Pollination

Flexible style that encourages outcrossing

Despite the convenience of self-pollination (selfing) in flowering plants[1–3], the detrimental effects of inbreeding that follow repeated selfing[3,4] have promoted strong natural selection for mating systems that ensure successful cross-fertilization (outcrossing). Here we describe a mechanism deployed by some tropical ginger flowers to avoid self-pollination — the flower moves its stigma (style), which normally acts as the pollen receptor, out of the way while its anther is releasing pollen. This cunning evasion adds to the diversity of pollination strategies that have contributed to the evolutionary success of flowering plants.

Alpinia is an Asian genus in the ginger family (Zingiberaceae) containing more than 250 species[5]. These are perennials with terminal inflorescences that produce between two and ten open flowers every day; each flower is hermaphrodite and lasts for only a day. We have monitored how the flower parts behave in nine species of *Alpinia*, both native and introduced, in a tropical seasonal rainforest in Xishuangbanna, Yunnan, in southwest China[6].

Each species of *Alpinia* has two phenotypes that coexist in all populations and which differ in the movement of the flower stigma (the phenotypes are termed cataflexistyled or hyperflexistyled flowers, depending on the direction of stigma movement during flowering). When cataflexistyled flowers are fully open (06:00–06:30), the stigma is held above the open (dehisced) anther from which pollen is being released (Fig. 1a). At the same time of day, the receptive stigma of hyperflexistyled flowers is curved downwards, below the indehiscent anther from which pollen has not yet been shed (Fig. 1b).

Flowers of both types retain these respective stigma positions until about midday, when the stigma of the hyperflexistyle form elongates and becomes erect above the anther (male phase). This movement prevents contact with insect visitors and creates an angle larger than 170° between the stigma and the anther's ventral face (11:45–13:30); the anther then dehisces and pollen is released (14:30–15:00; Fig. 1d).

The movement of the style of the cataflexistyle form is slower: here the stigma begins to move downwards and enter the receptive position (female phase; less than 170° from the anther's dorsal face) between 14:40 and 15:00 (several minutes after anther dehiscence in hyperflexistyle flowers; Fig. 1c). Flowering (or anthesis) ends in both forms after dark, when the anthers collapse and the corolla flops down.

The speed of stylar movement depends on the weather conditions, but all flowers of the same phenotype that open on the same day are strictly synchronous. The anthers of the hyperflexistyle flower never dehisce before all stigmas of the same phenotype have moved out of the receptive position (Fig. 2). It is likely that successful pollination only occurs between the two different forms, with the two phenotypes being associated with two genotypes (for example, in a natural population of *A. kwangsiensis* the ratio of individuals of the two phenotypes is about unity: 86:78; $\chi^2 = 0.39$, $P > 0.5$).

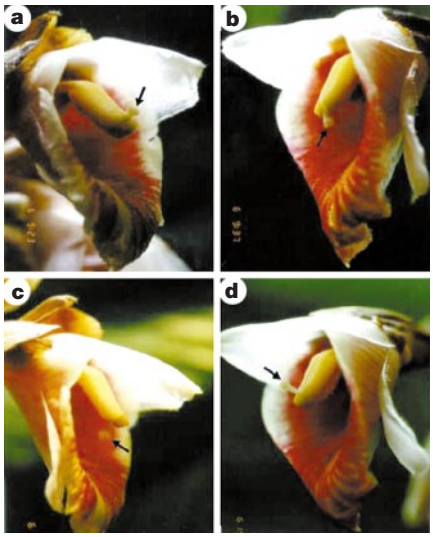

Figure 1 Positions of the stigma of the two flower forms in *Alpinia kwangsiensis* at different stages of flowering. **a,** Cataflexistyle flower in its male phase (before noon), in which the stigma is reflexed above the dehiscent anther. **b,** Hyperflexistyle flower in its female phase (before noon), in which the stigma is deflexed below the indehiscent anther. **c,** The same flower as in **a** during its female phase (afternoon), with the stigma below the anther; note that pollen has been removed from the anther by insect visitors (mainly xylocopid bees). **d,** The same flower as in **b**, but in its male phase (afternoon), with the stigma now erect above the anther, which then sheds its pollen. Arrows, stigma position.

We artificially manipulated different pollination combinations within and between phenotypes of *A. kwangsiensis* in the field. Our results indicate that fruit set resulting from cross-pollination between the two phenotypes is not significantly different ($F = 1.393$, d.f. = 1, $P = 0.242$) and that for the same treatments (self-pollination, cross-pollination, open pollination or controls), fruit-set rates did not differ significantly between the two phenotypes ($F = 2.251$, d.f. = 4, $P = 0.072$), indicating self-compatibility of the species. However, there was a significant difference between the treatments within the same phenotype ($F = 69.163$, d.f. = 6, $P < 0.001$): in both forms and during both gender phases, cross-pollination had a significantly higher fruit set than self-pollination, indicative of an inbreeding depression effect.

The floral strategy described here not only prevents self-pollination in a flower and within the same individual, but also among individuals of the same phenotype. It decreases inbreeding and promotes outcrossing in the plant by temporally and spatially separating the presentation of pollen and receptive stigmas through active floral movement. This mechanism, which we call flexistyly, differs from other passive outbreeding devices, such as dichogamy, herkogamy, enantiostyly and heterostyly[7], in that it combines some features of all of these mechanisms with the unique movement of floral parts.

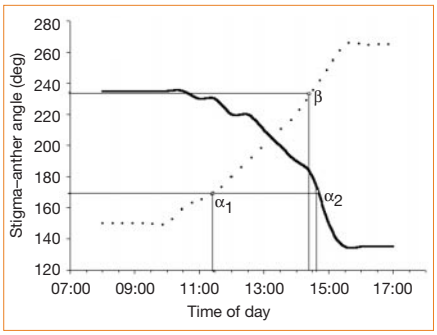

Figure 2 Floral behaviour of *Alpina kwangsiensis* during a single day of flowering. There is no overlap in the male and female phases of the two phenotypes (dotted line, cataflexistyle flower; full line, hyperflexistyle flower). α_1, Time when the stigma of a hyperflexistyle flower becomes reflexed out of its receptive position; α_2, time stigmatic receptivity of a cataflexistyle flower begins; β indicates the time of anther dehiscence of the hyperflexistyle flower.

We observed flexistyly in all nine *Alpina* species we studied[8]. In a molecular analysis of the phylogenetic relationships within the Zingiberaceae family (W. J. K. *et al.*, unpublished data), these nine species are distributed in three separate clades in the Alpineae, indicating that flexistyly either evolved independently several times in this Alpineae group or that it is widespread (though as yet unrecorded) in many taxa in the group (in *Amomum*, for example[9]).

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