

MERISTEM IDENTITY ON ANATOMIC SECTIONS OF REVERTED HOMEOTIC SEGREGANTS OF THE WINGED BEAN *PSOPHOCARPUS* *TETRAGONOLOBUS* (L.) DC UNDER LABORATORY CONDITIONS

Edward G.F. Benya

Key words: Homeotic gene, extra-morphologic meristem identity structure (EMIS), biformal meristematic location (BML).
Gene homeótico, estrutura extra-morfológica de identidade meristemática, locação biformal meristemática.

Abstract

Laboratory investigations on anatomic sections from reverted segregants of the winged bean *Psophocarpus tetragonolobus* (L.) DC, homozygous for a recessive homeotic gene in its activated state, revealed two forms of extra-morphologic meristem identity; rhizogenous and vegetative manifest in three steps: extra-vegetative, extra-rhizogenous, and both. This identity, in terms of number of structures at specific anatomic sites, showed significant concentrations at the ovary (i.e. carpel) or fourth floral whorl regions, plus the pre-whorl bracts regions. These results suggest that even in morphologically transformed sections of reverted segregants, anatomic and organ regions (e.g. the four floral whorls) maintain some definitive function or functions.

Endereço do Autor:

Escola Agrícola Santo Afonso Rodriguez; Socopo, C.P. 3910, 64051-971, Teresina, PI

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Resumo

IDENTIDADE MERISTEMÁTICA NAS SECÇÕES ANATÔMICAS DOS SEGREGANTES HOMEÓTICOS DO FEIJÃO-DE-ASA *PSOPHOCARPUS TETRAGONOLOBUS* (L.) DC EM LABORATÓRIO. Análises em laboratório de secções anatômicas originadas dos segregantes já revertidos do feijão-de-asa *Psophocarpus tetragonolobus* (L.) DC, homozigotos para um gene homeótico recessivo, no seu estado ativado, revelaram duas formas de identidade meristemática extra-morfológica; rizógena e vegetativa manifestadas em três classes: extra-vegetativa, extra-rizógena, e ambas. Estas identidades, em termos do número das estruturas surgindo em posições anatômicas específicas, mostraram concentrações significativas nas posições verticais florísticas dos ovários (i.e. carpelo) ou no quarto verticilo floral e nas posições pré-verticilares das brácteas. Estes resultados sugerem que, ainda em secções morfológicamente transformadas dos segregantes revertidos, as regiões anatômicas e os órgãos (e.g. os quatro verticilos florísticos) mantém alguma função ou funções definitivas.

Introduction

Homeosis is a developmental morphologic phenomenon where an anatomic region or structure (e.g. organ or organ system) changes its activity, form or regional position on a part or parts of an organism, changes that are variant from that which is morphologically normal (SCHWARZ-SOMMER et al., 1990; WEIGEL & MEYEROWITZ, 1994). Classic effects of homeosis including loss-of-function phenotypes (WEIGEL & MEYEROWITZ, 1993; 1994; PELAZ et al., 2000) and gain-of-function phenotypes (WEIGEL & MEYEROWITZ, 1994; BUSCH et al., 1999; WAGNER et al., 1999; DEVLIN & KAY, 2000) have been identified on numerous angiosperm species.

The winged bean *Psophocarpus tetragonolobus* (L.) DC is an exotic legume species to the Americas (NATIONAL ACADEMY OF SCIENCES, 1979) introduced into Brazil in 1976 (LORDELLO & de ALMEIDA, 1979). Populations of this species whose segregants are homozygous for a recessive homeotic gene, in activated form (BENYA, 1995), have shown effects of homeosis both at the levels of loss-of-function phenotypes (e.g. inactivation) and gain-of-function phenotypes (e.g. meristem identity) (BENYA, 1999a).

Main effects of inactivation occur in floral structures (i.e. flowers and flower buds) and in at least one related organ (i.e. fertilized ovary or pod). Flowers and flower buds of affected segregants revert from the sexual reproductive function to an non-reproductive, photosynthetic function with no further activity (BENYA, 1999b). With the beginning of reversion, fertilized ovaries (i.e. pods) on affected segregants, cease elongation and development becoming attenuated organs (BENYA, 1999a). Principal meristem identity effects are manifest as viviparous

(i.e. vegetative) activity at stem nodes of affected segregants, but also as extra-vegetative shoot apices and/or extra-rhizogenous structures that can develop at sites of organ systems (e.g. reverted flowers), organs (e.g. ovaries) and non-organ structures (e.g. stems) of affected segregants (BENYA, 1999a; 2000).

Previous laboratory experiments (BENYA, 2000) using anatomic sections from reverted segregants have qualitatively identified specific anatomic regions, including two of the four floral whorls (i.e. calyces [first whorl] and carpels or ovaries [fourth whorl]) plus the pre-floral (SCHWARZ-SOMMER, et al., 1990; KRAMER & IRISH, 1999; STERN, 1988) bracts regions, that showed significant levels of extra-morphologic (i.e. extra-vegetative and/or extra-rhizogenous) activity in terms of site numbers. Goal of this research was to quantitatively measure meristem identity, active or inactive, in terms of concentrations (i.e. numbers) of extra-vegetative and/or extra-rhizogenous meristem identity structures occurring at sites of specific anatomic regions of reverted flowers, flower buds, fusions and reverted stems. "Meristem" in these results refers exclusively to rhizogenous or shoot identity. The term "extra-morphologic meristem identity structure" (EMIS) defines meristematically active structures or those originating from such previous activity.

Material and Methods

Researchers analyzed 89 reverted anatomic sections from field grown segregants of this species. In laboratory, sections were cultured in plain and deionized water in 28 treatments of two to five reps per treatment as previously described (BENYA, 1999b). These sections represented three basic anatomic and/or organ categories: four fused floral and non-floral parts (i.e. "fusions"), six reverted stems, and 79 reverted flowers and flower buds. They had previously been analyzed qualitatively for presence of any form of hyper-anabolic, extra-morphologic (i.e. extra-rhizogenous and/or extra-vegetative) activity site at five major anatomic regions; four specific regions (i.e. calyx, floral stem, bracts, ovary) and one non-specific region (i.e. all other) (BENYA, 2000). White extra-morphologic structures were assumed to be meristematically rhizogenous. Virescent (i.e. chlorophyllized) structures were assumed to be meristematically vegetative. All 89 sections showed one or both forms of these meristem identity structures in at least one of these five regions. A total of 145 active sites were identified (BENYA, 2000). These 145 sites on the 89 anatomic sections were the basis of these quantitative analyses. ANOVA, X^2 and t-test statistical analysis served to identify and verify significant differences.

Results and Discussion

A total of 248 extra-morphologic meristem identity structures (i.e. EMIS, TABLE I), occurred on the 145 active sites. All structures were assumed to be organs or organ systems (i.e. leaves, roots and/or buds) even if no further activity followed. FIGURES 1 and 2 show rhizogenous and vegetative meristem identity structures respectively. Their mean distribution per active section was 2.78 ranging from one to nine. Frequency of occurrence (127 extra-rhizogenous, or 51.21 % of the total and 121 extra-vegetative or 48.79 % of the total) was about the 50:50 random frequency that would be expected ($X^2 = 0.1008$, NS). All extra-rhizogenous structures were meristematically active, showing some measurable form and period of tissue elongation. Extra-vegetative structures were either meristematically active or inactive. Their sudden appearance as virescent structures defined their meristematic identity as vegetative. However that identity might or might not represent further growth (i.e. indeterminate vs determinate growth) (WILSON & LOOMIS, 1967) in terms of shoot activity.

Distribution of these 248 EMIS on the 145 active sites occurred in significant concentrations at specific anatomic regions. Structural occurrence per site ranged between one and eight with an overall mean of 1.71 (s.d. = 1.34). Four sites on four distinct floral sections showed significantly higher presence of structures (i.e. six, seven, seven and eight respectively, ANOVA, $t = 7.9$, $P < 0.01$) and these were always vegetative, a phenomenon quite common when a stem (at an extra-vegetative site on a reverted flower) loses bud dormancy and all or most vegetative buds become active.

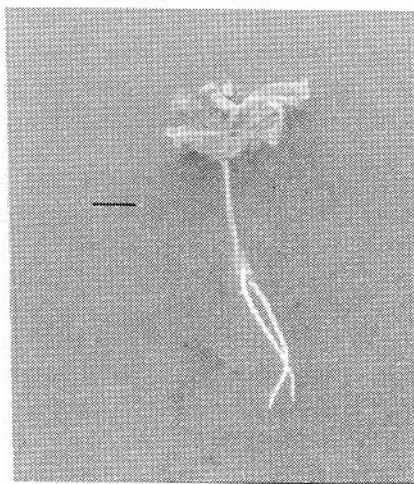


FIGURE 1 – Rhizogenous meristem identity structures (always active) occurred at all five major anatomic regions, but were significantly concentrated at sites of the bract regions. Scale bar: 1 cm

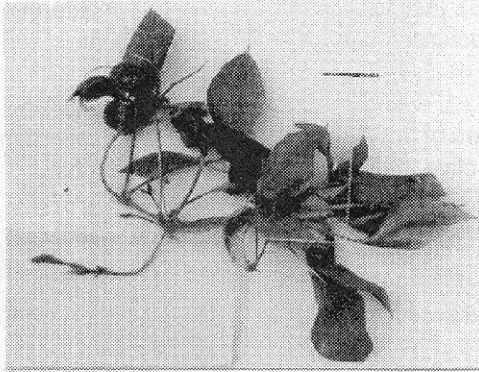


FIGURE 2 – Vegetative (shoot) meristem identity structures (active or inactive) occurred at three of the five major anatomic regions, but were significantly concentrate at sites of the ovary regions. Scale bar: 1 cm

The number of total structures was significantly higher (TABLE I) at sites of the bract regions (61 rhizogenous and vegetative structures at 37 sites of 36 specimens, $t = 3.004$, $P < 0.01$) and of the ovary regions (77 rhizogenous and vegetative structures at 38 sites of 35 specimens, $t = 3.243$, $P < 0.01$) in the 89 sections; the pre-floral region and fourth floral whorl respectively. Number of structures showed no significant variation from the overall regional distribution at the calyx, the first floral whorl (35 structures, all rhizogenous, at 27 sites of 27 specimens, $t = 0.731$, NS), the floral stem (25 structures, all rhizogenous, at 18 sites of 18 specimens, $t = 0.910$, NS) and the non-specific “all other” anatomic regions (50 structures both rhizogenous and vegetative at 25 sites of 23 specimens, $t = 0.1399$, NS).

Within the subgroup of extra-rhizogenous structures (TABLE II), total occurrence was significantly higher at the bract regions (60 structures at 36 sites of 36 specimens, $t = 3.464$, $P < 0.01$). It was significantly low at the ovary regions (three structures at three sites of three specimens, $t = 12.884$, $P < 0.01$) and at the “all other” regions (four structures at three sites of three specimens, $t = 9.419$, $P < 0.01$). Extra-rhizogeny at the calyx ($t = 1.601$, NS) and floral stem regions ($t = 0.007$, NS) remained non-significantly different from the overall regional distribution for this subgroup, just as it had been when considering all extra-morphologic structures as a group.

Within the subgroup of extra-vegetative structures (TABLE III), total occurrence was significantly higher at the ovary regions (74 structures at 35 sites of 35 specimens, $t = 2.470$, $P < 0.05$). It was significantly lower at the bracts regions (one structure at one site of one specimen, $t = 38.383$, $P < 0.01$) and totally absent at the calyx and floral stem anatomic regions. It remained statistically non-significantly different at the “all other” regions (46 structures at 22 sites of 22 speci-

mens, $t = 0.306$, NS), just as it had been when considering the group of all extra-morphologic structures.

TABLE I – Distribution of the 248 extra-morphologic meristem identity structures (EMIS) at the 145 active sites on the 89 active sections.

Anatomic region or subregion	Number of structures (A)	Type	t-value ¹	P	Number of sites (B)	Mean per site (A/B)	t-value ²	P
Calyx	35	rhizogenous	0.731	NS	27	1.2963	3.971	<0.01
Floral stem								
(shaft)	21	rhizogenous	1.619	NS	14	1.5000	1.036	NS
(base)	4	rhizogenous	13.475	< 0.01	4	1.0000	—	—
(total)	25	rhizogenous	0.910	NS	18	1.3889	1.954	NS
Bracts	60	rhizogenous	2.928	< 0.01	36	1.6667	0.233	NS
	1	vegetative	29.453	< 0.01	1	1.0000	—	—
(total)	61	both	3.004	< 0.01	37	1.6486	0.338	NS
Ovary	74	vegetative	3.107	< 0.01	35	2.1143	1.370	NS
	3	rhizogenous	16.047	< 0.01	3	1.0000	—	—
(total)	77	both	3.243	< 0.01	38	2.0263	1.086	NS
All other	46	vegetative	1.083	NS	22	2.0909	0.927	NS
	4	rhizogenous	11.810	< 0.01	3	1.3333	1.131	NS
(total)	50	both	1.399	NS	25	2.0000	0.696	NS
totals =	248				145			

¹ $\mu = 0.3669$

² $\mu = 1.7103$

TABLE II – Distribution of the 127 extra-rhizogenous structures.

Anatomic region or subregion	Number of structures (A)	t-value ¹	P	Number of sites (B)	Mean per site (A/B)	t-value ²	P
Calyx	35	1.601	NS	27	1.2963	1.568	NS
Floral stem							
(shaft)	21	0.692	NS	14	1.5000	0.198	NS
(base)	4	10.718	< 0.01	4	1.0000	—	---
(total)	25	0.007	NS	18	1.3889	0.431	NS
Bracts	60	3.464	< 0.01	36	1.6667	1.107	NS
Ovary	3	12.884	< 0.01	3	1.0000	—	—
All other	4	9.419	< 0.01	3	1.3333	0.379	NS
total =	127			87			

¹ $\mu = 0.3017$

² $\mu = 1.4598$

TABLE III – Distribution of the 121 extra-vegetative structures.

Anatomic region or subregion	Number of structures (A)	t-value ¹	P	Number of sites (B)	Mean per site (A/B)	t-value ²	P
Bracts	1	38.383	< 0.01	1	1.0000	—	—
Ovary	74	2.470	< 0.05	35	2.1143	0.095	NS
Convergence							
ovary-calyx	5	13.204	< 0.01	4	1.2500	3.345	< 0.05
All other	46	0.306	NS	22	2.0909	0.011	NS
totals =	121			58			

¹ $\mu = 0.4745$ ² $\mu = 2.0862$

An anatomic juncture, usually a point on normal flowers, the bract-calyx juxtaposition, underwent rapid elongation on 68 of 83 reverted flowers and fusions (81.9 %) which constituted the major portion of the 89 sections. This occurred soon after reversion (field stage) while still maintaining the convergence and positional unity of affected sections. It however changed the phyllotaxis (i.e. spatial arrangement of organs on the plant), ranging between one and 70 mm (mean = 12.24 mm), and could significantly distance the bracts from the calyx.

Overall mean values per active site for occurrence of all meristem identity structures at the five major anatomic regions ran from 1.2963 at the calyx to 2.0263 at the ovary, a range of 0.7300 (TABLE I). These values were quite consistent. Any subset of any of these regions might present a mean below or above this range (e.g. 1.000 rhizogenous structures per site at the ovary region, or 2.0909 vegetative structures per site at the "all other" region) but only the calyx as one of the five major anatomic regions presented a significantly low overall mean for an entire anatomic region (1.2963 structures/site, $t = 3.971$, $P < 0.01$). This low overall mean value may have been due to the change in bract-calyx phyllotaxis of 68 of the 89 sections. That in turn may have influenced transport, deposition and even effect of any possible morphogen responsible for extra-morphologic activity.

Extra-rhizogenous structures as a subgroup occurred at all five major anatomic regions. They showed mean values for occurrence per site running from 1.0000 at the ovary (three structures on three sites) to 1.6667 at the bracts (60 structures on 36 sites) (TABLE II), a range of 0.6667. Extra-vegetative structures as a subgroup occurred at three of the five major anatomic regions (TABLE III). They presented mean values for distribution per site running from 1.0000 at the bracts (one structure on one site) to 2.1143 at the ovary (74 structures on 35 sites), a range of 1.1143.

As had previously been detected in qualitative studies of active site distribution (BENYA, 2000), these analyses of EMIS distribution also revealed a gene-

ral quantitative gradient readily apparent on the 89 sections. Extra-vegetative structures significantly dominated at active sites of the ovary itself, the fifth or last organ region (i.e. fourth floral whorl) on most angiosperm reproductive systems (i.e. 74 of 77 structures, or 96.10 %). Extra-rhizogenous structures significantly dominated at sites from the calyx and regions below it (i.e. 120 of 121 structures or 99.17 %) ($\chi^2 = 181.5$, $P < 0.01$). This included the bracts (i.e. 60 rhizogenous structures), the first organ region (i.e. pre-floral) in most angiosperm reproductive systems.

The consistency of mean values for EMIS suggests the presence and maintenance of a governing mechanism or mechanisms responsible for organ establishment and development even after an organism or part of an organism has reverted. This governance continued within the group of extra-rhizogenous sites when analyzed separately (TABLE II). Mean occurrence of extra-rhizogenous structures at specific sites for four of the five major anatomic regions (i.e. calyx, floral stem, bracts, all other) showed no significant variation from the overall mean of 1.4598 structures per site for the subgroup. Only the mean at the ovary regions may have been significantly lower, but specific statistical calculation was impossible due to lack of variance. Any governance mechanism seemed less apparent in the mean values for extra-vegetative structures at specific sites (TABLE III). A significantly low statistical mean value was detected at the ovary-calyx convergence (1.2500, $t = 3.345$ $P < 0.05$), a subset of the ovary. The mean for the bracts regions may have been significantly low but lack of variance prevented statistical test for significance. Calyx regions presented no extra-vegetative meristematic identity of any kind.

The bracts and bracts regions may be the first organs to receive any hormone, hormones, morphogen or morphogens (COEN et al., 1990; SCHWARZ-SOMMER et al., 1990) that are synthesized in another part or parts of the plant and transported to the bud or flower. The distancing of these organs from the four floral whorls when the phyllotaxis changed had positive effects on extra-morphologic and meristematic identity activity at the bracts regions.

Six of the 89 anatomic sections presented six locations (one each) containing both extra-rhizogenous and vegetative meristem identity structures, for a total of 12 active (or previously active) sites (BENYA, 2000). Statistical analysis of the two forms of extra-morphologic activity called for treatment of each location as two distinct sites. Because these two forms of activity were or had been present, these six locations are termed "biformal morphologic locations" (BML). Their extra-rhizogenous structures were always meristematically active. However their extra-vegetative structures could be either inactive or meristematically active. Three of these locations were at ovary regions of three sections, two were at "all other" regions of two sections and one was at the bracts region of one section.

The three ovary locations contained one rhizogenous meristem identity structure each and two, one and three vegetative meristem identity structures respectively. Two of the vegetative structures (at least one on each of two of the-

se three floral sections) were apical, shoot meristematically active accompanied by one root meristem at the same ovary region.

The one bract location contained one extra-rhizogenous and one extra-vegetative structure. That extra-vegetative structure showed no apical meristematic shoot activity.

The first of the "all other" locations contained one extra-rhizogenous structure and six extra-vegetative, meristem identity structures, all active. The second of these locations contained two extra-rhizogenous and three extra-vegetative structures all active.

In all six cases extra-vegetative activity preceeded extra-rhizogenous. For some specific period (of days) in the metabolic persistence (BENYA, 1999b) of each anatomic section, both forms of extra-morphologic activity operated coincidentally on four of these six BML sections. In previous research (BENYA, 2000) where both extra-vegetative and extra-rhizogenous activities occurred concurrently on the same anatomic section but at different sites, the sections involved all failed to develop into photosynthetically self-sustaining autotrophic organisms. These six anatomic sections containing one BML each also failed to develop into self-sustaining autotrophs.

Significant concentrations of meristem identity structures at sites of the pre-whorl bract regions and sites of the fourth floral whorl ovary or carpel regions coincided with occurrence of two forms (not merely one) of meristem identity (i.e. vegetative and rhizogenous) at those two regions. They were the only two specific anatomic regions to show both forms of meristem identity although in vastly unequal proportions (i.e. 60 rhizogenous: 1 vegetative structure at the bracts [98.36 % of the total of 61] and 74 vegetative: 3 rhizogenous structures at the ovary [96.10 % of the total of 77], TABLE I). Besides being vastly disproportionate within each of these two regions, their distributions between the two regions were very obviously diametrically dissimilar.

Conclusion

Meristem identity in flowering plants can be manifest in clear and distinct forms: vegetative (BUSCH et al., 1999; SAMACH et al., 2000; SCHWARZ-SOMMER et al., 1990), inflorescence (BLÁZQUEZ & WEIGEL, 2000; PRUITT et al., 1993; WAGNER et al., 1999; WEIGEL & MEYEROWITZ, 1994) and floral (DEVLIN & KAY, 2000; KRAMER & IRISH, 1999) but also rhizogenous (STERN, 1988; WILSON & LOOMIS, 1967), the expression of which is regionally specific on an organism (WEIGEL & MEYEROWITZ, 1993; 1994). In the case of reverted floral, fusion and non-floral anatomic sections from the winged bean, the rhizogenous meristematic identity structures were always apically active. However the vegetative counterparts were only occasionally apically active.

ve. The coincidental presence of both forms of this activity on the same anatomic section or even at the same anatomic location of an anatomic section represented two activities that were never observed to be coordinated but always remained distinct and independent. This activity was significantly concentrated at two of the five organ regions of the reproductive system, the first region (i.e. pre-whorl bracts) and the last region (i.e. fourth floral whorl ovary or carpel region) but in significantly unequal and regionally dissimilar proportions. These proportions suggest that even in reverted (e.g. morphologically transformed) organisms, the four floral whorls plus the pre-whorl bract regions (i.e. five specific organ regions) maintain some definitive function or functions. The lack of coordinated activity suggests that one meristem identity gene may be operating at two different levels of morphogenic function, a function determined at least partially by the organs at which the morphogen is employed.

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