± 0.03	b	
226	EE				1.11 ± 0.02	a		1.16 ± 0.03	a		1.24 ± 0.02	a	
	Ger Hy				1.11 ± 0.01	a		1.17 ± 0.03	a		1.22 ± 0.04	b	
	Ger Li				1.12 ± 0.02	a		1.17 ± 0.03	a		1.23 ± 0.03	b	
227	EE							1.17 ± 0.03	a		1.27 ± 0.02	a	
	Ger Hy							1.17 ± 0.03	a		1.26 ± 0.04	b	
	Ger Li							1.17 ± 0.03	a		1.26 ± 0.03	b	
230	EE				1.08 ± 0.01	b		1.17 ± 0.03	a		1.26 ± 0.02	a	
	Ger Hy				1.10 ± 0.01	ab		1.19 ± 0.03	a		1.25 ± 0.04	a	
	Ger Li				1.10 ± 0.02	a		1.19 ± 0.03	a		1.26 ± 0.03	a	
231	EE				1.11 ± 0.01	c		1.19 ± 0.03	b		1.26 ± 0.02	a	
	Ger Hy				1.13 ± 0.02	b		1.21 ± 0.02	a		1.27 ± 0.03	a	
	Ger Li				1.14 ± 0.01	a		1.20 ± 0.03	a		1.27 ± 0.03	a	
234	EE				1.12 ± 0.01	b							
	Ger Hy				1.13 ± 0.02	a							
	Ger Li				1.14 ± 0.02	a							
236	EE	1.08 ± 0.02	b										
	Ger Hy	1.09 ± 0.01	b										
	Ger Li	1.10 ± 0.01	a										
238	EE	1.07 ± 0.01	b										
	Ger Hy	1.07 ± 0.01	b										
	Ger Li	1.09 ± 0.01	a										
240	EE				1.16 ± 0.01	b		1.15 ± 0.03	b		1.24 ± 0.02	b	
	Ger Hy				1.16 ± 0.01	ab		1.20 ± 0.02	a		1.29 ± 0.01	a	
	Ger Li				1.17 ± 0.01	a		1.19 ± 0.04	a		1.29 ± 0.02	a	
243	EE	1.03 ± 0.01	b										
	Ger Hy	1.03 ± 0.01	b										
	Ger Li	1.04 ± 0.01	a										
244	EE							1.14 ± 0.04	ab		1.18 ± 0.02	b	
	Ger Hy							1.11 ± 0.07	b		1.21 ± 0.01	a	
	Ger Li							1.15 ± 0.05	a		1.20 ± 0.02	a	
246	EE	1.02 ± 0.01	b					1.13 ± 0.02	b		1.28 ± 0.02	c	
	Ger Hy	1.02 ± 0.01	b					1.18 ± 0.02	a		1.33 ± 0.02	a	
	Ger Li	1.03 ± 0.01	a					1.17 ± 0.02	a		1.31 ± 0.02	b	
247	EE							1.11 ± 0.02	b		1.35 ± 0.02	c	
	Ger Hy							1.15 ± 0.02	a		1.39 ± 0.02	a	
	Ger Li							1.15 ± 0.02	a		1.37 ± 0.03	b	
249	EE							1.08 ± 0.02	b		1.09 ± 0.02	b	
	Ger Hy							1.11 ± 0.03	a		1.12 ± 0.03	a	
	Ger Li							1.11 ± 0.02	a		1.10 ± 0.03	b	
250	EE	1.00 ± 0.01	ab										
	Ger Hy	1.00 ± 0.01	b										
	Ger Li	1.01 ± 0.01	a										
253	EE							1.29 ± 0.03	b		1.27 ± 0.03	b	
	Ger Hy							1.32 ± 0.05	a		1.31 ± 0.06	a	
	Ger Li							1.31 ± 0.02	a		1.28 ± 0.04	b	

Table 34 (continued) WI values of each variety group in all trials.

DAS		WI											
		2017			2018			2019 Drought stress			2019 Irrigated		
		mean	sd	sig	mean	sd	sig	mean	sd	sig	mean	sd	sig
255	EE							1.04	± 0.02	b	1.04	± 0.02	b
	Ger Hy							1.06	± 0.04	a	1.07	± 0.04	a
	Ger Li							1.05	± 0.02	a	1.04	± 0.02	b
259	EE				0.90	± 0.01	b	1.04	± 0.02	a	1.01	± 0.01	b
	Ger Hy				0.91	± 0.02	a	1.05	± 0.04	a	1.03	± 0.05	a
	Ger Li				0.92	± 0.01	a	1.04	± 0.02	a	1.02	± 0.02	b
260	EE							1.03	± 0.01	a	1.00	± 0.01	a
	Ger Hy							1.04	± 0.05	a	1.01	± 0.06	a
	Ger Li							1.04	± 0.02	a	0.99	± 0.02	a
261	EE				0.90	± 0.01	b	1.06	± 0.01	a	0.98	± 0.01	b
	Ger Hy				0.90	± 0.02	b	1.07	± 0.05	a	1.00	± 0.04	a
	Ger Li				0.91	± 0.01	a	1.06	± 0.02	a	0.98	± 0.02	b
263	EE	0.91	± 0.01	b				0.99	± 0.02	a	1.01	± 0.02	b
	Ger Hy	0.91	± 0.01	b				0.99	± 0.05	a	1.03	± 0.04	a
	Ger Li	0.93	± 0.01	a				0.99	± 0.02	a	1.01	± 0.02	ab
264	EE	0.90	± 0.01	c									
	Ger Hy	0.91	± 0.01	b									
	Ger Li	0.93	± 0.01	a									
265	EE	0.87	± 0.01	b	0.93	± 0.01	a	0.97	± 0.01	a	0.96	± 0.02	a
	Ger Hy	0.87	± 0.01	b	0.93	± 0.01	a	0.98	± 0.03	a	0.97	± 0.04	a
	Ger Li	0.88	± 0.01	a	0.94	± 0.00	a	0.97	± 0.02	a	0.96	± 0.02	a
266	EE							0.97	± 0.01	a	0.95	± 0.01	a
	Ger Hy							0.97	± 0.03	a	0.95	± 0.03	a
	Ger Li							0.97	± 0.01	a	0.95	± 0.01	a
267	EE										0.94	± 0.01	a
	Ger Hy										0.94	± 0.02	a
	Ger Li										0.93	± 0.01	a
269	EE							0.99	± 0.01	a	0.96	± 0.01	a
	Ger Hy							0.99	± 0.01	a	0.96	± 0.02	a
	Ger Li							0.99	± 0.01	a	0.96	± 0.01	a
271	EE	0.84	± 0.04	a									
	Ger Hy	0.84	± 0.02	a									
	Ger Li	0.84	± 0.03	a									

DAS: Days after sowing; EE: Eastern European lines, Ger Hy: German hybrids, Ger Li: German Lines, mean: mean values per group of varieties, sd: standard deviation, sig: significant differences within one trial and DAS

8.5.3. REIP

Table 35 REIP values of each variety group in all trials.

DAS		REIP											
		2017			2018			2019 Drought stress			2019 Irrigated		
		mean	sd	sig	mean	sd	sig	mean	sd	sig	mean	sd	sig
221	EE							727.32	± 1.79	ab	730.64	± 0.97	b
	Ger Hy							728.64	± 1.45	a	732.08	± 0.62	a
	Ger Li							728.48	± 2.04	a	732.05	± 1.40	a
224	EE							726.73	± 1.68	b	731.06	± 0.86	b
	Ger Hy							728.18	± 1.16	a	731.28	± 0.66	ab
	Ger Li							728.00	± 1.73	a	731.64	± 1.44	a
225	EE							727.32	± 1.71	b	730.73	± 0.88	b
	Ger Hy							728.55	± 1.41	ab	730.86	± 0.51	ab
	Ger Li							728.76	± 1.95	a	731.42	± 1.36	a
226	EE				730.88	± 0.85	ab	726.89	± 1.69	b	731.08	± 1.00	b
	Ger Hy				730.33	± 0.69	b	728.31	± 1.28	a	731.46	± 0.59	ab
	Ger Li				731.04	± 1.05	a	728.47	± 1.83	a	731.87	± 1.34	a
227	EE							727.36	± 1.78	b	730.97	± 1.20	b
	Ger Hy							728.71	± 1.19	a	730.91	± 0.52	b
	Ger Li							728.83	± 1.76	a	731.59	± 1.24	a
230	EE				729.19	± 0.72	b	727.70	± 1.66	b	731.43	± 0.95	b
	Ger Hy				729.06	± 0.62	b	729.04	± 1.05	a	731.82	± 0.50	ab
	Ger Li				730.01	± 0.74	a	729.59	± 1.69	a	732.10	± 1.21	a
231	EE				731.09	± 0.79	b	727.37	± 1.59	b	731.27	± 1.05	b
	Ger Hy				730.55	± 0.76	b	729.08	± 1.13	a	731.72	± 0.48	ab
	Ger Li				731.75	± 0.88	a	729.31	± 1.73	a	731.88	± 1.42	a
234	EE				730.95	± 0.82	b						
	Ger Hy				730.70	± 0.91	b						
	Ger Li				732.02	± 0.97	a						
236	EE	730.13	± 0.87	b									
	Ger Hy	730.29	± 0.67	b									
	Ger Li	731.09	± 0.80	a									
238	EE	729.04	± 0.81	b									
	Ger Hy	729.34	± 0.63	ab									
	Ger Li	729.92	± 0.84	a									
240	EE				728.46	± 0.97	b	727.73	± 1.38	b	730.68	± 0.76	b
	Ger Hy				729.02	± 0.85	b	728.93	± 0.84	a	732.13	± 0.80	a
	Ger Li				730.12	± 1.05	a	729.49	± 1.24	a	732.05	± 1.12	a
243	EE	728.51	± 0.82	c									
	Ger Hy	729.28	± 0.62	b									
	Ger Li	729.90	± 0.72	a									
244	EE							727.32	± 1.37	b	728.46	± 0.87	b
	Ger Hy							729.50	± 1.32	a	730.26	± 1.20	a
	Ger Li							729.63	± 1.16	a	730.00	± 1.16	a
246	EE	728.36	± 0.84	c				726.54	± 0.99	b	727.81	± 0.95	b
	Ger Hy	729.18	± 0.69	b				728.43	± 1.31	a	729.65	± 1.32	a
	Ger Li	730.16	± 0.61	a				728.42	± 1.12	a	729.34	± 1.20	a
247	EE							725.85	± 0.87	b	726.36	± 1.02	b
	Ger Hy							727.21	± 1.22	a	728.24	± 1.42	a
	Ger Li							727.24	± 0.74	a	727.59	± 1.03	a
249	EE							725.04	± 0.90	b	725.37	± 1.15	c
	Ger Hy							726.14	± 1.26	a	727.43	± 1.66	a
	Ger Li							726.16	± 0.84	a	726.49	± 1.18	b
250	EE	726.18	± 1.00	c									
	Ger Hy	727.69	± 0.74	b									
	Ger Li	728.53	± 0.66	a									
253	EE							721.30	± 1.01	b	720.63	± 1.26	c
	Ger Hy							723.23	± 2.03	a	723.46	± 2.12	a
	Ger Li							722.51	± 0.88	a	722.14	± 1.03	b

Table 35 (continued) REIP values of each variety group in all trials.

DAS		REIP													
		2017			2018			2019 Drought stress			2019 Irrigated				
		mean	sd	sig	mean	sd	sig	mean	sd	sig	mean	sd	sig		
255	EE						720.54	± 1.08	b	719.85	± 1.30	c			
	Ger Hy						722.60	± 2.01	a	723.07	± 1.50	a			
	Ger Li						721.84	± 1.03	a	721.54	± 0.89	b			
259	EE				723.69	± 1.37	a	719.53	± 0.91	b	719.33	± 1.66	b		
	Ger Hy				721.15	± 0.93	b	721.57	± 1.66	a	722.16	± 1.60	a		
	Ger Li				720.19	± 0.96	c	721.32	± 0.67	a	721.18	± 0.72	a		
260	EE						718.20	± 1.11	b	717.78	± 1.61	b			
	Ger Hy						720.47	± 1.76	a	720.60	± 1.56	a			
	Ger Li						720.33	± 0.63	a	719.88	± 0.81	a			
261	EE				728.64	± 1.48	a	718.31	± 1.03	b	718.62	± 1.41	b		
	Ger Hy				722.89	± 2.88	b	720.51	± 1.06	a	720.31	± 1.15	a		
	Ger Li				722.32	± 1.90	b	720.09	± 0.76	a	719.67	± 0.72	a		
263	EE	725.33	± 1.34	a						717.11	± 1.56	b	715.85	± 2.78	a
	Ger Hy	723.86	± 0.48	b						719.11	± 1.18	a	716.77	± 2.15	a
	Ger Li	723.34	± 0.50	b						718.76	± 0.76	a	716.11	± 1.53	a
264	EE	726.29	± 1.37	a											
	Ger Hy	723.85	± 0.56	b											
	Ger Li	723.18	± 0.56	b											
265	EE	727.78	± 1.49	a	731.26	± 1.22	a	717.60	± 1.14	b	721.99	± 1.20	a		
	Ger Hy	725.43	± 1.40	b	726.45	± 3.66	b	718.67	± 1.02	a	720.51	± 1.05	b		
	Ger Li	723.85	± 0.76	c	728.42	± 2.01	b	718.02	± 0.77	ab	719.96	± 1.40	b		
266	EE						720.04	± 0.63	a	720.66	± 1.00	a			
	Ger Hy						720.06	± 0.52	a	720.06	± 1.12	ab			
	Ger Li						719.47	± 0.80	b	719.13	± 1.53	b			
267	EE									721.11	± 1.02	a			
	Ger Hy									720.03	± 1.59	b			
	Ger Li									719.40	± 1.66	b			
269	EE						720.53	± 0.90	a	723.37	± 1.18	a			
	Ger Hy						720.31	± 0.96	ab	722.45	± 1.50	b			
	Ger Li						719.96	± 0.95	b	722.63	± 1.44	b			
271	EE	729.21	± 1.64	a											
	Ger Hy	728.19	± 0.92	ab											
	Ger Li	727.67	± 1.29	b											

DAS: Days after sowing; EE: Eastern European lines, Ger Hy: German hybrids, Ger Li: German Lines, mean: mean values per group of varieties, sd: standard deviation, sig: significant differences within one trial and DAS

8.5.4. Canopy temperature (Fluke)

Table 36 Canopy temperature (Fluke) of all variety groups in all trials.

DAS		Canopy temperature (Fluke)											
		2017			2018			2019 Drought stress			2019 Irrigated		
		mean	sd	sig	mean	sd	sig	mean	sd	sig	mean	sd	sig
221	EE							24.64	± 1.40	a	23.96	± 1.22	a
	Ger Hy							24.14	± 1.29	a	22.93	± 1.84	a
	Ger Li							24.71	± 1.40	a	23.32	± 1.67	a
226	EE							22.30	± 0.97	a	21.89	± 1.00	a
	Ger Hy							20.44	± 1.46	c	20.85	± 0.94	b
	Ger Li							21.61	± 1.03	b	21.13	± 1.04	b
227	EE							23.09	± 1.30	a	21.91	± 0.84	a
	Ger Hy							22.23	± 0.90	a	21.90	± 0.73	a
	Ger Li							22.66	± 1.19	a	21.73	± 0.68	a
230	EE				21.89	± 0.85	a	23.26	± 1.18	a	21.65	± 0.58	a
	Ger Hy				21.62	± 1.06	a	21.69	± 0.46	b	21.08	± 1.05	b
	Ger Li				21.63	± 0.79	a	22.36	± 1.06	b	21.17	± 0.80	b
231	EE							26.27	± 0.79	a	24.61	± 0.34	a
	Ger Hy							24.88	± 0.54	c	24.32	± 0.30	a
	Ger Li							25.70	± 0.77	b	24.51	± 0.49	a
232	EE				26.16	± 0.90	a						
	Ger Hy				26.09	± 0.56	a						
	Ger Li				26.45	± 0.83	a						
234	EE				26.56	± 0.59	b						
	Ger Hy				26.95	± 0.56	ab						
	Ger Li				27.07	± 0.61	a						
237	EE				27.03	± 0.79	a						
	Ger Hy				27.50	± 0.83	a						
	Ger Li				27.43	± 1.28	a						
238	EE	24.83	± 0.79	a									
	Ger Hy	24.85	± 0.59	a									
	Ger Li	24.93	± 0.83	a									
239	EE				30.15	± 0.98	a						
	Ger Hy				30.33	± 0.98	a						
	Ger Li				30.58	± 1.00	a						
240	EE				32.64	± 1.13	a						
	Ger Hy				33.10	± 1.07	a						
	Ger Li				33.08	± 1.18	a						
243	EE	32.76	± 1.03	a									
	Ger Hy	32.71	± 0.85	a									
	Ger Li	33.05	± 1.12	a									
244	EE										28.35	± 0.53	a
	Ger Hy										28.15	± 0.39	a
	Ger Li										28.41	± 0.54	a
245	EE				31.18	± 1.10	a	30.26	± 1.11	a	28.71	± 0.68	a
	Ger Hy				31.40	± 0.89	a	30.41	± 1.76	a	28.22	± 0.26	b
	Ger Li				31.35	± 1.36	a	30.30	± 1.13	a	28.81	± 0.57	a
246	EE	28.57	± 0.98	a									
	Ger Hy	29.27	± 0.86	a									
	Ger Li	28.96	± 0.91	a									
249	EE				28.93	± 1.44							
	Ger Hy				28.49	± 1.65							
	Ger Li				28.69	± 1.86							
251	EE							34.42	± 1.91	a	31.24	± 1.51	a
	Ger Hy							33.97	± 1.44	a	28.88	± 0.78	b
	Ger Li							34.51	± 1.16	a	29.67	± 1.21	b
252	EE	29.38	± 1.38	a	35.78	± 1.67	a						
	Ger Hy	29.84	± 2.45	a	34.47	± 1.61	b						
	Ger Li	29.76	± 1.80	a	34.99	± 1.83	b						

Table 36 (continued) Canopy temperature (Fluke) of all variety groups in all trials.

Canopy temperature (Fluke)												
DAS	2017			2018			2019 Drought stress			2019 Irrigated		
	mean	sd	sig	mean	sd	sig	mean	sd	sig	mean	sd	sig
254	EE			29.37	± 0.69	a						
	Ger Hy			28.37	± 0.61	b						
	Ger Li			28.62	± 0.66	b						
255	EE						32.21	± 1.01	a	31.94	± 1.07	a
	Ger Hy			30.42	± 1.41	a	31.83	± 1.94	a	30.63	± 1.88	b
	Ger Li			30.15	± 1.86	a	31.92	± 1.02	a	31.37	± 1.07	b
259	EE											
	Ger Hy			34.61	± 0.77	a						
	Ger Li			35.14	± 1.05	a						
260	EE						35.89	± 1.94	a	34.43	± 1.12	a
	Ger Hy						34.37	± 1.94	b	33.13	± 1.52	b
	Ger Li						35.07	± 1.30	b	34.09	± 1.29	a
261	EE	34.38	± 1.23	a			36.74	± 1.78	a	35.01	± 1.47	a
	Ger Hy	34.89	± 0.65	a			35.06	± 3.25	b	34.27	± 2.06	a
	Ger Li	34.68	± 0.89	a			36.07	± 1.56	ab	34.73	± 1.25	a
265	EE	36.81	± 1.28	a								
	Ger Hy	37.48	± 1.21	a								
	Ger Li	36.90	± 1.14	a								
266	EE						39.54	± 1.88	a	36.98	± 1.00	b
	Ger Hy						38.90	± 2.05	a	37.51	± 1.64	ab
	Ger Li						39.48	± 1.77	a	37.76	± 1.11	a
267	EE						41.77	± 2.11	a	40.10	± 1.52	a
	Ger Hy						40.95	± 1.95	a	40.02	± 2.17	a
	Ger Li						42.05	± 2.19	a	40.82	± 1.85	a

DAS: Days after sowing; EE: Eastern European lines, Ger Hy: German hybrids, Ger Li: German Lines, mean: mean values per group of varieties, sd: standard deviation, sig: significant differences within one trial and DAS

8.6. Differences of NDVI, WI, and REIP between irrigated and drought stress plots 2018/2019

Table 37 Differences of NDVI, WI, REIP, and canopy temperature values between irrigated and drought stress plots 2018/2019.

DAS	NDVI			WI			REIP			Fluke				
	mean	sd	sig	mean	sd	sig	mean	sd	sig	mean	sd	sig		
221	Irrigated	EE	0.93	± 0.01	b	1.22	± 0.03	a	730.64	± 0.97	b	23.96	± 1.22	a
		Ger	0.95	± 0.01	a	1.22	± 0.03	a	732.06	± 1.28	a	23.24	± 1.70	b
	Drought stress	EE	0.90	± 0.02	d	1.16	± 0.03	b	727.32	± 1.79	d	24.64	± 1.40	a
		Ger	0.92	± 0.02	c	1.16	± 0.03	b	728.51	± 1.93	c	24.59	± 1.38	a
224	Irrigated	EE	0.94	± 0.01	a	1.25	± 0.02	a	731.06	± 0.86	a	±		
		Ger	0.94	± 0.01	a	1.23	± 0.03	b	731.57	± 1.32	a	±		
	Drought stress	EE	0.91	± 0.02	c	1.16	± 0.03	c	726.73	± 1.68	c	±		
		Ger	0.93	± 0.01	b	1.16	± 0.02	c	728.03	± 1.63	b	±		
225	Irrigated	EE	0.93	± 0.01	a	1.26	± 0.02	a	730.73	± 0.88	a	±		
		Ger	0.94	± 0.01	a	1.23	± 0.03	b	731.30	± 1.25	a	±		
	Drought stress	EE	0.91	± 0.02	c	1.13	± 0.03	c	727.32	± 1.71	c	±		
		Ger	0.92	± 0.01	b	1.13	± 0.02	c	728.72	± 1.84	b	±		
226	Irrigated	EE	0.94	± 0.01	a	1.24	± 0.02	a	731.08	± 1.00	b	21.89	± 1.00	a
		Ger	0.94	± 0.01	a	1.23	± 0.03	b	731.79	± 1.23	a	21.08	± 1.02	b
	Drought stress	EE	0.90	± 0.02	c	1.16	± 0.03	c	726.89	± 1.69	d	22.30	± 0.97	a
		Ger	0.92	± 0.01	b	1.17	± 0.03	c	728.44	± 1.72	c	21.38	± 1.21	b

Table 37 (continued) Differences of NDVI, WI, REIP, and canopy temperature values between irrigated and drought stress plots 2018/2019.

DAS			NDVI			WI			REIP			Fluke		
			mean	sd	sig	mean	sd	sig	mean	sd	sig	mean	sd	sig
227	Irrigated	EE	0.93 ± 0.01	a	1.27 ± 0.02	a	730.97 ± 1.20	a	21.91 ± 0.84	c				
		Ger	0.93 ± 0.01	a	1.26 ± 0.03	b	731.46 ± 1.16	a	21.76 ± 0.68	c				
	Drought stress	EE	0.90 ± 0.02	c	1.17 ± 0.03	c	727.36 ± 1.78	c	23.09 ± 1.30	a				
		Ger	0.92 ± 0.01	b	1.17 ± 0.03	c	728.81 ± 1.65	b	22.58 ± 1.14	b				
230	Irrigated	EE	0.93 ± 0.01	a	1.26 ± 0.02	a	731.43 ± 0.95	a	21.65 ± 0.58	c				
		Ger	0.94 ± 0.01	a	1.26 ± 0.03	a	732.04 ± 1.10	a	21.15 ± 0.84	d				
	Drought stress	EE	0.91 ± 0.02	c	1.17 ± 0.03	c	727.70 ± 1.66	c	23.26 ± 1.18	a				
		Ger	0.93 ± 0.01	b	1.19 ± 0.03	b	729.48 ± 1.59	b	22.23 ± 1.00	b				
231	Irrigated	EE	0.93 ± 0.01	a	1.26 ± 0.02	a	731.27 ± 1.05	a	24.61 ± 0.34	c				
		Ger	0.93 ± 0.01	a	1.27 ± 0.03	a	731.85 ± 1.29	a	24.47 ± 0.46	c				
	Drought stress	EE	0.90 ± 0.02	c	1.19 ± 0.03	c	727.37 ± 1.59	c	26.27 ± 0.79	a				
		Ger	0.92 ± 0.02	b	1.21 ± 0.03	b	729.27 ± 1.62	b	25.54 ± 0.80	b				
240	Irrigated	EE	0.92 ± 0.01	b	1.24 ± 0.02	b	730.68 ± 0.76	b	±					
		Ger	0.93 ± 0.01	a	1.29 ± 0.02	a	732.07 ± 1.06	a	±					
	Drought stress	EE	0.89 ± 0.02	d	1.15 ± 0.03	d	727.73 ± 1.38	d	±					
		Ger	0.91 ± 0.01	c	1.19 ± 0.03	c	729.38 ± 1.19	c	±					
244	Irrigated	EE	0.89 ± 0.01	b	1.18 ± 0.02	b	728.46 ± 0.87	b	28.35 ± 0.53	a				
		Ger	0.90 ± 0.01	a	1.20 ± 0.02	a	730.05 ± 1.16	a	28.36 ± 0.52	a				
	Drought stress	EE	0.87 ± 0.03	c	1.14 ± 0.04	c	727.32 ± 1.37	c	±					
		Ger	0.90 ± 0.02	a	1.14 ± 0.06	c	729.61 ± 1.18	a	±					
245	Irrigated	EE						28.71 ± 0.68	b					
		Ger						28.69 ± 0.57	b					
	Drought stress	EE						30.26 ± 1.11	a					
		Ger						30.32 ± 1.25	a					
246	Irrigated	EE	0.88 ± 0.02	b	1.28 ± 0.02	b	727.81 ± 0.95	c	±					
		Ger	0.90 ± 0.01	a	1.31 ± 0.02	a	729.40 ± 1.22	a	±					
	Drought stress	EE	0.85 ± 0.02	c	1.13 ± 0.02	d	726.54 ± 0.99	d	±					
		Ger	0.88 ± 0.02	b	1.17 ± 0.02	c	728.42 ± 1.15	b	±					
247	Irrigated	EE	0.84 ± 0.03	b	1.35 ± 0.02	b	726.36 ± 1.02	c	±					
		Ger	0.86 ± 0.02	a	1.37 ± 0.03	a	727.72 ± 1.14	a	±					
	Drought stress	EE	0.80 ± 0.03	c	1.11 ± 0.02	d	725.85 ± 0.87	d	±					
		Ger	0.84 ± 0.02	b	1.15 ± 0.02	c	727.23 ± 0.85	b	±					
249	Irrigated	EE	0.79 ± 0.04	b	1.09 ± 0.02	b	725.37 ± 1.15	c	±					
		Ger	0.84 ± 0.03	a	1.10 ± 0.03	a	726.68 ± 1.33	a	±					
	Drought stress	EE	0.76 ± 0.04	c	1.08 ± 0.02	b	725.04 ± 0.90	c	±					
		Ger	0.81 ± 0.04	b	1.11 ± 0.02	a	726.16 ± 0.93	b	±					
251	Irrigated	EE						31.24 ± 1.51	b					
		Ger						29.51 ± 1.17	c					
	Drought stress	EE						34.42 ± 1.91	a					
		Ger						34.40 ± 1.23	a					
253	Irrigated	EE	0.62 ± 0.06	c	1.27 ± 0.03	c	720.63 ± 1.26	c	±					
		Ger	0.74 ± 0.07	a	1.29 ± 0.05	b	722.41 ± 1.40	a	±					
	Drought stress	EE	0.66 ± 0.06	b	1.29 ± 0.03	b	721.30 ± 1.01	b	±					
		Ger	0.73 ± 0.05	a	1.31 ± 0.03	a	722.66 ± 1.21	a	±					
255	Irrigated	EE	0.52 ± 0.06	c	1.04 ± 0.02	b	719.85 ± 1.30	c	31.94 ± 1.07	a				
		Ger	0.66 ± 0.08	a	1.05 ± 0.03	ab	721.84 ± 1.20	a	31.22 ± 1.29	b				
	Drought stress	EE	0.57 ± 0.07	b	1.04 ± 0.02	b	720.54 ± 1.08	b	32.21 ± 1.01	a				
		Ger	0.66 ± 0.08	a	1.06 ± 0.02	a	721.99 ± 1.30	a	31.90 ± 1.23	a				
258	Irrigated	EE	0.39 ± 0.05	b	0.97 ± 0.01	a	717.85 ± 1.64	b	±					
		Ger	0.52 ± 0.09	a	0.97 ± 0.03	a	720.32 ± 1.32	a	±					
	Drought stress	EE						±						
		Ger						±						

Table 37 (continued) Differences of NDVI, WI, REIP, and canopy temperature values between irrigated and drought stress plots 2018/2019.

DAS		NDVI			WI			REIP			Fluke		
		mean	sd	sig	mean	sd	sig	mean	sd	sig	mean	sd	sig
259	Irrigated	EE	0.36 ± 0.04	c	1.01 ± 0.01	b		719.33 ± 1.66	b				±
		Ger	0.48 ± 0.09	a	1.02 ± 0.03	b		721.37 ± 1.02	a				±
	Drought stress	EE	0.42 ± 0.05	b	1.04 ± 0.02	a		719.53 ± 0.91	b				±
		Ger	0.50 ± 0.08	a	1.05 ± 0.03	a		721.37 ± 0.94	a				±
260	Irrigated	EE	0.29 ± 0.04	c				717.78 ± 1.61	b		34.43 ± 1.12	bc	
		Ger	0.40 ± 0.09	a				720.03 ± 1.03	a		33.90 ± 1.38	c	
	Drought stress	EE	0.35 ± 0.05	b	1.03 ± 0.01	a		718.20 ± 1.11	b		35.89 ± 1.94	a	
		Ger	0.41 ± 0.09	a	1.04 ± 0.02	a		720.36 ± 0.95	a		34.93 ± 1.46	b	
261	Irrigated	EE	0.26 ± 0.04	c	0.98 ± 0.01	b		718.62 ± 1.41	b		35.01 ± 1.47	c	
		Ger	0.37 ± 0.09	a	0.99 ± 0.03	b		719.79 ± 0.85	a		34.64 ± 1.44	c	
	Drought stress	EE	0.31 ± 0.05	b	1.06 ± 0.01	a		718.31 ± 1.03	b		36.74 ± 1.78	a	
		Ger	0.38 ± 0.07	a	1.06 ± 0.03	a		720.17 ± 0.83	a		35.87 ± 2.02	b	
263	Irrigated	EE	0.16 ± 0.05	c	1.01 ± 0.02	a		715.85 ± 2.78	c				±
		Ger	0.27 ± 0.08	b	1.02 ± 0.02	a		716.25 ± 1.67	bc				±
	Drought stress	EE	0.28 ± 0.06	b	0.99 ± 0.02	b		717.11 ± 1.56	b				±
		Ger	0.40 ± 0.08	a	0.99 ± 0.03	b		718.83 ± 0.86	a				±
265	Irrigated	EE	0.21 ± 0.03	d	0.96 ± 0.02	b		721.99 ± 1.20	a				±
		Ger	0.29 ± 0.06	b	0.96 ± 0.02	b		720.07 ± 1.35	b				±
	Drought stress	EE	0.24 ± 0.04	c	0.97 ± 0.01	a		717.60 ± 1.14	d				±
		Ger	0.32 ± 0.07	a	0.97 ± 0.02	a		718.15 ± 0.86	c				±
266	Irrigated	EE	0.17 ± 0.03	c	0.95 ± 0.01	b		720.66 ± 1.00	a		36.98 ± 1.00	c	
		Ger	0.22 ± 0.04	b	0.95 ± 0.02	b		719.32 ± 1.50	c		37.71 ± 1.22	b	
	Drought stress	EE	0.22 ± 0.04	b	0.97 ± 0.01	a		720.04 ± 0.63	b		39.54 ± 1.88	a	
		Ger	0.28 ± 0.05	a	0.97 ± 0.02	a		719.59 ± 0.79	bc		39.36 ± 1.82	a	
267	Irrigated	EE	0.16 ± 0.03	b	0.94 ± 0.01	a		721.10 ± 1.02	a		40.10 ± 1.52	b	
		Ger	0.19 ± 0.03	a	0.93 ± 0.01	a		719.53 ± 1.65	b		40.66 ± 1.92	b	
	Drought stress	EE									41.77 ± 2.11	a	
		Ger									41.83 ± 2.18	a	
269	Irrigated	EE	0.18 ± 0.03	b	0.96 ± 0.01	b		723.37 ± 1.18	a				±
		Ger	0.18 ± 0.02	b	0.96 ± 0.01	b		722.59 ± 1.44	b				±
	Drought stress	EE	0.24 ± 0.04	a	0.99 ± 0.01	a		720.53 ± 0.90	c				±
		Ger	0.24 ± 0.04	a	0.99 ± 0.01	a		720.03 ± 0.96	c				±

DAS: Days after sowing; EE: Eastern European lines, Ger: German varieties, mean: mean values per group of varieties, sd: standard deviation, sig: significant differences within one index and DAS

8.7. Differences of canopy temperature and NDVI between terrestrial and airborne measurements

Table 38 Differences in canopy temperature and NDVI of irrigated and drought stress plots between terrestrial (Fluke/HandySpec) and airborne (DuetT/Sequoia) measurements.

DAS		Temperature			NDVI		
		mean	sd	sig	mean	sd	sig
221	Irrigated	Airborne	23.72 ± 0.52	b	0.82 ± 0.02	c	
		Terrestrial	23.60 ± 1.52	b	0.94 ± 0.01	a	
	Drought stress	Airborne	24.64 ± 0.77	a	0.78 ± 0.04	d	
		Terrestrial	24.61 ± 1.39	a	0.91 ± 0.02	b	
224	Irrigated	Airborne			0.94 ± 0.01	a	
		Terrestrial					
	Drought stress	Airborne					
		Terrestrial			0.92 ± 0.02	b	

Table 38 (continued) Differences in canopy temperature and NDVI of irrigated and drought stress plots between terrestrial (Fluke/HandySpec) and airborne (DuetT/Sequoia) measurements.

DAS			Temperature			NDVI		
			mean	sd	sig	mean	sd	sig
225	Irrigated	Airborne Terrestrial				0.94 ± 0.01		a
	Drought stress	Airborne Terrestrial				0.91 ± 0.02		b
226	Irrigated	Airborne Terrestrial	19.89 ± 0.46		d	0.80 ± 0.02		c
	Drought stress	Airborne Terrestrial	21.48 ± 1.09		b	0.94 ± 0.01		a
227	Irrigated	Airborne Terrestrial	20.92 ± 0.83		c	0.76 ± 0.04		d
	Drought stress	Airborne Terrestrial	21.84 ± 1.19		a	0.91 ± 0.02		b
230	Irrigated	Airborne Terrestrial	22.23 ± 0.67		b	0.84 ± 0.02		c
	Drought stress	Airborne Terrestrial	21.84 ± 0.77		c	0.93 ± 0.01		a
231	Irrigated	Airborne Terrestrial	23.07 ± 0.88		a	0.82 ± 0.04		d
	Drought stress	Airborne Terrestrial	22.83 ± 1.24		a	0.91 ± 0.02		b
240	Irrigated	Airborne Terrestrial	21.40 ± 0.76		b	0.94 ± 0.01		a
	Drought stress	Airborne Terrestrial	22.74 ± 1.20		a	0.92 ± 0.02		b
244	Irrigated	Airborne Terrestrial	24.54 ± 0.41		b	0.93 ± 0.01		a
	Drought stress	Airborne Terrestrial	25.90 ± 0.87		a	0.91 ± 0.02		b
245	Irrigated	Airborne Terrestrial	26.54 ± 0.59		a	0.76 ± 0.03		c
	Drought stress	Airborne Terrestrial	26.22 ± 0.76		b	0.93 ± 0.01		a
246	Irrigated	Airborne Terrestrial	24.01 ± 0.45		c	0.72 ± 0.03		c
	Drought stress	Airborne Terrestrial	28.36 ± 0.52		a	0.90 ± 0.01		a
247	Irrigated	Airborne Terrestrial	24.86 ± 0.58		b	0.70 ± 0.04		d
	Drought stress	Airborne Terrestrial	±			0.88 ± 0.03		b
249	Irrigated	Airborne Terrestrial	26.89 ± 0.51		c			
	Drought stress	Airborne Terrestrial	28.70 ± 0.63		b			
251	Irrigated	Airborne Terrestrial	26.83 ± 0.77		c			
	Drought stress	Airborne Terrestrial	30.29 ± 1.17		a			
253	Irrigated	Airborne Terrestrial				0.70 ± 0.03		c
	Drought stress	Airborne Terrestrial				0.89 ± 0.02		a
255	Irrigated	Airborne Terrestrial				0.67 ± 0.04		d
	Drought stress	Airborne Terrestrial				0.86 ± 0.03		b
257	Irrigated	Airborne Terrestrial				0.85 ± 0.03		a
	Drought stress	Airborne Terrestrial				0.82 ± 0.04		b
259	Irrigated	Airborne Terrestrial				0.81 ± 0.04		a
	Drought stress	Airborne Terrestrial				0.79 ± 0.04		b
261	Irrigated	Airborne Terrestrial	30.38 ± 1.60		b			
	Drought stress	Airborne Terrestrial	34.41 ± 1.60		a			
263	Irrigated	Airborne Terrestrial				0.42 ± 0.10		c
	Drought stress	Airborne Terrestrial				0.69 ± 0.09		a
265	Irrigated	Airborne Terrestrial				0.46 ± 0.08		b
	Drought stress	Airborne Terrestrial				0.70 ± 0.07		a

Table 38 (continued) Differences in canopy temperature and NDVI of irrigated and drought stress plots between terrestrial (Fluke/HandySpec) and airborne (DuetT/Sequoia) measurements.

DAS			Temperature			NDVI		
			mean	sd	sig	mean	sd	sig
255	Irrigated	Airborne	27.43	± 1.10	d	0.27	± 0.12	b
		Terrestrial	31.58	± 1.23	b	0.59	± 0.10	a
	Drought stress	Airborne	28.53	± 1.13	c	0.29	± 0.10	b
		Terrestrial	32.05	± 1.14	a	0.62	± 0.09	a
257	Irrigated	Airborne				0.19	± 0.12	b
		Terrestrial						
	Drought stress	Airborne				0.22	± 0.10	a
		Terrestrial						
259	Irrigated	Airborne				0.10	± 0.09	d
		Terrestrial				0.42	± 0.09	b
	Drought stress	Airborne				0.17	± 0.10	c
		Terrestrial				0.46	± 0.08	a
260	Irrigated	Airborne						
		Terrestrial	34.16	± 1.28	b	0.35	± 0.09	b
	Drought stress	Airborne						
		Terrestrial	35.41	± 1.77	a	0.38	± 0.08	a
261	Irrigated	Airborne	31.48	± 1.10	d			
		Terrestrial	34.83	± 1.46	b	0.32	± 0.09	b
	Drought stress	Airborne	32.47	± 1.24	c			
		Terrestrial	36.30	± 1.95	a	0.35	± 0.07	a
263	Irrigated	Airborne				0.21	± 0.09	b
		Terrestrial						
	Drought stress	Airborne				0.34	± 0.09	a
		Terrestrial						
265	Irrigated	Airborne				0.25	± 0.06	b
		Terrestrial						
	Drought stress	Airborne				0.28	± 0.07	a
		Terrestrial						
266	Irrigated	Airborne				0.20	± 0.05	b
		Terrestrial	37.34	± 1.17	b			
	Drought stress	Airborne				0.25	± 0.05	a
		Terrestrial	39.45	± 1.84	a			
269	Irrigated	Airborne				0.18	± 0.03	b
		Terrestrial						
	Drought stress	Airborne				0.24	± 0.04	a
		Terrestrial						
271	Irrigated	Airborne	38.29	± 1.25	c			
		Terrestrial	40.38	± 1.75	b			
	Drought stress	Airborne	37.53	± 1.47	d			
		Terrestrial	41.80	± 2.13	a			

DAS: Days after sowing; mean: mean values per group of varieties, sd: standard deviation, sig: significant differences within one trial and DAS

9. Acknowledgement

I would like to thank Prof. Dr. Urs Schmidhalter for providing me the opportunity to carry out this project and to write my doctoral thesis at the Chair of Plant Nutrition. He brought trust to me, supported me, and encouraged me throughout the entire project. Thanks for helping me clear all hurdles, both formal and practical.

Special thanks to Prof. Dr. Boris Boincean and Prof. Dr. Alexei Postolati for having me at the Selectia Research Institute of Field Crops in Bălți. I was always welcomed with open arms and could experience a great time in Moldova. They introduced me to a new country and culture, and provided every help needed to make my stays unforgettable and successful. I am extremely grateful for the opportunity to work with them and the entire staff at the Selectia institute, expanding my horizon and making friends in a new place.

Thanks also to Jürgen Plass from the Chair of Plant Nutrition for technical support, drone knowledge and emergency help, in any case and any country.

Further, thanks to the entire crew in the lab and the secretariat for their help, and to all other colleagues for good company along the way, support, insightful discussions, and nice chats.