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Changes in the morphological traits of maize genotypes in China between the 1950s and 2000s

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ABSTRACT

Maize (*Zea mays* L.) morphological traits influence light attenuation within the canopy, and, ultimately, yield. The objectives of this 3-year field study were to: (i) examine the morphological characteristics of specific genotypes using varieties of maize that were widely used in Chinese agriculture from the 1950s to the 2000s; (ii) assess the canopies and yields of maize populations in relation to changes in their morphological characteristics. There were significant decrease on the ear ratio, center of gravity height and leaf angle with improved genotypes regardless of plant density. However, the ear leaves and adjacent leaves appeared to be longer in improved maize varieties. The mean leaf orientation value (LOV) and individual LOVs increased considerably during the time series of the genotypes, but more obvious changes in LOV occurred in the uppermost leaves. The average leaf area (LA) per plant and LA on the ears increased significantly from the 1950s to the 2000s. At the optimum density, current hybrid's canopy architecture was more compact, having short plant height and more upright leaf. The SDLA above or under ear significantly increased with improving genotypes, mainly due to new hybrids allowing the use of more individuals per area and thus increasing leaf area index (LAI). At the highest plant density, new hybrids had the rates of light transmittance (0.04–0.05), low attenuation coefficient (K = 0.47) and gained the highest yield. Leaf angle and LOV were highly correlated with TPAR/IPAR on ear, K, grain yield. Consequently, yield improvement in maize was probably a result of increased plant density tolerance through dependence on changes in leaf orientation characteristics.

1. Introduction

Maize grain yield in China has increased considerably, from 961 kg ha^{-1} in 1950 to 5166 kg ha^{-1} in 2007, during which time the yield has grown at an average annual rate of 85.8 kg ha^{-1} (Li and Wang, 2008). A similar trend has been reported for American maize production (Duvick, 2005). Improving hybrids and management practices have been vital to maize yield gains (Charles, 1999; Long et al., 2006; Li and Wang, 2010). On average, about 50% of the increase was due to breeding and 50% was due to management (Duvick, 2005).

Chinese maize hybrids have undergone five stages, from the use of landraces, between-variety hybrids, top-cross hybrids, and double-cross hybrids to single-cross hybrids, and plant populations have increased more than three times from the 1950s to the 2000s (Li and Wang, 2010). During the past 50 years, plant density in the corn belt of the central US increased at an average rate of about 1000 plants ha^{-1} year^{-1} by improving hybrids. Bavec and Bavec (2002) concluded that the information on suitable plant density for each maize cultivar is one of the key factors for planning maize production. As was suggested by several examinations of time series of maize hybrids and densities, open pollinated cultivars (OPCs) and old hybrids yielded more at lower densities, which were typical of the cultivation practices during their years of release, whereas newer hybrids produced their highest yields at higher planting densities, which are typical of recent years (Russell, 1991; Dong et al., 2006; Li and Wang, 2010). Duvick (1984) concluded that yield differences between old and new hybrids are mainly rooted in plant density tolerance. The enhanced plant density tolerance of modern

Abbreviations: LOV, leaf orientation value; LA, leaf area; SDLA, the spatial density of leaf area; PAR, photosynthetically active radiation; IPAR, intercepted photosynthetically active radiation; TPAR, transmitted photosynthetically active radiation; K, attenuation coefficient for Beer's Law.

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hybrids may be strongly dependent on changes in the architecture of the roots and stem, which have significantly improved plant lodging resistance (Hammer et al., 2009; Li and Wang, 2010).

Higher planting densities have been important for achieving genetic maize gains in the US (Duvick et al., 2004) and Canada (Tollenaar, 1989; Tollenaar and Lee, 2002; Liu and Tollenaar, 2009). However, at supraoptimal plant densities, further crowding can lead to worse canopy architecture (leaves above the ear intercepting almost all of radiation and a poor light in the middle and lower parts of the canopy) particularly during the period bracketing silking, which might make grain yield decline (Tollenaar and Wu, 1999; Maddonni et al., 2001; Christopher et al., 2009; Li and Wang, 2010). Estimating the effect of canopy architecture on light attenuation in maize crops has been simplified by means of exponential functions, which examine the light captured by a crop in relation to the leaf area index (LAI) (Jones and Kiniry, 1986). However, Maddonni (1996) reported that hybrids differed in total leaf number, individual leaf area, and leaf angle, creating different canopy structures and incoming photosynthetically active radiation (IPAR) levels. During the anthesis stage, hybrids with more horizontal leaves achieve greater light capture than hybrids with more erect leaves at the lower than optimum plant population (48,000, 58,500, 69,000 plants ha^{-1}), according to Xue et al. (1995).

Changes in maize morphological traits occurred as genotypes were improved during the last 50 years. Duvick et al. (2004) reported that American maize plant height was essentially unchanged, but ear height showed a weak trend. In comparison, maize plant and ear height increased in Chinese hybrids (Dong et al., 2006; Wang et al., 2011). The number of leaves per plant increased and the LAI tended to be higher for recent hybrids than for older ones over time (Dwyer et al., 1991; Tollenaar, 1991; Dong et al., 2006). However, some studies found no changes in the number of leaves or leaf area per plant (Crosbie, 1982; Russell, 1991; Duvick, 1997). Leaves became more upright with time in a study of US and Chinese hybrids, especially leaves above ears (Meghji et al., 1984; Crosbie, 1982; Russell, 1991; Duvick et al., 2004). Selection for more upright leaves was unintentional in the United States (Duvick et al., 2004), whereas intentional selection for more upright leaves occurred in China because erect leaf angle was hypothesized to increase tolerance to high planting densities (Wang et al., 1995; Tong, 2001). The development of Huangzao4 in 1974 and Ye478 in 1980s in China was the greatest proof. So the suite of changes in morphological traits in china might be expected to differ compared to the morphological changes in other countries.

Improved morphology was the key to improving light-use efficiency per plant (Yu et al., 1998; Li and Li, 2004), which affected canopy architecture, light attenuation, and, ultimately, yield (Maddonni et al., 2001; Stewart et al., 2003; Tollenaar and Lee, 2006; Li and Wang, 2010). Few studies have intensively examined the reasons for maize yield increases with the use of improved genotypes from the viewpoint of plant morphology. Thus, the primary objectives of this work were to: (i) report the changes in morphological traits within a time series of maize; (ii) analyze light interception within fully developed canopies and yield to determine if newer hybrids are more tolerant of higher plant densities than older genotypes; and (iii) test the hypotheses that the relationship of grain yield with those morphological attributes is linear well.

2. Materials and methods

2.1. Experimental design

The data used in this study were generated from field studies that were performed at the CAAS Northeast Research Station (Gongzhuling, Jilin Province, China; 43°30′ N, 124°50′ E, black soil) between 2009 and 2011. The study area was located in northeast China, pH 6.2, organic matter content 2.63%, total nitrogen content 0.15%, available nitrogen content 124.90 mg kg^{-1}, available phosphorus content 28.52 mg kg^{-1}, and available potassium content 184.47 mg kg^{-1} in the 0–30 cm soil layer. The area was a classic rainfed spring maize area. The area's rainfall during the maize growing period was respectively 301.4 mm in 2009, 673.5 mm in 2010, and 361.7 mm in 2011.

Individual hybrids were selected because they were known to be well-adapted to the agro-ecological conditions of the study area and seeds of proprietary parental lines were available, which allowed the creation of new F1 hybrid seeds.

In short, our study included eight maize hybrids and two OPCs that had been ever accumulatively used more than 2.8 million ha in popularly cultivated period in China (Li, 2007; Mi et al., 2011). All of the cultivars are considered to be successful, widely grown hybrids, representative of the elite germplasm of the period in this present paper (Table 1). They were tested at a range of plant population densities (37,500, 52,500, 67,500, and 82,500 plant ha^{-1}). The lowest density was typical in the 1950s, the 52,500 plant ha^{-1} density was typical of the 1960s or 1970s, the density of 67,500 plant ha^{-1} was the optimum in the 1980s, and the highest density was typical for maize grown in the 1990s and 2000s. N, P_2O_5, and K_2O were applied as fertilizer at 150, 42.5, and 42.5 kg ha^{-1}, respectively, before sowing. The experimental design of the studies was a split-plot design with densities as main plots and hybrids as subplots. Individual plots measured about $24 m^2$, and comprised six rows, 6 m in length and 0.65 m between rows, and were arranged in a randomized design with three replications each. Weeds and pests were chemically controlled.

2.2. Morphological trait measurements

At V3, five successive plants in the center row of each plot were tagged by applying red paint to their leaves. Tags were placed on leaves 5, 8, 12, and 15 to enable the identification of individual leaves and quantification of the total leaf number. Leaf angle (between the stem and a line from the leaf base point to the zenith of the leaf), leaf length, and h (the distance from the leaf base point to the zenith of the leaf) were recorded when a leaf was considered fully expanded. The following morphological traits were recorded for each of the five plants per plot at maturity: plant height (cm from the ground to the top of the tassel), ear height (cm from the ground to the highest node bearing an ear), and center of gravity height (cm from the ground to the balance point of the over-ground plant). All traits were measured according to the standards described by Subedi and Ma (2005). Indices were calculated using the following equations:

$$\text{Ear ratio} = \left(\frac{\text{ear height}}{\text{plant height}}\right) * 100\% \tag{1}$$

$$\text{Gravity ratio} = \left(\frac{\text{center of gravity height}}{\text{plant height}}\right) * 100\% \tag{2}$$

Leaf orientation value (Pepper et al., 1977)

$$(\text{LOV}) = \sum_{i=1}^{n}[(90 - a) * h/l] \tag{3}$$

(where a is the leaf angle, h is the distance from the leaf base point to the zenith of the leaf, l is the leaf length, and n is the number of leaves)

$$\text{The spatial density of leaf area (SDLA)} = \frac{LAI}{\text{plant height}} \tag{4}$$