Effect of water availability and genetic diversity on flowering phenology, synchrony, and reproductive investment in maize

Kristin Mercer[1]*, Lesley Campbell[2], Jing Luo[1]

[1]Department of Horticulture and Crop Science, The Ohio State University, 2021 Coffey Road, Columbus, OH 43210, USA
[2]Department of Chemistry and Biology, Ryerson University, 350 Victoria St, Toronto, ON M5B 2K3, Canada
*Corresponding author: E-mail: mercer.97@osu.edu

Abstract

Crop yield of monoecious species like maize (*Zea mays*) relies on simultaneous flowering of male and female inflorescences to ensure pollination. Yet productivity may be reduced if environmental conditions reduce floral synchrony or if plants within a field do not overlap sufficiently in flowering periods. We experimentally manipulated water availability and measured its effect on flowering, including the anthesis-silking interval (ASI) and crop yield components in open-pollinated (OP) and hybrid corn cultivars. Although watering treatments did not affect traits, we did detected cultivar-specific phenological and yield responses. Hybrid plants were earlier to silk than OP plants, which tasseled for longer, had a longer ASI, and lower yield components. The less diverse hybrids also expressed less variation in ASI. We suspect other methods for reducing moisture in the field, including earlier moisture removal, might have better elicited a biological response in maize. Nevertheless, because shorter ASI is genetically correlated with increased drought tolerance, we predict this hybrid may be more resilient than the OP under more extreme drought scenarios. Consideration for how genetic diversity found in OP varieties and crop landraces may respond to variation in moisture availability apparent with climate change may be warranted.

Keywords: anthesis-silking interval, corn, drought tolerance, reproductive development, yield loss

Introduction

Monoecious plants divide sexual function into distinct staminate (male) and pistillate (female) inflorescences (Frankel and Galun, 1977; Maynard Smith, 1978) and have repeatedly been domesticated as crops. Therefore, studying the sensitivities of their breeding system to environmental variation can inform a wide-range of agricultural programs. The separation of male and female structures may benefit hermaphroditic, wind-pollinated plants, like maize, because male flowers (e.g., tassels) are most successful at dispersing pollen when presented at elevated heights, whereas female flowers (e.g., silks) capture more pollen when they are below the source of pollen release (Friedman and Barrett, 2009; Niklas, 1985; Young and Schmitt, 1995). Further, monoecy allows plants to flexibly adjust resource allocation to male and female function which can be particularly advantageous when environmental conditions change (Bawa and Beach, 1981; Campbell et al, 2013). The phenology and phenological synchrony of ears and tassels in maize (also known as Anthesis to Silking Interval or ASI) are controlled by both genetic and environmental factors (Bolanos and Edmeades, 1993; Maddonni et al, 1999; Yuan et al, 2012).

Responses to environmental variation can alter plants' reproductive strategies (e.g., Gonzalez et al, 2014; Kawashima et al, 2011) in several ways. First, plants may change the number of viable gametes produced, which in maize can translate into the number of ears produced, viable ovules per ears, or viable pollen per tassels. All of these can be sensitive to variation in precipitation (Kawashima et al, 2011), soil fertility (Djaman et al, 2013), weed competition (Hall et al, 1992), pest pressure (Cardwell et al, 1997), and disease (Ward et al, 1999). Second, changes in environmental conditions can change synchrony within a plant or within the population. In maize, the phenologies of both ear and tassel anthesis are sensitive to variation in soil moisture (Bolanos and Edmeades, 1993), air temperature (Cicchino et al, 2010), latitude (Liu et al, 2013), agricultural history (Maddonni et al, 1999), and planting density (Shafi et al, 2012). These shifts may lead to changes in ASI and thereby change the degree of pollen limitation or rates of outcrossing, ultimately having an influence on yield (Campbell et al, 2013). Given the importance of maize worldwide, and given that climate change is predicted to change rainfall patterns (IPCC, 2013), it is important to examine the relative vulnerability of maize cultivars to reproductive failure or yield losses through altered phenology due to changes in soil moisture.

Where local variation in climatic conditions can create yield vulnerability in cropping systems, crop populations can improve short-term resiliency by exhibiting phenotypic plastic responses or by containing adaptive genetic diversity. Although plasticity is pervasive across plant populations, the degree and direction of response differs dramatically among species and individuals (Kawashima et al, 2011; Shaw

RECEIVED 09/02/2014

and Etterson, 2012). Moreover, phenotypic plasticity can have non-adaptive or maladaptive consequences (Bradshaw, 1965, 2006; de Jong, 2005; Maherali et al, 2008). Further, genetically diverse populations may be more likely to contain particular alleles that enhance crop resiliency and hardiness (Assmann, 2013). Specifically, increased crop genetic diversity can increase farm productivity by reducing the variance in yield (Di Falco, 2012; Marshall and Brown, 1973). However, breeding programs inherently reduce genetic diversity of populations (*e.g.*, Fufa et al, 2007) while increasing the frequency of traits that increase yield under particular sets of conditions. For cross-pollinating species such as corn, landraces and open-pollinated (OP) varieties have more genetic diversity within them than hybrid varieties. Despite concerted research effort that describes the qualities of OP and hybrid cultivars, there are very few direct comparisons of flowering phenology.

Within the context of climate change, we explored how water stress and the genetic diversity associated with hybrid versus open-pollinated crop varieties affected flowering and crop productivity. Using an economically important, monoecious crop, maize, we asked does water availability or crop diversity: i) affect male and female flowering phenology and components of individual yield? ii) influence synchrony of male and female flowers within a plant and within a plot? In cases where synchrony is reduced, does it affect components of yield?

Materials and Methods

Species description

Maize (*Zea mays*) is one of the world's three most important grain crops growing from temperate to tropical regions (Division, 2011). As a monoecious plant, it has separate male and female flowers that develop in separate locations. Male inflorescences, or tassels, grow at the top of the plant whereas female inflorescences, or ears, develop in leaf axils. Under favorable conditions, male anthesis usually occurs zero to three days before the female silks emerge (Edmeades et al, 1993), and delivery of pollen is facilitated by wind and honeybees. Anthesis usually lasts for five to eight days, and silk remains receptive for approximately one week after emergence, allowing for the possibility of self-pollination (Kiesselbach, 1980; Westgate, 1996).

Study location

This experiment was conducted at the Waterman Farm and Turf Grass Experimental Station of the Ohio State University in Columbus, OH, USA (40°80'N latitude and 83°01'W longitude) from May 21-November 3, 2009. The area has a temperate climate with a mean annual precipitation (1910-2009) of 978 mm and a July mean temperature of 23.9°C (National Weather Service data for 2009: http://www. weather.gov/). The precipitation total for 2009 (901mm) was slightly below this average. Soil type varied across the farm with areas characterized as both Crosby silt loam or Aeric Ochraqualf (USDA classification) and Stagnic Luvisol (Food and Agriculture Organization classification).

Seeds sources

We chose two modern varieties of maize for our experiment. The F_1 hybrid was P611XY (Doebler's Pennsylvania Hybrids, Inc, Jersey Shore, PA, USA). For the open-pollination (OP) population, we used a synthetic corn variety called 1776 (provided by Frank Kutka, North Dakota State University), which has a mix of genetics that include Stiff stalk (Iowa State), Ohio 43, and Lancaster (x2). These parents had relatively modern genetics and represented the breadth of classic heterotic groups; the OP was considered more stress resistant than many open-pollinated maize varieties. The F_1 hybrid was P611XY (Doebler's Pennsylvania Hybrids, Inc, Jersey Shore, PA, USA), which we chose because we expected its genetic background and maturity group to be similar to that of the OP.

Field experiment design

In 2009, we established a split-plot design with four blocks and the four watering treatments as main plots. Main plots were spaced 4.6 m apart and subplots of the maize varieties were located 2.4 m apart. We imposed four experimental watering treatments: irrigated, control, rain-in, and rain-out. To irrigated plots, we applied enough water to simulate a rainfall event of 2.54 cm once per week using drip tubes to distribute ground water from a local well. If the plots did not receive any natural rain in a given week, we irrigated those plots twice that week. The control plots experienced no experimental watering. To simulate drier conditions, we imposed a rain-out treatment, where we built rain-exclusion shelters over the experimental plots. The rain-exclusion shelters have been previously described in Campbell et al (2013, modified slightly from Yahdjian and Sala, 2002). We employed plexiglass shingles, which were bent at 120 degree and faced upwards, to intercept approximately 50% of the natural precipitation, which was subsequently carried off the field with tile line. The height of the shingles was adjusted throughout the growing season to be at least 20 cm above the crop foliage. To estimate the effect of the shelter itself (separate from the effect of reduced rainfall) on plants, we constructed rain-in shelters that were almost identical to the rain-exclusion shelters. The two shelter types differed only in the orientation of the shingles; on the rain-in shelters the shingles were faced down so that the rain ran into the plot.

Field plots were tilled on May 21, 2009 and seeds were planted on May 27th - 28th. We planted five rows in each plot and 11 seeds per row. Spacing was 76 cm between rows and 24 cm within rows. We irrigated the plots once immediately after planting. Seedling emergence of focal plants (see Data collection) was monitored every other day from June 5th - 13th, when seedling germination ceased according to two subsequent surveys. Seedling emergence was very low in three plots, so we replanted seeds on June 12th into the empty positions in these plots. The replanted seeds only served to create a competitive environment and their data were not included in analyses. Rain shelters were installed on June 26th, and the irrigation treatment started on July 16th. On June 30th, we controlled weeds. Due to an extremely dry period in early July 2009, we watered plots once on July 9th for about 2.5 cm of water. Fertilizer (19-19-19, Sure-Grow, Comanche, Texas, USA) were applied to all plots at the rate of 13.5 g m^{-2} of N on July 16th.

We measured soil moisture at the center of each plot, using a TDR (Trase System I, 6050X1, Soilmoisture Equipment Co, Santa Barbara, CA, USA), at 20 cm depths six times throughout the growing season. Between July 24th - September 15th, three measurements were taken immediately following large rain events (> 2.3 cm in 72 hours) and three measurements of which were taken during dry periods (> 6 days since the last rainfall event). Measurements were performed in all four blocks, expect during the first two dates when only two blocks were used.

Data collection

So that focal plants experienced a relatively uniform soil moisture and competitive environment, we collected data from the plants occupying the most central positions in each plot (seven positions each of the center three rows), though sample sizes were generally smaller than 21 (minimum sample size was seven plants). On July 9th, after a period of 13 days without rain, and coinciding with the installation of the rain-exclusion shelters, we assessed the health of each plot (ranging from 1 to 5, from least to most healthy), to be used as a covariate in the analysis. Flowering phenology was monitored three times a week. For each plant, we recorded the beginning and end of anthesis as the date when the first anthers appeared on the tassel and when no anthers remained in the tassel. Further, we recorded the beginning and end of silking as the date when the first silk was visible and when 95% of the silks turned brown, respectively.

We harvested the ears on November 3rd, when most ears on the non-focal plants had reached the «black layer» stage. The ear was recorded as «aborted» if no kernel was found. For each ear, we measured vacant area of cob (measured as the length of bare tip where no kernels developed). The kernels were then removed from the ear, dried at 55°C for 3 days, counted, and weighed.

Analysis

All analyses were performed using SAS 9.13 and SAS Enterprise 5.1 (The SAS Institute, Cary, NC, USA). Synchrony between male and female flowers was measured using a variety of approaches. The traditional approach to estimating synchrony in maize is the anthesis-to-silking-interval (ASI, calculated as the female flower begin date minus male flower begin date) (Edmeades et al, 1993); we estimated ASI for each plant. However, we were interested in exploring other synchrony indices, since ASI only accounts for synchrony in flowering initiation and not flowering duration. Therefore, we used three additional synchrony indices that assess synchrony based on both flowering initiation and duration: flowering overlap, reproductive overlap (Calabrese and Fagan, 2004), and available males. Flowering overlap (individual) was calculated as the number of days when both male and female flowers were open on a single plant divided by the number of days when there was at least one flower, regardless of gender, open on the plant. Flowering overlap (plot) was calculated in a manner similar to flowering overlap (individual), except that the flowering records of all plants within the plot were pooled. Reproductive overlap was calculated by summing individual flowering overlap across all male-female pairs. The number of available males (plot) was calculated as a season average of the number of males open on days when at least one female flower was open (Campbell et al, 2013).

For our statistical analysis, we ran two kinds of models. First, to assess whether the rainfall manipulation (rain-out, rain-in, control open, irrigated) altered average soil moisture, we used a general linear model repeated measures ANOVA with moisture treatment, plot and date of moisture measurement. This analysis included an interaction between moisture treatment and date of moisture measurement. *Post-hoc* comparisons among treatments were established using Tukey's HSD test.

Second, to determine whether our experimental factors affected flowering phenology, synchrony, and grain production, we performed a generalized linear mixed model that included moisture treatment, variety and their interaction as fixed effects. Block, block × moisture treatment, and block × moisture treatment × variety were random effects in the model; block × moisture treatment was used as the error term for tests of the main plot factor. Seedling emergence dates and health index were also included as covariates. *Post-hoc* comparisons of flowering phenology, synchrony, and grain production among fixed effects were accomplished using Tukey's HSD test. For flowering phenology, the response variables used were male flower begin dates, first female flower begin dates, male flower duration (calculated as male flower end date minus begin date), first female flower duration (calculated the same way as the male flower duration).

Results

Watering treatments altered soil moisture

Average soil volumetric moisture content (VMC, %) differed significantly among watering treatments ($F_{3,12}$ = 4.89, p = 0.019, Figure 1). In *post-hoc* tests, the soil moisture of the control and rain-in plots (our two control treatments) did not differ significantly (t = -0.55, df = 44, p = 0.95). Furthermore, and surprisingly, there was no difference in soil moisture between the rain-out and rain-in plots (t = 1.83, df = 44, p = 0.27). Irrigation plots did not have significantly higher soil moisture than the control plot (t = -1.97, df = 44, p = 0.22; unadjusted p-value = 0.055). The most dramatic difference in soil moisture occurred between irrigated and rain-out plots (t = 3.32, p = 0.0094), with the latter having lower moisture. Soil moisture declined significantly over the season (Repeated measure: $F_{5, 44}$ = 15.67, p < 0.0001), but did so differently across moisture treatments (moisture treatment × date of sampling interaction: $F_{15, 44}$ = 1.96, p = 0.043).

Cultivar identity determined phenological patterns

Although watering treatments did not have a significant effect on any variables measured, nor were there any significant interactions between watering treatments and cultivar identity, cultivar identity significantly affected several variables (Table 1). Initiation of silking occurred two days earlier in the hybrid relative to the OP variety and there was significantly less variation in initiation of silking in hybrid relative to OP plants (Table 1). The same was not true for tassels (Table 1). Nevertheless, tasseling lasted one day longer in OP relative to the hybrid variety, but the duration of silking did not differ between varieties (Table 1). There were significant differences in flowering synchrony between the two varieties. Specifically, the individual ASI was significantly longer in OP relative to hybrid at both the individual and plot level (Table 1). There was also greater variation in ASI in OP relative to hybrid plants (Table 1). Varieties did not differ significantly in synchrony as measured by proportion of phenological overlap, reproductive overlap, or ratio of available males (Table 1). Furthermore, cultivars differed in yield components. Hybrid plants produced more kernels that were heavier (Table 1). Cobs on open pollinated planted tended to have almost twice as many unpollinated ovules (Table 1).

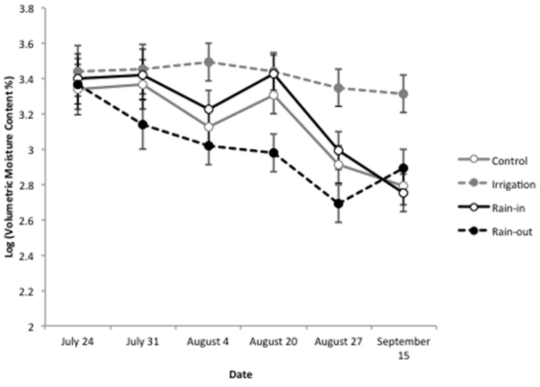

Figure 1 - The response of average soil volumetric moisture content (%, ± SE) to moisture treatments across the 2009 growing season in Columbus, Ohio, USA.

Discussion

This study failed to detect discernible main effects of maize flowering synchrony and yield in response to an experimentally induced soil moisture gradient. As expected, a variety possessing less genetic diversity (*i.e.*, hybrid) also expressed less variation in ASI than a variety with more genetic diversity (*i.e.*, OP). The hybrid plants were earlier to silk and tassel and expressed more synchrony (*i.e.*, shorter ASI) than open-pollinated plants, while also having higher yield components. Other methods for manipulating moisture may better elucidate how phenologies of varieties differentially respond to moisture gradients.

Response of maize flowering to soil moisture variation

Generally, other studies measuring the effect of moisture availability on flowering synchrony and yield of maize have noticed that genotypes with shortened ASIs tend to also exhibit drought tolerance whereas genotypes with long ASIs tend to exhibit less drought tolerance (*e.g.*, Edmeades et al, 1993; Gonzalez et al, 2014). Other studies have found little effect. Bolaños et al (1993) detected results similar to ours where experimentally imposed water stress did not induce phenological changes in maize cultivars. Further, Kamara et al (2003) found similar phenological responses to water limitation in hybrid and improved open-pollinated cultivars. However, given that we saw little effect of our experimental manipulations on soil moisture, we could not have expected much change in ASI or other metrics of phenological overlap. Nevertheless, in addition to differences in intensity of drought stress treatments, differences in the timing of the drought stress treatment itself might have had consequences for yield or phenology (Swanton et al, 2014), especially if applied early. For instance, research on drought adapted and drought sensitive inbred maize lines showed that early stresses from weed competition, intra-specific competition or drought reduced grain yield- and more so in the drought sensitive varieties (Gonzalez et al, 2014). Mechanisms of this reduced yield included increased ASI, smaller female inflorescences and reduced kernel production (Gonzalez et al, 2014). By contrast, in our study, drought stress was not applied until July 16th, approximately one month after seedlings emerged from the soil.

Alternative explanations and experimental constraints

We failed to detect significant biological effects of the rain-out shelters and here briefly outline three explanations. First, the shelter design we used may not have created enough variation in soil moisture in

Table 1 - ANOVA results (F-values for all fixed effects in the model, subscripts denote numerator, denominator degrees of freedom) and mean values of hybrid and OP plants for phenology, synchrony and yield across hybrid and open-pollinated cultivars grown under four watering treatments.

	ANOVA					Least Square Means	
	Trt	Var	Trt*Var	Emerge	Health	OP (SE)	Hybrid (SE)
Phenology traits							
Tassel initiation	$1.29_{3,8.06}$	$1.12_{1,9.21}$	$3.71_{3,9.08+}$	$1.40_{1,11.7}$	$229.31_{1,11.7***}$	220.0 (0.4)	220.0 (0.4)
Silking initiation	$0.70_{3,8.04}$	$18.10_{1,9.72**}$	$1.93_{3,9.41}$	$1.71_{1,18.5}$	$69.75_{1,18.5***}$	221.1 (0.6)	218.8 (0.6)
Tassel duration	$0.59_{3,10.8}$	$54.27_{1,8.86***}$	$0.13_{3,8.78}$	$0.28_{1,10.5}$	$2.20_{1,10.4}$	7.4 (0.2)	6.4 (0.2)
Silking duration	$2.59_{3,10.9}$	$0.22_{1,10.2}$	$3.22_{3,9.85+}$	$0.09_{1,20}$	$21.27_{1,20***}$	8.7 (0.2)	8.6 (0.2)
Synchrony traits							
CV of tassel initiation	$0.22_{3,18}$	$1.85_{1,17.1}$	$1.22_{3,17.1}$	$0.18_{1,20}$	$0.02_{1,20}$	1.77 (0.15)	1.51 (0.15)
CV of silking initiation	$0.24_{3,11}$	$12.41_{1,9.47**}$	$1.53_{3,9.25}$	$0.43_{1,16.3}$	$0.02_{1,17.4}$	0.78 (0.07)	0.49 (0.07)
CV of tassel duration	$0.31_{3,10.6}$	$1.56_{1,9.34}$	$0.29_{3,9.08}$	$1.73_{1,18.2}$	$0.26_{1,19.2}$	27.7 (2.1)	25.3 (2.1)
CV of silking duration	$0.26_{3,11}$	$3.99_{1,10.2+}$	$0.65_{3,9.91}$	$0.06_{1,19.8}$	$3.48_{1,20+}$	28.9 (1.9)	23.6 (1.9)
ASI (individual)	$0.93_{3,11.4}$	$48.17_{1,10.5***}$	$0.87_{3,10.2}$	$0.82_{1,19.9}$	$0.15_{1,19.2}$	0.90 (0.24)	-1.23 (0.24)
CV of ASI (plot)	$1.78_{3,8.7}$	$7.44_{1,10.3*}$	$1.01_{3,10}$	$0.36_{1,17}$	$0.12_{1,18}$	30.59 (2.85)	22.84 (2.85)
ASI (plot)	$0.52_{3,6.45}$	$13.31_{1,6.97**}$	$0.18_{3,6.71}$	$0.05_{1,17.2}$	$0.27_{1,18}$	0.01 (0.38)	-1.68 (0.38)
Prop. phenological overlap (individual)	$1.82_{3,20}$	$3.66_{1,20+}$	$1.49_{3,20}$	$0.02_{1,20}$	$0.80_{1,20}$	0.68 (0.02)	0.74 (0.02)
Prop. phenological overlap (plot)	$1.37_{3,16.6}$	$1.48_{1,16.2}$	$0.87_{3,15.9}$	$0.99_{1,17.1}$	$0.41_{1,18.6}$	0.73 (0.05)	0.80 (0.05)
Reproductive overlap	$0.18_{3,11}$	$1.17_{1,10.6}$	$1.65_{3,9.7}$	$0.81_{1,13.8}$	$1.66_{1,18.8}$	0.68 (0.02)	0.71 (0.02)
Avail. Male (plot)	$0.13_{3,10.8}$	$0.86_{1,8.83}$	$2.29_{3,8.37}$	$0.39_{1,9.9}$	$5.46_{1,12.4*}$	84.7 (3.1)	81.8 (3.1)
Yield components							
Kernel number	$0.36_{3,17.4}$	$34.39_{1,16.2***}$	$1.05_{3,16.2}$	$0.86_{1,18.5}$	$18.59_{1,20**}$	449.9 (16.7)	321.6 (16.6)
Kernel weight	$0.14_{3,17.7}$	$28.19_{1,16.9***}$	$0.80_{3,17}$	$0.03_{1,20}$	$11.74_{1,19.5**}$	102.9 (7.9)	149.02 (7.9)
Average kernel weight	$0.22_{3,17.9}$	$0.49_{1,17.3}$	$0.95_{3,17.3}$	$0.34_{1,20}$	$0.47_{1,19.5}$	0.33 (0.009)	0.32 (0.0008)
Vacant area (%)	$0.42_{3,17.6}$	$25.15_{1,16.9***}$	$1.68_{3,16.9}$	$0.04_{1,20}$	$18.33_{1,19.4***}$	25.7 (2.0)	14.7 (2.0)

Separate analyses for each trait were run with PROC MIXED. Data were collected in 2009 from maize plants grown in an experimental garden in Columbus, OH, USA. $^{+}p < 0.10$, $*p < 0.05$, $**p < 0.01$, $***p < 0.001$.

temperate conditions to elicit a biological response from maize. We employed a shelter design from arid and semi-arid ecosystems (Yahdjian and Sala, 2002), which, when used in a temperate area with high rainfall accompanied by strong winds may not have excluded enough moisture. Although we detected a significant difference in soil moisture among some treatments, this experimental manipulation was not as dramatic as we had expected, especially among the rain-in and rain-out treatments. Similar to these results, we found no differences in flowering phenology or yield among identical moisture manipulations applied to summer squash, although we did notice differences in relative production of male versus female flowers across the moisture gradient (Campbell et al, 2013). Differences between our temperate, agricultural ecosystem and arid native ecosystems may go beyond differences in quantity and quality of rainfall to include different soil types (especially with respect to their ability to absorb and retain moisture), the nature of plant responsiveness, and soil nutrient content.

Second, differences in soil moisture among our treatments increased across the season, but were relatively small early in the season. Maize is known to be particularly sensitive to water deficits at several stages of growth, including vegetative and silking stages, where deficits can result in up to 40% yield losses (*e.g.*, Barker et al, 2005; Çakir, 2004). Therefore, intercepting precipitation earlier in the season (or even during the previous winter) might have had created a greater biological effect than the treatments we imposed. Alternative soil moisture reduction methods, including applying impermeable plastic to the soil or shelter roofs or reducing necessary irrigation (as is done where irrigation is essential, *e.g.*, Barker et al, 2005) may have their own limitations. However, another technique may have been able to discern a drought response under temperate conditions. Given that winter precipitation is expected to change (IPCC, 2013), these types of manipulative treatments may produce very interesting basic and applied insights into the broader consequences of global climate change. Finally, advances in maize breeding (reviewed in Duvick, 2005) has improved the stress tolerance of current varieties, including drought tolerance (Barker et al, 2005; Bolanos and Edmeades, 1996), in part by reducing the ASI and selecting on other traits. Given that both varieties we used had more modern genetics, it would be interesting to know how large the moisture differences would have to be to see a stress response and how that relates to the kind of variation expected with climate change.

Cultivar effects

As expected, the hybrid cultivar, with less genetic diversity than the OP cultivar, expressed less variation in ASI, especially under drier conditions. The difference we noted in ASI between our improved varieties appears small once comparisons include open-pollinated landraces that typically express longer ASI than improved cultivars (e.g., ASI averaged > 8 days for open-pollinated landraces measured by Bolaños and Edmeades, 1996). Increased variation in ASI and silking initiation is an expression of the genetic diversity within a crop population and hence correlated to the number of genetically unique parents used to produce the cultivar group (*e.g.*, hybrids, open-pollinated improved and open pollinated landrace cultivars). Hybrids also silk earlier, creating not only a less variable ASI, but also a shorter ASI. Because shorter ASI is strongly genetically correlated with increased drought tolerance (Bolanos and Edmeades, 1996), this suggests that the hybrid we evaluated here have some greater drought tolerance than the OP, but that it was just not discerned here given our lack of moisture manipulation. Subsequent work with more OP and more hybrid varieties could better explore this question.

In sum, with the future challenges faced by agriculture with climate change, variation in moisture will continue to challenge crop growth and limit yield. Crops with complex mating systems may be especially at risk, but may also be able to adjust their flowering adaptively to maintain productivity. It remains to be seen whether genetic diversity for traits such as ASI can be adaptive under particular sets of environmental conditions, for particular kinds of farming systems, or in particular genetic backgrounds. Further work, for instance, with locally adapted landraces with high average ASI, but that outperform improved varieties with lower ASI, may prove fruitful in this regard.

Acknowledgements

The authors thank J Vent, B Snow, R Harrison, E Park, G Mills, B Pace, E Sanchez, D Snodgrass, A Weiss, K Lewis, and B Willson for amazing logistical assistance and two anonymous reviewers for helpful feedback. Funds from OARDC SEEDS Research Enhancement Grant 2009-027, The Ohio State University, Rice University and Ryerson University supported this work.

References

Assmann SM, 2013 Natural variation in abiotic stress and climate change responses in Arabidopsis: Implications for twenty-first-century agriculture. Int J Plant Sci 174: 3-26

Barker T, Campos H, Cooper M, Dolan D, Edmeades G, Habben J, Schussler J, Wright D, Zinselmeier C, 2005 Improving drought tolerance in maize. Plant Breeding Rev 25: 173-253

Bawa KS, Beach JH, 1981 Evolution of sexual systems in flowering plants. Ann Miss Bot Gard 68: 254-274

Bolaños J, Edmeades GO, 1993 Eight cycles of selection for drought tolerance in lowland tropical maize. 2. Responses in reproductive behavior. Field Crop Res 31: 253-268

Bolaños J, Edmeades GO, 1996 The importance of the anthesis-silking interval in breeding for drought tolerance in tropical maize. Field Crop Res 48: 65-80

Bradshaw AD, 1965 Evolutionary significance of phenotypic plasticity in plants. Adv Genet 13: 115-155

Bradshaw AD, 2006 Unravelling phenotypic plasticity - why should we bother? New Phytol 170: 644-648

Çakir R, 2004 Effect of water stress at different development stages on vegetative and reproductive growth of corn. Field Crop Res 89: 1-16

Calabrese JM, Fagan WF, 2004 Lost in time, lonely and single: reproductive asynchrony and the Allee effect. Am Nat 164: 25-37

Campbell LG, Luo J, Mercer KL, 2013 Effect of water availability and genetic diversity on flowering phenology, synchrony, and reproductive investment in summer squash (*Cucurbita pepo*). J Agric Sci, Camb 151: 775 - 786

Cardwell KF, Schulthess F, Ndemah R, Ngoko Z, 1997 A systems approach to assess crop health and maize yield losses due to pests and diseases in Cameroon. Agr Ecosyst Environ 65: 33-47

Cicchino M, Edreira JIR, Otegui ME, 2010 Heat stress during late vegetative growth of maize: Effects on phenology and assessment of optimum temperature. Crop Sci 50: 1431-1437

de Jong G, 2005 Evolution of phenotypic plasticity: patterns of plasticity and the emergence of ecotypes. New Phytol 166: 101-117

Di Falco S, 2012 On the value of agricultural biodiversity. Annu Rev Resour Econ, vol 4. 4: 207-223. DOI: 10.1146/annurev-resource-110811-114543

Division FS, 2011 FAOSTAT, vol. 2013. Food and Agriculture Organization of the United Nations, http://faostat3.fao.org/home/index.html

Djaman K, Irmak S, Martin DL, Ferguson RB, Bernards ML, 2013 Plant nutrient uptake and soil nutrient dynamics under full and limited irrigation and rainfed maize production. Agron J 105: 527-538

Duvick DN, 2005 Genetic progress in yield of United States maize (*Zea mays* L). Maydica 50: 193-202

Edmeades GO, Bolaños J, Hernandez M, Bello S, 1993 Causes for silk delay in a lowland tropical maize population. Crop Sci 33: 1029-1035

Frankel R, Galun E, 1977 Pollination mechanisms, reproduction and plant breeding. Springer Verlag, Berlin

Friedman J, Barrett SCH, 2009 The consequences of monoecy and protogyny for mating in wind-pollinated Carex. New Phytol 181: 489-497

Fufa F, Baum M, Grando S, Kafawin O, Ceccarelli S, 2007 Consequences of a decentralized participatory barley breeding programme on changes in SSR allele frequency and diversity in one cycle of selection. Plant Breed 126: 527-532

Gonzalez VH, Lee E, Lukens L, Swanton CJ, 2014 The effect of early stresses on ear development and mid season reproductive performance in corn. Annual Meeting of the Canadian Weed Science Society. Canadian Weed Science Society, Vancouver.

Hall MR, Swanton CJ, Anderson GW, 1992 The critical period of weed-control in grain corn (*Zea mays*). Weed Sci 40: 441-447

IPCC, 2013 Climate Change 2013: The Physical Science Basis. Contribution of Working Group I to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change [Stocker TF, Qin D, Plattner G-K, Tignor M, Allen SK, Boschung J, Nauels A, Xia Y, Bex V, Midgley PM, eds. Cambridge University Press, Cambridge

Kamara AY, Menkir A, Badu-Apraku B, Ibikunle O, 2003 Reproductive and stay-green trait responses of maize hybrids, improved open-pollinated varieties, and farmers' local varieties to terminal drought stress. Maydica 48: 29-37

Kawashima S, Nozaki H, Hamazaki T, Sakata S, Hama T, Matsuo K, Nagasawa A, 2011 Environmental effects on long-range outcrossing rates in maize. Agr Ecosyst Environ 142: 410-418

Kiesselbach TA, 1980 The structure and reproduction of corn. University of Nebraska Press, Lincoln

Liu Y, Xie R, Hou P, Li S, Zhang H, Ming B, Long H, Liang S, 2013 Phenological responses of maize to changes in environment when grown at different latitudes in China. Field Crop Res 144: 192-199

Maddonni GA, Carcova J, Perez MEI, Ghersa CM, 1999 Maize flowering dynamic in soils with contrasting agricultural history. Maydica 44: 141-147

Maherali H, Sherrard ME, Clifford MH, Latta RG, 2008 Leaf hydraulic conductivity and photosynthesis are genetically correlated in an annual grass. New Phytol 180: 240-247

Marshall D, Brown A. 1973 Stability of performance of mixtures and multilines. Euphytica 22: 405-412

Maynard Smith J, 1978 The evolution of sex. Cambridge University Press, Cambridge

Niklas KJ, 1985 The aerodynamics of wind pollination. Bot Rev 51: 328-386

Shafi M, Bakht J, Ali S, Khan H, Khan MA, Sharif M, 2012 Effect of planting density on phenology, growth and yield of maize (*Zea mays* L). Pak J Bot 44: 691-696

Shaw RG, Etterson JR, 2012 Rapid climate change and the rate of adaptation: insight from experimental quantitative genetics. New Phytol 195: 752-765

Swanton CJ, Gonzalez VH, Lee E, Lukens L, 2014 Why the anthesis-silking Interval is Important in understanding yield loss in maize. Annual Meeting of the Canadian Weed Science Society. Canadian Weed Science Society, Vancouver, BC, Canada

Ward JMJ, Stromberg EL, Nowell DC, Nutter FW, 1999 Gray leaf spot - A disease of global importance in maize production. Plant Dis 83: 884-895

Westgate ME, 1996 Physiology of flowering in maize: identifying avenues to improve kernel set during drought: developing drought- and low N-tolerant maize. CIMMYT, El Batán

Yahdjian L, Sala OE, 2002 A rainout shelter design for intercepting different amounts of rainfall. Oecol 133: 95–101

Young KA, Schmitt J, 1995 Genetic variation and phenotypic plasticity of pollen release and capture height in Plantago lanceolata. Funct Ecol 9: 725-733

Yuan LZ, Tang JH, Wang XP, Li CH, 2012 QTL analysis of shading sensitive related traits in maize under two shading treatments. Plos One 7: 11