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RESUPINATION IN FLOWERS OF TWO DENDROBIUM (ORCHIDACEAE) HYBRIDS: EFFECTS OF NODAL POSITION AND REMOVAL OF FLORAL SEGMENTS

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Removal of floral segments from *Dendrobium* (Orchidaceae) flowers indicates that resupination may be regulated or is at least affected by pollinia and/or stigmas. Other floral segments do not appear to have a direct effect. However, excision of the perianth may result in senescence and death, which could be caused by desiccation and/or ethylene evolution.

Introduction

Resupination, the turning of buds and flowers that places the labellum (the median, often highly modified petal) lowermost, is a common phenomenon in orchids and is considered to be a diagnostic character of the family. It is assumed to position the flowers in a manner that facilitates pollination (VAN DER PIJL and DODSON 1966; DRESSLER 1981). Although observed nearly 200 yr ago (SPRENGEL 1793) and described several times after that (SCHOMBURGK 1837; J. LINDLEY 1853 [cited by AMES 1938]; PFITZER 1882; VON MARILAUN 1896; DARWIN 1904; AMES 1938, 1945, 1946, 1947, 1948), resupination is still poorly understood (ZIMMERMANN 1933; ZIEGENSPECK 1936; GOH et al. 1982).

The amount of torsion by individual flowers depends on the angle of the inflorescence relative to the ground and the orientation of the pedicel. Flowers at adjacent nodes on an inflorescence turn either clockwise or counterclockwise alternately. Only buds and young flowers are capable of resupination (NYMAN et al. 1984). The physiological processes that regulate or affect resupination are unknown, and the effects on torsion of floral segments and/or the nodal position of a blossom have not been examined.

Material and methods

Observations, measurements, and surgical experiments were carried out on flowers of *Dendrobium* Tomie 'Tokyo' (figs. 1–3) and *D.* Indonesia at the Flora Sari Orchid Gardens, Jakarta, Indonesia. Bud diameters were measured with calipers, and angles were determined with a protractor (NYMAN et al. 1984). Floral segments were removed with scalpels.

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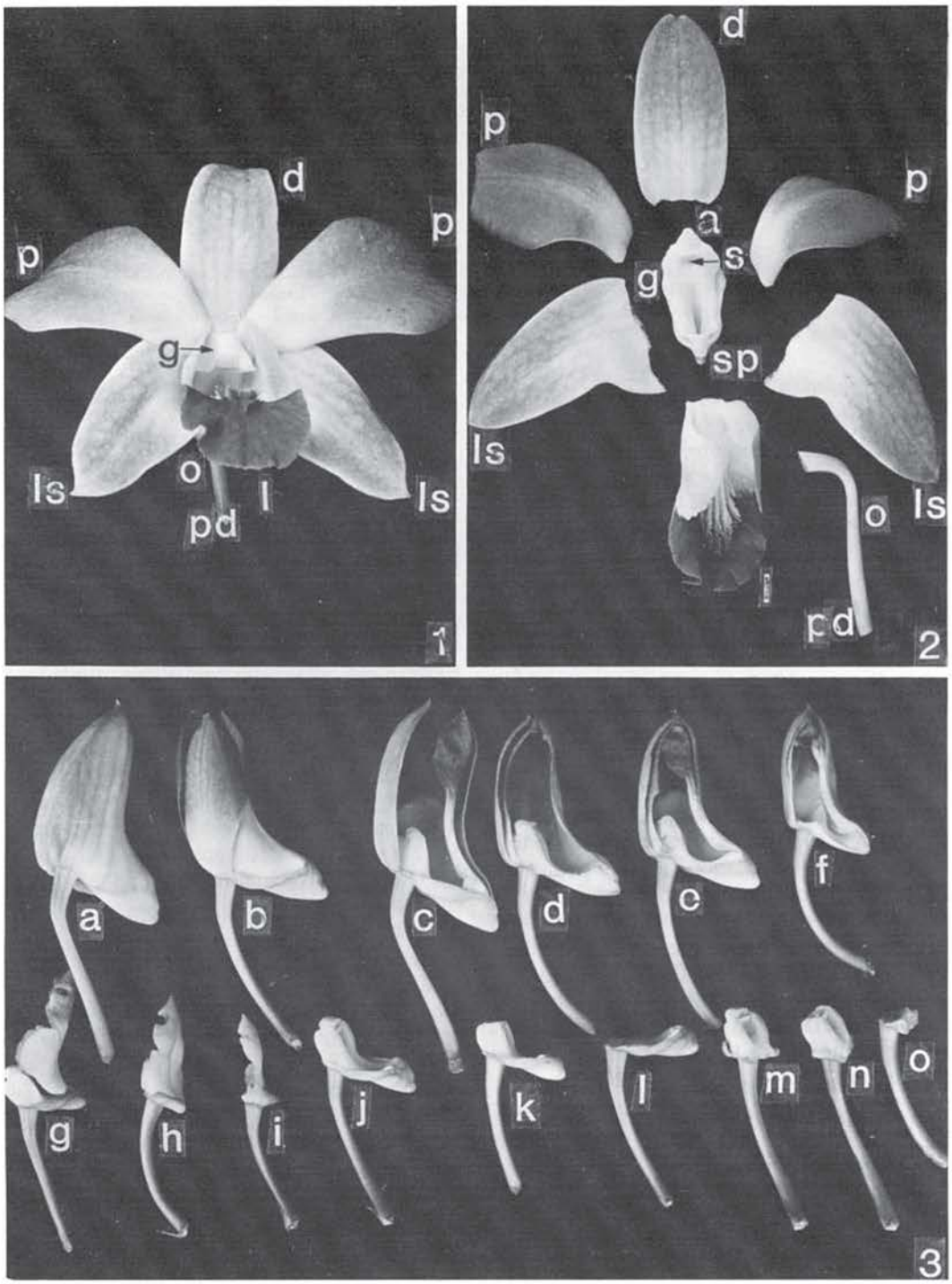
To ensure uniformity, buds on the fourth node from the base of inflorescences were selected; the lowermost flower was fully open, and the second and third buds were in the process of opening. Buds were at similar stages of development, 8.0 ± 1.4 cm in diameter; and their pollinia, stigmas, and perianths appeared to be mature or nearly so. Floral segments (figs. 1, 2) were removed singly or in groups to determine their effect(s) on resupination (fig. 3; table 1). Some buds were wrapped with aluminum foil to determine the role of light. Experiments were replicated at least three times with flowers on different plants.

Results

Intact buds and flowers turned rapidly during days 0–6; turning was considerably slower during days 5–12 and accelerated again thereafter (fig. 4).

Light exclusion had no appreciable effect on resupination (fig. 5, line 7). Removal of the petals (fig. 6, line 10) or the labellum (fig. 7, line 12) caused a delay during the early stages of resupination and extended the slow phase. Removal of the gynostemium (fig. 6, line 8); the pollinia and anther cap (fig. 8, line 13); sepals and lateral petals (fig. 6, line 9); sepals, petals, and the entire gynostemium (fig. 4, line 1); sepals, petals, labellum minus spur, anther cap, and pollinia (fig. 9, line 15); sepals, petals, and labellum with or without spur (fig. 9, lines 14, 15); sepals, petals, gynostemium, and labellum without spur (fig. 10, line 17); and sepals only (fig. 10, line 18) reduced torsion drastically and resulted in early yellowing and death of the buds. The buds did not turn at all when the sepals, petals, labellum with or without spur, and gynostemium were removed (fig. 5, line 5; fig. 10, line 16).

At the time of opening there were essentially no differences in diameter (table 2) between the buds of *Dendrobium* Tomie 'Tokyo' and *D.* Indonesia. Buds and flowers of *D.* Indonesia completed their resupination 1 day before they opened, on the day of opening, or 1 day thereafter. In *D.* Tomie 'Tokyo,' turning of flowers 1–6 stopped 1 day after



FIGS. 1–3.—Flowers of *Dendrobium* Tomie 'Tokyo.' Fig. 1, Intact flower. Fig. 2, Exploded flower. *a*, anther cap; *d*, dorsal sepal; *g*, gynostemium; *l*, labellum (median petal, lip); *ls*, lateral sepals; *o*, ovary; *p*, petals; *pd*, pedicel; *s*, stigma; *sp*, spurs. Fig. 3, Surgical treatments of *Dendrobium* flowers. Parts removed (line nos. are also given in figs. 4–10 and table 1). *a*, None (lines 2, 3, 4, 7); *b*, sepals (line 18); *c*, petals (line 10); *d*, labellum without spur (line 12); *e*, pollinia and anther cap (line 13); *f*, entire gynostemium (line 8); *g*, sepals and petals (line 9); *h*, sepals, petals, pollinia, and anther cap (line 11); *i*, sepals, petals, and gynostemium (line 1); *j*, sepals, petals, and labellum without spur (line 14); *k*, sepals, petals, labellum without spur, anther cap, and pollinia (line 15); *l*, sepals, petals, labellum without spur, and entire gynostemium (line 5); *m*, sepals, petals, and labellum with spur (line 6); *n*, sepals, petals, labellum with spur, anther cap, and pollinia (line 16); *o*, sepals, petals, labellum with spur, and entire gynostemium (line 17).

TABLE 1

TREATMENTS OF DENDROBIUM FLOWERS FOR STUDIES OF RESUPINATION

ILLUSTRATIONS		
Fig. and treatment	Effects, fig.-line	PARTS REMAINING[a]
3i	4–1	Labellum, ovary, pedicel, and spur
3a	4–2	All
3a	4–3	All
3a	4–4	All
3l	5–5	Ovary, pedicel, and spur
3m	5–6	Gynostemium, ovary, and pedicel
3a	5–7	All
3f	6–8	Sepals, petals, labellum, ovary, pedicel, and spur
3g	6–9	Labellum, gynostemium, ovary, pedicel, and spur
3c	6–10	Sepals, labellum, gynostemium, ovary, pedicel, and spur
3h	7–11	Labellum, gynostemium, ovary, pedicel, and spur
3d	7–12	Sepals, petals, gynostemium, ovary, pedicel, and spur
3e	8–13	Sepals, petals, labellum, gynostemium, ovary, pedicel, and spur
3j	9–14	Entire gynostemium, ovary, spur, and pedicel
3k	9–15	Part of the gynostemium, ovary, spur, and pedicel
3o	10–16	Ovary, pedicel, and part of gynostemium
3n	10–17	Pedicel and ovary
3b	10–18	Petals, labellum, spur, gynostemium, ovary, and pedicel

[a] *Dendrobium* flowers consist of three sepals, three petals (two lateral and one median, which is the labellum or lip), one gynostemium (which includes the stigma, pollinia, and anther cap), one ovary, and one pedicel. The parts that were removed are listed in figs. 4–10.

they opened. The torsion of flower 7 ceased on the day it opened. Flowers 8 and 9 stopped turning 1 day before they opened (fig. 11). In both hybrids, the amount of torsion decreased with proximity to the tip of the inflorescence (fig. 11).

Torsion of flower 4 on inflorescences of *D.* Tomie 'Tokyo' was generally within 1 SD of the theoretical value (fig. 11, table 2). Turning of flower 5 was within 2 SDs. Flowers 6 and 7 deviated by 2 SDs or more. In *D.* Indonesia, resupination of flower 5 was within 1 SD; flowers 7 and 8 differed by 2 SDs; flowers 4, 6, and 9, by more than 2 SDs.

Discussion

Differences in resupination among orchid hybrids, species, or plants may exist, but they are probably not of a fundamental nature. We selected clones of *Dendrobium* Tomie 'Tokyo' and/or *D.* Indonesia for our experiments because these hybrids were readily available and had well-shaped inflorescences and flowers of nearly uniform size.

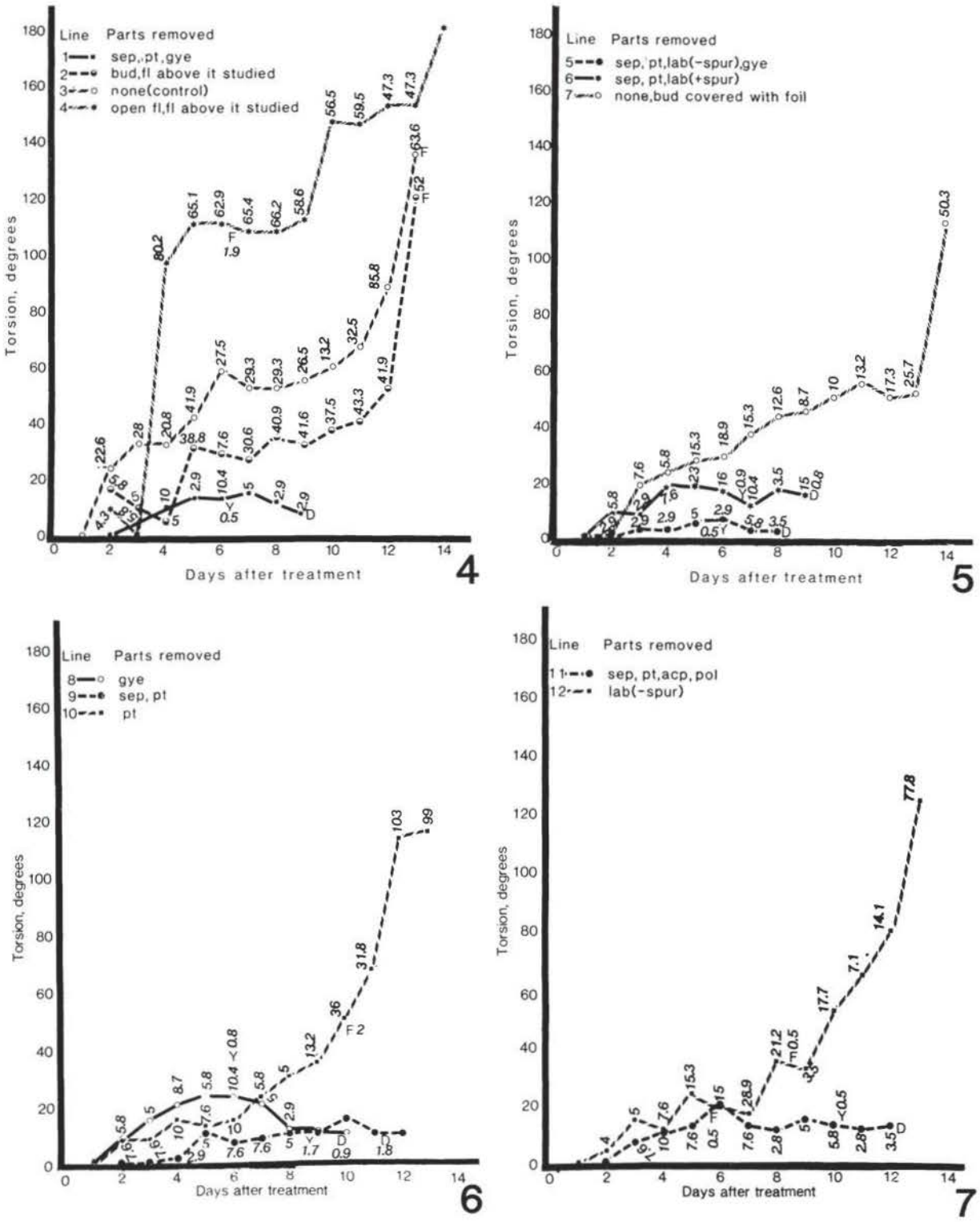
In *D.* Tomie 'Tokyo' and *D.* Indonesia, torsion by flowers 1–3 was alternately clockwise or counterclockwise in a 1:1 ratio (NYMAN et al. 1984). Turning ratios for flowers 4–9 of *D.* Tomie 'Tokyo' were the same. The turning ratios in *D.* Indonesia were more variable. In addition, variability in the extent of turning by upper flowers of both hybrids was higher. Movements of the pedicel may seem to play a larger role in the positioning of these flowers. Also, arching of inflorescences altered the orientation of some buds (figs. 12, 13).

When inflorescences are oriented at angles of 0°–90° relative to the ground, the buds are positioned with their labella uppermost (NYMAN et al. 1984). The amount of torsion necessary to place the labella lowermost in such cases is 90°–180° (fig. 12). In arching inflorescences, the labella are always in a dorsal position relative to the inflorescence tips. However, their orientation relative to the ground varies (fig. 13). As a consequence, the theoretical amount of turning required to position the labella of these buds downward is only 0°–90° (figs. 11–13). In fact, the observed range of torsion of upper buds was 20°–120° (fig. 11).

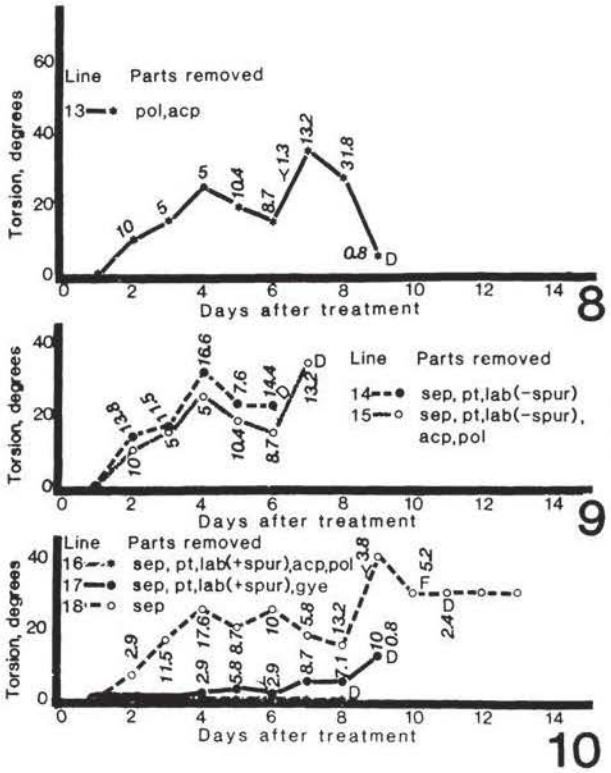
Turning of all flowers stopped on the day of opening or, at most, 24 h later. This is in line with reports (ZIEGENSPECK 1936) and our own finding (flowers 1–3 in NYMAN et al. [1984]) that resupination occurs only in buds or newly opened flowers.

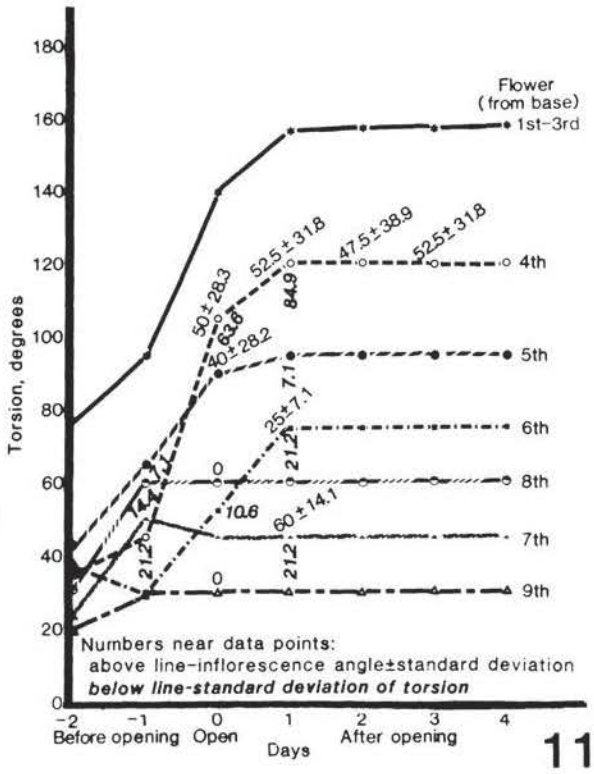
Missing buds did not affect the resupination of flowers below them (NYMAN et al. 1984). Removal of basal buds or flowers did not prevent the turning of those above. Therefore, it is reasonable to conclude that buds and flowers undergo resupination independently of each other. However, the shapes of the curves suggest that other buds or flowers may have a quantitative effect.

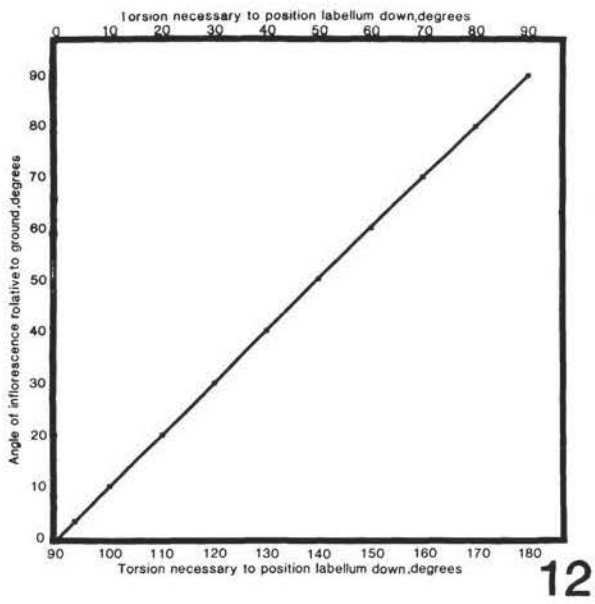
Resupination was reduced greatly when the pollinia were removed from young buds or following excision of the entire gynostemium or its upper part

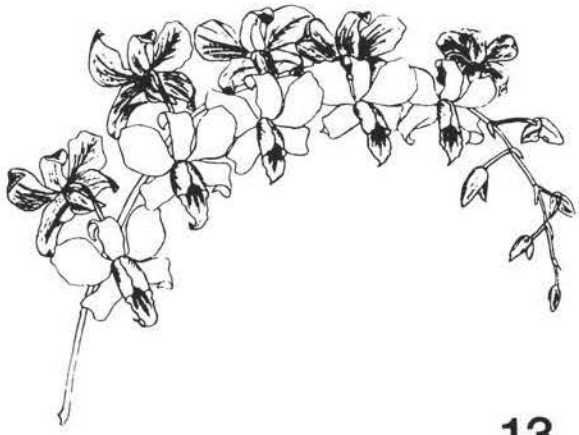


FIGS. 4–7.—Resupination of *Dendrobium* flowers: turning of controls and surgically treated flowers. *acp*, anther cap; *D*, dead; *F*, open flower; *fl*, flower; *gye*, entire gynostemium; *lab*, labellum; *pol*, pollinia; *pt*, petals; *sep*, sepals; *Y*, yellowing of floral segments. Italic numbers near data points and close to the letters *D*, *F*, and *Y* are SDs. Numbers are not repeated when values remained the same.









FIGS. 8–13.—Resupination of *Dendrobium* flowers. Figs. 8–10, Torsion of surgically treated flowers. Fig. 11, Torsion of flowers on different nodes of a flower stalk. Fig. 12, Torsion necessary to position labellum lowermost as affected by the angle of inflorescences (values were obtained from a cardboard and metal model). Fig. 13, Effects of arching of inflorescences on bud orientations. Symbols: same as in figs. 4–7.

TABLE 2

SIZE AND DIRECTION OF RESUPINATION AT THE OPENING OF FLOWERS OF DENDROBIUM TOMIE 'TOKYO' AND D. INDONESIA

FLOWER (from base)	BUD DIAMETER AT OPENING (mm)		CLOCKWISE/COUNTERCLOCKWISE RATIO	
	D. Tomie 'Tokyo'	*D.* Indonesia	*D.* Tomie 'Tokyo'	*D.* Indonesia
1–3[a]	12–17.9	8–16.9	1:1	1:1
4	14.6 ± .14	9.3 ± .46	1:1	1:1
5	13.5 ± 1.63	11.06 ± .72	1:1	5:1
6	14.35 ± .07	10.18 ± .62	0:1	1:1
7	12.4 ± .28	10.26 ± .88	1:0	0:1[a]
8	12.9[b]	9.88 ± .52	2:0	...
9	14.5[b]	10.7 ± .14	nt[c]	...
10	...	10[b]	...	...

[a] Summarized from NYMAN et al. (1984).
[b] One flower only.
[c] No turning.

(i.e., the pollinia and stigma were removed). This suggests that resupination may be regulated or at least affected by the pollinia and/or stigma. Suggestions that resupination may be gravitropic (ZIMMERMANN 1933; ZIEGENSPECK 1936; AMES 1946, 1948; BRIEGER 1970–1984) and a report that some flowers undergo deresupination after pollination (ZIEGENSPECK 1936) imply that auxin may be associated with this phenomenon. There is convincing evidence that, in orchid flowers, auxin moves basipetally through the gynostemium to ovaries (ARDITTI 1979; GOH et al. 1982; STRAUSS and ARDITTI 1982). In *Cymbidium*, removal of the pollinia from uppermost buds inhibits the elongation of inflorescences. Auxin (100 and 500 ppm naphthaleneacetic acid in lanolin) can replace the effect of pollinia on elongation (KAKO and OHNO 1980). In other flowers, styles and stigmas can be a source of auxin (KONING 1983). Altogether, the available evidence suggests that auxin and/or possibly other substances produced by the gynostemium or pollinia regulate resupination.

Removal of the sepals, petals, the entire gynostemium or parts of it, or the entire perianth resulted in large wound surfaces. This may have initiated the production of wound ethylene (TING 1982), which in turn induced yellowing (i.e., senescence) and abscission. Furthermore, the excision of what are essentially protective layers subjected the buds to desiccation, which may have (1) caused yellowing and abscission and (2) prevented resupination. This view is supported by the observation that (1) removal of only the petals or labellum did not prevent turning, probably because the remaining outer whorl (the sepals) provided substantial protection against desiccation, and (2) resupination was affected more severely by removal of the sepals. Another possibility is that perianth segments affect resupination by contributing growth factor(s) and/or metabolites. The movement of auxin and other substances from the perianth to the gynostemia, ovaries, and inflorescence axes (HARRISON and ARDITTI 1976; ARDITTI 1979) could be construed as evidence for this hypothesis. However, removal of the labellum and petals did not reduce torsion appreciably and argues against the likelihood that resupination is regulated physiologically by the perianth.

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