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Structure and function of dimorphic prop roots in *Piper auritum* L.[1]

Nancy Greig and James D. Mauseth[2]
Division of Biological Sciences and Department of Botany,
University of Texas, Austin, TX 78712

ABSTRACT

GREIG, N. AND J. D. MAUSETH (Division of Biological Sciences and Department of Botany, University of Texas, Austin, TX 78712). Structure and function of dimorphic prop roots in *Piper auritum* L. Bull. Torrey Bot. Club 118: 176–183. 1991.—Field observations on growth form and laboratory observations on structure were made of the root systems of *Piper auritum* L. (Piperaceae), a small weedy tree colonizing disturbed sites in humid lowland areas of the neotropics. Adventitious roots (prop roots, stilt roots) of *P. auritum* are dimorphic, with differences in form, structure, and orientation between above-ground and subterranean portions. Above ground the root is wide (mean diameter 1.78 cm), unbranched, and has numerous protoxylem poles ($\bar{x} = 42$) around a broad pith (mean diameter 0.72 cm). Upon penetration of the soil the root forms several branch roots, some of which grow vertically and provide anchorage and absorption, while others grow horizontally and produce new shoots (root suckers). Both subterranean types differ from the above-ground root and from each other. Horizontal roots are narrowest (1.01 cm diameter) with the fewest protoxylem poles (9) around the narrowest pith (0.04 cm diameter). Vertical subterranean roots have intermediate values (root diameter 1.06 cm; 22 protoxylem poles; pith diameter 0.44 cm). Vessels are on average wider in the xylem of the horizontal root portions (36 to 84 μm radius) than in either above-ground or vertical subterranean parts of the roots (24 to 60 μm and 36 to 72 μm in radius, respectively), and a greater percentage of total conduction is performed by wider vessel size classes in horizontal sections. Fast-growing vegetative shoots produced from the horizontal portions of the roots result in large stands of *P. auritum* and allow the species to persist in successional areas no longer favorable for germination of its light-dependent seeds.

Key words: *Piper auritum,* aerial (prop or stilt) roots, adventitious roots, vegetative propagation, root suckers, dimorphic roots, vessel conducting capacity.

Prop or stilt roots are aerial, adventitious roots usually produced on the lower portion of a shoot (Gill 1969; Gill and Tomlinson 1975; Jeník 1978). These roots eventually make contact with the substrate and provide anchorage in soft or shallow soils; they may also augment the plant's supply of water and nutrients (Jeník 1978). Unusual in temperate plants (except for *Zea mays*), prop roots occur in diverse groups within both monocots and dicots in humid tropical areas. Previous studies of aerial roots have noted their unusual structure and form, particularly the dramatic changes in external and internal structure once they enter the soil (e.g., Turner 1934; Kapil and Rustagi 1966). However, few authors have attempted to relate form and function in these roots. An exception is the work of Gill and Tomlinson (1969, 1971, 1977), which describes the dimorphic nature of red mangrove (*Rhizophora mangle*) aerial roots and discusses these features in relation to the functional role of these roots. In this paper we present observations on the anatomy and form of the prop roots of the tropical plant, *Piper auritum,* in relation to their functional roles.

Materials and Methods. STUDY ORGANISM AND FIELD SITES. *P. auritum* L. (Piperaceae) is a small, weedy tree with a widespread distribution in the American tropics, ranging from Mexico to Colombia in highly disturbed areas (roadsides, forest edges, and large treefall gaps) in lowland rainforest (Burger 1971, 1983). Its seeds are bat-dispersed (Janzen 1978) and bird-dispersed (B. Loiselle personal communication; Palmeirim *et al.* 1989), and they germinate and grow only in areas of high insolation (Vázquez-Yanes and Smith 1982). A typical heliophile spe-

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cies, *P. auritum* is extremely fast growing; it is essentially an overgrown herb with a large core of pith even in large woody specimens. Secondary growth is initiated within the first year when the plant is two to three meters tall. Plants reach sexual maturity in less than two years and probably live only about 5 years (N. Greig personal observation).

Observations on the growth habit of *P. auritum* were made in Corcovado National Park in southwestern Costa Rica and at the Organization for Tropical Studies' field station La Selva, in northeastern Costa Rica. Both areas are preserves of lowland tropical rainforest, receiving four or more meters of rain annually (see Hartshorn (1983) for site descriptions). At both sites *P. auritum* occurs typically in early successional stages of areas in regeneration, along with other heliophile species such as *Cecropia* and *Heliconia*.

ANATOMICAL STUDY. Field-collected material was cut into pieces and fixed in FAA. This material included above-ground portions of the prop root, vertical and horizontal subterranean portions of the same roots, and several small adventitious shoots. Younger stages of adventitious roots were obtained from *P. auritum* plants grown from seed in a greenhouse in Austin and also preserved in FAA. Sections were embedded in paraffin, cut at 10 μm on a rotary microtome, and stained with safranin and fast green. Macerations of above ground and subterranean root tissue were also prepared. Vessel diameters were measured with an ocular micrometer, then the fourth power of the radius, r^4, was calculated as an estimate of the conducting capacity of each vessel according to the Hagen-Poiseuille law (Mauseth 1988; Zimmermann 1983). Vessel radius classes 6 μm wide were used in presenting the results.

Results. MORPHOLOGY OF PLANTS AND ROOTS. Mature *P. auritum* plants average about 5 meters in height, with a mean DBH of approximately 8 cm. The leaf-bearing branches never become woody and those lower on the trunk are shed quickly as the tree grows in height, so that mature specimens have a long bare trunk with an umbrella-like crown of branches bearing the very large, thin leaves (35 × 25 cm). Occasional plants branch epicormically if growing at an angle to the ground, producing a forked trunk, but most plants have only one trunk. *P. auritum* flowers and fruits throughout the year; each infructescence, a long, pendant spike (30 cm × 1 cm), contains over ten thousand minute (0.14 mg) seeds.

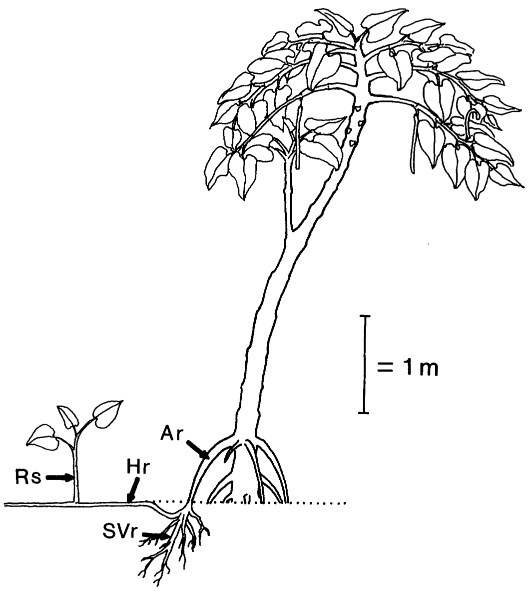


Fig. 1. *Piper auritum* habit. Ar = aerial root; SVr = subterranean vertical root; Hr = horizontal root; Rs = root sprout.

Almost all *P. auritum* individuals of over 3 cm DBH were found to have adventitious prop roots. These arise on the lowermost three or four nodes of the trunk and arch downward toward the ground as they elongate (Fig. 1). Several roots may arise at a single node, and large plants have 15–20 or more prop roots. Little secondary growth occurs until the root reaches the ground. Like the aerial roots of red mangrove and of many other tropical species (Gill 1969; Gill and Tomlinson 1975), these roots do not branch until they come in contact with the soil, unless the growing tip is injured. No root cap is present, but uninjured *P. auritum* root tips are sometimes coated with clear mucilage that forms a large droplet over the meristem. Injury to the above-ground root tips of *P. auritum* is common, and usually results in tip abortion, probably caused by fungal infection; the tips in such cases are black and appear to have rotted. Several lateral roots may emerge from just behind these aborted tips.

As it penetrates the soil, the previously unbranched prop root gives rise to three or more branch roots (Fig. 1). Some of these grow downward, are relatively short (<60 cm) and tapered, have numerous fine lateral rootlets, and probably function in absorption and anchorage. Other

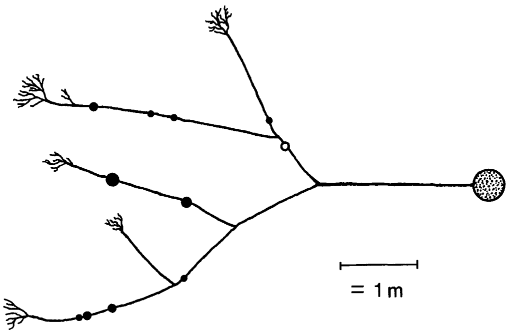


Fig. 2. Form of spread in horizontal extensions of the prop roots in *Piper auritum*. Filled dots represent root sprouts, size indicating size of sprout. Open dot represents scar where a sprout grew formerly. Large stippled dot represents the parent source plant (dots are not to scale with roots). Only one horizontal root is followed; there may be several radiating out from the parent plant.

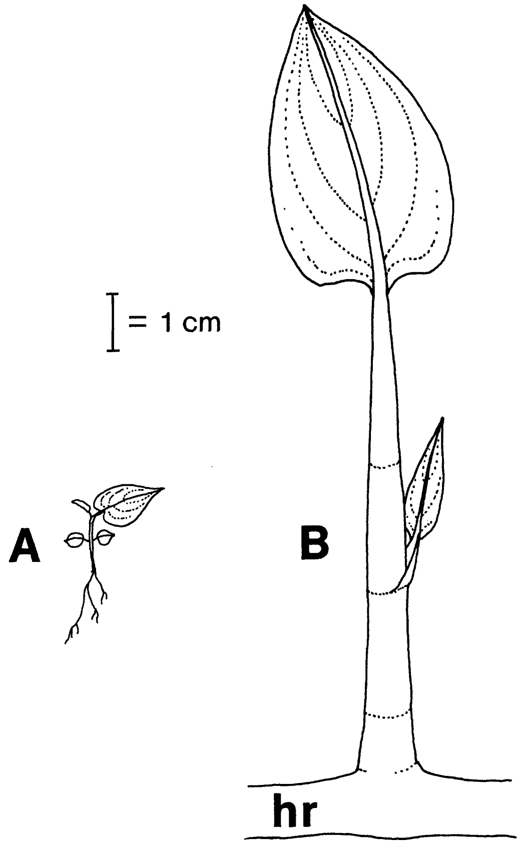


Fig. 3. A. Seedling, and B. root sprout of *Piper auritum*. Hr = horizontal root coming from adult plant.

branch roots reorient and grow horizontally at the soil surface, often becoming completely exposed or covered by a shallow layer of soil or leaf litter. The ground under a group of *P. auritum* plants may be criss-crossed by a number of these long sinuous roots. Some horizontal roots may extend for at least 9 meters from their point of origin. These roots branch only occasionally along their length, although they may be highly branched terminally (Fig. 2).

The above-ground portion of the prop roots undergoes considerable secondary thickening and may be 2–3 cm in diameter and very woody in large *P. auritum* specimens. The underground portion of these roots also undergoes secondary thickening. Vertical portions branch abundantly and taper rapidly. The horizontal portion may become nearly 2 cm thick in some specimens, but remains more flexible than its above-ground or vertical subterranean counterparts.

Adventitious shoots (root suckers) arise at irregular intervals from the horizontal roots (Fig. 1). Normally, buds are produced on roots at or near the soil surface, but occasionally we found root suckers growing as deep as 15 cm below ground. These shoots grow quickly and eventually produce their own adventitious roots. They appear to be produced randomly; the oldest shoots are not necessarily those on portions of the root closest to the parent plant (Fig. 2). Almost all juvenile *P. auritum* plants found at the study site could be traced to horizontally growing subterranean portions of prop roots from large plants in the vicinity. Very few wild plants were found that were unequivocally derived from seed, and these were found scattered in recently disturbed, sunny areas—a garden clearing and large treefall gaps in the forest, for example—usually with no large *P. auritum* individuals in evidence.

Seedlings can be distinguished from root-derived plantlets morphologically, at least in early stages (Fig. 3). Seedlings have small, ephemeral cotyledons, have extremely short internodes (2 to 5 mm), and produce their first leaves when only a few millimeters tall. All leaves, independent of size, have both petiole and blade. A taproot is present. Adventitious shoots, on the other hand, do not have cotyledons, and have much thicker stems and longer internodes (5 to 50 mm). Being buds of the parent root, they initially have no roots, and never produce a tap root; all of their roots are adventitious. The first few leaves of adventitious shoots are often scale-like, consisting of petiole only or petiole with a very reduced blade.

ANATOMY OF THE ROOTS. Table 1 shows several structural differences between above-ground

Table 1. Root diameter (cm), pith diameter (cm), and number of protoxylem poles in three root types ($\bar{x} \pm$ SE; range in parentheses).

Root position	Root diameter	Pith diameter	Protoxylem poles	N
Above ground	1.78 ± 0.13 (1.10–2.58)	0.72 ± 0.06 (0.33–1.04)	42 ± 3.2 (18–52)	12
Subterranean vertical	1.06 ± 0.29 (0.61–2.19)	0.44 ± 0.15 (0.13–1.03)	22 ± 2.3 (16–29)	5
Horizontal	1.01 ± 0.14 (0.59–1.64)	0.04 ± 0.01 (0.02–0.07)	9 ± 0.6 (7–13)	8

vertical, subterranean vertical, and horizontal portions of the prop root system. Mean root diameter is greatest in above-ground portions. Pith is also broadest in above-ground portions, but is wide in subterranean vertical portions as well. Narrowing of the pith in subterranean vertical branches is proportional to root width; i.e., in above-ground and below-ground root sections the proportion of pith to root diameter is approximately the same (0.40). Pith is narrow in horizontal portions, and the proportion of pith to total diameter is significantly less (0.04) than in the other two portions (ANOVA, $F = 75.976$, $P < 0.0001$; data were arcsine square root transformed to meet the assumptions of analysis of variance). The photograph (Fig. 4) of a bisected above-ground and horizontal root clearly illustrates the dramatic differences in their structure.

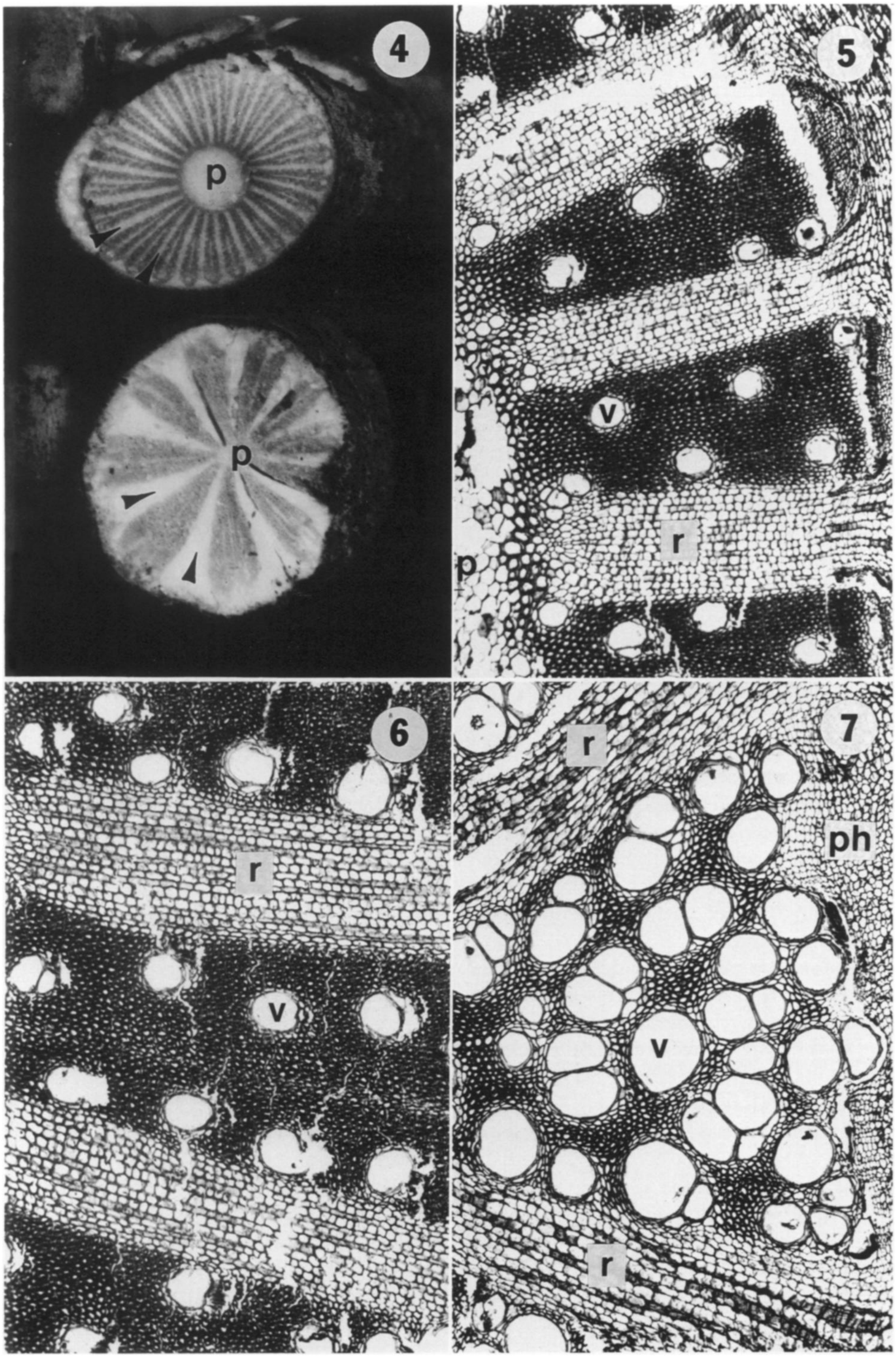
Number of protoxylem poles also differs among the three root regions (Table 1). Above-ground the roots have an average of 42, vertical subterranean branches have 22, while horizontal portions have only 9 protoxylem poles. Again, the ratio of protoxylem poles to total root diameter is approximately equal in both above-ground and subterranean vertical root sections (≈24 per cm diameter), while the ratio is much less in horizontal portions (≈9 per cm diameter) (ANOVA, $F = 24.171$, $P < 0.0001$; data were log transformed to meet the assumptions of analysis of variance).

The vascular tissues in the above-ground portion of the prop root system are located far from the center of the organ, and form a cylinder around the wide pith. Upon formation of a cambium in this section, ray parenchyma is formed opposite protoxylem poles, and axial secondary xylem and phloem are deposited opposite protophloem poles. Subsequent growth in this portion of the root results in a stem-like configuration, a cylindrical stele around a pith core (Fig. 4, upper). However, there are no scattered vascular bundles in the pith of the prop root, as there are in the stems of *P. auritum,* and in stems of other Piperaceae (Metcalfe and Chalk 1950). The configuration of the vascular tissues is similar in subterranean vertical portions. In horizontal branches of the root, however, protoxylem poles occur much closer to the center of the organ; the broad sections of secondary xylem, separated by broad rays, radiate out from the center (Fig. 4, lower).

Rays are wide in all three sections, but are widest in horizontal roots. In above-ground and subterranean vertical root sections, ray parenchyma has thick, lignified walls; ray parenchyma is not lignified in horizontal roots.

Vessels in the secondary xylem of all three root sections have scalariform pitting, and simple perforation plates. In the above-ground root, vessels are few and narrow, and are embedded in a dense matrix of fibers (Fig. 5). Secondary xylem in below-ground vertical roots is similar (Fig. 6). Horizontal roots have abundant, very wide vessels, clearly visible to the naked eye. Fibers in horizontal roots are correspondingly reduced in number and have thinner walls than in the other root categories (Fig. 7).

Figure 8 shows the distribution of vessels in different size classes (vessel radius) for three sample roots. Several roots were examined; those illustrated here are representative. In this particular above-ground root, vessels range from 24 to 60 μm in radius. The broadest vessels are not especially numerous, making up only about 15% of all the vessels present, but because of their very great r^4 value (Fig. 9), they account for about 35% of the total conducting capacity. (The fourth power of the radius of conducting cells, r^4, can be used to compare relative conducting capacities.) The most numerically abundant size classes were comprised of vessels with radii of 48 or 54 μm; about 43% of all vessels of this root fall into this size range. Despite their narrower diameter, which results in a lower r^4 value for each cell, there are so many cells in these classes that they account for over 50% of total conducting capacity. Vessels of 36 μm radius and less have such



Figs. 4–7. Structure of the root in *Piper auritum*. p = pith, ph = phloem, r = ray, v = vessel. — 4. Photograph of a bisected above-ground prop root (upper) and horizontal root (lower) of *Piper auritum*. Note the broad pith in the above-ground root, and the wide rays in the horizontal root. Arrows indicate rays in this figure. — 5. Cross-section of the above-ground portion of a prop root of *Piper auritum* (×58). — 6. Cross-section of a subterranean vertical root of *Piper auritum* (×58). — 7. Cross section of the horizontal (subterranean) portion of the root system of *Piper auritum* (×58). Note the large diameter of many vessels. Note also that the fibers in this part of the root have thinner walls than do fibers in the above-ground and subterranean vertical roots.

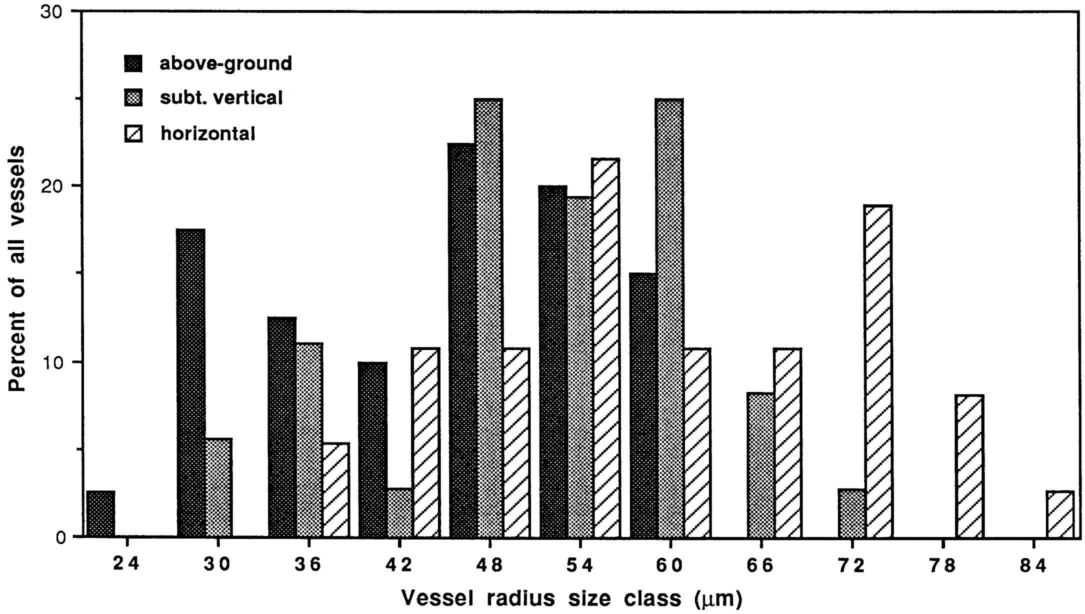


Fig. 8. Distribution of vessels (shown as percent of total vessels per root) among different vessel size classes (vessel radius) in representative above-ground, subterranean vertical, and horizontal portions of the root system in *Piper auritum.*

a low r^4 value and are so scarce that they contribute less than 7% of total conducting capacity of the above-ground portion of prop root.

Vessels in the subterranean vertical root of Figs. 8 and 9 are slightly larger, ranging from 30 to 72 μm in radius. The vessel size classes from 48 to 60 μm radius are both most abundant and account for about 70% of total conducting capacity.

Vessels in the horizontal roots are much wider than those in the vertical portions, either above-

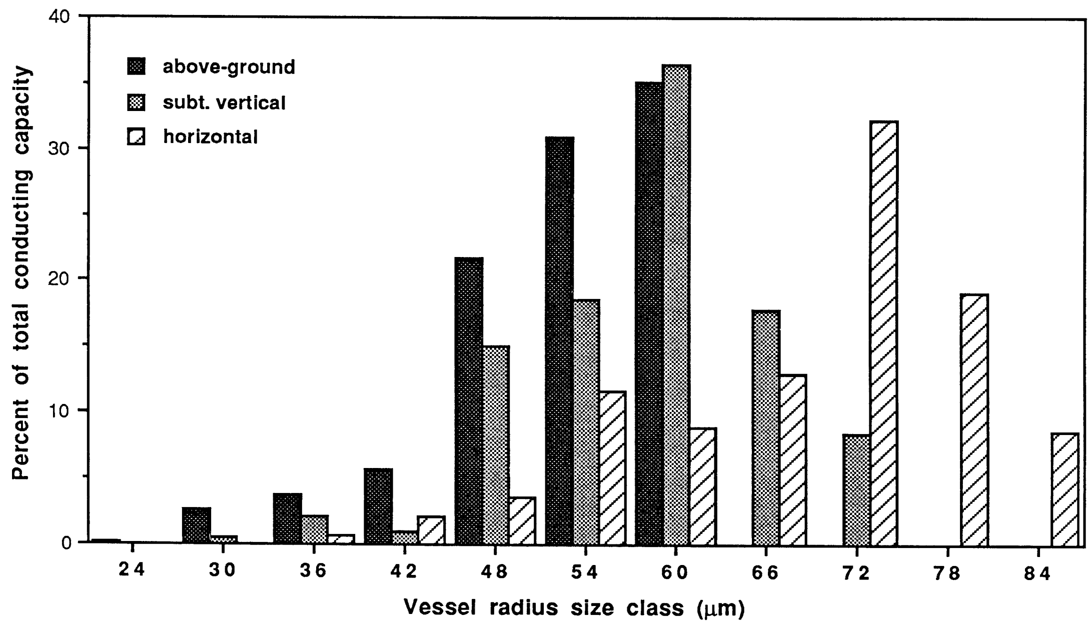


Fig. 9. Percent of total conducting capacity provided by vessels of different size classes in representative above-ground, subterranean vertical, and horizontal portions of the root system in *Piper auritum.*

or below-ground, with radii ranging from 36 to 84 μm; over 10% of all vessels have a radius greater than 78 μm (Fig. 8). Compared to the other root types, vessels in this horizontal root fall into a broader range of size classes, and a larger number of different vessel size classes contribute significantly to the root's conducting capacity (Fig. 9).

Phloem is particularly abundant in the horizontal root (Fig. 7). All root portions have a multiseriate band of persistant cortex outside the stele; the cortex is broadest in horizontal roots. Otherwise the cortex is unremarkable and similar in all root portions. Small groups of sclerified cells, about twice as long as wide, form a punctuated ring in the outer cortex in all three root types.

Mucilage canals are abundant throughout both shoot and root system in *P. auritum*. In roots, mucilage canals occur in the pith, in phloem rays, and occasionally in xylem rays. A single large mucilage canal may occupy the entire, narrow pith in horizontal branches of the prop root.

Discussion. Aerial root systems described to date in the literature serve as anchoring, conducting, and, *Rhizophora mangle* (Gill and Tomlinson 1977) and *Prestoea montana* (Arecaceae) (Frangi and Ponce 1985), as aerating organs, but have no role in regeneration (Gill & Tomlinson 1969). In contrast, the prop root system in *P. auritum* serves as a propagating/regenerating organ as well as providing anchorage and conduction. Propagation from roots is well-documented in a wide range of temperate taxa (Peterson 1975), though not usually attributed to specialized roots. The adventitious shoots produced on the horizontal roots of *P. auritum,* perhaps because of nutrients provided to them from adult plants via the connecting root, can grow and survive in areas where seedlings could not, e.g., sites in succession where light levels are lower than in new disturbances. Vegetative propagation is widespread among neotropical *Piper* (Gartner 1989; N. Greig in preparation), but most species regenerate from fallen stems or leaves or from adventitious shoots produced at the base of the trunk (N. Greig personal observation). Of 37 *Piper* species at Corcovado National Park, *P. auritum* is the only species to propagate from roots. At La Selva, *P. pseudobumbratum* C. DC. shares the root-cloning habit, but none of the 48 other *Piper* species at this site was found to propagate in this manner. *P. pseudobumbratum* and *P. auritum* are similar in growth form and stature, but the former occurs in primary forest and in small gaps, while *P. auritum* is confined to large, sunny disturbances.

Janzen (1978) suggested that "large even-aged stands" of *P. auritum* are due to bat dispersal of large numbers of seeds to concentrated areas. Evidence from our field study indicates that very few *P. auritum* individuals establish from seed, but plant numbers are increased via vegetative propagation within an area once a plant is established. Since *P. auritum* grows extremely rapidly (up to 3 m a year; N. Greig unpublished data), what appears to be an even-aged stand probably consists of one or a few older plants and their vegetatively-produced offspring.

The large droplet of mucilage over the meristem in young aerial roots of *P. auritum* presumably protects the growing tip and keeps it moist (cf. Mollenhauer 1967). A similar mucilage coating has been found on the tips of other aerial roots, for example *Hedyosmum arborescens* (Gill 1969), and on the adventitious roots of such epiphytes as *Cattleya* orchids (Mollenhauer 1967) and *Monstera* (N. Greig personal observation).

The anatomy of the adventitious aerial roots of *P. auritum* is unusual when compared to that of other dicot roots. Most dicot roots have two to several protoxylem poles and no pith. The above-ground portions of the aerial roots of *P. auritum,* like those of *Rhizophora mangle,* however, have numerous protoxylem poles in a ring surrounding a large pith, and thus more closely resemble the adventitious roots of some monocots, which are also polyarch and contain pith (Fahn 1982; Mauseth 1988). However, there is no secondary growth in the roots of these monocots. Below ground the parallels between the roots of *P. auritum* and those of *Rhizophora* or monocots are less striking. In *R. mangle* the subterranean portions of aerial roots, like the aboveground portions, have numerous protoxylem poles and abundant pith. The aerenchymatous tissue in these white and spongy organs has an obvious role in gas exchange in the waterlogged substrate where *R. mangle* occurs (Gill and Tomlinson 1977). In *P. auritum,* the horizontal roots have fewer protoxylem poles and less pith. The very wide vessels and abundant phloem may provide efficient transport of water and nutrients to adventitious shoots formed along the horizontal roots.

The diameter of a vessel is related not only to the ease of water movement through it but also to the ease of cavitation: wider vessels can cavitate and form an embolism, or "air bubble," more easily than can a narrow vessel. Xylem that has a wide range of vessel diameters conducts almost exclusively through the broadest vessels whenever water is freely available in the soil, but in times of water stress, the wide vessels may cavitate and the transpiration tension is shifted to water in narrower vessels, causing the latter to conduct more rapidly. If all vessels were of the same diameter, all might fail simultaneously (Zimmermann 1983).

Because of root pressure, cavitation is usually not a problem for subterranean roots. Their water is under pressure, not tension; only at a height of several centimeters above soil does transpiration tension take over from root pressure (Carlquist 1975; Mauseth 1988). The root system xylem of *Piper auritum* appears to be well-adapted to its environment: the aerial prop roots, which are not protected by root pressure, have the narrowest vessels. Vessel slenderness provides some resistance to cavitation (Zimmermann 1983). Also, these above-ground portions of the roots have the most rapid secondary growth, and any cavitated vessels can be replaced by newly formed vessels each season. In horizontal roots of most species, cavitation due to transpiration is not a danger, but these roots in *P. auritum* seem to be mostly conduits from absorptive root tips to transpiring adventitious shoots, which may be separated by many meters.

The dynamics of water flow through this complex root system would be a good subject for future field studies. *P. auritum* grows in sunny habitats and has large, non-xeromorphic leaves, which wilt easily (Chiariello *et al.* 1987). On a warm clear day during the dry season, transpiration could possibly exceed the horizontal roots' conducting capacity and cavitation might occur in the very widest vessels. If so, conduction might shift to the narrower vessels. But unlike vessels in vertical, aerial roots, it seems theoretically possible that low horizontal vessels could be refilled with water, at night or after a rain, so a large amount of secondary growth would not be necessary to replace them. If this does occur, these roots could remain narrow, with only a small amount of secondary growth after the first year.

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