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Impact of recent breeding history on the competitiveness of Chinese maize hybrids

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A B S T R A C T

The competitiveness of crop cultivars has been observed to decrease along with breeding progress. Changes in the competitiveness of maize (*Zea mays* L.) as a consequence of breeding over past decades have not been reported. The main objectives of this study were to (1) test Donald's concept of communal ideotype in maize, and (2) determine the specific changes in competitiveness of maize hybrids due to breeding. Field experiments were conducted in the 2013 and 2014 growing seasons, using a de Wit replacement series design. Three maize hybrids, ZD2 (1972), YD13 (1992) and ZD909 (2011), which differed in release dates, were used in this study. Each hybrid was grown in multiple row replacement series (0:6, 1:5, 2:4, 3:3, 4:2, 5:1, and 6:0), with a total plant density of 67,500 seeds/ha. Inter-cultivar competition reduced dry matter accumulation (DMA) and grain yield per plant of the cultivars in the replacement series. In each replacement series, plant DMA, grain yield and harvest index (HI) of hybrids decreased with increasing proportion of the older hybrid. Population grain yield exhibited the same trend. Based on competitive outcome and aggressivity (AG), maize hybrids differed in their competitiveness. Breeding reduced the competitiveness of maize hybrids, which ranked ZD2 > YD13 > ZD909, but the varying characteristics of plant traits were not at all consistent with competitiveness. The competitiveness of maize hybrids decreased during the past few decades, supporting Donald's communal ideotype, which states that modern high yielding hybrids should not perform well in competition with other genotypes. Shorter plants with erectophile leaves and lower root:shoot ratios could contribute to weak competitiveness. Based on an analysis of aggressivity (AG), the AG of ZD2 relative to YD13 ($AG_{ZD2\rightarrow YD13}$) was 0.121, the AG of YD13 relative to ZD909 ($AG_{YD13\rightarrow ZD909}$) was 0.091, the AG of ZD2 relative to ZD909 ($AG_{ZD2\rightarrow ZD909}$) was 0.153, and $AG_{ZD2\rightarrow YD13} + AG_{YD13\rightarrow ZD909} \neq AG_{ZD2\rightarrow ZD909}$, indicating that the changes in competitiveness were not consistent with the breeding process. Our results show that the competitiveness of maize bybrids was reduced by breeding, but that variation in architectural plant traits among genotypes was not completely consistent with the changes in their competitiveness.

1. Introduction

Competition is a common phenomenon in plant communities. Competitiveness contributes to plant resource acquisition, survival, growth and reproduction (Alexandra and Peter, 2003; Aarssen and Keogh, 2002). In nature, strong competitors are naturally selected. However, in agriculture production, breeders select the best performing genotypes at the crop population level, but not at the individual plant level (Weiner et al., 2010). New maize (*Zea mays* L.) hybrids were selected for their tolerance to crowding (Tollenaar and Wu, 1999; Sangoi et al., 2002); hence, modern hybrids should be less intra-specifically competitive. Previous reports provide evidence that for a crop to be high yielding, the individual plants should be weak competitors (Lemerle et al., 2001; Vandeleur and Gill, 2004; Murphy et al., 2008). Moreover, Donald (1968, 1981) suggested that, to increase yield potential in annual seed crops, breeders will be forced to develop a "communal ideotype", which would not perform well in competition with other genotypes.

Competitiveness differs among crops (Li et al., 2001; Misra et al., 2006; Zhang et al., 2011). Cultivar differences in competitiveness have also been reported. Radicetti et al. (2012) found that chickpea (*Cicer arietinum* L.) genotypes differed in competitiveness. Mennan et al. (2012) demonstrated differences in competitiveness of rice (*Oryza sativa* L.) cultivars. However, research on the determinants of competitiveness among cultivars has mainly focused

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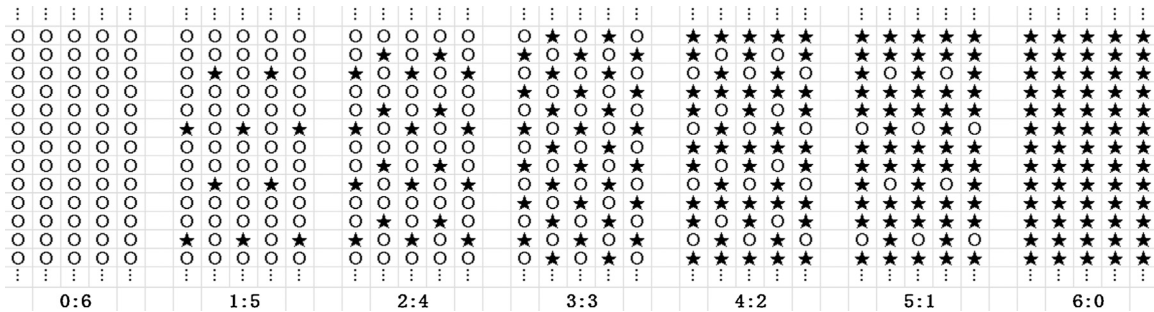

Fig. 1. Schematic diagram of the planting pattern used (white circles ○ and black five-pointed stars ⋆ represent the two cultivars of each combination).

on wheat (*Triticum aestivum* L.) (Reynolds et al., 1994; Vandeleur and Gill, 2004; Murphy et al., 2008; Song et al., 2009; Fang et al., 2011). Since the Green Revolution, wheat morphological traits, including root mass, plant stature and plant compactness, have changed and affected the competitiveness of cultivars. Reynolds et al. (1994) found that wheat cultivars with high yield potential are less competitive through improved adaption to the crop growth environment. Lemerle et al. (1996) reported that there is variability in competitiveness of Australian wheat genotypes.

Vandeleur and Gill (2004) tested 14 wheat cultivars to determine the impact of crop breeding on the ability to compete with weeds. These authors found a significant relationship between the year of cultivar release and crop yield loss, indicating inferior competitiveness of the modern wheat cultivars. A recent study of 63 spring wheat cultivars showed that the positive breeding effect on wheat yield over the past 150 years in the Pacific Northwest has led to slightly decreased weed suppression (Murphy et al., 2008). Similarly, other reports have shown that increased competitiveness might be associated with decreased wheat grain yield (Lemerle et al., 2001). All of these studies were based on crop/weed competition. In China, Zhang et al. (1999a,b) and Fang et al. (2011) used a de Wit replacement experiment to confirm that competitiveness of modern wheat cultivars is lower than that of older cultivars.

Maize grain yield has increased markedly in many countries during the past few decades. Genetic improvements have contributed to increased maize yield (Duvick and Cassman, 1999), which is mainly attributed to breeding for tolerance to crowding (Tollenaar and Wu, 1999). In the US, breeding has reduced total height of maize plants, the height of apical ear insertion, and the leaf insertion angle to stalks. Plant biomass has not been affected, while harvest index increased (Duvick, 2005). These plant traits reflect a trend toward reduced competitiveness of US maize hybrids (Begon, 1990; Evans, 1993).

Maize is one of the cereal species that is most sensitive to intra-specific competition (Maddonni and Otegui, 2006). In China, maize traits have changed substantially over the past decades. Such changes, which have been investigated extensively (Wang et al., 2011; Ma et al., 2014), have differed slightly from those in the US. The process of improving maize yield in China has led to an extended vegetative growth period, and to increased plant height, ear length, and plant biomass (Wang et al., 2011; Ma et al., 2014). These changes could contribute to enhanced competitiveness of modern hybrids. However, other traits, such as smaller leaf angles, smaller roots and higher harvest index (HI) have also been observed (Wang et al., 2011; Zhang et al., 2013; Ma et al., 2014). Changes in these plant attributes could contribute to reduced competitiveness (Donald, 1968; Zhang et al., 1999a,b).

Previous studies have reported that maize hybrids differ in competitiveness (Ford and Pleasant, 1994), but a standard competition experiment (i.e., replacement series and additive designs) has never been conducted. As modern maize hybrids are more compact and their tolerance to high densities has increased, we hypothesized that the competitiveness of maize hybrids recently released in China has decreased. Thus, growth of modern hybrids is likely to be significantly suppressed when grown in mixtures with older hybrids. To test this hypothesis, we imposed a de Wit replacement series design (de Wit, 1960). The main objectives of this study were to (1) test Donald's concept of communal ideotype in maize, (2) identify differences in competitiveness among maize hybrids and determine trends in variability of maize competitiveness, and (3) analyze the relationships among plant traits and competitiveness.

2. Material and methods

2.1. Experimental site and weather conditions

Field experiments were conducted during the 2013 and 2014 growing seasons at the Gongzhuling Experimental Station of the Chinese Academy of Agricultural Science (43°11′–44°9′N, 124°02′–125°18′E), which is located in a humid, continental monsoon climate in Gongzhuling county of the Jilin province. Spring maize is grown from late April to late September, under rainfed conditions and with ridge planting. The mean annual air temperature at the experimental station is 5.6 °C, the average annual precipitation is 594.8 mm (rainfall and snowfall), the average annual frost-free period is 144 days, and the average dates of last and first frosts are 27 April and 22 September. The primary soil of the area is Chernozem, with 2.63% organic matter, 0.15% total *N*, 124.90 mg kg^{-1} available *N*, 28.52 mg kg^{-1} available *P* and 184.47 mg kg^{-1} available *K* in the upper 0–30 cm of the soil profile.

The mean daily solar radiation for each month, total rainfall, and mean monthly temperatures during the two experimental years, are shown in Table 1. In 2014, low mean temperature was observed in May, which contributed to delayed emergence. In addition, total rainfall during the 2014 growing season was significantly lower than in 2013, particularly during August.

2.2. Plant materials

Three maize hybrids released in China during different eras were used in this study. Zhongdan 2 (ZD2) was an older maize hybrid, widely grown in northern China in the 1970s. Yedan13 (YD13) was widely grown in China in the 1990s. Zhongdan909 (ZD909), a modern maize hybrid released in 2011, is widely grown in China. These three maize hybrids were the most popular cultivars in their respective eras. The three maize hybrids differ in their morphological traits and are easily distinguished when grown in a mixture (Table 2).

2.3. Experimental design

Competitive ability was investigated using the de Wit replacement series design (de Wit, 1960). This design includes pure and mixed populations, in which the combined density of the components is held constant, and the proportion of each component

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