THE ECOLOGY OF AN ELFIN FOREST IN PUERTO RICO, 6 AËRIAL ROOTS [1]

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In temperate regions aërial roots are rare and although they may be found on a few vines they are absent from the trees and shrubs. In the moist elfin forest of Puerto Rico, however, many of the trees, shrubs, vines, and herbs form aërial roots. The tree fern *Cyathea* and the lowly *Selaginella* also form aërial roots in this environment.

Many of the aërial roots hanging freely from the plants are very characteristic of the species while some other species are difficult to distinguish by the characters of their aërial roots alone. In this study some of the distinctive characters of the roots are described and the frequency of aërial root formation on Pico del Oeste is documented.

Observations on the Distribution of Roots in toto

The roots in the study area are found in four general habitats: in the soil; immediately above the soil beneath a layer of cryptogams and/or leaf litter; appressed to the trunks and branches of the trees and shrubs; and hanging freely in the air.

All the roots in the last three habitats named may be considered "aërial." Those in the second category occur in a gaseous environment immediately below the forest floor and above the soil. A mat of roots up to five centimeters thick may be formed (Fig. 1) which appears to have arisen not merely by erosion of soil but by the growth of roots out of the soil and over its surface. On steep slopes roots of sufficient rigidity may even grow through the forest floor into the atmosphere. On gentle slopes this achievement has been attained by growth along tree trunks and fallen branches beneath a layer of cryptogams and thence out to the atmosphere.

The roots of many of the vines and of the bromeliad *Vriesea* are found closely attached to rigid organic surfaces. They are often found beneath a mantle of cryptogams but are also found where such a covering is lacking. This latter type of root may also be considered "aërial" but the affinity of the roots to their supports distinguishes them from the final group which is the main subject of this paper.

The aërial roots to be considered here are those found hanging freely in the atmosphere. They arise above ground and are not closely appressed

[1] The first two papers in this series were published in Jour. Arnold Arb. **49**: 1968. See: R. A. Howard, The Ecology of an elfin forest in Puerto Rico, 1. Introduction and composition studies, 381–418; and H. W. Baynton, 2. The Microclimate of Pico del Oeste, 419–430.

FIG. 1. Mat of roots immediately below the litter and cryptogam layer but immediately above the soil.

to any surface. They may become anchored in the substrate and undergo considerable secondary thickening and in such cases have been termed "prop" or "stilt" roots by other authors. The aërial portions of such anchored roots may exhibit phenomena different from roots of the same species in the freely-hanging stage — those to be considered here.

AËRIAL ROOTS OF THE TREES AND SHRUBS

Many of the data pertaining to the aërial roots of the trees and shrubs of the area are shown in TABLE 1.

Origin. Aërial roots usually arise from the undersides of branches and from the main axis of the plant. They are often associated with the formation of sprouts (probably arising from dormant buds) and in such cases are found at the base of the sprout where it joins the main stem. This condition was observed in *Ocotea*, *Ilex*, *Miconia pachyphylla*, *Calyp-*

TABLE 1. The aërial roots of the trees and shrubs

	Tip Properties					At root origin			
Species	Max. diam. (mm.)	Max. incre-ment before laterals (cm.)	Max. replace-ment tips	Color	Rigidity and alignment	Lateral roots without injury*	Min. stem diam. (mm.)	Min. distance to leaves (cm.)	Second. thick. before ground*
Prestoea montana	17	19	4	pale orange to pale pink	stiff & brittle, simple curves	+	58	45	–
Hedyosmum arborescens	3.5	80	3	white apex, then lemon, then green behind	unbent, flexible	–	4	5	+
Ocotea spathulata	6	36	4	pink to brown	unbent, flexible	–	12	30	+
Trichilia pallida	(1.2)	9	1	creamy brown to pink	unbent, flexible	–	7.5	15	?
Ilex sintenisii	0.7	5	3	white to brown	unbent, flexible	–	13.5	110	?
Torralbasia cuneifolia	0.6	12	5	orange	unbent, flexible	–	3	30	+
Clusia grisebachiana	6	89	2	white apex, yellow and brown behind	unbent, flexible	–	13.5	50	+
Calyptranthes krugii	1.2	14	1	white to red-brown	unbent, flexible	–	2.5	8	+
Eugenia borinquensis	1.8	24	1	white to red-brown	unbent, flexible	–	110	250	+
Calycogonium squamulosum	1.5	14	3	bright pink	unbent, flexible	–	4	2	+
Mecranium amygdalinum	1.2	9	2	white to pink	unbent, flexible	–	2	2	+
Miconia foveolata				pink		–	2	3	?
Miconia pachyphylla	0.9	10	2	white to pink	unbent, flexible	–	3.5	0	+
Grammadenia sintenisii	2.0	9	2	white to light brown	unbent, flexible	–	5	16	+
Wallenia yunquensis	1.0	10	4	white to pink	unbent, flexible	+	5	1	+
Micropholis garciniaefolia	2.7	17	?	white	unbent, flexible	–	47	150	?
Symplocos micrantha	0.8	4	6	white	unbent, flex. to hanging	–	5.5	6	+

TABLE 1 — *continued*

	Tip Properties					At root origin			
Species	Max. diam. (mm.)	Max. increment before laterals (cm.)	Max. replacement tips	Color	Rigidity and alignment	Lateral roots without injury*	Min. stem diam. (mm.)	Min. distance to leaves (cm.)	Second. thick. before ground*
Haenianthus salicifolius	1.5	23	6	cream ochre to brown	unbent to hang in cluster	–	8	15	+
Tabebuia rigida	2	10	5	creamy lime to weak yellow	unbent, flexible	–	11.5	6	+
Gesneria sintenisii	0.5	4	7	white to tan	unbent, flexible	–	3	3	?
Psychotria berteriana	0.7	7	2	beetroot to pale white	unbent flexible	—	4	11	?
Lobelia portoricensis	1.5			white to pale green	unbent, flexible	–	7	0	?

* + represents presence, – represents absence.

tranthes, Grammadenia and *Torralbasia.* The same thing may occur below the ground with some species of trees in temperate areas. In Massachusetts it has been seen in *Fraxinus americana*: when a tree is cut down and new shoots arise at the base from beneath the soil-surface, new roots may be formed at the junction of the new shoot and the parent stem.

No root was found within the leafy zone (distal to the most proximal leaf and with or without a few leafless nodes included) of the trees and shrubs except in *Lobelia.* In TABLE 1 the minimum distance of an aërial root from the leaf zone has been noted and also the minimum stem diameter on which an aërial root has been found. Most of the species have aërial roots very close to leaf zones but not within them. *Miconia pachyphylla* was recorded with roots at the junction of the leaf zone and for most of the species aërial roots have been found within 50 centimeters of the leaf zone.

The aërial roots are usually found too far away from the leafy zone to determine if there is any association between the root origin and the nodes of the stem. With *Miconia pachyphylla* (FIG. 2) one root was found at a node and no roots were observed where a definite lack of such an association could be seen. No anatomical observation of the origin of the aërial roots was made but association with a node would suggest development of a preformed primordium giving rise to the aërial root.

Aërial roots may also arise laterally from other aërial roots, a condition discussed in a later section.

Tip properties. The maximum diameters of the root tips vary widely between species. Maximum values were taken since they are more dis-

FIG. 2. Roots of *Miconia pachyphylla* with droplets of water at the apices. (Photo. courtesy of Dr. R. A. HOWARD.)

tinctive than average values. Tip size may decrease with the order of branching, with distance from the point of origin, and in some species with the size of plant (e.g. smaller plants of the palm *Prestoea* were observed with smaller tips than those on large trees). *Prestoea* has tips up to 17 mm. in diameter (FIG. 3) while the maximum recorded for *Torralbasia* was 0.6 mm. The root tips of the other species were of diameters intermediate between these values. The significance of tip size in between-species comparisons is not known, but in the roots of the trees in central Massachusetts at least, tip size within a given root system is an important parameter, and other properties of the root are associated with it, e.g., lateral frequency, number of protoxylem poles, and other anatomical features, as well as the probability of secondary thickening.

Color variations in the tips may be distinctive. *Torralbasia* roots are often orange in color, those of *Miconia* spp. usually a bright pink, and those

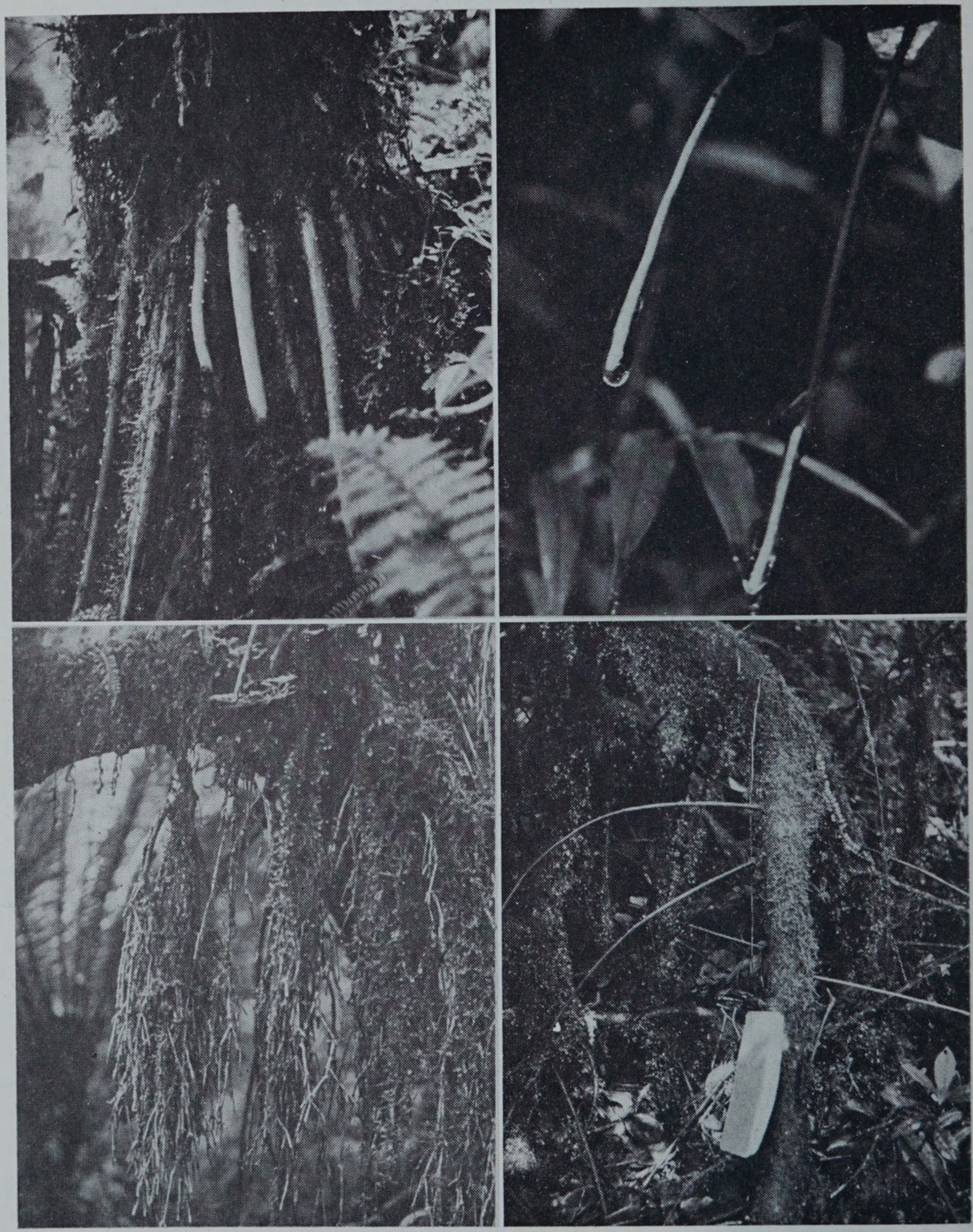

FIG. 3. Aërial roots of the palm, *Prestoea montana*, showing inhibited lateral root development in the absence of injury. FIG. 4. Gelatinous material on the aërial roots of *Hedyosmum arborescens*. FIG. 5. Broom-like cluster of aërial roots of *Tabebuia rigida*, developed as a response to repeated injury. Secondary thickening is also evident near the point of attachment. FIG. 6. Distally anchored aërial roots of *Clusia grisebachiana* showing development of root tips and considerable secondary thickening.

of *Hedyosmum* most often lemon. However, the color of the roots may be considerably muted under some conditions and for many of the species darker environments may cause all color to be lost from the root tips.

Most of the newly emerged tips are straight and flexible. The palm root tips, however, may be stiff and rather brittle and they may curve down towards the soil. When the roots are longer their alignment and rigidity may change. The roots of *Clusia* become long and rubbery and the roots of *Tabebuia* and *Torralbasia* tend to hang in clusters. The roots of *Ocotea*, however, usually maintain the initial direction of growth with some bias downward.

The living roots of *Hedyosmum arborescens* are usually bathed in a gelatinous fluid.[2] This may hang down from the apex of the tip for two millimeters as part of a drop around and below the apex (FIG. 4). Shortly above the apex the material becomes much thinner and is very thin 4 or 5 centimeters from the apex. Two roots with a considerable drop on their respective apices were stripped of their coating, using two fingers to remove it. The volume from both was approximately 2 milliliters.

An experiment was initiated in an attempt to discover how quickly the material covering the root was replaced. After a week there was partial replacement of the material. After this period approximately 1 milliliter of fluid was removed from the three stripped roots. It should be noted however, that similar stripping (with care not to exert pressure) eventually resulted in root death (R. A. Howard, personal communication). In addition it may be noted that the material does not occur on dead roots nor those with brown, apparently inactive, tips.

The gelatinous substance is common on the healthy roots of *Hedyosmum* but has been found only rarely on the aërial roots of other species in this area. It has been found only twice on the aërial roots of *Calycogonium* and once on a root of *Miconia pachyphylla*. Many aërial roots of the latter two species were observed, but in only these cited cases was the gelatinous material seen. On these specimens the material was less gelatinous and more readily removed than that on roots of *Hedyosmum*. However, it was not dislodged as easily as a drop of water might be and it was jelly-like in texture.

A cut in the aërial roots of three species caused drops of milky exudate to be formed. Such material is common in the leaves and stems of the three families represented and this observation indicates that the lactiferous system does extend into the aërial roots. The plants concerned are *Clusia grisebachiana*, *Lobelia portoricensis* and *Micropholis garciniaefolia*, members of the families Guttiferae, Campanulaceae, and Sapotaceae, respectively.

Lateral root formation. Patterns of lateral root development contribute to the specific character of many of the aërial roots. The rope-like *Clusia* roots and the broom-like *Tabebuia* roots (FIG. 5) are very distinctive for this reason. In many cases the lateral root formation from the freely hanging aërial roots appears to be entirely dependent upon injury. With such a stimulus, one to seven replacement tips may arise behind the

[2] This fluid has a high content of algae including diatoms and desmids. Some six carbon sugars were found in the material but no higher sugars (R.A.H.).

injured portion (TABLE 1). These tips may arise not only close to the injury but also several centimeters behind it (e.g. *Tabebuia* and *Torralbasia*).

With the aërial roots of the palm *Prestoea* lateral roots develop regularly without injury (FIG. 3) but have very limited growth. The laterals are short (up to 5 mm.) and pear-shaped. Their bases are narrow but their diameter increases markedly (to 2 mm.) within a short distance and then tapers to the apex. They arise in three to eight regular rows depending on parent root diameter.

Some roots may achieve great lengths before any lateral is formed. The length attained is a reflection of the growth rate and the interval between injuries, which in *Clusia* and *Hedyosmum* may amount to 2.5 to 3 meters. However, the maximum length without laterals for most of the aërial roots is usually between 4 and 40 centimeters in this area.

When a freely hanging aërial root becomes anchored in the substrate, prolific lateral root formation may occur in the subterranean portion. In addition, however, new laterals may arise on the aërial portion with no apparent stimulus from injury (FIG. 6). This contrasts with the development of lateral roots before anchorage and is evident in the aërial portions of anchored *Clusia* and *Ocotea* roots.

Growth rate. The growth rate appears to be very variable through time as single uninjured roots are found to have variations in diameter and color suggesting growth pulses. Injury, of course, prevents growth and a decrease in length may result. Injury may be environmentally induced and desiccation is a probable agent.

The growth in length of the aërial roots of ten species was measured as it occurred during a 7 to 11 day period in December, 1967. The growth rates varied from 0 to 2 millimeters per day. This may be contrasted with the rate of growth of the aërial roots of *Rhizophora mangle* (the red mangrove) in Miami, Florida, which grew up to 7 millimeters in length per day during the months of April and May, 1968 (P. B. Tomlinson and author). In the soils of New England, roots may achieve growth rates of 12 millimeters per day during summer (W. H. Lyford and author). Thus the growth rates of aërial roots in the equable climate of the elfin forest may be regarded as low.

Secondary thickening. Many of the aërial roots of trees and shrubs may commence secondary thickening well before they reach the substrate. Examples of this may be found among the roots of *Ocotea*, *Clusia*, *Miconia pachyphylla*, *Tabebuia*, *Haenianthus* and *Eugenia*. In FIGURE 5 thickening of the root of *Tabebuia* near the point of attachment to the branch may be observed readily.

The aërial roots of *Ocotea* near the base of the plant may become anchored and considerably thickened. In cross section these roots are oval with the larger axis vertical and the morphological center in the lower half. In *Clusia* however, similar roots are more nearly circular in cross section and arise from up to 3 meters above ground.

Aërial Roots of the Vines

Origin. The aërial roots of vines are often found within the leafy zone of the plant (in contrast to those of trees and shrubs). Not all roots are found within the leafy zone but this is a common occurrence. In the species under study here all the aërial roots were associated with a node in one way or another. This is not always the case with vines: in some vine species the roots are apparently formed at random along the stem as in the ornamental *Hydrangea anomala* ssp. *petiolaris* and in the native *Rhus radicans* in Massachusetts.

The associations with the node were varied. *Marcgravia sintenisii* has up to four aërial roots produced in a row parallel to the axis of the stem and running proximally from the leaf base. *Gonocalyx*, an ericaceous vine, has a similar arrangement of aërial roots but on the distal side of the leaf base. The genus *Mikania* of the family Compositae has roots formed between the leaf bases or in an axillary position. *Psychotria guadalupensis* (Rubiaceae) has aërial roots formed just distal to and between the nodes. Such specific positions of origin suggest a regular formation of root primordia in these positions as the shoot grows.

In *Marcgravia* at least, it appears that new roots may be formed on

Table 2. **The aërial roots of the vines**

Species	Roots in leaf zone?	Roots assoc. with nodes?	Max. number per node	Tip Properties: Max. diameter (mm.)	Tip Properties: Color	Tip Properties: Rigidity and alignment	Laterals without injury?
Rajania cordata	yes	yes	1	0.3	white	flexible, wrinkled	–
Peperomia emarginella	yes	yes	1	0.1	white	bent, flexible delicate	–
Marcgravia sintenisii	yes	yes	4	0.6 (2.0)	cream	unbent, tend to be rigid	–
Gonocalyx portoricensis	yes	yes	5	0.3	white	flexible, crinkled	+
Hornemannia racemosa	yes	yes	1	0.3	white to pale pink to brown	crinkled, flexible	+
Ipomoea repanda	yes	yes	2	0.5	white	weak flexibility, curves	–
Psychotria guadalupensis	yes	yes	4	0.5	cream to light green	flexible, crinkly	+
Mikania pachyphylla	yes	yes	3	0.5	white to pale green	flexible, crinkled	–

old parts of the vines where they may be 2 or 3 centimeters in diameter. In this case the tips produced may have different properties from those formed within the leaf zone. In TABLE 2 (summarizing the data collected for the vines) the value for tip diameter recorded on older wood is noted in parentheses. Whether these new roots develop from latent primordia formed in association with the leaves is not known.

Tip properties and lateral root formation. The tips of the aërial roots formed within or close to the leaf zone are usually very fine. Approximately 0.1 mm. to 0.6 mm. diameter is the range encountered. The larger value in this range was recorded for *Marcgravia*, which has rapidly tapering aërial roots — from 0.8 mm. to 0.4 mm. over one centimeter of length. In this species aërial roots with a length greater than a few centimeters have not been found free-hanging in or near the leafy zone.

Some of the species were observed to have lateral roots formed apparently without injury to the parent. The species in which this was observed are recorded in TABLE 2.

The aërial roots of vines appear rather fragile in comparison with those of trees and shrubs, both because of their small diameter and the fact that they are often irregularly bent.

AËRIAL ROOTS OF THE HERBS

Origin. The aërial roots of herbs may be found within the leafy zone in most species. In most cases also the roots are formed at well defined morphological positions. TABLE 3 presents a summary of the data. *Selaginella* and *Dilomilis* both form roots at the branch junctions. Most of the other species root only at the nodes but internodal roots have been observed in *Pilea yunquensis*.

Tip properties and lateral root formation. The roots of the *Selaginella* are green as are the apices of the aërial roots of *Dilomilis*. In the latter species the region of the tip behind the apex was creamy in color and green only at the apex.

A few of the species were observed to have lateral roots formed in the absence of injury and these are recorded in TABLE 3.

DISCUSSION

Frequency of formation of aërial roots in species. Some species such as *Miconia pachyphylla* are usually found with aërial roots but other species have been found to have no aërial roots. The reasons may be that too few specimens have been examined or that they do not in fact ever form them under the conditions experienced in this area. Woody plants such as *Cleyera* and *Ardisia* were not seen with aërial roots, but these species are not common on the site.

Some of the epiphytes, such as the bromeliad *Vriesea*, had readily visible roots but these were not observed hanging free of the host. Similarly no root of the vine *Peperomia hernandiifolia* was seen hanging free.

TABLE 3. The aërial roots of the herbs

Species	Min. distance leaf zone (cm.)	Roots only at nodes?	Tip Properties: Max. diameter (mm.)	Color	Rigidity and alignment	Laterals without injury
Selaginella krugii	0	branch junctions	0.4	green	flexible but wiry, unbent	—
Isachne angustifolia	0	yes	0.6	white to pale green	straight & flexible	—
Dilomilis montana	2	branch junctions	1.8	green apex, cream behind	corrugated, flexible	—
Pilea obtusata	0	yes	0.3	white to pink	curled, flexible	+
Pilea yunquensis	0	no	0.2	reddish brown	curled, flexible	+
Sauvagesia erecta	0	yes	0.2	pale cream	straight & flexible	—
Begonia decandra	1	yes	0.4	white to tan	straight & flexible	+

One large *Cecropia peltata* was examined and found to have secondarily thickened "prop" roots, but no tip was seen above ground and in this case it appeared that the roots had been exposed by erosion. Some of the grasses and carices had a preponderance of leafy tissue above ground, and very little stem tissue and no aërial root was observed. The scrambling grass *Isachne* has many stems above ground and in the most humid situations aërial roots are found. The tree fern *Cyathea* forms aërial roots in some cases but these were not studied. Other ferns were also omitted from the investigation.

The environment and aërial root formation. Two stages may be distinguished in aërial root formation. The first is the production of a primordium either in association with normal growth and development of the shoot or formed *de novo* under certain conditions and in older regions of the plant. The second stage is the growth of the primordium. At least some species appear to form primordia regularly on the shoot, among them many of the vines and herbs. *Selaginella* has roots associated with branch junctions and primordia are formed in these positions regularly during development (Webster & Steeves, 1967).

Several factors are known to influence the formation of aërial roots. In *Populus nigra* for example, root primordia are present in the aërial stem but no aërial root is formed. Under the proper conditions of moisture and darkness however, aërial roots may be forced into active growth (Shapiro, 1962). However, the "proper conditions" for the appearance of aërial roots in various species differ. The aërial roots of *Rhizophora mangle* in Florida, for example, often show great development in environments where there is always a high light intensity. In the elfin forest light intensities are low and roots often arise beneath a mass of cryptogams, but the importance of the light factor can only be surmised at present.

Mechanical tissue and/or lack of injury may be important in some species as roots are often associated with new shoots, which may cause wounding of the parent shoot as they grow and which are composed of relatively soft tissue. The humid environment may be essential to outgrowth of roots as desiccation seems to be an important cause of injury to apices.

Lateral root formation. The freely hanging aërial roots of the plants in the study area rarely produced laterals in the absence of injury. However, when these roots enter the soil they branch immediately. Thus there are two types of control to the lateral root formation, an external (environment) and an internal (through injury). In the external environment of the aërial root the high humidity appears to be incapable of inducing lateral root development in many of the species, and some other environmental factors such as light intensity and nutrient-environment may be involved.

Some plants with aërial roots fail to develop laterals in the absence of injury, although many herbs and vines do not. The major member of the latter group is the palm *Prestoea*, but its lateral roots are inhibited.

One cause of injury seems to be desiccation. The dead apices of the roots sometimes show no signs of physical injury but the rare periods of desiccation seem a likely cause of death. One case of physical injury was observed on a root of *Clusia*, which appeared to have been chewed.

Function of the aërial roots. Aërial roots may enable a plant to spread vegetatively to the surface of another plant or to the soil away from the base of the parent plant. If the roots from the shoot system reach the ground the path that nutrients have to travel will be shortened and this may be an advantage. Vegetative spread from detached portions of a tree is possible as broken branches with no connection to a parent tree or the soil have been seen with new roots and shoots. In an area where trees and shrubs may be pulled over by vines and/or the weight of epiphytes and water, or toppled on the steep slopes after a little soil erosion, the ability to form aërial roots may constitute a valuable property for survival.

The presence of copious quantities of a gelatinous material on the apices of the aërial roots of the *Hedyosmum* is remarkable. Samtsevitch (1965) has noticed relatively small gel-like caps on the roots of some plants such as *Zea mays* in soil and artificial media, and considers that they have several important functions including protection of the root apex from mechanical injury, improvement of the root penetration of soil, and promotion of root hair growth. In the area of study it seems that protection from desiccation is the most likely function of the material, as death of tips follows its removal (R. A. Howard, personal communication).

The anchored roots of *Clusia* and *Ocotea* certainly provide support to their parent trunks. In their absence however, subterranean roots may provide the plants with the same stability. Thus the adaptive value of these roots for support is questionable.

SUMMARY

In the humid conditions of the Puerto Rican elfin forest many freely hanging aërial roots are found on the trees, shrubs, vines, and herbs. Those of the trees and shrubs are not found in the leafy zone of the shoot system and lateral root development in the absence of injury is rare. In contrast the aërial roots of the vines and herbs arise in definite morphological positions within the leafy zone of the shoot system, and more commonly develop laterals in the absence of injury. Patterns of lateral root development may be distinctive, but other properties of the root tips such as color, rigidity, alignment, diameter, and the presence of secretions, may also contribute to the character of the aërial roots of the various species.

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