

First Record of a Natural Begonia Hybrid in Malaysia

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Abstract

Study of three begonia populations in montane forest at Cameron Highlands, Pahang, confirmed that hybridization had occurred between *Begonia decora* and *B. venusta*. The hybrids are fertile and calculation of the hybrid index indicates that introgression had taken place. Two populations are stable and are represented by hybrid swarms. Plants of the two parents were not located in the vicinity of these two populations. The third, comprising both parents and hybrids, is unstable and its composition has changed over the years. A further two populations have been destroyed by habitat disturbance, which is prevalent at Cameron Highlands.

Introduction

While hybrids of begonia are the norm in cultivation with over 10,000 hybrids and cultivars recorded (Mabberley, 1997), in contrast they are rarely encountered under natural conditions. In Peninsular Malaysia, 53 native species are known (Kiew, in prep.), but only one putative hybrid has been encountered. This was discovered at Cameron Highlands (Fig. 1) in 1983 (*Ruth Kiew RK1278*) and became the basis of a more detailed study, the results of which are reported below. The aim was to reassess diagnostic characters that distinguish the two putative parents, *Begonia decora* Stapf and *B. venusta* Ridl., to collect data from wild populations to test whether hybrid plants indeed existed, and to assess the fertility of hybrid plants.

Begonia decora was exhibited at the Royal Horticultural Society in London in 1892, where it was described as “a pretty dwarf-growing plant, with exceedingly ornamental foliage; the leaves are velvety-purple with greenish-yellow veins, and very hirsute” and where it was awarded a First-class Certificate (Anon., 1892). Towards the end of the nineteenth century, it was used in hybridization with *B. rex* Putzeys to impart a wide range of reds and a metallic sheen to the leaves (Thompson, M.L. and E.J. Thompson, 1981). In contrast, *B. venusta* (Fig. 2a), which has the largest flowers of any Peninsular Malaysian species, has yet to be introduced into cultivation. It is a larger, more robust plant with glossy, fleshy leaves that have earned it the common name of the cabbage-leaved begonia.

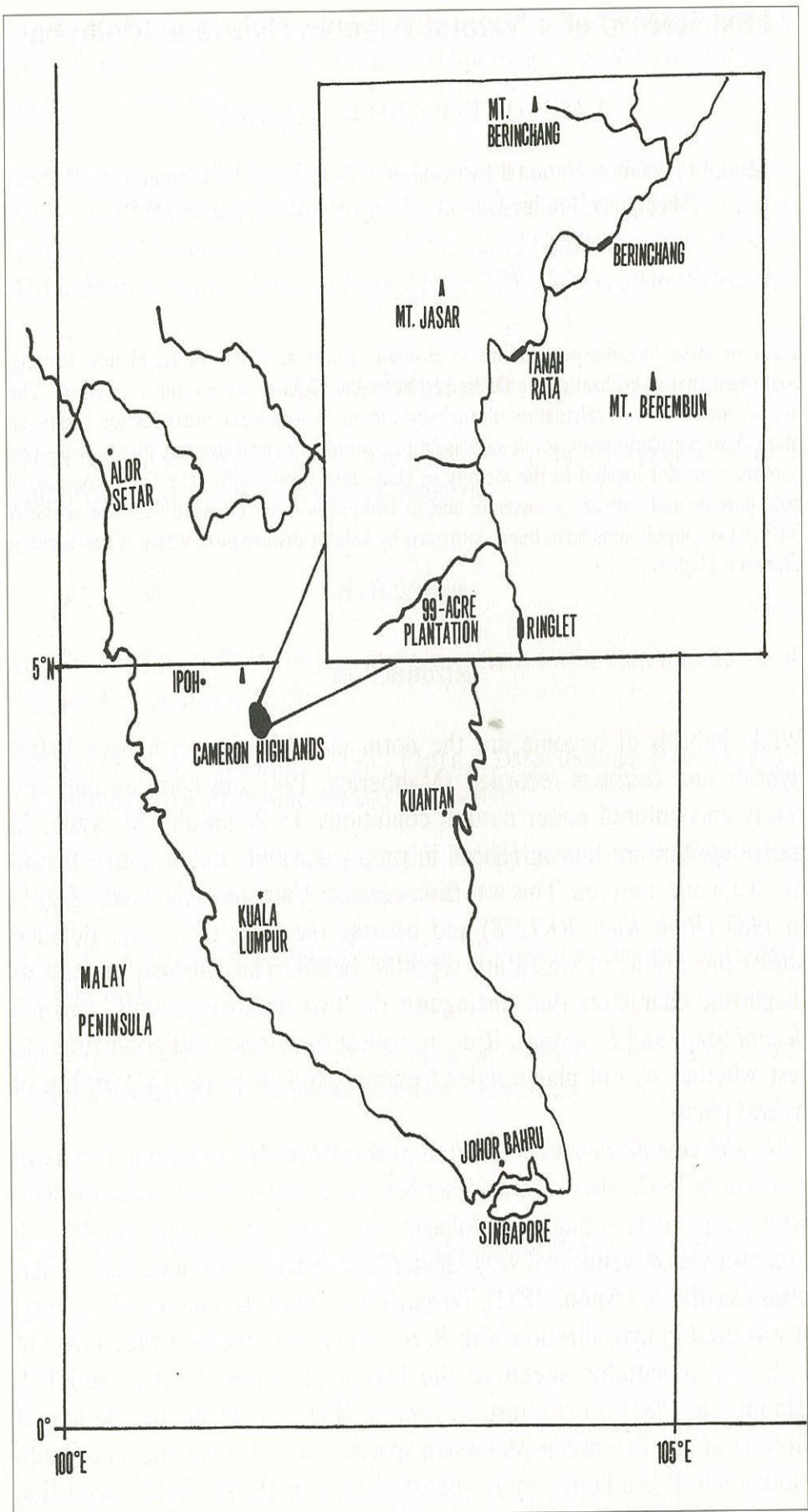


Figure 1. The study sites of the hybrid populations of begonia at Cameron Highlands, Malaysia.

Both species belong to the same group of species with markedly oblique leaves within the *Platycentrum* section, which includes creeping, rhizomatous species, which produce male flowers with four tepals and fruits with two locules and three wings, one of which is enlarged.

Plants in the first hybrid population discovered (Fig. 2b) more closely resembled plants of *B. venusta* (Fig. 2a) in having large cabbagey leaves but they had scattered hairs and were slightly purplish beneath, characters not seen in *B. venusta*. Other populations included hybrid plants (Fig. 2c) that more closely resembled *B. decora* (Fig. 2d) in having smaller leaves, which were more hairy and reddish-purple beneath, but not as small, densely hairy and deeply coloured as *B. decora* itself (Fig. 2d).

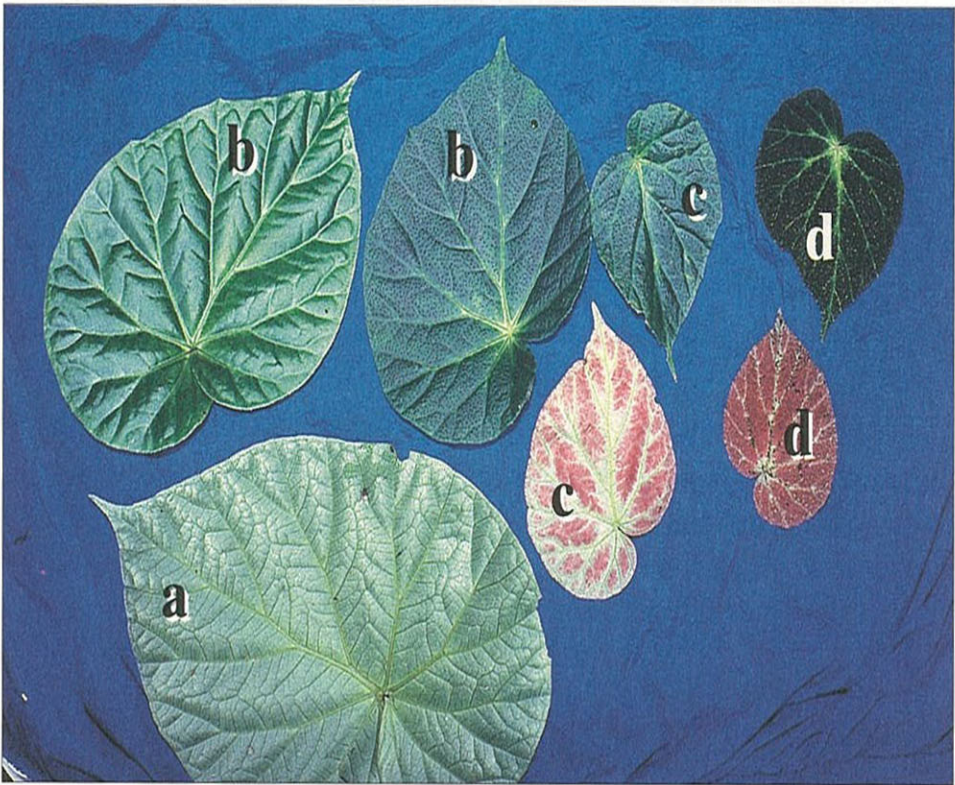


Figure 2. Laminas of the begonia hybrids and parent species.
(a. *Begonia venusta*; b. *venusta*-like hybrid; c. *decora*-like hybrid; d. *B. decora*)

Materials and Methods

Morphological study

Herbarium material (including type specimens) of *B. decora* and *B. venusta* was examined to draw up a list of clear and unambiguous diagnostic characters that would distinguish these two parent species. These characters were tested in the field to ensure that the complete range of variation was

captured (Table 1). No hybrids were found among the herbarium collections. Descriptions of the parent species are given in Appendix 1.

Table 1. Diagnostic characters used to differentiate *Begonia decora* from *B. venusta*.

Character	<i>B. decora</i>	<i>B. venusta</i>
Plant height (cm)	<20	28–55
Rhizome diam. (mm)	<6	8–16
Petiole length (cm)	<17	>22
Petiole indumentum	hairy	glabrous
Ratio lamina width:length (mean)	1:1.6–1.8	1:1.2–1.5
Lamina undersurface colour	red	green
Lamina indumentum	hairy	glabrous
Lamina base	overlapping	not overlapping
Lamina margin	serrulate	denticulate
Fruit wing	broad and blunt	tapered
Fruit wing texture	thin	thick and fibrous

Study sites

The hybrid is known only from Cameron Highlands, Pahang, a popular highland tourist resort. Search was made along accessible forest paths and along roads in the montane forest, which resulted in the discovery of six populations. Unfortunately, two of these have since been destroyed (by building construction and farming) before the more detailed study started in 1996.

All plants with both flowers and fruits in the remaining four populations (Table 2) were scored for the hybrid index using the eleven characters in Table 1.

Table 2. Number of individuals scored for the hybrid index in begonia populations at Cameron Highlands (Gunung=Mount)

Study sites	<i>B. decora</i>	hybrid	<i>B. venusta</i>
Gunung Beremban	NP	17	NP
Gunung Berinchang	11	30	41
Gunung Jasar	NP	20	NP
'99 Acre' Plantation	5	NP	NP

(NP=not present)

In the ideal situation, populations comprising only one parent should be scored. However, only one small population of *B. decora* could be found, while none of just *B. venusta* was located. Sample size was also limited by small population size and the fact that most plants were either sterile or had flowers or fruits (not both).

The sites at Gunung Beremban, G. Berinchang and G. Jasar were in upper montane forest in damp and deeply shaded conditions beneath a closed canopy although the canopy was slightly more open above streams. The G. Beremban site was relatively flat, while the other two were sited on steep slopes. The site at '99 Acre' Plantation was a forest fragment beside the road close to farms and was a more exposed steep slope, which was, however, shaded by overhanging trees.

Hybrid index

This was calculated based on the characters listed in Table 1. The presence of each character state for *B. decora* was scored as '2', those for *B. venusta* '0', while an intermediate character state was scored as '1'. The score for each plant was then totalled and results for each population expressed in a histogram (Anderson, 1949). Thus, in theory plants of *B. decora* should obtain a total of '22' for the eleven characters scored, *B. venusta* '0', while hybrid plants are identified by intermediate scores.

Anatomical study

Since differences in leaf texture and indumentum were so pronounced, the anatomy of the lamina of fresh leaves was also examined. Permanent slides of lamina T.S. (30 samples each for the two parents and the hybrid) were made by standard methods (Sass, 1958) being sectioned 15 μ m thick, stained in 1% safranin and 0.5% fast green and mounted in permount.

Indumentum was examined after clearing the lamina (one sample for each of the two parents and ten for the hybrid) with sodium hydroxide and chloral hydrate and mounting in permount. The number of trichomes visible in the optical field viewed at x40 magnification at eight points on each lamina was recorded and the mean calculated.

Pollen and seed viability

To assess pollen viability, five samples each of about 150 fresh pollen grains for each of the two parents and the hybrid were stained with methylene blue and made into a temporary mount in glycerol. The percentage viability was then calculated by counting the number of stained

(viable) and unstained (sterile) pollen grains for samples of *B. decora*, *B. venusta* and the hybrid.

To test seed viability, 50 seeds of both parents and six hybrid plants were sown on damp filter paper and the number of germinated seeds recorded at 2-day intervals until there was no further germination.

Results

Morphology

Compared with the character states of the parent species (Table 1), the hybrid plants displayed a complete range of morphological intermediacy in all qualitative (Fig. 2) and quantitative (Table 3) characters.

Table 3. Range in quantitative characters displayed by hybrid plants

Character	hybrid plants
Plant height (cm)	8–45
Rhizome diameter (mm)	4–14
Petiole length (cm)	9–41
Ratio lamina width:length (mean)	1:1.1–1.8

Hybrid index

Calculation of the hybrid index gave a score for *B. decora* of 22 when it grew alone (Fig 3d), and between 19 and 22 when it grew together with the hybrid (Fig. 3a). No population comprised only plants of *B. venusta* and on G. Berinchang, where it grew with hybrid plants, the distinction between it and the venusta-like hybrid was not disjunct.

Scores for the hybrid ranged widely. For the G. Beremban population (Fig. 3b), it ranged from 5 to 13 with a mean of 8 and a mode of 8–9, and for the G. Jasar population (Fig. 3c), it ranged from 7 to 17 with a mean of 14 and mode of 16. The structure of the G. Berinchang population (Fig 3a) was more complex. There was no clear distinction between scores for plants of *B. venusta* and the hybrid, and hybrid scores ranged up to 16.

Anatomy

The hybrid also showed intermediacy in characters such as lamina thickness,

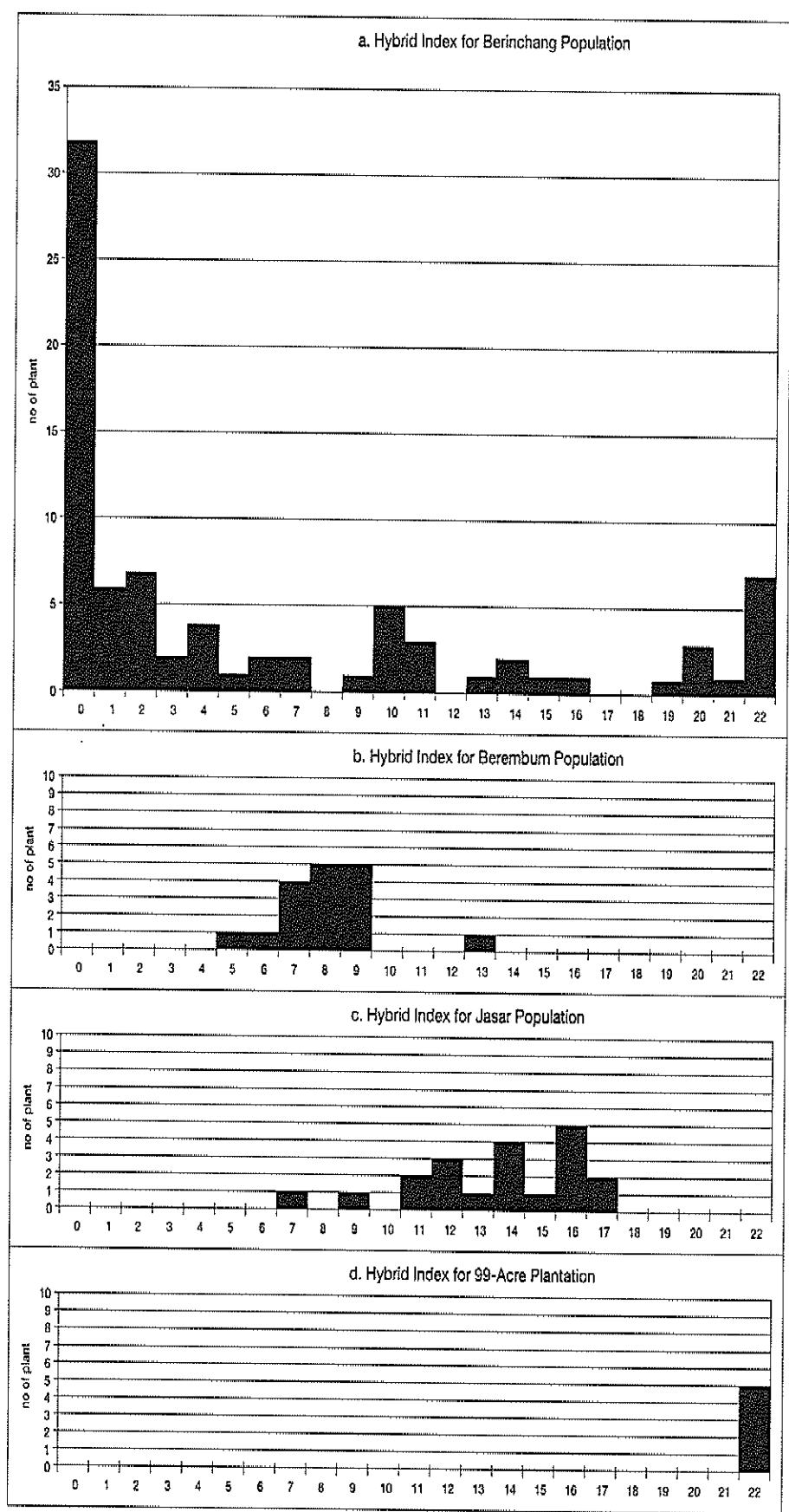


Figure 3. Hybrid index for begonia populations.
(a. Gunung Berinchang population; b. G. Berembum population; c. G. Jasar population; d. '99 Acre' Plantation population)

which was reflected by differences in the thickness of the tissue layers and number of mesophyll layers (Table 4, Plate 1).

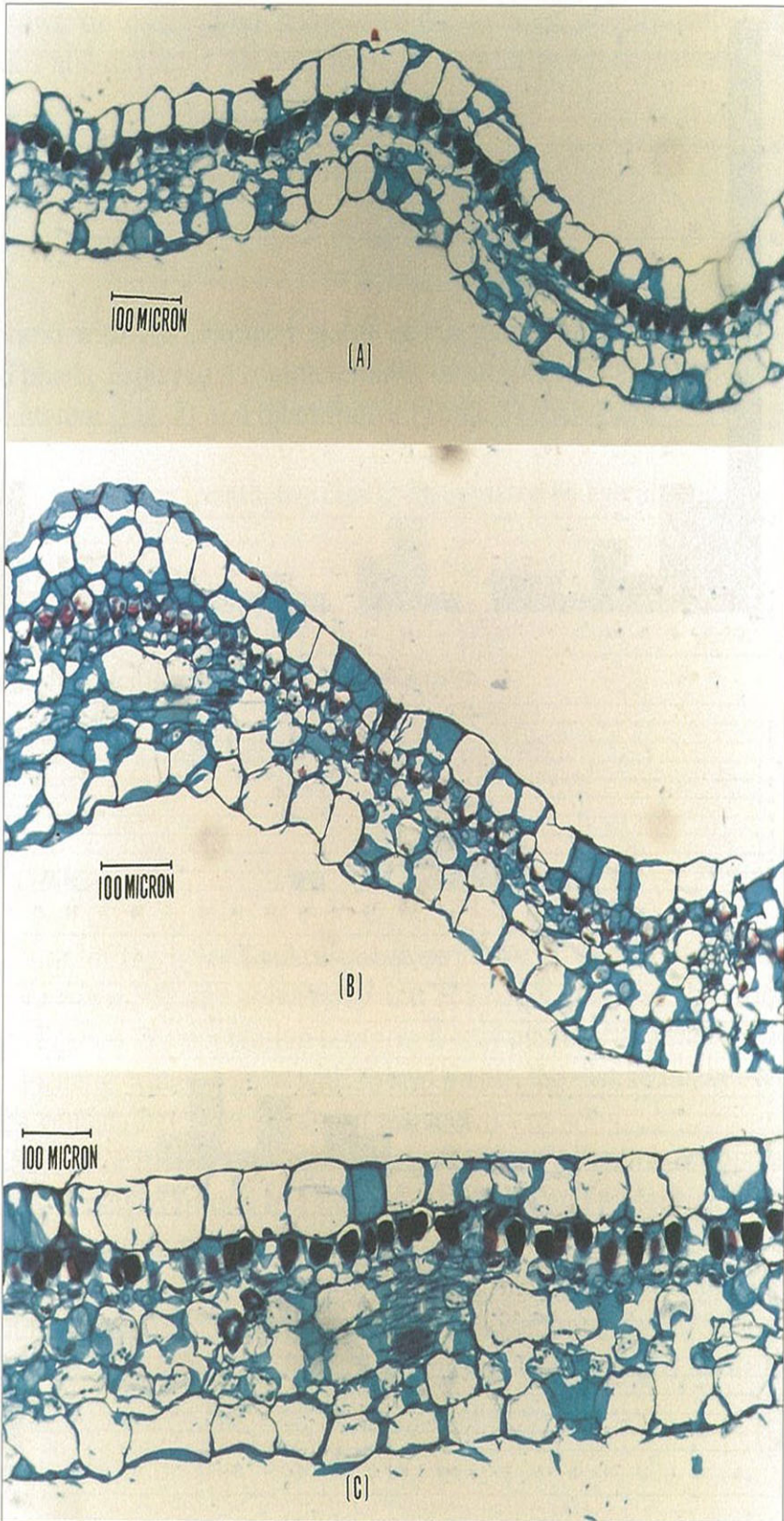


Plate 1. T.S. lamina of begonia species and hybrid.
(a. *Begonia decora*; b. hybrid; c. *B. venusta*)

Table 4. Differences in the lamina anatomy of the hybrid and its parents.
(mean±standard deviation)

Character	<i>B. decora</i>	hybrid	<i>B. venusta</i>
Thickness (μm)			
Lamina	166±25	234±35	312±16
Upper epidermis	48±9	57±9	83±14
Palisade mesophyll	29±5	40±7	52±8
Spongy mesophyll	29±8	43±14	52±15
Lower epidermis	38±7	49±7	64±13
No. spongy mesophyll layers	1-2	2-3	3-4

The hairiness of *B. decora* is very pronounced. Not only are the hairs dense but they are papillose (raised on a protrusion of the lamina) so that the underneath of the lamina appears pitted (Fig. 4). This is in complete contrast to *B. venusta*, which has glossy leaves that are completely smooth and glabrous. When counted per x40 optical field, the lamina of *B. decora* had (31-)35(-43) trichomes, *B. venusta* 0, 'venusta-like hybrid plants (0-) 2(-5) and 'decora-like' hybrid plants (20-) 27(-36) trichomes.

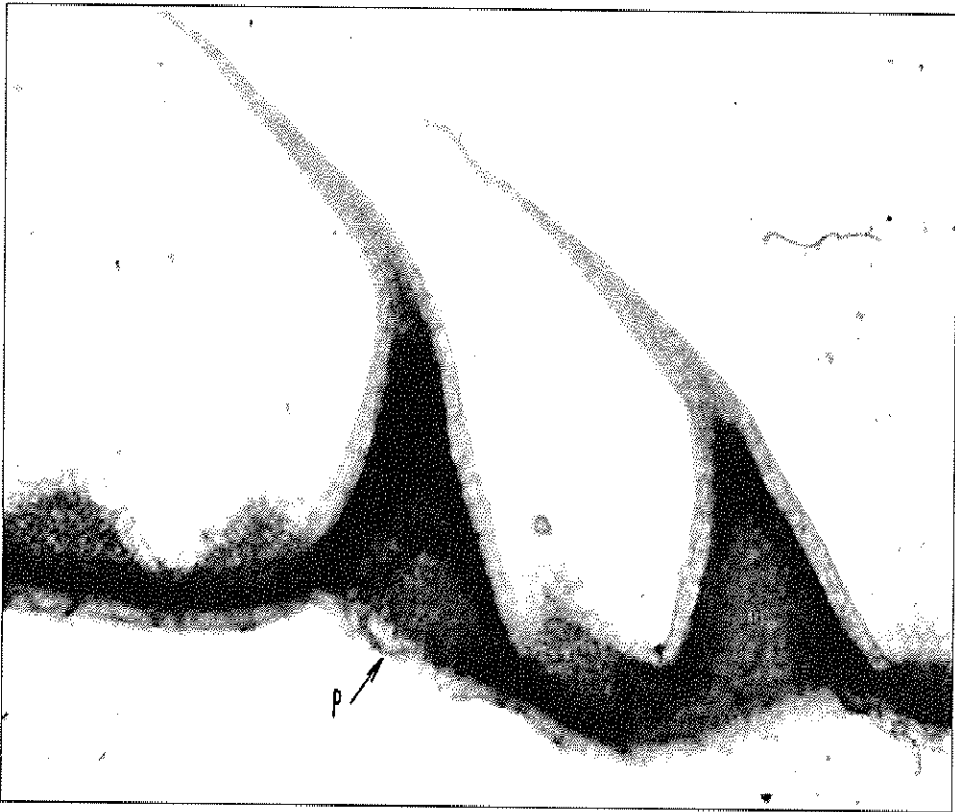


Figure 4. T.S. lamina of *Begonia decora*.
(P – papillose hair base)

Pollen and seed viability

The pollen viability for both parent and hybrid plants was high: (87.5–) 96 (–100)% for *B. decora*, (91.9–)97.4(–100)% for *B. venusta* and (91.9–)97.4(–100)% for hybrid plants.

Seed germination for all taxa was rapid (Fig. 5) beginning slightly earlier in seeds of the hybrid at Day 6 compared with Day 8 for seeds of *B. decora* and *B. venusta*, and while no further germination occurred after Day 14 for the hybrid, seeds of the two parental species continued to germinate up to Day 20. Percentage germination was high in all three taxa - 100% for *B. venusta* and 98% for *B. decora* and the hybrids.

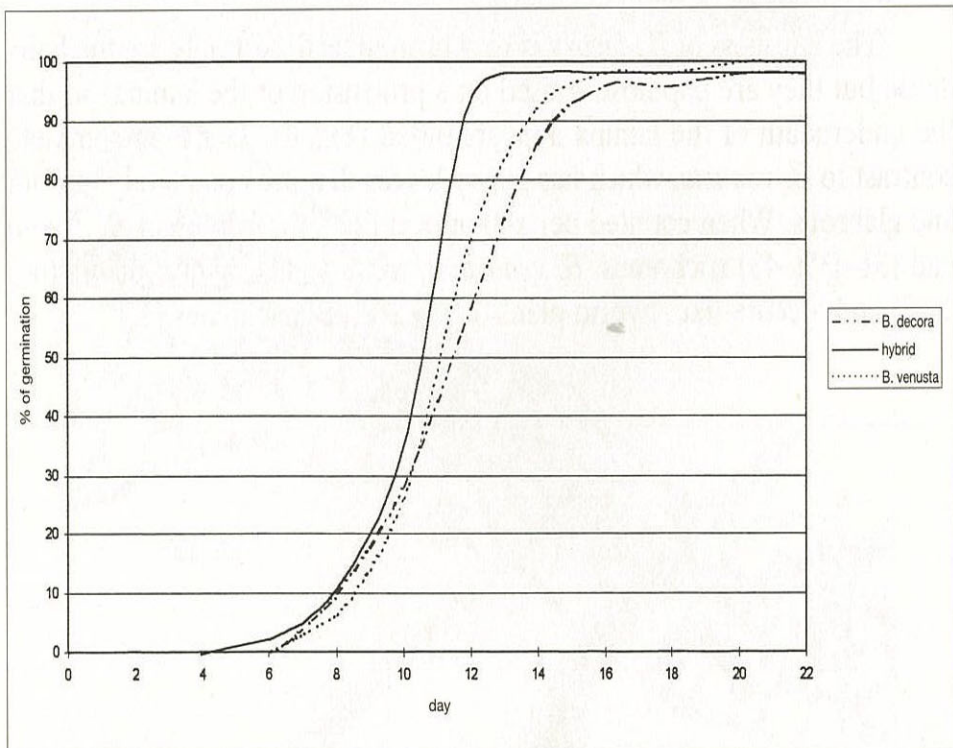


Figure 5. Rate of seed germination in *Begonia decora*, *B. venusta* and hybrids.

Discussion

The data from the hybrid index and anatomical study support the view that *B. decora* and *B. venusta* do produce hybrids in the wild and that the hybrid plants are fertile and backcross with the parental species to produce hybrid swarms. Arnold (1997), in reviewing cases of natural plant hybrids, concluded that, for the majority, the hybrid exhibits equivalent or superior fitness to the parents.

However, the structure of hybrid swarms is different at each site. On G. Berinchang, hybrid plants show a wide range of intermediate scores

between the two parents, while in the populations on G. Beremban and G. Jasar, the scores for majority of hybrid plants are skewed towards *B. venusta* and *B. decora*, respectively.

The high viability of seed from hybrid plants shows that there are no genetic barriers between these two closely related species. Thus, internal factors cannot play a role in isolating the two species.

In addition, flower characteristics and pollinator behaviour also do not serve to keep the two species reproductively isolated. The tepals of both species are similar in shape (broadly oval), size, colour (white or pale pink) and open widely to expose a similar cluster of yellow anthers in the male flower or twisted yellow stigmas in the female flower. Preliminary observations on the populations at G. Beremban and G. Berinchang indicated that a stingless bee, *Trigona* sp., is the most likely pollinator as it visits the male flowers of both species and hybrid plants to collect pollen. (No other flower visitors were observed). This bee also briefly visits the female flowers (so briefly as to appear to 'bump into' the flower before flying off). The female flowers of begonia do not offer any reward and pollination is by deceit, the bee visiting the female flower in mistake for the closely similar male flower. Ågren and Schemske (1991) have shown that in Costa Rica pollination by deceit in *Begonia involucrata* Liebm. is also by a *Trigona* species and is very effective. Although female flowers were visited infrequently and briefly (male flower were visited three times as frequently and for ten times longer), three quarters of the ovaries set fruit with about 50% seed set. In begonia species where a single inflorescence is produced, the male and female phases do not overlap (*B. decora* and *B. venusta* are protogynous; *B. involucrata* is protandrous), pollen will therefore be carried from one plant to another (xenogamous pollination). Therefore, when *B. decora* and *B. venusta* occur within the flight range of a *Trigona* bee, it is likely that crossing between the two species will occur.

This then raises the question as to what the isolating mechanisms are that enable the two species to remain distinct at Cameron Highlands. *Begonia decora* has a wider altitudinal range than *B. venusta* and at lower altitudes, e.g., at '99 Acre' Plantation, it occurs alone. *B. decora* also appears to tolerate more exposed conditions as it can grow on steep roadside banks at the edge of forest. Both species grow on damp, shaded steep slopes within the forest. The *venusta*-like hybrid shows some propensity to become weedy and colonises sandy banks or stream bottoms that frequently develop due to siltation of streams when earth has been exposed by man's activities. In these circumstances, it can form pure stands. This is interesting as in temperate floras, the occurrence of hybrids is often associated with man's disturbance of natural habitats, the greater variability of hybrid plants

compared with either parent is thought to contribute to their success in invading unstable habitats (Anderson, 1949).

However, the exact ecological requirements of the parental species and hybrid plants have yet to be tested experimentally because of the difficulty of growing montane plants in the hotter lowlands. It therefore cannot yet be proved that ecological factors are the major isolating factors that maintain the parental species as distinct entities. Elsewhere, for example on limestone, several species of begonia occur sympatrically and yet hybrids are not found. However, on limestone, the distinction between microhabitats is much clearer (Kiew, 1998).

The hybrid population on G. Berinchang appears to comprise both F1 plants that score between 9 and 11, as well as the progeny of backcrossing with scores ranging between 3 and 16. The wider scores for *B. decora* (19–22) and *B. venusta* (0–2) than the theoretical 22 and 0 and the intergrading of scores for *B. venusta* and the venusta-like hybrid (3–7) can be interpreted as earlier hybridization and introgression that have caused the parent species to be genetically less pure. Observation of this same population after three years showed the number of plants of the hybrid and *B. decora* were drastically reduced indicating that the composition of this population is not stable. (That the previous year, 1998, was a particularly dry year due to the El Niño effect may have been a contributing factor in this change.) Long-term studies in temperate floras indicate that in many cases the composition of hybrid populations is not stable (Stace, 1989).

The habitats beside the forest paths on G. Beremban and G. Jasar are deep inside the forest and have experienced little disturbance other than trampling along the narrow walking trail. These populations are interesting as plants of the parental species could not be located in the 1996 study, although plants of *B. decora* were growing nearby the study site on G. Jasar in 1983 (*Ruth Kiew RK1276*). It appears that in these two populations hybridization is of longstanding and that introgressive hybridization has occurred so that now plants of pure *B. decora* or *B. venusta* no longer exist. It also indicates that the hybrids swarm with its wide genetic variability may have superior fitness in this habitat compared to the parents (Arnold, 1997). It is likely that the difference in these two populations was due the numerical predominance of one of the two parent species, *B. decora* on G. Jasar and *B. venusta* on G. Beremban.

In temperate floras, some authors (e.g., Stace, 1989) considered that 'in general the ability to hybridize is the usual situation' and he cites 780 hybrids among the 2500 species in the British flora. Records of hybrids in tropical floras are much rarer and quantitative studies are almost non-existent. Two other genera, *Nepenthes* (Nepenthaceae) and *Rhododendron* (Ericaceae), are well-known as forming hybrids readily, both under natural

conditions or in cultivation because, like begonia, they have no internal barriers to crossing. In *Nepenthes*, there are 280 hybrids recorded in cultivation involving 34 of the 82 species known (Jebb and Cheek, 1997). In Peninsular Malaysia, where 11 species occur, two hybrids are so well known that they have been named (*x hookeriana* and *x trichocarpa*) and several other informal hybrids are known to exist both among the lowland as well as the montane species. Among the *Vireya* rhododendrons on G. Kinabalu, Argent *et al.* (1988) have observed several hybrids and note that these form hybrid swarms in inherently unstable or in disturbed habitats where they may be common and abundant.

However, populations of hybrids of *Nepenthes* and *Rhododendron* have not been subjected to detailed analysis. Only *Globba* hybrids have been studied in detail when Lim (1973) studied three populations at Cameron Highlands of hybrids between *Globba patens* Miq. and *G. cernua* Baker (Zingiberaceae). The hybrid index indicated that introgressive hybridization had occurred in the three populations and, similar to our study, her G. Jasar population no longer included plants of one parent (*G. patens*), although it was known earlier (in 1925) from that area.

Lim's results are interesting as they too show that changes have taken place in the montane flora at Cameron Highlands in the last 70 years, the period when it developed to become the largest highland resort in Malaysia. Leong (1992) chronicled the forest clearance, which started on a large scale in the 1930s when tea plantations and farms for temperate vegetables were established, to the 1970s when large scale resort development was encouraged and new areas were opened up to grow cut flowers, an industry that by 1990 had surpassed the value of the vegetable harvest. These developments have been at the expense of forest, which has resulted not only in the obvious effect of destroying habitats but also has had a more insidious effect in changing the environment. Leong reported that by 1985 the temperature at Tanah Rata had risen by 4°C, which would in turn affect other environmental factors, such as cloud formation, rainfall and humidity.

Conclusion

Analysis of morphological intermediacy to produce a hybrid index is a useful tool in confirming the occurrence of hybrids between *B. decora* and *B. venusta*. Intermediacy in anatomical characters also supports their hybrid status. That five hybrid populations have been found indicates that hybridization will occur wherever these two species occur sympatrically. The fertility of the hybrid plants enables introgression to take place resulting in hybrid swarms.

Disturbance by man on the one hand appears to favour the spread of the venusta-like hybrid, which grows lushly on wet sand resulting from soil erosion, while on the other hand to threaten these populations with habitat destruction as witnessed by two of the five populations having been cleared since they were discovered in 1983.

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Appendix 1: Description of the species

Begonia decora Stapf

Creeping plant with horizontal, slender reddish rhizomes, up to 6 mm diam. with internodes 5–7 mm long, foliage reaching up to 20 cm above ground. Stipules reddish, persistent, slightly hairy, narrowly lanceolate, c. 12–13 x 4–6 mm, apex acute. Petiole reddish, 7–17 cm long, slightly or densely hispid. Lamina malachite green or green-bronze and lighter green along veins on upper surface, rosy-purple or magenta and lighter red along veins on lower surface, obliquely ovate, 9–15 x 5.5–8.5 cm, base unequal, broadly rounded and overlapping, margin minutely serrulate, apex acuminate to cuspidate, densely hirsute above, hairs curved, magenta on raised whitish conical papilla, veins 7–9 radiating from junction with petiole, densely hispid and prominent beneath. Inflorescence axillary, few-flowered, long-stalked cyme, projecting above leaves, 1–3 flowers open simultaneously. Peduncle and pedicels reddish green, peduncle 9–21 cm long, hispid. Bracts reddish, c. 19 x 14 mm, at base broadly ovate, midway abruptly lanceolate narrowly to acute apex, caducous. Male flower: pedicel c. 2 cm long, tepals 4, white tinged pink or pale pink, outer two oval with apex acute, 27–32 x c. 18 mm, inner two narrowly oval, c. 20 x c. 9 mm; stamens many, clustered, filament short, anther golden yellow, c. 2 mm long. Female flower: pedicel 13–15 mm long, tepals 5, pinkish white to rosy pink, broadly rounded, isomorphic, outermost c. 24 x 16 mm, innermost c. 23 x 14 mm, ovary pale reddish-green, 3-winged, one wing wider, stigma pale yellow, lobes twisted. Infructescent peduncle elongating to 24 cm long. Capsule pendant hanging on a fine thread-like pedicel, 2-loculate, 10–12 mm long, two lateral wings rounded, 8–10 mm wide; posterior wing thin, broad with blunt apex, 17–26 mm wide.

Begonia venusta King

Creeping plant with slender rhizome 8–16 mm diam., at first with crowded internodes, then internodes elongating to 9–17 cm long to produce a weakly erect plant 28–55 cm tall, rooting at nodes, completely glabrous except for the bracts. Stipules persistent, lanceolate, c. 20 x 10 mm, apex pointed. Petiole slightly reddish, 22–45 cm long. Lamina plain dark

green and glossy above, paler green beneath, fleshily leathery, obliquely ovate, 12–26 x 10–17 cm, base unequally rounded not over-lapping, margin minutely and distantly denticulate, apex acuminate, veins 7–9 radiating from junction with petiole, prominent beneath. Inflorescence axillary, long-stalked cyme, at the level of or below the leaves, 1–4 flowers open simultaneously, protandrous. Peduncle in male phase 10–26 cm long, elongating in female phase to 45 cm long. Bracts in pairs, persistent, broadly lanceolate, 18–25 x c. 6 mm, apex apiculate, sparsely hispid outside with trichomes c. 1 mm long. Male flower: pedicel robust 2–2.5 cm long, tepals 4, white or white tinged pink, outer two broadly oval with rounded apex, 18–33 x 17–26 mm, inner two oval with rounded apex, 16–30 x 7–10 mm, stamens many, clustered, filament and anther yellow, filament 0.5–1 mm long, anther narrowly oblong, 1–1.25 mm long. Female flower: pedicel 1–2 cm long, tepals 5, pinkish white, broadly oval, isomorphic, outermost c. 18 x 14 mm, innermost c. 15 x 6 mm, ovary 3-winged with one wing wider, style c. 2 mm long, stigma yellow, twisted lobes 6 mm long. Peduncle of infructescence c. 29.5 cm long. Capsule c. 15–16 mm long, pendant on stiff pedicel c. 3 cm long, two lateral wings ovate, c. 8 mm wide, posterior wing fibrous, oblong, 19–20 mm wide, tapered to rounded apex.