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GREGARIOUS FLOWERING OF THE TERRESTRIAL ORCHID BROMHEADIA FINLAYSONIANA

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It is well known that certain epiphytic orchids flower gregariously. Several authors have made detailed observations of the behaviour of the species *Dendrobium crumenatum*, which is one of the commonest orchids in Malaya, occurring on nearly every old tree and producing a beautiful but short-lived display of fragrant white flowers several times during the year. Other less common species of Dendrobium behave similarly. The flower buds of these plants develop underneath their protecting bracts to a stage at which all parts are formed, and then rest, sometimes for some weeks, before entering upon their final period of growth, which ends in flowering after a definite number of days. The stimulus which causes the buds to resume growth appears to be an unusually prolonged cool period, of a temperature comparable to that of normal night temperature. The literature concerned is fully cited by Kerling (1941).

Other orchids besides Dendrobiums behave in this way (and indeed the phenomenon is not confined to orchids, as the behaviour of Zephyranthes, investigated by Kerling, is essentially similar). The species *Bromheadia alticola*, belonging to a rather isolated and peculiar genus of Western Malaysia, has an elongating inflorescence of conspicuous 2-ranked bracts, which thus appears very different from that of *Dendrobium crumenatum*, but its flower-buds rest in a similar manner and respond to cool temperature in the same way, opening their flowers a day before *D. crumenatum*. There is a very common terrestrial species of Bromheadia which has indications of a gregarious flowering, but its behaviour is so different from that of the

other orchids already mentioned that I was doubtful if it could be a response to the same kind of stimulus. The results of my investigations of this terrestrial Bromheadia are here reported, and they are interesting as indicating a behaviour mid-way between uninhibited flowering and the peculiar condition of *Dendrobium crumenatum*.

Bromheadia finlaysoniana is very common in the scrubby vegetation which develops in Singapore on land that has been cleared and abandoned. It grows in association with Gleichenia, Nepenthes, *Gahnia tristis*, Melastoma, *Wormia suffruticosa* etc. The soil is often a hard compacted clay and it takes a considerable time for a vegetation of trees to develop. The plants of the long-persistent scrub are exposed to full sun, and most of them have tough leaves. The roots of the Bromheadia are close to the surface of the soil, so that they must soon feel the effect of dry weather, though they are protected by the shade of the other plants around them. A week without rain in Singapore is a dry period; two weeks is very dry; three weeks very rare. A few days without rain under the tropic sun are a strain on most plants which have not a deep soil to supply their roots with water.

Plants of *Bromheadia finlaysoniana* have erect leafy stems two or three feet high, with a terminal inflorescence. The floral bracts alternate in close succession, and the inflorescence continues to elongate for several months; its tip commonly bears three flower buds at different stages of development (Fig. 1). Each bud takes 20–30 days to flowering from the time when it is first visible beyond its bract; the interval between the times of opening of successive buds varies considerably. Each flower lasts one day only.

If the inflorescences and their buds on all the plants continued to grow at a uniform rate, one would expect a random flowering, with no great differences in the number of flowers to be seen on different days. But when we grew a number of Bromheadia plants together in one bed at the Botanic Gardens, we found that at irregular intervals of about 6–12 days there were a considerable number of flowers open together (the number varying much on different occasions) with few flowers on other days. It seemed that there was some influence at work causing gregarious flowering of an irregular nature, even though all buds appeared to be developing continuously. In order to understand the matter better, I measured the lengths of buds on selected inflorescences daily over a period of several months. I did this in 1940, the plants measured being grown in pots

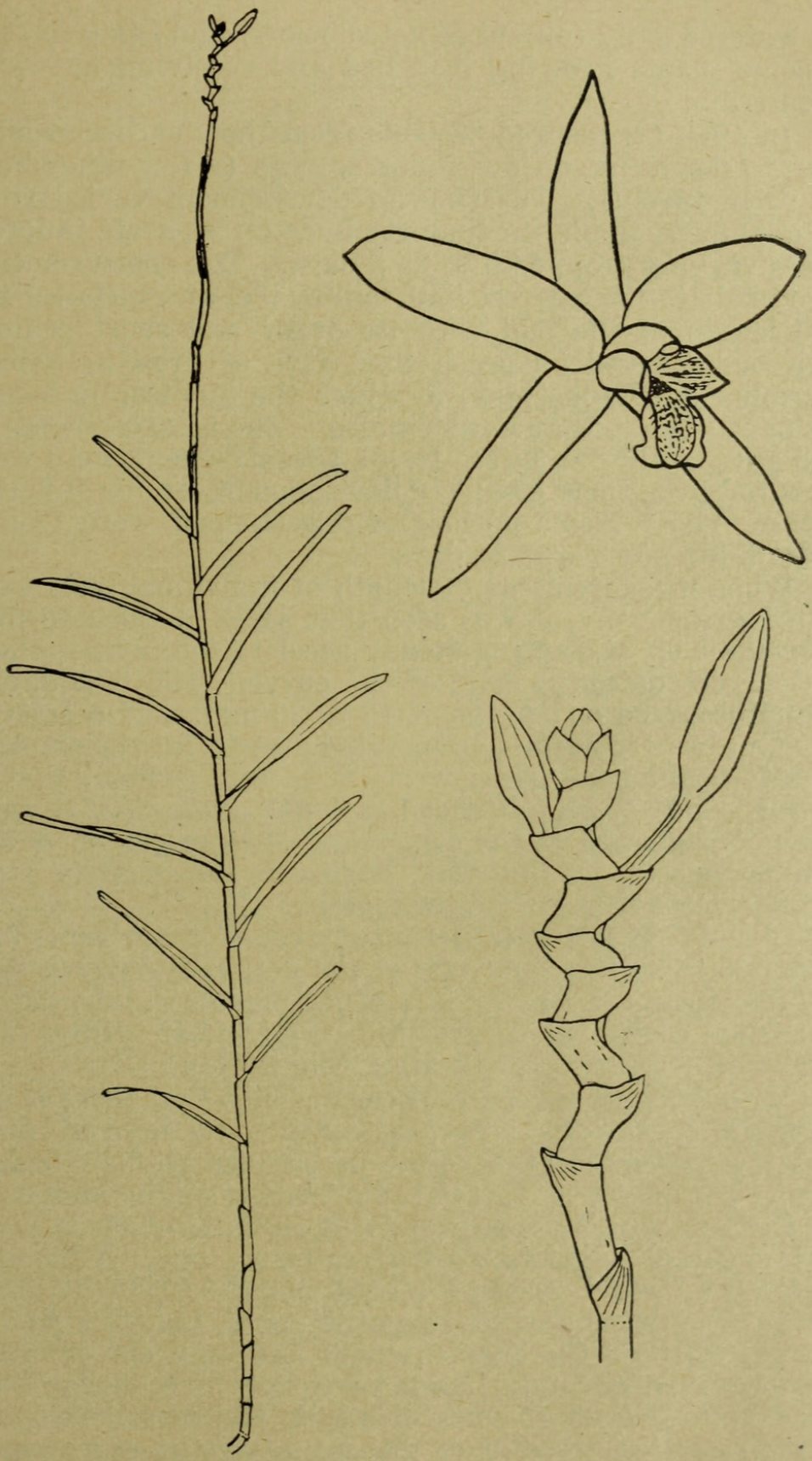

Fig. 1. On left, one complete stem of *B. finlaysoniana*, × ¼. On right, inflorescence with 3 flower-buds at different stages (× 2) and an open flower (× 1).

and watered daily (except as noted below) and again in 1948 on some plants growing in a bed and receiving no water except rain.

In 1940 I measured 32 buds from their earliest visible stage to flowering, on five inflorescences (a few other buds fell prematurely). The time of development varied from 20 to 30 days, the mean time for buds on separate inflorescences varying from 24.5 to 25.5 days. The measurements were made to the nearest half millimetre, and included the total length of the bud with its ovary and short pedicel. Each bud showed an accelerated rate of growth, with a maximum on the last day, in which the increase in length was usually more than a centimetre. The measurements of 1948 gave similar results. In all, seventy-one flowers were measured over their complete development, on six inflorescences. The extreme periods of development were 19 and 34 days, the mean was 24 days.

When measurements of length of individual buds were plotted graphically, it was seen that some of them formed an even curve, showing a steady acceleration, while others showed retardation in part of the curve. The retardation usually occurred at lengths of 13 to 20 mm., and sooner or later gave way to normal accelerated growth for the six days prior to opening of the flower. It is thus evident that if several buds with retarded growth resumed normal accelerated growth at the same time, they might all flower simultaneously. In this way, buds which started to grow on different days might flower together (fig. 2). There can be no doubt that such retardation and subsequent resumption of normal growth is the cause of the gregarious flowering.

Two questions now arise. What causes the retardation of normal accelerated growth? And what causes the resumption of such growth after retardation?

My observations lead to the conclusion that there is not one single cause of retardation, and there is need of much further investigation before the matter can be fully understood. The following facts have a bearing on the matter.

In 1940, a potted plant under observation had its roots much exposed, owing to wash from heavy rain. I thought to help the plant by adding a little burnt earth (the usual potting soil) to cover the exposed roots, but this had a contrary effect. The plant (which had only one inflorescence) responded in a remarkable way. A flower-bud, which had attained 15 mm. in length and was developing normally, ceased growth on the day after the extra earth was added, and made no further growth, persisting 22 days before falling. A smaller bud, 5 mm. long, ceased growth and fell after only one day. This is clear evidence of a

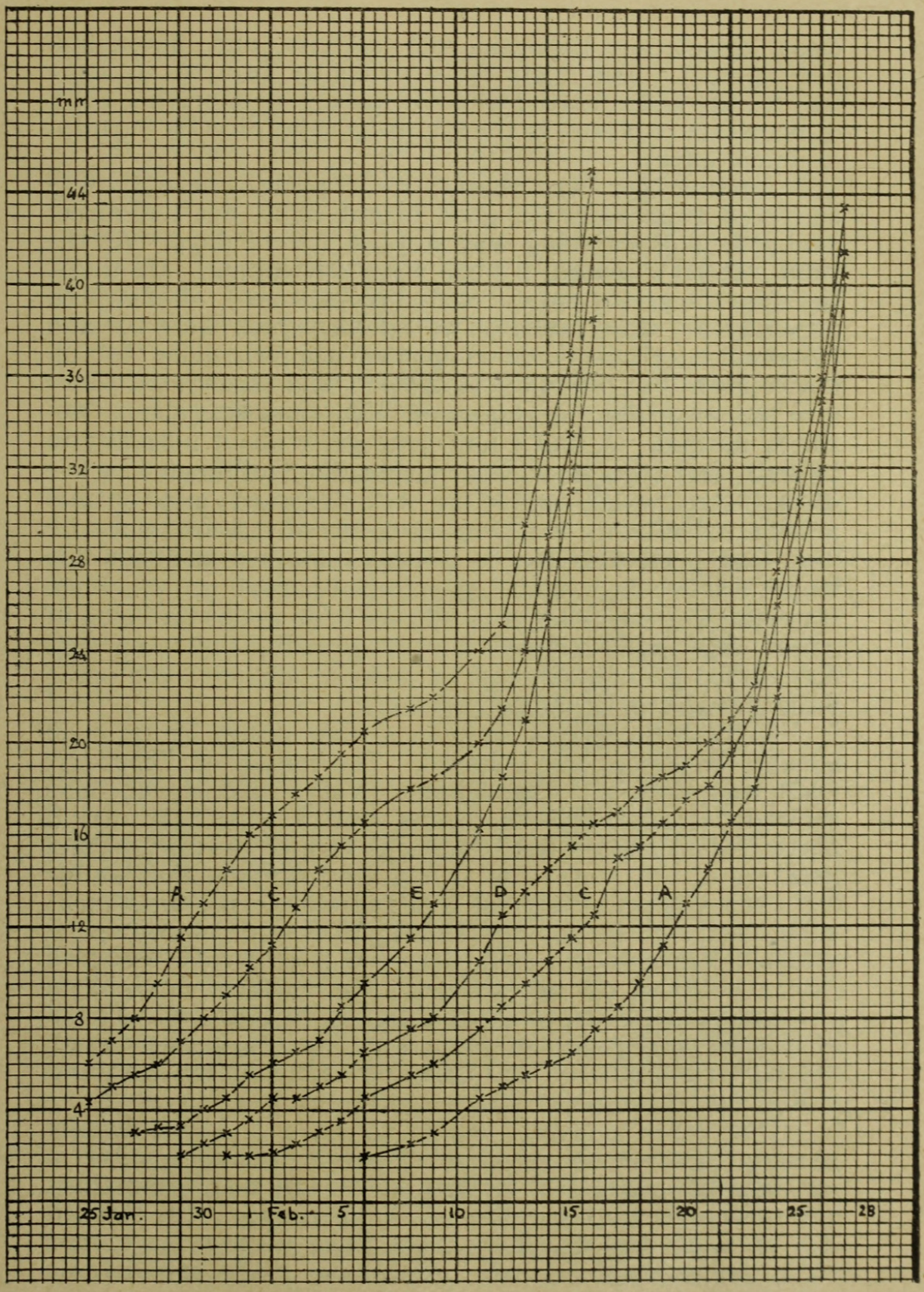

Fig. 2. Graphs showing growth of six flower-buds to the day before flowering. The left-hand group flowered on 17th February, the right-hand group on 28th February. Letters refer to the inflorescences on which the buds were borne; the first and last of the six buds were both on inflorescence A.

close association between root activity and flower-bud development. The roots were evidently injured in some way by the added earth; whether merely by depriving them of necessary exposure to the air, or by some directly harmful chemical effect.

Another pot was moved to a place where it was sheltered from rain (in good bright light, but not direct sunlight) and watering was stopped for 14 days. At the time watering ceased, 9 buds were developing. Of these, the four largest (one on each inflorescence) all flowered normally 2–7 days later. Two others, which were 5.0 and 5.5 mm. long when watering was stopped, grew to full development but failed to open; their final accelerated phase was less steep than normal, and their final size about two-thirds normal. A bud 4 mm. long grew about normally to 13 mm., and then grew less than another millimetre in five days, after which watering was resumed and normal accelerated growth to flowering occurred. A bud only 1.5 mm. long grew normally to 4 mm., remained at about this length for five days, and then resumed normal growth when watering was started again. There is no doubt that lack of water can cause retardation of growth, but also that accelerated growth (though of reduced amount) can occur even if water is seriously deficient.

In 1948 the plants were in a close group in the open ground, and were not watered. The month of February, 1948 was very wet throughout. Yet a number of buds showed retarded growth. It is well known that orchid plants resent unduly wet conditions (which prevent normal aeration of the roots) and I can only suppose that undue wet causes upset of normal root functions with consequent effect on flower buds. But this matter needs more experimental investigation. Retardation at later periods occurred in dry weather, but not always. The effect of drought on the root is not to be measured merely in terms of rainfall or its lack; it depends on many other factors, such as wind, atmospheric humidity, and duration of bright sunlight, and is difficult to assess.

Our other question seems to have a more definite answer. I have found that on every occasion when a considerable number of flowers were open on the same day (12 flowers or more, on about 30 inflorescences) the seventh day previous was decidedly cooler than average as judged by a thermograph record. I have not made any definite measurements of these records. Something more is needed than a comparison of maximum temperature, which may be of short duration. There was sometimes a sudden cooling due to a storm, such as that mentioned by Coster (1926),

but not always, and sudden cooling is certainly not essential. The results agree with those of Kerling already mentioned for Zephyranthes and Dendrobium.

It seems then that flower-buds of *Bromheadia finlaysoniana* grow to about 12 mm. in length, and then for the next week or so are susceptible to retarding influences which may extend over a period of as much as eight days but usually over a lesser period. When the plant experiences the next unusually cool day, the normal accelerated development begins, and flowering occurs on the seventh day. Under normal conditions, the retardation does not amount to a cessation of growth, but such might occur (as in the unwatered pot) under exceptionally dry conditions.

It is not a big step from such a condition to that of *Dendrobium crumenatum*, in which growth ceases altogether at a certain stage of development, to be resumed as a result of a cool-temperature stimulus. The significance of the cool temperature stimulus probably is that such temperatures are usually associated with wet days; and water is necessary for the rapid later stages of development of flower-buds. (In Zephyranthes it has been shown that both cool temperature and water are necessary as a stimulus to growth of dormant flower-buds). The terrestrial Bromheadia is somewhat better off as regards water supply than the epiphytic Dendrobium, so that a total cessation of growth of buds until rain comes may be unnecessary. The Bromheadia is evidently also sensitive to a less pronounced cool-temperature stimulus.

All other species of Bromheadia except one are epiphytic, and it seems possible that *B. finlaysoniana* is "secondarily" terrestrial; *i.e.* that it is derived from epiphytic ancestors. Its roots are of epiphytic type. Whether under such circumstances its behaviour as regards bud-development could be a regression from the epiphytic condition (shown by *B. alticola*) or whether it is an arrested stage of evolution, is an interesting matter for speculation.

Some buds of *Bromheadia finlaysoniana* develop quite evenly, with no trace of retardation. Whether a bud always does this if root conditions are satisfactory, or whether such buds always experience a cool day at the right stage of their development, is a matter for further observation. The whole behaviour of flowering in this species is an indication of extreme sensitiveness to external conditions, and is an interesting example of how plants in our apparently very uniform climate can respond to small climatic changes.

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