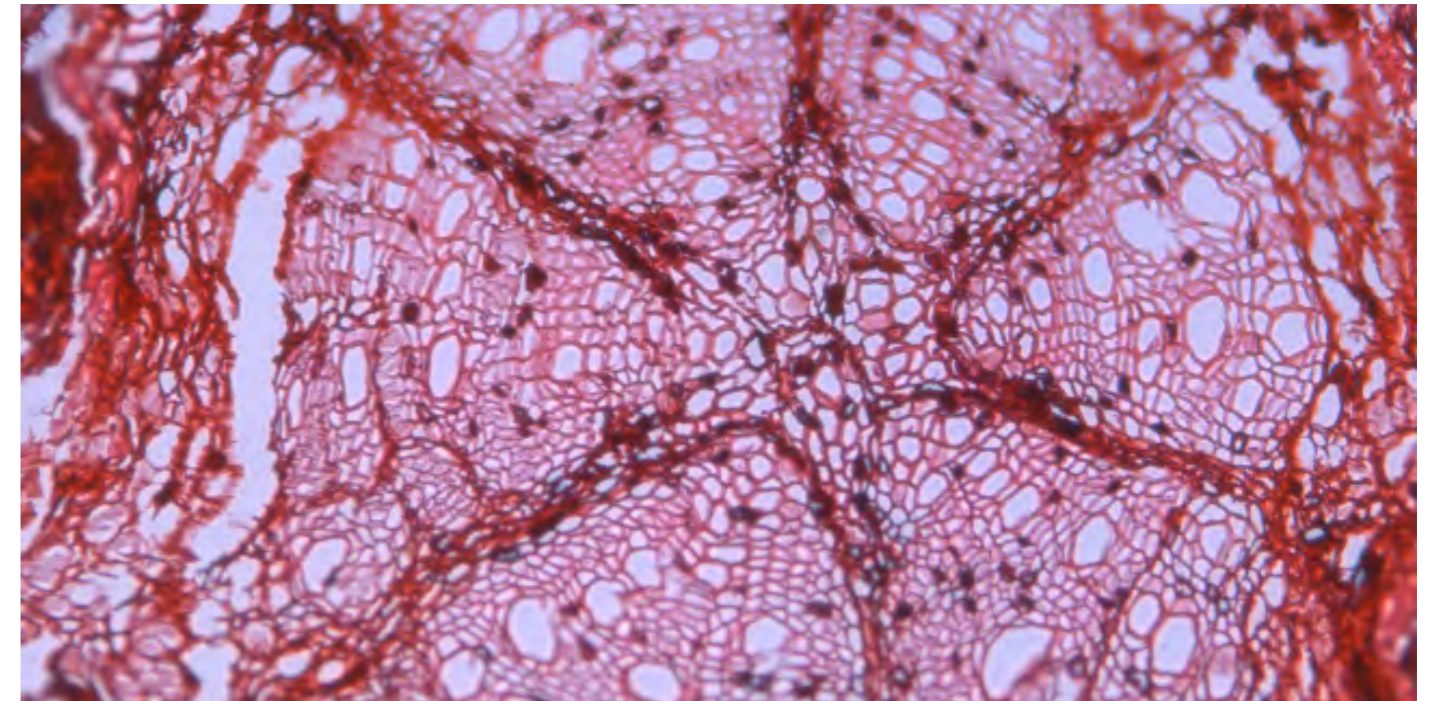


"Chinese Banyan grows rapidly with but little care, its foliage is of a glossy green colour, and it soon affords an agreeable shade from the fierce rays of the sun, which renders it particularly valuable in a place like Hong-kong'."

Robert Fortune, (1852).
A Journey to the Tea Countries of China

Aerial roots of *Ficus microcarpa*

Mathew Pryor and Li Wei



Section of flexible aerial root of *Ficus microcarpa*

This article reports on a study to investigate the nature of aerial roots in Chinese banyan trees, *Ficus microcarpa*, and the common belief that their presence and growth is associated with wet atmospheric conditions.

First, the form and distribution of free-hanging aerial roots on eight selected *Ficus microcarpa* trees growing in a public space in Hong Kong, were mapped on their form and distribution. Secondly the extension of selected sample aerial roots from each tree were measured over twelve months against prevailing atmospheric humidity. Lastly, section samples of aerial roots of different ages were taken, and the anatomical structure was observed and compared with that of terrestrial water-absorbing roots to assess the mechanism by which they might take up water.

The distribution and growth of aerial roots was observed to be highly variable, but there was a clear link between growth and high levels of atmospheric humidity. The anatomical structure of the aerial roots suggests that while aerial roots could absorb water under certain conditions, their growth was generated from water drawn from terrestrial roots via trunk and branches, and that the association with humid conditions was most likely to be due to the greater availability of ground water in such conditions.

Introduction

Chinese Banyan, *Ficus microcarpa*, is a native of Southern China and has been planted as a shade tree throughout the region for centuries. In Hong Kong, it has been planted as a roadside tree

since the beginning of the colonial period,² and was used almost exclusively for this purpose until the 1870s.³ The botanist Robert Fortune noted, as early as 1852,⁴ that the Banyan grew 'rapidly with but little care, its foliage is of a glossy green colour, and it soon affords an agreeable shade from the fierce rays of the sun, which renders it particularly valuable in a place like Hong-kong'. Even the Hongkong Governor, in 1881, observed that Banyans turned 'glaring roads to green avenues with the rapidity that would surprise arboriculturists in Europe'.⁵

It has been valued both for its shade and greenery, and its ability to cope with the typhoon winds and the poor growing environment in dense urban settings. The majority of Hong Kong's wall trees are *F. microcarpa*,⁶ and it is the species

that has been successfully transplanted most often at mature size within the Territory⁷.

‘Banyan’ is a generalized term used to refer to *Ficus* trees of the *Urostigma* subgenus of *Moraceae*, which includes tree species with aerial adventitious roots.⁸ A number of these grow in Hong Kong, e.g. *F. microcarpa*, *F. benjamina*, *F. benghalensis*, *F. elastica*, *F. macrophylla*, and *F. altissima*.⁹

The origin of aerial roots of *Ficus* trees has not been studied in detail. In Southern China, it is widely believed that the growth of aerial roots of Chinese Banyan is related to periods of high atmospheric humidity. Aerial root development is seasonal with the initiation and elongation of roots starting in spring with the rise in atmospheric temperature and humidity, and continuing until late autumn when humidity falls again.¹⁰ From this, it has been assumed that aerial roots are able to absorb water and nutrients from the atmosphere to sustain their growth. However, little research has been conducted on this point.

Gill (1975) notes that adult *F. microcarpa* trees produce slender, pendulous (free-hanging) aerial roots, i.e. roots exposed to air for at least of 50% each day and free of any support or substrate,¹¹ which under gravity grow downward. There is a high degree of variability between tree specimens in the number of aerial roots and their distribution within the canopy, but no clear indication of what factors influence this variability.

From simple field observations, there are three distinct stages in the development of aerial roots.

1. Growing tip – 1.5-2.0mm diameter, up to 120mm long, pale yellow, flexible but brittle,
2. Flexible aerial root – 2.0-5.0mm diameter, up to 10.0m long, dark reddish-brown, woody, flexible,
3. Lignified aerial root – >5.0mm (can be >100mm) woody, light grey, rigid.

In all three stages the longitudinal form of the root is variable from straight to very twisted, although they appear to become more twisted with the age. The growing tip will mature into a flexible aerial within two to three weeks. The



Typical pattern of aerial roots on a mature Chinese Banyan

flexible aerial will thicken into a lignified aerial within one to three years. The lignified aerial root has a similar appearance to a branch but does not bear foliage.

Aerial roots originate from a single point on a branch or stem, and as they grow they divide at the tip. Mature roots may have all three stages present, with a single lignified root giving rise to a cluster of many (can be <50 no.) individual flexible aerial roots and growing tips. The cluster is a self-contained system within which individual flexible aerial roots can intertwine, but do not fuse together.

Roots elongate very rapidly, and have been observed in a Miami based study to lengthen by up to 10mm per day.¹² Aerial roots arising in the upper canopy can

take several years to reach the ground or come into contact other stems or structures. Zimmermann, et al. (1968) describe the process of lignification of aerial roots in *Ficus benjamina*,¹³ a closely related species. When the flexible aerial root reaches soil it initiates and elongates terrestrial roots to absorb water and nutrients. This new terrestrial root system forms an anchor, allowing the above ground portion of the root to contract and straighten by producing tension wood. Finally, the root enters a consolidation phase, thickening to become prop stem to support lateral branches.¹⁴ Prop stems are noticeably straighter than lignified aerial roots that have not reached the ground.

Aerial roots produced from branches immediately around the main trunk or mature stems, may attach themselves to

the trunk or stem first as surface roots, and after they lignify may fuse with the stem, creating highly complex surface rooting structures.

Gill separately defines “clasping” aerial roots that are exposed, but remain appressed to some surface, as seen in the root fan of a wall tree. Aerial roots can also develop from the callus tissue around a bark injury which has severed the phloem,¹⁵ and have been observed to bridge over sizeable trunk wounds (spanning > 500mm), ultimately closing the wound altogether.¹⁶

Currently there has been no systematic study of the conditions under which flexible aerial roots occur on mature Chinese banyan trees, their presence and distribution within the tree, their growth rates, and how these might relate

to environmental conditions. Although aerial roots have been observed to absorb water under certain conditions,¹⁷ the mechanism by which they do so has not been investigated, and how this might affect the growth of the aerial root has not been assessed.

The objectives of this research study were to understand the role of flexible aerial roots in the growth and development of mature Chinese Banyan trees in Hong Kong. Specifically, to investigate:

- the occurrence of aerial roots within the tree, i.e. their number and broad distribution within the structure of the tree,
- the development and elongation rate of aerial roots, in relation to environmental conditions,
- the morphological structure of the



Mature *Ficus microcarpa* trees growing in a paved public space in Lei King Wan, HK

aerial roots at different developmental stages, and their potential for absorbing water from the atmosphere.

From these, an understanding of the nature of aerial roots and their role in the growth of the tree can be formed, which may help explain the predominance of Chinese banyans in manmade landscapes in Hong Kong.

Materials and methods

Eight mature *Ficus microcarpa* trees were selected for the study by random number from a set of 52 trees growing in paved areas in public spaces in Lei King Wan, Eastern District. They had all been planted at approximately the same time and were some 30 years old. The trees were healthy and vigorous, and growing in identical environmental conditions. They ranged from 9.0 to 12.0m in height, with trunk diameters of 0.24-0.55m (DBH), and average canopy spread of 9.0-13.0m. Landscape maintenance workers reported that free-hanging roots were periodically cut (typically twice a year) at approx. 2.0m above the ground, to prevent them from reaching the ground, and to avoid nuisance to park users.

First, the distribution of aerial roots within each tree was mapped. As no methodology for mapping aerial roots has previously been established, the following was devised for this study. The point of origin for each cluster of free-hanging aerial roots was identified and its distance from the centre of the tree was measured. The diameter of the stem at the point of origin was noted, together with its position within the cross section of the stem (stems divided into sectional quarters). The biomass of each cluster was calculated as the product of the aggregate diameter of aerial roots within the cluster and their average length (measured at the start of the study). Results for the percentage of total aerial root biomass for the tree by: (a) distance from the centre of the tree; (b) stem size; and (c) position of point of origin on the stem, are given in Table 1.

Second, the rate of elongation of roots was measured in relation to atmospheric humidity. Selected sample roots from each tree were tagged, and a reference point was identified on the root (typically the lowest branching junction). The



length of the root below the reference point was measured every week over a period of twelve months. The difference between successive measurements represented the elongation over the time interval. Records of the mean weekly atmospheric temperature and relative humidity for the period were obtained from the Hong Kong Observatory.

Lastly, specimens of flexible aerial roots were collected from two of the trees. Samples were taken from both the tip and the central portions of the aerial roots. These were cut into 10mm sections and fixed in FAA (Formalin-Acetic Acid - Alcohol) for at least 24 hours. Sections were embedded in paraffin after dehydration, then cut with 8-10µm on a rotary microtome, and finally stained with safranin and fast green. The sections were observed under a light microscope and photos taken with Motic Images Advanced 3.2 software. The anatomical structure was observed and analyzed to determine the ability of the different portions of the aerial roots to absorb water.

Results

Distribution of aerial roots

Amongst the eight trees, the number of root clusters varied considerably between the trees (from 1 to 44), with an average of 13.7 clusters per tree. The aerial root biomass also varied. The tree with just one small cluster measured at just 0.025 ltrs, while the largest tree with

the densest pattern of aerial roots, had a biomass of 38.5 ltrs. The radial distance of the point of origin of the roots from the centre of the tree was categorized into 1.0m intervals. The tree canopy spread (expressed as a radius) varied between 4.5m and 6.5m, although with the close arrangement of trees, canopies tended to be elongated along one axis. Nearly two thirds (62.3%) of the aerial root biomass was within 2.0m of the trunk which broadly reflects the proportion of the branch biomass within this distance of the trunk. 12.6% of the aerial root biomass was beyond 4.0m

from the centre. The majority (76.5%) was found on stems between 100 and 250mm diameter. Only one tree had roots on a stem >250mm, but only three of the trees had branches of this size. Only a few roots were found on small diameter stems (0-50mm), although on one tree these accounted for more than 10% of the total. Aerial roots were predominantly (85.8%) growing from the underside of stems, with only a small percentage growing from the two sides of the stem, and very few (1.7%) from the top side.

	Low	High	Average
Number of aerial root clusters (no.)	1	44	13.7
Total aerial root biomass (ltrs)	0.025	38.5	12.6
Distance from the trunk (m)	Proportion of aerial root biomass		
0-1.0m	0%	66.0%	37.6%
1.0-2.0m	21.8%	100.0%	24.7%
2.0-3.0m	0%	28.8%	15.3%
3.0-4.0m	0%	18.4%	9.9%
4.0-5.0m	0%	12.1%	7.5%
5.0-6.0m	0%	8.6%	5.1%
Stem diameter (mm)	Proportion of aerial roots		
0-50mm	0%	10.2%	3.8%
50-100mm	0%	25.1%	12.4%
100-150mm	7.6%	100.0%	17.6%
150-200mm	0%	59.8%	28.4%
200-250mm	0%	49.6%	30.5%
250-300mm	0%	19.1%	7.3%
Position on the stem cross section	Proportion of aerial roots		
underside	76.9%	95.5%	85.8%
side	4.5%	19.2%	12.3%
top	0%	4.4%	1.7%

Table 1. Distribution and position of aerial roots of *Ficus microcarpa*

Aerial root growth

Aerial roots selected for measurement were all active. They started elongating in late February and stopped sometime in October. Rate of root elongation varied over the course of the year, with April to August being the most active months (Table 2). There was little or no growth between November and February. In averaged measurements across samples from all eight trees, root elongation was greatest in May, with an average monthly increase 244.9mm. Roots extended on average by 1154.3mm over the year.

Individually the rate of elongation of flexible aerial roots varied very greatly between different roots. One root might elongate only a few millimeters in a month while its immediate neighbor within the same cluster might put on a few hundreds of millimeters of growth. The maximum elongation of any single root (from all samples) in one day was 17.4 mm, (321.8mm in one month 1983.4mm across the year)

Anatomical structure

The new aerial root tip, in section (Fig. 1), shows one layer of exodermis cells covering a broad cortex, consisting of 9-12 layers of parenchyma cells, arranged closely. The endodermis is not well defined. The roots have 4-5 xylem groups. A broad parenchymatous pith occupies the centre.

The radial longitudinal section through the new aerial root tip (Fig. 3), shows three distinct regions: division zone, elongation zone and differentiation zone, as would be expected in a terrestrial root structure. But the root tip has no root hairs in the differentiation zone. In the elongation zone, roots begin secondary growth. In detailed section (Fig. 4), the cork cambium differentiates cork outwards and phelloderm inwards. The epidermis, as the outmost cell layer, could be shed as the tree grows and includes many lenticels. Most lenticels on the epidermis are transversely orientated.

The mature flexible aerial root, in section (Fig. 2), shows many xylem vessels. Medullary rays cross the xylem. The broad cortex has been sloughed off and the parenchymatous pith has become lignified. Lenticels are raised. The radial longitudinal sections through the mature aerial root (Figs. 5 and 6), indicate more xylem vessels and some scattered sclereids.

Discussion

The distribution of aerial roots was highly variable. Some trees had very few or no aerial roots at all, while immediate neighbours (in the same environmental conditions), might have many hundreds. Although the trees were of the same age, their size (reflecting past growth) was very different. No relationship was observed between size of tree and presence of aerial roots. Small trunk diameter trees were as likely to have aerial roots, (and the same volume of aerial roots) as large trunk diameter trees.

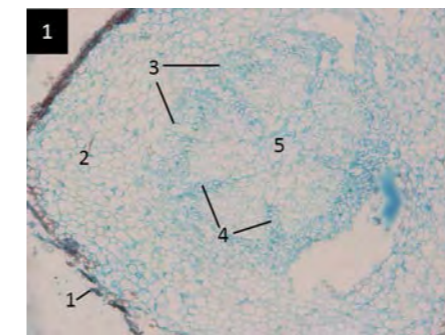


Fig. 1. Section of aerial root tip of *Ficus microcarpa*. X10. 1. Exodermis, 2. Cortex, 3. Endodermis, 4. Xylem, and 5. Broad pith.

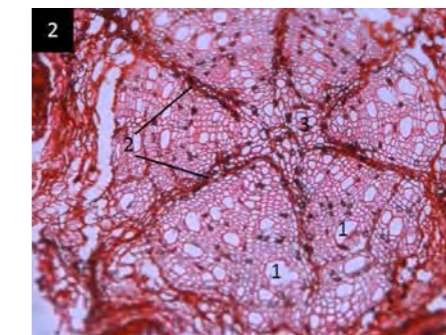


Fig. 2. Section of flexible aerial root of *Ficus microcarpa*. X10. 1. Xylem vessels 2. Medullary ray 3. Pith

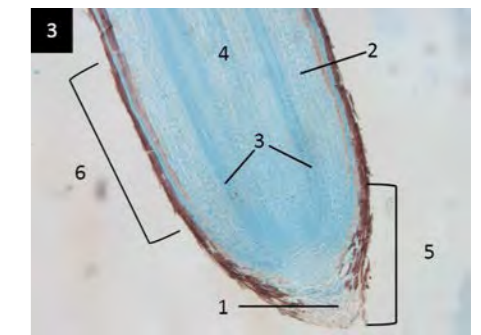


Fig. 3. Radial longitudinal section of an aerial root tip of *Ficus microcarpa*, (x5). 1. Root cap; 2. Cortex; 3. Xylem; 4. Pith; 5. Division zone; and 6. Elongation zone

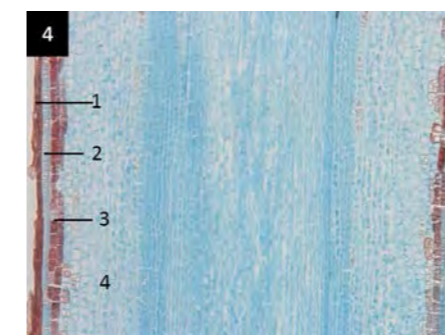
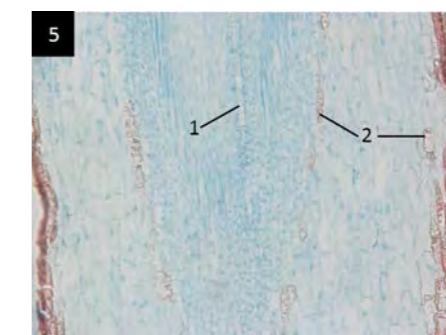


Fig. 4. Detailed radial longitudinal section of an aerial root of *Ficus microcarpa*, (x10). 1. Epidermis; 2. Cork; 3. Cork cambium; and 4. Phelloderm



Figs. 5 & 6. Detailed radial longitudinal section of a flexible aerial root of *Ficus microcarpa*, (two samples, x10). More xylem vessels exist in mature part of aerial root. 1. Xylem vessel; and 2. Sclereids.

The distribution of aerial root biomass within the canopy appeared to follow the distribution of branch and twig biomass within the canopy, with the greatest proportion being close to the trunk. Broadly, the distribution of aerial roots around the canopy was even, i.e. roots did not tend to grow just on one side.

Aerial roots were observed to originate from all sizes of branch, some as small as 25mm diameter. A higher proportion of aerial root biomass were growing from larger diameter branches, compared to smaller branches, but this was probably because of their relative age.

Aerial roots were initiated, very largely, from the underside of branches. This is likely to reflect the more humid conditions there, compared to the upper side, with rain water naturally draining to the lower side, and it being less exposure to sunlight. The fact that a few roots initiated on the sides and upper surfaces of branches suggests that initiation is not related to whether the wood is in compression or tension.

The pattern of growth in aerial roots was also highly variable, with some roots growing very vigorously alongside others, in the same conditions, that were hardly growing at all. Initiation of new roots and elongation of existing roots was clearly related to high levels of atmospheric humidity (relative humidity and rainfall). Substantial growth was recorded in the wet summer months, while no growth was observed during

the dry winter months. Rate of growth in individual roots was inconsistent. Some grew steadily throughout the summer, others would grow quickly then stop. Averaged maximum daily extensions for the five months June, July, August, Aril, and May ranged between 10.1 and 12.4. This is in line with measurements recorded in the Miami study.

With an average annual elongation of 1154.3mm, the vertical distance from the upper canopy to the ground, equated to several years growth. The rougher bark of the flexible roots, with raised lenticels, served to prevent them from fusing together (as was observed in the lignified aerial roots), allowing their free movement during this time.

It was noted that where a root tip stopped growing and had matured into a flexible aerial root structure, further growth tended to be initiated through side shoot rather than extension of the existing root i.e. roots divided (ramified) hence the multiple roots were usually found in clusters. Further, it was noted that aerial roots grew by elongation rather than by thickening, possibly to enable them to reach the ground as quickly as possible, while minimizing demand on energy resources.

Characteristics and ability to absorb water

The structural characteristics of aerial root tips and flexible aerial roots of *F. microcarpa* observed in this study can be compared with root tips, flexible aerial

roots and fine <2mm water absorbing terrestrial roots of *F. benghalensis* as described by Kapil and Rustagi¹⁸ (Table 2). The aerial roots of the two species are fundamentally alike, and both have distinct pith but lack of root hairs. These two characteristics make them more resemblance to stem than terrestrial roots. Kapil and Rustagi also note that the structure of aerial roots of *F. benghalensis* has greater resemblance to stems. More vessels exist in secondary xylem in *F. microcarpa* than *F. benghalensis*.

Root hairs, however, are just structures that substantially increase the absorbing surface of the roots, and the absence of root hairs would not prevent aerial roots from absorbing water. As Esau notes, hairless epidermal cells are capable of absorbing water.¹⁹

In terrestrial absorbing roots, water passes from the absorbing cells to the conducting tissues. Esau identifies that the notable features of this pathway are: the presence of abundant intercellular spaces in the cortex but the lack of such spaces in the vascular cylinder; together with the presence of a specialized endodermis between the cortex and vascular cylinder.

In new aerial root tips of *F. microcarpa*, cells in the cortex and vascular cylinder are closely arranged with few intercellular spaces. The endodermis is also not clearly defined. This would suggest that new aerial root tips cannot absorb water and conduct it to the xylem



Species	<i>Ficus microcarpa</i>		<i>Ficus benghalensis</i> (after Kapil and Rustagi 1966)		
	Aerial root (new)	Aerial root (mature)	Aerial root (new)	Aerial root (mature)	Terrestrial absorbing root
Root Hair	Absent	Absent	Absent	Absent	Present
Cortex	9-12 cells thick	Sloughed off	20-25 cells thick	Sloughed off	8-15 cells thick
Endodermis	Poorly defined	Poorly defined	Poorly defined	Poorly defined	Better defined
Xylem strands	4-5 groups	Absent	Usually 5-7, occasionally 10-15	Absent	Usually 3 or 4, rarely up to 7
Pith	Distinct and board	Lignified	Distinct and large	Lignified	Absent or scanty
Secondary vascular tissues	Absent	Less of parenchyma, many vessels, well developed medullary rays	Absent	Many fibres, less of parenchyma, fewer and smaller vessels, poorly developed medullary rays	Few fibres, more of parenchyma, numerous and large vessels, well developed medullary rays
Periderm Lenticels	Well developed Many	Well developed Many	Well developed Many, raised, transversely oriented	Well developed Many	Poorly developed Scanty, scattered

Table 3. Characteristics of aerial roots of *Ficus microcarpa* and *Ficus benghalensis*

in the same way as terrestrial roots.

In mature aerial roots of *F. microcarpa*, existing vessels serve as conduits. Water is actually drawn up from roots and transported to branches and leaves through vessels. The hanging aerial roots can be likened to branches of their parent stem. Water moves from branch to aerial roots through vessels in the flexible aerial roots.

The role of radially orientated ray tissue is the uptake of water through the outer surface of twigs²⁰. The well-developed rays observed in transection of the

flexible aerial roots of *F. microcarpa* might act in a similar way, allowing uptake water and movement to the conducting vessels.

In terrestrial roots of dicotyledonous plants, water usually flows from high soil water potential to low root water potential, and is then transported up the stem and leaf by evaporation. The reverse may occur if the water potential gradient is reversed.²¹ Some experiments show the water can flow into limbs under external pressure through xylem vessel of cut limbs.^{22,23} The external pressure plays an important role in uptaking water through leaves and branches. Aerial roots of other plant types such as epiphytic orchids have been shown to be anatomically adapted to absorb water.^{24,25} Epiphytic orchids uptake water and nutrients efficiently via a multilayered velamen arising from the epidermis.^{26,27} But aerial roots of *F. microcarpa* do not have such anatomical features.

Liu (2011) observed that aerial roots of *F. microcarpa* have CO₂ and water vapor exchange functions, and concluded that new aerial roots were active in CO₂ intake and H₂O release, and flexible aerial roots had weak respiration and transpiration activity. Aerial root tips could only absorb water in very high (almost 100%) relative humidity. In flexible aerial roots,

CO₂ intake was reduced but they could absorb water like a sponge/activated carbon in at least 75% relative humidity conditions.

Conclusion

The occurrence and distribution of aerial roots in *F. microcarpa* trees, and the initiation and elongation of aerial roots was highly variable. Trees growing in identical conditions often had very different aerial rooting patterns. Even in very wet conditions, some roots grew, others did not.

When aerial roots did grow, it was at times of the year, in environmental conditions, and at locations within the canopy and on the originating branch, that were associated with wet atmospheric condition. This supports the common belief that their presence and growth is linked to water availability.

From the detailed study of the cellular structure of the aerial root tips, however, it was clear that the secondary vascular tissues and cells are not closely arranged, and they do not have structures to absorb water. The more mature, flexible aerial roots were observed to have structures (lignified surface tissues, many vessels and medullary rays) that would allow the absorption and movement of some water, but as Liu²⁸



observed, this only occurred under high levels of atmospheric humidity. As roots were observed to be growing throughout periods where relative humidity was relatively low (70-80%), rapid elongation of the root tips is most likely to be based on water (and nutrients) drawn up from terrestrial roots and conducted along branches. The presence of many conducting vessels and well developed medullary rays in the cellular structure of flexible aerial roots suggest that their function is the transportation of water rather than its absorption from outside.

The link between the aerial root growth of Chinese Banyans and wet conditions, therefore, may be associated with their ability to take advantage of wet ground conditions, i.e. uptake water through their terrestrial roots and move it quickly within trunk and branch structures, rather than an added capacity of absorbing water through the aerial roots themselves.

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*Lignified aerial roots on *Ficus elastica*, on Lugard Road, The Peak*