



Genetic analysis in intra- and inter-specific crosses of tree willows

Punit Choudhary*, N. B. Singh¹ and Archana Verma¹

KVK, Sher-e-Kashmir University of Agricultural Sciences and Technology, Jammu; ¹Department of Tree Improvement and Genetic Resources, Dr. YSP University of Horticulture and Forestry, Solan, Himachal Pradesh

(Received: September 2014; Revised: July 2015; Accepted: July 2015)

Abstract

Twenty one full-sib families derived from intra- and inter-specific controlled crosses were analysed to study different genetic parameters. Estimates of the general combining ability (GCA) variance were found to be less than the specific combining ability (SCA) variance for all the parameters. The dominance variance was more than the additive variance for all the parameters studied. The degree of dominance ranged between 1.73 (per cent successful crosses) and 5.35 (% germination). Moderately high (0.42 for % successful crosses) to low (0.15 for seed per capsule) narrow sense heritabilities and high heritability in broad sense (0.74 to 0.99) for per cent successful crosses and seeds per catkin was recorded. GCA effects were positive and significant for *S. tetrasperma* (TFB), *S. tetrasperma* (TWE) and *S. tetrasperma* (LNM) male parents for all the parameters while *S. alba* (SE- 63-007) exhibited significantly positive effects for number of seeds/catkin. Among females, *S. tetrasperma* (LP), *S. tetrasperma* (LNF) and *S. tetrasperma* (LN) depicted positive and significant GCA effects for number of seeds/ catkin and per cent germination, respectively whereas crosses, *S. matsudana* (PN-227) x *S. alba* (Kashmiri) and *S. tetrasperma* (LNF) x *S. tetrasperma* (LNM) exhibited positive and significant SCA effects for per cent successful crosses. Cross *S. matsudana* (PN-227) x *S. alba* (Kashmiri) showed positive significant SCA effects for number of seeds/ capsule.

Key words: General combining ability, specific combining ability, dominance variance, diallel mating

Introduction

There is no doubt that the willows belong to a genus with a great abundance of inter-specific hybrids. Hybridization between few *Salix* species was found to be common with higher rates (Brunsfeld, 1992) than those known for many other genera. Hybrids of willows are often fertile and provided new range of various

forms through subsequent genetic segregation. Natural hybridization is supported by dioecism and is affected by diverse flowering phenologies in different *Salix* species (Choudhary et al. 2011). Researchers have reported 16 hybrids from Moscow, 177 hybrid combinations of different kinds from Fennoscandia, 181 from Central Europe and 210-220 interspecific hybrids from USSR (Skvortsov, 1999). Inter-specific hybrid [(*S. babylonica* x *S. alba*) x *S. matsudana* (*S. x jiangsuensis* cv. 'J172')] developed at Jiangsu Forest Academy, Nanjing China has recorded mean annual increment of 18.18 m³/ha under extensive culture. Inter-generic backcross hybrid (*S. x jiangsuensis* CL 'J194') between [(*S. matsudana* x *Ch. Arbutifolia*) x *S. matsudana*] recorded 57.45 % genetic gain for volume (Zhongyo, 1987). Extensive intra- and inter-specific hybridization among species of section *Salix* had resulted in excellent clones (*S. x jiangsuensis* CL 'J799' and *S. x jiangsuensis* CL 'J795') for production of high quality timber and pulpwood. Artificial hybrid developed between *S. babylonica* and *S. fragilis* could tolerate – 42°C and 0.4 % soil salt and 42.75 % faster in growth as compared to *S. matsudana* revealed that hybridization is effective in willows. Hybrids having high ornamental value 'golden weeping branches' and 'silver bud' were developed after successful inter-specific hybridization between *S. babylonica*, *S. alba* and *S. matsudana* (Pan et al. 2004)

Successful inter-specific hybrids between *S. matsudana* (PN-227), a native of northern China and various *S. alba* clones from Europe has been developed for timber production in New Zealand (Kraayenoord 1995). Several hybrids between *S. elaeagnos* x *S. daphnoides*, *S. glaucophylloides* x *S.*

*Corresponding author's e-mail: pmd.choudhary@gmail.com

viminalis were released for steam bank stabilization and roadside plantation in New Zealand. Fifty four species for biomass production which produced hybrids having high productive potential and better adaptability to climatic and edaphic factors were earlier identified (Newsholme 2003).

In India, various species of willows both indigenous and exotic, have assumed great importance in breeding programme. Arborescent species of willow like *Salix alba*, *S. humboltiana*, *S. excelsa*, *S. aemophylav*, *S. fragilis*, *S. nigra*, *S. matsudana*, *S. amygdaloides*, *S. argenteensis* and *S. tetrasperma*, their inter and intra-specific hybrids/clones can attain tree size of 20-30 meters, able to grow by vegetative propagation on great variety of edaphic, ecological and hydrological conditions. They are better adapted than poplar in monoculture as well as in agroforestry systems under short rotation of 6 to 9 years (Singh and Huse 2004).

Basic genetic studies such as crossability pattern, estimate of genetic parameters of traits of interest right from growth, adaptability, productivity to produce are very much needed. The combination of traditional breeding augmented with modern molecular tools could advance genetic improvement of the genus (Singh and Pawar 2005). The development of heterotic hybrids were planned by controlled crossing of *S. tetrasperma* with other arborescent willow species especially *Salix alba*, *S. babylonica*, *S. jessonensis*, *S. nigra* and *S. matsudana* so that increased adaptability and productivity can be combined. As a result, such hybrids can be successfully grown from temperate to tropical regions of the country in order to enhance the overall biomass production (Choudhary et al. 2013).

In order to obtain an effective improvement in different traits, information about the type of gene action involved, the combining ability of the parents and their crosses and the estimates of genetic component of variances are of great importance to the breeder. The common approach of choosing parents on the basis of performance, adaptation and genetic variability does not necessarily lead to useful results. This is because of the differential ability of the parents, which depends upon the complex interactions among the genes and cannot be judged by the performance alone (Allard 1960). It is of prime importance to pre evaluate the parents for combining ability. The parents which perform well in the cross combinations are of great importance to the breeders and the investigations on

general and specific combining ability would yield valuable information which can be used in various hybrid breeding programme. The most appropriate approach in preliminary screening of material for combining ability is to use diallel mating design (Griffing 1956). Therefore, the present study was carried out to evaluate five male and five female parents and their crosses with respect to combining ability.

Materials and methods

After initial screening of the promising clones of different *Salix* spp. under preliminary evaluation trials, selection of different species/clones was done for carrying out controlled pollination (hybridization). Controlled hybridization among selected indigenous and exotic species/clones was carried out at the experimental farm of the Department of Tree Improvement and Genetic Resources, Dr. Y S Parmar University of Horticulture and Forestry, Solan, H. P. India using incomplete diallel mating design for developing hybrids. The plant material (flowering branches) of selected female and male clones of *Salix* species used for control pollination (hybridization) in the present study are given in Table 1.

Freshly collected pollen grains of the male clones designated were applied to the receptive stigma of the female clones. Pollen of each male parent used in controlled hybridization was tested for *in-vitro* pollen viability through staining method using 2% acetocarmine (Mosseler 1989; Choudhary and Singh 2013). Every controlled cross involves single pollen and no pollen mixture was attempted. After pollination the catkins were bagged and tagged and observations on parameters viz., per cent successful crosses (Crossability %) (Jan and Pfeffer 1999), number of seeds per catkin, no of seeds per capsule fruit and germination per cent were recorded using standard procedures.

The data on crossability parameters obtained from twenty-one full-sib families pertaining to crosses 5x5 dialled set were subjected to RBD analysis for the estimation of main effects. The combining ability analysis and estimation of gene effects was done according to method four of diallel involving direct crosses only without involving parents. The combining ability analysis was done for the each crossability parameter separately. The estimates of variance for general and specific combining ability (gca and sca, respectively) and their effects were carried out as per the standard procedure (Griffing 1956) and methods

Table 1. Detail of female and pollen parents used in the breeding programme

Sex	Species/clones	Section	Source
Female parent	<i>S. tetrasperma</i> Roxb. (LP)	<i>Humboldtiana</i>	India
	<i>S. tetrasperma</i> Roxb. (LN)		
	<i>S. tetrasperma</i> Roxb. (LNF)		
	<i>S. tetrasperma</i> Roxb. (LG)		
	<i>S. matsudana</i> Koidz. (PN-227)	<i>Subalpine</i>	New Zealand
Pollen parent	<i>S. tetrasperma</i> Roxb. (TFB)	<i>Humboldtiana</i>	India
	<i>S. tetrasperma</i> Roxb. (TWE)		
	<i>S. tetrasperma</i> Roxb. (LNM)		
	<i>S. alba</i> Linn. (SI-63-007)	<i>Salix</i>	Italy
	<i>S. alba</i> Linn. (Kashmiri)		India

LNF = Local nala female (*S. tetrasperma*); LNM = Local nala male (*S. tetrasperma*); TFB = *S. tetrasperma* floriculture block; TWE = *S. tetrasperma* entomology field and LP = *S. tetrasperma* polyhouse

IV involving direct crosses only (Singh and Pawar 2005; Nadrajan and Gunasekaran 2005).

Results and discussion

Intra- and inter-specific controlled crossing was completed and twenty-one full-sib intra- and inter-specific families were produced using 5 × 5 incomplete diallel mating design. Four combinations appeared to be incompatible as no viable seeds were obtained from them (Table 2). However the reasons for incompatibility were not studied but non-compatibility between members of sub genus *Salix* and *Vetrix* may be attributed to the fact that *S. udensis* used as male in crossing belonged to a totally different section *Vimens* of sub genus *Vetrix*. Incompatibility between subgenus *Salix* and *Vetrix* have been earlier reported (Choudhary et al. 2013). Earlier Mosseler (1990) also reported several incompatible intra- and inter-specific combination during hybridization in a 6 × 6 full diallel set of willows. Similarly, twenty one and thirty three full sib families were also reported from 4 × 6 factorial mating between clones of *Populus nigra* and 6 × 6

factorial crossing involving clones of *Populus deltoides*, respectively (Pichot and Teissier 1989).

Many examples of successful inter- and intra-specific hybridization on willows has been reported. Attempts to breed *S. viminalis* were made in Eastern Europe, Britain and Sweden in the beginning of 19th century and later among species of subgenus *Salix* and subgenus *Vetrix* in Bulgaria, Czechoslovakia, Hungary, Romania and Yugoslavia (Stott, 1984). Inter-specific hybridization of willows had yielded superior clones through the combination of desirable traits, positive heterosis and greater phenotypic stability in varied environments. Artificial hybrids of *S. humboldtiana* × *S. babylonica* and *S. humboldtiana* × *S. alba* var *Caerulea* and some backcrosses with *S. babylonica* were made in 1965 and some of these progenies were then crossed with Italian *S. alba* that exhibited exceptional vigour in growth, wood quality, climate and pest resistance (Clone 131/25 and 131/27) (Kopp 2001).

Table 2. Estimation of variance components for different crossability parameters

S. No.	Variance components	Per cent successful crosses	Seeds/catkin	Seeds/capsule fruit	Per cent germination
1.	Variances of gca (σ^2_g)	132.41	95.55	0.13	26.21
2.	Variances of sca (σ^2_s)	200.29	894.53	1.17	375.82
3.	Additive variance (D)	529.67	382.21	0.53	104.87
4.	Dominance variance (H)	801.18	3578.12	4.69	1503.28
5.	Degree of dominance	1.73	4.32	4.19	5.35
6.	Heritability (ns)	0.42	0.17	0.15	0.16
7.	Heritability (bs)	0.74	0.99	0.84	0.98

Mean sum of squares due to parents and crosses were found significant for all the traits. Higher magnitude of sca variances (σ^2_s) as compared to gca variances (σ^2_g) for all the traits were observed and as such ratio gca to sca was found less than unity (Table 2). All the characters exhibited high dominance variances (H). Moderately high to low narrow sense heritabilities and fairly high value of broad sense heritabilities were estimated for all the traits. It showed the preponderance of non additive gene action governing these traits. Earlier Li and Wu (1997) reported that heterosis in F_1 was due to the over dominance interaction between two alleles, one from *P. tremuloides* and one from *P. tremula* at the same loci. Similarly, broad sense heritabilities were found to be 2-6 times higher than narrow sense heritabilities for growth and shoot components indicating the importance of dominance or over dominance in aspen growth (Bastien 1996).

The present findings are in agreement with those of Singh (2002) who concluded that dominance variance increased at a faster rate than additive variance in early stage in full sib progenies of selected clones of Poplar (*P. deltoides*). It is an added worth for species like *Salix* and *Populus* with ease of vegetative multiplication and being maintained under short rotation coppice in India, which can utilize dominance variance more effectively. Non additive type of gene action in willow genotypes provides basis for heterosis breeding and population improvement by recurrent selection for sca.

High percentage of successful crosses are desired for success of any breeding programme and as such the parents and crosses with positive general and specific combining ability effects, respectively should be selected for breeding programme. In the present study, high average seeds per catkin and per capsule (fruit) and high germination percentage were recorded for intra-specific crosses. In general, intra-specific crosses exhibited high crossability as compared to inter-specific crosses. High success rate and more number of average seeds per capsule among intra-specific crosses of *S. amygdaloides*, *S. discolor*, *S. eriocephala*, *S. exigua*, *S. lucida* and *S. petiolaris* reported earlier supports the above findings (Mosser 1987) and for inter-specific crossability and hybridization in willows (Jan and Pfeffer 1999).

The parents were classified as good, average and poor general combiners on the basis of gca effects of the traits. The female parent *S. tetrasperma* (LP) exhibited significantly positive gca effects for number of seed per catkin (Table 3) but positive but non-significant gca effects for number of seed per capsule. Parent *S. tetrasperma* (LNF) exhibited positively significant gca effect for germination per cent. Among the male parents *S. tetrasperma* (TFB) showed highest positively significant gca effect for all the characters. Male parents viz., *S. tetrasperma* (TWE) and *S. tetrasperma* (LNM) also exhibited significantly positive gca effects for all the characters except for per cent *S. tetrasperma* (TWE) which showed positive but non-significant gca effects. *S. alba* (SI-63-007) showed

Table 3. General combining ability effects of different parents for various crossability parameters

Parents		General combining ability effects			
		Per cent successful crosses	Seeds/catkin	Seeds/capsule fruit	Per cent germination
Females	<i>S. tetrasperma</i> (LP)	-1.20	7.20**	0.02	-10.00**
	<i>S. tetrasperma</i> (LNF)	-13.20**	-24.80**	-0.72*	10.00**
	<i>S. tetrasperma</i> (LG)	-5.20	-32.80**	-1.22*	-10.00**
	<i>S. tetrasperma</i> (LN)	-1.20	-24.80**	-0.72*	2.00*
	<i>S. matsudana</i> (PN-227)	-17.20**	-32.80**	-0.97*	-22.00**
Males	<i>S. tetrasperma</i> (TFB)	38.80*	39.20**	1.28*	14.00**
	<i>S. tetrasperma</i> (TWE)	6.80	39.20**	1.25*	14.00**
	<i>S. tetrasperma</i> (LNM)	14.80**	31.20**	1.02*	10.00**
	<i>S. alba</i> (SI-63-007)	-17.20**	7.20**	-0.23	-2.00*
	<i>S. alba</i> (Kashmiri)	-5.20	-8.80*	0.27	-6.00*
SE _{gi}		4.19	0.72	0.17	0.84

*Significant at 5 per cent level of significance; **Significant at 1 per cent level of significance

positively significant gca effect for number of seed per catkin. Significant positive link was recorded between intra- and inter-specific GCA for both *Populus deltoides* and *P. trichocarpa* parent clones (Bastien 1996). The present investigations are parallel to the findings that within and between family differences and large gca effects for willow clones used as parents in the breeding programme. The significant effect due to general and specific combining ability differences further suggested additive and non-additive genetic control among willows. Different parents expressing high desirable gca effects on various characters have been earlier reported in *P. deltoides* (Singh 2002) and *Morus* genotypes (Vijayan 2009).

Ten out of twenty one crosses revealed positive sca effects for per cent successful crosses (crossability %). Highest significantly positive sca effect was depicted by *S. matsudana* (PN-227) × *S. alba* (Kashmiri) which was followed by *S. tetrasperma* (LNF) × *S. tetrasperma* (LNM) (Table 4). However, cross *S. tetrasperma* (LN) × *S. tetrasperma* (TFB) exhibited lowest positive sca effects. For number of seeds per catkin hybrids *S. matsudana* (PN 227) × *S. alba* (Kashmiri), *S. tetrasperma* (LNF) × *S. tetrasperma* (LNM) and *S. tetrasperma* (LG) × *S. alba* (Kashmiri) with poor x poor combiners, *S. tetrasperma* (LNF) × *S. tetrasperma* (TFB), *S. tetrasperma* (LNF) × *S. tetrasperma* (LNM), *S. tetrasperma* (LG) × *S. tetrasperma* (TFB), *S. tetrasperma* (LG) × *S.*

Table 4. Specific combining ability effects of among different crosses for various crossability parameters

S.No.	Crosses	Specific combining ability effects			
		Per cent successful crosses	Seeds/ catkin	Seeds/ capsule fruit	Per cent germination
1.	Intra-specific crosses <i>S. tetrasperma</i> (LP) × <i>S. tetrasperma</i> (TFB)	11.26	7.74**	-0.24	11.64**
2.	<i>S. tetrasperma</i> (LP) × <i>S. tetrasperma</i> (TWE)	-3.47	2.33	0.03	9.53*
3.	<i>S. tetrasperma</i> (LP) × <i>S. tetrasperma</i> (LNM)	-11.15	-23.01**	-0.72	-13.51**
4.	<i>S. tetrasperma</i> (LNF) × <i>S. tetrasperma</i> (TFB)	3.34	4.61*	0.33	14.88**
5.	<i>S. tetrasperma</i> (LNF) × <i>S. tetrasperma</i> (TWE)	-12.14	-5.79*	-0.01	-14.22**
6.	<i>S. tetrasperma</i> (LNF) × <i>S. tetrasperma</i> (LNM)	24.26**	31.25**	0.65	11.92**
7.	<i>S. tetrasperma</i> (LG) × <i>S. tetrasperma</i> (TFB)	10.32	7.34**	0.75	8.44*
8.	<i>S. tetrasperma</i> (LG) × <i>S. tetrasperma</i> (TWE)	6.78	6.13**	-0.17	3.53
9.	<i>S. tetrasperma</i> (LN) × <i>S. tetrasperma</i> (TFB)	0.57	16.81**	0.36	4.72*
10.	<i>S. tetrasperma</i> (LN) × <i>S. tetrasperma</i> (TWE)	3.07	-15.19**	0.03	3.61
11.	<i>S. tetrasperma</i> (LN) × <i>S. tetrasperma</i> (LNM)	11.53	22.85**	0.68	21.76**
12.	Inter-specific crosses <i>S. tetrasperma</i> (LP) × <i>S. alba</i> (SI-63-007)	-20.74	-25.68**	-1.38*	-50.38**
13.	<i>S. tetrasperma</i> (LNF) × <i>S. alba</i> (SI-63-007)	-6.61	-13.42**	-0.51	7.64**
14.	<i>S. tetrasperma</i> (LNF) × <i>S. alba</i> (Kashmiri)	-2.06	-5.28*	0.18	-4.67*
15.	<i>S. tetrasperma</i> (LG) × <i>S. alba</i> (SI-63-007)	-2.43	3.30	0.31	-2.79*
16.	<i>S. tetrasperma</i> (LG) × <i>S. alba</i> (Kashmiri)	-3.35	5.04*	0.21	5.08*
17.	<i>S. tetrasperma</i> (LN) × <i>S. alba</i> (SI-63-007)	-12.21	-11.22**	-0.47	-13.71
18.	<i>S. tetrasperma</i> (LN) × <i>S. alba</i> (Kashmiri)	3.82	-1.88	0.02	-0.83
19.	<i>S. matsudana</i> (PN-227) × <i>S. tetrasperma</i> (TFB)	-19.16	-26.57**	-0.72	-26.08**
20.	<i>S. matsudana</i> (PN-227) × <i>S. tetrasperma</i> (LNM)	-17.50	-22.53**	-0.60	-12.44**
21.	<i>S. matsudana</i> (PN-227) × <i>S. alba</i> (Kashmiri)	35.87**	43.18**	1.23*	35.87*
	SE _{si}	11.03	1.89	0.45	2.20

*Significant at 5 per cent level of significance; **Significant at 1 per cent level of significance

tetrasperma (TWE) with poor and good combiners. Further, *S. tetrasperma* (LN) x *S. tetrasperma* (TFB) and *S. tetrasperma* (LN) x *S. tetrasperma* (LNM) with good x good combiner as their parents were observed giving significantly positive sca effects (Table 4).

Only hybrid *S. matsudana* (PN 227) x *S. alba* (Kashmiri) with poor and poor combiner was found as promising combination for number of seeds per capsule (fruit). Similarly, *S. matsudana* (PN 227) x *S. alba* (Kashmiri) and *S. tetrasperma* (LG) x *S. alba* (Kashmiri) with poor and poor combiner as its parents, *S. tetrasperma* (LN) x *S. tetrasperma* (LNM), *S. tetrasperma* (LN) x *S. tetrasperma* (TFB) and *S. tetrasperma* (LNF) x *S. tetrasperma* (TFB) with good x good combiners, *S. tetrasperma* (LNF) x *S. alba* (SI-63-007) with good x poor combiner and *S. tetrasperma* (LP) x *S. tetrasperma* (TFB) and *S. tetrasperma* (LP) x *S. tetrasperma* (TWE) and *S. tetrasperma* (LG) x *S. tetrasperma* (TFB) with poor x good combiner as parent showed positive specific combining ability effects (Table 4).

Majority of the cross combinations exhibiting desirable sca effect have at least one or both of their parents as good combiner except for *S. matsudana* (PN 227) x *S. alba* (Kashmiri), *S. tetrasperma* (LG) x *S. alba* (Kashmiri) and *S. tetrasperma* (LNF) x *S. tetrasperma* (LNM). Similar observations have also been expressed by earlier workers on *Populus* (Pichot and Teissier 1989). However for crosses that involved both the parents as poor combines lends support to these findings by Li and Wu (1997), Singh (2002) in Poplar and Ronnberg and Gulberg (1999) in willows. They are of the opinion that it was not necessary that parents having higher estimates of gca effects would always give higher estimates of sca effects. Usually the highest estimates of sca effects are obtained from crosses involving diverse parents. Sometimes specific interaction effects, of poor x poor crosses may perform better than good x good (high x high) and good x average (high x low) gca combinations. The resultant performance of traits from poor x poor cross indicates that a high magnitude of non-additive component was responsible for confirming the highest rank to the pertinent cross combination.

The male parents viz., *S. tetrasperma* (TFB), *S. tetrasperma* (TWE) and *S. tetrasperma* (LNM) recorded significantly positive gca effect for almost all the parameters can be used in for improvement breeding programme. The hybrids viz., *S. matsudana* (PN-227) x *S. alba* (Kashmiri), *S. tetrasperma* (LN) x *S.*

tetrasperma (LNM), *S. tetrasperma* (LN) x *S. tetrasperma* (TFB), *S. tetrasperma* (LNF) x *S. tetrasperma* (LNM), *S. tetrasperma* (LNF) x *S. tetrasperma* (TFB) and *S. tetrasperma* (LG) x *S. tetrasperma* (TFB) which recorded positively significant sca effects for most of crossability parameters are recommended for heterosis breeding.

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