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Heterosis and combining ability in a half-diallel cross of *Sesbania pachycarpa* DC.

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Abstract – Ten ecotypes of *Sesbania pachycarpa* DC. were crossed in a half-diallel mating scheme, and the parents and F1's were evaluated in a randomized complete block design with three replications. These ecotypes were examined for diameter of the principal stem, branch number per plant, pod number per plant and 100 seeds weight. All traits studied except the 100 seeds weight showed highly significant heterosis over mid-parent values. The general combining ability was highly significant for all traits studied, while the specific combining ability was highly significant for the 100 seeds weight and was just significant for pod number per plant. Hence, additive genetic variation was shown to be important in determining these traits.

Sesbania pachycarpa / combining ability / diallel

Résumé – Hétérosis et aptitude à la combinaison dans un demi-diallèle chez *Sesbania pachycarpa* DC.: Dix écotypes de *Sesbania pachycarpa* DC. ont été utilisés pour produire des hybrides F1 à travers un système de croisement de demi-diallèle (sans les hybrides réciproques). Les parents et leurs F1 ont été évalués dans un système en blocs complètement randomisés avec 3 répétitions. Les caractères observés ont été le diamètre à la base, le nombre de ramifications, le nombre de gousses et le poids de 100 graines. Pour tous ces caractères sauf le poids de 100 graines, les plantes ont manifesté un hétérosis hautement significatif par rapport à la moyenne des 2 parents. L'estimation des effets d'aptitude à la combinaison a montré des effets AGC hautement significatifs pour tous les caractères, tandis que les ASC ne sont hautement significatifs que pour le poids de 100 graines et à la limite de la signification pour le nombre de gousses. Les effets additifs apparaissent majoritaires dans le déterminisme génétique de ces caractères.

Sesbania pachycarpa / diallèle / aptitudes à la combinaison

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1. Introduction

Sesbania pachycarpa DC., a leguminous plant of the Fabaceae family, is widely spread in sahel. This species is found in semiarid and subhumid zones and on different types of soil [1, 5]. It has an important nitrogen fixation potential. Thirty days after germination the aerial part of the plant can contain about 5.38% of nitrogen. [2]. The leaves of the plant are used as fodder and in wound treatment [3]. The dry seeds eliminate guinea worm and its eggs [4]. They also contain an oil with a composition similar to soybean oil. However, the low content of oil in the seeds (6.58%) limits its economic interest [2]. We are interested in increasing the agronomic potential of this species. Previous studies have shown that genetic variability exists for traits associated with oil and nitrogen production [2].

This study was undertaken to estimate the amount of heterosis and to obtain estimates of general and specific combining ability for a range of traits in *S. pachycarpa*.

2. Materials and methods

Ten ecotypes of *S. pachycarpa* were selected to represent the genetic variability for four agronomic traits. The Fisher test indicated a highly significant difference at 1% for all the traits studied except pod number per plant (Tab. I). These ecotypes were crossed in all possible combinations excluding reciprocals because a previous study showed that there were no maternal effects [2]. In making crosses there were two phases, emasculation and pollination. In the first phase hermaphroditic plants considered as female were opened and their anthers removed. In the second phase flowers of plants considered as male were collected and their pollen was deposited on the stigma of emasculated flowers. The 10 ecotypes and 45 F1 hybrids obtained from the half-diallel cross were evaluated in the field at Léo (Burkina Faso) during 1995 in a randomized complete block design with 3 replica-

Table I. Trait mean for the ten ecotypes and tests indicating significant differences.

Ecotype	Dia (cm)	BNb	PNb	HSW (g)
1	2.2 _{abcd}	12.0 _{bcd}	232.8	2.6 _a
2	2.0 _{cd}	6.7 _{cd}	193.6	2.5 _{abc}
3	1.6 _d	10.7 _{bcd}	154.6	2.5 _{abc}
4	1.6 _d	5.3 _d	122.4	2.4 _{abc}
5	2.9 _{abc}	15.6 _{bcd}	337.1	2.3 _{abcd}
6	2.7 _{abc}	35.2 _a	130.6	2.6 _{ab}
7	2.9 _{abc}	20.7 _{bc}	244.4	2.2 _{cde}
8	3.1 _{ab}	22.5 _b	224.2	2.1 _{de}
9	3.5 _a	40.2 _a	285.4	2.2 _{bcd}
10	2.6 _{abc}	17.4 _{bcd}	318.8	1.8 _e
F	**	**	ns	**

Dia: stem diameter at maturity, BNb: branch number/plant, PNb: pod number/plant, HSW: 100 seeds weight, **: significantly different at 1% using a Fisher test, ns: not significantly different.

Values with the same subscript are not significantly different in a Newmann - Keuls test at the 5% level.

tions. Each ecotype was represented by a row of 8 m in length with rows 3 m apart. Three or four seeds were sown on each mound spaced 2 m apart. After germination, only one plant was left per mound. The traits studied were the main stem diameter (Dia) at maturity and the branch number per plant (BNb) (which represented the vegetative production characters), pod number per plant (PNb) and the 100 seeds weight (HSW) (which represented the oil production characters).

The data were analyzed statistically for combining ability according to Griffing's "method 4, model I" [6, 7]. Estimates of general and specific combining ability variance were also obtained using the diallel analysis described by Griffing [6, 7] as model I method 4. This analysis contains one set of F1's and neither parents nor reciprocal crosses are included.

Estimates of components of variance were obtained as follows.

For general combining ability variance:

$$S_{gi}^2 = \frac{M_g - M_s}{p - 2}.$$

For specific combining ability variance:

$$S_{si}^2 = M_s - M_e.$$

Where M_g is the mean square for general combining ability, M_s is the mean square for specific combining ability; M_e is the mean square for error from replicated experiments and p is the parent number.

Sum of squares were also estimated as follows.

For general combining ability:

$$S_g = \frac{1}{p-2} \sum_i X_i^2 - \frac{4}{p(p-2)} X^2.$$

For specific combining ability:

$$S_s = \sum_i \sum_j x_{ij}^2 - \sum_i X_i^2 + \frac{2}{(p-1)(p-2)} X^2.$$

Heterosis was expressed as a function of the average of the two parents i.e. $H = F1 - \text{mid parent}$ and $H\% = F1 \times 100 / \text{mid parent}$. This definition includes dominance as well as other non-additive (epistatic) gene effects.

3. Results

The analysis of mean performance of parents and their F1 hybrids showed that for diameter at maturity and pod number per plant, 27 F1 hybrids exceeded their better parents, 26 F1 hybrids achieved this performance for branch number per plant and only 8 F1 hybrids exceeded their better parent for 100 seeds weight (Tab. II). Average heterosis and heterosis expressed as a percentage of mid-parent values confirm this result. Thus, for all of the traits studied, F1 progeny on average significantly exceeded their mid-parent performance except for 100 seeds weight (Tab. III). Thus, F1 plants had more pods per plant, more branches per plant and a greater diameter than the average of their parents. Branch number (BNb) and the pod number (PNb) were the most heterotic characters. For pod number, the hybrid produced an increase of 94 pods compared to the average of the two

parents, as for branch number, the hybrid showed an increase of 3 branches.

In order to evaluate the hybrid combining potential value for these traits, an analysis of the variance for combining ability effects was carried out. Table IV shows that parents 2 and 4 have the best positive general combining ability for branch number per plant and parents 4 and 6 have the best general combining ability for pod number per plant. For the 100 seeds weight, parents 9 and 10 have the best general combining ability and for diameter, the best general combining ability is expressed by parents 4 and 6.

Variance analysis shows that the general combining ability (g_i) effects are highly significant for all traits studied. On the other hand, the specific combining ability (s_i) effects are only highly significant for the 100 seeds weight and are just at the significance level for pod number. The ratio of the general combining ability effect variances (s^2_{gi}) to the specific combining ability effect variances (s^2_{si}) is relatively high for stem diameter and branch number per plant, it is close to one for the 100 seeds weight and less than one for pod number (Tab. V).

Table VI shows the estimates of general combining ability variance (s^2_{gi}) and the specific combining ability variance (s^2_{si}) among the ten parents for all the traits studied. For stem diameter, parents 4 and 6 have similar specific combining ability variances; while for branch number per plant parents 2 and 4, have the largest general combining ability variances but they differ in specific combining ability variance. As for pod number per plant, parents 4 and 6 have the largest general combining ability variances but differ with regard to specific combining ability variance, while for 100 seeds weight parents 9 and 10 have similar specific combining ability variances.

4. Discussion

The ten parents selected for the diallel were chosen to represent a range of differences in the traits studied. Thus, the results of this investigation in

Table II. Mean performance for the ten ecotypes and their hybrids.

<i>Ecotype</i>	Dia (cm)	BNb	PNb	HSW (g)
1	2.53	09.66	279.27	2.17
2	2.18	09.11	146.27	2.79
3	3.53	16.33	318.22	2.41
4	4.08	20.05	376.50	2.11
5	2.99	13.88	228.88	3.07
6	2.33	08.44	195.44	2.72
7	2.51	09.86	119.66	3.34
8	2.29	10.22	093.22	3.18
9	2.82	11.33	199.10	3.62
10	2.40	07.49	151.94	3.65

<i>Hybrid</i>					<i>Hybrid</i>	Dia (cm)	BNb	PNb	HSW(g)
1 × 2	3.43*	19.77*	361.00*	2.33	5 × 6	2.87	14.85*	225.50	2.33
1 × 3	4.23*	13.94	470.77*	2.58*	5 × 7	3.19*	11.44	207.94	3.36*
1 × 4	3.39	21.44*	430.00*	2.60*	5 × 8	2.76	09.11	173.33	2.94
1 × 5	3.60*	19.00*	371.00*	2.46	5 × 9	3.21*	17.89*	287.22*	3.39
1 × 6	2.85*	10.88*	193.11	3.02*	5 × 10	3.20*	13.88	430.00*	3.05
1 × 7	2.94*	09.44	226.44	3.10	6 × 7	2.97*	11.33*	224.66*	3.07
1 × 8	3.05*	15.11*	280.88*	2.80	6 × 8	3.55*	15.22*	401.50*	2.79
1 × 9	3.06*	12.44*	246.33	3.21	6 × 9	3.03*	11.44*	283.94*	3.03
1 × 10	3.43*	14.00*	323.11*	3.07	6 × 10	3.59*	12.00*	297.11*	3.21
2 × 3	4.07*	17.11*	385.11*	2.32	7 × 8	2.06	05.33	127.05*	3.15
2 × 4	3.73	19.77	390.00*	2.33	7 × 9	3.63*	11.66*	366.78*	3.39
2 × 5	3.04*	14.00*	225.22	3.08*	7 × 10	3.31*	16.23*	364.61*	3.56
2 × 6	4.03*	22.66*	452.50*	2.67	8 × 9	2.49	07.50	158.83	3.31
2 × 7	2.59*	09.89*	182.22*	3.03	8 × 10	2.82*	12.99*	190.11*	3.45
2 × 8	3.41*	16.78*	255.00*	3.29*	9 × 10	2.81	10.66	206.28*	3.79
2 × 9	3.18*	13.78*	329.55*	3.19					
2 × 10	3.45*	19.89*	341.22*	3.10					
3 × 4	3.95	17.44	436.78*	2.81*					
3 × 5	3.27	14.88	256.77	2.44					
3 × 6	4.10*	20.44*	380.22*	2.36					
3 × 7	2.29	07.55	161.89	2.92					
3 × 8	2.78	13.33	246.33	2.88					
3 × 9	3.40	14.00	292.33	3.01					
3 × 10	3.49	14.66	302.89	3.41					
4 × 5	3.80	23.11*	368.33	2.35					
4 × 6	4.72*	24.33*	730.78*	2.54					
4 × 7	3.47	12.44	356.44	2.80					
4 × 8	3.09	09.66	189.88	3.21*					
4 × 9	3.67	13.44	288.77	2.94					
4 × 10	3.33	13.55	314.22	3.08					

*: hybrid which exceeded the better parent.

the strict statistical sense apply only to these specific parents. However, these parents do represent the range variability in a reasonable sample of the

lines available for breeding work and so some extrapolation of the findings is considered appropriate.

Table III. Average heterosis (H) and heterosis % F₁ (H%F₁).

Character	H	H%F ₁
Dia	0.52**	15.81
BNb	2.81**	29.52
PNb	94.35**	30.9
HSW	0.04 ^{ns}	1.34

Dia: diameter at maturity, BNb: branch number per plant, PNb: pod number per plant, HSW: 100 seeds weight, **: significantly different in a Fisher test at the 1% level of probability, ns: not significant.

Table IV. General combining ability of each parent.

Parent	Dia	BNb	PNb	HSW
1	0.042	0.745	19.481	-0.172*
2	0.173	2.947*	21.878	-0.151*
3	0.093	0.412	23.287	-0.226*
4	0.521*	3.141*	94.801*	-0.237*
5	-0.091	1.011	-25.185	-0.145*
6	0.748*	1.637	55.315*	-0.191*
7	-0.920*	-4.338*	-66.094*	0.229*
8	-0.615*	-3.129*	-90.483*	0.158*
9	-0.149	-2.157*	-35.844	0.338*
10	-0.031	-0.269	2.843	0.397*

Dia: diameter at maturity, BNb: branch number per plant, PNb: pod number per plant, HSW: 100 seeds weight, *: significantly different in a Fisher test at 5%.

Table V. General combining ability and specific combining ability effects and their variance ratio.

Characters	F _{GCA}	F _{SCA}	s _g ² /s _s ²
Dia	16.19**	1.94	3.7
BNb	5.23**	1.13	3.8
PNb	4.77**	1.71*	0.5
HSW	50.86**	4.59**	1.4

F_{GCA}: general combining ability effect, F_{SCA}: specific combining ability effect, Dia: diameter at maturity, BNb: branch number per plant, PNb: pod number per plant, HSW: 100 seeds weight, **: significantly different in a Fisher test at 1%, *: significantly different in a Fisher test at 5%.

On the basis of the heterosis estimates and the variance estimates for combining ability, additive gene effects were shown to predominate in determining stem diameter and branch number per plant which are the vegetative production characters. Comparable results have been found in crops such as cotton [12] and maize [10]. Similar studies with different crop species [8, 9, 11] found that when the effects of the specific combining ability were not significant in diallel crosses, the genetic variance depends mainly on additive gene effects. These were shown to be very important in determining the pod number per plant and 100 seeds weight in *Sesbania*. Not all of the genetic variation was attributable to additivity, however, as specific combining effects were also significant. Both general combining ability (GCA) and specific combining ability (SCA) were important in determining the oil production traits in *Sesbania pachycarpa* and may be improved by exploiting both additive and non-additive genetic effects.

With regard to individual ecotype effects, for stem diameter, parents 4 and 6 were similar in that they both exhibited high GCA and a low SCA variance. This means that both these parents consistently transmit their stem diameter characteristics to their progeny in a mainly additive and predictive way. For the number of branches per plant, parent 2 (having high GCA and low SCA variance) uniformly transmits this trait to its progeny. This trait is transmitted by parent 4 to its progeny in a more differential manner, i.e. there are specific combinations with parent 4 which yield considerably more than would be expected and other combinations which yield much less than expected. However parent 4 transmits pod number per plant uniformly to its descendants. Also consideration should be given to parent 6 as the best pod production is found in hybrids involving parent 6. Parents 2 and 6 come from the same climatic zone but they may belong to different genetic groups. With regard to 100 seed weight the best two parents, 9 and 10, have similar behaviour. They also come from the same climatic zone but may belong to different genetic groups.

With regard to individual ecotype effects, parent 4 is probably superior to the others for inclusion in

Table VI. Estimates of general combining ability and specific combining ability variances for each parent.

Parent	Dia		BNb		PNb		HSW	
	s^2_{gi}	s^2_{si}	s^2_{gi}	s^2_{si}	s^2_{gi}	s^2_{si}	s^2_{gi}	s^2_{si}
1	-0.02	0.01	-0.52	0.46	-206.5	3001.9	0.02	0.03
2	0.01	0.01	7.61	-0.56	-107.3	-1887.5	0.02	0.05
3	-0.01	-0.04	-0.90	-4.22	-43.7	-854.5	0.05	0.03
4	0.25	0.20	8.78	3.96	8401.1	8640.3	0.05	0.03
5	-0.01	-0.05	-0.05	2.47	48.2	1574.7	0.02	0.06
6	0.53	0.22	1.60	6.78	2473.7	14941.3	0.03	0.03
7	0.82	-0.02	17.74	1.59	3782.4	3566.4	0.05	0.01
8	0.35	0.06	8.71	-0.13	7601.1	-49.6	0.02	0.03
9	0.002	-0.01	3.57	-1.66	698.7	936.3	0.11	0.01
10	-0.02	-0.09	-1.004	2.37	-577.9	2316.1	0.15	0.01

Dia: diameter at maturity, BNb: branch number per plant, PNb: pods number per plant, HSW: 100 seeds weight.

a synthetic variety aimed at improving both vegetative growth and oil production traits. However, consideration should also be given to parents 2 and 6 because the best pod production was found in hybrids involving parent 6, and parent 2 produced a high number of branches.

This study has shown the importance of both GCA and SCA for the traits investigated. The genetic variability for each of the traits shows that it should be possible to make significant genetic changes in the generations following hybridization. Yield heterosis of F1 hybrids was quite pronounced but additive gene effects are also important.

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