Cereal Research Communications 40(2), pp. 246–255 (2012)
DOI: 10.1556/CRC.40.2012.2.9

Himalayan Maize – Potential Pollen Source for Maize Mediated System of Chromosome Elimination Approach in DH Breeding of Bread Wheat

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(Received 6 February 2011; accepted 8 August 2011)

To identify an efficient pollen source for maize mediated system of chromosome elimination, wheat genotypes (10 F_1s) were pollinated with eight diverse Himalayan maize genotypes. Among these, two were composite varieties Early Composite (Check) and Bajaura Makka (L 201) and rest six were locally grown traditional open pollinated maize varieties collected from diverse regions of North-west Himalaya. The data were recorded for three haploid induction parameters viz. pseudo seed formation, embryo formation and regeneration. In most of the crosses, haploid embryos were produced, asserting the potential of wheat × maize system as a genotype non-specific system as compared to androgenesis and *bulbosum* technique, where the genotype specificity limits the development of haploid plants. Frequencies of all the three haploid induction parameters in different crosses of wheat × maize clearly indicated that both wheat and maize genotypes were behaving differently for different crosses. The line × tester analysis also revealed significant influence of crosses, wheat, maize and their interaction on all the three haploid induction parameters. The results obtained suggest association of both additive and dominance gene action with all the haploid induction parameters. Over all proportional contribution of tester for embryo formation and regeneration parameters was found to be more, followed by line × tester interaction. On the basis of haploid formation efficiency (HFE) as well as general combining ability (GCA), Bajaura Makka has emerged to be the best general combiner among maize genotypes and also superior to the earlier identified variety, Early Composite. Also, HPW 155 × VL 852 and HPW 155 × HPW 211 were the top general combiners among wheat genotypes. Correlation between various haploid induction parameters revealed negative correlation between pseudo seed formation and embryo formation whereas embryo formation and regeneration were found to be significantly positively correlated; however the magnitude of correlation was not very high.

Keywords: wheat, maize, chromosome elimination, embryos, haploids, gene action, correlation

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Introduction

Doubled haploidy breeding provides a rapid means of genetic upgradation of bread wheat in a single generation, reducing the time required to attain absolute homozygosity and also enhancing the selection efficiency of crop breeding many folds. Among various techniques of haploid production, chromosome elimination approach has been studied to a varied extent, leading to its large scale application for haploid production nowadays.

The production of wheat haploid plants through chromosome elimination was first used successfully by crossing wheat with *Hordeum bulbosum,* which is commonly referred as the *bulbosum* technique (Barclay 1975). Most wheat varieties have the dominant incompatibility alleles *(Kr)* which reduce the crossability with *Hordeum bulbosum* but not with maize (Ito et al. 1997). Thus suggesting superiority of wheat × maize crosses over wheat × *Hordeum bulbosum* system (Suenaga et al. 1991).

For the first time, the production of haploid wheat plants through wheat × maize hybridization was reported by Laurie and Bennett (1988). Since then this technique has been used to produce haploid plants from many commercial wheat cultivars (Riera-Lizarazu and Mujeeb-Kazi 1990; Laurie and Reymondie 1991). The success rate of wheat × maize system depends upon the frequency of pseudo seed formation, embryo formation and regeneration, which in turn is influenced by wheat and maize genotypes (Suenaga and Nakajima 1989; Suenaga et al. 1991; Chaudhary et al. 2002; Singh et al. 2004).

The production of wheat haploids from intergeneric hybridization of wheat and maize is found to be influenced by the genetic make up of wheat as well as maize genotypes (Suenaga and Nakajima 1989; Inagaki and Tahir 1990; Verma et al. 1999; Chaudhary et al. 2002). Niroula et al. (2007) suggested that the production of doubled haploids (DHs) in wheat can be enhanced by using more responsive maize genotypes as pollinators. In another experiment, Cherkaoui et al. (2000) have reported that the haploid induction parameters viz. ovary development, embryo and plant formation were highly influenced by the wheat genotype, while only embryo formation was affected by the maize genotype.

Although many maize genotypes have already been evaluated in the Molecular Cytogenetics & Tissue Culture Lab, Department of Crop Improvement, CSK Himachal Pradesh Agricultural University, Palampur (India) for the induction of haploids in bread wheat (Chaudhary et al. 2002) and study the interactive influence of maize and wheat genotypes on haploid induction yet, there is a need to explore more diverse populations (open pollinated) and newly developed composites available in the maize growing regions of north-west Himalayas, with the objectives to further investigate the interactive influence of diverse maize and wheat genotypes on the haploid induction parameters in bread wheat and identify the highly efficient maize genotype (as pollen source) for enhancing the doubled haploid production efficiency in bread wheat.

Materials and Methods

Ten F_1 hybrids obtained from crosses of diverse wheat genotypes were pollinated with eight diverse Himalayan maize genotypes (Table 1). Early Composite, which was identified as the best pollen source in wheat × maize system for embryo formation and regeneration parameters by Pratap and Chaudhary (2006), was used as a Check Variety. The 10 wheat F_1s were raised in a completely randomized design, each sown individually in two rows, 1.5 m long with 25 cm row × row spacing. Staggered sowing was done for all the wheat and maize genotypes in three sets, so as to coincide their flowering times and to ensure regular availability of maize pollen for a long period of time. Thus solving problem related to variation between flowering time point in both crops, irrespective of number of genotypes involved. The wheat × maize hybridization was exercised as per the standard protocol of Laurie and Bennett (1987), further refined by Chaudhary et al. (2002). Five spikes of each wheat F_1 hybrid were hybridized with each of the eight maize genotypes in line (wheat F_1 hybrid) × tester (maize genotype) fashion under natural field conditions. Pollen availability is zero to very low on cloudy days, so all the pollinations were done on sunny days itself, between 9:00 am to 11:00 am. Also as maize plant produce quiet high amount of pollen, so a good amount of pollen was applied to every stigma of the wheat florets using camel hairbrush, thus providing equal chance to every floret to produce pseudo seeds. After 24 hours of pollination, 2,4-D solution of 100 ppm concentration was injected at the base of uppermost internode of each pollinated spikes for three consecutive days in order to ensure seed and embryo formation in each cross. The crossed spikes were harvested from the tiller base after 18–20 days of pollination.

Table 1. Parentage and source of different genotypes of maize

Genotype	Parentage	Source
Amarpur Local	Local collection (OPV)	Hamirpur
Bajaura Makka (L 201)	Composite of Early Composite, PS- 62,FH 3209, FH 3198, FH 3202, 10 half sib progenies of hill early yellow pool and Kullu Local	CSK HPKV, HAREC, Bajaura (1090 m a.m.s.l.)
Bhaleth Local	Local collection (OPV)	Sujanpur (Kangra)
Early composite	Composite of Kullu Local, Abaskajas, Maize No. 8, Mex-3CB, Bhodipur Yellow, JML603, VL1, YUZPSC-3, YUZPSC-4, YUZPSC-71C, YUZP-DC-775, YUZPSC-79C, VL2 and VL42	CSK HPKV, HAREC, Bajaura (1090 m a.m.s.l.)
Kilard Local	Local collection (OPV)	Pangi valley, Distt. Chamba
Sauni Local	-do-	Chamba
Shore Local	-do-	Pangi valley, Distt. Chamba
Sirmour Local	-do-	Sirmour valley

OPV= Open Pollinated Variety

The embryo-carrying seeds were identified by viewing from below under a light source as suggested by Bains et al. (1998). The embryos were excised and transferred to the test tube containing Murashige and Skoog medium supplemented with 0.5 mg/l kinetin, 150 mg/l glutamine, 20 mg/l each of L-arginine, L-cysteine and L-leucine, 30 g/l sucrose and 6 g/l agar agar under aseptic conditions. Cultured embryos were given cold treatment at 4ºC temperature in dark for 24 hours immediately after culturing. Following this, the test tubes containing the cultured embryos were transferred to the Plant Growth Room of the Molecular Cytogenetics & Tissue Culture Lab for regeneration into green plantlets at 20 ± 2°C, 80% RH with complete darkness.

After regeneration, test tubes were transferred to 10/14 h light dark regime at the same temperature for 15–20 days. In order to get profuse rooting, the haploid regenerants obtained from the cultured embryos (3–4 leaflet stage) were transferred to liquid rooting medium comprising half strength of MS salts, 1 mg/l each of nepthalene acetic acid and indole-3-butyric acid and devoid of sucrose and agar. The haploid plantlets were subsequently subjected to colchicines treatment (0.1% solution + 1.5% DMSO) for six hours and transplanted into pots and maintained up to maturity.

Observations were recorded with respect to pseudo seed formation, embryo formation and regeneration in each cross. The information was used to generate data with respect to pseudo seed formation frequency (number of pseudo seeds obtained/100 wheat florets pollinated with maize), embryo formation frequency (number of embryo-carrying seeds/100 pseudo seeds), haploid regeneration frequency (number of green haploid plantlets developed/100 embryos cultured) and haploid formation efficiency (HFE) (number of green haploid plantlets developed/ 100 wheat florets pollinated with maize). The mean data of all the crosses with respect to pseudo seed formation frequency, embryo formation frequency and haploid regeneration frequency were subjected to line × tester analysis as per Kempthorne (1957).

Results

The mean frequency of pseudo seed formation ranged from 20 to 100% in different crosses, while it was 0 to 42.4% and 0 to 100% for embryo formation and regeneration, respectively. Higher numbers of pseudo seeds were obtained from all the wheat genotypes when pollinated with various diverse maize genotypes. Frequency for pseudo seed formation was highest in case of HPW 155 × DBW 17 (93.31%) (Table 2a) followed by HPW 155 × HPW 288 (90.21%), though both were statistically at par. In case of maize genotypes, it was the Sirmour Local (91.2%) (Table 2b) which produced highest pseudo seed frequency followed by Bhaleth Local (85.99%). Highest embryo formation and regeneration frequency was observed in HS 420 × HPW 288 (8.74% and 80%) (Table 2a) followed by HPW 155 × HPW 211 (7.53% and 78.79%), where as in maize it was the Bajaura Makka which was showing highest embryo formation (17.3%) (Table 2b) and regeneration frequency (86.63%) followed by Early Composite having 11.83% embryo formation and 79.75% embryo regeneration frequency.

Table 2a. Mean performance of various wheat genotypes for response to various haploid induction parameters pooled over all the maize genotypes

S.No	Genotypes	Florets pollinated	Pseudo seed formation (%)	Embryo formation (%)	Embryo Regeneration (%)	Haploid formation efficiency (%)
Wheat crosses						
1	HPW 89 × HPW 211	1320	84.70 (1118)	6.26 (70)	71.43 (50)	3.79
2	HPW 89 × VL 852	1222	79.46 (971)	5.46 (53)	75.47 (40)	3.27
3	HPW 155 × HPW 211	1262	69.49 (877)	7.53 (66)	78.79 (52)	4.12
4	HPW 155 × HPW 288	1154	90.21 (1041)	5.38 (56)	73.21 (41)	3.55
5	HPW 155 × DBW 17	1330	93.31 (1241)	4.84 (60)	76.67 (46)	3.46
6	HPW 155 × VL 852	1153	84.00 (967)	6.72 (65)	73.85 (48)	4.16
7	HPW 249 × DBW 17	1332	83.11 (1107)	5.15 (57)	75.44 (43)	3.23
8	HPW 249 × VL 852	1293	89.87 (1162)	5.42 (63)	69.84 (44)	3.40
9	HS 420 × HPW 211	1205	73.78 (889)	6.41 (57)	70.18 (40)	3.32
10	HS 420 × HPW 288	1281	49.10 (629)	8.74 (55)	80 (44)	3.43
	MEAN	1255.2	79.69	6.19	74.49	3.57

Wheat genotype HPW 155 × DBW 17 was found to have the highest pseudo seed formation frequency (93.11%) but lowest embryo formation frequency (4.84%), same was the case with maize genotype Sirmour Local, which was superior for pseudo seed formation (91.23%), was also exhibiting quiet low embryo formation (1.60%) and regeneration (54.17%). The highest haploid formation efficiency (HFE) in wheat genotypes was exhibited by HPW 155 × VL 852 (4.16%) (Table 2a) followed by HPW 155 × HPW 211 (4.12%), while in maize genotypes Bajaura Makka showed highest haploid formation efficiency (11.75%) followed by Early Composite (7.38%) (Table 2b). Analysis of variance indicated that mean squares due to crosses, wheat genotypes, maize genotypes and wheat × maize interaction were statistically significant for all the three haploid induction parameters (Table 3), except for MS due to wheat genotypes for embryo regeneration which was found to be significant only when tested against error mean sum of squares.

Highest positive GCA effect was observed for HPW 155 × DBW 17 (10.14) followed by HPW 155 × HPW 288 (7.60) and HPW 249 × VL 852 (6.35) for pseudo seed formation, HS 420 × HPW 288 (3.61) followed by HPW 155 × HPW 211 (2.58) for embryo formation and HPW 155 × HPW 211 (9.59) followed by HPW 155 × VL 852 (6.03), HS 420 × HPW 288 (4.68), HS 420 × HPW 211 (3.62), HPW 249 × DBW 17 (3.59) and HPW 155

Table 2b. Mean performance of various maize genotypes for response to various haploid induction parameters pooled over all the wheat genotypes

S.No	Genotypes	Florets pollinated	Pseudo seed formation (%)	Embryo formation (%)	Embryo Regeneration (%)	Haploid formation efficiency (%)
1	Amarpur Local	1557	71.74 (1117)	4.66 (52)	73.08 (38)	2.44
2	Bajaura Makka	1489	78.71 (1172)	17.24 (202)	86.63 (175)	11.75
3	Bhaleth Local	1506	85.99 (1295)	2.55 (33)	48.48 (16)	1.06
4	Early Composite	1707	78.27 (1336)	11.83 (158)	79.75 (126)	7.38
5	Kilard Local	1586	81.53 (1293)	6.27 (81)	58.02 (47)	2.96
6	Saluni Local	1529	67.04 (1025)	0.78 (8)	37.5 (3)	0.20
7	Shore Local	1537	82.43 (1267)	3.47 (44)	68.18 (30)	1.95
8	Sirmour Local	1641	91.23 (1497)	1.60 (24)	54.17 (13)	0.79
	MEAN	1569	79.62	6.05	63.23	3.57

Figures in parenthesis represent original number obtained.

Table 3. Line × tester analysis for percent pseudo seed formation, embryo formation and regeneration in wheat × maize crosses

Source	d.f	MS		
		Pseudo seed formation	Embryo formation	Embryo regeneration
Crosses	79	1093.26**	351.77**	3646.12**
Wheat genotypes	9	647.37**††	37.52**†	421.21*
Maize genotypes	7	328.23**†	531.08**††	3708.68**††
Wheat × maize interaction	63	115.08**	16.57**	387.21**
Error	320	12.53	5.60	209.38
$(\sigma^2_D / \sigma^2_A)^{1/2}$		0.50	0.20	0.31

* P ≤ 0.05 and ** P ≤ 0.01 (Tested against EMS)

† P ≤ 0.05 and †† P ≤ 0.01 (Tested against MS (wheat × maize))

× HPW 288 (2.39) for embryo regeneration amongst the wheat F_1 hybrids. Amongst the maize, Sirmour Local (9.63) followed by Bhaleth Local (4.17) for pseudo seed formation, Bajaura Makka (11.53) followed by Early Composite (9.33) for embryo formation and regeneration exhibited highest positive GCA effect.

Estimates of variance due to general combining ability (σ^2_{gca}), specific combining ability (σ^2_{gca}), σ^2_A, σ^2_D and ((σ^2_D / σ^2_A)$^{1/2}$) indicated that in general the magnitude of additive genetic variance (σ_{A}^{2}) was higher than the dominance variance (σ_{D}^{2}) for all the three haploid induction parameters *viz.* pseudo seed formation, embryo formation and regeneration. The degree of dominance ($(\sigma_{\mathrm{D}}^{2}/\sigma_{\mathrm{A}}^{2})^{1/2}$) was also found to be less than one for all the three haploid induction parameters. Correlation studies exhibited a significant negative correlation pseudo seed formation with the embryo formation and non-significant negative correlation with embryo regeneration, while embryo formation and regeneration were found to be significantly positively correlated with each other.

Table 4. GCA effects of frequencies of pseudo seed formation, embryo formation and regeneration in wheat crosses and maize genotypes

Source	d.f	GCA		
		Pseudo seed formation	Embryo formation	Embryo regeneration
	Wheat crosses			
1	HPW 89 × HPW 211	2.77*	0.38	–4.48*
2	HPW 89 × VL 852	–1.76*	–2.19*	–14.18*
3	HPW 155 × HPW 211	–7.07*	2.58*	9.59*
4	HPW 155 × HPW 288	7.60*	–0.82*	2.39
5	HPW 155 × DBW 17	10.14*	–1.93*	–3.71
6	HPW 155 × VL 852	2.29*	0.53	6.03*
7	HPW 249 × DBW 17	4.03*	–1.94*	3.59
8	HPW 249 × VL 852	6.35*	–2.24*	–7.54*
9	HS 420 × HPW 211	–3.51*	2.03*	3.62
10	HS 420 × HPW 288	–20.81*	3.61*	4.68*
	SE(d)±			
	Maize genotypes			
11	Amarpur Local	–6.50*	–0.27	11.47*
12	Bajaura Makka	–1.70*	11.53*	21.99*
13	Bhaleth Local	4.17*	–4.71*	–15.38*
14	Early Composite	0.08	9.33*	12.79*
15	Kilard Local	1.10*	1.93*	5.80*
16	Saluni Local	–8.4*	–8.79*	–36.56*
17	Shore Local	1.63*	–2.49*	10.20*
18	Sirmour Local	9.63*	–6.51*	–10.30*
	SE(d)±	0.98	0.66	4.01

* $P \leq 0.05$

Table 5. Estimates of genotypic correlation for various haploid induction parameters

	Pseudo seed formation	Embryo formation	Embryo regeneration
Pseudo seed formation		–0.36**	–0.04
Embryo formation			0.32**
Embryo regeneration			

* $P \leq 0.01$

Discussion

Frequencies of all the three haploid induction parameters in different crosses of wheat × maize clearly indicated that both wheat and maize genotypes were behaving differently for different crosses. In most of the crosses haploid embryos were produced, asserting the potential of wheat × maize system as a genotype non-specific system as compared to androgenesis and *bulbosum* technique, where the genotype specificity limits the development of haploid plants (Inagaki and Tahir 1990; Suenaga 1994). It also suggests the insensitivity of maize pollen to the action of crossability inhibitor genes (*Kr1* and *Kr2*) located on the long arms of chromosomes 5B and 5A, respectively, which express in the style of many wheat genotypes and inhibit the penetration of pollen tube from alien species (Sitch et al. 1985; Laurie and Bennett 1987).

High pseudo seed formation has been observed, which is attributable to the application of 2,4-D resulting in ovary growth (Suenaga and Nakajima 1989; Suenaga 1994). Wide range of genetic variability for embryo formation and regeneration was also observed in the present study, substantiating the earlier reports of Amrani et al. (1993). Thus, the results suggests that high pseudo seed formation frequency does not ensure high embryo formation and regeneration frequencies but in most of the cases high embryo formation frequency leads to higher regeneration frequency.

The analysis of variance showed significant influence of crosses on all the three haploid induction parameters viz. pseudo seed formation, embryo formation and regeneration. Significant differences among wheat genotypes and maize genotypes for pseudo seed formation, embryo formation and regeneration (Table 3) were also found which clearly indicates the diversity among maize as well as wheat genotypes for the various haploid induction parameters. Wheat × maize interaction was also significant for all the three parameters indicating that both maize and wheat genotypes were behaving differently in wheat × maize cross for pseudo seed formation, embryo formation and regeneration and also give an indication of non-additive gene action involved with the traits. These results are in accordance with the findings of Kour et al. (2008); Suenaga and Nikajima (1989); Suenaga et al. (1991); Chaudhary et al. (2002) and Singh et al. (2004) who found significant effects of genotypes of wheat parents, maize pollinators and their interaction.

Significant values of general combining ability (GCA) for all the three haploid induction parameters in case of wheat as well as maize and less than one value of the degree of dominance (σ^2_A) indicates preponderance of additive genetic control of these parameters (Tables 3 and 4). Thus the results are in conformity with the findings of Sharma et al. (2005) in terms of association of both additive and dominance gene action with all the haploid induction parameters. Correlation between various haploid induction parameters was estimated. Pseudo seed formation and embryo formation were significantly negatively correlated (Table 5) whereas embryo formation and regeneration were found to be significantly positively correlated, however the magnitude of correlation was not very high. A perusal of the relative ranking of different genotypes for the two characters indicated that the regeneration frequency was not necessarily higher (Table 4) for high embryo formation in all the cases. This is in conformity with Brazauskas and Pasakinskiene (2001) who also found that, genotypes producing the highest embryo formation frequencies not necessarily exhibit high regeneration frequency also.

Based on significant estimates of positive GCA effects, HPW 155 × DBW 17 (Table 4), among the wheat F_1 hybrids and Sirmour Local of maize for pseudo seed formation frequency; HS 420 × HPW 288 among the wheat F_1 hybrids and Bajaura Makka of maize for embryo formation frequency, and HPW 155 × HPW 211 among the wheat F_1 hybrids and Bajaura Makka of maize for embryo regeneration frequency were identified to be outstanding genotypes influencing the haploid induction frequency. Over all proportional contribution of tester for embryo formation and regeneration parameters was found to be more, followed by line × tester interaction. Which is in accordance with Niroula et al. (2007), who suggested that the production of doubled haploids can be enhanced by using more responsive maize genotypes as pollinators.

Conclusively, on the basis of haploid formation efficiency (HFE) as well as general combining ability (GCA), Bajaura Makka has emerged to be the best general combiner among maize genotypes. Bajaura Makka with Haploid Formation Ffficiency (HFE) 11.75 (Table 2b), has also been found superior to the earlier identified varieties i.e. Early Composite (Pratap and Chaudhary 2006) and DEH 10503 (Kour et al. 2008) having 7.38 and 2.05 HFE, respectively. Utilization of this newly identified potential variety can further enhance the efficiency of DH production in bread wheat and save time and energy required to develop gene mapping populations and develop new varieties.

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