

Some Implications of Precocious Flowering in *Collospermum*¹

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IN HETEROBLASTIC DEVELOPMENT the juvenile and adult phases of a plant have the same genotype but the phenotypes are different, and Cook (1968, p. 97), noting that such phenotypic plasticity has undoubtedly led to a large number of "paper species," finds it rather shocking that so little information on phenotypic modification is presented in formal taxonomic work. In the case here described, in the Pacific genus *Collospermum* (Liliaceae), a single plant can, during its lifetime, display contrasts comparable to some that characterize species or sections in the closely related genus *Astelia*.

In setting up the genus *Collospermum*, Skottsberg (1934, pp. 72–88) recognized three species in New Zealand. Two, *C. bastatum* (Col.) Skottsberg and *C. microspermum* (Col.) Skottsberg, are certainly distinct, though vegetatively very similar. The third species, *C. spicatum* (Col.) Skottsberg, had been described independently by Carse (1926, p. 91) under the name *Astelia nana*, but Moore (1966, pp. 231–232) confirmed Skottsberg's suspicion that it was based on a "dwarfy" stage or on prematurely flowering seedlings. It is the inflorescence that shows the most striking contrasts at different stages; at the juvenile or "spicatum" stage, plants of the two species are very much alike and very different from their respective adults.

THE ASTELIAD INFLORESCENCE

The species of *Collospermum* and *Astelia*, conveniently referred to as asteliads, are perennial herbs in which a short erect stem with very short internodes bears trifariously arranged, long-linear leaves with broad sheathing bases, and the inflorescence is terminal. Dioecy is general, though functionally hermaphrodite flowers sometimes occur on predominantly male plants. The inflorescences of the two sexes are built on

the same plan, and they have been found to provide some good taxonomic characters at the specific level though not, as was once thought, a strong contrast between the two genera.

The leafless peduncle bears a panicle with a series of spathes in strict divergence of 1/3. The lower spathes are quite leaflike; upwards they become gradually smaller and in texture more like leaf-sheaths. The main axis ends in a raceme, and commonly each spathe subtends at least one lateral raceme. Each raceme bears flowers in a more or less close spiral, and each flower is usually associated with a bracteole. Bracteoles vary widely in size, even within one inflorescence.

Three types of inflorescence can be distinguished, though there are intermediates between them (Fig. 1):

Basic or type B. Spathes are well developed, each subtends a simple raceme and the terminal raceme is also simple; the total number of racemes, usually only one more than the number of spathes, rarely exceeds a dozen.

Complex or type C. Lower spathes subtend branched subinflorescences composed of two to five or more racemes; the part above the uppermost spathe usually resembles a lower lateral subinflorescence, and the total number of racemes greatly exceeds the number of spathes.

Reduced or type R. Spathes are few; each subtends, not a raceme, but only one to a very few flowers, and the terminal raceme is simple and short; ultimate reduction is to a single flower.

Types B and C occur both as lax open panicles with long or short racemes, and as more compact inflorescences, some female ones being very tightly congested.

Table 1 shows approximately how these inflorescence types are distributed in the subgenera and sections of *Astelia* and in *Collospermum*, and how they are related to size of flowering plants. Type C is characteristic of large to very large plants of predominantly lowland *Astelia*

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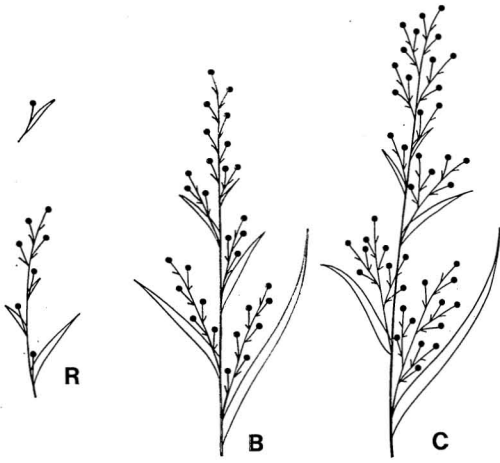


FIG. 1. Inflorescence types in asteliads. R, Reduced; B, basic; C, complex. (Drawn by B. McCulloch.)

species. At montane levels where plants are of medium size, some species have type C, some type B. Type R occurs only on small plants (i.e., less than ca. 30 cm tall), mostly in *Astelia* species of high altitudes or high latitudes, but also on precociously flowering small plants of *Collospermum* at low altitudes in New Zealand.

FLOWERING IN *Collospermum*

The two New Zealand species are predominantly epiphytic or rupestral, and in the wild neither is free flowering; it is possible (as in

some species of *Astelia*) to examine hundreds of plants at the right season without finding a single one in bloom. *Collospermum microspermum* flowers about November to January and *C. hastatum* a month or so later. Wheeler (1966, pp. 108–109) records that in both species buds are initiated some 10 months before flowering, while reduction division does not occur until 7 to 8 months later, in spring. (In six other asteliads Wheeler reports contrasting phenological patterns.) Inflorescences often develop very rapidly in the later stages, taking less than 2 weeks from first emergence to full flower. At the same time innovation shoots become obvious in the axils of one to three leaves immediately below, and these new shoots rarely flower in less than 3 years. As in the other two species of the genus (*C. samoensis* from Samoa and *C. montanum* from Fiji) inflorescences are normally of type B.

Type R inflorescences have been found on small single-tuft (seedling?) *Collospermum* plants in the wild, especially on those growing on or near the ground. Individual plants grown in pots have produced type R inflorescences singly, or two simultaneously, or up to three in succession at intervals of 3 to 12 months. These inflorescences appear irregularly through the year, and often remain only partly emerged for long periods. The highest proportion of flowering plants seen were in a group that had been grown on a wall under abnormally dry and sunny conditions where "hunger-forms" might

TABLE 1
INFLORESCENCE TYPES IN ASTELIADS
(Approximate range of leaf length of flowering plants in centimeters)

GENUS	SUBGENUS	INFLORESCENCE		
		TYPE R	TYPE B	TYPE C
		SECTION	SECTION	SECTION
<i>Astelia</i>	<i>Astelia</i>	<i>Astelia</i> 4 spp. (2–30 cm)	<i>Palaeastelia</i> 1 sp. (80–110 cm)	<i>Desmoneuron</i> 3 spp. (50–300 cm)
	<i>Asteliopsis</i>	<i>Micrastelia</i> 1 sp. (5–8 cm)	<i>Periastelia</i> 8 spp. (12–150 cm)	<i>Isonuron</i> 2 spp. (50–200 cm)
	<i>Tricella</i>	<i>Tricella</i> 1 sp. (8–16 cm)	<i>Tricella</i> 4–5 spp. (15–200 cm)	<i>Tricella</i> 4–5 spp. (30–350 cm)
<i>Collospermum</i>		Juvenile 2 (+?) spp. (10–30 cm)	Adult 4 spp. (—100 cm)	

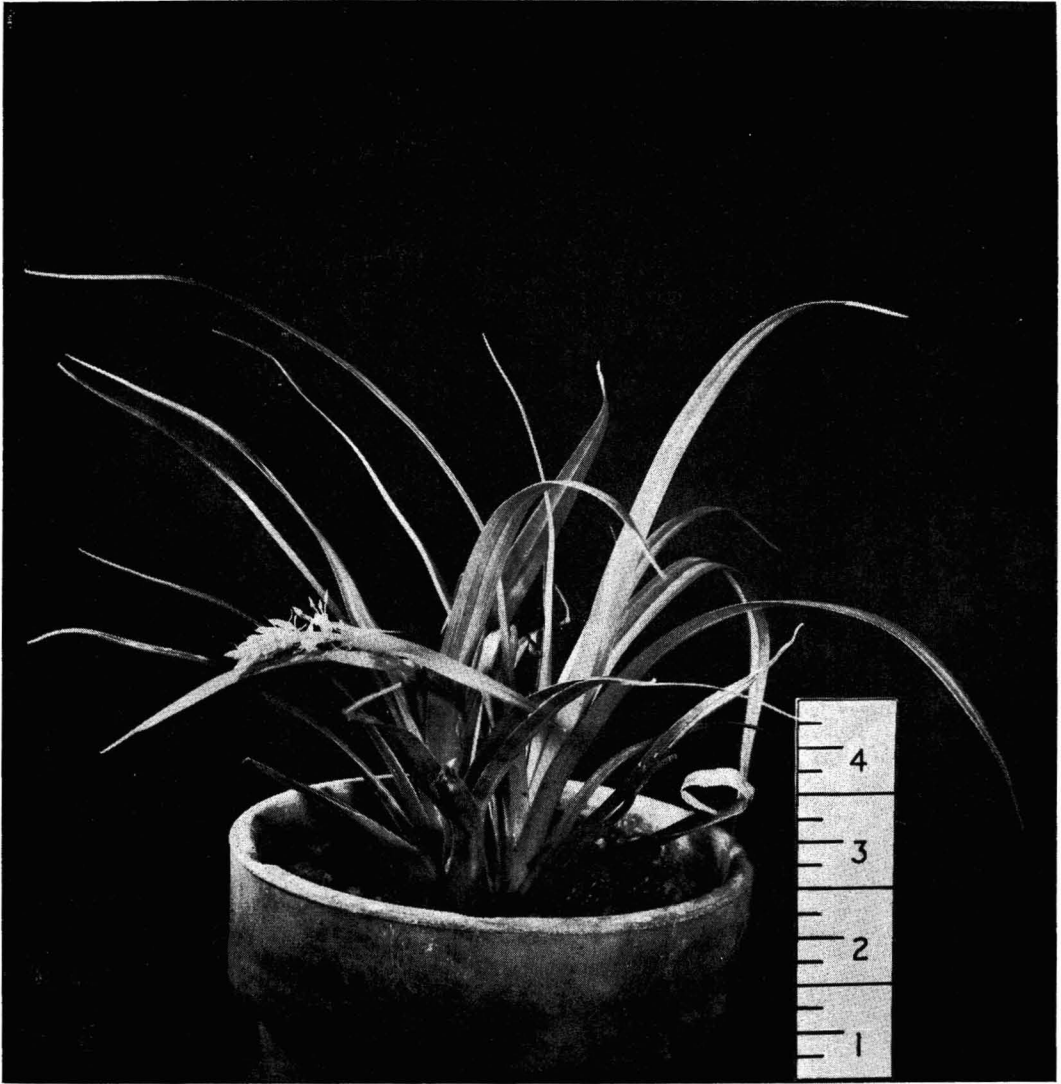


FIG. 2. *Collosperrum bastatum*: G3073, plant with male inflorescence, June 1962. Scale in inches. (Photograph by A. Underhill.)

be expected. On the other hand, an apparently vigorous small plant of either species can produce an unseasonable type R inflorescence and then grow on directly to produce, when it is very much larger, a good type B inflorescence at the time of the year normal for the species (Figs. 2, 3).

The type R inflorescence of *Collosperrum* is of rather uniform construction. The flowers are much smaller than in larger inflorescences, but

both male and female are well developed; in some plants flowers are of hermaphrodite form. Though fruit is rarely seen in the wild, some good seed can be set, and seedlings have been grown from the fruits of a type R inflorescence. In an intermediate form the lower one or two spathes subtend short narrow racemes with normally bracteolate flowers, the middle spathes have solitary flowers in their axils, and there is a short terminal raceme of bracteolate flowers.

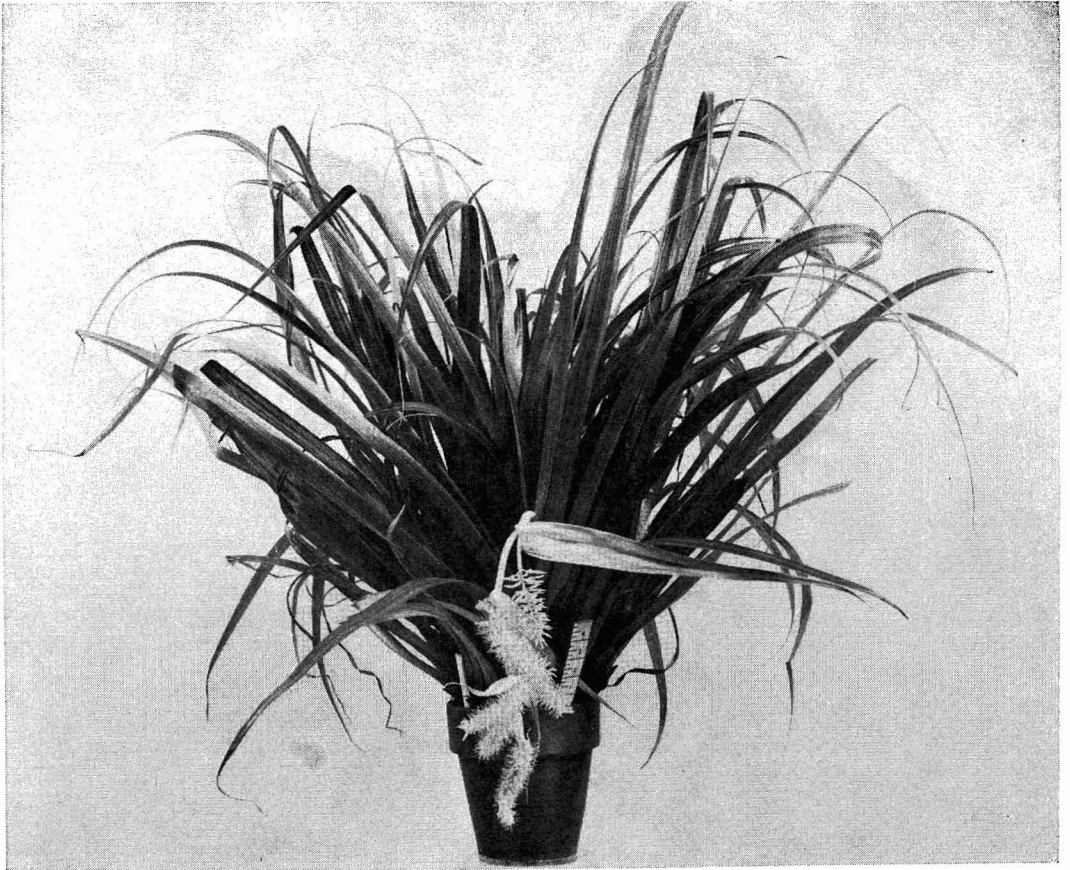


FIG. 3. *Collospermum hastatum*: G3073, plant with male inflorescence, February 1969. Scale in inches. (Photograph by C. J. Miles.)

DISCUSSION

Skottsberg pointed out that the type R inflorescence is homologous, not with the terminal raceme of other species, but with an entire panicle. In *Collospermum* the sporadic flowering habit and slow bud development make it difficult to locate appropriate young stages for anatomical investigation, but the early development could resemble that described for *Carex* by D. L. Smith (1966, pp. 483-484). If this is so, then the young spathe would subtend a rudimentary axis bearing two primordia: (a) a terminal primordium capable of developing into a raceme; (b) a lateral flower primordium. Normally one or the other would abort. One can imagine that in the juvenile plant it is the terminal primordium (a) that aborts, while the other primordium (b) develops into a flower

apparently in the axil of the spathe, resulting in the type R inflorescence. In older plants it is the terminal primordium that develops. Different conditions would no doubt favor one or other primordium. Smith (1969) reports elaborate experiments on *Carex*, using explants in aseptic culture, and he states (p. 513): "The implication of these results is that a factor produced by actively growing roots is involved in the control of branching of the inflorescence."

In *Collospermum*, while it seems possible to obtain type R inflorescences almost indefinitely if plants are kept small, it is not yet clear whether all plants flower while young, that is, whether heteroblasty is obligate. Several species of *Astelia*, of comparable adult size to *Collospermum*, have been grown from seed, and all these plants have been passed through their small stages without flowering. No type R in-

florescence has been seen on any large-growing *Astelia* in the wild, though type B sometimes precedes type C. Possibly precocious flowering occurs in extra-New Zealand species of *Astelia*, though it does not seem to have been recorded; certainly it should be watched for in the Pacific species of *Collospermum*.

The very small-growing astelias, some of them only 1 to 3 cm tall, show normal phenotypic plasticity in that larger plants of a species produce more flowers per inflorescence than do smaller ones, but almost all are of type R; only a few range from this to miniature type B inflorescences. Here no information is at hand about seedling performance or relation of inflorescence size to maturity of the plant as a whole or of the individual tuft.

Whereas small inflorescences in asteliads are always relatively simple, the largest are not necessarily the most complex, nor are the most complex inflorescences confined to the largest-growing species. *Astelia nervosa*, which is comparable in size to *Collospermum*, offers a special case in displaying divergent adult inflorescence patterns; these occur on geographical and/or ecological variants which differ infraspecifically in vegetative characters. In most or all North Island and some South Island populations, well-grown inflorescences characteristically have some branched racemes in at least the lowest one or two spathes, thus tending towards type C, whereas in other (usually more silvery-leaved) South Island populations the inflorescences are regularly of type B.

From observations to date the following points emerge:

1. The kind of precocious flowering characteristic of the two New Zealand species of *Collospermum* has not been seen in species of *Astelia* of similar size and habit.

2. Precocious flowering in *Collospermum* is prolonged under poor growing conditions.

3. The differences between juvenile and adult inflorescences in individual plants of *Collospermum* are of the same order as those found between small and large species of *Astelia*.

4. Both minimum and maximum complexity of inflorescence seems to be genetically controlled in asteliads.

SUMMARY

In the two New Zealand species of *Collospermum* (Liliaceae) much simpler inflorescences are produced on small plants than on large ones, and photographs record this kind of heteroblastic development in individual plants of both species. Matching precocious flowering is not known in the closely related and much larger genus *Astelia*, where three generalized inflorescence types can be recognized: one resembling that of young *Collospermum*, one closer to that of adult *Collospermum*, and one more elaborate still; these types are more or less characteristic of certain sections of *Astelia*. In both genera minimum and maximum complexity of inflorescence seem to be limited in any one species, and *Collospermum* displays the widest intraspecific range.

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