prepared from CaCarbide and water to make a 10% by volume atmosphere. Incubation vial volume for leaf and root samples was 20 ml and 250 ml for detritus. Vials were incubated in situ after the plant was re-attached to the bole. Vials with leaf samples were taped onto the leaves, the detritus samples inserted within the detritus mass, and the root samples taped to the encircling roots. The temperature inside a separate vial was monitored at 5-min intervals with a Li-Cor 1000 datalogger using a 64 μm diameter copper-constantan thermocouple, and the inner-vial temperature was compared to a second thermocouple taped to the leaf surface, root or inserted into the detritus. Only those samples that were within 2°C of the undisturbed root, detritus or leaf temperature were used for analyses to insure that incubation was at ecologically relevant temperatures.

The following controls were included in each sample set: (1) vials without leaf material were injected with C_2H_2 to detect contaminating C_2H_4; (2) vials were incubated with samples but without C_2H_2 to detect endogenously produced C_2H_4; (3) five vials were injected with a standardized gas mixture (Scotty I Analyzed Gases, 8.12 ppm C_2H_4) to detect C_2H_4 losses due to leakage, adsorption, and absorption during incubation or during transportation in the sampling syringe. The latter 5 vials generally showed C_2H_4 concentrations within 1% of specifications and exhibited statistically acceptable variations among samples (99th percentile). The Gow-Mac gas chromatograph model 69-750 fitted with a Porapak R filled stainless steel column at 40°C employing N_2 as carrier gas was calibrated using Scotty Analyzed Gases; calibration was rechecked every 20th sample. Conversion of ethylene concentrations to equivalents N assumed a N:C_2H_4 ratio of 3:1 (Hardy *et al.* 1968).

Root Mycorrhizae

Roots of *A. hookeri* were fixed in FAA and subsequently stained using the method of Brundrett *et al.* (1984). The roots were washed in distilled water, cut into 2 cm lengths and cleared in 5% KOH for 20 min at 60°C. After re-washing in distilled water, they were stained with 0.1% Chlorazol Black E (Sigma) for 1 hr at 90° and destained overnight in glycerol.

The total leaf area for the average 12–13 leaves per plant was measured with a surface area digitizer.

Results and Discussion

The constraints on epiphyte growth in many arboreal habitats include: 1) low light intensity; 2) isolation from the soil as a mineral source; and 3) a shift from soil to litterfall and canopy throughfall rainwater as mineral sources. Estimation of a plant's adaptation to the epiphytic habitat include: 1) mineral capture efficiency; 2) mineral requirement to produce biomass; and 3) mineral allocation to reproduction (Benzing 1981). Stresses exerted on epiphytes ultimately relate to the oligotrophic nature on the biotope they occupy. Adaptations to these stresses may be both morphological and physiological. For example, morphological adaptations as the development of a velamen in the epiphytic orchids, shootless morphology in the sub-tribe Sarcanthinae and certain species of the Bromeliaceae, and the trichome-lined interfoliar chambers of *Tillandsia circinnata* which facilitate nutrient absorption and conservation of biomass (Benzing & Ott 1981). An example of physiological adaptations is the employment of crassulation acid metabolism by some xerophytic species of orchid epiphytes as part of their moisture conservation strategy.

A hookeri, totally dependent on fine litterfall and canopy throughfall rain as mineral sources, exhibits a suite of adaptations that result in the accrual of sufficient N, P, and other macro-elements to sustain growth and provide sufficient excess for reproduction.

Growth Habit

A. hookeri has a short, thick stem from which a crown of vertically oriented leaves emerge (Figure 1). The basal stem produces two types of roots. One type grows upward into the mass of detritus that accumulates at the base of the leaves, while the second type encircles the bole of the host tree. Mean fresh weight of entire plants plus impounded detritus was 5.2 kg (SEM = $\pm$0.088, N = 8), and the mean dry weight was 0.765 kg (SEM = $\pm$0.045, N = 8).

Leaves

Leaf form and arrangement of *A. hookeri* permits the capture and retention of litter. Like the tank-form members of the Bromeliaceae, I interpret the reduction of stem length and the allocation of plant material into large litterfall-capturing leaves as an adaptation allowing *A. hookeri* to invade the nutrient-stressed canopy. Plants average 12.9 leaves (SEM = $\pm$0.125, N = 8), 104.1 cm in length (SEM = $\pm$1.65, N = 26), with a mean surface area per leaf of 1,744 cm^2 (SEM = $\pm$50.43, N = 26). The rosette display of these effectively intercepts and retains fine litterfall, and it funnels throughfall rainwater into the cen-

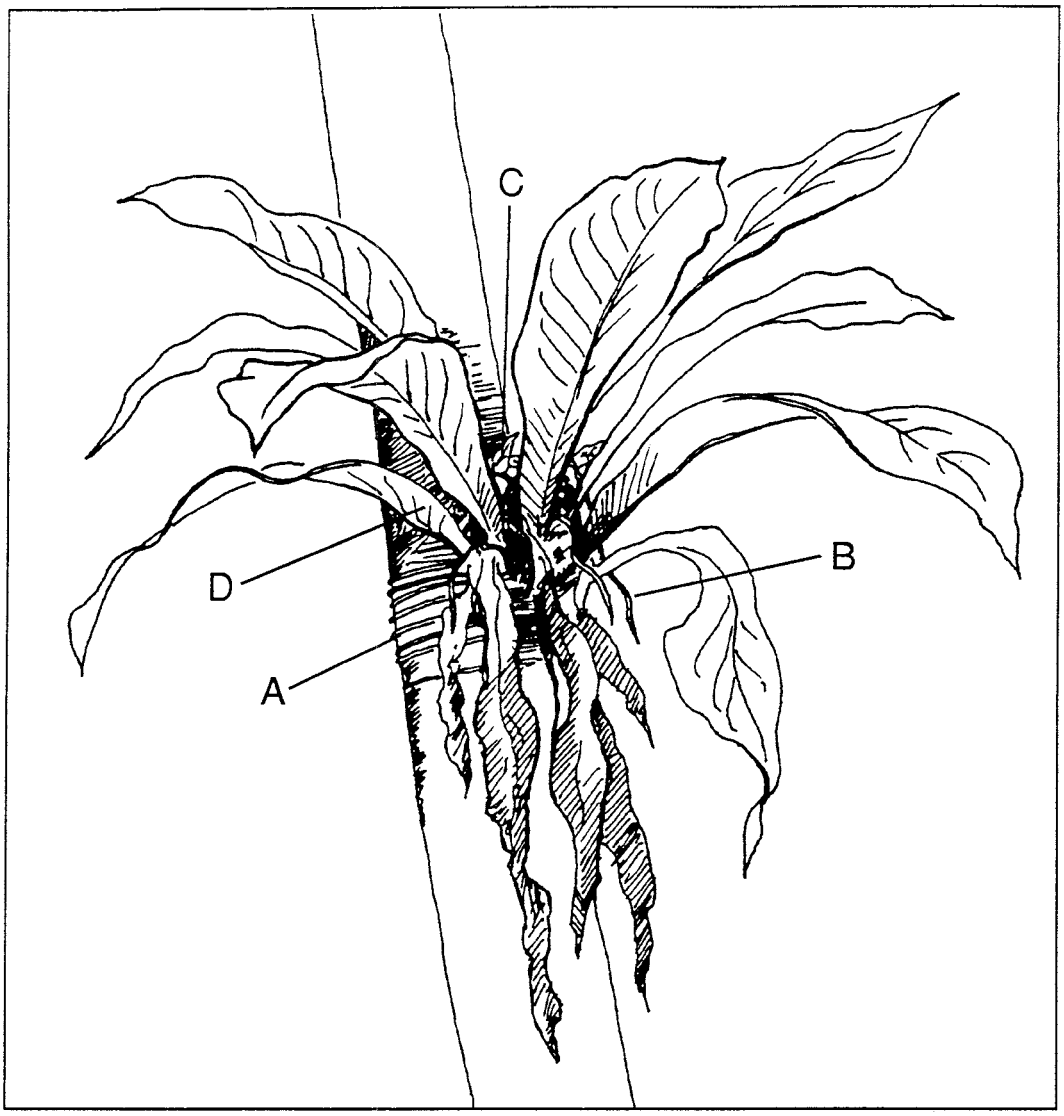

FIGURE 1. Growth habit of *Anthurium hookeri* Kunth. Shown are: A) anchoring roots encircle trunk of host tree; B) positively gravitropic absorbing roots intermixed with detritus derived from fine litterfall; C) captured fine litterfall; and D) rosette of fine litterfall capturing leaves.

tral mass of compost. Funneling of rainwater facilitates the acquisition of minerals in rainfall but also increases susceptibility to mineral loss by leaching. Mineral and water retention is facilitated by the mass of spongy compost. However, the vertical, overlapping leaf orientation of *A. hookeri* is sub-optimal for light absorption.

Stem

The reduced stem length of *A. hookeri* is shared by some epiphytic species of the family Orchidaceae of the sub-tribe Sarcanthinae (Benzing & Ott 1981). Elongated stems are expendable for epiphytes, which gain a competitive advantage by using the host tree for elevation into the canopy, allowing *A. hookeri* to allocate its resources to the more functional leaves that gather light in the low light intensity environment, funnel rainwater and fine litterfall to the axis, and serve as large substrate for nitrogen-fixing epiphyllae. A reduction in stem length and allocation of biomass to leaves are interpreted as adaptations conferring oligotrophic competence.

TABLE 1. Mineral content of Maison de la Forêt forest floor litter and detritus captured by *A. hookeri*.

ID	pH	%OM	Total %N	%P	μg·g⁻¹ K	Ca	Mg	Fe	Na
				Forest floor litter					
$\bar{x}$	—	—	1.42	0.0643	1,844	24,212	3,987	2,479	261
± SEM			0.080	0.0054	290	3,468	1,540	1,269	15
				Captured detritus					
1	6.55	87.8	2.44	0.125	6,817	6,009	3,848	4,229	1,139
2	6.60	85.8	2.56	0.129	9,329	9,283	5,206	4,085	859
3	6.59	86.0	2.51	0.125	10,540	8,701	5,572	3,796	909
4	6.50	85.5	2.50	0.127	7,959	8,607	4,743	4,394	745
5	6.50	85.2	2.58	0.129	8,693	8,494	4,677	4,515	771
6	6.33	87.9	2.58	0.126	5,380	5,909	3,437	4,412	799
7	6.36	88.6	2.47	0.114	6,489	6,168	4,100	3,812	1,057
8	6.33	88.3	2.66	0.127	5,664	5,842	3,406	4,274	826
$\bar{x}$	6.47	86.9	2.54	0.125	7,609	7,377	4,374	4,190	888
± SEM	0.004	0.491	0.025	0.0017	647	534	284	95.8	49.7

Mineral Content of Captured Detritus

Mean dry weight of captured fine litterfall was 149 g (SEM = ±11.5, $N = 8$). Decomposition of the captured detritus provides minerals and the resultant CO_2 may enhance photosynthesis. No other plants were rooted in the captured detritus. The composting fine litterfall of *A. hookeri* (TABLE 1) was slightly acidic (pH 6.47, SEM = ±0.004, $N = 8$). In comparison, the mean pH for epiphyte soil at La Selva was 4.42 ($N = 5$) and at Monteverde 3.54 ($N = 5$) (Lesica & Antibus 1991).

Mean percent organic matter was 86.9% (SEM = ±0.491, $N = 8$), and the mean N was 2.54% (SEM = ±0.02, $N = 8$) and P 0.126% (SEM = ±0.001, $N = 8$) (all dry wts.). Mean values for other elements reported as μg·g dry weight of detritus were: boron 16.1, aluminum 6,220, cobalt 2.31, copper 4.47, manganese 380, silicon 1,513, and zinc 47 ($N = 8$).

For comparison, the fine litterfall nutrient content is listed for the Maison de la Forêt forest floor (TABLE 1) and 10 other montane forests (TABLE 2). The mean % dry wt. N and P for the Maison de la Forêt was 1.42 N and 0.063 P compared to 1.2 N and 0.06 P for the ten other listed forests. In comparison, the mean nutrient concentrations for detritus impounded by *A. hookeri* were greater by a factor of 1.8 (N) and 2 (P) than Maison de la Forêt litter and 2.1 (N) and 2.0 (P) for litter listed in TABLE 2. The higher values for *A. hookeri* detritus were probably due to concentration by microbial activity, with most of the dry weight lost as CO_2, and accompanied by the conversion of fine litterfall carbohydrate and minerals into bacterial, fungal and invertebrate cellular material, thereby reducing leachability. The range for mineral content of suspended epiphyte soil at La Selva as & dry wt. was N 0.0187 to 0.2962 ($\bar{x} = 0.0898$), P 0.0050 to 344 ($\bar{x} = 0.0133$), and N 0.0040 to 0.0490 ($\bar{x} = 0.0241$) and P 0.0026 to 0.0050 ($\bar{x} = 0.0037$) at Monteverde (Lesica & Antibus 1991). the mineral status of detritus accessible to *A. hookeri* was 28 (N) and 9.4 (P) times higher than mean values determined for montane rain forest epiphyte soil at La Selva, and N 105 and P 33.9 times higher than those at Monteverde (Antibus & Lesica 1991). The N and P concentrations in *A. hookeri* detritus were 1.6 (N) and 1.8 (P) times higher than the mean values for epiphyte dead organic matter fraction determined by Nadkarni and Matelson (1992) in the Monteverde cloud forest. In comparison, *A. hookeri* is very successful at concentrating the low-nutrient litterfall into high-nutrient detritus soil.

TABLE 2. Litterfall nutrient content (values selected from Vitousek 1984).

Location	Forest type	%N	%P
Ivory Coast	Evergreen plateau	1.4	0.07
Ivory Coast	Evergreen talweg	1.4	0.02
Ivory Coast	Evergreen plateau	1.3	0.04
Columbia	Evergreen seasonal	1.1	0.04
Columbia	Evergreen seasonal	1.1	0.04
Guatemala	Rainforest mature	1.9	0.06
Jamaica	Monane mor ridge	0.6	0.02
Jamaica	Montane wet slope	0.6	0.04
Australia	Rainforest	1.5	0.1
Hawaii	Montane rainforest	0.6	0.03
$\bar{x}$		1.2	0.06

TABLE 3. Nitrogen from biological nitrogen fixation.

ID #	Total N mg N·kg dw·y^{-1}	Total N mg N·plant·y^{-1}	N Contribution mg N·kg dw·y^{-1}		
			Detritus	Roots	Leaves
1	640	440	398	11.9	29.9
2	6.2	5	2	1	2
3	6.8	5.2	1.8	0.2	3.2
4	372	247	215	4.9	27.1
5	12.3	8.8	8.2	0	0.6
6	7.6	6.0	1.2	0	0.2
7	19.2	16.1	14.7	1.3	0.1
8	28.2	21.4	20.9	0.2	0.3
$\bar{x}$	136	93.7	82.7	2.43	7.92
± SEM	84.5	57.5	51.9	1.47	4.51

Root Mycorrhizae

Most plants in natural ecosystems have mycorrhizal associations. Mycorrhizae are highly coevolved mutualistic associations between most plants and soil fungi of classes Zygomycetes, Ascomycetes and Basidiomycetes (rev. in Harley & Smith 1983). There are at least seven types of mycorrhizae when classified in the mature state. The most ubiquitous type of mycorrhiza is the VA mycorrhiza type which has been found in most angiosperms. Examination of *A. hookeri* roots did not conclusively show the presence of endomycorrhizal fungal colonization. Due to the lack of visible vesicles and arbuscules, the angularly branched hyphae could not be conclusively identified as vesicular-arbuscular (VA) mycorrhizal fungi. However it is noteworthy that fungi, possibly VA mycorrhizal fungi, were observed. The relation between a plant and VA mycorrhizal fungi is such that the host receives minerals from the fungus and the fungus obtains photosynthate from the host. VA mycorrhizae are formed by aseptate fungi of the Glomales (Morton & Benny 1990) that invaginate root cortical cells to produce arbuscules and vesicles (members of the Gigasporaceae do not produce vesicles). A VA mycorrhizal association would be clearly advantageous when the oligotrophic biotope of *A. hookeri* is considered (Lesica & Antibus 1990). The external hyphal network of the mycorrhiza would effectively extend the surface area of the roots and facilitate the uptake of minerals from the detritus before they are leached. Other fungi that did not conform to the description of the types of mycorrhizas were also observed within the roots.

Biologically Fixed Nitrogen

Mean N derived from biological nitrogen fixation (TABLE 3) was 136 mg N·kg dw^{-1}·yr^{-1}, 93.7 mg N·plant dw^{-1}·yr^{-1}. The distribution of N_2 fixation between the detritus, roots and leaves as the mean mg N·plant part dw^{-1}·yr^{-1} was 82.7, 2.43 and 7.92%, respectively. Nitrogen fixation was consistently highest for detritus, and there was considerable variation among the plants sampled. The annual N contribution by N_2-fixation ranged from 1.8% to 0.0002% of the total detritus N.

Roots

The remainder of *A. hookeri* phytomass is allocated to roots. Anchoring roots that encircle the host's bole are well adapted to secure *A. hookeri* in the event of bark exfoliation. A second set of positively gravitropic roots penetrate the accumulated fine litterfall composting in the leaf axils.

CONCLUSIONS

The adaptations by *A. hookeri* to the oligotrophic epiphytic biotope provide a detritus soil that exceeds the mineral content of fine litterfall. The epiphyte soil N and P concentrations of this "bird's nest" epiphyte greatly exceed those of the mat-forming epiphytes that cannot effectively exploit litterfall as a significant mineral source. Biological nitrogen fixation probably does not contribute significantly to the N budget of this epiphyte. *A. hookeri* exists in a eutrophic microenvironment due to its adaptations.

ACKNOWLEDGMENTS

I want to acknowledge the contribution of Susan Persad-Chinnery, Faculty of Natural Sciences, The University of the West Indies, Barbados which included the identification of root mycorrhizae, photography and text regarding these fungi. I also thank Professor Richard A. Howard of the Arnold Arboretum, Harvard University, for his taxonomic confirmation and discussion of *A. hookeri*. I am indebted to Professor Jacques Portécop, my host at the Université des Antilles et de la Guyane, Guadeloupe, for his advice, friendship, and his dedication to the conservation of the French West Indian ecosystems.

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