Density response of maize canopy architecture in adapted and unadapted synthetic populations

by

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ABSTRACT

Since the 1950’s, the average maize grain yield, on a per unit area basis, has risen exponentially and without a pause. Associated with this increase have been changes in shoot morphology which permit more light penetration into the canopy. Changes in plant traits including plant height, leaf number, individual leaf area, vertical leaf angle, tassel size and weight, and leaf area density distribution along the main stem have been reported in the literature; however, the response of canopy components to changes in plant density has not been examined in closed populations and at today’s densities. The objective of this study was to: (i) analyze canopy traits (leaf angle / leaf area) to determine how canopy architecture has changed; (ii) determine if canopy architecture interacted with density either directly or indirectly. Materials from unselected base populations, Iowa Stiff Stalk Synthetic (BSSS) and Iowa Corn Borer Synthetic no.1, were compared to the most advanced cycles of selection at four locations near Ames, Carroll, Crawfordsville, and Keystone, IA, in 2011.

Populations were compared at six densities ranging from 3.0 to 9.5 plants m⁻¹. Each breeding population by density combination was replicated once at each location and arranged in a split plot design. Increased densities resulted in reduced numbers of total nodes, lower ear height, shorter plant stature, smaller tassels, more upright leaf angles with smaller leaf areas at the top sector of the canopy and more horizontal leaf angles with larger leaf areas lower in the canopy. More importantly, the shape of the canopy was affected by plant height, ear height, node of attachment of the ear, and density.
CHAPTER I. INTRODUCTION

The era of hybrid maize (*Zea mays* L.) production is characterized by significant increases in grain yield (Duvick, 2005a, 2005b; Brekke, 2011). During the years 1930 to 1960, yield gains averaged 63 kg ha\(^{-1}\) yr\(^{-1}\) (Troyer, 2000; Duvick, 2005b). By the year 2000, the gains in yield averaged 110 kg ha\(^{-1}\) yr\(^{-1}\) (Troyer, 2000; Duvick, 2005b). In the U.S. Corn Belt, the average maize grain yield, on a per unit area basis, has increased from approximately 1.5 Mg ha\(^{-1}\), in the late 1930’s, to roughly 10.0 Mg ha\(^{-1}\), in 2004 (Duvick, 2005a, 2005b; Brekke, 2011).

Factors associated with the upward grain yield trends, in maize, include improved cultural practices, utilization of advanced plant breeding techniques, and the interdependencies between applied cultural practices and advancements in plant breeding techniques (Duvick, 2005a, 2005b). Duvick (2005a) estimates that improvements attributable to changes in applied cultural practices account for 40-50% of on-farm yield gains; while, the remaining 50-60% is associated with genotypic improvements resulting from advancements in plant breeding techniques.

Advancements in crop management practices, such as utilizing modern and more efficient harvesting equipment, application of chemical treatments for weed control, improved pest control through spatial planning and chemical application, and planting in a more timely fashion are some factors which have attributed to improved grain yields, in maize, over the years (Cardwell, 1982; Edmeades and Tollenaar, 1990; Osteen, 2000). Another factor, which has played a crucial role in driving the upward grain yield trend, is application of synthetic fertilizers (Duvick, 2005a, 2005b). During the time period from
1961 to 1992, nitrogen application has increased from 20 kg ha\(^{-1}\) to roughly 105 kg ha\(^{-1}\) (ERS, 1994; Daberkow, 2000; Duvick, 2005b).

However, perhaps the most determinant cultural practice, from the 1930’s to present, is increasing the density at which hybrid maize is planted. Over the past 50 years, the density at which maize was planted, in the U.S. Corn Belt, has increased at an average rate of 1000 plants ha\(^{-1}\) yr\(^{-1}\) (Duvick, 2005a). During the 1930’s, the average plant density was about 30,000 plants ha\(^{-1}\); by the 1960’s, the average plant density reached approximately 40,000 plants ha\(^{-1}\); in the 1980’s, the average plant density increased to 60,000 plants ha\(^{-1}\); currently, the average plant density is speculated to be in excess of 80,000 plants ha\(^{-1}\) (USDA, 1949-1992; Duvick 1977, 1984, 1992; Paszkiewicz and Butzen, 2001; Duvick \textit{et al.}, 2004, Duvick, 2005b).

In previous publications, Duvick (2005a, 2005b) explains that the observed increases in maize grain yields, since the early 1930’s, are associated with the increased adaptation, of newer hybrids, to higher planting densities, as opposed to increased production of grain on a per plant basis. Based on data published by Brekke (2011), the USDA NASS (2009, 2010) reported that in the State of Iowa, between the years 1965 to 2008, the average maize grain yield increased from 5.1 Mg ha\(^{-1}\) to 10.7 Mg ha\(^{-1}\) corresponding with increasing plant density from 37,000 plants ha\(^{-1}\) to 72,400 plants ha\(^{-1}\). At a per unit area basis, the increase in plant density has resulted in a 110% increase in maize grain yield since the 1930’s; however, on a per plant basis, an improvement, in maize grain yield, of only 7% is observed (Brekke, 2011).
Since the 1930’s, the average maize grain yield, on a per unit area basis, has increased significantly due to the adaptability of maize plants to higher planting densities (Duvick, 2005a, 2005b). Associated with this increase have been changes in shoot morphology which permit more light penetration into the canopy (Brekke, 2011; Edwards, 2011). In the literature, it has been noted that maize hybrids differ in plant height, leaf number, individual leaf area, vertical leaf angle, tassel size and weight, and leaf area density distribution along the main stem (Edmeades and Lafitte, 1993; Stewart and Dwyer, 1993; Maddonni and Otegui, 1996; Maddonni et al., 2001). However, the response of canopy components to changes in plant density has not been examined in closed populations and at today’s densities.

The objective of this study was to: (i) determine if direct selection for grain yield and agronomic performance in the Iowa Stiff Stalk Synthetic and Iowa Corn Borer Synthetic no. 1 has indirectly improved adaptation to high planting densities; (ii) analyze canopy traits (leaf angle / leaf area) to determine how canopy architecture has changed; (iii) determine if canopy architecture interacted with density either directly or indirectly. The long-term objective, for this research, was to develop a model for predicting leaf angle and leaf area at upper, middle, and lower sectors of the canopy with the hope of improving breeding strategies and cultural practices to increase grain yield.

References


CHAPTER II. REVIEW OF LITERATURE

The average maize grain yield, in the U.S. Corn Belt, began to increase following the introduction of hybrids, developed by conducting crosses between inbred lines, in the early 1930’s (Duvick 2005a, 2005b). In the U.S. Corn Belt, the first hybrids were actually introduced in the 1920’s (Duvick 2005a, 2005b). These early generation hybrids were double cross hybrids developed from inbred lines which were derived by self-pollinating higher quality open pollinated cultivars (OPC’s) (Baker, 1990; Duvick, 2005b). However, it was the introduction of single cross hybrids, in the 1950’s, that marked the increase in yield trends observed today (Bruce et al., 2002).

Contributions of Early Generation Lines to Hybrid Development

During the early 1930’s, George Frederick Sprague introduced the Iowa Stiff Stalk Synthetic population (BSSS) (Sprague, 1946). By the 1980’s, it was estimated that 19% of total maize acres planted, in the United States, were derived from BSSS inbred lines including B14, B37, B73, and B84 (Zuber and Darrah, 1980; Darrah and Zuber, 1986). The Iowa Stiff Stalk Synthetic population formation was conducted by intermating 16 inbred lines, consisting primarily of a Reid Yellow Dent background, exhibiting a higher than average stalk quality (Sprague, 1946; Lamkey, 1992). As a result of these intermatings, a half-sib recurrent selection program and a reciprocal recurrent selection program were generated (Holthaus and Lamkey, 1995); the selection criterion, for both programs, emphasized increases in yield (Lamkey et al., 1991; Lamkey, 1992; Holthaus and Lamkey, 1995) with some partial consideration for
decreased harvest grain moisture and improved resistance to root and stalk lodging (Lamkey et al., 1991; Lamkey, 1992; Holthaus and Lamkey, 1995).

The half-sib recurrent selection program consisted of seven cycles of half-sib selection and utilized the IA13 pedigree as a tester; the resulting population was then renamed BSSS(HT)C7 (Holthaus and Lamkey, 1995). From this population, the 29 best performing S1 lines were identified and selected to form the breeding population BS13(S)C0 (Lamkey, 1992). This population underwent five cycles of half-sib selection, with the pedigree B97 as tester, resulting in the formation of the population BS13(HI)C5 (Edwards, 2010).

The reciprocal recurrent selection program utilized the unselected base breeding populations BSSS and the Iowa Corn Borer Synthetic no. 1 (BSCB1) (Lamkey, 1992). BSCB1 was introduced in the 1940’s (Hallauer et al., 1974). It was synthesized from 12 inbred lines selected for improved resistance to whorl-leaf feeding by the European Corn Borer (Hallauer et al., 1974). The BSCB1 population was selected alongside the BSSS population for reciprocal recurrent phenotypic selection in order to simultaneously advance both populations and maintain their genetic variability (Holthaus and Lamkey, 1995). Comparable to the BSSS population, the BSCB1 population has remained a closed population with no migration.

The Iowa Stiff Stalk Synthetic population and the Iowa Corn Borer Synthetic no. 1 population are exemplary populations to study; unlike hybrids, the BSSS and BSCB1 populations have remained closed populations with no migration (Lamkey et al., 1991).
As a result, these populations provide a good model for the selection process which occurred in commercial maize hybrids.

**Genetic Gains in Grain Yield Associated With Upwards Yield Trends**

Genetic improvements, resulting in the increased adaptation of newer hybrids to higher plant densities, are associated with 50-60% of yield gains, on a per unit area basis (USDA, 1949-1992; Duvick 1977, 1984a, 1992; Paszkiewicz and Butzen, 2001; Duvick et al., 2004b; Duvick, 2005b). Based on published data, Russell (1991) reported positive and linear genetic grain yield gains, with estimates ranging from 33 Kg ha\(^{-1}\) yr\(^{-1}\) to 90 Kg ha\(^{-1}\) yr\(^{-1}\), for chronologically released maize hybrids from the years 1971 to 1991. Similarly, Duvick (1997) observed a positive and linear genetic grain yield gain of 74 Kg ha\(^{-1}\) yr\(^{-1}\) in a study involving sequentially released maize hybrids from the years 1930 to 1991 in the state of Iowa.

The works of (Edmeades and Tollenaar, 1990; Russell, 1991; Tollenaar et al., 1994) reveal that improvements in genetic grain yield gains, over the past 70 years, may have been accompanied by changes in other traits; Some of these traits are a result of direct selection, while others are the result of indirect selection (Duvick, 2005a, 2005b).

**Changes Accompanying Genetic Gain Yields in Hybrids**

Newer hybrids, by comparison to early hybrids from the 1930’s, exhibit a series of morphological and physiological variations congruent with selection for increased grain yield at higher planting densities. Such variations include changes in plant and ear
height, improved resistance to root and stalk lodging, a reduction in tassel size and branch number, and an increased tendency for more upright leaves. Researchers associate these characteristics with the increased adaptability of newer hybrids to high planting densities which consequently drives increases in per unit area yield.

**Plant and Ear Traits**

Since the 1930’s, researchers have reported changes in both plant height and in ear height. Based on data published by Meghji *et al.* (1984), a reduction in both plant and ear height was observed in sequentially released hybrid corn varieties. In a study containing sequentially released hybrids representative of the time period 1940 to 1980, Russell (1985) reported differences in plant and ear height as well. However, some research revealed a major reduction in ear height but a negligible change in plant height (Duvick, 2005a, 2005b); and, in some cases, research revealed no changes in plant or in ear height (Duvick, 1996).

The relationship between plant height and plant density can be examined in terms of neighboring effects. At high densities, plants are able to distinguish neighboring plants by detecting a low red:far-red ratio (Ballare *et al.*, 1990). As a result, a stem elongation response is activated which leads to taller plants (Ballare *et al.*, 1990). In a study conducted by Carena and Cross (2003), relating the effect of plant density on plant height, it was observed that increasing the plant density from 38,000 to 56,000 plants ha$^{-1}$ resulted in an increase in plant height; however, increasing the plant density greater than 56,000 plants ha$^{-1}$ had no effect on plant height. Similarly, the works of Tetiokagho
and Gardner (1988) showed a correlation between increased density and increased plant height; however, a decrease in plant height was observed when plant densities exceeded 100,000 plants ha\(^{-1}\).

Beginning in the 1970’s, next generation hybrids began developing a tendency to produce more upright leaf angles in the sector of the maize plant located above the developing ear (Crosbie, 1982; Meghji et al., 1984; Duvick, 1997; Duvick et al., 2004a, 2004b). Based on data published by Hesketh and Musgrave (1962), it was observed that the most efficient use of light energy occurred at light intensities of less than 100%. Specifically, maize leaves require roughly 50% of available sunlight intensity, in comparison to leaves exposed to the maximum sunlight intensity of 100%, to achieve a photosynthetic rate of 80% (Mock and Pearce, 1975). Thus, at higher densities, the vertical orientation of upper leaves, within a canopy, enables more light penetration to lower leaves (Williams et al., 1968) which increases the overall canopy photosynthetic rate.

In a hybrid study, conducted by Meghji et al. (1984), an increase in total number of leaves, from 12.2 to 13.8, was reported; the study contained a sample of 26 single-cross hybrids representative of hybrids available in the years 1930, 1950, and 1970. Seka and Cross (1995) reported an increase of 0.35 leaves per plant as density increased from 24,000 plants ha\(^{-1}\) to 72,000 plants ha\(^{-1}\). Based on data collected from modeling experiments, Hammer et al. (2009) observed an overall reduction in leaf size above the 10\(^{th}\) leaf at high plant densities; they hypothesize that at higher densities limited assimilate availability results in reduction in leaf size.
In a comparison study of single-cross hybrids, a reduction in tassel weight and tassel branch number was observed when comparing hybrids from the 1930’s to hybrids from the 1970’s (Meghji et al., 1984). In the study, Meghji et al. (1984) shows that over the past 75 years, a reduction of 0.5 gram/decade has occurred in terms of tassel weight as well as a reduction of 2.5 tassel branches/decade. Based on published data, Duvick (1997) reports a similar trend in reduction of tassel branch number and weight; the study was conducted in the state of Iowa and compared sequentially released hybrids from the year 1930 to 1991. Similar results were observed by Sangoi et al. (2002) when studying era hybrids grown in Brazil.

Other morphological and physiological changes which have been reported, when comparing first generation hybrids to next generation hybrids, include increased leaf rolling (Edmeades et al., 2003; Barker et al., 2005), delayed senescence (Crosbie, 1982; Meghji et al., 1984; Russell, 1991; Tollenaar, 1991; Duvick et al., 2004; Valentinuz et al., 2004; Barker et al., 2005; Duvick, 2005a, 2005b), and a reduction in the anthesis-silking interval when newer hybrids are grown under stressful environments (Crosbie, 1982; Meghji et al., 1984; Edmeades et al., 2003; Duvick et al., 2004; Barker et al., 2005). In a time-series based study, containing four hybrids representative of the time periods 1959 to 1989, an increase in leaf area index (LAI) was noted for recent hybrids (Dwyer et al., 1991; Tollenaar, 1991).

In a hybrid comparison study, Crosbie (1982) reports an increase, on a per plant basis, of both total as well as harvestable ears in newer hybrids; the study contains a sample of 20 sequentially released single-cross hybrids representative of hybrids
available from 1930 to 1970. The works of Crosbie (1982), Meghji et al. (1984), Cavalieri et al. (1985), and Russell (1985), based on four discrete time-series of hybrids, reveal a longer grain filling period is present in newer hybrids in contrast to older hybrids.

**Resistance to Root and Stalk Lodging**

In comparison to hybrids from the 1930’s, modern hybrids exhibit improved resistance to root lodging as well as stalk lodging (Duvick, 2005a, 2005b). In relation to resistance to root lodging, Duvick (1996) observed a linear increasing trend. However, various researchers have observed conflicting results; depending on the severity of root lodging tendencies, both improvement as well as lack of improvement was reported (Duvick, 2005a, 2005b).

In relation to resistance to stalk lodging, Duvick (2005a, 2005b) reported an increased resistance to stalk lodging. The increased resistance was most prevalent in high plant density situations and when newer hybrids where compared to hybrids present in the 1930’s. In comparison studies of hybrids of different era’s, improvement to stalk lodging was non-significant; however, it is speculated that stalk lodging presented a tendency towards increased resistance (Duvick, 2005a, 2005b).

A correlation between high planting densities and resistance to stalk lodging has been documented in a number of publications. The works of Widdicombe and Thelen (2002) and Carena and Cross (2003) have shown that as density increased from 56,000 plants ha$^{-1}$ to 90,000 plants ha$^{-1}$ an improvement of 0.6% was recorded; Although this is
a relatively small increase in resistance to stalk lodging, a larger improvement of 6.5% was recorded when density was increased from 38,000 plants ha\(^{-1}\) to 62,000 plants ha\(^{-1}\).

Based on data published by Duvick (2005b), Russell (1974, 1984), Duvick (1977, 1984b, 1992, 1997, and Duvick et al. (2004a) reported that both root and stalk lodging expressed a tendency for improvement expected to level off at approximately 95 to 100%.

Adaptability to Abiotic Stress

Modern hybrids, when compared to hybrids from the 1930’s, exhibit a higher adaptability to abiotic stress. In a study comparing sequentially released hybrids, Duvick (1997) reported that modern hybrids exhibited a linear increase in maize grain yields when grown in a hot and dry low yielding summer; the study was conducted in the State of Iowa and contains a sample of 26 sequentially released hybrids and one open-pollinated cultivar representative of hybrids available in the time period 1930-1991. In the same hybrid study, Duvick (1997) recorded a linear increase in maize grain yield when modern hybrids were grown in a very cool and wet season as well. Russell (1974) reported that newer hybrids, by comparison to older hybrids, yielded more in high stress drought environments; these results are based on a time-series study, conducted in the state of Iowa, and containing a sample of hybrids representative of the time period 1930 to 1970.
**Tolerance to High Planting Densities**

Since the 1950’s, the average maize grain yield, on a per unit area basis, has risen exponentially and without a pause (Duvick, 2005a, 2005b). Associated with this trend has been the increased adaptability and tolerance, of maize genotypes, to higher planting densities (Cardwell, 1982; Russell, 1991; Duvick 2005a, 2005b). Cardwell (1982) estimated that 21% of the observed maize grain yield gain, in newer hybrids, is associated with increased planting densities; this data is derived from a study which was conducted in the state of Minnesota and compared a sample of sequentially released hybrids representative of the time period 1930-1970. In a study comparing sequentially released hybrids, Hammer et al. (2009) reported that hybrids representative of the 1960’s achieved maximum grain yield at approximately 30,000 plants ha\(^{-1}\); while, hybrids representative of the year 2000 achieved maximum grain yield at or in excess of 80,000 plants ha\(^{-1}\). Furthermore, a study conducted by Tollenaar (1989) reveals that at a density of 40,000 plants ha\(^{-1}\), modern hybrids yielded 25% more than the oldest hybrid; however, at a density of 130,000 plants ha\(^{-1}\), modern hybrids yielded 190% more than the oldest hybrid. Currently, it has been reported that densities as high as 90,000 plants ha\(^{-1}\) were still below the potential maximum yield densities (Widdicombe and Thelen, 2002; Brekke, 2011).
Adaptation to High Planting Densities

Maize grain yield, on a per unit area basis, has increased exponentially and significantly since the early 1930’s; however, grain yield, on a per plant basis, has experienced an almost negligible increase (Duvick, 2005b; Brekke, 2011). Previous research, conducted on hybrids from the central Iowa region, revealed that yield potential, on a per plant basis, has remained stagnant over the years (Duvick, 2005a, 2005b). In fact, when the hybrids, from the central Iowa region, were grown at a very low density of 10,000 plants ha\(^{-1}\), a relatively stress free environment, yield, on a per plant basis, remained almost unchanged (Duvick, 1997; Duvick et al. 2004a, 2004b; Duvick, 2005a, 2005b). Thus, the exponential and continuous gains in maize grain yield, observed over the years, can be attributed to the adaptability of maize to higher planting densities, rather than an increased production of grain on a per plant basis (Duvick 2005a, 2005b).

The Effect of Canopy Architecture on Maize Grain Yield

Since the 1930’s, the average maize grain yield, on a per unit area basis, has increased significantly due to the adaptability of maize plants to higher planting densities (Duvick 2005a, 2005b). Associated with this increase have been changes in shoot morphology which permit more light penetration in to the canopy (Brekke, 2011; Edwards, 2011). The magnitude of photosynthetically active radiation (PAR), available on a per plant basis, is highly correlated to the frequency and spread of leaves within a plant; the greater the abundance and distribution of leaves, within a plant, the greater the
degree of intercepted PAR which, in turn, affects both the canopy photosynthesis as well as yield (Stewart et al., 2003). At higher densities, where shading effects are significant, increased light penetration into the canopy becomes an important factor; the photosynthetic capacity, of a canopy, is directly related to the total amount of leaf area exposed to sunlight; thus, the greater the amount of light penetration into a canopy, the greater the photosynthetic capacity (Pearce et al., 1967; Mock and Pearce, 1975; Brekke, 2011; Edwards, 2011).

The works of Hesketh and Musgrave (1962) and Mock and Pearce (1975) reveal that near maximum photosynthetic rates are attainable even when leaves are exposed to less than 100% of maximum available sunlight. Mock and Pearce (1975) explain that leaf exposure to a light intensity of 50% is sufficient enough to produce a photosynthetic rate of 80% by comparison to leaves exposed to the maximum available sunlight intensity. This infers that, at higher densities, horizontally oriented leaves, with a larger surface area, and a higher position in the canopy, intercept more sunlight than is needed to achieve sufficient photosynthetic rates while restricting light penetration to the lower portion of the canopy (Hesketh and Musgrave, 1962; Donald, 1968; Mock and Pearce, 1975; Brekke, 2011). Thus, at higher densities, possessing leaves with an upright angle and a smaller surface area, higher up in the canopy, allows for more efficient light interception and penetration which consequently results in higher photosynthetic rates specifically at leaves located in the lower portion of the canopy (Duncan et al., 1967; Donald, 1968; Williams et al., 1968; Duncan, 1971; Mock and Pearce, 1975; Brekke, 2011). In a simulation study conducted by Hammer et al. (2009), it was observed that
the presence of vertically oriented maize leaves, within the upper portion of the canopy, resulted in a reduction of the canopy light extinction coefficient, increased light penetration to the lower portion of the canopy, and more uniform photosynthetic rates within the canopy.

At higher densities, shading of underlying leaves by large maize tassels can decrease light penetration, within the canopy, resulting in reduced photosynthetic rates of lower leaves (Duncan et al., 1967). A study conducted by Duncan et al. (1967) revealed that at lower densities, tassel shading effects are negligible; however, at higher densities, the tassel shading effects become significant. At a planting density of 98,000 plants ha\(^{-1}\), Duncan et al. (1967) reported a 19.4% reduction in photosynthetic rates associated with tassel shading effects on underlying leaves. Furthermore, Duncan et al. (1967) displayed, through measuring differences in shadow sizes associated with tassels of varying dimensions, that larger tassels intercept more light than smaller tassels. This suggests that a decrease in tassel branch size and weight can be advantageous in terms of light attenuation within the canopy (Duncan et al., 1967; Brekke, 2011).

The significance of light attenuation, within a canopy, can also be expressed in terms of the photosynthetic rates of leaves closer to the developing ear shoots (Wardlaw, 1990; Hammer et al., 2009; Brekke, 2011). The availability of vertically oriented and smaller statured leaves, within the top portion of the canopy, enables more light penetration to the leaves closer to the developing ear shoots; which, in turn, increases the photosynthetic rates of these leaves (Wardlaw, 1990; Hammer et al., 2009; Brekke, 2011). Hammer et al. (2009), proposes that the increase in photosynthetic rates, of
leaves closer to the developing ear shoots, contributes a flux of carbohydrates to the
developing ear which results in a reduction in observed barrenness and an increase in
kernel count per ear. Thus, at higher densities, it is highly probable that there is a
correlation between the upright nature of upper maize leaves and increased assimilate
partitioning to the developing ear; consequently, resulting in reduced barreness and
increased grain set (Borras et al., 2004; Hammer et al., 2009).

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CHAPTER III. MATERIALS AND METHODS

Thirty-five populations and three inbreds were included in this study:

**BSSS.** Introduced in the 1930’s, the unselected base population BSSS was established by intercrossing 16 lines, consisting of primarily Reid Yellow Dent background, exhibiting above average stalk quality (Sprague, 1946; Lamkey, 1992).

**BSSS(R)C17.** This breeding population is the 17th cycle of the reciprocal recurrent phenotypic selection program utilizing BSSS and BSCB1 as base populations (Holthaus and Lamkey, 1995).

**BSCB1.** Developed in the 1940’s, the unselected base population BSCB1 was synthesized from 12 inbred lines selected for improved resistance to whorl-leaf feeding by the European Corn Borer (Hallauer et al., 1974).

**BSCB1(R)C17.** This breeding population is the 17th cycle of the reciprocal recurrent phenotypic selection program utilizing BSCB1 and BSSS as base populations (Holthaus and Lamkey, 1995).

**BS13(HI)C5.** The 5th cycle of half-sib selection of the population BS13(S)C0 using B97 as a tester (Edwards, 2010).

**B97.** BSCB1-derived inbred selected from the 9th cycle of reciprocal recurrent selection with BSSS (Hallauer et al., 1994).

**B73.** BSSS-derived inbred selected from the 5th cycle of recurrent selection (Russell, 1972).

**Mo17.** Inbred derived from 44 selected S1 plants from hybrid C103 x 187-2 (Hallauer, 2001).
The remaining pedigrees represented F1 crosses between populations, or F1 crosses between populations and inbred lines (Table 1). Each population was planted at six densities ranging from 3.0 to 9.5 plants m\(^{-1}\).

**Experimental Design**

The experiment was grown at four locations near Ames, Carroll, Crawfordsville, and Keystone, IA, in 2011 (Table 1). Each breeding population by density combination was replicated once at each location. Within each environment, the experiment was designed as a split plot design with planting densities as the whole plot factor and breeding population as the subplot factor. The experimental unit consisted of four rows spaced 0.76 meter apart and 6.10 meters in length for traits measured on plot basis;

**Measurements.** Prior to flowering, the number of intact or undamaged plants, within each plot, were recorded and converted into plants ha\(^{-1}\). Harvesting was conducted through the use of a New Holland TR-88 combine (Almaco Company, Nevada, IA). Prior to plot harvesting, the combine was calibrated for automatic acquisition of grain moisture, grain weight, and test weight. Within each plot, the number of plants discernably root and stalk lodged were totaled and converted into percentages of final stand. Plants were deemed root lodged if the base of the stalk was not perpendicular to the ground; plants were deemed stalk lodged if a break, in the stalk, was detected below the node of attachment of the uppermost ear.

Root and stalk lodging data was collected at Carroll, Crawfordsville, and Keystone. Due to a data collection error, involving incorrect rows, the Keystone...
location was excluded from the data analysis. As a result, root and stalk lodging data analysis included only the Carroll and Crawfordsville locations. Yield data was collected at all locations excluding Ames. All other traits including grain moisture and test weight were analyzed for all locations.

Beginning at anthesis, plots were visually inspected, on a daily basis, for plants shedding pollen and plants with visible silks. Dates of 50% pollen-shed and 50% silking were determined as the first day when at least 50% of the plants in the plot were shedding pollen and at least 50% of the plants in the plot had visible silks. Anthesis-silking interval (ASI) was calculated as date of 50% pollen-shed minus the date of 50% silking.

Plots were planted at the six densities, mentioned above, with no thinning. Immediately following pollination, measurements were collected on the center two rows, of the four row plots, for plant height, tassel branch number, leaf area, and leaf angle; 10 plant measurements, at a per plot basis, were generated by collecting data from 5 plants row$^{-1}$ beginning with the 5th plant from the outside of the plot.

Directly following pollination, data on tassel branch number was collected, at a location near Ames, by destructively removing the tassel and counting the number of branches deviating directly from the main branch. Branches stemming from other side branches were not counted (Bolanos and Edmeades, 1996). Data on plant height was collected after pollination as well; plant height was defined as the height of the flag leaf collar ((Maddonni et al., 2001, Bolanos and Edmeades, 1996).
Throughout the growing season, the number of leaves, on a per plant basis, was recorded in order to determine total number of leaves. Based on methods used in previous publications (Maddonni and Otegui, 1996; Maddonni et al., 2001; Elmore et al., 2005; Sangoi et al., 2002), leaves 5 and 11 on plants 6-10 were marked with a waterproof permanent marker during the year 2011. Marks were placed closed to the center of the leaf as to avoid accidental chipping. From these sets of marked leaves, the first 5 intact plants, in each of the two center rows, were used for data collection resulting in a maximum of 10 plants plot\(^{-1}\) observed.

At approximately v-stage 7, the 5\(^{th}\) leaf, on each plant, was determined by counting 5 leaves up from the very first true leaf. By v-stage 14, the 11\(^{th}\) leaf is marked. The purpose of marking the 11\(^{th}\) leaf is to provide a reference point for calculating total number of leaves; by the time the 11\(^{th}\) leaf has emerged, usually leaves 1-8 have already fallen; however, leaf marking proved unreliable as we were unable to locate the markings during data collection. So, the total number of leaves was determined as the total number of above ground nodes based on the assumption that the number of below ground nodes was fairly constant plus or minus one node.

Leaf angle was measured with a protractor. Vertical 0 degrees was established by placing the protractor against the stalk and measurements were then recorded as degrees from the vertical. The flag leaf was denoted as leaf 0 and is considered the top of the plant. Subsequently, this process was repeated for the third leaf from the top, the sixth leaf from the top, the ninth leaf from the top, and twelfth leaf from the top.
Leaf area measurements were collected through destructive sampling. Following pollination, the flag leaf as well as leaves three, six, nine, and twelve were removed from the maize plants; for this data set, the flag leaf is donated leaf 0 and is considered the top of the plant; thus, leaf 3 is the third leaf down from the flag leaf; the same rules apply to leaves six, nine, and twelve. Upon removal, an identifier is paper clipped to the leaf; the identifier contains a barcode containing information with regards to range, row, pass, plant, and leaf number. The tagged leaves were then set in a box and transported to the lab where they were fed through a LI-COR leaf area indexer.

**Data Analysis**

The following model was fit to plot data:

\[ Y_{ijkm} = \mu + \dot{e}_i + r(\dot{e})_j + \rho_k + \dot{\delta}(\dot{e})_{ijk} + \dot{p}_m + (\rho \dot{p})_{km} + (\dot{e} \rho)_{ik} + (\dot{e} \dot{p})_{ikm} + \epsilon_{ijkm} \]

Where:

- \( \mu \) = population mean,
- \( \dot{e}_i \) = effect of environment \( i \),
- \( r(\dot{e})_j \) = effect of replicate block \( j \) within environment \( i \),
- \( \rho_k \) = effect of planting density \( k \),
- \( \dot{\delta}(\dot{e})_{ijk} \) = Split plot error A for planting density \( k \), block \( j \), environment \( i \),
- \( \dot{p}_m \) = effect of breeding population \( m \),
- \( (\rho \dot{p})_{km} \) = interaction of planting density effect \( k \) with breeding population \( m \),
- \( (\dot{e} \rho)_{ik} \) = interaction of environment \( i \) with planting density \( k \),
- \( (\dot{e} \dot{p})_{ikm} \) = interaction of environment \( i \) with breeding population \( m \),
\((\hat{e}p)_{ik}\) = interaction of environment \(i\) with planting density effect \(k\),

\((\hat{e}p\theta)_{ikm}\) = three way interaction between environment \(i\), planting density effect \(k\), breeding population \(m\),

\(\varepsilon_{ijkm}\) = residual error.

All terms containing interactions with the environment were considered random effects. All other terms were treated as fixed effects. The model was derived using Henderson’s mixed model equations (Henderson, 1984). Variance components were estimated using restricted maximum likelihood (REML) (Searle et al., 1992). All mathematical computations were conducted using the Mixed procedure through the Statistical Analysis Software (SAS) (SAS Institute, Cary, NC).

Outlier detection was applied by computing the probability of attaining a larger absolute value, for each residual, using the t-distribution. A Bonferroni adjustment was applied to individual p-values associated with residuals and quantile-quantile (QQ) probability plots were generated for studentized residuals. Based on the results from the Bonferroni adjustments and the generated QQ plots, outliers were detected and discarded. Following outlier removal, the following covariate model was fit to the final data set:

\[
Y_{ijkm} = \mu + \hat{e}_i + r(\hat{e})_{ij} + \delta(\hat{e})_{ijk} + \theta_m + \beta_1x_{ijkm} + (\beta_2)_m x_{ijkm} + \beta_2x^2_{ijkm} + (\theta\beta_1)_m x_{ijkm} + (\theta\beta_2)_m x^2_{ijkm} + \varepsilon_{ijkm}
\]
Where:

\( \mu \) = population mean,

\( \dot{e}_i \) = effect of environment \( i \),

\( t(\dot{e})_j \) = effect of replicate block \( j \) within environment \( i \),

\( \delta(\dot{e})_{ijk} \) = Split plot error A for planting density \( k \), block \( j \), environment \( i \),

\( \beta_m \) = intercept of breeding population \( m \),

\( x_{ijkm} \) = observed plant density in subplot for environment \( i \), block \( j \), density \( k \), and with breeding population \( m \),

\( \beta_1 \) = average linear effect of plant density,

\( (\beta \beta_1)_m \) = interaction of breeding population \( m \) with average linear effect of plant density,

\( \beta_2 \) = average quadratic effect of observed plant density,

\( (\beta \beta_2)_m \) = interaction of breeding population \( m \) with average quadratic effect of plant density,

\( (\dot{e} \beta)_im \) = interaction of environment \( i \) with breeding population \( m \).

\( (\dot{e} \beta_1)_i \) = interaction of environment \( i \) with average linear effect of plant density,

\( (\dot{e} \beta_2)_im \) = three way interaction between environment \( i \), breeding population \( m \), linear plant density effect,

\( (\dot{e} \beta_2)_i \) = interaction of environment \( i \) with quadratic density,

\( (\dot{e} \beta \beta_2)_im \) = three way interaction among environment \( i \), breeding population \( m \), quadratic density,

\( \varepsilon_{ijkm} \) = residual error.
All environmental interactions were considered random effects. All other terms were considered fixed effects. Similar to the previous model, this model was fit using a Henderson’s mixed linear model equations and all variance components were attained through the use of REML (Henderson, 1984; Searle et al., 1992). All mathematical computations were conducted using the Mixed procedure provided in SAS (SAS Institute, Cary, NC). In order to identify the random effects to be retained in the model, Akaike’s information criteria (AIC) was employed. Random effects with zero variance estimates were discarded from the linear model. All combinations of the remaining random effects were fit. The final model with the lowest AIC value was used for subsequent analyses.

Non-significant plant density covariates and interactions between plant density and breeding population were systematically dropped from the model beginning with the highest order terms. If a random interaction containing a plant density covariate was found to be significant, the corresponding plant density fixed effect was retained automatically. If no random interactions containing plant density were identified, the highest order terms were examined by conducting a series of F-tests; All F-tests were conducted using type III sums of squares and a Satterthwaite (Satterth) approximation for the denominator degrees of freedom. If the highest order term in the model was non-significant, it was dropped and the next highest order term was tested and dropped if non-significant.

If the interactions between plant density and the breeding populations was significant, breeding population-specific covariates were estimated for each breeding
population. Non-significant covariate terms for individual breeding populations were dropped.

The procedure used to describe the analysis on a plot-basis is identical to the plant-basis analysis. However, a minor difference exists in the linear model. Since all the traits measured on a per plant basis were collected at a single location, the environmental effect was dropped.

The following model was fit to plant data:

\[ Y_{ijklm} = \mu + Q_i + \alpha(r)_{jk} + r_k + \rho_l + \delta(tp)_{kl} + p_m + (\rho p)_{lm} + \Phi_{klm} + \varepsilon_{ijklm} \]

Where:

\( \mu \) = population mean,

\( Q_i \) = effect of plot \( i \),

\( \alpha(r)_{jk} \) = effect of range \( j \) within block \( k \),

\( r_k \) = effect of replicate block \( k \),

\( \rho_l \) = effect of planting density \( l \),

\( \delta(tp)_{kl} \) = Split plot error A for block \( k \), planting density \( l \),

\( p_m \) = effect of breeding population \( m \),

\( (\rho p)_{lm} \) = interaction of planting density effect \( l \) with breeding population \( m \),

\( \Phi_{klm} \) = plot-level error for block \( k \), planting density \( l \), breeding population \( m \).

\( \varepsilon_{ijklm} \) = within-plot residual error.
Plots and range, nested within a block, were considered random effects. All other terms were treated as fixed effects. The model was derived using Henderson’s mixed model equations (Henderson, 1984). Variance components were estimated using restricted maximum likelihood (REML) (Searle et al., 1992). All mathematical computations were conducted using the Mixed procedure through the Statistical Analysis Software (SAS) (SAS Institute, Cary, NC).

Outlier detection was applied by computing the probability of attaining a larger absolute value, for each residual, using the t-distribution. A Bonferroni adjustment was applied to individual p-values associated with residuals and quantile-quantile (QQ) probability plots were generated for studentized residuals. Based on the results from the Bonferroni adjustments and the generated QQ plots, outliers were detected and discarded. Following the elimination of outliers, plant data was fit to the following covariate model:

\[ Y_{ijklm} = \mu + Q_i + \sigma(t)_{jk} + r_k + \rho_l + \delta(r\rho)_{kl} + \beta_1x_{klm} + (p\beta_2)_{m}x_{klm} + \beta_2x^2_{klm} + (p\beta_2)_{m}x^2_{klm} + \Phi_{klm} + \epsilon_{ijklm} \]

Where:
\( \mu = \) population mean,
\( Q_i = \) effect of plot \( i, \)
\( \sigma(t)_{jk} = \) effect of range \( j \) within block \( k, \)
\( r_k = \) effect of replicate block \( k, \)
\( \rho_l = \) effect of planting density \( l, \)
\( \delta(rp)_{kl} = \) Split plot error A for block \( k \), planting density \( l \),

\( \beta_m = \) intercept of breeding population \( m \),

\( x_{klm} = \) observed plant density in subplot for block \( k \), density \( l \), and breeding population \( m \),

\( \beta_1 = \) average linear effect of plant density,

\( (\beta \beta_1)_m = \) interaction of breeding population \( m \) with average linear effect of plant density,

\( \beta_2 = \) average quadratic effect of observed plant density,

\( (\beta \beta_2)_m = \) interaction of breeding population \( m \) with average quadratic effect of plant density,

\( \Phi_{klm} = \) plot-level error B for block \( k \), planting density \( l \), breeding population \( m \).

\( \epsilon_{ijklm} = \) within-plot residual error.

Plots and range, nested within a block, were considered random effects. Similar to the previous model, this model was fit using a Henderson’s mixed linear model equations and all variance components were attained through the use of REML (Henderson, 1984; Searle et al., 1992). All mathematical computations were conducted using the Mixed procedure provided in SAS (SAS Institute, Cary, NC). In order to identify the random effects to be retained in the model, Akaike’s information criteria (AIC) was employed. Random effects with zero variance estimates were discarded from the linear model. All combinations of the remaining random effects were fit. The final model with the lowest AIC value was used for subsequent analyses.

Non-significant plant density covariates and interactions between plant density and breeding population were systematically dropped from the model beginning with the
highest order terms. If a random interaction containing a plant density covariate was found to be significant, the corresponding plant density fixed effect was retained automatically. If no random interactions containing plant density were identified, the highest order terms were examined by conducting a series of F-tests; All F-tests were conducted using type III sums of squares and a Satterthwaite (Satterth) approximation for the denominator degrees of freedom. If the highest order term in the model was non-significant, it was dropped and the next highest order term was tested and dropped if non-significant.

If the interactions between plant density and breeding populations were significant, breeding population-specific covariates were estimated for each breeding population. Non-significant covariate terms for individual breeding populations were dropped.

Do to computational limitations, analysis of leaf traits was restricted to four populations: BSSS, BSSS(R)C17, BSCB1, and BSCB1(R)C17.

The following covariate model was fit for leaf angle and area:

\[ Y_{ij} = \mu + Q_i + y_j + 9X_1 + (9\eta)X_1X_2 + (9\theta)X_1X_3 + (9\epsilon)X_1X_4 + \rho X_5 + (9\rho)X_1X_5 + \epsilon_{ij} \]

Where:

\( \mu \) = population mean,
\( Q_i \) = effect of plot \( i \),
\( y_j \) = effect of plant \( j \),
\( X_1 \) = observed leaf position,
\( X_2 \) = observed ear node,
$X_3$ = observed ear height,
$X_4$ = observed plant height,
$X_5$ = observed plant density,
$\vartheta$ = average linear effect of leaf position,
$\eta$ = average linear effect of ear node,
$\Theta$ = average linear effect of ear height,
$\varphi$ = average linear effect of plant height,
$\rho$ = average linear effect of plant density,
$(\vartheta \eta)X_1X_2$ = effect of the product between observed leaf position $X_1$ and observed ear node $X_2$,
$(\vartheta \Theta)X_1X_3$ = effect of the product between observed leaf position $X_1$ and observed ear height $X_3$,
$(\vartheta \varphi)X_1X_4$ = effect of the product between observed leaf position $X_1$ and observed plant height $X_4$,
$(\vartheta \rho)X_1X_5$ = effect of the product between observed leaf position $X_1$ and observed plant density $X_5$,
$\epsilon_{ij}$ = within-plot residual error.

Plots and plant within a plot were considered random effects. All other terms were treated as fixed effects. The model was derived using Henderson’s mixed model equations (Henderson, 1984). Variance components were estimated using restricted maximum likelihood (REML) (Searle et al., 1992). All mathematical computations
were conducted using the Mixed procedure through the Statistical Analysis Software (SAS) (SAS Institute, Cary, NC).

Outlier detection was applied by computing the probability of attaining a larger absolute value, for each residual, using the t-distribution. A Bonferroni adjustment was applied to individual p-values associated with residuals and quantile-quantile (QQ) probability plots were generated for studentized residuals. Based on the results from the Bonferroni adjustments and the generated QQ plots, outliers were detected and discarded. Following the elimination of outliers, the plant-based data was fit to the following covariate model:

\[ Y_{ij} = \mu + Q_i + y_j + \theta_1 X_1 + \theta_2 X_1^2 + (\theta_1 \eta) X_1 X_2 + (\theta_1 \tau) X_1 X_3 + (\theta_2 \eta) X_1^2 X_2 + (\theta_2 \tau) X_1^2 X_3 + (\theta_2 \theta) X_1 X_4 + \rho_1 X_5 + \rho_2 X_5^2 + (\theta_1 \rho_1) X_1 X_5 + (\theta_1 \rho_2) X_1 X_5^2 + \epsilon_{ij} \]

Where:

\( \mu \) = population mean,

\( Q_i \) = effect of plot \( i \),

\( y_j \) = effect of plant \( j \),

\( X_1 \) = observed leaf position,

\( X_1^2 \) = observed quadratic leaf position,

\( X_2 \) = observed ear node,

\( X_3 \) = observed ear height,

\( X_4 \) = observed plant height,

\( X_5 \) = observed plant density,

\( X_5^2 \) = observed quadratic leaf position,
$\vartheta_1$ = average linear effect of leaf position,

$\vartheta_2$ = average quadratic effect of leaf position,

$\eta$ = average linear effect of ear node,

$\Upsilon$ = average linear effect of ear height,

$\Upsilon$ = average linear effect of plant height,

$\rho_1$ = average linear effect of plant density,

$\rho_2$ = average quadratic effect of plant density,

$(\vartheta_1 \eta)X_1X_2$ = effect of the product between observed leaf position $X_1$ and observed ear node $X_2$,

$(\vartheta_1 \Upsilon)X_1X_3$ = effect of the product between observed leaf position $X_1$ and observed ear height $X_3$,

$(\vartheta_1 \Upsilon)X_1X_4$ = effect of the product between observed leaf position $X_1$ and observed plant height $X_4$,

$(\vartheta_1 \rho_1)X_1X_5$ = effect of the product between observed leaf position $X_1$ and observed plant density $X_5$,

$(\vartheta_2 \eta)X_1^2X_2$ = effect of the product between observed quadratic leaf position $X_1^2$ and observed ear node $X_2$,

$(\vartheta_2 \Upsilon)X_1^2X_3$ = effect of the product between observed quadratic leaf position $X_1^2$ and observed ear height $X_3$,

$(\vartheta_2 \Upsilon)X_1^2X_4$ = effect of the product between observed quadratic leaf position $X_1^2$ and observed plant height $X_4$,

$(\vartheta_1 \rho_1)X_1X_5$ = effect of the product between observed linear leaf position $X_1$ and observed
linear plant density \( X_3 \),

\[(\beta_1 \rho_2)X_1X_5^2 = \text{effect of the product between observed linear leaf position } X_1 \text{ and observed quadratic plant density } X_5^2,\]

\( \varepsilon_{ij} \) = within-plot residual error.

Plots and plants within a plot were considered random effects. Similar to the previous model, this model was fit using a Henderson’s mixed linear model equations and all variance components were attained through the use of REML (Henderson, 1984; Searle et al., 1992). All mathematical computations were conducted using the Mixed procedure provided in SAS (SAS Institute, Cary, NC). In order to identify the random effects to be retained in the model, Akaike’s information criteria (AIC) was employed. Random effects with zero variance estimates were discarded from the linear model. All combinations of the remaining random effects were fit. The final model with the lowest AIC value was used for subsequent analyses.

Non-significant leaf position covariates were systematically dropped from the model beginning with the highest order terms. If the highest order term in the model was non-significant, it was dropped and the next highest order term was tested and dropped if non-significant. All F-tests were conducted using type III sums of squares and a Satterthwaite (Satterth) approximation for the denominator degrees of freedom.

References


CHAPTER IV. RESULTS AND DISCUSSION

Maize grain yield response was affected by the environment, breeding population, density, and the interactions between breeding population and density (Table 3). Grain yield for the unselected populations BSSS and BSCB1 initially increased at 30,000 plants ha\(^{-1}\); but, as density approached 70,000 plants ha\(^{-1}\), yield began to decrease (Figure 1). This trend was not observed in corresponding improved populations BSSS(R)C17 and BSCB1(R)C17 as grain yield continued to increase even at high densities. Unselected populations yielded more than corresponding improved populations at 30,000 plants ha\(^{-1}\); however, as density approached 55,000 plants ha\(^{-1}\), yield for the improved populations exceeded the unimproved. Grain yield for BSCB1(R)C17 plateaued at 90,000 plants ha\(^{-1}\); this was not observed for BSSS(R)C17 where yield increased past 100,000 plants ha\(^{-1}\).

The results in Figure 1 were consistent with commonly reported trends of increased yield gains with improved cycles of selection in the United States (Duvick, 2005a, 2005b; Brekke, 2011). Grain yield in the improved populations continued to increase even at higher densities and declined with increased densities for unimproved populations; and, at lower densities, unimproved BSSS and BSCB1 yielded more than corresponding improved populations BSSS(R)C17 and BSCB1(R)C17. These results supported previous publications stating that the observed increases in maize grain yields were associated with the increased adaptation, of newer hybrids, to higher planting densities, as opposed to increased production of grain on a per plant basis (Duvick, 2005a, 2005b); and, confirmed that selection response can be density dependent.
(Brekke, 2011). Furthermore, improved populations were able to maintain yield increases even at 85,000 plants ha\(^{-1}\) suggesting that selection at higher densities may be needed, in the future, to maintain upward yield trends (Brekke, 2011).

Grain moisture response was affected by the environment, breeding population, density, and the interactions between breeding population and density (Table 4). Grain moisture increased as density increased for improved populations BSSS(R)C17 and BSCB1(R)C17 (Figure 2). Unimproved BSSS and BSCB1 were not affected by plant density. At all stand densities, unimproved BSSS had higher grain moisture than the other populations. Improved BSSS(R)C17 had lower grain moisture than BSCB1(R)C17 at all stand densities.

There have been conflicting results, in the literature, with regards to grain moisture response to increased planting densities. Seka and Cross (1995) reported a linear response of grain moisture to increased density; Carena and Cross (2003) observed no difference in grain moisture with increased density. Our results were congruent with Seka and Cross (1995) with respect to improved BSSS(R)C17 and BSCB1(R)C17 and coincided with Carena and Cross (2002) for corresponding unimproved populations. The exact reasoning for increased grain moisture in modern hybrids is not fully understood; however, it has been hypothesized that increases in grain moisture might be associated with delayed initiation of reproductive stages in the maize plant (Carena and Cross, 2003). Although grain moisture increased with increasing density for BSSS(R)C17 and remained unchanged for BSSS, grain moisture was consistently lower for the adapted population than the unadapted population at all
densities. Perhaps these results are simply a response to selection since reduced grain moisture was one of the four selection criteria; or, it could be attributed to inbreeding depression (Edwards and Lamkey, 2002).

Test weight was affected by the same factors as grain yield and grain moisture (Table 5). Unselected populations BSSS and BSCB1 had constant test weight as plant density increased. Improved populations BSSS(R)C17 and BSCB1(R)C17 increased initially and then began to decrease as density increased (Figure 3). At all stand densities, BSCB1(R)C17 had a higher test weight than the other populations. Improved BSSS(R)C17 had a lower test weight than unselected BSSS at low densities and a higher test weight at high densities.

Our findings are consistent with reported trends of increased test weight in more advanced populations (Widdicombe and Thelen, 2002) and decreased test weight with increasing densities (Porter et al., 1997). Across all densities, the unimproved populations BSSS and BSCB1 had constant test weight indicating a lack of density effect; however, test weight increased with increasing density for improved populations suggesting a test weight response to increased density. Although test weight declined at the highest densities for improved populations, the consistently higher test weight of improved populations than corresponding unimproved populations indicated an increased adaptation of test weight to high plant density (Brekke, 2011).

Stalk lodging response was affected by the same factors as grain yield, moisture, and test weight (Table 6). Increasing plant density resulted in increased stalk lodging for all populations with the exception of unselected BSCB1 which decreased at 85,000
plants ha$^{-1}$ (Figure 4). Improved populations BSSS(R)C17 and BSCB1(R)C17 had lower stalk lodging percentages than unimproved populations BSSS and BSCB1 at all stand densities. By comparison to the other populations, improved BSSS(R)C17 had the greatest resistance to stalk lodging at all stand densities.

In comparison studies of hybrids of different era’s, improvement to stalk lodging was non-significant; however, it is speculated that stalk lodging presented a tendency towards increased resistance (Duvick, 2005a, 2005b). Both Carena and Cross (2003) as well as Widdicombe and Thelen (2002) reported trends of reduced stalk lodging at higher densities in commercial maize hybrids; the results in Figure 4 were congruent with these trends. Although the number of stalk lodged plants increased with increasing density, improved populations BSSS(R)C17 and BSCB1(R)C17 consistently had lower numbers of stalk lodged plants, at all densities, than corresponding unimproved populations indicating increased adaptation to high planting density.

Root lodging response was affected by the same factors as stalk lodging (Table 7). Increasing plant density resulted in increased root lodging for both improved and unimproved populations (Figure 5). Improved populations BSSS(R)C17 and BSCB1(R)C17 had lower root lodging percentages than corresponding unimproved populations at all stand densities. BSSS(R)C17 had lower root lodging percentages than BSCB1(R)C17 at all stand densities; and, BSSS had lower root lodging percentages than BSCB1 at all stand densities.

Depending on the severity of root lodging tendencies, both improvements as well as lack of improvements were reported in the literature (Duvick, 2005a, 2005b). Our
findings suggested linear increases in resistance to root lodging, in advanced populations, consistent with Duvick (1996). The percentage of root lodged plants increased with increasing densities for all populations; however, at all densities, improved populations had higher resistance to root lodging than corresponding unimproved populations suggesting an increased adaptation to higher planting densities.

Anthesis-silking interval response was affected by breeding population and density (Table 8). Anthesis-silking intervals increased as density increased for both improved and unimproved populations (Figure 6). Improved populations BSSS(R)C17 and BSCB1(R)C17 had consistently shorter anthesis-silking intervals than unimproved BSSS and BSCB1 at all stand densities. Across all densities, unimproved BSSS had higher anthesis-silking intervals than the other populations while BSSS(R)C17 had the lowest anthesis-silking intervals.

The trends in Figure 6 were consistent with hybrid maize studies indicating reduced ASI in improved populations (Russell, 1985) and increased ASI with increasing density (Sangoi et al., 2002). Although ASI increased as density increased for all populations, improved populations BSSS(R)C17 and BSCB1(R)C17 had consistently lower ASI than corresponding unimproved populations, at all densities. We speculate that reductions in ASI might be associated with reductions in number of tassel branches. In the literature, reduced numbers of tassel branches have been a commonly reported trend in modern hybrids (Duncan et al., 1967; Duvick, 1996, 2005a, 2005b). As the amount of available pollen decreased, due to reduced numbers of tassel branches, greater
synchrony between silk emergence and pollen shed could increase the probability of successful pollination resulting in increased grain yield (Brekke, 2011).

Ear height response was affected by breeding population, density, and the interactions between breeding population and density (Table 9). For three of the populations BSSS, BSSS(R)C17, and BSCB1, ear height increased as density increased (Figure 7). For BSCB1(R)C17, ear height increased initially and then decreased as density approached 90,000 plants ha\(^{-1}\). Improved populations BSSS(R)C17 and BSCB1(R)C17 had shorter ear heights than corresponding unimproved populations across all stand densities. BSSSRC17 had the shortest ear heights at lower densities while BSCB1(R)C17 had the shortest ear heights at higher densities.

There have been conflicting reports, in the literature, with regards to ear height response to increased planting densities. Some research had revealed a major reduction in ear height (Duvick, 2005a, 2005b); and, in some cases, research revealed no changes in ear height (Duvick, 1996). Our results suggested a decrease in ear height with advanced cycles of selection. Although ear height increased as density increased for all populations, improved populations BSSS(R)C17 and BSCB1(R)C17 had consistently lower ear heights than corresponding unimproved BSSS and BSCB1 at all densities. Reductions in ear height could be explained in terms of leaf angle. Modern hybrids developed a tendency to produce more upright leaf angles in the sector of the maize plant located above the developing ear (Crosbie, 1982; Meghji et al., 1984; Duvick, 1997; Duvick et al., 2004a, 2004b). Upright leaf angles enabled more light penetration into the canopy resulting in increased red:far-red ratios (Ballare et al., 1990). Increased
red:far-red ratios are associated with decreased plant stature; and, by nature, plants that are shorter in stature would have ears that are closer to the ground (Brekke, 2011).

Tassel branch number was affected by breeding population and density (Table 10). Tassel branch number decreased as density increased for all breeding populations (Figure 8). Improved populations BSSS(R)C17 and BSCB1(R)C17 had lower tassel branch numbers than corresponding unselected populations BSSS and BSCB1 at all densities. Unimproved BSSS had lower tassel branch numbers than BSCB1 at all densities. Similarly, improved BSSS(R)C17 had lower tassel branch numbers than BSCB1(R)C17.

Reduced numbers of tassel branches have been a commonly reported trend in commercial maize hybrids (Duncan et al., 1967; Duvick, 1996, 2005a, 2005b). Our results were consistent this trend. As density increased, number of tassel branches decreased for all populations; furthermore, improved populations BSSS(R)C17 and BSCB1(R)C17 had consistently lower number of tassel branches than corresponding unimproved populations BSSS and BSCB1 at all densities indicating an adaptation to high planting density. We speculate that a decrease in tassel branch number can be advantageous in terms of light attenuation within the canopy (Duncan et al., 1967, Brekke, 2011). At higher densities, shading of underlying leaves by large maize tassels could decrease light penetration, within the canopy, resulting in reduced photosynthetic rates of lower leaves (Duncan et al., 1967). Furthermore, reduced numbers of tassel branches could be explained in terms of ASI. Bolaños and Edemeads (1993) observed that selection for short ASI resulted in decreased tassel growth rates. We speculate that
as greater synchrony is attained between silk emergence and pollen shed, less pollen may be required to ensure successful pollinations (Bolaños and Edmeads, 1993). Reduced numbers of tassel branches could be explained in terms of neighboring effects. As density increased, plants were grown closer together. Perhaps, since pollen does not have to travel as far to ensure successful pollinations, reductions in tassel branches occurred.

Total number of nodes was affected by the same factors as tassel branch number (Table 11). The number of total nodes increased as density increased for all breeding populations (Figure 9). Improved populations BSSS(R)C17 and BSCB1(R)C17 had a lower number of total nodes than unimproved BSSS and BSCB1 at all densities. At all densities, unimproved BSSS had higher number of total nodes than the other populations while improved BSSS(R)C17 had lower number of total nodes.

In the literature, both reduction in number of total number of nodes (Sangoi et al., 2002) and lack of reduction (Duvick, 1996, 2005a, 2005b) were observed in advanced hybrids. Our findings were congruent with those of Sangoi et al. (2002). Although number of total nodes increased with increasing density for all populations, improved populations BSSS(R)C17 and BSCB1(R)C17 consistently had fewer number of total nodes than corresponding unimproved populations at all densities suggesting increased adaptation to high plant density. The reduction in number of total nodes, observed in advanced populations, could be explained in terms of leaf angle. At higher densities, improved populations tended to have more upright leaf angles in the portion of the canopy above the developing ear (Crosbie, 1982; Meghji et al., 1984; Duvick, 1997;
Duvick et al., 2004a, 2004b). It was reported that maize leaves required roughly 50% of available sunlight intensity to achieve a photosynthetic rate of 80% (Mock and Pearce, 1975). Thus, at higher densities, the vertical orientation of upper leaves, within a canopy, might enable more light penetration to lower leaves (Williams et al., 1968) which could result in increases in overall canopy photosynthetic rate. Another possible explanation may simply be that plants that are shorter in stature simply have less leaves (Brekke, 2011).

Plant height was affected by breeding population, density, and the interactions between breeding population and density (Table 12). For unselected BSSS and advanced BSSS(R)C17, plant height increased as density increased (Figure 10). Plant height for improved BSCB1(R)C17 initially increased at 30,000 plants ha\(^{-1}\); but, as density approached 85,000 plants ha\(^{-1}\), plant height plateaued. Plant height for unselected BSCB1 initially increased at 30,000 plants ha\(^{-1}\); but, as density approached 50,000 plants ha\(^{-1}\), plant height began decreasing. Improved populations BSSS(R)C17 and BSCB1(R)C17 had lower plant heights than corresponding unselected populations BSSS and BSCB1 at all densities.

The reduction in plant height observed in Figure 10 is consistent with findings of reduced plant height in modern hybrids (Meghji, 1984; Russell, 1985; Sangoi et al., 2002) and increased plant height at higher densities (Sangoi et al., 2002). At higher densities, plants are able to distinguish neighboring plants by detecting a low red:far-red ratio (Ballare et al., 1990); as a result, a stem elongation response is activated leading to taller plants. One possible explanation is that due to more upright leaf angles, improved
populations permit more light penetration into the canopy resulting in an increased red:far-red ratio, delayed stem elongation, and consequently shorter plants.

Leaf angle response was affected by leaf position for populations BSSS, BSCB1, and BSCB1(R)C17. Leaf angle had a quadratic response with respect to leaf position for all populations (Figure 11). Leaf angle was most upright at the flag leaf, most horizontal at intermediate leaves, and upright at lower leaves without surpassing the flag leaf angle. Improved populations BSSS(R)C17 and BSCB1(R)C17 had more horizontal leaves than corresponding unselected populations at all leaf positions. Unselected BSSS had more horizontal leaves than BSCB1 at all leaf positions. Similarly, improved BSSS(R)C17 had more horizontal leaves than BSCB1(R)C17. For advanced BSSS(R)C17, leaf angle response was affected by leaf position, the interaction between leaf position and ear height, and the interaction between leaf position and plant height (Table 13). Leaves became more horizontal as ear height increased for all leaf positions except the flag leaf (Figure 12); similarly, leaves became more horizontal as plant height decreased (Figure 13).

The results in Figure 11 corresponded with hybrid studies suggesting an increased tendency of modern hybrids to produce more upright leaf angles in the sector of the maize plant located above the developing ear (Crosbie, 1982; Meghji et al., 1984; Duvick, 1997; Duvick et al., 2004a, 2004b). Although no effect of density on leaf angle was detected in this experiment, shading of underlying leaves and leaf overlapping between neighbors increased with increasing density (Duvick, 2005a). Williams et al. (1968) reported that vertical orientation of upper leaves, within a canopy, enabled more
light penetration to lower leaves which increased overall canopy photosynthetic rates. Thus, the more upright leaf angles observed in advanced populations BSSS(R)C17 and BSCB1(R)C17 demonstrated their increased adaptability to higher densities. As the location of the ear increased from the ground leaf angles became more horizontal for all populations. The correlation between ear height and leaf angle had not been reported in past publications. We speculate that there is some sort of gradient up and down the plant that determines development of cells in the area of the leaf axil, and that gradient is affected by stature and placement of the ear. A hypothesis could be stated with regards leaf angle and increased plant height. As plant height decreases, the position of the ear relative to the ground becomes closer; thus, light has to penetrate deeper into the canopy in order to insure adequate assimilate to the developing ear; consequently, leaves closer to the developing ears became more horizontal. Brekke (2011) reported no effect of density on flag leaf angles. Our results contradicted this report. We believe that there might have been an error in data collection resulting in overestimation of flag leaf angles.

Leaf area had a quadratic response with respect to leaf position for all populations (Figure 14). Leaf area was smallest at the flag leaf, largest at intermediate leaves, and smaller at lower leaves without exceeding flag leaf areas. Improved populations BSSS(R)C17 and BSCB1(R)C17 had smaller leaf areas than corresponding unselected populations BSSS and BSCB1 at all leaf positions. Leaf area response was affected by leaf position for BSCB1 (Table 14); leaf position and the interaction between leaf position and node of attachment of the ear for BSCB1(R)C17 (Table 15). For
advanced BSCB1(R)C17, leaf area increased as node of attachment of the ear was lower on the plant and decreased with higher nodes of attachment of the ear at all leaf positions except flag leaf (Figure 15). Leaf area response was affected by leaf position, the interaction between leaf position and node of attachment of the ear, the interaction between leaf position and ear height, density, and the interaction between leaf position and density for BSSS (Table 16). When ear height and density were held constant, leaf area increased more rapidly at higher leaf positions, on the plant, when the node of attachment of the ear was higher from the ground; at lower leaf positions, leaf area decreased more rapidly when the node of attachment of the ear was higher from the ground (Figure 16). When ear node and density were held constant, leaf area increased more rapidly with respect to leaf position, on the plant, when the ear was closer to the ground; at lower leaf positions, leaf area decreased more rapidly when the ear was closer to the ground (Figure 17). When ear node and ear height were held constant, leaf area increased as density increased for all leaf positions (Figure 18). Leaf area response was affected by leaf position, the interaction between leaf position and node of attachment of the ear, and the interaction between leaf position and ear height for BSSS(R)C17 (Table 17). When holding ear height constant, leaf area increased rapidly at upper and intermediary leaves when the node of attachment of the ear was higher from the ground; at lower leaf positions, leaf area decreased more rapidly when the node of attachment of the ear was higher from the ground (Figure 19). When node of attachment of the ear was held constant, leaf area increased rapidly at all leaf positions when ears were higher off the ground; increased rapidly for upper and intermediary leaves and then plateaued at
the lower leaves when ear height from the ground was average; increased rapidly for upper leaves, plateaued at intermediary leaves, and declined at lower leaves when ear height was closest to the ground (Figure 20).

The results in figure 14 confirmed reports that leaf area decreased at the upper portion of the maize plant and increased at the intermediary portions (Duncan et al., 1967; Donald, 1968; Williams et al., 1968; Duncan, 1971; Mock and Pearce, 1975). The observed response pattern for flag leaf area was probably an indirect response for canopy architecture which permits more light to penetrate into the canopy. At higher densities, where shading effects are significant, increased light penetration into the canopy becomes an important factor; the photosynthetic capacity, of a canopy, is directly related to the total amount of leaf area exposed to sunlight; thus, the greater the amount of light penetration into the canopy, the greater the photosynthetic capacity (Pearce et al., 1967; Mock and Pearce, 1975; Brekke, 2011; Edwards, 2011). Thus, at higher densities, possessing leaves with upright angles and smaller surface areas, higher up in the canopy, allows for more efficient light interception and penetration which consequently results in higher photosynthetic rates at leaves located in the lower portion of the canopy (Duncan et al., 1967; Donald, 1968; Williams et al., 1968; Duncan, 1971; Mock and Pearce, 1975; Brekke, 2011). The availability of larger more horizontally oriented leaves next to the developing ear could be to insure sufficient carbohydrate flux to the developing ear. The reduction in leaf size associated with improved populations indicated an increased adaptation to higher densities. Our results have revealed an effect of node of attachment of the ear, ear height, and density on leaf area; this relationship has not been documented
in the literature; perhaps future research would provide an explanation for some of these observed trends.

References


CHAPTER V. CONCLUSIONS

Direct selection for grain yield and agronomic performance in the Iowa Stiff Stalk Synthetic and Iowa Corn Borer Synthetic no. 1 had indirectly improved adaptation to high planting densities. Improved populations BSSS(R)C17 and BSCB1(R)C17 exhibited reduced grain moisture, increased test weight, higher resistance to root and stalk lodging, and greater synchrony between days of silk emergence and pollen shed than corresponding unimproved populations BSSS and BSCB1 at higher densities.

Selection for grain yield and agronomic performance, at higher densities, in the Iowa Stiff Stalk Synthetic and Iowa Corn Borer Synthetic no. 1 had changed canopy architecture. Reduced numbers of total nodes, lower ear height, shorter plant stature, smaller tassels, more upright leaf angles with smaller leaf areas at the top sector of the canopy and more horizontal leaf angles with larger leaf areas lower into the canopy were observed for improved populations BSSS(R)C17 and BSCB1(R)C17.

Furthermore, we observed a relationship between leaf angle and leaf area. As leaf angles became more upright, leaf area decreased; while, as leaf angles became more horizontal, leaf area increased. It is important to reiterate that fact that leaves higher in the canopy tended to be more upright and smaller in size while leaves lower in the canopy tended to be more horizontal and bigger in size.

The shape of the canopy was affected by plant height, ear height, and the node of attachment of the ear, and density. The height of the ear from the ground changed canopy architecture by altering leaf angle and leaf area. As the height of the ear from the ground increased, leaf angles became more horizontal and leaf areas became smaller.
at all leaf positions except flag leaf. Plant height altered canopy architecture by affecting leaf angle; leaf angle became more horizontal as plant height decreased for all leaf positions except flag leaf. The node of attachment of the ear affected leaf area; leaf area increased as node of attachment of the ear was lower on the plant and decreased with higher nodes of attachment at all leaf positions except flag leaf. Leaf area increased with increased density at all leaf positions except flag leaf and 12th leaf position from the flag leaf.

The effect of plant height, ear height, and node of attachment of the developing ear on canopy architecture is undocumented in the literature. Perhaps a better understanding of these relationships could result in a prediction model for canopy architecture in the future.
APPENDIX A. TABLES

Table 1. Breeding Populations

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Table 3. Tests for fixed effects in the statistical model for grain yield. Fixed effects with p-values greater than 0.05 were dropped from the model.

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Table 7. Tests for fixed effects in the statistical model for root lodging. Fixed effects with p-values greater than 0.05 were dropped from the model.

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<th>Effect</th>
<th>Num DF</th>
<th>Den DF</th>
<th>F-Value</th>
<th>Pr &gt; F</th>
</tr>
</thead>
<tbody>
<tr>
<td>env</td>
<td>1</td>
<td>35.5</td>
<td>8.11</td>
<td>0.0073</td>
</tr>
<tr>
<td>blk(env)</td>
<td>12</td>
<td>282</td>
<td>1.36</td>
<td>0.1844</td>
</tr>
<tr>
<td>ped</td>
<td>37</td>
<td>86.6</td>
<td>2.25</td>
<td>0.0011</td>
</tr>
<tr>
<td>D</td>
<td>1</td>
<td>221</td>
<td>37.15</td>
<td>&lt; 0.0001</td>
</tr>
<tr>
<td>D*D</td>
<td>1</td>
<td>161</td>
<td>0.38</td>
<td>0.5362</td>
</tr>
<tr>
<td>D*ped</td>
<td>37</td>
<td>264</td>
<td>1.66</td>
<td>0.0133</td>
</tr>
<tr>
<td>D<em>D</em>ped</td>
<td>37</td>
<td>262</td>
<td>1.84</td>
<td>0.0034</td>
</tr>
</tbody>
</table>
Table 8. Tests for fixed effects in the statistical model for anthesis-silking interval. Fixed effects with p-values greater than 0.05 were dropped from the model.

<table>
<thead>
<tr>
<th>Effect</th>
<th>Num DF</th>
<th>Den DF</th>
<th>F-Value</th>
<th>Pr &gt; F</th>
</tr>
</thead>
<tbody>
<tr>
<td>blk</td>
<td>7</td>
<td>38.4</td>
<td>1.89</td>
<td>0.0982</td>
</tr>
<tr>
<td>ped</td>
<td>37</td>
<td>173</td>
<td>4.67</td>
<td>&lt; 0.0001</td>
</tr>
<tr>
<td>D</td>
<td>1</td>
<td>60.8</td>
<td>25.62</td>
<td>&lt; 0.0001</td>
</tr>
</tbody>
</table>

Table 9. Tests for fixed effects in the statistical model for ear height. Fixed effects with p-values greater than 0.05 were dropped from the model.

<table>
<thead>
<tr>
<th>Effect</th>
<th>Num DF</th>
<th>Den DF</th>
<th>F-Value</th>
<th>Pr &gt; F</th>
</tr>
</thead>
<tbody>
<tr>
<td>blk</td>
<td>7</td>
<td>38.9</td>
<td>6.01</td>
<td>&lt; 0.0001</td>
</tr>
<tr>
<td>ped</td>
<td>37</td>
<td>134</td>
<td>12.02</td>
<td>&lt; 0.0001</td>
</tr>
<tr>
<td>D</td>
<td>1</td>
<td>51.4</td>
<td>113.42</td>
<td>&lt; 0.0001</td>
</tr>
<tr>
<td>D*D</td>
<td>1</td>
<td>84.7</td>
<td>13.69</td>
<td>0.0004</td>
</tr>
<tr>
<td>D*ped</td>
<td>37</td>
<td>133</td>
<td>1.69</td>
<td>0.0168</td>
</tr>
</tbody>
</table>
Table 10. Tests for fixed effects in the statistical model for tassel branch number. Fixed effects with p-values greater than 0.05 were dropped from the model.

<table>
<thead>
<tr>
<th>Effect</th>
<th>Num DF</th>
<th>Den DF</th>
<th>F-Value</th>
<th>Pr &gt; F</th>
</tr>
</thead>
<tbody>
<tr>
<td>blk</td>
<td>7</td>
<td>193</td>
<td>1.48</td>
<td>0.1771</td>
</tr>
<tr>
<td>ped</td>
<td>37</td>
<td>193</td>
<td>18.90</td>
<td>&lt;0.0001</td>
</tr>
<tr>
<td>D</td>
<td>1</td>
<td>192</td>
<td>9.67</td>
<td>0.0022</td>
</tr>
</tbody>
</table>

Table 11. Tests for fixed effects in the statistical model for total nodes. Fixed effects with p-values greater than 0.05 were dropped from the model.

<table>
<thead>
<tr>
<th>Effect</th>
<th>Num DF</th>
<th>Den DF</th>
<th>F-Value</th>
<th>Pr &gt; F</th>
</tr>
</thead>
<tbody>
<tr>
<td>blk</td>
<td>7</td>
<td>38.4</td>
<td>6.64</td>
<td>&lt; 0.0001</td>
</tr>
<tr>
<td>ped</td>
<td>37</td>
<td>179</td>
<td>6.04</td>
<td>&lt; 0.0001</td>
</tr>
<tr>
<td>D</td>
<td>1</td>
<td>50.5</td>
<td>8.58</td>
<td>0.0051</td>
</tr>
</tbody>
</table>
Table 12. Tests for fixed effects in the statistical model for plant height. Fixed effects with p-values greater than 0.05 were dropped from the model.

<table>
<thead>
<tr>
<th>Effect</th>
<th>Num DF</th>
<th>Den DF</th>
<th>F-Value</th>
<th>Pr &gt; F</th>
</tr>
</thead>
<tbody>
<tr>
<td>blk</td>
<td>7</td>
<td>37.4</td>
<td>3.77</td>
<td>0.0035</td>
</tr>
<tr>
<td>ped</td>
<td>37</td>
<td>125</td>
<td>21.65</td>
<td>&lt; 0.0001</td>
</tr>
<tr>
<td>D</td>
<td>1</td>
<td>62.2</td>
<td>29.79</td>
<td>&lt; 0.0001</td>
</tr>
<tr>
<td>D*D</td>
<td>1</td>
<td>104</td>
<td>11.45</td>
<td>0.0010</td>
</tr>
<tr>
<td>D*ped</td>
<td>37</td>
<td>125</td>
<td>2.40</td>
<td>0.0002</td>
</tr>
</tbody>
</table>

Table 13. Tests for fixed effects in the statistical model for leaf angle (BSSS(R)C17). Fixed effects with p-values greater than 0.05 were dropped from the model.

<table>
<thead>
<tr>
<th>Effect</th>
<th>Num DF</th>
<th>Den DF</th>
<th>F-Value</th>
<th>Pr &gt; F</th>
</tr>
</thead>
<tbody>
<tr>
<td>leaf</td>
<td>1</td>
<td>93</td>
<td>12.55</td>
<td>0.0006</td>
</tr>
<tr>
<td>leaf*leaf</td>
<td>1</td>
<td>182</td>
<td>51.26</td>
<td>&lt; 0.0001</td>
</tr>
<tr>
<td>leaf*EH</td>
<td>1</td>
<td>184</td>
<td>5.16</td>
<td>0.0243</td>
</tr>
<tr>
<td>leaf*PH</td>
<td>1</td>
<td>167</td>
<td>6.63</td>
<td>0.0109</td>
</tr>
</tbody>
</table>
Table 14. Tests for fixed effects in the statistical model for leaf area (BSCB1). Fixed effects with p-values greater than 0.05 were dropped from the model.

<table>
<thead>
<tr>
<th>Effect</th>
<th>Num DF</th>
<th>Den DF</th>
<th>F-Value</th>
<th>Pr &gt; F</th>
</tr>
</thead>
<tbody>
<tr>
<td>leaf</td>
<td>1</td>
<td>254</td>
<td>54.44</td>
<td>&lt; 0.0001</td>
</tr>
<tr>
<td>leaf*leaf</td>
<td>1</td>
<td>254</td>
<td>22.84</td>
<td>&lt; 0.0001</td>
</tr>
</tbody>
</table>

Table 15. Tests for fixed effects in the statistical model for leaf area (BSCB1(R)C17). Fixed effects with p-values greater than 0.05 were dropped from the model.

<table>
<thead>
<tr>
<th>Effect</th>
<th>Num DF</th>
<th>Den DF</th>
<th>F-Value</th>
<th>Pr &gt; F</th>
</tr>
</thead>
<tbody>
<tr>
<td>leaf</td>
<td>1</td>
<td>344</td>
<td>86.67</td>
<td>&lt; 0.0001</td>
</tr>
<tr>
<td>leaf*leaf</td>
<td>1</td>
<td>272</td>
<td>513.42</td>
<td>&lt; 0.0001</td>
</tr>
<tr>
<td>leaf*EN</td>
<td>1</td>
<td>339</td>
<td>20.28</td>
<td>&lt; 0.0001</td>
</tr>
</tbody>
</table>
Table 16. Tests for fixed effects in the statistical model for leaf area (BSSS). Fixed effects with p-values greater than 0.05 were dropped from the model.

<table>
<thead>
<tr>
<th>Effect</th>
<th>Num DF</th>
<th>Den DF</th>
<th>F-Value</th>
<th>Pr &gt; F</th>
</tr>
</thead>
<tbody>
<tr>
<td>leaf</td>
<td>1</td>
<td>250</td>
<td>17.15</td>
<td>&lt; 0.0001</td>
</tr>
<tr>
<td>leaf*leaf</td>
<td>1</td>
<td>239</td>
<td>19.71</td>
<td>&lt; 0.0001</td>
</tr>
<tr>
<td>leaf*EN</td>
<td>1</td>
<td>245</td>
<td>5.63</td>
<td>0.0184</td>
</tr>
<tr>
<td>leaf<em>leaf</em>EN</td>
<td>1</td>
<td>243</td>
<td>7.42</td>
<td>0.0069</td>
</tr>
<tr>
<td>leaf*EH</td>
<td>1</td>
<td>248</td>
<td>6.26</td>
<td>0.0130</td>
</tr>
<tr>
<td>leaf<em>leaf</em>EH</td>
<td>1</td>
<td>237</td>
<td>9.96</td>
<td>0.0018</td>
</tr>
<tr>
<td>D</td>
<td>1</td>
<td>4.14</td>
<td>0.64</td>
<td>0.4680</td>
</tr>
<tr>
<td>D*D</td>
<td>1</td>
<td>4.18</td>
<td>0.51</td>
<td>0.5118</td>
</tr>
<tr>
<td>leaf*D</td>
<td>1</td>
<td>202</td>
<td>10.93</td>
<td>0.0011</td>
</tr>
<tr>
<td>leaf<em>D</em>D</td>
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<td>0.0004</td>
</tr>
</tbody>
</table>

Table 17. Tests for fixed effects in the statistical model for leaf area (BSSS(R)C17). Fixed effects with p-values greater than 0.05 were dropped from the model.

<table>
<thead>
<tr>
<th>Effect</th>
<th>Num DF</th>
<th>Den DF</th>
<th>F-Value</th>
<th>Pr &gt; F</th>
</tr>
</thead>
<tbody>
<tr>
<td>leaf</td>
<td>1</td>
<td>216</td>
<td>40.05</td>
<td>&lt; 0.0001</td>
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<tr>
<td>leaf*leaf</td>
<td>1</td>
<td>218</td>
<td>33.86</td>
<td>&lt; 0.0001</td>
</tr>
<tr>
<td>leaf*EN</td>
<td>1</td>
<td>215</td>
<td>6.02</td>
<td>0.0149</td>
</tr>
<tr>
<td>leaf<em>leaf</em>EN</td>
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<td>218</td>
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<td>0.0037</td>
</tr>
<tr>
<td>leaf<em>leaf</em>EH</td>
<td>1</td>
<td>216</td>
<td>35.19</td>
<td>&lt; 0.0001</td>
</tr>
</tbody>
</table>
Figure 1. Grain yield in Mg ha\(^{-1}\) at harvest.
Figure 2. Grain moisture percentage at harvest.
Figure 3. Grain test weight at harvest.
Figure 4. Percent stalk lodging.
Figure 5. Percent root lodging.
Figure 6. Anthesis-silking interval.
Figure 7. Height of the Ear from the ground.
Figure 8. Number of tassel branches.
Figure 9. Number of total nodes.
Figure 10. Plant height.
Figure 11. Leaf angle.
Figure 12. Changes in leaf angle as plant height is constant and ear height is variable.
Figure 13. Change in leaf angle as ear height constant and plant height varies.
Figure 14. Leaf Area.
Figure 15. Changes in leaf area as node of attachment of the ear varies.
Figure 16. Changes in leaf area when the node of attachment of the ear varies.
Figure 17. Changes in leaf area when ear height varies.
Figure 18. Changes in leaf area when density varies.
Figure 19. Changes in leaf area when node of attachment of the ear varies.
Figure 20. Changes in leaf area when ear height is varied.