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Effect of drought on yield components of maize hybrids (*Zea mays* L)

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Abstract

When investigating drought tolerance, it must not be forgotten that drought stress is a complex phenomenon exhibiting quite different characters in different years and locations. For this reason, the plant response to drought is also a complex process. In our study, 83 maize hybrids originating from various countries were investigated over a period of two years, under irrigated and non-irrigated conditions. The drought tolerance of plants in the non-irrigated plots was analysed in terms of flowering synchrony and yield components. It could be concluded from the results that in response to long-term water deficit the period between tasselling and silking became longer, while the analysis of yield components revealed the greatest reductions in the number of kernels per ear and in the proportion of seed set. As the degree of proterandry increased, there was a decline in the grain yield, confirming that the analysis of this trait could be a way of predicting drought tolerance. Considerable differences in drought tolerance were observed between the genetic materials included in the analysis, suggesting the presence among these parental lines and hybrids of genotypes resistant to long-term water deficit, suitable for cultivation under dry conditions. An analysis of correlations between the traits revealed that proterandry should be treated as a priority trait when investigating drought stress tolerance, as better predictions can be made of both drought tolerance and potential yields, leading to more reliable selection for higher yields.

Keywords: drought tolerance, yield components, proterandry, maize

Introduction

The timing and form of drought changes from year to year, so under non-irrigated conditions it is difficult to design experiments that will give reproducible results suitable for the selection of genetic materials with resistance to water deficit. Plants may be exposed to the various components of drought stress in many forms and combinations. The components of drought stress are the following: i) the duration and starting date of drought; ii) the relative humidity, temperature and movement of the air; iii) the intensity of solar radiation; iv) the quantity and distribution of precipitation; v) the texture (clay, loam, sand), water content and temperature of the soil, and the ground-water depth; vi) the species, variety, age and developmental stage of the crop, the stand density and the length of the vegetation period.

Plants may employ various strategies to overcome the consequences of drought: i) improvements in water use efficiency; ii) escape, i.e. completing reproductive processes, the development phase most sensitive to water deficit, before the onset of dry weather iii) an improvement in the *per se* drought tolerance of the plant (Ribaut et al, 2009).

Maize is most sensitive to drought during the flowering period. The most important symptoms of drought damage during flowering are the following:

delay in inflorescence development, flowering asynchrony, tassel blasting, reduction in pollen fertility and viability (possibly complete sterility), reduction in pistil receptivity (in some cases complete sterility), abortion of embryos (Westgate and Boyer, 1985). Maize is a cross-fertilised plant, so it is considerably more sensitive to drought and high temperature during flowering than other cereals, as the male and female flowers develop separately, at a distance of as much as 1 m from each other; in addition, both the pollen and the pistils are directly exposed to environmental effects. In the case of maize the kernels develop at the same time on a single ear, so stress at flowering may result in the simultaneous abortion of all the kernels (Tollenaar and Daynard, 1978). Due to the physical separation of the male and female flowers, dichogamy may occur (maturing of the anthers and pistils at different times). Male flowering generally begins before the appearance of the silk (proterandry), but in some cases female flowering may occur earlier (proterogyny), or the tassel and silk may flower simultaneously. In species where the maturing of the male and female flowers takes place at different times, relative humidity and temperature may affect proterandry to a substantial extent, which means that stress (such as drought) during the vegetation period may have a great influence on this synchrony

(Struik et al, 1986).

It is generally agreed that maize is the most sensitive to stress during the flowering period, when pollen shedding, silking and seed setting take place. Water deficit causes a much greater retardation in ear development, and consequently in the appearance of the pistils, than in the development of the male inflorescence, i.e. tasselling. This phenomenon is responsible for an increase in the length of proterandry. In response to stress at flowering, the yield quantity exhibits a close correlation with the kernel number per plant ($r > 0.8$), the occurrence of sterility ($r > 0.7$) and with proterandry ($r = 0.4-0.7$) (Bolaños and Edmeades, 1996).

If water deficit is accompanied by a long period of hot weather, the reduced number of viable pollen grains (Hall et al, 1982; Schoper et al, 1986) and the low water potential of the developing pistils (Herrero and Johnson, 1981; Westgate and Boyer, 1986) may further reduce the kernel number. Long periods of severe drought may also cause direct damage to the developing inflorescences (Moss and Downey, 1971). It has frequently been observed that during drought the interval between male and female flowering (proterandry) increases (DuPlessis and Dijkhuis, 1967; Hall et al, 1981; Herrero and Johnson, 1981). This is generally caused by the relative delay in the appearance of the pistils compared with that of the tassels (which is less affected by drought). Proterandry is thus a more important trait in determining the drought tolerance of a hybrid than the flowering date itself, and is independent of differences between varieties in different maturity groups (Edmeades et al, 1989). A delay in the appearance of the pistils may be caused by their slower growth, which is greatly influenced by the water supplies to the plant (Herrero and Johnson, 1981; Westgate and Boyer, 1986). Proterandry, which is a useful index of the degree of flowering asynchrony, increases in response to water deficit, primarily due to the later appearance of the ear primordium and the pistils and to their slower growth (Bolaños and Edmeades, 1993). Many authors also attributed an increase in proterandry to a lower quantity of assimilates in the plant, which could be caused, among other things, by greater plant density (Buren et al, 1974; Edmeades and Daynard, 1979a).

Proterandry is undoubtedly the secondary trait used most frequently for the improvement of drought stress tolerance (Beck et al, 1996; Troyer, 1983). According to Vega et al (2001) the degree of proterandry established during the flowering period is also an excellent trait for the measurement of the rate of ear formation and plant development. Newly developed, stress-tolerant genotypes respond to drought with a relatively small increase in proterandry compared with older hybrids (Bruce et al, 2001), though for many «modern» hybrids a comparison of proterandry and grain yield revealed a high level of variability for both traits.

Photosynthetic activity and tolerance of high temperatures both influence water use efficiency, while proterandry, ear growth and barrenness are correlated with the distribution of assimilates during grain filling. The yield formed during drought stress is closely correlated with the number of ears per plant, the kernel number per ear and short proterandry, and in moderately close correlation with leaf drying (senescence), leaf chlorophyll concentration and plant height. The kernel number per plant is decisively influenced by the flow of assimilates into the ear primordia at flowering (Edmeades and Daynard, 1979b). In genotypes selected for short proterandry and high yield under dry conditions it was observed that they generally accumulated less carbohydrate in the tassel and the vegetative organs, thus allowing a larger quantity of assimilates to be accumulated in the ear primordia (Edmeades et al, 1993).

The heritability of grain yield is very low in the case of drought, so it is difficult to achieve genetic gain by direct selection under such conditions. On the other hand, the heritability of a number of secondary traits remains high even under dry conditions. The heritability of proterandry and the number of kernels per plant, for instance, remains stable during drought stress, or may even be improved (Bolaños and Edmeades, 1996). The variability of these traits increases in the case of severe drought stress, making it possible to evaluate the performance of lines and hybrids, as these traits are closely correlated with the grain yield. In the case of proterandry, for example, the strong negative correlation can be used to estimate the yield under dry conditions (Bolaños and Edmeades, 1993; Monneveux and Ribaut, 2006; Ribaut et al, 1997). Selection under dry conditions is less efficient than in a stress-free environment, as it reduces the heritability of the grain yield (Rosielle and Hamblin, 1981; Blum, 1988).

Ribaut et al (2009) summarised the opportunities available in breeding for drought tolerance as follows: selection for genotypes with a smaller leaf area in the upper region of the plant, and selection for short, thick stalks, smaller tassels, erect leaves and later senescence (stay green). These authors consider smaller root biomass to be a relatively easily influenced trait, and suggest that the aim should be to produce deep-rooted genotypes with fewer lateral roots.

The aim in drought stress studies should be to find genotypes with short proterandry or complete flowering synchrony, as simultaneous selection is possible in these genotypes for drought tolerance and higher yields.

Materials and Methods

A panel of 83 hybrids has been evaluated over two growing seasons (2011, 2012) under well watered (WW) and water deficit (WD) conditions in the nursery of the Agricultural Institute at Martonvásár (Hungary). Hybrids were obtained by crossing a European flint

tester with a collection of inbred lines from different heterotic groups developed in the framework of the DROPS European project from UMR INRA-SUPAGRO, Institute de Biologie Intégrative des Plantes with a European flint tester (EFT). A total of 83 genotypes were included in the experiment. The female components of the hybrids were lines developed by the consortium members (firms and companies) involved in the DROPS project and belonged to various heterotic groups, so it was important to cross them with a partner that was unlikely to be related to any of these lines. This was why the European flint tester was chosen. The trial was a complete block design with five replications of the 83 genotype. Individual plots comprised two 5.6 m-long rows, with 76.2 cm between rows and 20 cm between plants in a row.

The experiments were set up in two years (2011 and 2012) in a random block design with two (irrigated: WW) or three (non-irrigated: WD) replications in the nursery of the Agricultural Institute, Martonvásár. The two-row plots were 5.6 m in length, with a plant distance of 20 cm and a plant density of 55-60 plants per plot. The soil of the experimental station is a chernozem with lime deposits, formed on loess, with a favourable water regime and loamy texture. The moisture status of the soil was logged throughout the vegetation period using soil moisture sensors (Decagon - Em20). Two sensors placed at 30, 60 and 90 cm depth at five locations, in each plot of a check genotype were placed on the irrigated area and three on the non-irrigated area in such a way that they gave a good representation of the water status of the whole area. The sensors were placed at depths of 30, 60 and 90 cm. Irrigation was always based on the moisture status of the soil. The measurements were made with Decagon - Em20 soil moisture sensors working on the principle of conductivity (v/v %), tensiometers

(cBar) and automatic data loggers.

On site temperatures (min, max, mean), global radiation, rainfall quantity and wind speed were recorded daily throughout the growing period.

The WW area was irrigated on 4-5 occasions each year (in summer, in the months of June and July), based on the data provided by the soil sensors. Irrigation was begun when to ensure that the soil water potential remained above -30 cB (20% volumetric water content). Linear irrigation equipment was used, which distributed a uniform quantity of water over the whole WW area. At each occasion, 40-50 mm water was supplied. The WD area was irrigated on a single occasion with 15 mm water to ensure that the soil water potential remained above -90 cB during the flowering period. Irrigation of the WW and WD areas after flowering allowed to avoid drought occurrence during grain filling.

Irrigation was discontinued after flowering (in mid- or late August) as the aim of the experiments was to model the plant responses to drought before, during or immediately after flowering, and not the effects caused by water deficit during the grain-filling period.

Male and female flowering were recorded daily. The plants in each plot were considered to be flowering when at least 50% of the plants had started shedding pollen, or when the silks were clearly visible on at least half the plants. Proterandry was expressed as the number of days between male and female flowering, while the flowering dates were given as the number of days from sowing.

The plots were harvested with a small-plot combine and the yield data (yield plot⁻¹, g, and grain moisture, %) were recorded simultaneously with a single instrument. Ear length and percentage fertilisation

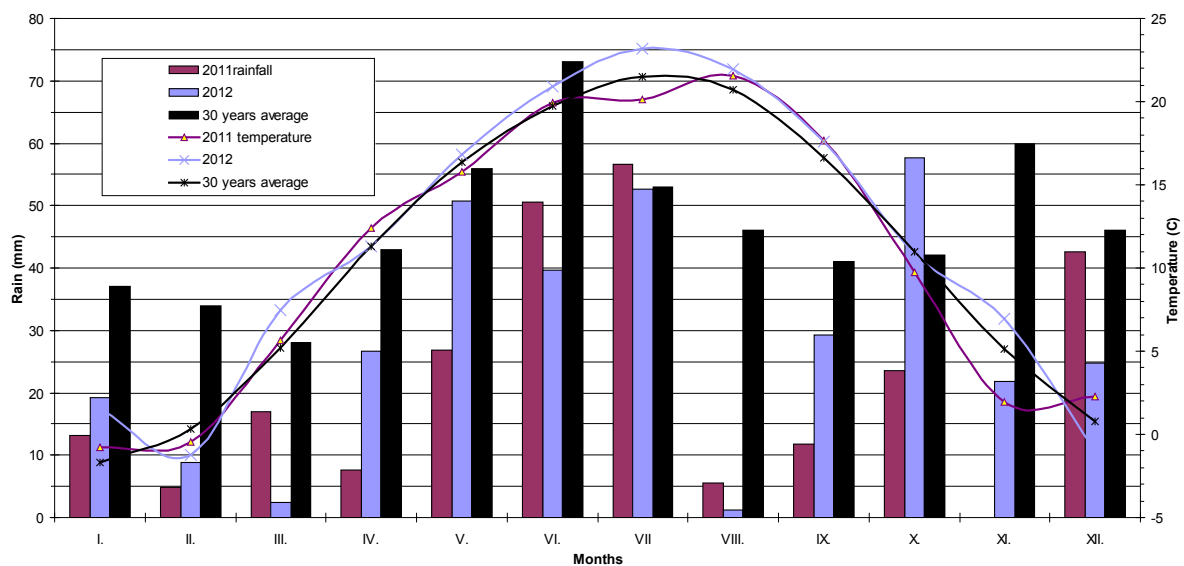


Figure 1 - Monthly average temperature and rainfall in the experimental years (2011 and 2012).

were recorded for sample ears (the yield of which was added to the plot yield during data processing), and the number of kernels per ear was counted. The thousand-kernel weight was calculated from the kernel number per ear and the kernel weight per ear.

The statistical evaluation was carried out using Agronomix Inc. Agrobases software. Analysis of variance (ANOVA) was performed for the traits and treatments and for interactions between the treatments (genotype, year, irrigation). Linear correlation analysis was used to reveal correlations between the traits.

Results and Discussion

Meteorological and soil moisture data

The experiments were set up in the nursery of the Agricultural Institute, Martonvásár in two years (2011-2012). Hungary is situated between latitudes 45°45' and 48°35'N, approximately half way between the Equator and the North Pole, and lies in the temperate zone. The climate is extremely variable, being in a moderately hot, but dry region. In Martonvásár, as in most of the country, the mean annual temperature is between 10 and 11°C. The temperature and rainfall distribution in 2011 and 2012 are illustrated in Figure 1.

In the two years, there was less rain than usual in almost every month. In June and July, the critical months for maize, there was a considerable water deficit due to the lack of rainfall during flowering and in the previous months. The situation was aggravated in 2012 by the fact that the total rainfall in the previous year was only 260.1 mm, compared with the 30-year mean of 559 mm (the total rainfall in 2012 was

334 mm). The rainfall deficiency was also largely pronounced in August, with only 5.5 and 1.2 mm instead of the 30-year mean of 46 mm.

The mean monthly temperatures did not deviate greatly from the 30-year mean, except in July, when the temperature was lower in 2011 (20.12°C) and higher in 2012 (23.18°C) than the mean (21.5°C), and in August, when the temperature was higher than the mean (20.7°C) in both years, being 21.56°C in 2011 and 21.94°C in 2012. It can be seen from the meteorological data that there was drought on several occasions in July and August in the two years, with maximum temperatures of 40-42°C for several days at a time in 2012 (with atmospheric drought as well as dry soil).

The water supplies available to the crop are better illustrated by considering the soil moisture in the experimental plots, based on the data obtained from the soil sensors placed in five replications at three depths (Figure 2).

On the irrigated area (WW), the irrigations were timed to ensure that the volumetric water content should not drop below 20% (v/v). Based on the tensiometer readings (data not shown) this meant that the water suction power of the soil did not decrease to below -30 cB (equivalent to a volumetric water content of 20 v/v % in Hungarian soils). The soil water content on the irrigated area was generally maintained at 25-30% (v/v), while on the non-irrigated area (WD) this value approached a value of 20% (v/v) by early June and fell below this value from the beginning of July until harvest, with the exception of a short period.

The combination of temperature, rainfall and soil

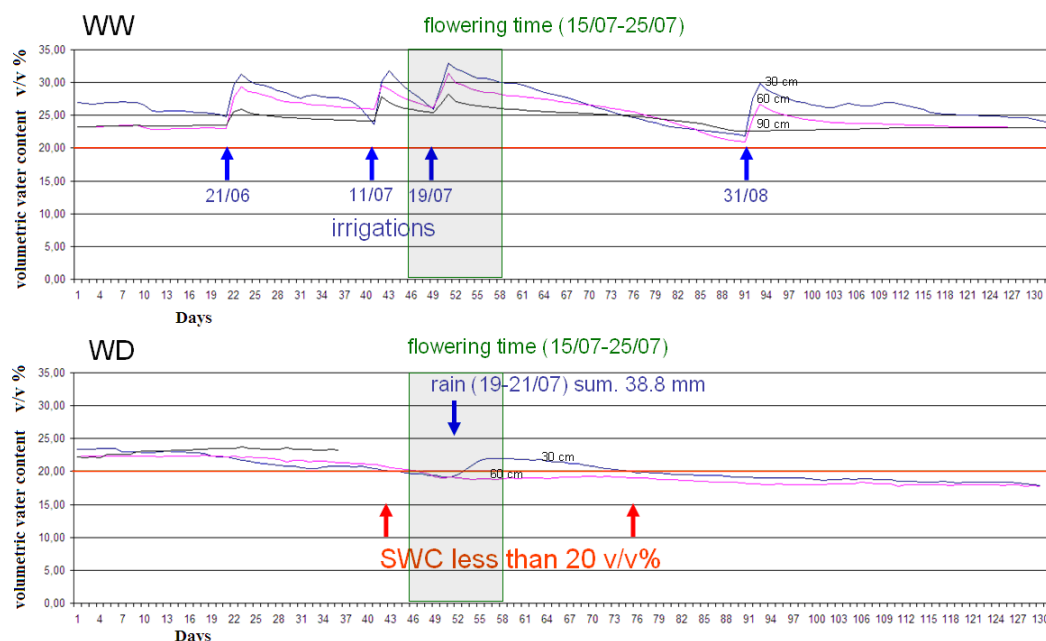


Figure 2 - Soil moisture content at three depths (30-60-90 mm) in 2011. WW - well watered; WD - water deficient area (rain fed); SWC- soil water content.

moisture data indicate therefore that WD plots experienced both soil and atmospheric drought in the two seasons, especially during the late vegetative and flowering phases. In July, in combination with high mean temperatures and rainfall deficiency, this caused drought stress on the WD area, while no water deficit was suffered on the irrigated (WW) area, except in the form of atmospheric drought.

Changes in flowering date and proterandry

The hybrids examined were produced by crossing 83 different female inbred lines with a European flint tester (EFT) as pollinator. The parental lines were developed by various research institutes and companies and belong to diverse maturity groups. The number of days from sowing to male flowering was 58.25 days for the earliest flowering hybrid (EP51*EFT) and 63.25 days for the latest (B73*EFT). This 5-day difference in flowering date is considerable, but the aim of the investigations was to determine the degree of proterandry rather than to determine maturity groups. Female flowering began at the earliest on the 59th day (CO109*EFT) and at the latest on the 65th day (B73*EFT). Both male and female flowering generally began later in WD compared to WW. A comparison of the years revealed that in 2011 flowering took place later than in 2012 and the differences were considerably smaller, in some cases being insignificant (Table 1).

Proterandry is a more important trait for judging the drought tolerance of hybrids than the flowering date itself, and is independent of differences between maturity groups (Edmeades et al, 1989). At the same time, recently developed stress-tolerant genotypes respond to drought with a relatively smaller increase in proterandry than earlier hybrids (Bruce et al, 2001). The analysis of flowering synchrony revealed that both the year and rainfall deficiency have a substantial effect on the appearance of male and female flowers and on the interval between male and female flowering. In the more favourable year, under irrigated conditions, the length of proterandry averaged 1.23 days (ranging from 0.25 to 3 days), while in response to drought stress, in years with rainfall deficit, it averaged 1.96 days (ranging from 0.25 to as much as 6 days). Longer proterandry was induced to a lesser extent by a delay in male flowering than by the protraction of female flowering. In both years of the experiment, under both irrigated and non-irrigated conditions, hybrids developed with the inbred lines Lp5, HMv5405, F924, CO109, B73, DKFBHJ, F912, F918, PHB09, PH207 and F98902 exhibited almost complete flowering synchrony (less than a day difference) between male and female flowering. In terms of proterandry these were thus the most outstanding lines, since the flowering synchrony of the hybrids was not affected by drought stress. Several authors previously reported that proterandry was the best trait for selection for stress tolerance under dry conditions (Troyer, 1983; Beck et al, 1996).

In drought tolerance analysis, proterandry should be treated as a priority trait, as it allows both drought tolerance and expected yields to be predicted more accurately, and selection for higher yields can be performed more reliably. In drought stress investigations, short proterandry or complete flowering synchrony is the aim, because in such genotypes the study of drought tolerance can be combined with selection for higher yields. Significant differences in proterandry were found; nevertheless, the flowering synchrony of all these hybrids, developed from newly selected lines, is satisfactory from the production point of view, as a longer period of proterandry, extending to as much as a week, was not detected in any case. It was confirmed, however, that the close negative correlation between proterandry and grain yield could be useful for the estimation of expected yields under dry conditions. In response to drought stress there may be a considerable delay in silking, so the dates when the ear primordia and the silks appear are ideal traits for predicting the drought tolerance of genotypes. In addition to the date of female flowering, it is also worth recording the way in which the ear appears. If it emerges from the leaf sheath at a clear angle from the stalk and has a satisfactory quantity of sufficiently long silks, this is indicative of a hybrid tolerant of drought stress. In such cases there is generally no great delay in silking. If the ear primordium remains covered by the leaf sheath throughout the flowering period and the silks are extremely short (1-2 cm), hardly emerging from the leaf sheath, the genotype is extremely sensitive to drought stress. In such cases there is a considerable delay in silking and the proterandry period increases substantially.

Analysis of yield components and grain moisture

The traits examined at harvest were the following: grain yield, kernel moisture content at harvest, thousand-kernel weight, kernel number per ear, ear length and fertilised ear length. Prolificacy was not investigated, as the genotypes tested did not produce secondary ears in any of the treatments when grown at normal plant density (65-70,000 plants ha⁻¹). Complete barrenness did not occur even in the case of drought stress. The yields per plot were adjusted to 15% grain moisture content. As expected, the grain yields were significantly different for each treatment and genotype. The 2011 season was dry, but otherwise favourable, so the grain yield averaged 7352.93 g plot⁻¹ on the irrigated area and 6096.14 g plot⁻¹ without irrigation (LSD5%: 146.58 g). The weather was drier in 2012, leading to average yields of 6997.36 g on the irrigated plots and 5104.6 g under non-irrigated conditions.

It is clear from the data, even for the best hybrids there were significant differences in yield between the dry areas and those with optimum water supplies the WW and WD treatments. The hybrids of three lines (HMv5325, F912, and F98902) did not exhibit significant yield losses in response to drought stress, and

Table 1 - Proterandria and days from sowing to male and female flowering in 2011 and 2012.

	Male flowering		Female flowering		Proterandria	
	irrigated	rain fed	irrigated	rain fed	irrigated	rain fed
2011	62.28 [‡]	62.91	63.29	64.34	1.006	1.434
2012	58.38	60.08	60.02	62.37	1.639	2.283
LSD _{5%}	0.08		0.18		0.161	

[‡]days

the yield of the hybrid developed using line HMv5325 was not substantially lower than that of the highest yielding hybrid (the progeny of line B97). Consequently, the combination HMv5325*EFT could be regarded as the best hybrid, having a high yield under optimum conditions and the least decrease in yield in response to drought stress. Averaged over the two years, the highest yield was recorded for the hybrid of B97 on irrigated plots (9285.78 g). Hybrids of the lines EZ34, HMv5325, Oh02, NDB8, LH38, F98902, F912, B106, and PH207 did not respond with significant yield losses to drought stress, so these were classified as having excellent yield stability. According to the grand mean, the highest yield was recorded on the irrigated area in 2011 (7,352.9 g) and the smallest on the drought-stressed area in 2012 (5,104.6 g).

The general mean for grain moisture content at harvest was 21.24%. Genotypic values related with the maturity groups of the parental material. The hybrids with the lowest grain moisture at harvest were combinations involving CO109 and Oh33 (17.45 and 18.33%, respectively), while those with the highest values were the hybrids of B104 and NC209 (25.66 and 25.13%, respectively). The year had a significant effect on the grain moisture at harvest. Irrigation caused a significant difference in 2011 but not in 2012. The similarity between the irrigated and non-irrigated areas could be attributed to the fact that irrigation was discontinued in both WW and WD and caused the kernels to dry at the same pace in both conditions.

Due to the similar watering conditions in WW and WD during grain filling, there was no difference in thousand-kernel weight between the treatments, nor were significant differences found over the average of the two years. Surplus yields could thus be attributed to the larger number of grain primordia developing on ears with better fertilisation, while the kernel weight remained the same.

In response to irrigation in June and July, larger ears developed on the control plots, with more kernel primordia and better fertilisation. This resulted in a higher kernel number per ear in both years compared to the non-irrigated plots. Of the two years, 2011 had better water supplies, resulting in better fertilisation than in 2012. The majority of the hybrids responded to drought stress with a reduction in the kernel number. The hybrids that produced almost the same number of kernels per ear under dry conditions as in the control environment had the following female parent

components: Pa405, LH145, AS5707, FR19, F748, N25, Oh02, EP10, PHB09, DK78371A, PHG83, W9, LH74, HMv5422 and Oh33. The hybrids of these lines had a favourable response to drought and the number of kernels per ear did not change significantly as a result of stress. As the thousand-kernel weight was almost unchanged throughout the experiment (276-278 g), the smallest yield fluctuation due to drought stress was observed for the progeny of these lines.

The evaluation of 83 hybrids in the present experiments revealed that long-term water deficit at flowering, often accompanied by extremely high temperatures, causes substantial yield losses, which can however be mitigated through a wise choice of hybrids and parental lines. Considerable differences exist between the genotypes, providing a possibility to develop hybrids capable of tolerating drought stress. In this work, water deficit at flowering caused a substantial decline in the yield as the result of poorer ear fertilisation and thus a smaller kernel number per plant. As irrigation was not applied during grain filling (except one occasion) even on the control area (WW), no great differences were observed in the thousand-kernel weights. The year had a significant effect on the grain yield and the kernel number per ear, i.e. the majority of the hybrids exhibited considerable fluctuations in the yield from one year to the next. It is worth selecting for kernel number per ear in treatments with optimum water supplies, as this allows genotypes with greater yield potential to be selected more efficiently. When studying drought tolerance, on the other hand, an evaluation of the number of fertilised kernels is ideal for the selection of drought-tolerant hybrids.

Correlations between the traits investigated

Linear correlations were calculated between the traits, averaged over the two years and the treatments, in order to determine how the traits changed in relation to each other and whether there was any correlation between the factors. The traits analysed were the yield, the thousand-kernel mass, the total ear length and fertilised ear length, the kernel number per ear and the degree of proterandria (Figure 3).

As expected, there was a significant correlation between the kernel number per ear and the total and fertilised ear length ($r=0.67$ and 0.90 , respectively). As a consequence of drought stress, the ear length decreased, and the fertilised part of the ear and thus the number of kernels per ear were also substantially reduced. In the present experiments, lower grain yields were clearly caused by poorer fertilisation during the

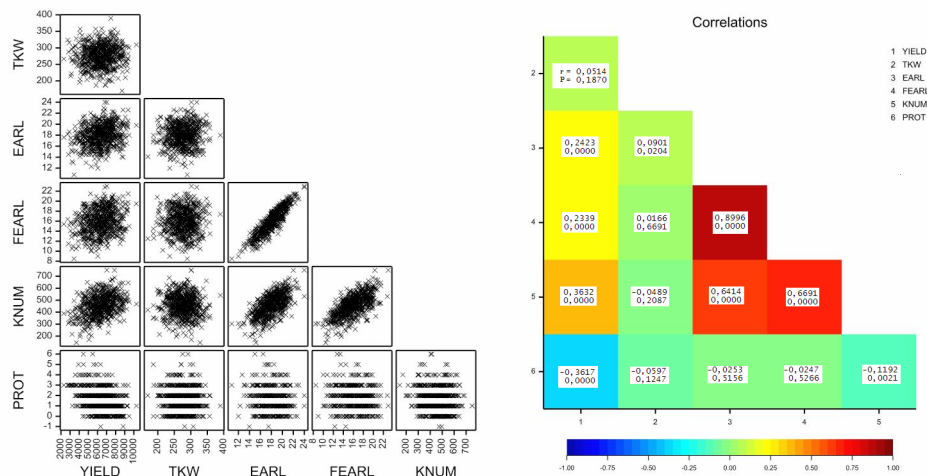


Figure 3 - Correlation matrix of the measured traits. TKW - thousand kernel weight, EARL - ear length, FEARL - fertile ear length, KNUM - kernel number, PROT- proterandria, r - correlation coefficients, P – probability

flowering period and a lower level of seed set. This was confirmed by the weak but significant correlation between the yield and these traits ($r=0.23-0.36$). At the same time, the yield was not influenced by the thousand-kernel weight ($r=0.05$), which could be attributed to the fact that the same water regime was supplied on the WW and WD areas during grain filling. The comparison of proterandry and other traits is of importance because proterandry is a major parameter in determining the drought tolerance of hybrids. A hybrid is considered to have good drought tolerance if it produces a satisfactory yield when subjected to drought stress. It was clear from the correlation analysis that proterandry was in negative correlation with all the parameters tested (in some cases the correlation was weak and non-significant). A substantial degree of flowering asynchrony has a negative effect on the yield ($r=-0.36$), primarily due to fertilisation problems (a smaller proportion of the ear is fertilised; lower number of kernels per ear). A delay in tasselling has little effect on proterandry; in general, later tasselling reduces the length of proterandry, while a delay in silking increases it (data not shown). Two factors should be mentioned, however, as having an influence on the evaluation of the results. The first is that the newly bred lines and hybrids included in the experiment did not exhibit differences in proterandry that were of significance from the point of view of seed production technologies. The 2-3-day difference observed on average under dry conditions for the majority of newly developed genotypes is not sufficient in itself to cause fertilisation problems. These drought-tolerant genotypes respond to drought with a relatively small increase in proterandry compared with earlier hybrids (Bruce et al, 2001). The other factor that should be considered is that the 83 genetically diverse hybrids included in the experiment did not flower at exactly the same time, so direct conclusions

could not be drawn on the correlation between flowering asynchrony and fertilisation, since there was viable pollen in the air throughout the flowering period, allowing even plants from hybrids exhibiting a considerable degree of flowering asynchrony to be fertilised by viable pollen from another genotype. It was clear, however, that the yield losses on the drought-stressed area were caused by the lower kernel number per ear. This could be explained by the fact that the atmospheric drought and the frequent occurrence of temperatures above 40°C led to a drastic reduction in the viability of the pollen grains, thus influencing their fertilisation ability. This phenomenon was of less importance on the irrigated area, because the frequent irrigation in July led to slightly lower temperatures in the plant stands, while the considerably higher relative humidity also improved pollen survival. On the dry area the abortion of kernels on fertilised ears may also have caused a reduction in the kernel number per ear and thus to lower harvestable yields. It was clear during the processing of the experiment that ears from the dry areas contained undeveloped, shrivelled kernel primordia which were probably initially fertilised.

A weak but significant correlation was thus found between the kernel number per ear and the grain yield, averaged over the years and treatments ($r=0.36$). When correlations between the traits were analysed for each treatment, averaged over the years, the strength of the correlation between the two factors differed (Figure 4). On the WD area the correlation proved to be negligible ($r=0.17$), while on the WW area, a weak but significant correlation was detected ($r=0.36$). It is thus advisable to select for kernel number per ear under optimum water supplies, as this allows genotypes with higher yield potential to be selected more efficiently. At the same time, the evaluation of the number of kernels fertilised is an excellent

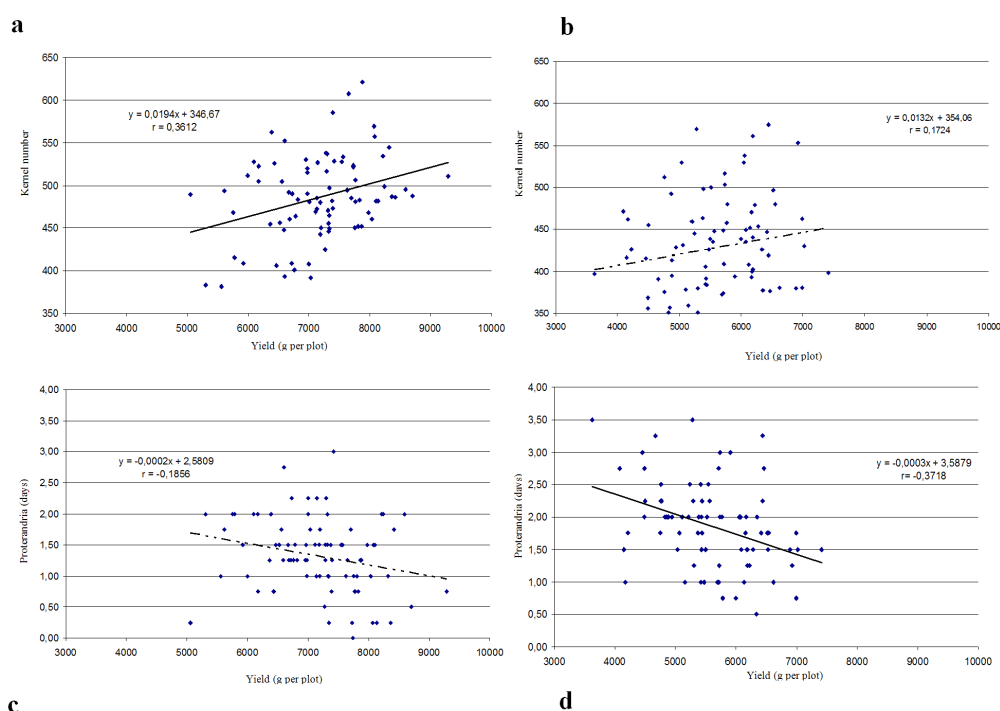


Figure 4 - Correlation between yield (x) and kernel number (y - upper figures) and proterandria (y - bottom figures) in irrigated (a, c) and drought stressed areas (b, d). Lines means sure correlation ($r > 0.2$), dashed lines means weak correlation and negligible connections ($r < 0.2$).

method for the selection of stress-tolerant hybrids in studies on drought tolerance.

The situation is different in the case of proterandry. Flowering asynchrony is in negative correlation with the grain yield ($r = -0.36$); in other words, greater proterandry is a prediction of lower yields. At the same time, it is worth carrying out selection under dry conditions, as this strengthens the differences between the genotypes, and the negative correlation between the traits is also closer ($r = -0.37$). If selection for proterandry is done in an optimum environment, differences between the genotypes become blurred and the correlation between the traits becomes negligible ($r = -0.18$). When investigating drought stress tolerance it is thus advisable to treat proterandry as a priority trait, as it makes it easier both to predict drought tolerance and to calculate expected yields, and selection for higher yields can be performed more reliably. In drought stress analysis, the aim is to achieve either short proterandry, as in such genotypes the study of drought tolerance can be combined with selection for higher yield.

If the aim is to select purely for greater yield potential, selection should be carried out with optimum water supplies, but even in this case it is worth repeating selection in a dry location to test for proterandry. In this case the results can be supplemented with the prediction of the expected yield stability of the hybrids.

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