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Flower production, male sterility and berry setting in andigena potato

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Summary. Unlike tuberosum, andigena potato germ plasm exhibits a high degree of genetic variation in morphological, biochemical and reproductive traits. Sixty-five percent of the 565 genotypes comprising 145 accessions of *Solanum tuberosum* ssp. *andigena* obtained from Argentina, Bolivia, Chile, Colombia and Peru remain totally vegetative and never develop any floral bud when cultivated in northern India. In 18% of genotypes, the floral buds develop but they drop off from the plants prematurely. Thus, 83% of genotypes do not develop mature flowers. The frequency of such genotypes is maximum in the Bolivian genotypes. Whereas 17% of genotypes produce mature flowers, only 2% develop berries. The highest proportion of floral bud formation and their subsequent development and differentiation into mature flowers occur in Peruvian and Colombian genotypes. Partial to high male sterility occurs in 93% of the flowering genotypes; their pollen sterility ranges from 15% to 91%. Seven percent of the flowering genotypes are completely pollen sterile. The male sterility is expressed variously, ranging from structural to sporogenous types. The floral bud formation, its development and retention to maturity, pollen and ovule functionability and fruit development are under the control of a large number of genes, most of which are unlinked and independent. Many of these genes are polygenic in nature.

Key words: *Solanum tuberosum* ssp. *andigena* – Floral bud drop – Male sterility – Berry development – Multigenic control

Introduction

Most of the present-day cultivars of potato, cultivated during winter in the subtropical plains, belong to the tuberosum group. Due to extensive cultivation and rigorous selection, the genetic variability in this crop is extremely reduced (Nayar 1986; Ross 1986; Birhman et al. 1988; Hosaka and Hanneman 1988). Since short-day photoperiod and low humidity prevail in winter in the Indian plains and the tuberosum potato genotypes require long-day photoperiods and high humidity, a majority of the cultivars do not flower. This nonflowering of tuberosum potato is a serious problem for true potato seed (TPS) production. Compared to the tuberosum group, the andigena group is genetically much richer and divergent (Glendinning 1969; Cubillos and Plaisted 1976; Tarn and Tai 1977; Nayar 1986; Ross 1986; Birhman et al. 1988; Hosaka and Hanneman 1988). Furthermore, it is very well adapted to Indian plains and its tuberization is very high (Birhman et al. 1988). Since the flower production and berry setting are the two basic requisites for TPS production, it is essential to identify andigena genotypes that have high rates of flower production and berry setting for use in TPS production and breeding. This was investigated by studying 565 genotypes collected from five South American countries and cultivated in India. The results obtained are presented in this paper.

Materials and methods

Five-hundred-sixty-five genotypes belonging to 145 accessions of the group andigena [*S. tuberosum* ssp. *andigena* (Juz et Buk Hawkes)] were obtained from Argentina, Bolivia, Chile, Colombia and Peru. The number of accessions and of genotypes from each country of origin are given in Table 1. These genotypes were planted in single rows with each row comprising 15 tubers per genotype in four replications at the Central Potato Research Station, Modipuram, Meerut, India (29 °N, 78 °E, 200 m above sea level). During the crop season, the mean day length ranged between 11.1 and 11.8 h, mean temperature between 14.3° and 26.3 °C and relative humidity between 41% and 63%.

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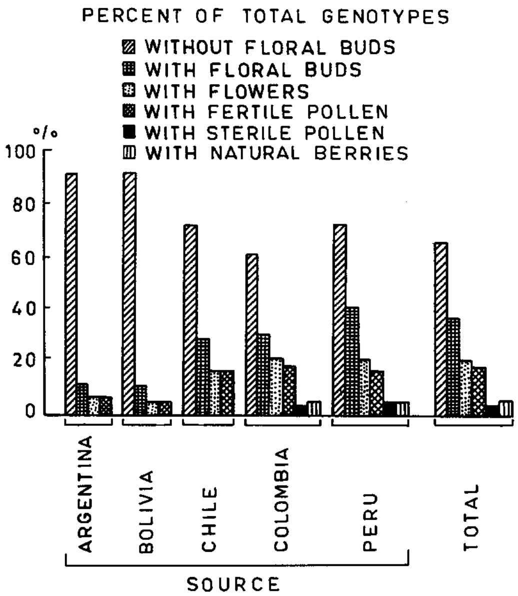

Fig. 1. Proportion of total genotypes of andigena potato from different countries with and without floral buds, with mature flowers, with fertile and sterile pollen and with natural berry formation

Table 1. Origin of andigena potato genotypes

Country of origin	No. of	
	Accessions	Genotypes
Argentina	26	43
Bolivia	14	34
Chile	9	18
Colombia	80	435
Peru	16	35
Total	145	565

Whereas all the plants of the 565 genotypes were evaluated for flower bud formation, flowering behaviour and berry production, only five flowers per plant of five randomly selected plants per genotype from each replication were used for the pollen sterility determinations. For this, the pollen was stained with 1% acetocarmine solution. The stained pollen was considered as fertile, the unstained as sterile. For testing the association of a trait with the country of its origin, the contingency χ^2 tests were carried out following the methods outlined by Gomez and Gomez (1984).

Results

Of the 565 genotypes investigated presently, 365 genotypes remain completely vegetative and never develop any flower bud (Table 2). In the remaining 200 genotypes, the floral buds are developed but they are prematurely dropped in 102 genotypes. Therefore, from a total of 565 genotypes, 467 genotypes do not have mature flowers, either due to non-initiation of floral buds in 365 genotypes or to premature floral bud drop in 102 genotypes. Ninety-eight genotypes produce mature flowers. Of these, 7 genotypes are completely pollen sterile. In the remaining 91 genotypes, the sterility is partial, ranging from 15% to 91% (Table 3; Fig. 4).

Floral bud formation

Over 90% of the Argentinian and Bolivian genotypes do not develop floral buds at all (Table 3; Fig. 1). About 70% of such non-budding genotypes occur in Chilean and Peruvian genotypes. In the Colombian genotypes, the proportion of such genotypes is about 60%.

Floral bud retention

The maximum proportion of Argentinian genotypes (75%) retain floral buds (Table 3; Fig. 2). In this respect they are followed by Chilian, Peruvian and Colombian

Table 2. Floral development, pollen sterility and berry formation in andigena potato genotypes

No.	Traits	No. of		Country of origin
		Genotypes	Accessions	
1	Floral buds not produced	365	135	Argentina, Bolivia, Chile, Colombia, Peru
2	Floral buds produced	200	84	Argentina, Bolivia, Chile, Colombia, Peru
2.1	Floral buds do not mature into flowers but drop off prematurely	102	61	Argentina, Bolivia, Chile, Colombia, Peru
2.2	Floral buds develop into mature flowers	98	58	Argentina, Bolivia, Chile, Colombia, Peru
2.2.1	Flowers with partially fertile pollen	91	54	Argentina, Bolivia, Chile, Colombia, Peru
	(a) berries not formed	79	49	Argentina, Bolivia, Chile, Colombia, Peru
	(b) berries formed	12	10	Colombia, Peru
2.2.2.	Flowers with completely sterile pollen (berries not formed)	7	7	Colombia, Peru
Total		565	458	

Table 3. Floral development, berry formation and pollen sterility in andigena potato[a]

Sr. No.	Country of origin	Total genotypes	No. of genotypes				Pollen sterility (%)	
			Without floral buds	With floral buds	With mature flowers	With mature berries	Range	Mean±SE
1	Argentina	43	39 (91%)	4 (9%)	3	0	22.2– 91.4	56.2a±5.9
2	Bolivia	34	31 (91%)	3 (9%)	1	0	55.3– 60.7	57.5a±1.6
3	Chile	18	13 (72%)	5 (28%)	3	0	31.5– 57.8	44.8b±3.5
4	Colombia	435	257 (59%)	178 (41%)	85	11	14.9–100	55.9a±2.7
5	Peru	35	25 (71%)	10 (29%)	6	1	29.8–100	70.3c±6.3
Total		565	365 (65%)	200 (35%)	98	12		
χ^2			30.3**		9.6*			

[a] For floral buds, the values in parenthesis are percent of total. Mean values for pollen sterility not followed by the same alphabet in the vertical line differ from each other at 5P level as indicated by Duncan's multiple range test.
χ^2 values: * $P<0.05$, ** $P<0.01$

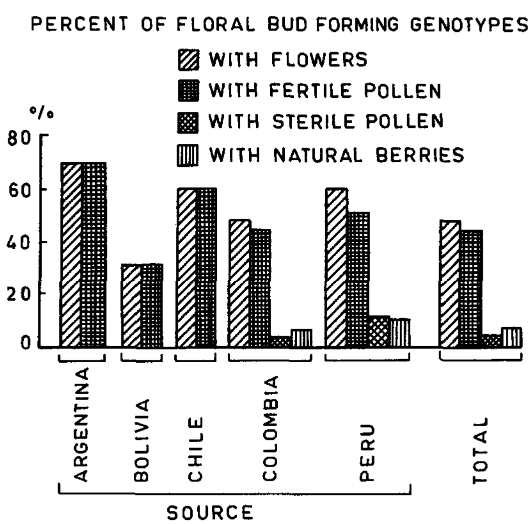

Fig. 2. Proportion of floral bud-forming genotypes of andigena potato from different countries having flowers with fertile and sterile pollen and natural berry formation

genotypes. The minimum proportion of Bolivian genotypes (33%) exhibit floral bud retention. Thus, maximum proportion (67%) of genotypes from Bolivia drop floral buds.

Berry formation

Of 565 genotypes, 98 produced mature flowers, but only 12 genotypes set berries. Of these, 11 were Colombian and 1 was Peruvian (Table 3). Thus, only 2% genotypes of andigena potato are able to set berries in the Indian plains.

Male sterility

Ninety-three percent of the flowering genotypes exhibit partial to high male sterility and the mean values of the genotypes range from 45% to 70% (Table 3; Figs. 3 and 4). The remaining 7% of genotypes are completely male sterile. Such genotypes occur only in the Colombian and Peruvian accessions. Some male steriles having pollen sterility up to 91% occur in Argentinian genotypes. Based on the mean values, the highest (70%) pollen sterility occurs in Peruvian genotypes and the lowest (45%) in Chilean genotypes; the mean difference between their male sterility is statistically significant (Table 3). In the Argentinian, Bolivian and Colombian genotypes, male sterility is medium: the mean ranges from 56% to 57.5%. The differences among their mean pollen sterility are insignificant.

Floral bud development

Nearly 65% andigena genotypes do not develop floral buds at all. In the remaining 35% of genotypes, the floral buds develop but they are retained and mature into flowers in only 17% of genotypes. The floral bud development or nondevelopment is not specific to any region or

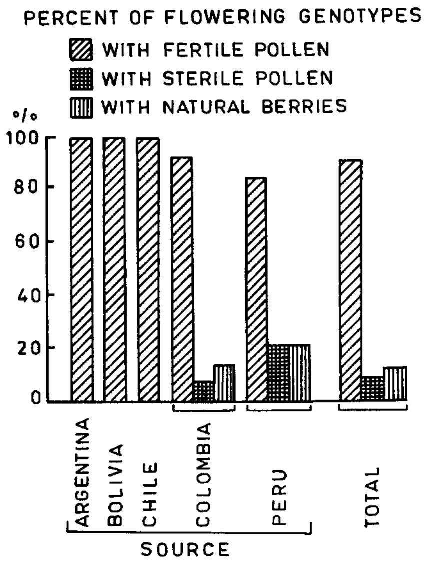

Fig. 3. Proportion of flowering genotypes of andigena potato from different countries having fertile and sterile pollen and natural berry formation

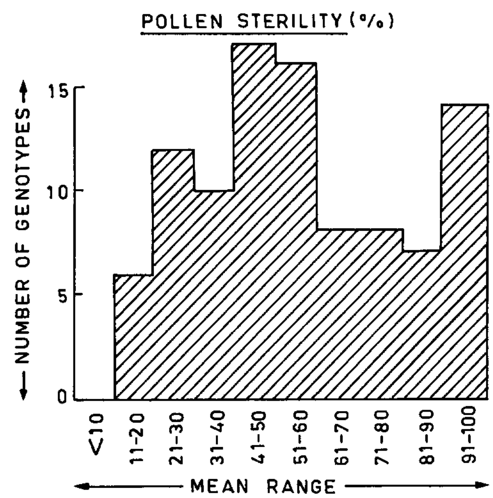

Fig. 4. Frequency distribution of mean pollen sterility in 98 andigena potato genotypes

country, but is scattered unevenly and is concentrated more in Chile, Colombia and Peru than in Argentina and Bolivia (Table 3). The frequency of genotypes that drop floral buds and those that retain them to flower maturity is nearly similar. Though mature flowers are retained in 17% of genotypes, only 2% produce berries. Male sterility occurs in all the genotypes that develop mature flowers. The sterility is partial in 93% of the genotypes and total in the remaining 7% of genotypes. The percentage of genotypes exhibiting total male sterility in andigena potato is only 1.2%.

Discussion

Unlike tuberosum, in which genetic variability is narrowed due to intense selection and domestication, andigena potato is a storehouse of genetic variation (Glendinning 1969; Cubillos and Plaisted 1976; Tarn and Tai 1977; Hosaka and Hanneman 1988). Most of this variability is untapped and has potential in potato improvement. This is not only due to the high diversity of andigena potato in phenotypic and biochemical characteristics (Birhman et al. 1988) but also to its possession of great variability in flower production, male sterility expression and berry setting. For instance, whereas the maximum genotypes from Peru produce flower buds, in most of them the buds abort prematurely so that the genotypes that finally retain flower buds are lesser in frequency than those from Argentina, in which the least number of genotypes produce flower buds, but almost all of them retain these to maturity and exhibit thereby the maximum floral bud retention capacity. Thus, there is no correlation between flower bud development and their final retention to maturity. This is further evidenced by the behaviour of genotypes from Bolivia. These have minimum capacity of floral bud formation and retain the floral buds until maturity. Likewise, there is no correlation between floral bud development or nondevelopment and its country of origin. Both these features, though prevalent in all the regions, are concentrated in Colombia, Peru and Chile.

In addition to nonproduction of floral buds or their premature drop off, the third major anomaly in potato is the gametic sterility, about 94% of the sterility being male sterility. The pollen sterility is also prevalent in the cultivated tuberosum potato (Kaul 1988). This led Livermore (cited by Grun and Staub 1981) to conclude that "nine times out of ten one of the clones that you wish to cross will not flower but if they both flower, then nine times out of ten, they will both be male or both female sterile". The same is true for the group andigena, in which about 83% of genotypes do not develop mature flowers. The remaining ones are male sterile; their sterility ranges from 15% to 100% (Fig. 4). Thus, the sterility is from partial to complete. The male sterility is conditioned by the interaction of *Fr* nuclear and *c* cytoplasmic genes (Kaul 1988) and is expressed as: (i) production of thin green anthers that do not mature or produce viable pollen grains; (ii) anthers malformed and fused with each other, partially to completely; (iii) formation of ministyles on the ventral surface of deformed anther sacs; (iv) indehiscence of anthers having shrivelled and aggregated microspores; and (v) formation of sporads or shrivelled microspores. Whereas anomalies (i) and (ii) fall in the structural male sterility types, the remaining are of sporogenous types. It is established that nonallelic dominant or recessive genes condition these two sterility types (Kaul 1988). Both the nature and number of genes controlling these two anomalies in the andigena potato material studied are presently not known. Determination of the gene control for these anomalies would facilitate the use of male sterility genes in hybrid potato breeding. Since three-way hybrids are not superior to two-way hybrids in vigour and tuber yield (Sanford and Hanneman 1982), male sterility assumes importance in a two-way hybrid breeding programme in the andigena potato and should be utilized for hybrid potato development and for true seed production. The utility value of male sterility is further enhanced in this tuber crop, as it is now possible to identify superior crosses on cross prediction basis in potato (Brown et al. 1988).

Conclusions

The development of floral buds, their retention to maturity, the production of flowers that bear ovules concealed in a hollow ovary and anthers approachable to stigma, the functionability of the anthers and ovules through the production of viable gametes, the fruit formation and the berry setting represent genetically conditioned events that render the angiosperms unique in the plant kingdom. All these events are sequentially programmed, controlled and coordinated by a large number of major genes, the majority of which are in a dominant state (Kaul and Murthy 1985; Kaul 1988). Mutation of any of these developmental genes causes absence of an event and loss of the further sequence of events. In the andigena potato, whereas the majority of the genotypes do not develop floral buds, in 50% of the remaining ones, the floral buds drop off before maturity. But in those in which the floral buds are retained and mature into flowers, male sterility is predominant. Thus, the main anomalies in andigena potato are: lack of floral bud development, premature dropping off of floral buds, nonproduction of berries and rampant male sterility. Since these anomalies are frequent in the genotypes collected from all five South American countries and are retained by the genotypes in successive generations, the presence of mutant genes governing these anomalies is inferred. That these genes are unlinked and independently functioning is inferred from the specific types of anomalies each genotype exhibits. Since these anomalies represent sequential steps for berry development, the presence of any one of these cuts off the further developmental sequence. Moreover, different nuclear *fr* genes in cooperation with the *c* cytoplasmic gene condition the male sterility type and expression in potato (Kaul 1988). How such a big gene array is maintained by each andigena genotype is not known. Tetraploidy coupled with clonal propagation appear to be the only answers.

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