Adapting maize crop to climate change

Ioannis S. Tokatlidis

Abstract Global weather changes compel agriculture to be adequately productive under diverse and marginal conditions. In maize, modern hybrids fail to meet this requirement. Although breeding has achieved spectacular progress in grain yield per area through improved tolerance to stresses, including intense crowding, yields at low plant population densities remain almost unchanged. Stagnated plant yield potential renders hybrids unable to take advantage of resource abundance at lower populations, designating them population dependent. Consequently, the optimum population varies greatly across environments. Generally, the due population increases as the environmental yield potential gets higher. As a remedy, relatively low populations are recommended for low-input conditions leading to inappropriate population in occasional adequacy of resources and considerable yield loss. For example, for a rain-fed hybrid tested at one location across 11 seasons, crop yield potential and optimum population on the basis of the quadratic yield-plateau model varied from 1,890 to 8,980 kg/ha and 4.56 to 10.2 plants/m^2, respectively, while 100 % yield loss is computed in the driest season if the optimum population for the most favorable season is used. The article reviews the consequences in terms of crop sustainability under widely diverse environments imposed by climatic changes and proposes crop management strategies to address the situation. The major points are: (1) variable-yielding environments require variable optimum populations, (2) population dependence is an insurmountable barrier in making a decision on plant population, (3) farmers suffer from considerable yield and income loss, (4) estimating the less population-dependent hybrids among the currently cultivated ones is a major challenge for agronomists, and (5) the development of population-neutral hybrids is a fundamental challenge for maize breeding. Honeycomb breeding is a valuable tool to pursue this goal since it places particular emphasis on the so-far stagnated plant yield potential that is essential for population-neutral hybrid development.

Keywords Crop yield potential · Honeycomb breeding · Optimum population · Plant yield potential · Population-neutral hybrids · Sustainable agriculture

Abbreviations

EYI	Environmental yield index (the experimental mean grain yield)
CYP	Crop yield potential (the maximum grain yield on the basis of the quadratic equation)
OP	Optimum population (the plant population per unit area necessary to obtain the maximum grain yield, i.e., OP(q) estimated by the quadratic model and OP (D) estimated by the Duncan's (1958) method)
PYP	Plant yield potential (the yield per plant under unlimited resources estimated indirectly by the Yan and Wallace's (1995) method)

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Contents

1 Introduction

Spatial and temporal heterogeneity of the environment may cause a considerable variation in crop yields (Williams et al. 2008; Rusinamhodzi et al. 2011). Tremendously variable weather conditions arise from climatic changes, and the pace of future environmental change will likely be unprecedented (Cutforth et al. 2007). Precipitation events, elevated temperatures, drought, and other types of damaging weather are becoming more intense and frequent (Lavalle et al. 2009; Hatfield et al. 2011). Agriculture is one of the sectors most vulnerable to the risk and impacts of global climate change (Tingem et al. 2009). Consequently, it is expected that these weather events will have implications for agro-ecosystems, with crop yields becoming more variable (Lavalle et al. 2009).

For agriculture to be sustainable in the future in a highly variable environment, it must be able to be adequately productive under diverse and marginal conditions. Moreover, agricultural systems are under increasing pressure to supply food to a growing human population (Hatfield et al. 2011; Jégo et al. 2011), and food demand globally is expected to double by 2050 (Stuber and Hancock 2008). Flexibility of agriculture has been highlighted as a determinant factor of sustainability, enabling agriculture to adapt to ongoing environmental changes and allowing the preservation of the ability to farm and produce food into the future (Lichtfouse et al. 2009). However, there are serious concerns that the forthcoming environmental changes will make the challenge of feeding additional people exceedingly difficult within the next 50 years (Vadez et al. 2012). In sequence, new cultivars, cropping systems, and agricultural management strategies are needed to provide options to farmers to counterweigh these changes.

At present, maize is of the highest tonnage cereal crops worldwide, providing feed, food, and fuel for more than 6,000 million humans while unprecedented growth in global demand for cereals is expected (Troyer and Wellin 2009). Maize grain yield increased from about 1,500 kg/ha in the early 1900s to 8,500 kg/ha at the beginning of the 2000s in the USA (Boomsma et al. 2009; Assefa et al. 2012). Despite this spectacular achievement, maize grain yield is closely related to plant population density (Van Roekel and Coulter 2011), and

the crop suffers from an agronomic weakness of prime significance, affecting its grain productivity and stability. Modern hybrids (Fig. 1) are usually population dependent (Tokatlidis et al. 2001, 2011), with the ideal plant number per area depending on several factors, including water availability, soil fertility, hybrid maturity group, and row spacing (Sangoi et al. 2002). Yet hybrids accomplish their per-area yield potential at high and narrow spectrum of populations, i.e., they follow the quadratic-plateau regression model (Van Roekel and Coulter 2011). Tokatlidis and Koutroubas (2004) reviewed the adverse effects of indispensable high plant population densities on grain yield stability because of considerable yield loss due primarily to missing plants, increased plant-to-plant variability, raised stalk lodging, and augmented barrenness. This review deals with the issue from another point of view, with more emphasis on the great variability in optimum populations, either on the environmental or on the hybrid basis. The main hypothesis comprises: (1) yield potential varies across environments (locations and/or seasons), and the same applies for optimum population, (2) hybrids usually fail to meet the requirements of the diversified environments due to their capacity to attain yield potential at a particular population, resulting in yielding penalty, (3) hybrids that accomplish their crop yield plateau at a relatively wide range of populations are more flexible, and (4) low threshold of a wide spectrum of optimum population, thanks to improved single-plant yield potential, is a determinant of ideal hybrids for flexible agriculture under variable conditions. In brief, this work presents a challenge for agronomists to seek among currently cultivated hybrids for likely population-neutral ones and for maize breeders to set such a target in future projects.

Fig. 1 Modern maize hybrids usually accomplish their per area yield potential, i.e., crop yield potential, at high and narrow spectrum of populations with OP depending on climate and availability of resources, thereby designating them population dependent

2 Source data and analysis

Data were obtained from a number of the most recent papers dealing with maize grain yield response to population, particularly those including variable environments and different hybrids. Key measures, either provided or estimated from the available data, were: (1) the grain yield potential at the area level through either the experimental mean yield (EYI, environmental yield index) or the max yield (crop yield potential (CYP)), (2) the optimal plant population to effectively exploit resources at the per-area level (optimum population (OP)), and (iii) the grain yield potential at the single-plant level (plant yield potential (PYP)).

Numerous studies demonstrated the use of the quadratic model ($y=a+bx-cx^2$) to best describe the grain yield response to population changes (Echarte et al. 2000; Sangoi et al. 2002; Blumenthal et al. 2003; Shanahan et al. 2004; Hashemi et al. 2005; Stanger and Lauer 2006; Sarlangue et al. 2007; Berzsenyi and Tokatlidis 2012). Consequently, the per unit ground area maximum yield and the required number of plants were computed from the quadratic equation, corresponding to the CYP and optimum population (OP(q)), respectively. Duncan's (1958) method was used to calculate optimum population (OP(D)) when the quadratic model did not fit or the range of plant densities included fewer than four treatments. According to this method, optimum density equals $1/b$, where b is the slope of the linear regression of natural logarithm of yield per plant over density (Tollenaar 1992; Tokatlidis 2001; Tokatlidis et al. 2011; Berzsenyi and Tokatlidis 2012). Although Duncan's (1958) method is, in part, an artifact of the estimation of OP, it approaches the differences among estimated values fiducially (Tollenaar 1992; Tokatlidis and Tsialtas 2008; Berzsenyi and Tokatlidis 2012). Indeed, strong positive correlation ($P<0.001$) between OP(q) and OP(D) values is drawn from the data of Berzsenyi and Lap (2005) and Luque et al. (2006), as shown in Fig. 2. Likewise, positive correlation between the two OP estimates is detectable from other studies as well, e.g., Farnham (2001)—$r=0.81$, $P<0.005$; Blumenthal et al. (2003)—$r=0.98$, $P<0.001$; and Stanger and Lauer (2006)—$r=0.89$, $P<0.001$.

Plant yield potential (PYP), defined as the maximum yield per plant when any kind of stress is absent, i.e., in the absence of competition, was measured indirectly by the Yan and Wallace (1995) procedure, i.e., through the intercept of the linear regression analysis of yield per plant over plant population (Tokatlidis 2001). Tokatlidis and Tsialtas (2008) studied this artifact statistic and discovered that, even though it is greatly affected by the level of the lowest population included in the analysis, hybrids' rank does not change and PYP is a solid criterion to comparatively estimate the hybrids for yield potential at the single-plant level. Limited experimental data exist on hybrid performance at very low densities. In a
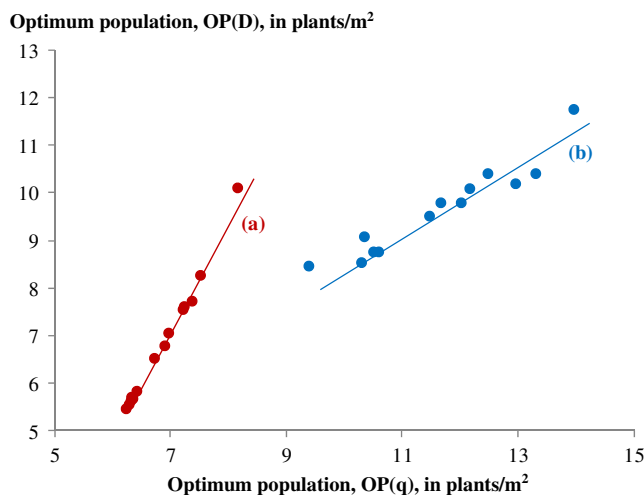

Optimum population, OP(D), in plants/m²

Fig. 2 The relationship between OP values estimated through the quadratic equation of yield response to population changes (*OP(q)*), and the Duncan's (1958) method (*OP(D)*). Data *a* across five hybrids and three seasons ($y=2.28x-8.80$; $R^2=0.99$; $P<0.001$) from Berzenyi and Lap (2005) and *b* across seven hybrids and two environments ($y=0.67x-1.93$; $R^2=0.92$; $P<0.001$) from Luque et al. (2006)

relevant study, Tokatlidis et al. (2010) discovered that a population proximal to 0.74 plants/m² precludes plant-to-plant interferences and approximates absence of competition in maize. Data from Tokatlidis et al. (2011) regarding two separate hybrid sets reveal a strong positive linear relationship of yield per plant at 0.74 plants/m² with their PYP values (Fig. 3). A similar strong positive correlation is computed from Tollenaar (1992) who evaluated four hybrids across 0.5–24 plants/m². Thus, it is verified that the PYP constitutes
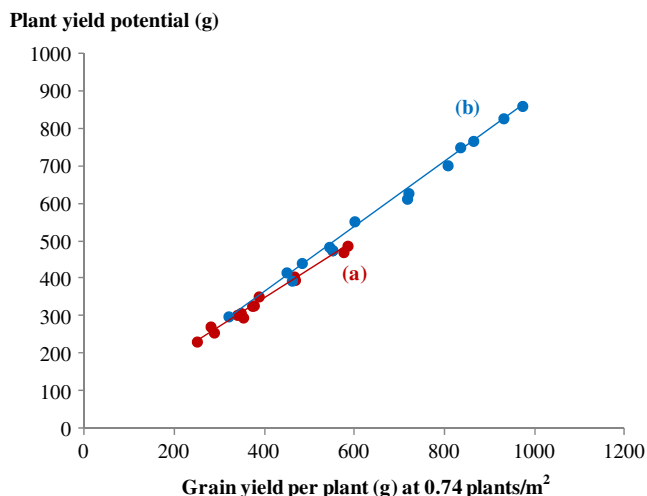

Plant yield potential (g)

Fig. 3 The relationship of the direct estimate of plant yield potential, i.e., grain yield per plant at the ultra-low population of 0.74 plants/m² deemed to proximate absence of competition, with the indirect estimate of PYP by the Yan and Wallace (1995). Data across two seasons from a set of seven, *a* short-season ($y=0.76x+45.3$; $R^2=0.99$; $P<0.001$) and *b* long-season hybrids ($y=0.86x+14.4$; $R^2=0.99$; $P<0.001$) from Tokatlidis et al. (2011)

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a comparatively good estimate of individual-plant yield capacity at very low populations. Tokatlidis (2001) came to the same conclusion. Consequently, calculation of PYP could be adopted as a procedure to investigate the degree of impact of individual plants on hybrid dependence on population, as well as on the optimal population. Tokatlidis and Tsialtas (2008) found that the level of OP(D) decreased and that of PYP increased with decreasing level of the lowest population involved in the calculation, but the hybrids' rank for both measures did not change.

3 Interactions among environments, hybrids, and populations

This section mainly deals with the implications of the interactions between yield potential of the environment (location and/or season), hybrid, and plant population density. From studying research works dealing with different hybrids it becomes apparent that hybrids may respond differently to population changes. Moreover, it is well documented that the environmental conditions determine the optimal number of plants per unit ground area. According to the general conclusion emerging from the published data, the higher the yield potential of the environment, the higher the due plant population density should be. Simply, the OP may differ not only among different hybrids, but even for the same hybrid across environments, i.e., across locations or across seasons at the same location. Thus, it is hard to reach a particular recommendation on appropriate plant population, devoid of the risk of considerable yield loss and limitation of farmers' income.

3.1 Implications of environmental variability on optimum population

The problem of population dependence becomes more acute when the crop is produced under rain-fed conditions. Considering the EYI or the CYP of maize grown under moisture-limited conditions, a tremendous variability in grain yield becomes apparent. Diversifying environmental conditions reflect an analogous diversity in OP. The interaction among hybrid, population, and environment, stemming from the hybrid dependence on population, constitutes the root cause of the variability in OP among different hybrids and, more importantly, of the wide variability in OP for the same hybrid across seasons and/or locations.

Blumenthal et al. (2003) reported the results of a 2-year study (1999 and 2000) aiming to determine appropriate plant population density for dryland maize grown in western Nebraska, USA. Field studies were conducted across four locations, where the hybrid PR3893 was no-till seeded into wheat or proso millet stubble at the population range of 1.73–5.68 plants/m^2. For three out of the four locations, the

over year EYI was 1,430 (Kimball), 3,050 (Box Butte), and 3,870 kg/ha (Cheyenne), and the respective OP(q) values were 2.60, 4.70, and 5.55 plants/m^2. Because of the difference in summer precipitation between the two years during the grain fill period, the EYI range across locations and seasons was much greater, varying from 1,220 (Kimball, 2000) to 5,550 kg/ha (Cheyenne, 1999), accompanied by an analogous increased range of the respective OP(q) values (i.e., 0.14–10.3 plants/m^2). Worthy of notice is the enormous gap (>200 %) in both CYP and OP(q) between the two consecutive seasons at the Cheyenne location (Table 1). Intriguingly, at the Kimball location, where the EYI of two seasons differed by 35 %, OP(q) for 1999 was 30 times higher compared with OP(q) for the drier 2000 (4.33 vs. 0.14 plants/m^2). These calculations might be exaggerated and beyond the expected limits. Nevertheless, they pinpoint the question of variation in OP on account of the environmental variance in yield potential.

Across 11 consecutive growing seasons (from 1989 through 1999) at the same location (Martonvásár, Hungary), total precipitation ranged between 68 % above and 55 % below the 30-year average (Berzsenyi and Tokatlidis 2012). Over four N-fertilizer treatments at 3, 5, 7, and 9 plants/m^2, rain-fed maize crop averaged a grain yield from 1,460 to 7,670 kg/ha, showing an EYI gap of up to 425 % across seasons (Fig. 4). The corresponding CYP range was 1,600–9,130 kg/ha. The lowest yield was in the driest season of 1990, which lagged behind 1989 by 75 %. For this extremely stressful season, an OP(q) value of 5.29 plants/m^2 was calculated while for the remaining ten seasons, OP(q) varied from 5.34 to 13.2 plants/m^2.

Norwood (2001) reported a 200 % gap in EYI (i.e., 2,820–8,480 kg/ha) when five hybrids were tested at 3, 4.5, and 6 plants/m^2 across eight environments and under rain-fed conditions at the Southwest Research Extension Center near Garden City, Kansas, USA. The eight environments consisted of four seasons (1996–1999) and two planting dates. Interestingly, the planting date of 17 April 1997 gave the lowest yield of 2,820 kg/ha, while planting date of 6 May of the same season averaged almost twofold higher yield (5,550 kg/ha). The researcher stated that because of favorable climatic conditions, higher populations usually resulted in higher yields. However, to minimize yield losses in dry years without causing much yield loss in wet years, early-maturing hybrids at populations not exceeding 4.5 plants/m^2 were recommended.

The phenomenon of variation in OP is presumably more intensive in widely diverse environments. Nevertheless, substantial variation in OP is apparent even from studies conducted in less diverse environments. Farnham (2001) evaluated the hybrid N4640Bt at six locations in Iowa, USA. Over four plant populations, two row spacing, and three seasons, experimental mean yields were from 9,950

Table 1 Data from studies concerning two contrasting environments and regarding the crop yield potential (CYP) and optimum population (OP(q)), as well as the yield loss (YL) whether in each environment a population equal to the OP(q) of the other was established

Hybrid	Environment		Quadratic equation	CYP (kg/ha)	OP(q) (plants/m^2)	YL (%)	Source
PR3893	Cheyenne, Nebraska	1999	$y=2{,}701+972.9x-47.2x^2$ ($R^2=0.97$)	7,720	10.3	35	Blumenthal et al. (2003)
		2000	$y=1{,}824+445.5x-80.6x^2$ ($R^2=0.99$)	2,440	2.76	100	
PR3860	Anton, Colorado, 1998	Low-yielding field	$y=1{,}839+1{,}283x-110x^2$ ($R^2=0.91$)	5,580	5.83	17	Shanahan et al. (2004)
		High-yielding field	$y=2{,}469+1{,}230x-70x^2$ ($R^2=0.92$)	7,870	8.78	8.8	
Non-Bt group	North Central Wisconsin-zone	Seynour	$y=3{,}020+1{,}560x-70x^2$ ($R^2=0.94$)	11,710	11.2	17	Stanger and Lauer (2006)
		Chippewa Falls	$y=8{,}020+320x-28x^2$ ($R^2=0.96$)	8,930	5.78	9.3	
Short-season group	Turda, Romania	2006	$y=2{,}696+1{,}252x-116.3x^2$ ($R^2=0.98$)	6,070	5.38	27	Tokatlidis et al. (2011)
		2007	$y=1{,}443+1{,}383x-75.82x^2$ ($R^2=0.99$)	7,750	9.12	14	
Norma	Martonvásár, Hungary	1990	$y=491.2+615x-67.49x^2$ ($R^2=0.98$)	1,890	4.56	100	Berzsenyi and Tokatlidis (2012)
		1997	$y=3{,}763+1{,}022x-50.13x^2$ ($R^2=0.87$)	8,980	10.2	18	

(Crawfordsville location) up to 11,060 kg/ha (Ames location), implying a gap in EYI of only 11 %. However, a high range of OP(q) values was derived from the quadratic regression analysis, i.e., 7.6 (Crawfordsville), 7.88 (Kanawha), 9.1 (Nashua and Sutherland), 11.7 (Ames), and 14 plant/m^2 (Lewis).

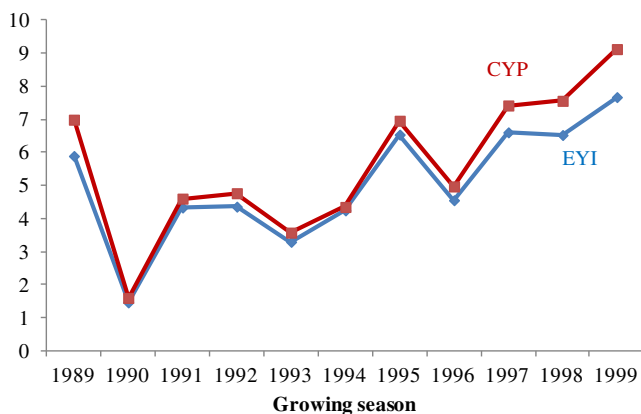**Environmental yield index (EYI) & Crop yield potential (CYP) (thousand kg/ha)**

Fig. 4 The degree of variability in environmental yield index, (*EYI*) and crop yield potential (*CYP*), are indicative of the across-season at a single-location environmental diversity in dryland maize production. Data over four hybrids and four N-fertilizer treatments at four densities from Berzsenyi and Tokatlidis (2012)

With the main objective to determine the OP for maize in Wisconsin, USA, Stanger and Lauer (2006) evaluated hybrids with non-Bt and Bt traits at the target populations of 6.18–12.35 plants/m^2 for three growing seasons (2002–2004) and across ten locations belonging to three maize zones. They predicted for the non-Bt hybrid group in particular an across-location CYP varying from 8,900 to 15,200 kg/ha, accompanied by a variation in OP(q) from 5.78 to 11.5 plants/m^2.

Popp et al. (2006) evaluated the profit-maximizing plant population of several maize hybrids at two locations of Arkansas, USA, i.e., Fayetteville and Keiser. They reported considerably different profit-maximizing plant populations for the same hybrid across locations and/or seasons. For example, the profit-maximizing population of hybrid PR39W54 was 11.9 (2001), 17.5 (2002), and 18.9 plants/m^2 (2003) at Fayetteville and 10.4 plants/m^2 at Keiser (2003). For hybrid 39T68, reported values of profit-maximizing plant population were 14.3 and 10.4 plants/m^2 for 2002 and 2003, respectively, at Keiser, and 18.9 plants/m^2 for 2003 at Fayetteville. The researchers concluded that the highest yielding hybrid does not always coincide with the profit-maximizing hybrid, due primarily to high seed costs to attain maximum yields.

In the research of Boomsma et al. (2009), population interacted significantly with N availability, and lower populations were more suited to environments devoid of N. Over three years, per-area data gave OP(D) of 5.2 plants/m^2 for the low yielding

treatment of 0 Nkg/ha. For the similarly yielding treatments of 165 and 330 Nkg/ha, OP(D) values were 7.4 and 7.9 plants/m^2, respectively. These data support the belief that lower populations are more suitable for low-input conditions.

The aforementioned data are indicative of a positive association between the environmental yield potential and the required plant population in the field. For instance, Norwood (2001) found that the higher populations of 6 plants/m^2 usually produce more grain at favorable climatic conditions, but for the stressful season and planting date, average yield decreased from 3,390 to 2,600 kg/ha when population increased from 3 to 6 plants/m^2. When the data of Norwood (2001) are considered over the five hybrids across four growing seasons by two planting date treatments, a significant linear correlation between EYI and OP(D) is found ($r=0.81$; $P<0.02$). Likewise, when data for the hybrid N4640Bt from Farnham (2001) are analyzed across the location by row spacing combinations, for 10 out of the 12 environments a positive correlation between hybrid CYP and OP(q) is found (Fig. 5). According to the linear regression analysis ($r=0.82$; $P<0.001$), for a per thousand kilograms per hectare increase in yield potential, 3.13 more plants/m^2 are needed for this potential to be fully exploited. It is worth noting the within-location differences between hybrid OP(q) of the inter-row spacing—38 cm vs. 76 cm—as shown in Fig. 5 (10.4 vs. 14.4 plants/m^2, 15.2 vs. 12.8 plants/m^2, and 8.47 vs. 11.2 plants/m^2 for the Ames, Lewis, and Nashua locations, respectively), emphasizing the strong environment/population interaction which appears an insurmountable obstacle in deciding on either hybrid- or site-specific OP density.

Linear regression analysis of data from Berzsenyi and Tokatlidis (2012) over four hybrids and four N-treatments across 11 growing seasons gave a positive correlation between CYP and

Fig. 5 The positive relationship between CYP and the OP(q) (i.e., $y=3.13x-24.2$; $R^2=0.67$; $P<0.005$), regarding the hybrid N4640Bt over three years at four populations and across six locations (*1* for Ames, *2* for Kanawha, *3* for Nashua, *4* for Sutherland, *5* for Crawfordsville, and *6* for Lewis) by two row-spacing, i.e., *brown dots* for 38 cm and *blue dots* for 76 cm. Data from Farnham (2001)

OP(q) ($r=0.67$; $P<0.03$). They reported significant positive linear correlations between EYI and OP(D) values for three out of the four hybrids when the hybrids were considered separately and across the N-rates. Similarly, the 20 CYP–OP(q) pairs from Stanger and Lauer (2006) showed a tendency for positive correlation ($r=0.57$; $P<0.007$).

3.2 Implications of optimum population variability on grain yield productivity and stability

Interactions among environments, hybrids, and populations create a necessity for hybrid- and/or site-specific crop management. However, the enormous variation in yield potential and OP across environments mirrors the difficulty in predicting the most suitable plant population and applying the corresponding seeding rate. As a consequence, accounting for the divergence from the OP in the degree of hybrid dependence on population, these interactions are the ultimate cause of substantial yield losses. Table 1 presents the maximum grain yield loss drawn from reported results, presumably expected at the most stressful environment if the applied population approaches that suitable for a very favorable environment and vice versa.

Data from Blumenthal et al. (2003), obtained under extremely extensive cultivation (rain-fed and no-till seeded), are sufficiently explanatory. The authors noted that growers in western Nebraska are advised to plant for an expected harvest population of 2.72 plants/m^2. Indeed, in the Cheyenne location during 2000, this population was computed as optimal to allow the hybrid/crop to fully exploit its yield potential (i.e., 2,440 kg/ha). For this season, however, the quadratic model estimated complete yield loss under a population similar to the optimum for the more favorable 1999. On the other hand, farmers would produce 35 % less grain than in 1999 under the recommended population of 2.72 plants/m^2. Let us accept that OP(q) of 10.3 plants/m^2 for 1999 was computed to exaggeration and that the derived as an over-season OP(q) of 5.55 plants/m^2 is now recommended in the area. By applying the respective quadratics, a grain yield loss of 1,069 (14 %) and 625 kg/ha (26 %) would result for seasons like the favorable 1999 and stressful 2000, respectively. Intriguingly, for the Kimball location, a loss of up to 39 (2000) and 55 % (1999) could occur during one of these two seasons under a population optimal for the other, even though the two seasons were of the same yield potential (Fig. 6).

Such an adverse implication may arise even for less variable environments. For example, in the study of Shanahan et al. (2004) the low-yielding environment of 1998 (CYP= 5,580 kg/ha) exhibited an OP of 5.83 plants/m^2 while the high-yielding environment of the same season (CYP= 7,870 kg/ha) gave OP(q) of 8.78 plants/m^2. Computed maximum yield losses were 17 and 8.8 %, respectively (Table 1).

Even though data from Stanger and Lauer (2006) did not depict severe dependence overall, since for either Bt or non-Bt hybrids 95 % of the maximum yield was attainable at
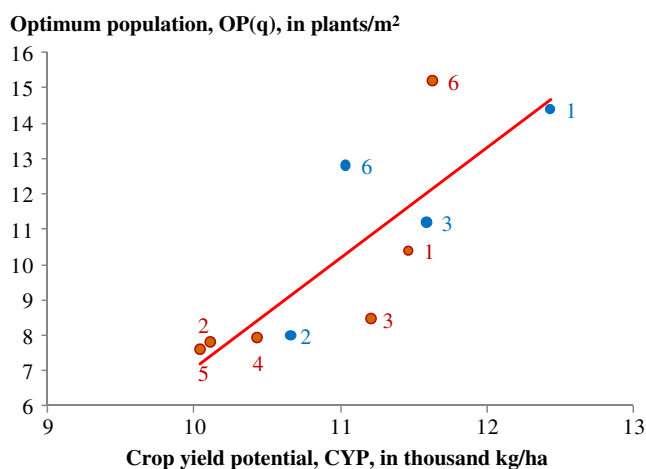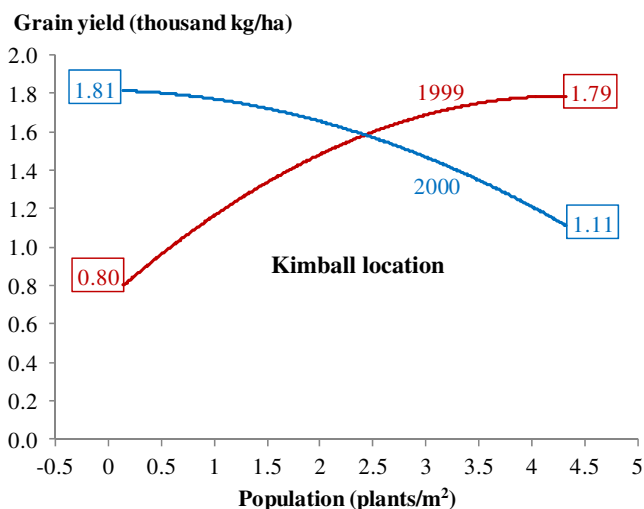
Grain yield (thousand kg/ha)

Fig. 6 Under marginal conditions the strong population by environment interaction may cause considerable yield loss even in seasons of similar yield potential, i.e., *the two numbers at the edges of each line* correspond to yields at the OPs in the two seasons, indicating yield loss up to 55 % for 1999 and up to 39 % for 2000. Data relevant to the hybrid PR3893 across the 1999 season ($y=731.5+487.3x-56.32x^2$; $R^2=0.94$) and 2000 ($y=1,814-9.977x-35.29x^2$; $R^2=0.98$) from Blumenthal et al. (2003)

populations 30 % lower, interesting inferences are made considering the edge values of CYP and OP(q) regarding the non-Bt group of hybrids. In the Southern zone, Arlington exhibited the lowest yield potential (12,000 kg/ha) attainable at 8.38 plants/m^2, while yield potential of the most favorable Janesville (13,600 kg/ha) could be accomplished at 11.5 plants/m^2. This range of OP implies a yield loss up to 4.5 % for Janesville and up to 6.8 % for Arlington if the applied population is within this range. More severely, the wider range of yield potential in the North Central zone (8,930–11,710 kg/ha) reflected a wider range of OP also (5.78–11.2 plants/m^2). Therefore, higher potential yield losses were estimated, i.e., up to 9.3 % for Chippewa Falls and 17 % for Seymour (Table 1).

Regarding seven short-season hybrids in Romania under dryland conditions for the dry 2006 season, the over-hybrid OP(q) was 5.38 plants/m^2, fairly approaching that recommended for the area (Tokatlidis et al. 2011). The next season, however, 9.12 plants per square meter was the required population to take advantage of the adequate rainfalls, implying a 14 % yield loss with the population commonly used in the area. If the OP for the well-rained season was chosen for the dry 2006 season, the yield loss would reach 27 %.

Extremely high potential losses have been reported for the population-dependent hybrid Norma (Berzsenyi and Tokatlidis 2012). Total yield destruction could result for seasons like the very dry 1990 in cases where the applied population is high enough to satisfy the requirements of favorable seasons similar to 1997 (Table 1). The authors compared the marginal season of 1990 with the favorable 1998. They found that the first would produce 830 kg/ha, 56 % lower compared with its CYP

when the crowding level approached the OP for 1998. On the other hand, the 1998 season would produce 6,960 kg/ha if the optimum seeding rate for 1990 was used, implying up to 20 % yield loss. Although a proportionately higher risk of yield loss existed in the stressful rather than the favorable environment, when these ratios were adjusted to the respective CYP values, the yield loss reached the levels of 1,067 kg/ha for the stressful season and 1,710 kg/ha for the favorable season. From these values, it can be deduced that choosing the OP for a favorable rather than a stressful season is seemingly a good decision to moderate a crop's instability. However, reanalysis aiming to estimate the over-season yield loss leads to a different conclusion. For each of the eight provided OP(q) values, the yield losses across seasons relative to the respective CYPs were computed and averaged. The loss by population interaction (Fig. 7) illustrates that the lowest over-season yield loss (3.6 %) would be at 7.5 plants/m^2. In fact, this population is proximal to the reported over-season OP (8.11 plants/m^2). Similar analysis of data from Blumenthal et al. (2003) parallels the above interaction model ($y=48.69-13.18x+1.33x^2$; $R^2=0.97$) and gives the lowest over-location and season yield loss (16 %) for a population approaching the OP(q) obtained when grain yield response to population change was considered over environment, i.e., ≈5.0 plants/m^2 ($y=2081+453.5x-43.32x^2$; $R^2=0.86$). Hence, to cope with the problem of population dependence and make a good decision on population recommendation, a long-term study of the yield by population interaction across the locations targeted is essential. The same inference is reached from the work of Farnham (2001) concerning ten locations by row spacing environments, i.e., the lowest over-environment yield loss (2.9 %) occurs when the population is consistently around 9.0 plants/m^2 and is equal to the OP(q) obtained from over-environment pooled data.

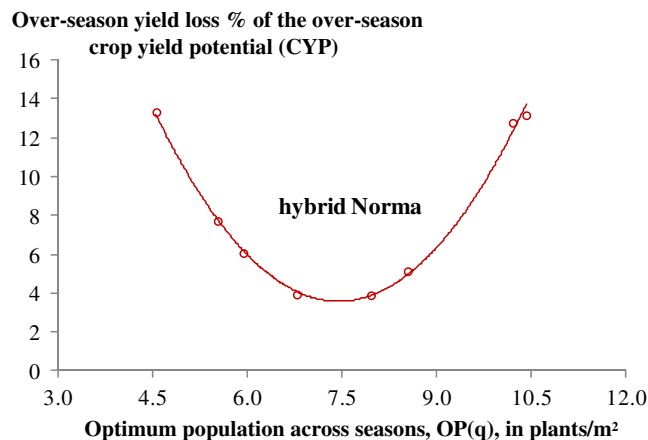**Over-season yield loss % of the over-season crop yield potential (CYP)**

Fig. 7 The over-season grain yield loss relative to the respective crop yield potential (*CYP*) across the optimum population (OP(q)) of eight seasons ($y=67.46-17.15x+1.15x^2$; $R^2=0.99$). Data from Berzsenyi and Tokatlidis (2012)

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3.3 The role of plant yield potential

Differences in grain yield per unit area between older and newer maize hybrids have been shown to be primarily a function of plant population density. Contrary to improvements in tolerance to biotic and biotic stresses, the single-plant yield potential has stagnated when expressed under minimal competition for light, water, and nutrients (Sangoi et al. 2002; Duvick 1997, 2005; Tollenaar and Lee 2002; Brekke et al. 2011). Hammer et al. (2009) examined the yield of hybrids from eras of release ranging from 1930s to 2000s in different populations and concluded that much of the yield increase associated with newer hybrids was due to increased stress tolerance, which allowed growers to adopt higher populations. Consequently, strong hybrid dependence on population is largely due to the inability of individual plants to exploit larger input-shares at lower populations. In contrast, the low threshold of the OP could be justified by the ability of individual plants to take advantage of more resources at lower populations. Indeed, Tokatlidis (2001) emphasized the improved plant yield potential as a mechanism that decreases the threshold of plant number that optimizes productivity and renders the hybrids less population dependent. How stagnation in plant yield potential determines the dependence of hybrids on population and adversely affects their stability because of the necessity to be grown at high populations has been discussed in detail by Tokatlidis and Koutroubas (2004). The role of plant yield potential in terms of the current paper's scope is discussed further hereafter based on more recent research.

In order to investigate reliably the impact of plant yield potential on OP and stability, the availability of data regarding hybrids equivalent in CYP is desired. Although such data are generally scarce, data provided by Thomison et al. (2011) meet such a presupposition. For four hybrids tested across 5.90 to 10.4 plants/m^2 at S. Charleston, Ohio, CYP values were found to be almost equal (12,670–13.080 kg/ha). Their OP(q), though, varied from 6.75 to 10.9 plants/m^2 and PYP from 297 to 341 g. These two measures were inversely correlated ($r=-0.94$; $P<0.06$), reflecting the message that improved yield at the single-plant level may extend the lower limit of the plant population range for optimal resource use and crop yield. Similarly, among the three hybrids evaluated by Sangoi et al. (2002), two (Ag12 and C929) exhibited similar CYP, but for the first, lower OP(q) and higher PYP are estimated.

Data from Norwood (2001) and from Sarlangue et al. (2007) deserve special consideration. Figure 8 reveals that high yield potential at the per-unit ground area level, i.e., EYI of a hybrid, does not necessarily require high plant population. In contrast, the higher yielding hybrids had lower OPs, owing to improved plant yield potential. Assuming the hybrid with the lowest PYP as the baseline (H1), the
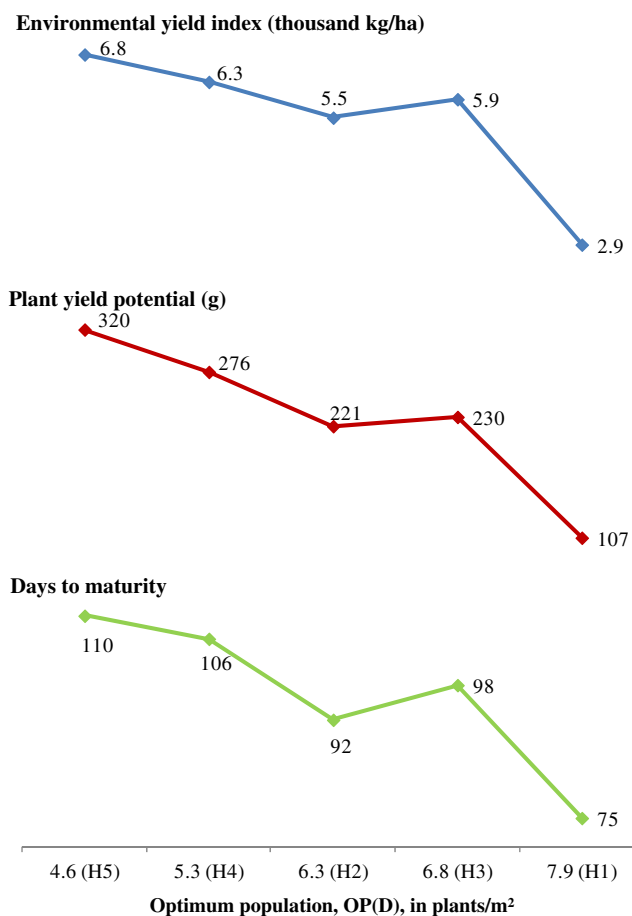

Fig. 8 The OP(D) of five hybrids (H1, …, H5) is negatively correlated with their EYI ($r=-0.89$; $P<0.05$), PYP ($r=-0.96$; $P<0.009$) and days to maturity ($r=-0.94$; $P<0.02$), indicating that (1) high environmental yield potential does not always require high plant population, (2) Plant yield potential is crucial for lower optimal population, and (3) early-maturing hybrids may generally require higher populations. Data over 3–4 years and two sowing dates from Norwood (2001)

hybrid H5 exhibited threefold higher PYP and almost half OP(D). A parallel declining pattern for OP and increasing pattern for CYP when plant yield potential increases is drawn from Sarlangue et al. (2007). They evaluated three hybrids, the short-season Romario, the mid-season P37P73, and the long-season DK688. Yield response to population was estimated on the basis of the provided quadratic lines for two seasons, and average values of PYP, CYP, and OP (q) were respectively: 136 g/plant, 9,170 kg/ha, and 13.6 plants/m^2 for Romario; 195 g/plant, 10,780 kg/ha, and 12.7 plants/m^2 for P37P73; and 267 g/plant, 12,460 kg/ha, and 10.9 plants/m^2 for DK688. Obviously, improved PYP influenced CYP favorably and OP(q) inversely. These findings indicate that very high population is not an imperative condition for high grain yield per unit area to be attained, on the premise that individual plants have the potential to take advantage of more available resources with less crowding.

Other works similarly report a significant (P<0.01) negative association between plant yield potential and OP. For example, a significant negative correlation between PYP and OP(q) is computable from data of Berzsenyi and Lap (2005) including five hybrids across three seasons (r=−0.59; P< 0.08). A negative correlation between PYP and OP(D) is also computed from data of Tokatlidis et al. (2011) regarding each of two sets of seven hybrids tested across two seasons, i.e., r=−0.78 (P<0.001) and r=−0.69 (P<0.007), as well as from data of Berzsenyi and Tokatlidis (2012) across three hybrids equivalent in CYP, 11 seasons, and three N-fertilizer treatments (100–300 Nkg/ha), i.e., r=−0.43 (P<0.001). Other studies providing additional evidence of this negative correlation are discussed in the following sections.

Plant yield potential is obviously crucial for lower optimal populations and thus a desirable agronomic trait of hybrids sought for variable conditions. When non-Bt and Bt hybrids of Stanger and Lauer (2006) were scored for PYP across 10 locations, a positive linear correlation of single-plant yield potential with CYP was found (r=0.91; P< 0.001). The finding is in agreement with those of Fig. 8 and corroborates a similar linear relationship found by Tokatlidis (2001). By inference, potential linkage between these two advantageous attributes determines high-yielding population-neutral hybrids.

Despite its beneficial agronomic attribute, whether plant yield potential has improved over time is questionable, and this is partially attributed to stagnation in harvest index (HI) (Duvick 2005; Tollenaar and Lee 2002, 2006). Vega et al. (2000) highlighted that maize has limited capacity to adjust the number of ears in response to resource availability, and low stability in HI. Improvement of yield potential of single plants is expected to be associated with improved HI and prolificacy at lower populations. Hashemi et al. (2005) reported higher and almost stable HI at lower populations (49–53 %) for the hybrid Northrup King Max 21, while HI of the hybrid SC704 declined dramatically (44→31 %) with decreasing population below the optimal (9→3 plants/m^2). Their data result in PYP 28 % higher for the first vs. the latter hybrid. Shapiro and Wortmann (2006) also found that population affected HI, the highest HI being obtained at lower populations (55 % at 5.5 plants/m^2). Echarte and Andrade (2003) found that prolificacy stabilized HI and advanced hybrid reproductive plasticity at low populations. Improved prolificacy was regarded by Tokatlidis et al. (2005) as the key factor for hybrids of low and broad OP. Sarlangue et al. (2007) reported optimum for HI populations of 12.7 plants/m^2 for hybrid Romario that exhibited the lowest PYP, 10.6 plants/m^2 for hybrid P37P73 with an intermediate PYP, and only 6.5 plants/m^2 for the highest yielding at low population DK688. Boomsma et al. (2009) discovered that strong responsiveness of grain yield per plant to reduced plant crowding accompanies higher HI

values and better nitrogen use efficiency, suggesting a relatively high level of reproductive partitioning and plasticity.

4 Current crop management status

Periodically re-evaluating the response of maize grain yield to population is encouraged, since OP can differ among hybrids (Cox 1996; Widdicombe and Thelen 2002; Stanger and Lauer 2006). However, OP has trended upward over time (Hammer et al. 2009), and thus the economically optimum seeding rate commonly differs among hybrids (Van Roekel and Coulter 2011). In other words, the strong reliance of maize crop upon plant population density makes the assessment of hybrid- and site-specific optimum plant population densities imperative. Nevertheless, under variable climate conditions the hybrid–population interaction constitutes an almost insurmountable constraint to deciding on a particular population. Due to close connection of the optimal population with the environmental yield potential, unpredictable environmental conditions for the contemporary growing season may result in a non-appropriate plant population in the field. The ultimate outcome might be a considerable yield loss on account of departure from the optimal population.

A representative example of the difficulty in addressing the issue of optimal population is the crop production for rain-fed conditions with precipitation commonly varying across seasons. Norwood (2001) concluded that risk-averse farmers would probably choose lower populations. He stated that hybrid maturity, plant population, and planting date should be diversified for risk management under drought conditions and to ensure acceptable yields across environments. Variable seeding rate, however, has been suggested as economically unprofitable (Bullock et al. 1998). Blumenthal et al. (2003) advised growers to plant maize at specific plant population and to increase above this level only if they are willing to accept the associated risks. Shanahan et al. (2004) reported results contrasting with the recommendation for hybrid maturity to be diversified and suggested using variable site-specific management of the plant population. Although the problem is less severe in conventionally irrigated and fertilized maize, Popp et al. (2006) found it hard to reach a particular optimal population. Moreover, they discovered that the highest yielding hybrid does not always coincide with the profit-maximizing hybrid, due primarily to the high seed costs incurred to attain maximum yields.

Planting at lower populations is recommended in drought-prone environments, where the available resources cannot support a high plant population (Norwood 2001; Kiniry et al. 2002; Blumenthal et al. 2003; Shanahan et al. 2004; Duvick 2005; Tokatlidis et al. 2011; Berzsenyi and Tokatlidis 2012). In addition, special emphasis has been

placed on the time required for a hybrid to reach maturity. It is believed that early- rather than late-maturing hybrids are more adaptable to lower densities in stressful seasons, plus they seemingly have potential for avoiding drought (Larson and Clegg 1999; Norwood 2001; Shanahan et al. 2004; Edwards et al. 2005). However, higher OPs were scored up for shorter-than longer-season hybrids when resources were in abundance, implying that the short-season hybrids are usually more variable in OP. Where hybrids largely varying in OP are preferred, maize crop production under diverse environments becomes exceptionally problematic.

Results obtained from Norwood (2001), i.e., Fig. 8, as well as from Sarlangue et al. (2007) are not supportive of early-maturing hybrids. In both studies, earliness was accompanied by lower yield per area potential and higher OP, i.e., stronger dependence on population. For example, Sarlangue et al. (2007) reported that a decrease in plant population from 10 to 5 plants/m^2 resulted in a 52, 37, and 23 % decrease in grain yield for the short-season Romario, the mid-season P37P73, and the long-season DK688, respectively. The researchers characterized the long-season DK688 hybrid as being more plastic on account of its ability to explore more resources at low plant populations. Shanahan et al. (2004) studied the potential for the use of site-specific management of maize hybrids and plant populations in dryland landscapes. Treatments consisted of a combination of two hybrids (the early-maturing PR3860 and the late-maturing PR3752) and four plant populations (2.5–6.2 plants/m^2) across low-, medium-, and high-yielding environments. They reported on quadratic equations indicating that the two hybrids were of similar CYP but of different OP. OP increased with increasing environmental potential for the early-maturing hybrid (i.e., 5.83→8.78 plants/m^2), while it remained almost unchanged for the late-maturing hybrid (i.e., 6.12→6.57 plants/m^2). Their results were contrary to their initial hypothesis that shorter season hybrids would have an advantage over longer seasons hybrids in lower yielding- more drought prone regions, while longer season hybrids would flourish in high-yielding areas.

Berzsenyi and Tokatlidis (2012) reported results with reference to OP(D) values across 11 seasons and four N-rate treatments for three hybrids characterized as short- (Mara), mid- (Norma), and long-season (Maraton), verifying stronger dependence on population for the short- and least dependence for the long-season hybrid. The differences between highest and lowest OP(D) were 12.2 (2.96–14.2), 11.9 (2.72–14.7), and 6.12 (3.69–9.81) plants/m^2 for the short-, mid-, and full-season hybrid, respectively. Edwards et al. (2005) found that short- and full-season hybrids had equivalent asymptotic yield potential as a function of plant population. Nevertheless, the threshold of plant population required to achieve maximum yield differed greatly between them. The highest production was approached at 19 and 8 plants/m^2 by the short- and full-season hybrid, respectively. They commented that, in terms of plant physiology, plant populations higher than current recommendations are required for short-season hybrids to ensure rapid canopy closure and full light interception. Popp et al. (2006) found that the higher the maturity of the hybrid, the higher the potential for lower plant population requirements to achieve required yields.

Avoidance of water deficiency at the crucial stages of grain formation and filling is of the utmost importance for the crop to withstand the drought stress. The aforementioned studies, though, highlight that the hypothesis of short-season hybrids is valid only on the premise that population-neutral hybrids are available. However, accumulated evidence regarding earlier-maturing hybrids supports the population dependence more so than the population neutrality.

5 Future crop management

Under cultivation conditions varying in climate, soil, precipitation, and other constituent parts of agro-ecosystems, the availability of flexible hybrids is imperative. Additionally, farmers need information on plant populations to optimize grain productivity consistently across such variable situations. For these presuppositions to be met, hybrids of high-yield potential should be able to fully exhibit their potential at a wide range of low-threshold plant populations. Because Popp et al. (2006) found profit-maximizing yield to be lower than the CYP, they suggested as ideal the grain yield response to population according to the asymptotic pattern, plus high-yielding hybrids at lower populations. They speculated that the ideal hybrid essentially accomplishes higher profit-maximizing yields at lower populations, on the condition that CYP, seed cost, and maize price are the same across the hybrids. Hence, they mirrored a population-neutral hybrid cultivatable at lower populations and therefore flexible to attain optimal productivity under either marginal or favorable conditions. It is evident that the goal of asymptotic pattern presumes, beyond tolerance to high populations, improved plant yield potential. Henceforth, crop management could be characterized by two challenges: the short-term target of investigation of the less population-dependent among currently cultivated elite hybrids and the mid-term target of developing population-neutral hybrids.

5.1 Seeking for the less population-dependent elite hybrids

Population-dependent genotypes might differ in OP for grain yield per unit ground area. Consequently, the common practice of evaluation of different hybrids at dense stand includes the risk of biased judgment, particularly when the evaluation

is conducted under a single dense stand. From this viewpoint, the study of Thomison et al. (2011) is exceptionally informative. They evaluated four hybrids, the early to mid-maturity hybrids 34B23 and 34M94 and the full-season hybrids 33G26 and 33J56, at plant populations of 5.9, 7.4, 8.9, and 10.4 plants/m^2 across three seasons and three harvest dates at South Charleston, Ohio. They did not find evident differences in yield among hybrids at the different population levels, implying hybrids of equivalent value. Consideration of the extended downward quadratic pattern of the yield to population response for the full-season hybrid 33J56 and the mid-maturity hybrid 34M94 in particular (Fig. 9) denotes different inferences, nevertheless. For a number of reasons, the first is less reliant on population and thus of higher value: (1) its OP is 26 % lower, implying a lower cost of planting; (2) it satisfies better the requirements of stressful environments for less plant crowding; (3) when plant population varies within the ±30 % limits of the optimum, yield loss is up to 2.1 %, while the corresponding yield loss of the second hybrid is 6.2 %. Indeed, only the 34M94 hybrid was yielding significantly lower at 5.9 compared with 8.9 plants/m^2 (Thomison et al. 2011). Consequently, 33J56 is more likely to accomplish its yield potential under variable conditions, while the seemingly higher yield of 34M94 at very high populations does not compensate for the lack of stability. However, this desirable attribute of the 33J56 hybrid can be revealed only when hybrid performance is considered at very low populations. Berzsenyi and Tokatlidis (2012) reported results for the relatively longer-season hybrid Maraton and the shorter-season Norma. For a

number of reasons similar to the above, the first exhibited less dependence on population and was found to be more appropriate for long-term dryland cultivation. Indicatively, the two hybrids had similar CYP under the optimal fertilizer treatment of 200 N kg/ha, and thus they might be evaluated as equivalent in yield potential. When results were considered over all N treatments, however, inducing low-input conditions (i.e., 0 and 100 N kg/ha), Maraton yielded consistently higher than Norma during 10 of the 11 seasons (Fig. 10), exhibiting the versatility to either adapt to the low-input environments or flourish during favorable seasons.

By inference, among currently elite hybrids the less population-dependent have to be qualified. The justified crucial role of plant yield potential highlights the necessity of evaluating hybrids to target this character. The first option to meet this demand is to estimate the PYP measure suggested by Yan and Wallace (1995) in cases where data across a range of populations are already available. An alternative option is evaluation of the hybrids in the absence of competition, where plant yield potential is directly measurable. An innovative statistic is now available, designed for accurate whole-plant field evaluation for high and stable crop yield and breeding population-neutral cultivars, described in the next section. Among hybrids already known to perform well at high populations, those which rank top for PYP are expected to be better suited to variable situations. For example, on the basis of the provided data (Thomison et al. 2011), PYP of hybrid 33J56 is computed as 15 % higher compared with PYP of 34M94 (Fig. 9). Similarly, from the provided data (Berzsenyi and Tokatlidis 2012) for the less dependent on population hybrid Maraton, the estimated PYP value is 18 % higher than PYP of the more dependent hybrid Norma. Also noteworthy
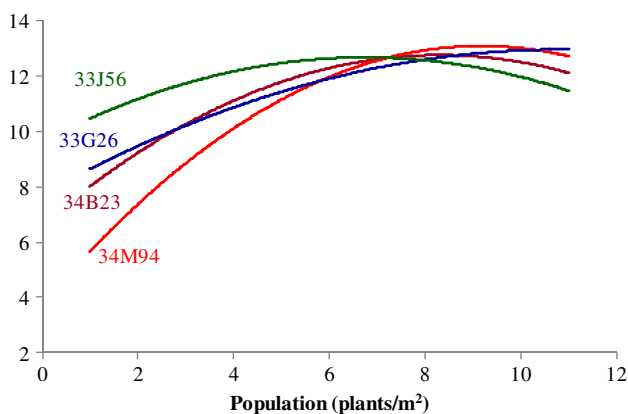
Grain yield (thousand kg/ha)

Fig. 9 The grain yield response to plant population of the early to mid-maturity hybrids 34B23 and 34M94, as well as of the full-season hybrids 33G26 and 33J56. Quadratic equations, OP(q) in plants per square meter, and CYP in kilograms per hectare are: 34B23, $y=6,628+1,476x-88.89x^2$ ($R^2=0.84$), 8.38, and 12,750; 34M94, $y=3,735+2,038x-111.1x^2$ ($R^2=0.99$), 9.17, and 13,080; 33G26, $y=7,717+964.4x-44.44x^2$ ($R^2=0.96$), 10.9, and 12,950; 33J56, $y=9,631+900x-66.67x^2$ ($R^2=0.98$), 6.75, and 12,670. Comparison of the full-season 33J56 against the early to mid-season 34M94 show that hybrids equivalent in crop yield potential are not always of the same value. Data across four populations and over three locations and three harvest dates were from Thomison et al. (2011)

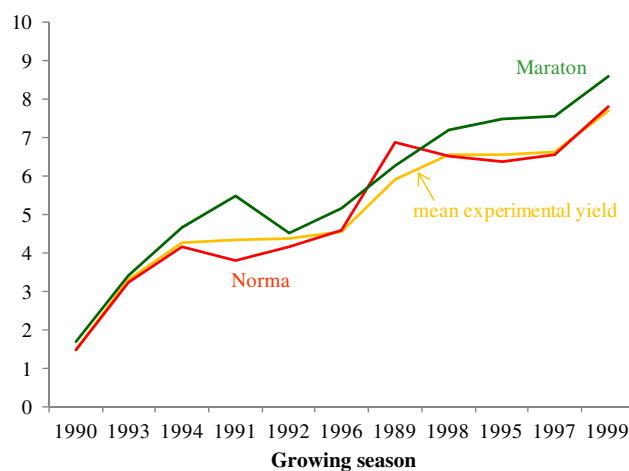**Grain yield (thousand kg/ha)**

Fig. 10 The grain yield of the mid-season hybrid Norma and the full-season hybrid Maraton compared with the mean of four-hybrid experimental yield across 11 seasons. Data over four populations and four N-treatments were from Berzsenyi and Tokatlidis (2012)

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are the beneficial implications of high PYP on OP level in the study of Norwood (2001), depicted in Fig. 8.

5.2 Development of population-neutral hybrids

The so-far spectacular gain in grain yield per unit area has been primarily due to improvement in tolerance to various stresses, including increased crowding, while responsiveness to enhanced inputs is another cause of higher yields of newer vs. older hybrids (Duvick 1997, 2005; Tollenaar and Lee 2002; Sangoi et al. 2002; Tokatlidis and Koutroubas 2004; Liu and Tollenaar 2009). On the other hand, grain yield stagnation at the individual plant level has been widely recognized (Duvick 1997, 2005; Sangoi et al. 2002; Tollenaar and Lee 2002; Tokatlidis and Koutroubas 2004; Hammer et al. 2009; Brekke et al. 2011). Indicatively of this discrepancy, Duvick (2005) stated that newer hybrids exhibit higher HI than older ones when plants are subjected to stresses, but in general, HI has not improved when modern hybrids are grown at their optimal populations or lower. Similarly, Tollenaar and Lee (2002, 2006) suggested a general lack of improvement in HI. On the contrary, Echarte and Andrade (2003) and Luque et al. (2006) reported on parallel improvement in HI and plant yield potential among Argentine hybrids.

Actually, when Duvick (1997) discovered that there was no increase in grain yield over time at very low populations, he focused on the necessity of improvement in tolerance to crowding stress combined with improvement in plant yield potential under low stress environments. Just a year later, Tokatlidis et al. (1998) published the results of a honeycomb breeding project in the absence of competition (0.74 plants/m^2), i.e., a Ph.D. project, indicating considerable improvement in plant yield potential. Forty $S_5 \times S_5$ hybrids drawn through single-plant selection within the F_2 of the PR3183 hybrid averaged 67 % and up to 115 % higher plant yield potential than the original hybrid, even though the whole process was conducted at a single location and genes of homeostasis might have been lost. Six of these recycled hybrids tested across two locations and seasons were found to be considerably less dependent compared with PR3183 (Tokatlidis 2001; Tokatlidis et al. 2001), allowing the researchers to suggest their procedure for development of population-neutral hybrids. With this work in mind, Duvick (2005) remarked: "The lack of increase in yield potential per plant is surprising until one reflects on the fact that up until now, the sole method of increasing yield per unit area has been to increase density while maintaining constant grain weight per plant. Although theoretically it may be possible to raise yield per unit area by yield per plant while holding population constant, for one reason or other this has not been done. Such a goal might be practical, however, for hybrids suited for drought-prone environments, where planting at lower density is prudent but the ability to utilize occasional higher rainfall by increasing yield per plant would be desirable."

Honeycomb breeding methodology was established by Prof. Fasoulas (Tsaftaris 2005). One of the first inviolable principles was selection in the absence of competition (Fig. 11), meaning that particular emphasis was placed on plant yield potential from the very beginning (e.g., Fasoulas 1973). Since then, further advancement in the methodology, and particularly the thorough explanation of the suspending role of competition in breeding (Fasoulas 1973, 1988, 1993; Fasoulas and Fasoula 1995; Fasoula and Fasoula 1997), has opened the possibility of even more progress through honeycomb breeding. To couple in parallel performance in the absence of competition and farming conditions, whole-genome phenotype is accomplished by partitioning the CYP into three components, which are plant yield potential, tolerance to stresses, and responsiveness to inputs (Fasoula and Fasoula 2000, 2002). Improved plant yield potential and tolerance to stresses extend the lower and the upper limits of optimum plant population, respectively, while genotypes carrying genes for responsiveness to inputs are capable of exploiting favorable growing conditions. Tolerance to stresses and responsiveness to inputs tie together plant yield potential and CYP and lead to the development of population-neutral cultivars (Fasoula and Fasoula 2000, 2002; Tokatlidis et al. 2001; Tokatlidis and Tsialtas 2008). For comparison purposes, in the absence of competition, the aforementioned CYP components were incorporated by Fasoula (2008) into two equations to evaluate individual plants

Fig. 11 The primary and inviolable principle of the honeycomb breeding is selection among widely spaced individual plants that allows them to grow in the absence of competition, thus placing particular emphasis on the determinant factor of density neutrality, i.e., the plant yield potential

and entries (i.e., progeny lines or cultivars), respectively. In a recent article, Fasoula and Tokatlidis (2012) analyzed the major principles of the method to develop cultivars which use resources effectively, tolerate biotic and abiotic adversities, and are capable of broad adaptation. Briefly, the equation A assesses the CYP of individual plants (PCYP), and the equation B the CYP of the entries (ECYP), enabling the breeder to apply single-plant selection based on equation A within lines singled out through equation B. Evaluation according to these equations is reliable only when individual plants and entries are assessed in the absence of the confounding effects of competition and soil heterogeneity, which is achieved with the utilization of the honeycomb selection designs that enable the application of ultra-high selection pressures. Each equation consists of two parameters; the first measures the plant yield potential in equation A and entry yield potential in equation B, while the second, which is common in both equations, measures the entry's stability of performance. More specifically, single-plant yield (x) is expressed as its ratio to the average yield of the surrounding plants within a ring of a chosen size ($\bar{x}_r$). The square of this ratio $(x/\bar{x}_r)^2$, called the coefficient of plant yield, devoid of the masking effect of soil heterogeneity, allows plants to be ranked objectively according to their true yield potential. Stability of the entry to which each plant belongs is measured by the coefficient of homeostasis $(\bar{x}/s)^2$, where $\bar{x}$ and s are the mean and the standard deviation, respectively. The product of the two coefficients, $\text{PCYP} = (x/\bar{x}_r)^2 \cdot (\bar{x}/s)^2$, represents the CYP at the plant level. Entry CYP, $\text{ECYP} = (\bar{x}/\bar{x}_t)^2 \cdot (\bar{x}/s)^2$, comprises the coefficient of entry yield, $(\bar{x}/\bar{x}_t)^2$, where $\bar{x}_t$ is the overall mean in the trial, and the coefficient of homeostasis, $(\bar{x}/s)^2$.

Reliability of the ECYP to assess the value of hybrids was investigated recently by Tokatlidis et al. (2011). They included one set of seven population-dependent hybrids, while the second set consisted of six experimental hybrids from those improved via honeycomb breeding for plant yield potential (Tokatlidis et al. 1998) and found to be partially population-neutral (Tokatlidis 2001; Tokatlidis et al. 2001). The first set was rain-fed tested across 2006 and 2007 seasons at a single location in Romania. The second set was evaluated with normal irrigation across 2006 and 2007, at a different location in Greece each season. The results justified the suitability of the population-neutral hybrids for drought-prone environments as opposed to the dependent ones, as well as the ability to anticipate hybrid performance at crop populations from evaluation in the absence of competition. The major results were: (1) large crossover type of genotype by season interaction for the population-dependent hybrids, (2) reduced hybrid–population interaction for the population-neutral set, and (3) significant correlations between ECYP and yield per unit area for both sets. Additional evidence of suitability of the second against the first set for diverse conditions is given in Fig. 12. For the first set, EYI was almost equal for the two seasons (though 2006 was drier), but the over-hybrid OP(D) was 69 % higher for 2007. Despite the 33 % higher EYI in 2007 for the hybrids bred for neutrality, they had the same OP(D) value across the two environments, which was almost half of the OP(D) for their check hybrid B73xMo17 (not shown).

To combat the challenge of climatic changes through population-neutral hybrids, the so-far neglected yield potential at the single-plant level merits special consideration in future maize breeding. Because the honeycomb breeding methodology essentially handles this attribute as the key constituent of advanced cultivars, it constitutes a unique breeding tool to meet the demand for population-neutral hybrids. The available relevant investigations are encouraging, while the recently proposed criteria promise greater success. Apart from a number of studies which are supportive of the method in maize and other crops (Fasoula and Tokatlidis 2012), regarding the recently suggested equations, Vlachostergios et al. (2011) found that PCYP was an effective selection tool for organic breeding in lentils while Papadopoulos and Tokatlidis (2011) qualified the ECYP as a stability criterion in dry beans and classified it according to the agronomic concept of stability, i.e., to designate cultivars performance in accordance with the available inputs.

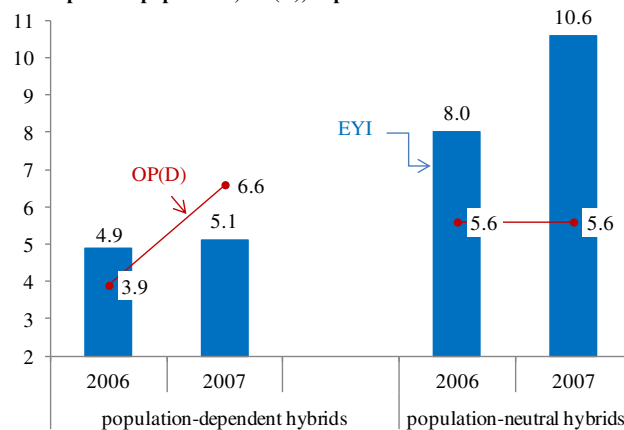**Environmental yield index, EYI, in thousand kg/ha & Optimum population, OP(D), in plants/m²**

Fig. 12 The environmental yield index (*EYI*) and optimum population (*OP(D)*) over seven density-dependent hybrids evaluated in Romania (across two seasons at the same location), as well as over six experimental hybrids improved partially for density neutrality evaluated in Greece (two seasons at different locations). Data were from Tokatlidis et al. (2011)

6 Synopsis

To meet the requirement for effective resource use and optimize grain productivity in maize, farmers have to be provided with suitable hybrids and information on optimum plant populations. For these requirements to be met, in particular due to continuously changing climate scenarios, the availability of plastic hybrids characterized by general adaptability in the matter of population is imperative. Feasibility of this target, however, is complicated by the hybrid–population interaction.

Future maize producers may have to make crop management decisions in a highly variable climate. Hybrid response to spatial and temporal heterogeneity differs among hybrids (Williams et al. 2008). Hence, in diverse environments, the hybrid–population interaction is commonly strong. The level of this interaction reflects the degree of hybrid reliance on population. The problem of hybrid dependence on population has long been acknowledged. Cox (1996) discovered that different hybrids respond differently to plant population. In addition, the plant population at which hybrids achieve maximum grain yield has increased throughout the hybrid era (Duvick 1997, 2005; Tollenaar and Lee 2002; Boomsma et al. 2009; Brekke et al. 2011). In a similar manner, Widdicombe and Thelen (2002) stated that continued improvement in hybrid ability to tolerate stress from high crowding requires periodical reassessment of OP. Popp et al. (2006) discovered that the profit-maximizing population is lower than the yield-maximizing population primarily because of the seed cost.

Population dependence, though, is a major barrier to reaching a site- and hybrid-specific decision on optimal population. Indicatively, researchers working under greatly variable conditions found it hard to recommend a population (Norwood 2001; Blumenthal et al. 2003; Shanahan et al. 2004; Berzsenyi and Tokatlidis 2012). Such a problem is detectable even in studies under less variable environments (Farnham 2001; Popp et al. 2006; Stanger and Lauer 2006; Tokatlidis et al. 2011). Boomsma et al. (2009) established the populations of 5.4 and 7.9 plants/m^2 deemed as suboptimal and optimal, respectively. Indeed, quadratics of their data at normal N fertilization showed that the second approached the OP. Nevertheless, under low-input conditions (i.e., without N-fertilizer) the first was closer to the OP.

Maize hybrid dependence on population adversely affects crop stability in grain yield due to a number of causes, e.g., occasional missing plants, deteriorated stand uniformity, inefficient resource use, increased lodging, asynchronous flowering, and increased barrenness (Tokatlidis and Koutroubas 2004). Furthermore, when farmers grow maize under variable climatic conditions, e.g., as dryland crop, enormous variability in OP may cause substantial grain yield and income penalty. Several relevant studies provide data supporting such an implication (Norwood 2001; Blumenthal et al. 2003; Shanahan

et al. 2004; Stanger and Lauer 2006; Boomsma et al. 2009; Tokatlidis et al. 2011; Berzsenyi and Tokatlidis 2012).

Important direct effects of the ongoing global weather changes on crop yields will be through changes in temperature, precipitation, length of growing season, and timing of extreme or critical threshold events relative to crop development (Southworth et al. 2000; Cutforth et al. 2007; Tingem et al. 2009; Hatfield et al. 2011). Because of these events crops might encounter more sharply fluctuating environmental situations in the future than currently occur. Vulnerability of agricultural systems to climate variance might reasonably be more severe in crops that interact strongly with population. As a consequence, maize instability due to severe population dependence would probably worsen and thus sustainability of the crop under such circumstances would be in danger.

Stagnation in plant yield potential alone accounts for severe maize hybrid dependence on high populations. Differences in grain yield per unit area throughout the hybrid era have been shown to be a function of plant population density rather than yield potential per se (Duvick 1997, 2005; Tollenaar and Lee 2002; Hammer et al. 2009; Brekke et al. 2011). For example, Van Roekel and Coulter (2011) quote the average population of maize in Minnesota as 3.07, 4.98, and 7.39 plants/m^2 in 1930, 1979, and 2010, respectively. Results from Thomison et al. (2011), however, indicate that high yield per area is not solely accomplishable at very high populations on the condition that the hybrid has improved plant yield potential (Fig. 9). Other studies (Norwood 2001; Sarlangue et al. 2007; Berzsenyi and Lap 2005; Tokatlidis et al. 2011; Berzsenyi and Tokatlidis 2012) verify that improved plant yield potential is a determinant of adaptation to low plant populations. Improved plant yield potential coupled with high CYP can exist, as suggested by Tokatlidis (2001), Luque et al. (2006), and Popp et al. (2006) and depicted by data of Stanger and Lauer (2006). Hence, hybrids which combine both these attributes and tolerate high populations are designated plastic hybrids, i.e., population-neutral hybrids that accomplish their CYP at a wide population range.

Planting at lower populations when the available resources cannot support a high plant population is an inevitable option (Norwood 2001; Kiniry et al. 2002; Blumenthal et al. 2003; Shanahan et al. 2004; Duvick 2005; Tokatlidis et al. 2011; Berzsenyi and Tokatlidis 2012). On the other hand, earliness in maturity is considered a drought-avoidance mechanism at the critical grain filling stage (Larson and Clegg 1999; Norwood 2001; Shanahan et al. 2004; Edwards et al. 2005). In the matter of maturity, however, relevant studies provide data showing that, in general, short-season hybrids may require very high populations to optimize resource use when high rainfalls occur (Norwood 2001; Shanahan et

al. 2004; Edwards et al. 2005; Popp et al. 2006; Sarlangue et al. 2007; Berzsenyi and Tokatlidis 2012), implying for producers considerable yield and income loss at favorable seasons. Consequently, hybrid maturity alone cannot address the major challenge of adapting maize crop to conditions of great variance. Seeking population-neutral hybrids is of utmost importance for their plasticity and ability to optimize resource use under various circumstances. Owing to their capacity to explore more resources at low populations, they could yield sufficiently when availability of resources would not support large plant numbers per unit area and, in parallel, they could take advantage when resources are in abundance. Actually, the asymptotic response to population described by Popp et al. (2006) on the premise that low populations are required to attain their CYP constitutes the ideal population-neutral hybrid, regardless of the environment targeted.

Data from Shanahan et al. (2004) as well as from Thomison et al. (2011) (Fig. 9) are indicative that seeking among elite hybrids, those which are less dependent on population is sound advice. Berzsenyi and Tokatlidis (2012) set the issue as a primary hypothesis and managed to discover a particular hybrid that was substantially the most suitable for extremely diverse seasons (Fig. 10). Apparently, improved plant yield potential is a determinant of population neutrality (i.e., Fig. 8). In turn, the estimation of this constituent element of CYP in hybrids allocated for cultivation is a major challenge for agronomists.

Obviously, breeding of population-neutral hybrids is a fundamental issue for future agriculture. Tokatlidis et al. (2001) opened the possibility of obtaining such hybrids through honeycomb breeding targeted directly at plant yield potential (Tokatlidis et al. 1998). Advanced selection criteria were suggested by Fasoula and Tokatlidis (2012) to create new cultivars with the potential to exploit effectively even marginal environments and meet the needs of sustainable agricultural systems. They speculated that since the method places particular emphasis on selection at ultra-low population to counteract the disturbing effects of plant-to-plant inference in equal share of inputs, it substantially improves plant yield potential, thereby expanding the lower limit of the OP. On the other hand, selection criteria consider the genotype ability to withstand stresses, and thus new cultivars are able to perform well at high populations. Other implications of population-neutral hybrids include advantages like reduced seed cost, limitation of re-sowings, greater persistence (less stalk lodging), and better anthesis and silking synchronization (Tokatlidis and Koutroubas 2004). The unique qualities of population-neutral hybrids guarantee their advantageous position to adapt well to climatic and other environmental changes and promote sustainable agricultural systems.

7 Conclusions

Global weather changes are expected to cause great environmental variability for agricultural systems. Therefore, for agriculture to be sustainable in the future, cultivars should be able to optimize yield in accordance with the occasionally available inputs, otherwise sustainability of agriculture is questioned. In maize, even though breeding has resulted in spectacular achievements for grain yield per area, modern hybrids fail to meet this presupposition, and the issue is of utmost importance. Stagnation of yield per plant makes them strongly interact with plant population density due to an inability to take advantage of resource abundance at lower populations and designates them population-dependent. On account of this dependence, optimum plant population varies greatly across environments, i.e., locations and/or seasons. According to the general conclusion emerging from the published data, the higher the yield potential of the environment, the higher the due plant population should be so as to reach the maximum grain yield, and vice versa. In dryland maize production, the application of relatively low populations is usually suggested in order to best adjust to the limitations of the driest seasons. In addition, short-season hybrids are preferred, because at the marginal seasons they require lower populations than the full-season ones to perform well and are also able to evade the severe drought stress during the critical grain-filling stage. Nevertheless, the reliability of this approach should be critically questioned in terms of whether a hybrid's maturity time alone is actually the crucial factor to determine which hybrid is the most suitable for dryland production. In fact, the short-season hybrids currently available require much higher populations during favorable seasons as opposed to the populations required at the driest seasons to achieve the highest production. As a result, these hybrids are unable to take advantage of occasional high rainfalls, merely because they happened to grow at low populations, seriously limiting the farmers' income in such cases. In order to overcome the problem, breeding ought to switch to population-neutral hybrids, i.e., hybrids that can accomplish their CYP at a wide spectrum of populations, and especially those of a low threshold level, i.e., with OPs starting at small numbers. Such hybrids could be cultivated at low populations so as to meet the requirements of the driest environments but at the same time be able to take advantage of occasional rainfalls. Consequently, hybrids that combine population neutrality with a relatively short time to reach maturity constitute the ideal solution for greatly varying environments. Therefore, two challenges arise, one for agronomists and the other for maize breeders. Firstly, among currently elite hybrids the less population-dependent have to be qualified. Secondly, the development of population-neutral hybrids is a serious challenge for maize breeding, serving

the needs of sustainable agriculture. Experimental data are now available indicating that this could indeed be a realistic goal. Population-neutral hybrids are of sufficient importance to justify breeding programs because their availability is an anticipatory response to the challenge of climate variation.

References

Assefa Y, Roozeboom KL, Staggenborg SA, Du J (2012) Dryland and irrigated corn yield with climate, management, and hybrid changes from 1939 through 2009. Agron J 104:473–482. doi:10.2134/agronj2011.0242

Berzsenyi Z, Lap DQ (2005) Responses of maize (Zea mays L.) hybrids to sowing date, N fertilizer and plant density in different years. Acta Agron Hungar 53(2):119–131. doi:10.1556/AAgr.53.2005.2.1

Berzsenyi Z, Tokatlidis IS (2012) Density-dependence rather maturity determines hybrid selection in dryland maize production. Agron J 104:331–336. doi:10.2134/agronj2011.0205

Blumenthal JM, Lyon DJ, Stroup WW (2003) Optimal plant population and nitrogen fertility for dryland corn in Western Nebraska. Agron J 95:878–883. doi:10.2134/agronj2003.8780

Boomsma CR, Santini JB, Tollenaar M, Vyn TJ (2009) Maize morphological responses to intense crowding at low nitrogen availability: an analysis and review. Agron J 101:1426–1452. doi:10.2134/agronj2009.0082

Brekke B, Edwards J, Knapp A (2011) Selection and adaptation to high plant density in the Iowa stiff stalk synthetic maize (Zea mays L.) population: II. Plant morphology. Crop Sci 51:2344–2351. doi:10.2135/cropsci2010.09.0562

Bullock DG, Bullock DS, Nafziger ED, Doerge TA, Paszkiewicz SR, Carter PR, Peterson TA (1998) Does variable rate seeding of corn pay? Agron J 90:830–836. doi:10.2134/agronj1998.00021962009000060019x

Cox WJ (1996) Whole-plant physiological and yield responses of maize to plant population. Agron J 88:489–496. doi:10.2134/agronj1996.00021962008800030022x

Cutforth HW, McGinn SM, McPhee KE, Miller PR (2007) Adaptation of pulse crops to the changing climate of the northern Great Plains. Agron J 99:1684–1699. doi:10.2134/agronj2006.0310s

Duncan WG (1958) The relation between corn populations and yield. Agron J 50:82–85. doi:10.2134/agronj1958.00021962005000020008x

Duvick DN (1997) What is yield? In: Edmeades GO et al (eds) Developing drought and low N-tolerant maize. CIMMYT, El Batan, Mexico, pp 332–335

Duvick DN (2005) The contribution of breeding to yield advances in maize (Zea mays L.). Adv Agron 86:83–145. doi:10.1016/S0065-2113(05)86002-X

Echarte L, Andrade FH (2003) Harvest index stability of Argentinean maize hybrids released between 1965 and 1993. Field Crops Res 82:1–12. doi:10.1016/S0378-4290(02)00232-0

Echarte L, Luque S, Andrade FH, Sandras VO, Cirilo A, Otegui ME, Vega CRC (2000) Response of maize kernel number to plant density in Argentinean hybrids released between 1965 and 1993. Field Crops Res 68:1–8. doi:10.1016/S0378-4290(00)00101-5

Edwards JT, Purcell LC, Vories ED (2005) Light interception and yield potential of short-season maize (Zea mays L.) hybrids in the Midsouth. Agron J 97:225–234. doi:10.2134/agronj2005.0225

Farnham DE (2001) Row spacing, plant density, and hybrid effects on corn grain yield and moisture. Agron J 93:1049–1053. doi:10.2134/agronj2001.9351049x

Fasoula VA (2008) Two novel whole-plant field phenotyping equations maximize selection efficiency. In: Prohens J, Badenes ML (eds) Modern cultivar breeding for present and future needs. Proc. 18th Eucarpia General Congress, Valencia, Spain, 9–12 September 2008, pp 361–365

Fasoula DA, Fasoula VA (1997) Competitive ability and plant breeding. Plant Breed Rev 14:89–138

Fasoula VA, Fasoula DA (2000) Honeycomb breeding: principles and applications. Plant Breed Rev 18:177–250

Fasoula VA, Fasoula DA (2002) Principles underlying genetic improvement for high and stable crop yield potential. Field Crop Res 75:191–209. doi:10.1016/S0378-4290(02)00026-6

Fasoula VA, Tokatlidis IS (2012) Development of crop cultivars by honeycomb breeding. Agron Sustain Dev 32:161–180. doi:10.1007/s13593-011-0034-0

Fasoulas AC (1973) A new approach to breeding superior yielding varieties. Pub. 3. Department of Genetics and Plant Breeding, Aristotle University of Thessaloniki, Thessaloniki, Greece

Fasoulas AC (1988) The honeycomb methodology of plant breeding. A.C. Fasoulas, P.O. Box 1555, GR 54006, Thessaloniki 17, Greece

Fasoulas AC (1993) Principles of crop breeding. A.C. Fasoulas, P.O. Box 1555, GR 54006, Thessaloniki 17, Greece

Fasoulas AC, Fasoula VA (1995) Honeycomb selection designs. Plant Breed Rev 13:87–139

Hammer GL, Dong Z, McLeand G, Doherty A, Messina C, Schussler J, Zinselmeier C, Paszkiewicz S, Cooper M (2009) Can changes in canopy and/or root system architecture explain historical maize yield trends in the U.S. Corn Belt? Crop Sci 49:299–312. doi:10.2135/cropsci2008.03.0152

Hashemi AM, Herbert SJ, Putnam DH (2005) Yield response of corn to crowding stress. Agron J 97:839–846. doi:10.2134/agronj2003.0241

Hatfield JL, Boote KJ, Kimball BA, Ziska LH, Izaurralde RC, Ort D, Thomson AM, Wolfe D (2011) Climate impacts on agriculture: implications for crop production. Agron J 103:351–370. doi:10.2134/agronj2010.0303

Jégo G, Pattey E, Bourgeois G, Drury CF, Tremblay N (2011) Evaluation of the STICS crop growth model with maize cultivar parameters calibrated for Eastern Canada. Agron Sustain Dev 31:557–570. doi:10.1007/s13593-011-0014-4

Kiniry JR, Xie Y, Gerik TJ (2002) Similarity of maize seed number responses for a diverse set of sites. Agronomie 22:265–272. doi:10.1051/agro:2002010

Larson EJ, Clegg MD (1999) Using corn maturity to maintain grain yield in the presence of late-season drought. J Prod Agric 12:400–405

Lavalle C, Micale F, Houston TD, Camia A, Hiederer R, Lazar C, Conte C, Amatulli G, Genovese G (2009) Climate change in Europe. 3. Impact on agriculture and forestry. A review. Agron Sustain Dev 29:433–446. doi:10.1051/agro/2008068

Lichtfouse E, Navarrete M, Debaeke P, Souchére V, Alberola C, Ménassieu J (2009) Agronomy for sustainable agriculture. A review. Agron Sustain Dev 29:1–6. doi:10.1051/agro/2008054

Liu W, Tollenaar M (2009) Response of yield heterosis to increasing plant density in maize. Crop Sci 49:1807–1816. doi:10.2135/cropsci2008.07.0422

Luque SF, Cirilo AG, Otegui ME (2006) Genetic gains in grain yield and related physiological attributes in Argentine maize hybrids. Field Crop Res 95:383–397. doi:10.1016/j.fcr.2005.04.007

Norwood CA (2001) Dryland corn in western Kansas: effects of hybrid maturity, planting date, and plant population. Agron J 93:540–547. doi:10.2134/agronj2001.933540x

Papadopoulos II, Tokatlidis IS (2011) A novel statistic estimated in the absence of competition to foresee genotype performance at the farming conditions parallels the agronomic concept of stability. Austr J Crop Sci 5:822–830

Popp M, Edwards J, Manning P, Purcell LC (2006) Plant population density and maturity effects on profitability of short-season maize production in midsouthern USA. Agron J 98:760–765. doi:10.2134/agronj2005.0201

Rusinamhodzi L, Corbeels M, van Wijk MT, Rufino MC, Nyamangara J, Giller KE (2011) A meta-analysis of long-term effects of conservation agriculture on maize grain yield under rain-fed conditions. Agron Sustain Dev 31:657–673. doi:10.1007/s13593-011-0040-2

Sangoi L, Gracietti MA, Rampazzo C, Bianchetti P (2002) Response of Brazilian maize hybrids from different eras to changes in plant population. Field Crops Res 79:39–51. doi:10.1016/S0378-4290(02)00124-7

Sarlangue T, Andrade FH, Calvino PA, Purcell LC (2007) Why do maize hybrids respond differently to variations in plant density? Agron J 99:984–991. doi:10.2134/agronj2006.0205

Shanahan JF, Doerge TA, Johnson JJ, Vigil MF (2004) Feasibility of site-specific management of corn hybrids and plant densities in the great plains. Prec Agric 5:207–225

Shapiro CA, Wortmann CS (2006) Corn response to nitrogen rate, row spacing, and plant density in Eastern Nebraska. Agron J 98:529–535. doi:10.2134/agronj2005.0137

Southworth J, Randolph JC, Habeck M, Doering OC, Pfeifer RA, Rao DG, Johnston JJ (2000) Consequences of future climate change and changing climate variability on maize yields in the midwestern United States. Agric Ecosyst Environ 82:139–158. doi:10.1016/S0167-8809(00)00223-1

Stanger TF, Lauer JG (2006) Optimum plant population of Bt and non-Bt corn in Wisconsin. Agron J 98:914–921. doi:10.2134/agronj2005.0144

Stuber CW, Hancock J (2008) Sustaining plant breeding-national workshop. Crop Sci 48:25–29. doi:10.2135/cropsci2007.07.0406spp

Thomison PR, Mullen RW, Lipps PE, Doerge T, Geyer AB (2011) Corn response to harvest date as affected by plant population and hybrid. Agron J 103:1765–1772. doi:10.2134/agronj2011.0147

Tingem M, Rivington M, Bellocchi G (2009) Adaptation assessments for crop production in response to climate change in Cameroon. Agron Sustain Dev 29:247–256. doi:10.1051/agro:2008053

Tokatlidis IS (2001) The effect of improved yield potential per plant on crop yield potential and optimum plant density in maize hybrids. J Agric Sci 137:299–305. doi:10.1017/S0021859601001496

Tokatlidis IS, Koutroubas SD (2004) A review study of the maize hybrids' dependence on high plant populations and its implications on crop yield stability. Field Crops Res 88:103–114. doi:10.1016/j.fcr.2003.11.013

Tokatlidis IS, Tsialtas IT (2008) Comparative analysis of two crop yield potential models based on yield potential per plant of maize and bread wheat genotypes. Asian J Plant Sci 7:241–250

Tokatlidis IS, Koutsika-Sotiriou M, Fasoulas AC, Tsaftaris AS (1998) Improving maize hybrids for potential yield per plant. Maydica 43:123–129

Tokatlidis IS, Koutsika-Sotiriou M, Fasoulas AC (2001) The development of density-independent hybrids in maize. Maydica 46:21–25

Tokatlidis IS, Koutsika-Sotiriou M, Tamoutsidis E (2005) Benefits from using maize density-independent hybrids. Maydica 50:9–17

Tokatlidis IS, Has V, Mylonas I, Has I, Evgenidis G, Melidis V, Copandean A, Ninou E (2010) Density effects on environmental variance and expected response to selection in maize (Zea mays L.). Euphytica 174:283–291. doi:10.1007/s10681-010-0160-9

Tokatlidis IS, Has V, Melidis V, Has I, Mylonas I, Evgenidis G, Compandean A, Ninou E, Fasoula V (2011) Maize hybrids less dependent on high plant densities improve resource use efficiency in rainfed and irrigated conditions. Field Crops Res 120:345–351. doi:10.1016/j.fcr.2010.11.006

Tollenaar M (1992) Is low plant density a stress in maize? Maydica 37:305–311

Tollenaar M, Lee EA (2002) Yield potential, yield stability and stress tolerance in maize. Field Crops Res 75:161–169. doi:10.1016/S0378-4290(02)00024-2

Tollenaar M, Lee EA (2006) Dissection of physiological processes underlying grain yield in maize by examining genetic improvement and heterosis. Maydica 51:399–408

Troyer AF, Wellin EJ (2009) Heterosis decreasing in hybrids: yield test inbreds. Crop Sci 49:1969–1976. doi:10.2135/cropsci2009.04.0170

Tsaftaris AS (2005) Apostolos fasoulas, a laudation. Maydica 50:3–8

Vadez V, Berger JD, Warkentin T, Asseng S, Ratnakumar P, Rao KPC, Gaur PM, Munier-Jolain N, Larmure A, Voisin A-S, Sharma HC, Pande S, Sharma M, Krishnamurthy L, Zaman MA (2012) Adaptation of grain legumes to climate change: a review. Agron Sustain Dev 32:31–44. doi:10.1007/s13593-011-0020-6

Van Roekel RJ, Coulter JA (2011) Agronomic responses of corn to planting date and plant density. Agron J 103:1414–1422. doi:10.2134/agronj2011.0071

Vega CRC, Sadras VO, Andrade FH, Uhart S (2000) Reproductive allometry in soybean, maize and sunflower. Ann Bot 85:461–468. doi:10.1006/anbo.1999.1084

Vlachostergios ND, Lithourgidis AS, Roupakias DG (2011) Effectiveness of single-plant selection at low density under organic environment: a field study with lentil. Crop Sci 51:41–51. doi:10.2135/cropsci2010.03.0137

Widdicombe WD, Thelen KD (2002) Row width and plant density effects on corn grain production in the Northern Corn Belt. Agron J 94:1020–1023

Williams CL, Liebman M, Edwards JW, James DE, Singer JW, Arritt R, Herzmann D (2008) Patterns of regional yield stability in association with regional environmental dharacteristics. Crop Sci 48:1545–1559. doi:10.2135/cropsci2006.12.0837

Yan W, Wallace DH (1995) Breeding for negatively associated traits. Plant Breed Rev 13:141–177