

GENETIC ASPECTS OF FLOWER REVERSION IN THE WINGED BEAN BEAN [*PSOPHOCARPUS* *TETRAGONOLOBUS* (L.) DC]

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KEY WORDS: winged bean, phenotypic plasticity, reversion, virescence, vivipary, feijão-de-asa, plasticidade fenotípica, reversão, viriscência, viviparidade.

ABSTRACT

*Flower buds of the winged bean [*Psophocarpus tetragonolobus* (L.) DC] growing in Teresina, Piauí, Brazil reverted from their normal sexual reproductive function to a photosynthetic, vegetative function. In comparison with normal flowers, reverted flowers were characterized by a transition from a tetragonolobanus to a digonolobanus form (100% of samples observed) and by virescence of flower parts (99.4% of samples observed). Reversion was further characterized by vivipary which depends on the degree of evocation (i.e. induction) of vegetative buds to flower buds and on foliation of reverted ovules in flowers. Statistical analysis of data from field experiments indicated a single gene, in the homozygous recessive form in all reverting individuals, to be the genetic basis of this reversion phenomenon.*

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RESUMO

Botões de flores de feijão-de-asa [Psophocarpus tetragonolobus (L.) DC] cultivados em Teresina, Piauí, Brasil reverteram de sua função normal (i.e. reprodução sexual) à função vegetativa fotossintética. Em comparação com flores normais, flores revertidas foram caracterizadas por uma transição da forma tetragonoloba à forma digonoloba (100% das amostras observadas) e por viriscência dos componentes das flores (99,4% das amostras observadas). Reversão foi ainda caracterizada por viviparidade que depende do grau de evocação (i.e. do grau de indução) dos botões vegetativos aos botões florais, e na foliação dos óvulos revertidos dentro das flores. Os resultados sugerem homozigose para um gene recessivo como responsável pelo fenômeno de reversão em [P. tetragonolobus].

INTRODUCTION

Reactions and adjustments of exotic species to their new environments are processes that merit specific, continuous attention and study. These reactions and/or adjustments can run a broad gamut involving genetic, physiologic and pathologic factors effecting anything from internal chemical changes to gross morphologic transitions. Flower reversion is one such transition. Reversion is, as SWARTZ (1971), has said "...the reappearance of an ancestral character not exhibited by the immediate parent". It refers to a change in form but ^{not} in structure of an organ or organ system at the morphologic level. The organ system (e.g. flower) assumes a function (e.g. photosynthetic) which is different from that of its principal, normal function (e.g. sexual reproduction) but commensurate with the developmental history of that organ system (e.g. flower as a leaf or leaves specialized for reproduction). Reversion is a type of homeosis in that it is, as SATTLER (1988) has stated, a "...case of shifting in which one part of an organism becomes more or less like another.", (e.g. flower and floral organs become more like photosynthesizing leaves). Reversion may affect entire individuals or only sections. Manifestations appear to be temporal responses by the organism or section of said organism to environmental factors rather than any permanent changes at the mutation or pure DNA level in the organism (BENYA & MALLMANN, 1986).

Phenotypic plasticity refers to any alteration or alternation (temporary or permanent) in the expression of a genotype at the morphological and/or physiological levels caused by strictly environmental influences (BRADSHAW, 1965; TRIVEDI & RAJESH, 1984; VIA & LANDE, 1985; SCHLICHTING, 1986; BOWMAN et al., 1989). In any specific environment some organisms may show a response while others of the same species may not. This may be a result of micro-environmental or of qualitative factors influencing the unique established genotype of any one individual permitting that individual to demonstrate a plasticity of form.

The winged bean is a species whose native origin appears to be South Asia, Oceania, Mauritius and Madagascar (NATIONAL ACADEMY OF SCIENCES, 1981). The species is naturally short-day in its flowering habits. However HERATH and ORMROD (1979) and WONG & SCHWABE (NATIONAL ACADEMY OF SCIENCES, 1981) have shown that both temperature and day length are equally important in controlling flowering. Introduced into Brazil in the 1970's, the species is adapted to a broad range of humid, tropical and subtropical climates (MALL-MANN, 1984; BENYA *et. al.*, 1985).

This report addresses genetic aspects of flower, flower bud and vegetative bud reversion as observed and analyzed during a 7 year study period from 1987 to 1993.

MATERIAL AND METHODS

Data were recorded over a 7 year period; 1987 to 1993. Soil of the area is an entisol silt. Teresina, Piauí, Brazil lies at an altitude of 64 m, 05°05'S; 42°49'W and is therefore environmentally tropical equatorial.

Climatically the region has an annual average precipitation, seasonally distributed, of 1339 mm and an ETP (Evapo-Transpiration Potential) of just over 1700 mm (GADELHA DE LIMA, 1987). Monthly ETP usually surpasses monthly precipitation during eight and sometimes during nine months of each year.

A government agency, EMBRAPA (Empresa Brasileira de Pesquisa Agropecuária) furnished specific raw monthly meteorologic data. General meteorologic data over the 30 year period 1952-82 came from a regional source (GADELHA DE LIMA, 1987).

The region naturally supports vegetative ecologic association classified according to the Holdridge system as Semi-arid Dry Forest. More specifically the natural vegetative association (in or near equilibrium) can be classified as seasonally humid, semi-arid, tropical, semi-deciduous forest (SANCHEZ, 1976) having a canopy composed of 1.5 to 2.0 established strata.

Data were collected by regular observation (generally every 2 to 10 days) of sites during the cultivation, staking and cropping season. The data described here in are both of an empirical, observational as well as of a controlled, experimental origin.

Plants ($N = 74$) were allowed to self-pollinate, as is normal for the species (KHAN, 1982) in the first phase of investigations. Reversion rate for these initial, self-pollinating populations, termed P_1 , was recorded and statistically analyzed. The second phase of investigation involved isolating and saving seed from sample specimens of a P_1 planting and then noting if the plant yielding the seed later reverted (since a reverted plant normally loses its capacity to produce seed). Seed from reverted specimens was mixed and planted. Specimens of the resulting F_1 generation were then observed for reversion frequency.

Simple qualitative biological analysis (i.e. a local-lesion analysis using the winged bean as the indicator plant) was conducted to test for possible pathologic influences (CORBETT & SISLER, 1964; AGRIOS 1978). Liquid extract from newly reverted flowers in aqueous (i.e. sterilized, deionized water) solution served as an inoculum on 36 flower buds representing 5 plants. Inoculum was dripped over the 36 buds soaking same. Another 32 flower buds from the same 5 plants served as a control receiving simple sterilized, deionized water as the treatment.

Chi-squared statistical analysis were calculated for frequency of reversion of mature plants in sample plantings representing 74 plants where 18 reverted. Standard linear correlations were calculated for frequency of reversion of 35 plants (reverting from July, 1987 to December, 1988) with various meteorologic components of ETP (GOMEZ & GOMEZ, 1984).

RESULTS

The presence of a morphologic flower reversion was first confirmed on a vine on 21 July, 1987. Reversion is marked by: transition of ovaries from the tetragonolob to a digonolob form, virescence (i.e. chlorophyllization) of flower parts (e.g. petals, ^{stamens}stamens, pistil); a curled appearance to affected parts especially petals and ovaries (FIGURE 1), and vivipary (i.e. foliation of ovules within the reverted ovary and/or foliation of incompletely induced vegetative-floral buds).

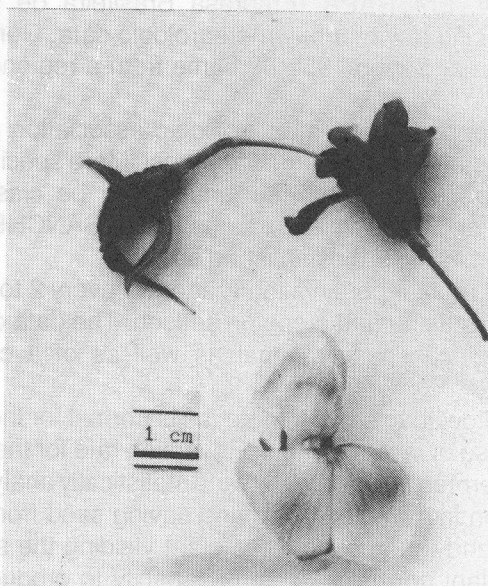


FIGURE 1 - Reverted flower (top): virescent, vascularized, curled appearance. Normal flower (bottom).

Vivipary is a profuse vegetative growth characterized by the quite sudden and numerous development of dense, usually weak-structured mats of petals and/or apices and/or leaves of varying form, but always of diminished dimensions. They never grow to normal size. Nodal vegetative buds are meristematically active.

Viviparous mats apparently can arise from numerous flower buds whose evocation (i.e. induction) is incomplete (BATTEY & LYNDON, 1990). It is herein treated as a sign of reversion because of its high frequency of appearance (100%) in a sample of 20 plants showing reverted flowers, plus its independent appearance on adult plants during the vegetative or non-flowering (i.e. increasing day-length) season. These mats could appear alone, prior to the appearance of, simultaneously with reverted flowers or up to 1.5 months later.

Spontaneous, natural meristematic vegetative apical activity arose on many reverted flowers (e.g. from reverted ovules) an average of 0.75 months, or about 3 weeks, from the time of initial reversion. This apical activity contributed to the viviparous phenomenon.

Local-lesion analyses of 36 inoculated normal flower buds from 5 normal winged bean plants was oriented toward identifying, by means of recognizable symptoms (e.g. flower reversion), any substance that might be associated with the entire reversion sequence. The experiment ran 22 days during which 18 of the 36 treated buds and 6 of the 32 control buds bloomed producing normal flowers. The 44 buds that did not bloom were lost because of natural causes (normal abscission, insect damage).

Initiation of the reversion sequence either by reverted flowers, viviparous growth or both showed highly significant linear correlation with the meteorologic variables "mean monthly evaporation" ($r = 0.710$; $P < 0.01$) and "mean daily range in temperature" for each month ($r = 0.636$; $P < 0.01$). Both of these variables influence ETP with which reversion was also significantly correlated ($r = 0.631$; $P < 0.01$).

The P_1 , 74 sexually mature plants (all at least 7 months of age) showed 56 normal and 18 reverted. This ratio significantly ($X^2 = 0.018$, $P < 0.001$) approaches the 3:1 phenotypic ratio indicative of a single dominant-recessive gene effect. Seed from reverted plants produced a sample of 13 F_1 plants all of which (100%) reverted.

Transition of pods from the tetragonolob to the digonolob form was the abnormality most commonly associated with the reversion sequence. Of 284 reverted flowers sampled, 100% showed this abnormality. Virescence of flower parts showed a 99.4% (i.e. 336 of 338 reverted flowers sampled) association with reversion.

DISCUSSION

Prerequisites for reversion by an individual plant included: the occurrence of a recessive gene responsible for the reversion phenomenon as a homozygous recombinant; and presence of the necessary meteorologic force or forces (e.g. evaporation, broad thermal range), factors influencing plant ETP (GADELHA DE LIMA, 1986). This meteorologic force or forces could easily be buffered or attenuated by the presence of micro-climates caused by companion species to the winged bean in any planting.

Factors that were highly desirable but not absolutely necessary for reversion were: sexual maturity of the individual plant (i.e. the presence of flowers buds) and use of the pods in their green, immature form rather than as mature seed pods.

The overall morphologic form of digonolob pods and of reverted flowers in general can present a "curled" effect very similar to that exhibited by normal leaves infected by a leaf curl pathogen (KHAN, 1982). Yet tests using a local-lesion analysis method revealed no pathological agent to be associated with this phenomenon.

Considering the implied and expressed cases of phenotypic plasticity already reported for the winged bean for tropical, subtropical and temperate climates (BENYA *et al.*, 1980; BENYA, 1985; BENYA & MALLMANN, 1986), the dearth or want of evidence linking any pathogen with this type of reversion, the specificity of effect of phenotypic changes cited herein (i.e. the close approximation of reversion rate in mature, random samples to the ideal 3:1 phenotypic ratio; the 100% reversion rate in sample F_2 plants resulting from seed of plants that had reverted), one must consider a phenotypic plasticity of the species basically caused by a single recessive gene in homozygous form, as the most plausible explanation for these morphologic changes.

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