# SEED-GERMINATION AMONG THE LEGUMINOSAE

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# CONTENTS

Page

1. Introduction 1
   Abstract “
2. Material and method “
3. General features of germination among the legumes 2
4. Modes of germination 4
   a. Mode 1 germination “
   b. Mode 2 “ 6
   c. Mode 3 “ 15

Figures 1 – 9 7

5. Germination among geocarpic legumes 16
6. Ambivalent germination 17
7. Discussion “
8. Acknowledgements “
9. References 18

Appendices 19
   A. Explored species germinating in Mode 1 “
   B. “ “ “ in Mode 2 21
   C. “ “ “ in Mode 3 22

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## 1. INTRODUCTION

Extensive experience in raising leguminous seedlings, in studies of their nodulation, has shown current terminology of germination, as embodied in the words **epigeal**, **geal**, and **hypogeal**, to be inadequate in distinguishing the three modes occurring. This study seeks to remedy this.

## 2. MATERIAL AND METHOD

Species explored for their mode of germination, most of them comparatively large-seeded, and chosen for that reason for ease of study, are listed in the Appendices, while those of which the embryos are depicted in Figure 1 are used to illustrate the three modes found.

To secure quick and even germination, impervious seed was etched with concentrated sulphuric acid and/or nicked with a miniature hacksaw. Seeds were germinated in moist vermiculite – a loose rooting-medium amenable to the movements of germination.

Seeds destined to be germinated underground were sown with the radicle vertical and the cotyledonary node either uppermost or lowermost, with these two postures being achieved by gumming the seeds to plates of glass shaped to fit the pots being used, as depicted in Figure 2. For ease of reference, these extreme postures are dubbed **obverse** and **reverse** respectively. Seeds destined to be surface-germinated were simply scattered on the surface.

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ABSTRACT

Current terminology of germination, as embodied in the words **epigeal**, **geal**, and **hypogeal**, is found to be wanting in distinguishing the modes occurring among the legumes. The three modes found, including the hitherto unrecognized mode of *Arachis,* are described and illustrated. 22 pages.

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Key words: *Arachis* germination Leguminosae seed

In exploring the behaviour of the embryonic axis during germination, the radicle was benchmarked by branding it. ( Pigments were found to be unreliable markers, often stretching to uncertainty, or vanishing, during subsequent growth.) In preparing seeds for branding, those with a bent axis were softened sufficiently in water to facilitate excising a small piece of the seedcoat to uncover the basal half of the radicle; seeds with a straight axis, on the other hand, were germinated sufficiently to extrude about 5 mm of the radicle. Thus exposed, radicles were then marked, indelibly and as required, by scorching them lightly with the side of a fine needle brought to a gentle heat in a candle-flame.

In drawings, for ease of recognition, hypocotyls and seedcoats are tinted pink and grey respectively, and, for clarity, lateral roots are omitted.

## 3. GENERAL FEATURES OF GERMINATION AMONG THE LEGUMES

The general features of germination among the legumes, many of them well-publicised ( e.g. in Raven, Evert & Eichhorn, 2007 ), are noted here for ease of reference.

Smith ( 1983 ) recognises four forms of cotyledon among the legumes, as set out in Table 1. Since his Forms 1 and 3 are photosynthetic organs, they are constrained to come to the light for successful function. His Forms 2 and 4, on the other hand, whilst capable of superficial greening, have no photosynthetic palisade: they, therefore, are not so constrained, and it is among them, and only among them, that germination may be successful with the cotyledons remaining underground during the process. Other properties material to the germination of the commoner leguminous seeds – those with Forms 1 or 4 cotyledons – are contrasted in Table 2. ( The less common types of seed – those with Forms 2 or 3 cotyledons – tend to have intermediate features, and are given only passing mention to avoid overburdening this account.)

Embryos are found to range in size from that of *Trifolium bocconei* with Form 1 cotyledons, to that of *Mora oleifera* with Form 4 cotyledons, with typical dry weights of 0.1 milligram and 330 grams respectively. Those with Form 1 cotyledons tend towards the lower reaches of this vast size-range, and those with Form 4, usually relatively large and heavy with a store of nutrients, towards its upper reaches.

The radicle – the root-tipped hypocotyl – is always the first part of the embryo to emerge from the seedcoat during germination, doing so in the direction in which it had pointed in the dormant seed. Once the radicle has emerged, the root proper rapidly extends and ramifies, thus, among other things, rapidly providing a firm base for the forceful thrusts of germination about to occur.

Table 1. Forms of cotyledon, and frequency of their occurrence, among leguminous seeds *

| Form of cotyledons | Incidence of photosynthetic palisade parenchyma | |
|---|---|---|
| | Present | Absent |
| Slim | Form 1 (58% **) | Form 2 (< 2%) |
| Plump | Form 3 (10%) | Form 4 (30%) |

* Adapted from Smith (1983). ** Estimated proportional frequency of occurrence within family

From the chance posture of the seed at the outset of germination, both root and shoot develop on circling courses until the seedling is geocentrically aligned, as depicted in Figure 3A.

Meanwhile, except in *Arachis,* the leader – the hypocotyl or the epicotyl, as the case may be – arches outwards from the seedcoat to pull its appendages ( the cotyledons and/or the plumule ) backwards from within the seedcoat, and thence to the surface. This arching involves the rolling motion depicted in Figure 3B – a motion that also eases the jostling thrust to the surface. As its appendages clear the surface, the tensely arched leader, tension released, straightens to swing them **aloft**, well above the surface, as depicted in Figure 3C.

The thrust to the surface is often helical – a twist which is usually discernable in the grain of the epidermis, and one which must be taken into account in interpreting events. Thus, in Figure 8 for example, in the Reverse row, the epicotyl is reflexed towards the cotyledons ( to the left as drawn ), whereas in the right-hand drawing it is reflexed away from them ( to the right as drawn ): this difference in orientation proclaims that such a twist has occurred.

Seedlings from a fully obverse start develop a more or less straight axis, while those starting otherwise are, at least temporarily, more or less sinuous through the cotyledonary node. This may be seen in the contrast between the outcomes of the obverse and reverse starts within each of Figures 4 to 9. A fully reverse start may retard the seedling's arrival at the surface by a day or more: it is clearly a handicap in this respect.

The root simply circles as necessary to orientate itself downwards, apparently having no feature distinctive of mode of germination.

Table 2. General features of the germination of the two main forms of leguminous seed*

| Feature | Seeds with Form 1 cotyledons | Seeds with Form 4 cotyledons |
|---|---|---|
| Modes of germination | Mode 1 only | Any one of the three modes found, but see Section 6 |
| Incidence of endosperm in the mature seed | Usually present. Rapidly absorbed into the embryo during germination | Usually absent as such, having been absorbed into the embryo during seed-development |
| State of embryonic axis in mature seed | Usually relatively large and well-developed | Usually relatively small and rudimentary |
| Working position of cotyledons during germination | Perforce aerial | Immaterial |
| Change of cotyledons during and after germination | Expanding, to become foliaceous for photosynthesis | Shrinking, as nutrients are transferred to the rest of seedling |
| Duration of cotyledons after the start of germination | Usually photosynthetically active for several weeks before falling | Falling when, early or late, their substance has been exhausted |

* Table derived in part from Smith (1983)

# 4. MODES OF GERMINATION

The legumes appear to have three modes of germination, with these being best distinguished by the behaviour of the hypocotyl during the process. Briefly, the hypocotyl either **pulls**, as already described, or it **pushes**, or it **idles**.

The distinctive features of the three modes of germination about to be described are summarised in Table 3.

## *4a. Mode 1 Germination*

In Mode 1, loosely familiar as **‘epigeal’** germination, the hypocotyl arches into the lead to bring the seedling to the surface. Typical sequences are depicted for *Phaseolus vulgaris* and *Schizolobium parahyba* in Figures 4 and 5, and their embryos are shown in Figure 1.

Table 3. Summary of behaviour of leguminous seed during germination

| Behaviour of embryonic axis during germination | | Mode of germination | Nature of embryonic axis | Posture of seed at start of germination * | Geo-centralizing response of embryonic axis ** | Exemplary species |
|---|---|---|---|---|---|---|
| Hypocotyl active | Hypocotyl leads, arching to haul cotyledons *cum* plumule above surface. Epicotyl then develops. | Mode 1 | Bent | Obverse<br>Reverse | 1<br>2 | *Phaseolus vulgaris* (Figure 4) |
| | | | Straight | Obverse<br>Reverse | 2<br>1 | *Shizolobium parahyba* (Figure 5) |
| | Hypocotyl leads, ridgidly thrusting cotyledons *cum* plumule almost clear of surface. Epicotyl then develops. # # | Mode 3 | Bent | | | Not known |
| | | | Straight | Obverse<br>Reverse | 2<br>1 | *Arachis hypogaea* (Figure 9) |
| Epicotyl active | Epicotyl leads, arching to haul plumule above the surface. Hypocotyl remains more or less idle. | Mode 2 | Bent | Obverse<br>Reverse | 1<br>2# | *Phaseolus coccineus* (Figure 7) |
| | | | Bent | Obverse<br>Reverse | 1<br>3# | *Vicia faba* var. *major* (Figure 8) |
| | | | Straight | Obverse<br>Reverse | 2<br>1 | *Tylosema fassoglensis* (Figure 6) |

* In all cases, except that of *A. hypogaea,* the pattern of surface-germination resembles that of the obverse posture.

** See Figure 3A for notation.

\# The epicotyl develops sigmoidally **internally**, between the cotyledons, in *P. coccineus,* but loops **externally** in *V. faba.*

\## During surface-germination of *A. hypogaea* the hypocotyl swells rather than elongates.

Elongation of the hypocotyl is partly of tissue that had already existed in the dormant seed, and partly by new intercalary growth generated below the cotyledonary node in forming the rolling arch.

From an obverse start, the arching hypocotyl pulls the appressed cotyledons, with the fragile plumule sandwiched safely between, backwards from within the seedcoat and thence to the surface. As the cotyledons clear the surface, the tense hypocotyl straightens to swing them **aloft**, as depicted in Figure 3C. From a reverse start, the hypocotyl roll-thrusts **droupwards** ( = down-round-and-upwards ) to the same end – in the process somersaulting the cotyledons to the degree necessary to bring the node uppermost for the haul to the surface. In germination on the surface, the characteristic sequence of arching, pulling, and straightening is still enacted.

Occasionally, the arching hypocotyl fails to extract the cotyledons fully from the seedcoat, and thus draws them to the surface still partly encased. In this event, the cotyledons bend, as shown in both Figure 3D and in the Surface row of Figure 5, to cause slippage ( as occurs, for example, in bending a ream of paper ), and thus to shrug off the seedcoat.

Most leguminous seeds get buried, in one way or another, before they germinate. Some, however, are so large, and/or shed so late, and/or germinate so quickly, that they habitually preëmpt burial by germinating on the surface. With some of these the hypocotyl swings the cotyledons aloft – indisputably, they are behaving in this Mode 1. Those behaving otherwise are dealt with later in describing Mode 2.

Most leguminous seeds germinate in this mode. It occurs with all four forms of cotyledon, but is, perforce, the only mode with the photosynthetic forms ( Forms 1 and 3 ). It is characteristic of, but not confined to, groups typically comprising the smaller-seeded species, such as the tribes Crotalarieae, Indigofereae, and Trifolieae. Species explored are listed in Appendix A.

### *4b. Mode 2 Germination*

In Mode 2, confusédly and confusingly called **'hypogeal'** germination, the hypocotyl fails to develop significantly: it more or less idles, with the epicotyl arching into the lead to bring the seedling to the surface. Typical sequences are depicted for *Tylosema fassoglensis, Phaseolus coccineus,* and *Vicia faba* var. *major*, in Figures 6 to 8, and their embryos are shown in Figure 1.

Such elongation of the hypocotyl as occurs suffices only to breach the seedcoat by extruding the tip of the root-tipped radicle: rarely does such elongation attain half the greatest diameter of the seed.

This idling of the hypocotyl is well-exemplified in the germination of the familiar culinary bean, *P. coccineus.* Germinate it underground, as in garden practice,

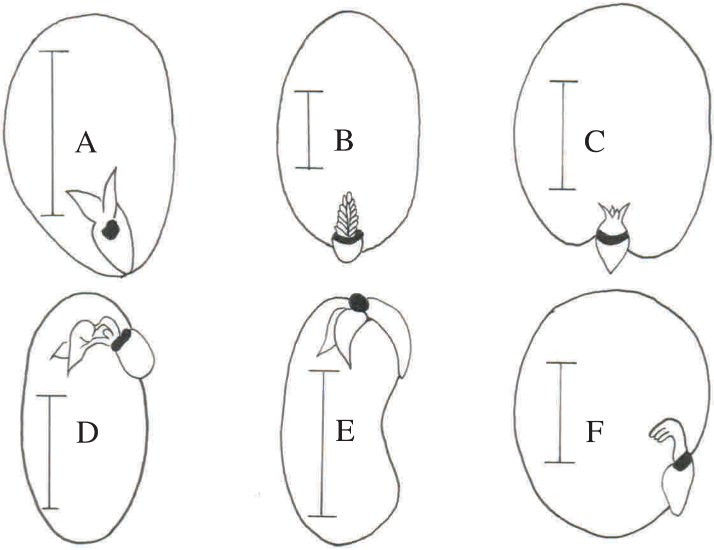

**Figure 1.** Internal view of mature dormant embryos of seeds of which germination is herein described. Cotyledonary nodes, black. Scale bars = 10 mm.
***Upper row***: embryos with a straight axis. **A** – *Arachis hypogaea.*
**B** – *Schizolobium parahyba.* **C** – *Tylosema fassoglensis.*
***Lower row:*** embryos with a bent axis. **D** – *Phaseolus coccineus.*
**E** – *Phaseolus vulgaris.* **F** – *Vicia faba* var. *major.*

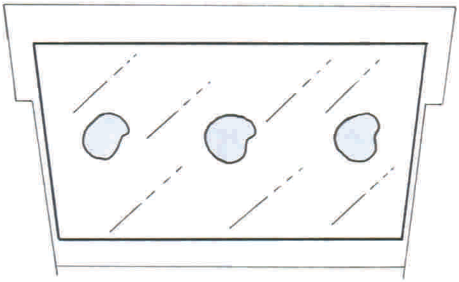

**Figure 2.** Shaped pot-diameter-fitting glass plate to which seeds may be affixed, with water-softenable gum (gum arabic), to pose them for germination

*HDLC*

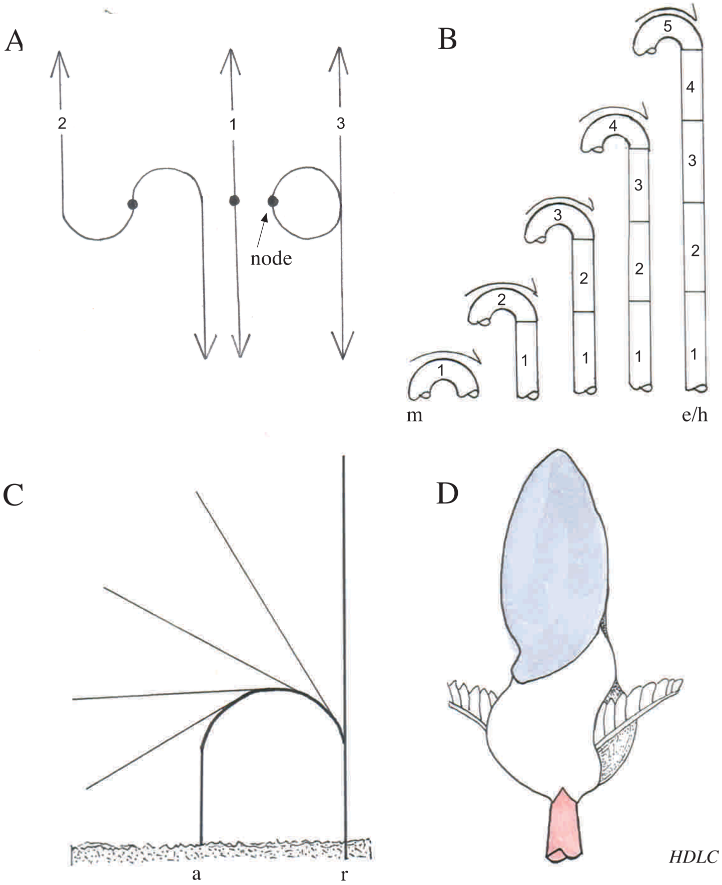

**Figure 3. The evolutions of germination.**
**A.** Circling growth, with all modes, to achieve geocentric alignment of seedling.
1 = Obverse start. 2 = Reverse start with sigmoid alignment of shoot.
3 = Reverse start with looping alignment of shoot.
**B.** Rolling extension of leader in Modes 1 and 2. Extension is in order of number.
m = position of meristem. e/h = position of epicotyl or hypocotyl.
**C.** Lofting of the cotyledons *cum* plumule in Mode 1, or of the plumule in Mode 2.
a = position of appendages. r = position of radicle/root. (In straightening, the arch raises its appendages about twice its own height above the surface).
**D.** Late discard of seedcoat, by bending of the cotyledons, in Mode 1. *Acacia* sp.

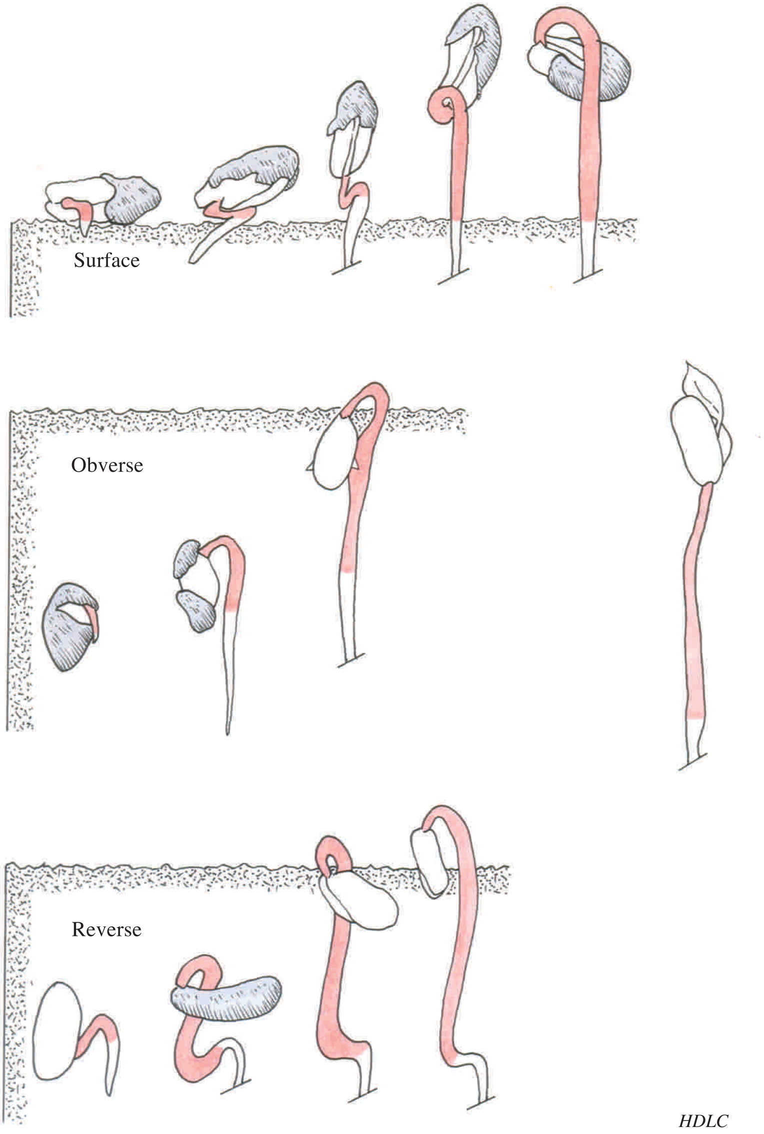

**Figure 4.** Mode 1 germination of a seed with a bent embryonic axis. *Phaseolus vulgaris.*

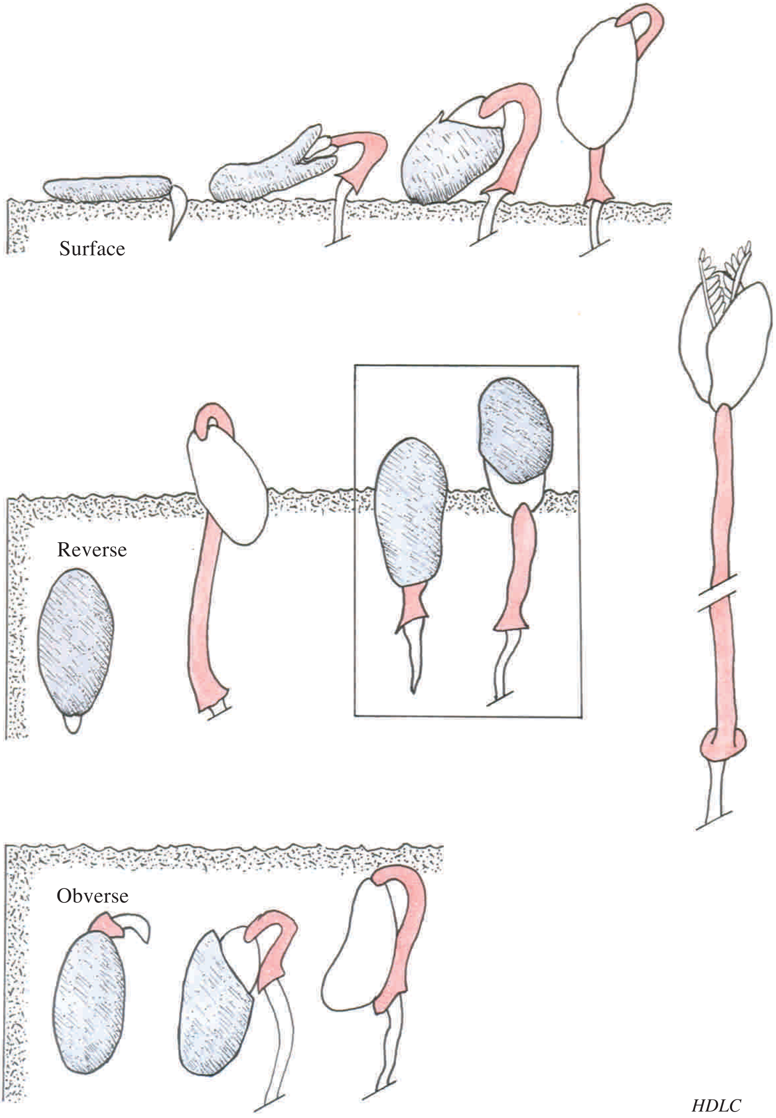

**Figure 5.** Mode 1 germination of a seed with a straight embryonic axis. *Schizolobium parahyba.* (**Inset – Shallow** obverse start, inducing part-simulation of Mode 3.)

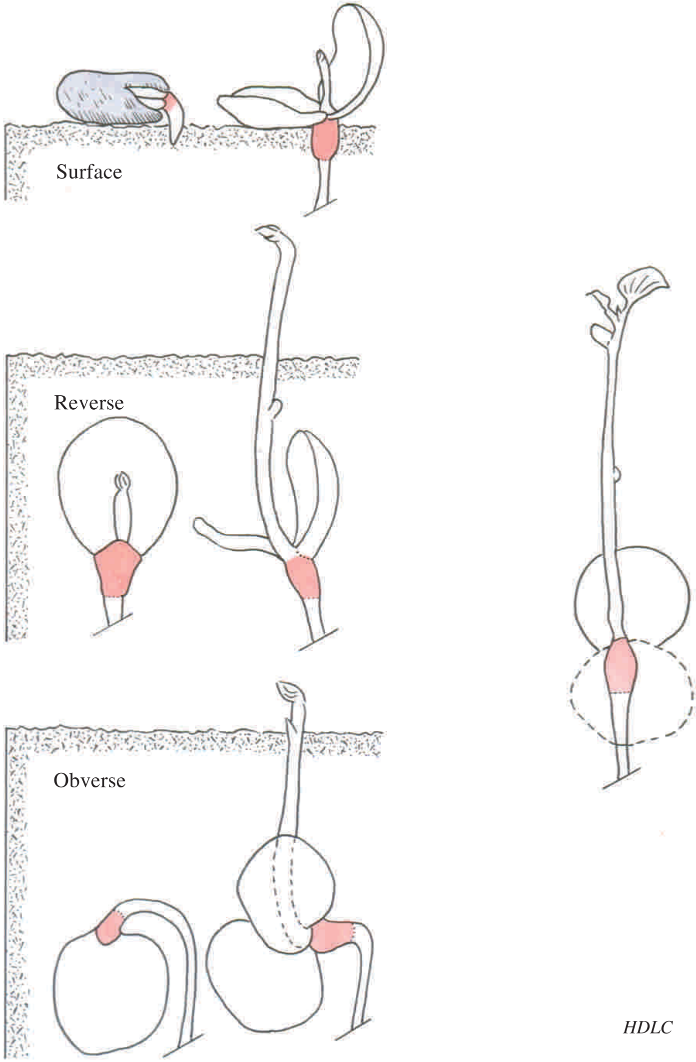

**Figure 6.** Mode 2 germination of a seed with a straight embryonic axis. *Tylosema fassoglensis.* (Reflexion of one of the cotyledons is typical of the germination of this species.)

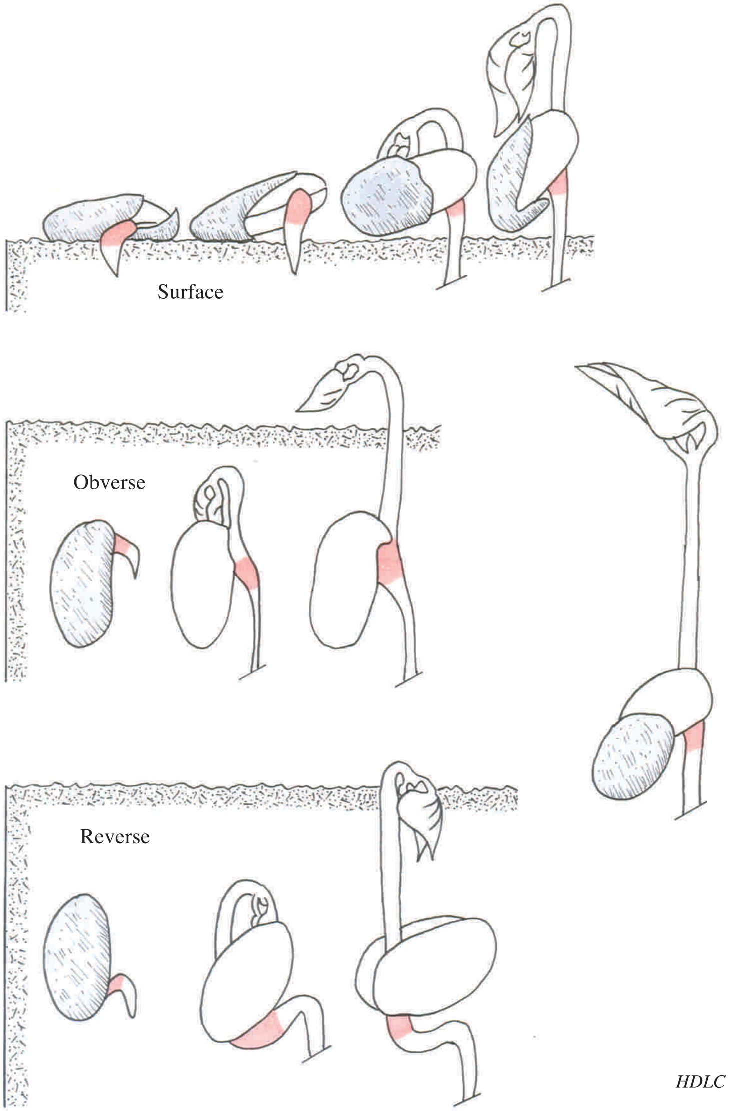

**Figure 7.** Mode 2 germination of a seed with a bent embryonic axis, with sigmoid geocentric alignment of the shoot. *Phaseolus coccineus.*

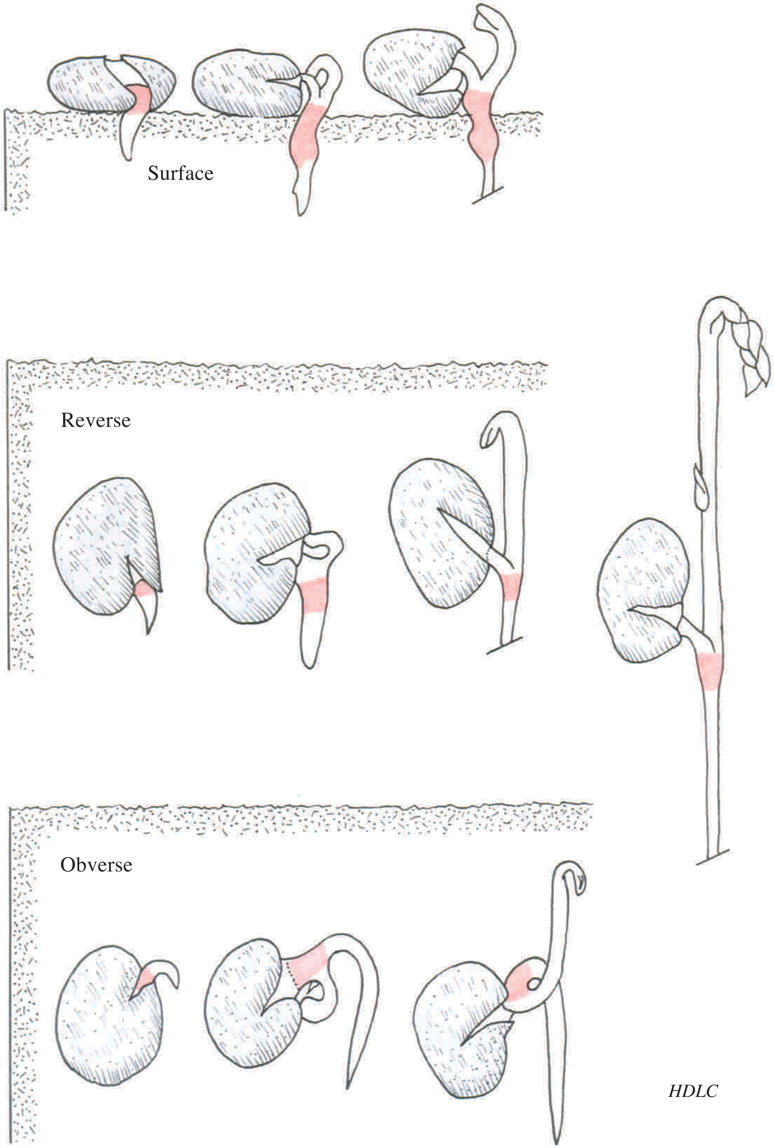

**Figure 8.** Mode 2 germination of a seed with a bent embryonic axis, with looping geocentric alignment of the shoot. *Vicia faba* var. *major.*

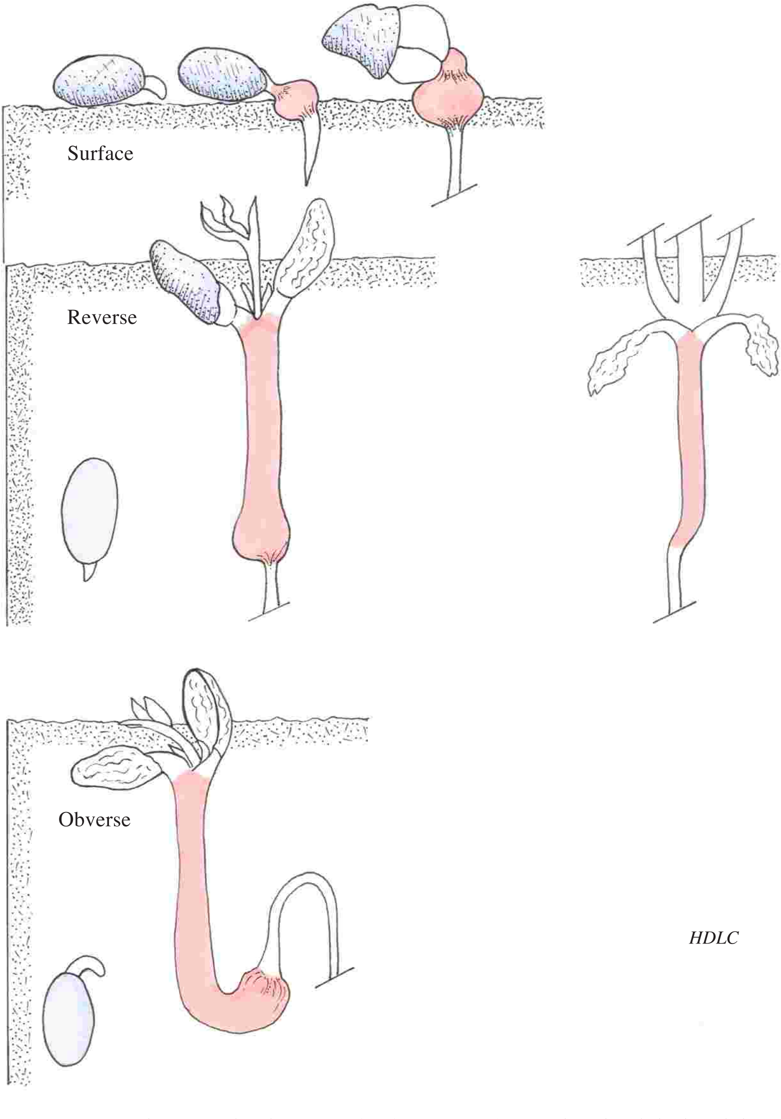

**Figure 9.** Mode 3 germination. *Arachis hypogaea.* ( Note that the right-hand drawing is of a plant aged 11 weeks, with the temporary stiffening sheath no longer present. Note also that the cotyledonary node remains subsurface.)

and there the cotyledons remain, more or less unmoving, where sown; germinate it on the surface, as on damp paper in the classroom demonstration of germination, and there the cotyledons remain, again more or less unmoving, where placed.

The epicotyl appears to have three ways of leading the seedling to the surface, with these being exemplified by the three species comprising the lower half of Table 3. In all cases, as the plumule clears the surface, the tensely arched epicotyl straightens, as depicted in Figure 3C.

Among the habitually surface-germinating species already mentioned in describing Mode 1, are those of which the hypocotyl does **not** significantly elongate, and of which the cotyledons are **not** swung aloft. But, germinate such species underground, and there their cotyledons remain: their behaviour is that of *P. coccineus* – that of this Mode 2. It was for these that the term **'geal'** was coined ( Duke & Polhill, 1981 ).

The variations in seedcoat-retention described as **'phanerogeal'** and **'cryptogeal'** ( Duke & Polhill, *loc. cit.* ), although they may have other functions, appear to be immaterial to the process of germination.

The treatment of the germination of *Isoberlinia angolensis* by Léonard ( 1957 ) exemplifies the confusion attending the term **'hypogeal'.** He depicts its large seed as germinating on the surface, as indeed it usually does, but was constrained by then-current terminology to describe its germination as hypogeal.

Compton ( 1912 ) cites several species of *Bauhinia* as spreading their cotyledons near the surface. Judging by the behaviour of related species ( *B. galpinii, B. variegata,* and *T. fassoglensis* ) this is because there is no significant elongation of the hypocotyl: this marks them as germinating in this Mode 2. ( In gaping, the shallowly buried cotyledons lever themselves to the surface, breaststroke-swimming fashion. ) Duke (1969 ) also has noted this behaviour, in *Pentaclethra macroloba.* And Ng (1992 ) notes that, during the germination of *Saraca thaipingensis*, the hypocotyl fails to develop, thus proclaiming this Mode 2.

This mode is much less common among the legumes than is Mode 1, being, presumably, limited to species with palisade-less non-photosynthetic cotyledons ( Forms 2 and 4, but not actually known with Form 2 ). It is characteristic of, but not confined to, groups with the typically larger-seeded, nutrient-laden, species, such as the tribes Detarieae, Phaseoleae, and Sophoreae. Species explored are included in Appendix B.

### *4c. Mode 3 Germination*

Whereas, in Modes 1 and 2, appendages are **pulled** to the surface during germination, in this Mode 3 they are **pushed.** The typical sequence is depicted for *Arachis hypogaea* in Figure 9, the embryo of which is shown in Figure 1.

Both Candolle ( 1825 ) and Compton ( *loc. cit.*) note that the cotyledons of *A. hypogaea* come to the surface during germination. Yarbrough ( 1949 ) gives a good partial account of its germination – an account which is borne out by the fuller description given here. Purseglove ( 1968 ) notes that germination is neither epigeal nor hypogeal. However, none has gone so far as to declare that *Arachis* has a distinct mode of germination.

With a reverse start, the sturdy broad-based hypocotyl elongates to **push** the whole seed, within its seedcoat, upwards, distal end foremost, until the distal end breaks the surface. With an obverse start, the hypocotyl thrusts droupwards, thus somersaulting the seed to align it for the headfirst drive to the surface. In surface-germination, the hypocotyl usually expends its energy by swelling rather than elongating, as depicted in the Surface row of Figure 9. Having been thrust to the surface, the cotyledons gape and, when drained of their nutrients, lie limp and empty on the surface, with their long limp petioles still attached to their subsurface node.

For its thrust to the surface, the hypocotyl is temporarily broadened at its base and stiffened throughout by a thickening of its cortex with dense parenchyma, as shown in cross-section by Yarbrough ( *loc. cit.* ) in his Figure 25 – a figure which is reproduced by Arant *et al.* ( *1951* ) as their Figure 6. Having served its purpose, this stiffening tissue shrinks, loosens, and sloughs off. However, the authors just quoted have misconstrued the thickening as storage tissue.

The nineteen species of *Arachis* explored for this paper all behave in this Mode 3. One of them however, namely *A. prostrata*, is atypical in that it habitually thrusts its cotyledons well above the surface, thus simulating the lofting of Mode 1.

In passing, it is noteworthy that *S. parahyba,* which normally germinates in Mode 1, may be induced to simulate the behaviour of *A. prostrata*, as just described. If its seed be shallowly sown in the reverse posture, the stout broad-based hypocotyl, lacking soil-depth for manoeuvre, thrusts the seed headfirst to the surface as in this Mode 3, and as depicted in the Inset in Figure 5, but then continues upwards in a belated assertion of its true, Mode 1, nature.

This mode has been found only in *Arachi*s, where it appears to be an inherent generic feature. Species explored are listed in Appendix C.

## 5. GERMINATION AMONG GEOCARPIC LEGUMES

Whilst most leguminous seeds germinating underground are there by chance, those of geocarpic fruits are there by design. All three modes of germination occur amongst such species: examples follow. *A. hypogaea* has Mode 3, as just described; *Vigna subterranean*, on the other hand, has Mode 2. *Amphicarpeae bracteata* and *Centrosema rotundifolium,* both of which are not only geocarpic but also amphicarpic, also have Mode 2 with both forms of their seed. Both *Medicago aschersoniana* and *Trifolium subterraneum* have Mode 1.

## 6. AMBIVALENT GERMINATION

*Abrus precatorious* usually germinates in Mode 1, but I have occasionally found it germinating in Mode 2, and Sousa and Sousa ( 1981 ) have reported similar ambivalence in *Lonchocarpus rugosus* in defined geographic circumstances. Both these species have the palisade-less cotyledons to which such ambivalence is, perforce, confined.

## 7. DISCUSSION

As stated at the outset, current terminology of germination, as applied to the legumes, has its shortcomings: its terms are insufficiently discriminate.

**'Epigeal'** fails to make it clear that the distinctive locative outcome of Mode 1 is its **lofting** of the cotyledons, and thus fails to distinguish it from the also-epigeal, but non-lofting outcomes of Mode 3, and of Mode 2 when it chances to occur above ground.

**'Hypogeal'** aptly describes the locative outcome of Mode 2 when germination chances to occur underground, but the term becomes self contradictory and confusing when stretched to include its outcome when chancing to occur above ground. Hypogeal germination, at any rate among the legumes, is not inherent: it is merely the outcome, in seeds with an inactive hypocotyl, of their chance location underground at the time. The inherent feature appears rather to be the relative inertia of the hypocotyl.

**'Geal'** relates to non-lofting appearances of the cotyledons above ground, and is ambiguous in not distinguishing between them.

Current terminology fails to accommodate Mode 3 as a distinct mode of germination.

## 8. ACKNOWLEDGEMENTS

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# APPENDICES

Note. Species marked with an asterisk are known to be habitually surface-germinating: others among the larger-seeded species listed may well be so.

## Appendix A. Explored species germinating in Mode 1

| Species | Form of cotyledon | Typical dry wt. of embryo (mg) |
|---|---|---|
| *Abrus precatorius* L. (Ambivalent: also in Mode 2) | 4 | 48 |
| *Acacia galpinnii* Burtt Davy | 3 | 150 |
| *Adenanthera pavonina* L. | 4 | 110 |
| *Albizia julibrissin* Durazz. | 1 | 20 |
| *Baikiaea plurijuga* Harms * | 4 | 840 |
| *Bolusanthus speciosus* (Bolus) Harms | 1 | 16 |
| *Brachystegia spiciformis* Benth. * | 4 | 310 |
| *Caesalpinia pluviosa* DC. | 1 | 170 |
| *Cercidium microphyllum (* Torrey) Rose & I.M. Johnston | 1 | 80 |
| *Colophospermum mopane (*Benth.) J. Léonard * | 1 | 250 |
| *Crotalaria ocholeuca* G. Don | 1 | <2 |
| *Dalbergia martinii* F. White | 4 | 50 |
| *Glycine max* (L.) Merr. | 3 | 160 |
| *Julbernardia globiflora* (Benth.) Troupin * | 4 | 230 |
| *Laburnum anagyroides* Medik. | 1 | 13 |
| *Lonchocarpus rugosus* Benth. (Ambivalent: also in Mode 2) | 4 | - |
| *Lupinus pubescens* Benth. | 1 | 10 |
| *Medicago aschersoniana* Urb. | 1 | - |
| *Paraserianthes lophantha* (Willd.) I. Nielsen | 3 | 23 |
| *Peltophorum africanum* Sonder | 1 | 50 |

(continued)

## Appendix A. Explored species germinating in Mode 1

(continued)

| Species | Form of cotyledon | Typical dry wt. of embryo (mg) |
|---|---|---|
| *Pericopsis angolensis* (Baker) van Meeuwen | 3 | 240 |
| *Phaseolus lunatus* L. | 4 | 870 |
| *Phaseolus vulgaris* L. | 4 | 300 |
| *Piscidia piscipula* (L.) Sarg. | 1 | 16 |
| *Robinia pseudoacacia* L. | 1 | 10 |
| *Schizolobium parahyba* (Vell.) S.F. Blake * | 2 | 390 |
| *Tamarindus indica* L. | 4 | 580 |
| *Trifolium bocconei* Savi | 1 | <1 |
| *Trifolium subterraneum* L. | 1 | <4 |
| *Ulex europaeus* L. | 1 | <2 |
| *Vigna aconitifolia* (Jacq.) Maréchal | 4 | 20 |
| *Vigna mungo* (L.) Hepper | 4 | 36 |
| *Vigna radiata* (L.) R. Wilczek | 4 | 53 |
| *Vigna unguiculata* (L.) Walp. | 4 | 220 |

## Appendix B. Explored species germinating in Mode 2

Note. All species have Form 4 cotyledons

| Species | Typical dry wt. of embryo (mg) |
|---|---|
| *Abrus precatorius* L. (Ambivalent: also in Mode 1) | 48 |
| *Afzelia quanzensis* Welw. * | 1440 |
| *Amblygonocarpus andongensis* (Oliver) Exell & Torre | 220 |
| *Amphicarpaea bracteata* (L.) Fernald (Aerial seed) | 22 |
| (Subterr. seed) | 320 |
| *Bauhinia galpinii* N.E. Br. | - |
| *Bauhinia variegata* L. * | 97 |
| *Caesalpinia decapetala* (Roth) Alston | 110 |
| *Cajanus cajan* (L.) Millsp. | 130 |
| *Castanospermum australe* Cunn. & Fraser * | 16900 |
| *Centrosema rotundifolium* Benth. (Aerial seed) | 53 |
| (Subterr. seed) | 90 |
| *Cicer arietinum* L. | 330 |
| Dioclea violacea Benth. | 3100 |
| *Entada rheedii* Spreng. | 5700 |
| *Erythrina abyssinica* DC. | 86 |
| *Erythrina lysistemon* Hutch. | 78 |
| *Gymnocladus dioicus* ( L.) K. Koch | 550 |
| *Inga semialata* (Vell.) C. Mart. * | 370 |
| *Isoberlinia angolensis* (Benth.) Hoyle & Brenan * | 3670 |
| *Lathyrus latifolius* L. | 41 |
| *Lonchocarpus rugosus* Benth. (Ambival: also in Mode 1) | - |
| *Mora oleifera* (Hemsley) Ducke * | 330000 |
| *Mucuna pruriens* (L.) DC. var. utilis (Wight) Burck | 750 |
| *Pentaclethra macroloba* (Willd.) Kuntze | - |
| *Phaseolus coccineus* L. | 940 |
| *Pisum sativum* L. | 120 |
| *Saraca thaipingensis* Prain | 7100 |
| *Tylosema fassoglensis* (Schweinf.) Torre & Hillc. | 1200 |
| *Vicia faba* L. var. major Harz | 880 |
| *Vigna angularis* (Willd.) Ohwi & Ohashi | 75 |
| *Vigna oblongifolia* A. Rich. | 14 |
| *Vigna subterranea* (L.) Verdc. | 560 |

## Appendix C. Explored species germinating in Mode 3

Note. Only *Arachis* is known to have this mode.
*A. hypogaea* has, and the other species listed
presumably have, Form 4 cotyledons.

| Species | Typical dry wt. of embryo (mg) |
|---|---|
| A. batizocoi Krapov. & W.C.Greg. | 160 |
| A. benensis Krapov., W.C.Greg. & C.E. Simpson | 110 |
| A. cruziana Krapov., W.C.Greg. & C.E. Simpson | 250 |
| A. dardani Krapov. & W.C.Greg. | 180 |
| A. diogoi Hoehne | 150 |
| A. duranensis Krapov. & W.C.Greg. | 140 |
| A. glandulifera Stalker | 420 |
| A. helodes Krapov. & Rigoni | 85 |
| A. hoehnei Krapov. & W.C.Greg. | 140 |
| A. hypogaea L. | 450 |
| A. matiensis Krapov., W.C. Greg. & C.E. Simpson | 150 |
| A. monticola Krapov. & Rigoni | 230 |
| A. paraguariensis Chodat & Hassl. | 190 |
| A. pintoi Krapov. & W.C. Greg. | 100 |
| A. prostrata Benth. | 65 |
| A. stenosperma Krapov. & W.C. Greg. | 260 |
| A. sylvestris (A. Chev.) A. Chev. | 150 |
| A. valida Krapov. & W.C. Greg. | 190 |
| A. villosa Benth. | 180 |