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EPICOTYL MORPHOPHYSIOLOGICAL DORMANCY IN SEEDS OF *DAPHNIPHYLLUM GLAUCESCENS*, A WOODY MEMBER OF THE SAXIFRAGALES

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Available information on seed dormancy for various members of the Saxifragales and phylogenetic relationships within this order allowed us to accurately predict that *Daphniphyllum glaucescens* seeds have morphophysiological dormancy (MPD). However, our hypothesis that seeds had deep simple epicotyl MPD, i.e., nondeep physiological dormancy (PD) in root and deep PD in shoot, was not supported. Both the root and the shoot (cotyledons) of the underdeveloped embryo of *D. glaucescens* have nondeep PD. Exposure to moderate (15°/6°, 20°/10°C), rather than high (25°/15°C), temperatures for 10–12 wk broke the PD of the hypocotyl/root. After hypocotyl emergence, seeds with an attached developing root system did not require cold stratification to break the PD of the shoot. The PD of the shoot was broken by an additional 10–12 wk at moderate temperatures, during which time cotyledons slowly grew inside the seed. As cotyledons grew, all of the hypocotyl was pushed out of the seed, and the final cotyledon length was almost twice that of the seed; at this point, the folded cotyledons emerged. Since the level of PD in root and shoot may or may not be the same, we advocate stating the level of PD in both root and shoot when epicotyl MPD is described in a species. Thus, seeds of *D. glaucescens* have nondeep simple (root)–nondeep simple (epicotyl) MPD, which is written as C_{1b}B(root)-C_{1b}B(shoot) in the formula system of Nikolaeva. This is the first report of this level of epicotyl MPD in the Saxifragales.

Keywords: epicotyl dormancy, morphophysiological dormancy, seed dormancy, seed germination, underdeveloped embryo.

Introduction

Dormant seeds cannot germinate under any set of normal environmental conditions that otherwise would be favorable for germination after seeds come out of dormancy (Baskin and Baskin 2004). Seed dormancy, including when and how it is broken, plays an important role in controlling the timing of germination in nature so that it occurs when conditions in the habitat are optimal for seedling establishment and growth of plants (Baskin and Baskin 1998; Finch-Savage and Leubner-Metzger 2006). To better understand this key step in the life cycle of seed plants, the physiology, biochemistry, molecular genetics, ecology, and evolution of seed dormancy have been given considerable attention (Finch-Savage and Leubner-Metzger 2006). Regardless of the research approach, it is clear that there are different kinds of dormancy, resulting in a need for a classification system of seed dormancy, and several have been devised (see Baskin and Baskin 2004). The classification system of Nikolaeva (1969, 1977) is the most comprehensive one, and it has proven to be useful to people in various disciplines who study seeds (Finch-Savage and Leubner-Metzger 2006). This system has been revised several times, and it has also been expanded into a hierarchical scheme of classes, levels, and types of seed dormancy (Baskin and Baskin 2004). A seed dormancy classification system not only organizes information but also facilitates exploration of questions about evolutionary relationship of various classes, levels, and types of dormancy.

Plotting information related to seed dormancy, e.g., various classes and levels of dormancy, on phylogenetic diagrams is potentially an important way to identify gaps in our knowledge about seed dormancy in a plant lineage. That is, if we know about seed dormancy in some members of a lineage, it may be possible to generate meaningful hypotheses about seed dormancy in other members of the lineage. However, some lineages, such as the Saxifragales, have a diversity of embryo types—i.e., spatulate–fully developed, rudimentary (underdeveloped), linear-underdeveloped, and linear–fully developed (Martin 1946; Baskin and Baskin 2007)—and classes/levels of dormancy—i.e., physiological dormancy (PD), deep simple morphophysiological dormancy (MPD), nondeep simple MPD, intermediate simple MPD, and deep simple epicotyl MPD (Nikolaeva et al. 1985; Baskin and Baskin 1998). Thus, an unstudied member of such a diverse lineage could have any one of several classes/levels of seed dormancy. In the case of the Saxifragales, however, phylogenetic relationships within the order may provide insight into the possible dormancy class/level to be found in a family, for example, the Daphniphyllaceae.

The Daphniphyllaceae constitute a monogeneric family of ~10 species of trees and shrubs ranging from New Guinea to India and north to central China and Japan (Huang 1965, 1993). Depending on the species, seeds require at least 45 d to several months (Huang 1965; Boyce 1999; Srivastava 2000) to germinate, indicating that they are dormant. Further, each

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seed of *Daphniphyllum himalayense* (Bhatnagar and Kapil 1982) and *Daphniphyllum glaucescens* (Huang 1965) has a small embryo in copious endosperm. These small embryos may be underdeveloped, i.e., grow inside the seed before radicle emergence, in which case the seeds would have MPD. However, it is not known whether the small embryos in *Daphniphyllum* seeds are underdeveloped; not all small embryos are underdeveloped (Baskin and Baskin 2005). Nikolaeva et al. (1985) list *D. glaucescens* as having seeds with only intermediate PD (but not MPD); however, Nikolaeva (1988) described the family Daphniphyllaceae as having seeds with intermediate complex MPD (which means that each seed has a small embryo that grows only during cold stratification).

A recent parsimony analysis of five genes resulted in a weakly supported clade in the Saxifragales consisting of Peridiscaceae, Paeoniaceae, Hamamelidaceae, Altingiaceae, and Daphniphyllaceae; the Cercidiphyllaceae are the sister to this clade (Soltis et al. 2007). A closer look at this analysis reveals that Peridiscaceae, Paeoniaceae, and Hamamelidaceae are a clade and that Altingiaceae plus Daphniphyllaceae are sister to it. Embryo type in these five families varies: Peridiscaceae has a small embryo, but its type has not been determined (Soltis et al. 2007); Paeoniaceae linear-underdeveloped and rudimentary ones; Hamamelidaceae a spatulate–fully developed one; Altingiaceae a spatulate–fully developed one (Martin 1946); and Daphniphyllaceae a small, linear, and possibly underdeveloped one (Huang 1965; Bhatnagar and Kapil 1982). Linear-underdeveloped and rudimentary embryos grow before seed germination, but spatulate–fully developed embryos do not. From the size/shape of Daphniphyllaceae embryos, we can see that they are more like those of the Paeoniaceae and possibly the Peridiscaceae than like those in the other woody families, Hamamelidaceae and Altingiaceae.

Seed dormancy has been studied in 11 species of Paeoniaceae, and all have MPD; nine have deep simple epicotyl MPD (Barton 1933; Nikolaeva et al. 1985; Wang and van Staden 2002), and seeds of *Paeonia officinalis* have intermediate simple MPD (Nikolaeva et al. 1985). Also, seeds of *Paeonia californica* germinate in autumn ~4 wk after the beginning of autumn rains, and shoots appear above ground in 10–12 wk (Schlising 1976), suggesting that seeds have some kind of epicotyl dormancy. Thus, we hypothesized that seeds of Daphniphyllaceae have MPD and that its level is deep simple epicotyl MPD. Our specific objectives were to determine whether seeds of *D. glaucescens* Blume ssp. *oldhamii* (Hemsl.) var. *oldhamii* (Hemsl.) Huang (hereafter *D. glaucescens*) have MPD and, if so, to determine the level of MPD and when embryo growth occurs.

Material and Methods

Ripe fruits were collected from trees of *Daphniphyllum glaucescens* growing at Yang-Ming-Shan, Taiwan (lat. 25°09′N, long. 121°33′E, 500 m asl) on October 19, November 10, and December 1, 2005, and October 5, 2006. The fruits are drupes; therefore, the exocarp and fleshy mesocarp were removed, leaving the endocarp around the true seed (hereafter, the germination unit consisting of the endocarp plus the true seed is called a "seed"). Seeds were washed with water and allowed to dry at room temperatures for several days, after which they were sent by air mail to the University of Kentucky. Germination studies were initiated within ~3 wk of seed collection. Seeds were incubated on sand moistened with distilled water in 9-cm-diameter plastic Petri dishes.

Hypocotyl and Shoot Emergence

For seeds collected in October 2005, rates of hypocotyl and shoot emergence were determined at alternating temperature regimes of 5°/1°, 15°/6°, 20°/10°, and 25°/15°C. In the 5°/1°C regime, seeds were exposed to 12 h of light each day at 5°C and 12 h of darkness at 1°C. In the other temperature regimes, seeds were incubated in light for 14 h each day; lights in the incubators were set to come on 1 h before the beginning of the high-temperature period and to go off 1 h after the beginning of the low-temperature period. Seeds were exposed to 40 μmol m^{-2} s^{-1} of cool white fluorescent light, 400–700 nm. Three replicates of 25 seeds each were placed in light at each temperature regime, and seeds were monitored at 2-wk intervals for 46 wk. The first indication of germination was emergence of the hypocotyl, and when it was $\geq$1 mm long, the seed was moved to another Petri dish (at the same temperature). After hypocotyl emergence, seeds were monitored for cotyledon emergence. This study was repeated with seeds collected on the other three dates, with similar results.

To determine whether rates of hypocotyl and cotyledon emergence are promoted by simulated seasonal temperature changes, seeds collected in December 2005 were subjected to increasing and decreasing temperatures, i.e., a move-along study, using three replicates of 25 seeds each as described above (see legend in fig. 2 for the sequences of moves to different temperatures). All seeds were monitored for hypocotyl and cotyledon emergence at 2-wk intervals for 46 wk. This study was repeated using seeds collected in October 2006, with very similar results. Mean (±SE) percentages of seeds with an emerged hypocotyl and shoot were calculated. Percentage of seeds with an emerged hypocotyl was based on number of viable seeds in each dish, and percentage of seeds with an emerged shoot was based on number of seeds with an emerged hypocotyl in each dish.

Temperature Requirement for Cotyledon Emergence

To determine whether cotyledon emergence was promoted by daily exposure to cold-stratifying temperatures (10°C each day under the 20°/10°C regime and 6°C each day under the 15°/6°C regime), seeds with and without emerged hypocotyls were transferred from 20°/10° to 25°/15°C. Seeds collected in October 2006 were incubated on wet sand in light at 20°/10°C for 0, 6, 8, 12, and 14 wk and were then transferred to 25°/15°C; a control was kept at 20°/10°C. Three replications of 25 seeds each were used for each condition, and all seeds were checked for hypocotyl and cotyledon emergence at 2-wk intervals for 28 wk. Mean ± SE percentages of seeds with an emerged hypocotyl (based on number of viable seeds) and emerged cotyledons (based on number of seeds with emerged hypocotyls) were calculated.

Embryo Growth before Hypocotyl Emergence

To determine whether embryos grow inside seeds before germination, embryo growth was monitored in seeds collected in October 2005. Seeds were incubated on moist sand in light

(14 h daily light period) at 15°/6°, 20°/10°, and 25°/15°C. At 2-wk intervals for 10 wk, embryos were excised from each of 15 seeds at each temperature and measured. Embryos were excised with a razor blade and a dissecting microscope equipped with a micrometer, which was used to measure embryos. To determine the length that embryos must reach before germination occurs, embryos were excised and measured from 15 seeds that were beginning to germinate, i.e., in which the seed coat (endocarp) had split but none of the hypocotyl had emerged; these seeds had been incubated at 20°/10°C for 8 or 10 wk. Each time embryos were measured, mean embryo length ± SE was calculated.

Embryo Growth after Hypocotyl Emergence

At the time of hypocotyl emergence, the shoot (consisting of part of the hypocotyl, the cotyledons, and the axis) remains inside the seed, and our observations indicated that it could be many weeks before shoot emergence occurred. To determine whether additional embryo growth occurs after hypocotyl emergence and before cotyledon emergence, shoot length (inside the seed) was monitored between time of hypocotyl emergence and cotyledon emergence. Seeds collected in November 2005 were incubated in light at 20°/10°C; 25 dishes with 25 seeds each were used. At 6 wk, seed coats (endocarp) began to split on a few seeds, and at 10 wk, the hypocotyl began to emerge from a few seeds. At 1-wk intervals (starting at 6 wk), seeds in all dishes were examined, and the length of the protruding hypocotyl (or hypocotyl plus root) was measured. Eventually, 15 seeds with a split seed coat and an external (protruding) hypocotyl/root length of 1, 2, 4, 6, 8, 10, 12, 14, 16, 18, 20, 22, 24, 26–32, 40–60, and 70–120 mm were found, and embryos were excised from them. After embryo excision, the length of the hypocotyl and/or cotyledons inside each seed was measured. It took 34 wk to find 15 seeds in each size category. The length of the external hypocotyl plus root was used to judge size categories instead of time of incubation because on any given date there was a range of sizes; i.e., seedlings grew at different rates. Also, at the beginning of the study, the length of 15 intact, imbibed seeds was measured, and then their embryos were excised and measured.

Results

Hypocotyl and Shoot Emergence

The hypocotyl was the first thing to emerge from seeds, and when the hypocotyl was ~1 cm long, the root emerged from it. Hypocotyl and shoot emergence occurred only while seeds were incubated at 15°/6° or 20°/10°C. Hypocotyl emergence in seeds incubated continuously at 15°/6° or 20°/10°C began after 10–12 wk, and most (especially at 15°/6°C) had emerged after ~30 wk. However, a few roots emerged at 20°/10°C after 32–40 wk. In seeds incubated continuously at 15°/6° or 20°/10°C, cotyledons began to emerge 10–12 wk after the hypocotyl emerged (fig. 1).

In the move-along study, moving seeds from high to low or from low to high temperatures had little effect on percentage of hypocotyl emergence (fig. 2). However, starting seeds at 5°/1° or 25°/15°C delayed the beginning of hypocotyl emergence by ≥10 wk. That is, hypocotyl emergence in seeds at 15°/6°C began at 12 wk, but in seeds moved from 5°/1° to 15°/6°C and from 25°/15° to 20°/10°C, it did not begin until 22 and 24 wk, respectively. After the hypocotyl emerged in seeds started at 5°/1°, 15°/6°, and 25°/15°C, it was another 10–12 wk before cotyledons began to emerge.

Temperature Requirement for Cotyledon Emergence

Cotyledons did not emerge from any seeds kept continuously at 25°/15°C (table 1). Regardless of (1) how long seeds were incubated at 20°/10°C before being moved to 25°/15°C and (2) whether the hypocotyl had emerged before the transfer to 25°/15°C, both hypocotyl and cotyledons emerged at 25°/15°C. The time (from beginning of experiment) for emergence of all hypocotyls and cotyledons (that did emerge) was 12–20 and 18–28 wk, respectively.

Embryo Growth before Hypocotyl Emergence

Mean (±SE) embryo length in fresh seeds collected in October 2005 was 1.59 ± 0.05 mm, and it was 2.73 ± 0.16 mm in seeds at 20°/10°C with a split seed coat. Thus, embryo length increased 72% before emergence of hypocotyl. Increase in mean embryo length did not exceed 15% at any temperature until

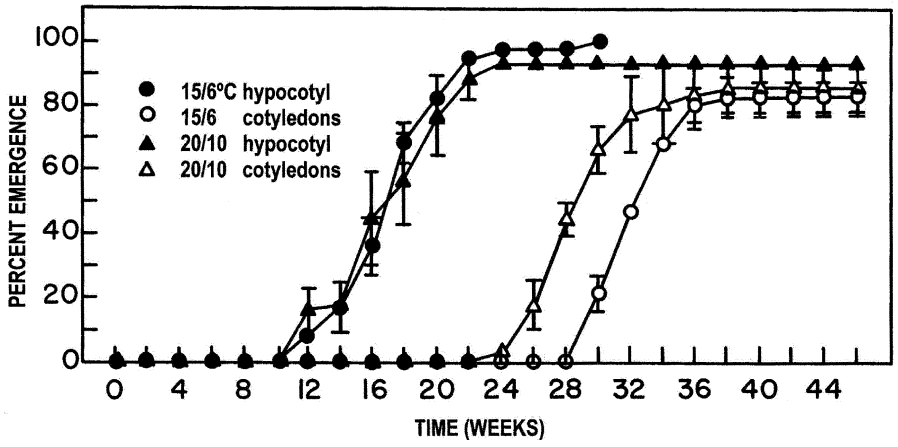

Fig. 1 Percentage (mean ± SE, if ≥5%; $n = 3$ replicates of 25 seeds each) hypocotyl and cotyledon emergence of *Daphniphyllum glaucescens* seeds collected in Taiwan in October 2005 and incubated at 5°/1°, 15°/6°, 20°/10°, and 25°/15°C. No hypocotyls or cotyledons emerged at 5°/1° or 25°/15°C.

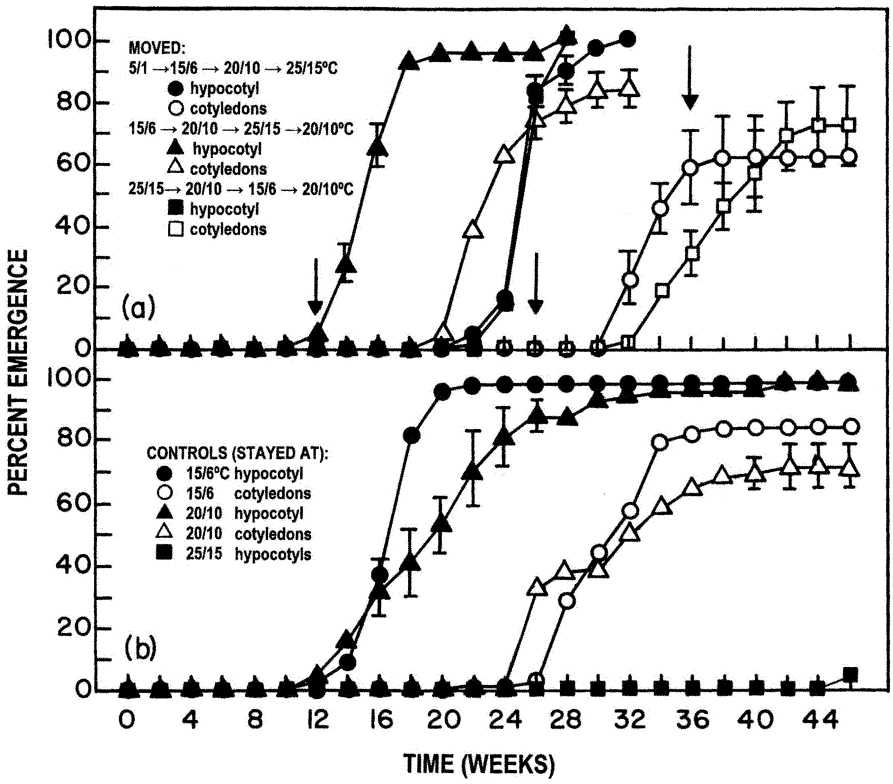

Fig. 2 Percentage (mean ± SE, if ≥5%; $n = 3$ replicates of 25 seeds each) hypocotyl and cotyledon emergence of *Daphniphyllum glaucescens* seeds collected in Taiwan in December 2005 and incubated at 5°/1°, 15°/6°, 20°/10°, and 25°/15°C. *a*, Seeds moved from 5°/1° to 15°/6° to 20°/10° to 25°/15°C; from 15°/6° to 20°/10° to 25°/15° to 20°/10°C; and from 25°/15° to 20°/10° to 15°/6° to 20°/10°C. Arrows indicate times when seeds were moved. *b*, Seeds kept continuously at 5°/1°, 15°/6°, 20°/10°, and 25°/15°C. No hypocotyls or cotyledons emerged at 5°/1°, and no cotyledons emerged at 25°/15°C in either the move-along (*a*) or the control (*b*) treatment.

after 6 wk (fig. 3). After 10 wk, embryos at 20°/10° and 15°/6°C had increased in length by 45% and 44%, respectively, but 4 of the 15 embryos measured from each temperature were still 1.55 ± 0.08 and 1.65 ± 0.11 mm long, respectively, indicating that they had grown very little, if at all.

Embryo Growth after Hypocotyl Emergence

Mean (±SE) length of imbibed seeds was 6.06 ± 0.12 mm, and length of embryos in these seeds was 1.47 ± 0.05 mm; cotyledons and hypocotyl (inside seed) were 0.59 ± 0.03 and 0.88 ± 0.03 mm long, respectively (fig. 4). As the emergent hypocotyl/root elongated from 1 to 70–130 mm, a series of changes occurred inside the seed. (1) The total length of the embryo inside the seed increased, reaching a maximum of 13.6 mm at the time cotyledons began to emerge. (2) The length of both the hypocotyl and the cotyledons increased. The hypocotyl was longer than the cotyledons until the embryo reached the 6-mm size category, at which time hypocotyl and cotyledons were the

Table 1

Effect of Moving Seeds of *Daphniphyllum glaucescens* from 20°/10° to 25°/15°C on Emergence of Hypocotyl and Cotyledons

Time at 20°/10°C before moving to 25°/15°C (wk)	Percentage with emerged hypocotyl when moved to 25°/15°C	Final percent emergence		Total time to emergence (wk)	
		Hypocotyl[a]	Cotyledons[b]	Hypocotyl	Cotyledons
0 (control, 25°/15°C)	0	4 ± 3	0	26	NA
6	0	52 ± 7	60 ± 2	12	22
8	1 ± 1	80 ± 3	60 ± 2	16	28
10	11 ± 1	67 ± 5	62 ± 1	14	18
12	20 ± 2	69 ± 3	61 ± 8	20	22
14	33 ± 1	72 ± 2	75 ± 9	18	22
28 (control, 20°/10°C)	NA	73 ± 4	61 ± 2	18	28

Note. Data presented as mean ± SE. NA = not applicable.

[a] Based on number of viable seeds; $n = 3$ replicates of 25 seeds each.

[b] Based on number of seeds with emerged hypocotyl; $n = 3$ replicates of 25 seeds each.

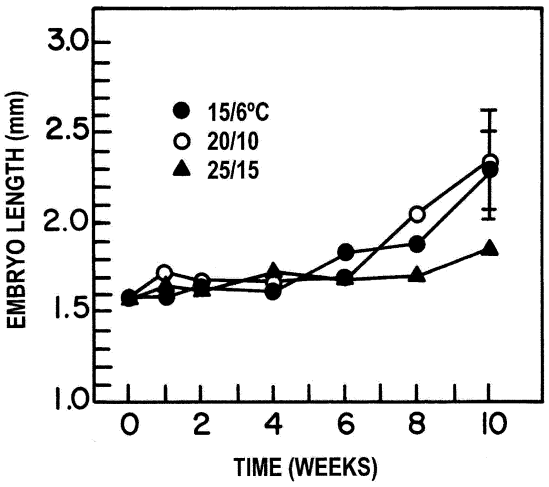

Fig. 3 Embryo length (mean ± SE, if ≥0.1 mm; $n = 15$ seeds) of *Daphniphyllum glaucescens* seeds collected in Taiwan in October 2005 and incubated in light at 15°/6°, 20°/10°, and 25°/15°C for 10 wk.

same length. (3) From the 8-mm to the 12-mm size category, the cotyledons increased more in length than did the hypocotyl (inside the seed). (4) From the 14-mm to the 70–130-mm size category, the cotyledons increased and the hypocotyl (inside seed) decreased in length. The cotyledons were growing, but the hypocotyl was being pushed to the outside of the seed. (5) Finally, all of the hypocotyl was pushed out of the seed, and at this time the greatly folded (or "bowed") cotyledons were 13.5 mm long; all of the endosperm was gone. (6) When all of the hypocotyl was pushed out of the seed, cotyledons emerged immediately. At the time of cotyledon emergence, the (full) hypocotyl and true root were 52 ± 3.2 and 38.19 ± 1.73 mm long, respectively (fig. 5).

Discussion

The first structure to emerge from germinating seeds of most dicots is the radicle, but it may be the hypocotyl or even the cotyledons, depending on the species (Werker 1997). Our observation that the hypocotyl is the first structure to emerge from *Daphniphyllum glaucescens* seeds confirms those made by Huang (1965), who published a series of drawings on germination of this species. These drawings show emergence of the hypocotyl, then appearance of the radicle, and finally, development of the root system. Also, as indicated by Huang (1965), we saw no evidence of root emergence until the emerged (from seed) part of the hypocotyl was ~1 cm in length. Further, it should be noted that Huang's drawings do not show what happens inside the seed before cotyledon emergence.

The small, linear embryo in *D. glaucescens* seeds increased in length by 72% before hypocotyl emergence, showing that the embryo is underdeveloped. Even at optimum temperatures for hypocotyl emergence (15°/6° and 20°/10°C), little or no embryo growth occurred until after 4–6 wk, and hypocotyls did not begin to emerge until after 10–12 wk. Thus, underdeveloped embryos also have PD, which delays onset of embryo growth and emergence of the hypocotyl and shoot, and, as hypothesized, seeds of *D. glaucescens* have MPD. Hence, the report by Nikolaeva et al. (1985) that seeds of this species have only intermediate PD is not supported by our data.

The long delay between emergence of hypocotyl and that of cotyledons in *D. glaucescens* seeds can generally be described as epicotyl dormancy; thus, seeds of this species have epicotyl MPD. Epicotyl MPD is found in Piperales, Liliales,

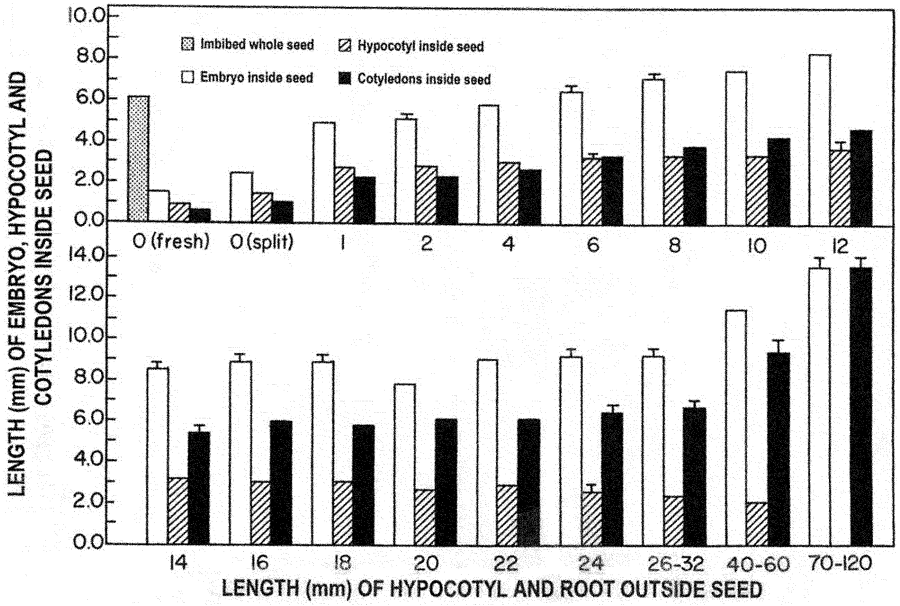

Fig. 4 Length (mean ± SE, if ≥0.1 mm; $n = 15$ seeds) of whole seed and of embryo of fresh imbibed seeds (*0 (fresh)*) of *Daphniphyllum glaucescens* collected in Taiwan in November 2005 and length of embryo, hypocotyl, and cotyledons inside seed at time seed coat split (*0 (split)*, just before hypocotyl emergence) and when emerged part of hypocotyl or hypocotyl plus root was from 1 to 70–120 mm in length.

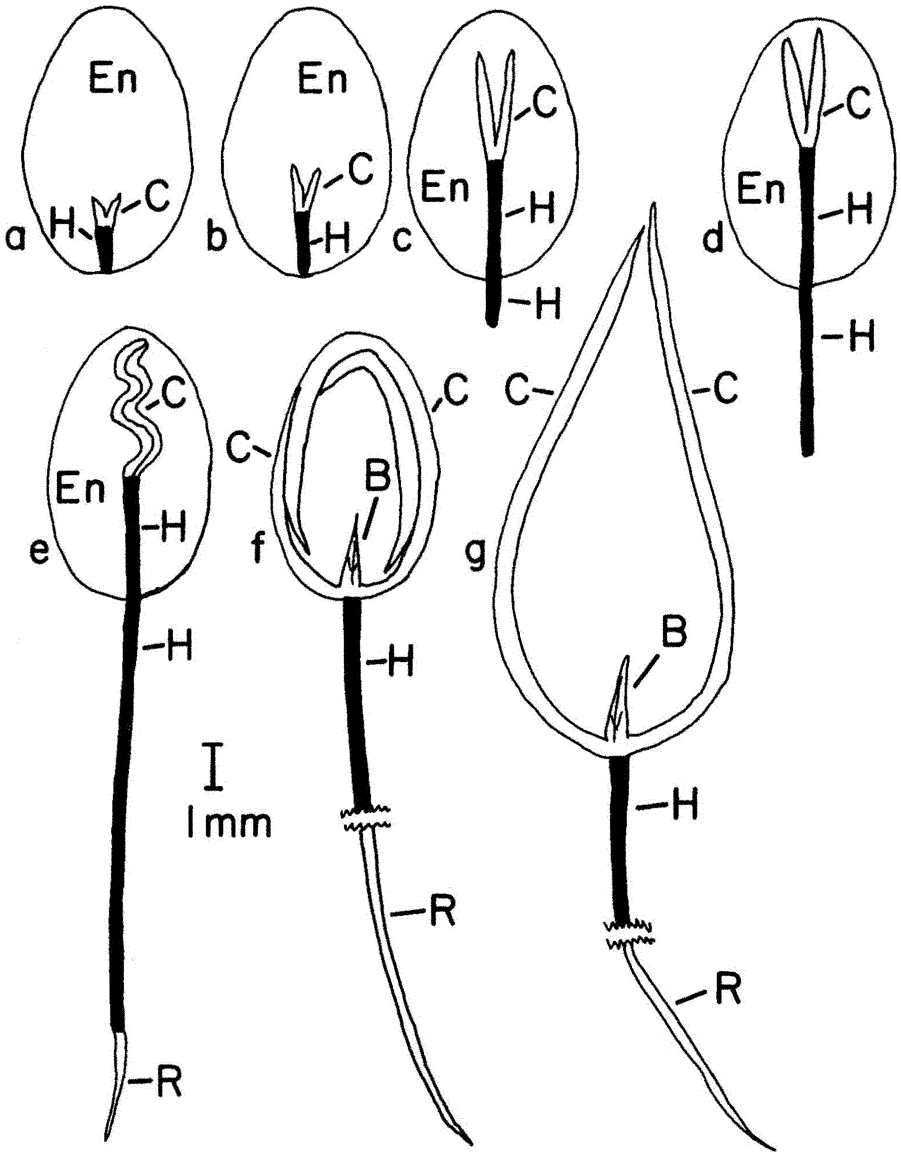

Fig. 5 Various stages in the germination morphology of *Daphniphyllum glaucescens*. *B* = apical bud, *C* = cotyledons, *En* = endosperm, *H* = hypocotyl, *R* = root. *a*, Fresh seed with linear embryo and endosperm. *b*, Embryo has increased in length, and at this point the seed coat splits (not shown). *c*, Embryo has increased in length, and hypocotyl has emerged. *d*, Hypocotyl has emerged from seed, and the portion of the hypocotyl inside the seed, as well as cotyledons, has increased in length. *e*, Cotyledons have increased in length and are bent. Also, portion of hypocotyl outside the seed has increased in length, and root has emerged from end of hypocotyl. *f*, All of the hypocotyl has been pushed out of seed, cotyledons have reached maximum length and are bent or folded in various ways, apical bud has grown to a length of ~2 mm, and all of the endosperm has been used. *g*, Cotyledons have emerged from the seed, at which time mean ± SE hypocotyl and root length were 52 ± 3.2 and 38.19 ± 1.73 mm, respectively.

Ranunculales, Saxifragales, Dipsacales, and the Boraginaceae (unplaced in Euasterids I), and with the exception of *Daphniphyllum* and *Viburnum*, it is known only in herbaceous plants (Baskin and Baskin 1998). Several woody plants, e.g., *Chionanthus retusus* (Chien et al. 2004), *Psychotria* sp. (C. C. Baskin, J. M. Baskin, and A. Yoshinaga, unpublished data), and *Quercus* spp. (Allen and Farmer 1977; Farmer 1977), have epicotyl dormancy, but the embryo is fully developed. However, in *C. retusus* seeds, there is further differentiation of the shoot apex before radicle emergence (Chien et al. 2004). After the root emerges from seeds of these taxa, PD of the shoot must be broken before the shoot emerges. In all seeds with epicotyl dormancy, the root system is well established before the shoot emerges. For example, by the time cotyledons emerge from *D. glaucescens* seeds, the hypocotyl not only has emerged but also has produced the main root; often lateral roots also are present (drawings in Huang 1965; our measurements and observations). However, the consequences of epicotyl dormancy in seeds with either underdeveloped or fully developed embryos on fitness of the species have yet to be determined.

Nikolaeva (1977) classified seeds that had underdeveloped embryos and inhibition of epicotyl growth until after a seed with its developing root system had been given a cold-stratification treatment as having deep simple epicotyl MPD. That is, the epicotyl had deep PD. However, research on temperate woodland species with epicotyl dormancy revealed that the radicles of the underdeveloped embryos also had PD and that only warm stratification was required to break it (Baskin and Baskin 1983, 1986). According to Nikolaeva's (1969, 1977) criteria, the level of PD in the radicles is nondeep. Thus, in the field, the nondeep PD of radicles is broken in summer, radicles emerge in autumn, and the deep PD of the epicotyl is broken by cold stratification during winter.

Warm stratification is the only dormancy-breaking requirement of *D. glaucescens* hypocotyls, but exposure to high summer temperatures (25°/15°C) did not promote hypocotyl emergence in *D. glaucescens* seeds. After seeds were moved from 25°/15° to 20°/10°C, there was a delay of 10–12 wk before hypocotyls started to emerge, indicating that PD was not broken while seeds were at 25°/15°C. In *D. glaucescens* seeds incubated in darkness at a constant temperature of 15°C, 0%, 5%, 80%, and 95% of them had emergent hypocotyls after 1, 2, 3, and 4 mo, respectively (C.-T. Chien and S.-Y. Chen, unpublished data).

The epicotyl in seeds of *D. glaucescens* is dormant, but unlike those of seeds with deep simple epicotyl MPD (described above), cotyledons of *D. glaucescens* emerged at high temperatures (25°/15°C) without the seed and its emerged/attached root system having been given a cold-stratification treatment. In fact, after 6 and 8 wk at 20°/10°C, when embryo growth had just been initiated inside the seed (but the hypocotyl had not yet emerged), both hypocotyls and cotyledons emerged in seeds moved from 20°/10° to 25°/15°C. After hypocotyl emergence in seeds of *D. glaucescens*, there was a long delay until cotyledons emerged, both in seeds kept at 20°/10°C and in those moved from 20°/10° to 25°/15°C. Thus, we conclude that the PD part of the MPD of the cotyledons is broken relatively slowly and that the maximum rate of cotyledon growth does not occur until all the PD is broken. Further, judging from growth of cotyledons inside the seed (fig. 4), it appears that the external hypocotyl/root is ~12–14 mm long before most of the PD is broken. After the hypocotyl/root length surpasses 26–32 mm, all PD of cotyledons is broken, after which cotyledons grow rapidly.

Since seeds (both the hypocotyl and shoot) of *D. glaucescens* require only relatively high temperatures for embryo growth and emergence of hypocotyl and cotyledons (15°/6° and 20°/10°C, respectively), they fit Nikolaeva's (1977) general category of simple levels of MPD. Thus, seeds of *D. glaucescens* have a simple level of epicotyl MPD. If seeds required cold stratification for embryo growth and germination, they would fit her general category of complex levels of MPD. However, because cold stratification delayed dormancy break and germination of *D. glaucescens* seeds, the description of intermediate complex MPD given by Nikolaeva (1988) for Daphniphyllaceae does not fit seeds of *D. glaucescens*. Further, because the hypocotyl and epicotyl in *D. glaucescens* embryos are about equally dormant (requiring 10–12 wk of exposure to moderately high temperatures for dormancy break to occur in each of them), we conclude that both the hypocotyl and the epicotyl have nondeep PD. Thus, seeds of *D. glaucescens* have nondeep simple epicotyl MPD, and this is the first report of this level of epicotyl MPD in the Saxifragales.

It should be noted that deep PD that can be broken only by long periods (16 to ≥162 wk) of warm stratification has been identified in seeds of *Leptocophylla tameiameiae*, a shrub from the montane zone of Hawaii (Baskin et al. 2005). Nikolaeva (1969, 1977) described deep PD as being broken only by long periods of cold stratification. Given the relatively long periods of time required to break PD in the hypocotyl and shoot of *D. glaucescens*, we cannot entirely rule out the possibility that the PD part of MPD in the hypocotyl and shoot of *D. glaucescens* could be the intermediate level.

Nondeep simple epicotyl MPD has been reported in seeds of *Viburnum odoratissimum* (Baskin et al. 2008). The dormancy-breaking and germination requirements of *V. odoratissimum* (seeds also from Taiwan) and *D. glaucescens* seeds (both root and shoot) are similar in that 15°/6° and 20°/10°C are optimal temperatures for root and shoot emergence in both species. However, rates of root and shoot emergence were faster at these temperatures for seeds of *V. odoratissimum* than for those of *D. glaucescens*, indicating that the seeds of *D. glaucescens* had more PD those of *V. odoratissimum*.

Given that (1) there are three levels of PD (Nikolaeva 1969, 1977) and (2) the root and shoot can have different levels of PD (Baskin and Baskin 1983, 1986), there can be nine different kinds of simple epicotyl MPD. Thus, it appears that if we want to accurately describe the dormancy in seeds with epicotyl MPD, we must state the level of PD in both the root and shoot. In such a system, the name for dormancy in seeds of *D. glaucescens* would be nondeep simple (root)–nondeep simple (epicotyl) MPD, and in Nikolaeva's formula system (Baskin and Baskin 2008), it would be written as $C_{1b}B$(root)-$C_{1b}B$(shoot). Further, the name for seeds with deep simple epicotyl MPD, e.g., 11 species of Paeoniaceae (Barton 1933; Nikolaeva et al. 1985; Wang and van Staden 2002), would be nondeep simple (root)–deep simple (epicotyl), with the formula $C_{1b}B$(root)-$C_{3a}B$(shoot). In these formulas, C_{1b} indicates nondeep PD broken by warm stratification, C_{3a} indicates deep PD broken by cold stratification, and B indicates underdeveloped embryo.

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