

A new type of epicotyl dormancy in crypto-viviparous fruits of *Aegiceras corniculatum* (Primulaceae), the first report from a true mangrove species

Malaka Madhuranga Wijayasinghe^{1,2,3}, Kariyawasam Marthinna Gamage Gehan Jayasuriya^{1,2}, Savitri Gunatilleke^{1,2}, Nimal Gunatilleke^{1,2}, Jeffrey Walck⁴

¹ Department of Botany, University of Peradeniya, Peradeniya, Sri Lanka

² Postgraduate Institute of Science, University of Peradeniya, Peradeniya, Sri Lanka

³ Department of Biological Sciences, Faculty of Applied Sciences, Rajarata University of Sri Lanka, Mihintale, Sri Lanka

⁴ Department of Biology, Middle Tennessee State University, Murfreesboro, USA

Corresponding author: Malaka M. Wijayasinghe (malakamadhu@gmail.com)

Academic editor: Sergey Rosbakh ♦ Received 2 March 2025 ♦ Accepted 8 May 2025 ♦ Published 3 July 2025

Abstract

Background and aims – Although viviparous seeds of mangrove species have traditionally been considered non-dormant, our previous study has shown that *Aegiceras corniculatum*, a crypto-vivipary species exhibits epicotyl dormancy. However, the kind of epicotyl dormancy in this species has not yet been explored. Thus, the aim of this study was to ascertain the kinds of epicotyl dormancy present in *A. corniculatum*.

Material and methods – Mature fruits were collected in Sri Lanka. The effects of scarification, light, and temperature on root emergence and the effects of scarification, gibberellic acid (GA₃), salinity, light, and root stability on shoot emergence were tested. In addition, the morphology and anatomy of the fruits in relation to shoot emergence and growth were documented.

Key results – Under both light/dark and darkness, > 70% of non-scarified and scarified fruits had an emerged root within 30 days, and thus, we considered them non-dormant. Root emergence was dependent on temperature, with reduced root emergence at higher temperatures. In contrast, a substantial time delay occurred between root and shoot emergence. Environmental conditions influenced shoot emergence, with emergence slower (1) in low NaCl solutions than in high solutions, (2) in darkness than in light/dark, and (3) when fruits were laid horizontally on a substratum as compared to being planted vertically. When fruits were treated with GA₃ or were scarified, the time delay between root and shoot emergence was shortened.

Conclusion – Since fruits of *A. corniculatum* contain a fully developed embryo, we conclude that they exhibit epicotyl physiological dormancy (PD). Furthermore, we propose that this dormancy represents a new type of epicotyl PD, symbolized by the formula: C_{cry}(root)-C_{ib}^P(shoot), where “cry” depicts the crypto-viviparous nature of the radicle or the hypocotyl.

Keywords

embryo, epicotyl physiological dormancy, salinity, shoot emergence, temperature

INTRODUCTION

Although reports of epicotyl dormancy in seeds with fully developed embryos of tropical glycophytic species are common (Carvalho et al. 1998; Chien et al. 2004; Agyili et

al. 2007; Jayasuriya et al. 2010, 2012; Athugala et al. 2018), there is a lack of information regarding this phenomenon in halophytes. In a recent publication by Wijayasinghe et al. (2023), the presence of epicotyl dormancy in *Aegiceras corniculatum* (L.) Blanco, a true mangrove species, was

reported for the first time. However, the study did not investigate the exact kind of dormancy present in this species, sparking renewed interest in understanding its specific nature. Understanding the type of epicotyl dormancy observed in *A. corniculatum* is crucial because it allows us to understand the ecological significance of this dormancy type and draw inferences about the evolution of seed dormancy across different species and habitats.

Aegiceras corniculatum is a crypto-viviparous species, which falls under the broader category of vivipary. In crypto-vivipary, the hypocotyl pierces the seed coat but not the fruit coat before seed dispersal (Tomlinson 1994). In contrast, vivipary involves the embryo continuously growing, piercing both the seed coat and fruit coat before dispersal while still attached to the mother plant (Goebel 1905; Elmqvist and Cox 1996). However, unlike seeds of other viviparous or crypto-viviparous species, mangrove species undergo a unique development process. They develop the hypocotyl while still attached to the mother plant, but the epicotyl remains dormant during this period (Juncosa 1982; Tomlinson and Cox 2000). As a result, the hypocotyl grows and protrudes from the seed coat, but the epicotyl remains in a dormant state.

Epicotyl dormancy in seeds with fully developed embryos is referred to as “physiological epicotyl dormancy” (Jayasuriya et al. 2010). In their latest dormancy classification system, Baskin and Baskin (2014, 2021) introduced a subclass called “physiological epicotyl dormancy (epicotyl PD)” within the broader class of physiological dormancy. This subclass is further divided into two levels: nondeep and deep. Each level comprises three types (Baskin and Baskin 2014, 2021).

Therefore, the main objectives of this research were to confirm epicotyl dormancy, categorize its type, and assess the effects of environmental factors on epicotyl dormancy in *Aegiceras corniculatum*. To evaluate the root emergence requirements of *A. corniculatum*, the effects of two temperature regimes to which these plants are exposed were studied. To test the presence of physiological dormancy, gibberellic acid (GA_3) was applied to fruits since it is well known to overcome physiological dormancy, and manual scarification was performed on fruits since it tests whether the embryo can overcome the mechanical constraints of the seed/fruit coat (Baskin and Baskin 2014). The effects of these two treatments were determined for both root and shoot emergence. NaCl is the most abundant salt in the sea and brackish water to which mangrove species are naturally exposed (Scholander et al. 1962). Therefore, the effects of a NaCl concentration gradient were studied to test the hypothesis that shoot emergence may be limited to favourable salinity conditions for seedling production. Jayasuriya et al. (2010) hypothesized that epicotyl PD may be an adaptation to survive seed predation and pathogenesis under low light conditions which prevail in tropical rainforests. Thus, the effects of light versus darkness on root and shoot emergence

were studied to test the validity of this hypothesis for *A. corniculatum* fruits. Tomlinson and Cox (2000) reported that in *Bruguiera gymnorhiza* (L.) Lam. ex Savigny and *Rhizophora mangle* L., 5 weeks were required for shoots to become erect when the hypocotyls were planted vertically, but 7 weeks were needed when the hypocotyls were planted horizontally. To test the effects of type and orientation of planting (hereafter, referred to as root stability) on *A. corniculatum*, we inserted the hypocotyl vertically into or laid it horizontally on a substratum and followed shoot emergence. Lastly, we described the morphology and anatomy of *A. corniculatum* fruits in relation to shoot emergence and growth.

MATERIAL AND METHODS

Study species

Aegiceras Gaertn. (Primulaceae sensu lato) is a genus comprised of two species: *A. corniculatum* and *A. floridum* Roem. & Schult., both confined to Asian tropical mangrove ecosystems (Tomlinson 1994). Among these, *A. corniculatum* is the only *Aegiceras* species found in Sri Lanka, and it is an evergreen treelet or shrub and is widely distributed throughout the country with a common occurrence (Ellison et al. 2010). As a result, it has been classified as a least concern (LC) species in the Sri Lankan Red Data list (2020). This species grows in mangroves within Sri Lanka's dry, intermediate, and wet zones (Jayatissa et al. 2002), and it is often found near estuarine banks (Ellison et al. 2010). A unique characteristic of this species is its crypto-vivipary fruit morphology, which distinguishes it from other genera in Primulaceae (sensu stricto) (Tomlinson 1994).

Fruit collection and storage conditions

Mature (yellow-brown) fruits were collected in Sri Lanka from Kalamatiya (dry zone mangrove) in December 2012 (KLM1) and again in June 2013 (KLM2), and from Pambala (wet zone) in February 2014 (PM1). Fruits were collected from at least five trees at each site and brought in labelled polythene bags to the University of Peradeniya, Sri Lanka. For each collection date, fruits were pooled and randomly selected for the laboratory experiments which were initiated within a week maximum following fruit collection. For the experiments, the entire fruit coat was kept intact (hereafter referred to as non-scarified) or was manually removed by hand using a scalpel from the entire fruit (hereafter, manually scarified, i.e. de-coated).

Laboratory conditions and procedures

Unless otherwise stated, the studies were done in the laboratory at a temperature of 27°C and a relative humidity of approximately 80% (hereafter ambient laboratory conditions). Two light conditions were used: a 14/10 hour light/dark cycle with fluorescent ceiling

lights, and diffuse sunlight from windows, or darkness provided by placing the Petri dishes in a closed box covered with aluminium foil. Fruits were placed on tissue papers moistened with distilled water in 9 cm diameter plastic Petri dishes during the experiments unless otherwise stated. The emergence of the radicle (by at least 1 mm) from the hypocotyl was the criterion for root emergence, and protrusion of the plumule axis through the cotyledons (by at least 1 mm) was the criterion for shoot emergence (Fig. 1B).

Effects of manual scarification on root emergence under different light conditions

Two sets of samples were prepared, each consisting of three replicates. Within each replicate, there were 15 non-scarified and 15 manually scarified fruits from KLM1. These samples were placed on moist tissue papers inside plastic boxes and exposed to a light/dark (14/10 h) cycle at ambient laboratory conditions. Similarly, another set of experimental setups was arranged with the same characteristics and exposed to darkness. Root emergence

was scored at 3-day intervals for 30 days, and percentages were compared by binary logistic regression (Minitab Inc., State College, PA, USA).

Effects of temperature on root emergence under different light conditions

Four samples, with three replicates each containing 15 non-scarified fruits from KLM2, were placed on moist tissue papers inside Petri dishes in light/dark (14/10 h) or in complete darkness at ambient laboratory conditions (27°C) and in a seed incubator (MGC 450 BP, Hinoteck, China) at 35°C. Samples were checked for root emergence at 3-day intervals for 30 days. Root emergence percentages were compared by binary logistic regression.

Effects of scarification and GA₃ on shoot emergence under light/dark condition

Two samples of three replicates each, consisting of 20 non-scarified and 20 manually scarified fruits from KLM1 were placed on moistened tissue papers with

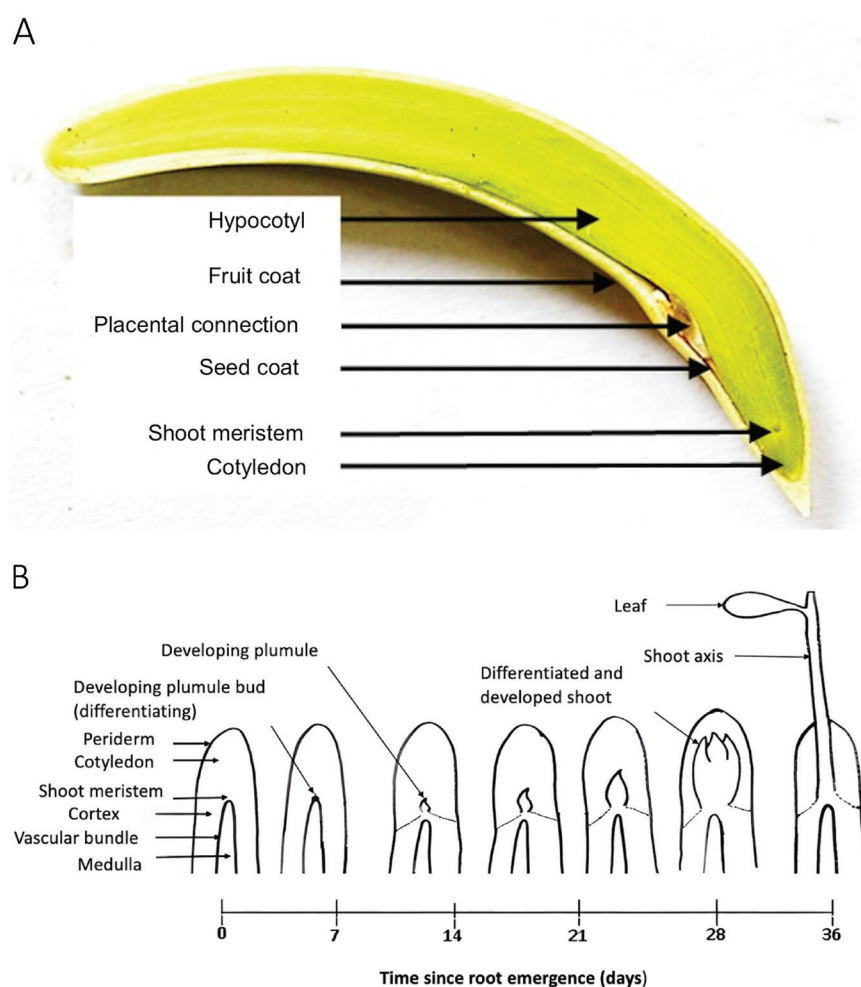


Figure 1. A. Longitudinal section of a mature fresh fruit showing the undifferentiated shoot and well-developed hypocotyl. B. Longitudinal section of the epicotyl region of an *Aegiceras corniculatum* seedling showing shoot development in light/dark conditions at ambient laboratory conditions over 36 days for the PM1 collection.

distilled water inside Petri dishes under light/dark (14/10 h) at ambient laboratory conditions. Another sample of three replicates, each consisting of 20 non-scarified fruits was placed on tissue papers moistened with GA₃ (500 ppm) inside Petri dishes under the same light/dark condition. Observations were made daily, and dates of root and shoot emergence of each fruit were recorded. The time taken to shoot emergence from root emergence was calculated and compared by non-parametric Mood's median test (Minitab Inc., State College, PA, USA).

Effects of salinity on shoot emergence under light/dark condition

Six samples, each containing three replicates of 15 KLM1 seeds, were subjected to an experiment involving different osmotic potentials of NaCl solutions (0.0, -0.1, -0.3, -0.5, -1.0, and -2.5 MPa). These samples were placed onto tissue papers moistened with the respective NaCl solutions and exposed to light/dark (14/10 h) at ambient laboratory conditions. Observations were made daily, and dates of root and shoot emergence of each fruit were recorded. Time taken for shoot emergence from root emergence was calculated and compared by Mood's median test.

Effects of scarification on shoot emergence under different light conditions

The experiment utilized fruits from KLM2. In total, two sets of samples were prepared, each comprising three replicates. Each replicate consisted of 15 non-scarified fruits and these fruits were placed on sandy soil moistened with distilled water under light/dark (14/10 h) conditions. Similarly, the second set of replicates, each containing 15 non-scarified fruits were placed on sandy soil moistened with distilled water in darkness. These arrangements were established at ambient laboratory conditions (Suppl. material 1).

Observations were conducted at 3-day intervals to monitor the root emergence of the fruit samples. After root emergence, one sample from the light/dark regime was transferred to a completely dark environment (light/dark to dark), while the other sample continued in light/dark conditions (light/dark to light/dark). After root emergence occurred for fruits incubated in darkness, one sample was transferred to the light/dark (dark to light/dark), while the remaining sample was kept in darkness (dark to dark).

Two samples, with three replicates each containing 15 manually scarified fruits from KLM2, were placed in light/dark on soil moistened with distilled water at ambient laboratory conditions. After root emergence, one sample was transferred from light/dark to darkness (light/dark to dark) and the remaining sample was kept in light/dark (light/dark to light/dark).

Individual fruits of all of the above samples were checked for shoot emergence in 3-day intervals. Date of shoot emergence was recorded for each fruit. Samples

kept in darkness were observed under very low light conditions, with each replicate exposed to light for only a brief period (~2 minutes) during observations. Time duration between root emergence and shoot emergence was calculated and compared by Mood's median test.

Effects of root stability on shoot emergence

Four samples of fruits each containing 20 non-scarified fruits from PM1 were placed on moist tissue papers in light/dark (14/10 h) at ambient laboratory conditions (Suppl. material 2). Following root emergence, two of the samples were retrieved and planted vertically by hand with ~1.5 cm of the hypocotyl being inserted into coconut coir substratum moistened with distilled water and exposed to light/dark or darkness at ambient laboratory conditions. The remaining two samples were laid horizontally on the coconut coir substrate and kept in light/dark and darkness at ambient laboratory conditions. The date of shoot emergence for each fruit in each sample was recorded, and the time interval between root emergence and shoot emergence was calculated and compared using Mood's median test.

Morphology and anatomy of fruits in relation to shoot emergence and growth

Fresh fruits from the PM1 collection were cut in half lengthwise and observed under a dissecting microscope. A sample of 25 non-scarified germinated fruits in each was placed by hand vertically on coconut coir substratum in light/dark at ambient laboratory conditions. At regular intervals over 36 days, five fruits were dissected each time, all parts of the fruit were identified, and the length of the shoot was measured. Photographs were taken using a digital camera (Nikon D3100), and hand drawings were made to explain the observations.

RESULTS

Effects of manual scarification on root emergence under different light conditions

Root emergence of non-scarified fruits was $80.0 \pm 6.7\%$ (mean $\pm$ SE) in light/dark at ambient laboratory conditions within 30 days, while it was $73.3 \pm 19.9\%$ in darkness. Root emergence of manually scarified fruits was $91.1 \pm 17.4\%$ in light/dark within 30 days. All non-scarified and manually scarified fruits that did not emerge roots were non-viable. Root emergence percentages did not differ among the three treatments ($G = 5.15$, $P = 0.076$).

Effects of temperature on root emergence under different light conditions

Root emergence of non-scarified fruits was $80.0 \pm 6.7\%$ (mean $\pm$ SE) in light/dark at ambient laboratory conditions (27°C) within 30 days and was $62.2 \pm 15.4\%$

Table 1. Time between root and shoot emergence for non-scarified *Aegiceras corniculatum* fruits on tissue papers moistened with NaCl solutions of different osmotic potentials and in light/dark at ambient laboratory conditions. Different lowercase letters indicate significant differences between treatments (Mood's median test, $P < 0.001$).

Osmotic potential (MPa)	Days (mean $\pm$ SE)
0.0	115 $\pm$ 17 ^a
-0.1	128 $\pm$ 26 ^a
-0.3	96 $\pm$ 29 ^a
-0.5	173 $\pm$ 1 ^b
-1.0	173 $\pm$ 1 ^b
-2.5	173 $\pm$ 0 ^b

Table 2. Time between root and shoot emergence for non-scarified or manually scarified *Aegiceras corniculatum* fruits in different light treatments at ambient laboratory conditions. Fruits emerged root in one light condition (light/dark or dark) and then kept in the same or transferred to a different light condition (light/dark or dark). Different lowercase letters indicate significant differences between treatments (Mood's median test, $P < 0.05$).

Light treatment	Days (mean $\pm$ SE)
Non-scarified fruits	
Light/dark to light/dark	103 $\pm$ 34 ^a
Light/dark to dark	135 $\pm$ 40 ^a
Dark to light/dark	164 $\pm$ 0 ^a
Dark to dark	187 $\pm$ 0 ^b
Scarified fruits	
Light/dark to light/dark	28 $\pm$ 8 ^c
Light/dark to dark	176 $\pm$ 6 ^a

at 35°C ($G = 3.505$, $P = 0.06$). All non-germinated fruits were non-viable. In the darkness at ambient laboratory conditions (27°C), 73.3 $\pm$ 19.9% of the fruits germinated but at 35°C none of the fruits did so. These non-germinated fruits were non-viable possibly due to fungal infection.

Effects of scarification and GA₃ on shoot emergence under light/dark condition

Non-scarified fruits placed on tissue papers moistened with distilled water took 115.7 $\pm$ 17.3 days (mean $\pm$ SE) for shoot emergence following root emergence, but with GA₃ it took 63.6 $\pm$ 30.0 days ($\chi^2 = 5.32$, $P = 0.02$). The interval between root and shoot emergence was only 24.7 $\pm$ 1.0 days for manually scarified seeds with distilled water, and it significantly differed from non-scarified fruits with distilled water ($\chi^2 = 35.0$, $P < 0.001$).

Effects of salinity on shoot emergence under light/dark condition

Fruits placed on tissue papers moistened with NaCl solutions with relatively low osmotic potentials (0.0, -0.1, and -0.3 MPa) took fewer days (from root emergence) for shoot emergence than those placed on high osmotic potentials (-0.5, -1.0, and -2.5 MPa) (Table 1; $\chi^2 = 23.43$, $P < 0.001$).

Effects of scarification on shoot emergence under different light conditions

There was a significant effect of the light regime on the shoot emergence of both non-scarified and manually scarified fruits (Table 2; $\chi^2 = 32.25$, $P > 0.001$). Non-scarified fruits kept in darkness took the longest time for shoot emergence, and manually scarified fruits kept in light/dark exhibited the shortest time.

Effects of root stability on shoot emergence

The time between root and shoot emergence was the shortest for fruits planted vertically in a coconut coir substratum in light/dark, as compared to vertical planting in darkness or being laid horizontally in either light regime ($\chi^2 = 8.82$, $P = 0.003$; Fig. 2, Table 3).

Morphology and anatomy of fruits in relation to shoot emergence and growth

Fresh mature fruits have a well-developed embryo. The hypocotyl and cotyledons were well-developed and differentiated. However, the plumule only consisted of a shoot meristem at the earliest stage of development (Fig. 1A). There was no cell differentiation observed in the plumule at dispersal time. When fruits were placed on a moist substrate in light/dark conditions, the shoot

Table 3. Time between root and shoot emergence for non-scarified fruits of *Aegiceras corniculatum* planted vertically or laid horizontally on coconut coir substratum in different light conditions at ambient laboratory conditions. Different lowercase letters indicate significant differences between treatments (Mood's median test, $P < 0.05$).

Position	Light treatment	Days (mean $\pm$ SE)
Planted vertically	Light/dark	50 $\pm$ 7 ^a
	Dark	89 $\pm$ 9 ^c
Laid horizontally	Light/dark	78 $\pm$ 8 ^b
	Dark	98 $\pm$ 10 ^c

meristem produced a small shoot bud, with differentiated vascular cells and epidermal cells in the plumule after 7 days from root emergence (Fig. 1B). The plumule gradually developed between the two cotyledons. Shoots emerged after about 40 days from the root emergence.

DISCUSSION

The radicle of *A. corniculatum* is non-dormant irrespective of the light requirement. Despite differences in the collection sites, a higher percentage of *A. corniculatum* fruits had an emerged root at $\sim 27^{\circ}\text{C}$ than at 35°C . Further, the development of the radicle was hampered at 35°C , leading to higher seedling mortality (data not shown). Therefore, root emergence in darkness

and consequent establishment of seedlings in light/dark of *A. corniculatum* may be challenging at relatively high temperatures.

In contrast to radicle emergence, a significant delay in shoot emergence (after root emergence) was observed in non-scarified fruits of *A. corniculatum* by up to 90 days. Several environmental factors affected the length of time for shoot emergence. First, shoot emergence took at least 3 months regardless of NaCl concentration (i.e. osmotic potential). The time between root and shoot emergence was significantly less in low NaCl solutions than in high solutions. This may be an adaptation to produce root and subsequently develop into a seedling during a favourable time period. NaCl concentration of lagoon water fluctuates with precipitation. During the rainy

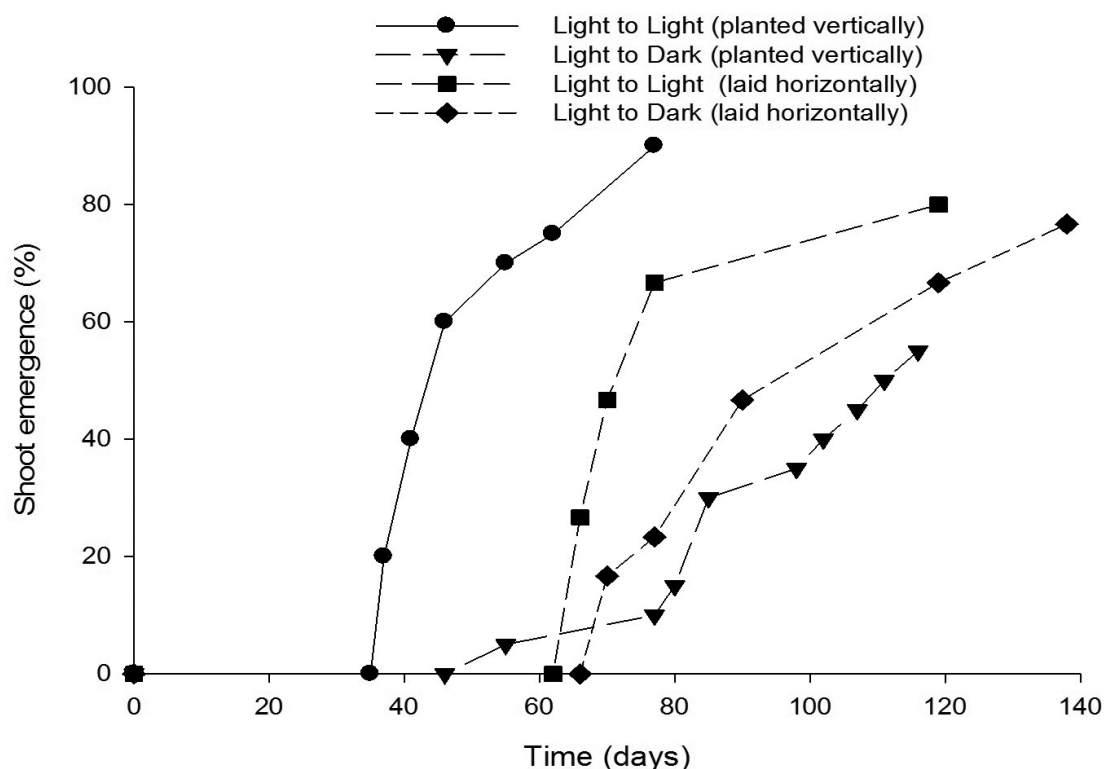


Figure 2. Cumulative percentages of shoot emergence for non-scarified *Aegiceras corniculatum* root-emerged fruits placed on coconut coir substratum moistened with distilled water and kept in light/dark or dark conditions at ambient laboratory conditions. Light to light: kept in light/dark conditions throughout experiment; Light to dark: radicles emerged in light/dark and then the seedling was transferred to darkness. Planted: root-emerged fruits were placed vertically with the radicle inside the substratum; Laid: root-emerged fruits were laid down on the substratum.

season, an increased amount of fresh water enters the lagoon causing a decrease in salinity (Sugirtharan et al. 2014). Thus, a low NaCl concentration may be a cue for seedlings to detect the favourable rainy season for shoot emergence and seedling establishment.

Darkness increased the length of time for shoot emergence after root emergence. For example, shoots from manually scarified fruits took about 176 days to emerge in darkness, whereas they took about 28 days in light/dark condition. The delay in shoot emergence may be a strategy to survive in the dark conditions that prevail under the thick mangrove forest canopy. Our experiments clearly showed that shoot emergence is faster under light conditions than under dark conditions. Thus, we can speculate that as soon as light penetrates through a gap in the canopy, shoots may be produced quickly to capture the available light. In dark conditions, the seedlings (with an exposed shoot) may be susceptible to predation or pathogens. By delaying shoot emergence, this vulnerability may be reduced during the quiescent period of the seedlings. Supporting our hypothesis, we have observed large numbers of seedlings under the canopy of other mangrove trees that were only in a root-emerged condition but without emerged shoots. However, we did not compare this observation under the canopy of mangroves with canopy gaps.

Third, shoots from root-emerged fruits manually planted vertically into the substratum took about 50 days for emergence, whereas those from fruits laid horizontally took more than 78 days. This time delay may have to do with the time required for the plant to develop a root system into the substratum and become stabilized before growing vertically. If naturally dispersed fruits of this species fall into a muddy substratum and are positioned vertically, they do not need time to become stabilized before growing upright. However, if the fruits were positioned horizontally after dispersal, it would take much more time to produce shoots. A similar observation was recorded for *Bruguiera gymnorhiza* and *Rhizophora mangle* by Tomlinson and Cox (2000).

The time gap between root and shoot emergence was greatly reduced (by about 30 days) when fruits were treated with GA_3 . When the fruit coats were removed, shoot emergence occurred within about 25 days. Thus, *A. corniculatum* fruits apparently have epicotyl dormancy. The lack of growth potential of the epicotyl to overcome the fruit coat resistance may be the primary reason for the epicotyl dormancy. We suggest that the level of physiological dormancy in the epicotyls is nondeep because GA_3 alleviated dormancy and normal seedlings developed after the removal of fruit coats (Baskin and Baskin 2014). Since the embryo is fully developed, fruits of this species have epicotyl PD. Although there are many records of species producing seeds with epicotyl MPD, only a few species have been reported as having seeds with epicotyl PD (Jayasuriya et al. 2012; Baskin

and Baskin 2014; Athugala et al. 2018). To the best of our knowledge, our study on *A. corniculatum* is the first report of epicotyl dormancy in a species with crypto-viviparous fruits and in a true mangrove species.

Epicotyl PD seeds/fruits have either non-dormant (e.g. *Humboldtia laurifolia* Vahl, Jayasuriya et al. 2010; *Brownea coccinea* Jacq., Jayasuriya et al. 2012) or dormant radicles (e.g. *Garcinia kola* Heckel, Agyili et al. 2007; *Chionanthus retusus* Lindl. & Paxton, Chien et al. 2004). As described above, the radicles of *A. corniculatum* are non-dormant. According to Baskin and Baskin (2014, 2021), epicotyl dormancy of *A. corniculatum* should be categorized as Type 2 nondeep epicotyl PD, which is formulated as $C_{nd}^{(root)-C_{ib}^p}$ (shoot). However, viviparous/crypto-viviparous seeds/fruits are different from other species with this same formula, especially those with recalcitrant seeds, due to their ecological, physiological, and anatomical features during development and dispersal. Viviparous or crypto-viviparous fruits precociously germinate without undergoing maturation drying, while they are still attached to the mother plant (Farnsworth 2000; Hartmann et al. 2002). Recalcitrant seeds reduce the fresh weight at maturation drying to a certain amount and become quiescent for a certain period of time. In contrast, viviparous or crypto-viviparous seeds/fruits do not attain a quiescent phase, instead, they directly continue the development phase to the germination phase (Hartmann et al. 2002). Thus, epicotyl dormancy of *A. corniculatum* cannot be categorized as Type 2 nondeep epicotyl dormancy. Hence, we propose that the dormancy of *A. corniculatum* is recognized as a new type of epicotyl dormancy under nondeep epicotyl PD and is formulated as $C_{cry}^{(root)-C_{ib}^p}$ (shoot), where “cry” indicates the crypto-viviparous nature of the radicle or the hypocotyl.

CONCLUSION

Aegiceras corniculatum is a true mangrove species that produces recalcitrant fruits with crypto-viviparous behaviour. The radicle is non-dormant and does not have a light requirement for emergence, although at high temperatures emergence and viability decreased. In contrast, a delay in shoot emergence occurred indicating the presence of epicotyl PD. Removal of the fruit coat and addition of GA_3 relieved epicotyl PD, and light regime and salinity significantly affected shoot emergence. Shoots do not emerge until the seedling is stabilized in a vertical position. Fruits/seeds of *Aegiceras corniculatum* have nondeep epicotyl PD, which is formulated as $C_{cry}^{(root)-C_{ib}^p}$ (shoot). This information on the germination ecology of *Aegiceras corniculatum*, particularly its responses to temperature, light, salinity, and fruit coat removal, is crucial for effective mangrove restoration, as it informs optimal conditions for seedling establishment and growth in conservation efforts.

ACKNOWLEDGEMENTS

This work was supported by the National Science Foundation, Sri Lanka [RG/2011/NRB/08]. We sincerely thank the reviewers for their insightful comments and constructive suggestions, which have greatly improved the quality of this paper. Also, we would like to thank Dr Yasoja S. Athugala who helped in collecting seeds.

REFERENCES

- Agyili J, Sacande M, Koffi E, Peprah T (2007) Improving the collection and germination of West African *Garcinia kola* Heckel seeds. *New Forests* 34(3): 269–279. <https://doi.org/10.1007/s11056-007-9054-7>
- Athugala YS, Jayasuriya KMG, Gunarathne AMTA, Baskin CC (2018) Diversity of epicotyl dormancy among tropical montane forest species in Sri Lanka. *Plant Biology* 20(5): 916–925. <https://doi.org/10.1111/plb.12846>
- Baskin CC, Baskin JM (2014) *Seeds: Ecology, Biogeography, and Evolution of Dormancy and Germination*. Second edition. Academic Press, San Diego, 1–1584. <https://doi.org/10.1016/C2013-0-00597-X>
- Baskin JM, Baskin CC (2021) The great diversity in kinds of seed dormancy: a revision of the Nikolaeva–Baskin classification system for primary seed dormancy. *Seed Science Research* 31: 249–277. <https://doi.org/10.1017/S096025852100026X>
- Carvalho JEU, Muller CH, Leao NVM (1998) Chronology of morphological events associated to germination and desiccation sensitivity of *Platonia insignis* Mart. seeds—Clusiaceae. *Revista Brasileira de Sementes* 20: 236–240.
- Chien C-T, Kuo Huang L-L, Shen Y-C, Zhang R, Chen S-Y, Yang J-C, Pharis RP (2004) Storage behavior of *Chionanthus retusus* seed and asynchronous development of the radicle and shoot apex during germination in relation to germination inhibitors, including abscisic acid and four phenolic glucosides. *Plant and Cell Physiology* 45: 1158–1167. <https://doi.org/10.1093/pcp/pch129>
- Ellison J, Koedam NE, Wang Y, Primavera J, Jin Eong O, Yong W-H, Ngoc Nam V (2010) *Aegiceras corniculatum*. The IUCN Red List of Threatened Species 2010: e.T178797A7608891. <https://doi.org/10.2305/IUCN.UK.2010-2.RLTS.T178797A7608891.en>
- Elmqvist T, Cox PA (1996) The evolution of vivipary in flowering plants. *Oikos* 77(1): 3–9. <https://doi.org/10.2307/3545579>
- Farnsworth E (2000) The ecology and physiology of viviparous and recalcitrant seeds. *Annual Review of Ecology, Evolution, and Systematics* 31: 107–138. <https://doi.org/10.1146/annurev.ecolsys.31.1.107>
- Goebel KE (1905) *Organography of Plants*. Clarendon Press, Oxford, 1–270. <https://doi.org/10.5962/bhl.title.3802>
- Hartmann HT, Kester DE, Davies FT, Geneve RL (2002) *Hartmann and Kester's Plant Propagation: Principles and Practices*. Seventh edition. Pearson Education, Inc, Upper Saddle River, New Jersey, 1–840.
- Jayasuriya KMG, Wijetunga ASTB, Baskin JM, Baskin CC (2010) Recalcitrancy and a new kind of epicotyl dormancy in seeds of the understory tropical rainforest tree *Humboldtia laurifolia* (Fabaceae, Caesalpinioideae). *American Journal of Botany* 97(1): 15–26. <https://doi.org/10.3732/ajb.0900213>
- Jayasuriya KMG, Wijetunga ASTB, Baskin JM, Baskin CC (2012) Physiological epicotyl dormancy and recalcitrant storage behaviour in seeds of two tropical Fabaceae (subfamily Caesalpinioideae) species. *AoB PLANTS* 2012: pls044. <https://doi.org/10.1093/aobpla/pls044>
- Jayatissa LP, Dahdouh-Guebas F, Koedam N (2002) A review of the floral composition and distribution of mangroves in Sri Lanka. *Botanical Journal of the Linnean Society* 138(1): 29–43. <https://doi.org/10.1046/j.1095-8339.2002.00002.x>
- Juncosa AM (1982) Developmental morphology of the embryo and seedling of *Rhizophora mangle* L. (Rhizophoraceae). *American Journal of Botany* 69(10): 1599–1611. <https://doi.org/10.1002/j.1537-2197.1982.tb13413.x>
- Scholander PF, Hammel HT, Hemmingsen E, Garey W (1962) Salt balance in mangroves. *Plant Physiology* 37(6): 722–729. <https://doi.org/10.1104/pp.37.6.722>
- Sugirtharan M, Pathmarajah S, Mowjood MIM (2014) Variation of salinity in Batticaloa Lagoon in Sri Lanka during wet season. *Tropical Agricultural Research* 25(3): 403–411. <https://doi.org/10.4038/tar.v25i3.8048>
- Tomlinson PB (1994) *The Botany of Mangroves*. Cambridge University Press, Cambridge, 1–420.
- Tomlinson PB, Cox PA (2000) Systematic and functional anatomy of seedlings in mangroves Rhizophoraceae: vivipary explained? *Botanical Journal of the Linnean Society* 134(1–2): 215–231. <https://doi.org/10.1006/bojl.2000.0371>
- Wijayasinghe MM, Jayasuriya KG, Gunatilleke CVS, Gunatilleke IAUN, Walck JL (2023) Seed dormancy diversity of the mangrove plant community in Sri Lanka to assist in direct seeding and seedling transplanting restoration. *Seed Science Research* 33(2): 107–117. <https://doi.org/10.1017/S0960258523000120>

SUPPLEMENTARY MATERIALS

Supplementary material 1

Experimental setup of non-scarified and scarified seeds in root and shoot emergence under different light conditions. <https://doi.org/10.5091/plecevo.151630.suppl1>

Supplementary material 2

Experimental setup to ascertain the effects of the direction of the position on shoot emergence of *A. corniculatum* under different light conditions. <https://doi.org/10.5091/plecevo.151630.suppl2>