A chlorophyll-deficiency factor in the natural populations of *Tephrosia purpurea* (L.) Pers.*

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ABSTRACT

The selection coefficient for the deficiency allele and the proportion of the two alleles in the populations are estimated. The apparent vegetative and reproductive vigour in the populations with the factor is attributed to the combined effect of low population density caused by the death of the double recessives and the higher selective value of the heterozygotes in these populations. A model of balanced polymorphism involving a recessive lethal is suggested to explain the results.

1. INTRODUCTION

THERE is vast literature on the occurrence and evolutionary significance of recessive lethal genes in natural populations.[1-3] Although work of this kind is almost exclusively on *Drosophila*, high frequencies of sickle cell trait [4,5] and several deleterious genes[6] in human populations have been explained on the basis of balanced polymorphism. A case of balanced polymorphism in plants involving a chlorophyll lethal in the natural populations of *Dactylis glomerata* L., a self-incompatible species, has also been reported.[7]

During the course of a study on the structure of natural populations of *Tephrosia purpurea* (L.) Pers., a predominantly self-pollinated species, this author came across the presence of a chlorophyll-deficiency factor (*cdf*) of a rather low frequency in 16 samples from five out of about 35 localities in peninsular India. The results of a study on the frequency of occurrence of this factor, its probable origin and role in population dynamics are presented here.

2. MATERIAL AND METHODS

The seed samples used in the present study form a part of several collections of *Tephrosia purpurea* from about 35 localities in peninsular India. The samples collected from each plant were maintained separately althrough. Only those samples yielding chlorophyll-deficient seedlings were analyzed further for purposes of this paper. Details of the sources of samples are given in table 1.

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Table. 1 Data on the chlorophyll deficiency factor

Locality	No. of samples	Total No. of seeds	Germi-nation %	Chloro-phyll defi-cient seedlings (aa) %	Hetero-zygotes (Aa) de-tected %	Gametic frequen-cy of allele a %	Selection coeffi-cient	Propor-tion of A : a in the population
1. Konarak (Orissa)	3	32	78·12	16·00	19·00	9·50	0·895	1 : 0·1050
2. Markhandi Udadoan (Madhya Pradesh)	4	44	77·29	8·82	plants did not survive			
3. Anakapalli (Andhra Pradesh)	2	38	78·94	10·00	7·40	3·70	0·961	1 : 0·0384
4. Vijayawada (Andhra Pradesh)	4	55	80·00	11·36	10·23	5·11	0·946	1 : 0·0538
5. Pamban (Tamil Nadu)	3	57	80·70	8·69	7·14	3·57	0·963	1 : 0·0370
Total/Average	16	226	79·01	10·97	10·94	5·47	0·942	1 : 0·0578

Normal plants from all the samples yielding chlorophyll-deficient seed-lings were allowed to grow and flower. At the time of flowering three inflore-scences of each plant were enveloped in butter paper bags. Seeds collected from the protected inflorescences were used for progeny tests to detect hetero-zygotes. Plants showing at least one chlorophyll-deficient seedling in the progeny were considered as heterozygotes.

Data presented in table 2 were gathered from natural populations at the localities indicated.

3. RESULTS AND DISCUSSION

Data relating to the frequency distribution of the *cdf* and the results of progeny tests locating heterozygotes are given in table 1. Basing on these findings it is assumed that the factor is a simple Mendelian trait involv-ing a recessive lethal, the double recessive resulting in chlorophyll-deficient seedlings that die off in about a week after germination. The heterozygotes were morphologically indistinguishable from the homozygous dominants.

The occurrence of the *cdf* both in inland and coastal populations, at the northern and southern-most parts of peninsular India and in sandy and hard red soils shows a lack of correlation between geographical and eco-logical factors and the occurrence of the deficiency allele which might have initially come into being through a spontaneous mutation.

Table 2. Some differences between populations with and without the chlorophyll deficiency facto; from two localities.

Character	Konarak populations		Vijayawada populations	
	with *cdf*	without *cdf*	with *cdf*	without *cdf*
1. Density (number of plants per m^2) (5 quadrats each)	7–16	10–22	6–13	8–20
2. Plant height (25 observations each)	30–45 cm	27–42 cm	31–47 cm	30–43 cm
3. Length of the terminal leaf-let (50 observations each)*	1·38 cm	1·33 cm	1·35 cm	1·29 cm
	±0·0584	±0·0714	±0·0599	±0·0632
Coefficient of variation	4·23%	5·37%	4·44%	4·89%
4. Number of inflorescences per plant (25 observations each)	7–10	6–8	6–9	5–7
5. Number of seeds per fruit (50 observations each)	2–5	1–4	1–6	1–4
6. Seed germination (%) (3 samples each)	78·12	79·00	80·00	81·30

* Differences between the corresponding means are significant at 0·01 level.

The gametic frequency of the gene as estimated through progeny tests is rather low (table 1) when compared to the situation in *Dactylis glomerata*, where a similar gene occurs at a gametic frequency as high as 24 per cent, the lowest being 2·5 per cent in some populations.[7] The author is aware that some heterozygotes and homozygous recessives might have gone undetected in germination studies or progeny tests. Nevertheless, it is believed that the general picture of the frequency distribution of the gene would nearly be the same as shown in table 1.

Some differences observed between populations with and without the *cdf* in two localities are given in table 2. One important difference relates to the density of the populations. Population size is regulated at or below some level which is known as the carrying capacity of the environment.[8] The deleterious effects of a population density beyond this level are well known. Evidence for density induced mortality has been provided recently for some leguminous and non-leguminous species.[9,10] The present author also found a fall in dry weight with increase in the population density in some populations of *T. purpurea* and *T. candida* DC. (unpublished data). Table 2 indicates the benefits accrued by the populations with the *cdf* resulting

in an increase of the reproductive capacity. Neither the gene nor population density seem to have any effect on the rate of seed germination.

Recessive lethals are known to play a role in regulation of population density in some organisms.[11] One effect of such genes is the maintenance of population density at or below the carrying capacity of the environment.

The differences between the populations with and without the *cdf* cannot exclusively be attributed to density differences. There is evidence that apparent vegetative vigour can be a consequence of heterozygosity for recessive chlorophyll-blocking genes in barely,[12,13] cherry[14] and *Dactylis glomerata*.[7] Basing on the evidence presented here, the higher vegetative and reproductive vigour found in the populations of *T. purpurea* with the *cdf* may, therefore, be attributed to the combined effect of lower population density and heterozygosity for the gene. The fact that the populations are not entirely composed of heterozygotes is borne in mind while making this suggestion.

A recessive lethal gene can be maintained in populations by three ways : (*a*) repeated mutation at the same locus, (*b*) heterozygotes resulting from heterozygote-heterozygote or homozygous dominant-heterozygote matings within the population and (*c*) gene flow between populations. In view of the estimated limits of the rate of mutations ($0 \cdot 0001$ to $0 \cdot 000001$ per locus per generation[11]), it is very unlikely that a lethal gene can be maintained in a population at frequencies found in the present case exclusively through repeated mutations at the concerned locus. Moreover, the mere occurrence of a mutation is not enough; the mutant allele must have a chance to be included in the gametes. In view of the discontinuous distribution of the *cdf* and the closed breeding behaviour of the species, the role played by gene flow, if any, is considered negligible. Heterozygotes are, therefore, the only major source of maintenance of the lethal gene indefinitely in the populations. *T. purpurea* is a predominantly self-pollinated species. The author's unpublished data, however, indicate that there exists some limited amount of natural outcrossing. In self-pollinated species heterozygote-heterozygote matings, whatever their proportion, are more a matter of certainty than in outbreeding populations and this ensures the continued representation of the heterozygotes in the population although the actual proportion may vary from time to time.

The frequency of the heterozygotes and so the gametic frequency of the lethal gene would be high in a population only if the heterozygotes have a higher selective value. The frequency of heterozygotes, hence, can be taken as a direct indication of the selective value of the gene. The process that

operates to change the allele frequency, *viz.*, selection, can be represented as a coefficient using the formula

$$s = 1 - L/M$$

where s is selection, L the frequency of the recently appearing allele and M the frequency of the other allele[15]. In the present case values of s vary from 0·895 to 0·963. The proportion of the alleles expressed by the coefficient of selection is represented as $A = 1$ and $a = 1 - s$. Here the values of a vary from 0·1050 to 0·0370. Understandably, the ratio $A : a$ is indeterminant in the populations studied here since the allele a is a lethal. Nevertheless, the data indicate that the proportion of the lethal allele is appreciably high. The data presented heretofore indicate that populations of *T. purpurea* with *cdf* have some advantages over the populations without the same and so are to be considered to be having a higher selective value. Therefore, an equilibrium of adaptive polymorphism with a higher selective value for the heterozygote populations is suggested to explain the results. Such a proposal was made for *Dactylis glomerata* along with a suggestion that this kind of a recessive lethal may be of a more general occurrence in the natural populations of cross-pollinated species.[7] The present findings point out to a similar possibility even in predominantly self-pollinated species.

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