Pneumatophores on *Acoelorrhaphe wrightii*

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1. Pneumatophores growing around an upright stem of *Acoelorrhaphe wrightii* at Fairchild Tropical Botanic Garden, Miami, Florida, USA. The white pneumatozones are visible.

Upward-growing (negatively geotropic) roots were recently observed in both cultivated and wild individuals of *Acoelorrhaphe wrightii*, a rhizomatous wetland palm. Upward-growing roots occur in the vicinity of the rhizomes and arise from horizontal roots. These upward-growing roots usually grow 2–5 cm above the soil surface and are 3–7 mm diameter. They have white bands or sectors that are similar to pneumathodes described on pneumatophores of other palms (Yampolsky 1924). Morphological and anatomical study supports the conclusion that upward-growing roots are pneumatophores.

Pneumatophores are erect aerial roots and are very common in palms growing in swampy conditions (Tomlinson 1990). In swampy conditions, the soil is often waterlogged and deficient in oxygen making it is difficult for roots to respire (Vartapetian & Jackson 1997). In order to overcome this deficiency, some roots are able to project above water surface of flooded soil (Esau 1977). These erect, aerial roots are called pneumatophores and it is presumed that the pneumatophores aid in gas exchange (de Granville 1974, Tomlinson 1990). Pneumatophores are often second order roots that arise from first-order, underground roots (Tomlinson 1990).

Upward-growing roots that resemble pneumatophores were recently found in *Acoelorrhaphe wrightii* (Griseb. & H. Wendl.) H. Wendl. ex Becc., commonly called paurotis or Everglades palm. *Acoelorrhaphe wrightii* grows abundantly around the Caribbean basin, mostly in seasonally or constantly flooded habitats, and is widely cultivated in the tropics and subtropics (Dransfield et al. 2008, Meerow et al. 2001). *Acoelorrhaphe wrightii* is a multi-stemmed palm that creates large, circular clumps through rhizomatous branching. Prolific root formation occurs along the rhizomes.

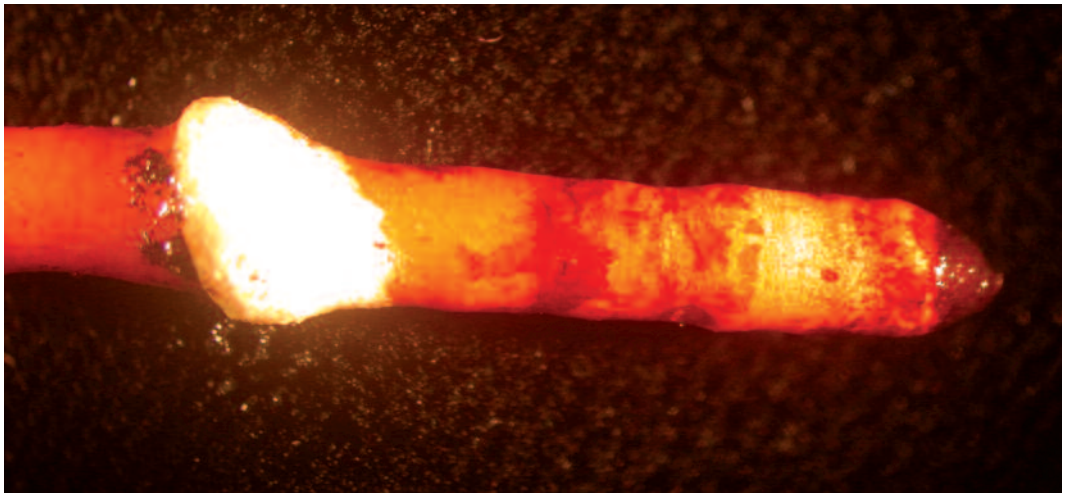
Upward-growing roots were observed on *A. wrightii* first at Fairchild Tropical Botanical Garden and Montgomery Botanical Center, on plants growing in Everglades National Park, and on saplings growing in a mesocosm (large tanks that simulate the Everglades ecosystem on small scale) for a developmental study. These upward-growing roots were found in all observed clumps of *A. wrightii*, both in the wild and in cultivation (Fig. 1). Since they were present in both wild and cultivated individuals these roots are most likely an early adaptation to its wetland habitat that become a typical morphology for the species.

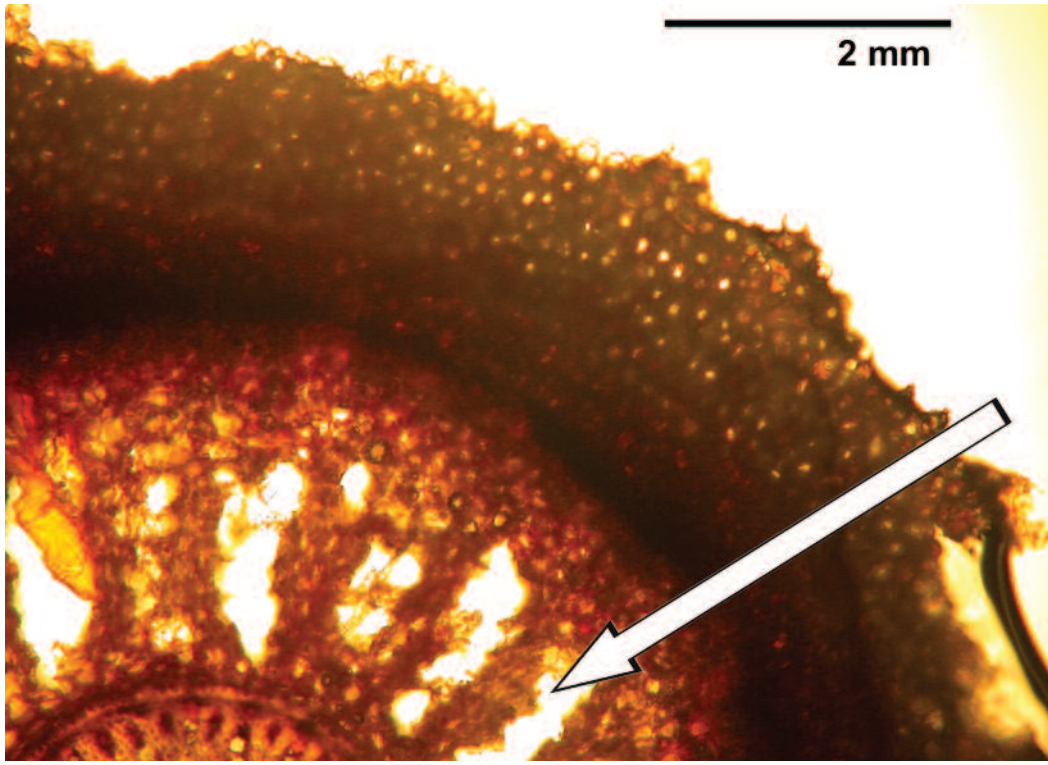
Upward-growing roots are found up to 0.15 m away from the nearest rhizome, mostly on or near the rhizomes. The upward-growing roots initiate from horizontal roots, not directly from the rhizome. Upward-growing roots are commonly between 3–7 mm diameter, which is often smaller than parent roots, and can grow vertically to 2–5 cm above soil level. They have 1–4 white bands or localized sectors that occur around the circumference (Figs. 1 & 2). Upward-growing roots generally do not occur singly, but their density is variable. They are found both sparsely and densely distributed around a rhizome.

Anatomical analysis has shown that upward-growing roots have large air channels (Fig. 4) and pneumathodes (Figs. 2 & 4). The air channels form a longitudinal system that is located in the inner-cortex (Figs. 3 & 4) (Tomlinson et al. 2011). These air channels are aerenchyma tissue and enhance gas exchange in the roots (Tomlinson 1990).

It is not surprising that pneumatophores are present on *A. wrightii* since most wetland palms have this morphological feature and it is common in Coryphoid palms. However, the pneumatophores are very well developed in *A. wrightii*, unlike most Coryphoid relatives. *Serenoa repens*, sister to *A. wrightii*, has second and third-order roots that are upward growing (negatively geotrophic) but do not project

2. A. Pneumatozone (white band) on upward-growing root of *Acoelorrhaphe wrightii*. Root cap to right.



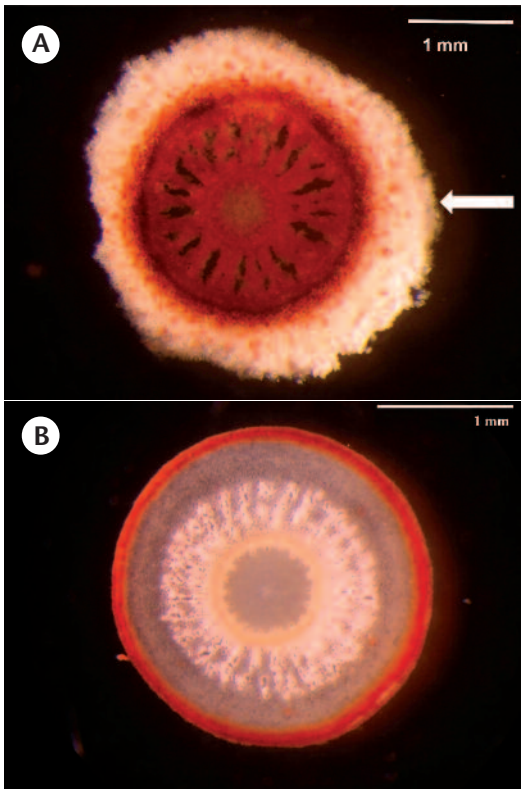


3. Cross-section of upward-growing root. Arrow points to large air channels in the inner cortex; vascular stele occupies interior of root, while loose pneumatozone tissue occurs in the outer cortex and displaces the epidermis.

above the soil (unlike *A. wrightii*) (Fisher & Jayachandran 1999). They do not aid in gas exchange (are not pneumatophoric) but instead have arbuscular mycorrhizal fungi that facilitate nutrient uptake. The upward-growing roots of *A. wrightii* are also quite distinct from other Coryphoid relatives. In most Coryphoid palms, pneumathodes exist in their simplest state as mealy excrescences on the surface of seemingly normal roots (Tomlinson 1990). But, the pneumathodes in *Acoelorrhaphe wrightii* have expanded to create white bands or sectors around the pneumatophore, called pneumatozones (de Granville 1974). Pneumatozones are localized regions on the erect root that have specialized modifications that assist in gas exchange (Jost 1887, Yampolsky 1924). The mealy white bands and localized white sectors on the upward-growing roots of *Acoelorrhaphe wrightii* are similar in morphology to pneumathodes described in *Elaeis* and *Livistona* (Jourdan & Rey 1997, Yampolsky 1924) and resemble the pneumatozones described in *Mauritia flexuosa* (de Granville 1974). The pneumatozones of *A. wrightii* appear to develop from exodermis (under the epidermis) outer cortical region of the root. The outer cortex is parenchymatic in regions of the upward-growing root lacking pneumathodes (Fig. 4). These pneumatozones were observed on first-order roots and well as upward-growing roots.

The upward-growing roots of *A. wrightii* have all the common characteristics of pneumatophores including an upward-growing habit, presence of pneumathodes, pneumatozones and/or pneumatorhiza, and presence of aerenchyma tissue. Pneumatophores are well-documented in a number of other palms: *Livistona australis* (Jost 1887), *Raphia hookeri* and *Phoenix reclinata* (Jeník 2008), *Elaeis guineensis* (Jourdan & Rey 1997, Yampolsky 1924), *Metroxylon sagu* (Flach 1997), *Euterpe oleracea* (de Granville 1974) and *Mauritia flexuosa* (Balslev et al. 2011). Pneumatozones are also present on pneumatophores of *Mauritia*, *Raphia*, *Metroxylon*, *Livistona* and *Phoenix* (de Granville 1974).

Anatomical and morphological work supports the conclusion that the upward-growing roots observed in *Acoelorrhaphe wrightii* are pneumatophores. The pneumatophores, with their pneumathodes, pneumatozones and large air channels, are likely an adaptation to this palm's semi-aquatic environment.



4. Cross-section of upward-growing root in pneumatozone (A) and in region of root without pneumatozone (B). Arrow points to pneumatozone, which forms in the outer cortex of the root; air channels form radiating dark discs in inner cortex.

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