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Rhododendron mucronatum G. Don grown in subtropical Taiwan does not manifest endodormancy

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Abstract. Microscopic observation of bi-weekly sampled terminal buds revealed that most flower buds of *R. mucronatum* were formed between late-July and mid-August and differentiation of specific floral organs was completed before mid-October. Flower buds continued to enlarge through the winter. When flower buds on two-year-old plants from rooted cuttings were allowed to grow at day / night temperature of 15/13°C, 20/15°C, 25/20°C or 30/25°C, the 30/25°C treatment was observed to inhibit their growth; those subjected to the 15/13°C treatment grew the fastest during the early stages. Neither treatment, however, enabled attainment of anthesis by the end of the experiment. The 20/15°C treatment hastened flower bud growth and reduced the number of days to flowering. Bud growth was slower and flowering percentages were lower at 25/20°C, than at 20/15°C. When plants were transferred to 30/25°C after 2, 4, or 6 weeks in the 15/13°C treatment, the growth rate of flower buds increased greatly. Also, when the 15/13°C treatment was extended, the growth rate of flower buds increased, while the number of days needed for flowering after transferring from the low temperature treatment was reduced. The 15/13°C treatment simulated the winter temperatures in Taiwan. Our finding disclosed that bud growth was fastest, rather than ceasing, under this temperature regimen. Although growth rate decreased near the end of the experiment, it increased immediately and bloomed quickly when plants were transferred to higher temperatures. Thus, our observation indicated that *R. mucronatum* does not enter endodormancy during winter in subtropical Taiwan lowlands.

Keywords: Dormancy; Ecodormancy; Endodormancy; Flower bud development; Flowering; Temperature.

Introduction

Traditionally, it is believed that azalea flower buds enter dormancy before flowering and that the dormancy is overcome by low temperature. Hence, treatment of 4-6 weeks at 2-9°C is used to break flower bud dormancy for commercial production of potted azaleas (Larson, 1992; Seeley, 1981; Hamrick, 1991). When some azaleas, such as "Redwing" and "Reinhold Ambrosius," are grown at 20°C, they can attain anthesis without low temperature treatments; nevertheless, the uniformity of flowering is lower (Pettersen and Kristofferson, 1969). Brown and Box (1971) and Brown (1973) reported that some azalea cultivars, when grown at 18°C and under a 18-hour daylength, flowered about one-half to one month earlier than when given the traditional cold temperature treatment (5-week at 3°C); the uniformity of flowering was also very high. With temperate zone deciduous fruit species that are grown in tropical regions, Saure (1985) proposed that dormancy may be avoided because the warm temperature, together with the long daylength, is suitable for plant growth. This may be why some deciduous species can bear fruits twice a year. Accordingly, the early flowering of some azalea cultivars as reported by Brown and Box (1971) and Brown (1973) may be the result of the warm temperature and long daylength having prevented dormancy from occurring in the flower buds. The relationship between temperature and azalea flower bud dormancy needs to be clarified more precisely.

Rododendron mucronatum is widely found in northern Taiwan lowlands. It was introduced in 1925, but there have been very few studies on its flowering habits and flower bud dormancy. Tang (1975) reported on its morphological changes, from vegetative growth to flower bud formation, but did not investigate flower bud dormancy. The purpose of our study has been to observe the flowering habit of *R. mucronatum* in Taiwan lowlands, and to evaluate the effect of temperature on flower bud development and dormancy. Our findings described here may help to control the flowering behavior of azalea in subtropical regions.

Materials and Methods

Determination of Flower Bud Developmental Stages

The flowering of ten azalea (*R. mucronatum*) plants, about 50-years-old and in good condition on the National Taiwan University campus, was observed from mid-July,

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1995 to mid-March, 1996. One bud was randomly sampled from each plant at two-week intervals, and the developmental stage was observed microscopically using fixed and fresh sections. The developmental stages were identified according to the nine stages of Kohl and Scaroni (1956), Tang (1975), and Bodson (1983). These stages are shown in Table 1. In addition, the lengths of buds, corollas, stamens and styles, the dates of emergence of buds with color, and the dates of anthesis were recorded.

Temperature Treatments

Two-year-old plants from rooted cuttings of *R. mucronatum* were bought from a nursery in Yang-Ming Mountain, Taipei, in mid-February 1995. Each plant was about 60-cm tall and had 4-5 main shoots. They were potted in 15.3-cm plastic pots, containing a mixture of 5:2:2:1, V: V: V: V, soil: peat moss: vermiculite: perlite. The plants were placed in an open area of the Experimental Farm of National Taiwan University, Taipei, Taiwan. The plants were given 50% shade from May to September, and watered daily during the summer and at 2- to 3-day intervals during autumn and winter. A 20-20-20 fertilizer mixture (Peter's) was dissolved at a rate of 1 g / liter of water and applied weekly from March to October and at three-week intervals from October to anthesis, each pot receiving 250 ml of solution. Ten flower buds of about 1.0 cm length were sampled from each plant, and a total of three plants were employed per treatment. Plants were moved into growth rooms at day/night temperatures of 30/25°C, 25/20°C, 20/15°C, and 15/13°C. Because a long day may prevent dormancy occurring, the temperature experiment was conducted under short-day conditions to avoid the influence of daylength. The temperature experiment was conducted under natural daylengths because days in Taiwan were short during the experimental period. The natural daylength ranged from 11.5 to 12.6 hours during the experimental period, which spanned from 27 October 1995 to 2 February 1996. Bud growth, measured at two-week intervals, was based on total bud length. The dates of flower buds showing color and undergoing anthesis were also recorded.

Temperature Shift Treatments

Six flower buds, each about 1.2-1.3 cm long, were sampled from each plant. The plant source and cultivation methods were the same as for those used in temperature treatment investigation. Twelve plants were moved into a 15/13°C growth room on 16 November 1995. The natural daylength ranged from 11.5 to 12.6 hours during the experiment period. After 2, 4, and 6 weeks, three plants were transferred to a 30/25°C growth room. All treatments ended on 31 January 1996. Total bud lengths were measured at two-week intervals, and dates when all buds showed color and underwent anthesis, as well as flower diameter, were recorded. The percentage of total flower buds that bloomed before the experiment ended was also calculated as flowering percentage.

Table 1. The developmental stages of azalea terminal buds.

Stages	Description
0	Vegetative growth
1	Apex broadens
2	Sepal formation
3	Petal formation
4	Stamen formation
5	Carpel formation
6	Elongation of style
7	Bud shows color
8	Full bloom

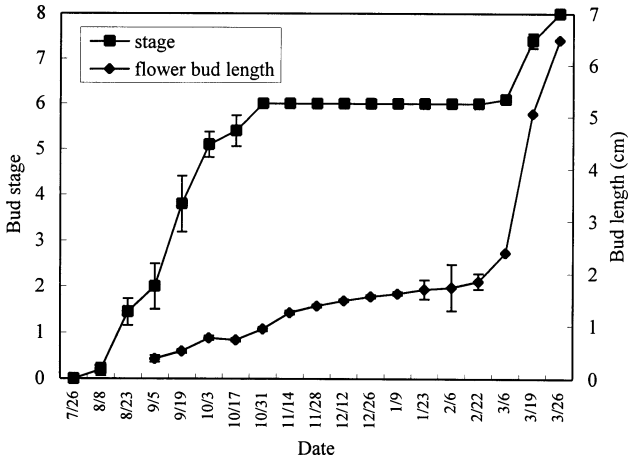

Figure 1. Flower developmental stage and flower bud length of *R. mucronatum* grown on campus of National Taiwan University.

Results

In the Taiwan lowlands, flowers of *R. mucronatum* that bloomed during the main flowering season were formed between mid-July and mid-August (Figure 1). Differentiation of flower organs was completed by late October, after which the buds grew slowly, but steadily. Flower buds developed color in late February, and underwent anthesis in mid-March. During the period of our observations, there were about four months during which the flower buds remained in Stage 6, but the buds did not cease growing because of the lower winter temperatures. Although the length of corollas, styles, and stamens did not increase significantly in January 1996 (Figure 2), an increase in standard errors of means indicated that a large variance existed in the development of buds.

The growth rate of flower buds increased when the temperature was lowered (Figure 3). In the early stages, buds of the 15/13°C treatment grew significantly faster than those of the other temperature treatments. Unlike flower buds of the 20/15°C treatment, which grew dramatically at the end of experiment and attained anthesis, those of 15/13°C declined in growth after 2 months. The growth rate of buds in the 25/20°C and 30/25°C treatments did not differ greatly, although a few flowers opened at the end of

25/20°C treatment. The growth rate was the lowest among buds of the 30/25°C treatment; furthermore, about 30% of the buds aborted (data not shown). Except for the 15/13°C treatment, no flower buds of *R. mucronatum* ceased growing during the experiment.

Flower buds grew slowly at 15/13°C and remained so when left continuously in the temperature regime (Table 2). The slower growth rate in continuous 15/13°C was attributable to decreased growth toward the end of the experiment. The flower bud growth rate increased twofold with a change in temperature regimes. Buds that received only two weeks of 15/13°C temperature treatment displayed color and bloomed the earliest, but the flowering percentage was only 58.82%. Plants that received 4 and 6 weeks of 15/13°C did not differ in dates of color display or in anthesis and flowering percentage. Nevertheless, as is evident in Table 3, the longer the low temperature treatment, the faster did the buds show color and attain anthesis. However, because of the shorter development time, the diameter of flowers was smaller.

Discussion

In the temperate zone, winter temperatures range from 0°C to 10°C, unsuitable for azalea plant growth. Their flower buds become dormant. However, in the subtropical Taiwan lowlands, the winter temperature is about 15°C with a minimum temperature always above 10°C (Chen and Wu, 1978). The continuous increase in the length of the flower buds as observed in this study indicated that the flower buds did not cease growing. The lengths of individual flower organs also increased in early winter, but ceased in late winter. Phytotron experiment confirmed that when buds were subjected to a 15/13°C regimen, simulating winter temperatures of north Taiwan lowlands, they grew faster than at higher temperature treatments during

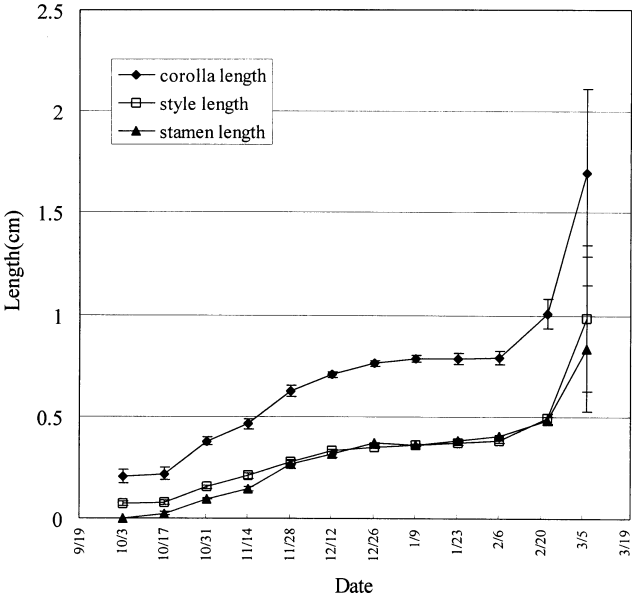

Figure 2. Lengths of floral organs of *R. mucronatum* grown on campus of National Taiwan University.

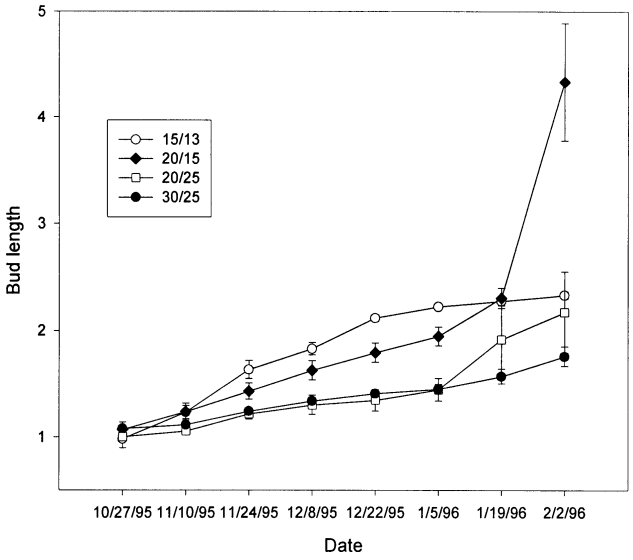

Figure 3. Effect of temperature on flower bud growth of *R. mucronatum*.

Table 2. Effect of temperature shift on flower bud development of *R. mucronatum*.

Temperature treatment	Average bud growth rate (mm/day)		Days to buds show color	Days to flowering	Flowering percentage (%)
	Before shift	After shift[a]			
15/13°C 8 weeks	0.085b[b]	–	–	–	–
15/13°C 6 weeks→30/25°C 2 weeks	0.110aB[c]	0.333aA	68.4a	77.6a	97.43a
15/13°C 4 weeks→30/25°C 4 weeks	0.111aB	0.199aA	64.4a	74.5a	86.33a
15/13°C 2 weeks→30/25°C 6 weeks	0.114aB	0.228aA	53.8b	66.2b	58.82b

[a] Means the average growth rate before flower buds showed color.
[b] Means within the same column followed by different lowercases were significantly different at the 0.05 level of Duncan's Multiple Range Test.
[c] Means within the same row followed by different uppercases were significantly different at the 0.05 level of Duncan's Multiple Range Test.

Table 3. Effect of temperature shift on flowering of *R. mucronatum*.

Temperature treatment	Days from temperature shift to buds show color	Days from temperature shift to anthesis	Flower diameter
15/13°C 6 weeks→30/25°C 2 weeks	18.4b[a]	27.6c	7.14b
15/13°C 4 weeks→30/25°C 4 weeks	29.4a	39.7b	7.06b
15/13°C 2 weeks→30/25°C 6 weeks	33.8a	46.2a	7.71a

[a] Means within the same column followed by different lowercases were significantly different at the 0.05 level of Duncan's Multiple Range Test.

the early stages. Lang (1987) suggested that dormancy should be defined as "the temporary suspension of visible growth of any plant structure containing a meristem." Applying that definition, it can be concluded that *R. mucronatum* did not manifest dormancy in the northern lowlands of Taiwan. The bud growth rate, however, decreased after about two months at 15/13°C. When buds from the 15/13°C treatment were transferred after 2-6 weeks to a higher (30/25°C) temperature, growth resumed and flowering quickly followed. These results also indicated that *R. mucronatum* does not enter "endodormancy," or dormancy that is controlled by physiological factors within the dormant structure (Lang, 1987). The growth rate only decreased among flower buds that were kept at 15/13°C continuously. It is possible that buds treated continuously in 15/13°C gradually entered "ecodormancy," or dormancy that is controlled by environmental stresses evoking nonspecific responses (Lang, 1987). The temperature was unfavorable to the final developmental stage of the flower buds, possibly explaining why the lengths of corollas, styles, and stamens did not increase continuously in January 1996. Pemberton and Wilkins (1985) also pointed out that the "Prize" azalea may not exhibit endodomancy. Therefore, it seems that the flower buds of some azalea species do not necessarily enter endodormancy before flowering, but they can enter endodormancy because of unsuitable growth temperatures in winter.

The four temperature treatments in our experiment caused the buds to grow faster as the temperature decreased, indicating that high temperatures inhibited flower bud development of *R. mucronatum*. This finding is similar to the report by Larson and Biamonte (1972), that "Red American Beauty" azaleas formed flower buds rapidly at 30°C, but subsequent development was delayed if the plants were retained at this temperature. Bud growth resumed only after the plants were moved to a cooler temperature (22-18°C). In our investigation, flower buds grown at 15/13°C grew faster in the early stages than at other temperatures, rather than entering dormancy. It is possible that azalea flower buds require low temperatures during flower development, but the low temperatures may be involved in physiological processes other than in overcoming dormancy. However, the length of the buds grown in 15/13°C did not continue to increase, but possibly ceased, and anthesis was unattained by the end of our experiments, indicating a need of higher temperature for completing the final developmental stage preceding anthesis. Base on results of our temperature shift treatments, we propose that four weeks of the low temperature treatment should be sufficient to satisfy the low temperature requirement of *R. mucronatum.*

To summarize, when *R. mucronatum* plants were placed under a 15/13°C treatment, similar to the average winter temperature in the northern Taiwan lowlands, the growth rate of their flower buds increased, instead of ceasing. Even though growth rate of buds decreased, it could be immediately increased and hastened to flower by transferring the plants to a higher temperature. Hence *R. mucronatum* grown in lowlands of subtropical Taiwan show no endodormancy, but may show ecodormancy in later developmental stages in winter. We conclude that *R. mucronatum* flower buds need about a month of low temperature to induce blooming. The low temperature requirement is related to some physiological reactions other than overcoming endodormancy.

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白琉球杜鵑（*Rhododendron mucronatum* G. Don）在亞熱帶的台灣應未存有內生性休眠

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針對台灣平地數十年生白琉球杜鵑定期逢機抽取 10 個花芽以鏡檢觀察，結果顯示白琉球杜鵑於七月底至八月中旬形成花芽，在十月中旬各花器發育完成。調查顯示白琉球杜鵑花芽及各花器在冬季持續生長，並未因氣溫降低而停止。以具有花芽的二年生白琉球杜鵑盆栽置於人工氣候室下四種溫度處理，日／夜溫 30/25℃ 的高溫會抑制粉白花芽發育，15/13℃ 的低溫可使初期花芽發育最快，但後期並不能使花芽達到開花階段。而 20/15℃ 不但可加速花芽發育，亦可提早開花，25/20℃ 處理花芽發育速度明顯較 20/15℃ 處理為慢，且開花率下降。另將白琉球杜鵑於人工氣候室以 15/13℃ 處理 2、4、6 週後移入 30/25℃，結果顯示低溫處理移溫後後花芽發育速率更行增加。且低溫處理越久，移至高溫後花朵發育越快，到開花天數越短。由於 15/13℃ 相當於北台灣冬季之平均氣溫，而此溫度試驗結果顯示在此溫度下白琉球杜鵑花芽並未停止生長，反而加速生長，即使至後期花芽發育減緩，但一移至高溫可迅速恢復生長以至開花，因此白琉球杜鵑在北台灣平地冬季應未進入內生性休眠。

關鍵詞：休眠；外生性休眠；內生性休眠；花芽發育；開花；溫度。