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Genetic improvement of pyrethrum

4. Selective divergence, heterosis and potential hybrid clones*

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Summary. Pyrethrum (*Chrysanthemum cinerariefolium*), an important paramedicinal plant is a potential source of pyrethrins, which have a long history of safe uses against mosquito larvae – a carrier of malarial parasite. It was introduced in India from Kenya in 1931. Considerable genetic diversity has been generated over the years. Repeated clonal selection could lead to isolation of a number of divergent clones representing selective divergence. Planned hybridization among some of the chosen clones could further enlarge the spectrum of variation as measured by multivariate analyses (D^2-statistic and canonical analysis). The resulting hybrids manifested a variable degree of heterosis which was found to be, by and large, positively associated with the degree of divergence between the two constituent parents of a hybrid. However, the choice of the potential hybrid clone(s) for commercial exploitation was most viable when parents for hybridization were short-listed on the basis of parental divergence coupled essentially with per se performance for specific traits. The latter criterion assumes greater significance since low × low or medium × low parental hybrids also tended to register high heterosis for both the pyrethrins content and yield. Four hybrids: 234 × L, 8 × L, 326 × 395 and 319 × L were identified to be the most promising for clonal selection.

Key words: *Chrysanthemum cinerariefolium* – Selective divergence – Heterosis – Hybrid clones – Crop improvement

Introduction

The acute and chronic mammelian toxicity associated with synthetic insecticides/pesticides employed for controlling domestic insects pests poses severe restriction on their continuous and indiscriminate use. Development of safer toxicants, preferably natural ones, is therefore a key to a sound health care programme. Natural pyrethrins comprising two main components of flower extract – pyrethrin I (including Jasmolin I, Cinerin I and pyrethrin I) and pyrethrin II (including Jasmolin II, Cinerin II and pyrethrin II) (Dickinson 1987) – have a long history of safety due to their non-persistent and non-pollutant nature, also being easily biodegradable through the native enzyme system of mammals (Woodward et al. 1987; Matsumura 1975). Their potential bio-efficacy against mosquito larvae – a carrier of malarial parasite (Hobbs 1976), *Varroa jacobsoni* – an ectoparasitic mite of honey bees in apiculture (Nijhuis et al. 1987), *Culicoides variipennis* – a biting pest of man and livestock (found in alkaline/saline lake water) and a vector of bluetongue viral disease of sheep and cattle (Woodward et al. 1987), and against *Mesocyclops leuckarti Sensu Lato* (Cyclops) – a carrier of dranculiasis (Kamal and Mangla 1987), among others, is now well established. Moreover, natural pyrethrins are virtually non-toxic, inexpensive, and do not have a build-up of secondary resistance to pests. Therefore, unlike with 'hard' insecticides, no precautions need to be taken where pyrethrum-based formulations are in use. As such, they can conveniently be incorporated into integrated pest management programmes.

Pyrethrins are obtained from pyrethrum (*Chrysanthemum cinerariefolium*), which is self-incompatible allogamous perennial plant of the Compositae family, brought under cultivation in India in 1931 (Bhat and Pandita 1977). A great deal of genetic variability is encountered in the commercial bulk populations grown in the Kashmir valley in the north and the Palani hills in south peninsular India. Selection within such a variable population might lead to divergence from the base popu-

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lation and also among selected genotypes (Hanson 1987). Hence, repeated clonal selection was exercised and a number of diverse clones were developed, as reported in earlier parts of this investigation (Singh et al. 1987, 1988 a, b).

The degree of diversity so generated can be measured by three principal methods: (i) using genetic loci (genes, isozymes, restriction fraction length polymorphism, etc.) as indicated by Troyer et al. (1988) and Burr et al. (1983); (ii) by direct measurement or qualification of divergence using potent multivariate analyses, such as D^2 and principal component analyses or factor analysis (cf. Godshalk and Timothy 1988); and (iii) using the diversity analysis of Hanson and Moll (1986) utilising heterotic differences among single crosses, as abundant heterosis reveals genetic diversity among parents (Mungoma and Pollak 1988). We applied the latter two approaches on 12 parental clones plus 27 related half sibs in pyrethrum to achieve the following twin objectives: (a) To determine the degree of selective divergence among three pollen parents, nine seed parents (all selections) and their 27 hybrids through multivariate analyses. (b) To ascertain the degree of heterosis in a cross vis-a-vis quantified divergence between the parents involved for establishing the relationship, if any, between heterosis and genetic diversity and also for locating the best hybrid clone(s) of pyrethrum for commercial exploitation.

Materials and methods

Three pollen parents (testers) and nine selected seed parents (lines/clones) of *Chrysanthemum cinerariefolium* were crossed in line x tester fashion to generate 27 hybrids (half-sib families). Owing to the intense incompatibility reaction in each clone, selfing was not possible; even 'bud pollination' could not succeed. Conversely, cross-pollination was easy. All 39 genotypes (12 parents and 27 hybrid progenies), as detailed in Table 3, were transplanted through seed-nursery under standard agronomic management in randomised block design, with three replicates at the CIMAP Regional Centre, Kodaikanal (Tamil Nadu) situated at 1,650 m above sea-level. A plot comprised triple rows of 3.5 m each with 45 x 45 cm inter- and intra-hill spacings.

Metric observations were recorded three times a year on 15–20 random plants sampled from the middle row in each plot, for plant height (cm), bush diameter (cm) and flower diameter (cm) of at least 25 flowers per hill. Flowering commenced 4 months after planting and picking of flowers was carried out at 10- to 15-day intervals thereafter. Flowers were then sun dried or oven dried at 50 °C to a constant weight which represented (dried) flower yield (g/plant). Pyrethrin content (all six rethrins pooled) was estimated in dried flower powder by a modified spectrophotometer (Beckley 1950). Pyrethrin yield (mg/plant) was obtained as a product of dried flower yield and pyrethrin content (%).

Statistical analysis of data was performed for quantified/generalized (D^2-statistic) and spatial distances (canonical variates) as outlined in Rao (1952). Realized heterosis was computed by standard methods over the better parent (BP) as well as over the check (EP), the latter being 'economic heterosis'.

Results and discussion

Though other plant species containing natural pyrethrins, viz. *Tagetes minuta* and *T. pitula,* occur in India, they possess low pyrethrin content: 0.20%–0.65% (Kamal and Mangla 1987) as compared to >0.65% in pyrethrum. Hence, judicious exploitation of the latter assumes greater significance. Introduction and subsequent adaptation of this crop in temperate agroclimatic zones of India facilitated its successful commercial use. However, since a heterogenous material was introduced from Kenya some six decades ago (cf. Bhat and Pandita 1977), a tangible amount of genetic variation seems to have been accumulated over the years (Singh et al. 1987). Nearly absolute allogamy as a result of by self-incompatibility could further enlarge this spectrum. Vegetative multiplication coupled with seed propagation is employed to perpetuate it.

Selective divergence

From this variability, several elite clones were selected. From these, the two clones along with the local bulk were used as testers and nine as female lines to develop 27 half-sib (HS) families. The quantified degree of divergence among testers ranged from 9.9 to 68.6 ($D^2 = 35.4$); among lines from 0.6 to 41.1 ($D^2 = 12.9$) and among HS families from 2.7 to 191.9 ($D^2 = 34.7$) (Table 1). A group constellation of 39 genotypes D^2 analysis) resulted in six clusters where the three testers (Sl. Nos. 1–3) fell in three separate groups, while all the lines (Sl. Nos. 4–12), except No. 11, formed a single cluster (Table 2). Hybrids formed five clusters, signifying the presence of considerable diversity among them. When all these genotypes were examined with respect to their distribution on the first two canonical axes (spatial relationship) (Fig. 1), it became apparent that they followed the group constella-

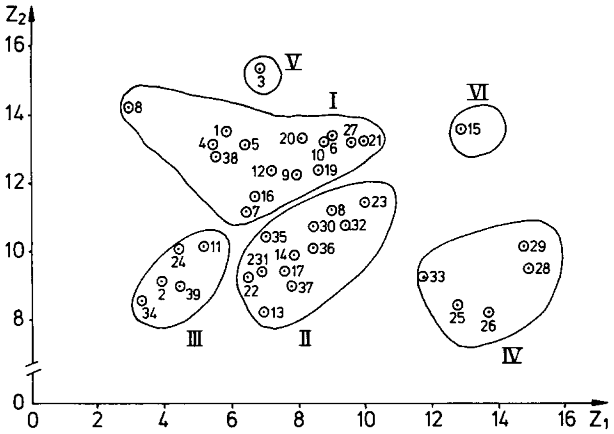

Fig. 1. Spacial distance among parents and hybrids of pyrethrum in Z_1-Z_2 chart of principal component analysis

Table 1. Group divergence (D^2) in pyrethrum populations

Group of populations	Mean D^2			Range of D^2		
	Testers	Lines	Hybrids	Testers	Lines	Hybrids
Testers	35.4	20.7	70.1	9.9–68.6	6.2–49.8	2.1–113.7
Lines	–	12.9	30.4	–	0.6–41.1	2.9– 97.5
Hybrids	–	–	34.7	–	–	2.7–191.9

Table 2. Group constellation and inter-cluster divergence (D^2) in pyrethrum

	I	II	III	IV	V	VI	AV.D^2	Cluster-constellation[a]
I	13.9	23.6	36.5	58.3	23.0	38.8	36.0	1, 4–10, 12, 16, 19–21, 27, 38
II		16.4	23.7	47.5	51.1	47.0	38.6	13, 14, 17, 18, 22, 23, 30–32, 35–37
III			18.0	85.7	58.1	85.0	57.8	2, 11, 24, 34, 39
IV				15.8	84.6	27.0	60.6	25, 26, 28, 29, 33
V					–	43.5	52.1	3
VI						–	48.3	15

[a] Numbers are the Sl. No. denoted in Table 3

tions arrived at by D^2 analysis (Table 2). Thus, testers were diverse in satisfying their requirements to be used as pollen parents, and the divergence among hybrids was greatly extended.

Ostensibly, heterozygosity stemming from hybridization among clones would have been the principal cause of such an inflated variation among hybrids. But the parental clones were already highly heterozygous. The question arises: where did this additional variation arise from? Could it be due to a combination of more desirable or complementary alleles on selective hybridization among superior clones? Or could it occur from higher frequency of syngamy on artificial/controlled pollination of female clones? Perhaps both factors might be responsible to an unknown extent. The latter seems to attract attention on two counts. First, entomophilous pollination, which is common in pyrethrum, may not be good enough to get all the female gametes fertilised under open conditions. Also, such open pollination does not exclude poor genotypes (inferior gametes) from participating in fertilisation, resulting in poor progenies. And second, vegetative multiplication of the same planting stocks, which is a common practice, would block new genotypes from appearing in the population, even if pollination has been complete and has involved superior gametes.

Thus, a judicious hybridisation between chosen superior parents in unision with sexual propagation yielded superior (diversified) full-sib families in pyrethrum. It can, therefore, be inferred that 'selective divergence' might be a potential force of differentiation in crop plants, particularly where vegetative propagation prevails over sexual propagation.

Heterosis vis-a-vis selective divergence

Since high heterosis indicates high genetic diversity between the two parents involved in a cross (Mungoma and Pollak 1988), it would be interesting to examine the mean performance and realised heterosis over the better parent (regardless of signs) vis-a-vis the corresponding D^2 values associated with the two constituent parents for three economic traits, viz., flower yield and pyrethrin content and yield in pyrethrum (Table 3). An over-all correlation between D^2 and heterosis for any of the three traits revealed that while divergence and heterosis were correlated positively for flower yield ($r = 0.40^*$) and pyrethrin yield ($r = 0.34$), they showed no correlation with pyrethrin content. The percentage frequency distribution of all 27 cross-combinations based on a defined classification of divergence and heterosis over better parent for flower yield, pyrethrin content and pyrethrin yield, as presented in Table 4, reinforced this fact.

Thus, narrow-to-average (N-A) divergence was associated with low-to-medium (L-M) heterosis in 85%–89% of crossses for all three traits. Conversely, a wide divergence between selected parents might be construed to correspond with high heterosis in the resulting hybrid, though such a relationship was absent in the present set of materials, probably because nearly all the selected female parents were closely related and least divergent from each other. However, there appear to be two exceptional cases: in two cross-combinations involving widely divergent parents, viz. 234 × L ($D^2 = 43.3$) and 326 × L ($D^2 = 49.8$), the degree of heterosis was low to medium, not high, for all three traits, and the reverse was true with

Table 3. Heterosis (%) in relation to divergence (D^2) between parents involved in crosses in pyrethrum

Sl. No.	Parents/ hybrids	Divergence (D^2)	Flower yield (g/plant)		Pyrethrin content (%)		Pyrethrin yield (mg/plant)	
			Per-se mean	Heterosis	Per-se mean	Heterosis	Per-se mean	Heterosis
1	2	3	4	5	6	7	8	9
1.	395		56.0		1.2		672.0	
2.	L		46.3		0.80		370.6	
3.	D16-6		72.7		1.43		1,039.2	
4.	333		54.7		1.23		672.4	
5.	387		73.0		1.17		846.8	
6.	326		93.7		1.27		1,189.6	
7.	154		78.7		0.93		731.6	
8.	319		73.7		1.30		957.7	
9.	216		81.0		1.13		915.3	
10.	234		86.0		1.30		1,118.0	
11.	8		76.7		0.90		690.0	
12.	151		79.7		1.20		956.0	
13.	333 x 395	4.0	83.0	48.2	0.73	−40.7	605.9	−9.9
14.	387 x 395	6.3	84.8	16.2	0.90	−25.0	763.5	−9.8
15.	326 x 395	11.8	128.7	37.3	1.43	12.6	1,852.7	55.7
16.	154 x 395	19.9	71.0	−9.8	1.03	−14.2	731.3	−0.1
17.	319 x 395	6.2	83.5	13.3	0.90	−30.8	751.5	−21.5
18.	216 x 395	10.8	89.8	10.9	1.14	−5.0	1,024.2	11.9
19.	234 x 395	13.7	73.7	1.5	1.19	− 8.5	1,039.3	−7.0
20.	8 x 395	13.9	80.3	4.8	1.26	5.0	1,012.3	46.7
21.	151 x 395	9.6	105.3	32.1	1.23	2.5	1,295.6	35.5
22.	333 x L	26.5	75.2	37.5	0.79	−35.8	593.8	−11.7
23.	387 x L	28.6	110.0	50.7	1.13	−3.5	1,254.0	48.1
24.	326 x L	49.8	46.2	−50.7	0.82	−35.4	378.6	−68.2
25.	154 x L	31.4	135.3	84.6	0.87	−6.5	1,264.4	72.8
26.	319 x L	39.1	155.5	110.9	0.92	−29.2	1,430.6	49.4
27.	216 x L	21.3	94.2	16.3	1.31	15.9	1,233.6	34.8
28.	234 x L	43.3	164.0	90.7	1.29	−0.8	2,115.6	89.2
29.	8 x L	17.8	154.8	101.8	1.22	35.6	1,888.9	173.7
30.	151 x L	26.9	87.2	9.4	1.04	−13.3	906.6	−5.2
31.	333 x D16-6	14.8	79.0	8.7	0.80	−44.1	632.0	−39.2
32.	387 x D16-6	13.7	118.7	62.6	1.15	−19.6	1,364.7	31.3
33.	326 x D16-6	10.4	141.7	51.2	0.92	−35.7	1,303.4	9.6
34.	154 x D16-6	33.5	78.7	0.00	0.83	−41.9	653.0	−37.2
35.	319 x D16-6	7.8	69.8	5.3	0.98	−31.4	684.3	−34.2
36.	216 x D16-6	24.1	81.7	0.8	0.89	−37.8	726.9	−30.1
37.	234 x D16-6	18.5	84.7	−1.5	0.86	−39.9	728.2	−34.9
38.	8 x D16-6	35.8	53.4	−30.4	1.15	−19.6	613.3	−40.9
39.	151 x D16-6	19.4	51.0	−35.0	0.69	−51.8	357.0	−65.6

the cross 8 x L (Table 3), both being two facets of the same phenomenon. Nevertheless, going by relative frequency, there seems to be a positive relationship between parental diversity and realised heterosis in pyrethrum as in several other crops (cf. Moll et al. 1965; Cress 1966; Moll and Stuber 1974). Whether these relationships have a bearing on detecting the crosses showing high realised economic heterosis may be examined further.

Choice of economically viable hybrid clones and potential parents

The check, clone 387 (var. *Hansa*), was released in 1985 for commercial cultivation under Palani hill conditions (Anon 1986). Against this, at least four hybrids, namely 234 x L, 8 x L, 326 x 395 and 319 x L, in order, registered 150%–69% superiority in pyrethrin yield (Table 5). The first three of these were consistently superior over the check for flower yield (125%–76%) and also for pyrethrin content (22%–4%); the fourth one was more than twice as good as the check for flower yield, but was poor in pyrethrin content. The two other promising hybrids were 216 x L and 8 x 395, which gave 12%–8% superiority over the check for pyrethrin content, 46%–20% for pyrethrin yield and 29%–10% for flower yield. One more hybrid, 154 x L, was nearly one-and-a-half times better than the check for pyrethrin yield and two times better for flower yield, but possessed low pyrethrin content. The rest of the hybrids manifested low/poor (or negative) heterosis, and hence are not presented in Table 4.

A careful perusal of the parental components of the above top few hybrids reveal that among testers it was L, the local bulk, which constituted the pollen parent of almost all the superior hybrids; clone 395 was involved in two hybrids only. Among the nine female lines, clones 234, 8, 326, 319, 154 and 216, in that order, were useful parents. This brings out two important points, one relating to divergence between parents involved in a cross, and the other to the agronomic properties of the pollen parent. With regard to divergence, it is apparent that widely divergent parents, viz., 234 and L, produced the highest productive hybrid for both pyrethrin and flower yield. This confirms our earlier statement generalising on the positive association between parental diversity and hybrid performance. Notwithstanding, however, the two next best hybrids (8 x L and 326 x 395) involved narrowly divergent parents, and the following hybrids (319 x L and 216 x L) had average divergence between parents. Since their performance was also significantly high, it would not be misplaced to suggest that some of even narrowly or mildly divergent parents can also yield productive hybrids. Consequently, a question arises axiomatically: what should the criteria be in choosing parents from amongst the less divergent ones (with low D^2 values) to realize high heterosis?

Table 4. Divergence and heterosis relationship for different traits in pyrethrum

Magnitude of divergence-heterosis	% frequency of crosses for different traits		
	Flower yield	Pyrethrin %	Pyrethrin yield
W-H	0	0	0
W-M	7.40	3.70	3.70
W-L	0	3.70	3.70
A-H	3.70	0	0
A-M	7.40	14.81	0
A-L	22.23	18.53	33.34
N-H	3.70	3.70	3.70
N-M	7.40	29.63	0
N-L	48.17	25.93	55.56
Correlation (r)	0.40*	−0.06	0.34

W, A and N – Wide ($D^2 > 40$), Average ($D^2 = 20-40$) and Narrow ($D^2 < 20$) divergence, respectively; and H, M and L – High, Medium and Low representing >100%, 50%–100% and <50% for flower yield, >45%, 25%–45% and <25% for pyrethrin content and >125%, 75%–125% and <75% for pyrethrin yield, respectively

The study reveals that the choice of parents for hybridisation to effectively exploit hybrid vigour should be based on multivariate generalized distance (D^2 values) between parents coupled with per se performance for specific traits, as specified in pyrethrum (Table 6).

Notably, when parental divergence is narrow or mild, low x low or medium x low crosses tend to register high heterosis, and when diversity between parents is wide, the same is accomplished by high x low crosses. An exception to the latter situation is obtained in the cross 326 x L, where parental divergence was the highest and per se means of the two parents were also highest and lowest, respectively, for flower and pyrethrin yields (Table 3); still F_1s for all three traits were, by and large, the lowest. Negative heterosis was the consequence. Perhaps, as stated by Moll et al. (1965), a positive relationship between heterosis and parental divergence works within a reasonable range of divergence. But clone 326 and the local bulk (L) do not seem to be exceptionally divergent ($D^2 = 49.8$ only). Whether allelic differences for specific traits might be responsible for such a situation cannot be ruled out.

Insofar as the agronomic worth of the L – the tester parent involved frequently in top hybrids – is concerned, it is well adapted to the local ecological milieu. Hence, hybrids based on the L are likely to be well favoured under Palani hill conditions. Since the crop can be vege-

Table 5. Superior crosses and parental performance for three economic traits in pyrethrum

Superior crosses or check (D^2)[+]	Pyrethrin yield (mg/plant)				Flower yield (g/plant)				Pyrethrin content (%)			
	Line	Tester	$\bar{F}_1$	EH[a]	Line	Tester	$\bar{F}_1$	EH[a]	Line	Tester	$\bar{F}_1$	EH[a]
234 x L (W)	1,118	371	2,116	150	86	46	164	125	1.30	0.80	1.29	10
8 x L (N)	690	371	1,889	123	77	46	155	112	0.90	0.80	1.22	4
326 x 395 (N)	1,190	672	1,853	119	94	56	129	76	1.27	1.20	1.43	22
319 x L (A)	958	371	1,431	69	74	46	156	113	1.30	0.80	0.92	−21
154 x L (A)	732	371	1,264	49	79	46	145	99	0.93	0.80	0.87	−26
216 x L (A)	915	371	1,234	46	81	46	94	29	1.13	0.80	1.31	12
8 x 395 (N)	690	672	1,012	20	77	56	80	10	0.90	1.20	1.26	8
387 (Check)	847	–	–	–	73	–	–	–	1.17	–	–	–

[a] EH – Economic heterosis (%) over the check

[+] D^2 (W, A, N)–divergence between parents being Wide, Average and Narrow, respectively

Table 6. Choice of parents based on divergence and per-se performance for different traits in pyrethrum

Character	Parental divergence (D^2)	Per-se performance of two parent
Flower yield	Wide	High x Low
	Narrow/Mild	High x Low
Pyrethrin yield	Wide	High x Low
	Narrow/Mild	Low x Low or Medium x Low
Pyrethrin %	Wide	High x Low
	Narrow/Mild	Low x Low or Medium x Low

tatively propagated as successfully as sexually, the hybridity so generated would stay fixed under asexual propagation. As such, after thoroughly evaluating them further against the check (var. *Hansa* – clone 387) in bench scale and pilot scale trials, the best of the top four hybrids, viz., 234 x L, 8 x L, 326 x 395 and 319 x L may be exploited commercially to maximise the production of pyrethrins to combat mosquito menace effectively.

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