

Evolutionary Significance of Economy in the Pollen Grain to Ovule Ratio in the Process of Crop Domestication

R UMA SHAANKER and K N GANESHAIAH

*Department of Agricultural Botany, University of Agricultural Sciences,
Hebbal Campus, Bangalore 560 024*

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A positive shift in the probability of success of pollen grain and ovule in few crop species during the process of domestication is traced. The consequent decrease in the pollen grain to ovule ratio from the wild to domesticated crop species is discussed in relation to the changes in the breeding behaviour. A method of characterising the wild and domesticated species on the basis of their pollen grain to ovule ratio and corresponding probability of success of gametes is arrived at.

Key Words : Pollen grain to ovule ratio, Probability of success of pollen grain and ovule, Crop Domestication, Crop adaptive strategies

Introduction

During the process of domestication, crop species have undergone considerable changes in their reproductive strategies because of intentional or unintentional selection pressures (Morishima et al. 1963, Harlan et al. 1973 and Kaltz-nelson 1976). These changes are generally directed towards an economized use of energy and a guaranteed reproductive success. Such assured reproductive success may be brought about through several ways like increased probability of the male and/or female gametic success in fertilization, faster and ensured development of seed etc. The increased probabilities of success of gametes in fertilisation may result in large decreases in pollen grain to ovule ratio without any

loss in fitness (Uma Shaanker & Ganeshaiah 1980). The decrease in pollen grain to ovule ratio from xenogamous to autogamous plants has been traced by Cruden (1977). In this communication we provide evidence for such altered reproductive strategies brought about through changed pollen grain to ovule ratio under domestication and arrive at a method of characterising the domesticated varieties and their wild relatives on the basis of their pollen grain to ovule ratio and corresponding gametic success. The results are extended to explain the progress of crop species from varying levels of out-crossing to self fertilisation.

Material and Methods

The study was conducted on few species mostly leguminous, except *Eleusine*—a cereal, where the relation between the domesticated and their related wild species was known (table 1). Their respective breeding behaviours are also indicated in the table. The species studied were censured for the number of pollen grains per flower (P), number of ovules per flower (O) and the number of ovules successfully developing into mature seed (X). The number of pollen grains per anther was counted following the method of Cruden (1977) and Uma Shaanker and Ganeshiah (1980). Twenty anthers from twenty flowers were used from 5–6 randomly selected plants of each species. Each anther was crushed with acetocarmine stain on a slide and smeared over sufficiently to make possible to counting under a microscope. By moving the microscopic field to cover the entire area of spread, the pollen grains per anther was counted. From the data, the probabilities of success of an ovule developing into mature seed ($\beta = X/O$) and the pollen grain to ovule ratio (P/O) were computed. Since the number of pollen grains that can succeed in fertilisation cannot be more than the number of ovules, the probability of success of pollen grains in fertilising an ovule was calculated as the ratio of number of ovules to pollen grains ($\alpha = O/P$). Notwithstanding the individual probabilities of success of the pollen grain and ovule, the net success in terms of the total genome contribution to a successive generation in a hermaphrodite depends on the product of their individual probabilities ($\alpha\beta$), which was also found. This, in other words, will represent the net probability of success of the pollen ($\alpha\beta = X/P$).

Results and Discussion

All domesticates showed a reduced P/O ratio as compared to their wild species (table 1). This is particularly evident in the genera *Macrotyloma*, *Cajanus* and *Glycine*. Both in *Macrotyloma* and *Glycine* the related wild species showed twice as high a P/O ratio as their domesticated relatives. Such differences were also observed between the wild species *E. africana* and its domesticated form *E. coracana*.

These changes in the P/O ratio between the domesticated species and their wild relatives essentially reflect on the proportionate increase or decrease of their gametic success, α and β (table). As shown in figure 1 there exists an inverse relation between the P/O ratio and the net probability success of the male gamete ($\alpha\beta$). This may be largely a consequence of the ensured

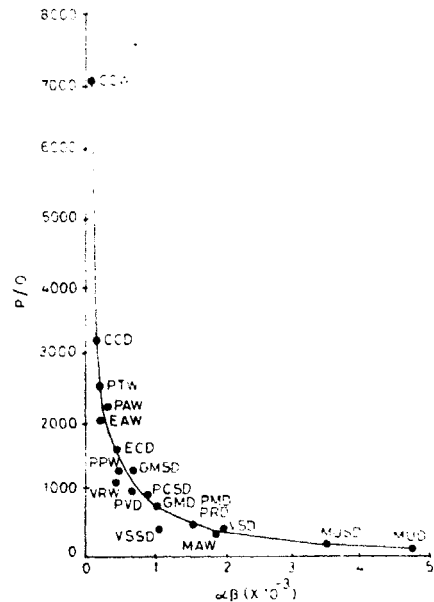


Figure 1 An inverse relation between the net probability of success of pollen ($\alpha\beta$) and the pollen grain to ovule (P/O) ratio (for details of the abbreviations refer table 1)

Table 1 Pollen grain to ovule (P/O) ratio, probability success of pollen (α) and ovule (β) and the net success of pollen ($\alpha\beta$) for a few domesticated and wild species

Name	Abbreviation†	Breeding behaviour*	Pollen No. per anther‡		Ovule Number	P/O ratio‡ ($\times 10^{-3}$)	α ($\times 10^{-3}$)	β ($\times 10^{-1}$)	$\alpha\beta$ ($\times 10^{-3}$)
			Range	Mean					
<i>Macrotyloma uniflorus</i>									
(a) Determinate type	MUD	SF	76 — 115	87.54	5	175.08	5.71	8.43	4.8135
(b) Indeterminate type	MUSD	SF	108 — 176	140.00	6	233.33	4.28	8.40	3.5952
(c) <i>M. acclare</i>	MAW	SF	230 — 340	248.00	7	354.28	2.82	6.79	1.9147
<i>Vigna Sinensis</i>	VSD	SF	442 — 612	559.80	12	466.50	2.20	9.14	2.0128
<i>V. sesquipaetalis</i>	VSSD	SF	817 — 959	908.10	20	454.55	2.14	5.00	1.0700
<i>V. repens</i>	VRW	SF	1100 — 1412	1308.00	11	1189.77	0.84	4.83	0.4057
<i>Phaseolus mungo</i>	PMD	SF	338 — 649	505.00	10	505.00	1.98	8.00	1.5840
<i>P. radiata</i>	PRD	SF	456 — 556	505.00	10	505.00	1.98	8.00	1.5840
<i>P. vulgaris</i>	PVD	SF	842 — 1040	983.70	8	894.33	1.11	5.41	0.6000
<i>P. calcaratus</i>	PCD	SF	648 — 967	793.25	8	981.00	1.09	8.00	0.8720
<i>P. atropurpureus</i>	PAW	OSF	2926 — 3445	3377.50	15	2251.00	0.44	8.76	0.3871
<i>P. trilobus</i>	PTW	OSF	3324 — 3827	3764.00	15	2509.00	0.39	6.48	0.2582
<i>P. panduratus</i>	PPSD	OSF	983 — 1120	1072.00	8	1340.00	0.74	6.48	0.4795
<i>Glycine max</i>									
(a) var. Jupitore	GMD	SF	230 — 240	225.00	3	750.00	1.33	7.50	0.9997
(b) Black Kulti	GMSD	SF	336 — 523	377.00	3	1256.67	0.79	7.50	0.5962
<i>Cajanus cajan</i>									
(a) Annual	CCD	OCF	1208 — 1744	1614.50	5	3329.10	0.30	7.52	0.2328
(b) Perennial	CCW	OCF	2715 — 3001	2853.60	4	7134.00	0.14	7.01	0.0980
<i>Eleusine coracana</i>									
E. africana	ECD	SF	454 — 569	511.30	1	1534.00	0.65	8.00	0.5215
	EAW	SF	587 — 720	692.60	1	2078.00	0.48	6.50	0.3127

‡ Significant at P 0.01 level (analysis carried out for each genus separately).

Sample size — 20 anthers/20 flowers for ovules

† D, domesticate; SD, semi-domesticate; W, wild

* Drawn mainly from Fryxell (1957), others from consultations with local breeders; SF, self fertilised, OSF, often self fertilised, OCF, often cross fertilised.

conditions of fertilisation and development under domestication, resulting in an increased α and β .

Any change in α and/or β should correspondingly bring about changes in the number of pollen grains, ovules or both, to bring the plant to an Evolutionary Stable Strategy (ESS) (Maynard Smith & Price 1973). An ESS in the case of fertilisation shall aim at maximising the reproductive success with a minimum possible reproductive cost. Expressed in gamete numbers, it should indicate the ideal balance between the pollen grain and ovule numbers for a given situation without imposing on the plant a heavy reproductive cost. Plants that do not conform to this principle would impose a liability on themselves and would be selected against (see the alternative discussed later).

Under domestication increase in α is brought about among other factors through increased plant density, change in floral structure including spatial and temporal features and reduced pollinator activity. Indeed, such factors are shown to be responsible for the reduced P/O ratio in the domesticated forms of *Eleusine* (Ganeshaiyah & Uma Shaanker 1982). Such factors may restrict outward movement of pollen and confer no selective advantage on plants possessing high α and high P , while increased selfing as indicated by a decrease in P/O ratio (Cruden 1977), may be highly advantageous and would confer a selective advantage on these individuals. Indeed, it is evident from figure 1 that the P/O ratio is directly proportional to the cross pollination rate, thus confirming the thesis of Cruden (1977). For instance, *Cajanus* which has a high cross pollination rate of 40 per cent (Bhatia et al. 1980), recorded the highest P/O ratio, while in *Glycine* and *Macrotyloma* which have

relatively low cross pollination rates of 2-5% the P/O ratios were found to be low.

A large decrease in pollen-grain number during domestication cannot occur without change in the resource allocation to the reproductive parts—the pollen grains and the ovules. Almost always, change in the number of pollen grains is associated with a corresponding redistribution of resource to ovules or seeds, most commonly expressed in the form of increased seed sizes (Wells 1976). This is true, assuming that the total production of male and female gametes is limited by a common resource pool, which often is the case in bisexual reproductive systems, (Charnov et al. 1976). However, it is not necessary that under an ESS, a hermaphrodite divides its reproductive resource equally between the male and female gametes as suggested by Maynard Smith (1971, 1976). The responses to changed α and β appear to be more frequently adjusted by changes in the number of pollen grains than ovules.

The net probability of success of pollen ($\alpha\beta$) is greater for all domesticated species of all the crops studied (table 1). The extent of domestication, (if that can be a measure) is found to be directly proportional to the product $\alpha\beta$. This is further justified when the species across different genera are compared on a common scale, wherein the standardised or normalised "Z" values of the P/O ratio and $\alpha\beta$ values of each species were plotted against each other (figure 2). An interesting observation from this figure, was the clear dispersion or characterisation of the domesticated species and their wild relatives into distinct quadrants of P/O ratio and $\alpha\beta$.

Most of the domesticated species grouped in the IV quadrant, with a low P/O ratio and high $\alpha\beta$. The limits of

domestication could be traced following the diagonal line drawn through the origin. Theoretically, the line can be extended to a point where $Z_1 = -3$ and $Z_2 = 3$, where the P/O ratio = 1, that is when the number of pollen grains equals number of ovules and $\alpha\beta = 1$. This will then represent the case of an "ideal hermaphrodite". Decrease in P/O ratio less than unity would indicate entry into increased femaleness or gynodioecy (if considered on the gametic sex ratio). However, this state would be very transient and would be eventually either selected against or may frequently slip into female dioecism, (Case 'a').

The II quadrant comprised the wild species and is characterised by high P/O ratio and low $\alpha\beta$. Although, here too the theoretical extrapolation of the limits

of wildness should continue upto the point $Z_1 = 3$ and $Z_2 = -3$, there is no condition on what the maximum P/O ratio should equate to numerically. However, when $\alpha\beta$ decreases *ad infinitum* (paralleled by increase in pollen number) a stage will soon be reached when any further decrease in $\alpha\beta$ level makes the plant inviable as a hermaphrodite. This would make the progress into increased maleness or androdioecy or vegetative reproduction (Case 'b').

In both the cases 'a' and 'b', the process of moving to either complete femaleness or maleness is only a question of becoming a specialist—in channelising the reproductive resources into either being an efficient pollen-recipient or pollen-donor.

Though none of the test species were found in the I quadrant of high P/O ratio and high $\alpha\beta$, it may be possible in a larger survey to find few individuals, especially those possessing an unlimited reproductive resource, extremely high ovule number and high P —for instance, certain perennial crops. The absence of species in the III quadrant of low P/O ratio and low $\alpha\beta$ can be explained as due to the high negative selection pressure imposed here. However, the presence of two species may be due to their selective maintenance under domestication for their pod or vegetative value, irrespective of their α and β .

It may be concluded from the foregoing, that gamete success is vital in influencing to a large extent selection for P/O ratio apart from the influences of specific breeding behaviours. In this regard, we consider three reasons to broadly explain the higher P/O ratio in wild relatives of the crop species:

1. In the natural habitats of the wild species where absence of conspecific crowding of plants, irregular pollinator

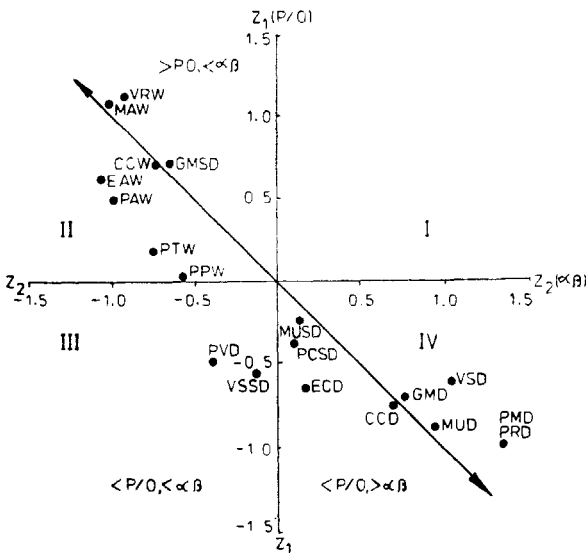


Figure 2 Characterization of domesticated and wild crop species based on normalised z transformation of P/O ratio and corresponding $\alpha\beta$ values. Details of the abbreviations are given in table 1. Note the general absence of co-ordinates in quadrants of $>P/O$, $>\alpha\beta$ and $<P/O$, $<\alpha\beta$

activity etc., render pollination and fertilisation unreliable, selection favours an increased P/O ratio.

2. In continuously changing and pioneering habitats which are inhabited by wild species, a need for genetic variability in the population arises (Maynard Smith 1976). Only a viscous population with members sharing different proportions of the main gene pool is able to survive and reproduce. High P/O ratio, selectively maintained through outcrossing would facilitate this. The case of *Cajanus* may be recalled which possesses the highest P/O ratio and outcrosses to an extent of 40%. Contrarily, due to enforced uniformity (i.e. also genetic uniformity) the highly domesticated types have shifted to increased autogamy with reduction in P/O ratio. However, the underlying assumption here is that, the high P/O ratio of the wild relatives is also associated with a high variance, which warrants a further investigation.

3. Under the conditions of adaptive colonisation (as in wild habitats) all individuals attempt to increase their fitness and eventually swamp their neighbourhood populations (by fitness we mean the individuals' ability to perpetuate; by swamping we mean the same as

infertive principle (Stebbins 1965). The total fitness accrued by any individual in a population is the sum of fitnesses contributed through the male and female gametes). By the conditions of adaptive colonisation and viable hermaphroditism, a self fertilising species would increase its fitness twice as much as, if it were to get cross fertilised—either by allowing its ovule to be fertilised by a foreign pollen or by allowing its pollen to fertilise a foreign ovule. The increase in fitness through either of the two alternatives, though similar, will be more costly through first than second alternative, when the total cost required to produce a pollen grain and the cost involved development of an ovule to seed are compared. So, given the choice (resource being available) selection would be for increasing the pollen grain number. That is, selection will be for plants that multiply their genes at a minimal cost to themselves, but at a high cost to others—a sort of cuckoo's behaviour. This would entail an active and substantial amount of outcrossing. The game of which beats the other in preventing its ovules getting cross fertilised is however confined to the limits of what one is allowed to be—either a hermaphrodite or dioecious.

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