in animals. Determination of the probable mode of action will explain the therapeutic profile. The safe and stable herbal extract may be marketed if its therapeutic use is well documented in indigenous systems of medicine, as also viewed by WHO. A limited clinical tribal to establish its therapeutic potential would promote clinical use. The herbal medicines developed in this mode should be dispensed as prescription drugs or even OTC products depending upon disease consideration and under no circumstances as health foods or nutraceuticals.

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ACKNOWLEDGEMENT. I thank EMR (HRDG), CSIR, New Delhi for the grant of Emeritus Scientist Scheme.

Received 30 August 1999; accepted 14 September 1999

The underground flower

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There are about 250,000 species of flowering plants in the world. Most of these produce flowers above ground. Thirty six species bear flowers on underground shoots. Flowers produced above ground may be of two types – chasmogamous and cleistogamous. The former are the normal flowers which open to receive pollen and/or pollinators. The latter type do not open and pollination is accomplished when they are closed. Flowers borne on underground shoots are invariably cleistogamous. The chasmogamous flowers are larger in size, produce copious amounts of pollen and large number of small seeds. Contrarily, the cleistogamous flowers are generally reduced in size, produce little pollen and few but heavier seeds[1].

FLOWERING involves transformation of a foliar into a floral bud through a series of histological, physiological and biochemical changes[2–4]. Since flower represents a modified shoot, and shoot is negatively geotropic, flowers almost invariably differentiate above ground. If flowers had been underground, the world would be devoid of the range of colours, variety of scents, and innumerable patterns and forms we see around us. The immense variety and enormous beauty of flowers benefits the plants and appeals the human eye. However, for the plant, underground flower formation could be an asset, as it substantially cuts down resource allocation involved in differentiation of accessory floral parts, biosynthesis of pigments and production of large quantities of pollen and nectar to reward pollinators. Importantly, underground flowers have assured pollination and seed set, with security against predators and vagaries of environment. Nevertheless, the invariable differentiation of flowers above ground has deprived plants of all the above advantages. However, as compensation the above-ground flowers confer on plants the ability for (i) cross-pollination, which generates variability, assures adaptability and evolutionary plasticity, and (ii) wider dispersal of pollen and seed for greater distribution and reducing intrapopulation competition.

That pollination and seed dispersal are the only major events which aerial flowers help to accomplish is reflected by *Tulipa*, *Sternbergia*, *Ixilioron* and such other bulbous angiosperms in which flower development is completed within the bulb, underground. The hidden flower is thrust above ground for accomplishing pollination, whereafter, seeds and fruits develop above ground.

Geocarpy

Have plants ever tried to combine the advantages of above ground flowering and underground development of fruits? The answer is provided by a few plants of which peanut is the most common example. In this legume, flowers differentiate above ground. Soon after pollination, they shed their petals and bend with the help of a peg to first

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come close to soil surface, and finally become subterranean. Pods and seeds mature underground[5]. This phenomenon of development of fruits underground is called geocarpy.

Besides *Arachis hypogaea*, development of aerial flowers and subterranean fruits is also known in *Trifolium subterraneum*, *Voandzeia subterranea* (L.) Thouars[6] and *Kerstingiella geocarpa* Harms[6].

There are also reports of the differentiation of fertile, cleistogamous flowers on the underground shoots of peanut[7–11]. Development of seed from flowers which are *ab initio* underground, is called amphicarpy. However, when these underground buds are brought above the ground and exposed to light, they open readily, and follow normal course of development[5], suggesting that these flowers are not truly cleistogamous and the plants are not truly amphicarpic. Some scientists believe that such flowers differentiate in response to the environment created by farmer's 'plow'[5].

Amphicarpy

During their evolutionary history, differentiation of true underground flowers has been attempted by flowering plants more than once. Of the nearly 250,000 flowering plants, only 36 (Table 1; refs 12–39) are amphicarpic.

Table 1. List of species that bear cleistogamous flowers on subterranean shoots

Family	Valid name of the species	Reference
Dicotyledons		
Asteraceae	*Catanche lutea* L.	12–15
(Compositae)	*Gymnarrhena micrantha* Desf.	14–17
Brassicaceae	*Cardamine chenopodifolia* Pers.	18, 19; Fig. 1 *a*
(Cruciferae)	*Geococcus pusillus* J. Drumm	14
Fabaceae	*Amphicarpa monoica* (L.) Ell.	18
(Leguminosae)	*Vicia sativa* ssp. *amphicarpa* (Dorth) Aschers & Graebn.	12–15; Fig. 1 *b*
	Vigna minima (Roxb.) Ohwi & Ohashi	20
	Lathyrus ciliolatus Sam. ex. Rech. f.	13–15, 21
	Pisum fulvum Sibth & Sm. var. *amphicarpum* Warb & Eig.	13–15, 22
	Amphicarpaea bracteata (L.) Fern.	23, 24
	Lathyrus amphicarpos L.	cf. 15
	L. setifolius L. var. *amphicarpos* DC	cf. 15
	Phaseolus sublobatus Roxb.	cf. 15
	Tephrosia lupinifolia DC Prod.	cf. 15
	Trifolium polymorphum Poir.	cf. 15
	Galacita canescens (Scheele) Benth.	cf. 15
Polygalaceae	*Polygala polygama* Walt.	18
	P. pauciflora	
Polygonaceae	*Emex spinosa* (L) Campd.	15, 25
	Polygonum thunbergii Sieb. et Zucc.	26
Scrophulariaceae	*Scrophularia arguta* Soland.	cf. 15
Urticaceae	*Fleurya podocarpa* var. *amphicarpa* Engl.	cf. 15
Violaceae	*Viola cucculata* Ait., *V. purpurea* Kell., *V. sciaphila**	18
Monocotyledons		
Commelinaceae	*Commelina virginica* L.	18, 27
	C. nudiflora L.	28, 29
	C. indehiscens Barnes.	30
	C. forskalaei Vahl.	18, 31–34; Fig. 1 *c*
	C. benghalensis L.	18, 32, 33, 35; Fig 1 *d*
Poaceae	*Amphicarpum purshii* Kunth	14, 15, 36–39
(Gramineae)	*A. floridanum* Chapman.	36
	A. muhlenbergianum (Schult) Hitchc.	cf. 15
	Chloris chloridea (Presl.) Hitchc.	37
	Eremetis (ca 4 species)	cf. 15
	Paspalum amphicarpum Ekman	36, 37

*Subterranean cleistogamy not confirmed.

These are distributed over 10 phylogenetically distantly related groups with a maximum concentration in the Fabaceae (~ 10 species) and Poaceae (8 species). Most amphicarpic plants are annuals; only a few are perennial. With a few notable exceptions, the amphicarpic taxa grow well in aerated, well drained sandy or gravely soils.

The characters shared by most amphicarpic plants (see Figure 1 *a–d*) include the presence of (i) self-fertile subterranean flowers that mature into large fruits and seeds with limited dispersal, and (ii) aerial flowers that are capable of cross-pollination and set many smaller fruits and seeds suited to long distance dispersal.

Flowers of aboveground capitula of *Gymnarrhena micrantha* Desf. a dwarf, annual desert composite, are chasmogamous, while those comprising the subterranean capitula are cleistogamous. The aerial capitula bear a large number of small, wind dispersed fruits. On the contrary, the

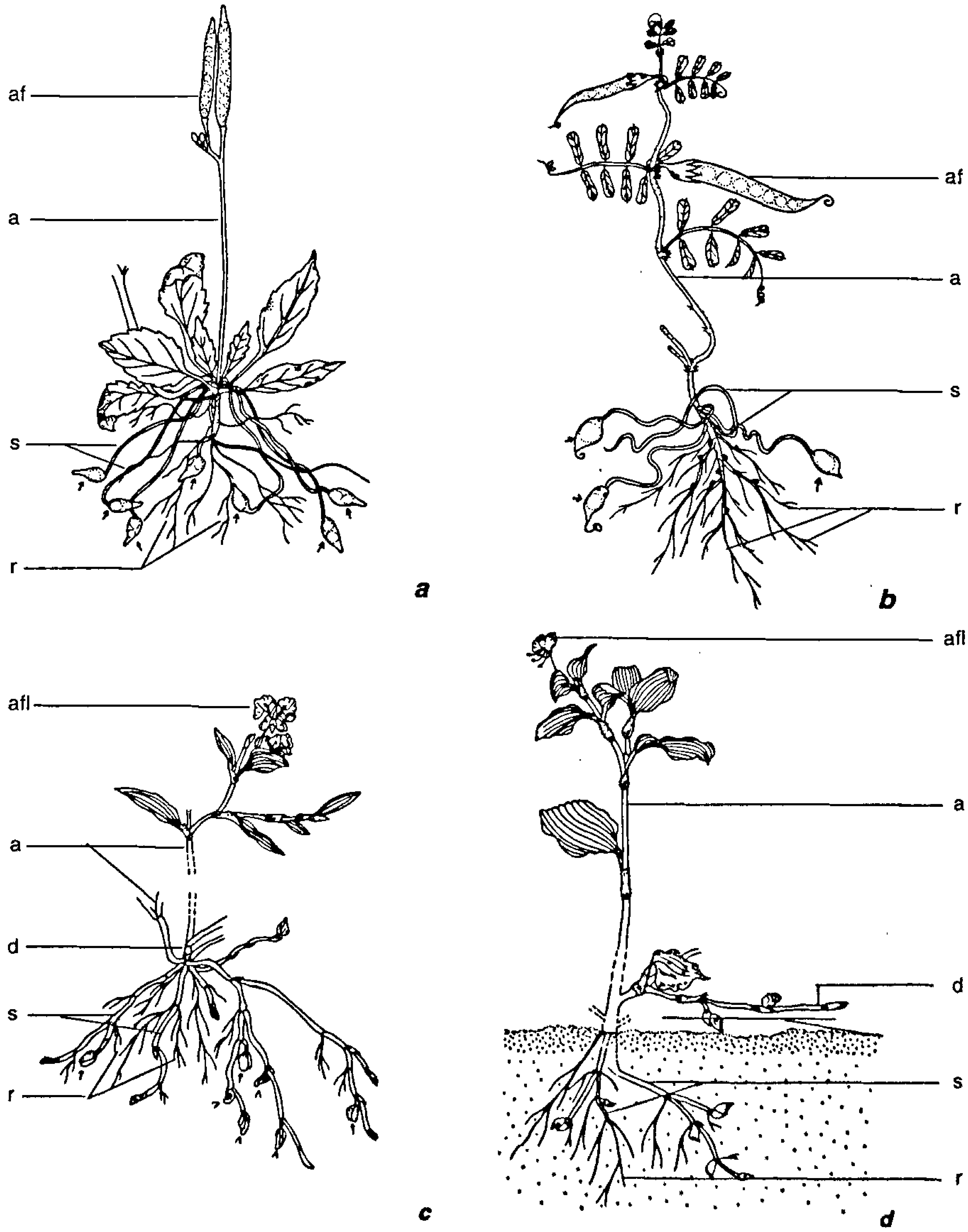

Figure 1 ***a–d.*** Hand drawings of plants of (*a*) *Cardamine chenopodifolia*; (*b*) *Vicia sativa amphicarpa*; (*c*) *Commelina forskalaei*; and (*d*) *C. benghalensis* showing fruits/flowers (marked by arrows) on aerial and underground shoots. r, roots; a, aerial; s, subterranean and d, diageotropic shoots; af, fruits; afl, flowers on aerial shoots.

subterranean fruits are large sized and fewer. They are never shed; their seeds germinate *in situ*[16].

Aerial flowers of the plant are potentially open-pollinated, which helps in increasing the genetic variability of the population. The wind dispersed achenes widen the distribution of the species to distant habitats. Subterranean flowers are invariably self-pollinated and are therefore, instrumental in preserving the parental genotype. Underground fruits and seeds improve chances of survival of these plants at specific microhabitats.

Amphicarpum purshii Kunth., an annual panicoid grass, also bears aboveground and subterranean spikelets on the same individual. The former are small and chasmogamous, while the latter are large and cleistogamous. The subterranean seeds are few but heavy. These account for most progeny seedlings. Aerial florets outnumber the subterranean flowers and contribute to the widening of genetic variability of the species[38].

Relative cost of aerial and underground flowers as exemplified by *Commelina* sp.

In the genus *Commelina* of Commelinaceae, five species are known to produce underground cleistogamous flowers. *Commelina forskalaei* (Figure 1 *c*) and *C. benghalensis*

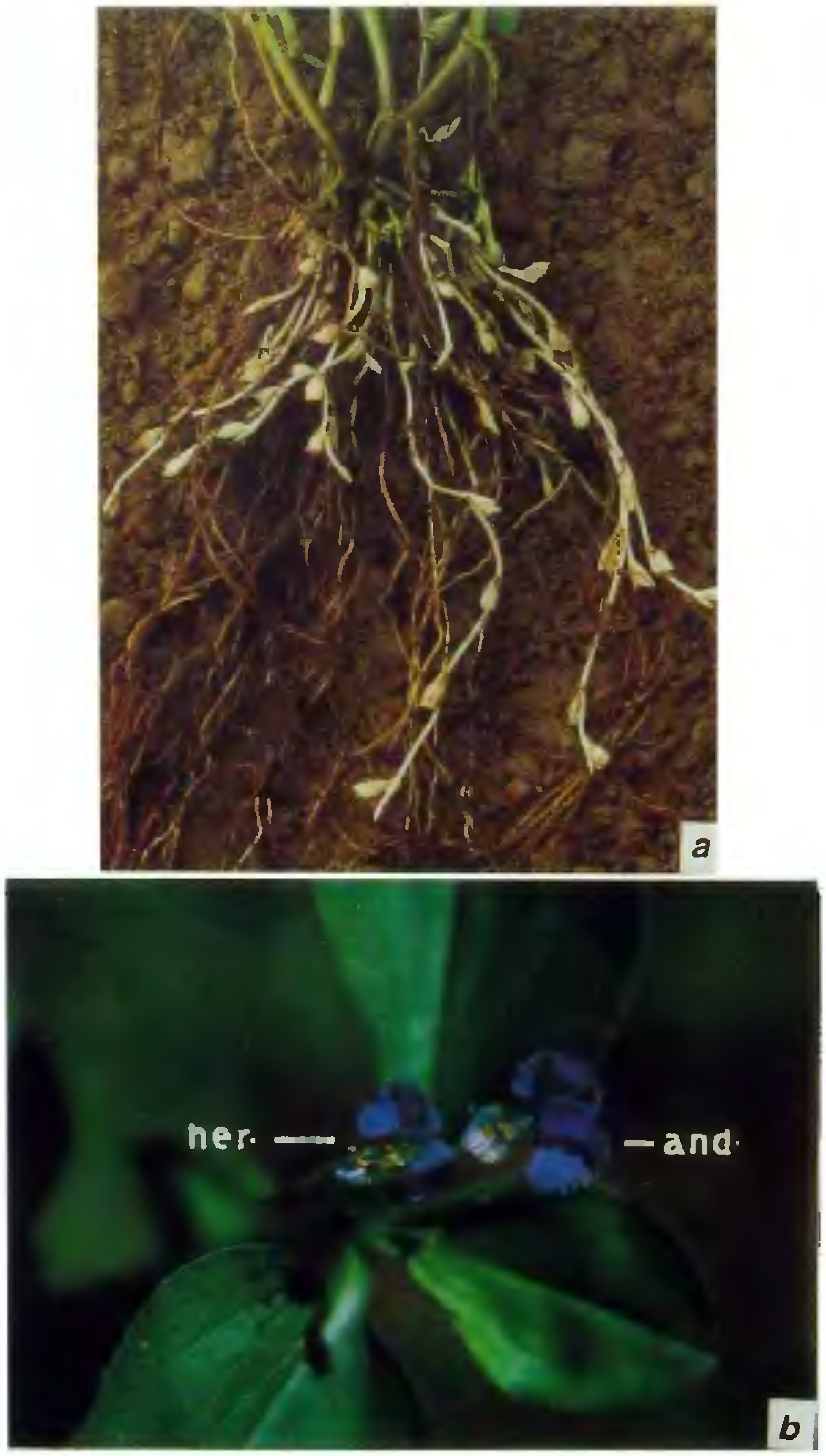

Figure 2. *a*, An uprooted plant of *C. benghalensis* with exposed roots (brown) and underground shoots (white) laden with flower containing spathes (white). *b*, Male (androgenic; and.) and hermaphrodite (her.) flowers of an aerial spathe of *C. benghalensis* in bloom (× 3).

(Figure 1 *d*) bear flowers on three types of shoots[33,34]; positively geotropic subterranean shoots, negatively geotropic cauline shoots and diageotropic shoots which run parallel to soil surface. The positively geotropic leafless shoots grow deep into the soil, and carry flowers inside colourless spathes (Figure 2 *a*). Flowers on other two types of shoot differentiate in green spathes and vary in number as well as structure. In *C. benghalensis* spathes on the diageotropic and subterranean shoots have a single hermaphrodite flower each, but aerial spathes have three and occasionally four flowers each. Flowers of aerial spathes are trimorphic; the oldest is male and chasmogamous, the second is hermaphrodite and chasmogamous and the youngest is hermaphrodite and cleistogamous (Figure 2 *b*). Flowers of the diageotropic spathes are always chasmogamous, and those of the subterranean spathes are invariably cleistogamous.

The subterranean cleistogamous flowers are obligately self-pollinated. Their floral parts are small. The ratio between the resources consumed in the differentiation of their essential (stamens and carpels) and accessory organs (sepals and petals) is 3 : 2 (60 : 40%). Resource expenditure on pistil differentiation is 20% higher than that on the differentiation of stamens. This is reflected in the greater biomass of the pistil. Cleistogamous flowers have fewer pollen grains and their pollen–ovule ratio is 2,305 : 1. They also produce fewer but larger and heavier seeds than their counterparts on aerial and diageotropic shoots. This increase in size and weight of seeds is caused by the diversion of resources saved from male function and differentiation of extrafloral parts to the female function. The diversion is made possible by assured pollination due to cleistogamy despite the availability of fewer ovules borne by the pistil.

On the contrary in all chasmogamous flowers, aerial as well as diageotropic, greater share of resources is invested in floral advertisement; it approaches 62% in male and 42–50% in hermaphrodite chasmogamous flowers. From the total reproductive investment on chasmogamous hermaphrodite flowers, 56–61% investment is channelized to male function. Even in cleistogamous flowers of the aerial branches, the ratio between pistil and stamen biomass is male biased unlike their subterranean counterparts.

Although anther dehiscence and stigma receptivity overlap in hermaphrodite chasmogamous flowers leading to self-pollination, these flowers hold the potential for cross-pollination because of their colourful petals and anthers, profuse pollen production and very frequent visitation by a variety of hymenopteran insects. The potential for cross-pollination can get expressed in the event of the failure of self-pollination.

From what has been stated above, it follows that reproduction through underground flowers is less expensive, yet more assured. In terms of investment/allocation of the resources, the seed produced underground is cheaper than that set above-ground. If selection pressure has not worked against above ground flowers, and they continue to differentiate on the plant, it is because they help in retrieving one of the costs of sex, that of sharing gene(s)[40] through occasional outcrossing.

In most amphicarpic plants including *C. benghalensis*, seedlings produced by subterranean seeds are more vigorous than those produced by aerial seeds. As a consequence, they have greater competitive ability and better survival compared to seedlings resulting from aerial flowers/fruits.

According to Cheplick and Quinn[14], it is perhaps on account of the importance of subterranean seeds to individual fitness that they are produced early in ontogeny, well in advance of aerial seeds. Zeide[17] has termed early production of subterranean seeds and fruits a 'pessimistic' strategy of plants, suited to highly disturbed habitats, where survival even up to the end of growing season is uncertain. In such situations it is a definite advantage if plants produce fruits as early as possible. In contrast, the formation of aerial fruits is an 'optimistic' strategy, whereby reproduction is delayed until the end of growing season, when time and growth conditions have resulted in accumulation of sufficient resources in the plant body[15].

Evolution of amphicarpy

What factors have led to the evolution of amphicarpy is a question that remains to be answered. A number of hypotheses have been proposed from time to time. Since subterranean seed production has evolved independently in phylogenetically unrelated taxa, the factors underlying their evolution are most likely to differ from species to species. Mattatia[13,21] believes that amphicarpy in the genus *Lathyrus* has arisen independently at least three times.

According to one hypothesis, the adaptive significance of subterranean seeds is to expose them and the plants differentiating therefrom to similar, presumably favourable, microhabitat as that of the parent. However, in experiments conducted on *Amphicarpum purshii*, plants raised from subterranean seeds close to the parent did not always outperform the plants raised at places far removed from the parent[15]. A related possibility is that being better shielded from the extreme fluctuations of microclimate at the soil surface, the buried seeds retain viability, germinate and establish seedlings far better than the seeds lying exposed on soil surface. This hypothesis seems particularly plausible for those amphicarpic plants which inhabit dry habitats since 'active seed burial will, for instance, ensure availability of greater soil moisture'[15]. Supporting evidence for this comes from *Emex spinosa*[25], *Amphicarpum purshii*[15] and to a certain extent *Commelina benghalensis*. In all these taxa, none (some in *C. benghalensis*) of the subterranean seeds germinated when they were spread on the soil surface. However, this hypothesis does not explain evolution of subterranean seed production in species inhabiting mesic environments.

Another hypothesis is that severe predator pressure must have led to the evolution of subterranean seed production which is understandable since buried flowers, fruits and seeds are comparatively safe from foraging animals. 'In grasses, it is easy to envisage the selective advantage of subterranean seed production under conditions of intense grazing[15].' Even in deserts where animals can be a major cause of seed predation, seed burial might be an adaptive response.

Detailed comparative data on the effect of herbivory on aerial and subterranean flowers, fruits and seeds are required to confirm this hypothesis.

Another advantage which can accrue to a plant from subterranean seeds becomes explicit during a major disturbance which periodically destroys the aerial portion of a herbaceous plant. At this critical juncture in plant's life cycle, only individuals producing subterranean propagules would contribute to the formation of next generation. This would be true especially for annuals which usually lack vegetative propagation and therefore, have a single means of reproduction. In *Amphicarpum purshii*[15], *Vigna minima*[20] and *Commelina virginica*[27], amphicarpy has been viewed as possible adaptation to escape fire.

All the above hypotheses concede selective advantage to subterranean reproduction. If this were so, why do amphicarpic plants still produce aerial seeds? Is it for combating the constraints associated with subterranean reproduction? The retention of aerial flowers may be a selective compromise between the risks associated with production of either of the two types of flowers.

Detailed ecological, evolutionary and physiological studies are required to fully appreciate the actual significance of underground flowers.

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ACKNOWLEDGEMENTS. V.K. thanks the Head, Depa Botany, University of Jammu for providing the necessary l laboratory facilities and to Council of Scientific and Research, New Delhi, for the award of Junior and Senior Fellowships.

Received 15 June 1999; revised accepted 28 October 1999