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Factors affecting the initiation and growth of aboveground adventitious roots in a tropical cloud forest tree: an experimental approach

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Abstract Some of the proximate factors that would induce aboveground stems to produce adventitious roots were investigated experimentally on *Senecio cooperi*, a tropical cloud forest tree. Stem segments were air-layered with different treatments to promote root formation, and the number of roots initiated and rates of root growth were monitored for 20 weeks. Treatments were the application of wet epiphytes or dry epiphytes plus associated humus, sponges wetted with either water or nutrient solutions, or dry sponges. Controls (stem segments with nothing applied) were also monitored. Numbers of adventitious roots formed and rates of subsequent root growth differed among treatments. Wet epiphyte/humus and nutrient solutions were most effective in producing roots, which suggests that epiphytes and the nutrients they intercept and retain within the canopy may cue adjacent host tissue to exploit this resource.

Key words Adventitious roots · Epiphyte · Mineral nutrition · Tropical cloud forest · *Senecio cooperi*

Introduction

Aboveground adventitious roots (AARs) characterize many species of tropical and temperate wet forest trees (Table 1) (Lanner 1966; Jenik 1973; Nadkarni 1981, 1983; Grier and Nadkarni 1987; Moore 1989) and have been termed "canopy roots" (Nadkarni 1981), "aboveground adventitious roots" (Herwitz 1991), and "apogeo-tropic roots" (Sanford 1987). They are structured much like their belowground counterparts and have similar capacities to absorb nutrients and water (Nadkarni and Primack 1989). These organs are often (but not always, Herwitz 1991) directly associated with and/or penetrate accumulations of epiphytes and accompanying humus suspended in host tree crowns. These AARs contrast

Table 1 Genera and species of trees that have been documented as putting forth aboveground adventitious roots. Locations of trees are designated by numbers; sources are designated by letters

NEW WORLD FORESTS	OLD WORLD FORESTS
TEMPERATE	TEMPERATE
<i>Acer macrophyllum</i> ^{1a}	<i>Coprosma</i> sp. ^{2b}
<i>Acer circinatum</i> ^{1a}	<i>Griselinia lucida</i> ^{2b}
<i>Alnus rubra</i> ^{1a}	<i>Leptospermum</i> sp. ^{2b}
<i>Populus trichocarpa</i> ^{1a}	<i>Meterosideros umbellata</i> ^{2b}
	<i>Nothofagus fusca</i> ^{2b}
	<i>Podocarpus totara</i> ^{2b}
	<i>Weinmannia racemosa</i> ^{2b}
TROPICAL	TROPICAL
<i>Clusia alata</i> ^{3b}	<i>Acronychia</i> sp. ^{5b}
<i>Didymopanax pittieri</i> ^{3b}	<i>Cinnamomum</i> sp. ^{5b}
<i>Nectandra</i> sp. ^{3b}	<i>Dacrydium</i> sp. ^{5b}
<i>Ocotea</i> sp. ^{3b,4c}	<i>Podocarpus merifolium</i> ^{5b}
<i>Senecio cooperi</i> ^{3b}	<i>Schizomeria</i> sp. ^{5b}
<i>Weinmannia pinnata</i> ^{3b}	<i>Weinmannia</i> sp. ^{5b}
<i>Xylosma</i> sp. ^{3b}	<i>Meterosideros collina</i> ^{6d}
<i>Ilex</i> sp. ^{4c}	<i>Cheirodendron trigynum</i> ^{6d}
<i>Miconia pachyphylla</i> ^{4c}	<i>Ceratopetalum virchowii</i> ^{7e}
<i>Calypttranthes</i> ^{4c}	
<i>Grammadenia</i> ^{4c}	

¹ Olympic Peninsula, Washington, U.S.A.

² Urewāra National Park, New Zealand

³ Monteverde, Costa Rica

⁴ Mt. Missim, Papua New Guinea

⁵ Luquillo Elfin Woodland, Puerto Rico

⁶ Cloud forest, Hawaii, U.S.A.

⁷ Atherton tableland, Australia

^a Nadkarni, 1981

^b Nadkarni, 1983

^c Gill, 1969

^d P. Vitousek personal communication

^e Herwitz 1991

with the wide array of "aerial roots" which differ morphologically from "normal" subterranean roots (Gill 1969; Gill and Tomlinson 1975). The latter putatively provide protection from large animals, ventilate roots in anaerobic soils, increase mechanical support for horizon-

tal branches and entire shoots without secondary thickening, or host symbiotic micro-organisms.

AARs have attracted interest as a peculiar morphological phenomenon. Nadkarni (1981) suggested that these roots can effect a "short-cut" in nutrient cycles by allowing host trees to exploit the abundant nutrients contained in organic matter suspended within their own crowns. Herwitz (1991) proposed that certain trees with AAR may enhance nutrient use efficiency by retrieving leached nutrients from stemflow. Little is known about the anatomy of AARs, their absorptive capacities of water and/or nutrients under natural conditions, or the physiology of their initiation and growth. Hormones triggered by the presence of moisture, darkness, dead organic matter, or nutrients induce some other types of adventitious roots (Gill 1975; Fink 1983; Davies and Hartmann 1988). Certain plants denied oxygen (for example by seasonal flooding), produce adventitious roots (Haissig 1974; Gill 1975; Pereira and Kozlowski 1977; Angeles et al. 1986).

Epiphytes and crown humus-produced or related factors possibly responsible for inducing AAR include darkness, moisture, inorganic nutrients, hormones, or other organic exudates. This report presents results of an experiment designed to identify stimuli that may promote the growth of AARs in the crown of *Senecio cooperi* Greenman, a tropical cloud forest tree.

Materials and methods

Experiments were performed between 5 May and 22 September 1982 in the Monteverde Cloud Forest Reserve (MVCFR), in north-western Costa Rica (10°12'N, 84°42'W). The approximately 2-ha study area was located immediately to the windward side of the area known locally as "La Ventana," which directly straddles the Continental Divide of the Cordillera de Tilaran. The area experienced a landslide approximately 12–15 years before the study (W. Guindon, personal communication). Such landslides are frequent on the steep windward slopes of these mountains.

Recorded annual precipitation in the MVCFR is c. 2500 mm, but actual wet deposition is higher because of the large amounts of wind-driven mist and fog that occur throughout the year. Temperatures vary little through the year, with diurnal ranges exceeding yearly ranges (Nadkarni, unpublished data). The physiognomy of the Penas Blancas watershed to the west causes winds to funnel directly through La Ventana before pouring over to the leeward side of the forest. Strong winds occur throughout the year, but are particularly intense during the misty and dry seasons (Lawton and Dryer 1980). No records exist for the study area, but Lawton (1982) estimated wind speeds exceeding 100 km h⁻¹.

Soils in the area are derived from volcanic rhyolites (Vance and Nadkarni 1989). The soils of the study area contained very small amounts of organic matter and were extremely clayey and bright orange in color. Six soil samples (10×10×10 cm aliquots) at two depths were collected near the center of the site at the midpoint of the study; mean bulk density was 1.2 g cm⁻³ (SD 0.24) for 0–10 cm depth, and 1.3 g cm⁻³ (SD 0.20) for 10–20 cm depth. Mean percent moisture [(field weight/dry weight)/field weight] was 38% for 0–10 cm depth and 31% for 10–20 cm depth.

Local vegetation consists of a thick cover of arborescent shrubs with a uniform 3–4 m canopy dominated by *Senecio cooperi* Greenman (Compositae). These shrubs are multi-branched, with all of the foliage restricted to the ends of branches, leaving the crown interiors relatively unobstructed and hence easily accessi-

ble. Other common landslide-following plants such as *Gunnera m-vignis* (Oersted) A. DC. (Gunneraceae) and *Bocconia frutescens* L. (Papaveraceae) ringed the study area. There was almost no herbaceous understorey. Terrestrial roots were exposed in places, but trees were firmly anchored.

Senecio cooperi was used because of its uniform height, low stature, and propensity for forming AARs under natural conditions (personal observations). An aggressive pioneer following major disturbances, this tree can reach 6 m. Much like many other cloud forest trees, its branches frequently produce AARs that are usually beneath mats of cryptogamic epiphytes and associated dead organic matter.

Thirty-nine *S. cooperi* trees were chosen for uniform height and structure, all of which were located within 5 m inside the plot. Sixty stem segments adjacent to accessible branch nodes (maximum of three per tree) between 2 m and 3.5 m were marked on the experimental trees. Each designated stem segment was subjected to one of the following six treatments and the number of roots initiated and their lengths were recorded. Factors tested were the presence of: (1) wet epiphytes (live epiphytes, crown humus, water); (2) dry epiphytes (air-dried epiphytes and crown humus); (3) wet sponges (foam sponges saturated with distilled water); (4) inorganic nutrient solution sponges (foam sponges, water, and dissolved commercial nutrient solution, equivalent to a Hoagland's solution); (5) dry sponges (air-dried foam sponges); and (6) control (nothing applied to stem). Epiphytes and crown humus (a mixture of mosses, liverworts, filmy ferns, and dead organic matter) from three *Didymopanax pittieri* trees were collected from the adjacent primary elfin woodland. The material was divided into uniform portions of c. 50 g wet weight (250 cm³), half of which were air-dried to a constant weight for 3–4 days and used for the "dry epiphytes" treatment. The other half were used for the "wet epiphytes" treatment.

Modified techniques of air-layering (Hartmann and Kester 1975) were used to stimulate shoot segments to root. A clump of epiphytes (wet or dry) or a sponge (saturated with distilled water, nutrient solution, or dry) was wrapped around each stem section. Treatment materials were wrapped securely with a 50×50 cm gas-permeable polyethylene sheet and tied off at each end with nylon cord to exclude throughfall and stemflow. Every 2 weeks, 10 ml distilled water or nutrient solutions were applied with a syringe to maintain desired conditions. The plastic coverings were periodically removed for several minutes to expose the branch site. During the first 4 weeks, observations were made every 4–6 days and subsequently every 4th week for 16 weeks to record the number and lengths of roots. The material was re-wrapped and tied off again. The number of roots per treatment were tallied, and the total length of the roots were summed for each sample. Each stem segment was treated as an independent sample. Analysis was performed with the statistical package SYSTAT (Systat Inc., Evanston, Illinois).

Results and discussion

The adventitious roots that appeared on stems appeared to be derived from hypertrophied lenticels and aerenchyma tissue and were observed as early as 8 days after the experiment began. As early as 4 days after root initiation, thick white roots with no obvious root hairs had grown into the media or between the sponges and the bark. Three days later, many of the roots had branched and possessed root hairs just above the root cap. After 4 weeks, the larger roots developed a light purple color, which darkened as they thickened.

The sequence of AAR formation was similar to the sequence described for flooded individuals of *Fraxinus pennsylvanica* (Sena Gomes and Kozlowski 1980),

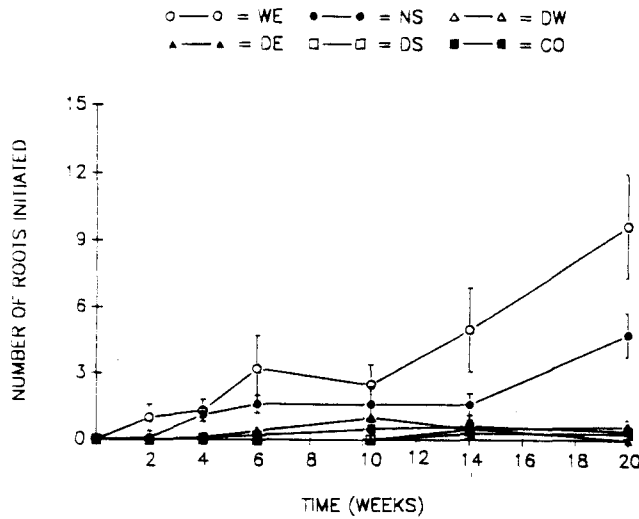


Fig. 1 Mean (and SE) number of aboveground adventitious roots initiated by *Senecio cooperi* trees over the 20-week study period for each of six treatments (WE wet epiphytes, including crown humus, DE air-dried epiphytes, NS nutrient solutions with foam sponges, DW distilled water with foam sponges, DS dry foam sponges, CO control)

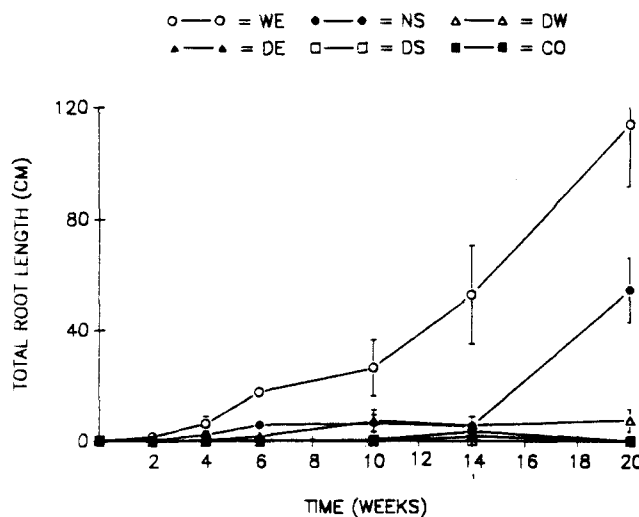


Fig. 2 Mean (and SE) length (cm) of aboveground adventitious roots initiated by *Senecio cooperi* trees over the 20-week study period for each of six treatments (WE wet epiphytes, including crown humus, DE air-dried epiphytes, NS nutrient solutions with foam sponges, DW distilled water with foam sponges, DS dry foam sponges, CO control)

Ulmus americana (Angeles et al. 1986), and *Tamarix* (Ginzburg 1967). Hypertrophied lenticels preceded the presence of white and then colored roots. The roots appeared to differentiate from the lenticels themselves, with subsequent connection of procambial strands to those of the parent stem.

Treatments differed in their effects on root initiation (one-way ANOVA, $F=11.56$, $df=49$, $P < 0.01$ for total number of roots present on final date) (Fig. 1). Wet epiphytes and nutrient solutions were most effective.

Several of the others, including the control treatment, induced roots, but these appendages disappeared within days, probably through desiccation.

Root growth responded similarly; those stimulated by epiphytes were longest (mean root length per segment=114.0 cm, mean single root length=9.7 cm) followed by those growing from stems subjected to the nutrient solution treatment (mean root length per segment=54.7 cm, mean single root length=4.8 cm) ($F=16.79$, $df=45$, $P < 0.001$ for roots present on final date) (Fig. 2). Distilled water affected root initiation and elongation only slightly (mean root length per segment=6.2 cm, mean single root length=0.6 cm).

The inducement of AARs by the wet epiphyte and nutrient solution treatments indicates that stimuli involving more than simply moisture or darkness trigger the growth of AARs as has been suggested in other studies (e.g., Gill 1969). Further studies are needed to determine the factors which induce the formation of these roots and to determine the functional capacity of these roots.

A positive feedback mechanism between the growth of epiphytes and the nutrition of their host trees may exist. A variety of inorganic nutrients (Nadkarni 1986) and organic nutrients (Coxson et al. 1992) are leached from epiphyte communities (especially those dominated by bryophytes) to which trees gain access via these root systems (Nadkarni and Primack 1989). As epiphyte communities colonize, grow, and accumulate dead organic matter, more AARs initiate and elongate. The presence of root systems appears to provide better substrate for epiphyte colonization than does bare bark by "roughening" the surface of the stem and providing more locations for colonization by epiphyte propagules and retention of water and nutrient. As the epiphyte community develops, the host tree may derive more leachates from the epiphytes and put forth more AARs, which would in turn create a better substrate for further epiphyte colonization.

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