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Phenotypic Variation and Plasticity in the Colonizing Species *Xanthium strumarium* L. (Noogoora Burr)

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Abstract

Levels of genotypic (σ_G^2) and environmentally induced (σ_E^2) variation for 15 quantitative characters were estimated in seven populations of the four naturalized races of *X. strumarium* in Australia. Estimates of σ_G^2 indicated that populations of *X. strumarium* were often genetically variable for quantitative traits. However, for the majority of the characters studied, σ_E^2 was a larger component of the total phenotypic variation than was σ_G^2, indicating that phenotypic plasticity is the major mode of adaptation of this species to variable and varying environments. Few significant differences were found among the races, or among populations within a race, in either σ_G^2 or σ_E^2. This suggests that marked differences in colonizing ability of the four races of *X. strumarium* are probably not due to differences in phenotypic plasticity (individual buffering) or genotypic variation (populational buffering) but to differences in such factors as their reproductive strategies and photoperiodic requirements for flowering.

Introduction

Four races of *Xanthium strumarium* L. (*X. chinense*, *X. italicum*, *X. cavanillesii*, and *X. pennsylvanicum*), a predominantly self-pollinated monoecious annual (Löve and Dansereau 1959), were introduced into Australia from the new world. All races occupy similar highly unstable and unpredictable habitats, principally river banks and associated flood plains and, more rarely, man-disturbed waste areas. However, because the races were introduced at different points on the Australian continent, are predominantly self-pollinated and have different photoperiodic requirements (McMillan 1975), they rarely hybridize in the field and have largely maintained their genetic integrity since their introduction. The four racial groups can be readily distinguished on the basis of their burr morphology (Löve and Dansereau 1959) or allozyme phenotypes (Moran and Marshall 1978).

Despite the broad similarities among the four races of *X. strumarium* in the sorts of environments they occupy, they differ in their colonizing ability and occupy markedly different-sized geographic areas within Australia (Moran and Marshall 1978). *X. chinense* is by far the most successful race, having colonized a large area of eastern Australia, whereas *X. italicum* occurs only in central New South Wales and *X. pennsylvanicum* is restricted to an even smaller area along the Murray River. *X. cavanillesii*, the least successful race, is found only in the Hawkesbury River region west of Sydney. It has long been recognized that there are two ways colonizing species adapt to the varying and variable environments they occupy (Thoday 1953; Lewontin 1957; Allard and Bradshaw 1964; Bradshaw 1965; Jain 1976). One

way is through individual buffering or homeostasis whereby individuals adjust their phenotypic responses so that each member of the population can cope with a wide range of environments. An important component of individual buffering is phenotypic plasticity, i.e. adaptive environmentally induced variation in morphological characters and growth form (Bradshaw 1965; Harper 1967; Marshall and Jain 1968). The alternative mechanism is populational buffering which results from the co-existence of different genotypes, each adapted to somewhat different environments, in the one population (Allard and Bradshaw 1964). The broad aim of the present study was to determine the relative roles of individual and populational buffering in the adaptation of *X. strumarium* to Australian environments and to establish if differences in either of these mechanisms were responsible for differences among the four races of this species in their colonizing ability.

In the previous paper (Moran and Marshall 1978), we reported levels of allozyme variation within and between the four introduced races of *X. strumarium*. Very little variation was found within races at the 13 loci studied but there was considerable interracial differentiation at several loci. On this basis, we concluded that allozyme polymorphism has played only a minor role in the adaptation of *X. strumarium* to Australian conditions. We further suggested, therefore, that the marked differences in colonizing ability of the four races of *X. strumarium* are due to differences in the levels of within-race genetic variation in quantitative, morphological, or physiological traits or to differences in their levels of phenotypic plasticity. Under the first suggestion, we would expect little relationship between the levels of allozyme variation and adaptive variation for quantitative characters in *X. strumarium*.

As a consequence, the present study was designed to compare for *X. strumarium* estimates of levels of (i) genetic variation of quantitative characters within races and (ii) phenotypic plasticity exhibited by the four races in response to a range of glasshouse and field environments, to determine the relative importance of genetic variation and phenotypic plasticity in adaptation of each to local environments.

Materials and Methods

The four races of *X. strumarium* were grown in five different environments chosen to represent a range of environmental conditions encountered by the species in Australia. Two of the environments were different glasshouses with different soil and nutrient regimes: one a growth cabinet with different photoperiod and temperature levels and the other two field sites with differing moisture and nutrient regimes. Three populations of the race *X. chinense* (designated 11, 22 and 42 as in Moran and Marshall 1978), two populations of *X. pennsylvanicum* (25 and 26) and one population each of *X. cavanillesii* (44) and *X. italicum* (46) were selected to cover the geographic range of the four races. For each of the seven populations, 10 families were randomly chosen to represent the genotypic variation at the site. Within each environment there were two replicates, each consisting of 70 plants, one from each family for each population. The position of plants was fully randomized within each replicate. *Xanthium* sp. fruit are dimorphic and only the non-dormant lower seeds were used to raise seedlings for the experiments reported here. Since *X. strumarium* is a highly inbreeding species (Moran and Marshall 1978), the progeny within each family were assumed to be genetically identical. Hence, it is expected that most of the variation among the plants exposed to different environmental treatments will be environmental while most of the variation shown among the plants within any one environmental treatment will be due to genetic differences between families.

A total of 15 quantitative characters was measured for each plant (see Table 1). Leaf width and leaf length were of the largest leaf. Minor leaves were those leaves that developed after the onset of the reproductive phase in the leaf axils on the main stems and branches. Plant dry weight included all of the plant above ground level. For each plant mean fruit length and mean fruit weight were estimated from a random sample of five fruit.

Because the five environments provided a large range of conditions, values of most characters changed substantially from one environment to another, with greater variation when values were larger. Thus to stabilize the variance, all values were log transformed before statistical analysis. Since values of the 15 characters were pairwise highly correlated in many instances, the characters could not be treated as independent. To identify groups of related characters and hence obtain an idea of the effective number of independent attributes being measured, a principal component analysis was performed on the correlation matrix of the log-transformed values for the 15 characters.

To investigate environment and population effects, analyses of variance were performed for each character on the means over the 10 families of the log-transformed values, i.e. on five environments × two replicates × seven populations. Variances within each replicate were calculated over the 10 families for each character for each population, using log-transformed data. These variances could be regarded as measures of genotypic variation for each population within each of the 10 replicates (five environments × two replicates). Analyses of variance, similar to those on the means, were then performed on the variances, with another log transformation of the variances being necessary to stabilize variation.

An alternative approach was also adopted within each population to investigate environmental and genetic components of variation. For each population, the basic data for any character consists of n_{ij} observations for the jth replicate under the ith environment. Under the design, n_{ij} should be 10 for each replicate. However, there were a large number of plants which did not grow, so that n_{ij} values observed ranged from 4 to 10. Thus, family could not be treated as a factor and a nested analysis of variance (Kempthorne 1957) of the form shown in the following tabulation performed was on log-transformed data for each character.

Source	d.f.	m.s.	Expected m.s.
Between environments	$E-1$	M_E	$\sigma_G^2 + K_1\sigma_R^2 + K_2\sigma_E^2$
Between replicates within environments	E	M_R	$\sigma_G^2 + K_3\sigma_R^2$
Between plants within replicates	$\sum_{ij}(n_{ij}-1)$	M_G	σ_G^2
Total	$n..-1$		

$n..$ is the total number of plants, $n_{i.}$ is the number of plants in environment i, n_{ij} is the number of plants in environment i, replicate j, E is the number of environments in which the population was grown, and

$$\hat{\sigma}_G^2 = M_G, \qquad \hat{\sigma}_R^2 = (1/K_3)(M_R - M_G), \qquad \hat{\sigma}_E^2 = (1/K_2)[M_E - M_G - (K_1/K_3)(M_R - M_G)],$$

$$K_1 = \left[1/(E-1)\right]\left[\sum_{ij}(n_{ij}^2/n_{i.}) - (1/n..)\sum_{ij} n_{ij}^2\right],$$

$$K_2 = \left[1/(E-1)\right]\left[n.. - (1/n..)\sum_{i} n_{i.}^2\right],$$

$$K_3 = (1/E)\left[n.. - \sum_{ij}(n_{ij}^2/n_{i.})\right].$$

From these analyses, three variance components were calculated. The between-environment variance component (σ_E^2) measures the phenotypic plasticity of each population for the character and the specific environments used. The between-replicate variance (σ_R^2) is largely due to variation in establishment of replicates within environments. The between-plant variance (σ_G^2) contains components due to differences between families, family × environment interactions and replicate × family interactions within environments. Thus it is measuring mainly genetic variation but there will also be some microenvironmental sources of variation.

To test whether variance components differed between populations, the F_{max} test was used. This test was introduced by Hartley (1950) as a test for homogeneity of a number of independently estimated variances, and exact tables of upper 5 and 1% points of the maximum F ratio were given by David (1952). Levy (1975) showed that the test performed satisfactorily for data obtained from normal populations, and was preferable to other tests as it was most easily performed. Use of the test for the genetic component σ_G^2 posed no problems as σ_G^2 is directly estimated by the mean square

M_G. However, for our data, $K_2\sigma_E^2$ is the major component of mean square M_E, hence σ_E^2 will be approximately distributed χ^2 and the F_{max} test performed directly on estimates of σ_E^2 is a reasonable approximation.

Results

The first four principal component vectors, which account for 93% of the variation, are presented in Table 1. Rather than attempt to interpret each vector and hence create four new variables, original characters which had similar loadings for each component were subjectively grouped. This approach was preferred as it meant that characters discussed would be biologically meaningful, while high pairwise correlations would still be recognized in the interpretation of results. Five groups of variables were identified in this manner, and could broadly be described as plant size, leaf size, plant length, fruit size and reproductive timing.

Table 1. Results of principal component analysis on 15 characters

Character	Principal component vectors			
	1	2	3	4
Plant Size				
Basal diam.	−0·32	−0·12	0·01	−0·03
No. of clusters	−0·31	−0·11	−0·15	−0·25
No. of branches	−0·31	−0·14	−0·13	−0·19
No. of minor leaves	−0·31	0·01	−0·20	−0·09
No. of major leaves	−0·32	−0·05	−0·09	−0·16
No. of fruit	−0·31	−0·08	0·02	−0·26
Plant weight	−0·31	−0·13	0·08	−0·22
Leaf Size				
Leaf width	−0·29	0·11	−0·06	0·29
Leaf length	−0·25	0·09	−0·11	0·54
Plant Length				
Plant height	−0·24	−0·21	0·26	0·39
Internode distance	−0·14	−0·41	0·29	0·39
Fruit Size				
Mean fruit length	0·18	−0·42	0·22	−0·10
Mean fruit weight	0·13	−0·50	0·30	−0·18
Reproductive Timing				
Days to flowering	−0·14	0·38	0·56	−0·10
Days to pollination	−0·16	0·35	0·54	−0·14
% variance accounted for	61·2	16·9	9·5	5·6

Although the population × environment interaction was significant for many characters, the environments were of no interest in themselves, being only arbitrarily chosen to give a range of conditions. Thus, it was felt that means over environments would be useful to present a general idea of the relative magnitude of the characters for each population. These means are presented in Table 2. The smaller means for such characters as number of fruit and number of leaves in populations 25, 26 and 44 are a consequence of the shorter period of vegetative growth of the races

X. pennsylvanicum and *X. cavanillesii*. Likewise, the differences in fruit length and fruit weight means are due to racial differences in burr morphology. The bigger maximum internode distances for *X. pennsylvanicum*, and to a lesser degree for *X. cavanillesii*, and the concomitant smaller number of major leaves but similar plant heights compared to other races, are indicative of the faster growth rates of these two races.

Table 2. Overall means for each character and population of *X. strumarium* races

Values are obtained as back transformations of means of transformed data

Character	*X. chinense*			*X. pennsylvanicum*		*X. cavanillesii*	*X. italicum*
	11[A]	22	42	25	26	44	46
Plant Size							
Basal diam. (mm)	11·4	11·9	11·7	9·2	10·3	9·1	10·6
No. of clusters	38·7	42·8	41·9	28·4	39·6	16·4	44·6
No. of branches	4·4	5·0	4·9	3·1	4·4	2·2	5·5
No. of minor leaves	67·9	73·1	66·7	37·8	49·2	32·3	81·7
No. of major leaves	54·1	58·2	58·5	31·1	42·7	27·5	68·2
No. of fruit	69·7	88·7	85·5	41·4	65·8	21·9	66·1
Plant weight (g)	34·3	40·7	42·8	22·5	34·4	18·0	41·7
Leaf Size							
Leaf width (mm)	134·8	141·4	143·1	105·3	111·0	106·1	114·7
Leaf length (mm)	123·2	128·6	132·5	103·4	111·3	108·2	112·3
Plant Length							
Plant height (cm)	59·7	60·9	63·1	57·0	62·4	57·9	73·2
Internode distance (mm)	49·1	49·2	51·8	65·4	67·9	57·3	52·8
Fruit Size							
Mean fruit length (mm)	18·4	18·7	18·3	21·0	21·1	22·5	20·2
Mean fruit weight (mg)	138·7	158·1	142·4	291·6	278·6	424·4	189·5
Reproductive Timing							
Days to flowering	102·0	98·3	100·3	61·7	60·0	81·3	99·6
Days to pollination	118·6	115·2	117·0	75·9	73·9	95·8	116·5

[A] Population numbers are those used in Moran and Marshall (1978).

Significant differences were observed between populations for means of all measured characters (Table 3). There was also a significant environment × population interaction for some characters in the plant size group and all characters in the other groups. Thus, these significance levels and the means over environments (Table 2) demonstrate a high level of variation in character means for the seven *X. strumarium* populations, with expression of this variation differing in many instances from one environment to another. Some differences were also observed between environments and populations in variance between families (Table 3). Population differences occurred for fruit size, reproductive timing and some plant size characters, and environment differences occurred for all plant size and reproductive timing characters. Thus, certain types of characters showed greater relative variation between families in some populations than in others, or in some environments than in others.

Table 3. Variance ratios and significance of population, environment and population × environment effects on the means and variances of each character

* $P < 0{\cdot}05$; ** $P < 0{\cdot}01$; *** $P < 0{\cdot}001$

Character	Means			Variance between families		
	Environment	Population	Environment × population	Environment	Population	Environment × population
Plant Size						
Basal diam.	99·89***	6·77***	2·85**	56·25***	1·49	1·89
No. of clusters	314·25***	11·14***	1·72	42·75***	2·08	2·45*
No. of branches	919·92***	10·55***	2·20*	1818·43***	20·45***	21·77***
No. of minor leaves	74·44***	22·88***	6·01***	13·96**	1·44	3·67***
No. of major leaves	108·64***	17·05***	1·79	111·44***	3·48**	1·56
No. of fruit	223·31***	15·39***	1·62	14·30**	1·00	2·14*
Plant weight	304·54***	6·57***	1·84	21·84**	1·25	1·15
Leaf Size						
Leaf width	49·09***	27·39***	4·04***	2·82	2·08	1·70
Leaf length	32·80***	13·41***	2·96**	1·04	1·12	1·61
Plant Length						
Plant height	112·60***	3·76**	3·04**	1·44	1·37	1·90*
Internode distance	94·03***	12·32***	3·61***	4·79	1·00	0·71
Fruit Size						
Mean fruit length	5·70*	102·54***	14·79***	1·52	4·33**	1·05
Mean fruit weight	12·77**	213·03***	12·37***	1·68	10·95***	2·00*
Reproductive Timing						
Days to flowering	1487·36***	1737·66***	164·11***	8·09*	9·33***	2·44*
Days to pollination	1802·38***	1461·62***	127·11***	5·56*	5·86***	2·13*

Table 4. Estimates of the environmental variance (σ_E^2) and the between-plant variance (σ_G^2) for each character for seven populations from four races of *X. strumarium*

* $P < 0.05$; ** $P < 0.01$

Character	Component	*X. chinense*				*X. pennsylvanicum*			*X. cavanillesii*	*X. italicum*	F_{max}[B] value
		11	22	42	Mean[A]	25	26	Mean[A]	44	46	
Plant Size											
Basal diam.	σ_E^2	0·048	0·046	0·040	0·045	0·020	0·036	0·028	0·016	0·065	4·06
	σ_G^2	0·010	0·011	0·012	0·011	0·011	0·013	0·012	0·015	0·014	1·36
Plant weight	σ_E^2	0·497	0·469	0·429	0·449	0·234	0·387	0·311	0·246	0·662	2·69
	σ_G^2	0·076	0·076	0·106	0·091	0·112	0·107	0·110	0·124	0·097	1·36
Leaf Size											
Leaf width	σ_E^2	0·0080	0·0066	0·0052	0·0066	0·0036	0·0022	0·0029	0·0047	0·0106	3·66
	σ_G^2	0·0060	0·0058	0·0061	0·0060	0·0111	0·0043	0·0077**	0·0093	0·0049	2·27*
Leaf length	σ_E^2	0·0032	0·0039	0·0021	0·0031	0·0039	0·0029	0·0034	0·0029	0·0039	4·34
	σ_G^2	0·0037	0·0042	0·0041	0·0040	0·0087	0·0041	0·0064**	0·0046	0·0037	2·35*
Fruit Size											
Mean fruit length	σ_E^2	0·0016	0·0012	0·0016	0·0015	0·0005	0·0005	0·0005	0·0002	0·0002	7·50
	σ_G^2	0·0011	0·0010	0·0005	0·0009**	0·0007	0·0006	0·0006	0·0019	0·0010	2·20*
Mean fruit weight	σ_E^2	0·0071	0·0125	0·0097	0·0098	0·0133	0·0147	0·0140	0·0042	0·0045	3·33
	σ_G^2	0·0121	0·0099	0·0081	0·0100	0·0077	0·0076	0·0076	0·0321	0·0194	4·22**
Reproductive timing											
Days to flowering	σ_E^2	0·0086	0·0116	0·0104	0·0102	0·0105	0·0124	0·0114	0·0028	0·0062	4·07
	σ_G^2	0·0001	0·0002	0·0002	0·0002	0·0021	0·0008	0·0014**	0·0012	0·0004	10·50**
Days to pollination	σ_E^2	0·0092	0·0127	0·0124	0·0114	0·0073	0·0084	0·0078	0·0034	0·0078	3·35
	σ_G^2	0·0002	0·0002	0·0003	0·0002	0·0016	0·0008	0·0012*	0·0010	0·0003	8·00**

[A] Significance of differences between populations within races is indicated.

[B] F_{max} value for testing difference between variance components of four races. Where populations differed significantly within races, separate variance component values for each population were used for the F_{max} test.

Environmental (σ_E^2) and genetic (σ_G^2) components of variation obtained from the nested analyses of variance on each population are given in Table 4 for the leaf size, fruit size and reproductive timing groups, and for two typical characters in the plant size group. Components are not given for the plant length group and the remainder of the plant size group as no significant differences were obtained between populations or races for these groups. In all cases the between-replicate variance component (σ_R^2) was either zero or very small compared to σ_E^2 and σ_G^2, so is not presented. For all populations in the plant size and reproductive timing groups, and for *X. chinense* in the plant length group (not presented), σ_E^2 was generally greater than σ_G^2. Conversely, σ_G^2 was generally greater than σ_E^2 for *X. pennsylvanicum* and *X. cavanillesii* in the leaf size group, *X. pennsylvanicum* in the plant length group (not presented), and *X. cavanillesii* and *X. italicum* in the fruit size group.

Mean values of σ_E^2 and σ_G^2 over populations within *X. chinense* and *X. pennsylvanicum* and significance of differences between the populations are also presented in Table 4. Few significant differences were observed between populations within races occurring only in σ_G^2 for mean fruit length in *X. chinense* and for the leaf size and reproductive timing groups in *X. pennsylvanicum*. Thus, F_{max} values were obtained for comparison of the four race means (Table 4). These indicated significant differences between races for σ_G^2 values in the three groups leaf size, fruit size and reproductive timing.

Comparisons between races of environmental variance components for each character using the F_{max} test detected no significant differences, but the power of the test is severely limited with these data since a much larger number of environments would have been needed to give a reasonable number of degrees of freedom. Nevertheless, general trends observed in σ_E^2 values could be an indicator of differences in environmental variation between populations and races. Within *X. pennsylvanicum*, σ_E^2 values for population 26 were greater than values for population 25 in the plant size group, and values for population 42 were less than values for the other two *X. chinense* populations for the groups plant size and leaf size. Comparison between races also yielded some trends, with *X. italicum* and *X. chinense* generally having higher σ_E^2 values than *X. pennsylvanicum* and *X. cavanillesii*. For example, in the plant size group *X. italicum* > *X. chinense* > *X. pennsylvanicum* > *X. cavanillesii* for all characters, and in the reproductive timing group *X. cavanillesii* values were lowest for both characters.

Discussion

The results of this study indicate that there is measurable genetic variation for many quantitative characters within Australian populations of *X. strumarium*. They also indicate that for six characters there are significant differences among the four races in within-population levels of genetic variation, and for three of these, significant differences among population within a race. These results contrast sharply with our previous findings with respect to allozyme variation, which indicated that three of the races, *X. chinense*, *X. cavanillesii* and *X. pennsylvanicum*, were genetically uniform both within populations and among populations within a race. They also contrast sharply with patterns of variation at the loci governing burr morphology, which are also invariant within and among populations within a race (Moran 1975 and unpublished data) but polymorphic among races. In *X. strumarium* in Australia, therefore, the pattern of variation at allozyme marker loci is highly correlated with

those for morphological markers, but not with patterns of variation for quantitative traits.

Similar results have been reported for the slender wild oat *Avena barbata* in California. In particular, Marshall and Allard (1970) reported a significant correlation between patterns of variation for allozyme and morphological markers in the species. However, more recently Allard *et al.* (1978) and Kahler *et al.* (1980) reported significant genetic variability for measurement characters, both within and between populations of *A. barbata*, monomorphic for both morphological and allozyme marker loci. Kahler *et al.* (1980) concluded as a result: 'It is therefore apparent that no single class of loci such as those governing enzyme variants, or those governing morphological polymorphisms, or those governing measurement characters, gives a complete picture of the extent of genetic variability within populations or of degree of evolutionary divergence among populations in this species'. This conclusion applies equally well to *X. strumarium* populations in Australia.

The basis of the differences in the patterns of variation for qualitative and quantitative characters in *X. strumarium* is unknown. Such differences may reflect differences in the level of polymorphism at each of the loci governing these traits. Alternatively, such differences may simply reflect the fact that we assay many more loci in studying quantitative characters compared to qualitative characters.

All four races of *X. strumarium* in Australia also exhibited considerable phenotypic plasticity for the characters and environments studied. Indeed, plasticity (σ_E^2) for most races and characters was a larger component of the total phenotypic variation than was genetic variance, suggesting that phenotypic plasticity is the major mode of adaptation of this species to varying environments. The low levels of both quantitative genetic variation and allozyme variation, particularly in *X. chinense*, the most successful colonizer of the races of *X. strumarium* in Australia and also probably the world (McMillan 1975), supports this contention. Apparently, all races of *X. strumarium* in Australia have ample plasticity to cope successfully with fluctuating environments without being dependent on extensive genetic variation.

The present results indicate that the differences in colonizing ability among the four races of *X. strumarium* in Australia are probably not correlated with either differences in phenotypic plasticity (individual buffering) or genetic variation (populational buffering). Consequently, we have to look to other factors, such as differences in photoperiod requirements for flowering (McMillan 1975), or in reproductive strategies, to account for the racial differences in the colonizing success. With respect to differences in reproductive strategies, our results revealed substantial differences in fecundity within and among the five environments used here. *X. chinense* produced the greatest number of seeds, whereas the least successful colonizer, *X. cavanillesii*, produced the least. In fact, our data suggest that there is a correlation between decreasing fruit weight, increasing fruit number, and success in colonization for the races of *X. strumarium*. Thus, the greater success of *X. chinense* as a colonizer appears to be due to the fact that it produces a greater number of smaller seeds than the other races and has less restrictive photoperiodic requirements for flowering.

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