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Permutation of ground state phylloid buds and flowers from a paleobotanically reverted recombinant of psophocarpus

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ABSTRACT

Paleochronic (anachronic) reversion is an atavism (transition) of angiosperm flowers, a transmutation that nullifies the sexual reproductive dynamic reducing the reproductive system to a phylloid state. This seldom remains stable as a permutative stage usually follows spatially transforming anatomic zones (i.e. whorls and bracts), regions within zones (e.g. floral whorls), or even sites within regions (e.g. carpel components). Permutation can be augmented, accompanied or followed by vascularization, deadnation and/or spiralling in a scenario of transformations. This research focused on 51 reverted floral specimens from a reverted recombinant of Psophocarpus tetragonolobus. The recombinant, verified phenotypically as homozygous recessive for a master homeotic gene (srs) responsible for this reversion, was also dominant for four major "reversion dependent genes". Transition presented (in planta) the two stages characteristic of paleochronic reversion; transmutation and permutation. A general chronology for floral permutation occurred. Parallel and tangent carpel clefts underwent distancing of central portions of these clefts by means of a "webbing" function. Decompression permutation occurred at the inter-zonal (i.e. pericladial stalk), inter-regional (i.e. inter-bracts stem) and inter-whorl (e.g. gynophore and/or cupule-like structure) anatomic levels. Spiralling of carpels frequently occurred as did vascularization and deadnation of carpels to a lesser extent. The order of events presented a sequence that was "paleoanachronic"; a development of anachronic characteristics whose succession was variable yet significantly ordered.

KEYWORDS

Atavism;
Floral decompression;
Genetic activation;
Paleochronic reversion;
Permutative sequence.

INTRODUCTION

In angiosperms the inductive conversion of the shoot apical meristem (SAM) to the floral meristem (FM) involves a transformation of the SAM from an entity of non-sexual, indeterminate growth to one of sexual reproduction with determinate growth[1]. This conversion can include the specification and generation of an intermediate inflorescence meristem (IM) (Figure 1A)[2-5]. Floral components of IMs must then receive specifica-

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tion of organs positioned at one of two floral anatomic zones; the pre-whorls bracts zone (and region) plus sepals, petals, stamens and carpel(s) at the floral whorls anatomic zone. These latter four organ types occupy regions organized in specific, concentric whorls[6-8] forming respectively the calyx, corolla, androecium and gynoecium of each flower.

Thus floral induction involves a sequential metamorphic conversion of the shoot to an inflorescence and then to a flower or direct conversion of SAM to FM[4,9,10]. The FM is the result of specific compression morphogenesis where anatomic zones and regions of homologous organs are specified and developed in a tightly compressed phyllotaxy, of highly exact forms and sequence where internodal development is minimal or nil in a compact floral architecture[11].

Inflorescence decompression by means of elongation of each floral pedicel is necessary in order to establish distance between component flowers (Figure 1A) and generate sufficient space for normal flower bloom (Figure 1B, 2A). Established terminology concerning "floral axis… compression"[12] and "com-

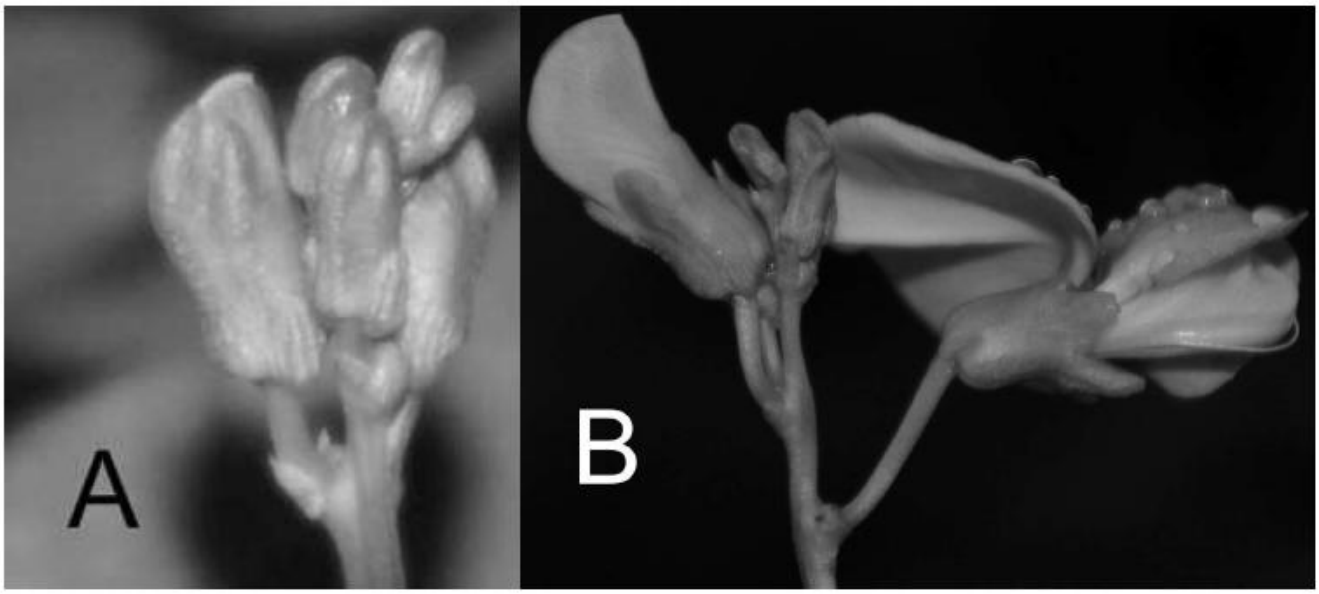

Figure 1 : (A) Compressed inflorescence of normal (non-reverted) recombinant (in planta) of Psophocarpus with initial decompression beginning; (B) Normal decompression, bud burst and flower bloom

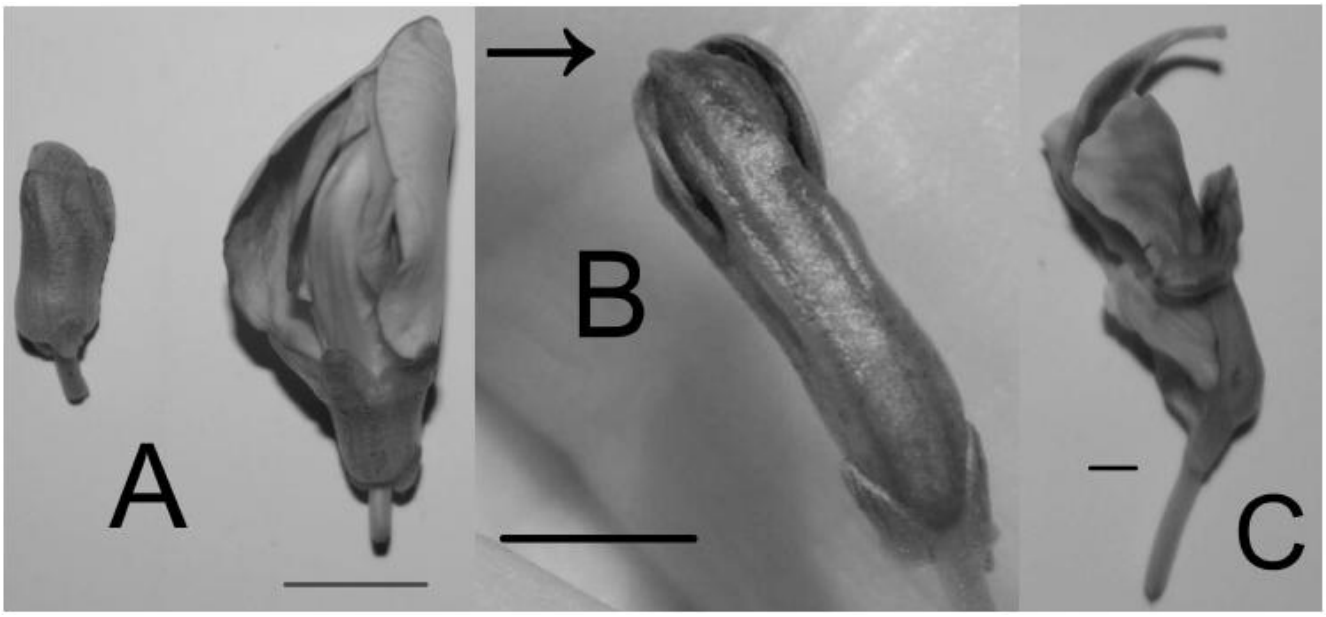

Figure 2 : (A) Normal (non-reverted) flower bud (left), flower in bloom (right). Sexual reproductive state; (B) Reverted flower bud, cancelled floral meristem, "rifted" distal end, a phylloid ground state; (C)Reverted flower, cancelled floral meristem; (scale: A and B, 1 cm, C, 2 mm)

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pressed… habit"[11] involving morphologic compression indicates an essential dynamic established and maintained in the compact flower structure[2,13,14]. The term "decompression" (a type of "unfolding") then continues from this established terminology.

The sequence of compression floral morphogenesis can be modified and/or multiplied through the activity of floral homeotic genes leading to conversion or reversion transformation of the flower or of regions within the flower[2,15,16]. Reversion can completely cancel FM and floral organ activity resulting in floral organs of a phylloid state[17,18] and even result in atavism (i.e. appearance of phyllome ancestral forms)[19,20,21].

A phylloid floral ground state has been recognized in anachronically reverted floral specimens of the legume species Psophocarpus tetragonolobus (L.) DC (Fabaceae)[18]. The essential reversion responsible for this ground state is controlled by a master homeotic gene termed "SEXUAL REPRODUCTIVE STATE" (SRS) whose recessive allele (srs), in its homozygous activated form, terminates the process of floral development and cancels a reproductive dynamic, necessary for sexual function of flowers, thus reducing them to a phylloid state.

Two principal stages, a transmutative followed by a permutative, characterize this ground state. The transmutative is precise, resulting in a phylloid flower (Figure. 2B, C) after activation of the srs allele. The permutative stage however is not as distinct. After activation of the master srs allele, alleles of at least four other genes can be activated to initiate permutation (e.g. decompression, spiralling) and/or vascularization, in variable combinations and sequences, of floral unfolding of the ground state flower[18]. Three of these genes (i.e. formed "Gynophore", formed "Pericladial stalk" and "Vascularized" carpel) present dominant alleles (i.e. "GNF", "PCL" and "VSCARP" respectively) that directly influence reverted floral permutation and/or foliation. The fourth gene "Parallel Bracts" presents a dominant allele (i.e. "PRL:BCT") that, when activated, maintains the bracts at opposite loci. Each of these genes present phenotypes in a distinctly Mendelian scenario of inheritance[18].

Purpose of this research was to document any sequence(s) of floral permutation and/or foliation for reverted floral specimens in planta originating from a single reverted recombinant plant thus identifying possible intensive regions of floral permutation.

MATERIALS AND METHODS

Psophocarpus tetragonolobus (L.) DC (Fabaceae) is a highly selfing taxon[22]. The variety GRWB-26 was introduced to Brazil from India. That seed carried the recessive allele (srs) of the master homeotic gene (SRS) as well as the four "reversion dependent genes" associated with that allele. The srs allele was isolated in a population (homozygous presence), then verified phenotypically over multiple generations in the Teresina region of Piaui, Brazil as previously described[18]. This population was then designated GRWB-26r to distinguish the homozygous presence of the *srs* allele. It was used to establish a seedling population during both the wet (March to June) and dry (July to February) seasons, in the tropical equatorial semiarid environment of Russas, Ceara, Brazil (04°, 55' S; 37°, 58'W; alt. 38 m). Meteorological data are available at (http://tempoagora.uol.com.br). Recombinants in this planting reverted naturally and yielded both reverted and normal floral specimens. Research then concentrated on one recombinant verified as dominant (homozygous or heterozygous) for all four permutation or foliation "reversion dependent genes", documenting morphologic changes, sequence(s) and frequencies of change for 51 reverted floral specimens of that recombinant. Subsets from these 51 specimens (ranging in size from one to 29 specimens each) then furnished clusters ($y_{(i,...j)} = n$ = numbers of specimens) for statistical analysis of selected permutative events and/or multiples of those events on individual floral specimens. A specimen could thus appear in more than one cluster.

"Reversion age" of a floral specimen was defined as the time ($\mathbf{T}_{(k,...1)}$) from initiation of reversion (day zero; $\bar{\mathbf{x}}_{\mathbf{T}_1} = \mathbf{0.00}$; TABLE 1) on the recombinant, to the date when any reverting floral specimen from that recombinant was incorporated into this study. It is the time in days, counting from the onset of reversion on the recombinant to the date of reversion of that floral specimen (its "reversion age"), in accord with similar procedure[23]. This served as a timing reference for analysis of morphologic permutative transformation(s) and their sequential manifestation at specific anatomic regions of each specimen furnishing "mean generative times" ($\bar{\mathbf{x}}_{\mathbf{T}_{(k,...1)}} = \sum \mathbf{T}_{(k,...1)} / \mathbf{n}_{y(i,...j)}$) for documentation of permutations and there combinations being either above or below the standard mean reversion age ($\bar{\mathbf{x}}_{\mathbf{T}_0} = \sum \mathbf{T}_0 / \mathbf{n}_{y_0} = \mathbf{190 / 29 = 6.552}$). Digital photography

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TABLE 1 : General permutative sequence: Statistical "t-test" values of "mean generative times" ($\bar{x}_{T_{(k,...1)}}$), in days, for selected permutative functions on "number of reverted floral specimens" ($y_{(i,...j)}$=n) relative to the standard mean reversion age ($\bar{x}_{T_0}$ = 6.55 days).

Reverted condition	$\bar{x}_{T_{(k,...l)}}$	$y_{(i,...j)} = n$	"t" value	p	Distancing effect
1. phylloid ground state	$\bar{x}_{T_1}$ =0.00	y_1= 4	----------	--------	none
2. webbed carpel	$\bar{x}_{T_2}$ =3.57	y_2= 21	-4.779	<0.000**	intra-regional Between carpel clefts
3. carpel spiral rotation	$\bar{x}_{T_3}$ =5.17	y_3= 6	-1.284	0.255 NS	none
4. pericladial stalk	$\bar{x}_{T_4}$ =7.38	y_4= 21	0.656	0.519 NS	inter-zonal Whorls zone from non-whorls zone
5. bracts dislocation	$\bar{x}_{T_5}$ =8.07	y_5= 15	1.227	0.240 NS	intra-regional IB (inter-bracts stem)
6. gynophores and/or cupule-like structure	$\bar{x}_{T_6}$ =12.36	y_6= 11	4.513	0.001**	inter-regional Fourth whorl from preceding whorls
7. vascularised carpel	$\bar{x}_{T_7}$ =14.38	y_7= 8	7.444	<0.000**	intra-regional Expansion of inter-cleft webbing
8. collective permutative	$\bar{x}_{T_8}$ =15.00	y_8= 3	8.450	0.014*	collective anatomic

(PENTAX K10D) and statistical analysis (correlations, t-test, χ^2, SPSS program) were used to document, archive and distinguish results according to significance.

RESULTS

An anachronic paleochronic (paleobotanic) reversion of a recombinant plant homozygous for the recessive allele (srs) of the master homeotic gene "SEXUAL REPRODUCTIVE STATE" (SRS)[18], caused an atavism in the form of cancelled floral meristem activity, transforming sexually reproductive flowers to a non-sexual phylloid floral ground state. Normal flowers and buds, at varying degrees of development, reverted from the sexual reproductive state, over a period of time, (Figure 1B, 2A, [Supplementary Information Figure 1 "1", "2"]) to a non-sexual phylloid state (Figure. 2B, C). Most floral whorls and their respective organs underwent virescence of their organ parts with the notable exception of the third whorl (i.e. stamens) which desiccated (Figure 3A, B, C). The pre-whorl bracts remained virescent. By definition mean generative time for appearance of the phylloid state was zero ($\bar{x}_{T_1}$ = **0.00; n = 4**); day zero of reversion (TABLE 1).

A conduplicate digonolobe carpel (Figure 4A, B) was a constant characteristic of this reversion, at initia-

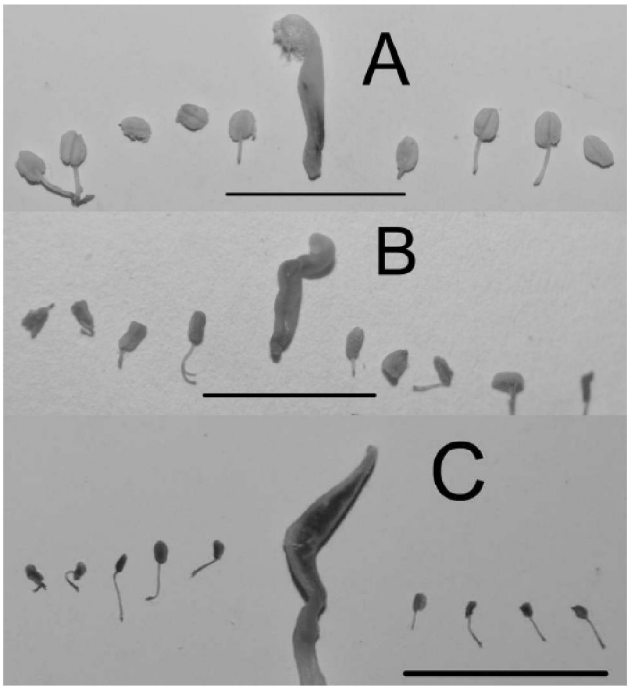

Figure 3 : (A)Normal carpel (conduplicate, digonolobe form) and fertile stamens; (B) Reverted carpel (conduplicate digonolobe form; virescence, tangent abaxial and adaxial clefts; spiralling 270°) and desiccating stamens; (C) Reverted carpel (conduplicate digonolobe planar webbing form; virescence, separated abaxial and adaxial clefts, spiralling 180°) desiccated stamens; (scale bars = 1 cm)

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tion of the transmutative stage as was "rifting", (i.e. "irregular point-release") of distal sepal margins (Figure 2B, [Supplementary Information Figure 1 "3", "4", "5", "6", "7", "8"]). This lead to a "rifted bud" rather than the neat convergence of sepal points (Figure 1A) on normal flower buds.

Dissection of pre-bloom reverted buds revealed that "carpel clefts" (abaxial and adaxial) were parallel and juxtaposed (i.e. tangent to each other [Figure 4A]). A "webbing" function then ensued at this intra-region (intra-whorl) carpel cleft site, which gave rise to a flat "planer" digonolobe conduplicate carpel that was prevascular and pre-foliar in form[20]. Webbing occurred between the two carpel clefts. Points (acropetal and basipetal) of both clefts remained joined but development of the "web" then distanced central regions of the two clefts from each other eliminating their tangential juxtaposition thus giving rise to the "planed" flat digonolobe carpel (Figure 3C) common to most normal flowers of the family Fabaceae.

Mean generative time for the planar digonolobe carpel, because of its origin internal to and prior to bud bloom, was significantly less ($\bar{x}_{T_2}$ **= 3.57; n = 21; t = –4.779; p < 0.000**) than that of the standard mean reversion age ($\bar{x}_{T_0}$ **= 6.55**) for reverted specimens (TABLE 1). This planar digonolobe carpel could be preceded, accompanied or succeeded by a spiral rotation to the carpel itself (Figure 3B, C). All dissected buds and numerous buds showing pre-bloom organ emergence [Supplementary Information Figure 1 "9", "10"] presented this "spiral rotation". Its presence was not absolute. Its mean generation time was less than but not significantly variant ($\bar{x}_{T_3}$ = 5.17; n = 6; t = –1.284; NS) from the standard mean reversion age (TABLE 1).

The digonolobe carpel within the floral bud could be terminal. Yet as anticipatory to permutation, it preceded all characteristics of reversion that are external to the bud. Thus the rifted bud, digonolobe tangentially juxtaposed clefted carpel and virescent floral organs were the three characteristics that defined a phylloid ground state for a reverted flower.

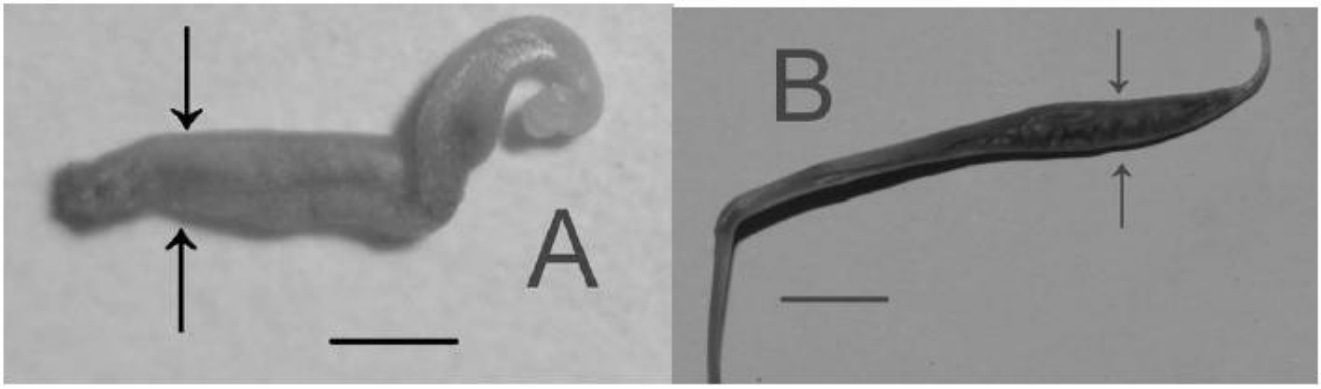

Figure 4 : (A) Conduplicate digonolobe carpel parallel and tangent adaxial (↓) and abaxial (↑) clefts (scale = 2 mm); (B) Conduplicate digonolobe carpel, separated adaxial (↓) and abaxial (↑) clefts, planar webbing of the separating clefts (scale = 1 cm)

The phylloid ground state however was seldom terminal being highly unstable. A sample of 51 reverted floral specimens, presented four (7.84%) (TABLE 1) at a ground state, but 47 (92.16%) presenting some succeeding state of floral permutation. This permutation is governed by at least four other genes[18] herein termed "reversion dependent genes" whose individual or combined activation is dependent on the homozygous presence, activation and manifestation of the recessive allele (srs) of the master gene. This permutative stage was manifest at specific floral zones, regions and/or sites in temporal intervals (in days) that were predictable and even statistically significant.

Inter-floral permutation begins with the decompression of the inflorescence. Such decompression however can also occur on non-reverted inflorescence (Figure 1A, 1B). Thus individual intra-floral decompression permutation (Figure 5A, B) was the most objective indicator of reverted decompression.

Three of the four genes, presenting a simple Mendelian dominant:recessive scenario of gene action (i.e. formed Gynophore [GNF], formed Pericladial stalk [PCL] and Vascularized carpel [VSCARP])[18] permitted uncomplicated measurements of permutation at anatomic zones and morphologic regions and sites for direct verification of any effects. The fourth gene, Parallel Bracts (PRL:BCT), presented complications, because its dominant allele, a loss-of-function allele,

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prior to activation apparently allows bract dislocation giving rise to an inter-bracts (IB) stem (Figure 5B). This effect is indistinguishable from the dislocation caused by its recessive allele (prl:bct). Statistical analysis of mean reversion age with "mean generative times" T_4 to T_6 of functions for the "reversion dependent genes" revealed a general sequence (TABLE 1) of ontogenetic morphologic decompression related to three of those four genes.

Pericladial stalk development (Figure 5B) is the first and only anatomic inter-zonal decompression permutation. It distances the entire whorls anatomic zone, from the entire pre-whorls bracts anatomic zone (and region). At initiation of reversion this was usually the first and most obvious sign of floral decompression permutation. Its mean generation time in days ($\bar{x}_{T_4} = 7.38; n = 21; t = 0.656;$ NS) presented no significant variation from the standard mean reversion age of all floral specimens.

Expectation of bract dislocation on specimens originating from a recombinant containing the dominant PRL:BCT allele(s) would be nill. Yet bract dislocation (Figure 5B) frequently accompanied (11 of 22 specimens) pericladial stalk formation. An intra-zonal (intra-regional) function, at a mean of 8.07 days, it was second in a general sequence of inter-regional decompression events, greater than that for pericladial stalk development but not significantly variant ($\bar{x}_{T_5} = 8.07;$ $n = 15; t = 1.227;$ NS) from the standard mean.

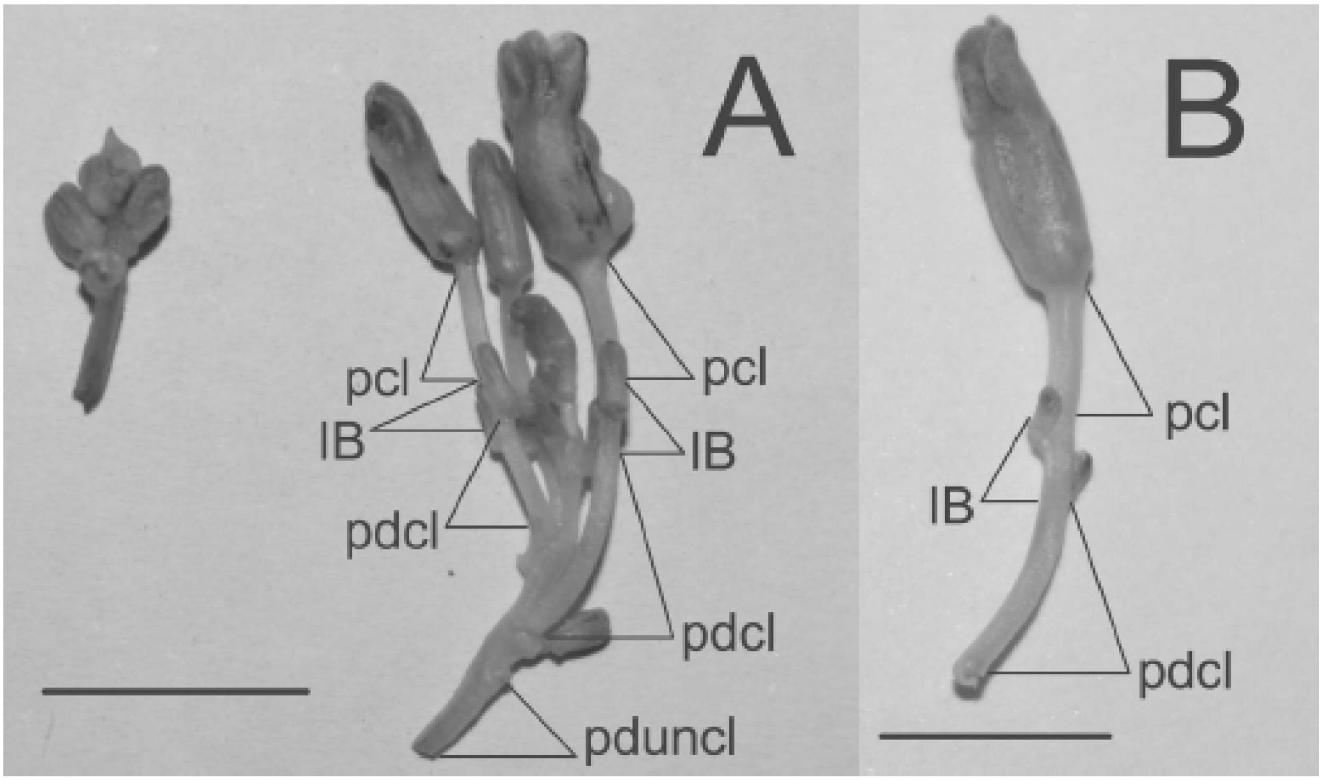

Figure 5 : (A) Normal inflorescence point (left), compression of internodes of normal flower buds, in compact cluster. Reverted inflorescence (right), decompression of a cluster of reverted flower buds. Elongation of individual pericladial stalks (pcl), inter-bracts (IB) stems, floral pedicels (pdcl) and peduncle of inflorescence (pduncl). (scale bar = 1 cm). (B) Reverted floral bud, floral decompression (permutation) beginning with distinct pericladial stalk (pcl), inter-bracts stem (IB) and pedicel (pdcl) clearly present (scale bar = 1 cm).

Development of the gynophore and/or cupule-like structure (Figure 4B, 6), an inter-whorls (inter-regional) permutation function, was usually next in the sequence of decompression events. It distanced the stamen and carpel whorls regions from each other. This was significantly higher than the standard mean reversion age of floral specimens ($\bar{x}_{T_6} = 12.36; n = 11; t = 4.513; p = 0.001;$ TABLE 1).

The combined permutation effect of gynophore and/or cupule-like structure development was complicated by the fact that what was previously considered to be a single structure (i.e. gynophore) composed of one node and two internodes[18] was more clearly recognized as a structure composed of a single internode[24] but at juncture (and with continuing decompression) with a

"cupule-like" structure. Homology of this second structure however is unclear (G.W. Rothwell, personal communication). Thus it is not recognized as a cupule, but as "cupule-like". Elongation of this structure is preceded, accompanied or succeeded by development of the gynophore. Thus decompression permutation by means of gynophore development alone and/or development of a "cupule-like" structure is analysed as a single operation, but is treated as two distinct events because biophysical functions governing their development may be quite distinct.

Vascularization of the carpel, an intra-whorl (intra-regional, intra-site) function, was generally next in the timing sequence of atavism functions, also significantly above the standard mean floral reversion age ($\bar{x}_{T_7}$ **= 14.38; n = 8; t = 7.444; p < 0.000**). It consumed a lengthy period of time (over 24 hours) permitting closer scrutiny of associated functions.

Deadnation of the vascularized carpel, was one of these associated functions (Figure 7). As a point of decompression, previous research had recognized carpel deadnation as a rarity[18]. Partial deadnation of fully vascularized reverted carpels allowed more accurate analysis of carpel clefts and direction of any deadnation which was always adaxial, initiating basipetally and running

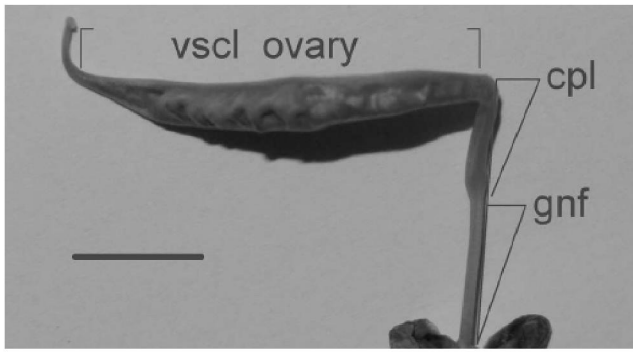

Figure 6 : "Cupule-like" structure (cpl) at juncture with and succeeding the gynophore (gnf) but preceding a vascularized ovary (vscl ovary) (scale bar = 1 cm).

acropetally (Figure 7).

Analysis of the main intra and inter-regional decompression events plus carpel vascularization in combinations allowed recognition of major states of compression and decompression. The phylloid ground state, where the reverted flower maintains "compressed" architecture of the non-reverted flower, preceded the beginning of any permutation on all 51 specimens. Collective permutation events on solitary specimens (i.e. vascularized carpel, formed gynophore and/or cupule-like structure, formed pericladial stalk and inter-bracts [IB] stem), rare in occurrence (n=3), were temporally significantly higher than ($\bar{x}_{T_8}$ **= 15.000; n = 3; t = 8.450; p = 0.014**) the standard mean reversion age (TABLE 1).

A comparison of archival meteorological variables from 1952 to 1982 for the region of Teresina, Piaui[25] with sample meteorological measurements from 2005 and 2006 for Russas, Ceara (http://tempoagora.uol.com.br) revealed a significant difference (t=-2.400;p=0.035) between mean annual relative atmospheric humidity (70% vs 60% respectively) for both regions. Reversion of recombinants in Russas, was significantly correlated (r=0.660;p=0.019) with "mean daily range in temperature" for each month, very similar (r=0.636;p<0.01) to that reported for previous research[26].

Qualitatively, soils in both areas were appreciably different. Those in Teresina are entisol silts[27] presenting pH values usually ranging between 4.9 and 5.8. Soils in Russas are principally alfisol loams with ph values generally from 6.0 to 7.0.

Figure 7 : Deadnation of reverted vascularized carpel (partial, about 60%) from basipetally to acropetally along adaxial cleft (scale bar = 1 mm)

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DISCUSSION

As in the previous research[18], reversion in the Psophocarpus population in Russas began with a transmutative stage closely followed by a permutative stage. The permutation documented here however was slower and less complete thus permitting more specific observation and analysis of certain permutative events. Reverted floral specimens, originating from one recombinant permitted morphogenerative and timing analyses of these events; their operations, functions, frequencies, general sequence and selected combinatorial manifestations while controlling for genome composition.

More accurate distinction of structures permitted clearer recognition of anatomic components and morphologic forms. As in the case of autonomous permutation site analysis, development of the pericladial stalk, in combinatorial analyses with the two inter-regional permutation functions, was usually the initiatory inter-zonal and inter-whorl decompression function. Stalk development distanced the entire pre-whorls bracts' anatomic zone from the entirety of the floral whorls anatomic zone. This general primacy of pericladial stalk development, usually preceding development of structures determined by dominant alleles of other "reversion dependent genes" (e.g.gynophore, cupule-like structure), supports a theory of essential differences in basic identity of the floral whorls zone and its organs regions from the basic identity of the non-whorl bracts zone (a single-region zone).

Genesis of the pericladial stalk is treated here as an extension of the calyx because of its phenotypic continuance with the first floral whorl (Figure 5B). The significant timing and sequential variables t=-9.696;p=0.001 for separating both zones suggest floral identity and architectural influences whose functions and manifestations reflect a dynamic of continuous and necessary canalization[28] and maintenance well documented in normal, non-reverted flowers[13,28-31] and extending to and including paleobotanically anachronically reverted flowers. The absence of that canalization and floral dynamic leads to a phylloid ground state that quickly enters a permutative dynamic that is governed by distinct biophysical functions, all or parts of which can be impeded, redirected and/or attenuated by specific silencing or interference genes.

Dislocation of bracts on this recombinant, homozygous or heterozygous for the dominant allele PARALLEL BRACTS (PRL:BCT), raises the question of gene activation, manifestation and control. Previous research demonstrated a simple Mendelian inheritance of traits as dominant or recessive[18]. The present results raise the possibility that at least one allele of one of these "reversion dependent genes" (i.e. the recessive "prl:bct" allele) is a "null allele" (i.e. one that does not produce or code for any functional transcript or product but is phenotypically manifest as a recessive) at least under certain conditions[3]. The PRL:BCT allele, in activation, is then a "dominant-negative", a dominant loss-of-function allele in its maintenance function[2]. Genetic nullity, timing indolence of dominant allele activation (PRL:BCT etc.) and/or genetic silencing (e.g. "dominant-negativity") would explain the expression of a phenocopy of a homozygous recessive phenotype (i.e. prl:bct/prl:bct) on various floral specimens originating from a recombinant that in all other aspects presents phenotypes of dominant alleles.

Analyzing decompression permutation through manifestation of floral ontogenetic anatomic sequence(s) reveals differences in morphologic diversity, beginning acropetally at the pre-whorls bracts zone and continuing to the whorls zone and two of its four regions. Diversity of permutation was notable at bracts (1 of 8 permutation events) and calyces (1 of 8), absent at the corolla (0) and androecium (0) but significantly concentrated (6 of 8 events) ($\chi^2 = 15.750 > \chi^2_{\alpha=0.01} = 13.227$; $df = 4$) at the gynoecium (TABLE 2). These six permutative events included intra-whorl webbing, vascularization, deadnation, inter-whorl distancing of androecium from gynoecium (through development of the gynophore and/or cupule-like structure) and spiralling of the carpel. This concentrated activity reflects the complexity and range of anatomic components that constitute the fourth whorl carpel region and sites therein[20,24] and at least some of the distinct morphologic reversion events associated with that complexity.

Decompression intra-floral permutation (i.e. bloom) is a dynamic that can occur on both sexually functional[24] and paleochronic reverted (ground state) flowers. Such decompression in regular, sexually reproductive flowers is a phenotypic trait or series of traits whose heritability (h^2) can be measured, calculated and predicted for succeeding generations[32]. However, paleochronic intra-floral decompression is a permutative capacity, manifest ([de novo] in each generation) or not manifest. Its heritability of phenotype cannot be calculated. Intra-floral permutation in paleochronically reverted ground state flowers is extensive (TABLE 2). It presents a distinctly varying yet estimable chronology

of events. The sequence of permutation events documented here indicates a chronology whose succession, although variable, is significantly ordered suggesting distinct biophysical function(s) of canalization. This adds credence to a "sequential" aspect of this paleobotanic anachronic reversion. It supports the rationale for the genesis of the more recent term "paleochronic reversion"[18] as an atavism where ancestral botanic characteristics of a paleobotanic form arise in a variable yet predictable paleo-anachronic order.

TABLE 2 : Regional permutative diversity: Ontogenetic development of atavistic character(s) at floral organs regions on reverted floral specimens of a single recombinant plant.

Component	organ(s)	form	Permutative event (type)	Regional subtotal	diversity Σ events[a]
Entire flower					
whorls & pre-whorls	Sum	Phylloid state	none (gs)[b]		
Pre-whorl	bracts	bracts dislocate, (IB) stem forms	intra-zonal	(1)	1
Whorl 1 (calyx)	sepals	normal virescent	none (gs)		
pericladial stalk		semi-internode	inter-zonal	(1)	1
Whorl 2 (corolla)	petals	virescent	none (gs)	(0)	0
Whorl 3 (androecium)	stamens	desiccated	none	(0)	0
Whorl 4 (gynoecium)	carpel	digonolobe			
		clefts tangent	none (gs)	(0)	
		clefts webbed	intra-whorl	(1)	
		vascularised	intra-whorl	(1)	
		deadnation	intra-whorl	(1)	
(gynophores and/		internode	inter-whorl	(1)	
or cupule-like)		cylindrical	inter-whorl	(1)	
		spiral	intra-whorl	(1)	6
				Σ_{events} =	8

[a]($\chi^2 = 15.750 > \chi^2_{\alpha=0.01} = 13.277; df = 4$); [b]"gs" = ground state

CONCLUSION

Atavism as anachronic reversion, also termed "paleochronic" is now recognized in two related but significantly distinct tropical, equatorial, semi-arid environments. Both cultures used seed of the same taxon and genetic origin but planted in localities of about 520 km apart. These localities are distinguished by the significant differences in their overall annual relative humidity and appreciable differences in soil texture and density. Therefore the differences in results from both regions may be associated with variables still to be investigated. Research concerning extant arboreal species[33] under specific environmental conditions (i.e. meteorological and edaphic) compared to fossil records of the same or similar taxa within their paleobotanic conditions has led to valuable comparisons of the adaptability of taxa to varying conditions over the ages. Paleoanachronic reversion permits comparisons of extant species forms with extant paleochronic forms of the same species.

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SUPPLEMENTARY INFORMATION

Supplementary Information in the form of one figure (photograph) presents a numbered general sequence of decompression permutation on normal, "non-reverted" inflorescence (1), a solitary non-reverted flower bud (2) and sequential decompression of paleobotanically "reverted" buds. (3-10).

REFERENCES

[1] S.Melzer, F.Lens, J.Gennen, S.Vanneste, A.Rohde, T.Beeckman; Nature Genetics, **40**, 1489-1492 **(2008)**.
[2] F.Parcy, K.Bomblies, D.Weigel; Development, **129**, 2519-2527 **(2002)**.
[3] E.Souer, A.B.Rebocho, M.Bliek, E.Kusters, R.A.M.de Bruin, R.Koes; The Plant Cell, **20**, 2033-2048 **(2008)**.
[4] S.J.Park, K.Jung, M.C.Schatz, L.B.Lippman; Proceedings of the National Academy of Sciences, USA, **109**, 639-644 **(2012)**.
[5] S.Torti, F.Fornara, C.Vincent, A.Fernando, K.Norström, U.Göbel, D.Knoll, H.Schoof, G.Coupland; The Plant Cell, **24**, 444-462 **(2012)**.
[6] E.S.Coen, E.M.Meyerowitz; Nature, **353**, 31-37 **(1991)**.
[7] D.Weigel, E.M.Meyerowitz; Cell, **78**, 203-209 **(1994)**.
[8] A.Goldsmith, J.P.Alvarez, J.L.Bowman, Y.Eshed; The Plant Cell, **20**, 1217-1230 **(2008)**.
[9] A.Fahn; 'Plant Anatomy', Pergamon Press, Oxford, **(1985)**.
[10] M.R.Karim, A.Hirota, D.Kwiatkowska, M.Tasaka, M.Aida; The Plant Cell, **21**, 1360-1372 **(2009)**.
[11] C.Gómez-Mena, R.Sablowski; The Plant Cell, **20**, 2059-2072 **(2008)**.
[12] N.Prunet, P.Morel, A.M.Thierry, Y.Eshed, J.L.Bowman, I.Negrutiu, C.Trehin; The Plant Cell, **20**, 901-919 **(2008)**.
[13] J.K.Okamuro, B.G.W.Denboer, K.D.Jofuku; The Plant Cell, **5**, 1183-1193 **(1993)**.
[14] T.Ishida, S.Fujiwara, K.Miura, N.Stacey, M.Yoshimura, K.Schneider, S.Adachi, K. Minamisawa, M.Umeda, K.Sugimoto; The Plant Cell, **21**, 2284-2297 **(2009)**.
[15] M.Ng, M.F.Yanofsky; The Plant Cell, **13**, 739-753 **(2001)**.
[16] E.R.Álvarez-Buylla, B.A.Ambrose, E.Flores-Sandoval, M.Englund, A.Garay-Arroyo, B.García-Ponce, E.de la Torre-Bárcena, S.Espinosa-Matías, E.Martínez, A.Piñeyro-Nelson, P.Engström, E.M.Meyerowitz; The Plant Cell, **22**, 3543-3559 **(2010)**.
[17] Z.Schwarz-Sommer, P.Huijser, W.Nacken, H.Saedler, H.Sommer; Science, **250**, 931-936 **(1990)**.
[18] E.G.F.Benya, P.G.Windisch; Flora, **202**, 437-446 **(2007)**.
[19] N.H.Battey, R.F.Lyndon; The Botanical Review, **56(2)**, 162-189 **(1990)**.
[20] W.N.Stewart, G.W.Rothwell; The origin and early evolution of angiosperms, in: 'Paleobotany and the Evolution of Plants', 2nd Edition, Cambridge University Press, Cambridge (UK), 438-467, **(1993)**.
[21] C.Surridge; Nature, **432**, 161 **(2004)**.
[22] Volume T.N.Khan; 'Winged bean production in the tropics'. FAO Plant Production and Protection Paper, FAO, Rome, 38 **(1982)**.
[23] D.Lohmann, N.Stacey, H.Breuninger, Y.Jikumaru, D.Müller, A.Sicard, O.Leyser, S.Yamaguchi, M.Lenhard; The Plant Cell, **22**, 335-348 **(2010)**.
[24] Volume R.C.McLean, W.R.Ivimey-Cook; Textbook of Theoretical Botany, Longmans, Green and Co, London, **2**, **(1961)**.
[25] [DEAS] M.Gadelha de Lima; O Clima de Teresina, Fundação Universidade Federal do Piauí Pro-Reitoria de Extensão; Teresina, Piauí, Brasil, **(1987)**.
[26] E.G.F.Benya; Acta Biologica.Leopoldensia, **17**, 65-72 **(1995)**.
[27] Edition P.A.Sanchez; 'Properties and management of soils in the tropics', John Wiley and Sons, New York, **(1976)**.
[28] T.Casci; Nature Reviews Genetics, **6**, 89 **(2005)**.
[29] V.Debat, P.David; Trends in Ecology & Evolution, **16**, 555-561 **(2001)**.
[30] K.Ikeda, N.Nagasawa, Y.Nagato; Developmental Biology, **282**, 349-360 **(2005)**.
[31] S.E.Parkinson, S.M.Gross, J.B.Hollick; Developmental Biology, **308**, 462-473 **(2007)**.
[32] W.S.Klug, M.R.Cummings; Quantitative inheritance, phenotypic expression and heritability, in 'Concepts of Genetics', Merrill Columbus (Ohio), 149-162 **(1986)**.
[33] T.Denk; Feddes Repertorium, **109**, 435-463 **(1998)**.