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Summary on Inheritance and Utilization Research of Chinese Waxy Corn Heterosis

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Since around 1570, corn variety was introduced into China, a special corn with waxy performance first formed in Guangxi province of China, after it was introduced American at beginning of Twentieth Century. Collins, C.H. first reported that gene mutation of the corn changes endosperm carbohydrates (including the type and amount of starch) and defined the corn as the waxy endosperm, and then named wx gene as a wax marker in 1909.

Because of these special properties of waxy endosperm, corn breeders proposed that the corn was found in China at the beginning of the twentieth Century was called Chinese Waxy Maige that is Chinese waxy maize (wx-c).

Since 1909 Chinese glutinous corn was introduced into American until mid twentieth Century, geneticists have revealed a series of basic genetic phenomenon, promoted the development of the genetics theory by using wx-c as a marker gene in genetic research and trialing system.

USA corn breeder Sprague, G.F. began to make use of these specific genetic resources in breeding programs in 1930s, and USA maize breeder Jenkins, M.T. had bred the earliest glutinous corn hybrids in Iowa in the early 1940s.Waxy corn planting area increased significantly in America because of the new discovery of waxy corn starch application in 1960s. Thus, America development of waxy maize breeding has always been closely linked with the use of waxy corn as raw materials in starch industry.

Ⅰ Improvement and innovation of Chinese Waxy Maige germplasm

1 Germplasm

Breeders have revealed open pollinated varieties have significant genetic variation by researching the distribution of the yield traits additive genetic variance in different types of groups. Therefore, it is easier to obtain favorable genes and get the effective choice by selecting free pollination varieties as the original group of germplasm improvement. China is origin of waxy maize, contains abundant germplasm resources, no doubt, these landraces have experienced a long period of natural and artificial selection and have enough traits variation.

Yunnan, Guizhou, Sichuan provinces and Guangxi mountains, where are located in the upper areas of the Yangtze River, are the birthplace of waxy corn in China and are also the most concentrated distribution areas of landraces. Later, these waxy corn species have gradually spread to the lower areas of the Yangtze River that become a concentrated areas of local varieties of Waxy Maize later including Qidong, Haimen in Jiangshu province, Chongming in Shanghai and Hangjiahu plain in Zhejiang province. The waxy corn varieties in these areas become the core germplasm and representative germplasm of Chinese waxy corn because of the advantages including high quality, early maturity , various types of varieties and high temperature, plentiful rainfall, long growing period in the areas, especially in Qidong, Haimen

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and Chongming county.

In 1980s, I devoted to waxy corn germplasm research in the lower areas of the Yangtze River. I had ultimately bred 8 waxy open pollinated varieties including Qidong large particles of dent, Qidong purple dent, Qidong early mature flint, Haimen large particles of dent, Haimen early mature flint, Haimenxuehua nuo, Chongming large particles of dent and Chongming early mature flint after observation, identification of long-term and comparison. The composite variety groups were produced through the diallel cross and two rounds of isolation free pollination and were taken as original groups for applying to population improvement.

2 Population improvement

A Selection of goal traits

Starting from the study on morphology and physiological basis of high yield of waxy corn, determine the key target traits of selection that are as follows: Northern leaf blight-resistance (a)，southern leaf blight -resistance (b)，shorter internodes and good stem strength under ear (c)，developed root system (d)，compact plant type, lower plant height (e) according to the important degree. The genetic background (genotype) of selection indicated effectiveness of selection (Table 1).

Table 1 Genotype of target traits and selection effect

Genotype	Phenotype	Selection effect
Ht	Northern leaf blight-resistance	Genetic disease resistance controlled by multiple genes, Can effectively select
rhm	Southern leaf blight -resistance	Pathogenic type cytoplasm control specific resistance, similar with the major gene resistance, can effectively select
br、br2、br3	Shorter internodes and good stem strength under ear	Morphological variation of genetic simple controlled by main gene, can be used by selecting
Ct、Ct2、rd、rd2	Compact plant type, lower plant height	Morphological variation of genetic simple controlled by main gene, can be used by selecting

According to this goal, I designed the unique selection scheme in order to improve the effect of selection and recombination. Selection procedure is as follow. (1)In the original group, selected a large number of excellent plants to mate pairwise according to the 5 target traits, while a part of individual inbred, a part of individual pollinate freely, and then threshed in hybrid ear, inbred ear and free pollination ear ,and took equal seed from the 3 groups to mix ,then divided into 5 small groups. (2) planted the 5 small groups respectively, then the 5 small groups were allowed to self-copulate artificially by selecting strains in consecutive two-generations and ear row selected strains ,lastly even mix self-copulated seed when S2 generation are established. (3)S2 early generation mixed seeds with the 5 target traits were planted respectively ,then hybridize by a × b, a × c, a × d, a × e, b × c, b × d, b × e, c × d, c× e and d× e, lastly threshed from hybrid spike ,got equal seed and mix the seed. (4)Planted the

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mix the seed of combination of the various groups in the isolation zone, let it pollinate freely, and produced comprehensive population that obtained simultaneously improving in the 5 target traits.

B Combining ability selection

(1) General combining ability selection

In the comprehensive population（S0）, carried out selfing for continuous two generation and selecting plants according to number of ear rows, and then carried out progeny test of general combining ability by taking a waxy free pollinated variety as the female parent test variety by the time of S2 generation. According to the yield comparison test results of test crosses combination, even mixed the corresponding inbred line seed of high yield combination, after isolation free pollination , took the inbred line seed as the basis population of the next round of general combining ability selection （S0）.The second round of progeny test of general combining ability was carried out by taking a waxy corn hybrid variety- YandanNo.5 (Hengbai 522×Bai525) as the female parent test variety in the basis population, even mixed the corresponding inbred line seed of high yield combination, then produce improved population composited by the homozygous lines with a plurality of high general combining ability.

(2) Specific combining ability selection

If plant larger improved population (more than 0.2 hectares),so planting density cannot be lower than 45,000 plants per hectare. Select excellent single plant by batches and partition (at least 50 plants in each batch) from the improvement population to collect pollen, and mix the pollen. Use the mixed pollen to test cross with Hengbai 522 that is taken as improving line of female parent, at same time, pollinate the mixed pollen each plant that is collected pollen (hung signs according to the 1 to 50 sequence number for avoiding self pollen in pollination) ,then produce a series of small separation groups. Carry out Comparative experiments of testcrosses combinations yield Select several productive testcross combinations; use the small separation groups corresponding with productive testcross combination as the basic population of selection inbred line. The original group and groups after selection changed in the yield and character in the selection process (Table 2).

Table2. Changes of root & stem lodging rate in different groups within the selection trial

Population	Modified methods	Yield（g/m2）	Lodging rate（%）	
			Root	Stem
Compound variety Population	Original group	431	17	15
Comprehensive population	Combining ability selection	521	8	7
Modified population	General combining ability selection	575	3	2
Separation small population	Specific combining ability selection	603	0	0

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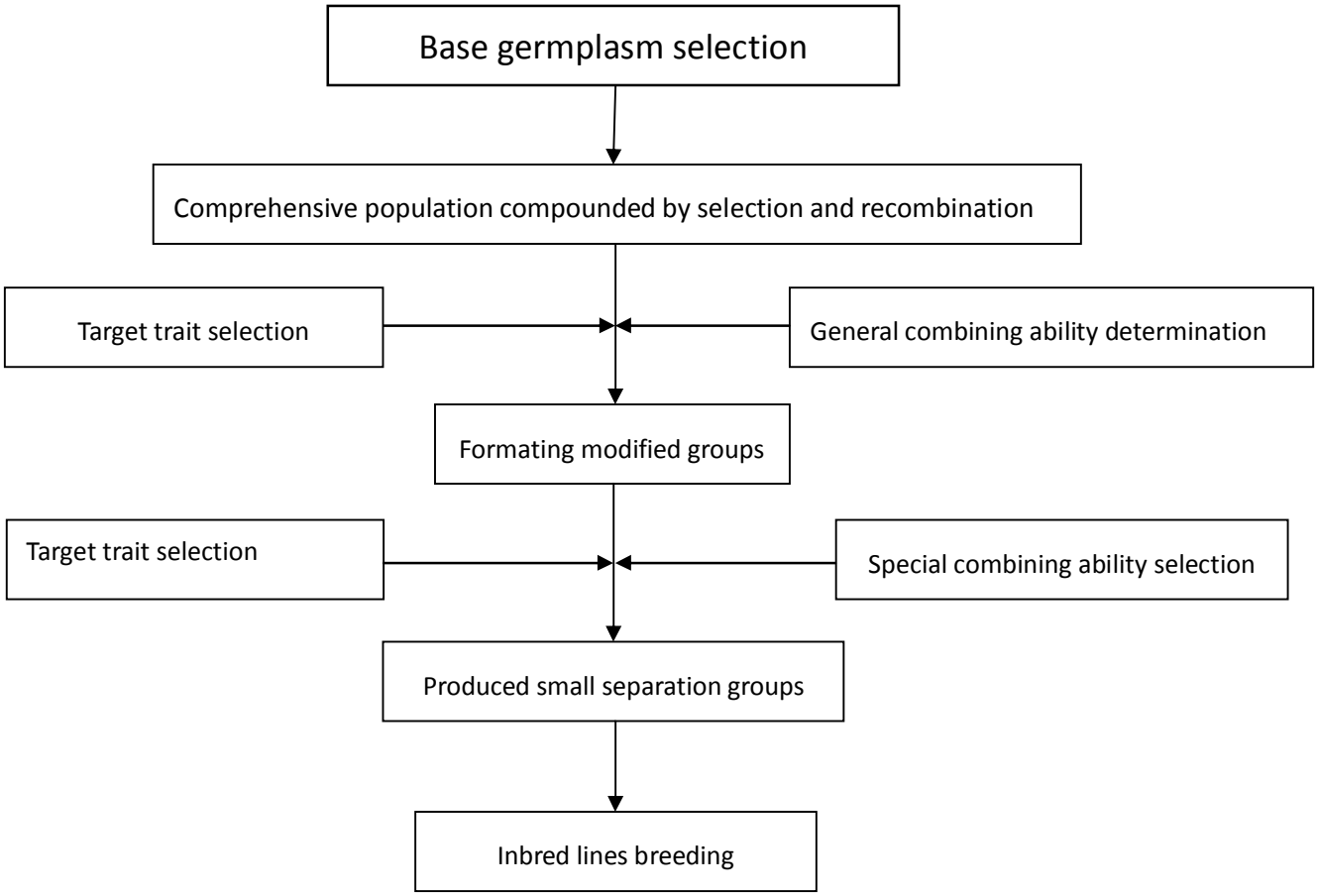
The small separation population is a new concept of population genetics proposed by the author who based on breeding practice and basic research. Its basic meaning is that improved population with continuous yield improvement effect produced by cycle options of the target traits and general combining ability, as well as the effective self-separation in free pollinated varieties population with the large genetic variability. It was screened out to basic population of lines newly selected (small separation population) that effectively polymerized Excellent genes (including roots strength, resistance to disease, combining ability) through specific combining ability selection of pollen group that synthesized by Excellent single plant pollen In the improved group (Figure 1).

Figure1. Production process of small separation groups



C Breed inbred lines by using the small groups of separation

The pertinence of breeding inbred lines strengthen, probability of breeding excellent inbred lines naturally become high by using the small groups of separation, because the most important factors(lodging resistance, disease resistance and combining ability), which affect the waxy maize yield, have been improved through genetic improvement in the small groups of separation.

Shull, G.H. (1909, 1910) pointed out that self-segregating is the fastest method to select homozygous lines by using free pollination varieties. A ring of originality-inbred line---Tongxi 5

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with typical high combining ability was successfully bred by using self-segregating method in TP5 separation small groups that originate free pollination varieties.

Tongxi 5 has become the core germplasm of Chinese waxy maize breeding, because its upper leaves are strong and vertical, its plant type is compact, its lodging resistance and disease resistance is extremely strong, its adaptability is extremely wide(Figure 2, figure 3).

Figure 2. Plant type of Tongxi 5 and its ear

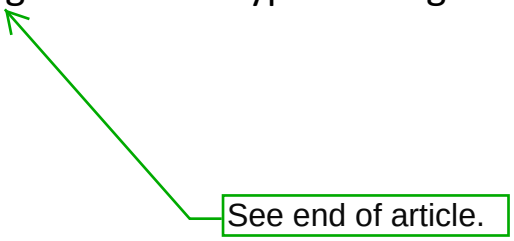

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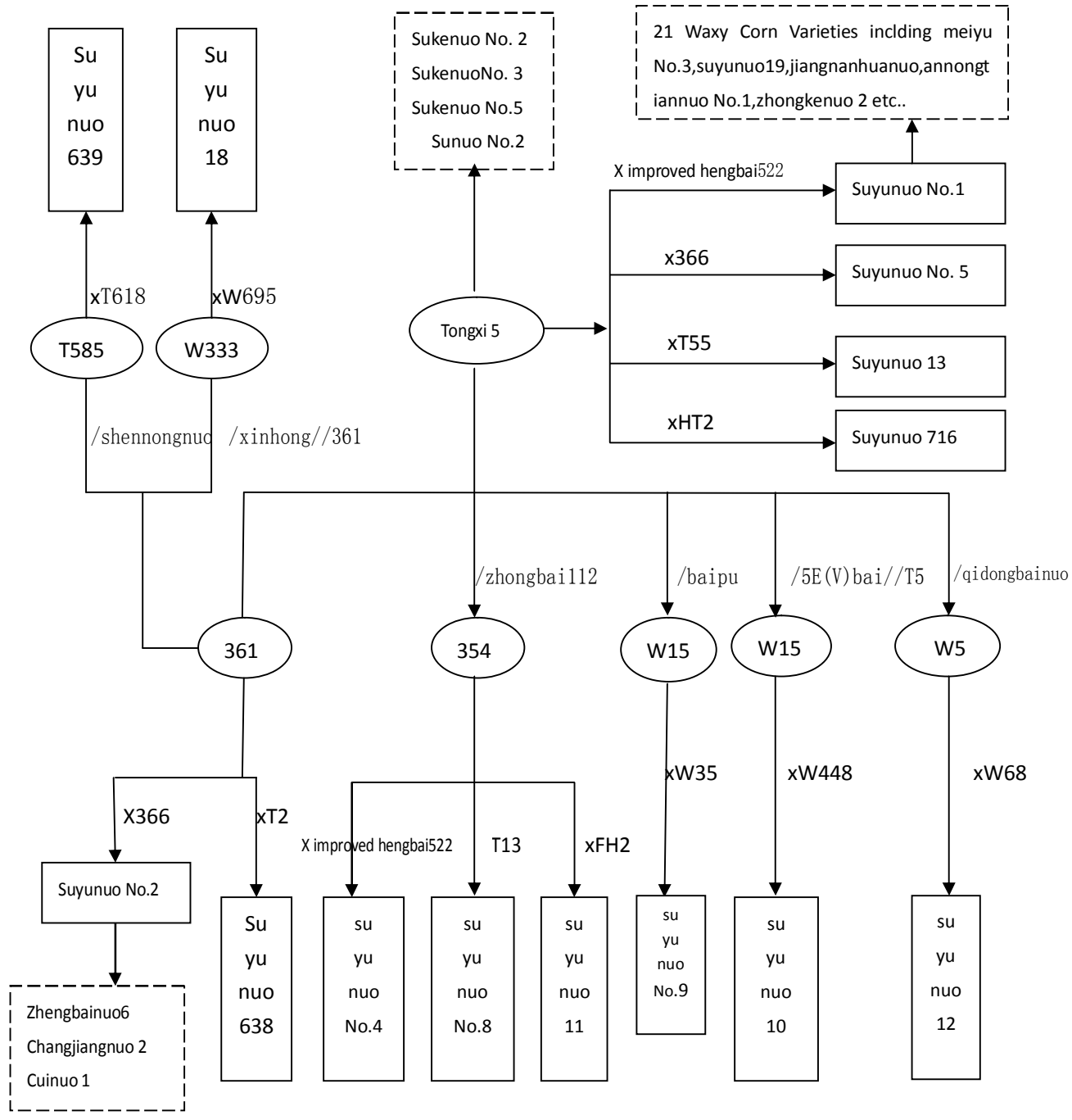
Figure 3. Pedigree of Germplasm use on Tongxi 5 and its derivative lines



Note:

Represents Tongxi 5 and its derivative lines;

Represents varieties bred by this unit;

Represents varieties bred by other units using Tongxi 5 and its derivative lines.

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Taking Tongxi No.5 as female parent cross with modified hengbai 522, had bred the first typical waxy maize hybrid Suyunuo No. 1 with high yield and quality in China, Suyunuo No. 1 also is the largest promotion area and longest waxy maize hybrids in China (Fig. 4).

Fig.4. Plant type of Suyu waxy No.1 and its ear

See end of article.

In Jiangsu province, 15 breeding units, such as Jiangsu agricultural academy of Sciences, Nanjing Agricultural University etc, bred a series of waxy maize hybrid by taking Tongxi No.5 or its derivative lines as parents. Statistics showed that 14 varieties contain blood of Tongxi No.5 in 23 waxy maize hybrids approved by Jiangsu variety approval committee, accounted for 60.8%. The result showed the 28 varieties contain blood of Tongxi No. 5, accounted for 70% through analyzing on the national Huanghuaihai and National Southeast waxy corn regional test covering 12 provinces (regions) in China.

II Study on inheritance and utilization of Chinese waxy maize heterosis

1 Genetic characteristics of Tongxi No.5

A Genetic specificity of basic Germplasm

It analyzed to Genetic diversity of 184 maize inbred lines (including 73 waxy maize inbred lines and 111 ordinary maize inbred lines) by using SSR markers. According to UPGMA method, 184 maize inbred lines were clustered into 9 subgroups: there are 6 inbred lines (including 3 waxy maize inbred lines from the Jiangsu Nantong area and 3 selection lines from tropical ordinary maize improvement group) in subgroup Ⅰ; there are 7 waxy maize inbred lines that all derived from T4 germplasm in Thailand subtropical region in subgroup II; there are 26 inbred lines (including 21 waxy maize inbred lines derived from improved Hengbai522 & T4 germplasm and 5 selection lines from tropical ordinary maize improvement group) in

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subgroupⅢ; there are 50 inbred lines (including 36 waxy maize inbred lines almost derived from T4 germplasm and 14 inbred lines almost derived from ordinary maize inbred lines that have kinship with Huangzaosi in subgroupⅣ;The remaining subgroups are common maize inbred lines.

The Genetic diversity analysis showed that: (1) the waxy corn is mainly distributed in the subgroups Ⅰ ~ Ⅳ, Tongxi No.5 and its derivative lines is in the subgroup IV, improved hengbai 522 and its derivative lines and T2 are in subgroup III and the subgroup II respectively; (2) Tongxi No.5 is a excellent germplasm with unique inheritance basis and genetic specificity; (3) Tongxi No. 5, improved hengbai 522 and T2 formed heterosis groups respectively, they provides a theoretical basis for utilization of heterosis (Figure 5)

Fig.5. Genetic specificity of basic germplasm of Tongxi No.5

See end of article.

B High combining ability

The Diallel cross analysis showed that Tongxi No.5, which is derived from the lower areas of the Yangtze River , has not only very high combining ability with improved hengbai 522 ,which is derived from the north area of China ,but also has more higher combining ability with subtropical germplasm T2, which is derived from Thailand (Table 3). This provides a genetic basis for taking Tongxi No.5 as core germplasm to construct heterosis models between the southern germplasm and Northern germplasm, as well as between temperate germplasm and subtropical germplasm.

Table 3.Combining ability of Tongxi No.5 ×temperate germplasm and Tongxi No.5 ×subtropical germplasm

Inbred lines	Tongxi No.5	361	354	W152	W331	GCA
T2	4.3	3.7	1.25	-0.9	2.3	4.0
RF	-0.4	5.7	-1.1	-2.9	-3.1	1.8

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R8	0.2	-8.5	-3.1	0.4	-4.6	-4.5
Improved Hengbai 522	3.1	2.9	2.6	2.9	-1.5	0.8
Hu-1	3.3	1.9	1.9	3.0	1.1	2.0
366	3.9	4.2	2.8	1.7	3.3	2.7
Nanzi	1.3	-0.3	-8.9	-7.2	-4.2	-6.8
GCA	3.5	3.6	-4.3	-1.5	-1.3	—

2 Tongxi No.5 ’quality characteristics for starch industry

Glutinous corn is mainly used for wet milling industry, research and breeding of waxy corn is to meet the needs of wet milling industry in developed countries such as America and Europe. Waxy endosperm hybrids Combined by selecting and breeding inbred lines, which are suitable for wet grinding process, can be used to extract the waxy starch modified. Tongxi No.5 has excellent quality of food and wet grinding industrial corn (Table 4), it will enable this unique high molecular material expand its application in wet grinding industry to combine waxy endosperm hybrids with Tongxi No.5.

Table4. Tongxi No.5 ’quality characteristics for starch industry

Inbred lines	Peak of viscosity （cp）	Valley of viscosity（cp）	Finality of viscosity （cp）	Sediment ation of viscosity （cp）	Cut of viscosity（cp）	Pasting time （min）	Pasting temperature（℃）
Tongxi No.5	1808	883	991	924	-817	4.1	74. 7
Improved Hengbai 522	749	678	786	70	37	5.5	75.5
T2	1320	620	714	700	-606	3.9	72.3
361	1069	348	446	721	-623	3.7	71.6
366	1615	850	969	766	-646	4.1	74.5

3 Heterosis utilization

A Constructing model of Tongxi No. 5 heterosis group × modified hengbai 522 heterosis group

Tongxi No.5 and improved Hengbai 522 are 2 parental inbred lines of Suyunuo No.1, WA4 and HTB42 are 2 parental inbred lines of a common corn single hybrid. It carried out to use tongxi No.5 and improved Hengbai 522 cross with WA4 and Htb42 each other, and carried out the comparative trials of yield in the different cross combinations. The results showed that yield of 361 (derived from Tongxi No. 5 × WA4) × 366 (derived from improved hengbai 522×HTB42) is the highest; finally, Suyunuo No.2 was bred (361 × 366).

A series of derivative lines were bred by further using Tongxi No.5 and modified hengbai 522 as ancestry, Hybridization between a large amount of derivative lines of Tongxi No.5 and modified hengbai 522 showed high special combining ability, it approved the first heterosis model of contemporary waxy corn single cross as follows (Table 5 and table 6).

Table 5.A series of hybrids bred by using Tongxi No.5 as core germplasm

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Heterosis models	Varieties	Parental combinations	Variety certification
TongxiNo.5 group × Improved Hengbai 522 group	Suyunuo No.1	TongxiNo.5×Improved Hengbai 522	National approval in 1999
	Suyunuo No.2	361（Derivative line of Tongxi No.5）×366（Derivative line of Improved Hengbai 522）	National approval in 2003
	Suyunuo No.3	365（Derivative lines of Tongxi No.5）×359（Derivative line of Improved Hengbai 522）	Nantong government approval in 1998
	Suyunuo No.4	354（Derivative line of Tongxi No.5）×Improved Hengbai 522	National approval in 2003
	Suyunuo No.5	Tongxi No.5×366（Derivative line of Improved Hengbai 522）	National approval in 2003
	Suyunuo No.8	354（Derivative line of Tongxi No.5）×T137（Derivative line of Improved Hengbai 522）	National approval in 2004
	Suyunuo No.9	W15（Derivative lines of Tongxi No.5）×W35（Derivative lines of Improved Hengbai 522）	Zhejing provincial government approval in 2004
	Suyunuo No.10	W150（Derivative line of Tongxi No.5）×W448（Derivative line of Improved Hengbai 522）	Jiangsu provincial government approval in 2005
	Suyunuo No.11	354（Derivative line of Tongxi No.5）×FH2（Derivative line of Improved Hengbai 522）	Jiangsu provincial government approval in 2006
	Suyunuo No.13	T55（Derivative line of Improved Hengbai 522）×Tongxi No.5	National approval in 2007
	Suyunuo No.18	W333 Derivative lines of Tongxi No.5）×W695（Derivative line of Improved Hengbai 522）	Jiangsu provincial government approval in 2008
Tongxi No.5 group×T2 group	Suyunuo No.12	W5（Derivative lines of Tongxi No.5）×W68（Derivative line of T2）	Shanghai municipality government approval in 2006
	Suyunuo No.716	Tongxi No.5×HT2（Derivative line of T2）	Zhejing provincial government approval in 2010
	Suyunuo No.638	361（Derivative lines of Tongxi No.5）×T2	National approval in 2008
Tongxi No.5 group×the other germplasm group	Suyunuo No.639	T585（Derivative lines of Tongxi No.5）×T618（Derivative lines of the other germplasm）	National approval in 2010
	Suyunuo No.901	W935（Derivative lines of Tongxi No.5）×W8（Derivative line of the other germplasm）	National approval in 2013

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Table 6.Model of Tongxi No. 5 heterosis group × modified hengbai 522 heterosis group

Heterosis group	Tongxi No. 5 group	Modified Hengbai 522 group
Germplasm source	Local varieties come from the lower areas of the Yangtze River including Qidong and haimen in Jiangsu, Chongming in Shanghai.	Local varieties come from Hengshui area in Hebei province
Core Germplasm	TP5 small group of separation	Mixed pollen group consist of selecting modified Hengbai 522
Originality line （representative line）	Tongxi No. 5 group	Modified Hengbai 522
Typical derivatives lines	354、361	366
Typical combination	Tongxi No. 5× modified hengbai 522	

A reasonable principle of tester selection has been drawn from this model of heterosis that is that tester is selected according to sources of inbred line. For example, if you want to test inbred lines with Tongxi No.5 germplasm, you will mainly take the inbred lines with Tongxi No.5 blood kinship as tester, and vice versa.

It provides basis of reasonable parent selection for breeding second cycle lines to construct the basic material of breeding new inbred lines according to heterosis patterns and select corresponding parent for combining new hybrids, and then the breeding technology come into the theoretical thinking mode.

B Constructing model of Tongxi No. 5 heterosis group × T2 heterosis group

In the early 1990s, I got a free pollination waxy corn variety (a subtropics germplasm) from the Thailand NaKhonra jsrima through the international wheat and Maize Improvement Center (IMMYT).

After a year of planting the variety, this variety showed very large variability, its plant and yield are all high, but its mature period is late, must first modify mature period of the variety. Early silking of corn is dominant genetic trait to late silking of corn, it can separate earliness gene from germplasm through mixing selection of early silking plants. The objective of mixing selection of successive 2 rounds of early silking plants in the variety population, is to make the selection offspring conducted for early mature adapt to the growth condition of temperate zone. At same time, the plant height and ear height also reduced, this Improved varieties groups named T2 improved varieties group.

T2, which comes from free pollination varieties, contains a series of the heterozygous genotype, was used as the basis group of inbred lines breeding, such, frequency of getting excellent pure lines is high. The initial population of selection is large (3000 plants), a large number of selecting plants self, and then strictly eliminate according to trait selection.

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Eliminate 50% of plants in the S1 generation by visual inspection, go on eliminating in S2, S3 and S4 generation, selfing and test crossing are conducted in same plant at same time, timely eliminate plants according to testcross yield. In S4 generation, collect pollen of excellent plants with 2 or 1 of lodging resistance, disease resistance and good combining ability, to form some small groups of mixing pollen. Plant these small group, self and separate respectively until S2 generation, equally mix seeds of early generation inbred lines, plant the mixed seeds in isolation area and continue to self and separate. Lastly, determinate the combining ability when the varieties become homozygote.

73 testcross combinations were obtained by selecting Tongxi No.5 and its derivatives 354, 361 and improved Hengbai 522 and its derivatives 366 to testcross with excellent early generation lines of T2 improved varieties group, carried out yield comparison trial of 73 testcross combinations by taking Suyunuo No. 2 as CK. The results showed that high yield combinations in more than 50% of the increase, mainly concentrated in 361× T2 and 354×T2. Diallel cross analysis showed that heterosis of 361 × T2 lines and 354 × T2 lines are particularly strong, especially heterosis of 361 × T2 lines (Suyunuo 638) is the most prominent.

Based on the above findings, combined with performance of combination ability of 361 and 354 in the pattern of Tongxi No.5 ×modified hengbai 522: 361 ×366 (Suyunuo No.2), 354 × improved Hengbai 522 (Suyunuo No.4), 354 × T137 (Suyunuo No.8) and 354 × FH2 (Suyunuo 11). The results of the above comprehensive analysis showed that (1) T2 is a typical subtropical high combining ability group, from which a series of high combining ability inbred lines have been bred for example T2-1, T2-2 and so on. (2) The model of Tongxi No. 5 ×T2 has extremely high heterosis and combining ability. (3) The models of 361×derived lines of 354 and 361 ×T2 can be used as sub models to apply for heterosis breeding.(4) 361 and 354 can be used as subgroup of Tongxi No.5 to apply for heterosis breeding and basic theory research .

Table 7.The model of Tongxi No.5 heterosis group× T2 heterosis group

Heterosis group	Tongxi No.5 group	T2 group
Germplasm soures	Germplasm in the lower area Yangtze river	Germplasm in Sub-tropical areas
Core Germplasm	TP5 small group of separation	T2 improved variety group
Originality line （representative line）	Tongxi No.5	T2-1,T2-2
Typical derivatives lines	354,361	W68,HT2
Typical combinations	361×T2,354×T2	

III. Summary and conclusions

1 Use open pollinated varieties with large heredity variability form compound variety population as the original group of population improvement. Lastly, the basic group (TP5 small group of separation) with high combination ability are bred by using selection scheme is designed for improving selection and recombination effect and through continuous selection of more than 10 years. TP5 is a typical high combining ability groups, and are widely used for the waxy maize breeding (including the breeding of inbred lines and basic theory research) as the basic breeding groups. The secret of successfully selecting high combining ability breeding

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population is that (1) select appropriate original germplasm, and the original groups have larger selectivity; (2) insist on continuous selection; (3) the selection should closely combined with breeding application.

2 Tongxi No.5 and a series of excellent derivatives with typical high combining ability were bred by using the small group of separation select inbred lines, this indicates that this method is successful; it is tenable to taking small groups of separation as the new concept of population genetics. Tongxi No.5 has become a core germplasm of Chinese waxy maize breeding and widely used. However, the ultimate success of any well-designed breeding method must depend on ability and wisdom of breeders who select positive influence offspring individual to whole breeding work.

3 High Inbred lines with high combining ability are only selected and obtained from high combining ability groups .Therefore, corn breeding program of science should take the breeding of high combining ability breeding population as a primary objective , Only on the basis of breeding groups with high combining ability, can breeding techniques of inbred lines be effective.

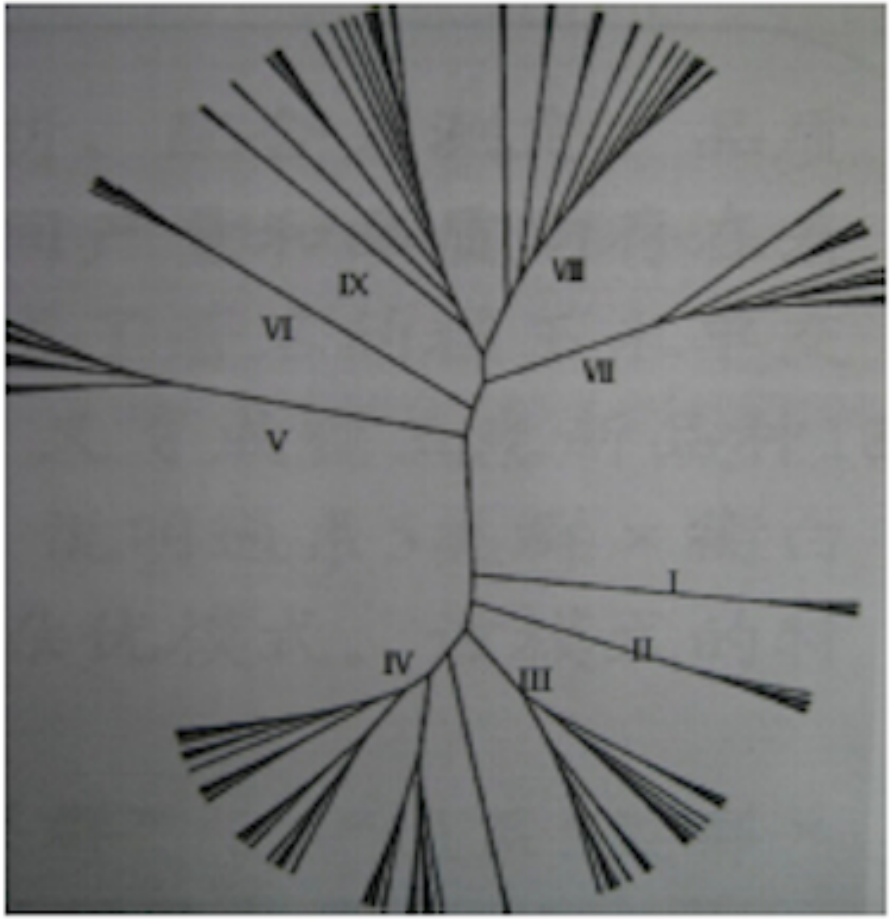
4 Corn breeders generally accept concept of heterosis pattern because of the tremendous contribution of the heterosis pattern on developing corn heterosis breeding nearly 20 years. Maize Heterotic Patterns mainly generated in the local germplasm and tropical and subtropical germplasm (all are open pollinated varieties). Heterosis pattern is natural law in which contains in the germplasm of open pollinated varieties during long-term natural selection and artificial selection process ,often found by breeders in the process of breeding . Therefore, the breeders may find unexpected genetic information when they have used open pollinated varieties as basic germplasm to carry out selection trials that combine with application breeding. New heterosis patterns will gradually form along with the new germplasm improvement and innovation. Therefore, the existing heterosis patterns can be used as dynamic framework of heterosis utilization, and breeders continuously explore and summarize the new patterns.

5 It has become the main model of waxy corn Heterosis utilization in Huang Huai Hai and southeast area of China to Tongxi No. 5 heterotic group× modified Hengbai 522 heterotic group and Tongxi No. 5 heterotic group × T2 heterotic group. I thinks that the countries (such as the United States), who develop waxy starch industry as the main purpose ,can take represents lines of this two tropical model and Tuxpeno with particularly high special combination ability to cross with represents lines of ETO each other respectively. Lastly, select temperate zone inbred lines for breeding corn varieties with high yield and good quality to meet requirements of starch industry.

Figure 2. Plant type of Tongxi 5 and its ear

Fig.4. Plant type of Suyu waxy No.1 and its ear

Fig.5. Genetic specificity of basic germplasm of Tongxi No.5



II -T2
III-Improved Hengbai522
IV-Tongxi No.5