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SEED MORPHOLOGY AND EARLY DEVELOPMENT OF THE GROUNDNUT  
(*ARACHIS HYPOGAEA* L.)

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# SEED MORPHOLOGY AND EARLY DEVELOPMENT OF THE GROUNDNUT (*ARACHIS HYPOGAEA* L.)\*

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## SUMMARY

The morphogenesis of groundnut plants from an age of 0 to 21 days is described. The opinion that flower primordia are present in groundnut seeds is not confirmed. Further observations prove that the early development of the groundnut is less fixed than former conceptions about the structure of the seed suggest.

## 1. INTRODUCTION

The embryo in the mature seed of the groundnut is unusually advanced in morphological development. This feature brought GREGORY, SMITH & YARBROUGH (1951) to the more or less animalculistic statement: "All of the leaves and above-ground parts which the seedling will have for the first 2 to 3 weeks of growth are already present in the dormant seed. The epicotyl consists of three buds, one terminal and two cotyledonary laterals. In the terminal bud there are four foliage leaves and in the cotyledonary laterals one or two leaves. Thus the dormant embryo has from six to eight differentiated leaves, all of them ready to expand and go to work immediately upon germination".

BALLY (1962) wrote about the vegetative development of the embryo in the seed: "Zwischen den Keimblättern sind die Anlagen des Stengels, der Hypokotyle und der Hauptwurzel eingebettet. An der Stengelanlage lassen sich schon deutlich neun oder mehr Blattanlagen wahrnehmen. Bei jedem Blatt kann man den Blattstiel, die Blattspindel und vier Fiederblättchen unterscheiden". That means; nine or more embryonic leaves, all of them with a petiole, a rachis, and four leaflets are present in the seed.

MAEDA (1972) provided more modest information based on an investigation of the morphological differentiation of leaves on the main axis of embryos of six groundnut cultivars. He found five well developed primordia and one less developed in big-seeded cultivars, and four well developed and one to two less developed primordial leaves in small-seeded.

The generative development of the embryo in the seed is also discussed in the literature. PRÉVOT (1949, 1950) gave a start to speculations about an early flower development. VAN ROSSEM (1952) and VAN ROSSEM & BOLHUIS (1954) presented morphological evidence from which FORTANIER (1957) concluded that the presence of flower primordia in the seed had actually been observed.

\* Dedicated to Professor Karstens on the occasion of his retirement.

\*\* Most of the work on which this article is based, was curried out at the Centre for Agricultural Research in Surinam (CELOS), Paramaribo, Surinam.

WELLENSIEK (1957, 1958, 1962 and 1967), impressed by this "highly exceptional" phenomenon, gave the world-wide diffusion to this observation. Thus SCHWABE (1971) could write: "The peanut or groundnut (*Arachis hypogaea*) actually carries flower initials in the seed even before their germination".

However, preliminary observations by the author in 1965 did not reveal the presence of flower primordia in the seed of the groundnut. In order to trace the first flower primordia, further investigations were made with young plantlets grown under controlled environmental conditions in Wageningen and under natural conditions in Surinam, South America (STARITSKY 1971).

## 2. MATERIAL AND METHODS

In the experiments two cultivars of *Arachis hypogaea* L. were used: 'Schwarz 21' and 'Matjan'. 'Schwarz 21', an Indonesian selection, has an upright carriage (bunch) and belongs to the Spanish type (GREGORY, SMITH & YARBROUGH 1951). 'Matjan' is very closely related to 'Schwarz 21' and is widely cultivated in Surinam.

In Wageningen the experiments were carried out with 'Schwarz 21'. Selected seeds were sown in culture pots, with the root end oriented downward at a sowing depth of 3 cm. Plantlets were carefully grown in a dark germinating cabinet and in a plant growing chamber. The temperature in the dark cabinet was 28°C; in the growing chamber a light period (Philips 40 W TLF 55 fluorescent tubes) of 12 hours at a temperature of 28°C alternated with a dark period of 12 hours at a temperature of 23°C.

Every 24 hours for 12 days 4 to 5 plants of each treatment were collected. One intact plant was preserved in alcohol 70% for macromorphological observations. The other plants were dissected for microtechnical treatment and fixed in FAPA. Plumules of untreated seeds (0 days germination) were also fixed in FAPA. Buds and plumules were dehydrated by the TBA (tertiary butyl alcohol) method and embedded in "Paraplast". The material was sectioned with a rotary microtome at a thickness of 10 or 12 µm. The microscopic preparations were stained by safranin-fast green.

In Surinam the experiments were carried out with 'Matjan'. Half of the plantlets were grown in a dark room at a temperature of 28–29°C. The other plants were grown in a greenhouse in which the night temperature was 23–24°C and the day-time temperature went up to 35°C, with peaks on sunny days of about 40°C. Material was collected 0, 3, 6, 9, 12, 15 and 21 days after sowing and processed in the same way as in Wageningen.

The complex image from the microscopic slides was translated into simple botanical diagrams presenting the orientation of the branching system and the position of each flower, leaf, bract, bracteole and prophyll, or their primordia.

### 3. RESULTS

#### 3.1. Plant description

The species *Arachis hypogaea* L. is highly variable morphologically. Branching pattern and growth habit are important characters in the classification of variety groups and cultivar clusters (GIBBONS, BUNTING & SMARTT 1972). Normally 'Schwarz 21' and 'Matjan' plants develop lateral branches in the axils of the cotyledons and the two lowermost foliar leaves. These four primary axes are virtually always formed. Depending on external conditions more vegetative laterals may be formed. By preference these appear in the axils of the prophylls (cataphylls) of the cotyledonary branches and at the higher nodes of the main stem. However, FORTANIER (1957) demonstrated that each axillary bud has the potential to develop into a vegetative branch.

The complex structure of the groundnut plant becomes quite clear from *figs. 1, 2 and 3*. *Fig. 1* is a photograph of an exceptionally well developed 21 day old 'Matjan' plant. *Fig. 2* is a schematical drawing of the same plant. *Fig. 3* explains the symbols used in *fig. 2*.

Noteworthy are:

1. A difference between vegetative branches and generative branches. According to PURSEGLOVE (1968): "Branching dimorphic with monopodial vegetative branches and reduced reproductive branches".
2. The presence of solitary flowers in the axils of bracts or prophylls only.
3. The presence of two partly fused but clearly distinct bracteoles at the base of the pedicel of each flower.



Fig. 1. 'Matjan' plant, 21 days old.

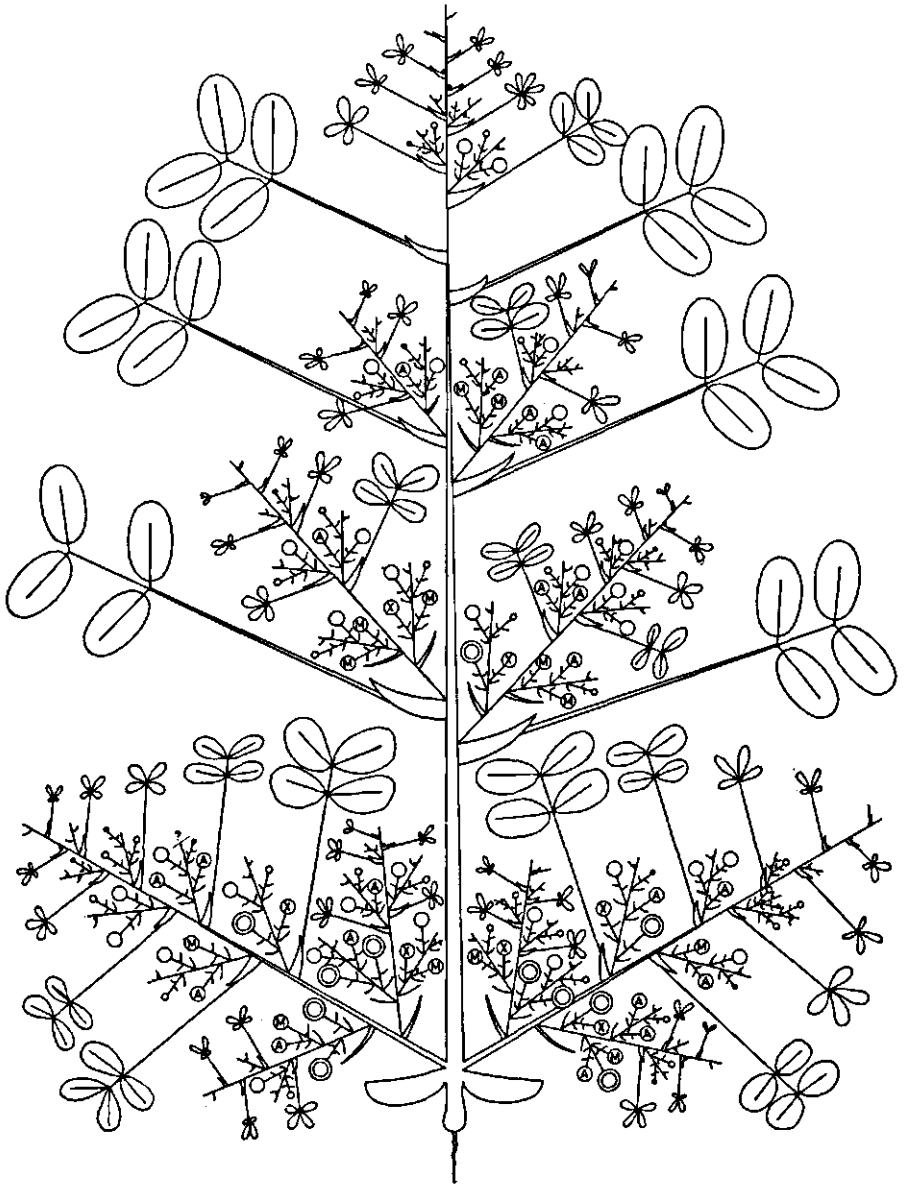


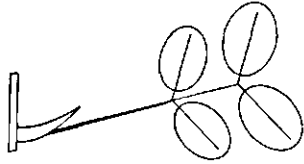
Fig. 2. Schematic representation of the plant shown in *fig. 1*. Note the absence of laterals in the axils of the fifth and sixth foliage leaf.

VEGETATIVE ORGANS

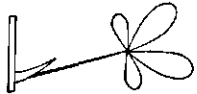
GENERATIVE ORGANS



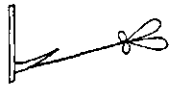
Lateral prophylls (cataphylls) close to the base of side branches, quite often one or three



Expanded leaves, at the base two long pointed, partly fused (adnate) stipules



Well developed primordial (not expanded) leaf



Primordial leaf, only the two terminal leaflets are well developed



Only the two terminal leaflets visible in a very early stage of development



Undivided lamina primordial flanked by two stipule primordia



One undivided primordial near the tip of an axis



Flower primordium and bracteole primordia separated



Sepal differentiation



Stamen differentiation



Archesporium differentiation in the anther sacs



Differentiation of pollen mother cells



Meiosis and differentiation of pollen tetrads



Pollen grains are separated

INTERMEDIATE



Undetermined primordial in the axil of a prophyll, bract, or leaf (see also *fig. 16*).

Fig. 3. Symbols used in *figs. 2, 4 and 14*.

4. The abundance and maturity of flower buds and primordia on the branches in the axils of the prophylls of the cotyledonary laterals.

Apical dominance does not seem to inhibit the vegetative growth of the four primary laterals (YARBROUGH 1957a). These become as long and as well developed as the main axis. Other vegetative branches also develop and grow out very well. The generative branches are short so that a compact mass of flowerbuds is hidden between stipules and/or bracts in the axil of a foliage leaf or prophyll. Often the generative character of such branches is completely lost by extension after the formation of foliage leaves at the tip. Thus a definite distinction between vegetative and generative axes is not possible (FORTANIER 1957). According to PURSEGLOVE (1968) the flowers are: "Borne on compressed spikes in the axils of foliage leaves and never at the same node as vegetative branches".

As a result of the compact structure of the generative axes the position of the flower to the axis and the presence of two bracteoles instead of one bifid one was not clearly observed by earlier investigators (SMITH 1950; GREGORY, SMITH & YARBROUGH 1951; FORTANIER 1957; GILLIER & SILVESTRE 1969). This became quite obvious from the microscopic slides (*fig. 4*). Additional evidence for the presence of two bracteoles is provided by the occasional occurrence of flowerbuds in their axils. The cyme formed in this way is a very unusual structure in the Leguminosae (*fig. 5*). The more or less adaxial position of the bracteoles makes it possible at a very early stage to distinguish a floral primordium with its two bracteole primordia from a "branch" primordium with its prophyll primordia in lateral position (*fig. 4C*).

### 3.2. Structure of the embryo in the mature seed

When one of the cotyledons is broken off from the straight embryo, a well developed plumule becomes visible (*fig. 6*). Close observation reveals a cotyledonary bud enveloped in two prophylls or cataphylls (*fig. 7*). After micro-technical treatment all parts of the plumule are distinguishable in the slides.

There is a small difference in morphological development between well and less developed embryos. *Fig. 8* shows a diagram of one of the most developed 'Matjan' seeds. The number of leaves at the main axis is in agreement with the observations of GREGORY, SMITH & YARBROUGH (1951), FRANQUIN (1970), and MAEDA (1972). The first two leaves are well developed. These leaves, like the cotyledons, are more or less opposite. The third and fourth leaf are less developed but complete. The fifth leaf is hardly formed (*fig. 9*).

The leaf at the third node of the cotyledonary laterals is not very far developed in the seed (*fig. 10*). At the fourth node only a primordium is present. This seems in contradiction to the observation of two embryonic leaves by GREGORY, SMITH & YARBROUGH (1951). However, the prophyll at the second node of the cotyledonary laterals quite often bears three, or less frequently one, two, or even four leaflets at the tip. This leafy prophyll might be regarded as a second foliage leaf. The observation of FRANQUIN (1970) that the prophylls are always leafy seems to be incorrect.

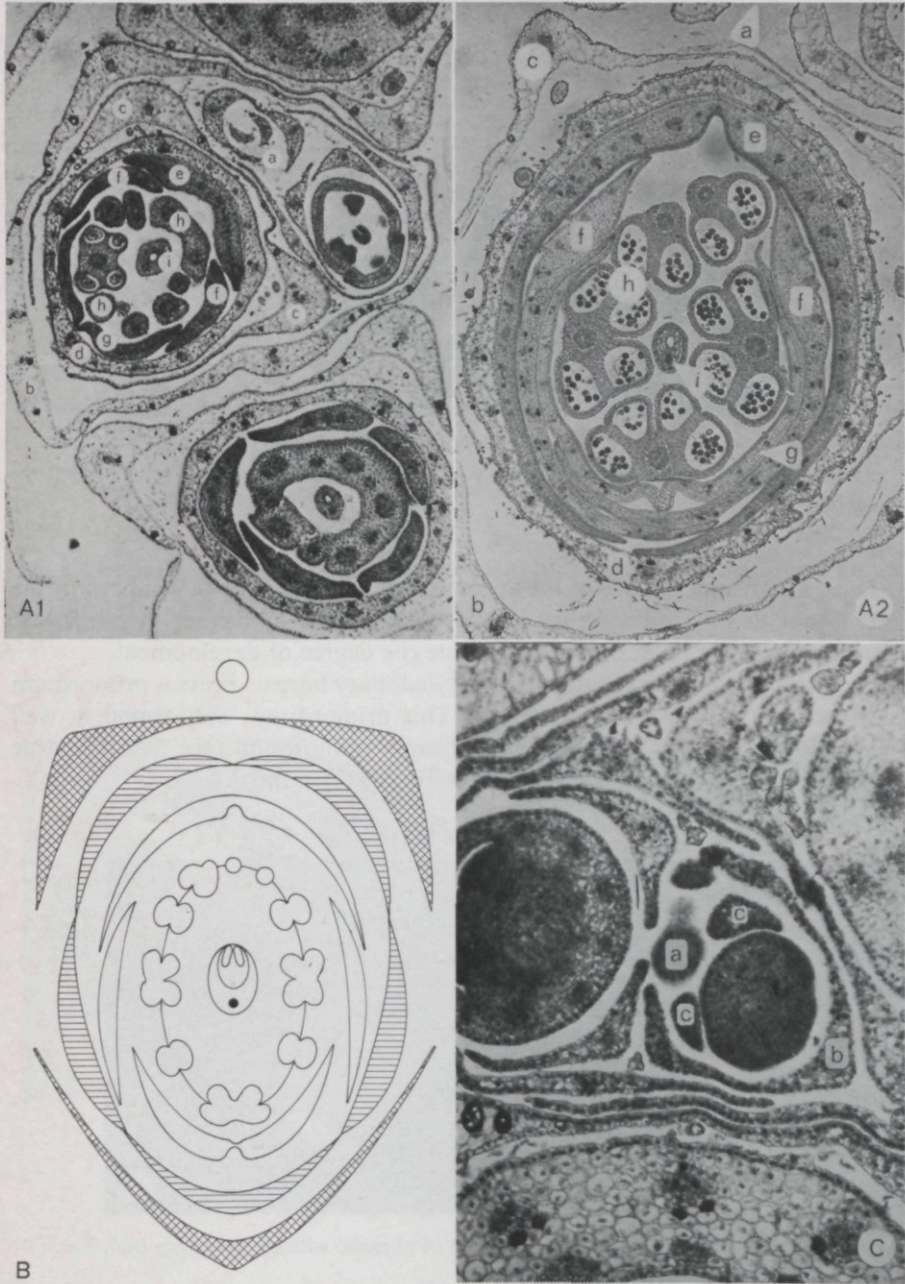


Fig. 4. A1-2. Structure of the *Arachis* flower, 36 $\times$ . A1. Differentiation of pollen mother cells. A2. Pollen grains are separated; B. Floral diagram; C. Young flower primordium, 100 $\times$ . Take note of the adaxial bracteoles.

a. axis; b. bract; c. bracteoles; d. calyx; e. standard; f. wings; g. keel; h. monadelphous androecium, usually eight functional stamens and two sterile filaments; i. style with styler canal of the superior gynaecium.



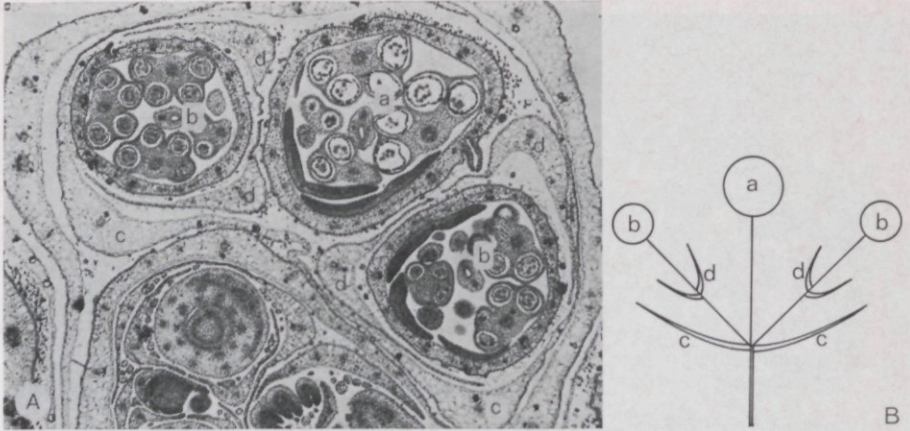


Fig. 5. A. Microphotograph of a cyme,  $32\times$ ; B. Schematic representation of a cyme. a. terminal flower; b. lateral flowers; c. bracteoles of the terminal flower; d. bracteoles of the lateral flowers.

Thus, the overall picture of the vegetative development of the embryo in the seed is not at all contradictory to the observations of former investigators. However, some of them highly exaggerate the degree of development.

The branch at the first node of the cotyledonary laterals bears a primordium in the axil of the lowermost prophyll. This primordium, only found in well developed embryos, is definitely not a flower primordium (*fig. 11*). The true nature of this primordium will be discussed in paragraph 3.4.

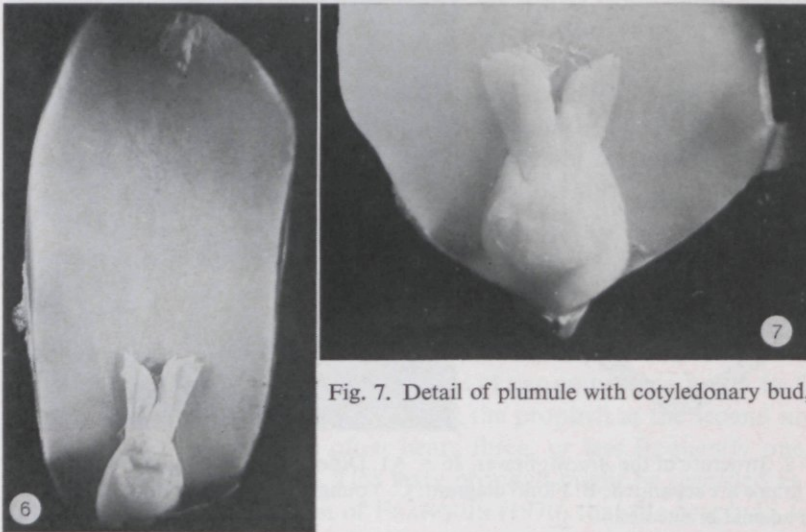


Fig. 7. Detail of plumule with cotyledonary bud,  $7\times$ .

Fig. 6. Plumule with cotyledon in background,  $4.5\times$ .

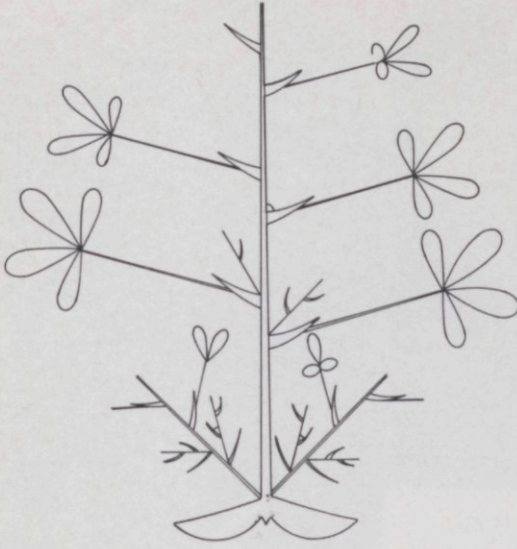


Fig. 8. Schematic representation of the morphological development of the embryo in the seed.

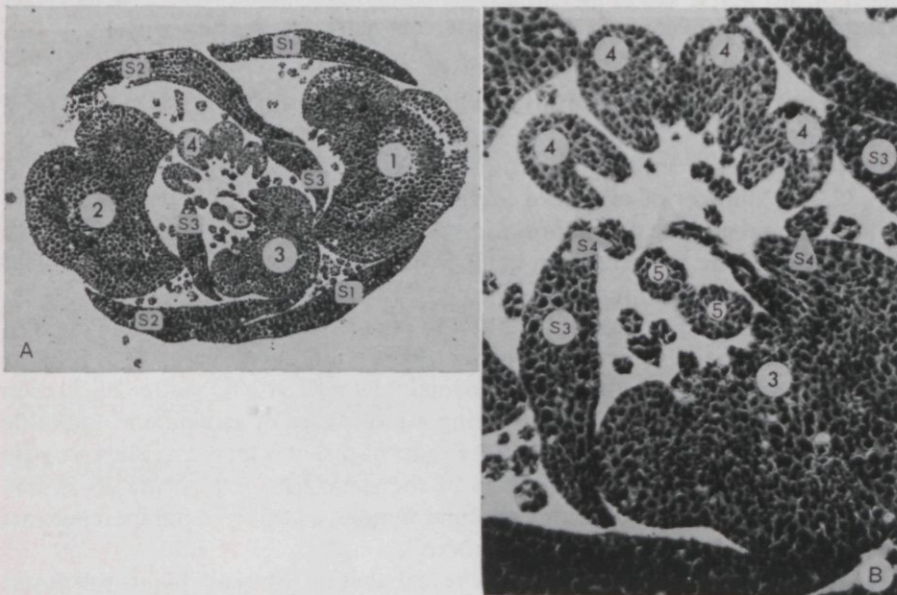


Fig. 9. Transverse section of plumule. A. General view, 28 $\times$ . B. Enlargement, 90 $\times$ .  
 1. first leaf with its stipules S 1.; 2. second leaf with its stipules S 2.; 3. third leaf with its stipules S 3.; 4. fourth leaf with its stipules S 4.; 5. fifth leaf.

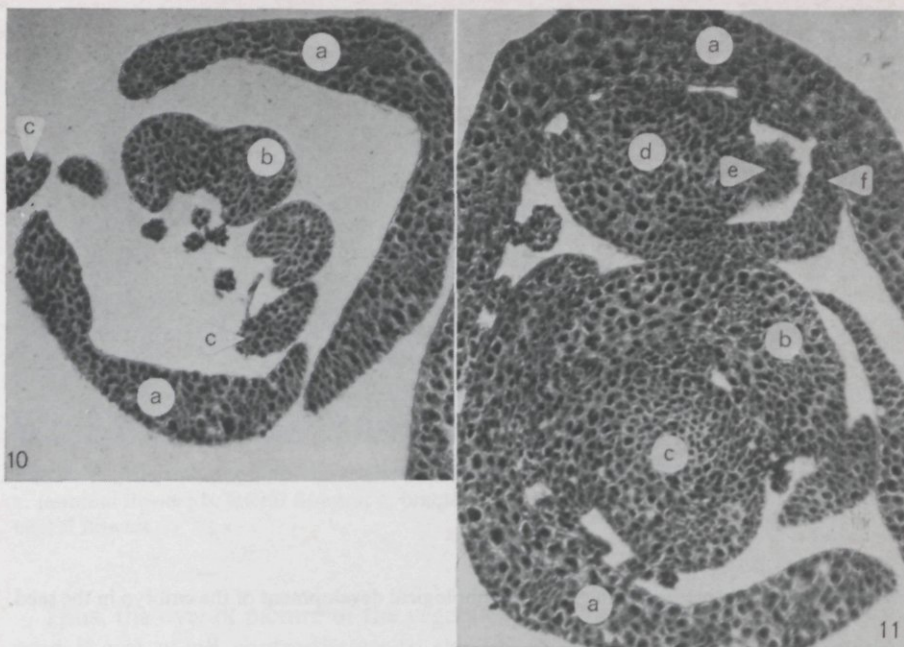


Fig. 10. Transverse section of a cotyledonary bud, 100 $\times$ . a. prophylls; b. first leaf with stipules (c).

Fig. 11. Transverse section of a cotyledonary bud, 100 $\times$ . a. prophylls of the cotyledonary lateral; b. first leaf; c. axis of the cotyledonary lateral (branch first order); d. second-order branch with a primordium (e) in its lowermost prophyll (f).

### 3.3. Vegetative development of the plumule during the first 21 days of growth

The vegetative development in situ of three groundnut cultivars is shown in *fig. 12*. The number of expanded leaves on three-week old plants corresponds with the number of leaf primordia in the seed. The four primary laterals (see paragraph 3.1) are not yet grown out. The rate of leaf expansion is not very fast and in fact slows down further in the period between 15–30 days after sowing. YARBROUGH (1957b) concluded: "It will be recalled that in the dormant embryo of *Arachis* as many as five foliar primordia are found on the main axis alone and four or five more on the two cotyledonary laterals. It is only after 20–30 days of growth, when the seedling is entering a new phase of growth and initiating new internodes and foliar organs, that results of this new tempo in physiological processes is reflected in the products of the stem apex. Up to the 20–30-day interval the pattern of internodes, vascular bundles and files of pith parenchyma has been largely preformed in the embryo".

However, microscopic observations reveal that in 'Matjan' plants this is not true. In *table 1* the counts of all foliar and generative organs are given for plants from 0 to 21 days old. At least 60 leaf primordia are formed during the first 21 days of growth.

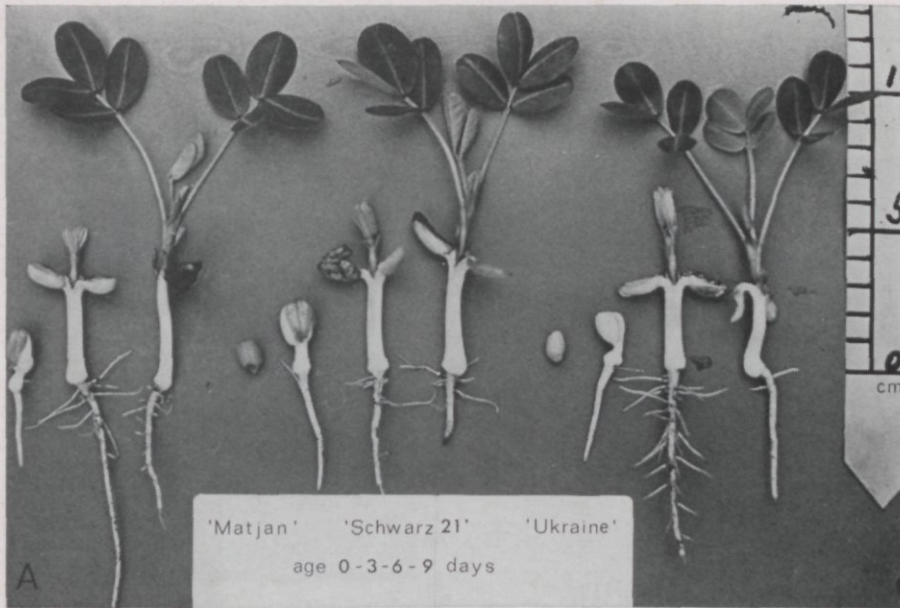


Fig. 12 A-B. Development in situ of the plants of three groundnut cultivars. A. 0-3-6-9 days; B. 12-15-21 days.

Table 1. Development of 'Matjan' plants during the first 21 days of growth

age (in days)		plumule length (mm)	number of leaves and leaf primordia	number of expanded leaves	number of flowerbuds and primordia
0	plant 1	c. 3	9	0	0
	2	c. 3	10	0	0
	3	c. 3	10	0	0
3	plant 3	5	12	0	0
	4	2	10	0	0
	5	4	12	0	0
6	plant 2	32	21	2	0
	3	36	27	2	0
	4	28	26	2	0
9	plant 2	—	44	5	26
	3	—	43	5	11
12	plant 2	119	51	7	39
	3	109	56	7	46
15	plant 2	160	60	9	65
	3	145	57	9	53
21	plant 2	205	79	18	125
	3	180	71	10	98

### 3.4. Generative development of the plumule during the first 21 days of growth

During the first two days of germination the plumule does not change morphologically. New primordia do not become visible until three days after sowing. Then a rapid development follows. The first flower primordia were observed in 6-day old 'Schwarz 21' plants grown in the dark. Plants of the light treatment did not show their first flower primordia until 8 days after sowing (*fig. 13*). This is not remarkable, since it is known that light slightly inhibits germination (MONTENEZ 1957). Moreover, the mean germination temperature was lower than in the dark treatment.

In *table 1* the very rapid increase and development of flower primordia in the period of 9 to 21 days after sowing is demonstrated. Up to 125 flower primordia were counted in a well developed 'Matjan' plant of three weeks. Most of the flowers are situated on the cotyledonary laterals. Their development is shown in the diagrams in *fig. 14*. The primordium (discussed above: see 3.1) in the axil of the lowermost prophyll of the branch at the first node of the cotyledonary axis develops into a compound structure and never into a single flower. In *fig. 15* the development of this primordium is shown in a sequence of microscopic

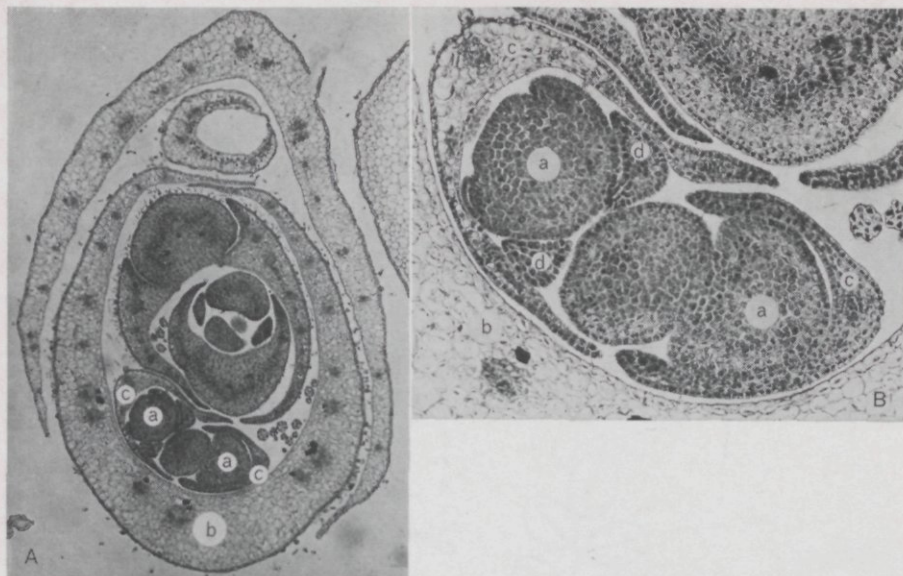


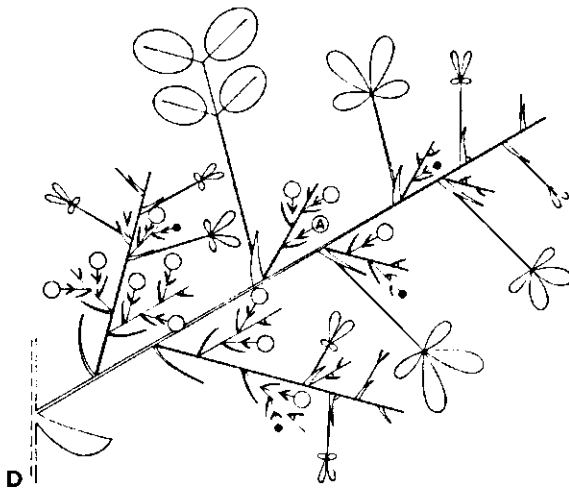
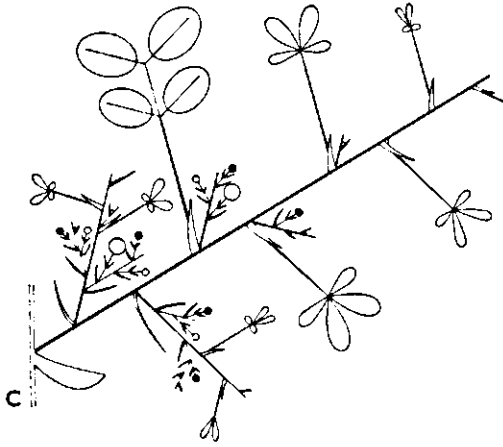
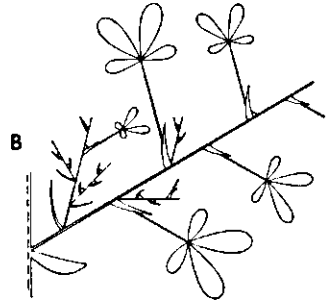
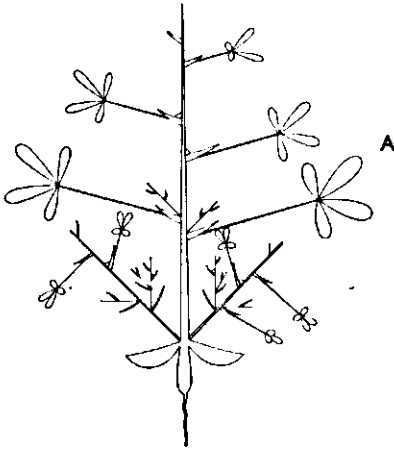
Fig. 13. Microphotograph of the first flower primordia (a) in the axil of the second prophyll (b) of a cotyledonary lateral of a "Schwarz 21" plant eight days after sowing. Take note of the lateral position of the prophylls (c) of the branch second order and the adaxial position of the bracteole primordia (d). A 33 $\times$ ; B 100 $\times$ .

photographs. Although at this location single flower primordia were never found in less developed "Schwarz 21" plants, it is quite common to find them in the axils of the prophylls of the second side branch of the cotyledonary lateral. In exceptional cases they may also appear in the axils of prophylls of the first side branch. This, then, could be the source of the misconception of earlier investigators.

#### 4. CONCLUSIONS

The observation that flower primordia are not present in the seed of the groundnut has consequences. The formation of a single flower is the closure of that particular axis and means the end of growth and flower initiation at this location. The formation of a generative branch at the same location means not only more flowers, but opens the way to further vegetative growth and flower initiation (see *fig. 16*). It is quite obvious, and in accord with the author's actual findings, that environmental conditions during the first few days of germination can interfere with the balance between the initiation of a single flower (or a cyme) and an open compound structure. This is particularly true of the axes at the lower nodes of the four primary laterals.

In bunch cultivars the majority of the pods arise from these nodes. Therefore this less fixed character in the early stages of growth may be of significance for the growing of the "unpredictable legume" (LONG 1951).



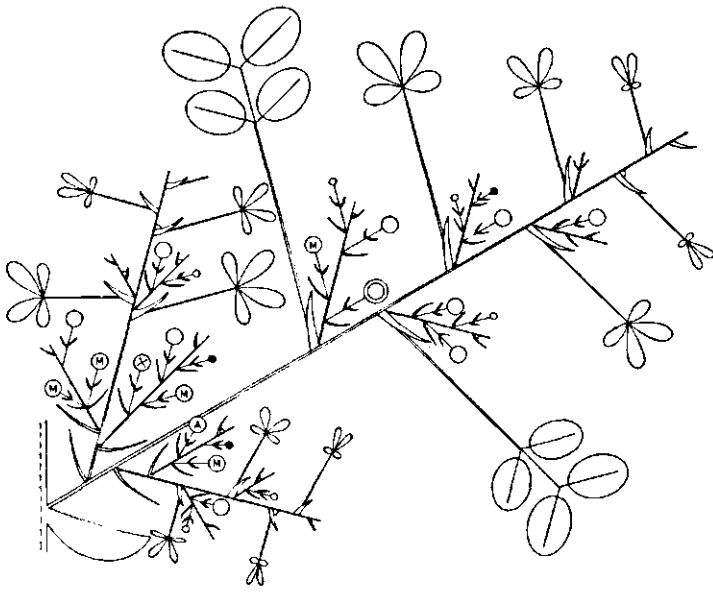
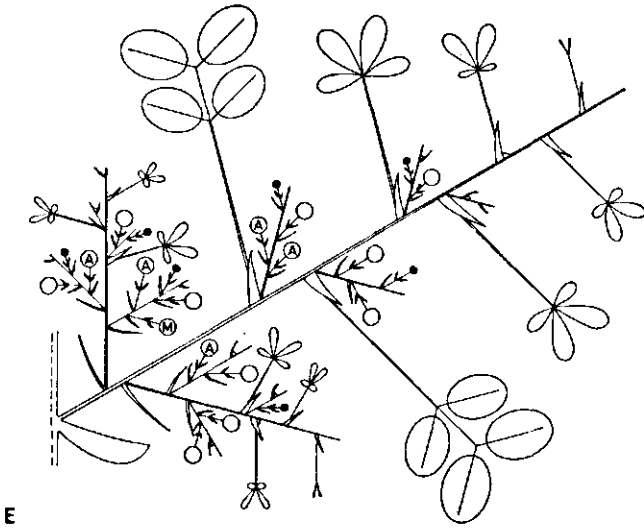


Fig. 14. Schematic representation of the development of the cotyledonary laterals of 'Matjan' plants, from 3 to 21 days old. A 3 days; B 6 days; C 9 days; D 12 days; E 15 days and F 21 days old.



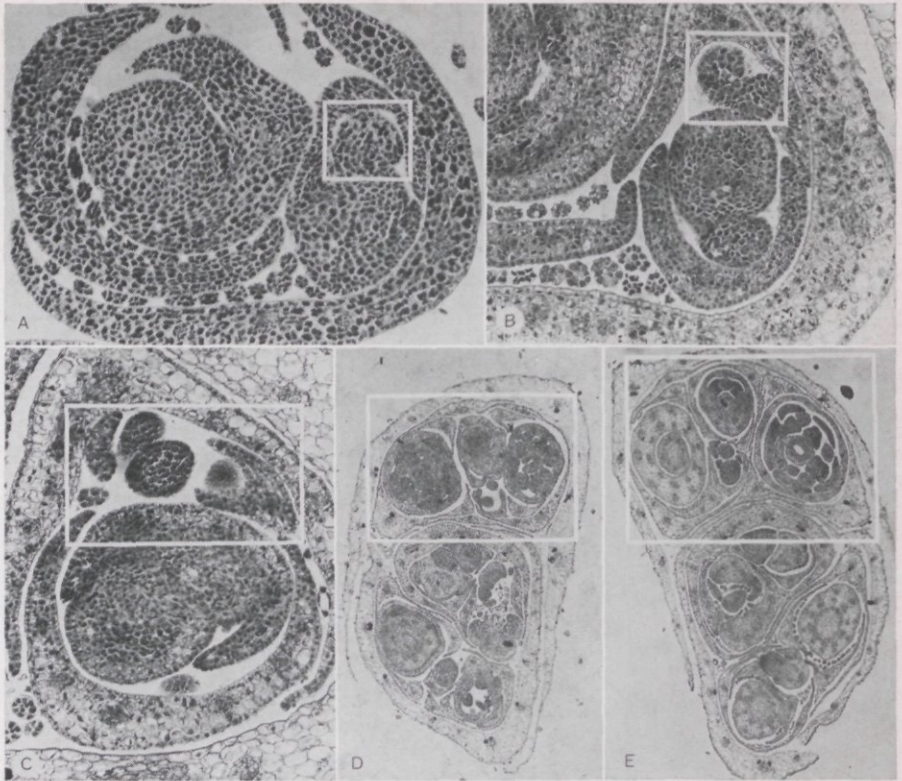


Fig. 15. Microphotographs of the development of the primordium shown in fig. 11. A 0 days old; B 3 days; C 6 days; D 12 days and E 15 days. A, B and C 80 $\times$ ; D and E 26 $\times$ .

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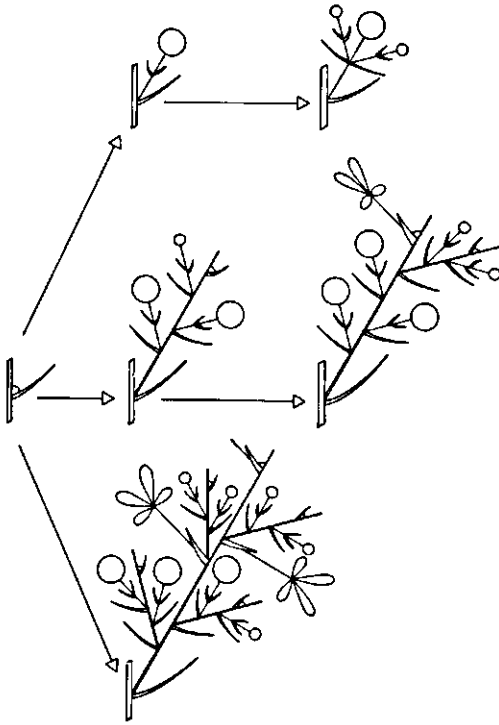


Fig. 16. Hypothetical development of an (embryonic) primordium into a flower, a closed system, or into an inflorescence or vegetative lateral, both open systems.

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