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Plasmon Divergence in Peanuts *(Arachis hypogaea)*: A Third Plasmon and Locus Affecting Growth Habit

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Summary. In a series of reciprocal crosses between peanut (*Arachis hypogaea* L.) cultivars from different regions and known testers, the cultivar HG1 from India was shown to have a third plasmon type, designated [G]. HG1 also has a third locus, Hb_3, which interacts with the plasmons and the loci described earlier. In the [G] plasmon, Hb_1 and Hb_3 are additive: plants having three or four dominant alleles have a trailing habit while the other nuclear genotypes produce in [G] erect plants. In the [V4] plasmon, Hb_1 and Hb_3 are complementary, [V4] Hb_1 –, Hb_3 – plants being trailing, the others erect. In the [G] plasmon, Hb_1 and Hb_3 are complementary, while in the [0] plasmon they are additive.

Introduction

Much insight on cytoplasmic inheritance has been derived in recent years from studies on the transmission of genetic information contained in the plastids and the mitochondria in *Chlamydomonas*, yeast and other organisms (Gilham 1974; Preer 1971; Sager 1972). At the same time, the role of cytoplasmic inheritance in higher plants also received more attention, especially male sterility which is economically important (Beckett 1971; Edwardson 1970; Harvey et al. 1972; Sager 1972; Smith 1968). It is now realized that the plasmon can also affect disease reaction, e.g. in corn (Harvey et al. 1972) and wheat (Washington and Mann 1974), affect various other traits in higher plants (Harvey et al. 1972; Oehlkers 1964; Sager 1972) and has a role in the evolution of higher plants (Grun 1973; Hagemann 1965; Harvey et al. 1972; Michaelis 1954; Mann 1973; Sager 1972; Stubbe 1964) and animals (Sager 1972). Thus, the study of natural plasmon variability is important, both to our understanding of the role of the plasmon in evolution and in differentiation, and for the reduction of genetic vulnerability in important crops such as corn and sorghum. The genic-cytoplasmic interactions affecting growth habit in peanuts (Ashri 1964; Ashri 1968) can serve as an excellent system for the study of cytoplasmic inheritance and for assessing natural plasmon variability in this trait, which is quite different from male sterility. The two growth-habit types known in peanuts are bunch (= erect) and runner (= trailing). Runner and bunch plants are normal, fully self-fertile and productive; very successful commercial cultivars of both types are known (Hammons 1973; Norden 1973). Inheritance studies on growth habit have been conducted since the 1920's and were reviewed recently by Hammons (1973). Most authors reported only nuclear genes (Coffelt 1974; Hammons 1973). Cytoplasmic components were first reported by Husted (see Hammons 1973). Ashri (1964, 1968) showed that growth habit was controlled by genic-cytoplasmic interactions. Two plasmons were found, [V4] in the V4 cultivar (see below) and [0] in a series of other varieties, and two nuclear genes, Hb_1 and Hb_2 (Ashri 1964, 1968). It was concluded (Ashri 1968) that in the [V4] plasmon Hb_1 and Hb_2 were complementary, while in the [0] plasmon they were additive and possibly also complementary. The F_2 ratios obtained were 9 runner : 7 bunch in the [V4] plasmon, while in the reciprocal, in the [0] plasmon, they were 5 runner : 11 bunch (Ashri 1968). The 5/16 runner are those that have four and three dominant alleles in the two possible combinations.

Cytoplasmic factors were implicated in the genetic control of pod constriction (Coffelt and Hammons 1974) and maternal effects were shown for some traits in peanuts (Parker et al. 1970).

Halevy, Ashri and Ben-Tal (1969) found that runner and bunch plants, including tests with reciprocal F_1 hybrids, had similar levels of endogenous gibberellins but differed in the levels of two gibberellin antagonists, one being found in the runner plants only. Subsequently Ziv et al. (1973) reported that the runner habit is induced by blue+far-red light of a cer-

tain minimum intensity. Hence, the genic-cytoplasmic interactions which determine growth habit must act by controlling the biosynthetic pathways in which the phytohormones and their inhibitors are produced. These findings indicate that a complex mode of inheritance of growth habit in peanuts should be expected, involving several loci interacting with each other and with the cytoplasms. Evidence for a third plasmon and a third nuclear locus which affect growth habit is presented here.

Materials and Methods

The three cultivars mainly used in this study were:
V4 = Virginia Beit Dagan No.4. It is a Virginia type (Gregory et al. 1973) bunch cultivar developed in Israel by E. Goldin. Its origin, whether through natural hybridization or contamination, could not be ascertained, but it is known to have the [V4] plasmon and Hb_1Hb_1 hb_2hb_2 (Ashri 1968).

VSM = Virginia Sihit Meshubahat. This bunch Virginia type cultivar was selected by E. Goldin from a U.S. introduction. It has the [0] plasmon and hb_1hb_1 Hb_2Hb_2 (Ashri 1968).

HG1. A bunch cultivar requested from India because in a cross with another bunch cultivar, it (as female) gave runner F_1 hybrids and the F_2 segregated for trailing vs. bunch (Patel et al. 1936). HG1 originated from a natural cross in a spreading variety *(Ibid.)*.

The other cultivars which were used in this study were obtained either from the Israel colletion (Goldin and Har-Tzook 1966) or from the USDA germ plasm collection (Langford and Sowell 1974).

Hybridizations were made in the greenhouse. The F_1, F_2 and F_3 hybrids and the parents were grown in the field at the optimal time (late April or early May sowing) and were sprinkler-irrigated regularly. The F_1 hybrids were spaced 66 × 60 cm or 66 × 120 cm and the F_2 and F_3 plants 60 × 66 cm or 40 × 66 cm, depending on the season.

The plants were classified for growth habit at the age of 6-8 weeks. No difficulties were encountered in classification at this stage, except for a few plants (usually late to germinate) which had to be scored later. Plants that were typically runner, with trailing side branches and usually a short main axis, were classified as runner. All other plants, with appressed or open side branches, were classified as bunch.

Results and Discussion

HG1 was crossed reciprocally to V4 and to 28 other bunch accessions; in addition it was the female parent in crosses with VSM and 17 other bunch accessions and was the male parent in crosses with 21 other lines (Ashri 1975). The growth habits of the reciprocal and some unidirectional hybrids with HG1 are shown in Table 1, together with the phenotypes of hybrids of the same accessions with V4 ([V4] plasmon) and VSM ([0] plasmon).

There were reciprocal differences between the hybrids of nearly all the accessions and HG1 (Table 1). In most crosses with VSM the same accessions produced no reciprocal differences, while in those with V4 there were such differences. The phenotypes of the hybrids between the accessions and HG1 were nearly always the same as in the hybrids of these accessions and V4 (Table 1), but there were a few important differences in the breeding behavior of HG1 and V4. Most significantly, there were differences between the reciprocal hybrids of HG1 and V4, indicating that the plasmons of HG1 and V4 are different. This conclusion is strengthened by the differences between the hybrids of V4 and HG1 as females and Tarapoto (Short), PI 259, 671 and PI 288, 215 as males (Table 1).

The F_2 segregations are summarized in Table 2. They show that HG1 and V4 differ by two genes: when V4 was female the F_2 segregated 9 runners: 7 bunch and when HG1 was female the F_2 segregated 5 runner: 11 bunch as expected in crosses with V4 (Ashri 1968). These ratios were confirmed in the F_3. Thus, the previously described (Ashri 1968) complementary or additive modes of action were obtained, depending on the direction of the cross.

Only HG1 × VSM hybrids were obtained, but the behavior of HG1 in crosses with other [0] plasmon cultivars can be studied. The HG1 × VSM F_2 segregation gave a good fit with a 9 runner: 7 bunch ratio, indicating that two complementary genes were involved. This was confirmed in the F_3. Thus, HG1 and VSM differ by two loci controlling growth habit. These findings are confirmed by the crosses of HG1 with the other bunch cultivars which were crossed reciprocally with VSM (Tables 1 and 2). All these accessions gave only bunch F_1's in reciprocal crosses with VSM, yet when crossed to HG1 they gave (with one exception) reciprocal differences: the F_1 hybrids were runner when HG1 was female and bunch when it was male (other exceptions (Table 1), in unidirectional crosses, require further checking). It is concluded that HG1 has a plasmon which differs from the [0] plasmon. The F_2 data in crosses with VSM and the additional [0] type cultivars (Table 2) also show that HG1 differs from them in two genes.

In view of these findings HG1 must have a third plasmon, to be designated [G], and another nuclear

Table 1. Growth habit phenotypes (B = bunch, R = runner) of reciprocal F_1 hybrids between bunch accessions and HG1, with phenotypes of the F_1 hybrids of the same accessions and V4 and VSM (F = female, M = male)

Accession crossed		Testers					
		V4		VSM		HG1	
Name or No.	Origin	F	M	F	M	F	M
V4	Israel	-	-	B	R	B	R[4]
VSM	Israel	R	B	-	-	R[2]	-
HG1	India	R[4]	B	-	R[2]	-	-
Ga. 119-20	USA	R	B	B	B	R	B
Tarapoto (Short)	Venezuela	B	-	B	-	R	-
Improved Small Japan	Japan	R	B	-	-	R	B
Large White Spanish	Australia	R	-	B	B	R	B
TMV-2	India	R	B	B	B	R	B
Muitunde 7	Tanzania	R	B	B	-	R	B
C-501	India	R	-	B	B	R	B
P.I. 261,994	Paraguay	R	B	B	-	R	B
P.I. 262,075	Brazil	R	B	B	B	R	B
P.I. 262,123	Peru	R	B	B	B	R	B
P.I. 268,494	Rhodesia	R	B	-	B	R	B
P.I. 290,606	India	R	B	R[3]	-	R	B
P.I. 290,611	India	R	B	B	B	R	B
P.I. 290,680	Japan	R	B	-	B	R	B
P.I. 298,863	Gambia	-	B	-	B	R	B
P.I. 298,866	Volta	R	B	B	B	R	B
P.I. 300,242	Nigeria	R	B	-	-	R	B
P.I. 324,504	Taiwan	B	B	B	B	B	B
P.I. 331,333	Argentina	R	-	B	B	R	B
P.I. 239,038	Senegal	-	B	B	B	R	B
P.I. 240,568	India	R	B	B	B	R	B
P.I. 275,500	Korea	B	B	B	B	B	-
P.I. 269,685	Tanzania	-	-	-	B	R	B
P.I. 311,003	Guiana	R	-	B	B	R	B
P.I. 259,583	Jamaica	R	B	B	-	R	B
P.I. 259,641	Cuba	R	-	R	-	R	B
P.I. 259,659	Cuba	R	-	-	B	R	B
P.I. 259,671	Cuba	R	B	B	B	B	-
P.I. 259,675	Cuba	-	B	B	B	R	B
P.I. 280,688	Mexico	R	B	B	-	R	B
P.I. 288,215	Jamaica	R	B	R	B[4]	B[5]	-

[1] Five plants runner, one additional plant (from a separate pod) bunch.
[2] Two plants runner, an additional plant (from a separate pod) bunch.
[3] Classification difficult, closest phenotype at the end of the season is listed.
[4] Two plants bunch, two additional plants (from a separate pod) runner.
[5] Three plants bunch, an additional plant runner.

gene, to be called Hb_5 (Hb_3 and Hb_4 were assigned to other materials by Coffelt (1974)). It is proposed that the genotypes of the test cultivars are:

V4 = [V4] Hb_1Hb_1, hb_2hb_2, hb_5hb_5

VSM = [0] hb_1hb_1, Hb_2Hb_2, hb_5hb_5

HG1 = [G] hb_1hb_1, hb_2hb_2, Hb_5Hb_5 .

According to the F_1 and F_2 data (Tables 1, 2) Hb_5 interacts with Hb_1 and Hb_2 in much the same fashion as the latter two interact with each other in the [V4] and [0] plasmons. In the [G] plasmon Hb_2 and Hb_5 are complementary, while in the [0] plasmon they are usually additive: three or four dominant alleles, in any combination, are needed to produce the runner phenotype. In the [V4] plasmon Hb_1 and Hb_5 are complementary and in the [G] plasmon they are additive - plants having three or four dominant alleles are runner, while the others are bunch. In three exceptions (240, 568 × HG1, C-501 × HG1 and 268,494 × HG1) the F_2 segregations gave a good

Table 2. F_1 phenotypes and F_2 segregations in reciprocal crosses of HG1 with bunch accessions where reciprocals were obtained also with V4 and/or VSM, and χ^2 tests

Cross*	F_1 hybrids		No. F_2 plants			Ratio	P
	No.	Habit	Runner	Bunch	Total		(1 df)
Reciprocals obtained with both V4 and VSM:							
HG1 × V4	4	B	36	65	101	5:11	.50-.30
Recip.[1]	5	R	52	40	92	9: 7	.98-.95
HG1 × VSM[2]	2	R	81	67	148	9: 7	.80-.70
HG1 × 262,075	3	R	87	74	161	9: 7	.70-.50
Recip.	4	B	64	107	171	5:11	.10-.05
HG1 × 262,123	2	R	94	67	161	9: 7	.70-.50
Recip.	3	B	48	100	148	5:11	.80-.70
HG1 × 290,611	2	R	89	86	175	9: 7	.20-.10
Recip.	2	B	37	66	103	5:11	.50-.30
HG1 × 298,866	5	R	86	73	159	9: 7	.70-.50
Recip.	6	B	57	106	163	5:11	.50-.30
HG1 × 324,504	4	B		All Bunch		-	-
Recip.	2	B		All Bunch		-	-
HG1 × 240,568	1	R	44	92	136	?	-
Recip.	2	B	79	110	189	5:11	.01-.001
						1: 9	.50-.30
Reciprocals obtained with VSM:							
HG1 × C-501	2	R	86	72	158	9: 7	.70-.50
Recip.	1	B	51	67	118	5:11	.01-.001
HG1 × 331,333	1	R	88	78	166	9: 7	.50-.30
Recip.	3	B	57	113	170	5:11	.70-.50
HG1 × 239,038[3]	6	R	69	65	134	9: 7	.30-.20
HG1 × 311,003	4	R	100	77	177	9: 7	.98-.95
Recip.	4	B	46	102	148	5:11	.98-.95
HG1 × 259,675[4]	3	R	85	87	172	9: 7	.10-.05
Recip.	3	B	47	104	151	5:11	.98-.95
Reciprocals obtained with V4:							
HG1 × 268,494	3	R	46	40	86	9: 7	.70-.50
Recip.	2	B	79	85	164	7: 9	.30-.20
HG1 × 290,606	1	R	94	76	170	9: 7	.90-.80
Recip.	6	B	48	112	160	5:11	.80-.70
HG1 × 290,680	2	R	86	74	160	9: 7	.70-.50
Recip.	3	B	43	94	137	5:11	.98-.95
HG1 × 259,583	2	R	82	78	160	9: 7	.30-.20
Recip.	6	B	48	78	126	5:11	.10-.05
HG1 × 280,688	5	R	94	76	160	9: 7	.90-.80
Recip.	1	B	27	46	73	5:11	.50-.30

* Numbers are USDA P.I. Nos.
[1] In addition to the 5 runner hybrids, one F_1 plant (from a separate pod) was bunch.
[2] In addition to the 2 runner hybrids, one F_1 plant (from a separate pod) was bunch.
[3] F_2 data on reciprocal not available at this time.
[4] F_2 classification was difficult.

fit with 7 runners : 9 bunch. Such a segregation could imply some variation in potency of the Hb_2 or Hb_5 alleles in different [0] plasmons, i.e., possible further plasmon variations. Or, it could imply the presence of alleles of Hb_2 with differing potency, i.e., further allelic variation. It could also be that there is further variability in the interactions of Hb_5 with the plasmon and/or Hb_2. It is interesting that C-501 and 240,568 are from India (where HG1 originated).

Alternative genetic mechanisms and genotypes for HG1 have also been explored. For example, a hypothesis that HG1 has a third plasmon [G] but instead of a third locus it has different alleles in the Hb_1 and Hb_2 loci, i.e., that it is [G] $hb_1'hb_1'$, $hb_2'hb_2'$, was tested. However, it was not corroborated by the data.

On the other hand, the 3 loci mechanism which gave a good fit to most of the F_2 segregations in the crosses of bunch accessions with HG1, met with some

difficulties in studies of the crosses of HG1 with runner cultivars. These will be studied further.

It is significant that in a sample of less than 50 peanut cultivars at least three different plasmon types were found. This may be compared with eight cytoplasmic male sterility types known in tobacco (Smith 1968) and only three distinctly different male sterility plasmon types recognized in corn (Beckett 1971), despite large scale investigations. Evidently the plasmon component in the peanut growth habit system (whose identity is still unknown) is mutable. The plasmon variability reported here demonstrates the hereditary contribution of the plasmon components, that they can be modified through mutations and that variability for them may exist in the germ plasm resources of the species.

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