

The formation of Maize Foundation Inbred Lines: Analysis in Different Perspective

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Abstract— Maize breeding has made a greater contribution to the increases of maize yield. Maize foundation inbred lines play an irreplaceable role in maize breeding. The formation of foundation lines were the results of many factors, the key factors of which were accord with breeding trends, adapt to environment in much of region, and have appropriate representativeness for particular heterotic group. Foundation lines possess well structure of source and better yield stability, this contribute to their combinations with coordinated source-sink relationship and adapt to close planting. Foundation lines resist major stress factor and adapt to the cropping systems and cultural practices of main maize producing areas. And foundation lines concentrate numerous unique alleles of particular heterotic group, so they are easy to generate heterotic with lines from other heterotic group. For new foundation lines breeding, the existing foundation lines are preferred basic germplasm and cross breeding unites with pedigree selection is effective breeding method. Moreover, we give a integrate breeding method base on rapid advances in plant-breeding technology.

Keywords— Maize, Foundation inbred lines, China, formation.

I. INTRODUCTION

Maize (*Zea mays L.*) is one of the most important crop which extensive as food, fodder and industrial raw materials. According to investigation statistics by Food and Agriculture Organization of the United Nations(FAO, <http://faostat.fao.org>), maize total production in the world more than rice and wheat from 2001 to 2011 and reached 885milliontons in 2011. China is the second largest maize producer, planted area and total yield, in the world. The area planted of maize in China over wheat in 2002 and over rice in 2007. The average yields of China maize from 0.96 tons per hectare in 1949 rose to 5.87 tons per hectare in 2012, more than six fold increase(<http://www.stats.gov.cn/>). It is estimated that40-60% of total gain in maize yield was contribution by genetics improve (Ci et al2011a; Duvick1992, 2004; Li2009a; Russell1991). Maize is one of the earliest and largest grown area crop which utilization of heterosis in crops, and over 97% of maize plantings are hybrid in China(Duvick1992, 1999; Li2009a). The chiefly process of maize breeding and utilization of heterosis is breeding inbred lines and test cross to testers. Foundation inbred lines, such as B73, Mo17, Oh43, Huangzao4, Ye478, Dan340 et al., play an important role in maize breeding (Li and Wang2010; Teng et al.2004; Troyer1999,2004).

Several lines of evidence indicate that maize was domesticated approximately 10,000 years ago in the Balsas River Basin of southwestern Mexico (Matsuoka et al.2002; Piperno et al.2009; Van Heerwaarden et al.2011). It was undergoing narrow selection in domestication from teosinte (*Zea mays ssp. parviglumis or spp. mexicana*) to maize(Wang et al.1999).The variation in a few critical regions of genome between maize and teosinte generate their obvious difference of morphological (Doebly2004).The chief process of maize domestication are increase apical dominance, and decrease branches, unfallen, number of female inflorescences per plant, thus enhance single ear grain weight (Doebly1997, 2006). And the main process of maize improvement are enhance grain yield, improve plant type, and increase tolerances to biotic and abiotic stress (Crosbie et. al.2006; Duvick2005; Russell1991). The ultimate aim of maize domestication and improvement is increase yield potential, and convenient for manage and harvest.

This paper reviews the formation of foundation maize inbred lines, by means of analyze yield-related traits in level of performance and genes (Figure 1).In the level of performance, the foundation lines with fine plant type could harmonize individual growing development and the construct of population structure, even more it could coordination of source and sink. At the genetic level, on the one hand the foundation lines own high general combining ability (GCA) effects because it

get together a lot of favorable alleles; on the other hand the foundation lines own some distinctive alleles so that it is apt to generate heterosis with different heterotic group material.

1.1 Ideal performance of foundation maize inbred lines

What characteristic should be of foundation maize inbred lines? The fundamental use of inbred lines is in hybrids, there are correlations between parental inbred lines traits and their hybrid same traits (Flint-Garcia et al.2009; Gama et al.1977; Jenkins1928). DuVick (2005) indicate that hybrids traits changes result from selection during inbred lines development and evaluation, and relative heterosis for grain yield is slightly reduced. The additive effect is the preponderance genetic components of total genetic variance in most of maize traits (Hallauer et al.2010). Hence, it is likely to be more effective that select inbred lines with ideotype during maize breeding. It always is a desired trait for maize cultivars that obtain a higher yield, or an acceptable and dependable level of yield. The nature of yield formation is plants efficiency in the use of resources to capture and convert solar energy into chemically available forms. Thereby, the trait of plant type, root type, ear type and dry matter production, dry matter distribution and stress resistance are the key problems to be researched.

1.2 What kind of source ought to have of foundation maize inbred lines

1.2.1 Plant Morphology

Many researchers have studied of genetic correlations among plant and ear trait with yield. Hallauer et al. (2010) summary their studies found that kernel depth, kernels/row, ears/plant, ear diameter, ear length, ear height, and plant height had greater genetic correlations with yield. These agronomic traits are the easiest observe and measure characters by breeders in maize breeding. Selection and improvement of foundation maize inbred lines based on trade-offs about key plant traits and ear traits.

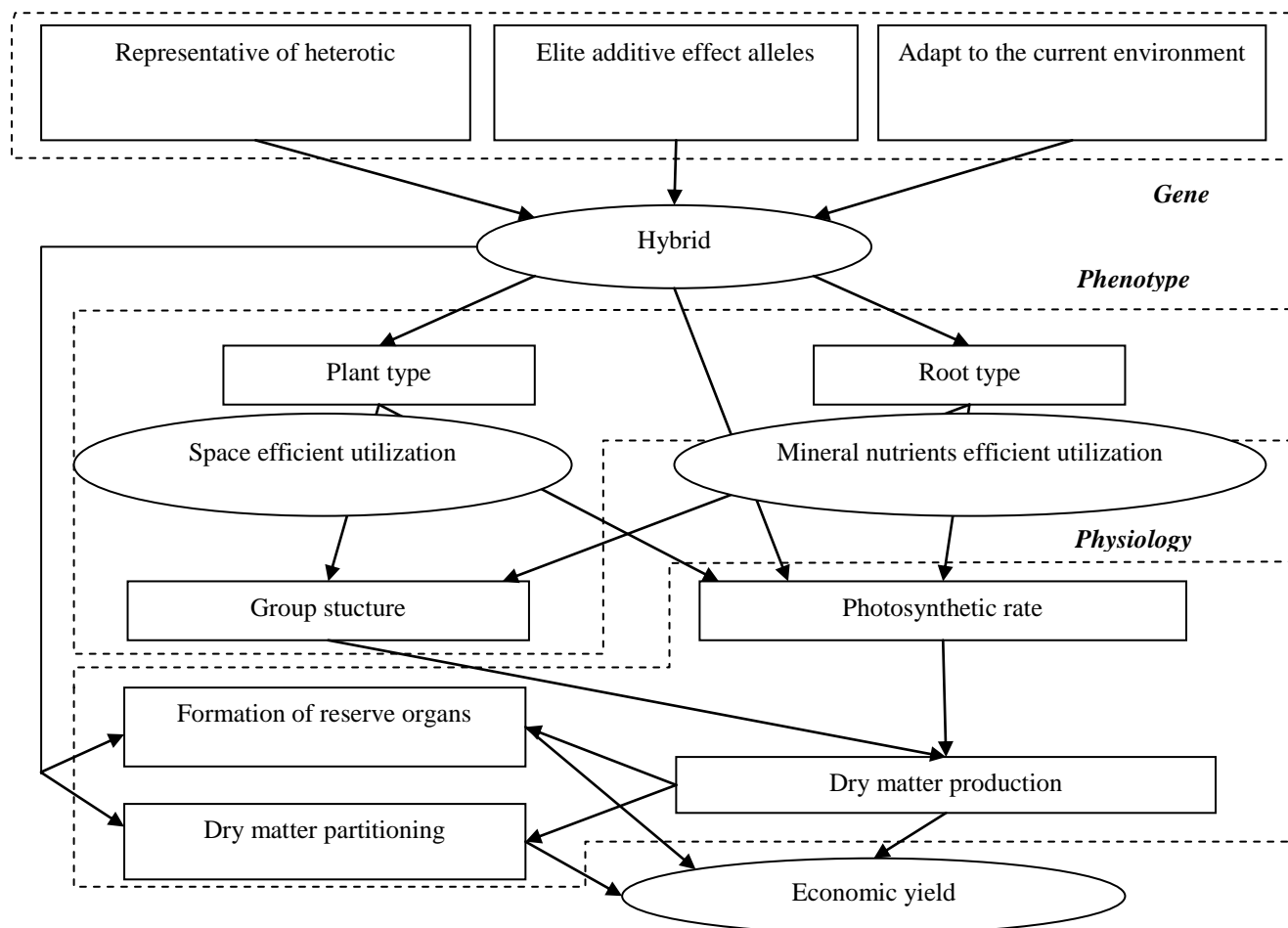


FIGURE 1 SCHEMATIC OF DISPLAY OF ELITE MAIZE INBRED LINE IN DIFFERENT LEVELS.

The most typical features of maize foundation lines are they have favorable plant type. It is the reason for they showed excellent coordinate of photosynthesis source structure and population yield in hybrids (Pagano et al.2007).The canopy architecture of high yield maize is solar radiation appropriately spatial distributed and plant-to-plant uniform which reduce intra-specific competition and enhance spatial resource utilization (Bavec and Bavec2002; Pagano and Maddonni2007; Rossini et al.2011; Tokatlidis and Koutroubas2004).There are several significant manifestations: the development aspect, where in the earlier stage fast growth and formation canopy, in the middle stage with high leaf area index (LAI) and keep a long time, and in the later stage maintain high photosynthetic efficiency at functional leaf; the canopy aspect, where the upper leaf smaller and compact and with a large leaf interval, the middle to lower leaf medium length, and loosely and with shorter leaf interval; the supporting part aspect, where with stiffness stalks and flourishing roots; the population aspect, where with higher uniformity(Allison and Watson1966; Crosbie1982; Lynch1995; Tollenaar and Dwyer1998; Lindquist and Mortensen1999; Lindquist et al.2005; Rodermeel and Spalding2001; DuVick2005; Stöckle2009; Ci et al.2012; Li2009; Westgate et al.1997). Hence, photo synthetically active radiation (PAR) and carbon dioxide (CO₂) could reasonable distribution, more PAR and CO₂ to ear leaf to increase the proportion of LAI operating at non-saturating irradiance, in vertical direction of maize population to enhance individual yield (Figure 2).So, the planting density could be increased and with an acceptable intra-specific competition in horizontal direction of maize population to increase population yield. Besides that, maize population microenvironment also could be improved by improvement in plants type, thus inhibiting microorganism who fond of dankness environment reproduction and reducing wind loading of plants.

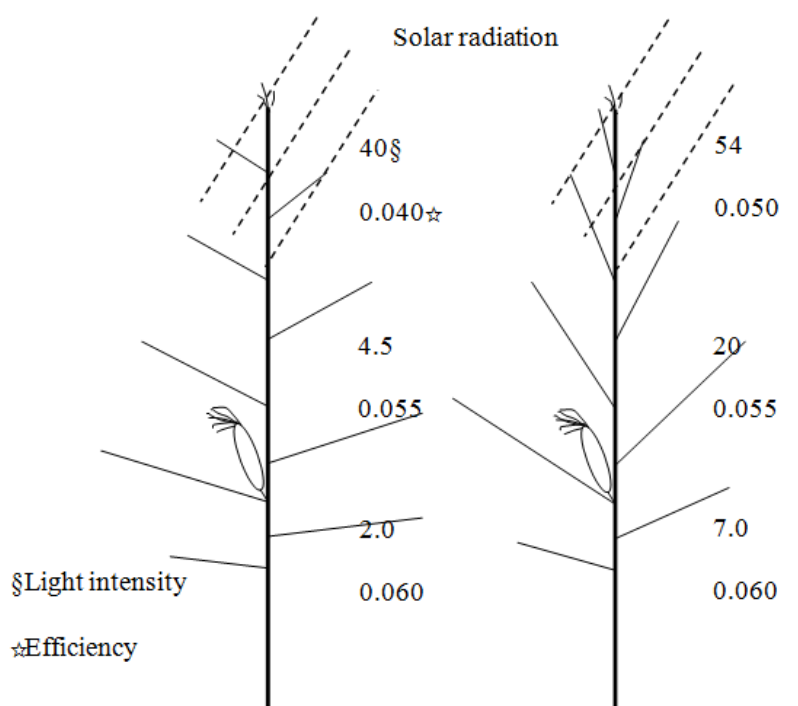


FIGURE 2 SCHEMATIC OF THE MICROENVIRONMENT IN TWO PLANT TYPE MAIZE CANOPY, ON LIGHT INTENSITY (KILOLUX), ON RADIATION USE EFFICIENCY (MOL C PER MOL PHOTOSYNTHETICALLY ACTIVE RADIATION), ON CO₂ CONCENTRATION (PPM). DATA FROM SU ET AL.(1990), WANG ET AL.(1996) AND NATR ET AL.(2005).

1.2.2 Photosynthesis

The formation of efficient maize source not only require coordinated canopy architecture of population as morphology base to capture and distribution PAR but also need high rates of photosynthesis as physiology base to take advantage of incoming PAR.Three approaches to which enhance the accumulate of dry matter and carbohydrate were frequently-used: improve cultivation and management measures; increase leaf area index and its duration; enhance photosynthetic rate. (Athar et al.2005; Bavec2002; Ning et al.2013; Rychter et al.2005; Tollenaar1988, 1992).

Enhance leaf photosynthetic rate (especially after pollination) is one crucial effort of maize genetic improvement. Photosynthetic rate have a significant variation in different maize genotypes (Prioul et al.1990; Otegui et al.1995).And new maize hybrids have higher photosynthetic rate than older (Li2009b; Wang2011). High photosynthetic rate maize hybrids

possess common physiological basis and enzyme system: high levels of leaf chlorophyll concentration and leaf soluble protein content; low membrane lipid per oxidation products content; efficient protective enzymes; high activity of ribulose 1,5-bisphosphate carboxylase/oxygenase (Rubisco) and C4-specific phosphoenolpyruvate carboxylase (PEPC) (Ding et al.2005; Dwyer and Tollenaar1989; Fromme et al.2003; Ge et al.2006; Li2009b; Li et al.1999; Parry et al.2013; Schäffnef et al.1992; Usuda1984; Wang2011; Zhu et al.2010).The indirect physical manifestations of maize hybrids are gradient distribution of inorganic nutrients (especially N P K) in leaves at different light intensities, better stay-green of functional leaves, and extended grain filling period (Duvick1999, 2005; Edmeades and Tollenaar1990; Jacob et al.1992; Peaslee et al.1966; Sinclair et al.1989).

1.3 Which kind sink should be in maize foundation lines

Grain yield in maize is a function of the relationship between source produce and inherent potential of the sink to accommodate this produce. The sink in maize foundation lines should be high-effect and high-capacity. The main jobs of maize breeders are to breeding high yield inbred lines. The yield components can be formalized as follow:

$$Y = PN \times E/P \times KRN \times KPR \times KW$$

where Y is grain yield ($g\ m^{-2}$), PN plant number(m^{-2}), EN ears per individual plant, KRN kernel-row number, KPR kernel per row, KW mean weight per kernel(g) (Engledow and Wadham1923).The equation indicates that breeders could pay attention to ear characters as the sink capacity selection index in maize breeding.

Grain yield per plant, composed of kernel number and weight per kernel, is the final sink and is the chiefly goal for maize produced. The number of kernels per plant (KNP) depends on the number of ears per plant, the row number of per ear and the number of kernels per row that achieve physiological maturity. There are the wide ranges of natural variation in ears size among different inbred lines (<http://www.panzea.org>), and it's reflecting the diversity of allelic. The improve trends of ear traits of maize hybrids might not be as clear inductive of plant morphology traits. It is not entirely consistent in different regions and at different ages (Ci2011b; Duvick1997; Li2009b; Russell1985; Wang2011). But we could summarize that US and Chinese maize hybrids underwent different breeding process to adapt to local agricultural conditions, and ear traits dependent on the trade-offs of source-sink relationship and individual-population relationship and yield-cultivation relationship. The possible performances of ear are medium kernel rows, more kernels per row, and higher 100 kernel weight. Besides, ears should be uniform, have loosely and moderate number husk and low grain moisture content when mature to facilitate machinery harvest, enhance shelling efficiency, improve grain quality and reduce additional drying cost (Anazodo et al.1981; Hellevang and Reff1987; Troyer and Ambrose1971; Waelti and Buchele1969).

1.4 From source to sink: coordination is important

The harvest index (HI) is a key determinant of maize yield estimation and source-sink relationship ((Westgate et al.2004). The increase of maize yield was attributable mainly to improvement of both total biomass yield and HI (Yamaguchi1974). The other one yield components equation as follow:

$$Y = HI \times BIO$$

where Y is grain yield ($g\ m^{-2}$), BIO biomass produced per unit area ($g\ m^{-2}$), HI the harvest index or ratio of harvestable material to total biomass at harvest.

How high the HI is appropriate in maize hybrids is need some trade-off: population yield versus individual yield, and yield potential versus yield stability. Several studies show that the HI of maize varieties in U.S. and China around 0.5 may be an ideal balanced and the stabilization of HI in higher plant density or in the adversity need to be improved (Duvick et al.2004; Li2009b; Russell1985; Tollenaar1989). Therefore breeders could pay more attention to enhance HI stabilization of inbred lines. The essence of HI in physiology viewpoint is fluxes which regulatory photo synthetically assimilated carbon product from sources to sinks. Nutrient fluxes via the phloem to long-distance supply no photosynthetic organs with energy and carbon resources and the major transport forms are sucrose and its derivatives (Lalonde et al.1999; Slewinski et al.2009). Sucrose enters and exit the phloem generating turgor pressure provides the driving force for its long-distance transport and determine carbon partitioning (Bush1999; Hellmann et al.2000). However, many studies found abiotic stress factors, such as

chilling and mineral deficiency, can obviously affect sucrose loading rate (Turgeon et al.2001). Hence, we may need to increase source organs phloem sucrose loading rate in a volatile environments to enhance the stabilization of HI.

The transition from vegetative growth to reproduction growth is one of the most importance and dramatic developmental processes during the life of maize. There into, the coordinative level of source-sink relationship was taken as a comprehensive index to select the maize variety of high yield. Ears, the sink of maize, are produced at the axial of leaf primordial began at or very near the 6 leaves stages (V6)and terminate all lateral axillaries buds. Thereafter, the maximum number of kernel rows around the ear is being determined from V7 to V8. And the maize plant determined the length of the ear during the period from about V7 to pollination (Ritchie1992; McMaster et al.2005).The number of kernels per plant is established during the period bracketing flowering of kernel development (Jacobs et al.1991; Andrade et al.1999).Grain fill is the period from flowering to physiological maturity and is the stage of final yield determined. Thus, grain yield is influenced not only by vegetative growth phase and kernel development stage, but by the interaction between source and sink. The processes of photosynthesis and carbon partitioning in maize when kernel development stages are highly interdependent, and sinks as determinants of assimilate distribution (Connell et al.1987;Crafts-Brandner et al.1984; Tanaka and Yamaguchi1972).In the main variety, the remobilization of carbon and nutrition which reserves accumulated in the stalk and senescent leaves for the ear growth is an important factor in crop yield (Cliquet et al.1990).

1.5 Important guarantee for yield: stress tolerance and resource-uptake ability

Maize, as the main field crops, needed to overcome adversity and to take full advantage of environmental resources to achieve high and stability yield. The key processes of maize yield formation are the extended period of grain-filling and the photosynthetic efficiency in grain-filling period (Yang and Zhang2006). So, it should be no surprise that increase tolerances to biotic and abiotic stress are the key trends in maize breeding. Meanwhile, the resource-uptake ability of hybrids has improved with time.

Tollenaar and Wu (1999), Tollenaar and Lee (2002), and Duvick (2005) retrospective analysis of the key factor of maize genetic yield improvement indicate that new maize hybrids have a better performance than older hybrids at the drought, high temperatures, low temperatures, excessive soil moisture, diseases, high density and so on environmental stress. Foundation maize inbred lines don't have to resistance all stress, but to tolerance or resistance main stress of where it's widespread use region.Huangzao4 possess drought resistance and maize Dwarf Mosaic Virus resistance, Ye478 possess lodging-resistance, which makes they popular in Yellow and Huai River maize zone; Mo17resistant to head smut, which makes it turn into core germplasm in Northeast China maize zone; Dan340 tolerate to water-logging and saline-alkaline, which makes it widely used in Liaoning province (Cao and Xu2000; Li and Wang2010).

Maize yield is the result of capture and use of resources. The main resources are solar radiation and nutrients and water. The capture of solar radiation have be discussing in the first section, so we only review of the nutrients and water capture and use by the root and the related plant tissue. Nutrients and water uptake correlated with root mass and root system architecture (the spatial configuration of a root system in the soil; Wiesler and Horst1994). Tollenaar and Migus (1984) and Nissanka (1995) reported that newer hybrid root/shoot ratio greater than the older hybrid. Hammer et al. (2009) simulation study cropping system in maize suggested that the improvement of root architecture make an importance contribution to the continuous increase in the yield of maize in the U.S. Corn Belt. Campos et al. (2004) indicate that modern maize hybrids can capture more water in deep layer soil than old hybrids during a period of water limitation.

II. REALITY PERFORMANCE OF MAIZE FOUNDATION LINES

We could speculate on desirable characteristics of maize foundation lines by summarize the trend of maize breeding above: reasonable plant canopy architecture to capture and distribution PAR and decrease competition between individuals; excellent ear characters to store dry matter and promote source efficiency; coordinated source-sink relationship. Otherwise, popularized production maize hybrids must adaptation to accelerated climate change, frequent diseases outbreaks and cropping systems, economic environment to ensure economic benefit and food security. The above considerations led to breeders improve and selection of inbred lines for superior maize hybrid combinations. In this part, we enumerate four inbred lines (Ye478, Huangzao4, Dan340 and Mo17) who stand of trend of China maize breeding to analysis foundation lines possess which outstanding performance and how to adapt environment (Figure 3).

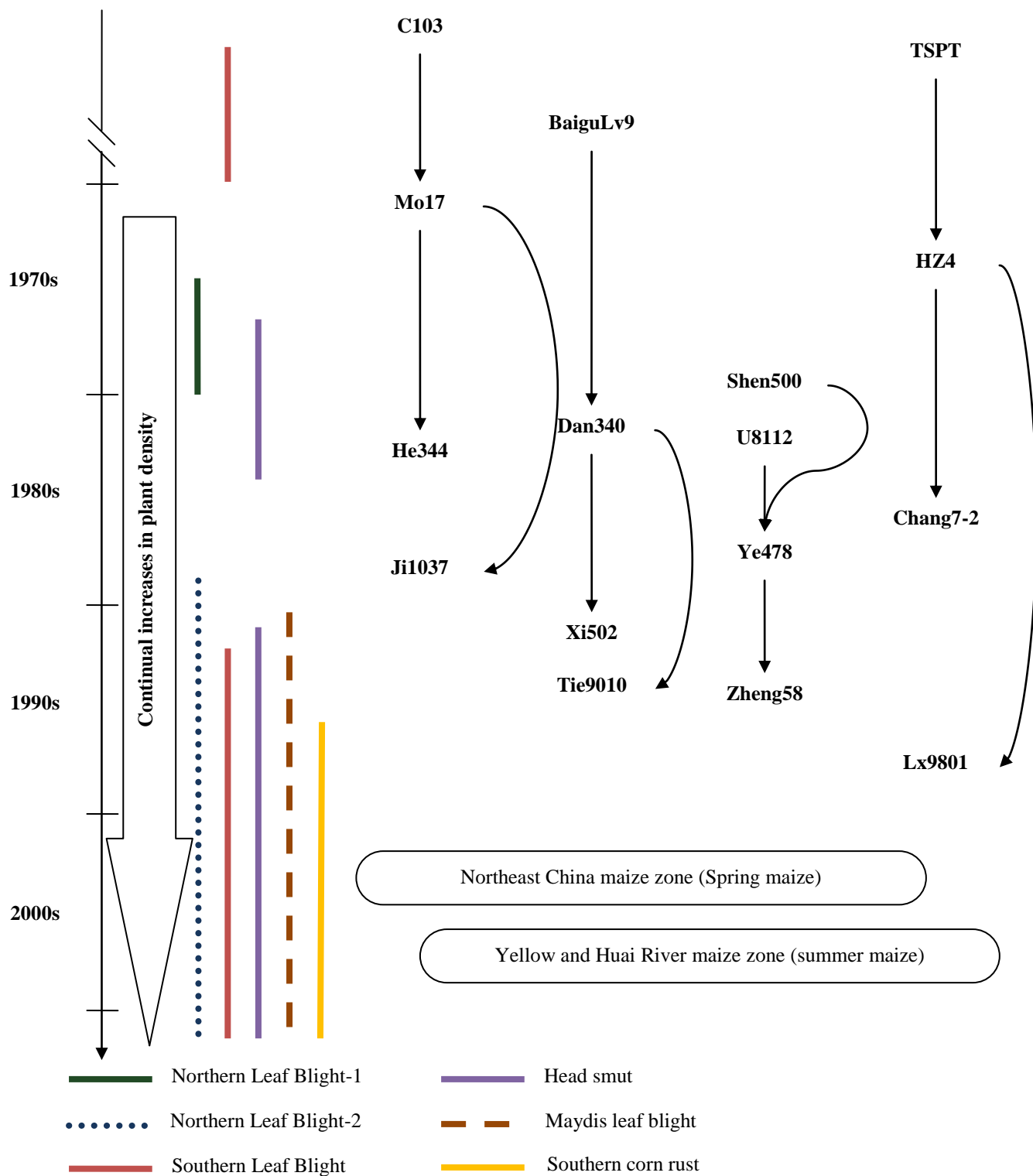


FIGURE 3 ELITE MAIZE INBRED LINES ADAPT TO DEMAND OF BREEDING. NORTHERN LEAF BLIGHT-1 CAUSED BY EXSEROHILUM TURCICUM RACE 1 AND NORTHERN LEAF BLIGHT-2 CAUSED BY EXSEROHILUM TURCICUM RACE 2. DATA FROM LI AND WANG (2010), WANG ET AL. (2006).

2.1 Ye478

Inbred Line Ye478 was important maize inbred line in the Yellow and Huai River maize zone where one main maize production region in China. Mr. Li Denghai, Laizhou academy of agricultural sciences, developed Inbred line Ye478 from hybrid Shen5003 × U8112. The most obvious trait of Shen5003 is dwarf and U8112 is upright-leaf. Ye478's plant

characteristics are short, low ear attachment, thick and stiffness stalks. The leaves are upright, medium length, relatively width, and dark green with relatively stay-green and high net photosynthetic rate. The ear has medium length, with 12-14 kernel rows and medium channels between rows. The kernels are medium size, primrose yellow and dent type. It has a compact tassel with short and stand upright branches, medium of pollen quantity. It contributes resistant to lodging, drought and suitable for close planting. It possesses good combining ability, excellent yield, high nitrogen accumulation and wide-adaptation (Cao and Xu2000; Chen2012; Kong2009; Li et al.1999; Li and Wang2010; Liu et al.2009). Inbred line Ye478 was a parent of Yedan No. 13 which was the first popular, compact and large-eared single-cross hybrid (<http://www.most.gov.cn/>). The derived lines of Ye478 all inheritance plant characters from Ye478 and improve disease resistance (Northern Leaf Blight, Southern Leaf Blight, Maize Rough Dwarf Disease and so on) and ear characters (Kong2009; Liu2010). A very important improved line of Ye478 is Zheng58 which is a parent of Zhengdan958, the most widely grown cultivar at present in China (<http://www.most.gov.cn/>), and with better disease resistance than Ye478. Ye478's succeeded in renewed of varieties on account of it accommodates the changes of cultivation pattern which increase of plant density and changes of harvest equipment.

2.2 Huangzao4

Inbred line Huangzao4 (HZ4) was a typical example of China breeders take advantage of domestic maize germplasms and was widely used in the Yellow and Huai River maize zone (Zhang et al.2002). HZ4 was released in 1975. Breeders at Institute of crop of BAAFS (Beijing academy of agricultural and forestry sciences) and breeders at Institute of crop breeding and cultivation of CAAS (Chinese academy of agricultural sciences) worked together to developed HZ4 from open pollinated plant of inbred line Tangsipingtou (TSPT) (Zeng et al., 1996; <http://www.most.gov.cn/>). Its plant characteristics are medium plant height, medium ear attachment and stiffness stalks. The upper leaves are upright, middle part leaves with bigger angle between leaf and stem than upper, all leaves have dark green with medium length and width and high net photosynthetic rate. Ears are medium-short and with 14-16 kernel rows. The kernels are medium size, yellow with white on the top and flint type. Its tassel is compact, and with short and stand upright branches, and possess abundant pollen quantity. HZ4 has good combining ability, high harvest index, and efficient nitrogen utilization. It tolerate to cold, drought, high-density, and resistant to maize Dwarf Mosaic Virus, Southern Leaf Blight, Northern Leaf Blight (Cao and Xu2000; Chen2012; Kong2009; Li et al.1999; Zeng et al.1996). Besides the above characteristics, HZ4 is a medium-earlier maturity inbred line. So it was more popular in summer maize zone where unusual annual double-cropping rotation with wheat is. HZ4 showed excellent yield in hybrids that it with compact plant-type and shorter growth period. Hybrid Yandan No. 14 (HZ4 × Mo17) and hybrid Yedan No. 2 (Ye107 × HZ4) were particularly outstanding and popular. HZ4's shortcomings were poor lodging resistance, poor stay-green, susceptible to *Curvularia* Leaf Spot, Head smut, Gray leaf spot, and Common rust. Therefore, breeders put their effort to developed HZ4 for overcoming its short comings. Inbred lines Chang7-2 (another parent of Zhengdan958) and Lx9801 (a parent of Ludan981) and Ji853 (have bred at least 26 varieties) are the successful HZ4's descendants who inheritance HZ4's high combining ability and upright-leaf plant type. The reasons of HZ4's widespread use were it adapt require of high density and earlier maturity breeding in summer maize area.

2.3 Dan340

Another typical example of China breeders utilizes domestic maize landraces was Dan340. It has widespread used in northeast of China (especially in Liaoning province) where is the largest maize zone of China. Mr. Zhou Baolin and his colleagues, Dandong academy of agricultural sciences, developed inbred line Dan340 from cross Baigu Lu9 × Pod corn which irradiated by Cobalt-60. Dan340 inheritance high yield phenotypic traits from Baigu Lu9 and stress resistance from Pod corn, thus adapt the environment of Liaoning peninsula where flower-season weather is humid, rainy, warmth and sunless. Its plant characteristics are medium plant height, medium ear attachment, stiffness stalks and flourishing roots. The leaves are upright, medium length, width, yellow-green with relatively stay-green. Ears are long, thick with 18-20 kernel rows. The kernels are medium size, primrose yellow and half-dent type. Its tassel is flourishing with 9-11 branches, and possesses abundant pollen quantity. Dan340 has good combining ability, high harvest index, efficient nitrogen utilization, and wide-adaptation. It tolerate to drought, water-logging, saline-alkaline, and resistant to Northern Leaf Blight, Southern Leaf Blight and Head smut (Cao and Xu2000; Li and Wang2010; Liu et al.2009). Inbred line Dan340 was another parent of Yedan No. 13. Breeders make efforts to improve Dan340's disease-resistant ability with Gray leaf spot has already been a main plant disease at 1990s in northeast of China. Inbred line Xi502, developed from HZ4 × Dan340 and inherited combining ability advantages from parents, is an excellent improved inbred line which is the male parent of Xiyu No. 3 and

Yedan No. 20.Dan340 can turn into popular foundation inbred line in China because of it has strong resistance and excellent ear characters.

2.4 Mo17

Inbred line Mo17 is the most successful practice of direct utilizes exotic maize germplasm. Dr. Grogan Clarence Orval, under the direction of Prof. Zuber Marcus Stanley in University of Missouri, developed Inbred Line Mo17 from hybrid C103 × 187-2. Dr. Li jingxiong and crop breeding and cultivation of CAAS respectively introduced it from Canada in 1971 and from USA in 1974. The selection chief purpose of Mo17 was improved C103's lodging resistance. So its ear characteristics from both parents, more plant type characteristics from Inbred Line C103, and root characteristics from Inbred Line 187-2. Its plant characteristics are tall, medium high ear attachment and slender stalks with long internodes. The upper leaves are slope upward flat, middle part leaves are spread as parabolic, medium length, relatively narrow, and greenness with high net photosynthetic rate and long duration. Ears are long length, with 12 kernel row and medium channels between rows. The kernels are large size, with rust colored wall and little dent. Its tassel is spreading with 3-6 rigid branches, and possesses a small number of pollen. Mo17 has good combining ability, high nitrogen accumulation, efficient nitrogen utilization, medium growth duration, and wide-adaptation. It resistance to Northern Leaf Blight, Southern Leaf Blight and Head smut (Cao and Xu2000;Kong2009; Liu et al.2009; Troyer1999). But it popular in China, particularly in northeast of China, was due to it disease resistance and long internodes, so it could quick replace the use of Goldqueen germplasm. The improvements of Mo17 were aimed at stress resistance. Mo17 was the female parent of Zhongdan No. 2 which very popular in main maize production province other than Heilongjiang in the 1980s (<http://www.most.gov.cn/>). The most successful descendant of Mo17 is He344 which was the parent of more than 9 hybrid varieties (Li and Wang2010). The reasons of Mo17's widespread use were it has high disease resistance and suitable growth period.

III. FOUNDATION MAIZE INBRED LINES STACK A LOT OF EXCELLENT ALLELES

3.1 Foundation maize inbred lines are the combinations of favorable allelic

A majority of economically important plant agronomic traits are quantitative trait, and vulnerability to environmental influences (Lynch and Walsh1998). The basic process of maize improvement is to increase the frequency of favorable allelic (both major and minor genes), thereby obtain good synthetic traits (Olsen and Wendel2013; Wu et al.2014; Yang et al.2013). Classic maize breeding is a hybridization and selection process. And foundation maize inbred lines generate is a continuous favorable allelic pyramiding process that breeders unceasing make crosses of parents that possess desirable characteristics to create new gene combinations (Hallauer and Carena2009; Yamasaki et al.2005; Jiao et al.2012; Li et al.2009). And foundation lines with higher combining ability on account of their key allelic which have favorable additive effects and positive effect loci of general combining ability (GCA) (Rojas1952; Revilla et al.1999; Qu et al.2012; Qi et al.2013).

The quantitative genetics is an effective tool to study complex trait, and it can provides many genetic information for make genetic advances. Today, quantitative trait locus (QTL) mapping and association analysis are two common approaches to obtain the genetic information of phenotypic variation (Tanksley1993; Jannink and Walsh2002). Many researchers have application of QTL mapping strategy and association analysis to study of numerous economically important traits in foundation maize inbred lines. In the Ye478, dwarf trait is an important cause of it been widely used in maize breeding in China and the research hotspot of dissect it genetic base. Several studies found that Ye478 have more favorable locus which can reduce plant height or ear height than other inbred lines which include foundation lines (Zhang et al.2007; Yang et al.2008; Zhang et al.2010; Zhao et al.2011). A genome-wide association study (GWAS) for plant height by 277 maize inbred lines found that a favorable allele for the dwarf trait in bin 5.05-5.06 from Shen5003 propagate its derivatives Ye478 and Zheng58 (Weng et al.2011). For the Huangzao4, a short growth duration inbred line like the meaning of its name in Chinese, days to silking and growth period are two reasons of its popular in Yellow and Huai River maize zone breeding. Researchers found that Huangzao4 pyramiding many favorable allelic (reduce days to pollen-shedding and days to silking) and have difference allelic with its derivatives K12 (Huangzao4 × Subtropical maize) and Huangye4 (Huangzao4 × Yejihong) by mapping and association analysis (Wang et al.2010a; Wang et al.2010b; Zheng et al.2012; Yang2012). As for the Mo17, highly resistant Head smut of maize probably is a key cause of it been widely used in Northeast China maize zone. Some studies have found Mo17 is a favorable resistant Head smut allele harbored and the Major Resistance QTL qHS2.09 passed on to its derivative Ji1037 (Mo17× Suwan1) by mapping and fine mapping analysis (Chen et al.2008; Ji et al.2012; Li et al.2008; Weng et al.2012). For the Dan340, it is a high kernel row number inbred line. Lu et al. (2011) found that Dan340 pyramiding more favorable allelic (enhance kernel row number) than Ye478 by F2:3 population from the cross Ye478× Dan340. Foundation lines not only pyramid favorable allelic of key traits but also pyramid many other favorable allelic of numerous economically important traits. Take Huangzao4 for example, researcher found that its synthetic traits excellent and

have many favorable allelic of agronomic traits and ear traits and adaptability (Li et al.2013; Liu et al.2010; Zheng and Liu2013; Wang et al.2010a; Ku et al.2012).

High-throughput single nucleotide polymorphisms (SNP) genotyping by BeadArray™ platform (Illumina, CA) or SNPlex™ platform (Applied Biosystems, CA) and whole-genome sequence by next generation sequencing technology are powerful tool in population genetics researches and inbred development studies (Kim and Misra2007;Ganal et al.2011; Gupta et al.2008;Flintoft2010; Huang and Han2012).A total of 44,927 SNPs of the MaizeSNP50 Bead Chip were used to genotype 42 Huangzaosi-related lines, contrast genotyping data detected 15 conservative genetic regions which in Huangzao4 and majority Huangzao4’s descendants and some conservative regions not exist in Tangsipingtou (one parent of Huangzao4) (Wu et al.2014).Genome-wide deep resequencing of Ye478-related lines (Ye478, Shen5003, U8112, Zheng58) and sequencing of 278 temperate maize inbred lines show that U8112 is a major donator for Ye478 and Zheng58and the proportions of rare alleles continuously increased from U8112 to Zheng58 following the breeding and improve of Ye478 (Lai et al.2010; Jiao et al.2012).

TABLE 1

PERFORMANCE OF FOUNDATION LINES AND COEFFICIENT OF VARIATION OF FOUNDATION LINE’S PROGENY. DATE ADAPTED FROM YAN’S LAB PHENOTYPIC DATA (<http://www.maizego.org/index.html>) AND LIU (2010)

		Plant height (cm)	Ear height (cm)	Ear leaf width (cm)	Ear leaf length (cm)	Leaf number above ear	Ear length (cm)	Ear diameter (cm)	Kerner number per row	100-grain weight (g)	Silkin g time	Pollen shed
Range	P ^b	107.2-220.5	17.6-103.4	6.23-11.37	54.4-93.83	4.3-7.4	6.88-17.35	2.52-4.71	12.9-32.9	11.8-30.6	59.7-82.7	57.6-82.2
HZ4	P	138	48.3	7.09	60.66	4.7	8.93	3.62	16	20.4	66.8	64.1
	C ^c	14	20.45				19.35	17	21.3	24.2		
Dan340	P	153.4	63.5	9.75	72.07	4.8	10.77	4.27	21.3	21.2	72.5	71.2
	C	14.14	22.76				19.52	12.02	26.02	26.28		
Mo17	P	176.6	55.4	8.3	61.42	5.2	13.35	3.32	23.1	23.6	71.2	67
	C	13.92	23.96				13.81	11.39	21.24	19.98		
Ye478	P	142.4	49.7	8.48	65.23	5	12.12	3.8	20.8	23.8	71	69.4
	C	12.77	23.63				9.74	12.13	18.36	14.57		
B73	P	173.3	66.6	8.05	67.35	5.5	11.22	3.61	21.8	19.2	73.8	69.2
Average ^a	P	173.2	64.7	8.49	71.55	5.7	12.17	3.7	21.2	16.6	72.2	70.2

^aAverage value of 508 lines; ^bPerformance of lines; ^cCoefficient of variation of foundation line’s progeny

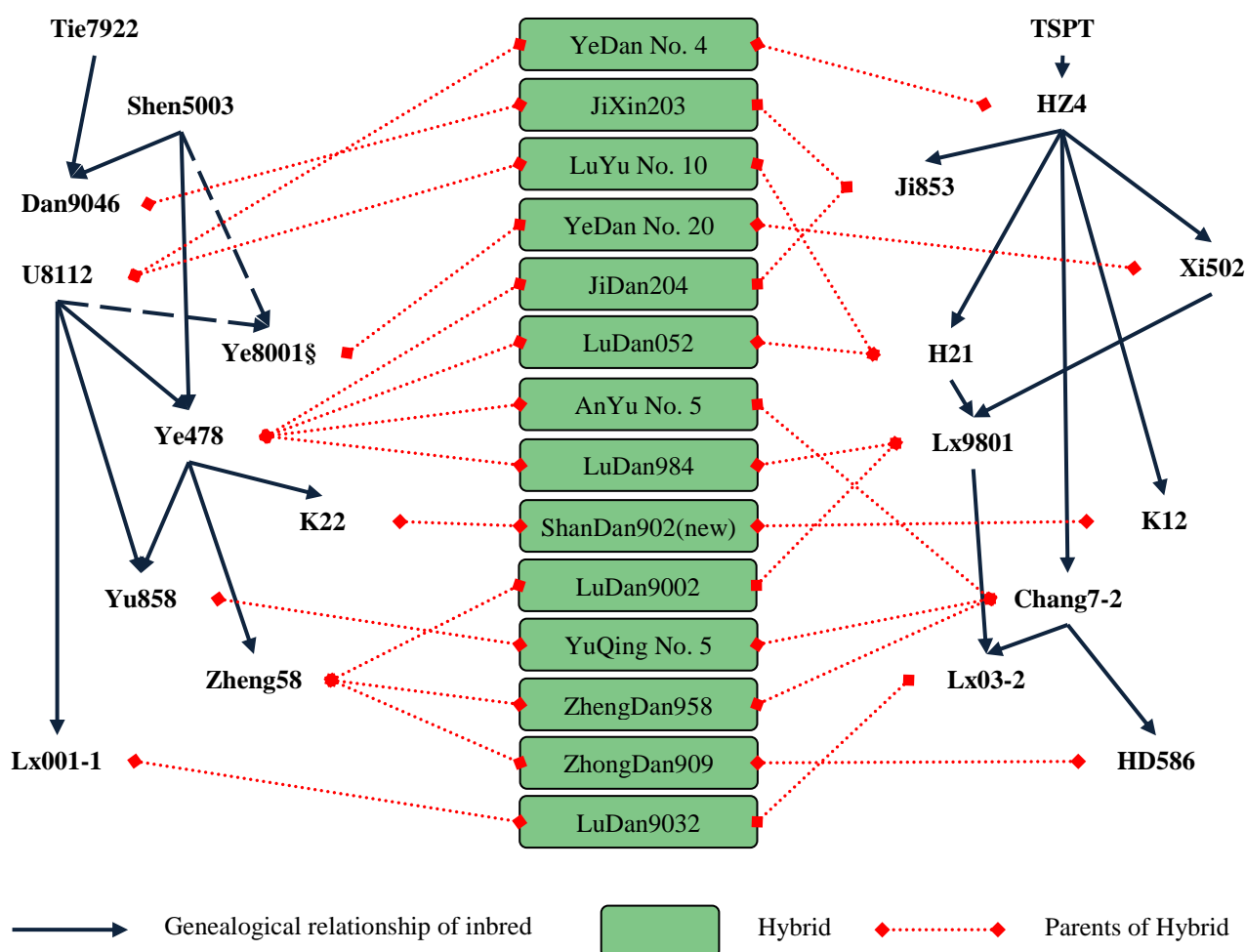
3.2 Foundation maize inbred lines are the representative of its heterotic group

Maize was one of the most successful examples of the utilization of heterosis in crops (Duvick1992, 1999).The development of foundation maize inbred line has close connection with the utilization of heterosis in maize (Teng et al.2004; Meng et al.2010; Wu et al.2010).

Since Shull formally defined the phenomenon of heterosis (or hybrid vigor) which hybrid offspring phenotypic performance superior to their parents in 1908, it has be researched and harnessed over 100 years (Shull1908). Some mechanisms have been proposed to explain heterosis. Classics hypotheses to understanding the genetic basis of heterosis at the level of genes are dominance, over dominance and epitasis (Schnable and Springer2013; Wallace et al.2014).The dominance hypothesis considers that the slightly deleterious recessive alleles were complemented by superior alleles in hybrid offspring (Jones1917; Crow1999).The over dominance hypothesis argues that allelic interactions within each of many genetic loci lead to superior performance over the homozygous parents’ inbred lines (Shull1908; Lippman and Zamir2007).And the epistasis hypothesis attributes that interaction between non-allelic genes at two or more loci generate superior phenotypic expression of a trait in hybrids (Powers1944; Goodnight1999).There have been many studies in which three hypotheses have been demonstrated in Arabidopsis, rice, tomato and maize (review in Lippman and Zamir2007; McKeown et al.2013; Schnable and Springer2013).Current explaining of the genetic basis of heterosis are gene balance hypothesis and allele-specific gene expression hypothesis. The gene balance hypothesis argues that heterozygous have more favorable dosage balances than homozygous in multiple genes framework (Birchler and Veitia2007, 2010).And the allele-specific gene expression hypothesis considers that heterozygous have a broad activity range than homozygous at the level of protein; therefore hybrids could selective favorable protein synthesis and metabolism in a given environment (Goff2011). The two hypotheses both don’t exclude the classics hypotheses but are the unifying theory for general multigenic heterosis. There are many researches in which transcriptomes and proteome and epigenomic demonstrate that many molecular mechanisms together produce

heterosis in complex traits (review in Chen2010, 2013; Goff and Zhang2013; Hochholdinger and Hoecker2007; McKeown et al.2013; Xing and Zhang2010). So, we could draw a conclusion that the utilization of heterosis requires widespread variation between the parents and the alleles have excellent performance.

Maize inbred lines possess highly variation at genome (Jiao et al.2012; Liu et al.2003; Wu et al.2014). The genome variations which mainly include SNPs, transposon insertions and indels engender abundant trait variations (Wallace et al.2014). And a series of studies indicate that many traits which from agronomic trait to physiological trait of maize show heterosis (Flint-Garcia et al.2009; Mehta and Sarkar1992; Tollenaar et al.2004). Quantitative trait loci, analysis of gene expression and researches of epigenetics in maize documented that heterozygous play an important role in its heterosis (Barber et al.2012; Guo et al.2006; Qin et al.2013; review in Schnable and Springer2013). Four major heterotic groups in China been widely used: Lancaster, where mainly meant Mo17 and its related lines; Reid, where from hybrids of Pioneer and their combining ability similar to U.S. Reid, such as Tie7922 and Ye478; Tangsipingtou, where from landrace Tangsipingtou and mainly meant Huangzao4 and its descendants; Luda Red Cob, where from landrace Luda Red Cob and mainly includ E28, Lu 28, Dan340 and their related lines (Teng et al.2004; Wang et al1997; Zhang et al.2000). Each heterotic group has its unique conservative genetic regions compared with other heterotic groups (Wu et al.2014). In conclusion, we could describe the foundation lines breeding process as follow: breeders make use of domestic landraces and exotic germplasm breeding inbred lines in early stage of China maize breeding; then, they found that some inbred lines easier obtain excellent hybrid than others, later they heavily utilized the better inbred lines to improve, and finally the best improved inbred lines turn into foundation lines and the representative of their related lines. In turn, foundation lines and their related lines been divided into several heterotic groups to guide maize breeding. Hence, the formation of foundation maize inbred lines in China was both a result which the utilization of heterosis, and a cause which the widely utilization of heterosis (Figure 4).



§Ye8001 from cross Ye488 × Ye3189, and the two parents both from Shen5003 × U8112.

FIGURE 4 FORMATION AND UTILIZE OF ELITE INBRED LINES AND ITS HETEROTIC GROUP, TAKE YE478 AND HZ4 FOR EXAMPLE.

IV. SUMMARY AND INTEGRATION

Foundation lines play an irreplaceable role in maize breeding (Troyer1999;Zhang et al.2000). Accordingly, there are important theoretical value and practical significance of that research inheritance and breeding law of maize foundation lines. In this review, we analyze the formation of maize foundation lines at three level which were source-sink-flow, environmental adaptation and molecular level. It's concluded that maize foundation lines pyramiding abundant favorable allelic and distinctive allelic to show excellent performance (plant type, net photosynthetic rate, yield, stress tolerance and so on) and heterosis in its hybrid.

The formation of maize foundation lines is a fascinating subject, but breeding new foundation lines is more exciting. Now, most inbred lines had been selection from narrow-based populations which include single-cross combinations, double-cross combinations and backcross populations (Hallauer and Carena2009; Liu2002). The long-term commercial breeding programs are used with continued selection within specific groups of inbred lines to create new inbred lines (Duvick2004; Hallauer and Carena2009; Troyer999).Summary the breeding and improving of China maize foundation lines found that intimating and recycling within better inbred lines from same germplasm sources is effective method to breeding new better inbred lines (Table 2). In addition, germplasm enhancement and innovation are equally important for foundation lines breeding because they maybe provide some rare allelic which aim at specific breeding goal. Along with the rapid change of environment and increased information of maize genetics, the breaking and forming of heterotic groups might more important for maize breeding, so cross-bred between heterotic groups could more common for breeding and improving of maize foundation lines in next cycle breeding.

TABLE 2
SUMMARY OF FOUR FOUNDATION LINES

Elite inbred line	Pedigree	Common characteristic	Typical characteristic	Heterotic group	Breeding method	Improvement method
Ye478	Shen5003× U8112	Plant-type compact or slender, high combining ability, wide adapted and high yield.	Dwarf plant and stalk stiffness.	Reid	Crossbreeding within heterotic group.	Crossbreeding within heterotic group.
Huangzao4	Open pollinated plant of inbred line TSPT		Medium-earlier maturity.	Tangsipingtou	Crossbreeding and germplasm enhancement.	Crossbreeding within heterotic group or between heterotic groups.
Dan340	Baigu Lu9 × Pod corn		Large ear and high resistance to adversity.	Luda Red Cob	Crossbreeding and germplasm innovation.	
Mo17	C103 × 187-2		High disease resistance.	Lancaster	Crossbreeding between heterotic groups.	Crossbreeding and germplasm enhancement.

The trend of maize breeding in China mainly consist of grain yield increased (particularly in high planting density), plant type changes to more upright and tolerance to lodging to accommodate high planting density and harvesting mechanization, and yield stability enhance through resistant improvement (Ci2011b; Ci et al.2012; Ma et al.2014).In China today there are some new challenges for maize production: first, more intense drought conditions for much of maize production region; second, rural labor shortages and the relatively low income of agricultural production impact on the traditional cropping patterns; besides, new maize disease prevalence in part or whole maize area, e.g. maydis leaf blight in the Yellow and Huai River maize zone or sugarcane mosaic virus (SCMV) and maize rough dwarf virus (MRDV) in the Yellow and Huai River maize zone and the north zone (Li2009a; Zhang and Bonjean2010; OECD-FAOOutlook2013).This trends and challenges present new requirements to the maize foundation lines breeding. Therefore, new maize foundation lines might manifest as semi-dwarf and low ear height, upright leaf above ear, lower spatial density of leaf area (LAI/ plant height) above ear and high spatial density of leaf area below ear, medium ear and with loosely and moderate number husk, tolerance to lodging and

drought, possess the resistance of main disease. According to these features, Zheng58, Chang7-2 and Lx9801 could replace the use of Ye478 and HZ4 and play an important role in maize breeding.

The basic germplasm selection was key element for new foundation lines breeding. In China, exotic germplasm which main introduced from the US Corn Belt and domestic germplasm which main from landraces or open-pollinated varieties (OPVs) also plays an important role in maize breeding, and maize breeders developed a number of important inbred lines based on these germplasm (Liu2002; Zhang et al.2000). These lines were divided into five major heterotic groups in breeding practice (Li and Wang2010).The normal mode of present-day maize breeding is development of improved inbred lines via recycling of foundation lines, and the predominant development method is continues to include crossing foundation by foundation to generate genetic variability and selfing to derive inbred lines (Hallauer and Carena2009; Li and Wang2010).These conclusions indicate that the new maize foundation lines breeding should mainly choose foundation lines which could better adapted to local environmental and with highly GCA as basic germplasm, and these basic germplasm should belong to same heterotic groups and overcome the respective defects. Moreover, we could choose some lines which possess particularly traits as donor to improve foundation lines through back-cross breeding.

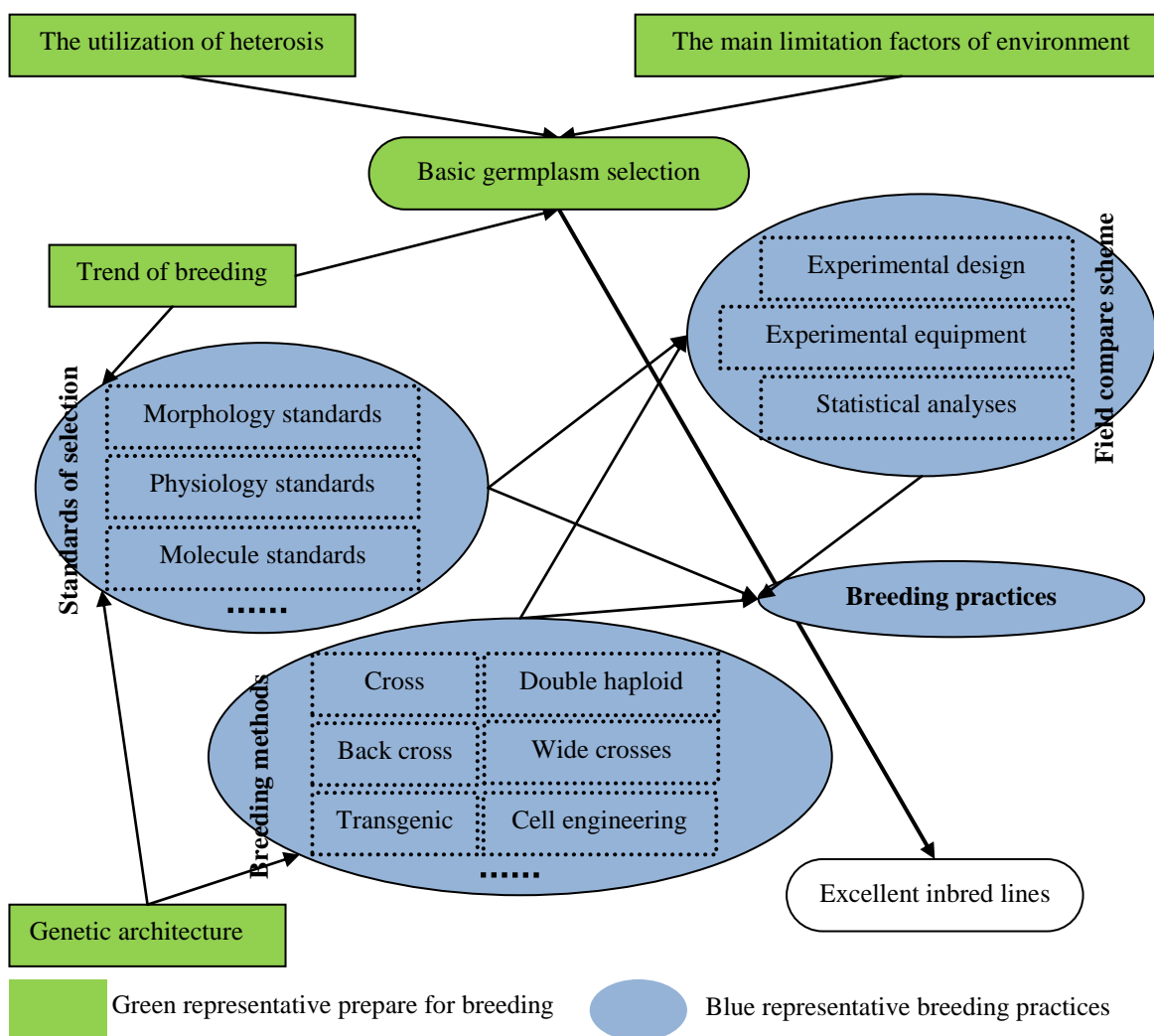


FIGURE 5 FLOWCHART OF MAIZE BREEDING.

Maize inbred lines breeding mainly include three steps that generate genetic variability, selfing, and evaluation and select expected allele combinations. The major method of generate genetic variability is cross breeding, because it could generate enough genetic variability and simple (Hallauer and Carena2009; Liu2002). Sometimes breeders take advantage of back-cross breeding to improve foundation lines. And now gene modification (GM), it could create new allele combinations which does not exist in nature, has already contributed to maize improvement to resistant pests and herbicides. The major method of select is pedigree select, because it could discard inferior genotypes before lines are further evaluated, compare the

performance of generations involves a different environment and estimate the genetic relationship of lines (Liu2002). Recurrent selection, could concentrate favorable genes scattered among a number of individuals, also often be used to develop inbred lines. Besides, molecular assisted selection (MAS) and genomic selection (GS) have been proven to be effective for some traits (Massman et al.2013; Steele et al.2013; Zhao et al.2012). But most of economically important plant agronomic traits are quantitative trait, foundation line concentrate numerous major and minor gene, and foundation line breeding involve many traits, so combine cross breeding and pedigree selection as the main approach and with other methods might be the better method for new foundation line breeding.

Rapid advances in plant-breeding technology directly and indirectly impacted maize breeding. Non genetic developments main include developments in experimental design and statistical analyses, experimental equipment, and computer hardware and software to collect and analyze data (Hallauer and Pandey2006). Genetics progress encompass developments in dissects for the genetic architecture of complex traits, analyze the structure of breeding populations, create genetic variation, and identify and select the best individuals with desirable genetic features (Xu2010). These developments provide many tools for integrate method of breeding (Figure 5):

- 1) The utilization of heterosis, the trend of maize breeding, and the main limitation factors of environment guide the selection of basic germplasm.
- 2) The trend of maize breeding, the genetic architecture of complex traits both determines breeding methods and standards of selection.
- 3) Breeding methods and standards of selection both determine field compare scheme.

The integrate methods of breeding will promote new foundation lines breeding because it can take advantage of many ways to create genetic variation and full considered phenotype (morphology performance and physical performance) and genotype to precise selection expected allele combinations into specific hybrids.

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CONFLICT OF INTEREST

The authors declare that they have no conflict of interest.

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