# The Development of Buttresses in Queensland Trees.

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Plates I.-VI. Text-figures 1-7.

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CONTENTS.



## 1.—GENERAL REMARKS.

One of the most impressive features of luxuriant rain forests is the wide buttresses or plank buttresses which radiate from the bases of the stems of certain species of trees. These buttressed trees abound in dense rain forests in tropical and subtropical parts of the world. A. R. Wallace[1] records them in the rain forests of the Amazon, T. F. Chipp[2] in the West African rain forests, A. F. Schimper[3] in the monsoon forests of Burma, H. N. Whitford[4] in the rain forests of the Philippine Islands, J. H. Maiden[5] in the rain forests of Northern New South Wales, and the writer[6] in the rain forests of Southern Queensland. They are also known to occur in the forests of Java, Borneo, and New Guinea.

From the foregoing statements it is evident that buttressed trees are found in all the continental land masses, which extend into the tropics, and in several of the large tropical islands. As the phenomenon is so widely distributed, it constitutes a problem of considerable biological interest, and it is probable that a number of the observations and conclusions derived from an investigation of buttressed trees in Queensland will be found to be applicable also to examples in other parts of the world.

## II.—A Comparision of the Distribution of Buttressed Trees in the Queensland and Extra-Australian Floras.

The occurrence of buttresses does not appear to have received general attention. In consequence, records of their distribution in Australia and abroad are very incomplete. The following table shows the distribution of buttressed trees in the Queensland flora and several extra-Australian floras so far as known to the writer. The extra-Australian portion of the table was compiled chiefly from the works of Schimper[7] and H. N. Ridley[8], and from those of Chipp and Whitford, which are referred to in the preceding section.

| Queensland Buttressed Trees. | Extra-Australian Buttressed Trees. |
|---|---|
| Moraceæ—<br>*Ficus* spp. Fig Trees. | Moraceæ—<br>*Ficus* (Tropical Asia).<br>*Cecropia* (Tropical America).<br>*Musanga* (West Africa). |
| Lauraceæ—<br>*Endiandra discolor*, Domatia Tree. | |
| Cunoniaceæ—<br>*Weinmannia Benthami*, Pink Marara.<br>*Weinmannia lachnocarpa*, Marara.<br>*Ackama Muelleri*, Rose-leaf Marara. | |
| | Leguminosæ—<br>*Cynometra* (West Africa).<br>*Piptadenia* (West Africa).<br>*Parkia* (West Africa). |
| Meliaceæ—<br>*Dysoxylum Pettigrewianum*, Spur-wood, Satin-wood<br>*Dysoxylum* sp. Red Bean.<br>*Cedrela toona* var. *australis*, Red Cedar. | Meliaceæ—<br>*Dysoxylum* (Java).<br>*Khaya* (West Africa).<br>*Entandrophragma* (West Africa). |
| Anacardiaceæ—<br>*Euroschinus falcatus*, Ribbon-wood. | Anacardiaceæ—<br>*Dracontomelon* (Philippine Ids.). |
| Elæocarpaceæ—<br>*Echinocarpus Woollsii*, Carribin.<br>*Elæocarpus grandis*, Quandong.<br>*Elæocarpus obovatus*, Blue-berry Ash.<br>*Elæocarpus Kirtonii*, Mountain Beech. | |
| | Malvaceæ—<br>*Bombax* (India, West Africa).<br>*Eriodendron* (West Africa).<br>*Triplochiton* (West Africa). |
| Sterculiaceæ—<br>*Tarrietia argyrodendron*, Booyong, Hickory, Crow's Foot Elm.<br>*Tarrietia actinophylla*, Black Jack. | Sterculiaceæ—<br>*Sterculia* (East Indies).<br>*Tarrietia simplicifolia* (Malay Pen.)<br>*Tarrietia utilis* (West Africa). |

| Queensland Buttressed Trees. | Extra-Australian Buttressed Trees. |
|---|---|
| | Dipterocarpaceæ—<br>*Shorea* (Malay Peninsula).<br>*Anisoptera* (Malay Peninsula).<br>*Dipterocarpus* (Philippine Ids.).<br>*Lophira* (West Africa). |
| Rhizophoraceæ—<br>*Ceriops Candolleana*, a Mangrove. | Rhizophoraceæ—<br>*Ceriops Candolleana* (India).<br>*Anopyxis* (West Africa). |
| | Combretaceæ—<br>*Terminalia* (West Africa). |
| Myrtaceæ—<br>*Eugenia Francisii*, Giant Watergum.<br>*Eugenia Luehmanni*, Small-leaved Watergum.<br>*Syncarpia subargentea*, Giant Iron-wood. | Myrtaceæ—<br>*Eugenia* (Philippine Ids.). |
| | Verbenaceæ—<br>*Vitex* (East Indies). |
| | Bignoniaceæ—<br>*Spathodea* (Tropical Africa). |

The Natural Order Dipterocarpaceæ, which comprises a large number of important trees widely and often densely distributed in rain forests of the Indo-Malayan region, is not represented in Australia.

### III.—The Distribution of Buttressed Trees in the Queensland Flora.

The occurrence of buttresses in the more southern or sub-tropical rain forests of Queensland is more particularly under consideration, as the Northern rain forests of the State have not as yet been thoroughly investigated.

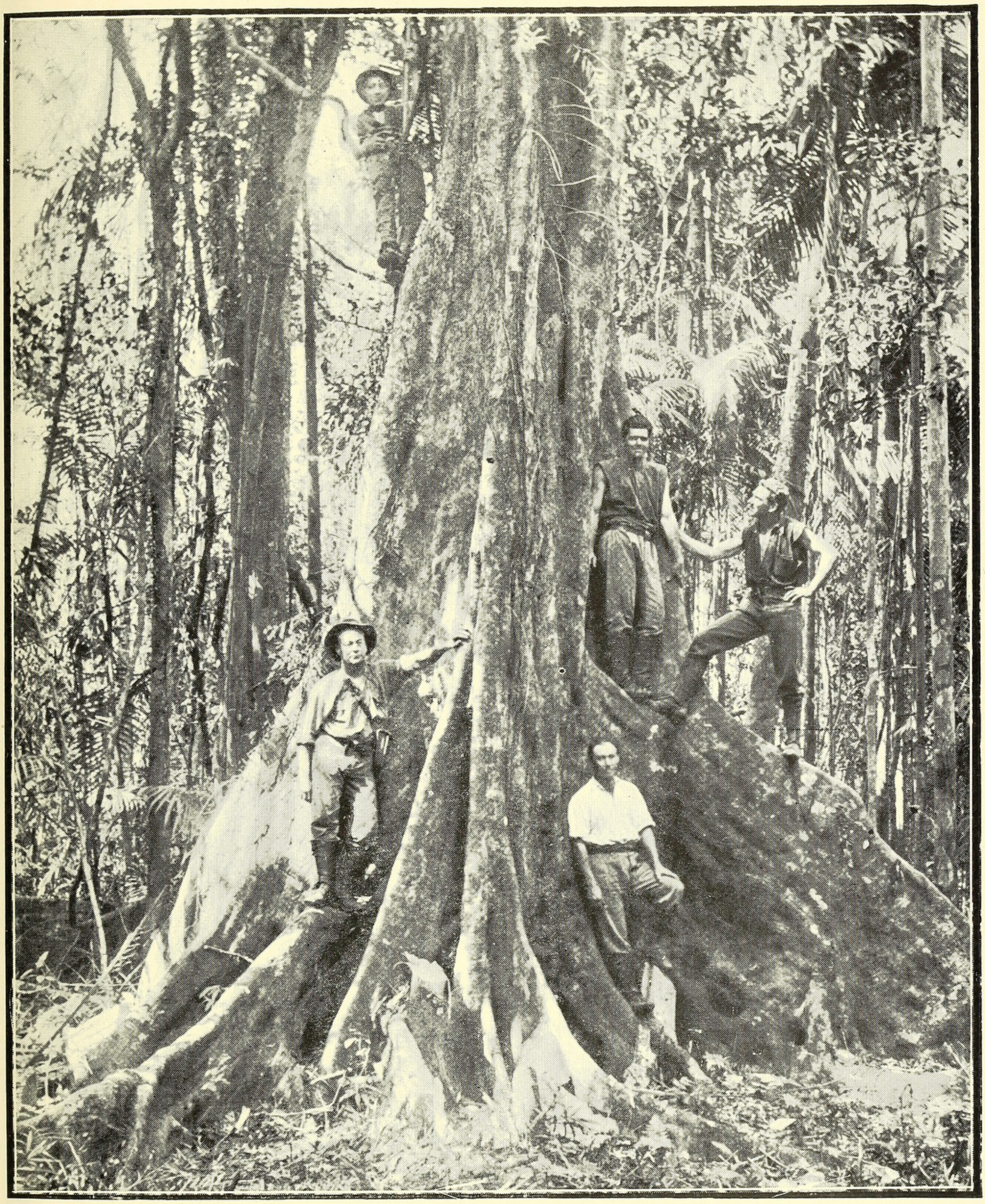
The Queensland buttressed trees, with the exception of *Ceriops Candolleana*, which is a mangrove on the shores of the East Indies, tropical Asia and Africa, are rain-forest species. The majority of them belongs to genera which attain a relatively high numerical development of species in a region comprising India, tropical Eastern Asia, the East Indies, and New Guinea. Examples of these genera are:—*Tarrietia, Echinocarpus, Elæocarpus, Dysoxylum, Euroschinus, Ficus,* and *Ceriops.* All of the Queensland buttressed species observed by the writer with one exception belong to genera which are represented in the tropics to the North and North-West from Australia. The single exception to this qualification, *Syncarpia subargentea,* belongs to a genus which is represented in tropical Queensland.

The table in Section II. shows that buttresses are not confined to any single Natural Order or circumscribed systematic group of plants, but that they occur in species and genera of Natural Orders often widely separated from one another. However, the very large systematic class of dicotyledonous plants includes the buttressed species referred to in this paper.

The same Natural Order may contain both buttressed and unbuttressed species. In the Natural Order Sterculiaceæ there are species of trees exhibiting singular contrasts in the shape of the bases of the stems. The two species of *Tarrietia* are very prominently buttressed, whilst the stem of the Queensland Bottle Tree (*Brachychiton rupestre*) is circular in transverse section and conspicuously bottle- or bulb-shaped. The Natural Order Malvaceæ also contains examples of similar contrasts, but the trees providing them are chiefly found beyond Queensland. Belonging to this Natural Order, *Bombax malabaricum* is a buttressed tree in India and perhaps also in North Queensland, whilst bulb-shaped or tumid stems are known to be very strongly developed in the Baobab Trees (*Adansonia Gregorii* of Western Australia and *A. digitata* of South Africa). Examples of unbuttressed, large, Queensland rain-forest species in Natural Orders containing buttressed species are the White Cedar (*Melia Azedarach*) of Meliaceæ, *Callicoma serratifolia* of Cunoniaceæ, and White Myrtle (*Rhodamnia argentea*) of Myrtaceæ.

H. N. Whitford[9] states that buttresses appear to be correlated with broadly developed crowns and with the dominance of certain trees over others. The occurrence of buttresses in Southern Queensland rain forests is not definitely associated with either of these conditions as a general rule. The following species are examples of trees which are sometimes dominant, often produce large spreading crowns, frequently attain large dimensions, and are generally unbuttressed:—Crow's Ash (*Flindersia australis*), Cudgeree (*Flindersia Schottiana*), Yellow-wood (*Flindersia Oxleyana*), Bogum (*Flindersia Bennettiana*), Marblewood (*Acacia Bakeri*), and Coondoo (*Sideroxylon Richardi*). A large number of species of the Natural Order Lauraceæ, which is copiously represented in Southern Queensland rain forests, could also be cited as examples of the largest and tallest trees which are without prominently developed buttresses. Some examples of the Lauraceæ of this kind are:—Sassafras (*Cinnamomum Oliveri*), Southern Maple (*Cryptocarya erythroxylon*), and Hard Bolly Gum (*Beilschmiedia obtusifolia*).

It should be remarked, however, that Southern Queensland rain forests differ from the Anisoptera-Strombosi formation of the Lamao Forest Reserve, where Whitford made his observations on buttresses. In the Southern rain forests of Queensland it is unusual to find representatives of a single Natural Order predominating in numbers over a large tract, as in the case of the Lamao Forest Reserve, in parts of which Whitford found that the Dipterocarpaceæ predominated both in numbers and volume.



WEINMANNIA LACHNOCARPA, rain forest, Cedar Creek, about 26.5° S. (Westward from Eumundi). Diameter of stem and measurements of buttresses are shown in the Table in Section VI. Leaves of the palm, *Archontophoenix Cunninghamii*, in background and a climbing aroid, *Pothos Loureiri*, on the tree stem in uppermost part of picture. An extension of a posterior buttress is shown on the left at about one-fifth of height of picture.

*Photo.: W.D.F.*

[*Face page* 24.]

Ficus eugenioides, rain forest, Kin Kin, about 26.2° S. (Eastward from Gympie). The meshwork of aerial roots is evident in the picture.

*Photo.: W.D.F.*

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Although it is convenient to describe certain species of trees as buttressed, or unbuttressed, the observer in the field is very frequently confronted with a large number of species exhibiting gradations between the buttressed and the unbuttressed conditions. In the more luxuriant rain forests the majority of the trees which are not positively buttressed has flanged or somewhat perpendicularly flattened roots.

*Ceriops Candolleana* is a small tree or shrub which flourishes on muddy shores of the sea, estuaries, and tidal streams. It has prominent buttresses which are well established in plants ·9-1·2 m. (3-4 ft.) high.

Of all Queensland buttressed trees the Booyong (*Tarrietia argyrodendron.* var. *trifoliolata*) is one of the most common and most widely distributed, as it abounds in rain forests of both Northern and Southern parts of the State. As indicated in the comparative table in Section II., this variety belongs to a genus which is represented by buttressed species in the Malay Peninsula and West Africa. These facts concerning the distribution of the Booyong and its alliance with buttressed trees in distant parts of the world are of interest, as the buttresses of this variety are described in this paper in more detail than those of other trees.

## IV.—The Stage of Growth at which Buttresses Appear.

The buttresses appear at a comparatively early stage of growth in a large number of rain-forest species. The dimensions of several examples of young buttressed trees are contained in the following table.

| Species. | Diameter of Stem above Buttresses. | Diameter of Stem. / Maximum Diameter of Stem of Species. | Height. | Height. / Maximum Height of Species. |
|---|---|---|---|---|
| *Tarrietia argyrodendron* var. *trifoliolata* | 7·2 cm. (2·86 in.) | $\frac{1}{10}$ | 9·9 m. (33 ft.) | $\frac{1}{4}$ |
| *Weinmannia lachnocarpa* .. | 6·3 cm. (2·5 in.) | $\frac{1}{17}$ | 8·4 m. (28 ft.) | $\frac{1}{4\cdot6}$ |
| *Echinocarpus Woollsii* .. | 8·8 cm. (3·5 in.) | $\frac{1}{9}$ | 10·3 m. (34 ft.) | $\frac{1}{4}$ |
| *Endiandra discolor* .. .. | 5·6 cm. (2·25 in.) | $\frac{1}{10}$ | 7·8 m. (26 ft.) | $\frac{1}{4\cdot2}$ |

The measurements contained in this table indicate that buttresses are well established in comparatively young trees of these four species when they have attained from one-seventeenth to one-ninth of their maximum stem diameter and from one-quarter to two-ninths of their maximum height. These young trees were all very slender in habit and much below the height at which they develop spreading crowns or become exposed to the strain-producing action of wind. The young buttressed *Tarrietia* whose dimensions are shown in the above table had two buttresses, one measuring 30·2 cm. (12 in.) along the base and 7·6 cm. (3 in.) in perpendicular height, the other 22·8 cm. (9 in.) along the base and 8·2 cm. (3·25 in.) in perpendicular height.

In discussing the development of buttresses in the Lamao Forest Reserve, Whitford has arrived at conclusions which are not apparent in Southern Queensland rain forests. He states[10]: "It will be seen that the same causes which operate to produce short, thick boles in open places in temperate regions are possibly also present here, with the difference that the buttresses, which take the place and perform the function of uniformly thick trunks, appear later in the life of the tree. This means that the tree in youth, while it is crowded in the forest, develops a regular bole, but that when it reaches above the surrounding vegetation, in response to the increased heaviness of the top, the buttresses appear at the base, enabling the tree to withstand the extra strain."

## V.—The Transition from Roots to Buttresses.

The modification of roots in the process of forming buttresses has been observed by the writer chiefly in *Tarrietia argyrodendron* var. *trifoliolata.* In all instances it was noticed that the young buttresses consisted of the main surface roots which were flattened in a perpendicular plane where they joined the stem of the tree. At the distal end they gradually tapered into the rounded root. The young buttress could be compared to a triangle in which the base is long and the perpendicular height proportionately very short. With subsequent development the difference in the measurement of the base and the perpendicular height is lessened until the perpendicular height approaches or often exceeds the length of the base. Instances in which the perpendicular hight of the buttresses exceeds the length of their bases are very frequent in mature trees. This condition is commoner than the reverse in mature trees of *Echinocarpus Woollsii* (*see* Plate V., fig, 2 and text-figure 4) and *Endiandra discolor,* for example. The following table shows the relationship of perpendicular height to length of base of buttresses at three stages of growth in *Tarrietia argyrodendron* var. *trifoliolata*:—

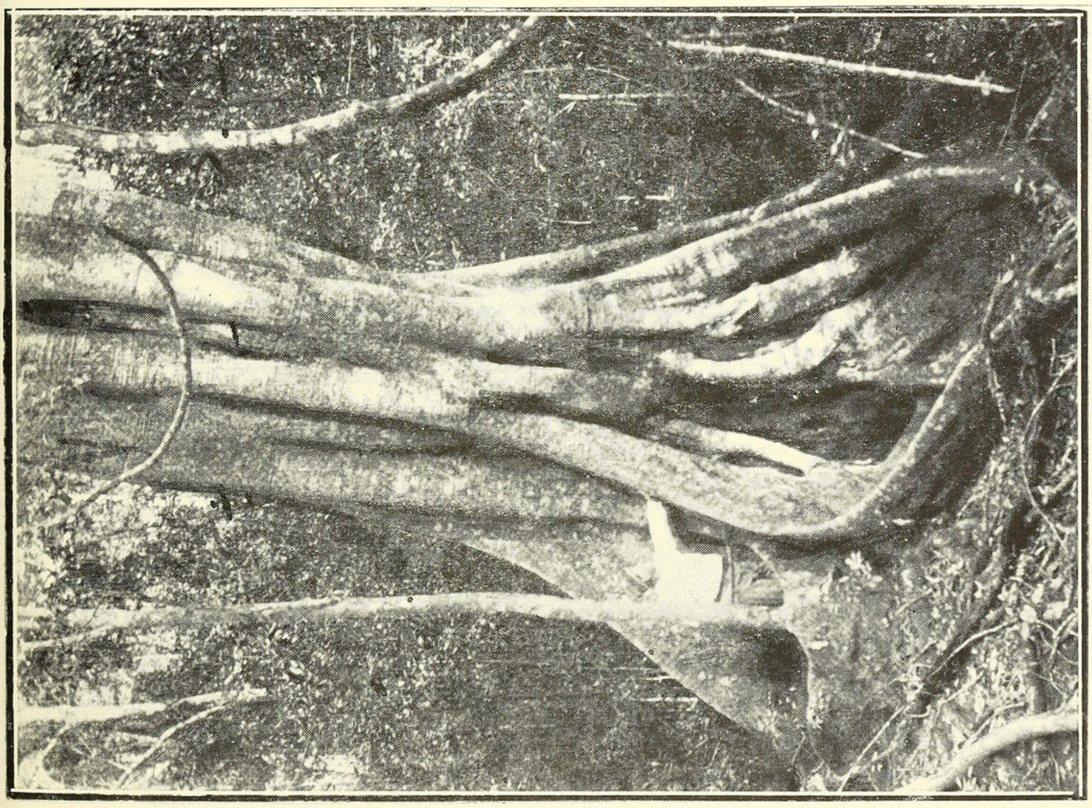


Fig. 1.—FICUS MACROPHYLLA, rain forest, Imbil, about 26.4° S. (Southward from Gympie).

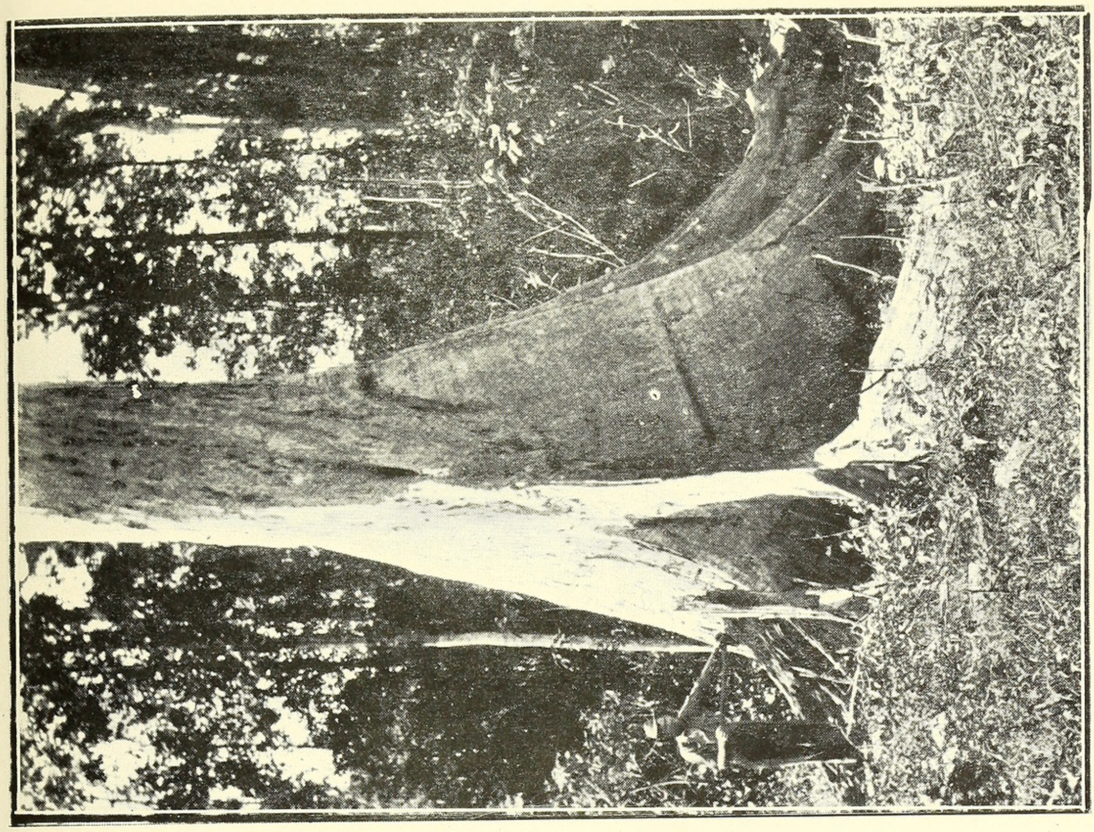


Fig. 2.—EUGENIA FRANCISII, rain forest, Kin Kin, about 26.2° S. (Eastward from Gympie). Measurements of buttresses shown in Table in Section VI.

*Photos.: W.D.F.*

[*Face page* 26.]

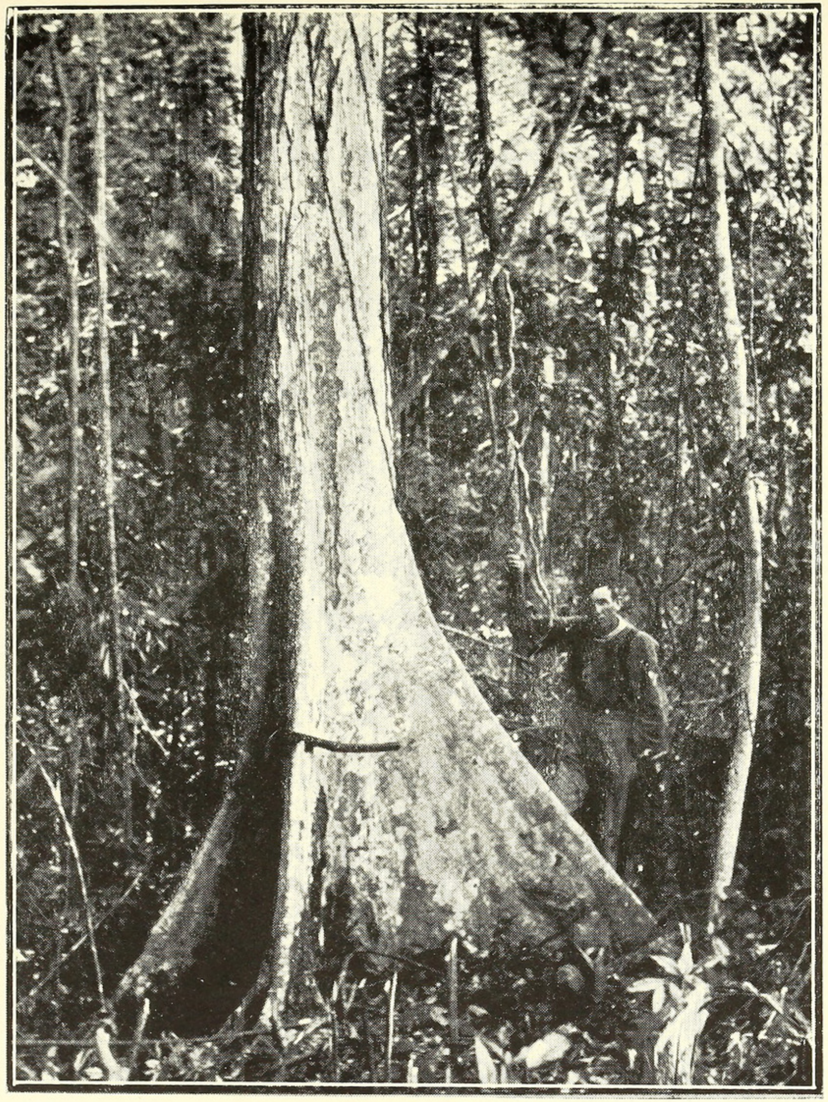


Fig. 1.—Tarrietia argyrodendron var. trifoliolata, rain forest, Kin Kin, about 26.2° S. (Eastward from Gympie).

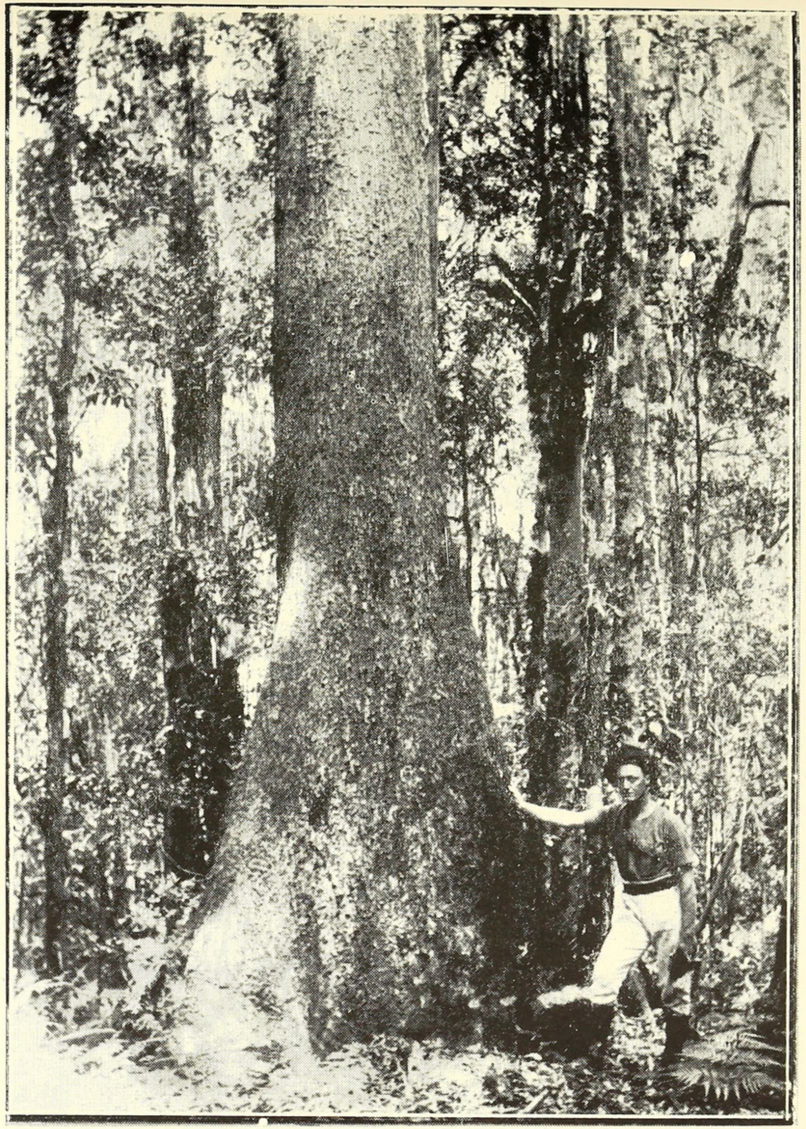


Fig. 2.—Tarrietia actinophylla, rain forest, Macpherson Range, about 28.3° S. (Eastward from Killarney).

*Photos.: W.D.F.*

[*Face page* 26.]

| Diameter of Stem of Tree above Buttresses. | Perpendicular Heights of Buttresses. | Length of Bases of Buttresses. | Ratio of Average Perpendicular Height to Average Length of Base. |
|---|---|---|---|
| 9·6 cm. (3·8 in) | 8·2 cm. (3·25 in.) | 20·3 cm. (8 in.) | 41 : 100 |
| | 10·1 cm. (4 in.) | 22·8 cm. (9 in.) | |
| | 8·2 cm. (3·25 in.) | 20·3 cm. (8 in.) | |
| | 7·6 cm. (3 in.) | 17·8 cm. (7 in.) | |
| | 6·3 cm. (2·5 in.) | 17·8 cm. (7 in.) | |
| | 9·5 cm. (3·75 in.) | 22·8 cm. (9 in.) | |
| 21·0 cm. (8·3 in.) | 45·7 cm. (18 in.) | 122·0 cm. (48 in.) | 45 : 100 |
| | 48·2 cm. (19 in.) | 76·2 cm. (30 in.) | |
| | 30·5 cm. (12 in.) | 50·8 cm. (20 in.) | |
| | 15·2 cm. (6 in.) | 60·9 cm. (24 in.) | |
| 60·5 cm. (2 ft.) (estimated) | 320·0 cm. (10 ft. 6 in.) | 396·2 cm. (13 ft.) | 98 : 100 |
| | 289·5 cm. (9 ft. 6 in.) | 274·3 cm. (9 ft.) | |
| | 289·5 cm. (9 ft. 6 in.) | 243·8 cm. (8 ft.) | |

One of the young buttresses of the smallest tree whose dimensions are shown in the above table is represented by text-figures 2 and 3.

The reverse process, in which the perpendicular height of the young developing buttresses greatly exceeds the length of their bases and in which subsequent growth by adding more to the length of the base tends to equalise the perpendicular and basal measurements, has not been observed by the writer.

## VI.—The Number and Dimensions of Buttresses in Various Species.

The number of buttresses in any one species of tree frequently varies considerably. In a few cases only one or, less rarely, two buttresses is strongly developed. Instances in which three are well developed are much more frequent. Examples of small trees of *Tarrietia argyrodendron* var. *trifoliolata* having respectively two and six relatively prominent buttresses are referred to in this paper. The mature trees of this variety exhibit a similar variation in the number of conspicuous buttresses, and in some instances as many as eight buttresses may be developed. These observations are also applicable in a general way to *Tarrietia actinophylla, Cedrela toona* var. *australis, Weinnmannia lachnocarpa, Eugenia Francisii, E. Leuhmanni,* and *Echinocarpus Woollsii.*

The dimensions of the buttresses in four species of mature rain-forest trees are shown in the following table:—

| Species or Variety. | Diameter of Stem above Buttresses. | Perpendicular Heights of Buttresses. | Length of Bases of Buttresses. | Estimated Thickness of Buttresses. |
|---|---|---|---|---|
| *Tarrietia argyrodendron* var. *trifoliolata* | 60·5 cm. (2 ft.) (estimated) | 320 cm. (10 ft. 6 in.)<br>289 cm. (9 ft. 6 in.)<br>289 cm. (9 ft. 6 in.) | 396 cm. (13 ft.)<br>274 cm. (9 ft.)<br>244 cm. (8 ft.) | 6·3 cm. (2 ft. 5 in.) |
| *Echinocarpus Woollsii* | 60·5 cm. (2 ft.) | 427 cm. (14 ft.)<br>408 cm. (13 ft. 6 in.)<br>229 cm. (7 ft. 6 in.)<br>229 cm. (7 ft. 6 in.) | 183 cm. (6 ft.)<br>183 cm. (6 ft.)<br>152 cm. (5 ft.)<br>142 cm. (4 ft. 8 in.) | 5·7 cm. (2·25 in.) |
| *Eugenia Francisii* | 106·6 cm. (3 ft. 6 in.) (estimated) | 437 cm. (14 ft. 4 in.)<br>437 cm. (14 ft. 4 in.)<br>345 cm. (11 ft. 4 in.)<br>345 cm. (11 ft. 4 in.)<br>437 cm. (14 ft. 4 in.)<br>437 cm. (14 ft. 4 in.) | 366 cm. (12 ft.)<br>274 cm. (9 ft.)<br>426 cm. (14 ft.)<br>335 cm. (11 ft.)<br>274 cm. (9 ft.)<br>183 cm. (6 ft.) | 10·1 cm. (4 in.) |
| *Weinmannia lachnocarpa* | 120·9 cm. (4 ft.) | 514 cm. (17 ft.)<br>302 cm. (10 ft.)<br>514 cm. (17 ft.)<br>196 cm. (6 ft. 6 in.) | 635 cm. (21 ft.)<br>756 cm. (25 ft.)<br>514 cm. (17 ft.)<br>408 cm. (13 ft. 6 in.) | 10·1 cm. (4 in.) |

## VII.—The Shapes of Buttresses.

In the paper by T. F. Chipp, which is referred to in Section I., the author discusses the outline of the outer edge (hypotenuse) of buttresses and the relative lengths of their base and height in West African trees, and applies these properties to the identification of species. The measurements given in Section V. show that the ratio of height to base in the buttresses of *Tarrietia argryodendron* var. *trifoliolata* is subject to variation as the tree develops. There are, however, more or less characteristic forms of buttresses which can be associated with several species of Queensland trees. The most conspicuous instances of this kind are *Echinocarpus Woollsii* and *Endiandra discolor*, which can be recognised very frequently by the edge (or hypotenuse) of the buttress curving outwards (*see* text-figure 4 and Plate V., fig. 2). In *Tarrietia argyrodendron* var. *trifoliolata* and *T. actinophylla* the edge of the buttresses is frequently almost linear or approximately straight (*see* Plate IV.). On the other hand, the majority of buttressed Queensland species has edges which curve inwards towards the axis of the tree, as exemplified in *Weinmannia lachnocarpa* (Plate I.), *Elæocarpus grandis* (Plate VI., fig. 1), and *Ficus* spp. (*see* Plates II. and III., fig. 1). The relative thickness of buttresses is of some value in identifying species in a few instances. Comparatively thick buttresses are often found in *Eugenia Francisii* and comparatively thin ones in *Echinocarpus Woollsii* and *Ficus* spp.

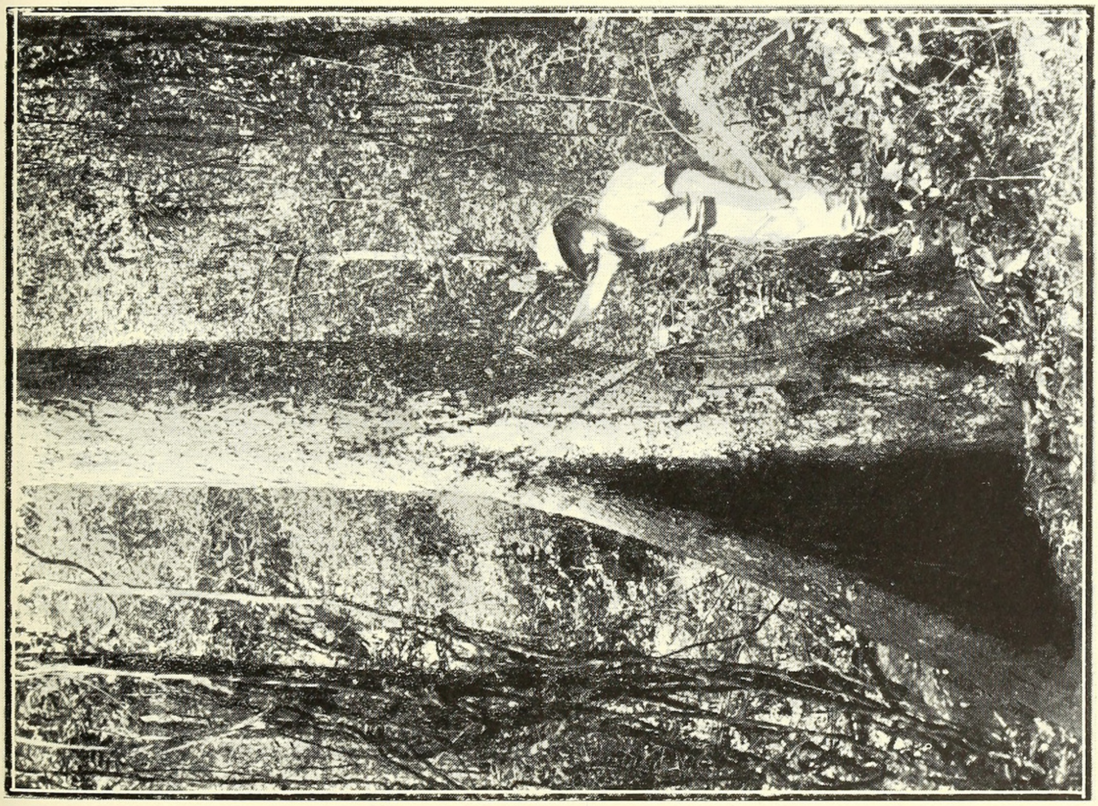


Fig. 1.—CEDRELA TOONA VAR. AUSTRALIS, rain forest, Macpherson Range, about 28.3° S. (Eastward from Killarney).

*Photo.: W.D.F.*

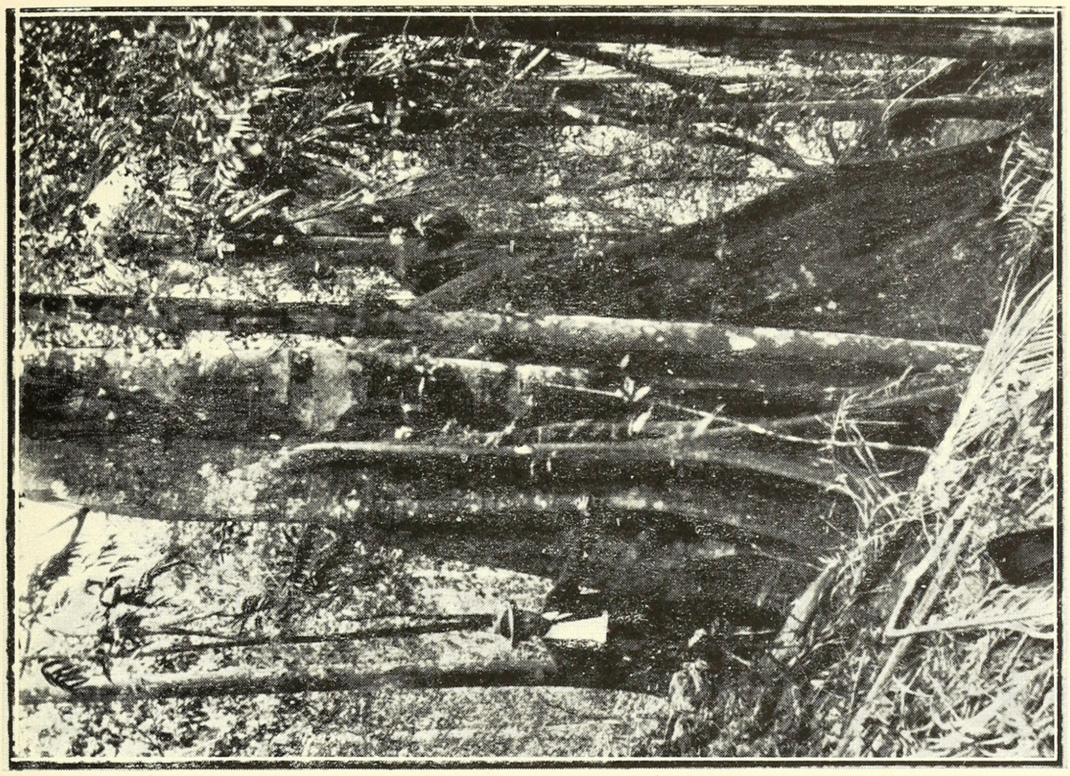


Fig. 2.—ECHINOCARPUS WOOLLSII, rain forest, Tamborine Mountain, about 28° S. (Southward from Brisbane).

*Photo.: J. E. Young.*

Fig. 1.—Elaeocarpus grandis, rain forest, Traveston, about 26.3° S. (South-Eastward from Gympie).

Fig. 2.—Elaeocarpus obovatus, rain forest, Macpherson Range, about 28.3° S. (Eastward from Killarney).

*Photos.: W.D.F.*

[*Face page 28.*]

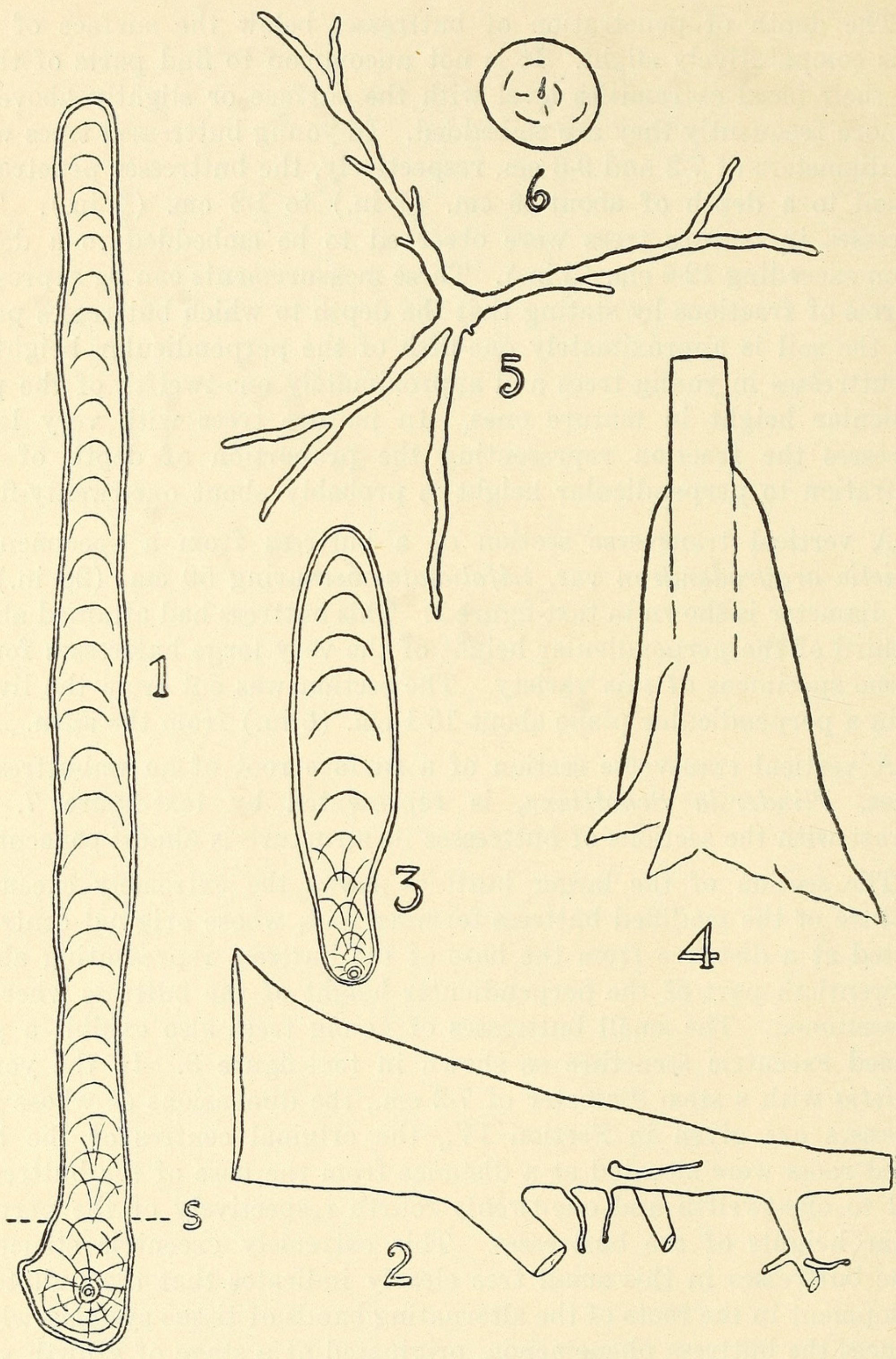
## VIII.—The Structure of Buttresses.

The depth of penetration of buttresses below the surface of the soil is comparatively slight. It is not uncommon to find parts of them with their basal extremities level with the surface or slightly above it, but more frequently they are embedded. In young buttressed trees with stem diameters of 7·2 and 9·6 cm. respectively, the buttresses penetrated the soil to a depth of about ·6 cm. ($\frac{1}{4}$ in.) to 1·8 cm. ($\frac{3}{4}$ in.). The buttresses in mature trees were observed to be embedded to a depth seldom exceeding 12·6 cm. (5 in.). These measurements can be expressed in terms of fractions by stating that the depth to which buttresses penetrate the soil is approximately one-fifth of the perpendicular height of the buttresses in young trees and approximately one-twelfth of the perpendicular height in mature ones. In mature trees with very large buttresses the fraction representing the proportion of depth of soil penetration to perpendicular height is probably about one-twenty-fifth.

A vertical transverse section of a buttress from a specimen of *Tarrietia argyrodendron* var. *trifoliolata* measuring 50 cm. (20 in.) in stem diameter is shown in text-figure 1. This buttress had attained about one-third of the perpendicular height of the very large buttresses found in some specimens of this variety. The section was cut from the living tree in a perpendicular plane about 15·1 cm. (6 in.) from the stem.

A vertical transverse section of a surface root of an unbuttressed species, *Flindersia Schottiana*, is represented by text-figure 7. In contrast with the sections of buttresses its structure is almost concentric.

The section of the larger buttress shows the extremely excentric structure of the modified buttress-forming root, whose original centre is situated at a distance from the base of the buttress representing about one-twentieth part of the perpendicular height of the buttress where it was sectioned. The small buttresses of young trees also exhibit a pronounced excentric structure as shown in text-figure 3. In the young *Tarrietia* with a stem diameter of 7·2 cm., the dimensions of whose two buttresses are given in Section IV., the original centres of the buttressed roots were situated at a distance from the base of the buttresses equal to one-twelfth and one-twenty-fourth respectively of the perpendicular heights of the buttresses. This extremely excentric structure of the buttresses in this small tree clearly indicates that the unilateral development in the roots of the alternating bands of tissue systems, which produces the buttress phenomenon, originated at a stage of growth very much earlier than that at which the tree was measured. The buttresses of the young trees of the other three species whose dimensions are shown in the table in Section IV. also exhibited a highly excentric structure in transverse section. The curving lines appearing in the sections represent some of the more conspicuous bands of wood parenchyma. They are not intended to be interpreted as ''annual rings.'' The lines intersecting them indicate some of the more prominent wood rays. G. Haberlandt[11] has figured a transverse section of a buttressed root of *Parkia africana*.

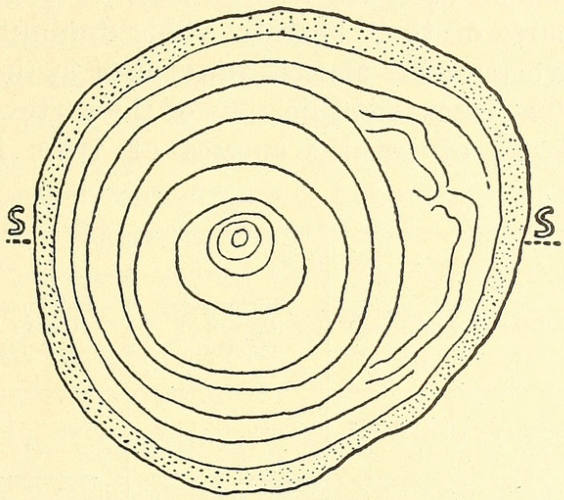



Text-figures 1-6.

1, Vertical transverse section of buttress of *Tarrietia argyrodendron var. trifoliolata* × $\frac{1}{6}$. 2, Buttress of young tree of foregoing variety which had attained 9·6 cm. in stem diameter × $\frac{1}{4}$. 3, Vertical transverse section of same buttress × $\frac{1}{2}$. 4, Diagram of basal part of stem of *Echinocarpus Woollsii* × $\frac{1}{96}$. 5, Transverse section of stem of same tree at the soil surface × $\frac{1}{48}$. 6, Transverse section of stem of same tree immediately above buttresses × $\frac{1}{48}$. S, surface of soil.

Some vertical sections of buttresses of *Ceriops Candolleana* were also made. They were similar to that of the young *Tarrietia* shown in text-figure 3, thereby indicating that the structural development of the buttresses is probably not very different in each case.

In all instances of prominently buttressed mature trees, which have been examined by the writer, a decided diminution was observed in the size of the stem or axis of the trees from just above the buttresses towards its point of contact with the soil. The extent of this diminution was measured in a large stump of *Echinocarpus Woollsii* (*see* text-figures




Text-figure 7.

Transverse section of surface root of *Flindersia Schottiana* $\times \frac{1}{2}$.
S, surface of soil.

5 and 6). The stem above the buttresses measured 60·4 cm. (2 ft.) in diameter, whilst its maximum diameter at the surface of the soil as the woody axis of the buttresses was only 22·6 cm. (9 in.), or three-eighths of its diameter above the buttresses. A similar tapering of the woody axis towards the surface of the soil was observed in large buttressed trees of *Cedrela toona* var *australis, Tarrietia argyrodendron* var. *trifoliolata,* and *Weinmannia lachnocarpa* It was also evident in a specimen of *Ceriops Candolleana.* This peculiar feature of the structure of buttressed trees is the reverse of the form generally found in the stems of trees, which as a rule gradually taper from the ground upwards. Several examples of comparatively young buttressed trees of *Tarrietia argyrodendron* var. *trifoliolata* were examined, and it was ascertained that the characteristic diminution in the size of the stem towards the earth was not evident in trees up to 20·16 cm. (8 in.) in stem diameter above the buttresses. A buttressed specimen of this variety attaining the foregoing dimensions was sawn off at the surface of the ground and it was found that its stem or woody axis had not undergone appreciable diminution towards the base.

Some microscopical examinations of the secondary wood in buttresses of *Tarrietia argyrodendron* var. *trifoliolata* indicated that this product contained tissues similar to those composing the stem in this variety.

## IX.—Some Characteristics of the Roots and Bark.

Large buttressed trees which have been uprooted by violent means, such as storms, generally show an extensive development of surface roots and no strongly developed tap-root, but the young *Tarrietia* with six buttresses and a stem diameter of 9·6 cm., which is referred to in Section V., had a large tap-root measuring 6·3 cm. (2·5 in.) in diameter.

Schimper[12] states that, owing to the prejudicial effect of humidity on the formation of cork, bark is only slightly developed on most of the tree stems in rain forest. The present writer has often observed that the bark is much thinner on the buttresses of rain-forest trees than that on the unbuttressed parts of their barrels. This diminution in the thickness of the cortex is often most marked towards or at the outermost edges of the buttresses. The measured thickness of the cortex on the stems and buttresses respectively of several species of trees is shown in the following table:—

| Species. | Diameter of Stem. | Thickness of Cortex of Stem. | Thickness of Cortex of Buttress. | $\frac{\text{Thickness of Buttress Cortex.}}{\text{Thickness of Stem Cortex.}}$ |
|---|---|---|---|---|
| *Tarrietia argyrodendron* var *trifoliolata* | 50·4 cm. (1 ft. 8 in.) | 1·2 cm. (·5 in.) | ·48 cm. (·19 in.) | $\frac{1}{2 \cdot 5}$ |
| *Echinocarpus Woollsii* .. | 60·48 cm. (2 ft.) | 1·6 cm. (·625 in.) | ·63 cm. (·25 in.) | $\frac{1}{2 \cdot 5}$ |
| *Weinmannia lachnocarpa* | 70·56 cm. (2 ft. 4 in.) | ·78 cm. (·312 in.) | ·48 cm. (·19 in.) | $\frac{1}{1 \cdot 6}$ |

## X.—The Extent to which Root and Stem Respectively Contribute to the Construction of Buttresses.

From the reversed or downwards taper of the lower part of the stem, which is characteristic of strongly buttressed, large trees, the respective contributions of the root and stem can be deduced to a certain degree. This reversed taper or downwards diminution of the stem can be readily and naturally explained by assuming that the deficient portion of the lower part of the stem has passed into the buttresses. Hence that stage of growth in buttressed trees which exhibits the beginning of the downwards diminution of the stem or axis indicates the period at which the stem has commenced to participate in the construction of the buttresses. As no appreciable diminution towards the base was observed in the stems of *Tarrietia argyrodendron* var. *trifoliolata* measuring from 15·12 cm. (6 in.) to 20·16 cm. (8 in.), it is concluded that the roots alone contributed to the construction of the buttresses in the stages of growth represented by these instances. The pronounced downwards diminution of the central stem of mature trees of this variety from above the buttresses towards its insertion in the soil, as stated in Section VIII., shows that the axis loses a large proportion of its normal dimensions through contributing to the development of the buttresses. It is, therefore, concluded that the stem performs a very large part in building up the buttresses in the latter part of the life of the tree.

Corresponding to the foregoing order of modification of the root and stem in the development of buttresses is the extension of the sides of the buttresses collateral with the root and stem respectively. This relationship is evident in the table in Section V., which shows that in the young trees of *Tarrietia argyrodendron* var. *trifoliolata* the base greatly exceeds the perpendicular height, whilst in mature trees the perpendicular height almost equals the length of the base. The table also indicates that the perpendicular height of the buttresses only shows a slight proportional increase upon the length of the base in stages of growth up to 21 cm. (8·3 in.) in stem diameter, whilst in the subsequent stage from 21 to 60·5 cm. in stem diameter a high proportional increase in the perpendicular measurement takes place. These facts conform with the respective shares attributed to the roots and stem in constructing buttresses, as they prove that the positive development of the buttresses proceeds along the sides respectively collateral with the root or stem during the stage of growth when the one or the other is computed to be the more active contributor.

The extent to which these conclusions are applicable to examples other than those mentioned in this section is a subject requiring further investigation.

## XI.—Conditions with which Buttressed Trees are Associated.

It has been remarked by Schimper[13] that buttresses are a pecularity of trees in a tropical climate with abundant rainfall, and that the amount of rainfall necessary for their appearance is not yet ascertained. The present writer[14] has shown that it can be definitely stated that in Queensland the phenomenon appears in rain-forest trees when the average annual rainfall approximates, equals, or exceeds 60 inches, and that it is not confined to tropical forests but occurs in Queensland in relatively temperate climates at an altitude of 3,500 in latitude 28·2 degrees south. The occurrence of buttresses further south in Eastern Australia has been recorded by J. H. Maiden[15] who has observed them in the Dorrigo Forest Reserve in about latitude 30·3 degrees. It is to be expected that in tropical rain forests in which buttressed trees abound the amount of the prevalent rainfall would be greater than that occurring in Southern Queensland rain forests on account of the more rapid evaporation in the tropics.

High relative humidity and deep shade are conspicuous accompaniments of rain forests containing buttressed trees. Unfortunately the humidity in Queensland rain forests does not appear to have been determined. A high relative humidity is also a condition of the environment of the buttressed mangrove *Ceriops Candolleana*, which grows on tropical and subtropical sea coasts.

An extensive development of surface roots is also a noticeable feature of rain forests in which buttressed trees abound. These surface roots often arise from unbuttressed as well as buttressed trees. They are more conspicuous in the heavy rain forests with a relatively high annual rainfall as at Kin Kin (57 in.) than in those where the vegetation is less luxuriant and the rainfall much lower, as at Goodna (37 in.).

## XII.—The Possible Causes of Buttresses.

Schimper[16] remarks that the physiological causes of buttresses and their significance to the life of the tree are still obscure. In discussing the excentric development of plant organs, of which buttresses are examples, Haberlandt[17] states that it is probable that the distribution of mechanical strains within an organ plays a leading part in producing asymmetrical thickening. A similar conclusion is assumed by Whitford, as the quotation from his work in Section IV. of this paper expresses the view that the buttresses appear at the base of the tree in response to the increased heaviness of the top, thus enabling the tree to withstand the extra strain.

Although buttresses are not specially mentioned, Pfeffer,[18] in discussing the stimulus of tension, remarks that the pull of the aerial parts upon the roots must act as a stimulus strengthening the latter, and that in general the mechanical demand largely determines the degree of development of the organs of attachment.

The hypothesis which attributes the origin of buttresses to the direct effects of strain or tension induced by the upper, aerial parts of the tree appears to be the most obvious explanation of the phenomenon, but there are circumstances which are not in accordance with this view. As shown in Section IV., buttresses appear in many young trees long before they have attained the height at which they develop large crowns or become exposed to the strain-producing force of winds.

Of all conditions with which buttressed trees are associated, high relative humidity appears to be the most characteristic, and it may possibly be a principal factor in causing the phenomenon. Other conditions which accompany buttressed trees, such as heavy rainfall, heavy crowns, and strain-producing factors such as wind, are also present in some temperate regions but do not induce the phenomenon there. Buttresses are essentially characteristic of the tropics and subtropics. In conjunction with a heavy rainfall in these regions, the solar heat, which directly increases the vapour pressure of water and the moisture-carrying capacity of the air, is known to profoundly stimulate vegetation, which luxuriates in the humid atmosphere and abounds in denseness and diversity of form unequalled elsewhere.

In Section XI. the association of buttressed trees with rain forests in which surface roots are prominent has been remarked upon. It is not improbable that surface roots anteceded buttresses, which are essentially perpendicularly extended forms of surface roots. Besides humidity, conditions which probably tend to develop surface roots are the moisture of the surface layer of rain-forest soils, the absence of much direct sunlight on the soil surface, and the fertile, humus-containing, upper layers of rain-forest soil. In addition to the nutriment it produces, the relatively high humus content of the soil towards the surface, because of its avidity for oxygen, would retard the oxygenation of the subsoil and exercise a further tendency towards the concentration of roots in the superficial layer of the soil.

It would appear that in those cases where buttresses have been evolved the upper part of the principal surface roots has acquired an aerial character and is subject to some of the conditions of growth operating in stems. The perpendicular elongation of stems is a very prominent characteristic of the trees and erect shrubs of rain forests in which buttresses abound, and it is attributed to the attractive agency of light (phototropism), acting in conjunction with the normal upward growth in opposition to gravity (negative geotropism). The upper part of the principal surface roots in buttressed species may be affected by negative geotropism and phototropism either directly or indirectly through the stem; and in this manner the perpendicular extension, which constitutes buttresses, may arise. Roots are most commonly subterranean organs, but in rain forests the roots of many plants possess an aerial or sub-aerial character. The adaptation of roots to an aerial environment is facilitated by the high relative humidity of the air and the exclusion of a great amount of direct sunlight in rain forests. These two conditions, therefore, are probably factors of considerable importance in the production of buttresses.

The prevalence of the buttress phenomenon in trees whose roots have assumed a definite aerial character is exemplified in the epiphytical species of Fig trees (*Ficus*), which are so common in Queensland rain forests. In all the large specimens of the various species of these trees which the writer has seen the flattening of the roots in a perpendicular plane near the surface of the soil was prominent.

It is also possible that hereditary factors are active, as several species of buttressed trees, such as the Figs (*Ficus* spp.), tend to retain their buttressed character when planted in parks and gardens away from their natural environment of the rain forest. In these cases, however, the buttresses are not so large and conspicuous as in trees of corresponding sizes in the rain forests.

The causes of buttresses, whatever they are assumed to be, are evidently to a great extent selective in their action as their effects are seen in species often widely separated from each other in the classified systems in which plants are arranged, whilst species allied to those in which buttresses are strongly developed remain unbuttressed, although subjected to the same external conditions.

## XIII.—Summary.

Buttresses occur in Queensland in certain species of trees belonging to that section of the flora which is closely allied to the flora of the Indo-Malayan region. They are not confined to any single Natural Order of plants, but occur in species and genera of Natural Orders which are often widely separated from each other.

Buttresses are well established in young trees of *Weinmannia lachnocarpa, Tarrietia argyrodendron* var. *trifoliolata, Endiandra discolor,* and *Echinocarpus Woollsii* when they have attained from one-seventeenth to one-ninth of their maximum stem diameter and one-quarter of their maximum height.

In young trees of *Tarrietia argyrodendron* var. *trifoliolata* the length of the base of the buttresses greatly exceeds their perpendicular height. In subsequent development the difference in the measurements of the base and perpendicular height is lessened until the perpendicular height approaches, equals, or exceeds the length of the base in mature trees.

The depth to which buttresses penetrate the soil varies from about one-fifth of the perpendicular height of the buttresses in young trees to about one-twenty-fifth of the perpendicular height of the buttresses in mature trees with very large buttresses.

Vertical sections of buttresses of *Tarrietia argyrodendron* var. *trifoliolata* show that their structure is extremely excentric. In a buttress, which had attained one-third of the maximum height of buttresses in this variety, the original centre of the root was situated at a distance from the base of the buttress represented by about one-twentieth of the perpendicular height of the buttress.

In all instances of prominently buttressed mature trees, which were examined, a decided diminution was observed in the size of the stem or axis of the tree from above the buttresses towards its point of contact with the soil. In a specimen of *Echinocarpus Woollsii* this reversed taper of the stem or axis of the tree reduced the axis at the soil surface to three-eighths of its diameter above the buttresses.

It is computed that in *Tarrietia argyrodendron* var. *trifoliolata* the roots alone contributed to the structure of the buttresses in trees up to 20·16 cm. (8 in.) in stem diameter, and that in subsequent development the stem performs a large part in building up the buttresses.

Conditions with which buttressed rain-forest trees are associated are a heavy rainfall, high relative humidity, the absence of much direct sunlight on the soil surface, and an extensive development of surface roots.

In discussing the causes of buttresses the following factors are suggested as possible originating or contributing agents:—High relative humidity, the absence of much direct sunlight on the soil surface, the humus content of the upper layer of rain-forest soil, negative geotropism and phototropism. The possible activity of hereditary factors is also suggested. The causes of buttresses are evidently to a great extent selective in their action.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