Differential aboveground adventitious root production by *Senecio cooperi* (Asteraceae)

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ABSTRACT

Previous studies have suggested that aboveground adventitious roots (AARs) are produced by plants in order to extract nutrients from the epiphytes they support (Nadkarni 1981 & 1984). I asked whether *Senecio cooperi*, a neotropical plant which produces AARs, generates these roots for nutrient absorption, fragmentation establishment, or structural support. I conducted a survey in which I measured multiple characteristics of *S. cooperi* and their AARs in Monteverde, Costa Rica. Naturally fragmented stems produced more AARs than expected by chance ($x^2 = 12.80$, df = 1, p < 0.05). No purely vertical stems contained AARs associated with the moss mats growing on them. However, vertical stems displayed basal AARs which increased in diameter as both plant height and DBH increased ($R^2 = 0.330$, P < 0.001, N = 50, $R^2 = 0.402$, P < 0.0001, N = 50 respectively). These findings suggest that the naturally occurring roles of AARs of S. cooperi are not for nutrient absorption, but rather for structural support and fragmentation regeneration. These functions of AARs allow *S. cooperi* to be more successful as a pioneer species in disturbed habitats, and highlight the need to reevaluate the functionality of AARs among other plants.

RESUMEN

Los estudios previos han sugerido que raíces adventicias en la superficie (AARs) son producidos por plantas para extraer alimentos nutritivos de las epifitas que ellos sostienen (Nadkarni 1981 & 1984). Pregunté si *Senecio cooperi*, una planta de neotropical que produce AARs, engendra estas raíces para la absorción de alimento nutritivo, para establecimiento de fragmentación, o para apoyo estructural. Realicé una inspección en la que medí múltiples características de *S. cooperi* y su AARs en Monteverde, Costa Rica. Los tallos naturalmente fragmentados produjeron más AARs que esperado por casualidad ($x^2 = 12.80$, df = 1, P <0.05). Ningunos tallos puramente verticales contuvieron AARs se asoció con las esteras de musgo que crecen en ellos. Sin embargo, los tallos verticales demostraron AARs elemental que aumentó de diámetro como ambas altura de planta y DBH aumentó ($R^2 = 0.330$, P <0.001, N = 50, $R^2 = 0.402$, P <0.0001, N = 50 respectivamente). Estas conclusiones sugieren que el papel naturalmente ocurriendo de AARs de *S. cooperi* no es para la absorción de alimento nutritivo, sino para la regeneración estructural de apoyo y fragmentación. Estas funciones de AARs permiten *S. cooperi* para ser más exitoso como una especie de pionero en hábitats perturbado, y destaca la necesidad de reevaluar la funcionalidad de AARs entre otras plantas.

INTRODUCTION

An intense challenge that many neotropical tree species face is the low amount of soil nutrients available. These tropical soil conditions require plants to have efficient nutrient capturing and processing mechanisms (Nadkarni 1981). A unique nutrient pathway has been suggested in which epiphyte host plants produce aboveground adventitious roots (AARs) that probe beneath the collected organic material of the epiphytes they support (Nadkarni 1981). AARs are distinguished from other aerial roots in that they have

morphological features such as root hairs, quickly regenerating root tips, and contain endomycorrhizal hyphae (Nadkarni 1981).

Other authors have proposed alternative reasons why plants may produce AARs. Kinsman (1990) experimentally fragmented stems of 22 neotropical plant species representing 14 genera Ten months after fragmentation, 35% of the fragments had survived by producing adventitious roots (Kinsman 1990). Schatz et al. (1985) suggested that some plants produce AARs close to their stem base for structural support, in an effort to compensate for lacking secondary growth Weiner et al. documented that intraspecific plant competition drives some plant species to grow horizontal stems in order to gain access to light resources (1990). In this horizontal form plants may produce AARs for increased structural support (Muzik & Cruzado 1956).

The apparent controversy over the function of AARs is complicated by the fact that AARs may take on varying roles throughout a plants development (Smith 1936). Additionally, AAR production may occur differently under experimental conditions versus natural circumstances. Comprehensive studies exploring AAR functional versatility and adaptability are lacking.

Nadkarni (1994) reported that a particular neoptropical tree species, *Senecio cooperi* (Asteraceae), responded to experimental applications of epiphytes by producing AARs. This suggested that the AARs of *S. cooperi* assist in nutrient uptake. In this study, I reexamine AARs of *S. cooperi* because initial observations revealed no association between moss mats and AARs. The principle objective of this study is to determine whether AARs of *S. cooperi* assist with nutrient uptake, structural support in horizontal or vertical growth forms, or fragmentation survival. I hypothesize that AARs of *S. cooperi* assist with structural support and fragmentation establishment. Therefore, I expect AARs to be present at the base of tall vertical stems as well as along the stem of horizontal growth forms. I also expect AARs to be present on fragmented stems.

METHODS

Study Site.—This study was conducted in forest edge near a rural road within one kilometer of the Santa Elena Cloud Forest Reserve (SECFR), Costa Rica (10˚20'N, 84˚45'W). The SECFR is located high on the Caribbean slopes of the Cordillera de Tilarán (1,500 m), very near Monteverde, Costa Rica. Average annual temperature at Monteverde is 18.5˚C, with a mean annual precipitation of 2519 mm (Clark et al. 2000). The study plant, *S. cooperi*, was abundant along the forest bordering this rural road and grew well in this frequently disturbed habitat. The study was conducted from 24 October 2007 to 13 November 2007.

Induced Fragmentation.—Twenty adult *S. cooperi* individuals were identified that displayed both horizontally and vertically growing stems. Horizontal and vertical segments were cut from each of the 20 individuals, resulting in 20 pairs of segments. Horizontal stems were classified as those stems whose angle between stem and soil was 0 to 45 degrees before being cut; while vertical stems were those whose original angle was 46 to 90 degrees. These fragmented stems were then placed on a natural soil plot (3 m x 1 m). Stems were checked every two days for AAR growth, with the last day of observation occurring ten days after the initial fragmentation event.

Natural Fragmentation.—Twenty random, previously fragmented *S. cooperi* stems were obtained from the forest edge bordering the study site. Each stem's diameter was measured with a digital caliper, along with the number of AARs per stem.

Moss and Basal Associated AARs.—Fifty adult *S. cooperi* individuals who exhibited a purely vertical growth form (90°) were selected for the survey. DBH, plant height, the number and diameter of basal AARs, total amount of moss cover occurring on stems, and the number of AARs associated with moss mats were recorded for all 50 individuals. Measurements were obtained using a digital caliper and a 20 m measuring tape.

Growth Angles and AARs.—Fifty adult *S. cooperi* individuals who displayed both horizontal and vertical stems were selected. Some segments (horizontal or vertical) often were continuous along the naturally curving stem of *S. cooperi*, and therefore were documented as two different segments. Plant height, estimated stem angle, the number of AARs associated with each stem, and the distance between plant base and AARs were recorded using a digital caliper and a 20 m measuring tape.

Statistical Analyses.—A Goodness of Fit test was used to analyze significance between the number of AARs and the original angle of stems (horizontal or vertical) prior to fragmentation. Another Goodness of Fit test was used to analyze significance between the number of naturally fragmented stems with or without AARs. A simple linear regression was run to investigate a relationship between stem diameter and the number of AARs present for naturally fragmented stems. To examine the relationship between vertical plant height or DBH and the average diameter of basal AARs, two simple linear regressions were run. Two more simple linear regressions were run to explore potential correlations between stem angle and the number of AARs and relationships between plant height and the distance between stem base and AARs.

RESULTS

Induced Fragmentation.—Both horizontal and vertical stem segments (N = 20) cut from adult *S. cooperi* produced AARs ten days after the induced fragmentation (Table 1). However, neither horizontal nor vertical stem segments displayed greater than expected AAR production ($x^2 = 0.94$, df = 1, P > 0.05).

TABLE 1. *Number of stems that generated aboveground adventitious roots (AARs) ten days after being cut from adult* Senecio cooperi *plants. Horizontal stems were classified as those stems whose angle between stem and soil was 0 to 45 degrees before being cut; while vertical stems were those whose original angle was 46 to 90 degrees. After being cut from the adult plant, all stems were placed on a natural 3 m x 1 m soil plot.*

Original Stem Orientation	Number of stems with AARs	Number of stems without AARs
Horizontal	3	17
Vertical	1	19

Natural Fragmentation.—Of the surveyed naturally fragmented stems (N = 20), the number of stems with AARs present was significantly larger than the number of stems without (x^2 = 12.80, df = 1, p < 0.05). Additionally, greater fragmented stem diameter (mean in mm ± SD; 15.471 ± 2.382) resulted in more AARs (10.850 ± 9.292; Figure 1).
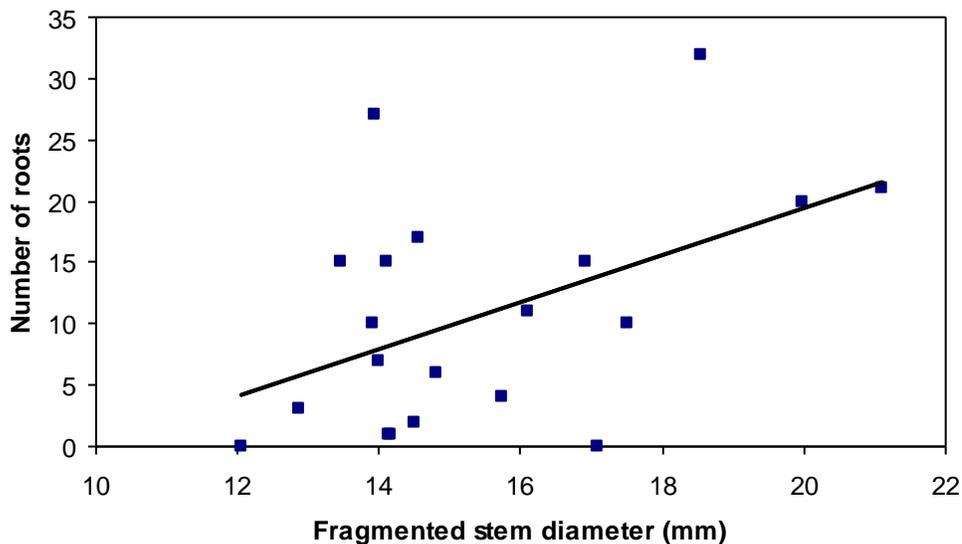

FIGURE 1. Relationship between the diameter and the number of aboveground adventitious roots found on fragmented stems of *Senecio cooperi*. (Y = 1.913x - 18.747 R^2 = 0.240, P = 0.0282, N = 20). The measured stems had all undergone previous natural fragmentation events.

Moss and Basal Associated AARs.—Moss cover on the vertical stems of the surveyed *S. cooperi* (N = 50) ranged from ¼ to complete coverage. None of these vertical growing *S. cooperi* individuals produced any AARs that grew into the moss mats present on their stems. Purely vertical forms of *S. cooperi* did produce basal AARs that probed into the soil. These basal AARs all grew between 0 and 100 mm along the stem of *S. cooperi*, and were not associated with the stem moss mats. *Senecio cooperi* stems are thin (mean in mm ± SD; 18.30 ± 2.32) and tall (1697.10 ± 189.89). Greater *S. cooperi* DBH and height resulted in larger average basal AAR diameter (Figure 2).

There was not a significant relationship between plant height or DBH and the number of basal AARs present (Table 2).
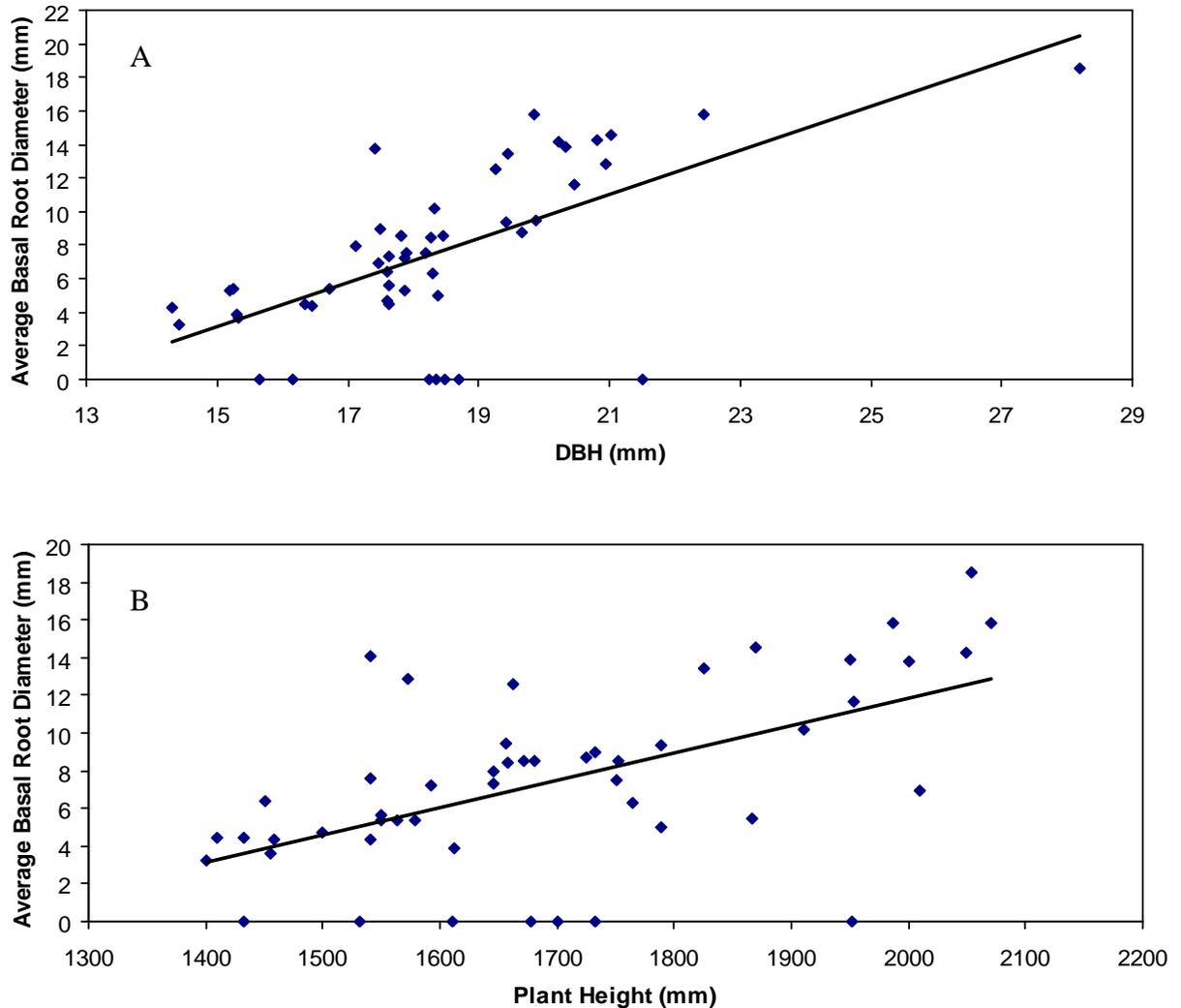

FIGURE 2. Relationship between (A) stem DBH and average basal root diameter (Y = 1.306x - 16.414, R^2 = 0.402, P < 0.0001, N = 50) and (B) plant height and average basal root diameter (Y = 0.0145x - 17.122, R^2 = 0.330, P < 0.001, N = 50) of *Senecio cooperi*. The measured plants all exhibited purely vertical growth.

Growth Angle and AARs.—Both horizontal and vertical *S. cooperi* individuals had stems that exhibited AARs. Out of all of the stems surveyed (N = 50), 42 horizontal stems contained AARs, compared to only two vertical stems. These AARs were distinguished from basal AARs in that they grew farther than 100 mm from the base of the stem. None of these AARs grew into the soil, and even the longest root (429. 43 mm) was solely attached to its anchoring *S. cooperi* stem. Stems that exhibited a smaller

growth angle in relation to soil displayed a higher number of AARs (maximum AARs found per stem = 5; Figure 3).
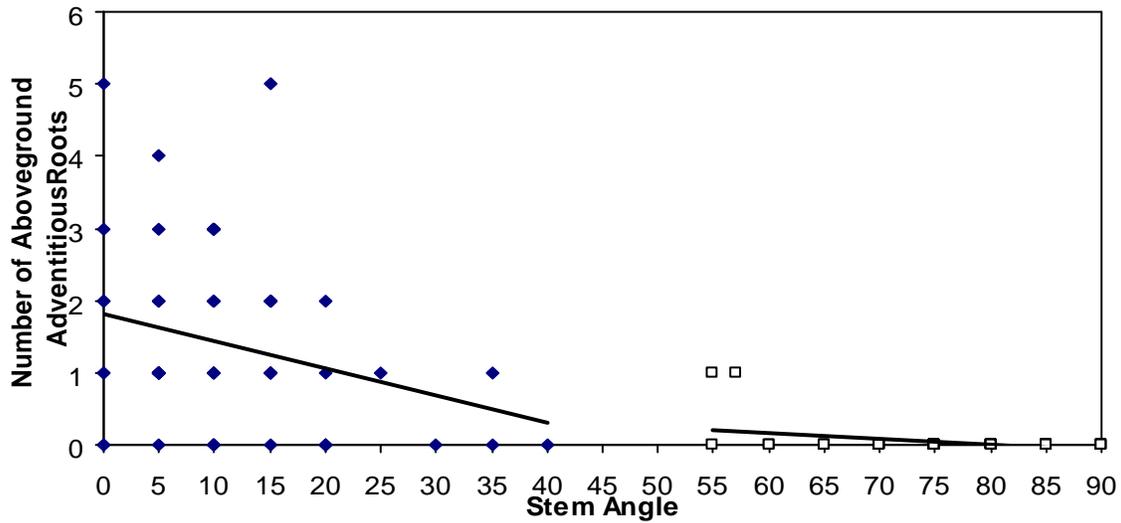

FIGURE 3. Relationship between stem angle and the number of aboveground adventitious roots (AARs) of *Senecio cooperi*. Regression analyses for both horizontal stems (Y = -0.0375x + 1.81, R^2 = 0.082, P = 0.0307, N = 50) and vertical stems (Y = -0.0087x + 0.6939, R^2 = 0.174, P = 0.0023, N = 50) reveal a negative correlation between stem angel and the number of AARs. Horizontal stems were classified as those stems whose angle between stem and soil was 0 to 45 degrees; while vertical stems were those whose angle was 46 to 90 degrees.

There was a significant correlation between horizontal stem segment length and the average distance between *S. cooperi* plant base and AARs (Figure 4), meaning longer stem segments had larger distances between plant base and their respective AARs. Variation was present, evident in that a stem of small length (1500 mm) had the largest distance between plant base and AARs (1236 mm).
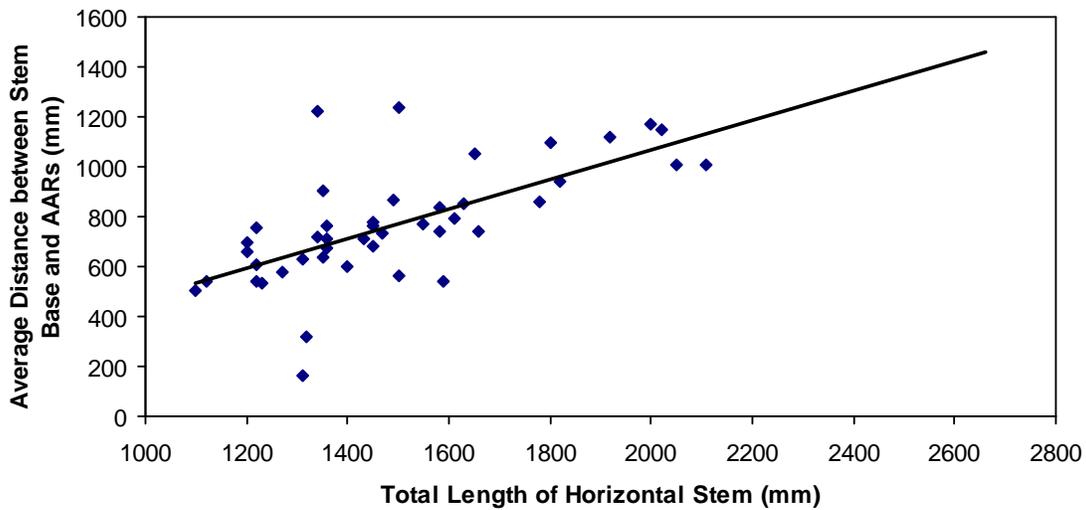
FIGURE 4. Relationship between total length of horizontal stems and the average distance between the plant base and the aboveground adventitious roots on that stem ($Y = 0.5956x - 121.4$, $R^2 = 0.430$, $P = < 0.0001$, $N = 45$) of *Senecio cooperi*

Additional regressions were run on other aspects of AARs, stem angle, and *S. cooperi* characteristics, but none revealed significant relationships (Table 2).

Table 2. *Additional statistical regressions concerning aboveground adventitious roots of* Scenecio cooperi. *None of these test yielded statistically significant regression (N = 50 for all regressions).*

Comparison	Regression Equation	R^2	P-value
DBH vs. number of basal adventitious roots (vertical plants only)	$Y = 0.1076x + 0.671$	0.013	0.42
Plant height vs. number of basal adventitious roots (vertical plants only)	$Y = 0.0011x + 0.8075$	0.009	0.51
Stem angle vs. average aboveground adventitious root (AAR) length	$Y = 2.1655x + 102.59$	0.018	0.40
Total number of stem segments per individual vs. number of AARs per individual	$Y = 0.0527x + 1.5378$	0.002	0.74
Length of stem vs. total number of AARs per stem	$Y = -0.0003x + 2.0726$	0.009	0.52
Average distance between stem base and AARs vs. number of roots per stem	$Y = 0.0008x + 0.7231$	0.030	0.92
Average distance between stem base vs. average AAR length	$Y = -0.058x + 167.52$	0.024	0.32

DISCUSSION

Prior to this study, I hypothesized that the AARs generated by *S. cooperi* were principally important for regeneration after fragmentation and structural support. As expected, some fragmented stems did produce AARs. However, there were only a small number of experimentally fragmented stems with AARs, resulting in no significant difference between the numbers of AARs produced by fragmented stems that were originally horizontal or vertical (Table 1). The small amount of AAR production can be explained by the short time period (ten days) allotted for fragmented stems to produce new AARs. Many AARs have been documented to take as long as one month to grow out of fragmented stems of neotropical species (Kinsman 1990).

Naturally fragmented stems had more AARs present than was expected by chance. This supports the idea that AARs assist in fragmentation survival and establishment. Structurally, *S. cooperi* stems are weak and thus are susceptible to fragmentation. It follows from this that *S. cooperi* stems would gain a fitness advantage if fragmented stems could reestablish, providing a form of asexual reproduction. This ability to fragment successfully, as a result of AAR production, explains *S. cooperi* abundance in disturbed areas.

A larger stem diameter resulted in a greater number of AARs (Figure 1). AARs likely originate from the cambium of fragmented stems (Smith 1936). Thicker stem fragments would have a greater amount of cambium and necessary nutrients for root growth, allowing them to generate more AARs. It is important to note that the fragmented stems that were collected were taken across a range of abiotic conditions. The varying amounts of light and nutrients across this range may explain how several stems with smaller diameters had a numerous AARs (Figure 1).

No vertical *S. cooperi* stems had AARs that probed into the moss mats they were supporting. This information suggests that AARs do not offer an alternative nutrient pathway for *S. cooperi* individuals. Furthermore, this datum suggests that the AARs produced by *S. cooperi* in response to experimental epiphyte treatments (Nadkarni 1994) do not reflect normal ecological growth patterns.

As expected, vertical *S. cooperi* stems did display basal AARs. Stems that were taller and exhibited a greater DBH had basal roots with thicker diameters (Figure 2). These results begin to suggest that basal roots offer structural support to vertical stems. It is also possible that these roots were primarily in place for nutrient absorption. If these basal AARs were produced for nutrient absorption, it would be more advantageous for larger plants to produce a greater number of AARs (instead of AARs with greater diameters) in order to maximize surface area. There was not a significant relationship between plant height or DBH and the number of basal AARs. This further supports the idea that basal AARs are used for structural support. *S. cooperi* stems are slim yet tall, which results from their rapid growth pattern characteristic of pioneer species. Producing thick basal AARs allows *S. cooperi* individuals to grow quickly to maximize sunlight absorption, while offering increased structural stability (Schatz et al.1985).

As stem angle increased towards 90°, the number of AARs decreased (Figure 3). Horizontal stems experience more gravitational pull (Wilkins 1977), and AAR growth may be facilitated by this increase. Interestingly, none of these AARs present on horizontal stems reached the soil, and therefore did not offer these stems additional

support. AARs may be produced on horizontal stems in order to anticipate fragmentation, which indeed is more likely to occur compared to vertically oriented stems (Wilkins 1977). Having a few AARs produced prior to fragmentation would allow more immediate nutrient uptake to occur in the fragmented stem.

Longer horizontal stems had a greater distance between their stem base and AARs (Figure 4). Again, horizontal stems are more likely to experience fragmentation, and the probability increases with distance along the stem. Therefore, longer stems would be benefited by producing AARs closer to a potential fragmentation area.

These results question previous studies that suggested AARs produced by *S. cooperi* were for epiphyte associated nutrient uptake (Nadkarni 1994) by highlighting their important role in fragmentation recovery and structural support. However, it is still unknown whether AARs of *S. cooperi* change function based upon microhabitat and other abiotic conditions. Furthermore, the absorptive capacities and rate of growth of AARs are poorly documented. Still, my results show the importance of reevaluating the functional role of AARs beyond nutrient absorption for many neotropical plant species.

ACKNOWLEDEMENTS

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