ART. XXXII.—*Observations on the Lianes of the Ancient Forest of the Canterbury Plains of New Zealand.*

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Plates XXIII–XXVI.

I. INTRODUCTION.

LIANES form, in the New Zealand forest, an ecological group of prime physiognomic importance, as pointed out by L. Cockayne (1908, p. 24). Further, within quite limited areas the various life-forms of this class of plants occur side by side, so that it is comparatively easy to study and compare their forms, adaptations, behaviour, and life-histories. Up to the present time such studies have been for the most part neglected; nor is this to be wondered at, since in a newly settled country the earliest botanical investigations must of necessity be floristical, while even in the Old World ecology is yet in its infancy. The work of L. Cockayne stands out as a notable exception to the above statement, for in a series of writings, commencing in 1898 and extending to 1915, he has given a good many details as to the methods of climbing and life-histories of lianes, and the evolution of the climbing habit; but he has not published any comprehensive account of the group. Nor in this paper is it possible for the writer to attempt anything really comprehensive—a matter that would have required several years' experience in the field in all parts of the botanical region. On the contrary, the study, for which no completeness is claimed, since New Zealand contains no less than forty-seven lianes, which belong to sixteen families and twenty-two genera, is confined to one definite forest area, Riccarton Bush, the last remnant of the ancient forest of the Canterbury Plains.*

Nor is the study of the lianes in this area complete. A complete account must of necessity include stem-anatomy. This in itself is of such importance that it should be made the subject of a separate paper, for thus only can it receive its deserved attention. There are experiments to be made dealing with water-conduction, mechanical principles, &c., and for this considerable time and observation are necessary. Moreover, the forest investigated is of such importance that it is rightly preserved closely; and the amount of material required for a complete stem account cannot be obtained without considerable destruction to the forest.

Riccarton Bush is a portion of an ancient kahikatea (*Podocarpus dacrydioides*) forest The members of this species do not here grow very closely together, but they attain a great size, their trunks, often 1·6 m. in diameter, rising straight up to a height of 30–40 m., with their lowest branches 20 m. from the ground On the surface of the ground their roots spread widely, many of them twisting up and forming knees about 50 cm. in height, and others, through the displacement of the soil by which they were formerly partially covered, forming a kind of reticulate platform round the base of the tree (Plate XXIV, fig. 2). Growing to the same level in the forest, but present in small numbers, are two other species of *Podocarpus*—*P. spicatus* (matai) and *P. totara* (totara)—and two species of *Elaeocarpus*—*E. dentatus* and *E. Hookerianus*.

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* For an account of this association see Armstrong, J. F., 1869, and Cockayne, L., 1914.

The smaller trees and the shrubs are represented by many more species which grow chiefly in the more exterior portions of the forest, where the light-conditions are more favourable. The shrub or low tree *Paratrophis microphylla* is especially abundant

On the forest-floor grow certain herbs and ferns, the diffuse light causing elongated thin shoots and broad membranous leaves, while seedlings of the most diverse inhabitants of the forest are here found in considerable numbers, forming a living floor of vegetation.

From their tall supports hang the rope-like stems of the lianes, often 12 cm. in diameter. These stems, which belong to the various species of *Rubus* and *Muehlenbeckia,* act as supports for still more lianes, the whole often forming impenetrable tangled masses. Where the support has died, or the liane slipped down, other stems form great coiling masses, extending along the ground for several metres The various twining-lianes, tendril-bearers, and many scramblers climb on the smaller trees and the shrubs, while the small shrubs and the herbs are excellent supports for the growing juvenile lianes.

The number of species of vascular plants in the forest is sixty-eight, consisting of—Trees and shrubs, 35 , lianes, 12 ; parasites, 2 , herbaceous plants, 12 ; ferns, 7.

The lianes dealt with in this paper may be classified as follows: (1.) Scramblers: *Rosaceae—Rubus australis* Forst f var *glaber* Hook f., *R. schmidelioides* A. Cunn., *R. cissoides* A. Cunn.,* *R. subpauperatus* Cockayne; *Onagraceae—Fuchsia Colensoi* Hook. f. (2.) Root-climbers: *Myrtaceae—Metrosideros hypericifolia.* (3.) Twining-plants: *Polygonaceae —Muehlenbeckia australis* (A. Rich.) Meissn., *M complexa* (A. Cunn.) Meissn.; *Apocynaceae—Parsonsia heterophylla* A Cunn., *P capsularis* (Forst. f.) R. Br. var. *rosea* (Raoul) Cockayne (4.) Tendril-climbers: *Ranunculaceae—Clematis indivisa* Willd , *Passifloraceae—Tetrapathaea australis* Raoul.

Before concluding this introduction, I wish to express here my indebtedness to those who gave me assistance in the preparation of this paper. I especially wish to thank Mrs Deans. through whose permission to make investigations in Riccarton Bush the work was able to be carried out; Dr C Chilton, C M Z S , who supervised the preparation of the paper and the laboratory-work; and Dr. L Cockayne, F.R.S., who suggested the outlines of the paper and gave valuable assistance in connection with the field-work.

II. AUTECOLOGY OF THE LIANES

1. FUCHSIA COLENSOI.

A. LIFE-FORM.

Although fairly abundant in the forest, the distribution of this species indicates that the conditions required for its growth are an abundance of moisture, but at the same time a well-drained soil The species is most abundant on the sides of and in the vicinity of the drains which run through the forest, and, further, at the edge of the swampy portion of the forest. In this swamp itself the species is entirely absent The individual plants, upon leaving the ground, give off numerous shoots, which may scramble up among the branches of an overhanging shrub, or trail along the forest-

* Dr. L. Cockayne informs me that there is some doubt as to what *R. cissoides* A. Cunn really is, but the plant here dealt with is *R cissoides* as defined by Cheeseman, 1906, p. 125.

floor for a distance of 5 m. The stems often attain a thickness of 3 cm. in diameter, and are covered with a papery bark. At intervals along these stems shoots arise, which may reach a support, or, failing this, they bend over till they touch the ground, where they continue their growth. As these shoots spread out in all directions, their branches are a considerable distance apart, and thus it is almost impossible that none of them reach a support. Roots arise in large numbers from these trailing-stems, and thus the food-supply available for the shoots is largely increased. The value of these roots may be seen from the fact that stems with roots attached which had been cut through by the writer continued to live, and the roots gained enough food-material from the soil to maintain in vigorous growth the shoots which were given off near the roots.

Shoots arising from the adult stem in the shade are very thin (5 mm. in diameter) and elongated (internodes are 7–8 cm. long). The stems which straggle upwards through the supporting branches are mostly unbranched, but maintain their upright position by twisting and turning through the network of supporting branches, and finally may attain a height of 4 m. The leaf-petioles are very thin and fragile, and thus, though they project from the stem at right angles, cannot be of great assistance in climbing But where the plants grow in more strongly illuminated positions the stems branch freely, and, as the branches project at right angles, they are of prime importance in obtaining and maintaining new positions of support. On the top of supporting shrubs, branches may stand erect for fully 50 cm , but most of the branches lie horizontally on the support and form a dense covering. Others, again, hang down from the edge of the support, and thus the leaves of the plant are borne in all positions suitable for assimilation.

In exposed situations the plants form dense, low bushes, about a metre high, and usually 2–3 m across The primary stem gives off, near its base, numerous branches, which spread out and branch further, the branches interweaving and forming masses of the divaricating life-form. From the tops of these masses stems may rise up, and by their mutual support gain a height of a metre above the main mass of branches. And thus, should they come into contact with the branches of any overhanging tree or shrub, the liane-branches may push their way into the support, and there continue their scrambling growth. Branches from these exposed plants at the edge of the forest may trail along the ground, and, rooting freely, give off shoots in the shade, where supports are abundant. And so efficient are these roots that sometimes the attenuated shoot may give off near these roots new shoots, which attain a thickness fully double that of the parent shoot.

Fuchsia Colensoi is one of the few New Zealand indigenous plants which are deciduous. Plants in exposed situations lose their leaves early in winter, but in the shade they are devoid of leaves for only a few weeks.

B. LEAF.

(i.) *Leaf-form.*

Leaves alternate, petiolate, thin, membranous; upper surface pale green, dull; lower surface greyish-green, shiny; veins purple; 2–4 cm. long; orbicular or orbicular-ovate; cordate or rounded at base; minutely and remotely serrate Petioles usually slightly longer than blade, translucent, upper surface slightly grooved

Sun leaves are slightly smaller and less membranous, and have shorter petioles.

(ii.) *Leaf-anatomy*

(*a.*) *Shade Leaf.*—Epidermis: Cells flattened, thin-walled, outer walls very convex; lower epidermal cells smaller; cells beneath midrib thick-walled. Stomata · Lower surface only, level with epidermal cells. Chlorenchyma · Palisade—1 layer cells, slightly elongated, and rather loosely packed Spongy—5–6 layers; upper cells nearly spherical, lower cells more or less elongated, parallel to leaf-surface, intercellular spaces large Chlorophyll abundant both in palisade and in spongy tissues Vascular bundles surrounded by poorly developed bundle-sheath Calcium oxalate in raphides

(*b.*) *Sun Leaf*—Epidermis Walls slightly thickened Chlorenchyma: Palisade—Cells more elongated and more closely packed than in shade leaves. Spongy—Cells more regular; intercellular spaces smaller.

2. The Species of Rubus.

There can be no doubt that the species of *Rubus* in New Zealand are poorly defined. Cheeseman did not recognize *R. subpauperatus* in the Manual, but from the following descriptions it will be seen that there are sufficient grounds for the establishment of Cockayne's species (1909A, p. 42). The different species show many points of similarity in their life-form, but there are some characteristics which, though common to all, are more noticeable in particular species *

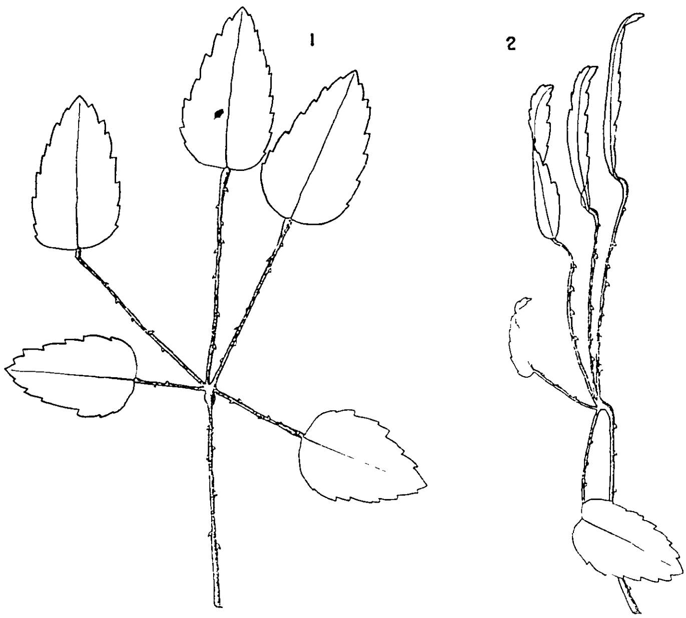


FIG 1 —*Rubus australis* Leaf, top view
FIG 2 —*Rubus australis* Leaf, side view

The leaves are alternate and palmately compound (see figs. 1 and 2), with 3–5 leaflets, which vary in size. Margins serrate, with incisions to

* In the descriptions below, therefore, the special points of each species are more fully dealt with. Further, the descriptions cannot be rigidly applied to all the members of a species, on account of the diversity of form of the individual plants, and, in fact. it is probable that hybrids are of common occurrence

varying depths. The distal end of subpetioles is bent up about 0·5 cm. from the lamina, and considerably thickened. Further, the lamina is at right angles to this thickened portion, and so lies parallel to the proximal portion of the subpetiole. Prickles may be present on the under surface of petiole, subpetiole, and midrib.

(*a.*) Rubus australis var. glaber.

A. LIFE-FORM.

This species is fairly abundant in the forest, and is found chiefly in the drier situations. Since these parts of the forest are the habitat of plants of varying habits, the liane is presented with abundant support, usually climbing up among the interlacing branches to a height of 12 m. or more. Very often the falling of trees forms large gaps in the forest vegetation, which provide excellent situations for plants which thrive best in bright sunlight. And it is on the plants surrounding such gaps that *R. australis* is found growing at its best. Its thick stem, often 4 cm. in diameter, covered with a hard, brown, scaly bark, gives off at right angles numerous lateral shoots, which branch further, and, finally, leafy masses borne on these branches form an impenetrable wall 3–4 m. high.

In the more shaded portions of the forest the stems give rise to very few lateral branches, but stretch up like ropes into the branches overhead, where their foliage is spread out in the light. In such cases, where the expanse of foliage is on the branches of a kahikatea, whose lowest branches, as stated above, are usually 20 m. from the ground, it is impossible to conceive how the liane could reach the support directly. However, the frequent presence of decaying stumps of trees near these taxads suggests that the lianes commenced their growth by scrambling up these trees, and from their top branches reached those of the neighbouring pines. Such a process as this is actually seen occurring on other trees which form supports for the liane. From almost any part of the liane-stem there arise adventitious shoots similar to those of *R. schmidelioides*, and if these shoots happen to arise within 2–3 m. of the branches of a neighbouring tree the shoots very often bridge the intervening space; then by the grasping action of prickles, which are borne on the stems, the new supports are firmly held. The stems of *R. australis* which have never reached a support or which have fallen away from such, and lie along the ground, show great tendency to adventitious rooting wherever in contact with moist soil. From these trailing-stems adventitious shoots often arise, which may reach a support, or which may bend over and, continuing their growth along the ground, give off still more roots. Now, the writer has proved by experiment that when these roots are well developed they are themselves capable of supplying sufficient nutritive material and water for the further growth of any adventitious shoot which arises near them. Thus an injury to the primary root or stem need not result in the death of the whole plant. On the contrary, this rooting is a means by which the plant can increase by vegetative reproduction, one such plant noted representing at least seven potential individuals.

B. LEAF.

(i.) *Leaf-form.*

Leaves 3–5-foliate; leaflets coriaceous, glabrous, 8–12 cm. long, ovate-oblong or ovate-lanceolate; base rounded or truncate, apex acute, margin serrate. Petiole 6–8 cm long, deeply grooved on upper surface along its entire length. Prickles in small numbers on petiole and subpetiole, absent from midrib The distal end of the petiole is often swollen and bent, and from it the leaflets project at varying angles so that they face the light

Both seedlings and adventitious shoots bear leaves which show all transitions from simple to compound. The first leaf is simple, and is often succeeded by a simple leaf with a lobe near its base Later, leaves with 2 lobes may appear, and may be succeeded by a leaf with a lateral leaflet in place of one of these lobes. From this stage to the adult 3–5-foliate leaf there are numerous transitional forms. Injury to the growing-point by frost or other means may lead to the development of lateral shoots, which bear leaves in an order similar to that on the primary stem, and, on lateral shoots from these, leaves may again develop in a corresponding order.

(ii.) *Leaf-anatomy.*

(*a*) *Shade Leaf.*—Epidermis: Cells slightly flattened; well-developed cuticle; stomata under surface only, level with epidermal cells. Hypoderm. One layer isodiametrical cells, continuous on upper surface; on lower surface confined to the regions near the vascular bundles. Chlorenchyma: Palisade—2 layers, cells rather elongated. Spongy—5–7 layers; cells mostly elongated in direction of palisade, and so no sharp boundary between the tissues; intercellular spaces fairly large Vascular bundles: Surrounded by sheath of collenchyma, which connects with the upper and the lower hypoderm; a small band of stereome is present at the base of the larger bundles. Leaf-margin: Very thick cuticle; hypoderm 2 layers; chlorenchymatous cells elongated and arranged radially Calcium oxalate: Aggregate crystals.

(*b*) *Sun Leaf*—Epidermis: Upper epidermis, cells with small lumina and much-thickened walls; cuticle very thick; lower epidermis, walls much thickened, but to a less extent than those of upper epidermis Chlorenchyma: Palisade—Cells very elongated and closely packed; tissue occupies almost one-half of leaf-thickness Spongy—Cells fairly regular; intercellular spaces smaller than in shade leaf. Vascular bundle Stereome at base of each bundle well developed, and composed of cells with walls greatly thickened Leaf-margin: Hypoderm forms a mass of 3–4 layers of cells with thick walls.

(*b*.) Rubus schmidelioides.

A. LIFE-FORM.

In the shade of the forest this liane often grows to a height of 8 m. or more before it reaches the sunlight It may be growing upright beside its support, or, if the support is a tree with smooth bark and few lateral branches in the shade, the liane-stems may be coiled in a tangled mass at the foot of the support, indicating that the liane has probably fallen down through the increased weight of its own body Between the liane's root and the support there is often a distance of 4–5 m, and in this intervening space the stem lies close along the ground, perhaps covered with debris Also, adventitious roots may be given off which anchor the stem, and doubtless are of further use with regard to the food-supply

The stem, growing to 4 cm in diameter, is dark brown in colour, and smooth; the nodes are 7–9 cm. apart, and usually slightly swollen. Prickles are practically absent From almost any portion adventitious shoots may arise, which are characterized by very vigorous growth. Although very slender, the stems may grow erect without support to a height of 1 m. or more, further growth resulting in the shoot bending over and finally touching the ground. Here they continue their rapid growth, and bear leaves, which stand upright with their expanded laminae facing the incident rays of light. As adventitious shoots frequently arise high up on the plant, they are important in reaching the new positions of support, either on the same tree or on adjacent trees. Lateral branches normally arise where the stem is growing in the sun. They are at first usually at right angles to the main axis, but upon reaching the branches of the support grow upwards and give rise to more shoots. At other times, failing to come into contact with a support, they hang down, forming with other branches a divaricating reticulation, upon which masses of leaves are borne. The divisions of the leaves assist further in the formation of a "leaf-mosaic," whose efficiency may be judged by the manner in which the supporting tree is often hidden from sight.

In the more exposed portions of the forest the species scrambles over low-lying shrubs, forming a dense mass, with interlacing branches, which have a tendency to droop, and thus often hide the support.

B. LEAF.

(i.) *Leaf-form.*

Leaves 3–5-foliate; leaflets 4–5·5 cm. long, orbicular-ovate or orbicular-oblong, coriaceous, acute, rounded or cordate at base, irregularly toothed, usually pubescent beneath. Petioles 4–6·5 cm. long; subpetioles vary in length, terminal 4–5·5 cm. long, basal 0·5–1 cm. long. Prickles numerous on petioles and less numerous on subpetioles, usually absent from midrib.

Shade leaves: Adult, subcoriaceous; juvenile, membranous, and often brightly pigmented, being reddish-brown in colour.

(ii.) *Leaf-anatomy.*

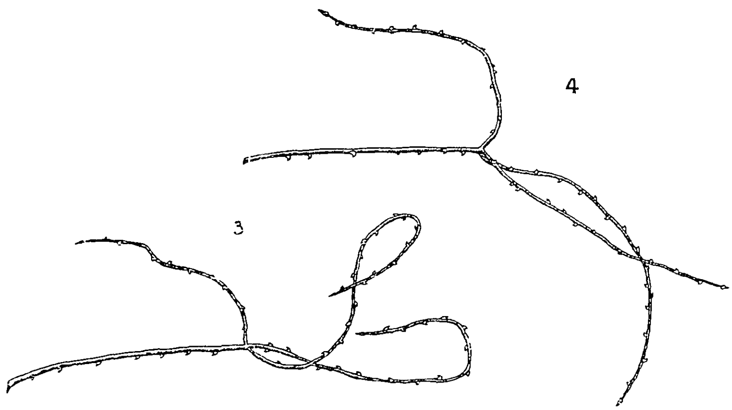
(*a.*) *Sun Leaf*.—Epidermis: Both upper and lower epidermis have a well-developed cuticle, the upper being especially thick; stomata on lower surface only, and level with the epidermal cells. Hypodermis: A single layer of large cells with collenchymatous walls inside both upper and lower epidermis. Chlorenchyma: Palisade tissue—2–3 layers of elongated cells, rather loosely packed. Pneumatic tissue—6–8 layers of irregular cells, more or less rounded; intercellular spaces very large. Vascular bundles: Collateral, surrounded by a well-developed sheath of thick-walled parenchyma, the cells below the vascular bundle having their walls especially thick. Leaf-margin is strengthened by 2–3 layers of collenchyma, which extend for a few cells' length along both surfaces. Crystals of calcium oxalate are present in the hypoderm and the chlorenchyma in the form of aggregate crystals.

(*b.*) *Shade Leaves.*—Shade leaves have most characteristics in common with exposed leaves. The variations are—(1) Many cells of the hypoderm have chloroplasts; (2) cuticle is not so well developed; (3) less strengthening of the leaf-margin; (4) *pigment* may be present. The cells of the upper hypodermis and the first row of palisade cells often contain abundant anthocyan, which is scattered to a less extent throughout the rest of the chlorenchyma.

(c.) Rubus cissoides.

A. LIFE-FORM.

This species occurs in the forest in most situations, and though not growing to a great size, nevertheless exhibits greatly varying habits of growth. On the smaller trees and on the shrubs its growth resembles that of other species of *Rubus*, but, like *R. subpauperatus*, it abounds on the outskirts of the forest, where it forms straggling masses with leaves reduced to midribs.* In numerous cases certain shoots scramble into a tree, in whose shade the leaf-blades are well developed. Other branches of the same plant stretch along the ground and form the wiry masses characteristic of the plant in these situations, while branches between these two portions bear leaves which exhibit all gradations in leaf-reduction (Plate XXIII). The prickles, unlike those in *R. subpauperatus*, are absent from the stem, and are practically absent on the leaf-lamina, although as many as three may sometimes be present. The stems are covered with a greyish-brown bark, and grow to a thickness of 5 cm. in diameter. Leaves



FIGS. 3, 4.—*Rubus cissoides.* Climbing-leaf.

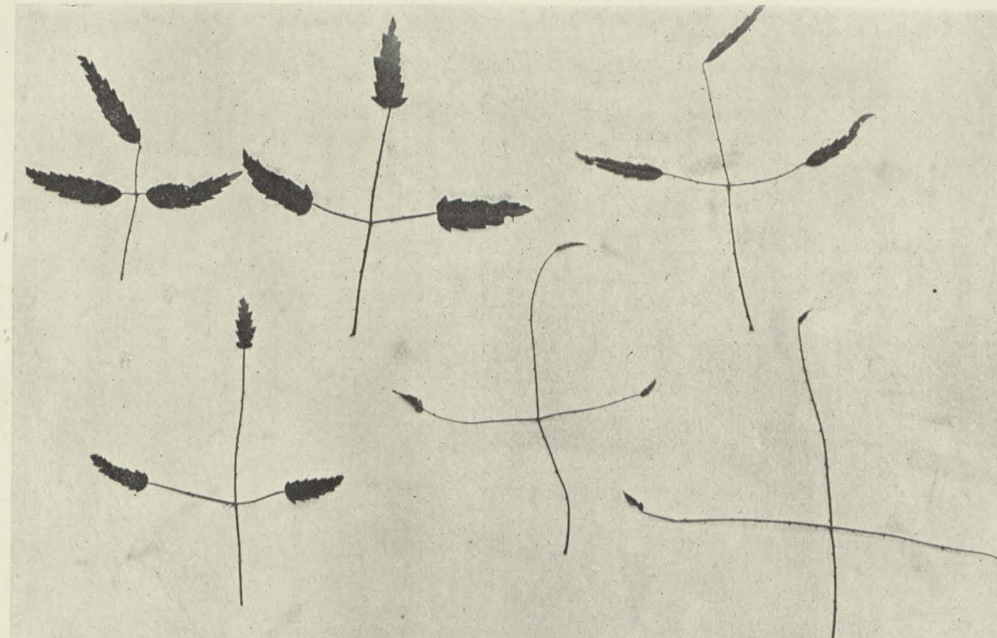
with smaller laminae possess more prickles, while in the final stages of reduction the midrib may bear as many as 25. The prickles form a feature by which this species can be readily distinguished from *R. subpauperatus*, for in *R. cissoides* they are yellowish, but in the latter red.

Especially characteristic of *R. cissoides* is the production of adventitious shoots. These are green, thus being fitted for photosynthesis, and the internodes are relatively long — *e.g.*, 15 cm. or more — and in some cases 1·7 cm. in diameter, and stand erect for 2·5–3 m. The leaves of such shoots are almost reduced to greatly elongated midribs. A typical shade leaf has a terminal leaflet 5–7 cm. in length, and rather shorter lateral leaflets; but the leaves of adventitious shoots may have their terminal midrib 21 cm. long and their lateral midribs 13 cm. As these leaves project from the stem at right angles, and bear large numbers of prickles, it can be seen how important they are in aiding the plant to reach new supports.

Very often the liane is found straggling along the forest-floor for nearly 10 m. In places where the undergrowth is scanty *Rubus cissoides* forms

* This is the so-called var. *pauperatus* (J. B. Armst.) T. Kirk.

Face p. 322.



Rubus cissoides. Leaves, showing stages in leaf-reduction.

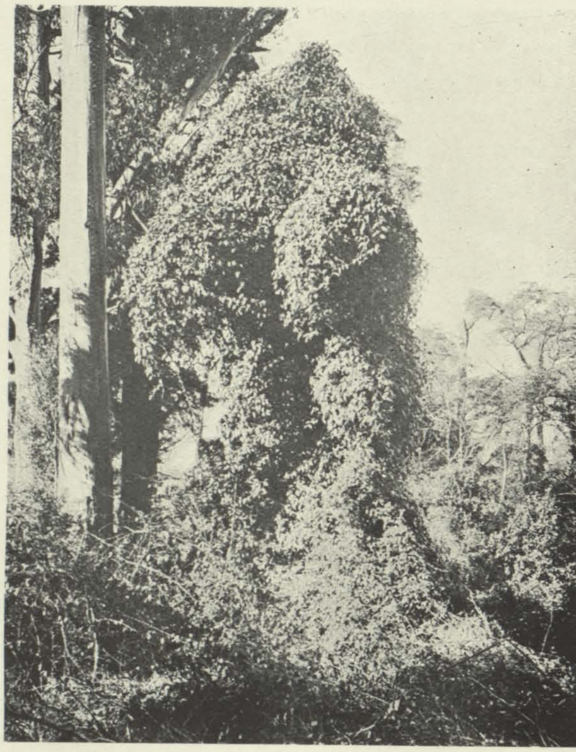


FIG. 1.—*Tetrapathaea australis* growing on support.

FIG. 2.—Interior of the forest, showing *Podocarpus dacrydioides* with reticulating roots.

FIG. 1.—*Rubus subpauperatus* stretching up beside a supporting white-pine.

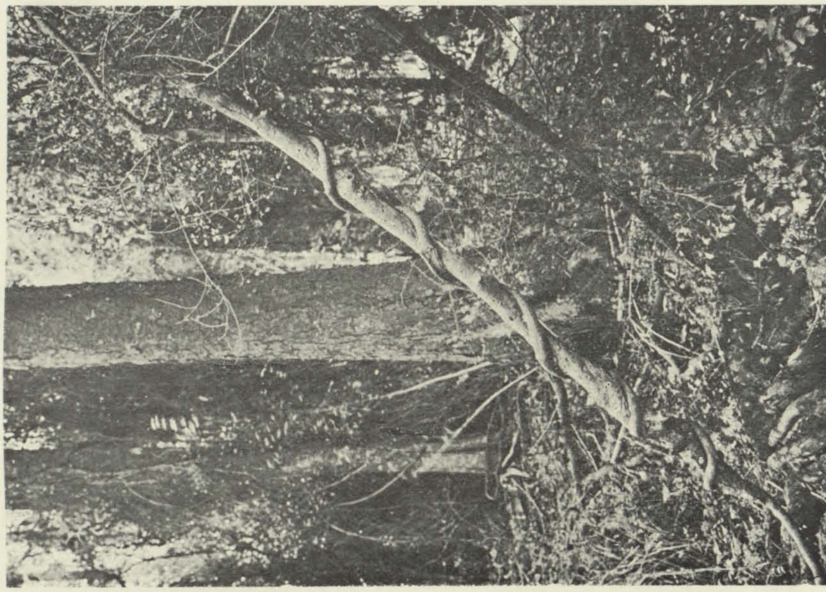
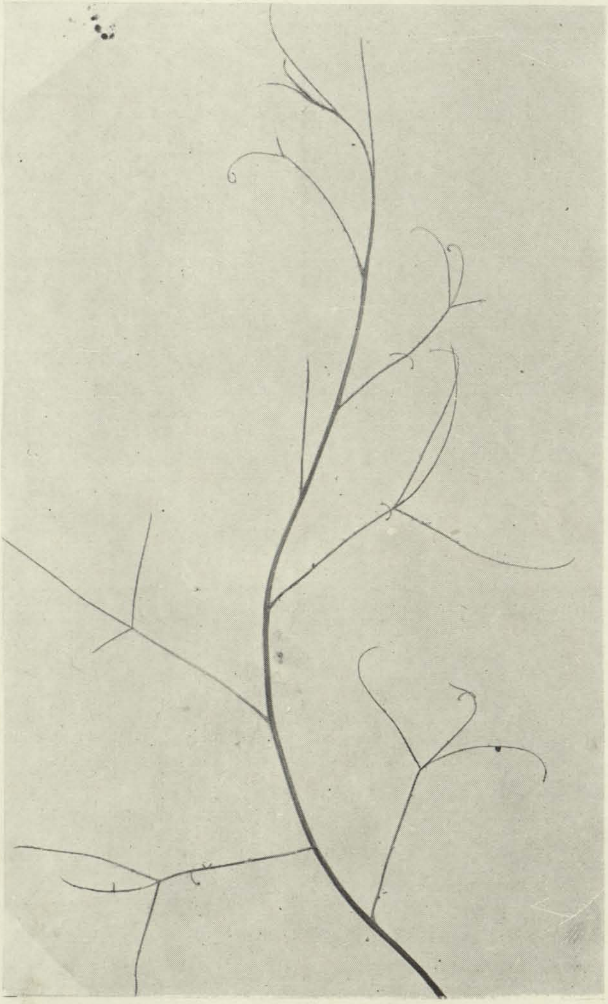


FIG. 2.—*Muehlenbeckia australis*. Twining-stem round former support.



Rubus cissoides. Showing curving of climbing-leaves.

extensive flattened masses, but where there is more abundant vegetation it may push its way among the tangled branches and increase the density of these masses.

It has been stated above that in exposed situations the leaves are reduced to midribs. However, the reduction in this species cannot always be a reaction to environmental factors, for in very damp shady stations certain individuals occur which have their leaves similarly reduced, while adjacent plants show no reduction. Possibly there may be two varieties—one in which the leaves show reduction in the open only in response to some environmental stimulus, and another in which leaf-reduction is a fixed hereditary character.*

B. LEAF.

(ii) *Leaf-anatomy.*

(*a*) *Shade Leaf* —Leaf 3–5-foliate ; laminae 4–7 cm. long, subcoriaceous, ovate-oblong or ovate-lanceolate, base truncate; margin deeply serrate. Yellow prickles on under surface of petiole ; few or absent on subpetioles and midribs

(*b*) *Sun Leaf.*—Leaf reduced almost to midribs; terminal 9–12 cm., lateral 7–9 cm. Petiole 6–7 cm. Prickles in large numbers on both petiole and midribs.

(i.) *Leaf-form.*

(*a*.) *Shade Leaf.*—Epidermis: Cells almost isodiametrical; well-developed cuticle; stomata lower epidermis only. Hypoderm: One layer of thick-walled collenchyma, extending a short distance from leaf-margins. Chlorenchyma: Palisade—2 layers cells; upper rather closely packed, second layer looser. Spongy—4–5 layers irregular cells; intercellular spaces large. Calcium oxalate in aggregate crystals. Vascular bundles surrounded by collenchymatous sheath; stereome scattered irregularly round the bundles; on under surface of midribs a strengthening mass of 4–5 layers of collenchyma.

(*b*) *Sun Leaf* —Epidermis: Cuticle very thick; stomata lower epidermis only Hypoderm: One continuous layer beneath epidermis; cells large, isodiametrical; beneath lower epidermis it forms patches of cells beneath the vascular bundles, and extending a short distance on each side. Chlorenchyma. Tissue separated by vascular bundles and their sheaths, which extend from the upper to the lower epidermis. Palisade—Cells elongated and very closely packed. Spongy—Not sharply separated from palisade; the cells are elongated in the same direction as the palisade, and intercellular spaces are small Mechanical tissue is more strongly developed than in shade leaves. Leaf-margin protected by 3–4 layers of collenchyma; chlorenchyma at the margin composed of palisade cells with small ends facing the leaf-surface.

(*c*) *Assimilatory Midrib* —Epidermis: Thick walls; outer walls convex; stomata distributed round whole surface. Hypodermis: One layer isodiametrical cells Chlorenchyma · A continuous ring 2–3 cells thick; on upper surface cells elongated, forming a palisade tissue; on under surface irregular cells and intercellular spaces which connect with the stomata through breaks in the hypoderm. Vascular system: A ring of bundles lies close to the chlorenchyma, the dorsal bundle being greatly enlarged Medulla composed of large spherical cells with thin walls.

* For a fuller discussion of this important topic see Cockayne, L., 1901, pp. 291–95.

(*d.*) Rubus subpauperatus.

A. LIFE-FORM.

Members of this species are scattered throughout most parts of the forest, and attain a size at least equal to that of any other of the lianes. Their foliage may be expanded upon the branches of the highest trees, and between the foliage and the ground, the stems stretching up, as in *R. australis*, beside the bare stems of supporting taxads, attain considerable thickness; sometimes they are as much as 16 cm in diameter, and are thickly covered with rough, dark-brown, scaly bark (Plate XXV, fig. 1). Even from such stems as these, adventitious shoots arise, which in the more open situations do not grow to a great length, but give off numerous leafy branches, so that the adult stem is often covered for a considerable portion of its entire height by these hanging leafy festoons Among the low-lying trees and shrubs the liane, as in other species of *Rubus*, scrambles over the support and among the branches In the more shaded stations the internodes are longer than those of more exposed plants, and from stems trailing along the ground numerous adventitious roots arise Beyond the outermost fringe of forest-trees *R. subpauperatus* forms dense masses 1–2 m. in height The plants here very quickly cover any low-growing shrub with their wiry interlacing branches, and spread over extensive areas. This is due to the rapid elongation of their shoots, which may bridge the spaces between adjacent shrubs, or which may trail along the ground, and thus reach supports many metres distant Both leaves and stems are thickly beset with prickles, which by their grasping action are especially suitable for this straggling growth over low supports. Moreover, the prickles enable the plants to use supports of greatly varying nature, such as branching shrubs and trees, tree-trunks with rough bark, and even vertical rock-faces.* The growth of plants in the open results in a shortening of the internodes and excessive reduction of leaf-surface This reduction appears to be correlated with increased transpiration, for when a plant is exposed to southerly winds the greatest reduction is on its south side, although this is shaded from the bright sun. Again, when the prevailing winds are from the north it is on the north side of the plant that the leaves are most reduced.

B. LEAF.

(i.) *Leaf-form*

(*a*) *Shade Leaf.*—Leaf 3–5-foliate, terminal leaflet, lamina 6–8 cm. long; lateral leaflets slightly shorter; when 5-foliate the 2 basal leaflets very small (2–3 cm). Leaflets subcoriaceous, glabrous, linear-lanceolate or linear, acute, base truncate or obtuse, margin serrate. Petiole 7–9 cm; terminal subpetiole 3–4 cm., but other subpetioles at most 5 mm. Prickles numerous on back of petioles, in smaller numbers on subpetioles and midribs.

(*b.*) *Sun Leaf*—Plan of structure similar to that of shade leaf, but much smaller. Lamina at most 5 cm. long, and very narrow; but there is no sharp distinction between the two types of leaves, for a single plant may bear leaves which show all gradations in leaf-reduction

* This does not refer to Riccarton Bush

(ii) *Leaf-anatomy*

(*a.*) *Shade Leaf.*—Epidermis: Cells slightly elongated in axis parallel to the leaf-surface; thick cuticle; lateral walls thinner and irregular. Hypoderm: A single layer of collenchymatous cells on both leaf-surfaces in the regions of the vascular bundles; cells are large and isodiametrical. Chlorenchyma: Palisade — In regions between two adjacent hypoderm layers the tissue touches the epidermis and is 3 layers in thickness; beneath the hypoderm it is composed of 2 layers. Cells are long and closely packed. Tissue occupies nearly one-half of leaf-thickness. Spongy—5–6 layers thick; cells are elongated and abutting by their ends, forming large intercellular spaces; chloroplasts are comparatively numerous. Vascular bundles surrounded by thick-walled parenchymatous sheath. Mechanical tissue: Each bundle-sheath is connected with the hypoderm by collenchyma, the whole forming an I-shaped girder, which is further strengthened by stereome at the base of each bundle; each half of a leaf-blade contains about 5 of these girders; at the base of the midrib the mechanical tissue is very abundant. Leaf-margin is strengthened by thickening of the walls of the epidermis and hypoderm; chlorenchyma cells are elongated and radially arranged. Calcium oxalate in aggregate crystals.

(*b.*) *Sun Leaf.*—Epidermis: Cuticle very thick. Hypodermis forms an uninterrupted ring beneath the epidermis. Chlorenchyma: Palisade—Cells more elongated, and more closely packed. Spongy—Cells more spherical, and intercellular spaces thus lessened.

The Leaf of the Species of Rubus as a Climbing-organ.

The value of the leaf as a climbing-organ arises from four characteristics: (*a*) The leaves extend from the shoot at right angles, and are therefore in the position most suitable to overcome vertical strains, so that the shoot may maintain its upright position and thus grow to a greater height. This is shown by the great height of many adventitious shoots. In many cases in which the leaves can find a support, and so prevent the shoot from slipping down, shoots as slender as 1·7 cm. in diameter may grow upright for 7 m. (*b*) Lateral strains are overcome by means of the prickles, which, on account of their hooked shape, form efficient anchors. The effect of the strain is minimized by the position of the prickles—a position which causes the strain to be distributed along the whole petiole. It is evident that the prickles also are an important factor in preventing the slipping-down of an upright shoot (*c.*) Assisting in overcoming such strains is the downward curvature of the apex of the lamina. The power of resistance of this is perhaps very small in comparison with that of a prickle, but it has the advantage that it acts where there is little resistance by prickles, the prickles being more commonly absent from the lamina. (*d.*) The strains may also be slightly overcome by the top of a leaf coming into contact with a support. This is due to the hooked arrangement which results from the irregular growth of the petioles at the base of each lamina.

The *Rubus* leaves of most importance in climbing are those of *R. cissoides* var. *pauperatus*. These are practically devoid of laminae, and the midribs, armed with sharp recurved prickles, grow to a great length—often 24 cm These usually project from the petiole at right angles, or may be variously curved and twisted, and so are highly efficient in grasping supports (figs. 3 and 4). In a few cases studied this tendency of the midribs to curve was so great that they were practically encircling supporting twigs to which they had become attached. *It may, therefore, be said that in this species the leaf has changed its function, and has become a distinct climbing-organ.*

Not only are the leaf-prickles of importance to the plants in climbing, but the stem-prickles, which persist for a great length of time, function to some extent in this regard. *They are practically absent from the stems of* R cissoides, *and it is interesting to note this absence going hand-in-hand with the great development on the leaf-midribs of that species* In *R. schmidelioides* a few prickles are present In *R australis* they are more numerous, and in *R. subpauperatus* they are very abundant. On stems of the last-named species 1 cm. in diameter, many of the prickles can individually withstand a strain of 900 grams The average for the species is about 650 grams, and in the other species this same strain is the maximum which they can withstand

3. Metrosideros hypericifolia.

A. Life-form.

This species is by no means common in the Riccarton Bush, there being only about six individuals These are confined to the damp shaded portions of the interior, where they grow on the trunks of large trees to a height of 10 m The stems are 3–4 cm in diameter, and at about 3 m from the ground they usually give off numerous branches, whose growth is often more or less erect, but which may be inclined to varying degrees. These branch again, so that the whole plant forms a mat-like growth round the support Leaves borne on these branches are arranged in two lateral rows, though small, they are in large numbers, forming a dense mass of foliage When brightly illuminated the branches hug the support, against which the leaves are closely pressed; but in shaded places growth is more vigorous, and branches may project from the support for 50 cm, and by their interweaving form dense masses Usually the climbing-roots at the basal portions of the liane are dead, and the stem swings freely Branches which arise near the ground often grow out over semi-exposed surface roots, and finally on to the surrounding forest-floor, where they become covered with debris and bear roots which penetrate the soil for a depth of 10–12 cm. From these stems leafy branches may arise erect for a few centimetres, or, as is more common, they lie along the ground-surface

These surface-growing shoots are mostly found in contact with the roots of the kahikatea, which extend along the surface of the ground for many metres The main shoots of the liane keep in contact with the roots, while lateral shoots branching off usually grow over the forest-floor, giving off absorbing-roots The stems which thus grow along the taxad-roots are often broken by animals and other means, but the severed portions continue their growth, thus showing the efficiency of the absorbing-roots * The anchoring-roots which attach the liane to the support are usually diageotropic, but it is evident that contact with the support may overcome the influence of gravity. The factors influencing the development of roots

* Cockayne, L. (1909A, p 14), describes how in the forest of Stewart Island there is often a stout creeping stem beneath the loose peaty soil many yards in length, from which climbing shoots may be given off, "the plants of adjacent trees in this manner being at times merely branches of one plant"

seem to be shade and moisture. Root-hairs are usually absent from the anchoring-roots, but in a moist chamber they arise in large numbers. If the roots fail to come in contact with a support they become attenuated, and remain unbranched, but in other cases they branch freely and grow to a length of 3–4 cm. In more exposed situations the plants thus growing along taxad-roots do not elongate very much, but tend to become more bushy. The leafy branches are very numerous, and by their interweaving support each other, so that the plants form small leafy clumps up to 40 cm. in height

B. LEAF.

(i) *Leaf-form.*

Leaves distichous, glabrous, subcoriaceous, sessile or subsessile, 0·8–1·5 cm long, ovate-oblong or ovate-lanceolate; acute, apiculate, or obtuse.

(ii) *Leaf-anatomy.*

(*a*) *Shade Leaf.*—Epidermis: Cells in transverse section of leaf isodiametrical, outer walls slightly thickened Stomata: Lower surface only; slightly raised above level of epidermal cells Chlorenchyma: Palisade—Usually 3 layers cells, elongated, but not closely packed. Spongy—Cells roundish or irregular; intercellular spaces very large; tissue comprises two-thirds of leaf-thickness. Vascular bundle: Surrounded by a sheath of thick-walled stereome, 1–2 layers thick. Calcium oxalate: In chlorenchyma in aggregate crystals Secretory cavities occur beneath the epidermis, and are lined by a distinct epithelium; they are described by Solereder (1908, p 353) as schizogenous in origin; more abundant on upper surface. Leaf-margin: Epidermal cells are here larger, and have thicker walls.

(*b*) *Sun Leaf*—Epidermis: Cell-walls thicker Stomata level, with epidermal cells, ratio of palisade to spongy tissue is greater than in shade leaves. Palisade cells are more closely packed, and intercellular spaces are smaller.

(*c*) *Climbing-organ.*—(i) Climbing-roots: The vessels of the central cylinder have small lumina and very thick walls. Endodermis forms a distinct ring of large, thin-walled cells Cortical cells in young roots contain chloroplasts, but in older roots the walls of the outer cells become lignified, and the cells lose their contents, forming a strong peripheral band of mechanical tissue. Root-hairs are absent, but can be induced by placing the roots in a moist chamber

(ii) Absorbing-roots. The vessels have slightly larger lumina, and the cortical cells continue their functions, this resulting in the absence of peripheral mechanical tissue. This distribution of mechanical tissue is in both types of root advantageous for resisting the particular strains to which the roots are exposed Thus the anchoring-roots must resist vertical strains, due to the weight of the plant, and lateral strains, due to the action of the wind and to growth in circumference of the support. In the absence of peripheral mechanical tissue the roots would be subject to injurious torsion; and, further, the tissue prevents injury to the living cells through crushing or attrition; but in the absorbing-roots the axile arrangement of mechanical tissue is the more advantageous, for they have to withstand pulls from various directions, and by the axile arrangement of mechanical tissue the stress is most evenly distributed.

4. Muehlenbeckia australis

A. Life-form.

This is one of the most widespread inhabitants of the forest, growing both in the shade and in the bright sun at the forest-edge; in the damp undrained area and in the neighbourhood of drains, and in the driest exposed situations. In the forest-interior it is found twining round the thin trunks of young trees and shrubs. Its direction of twining is not uniform, as in *Parsonsia*, but different individuals twine some right and some left Further, a single plant may commence its growth as a sinistrorse twiner, and after a few turns become displaced by a projecting branch of the support, beyond which it continues its twining in a dextrorse manner. The highest position of the liane is on the branches of the tallest trees, 30–40 m from the ground; but in no case does the liane twine round their trunks. On the contrary, the liane-stems usually hang freely from the supporting branches at a distance of 1–5 m from the large trunk, or perhaps quite near the latter, either growing fairly erect from the root or with their stems coiling first along the ground for a distance of fully 12 m. From these coiling stems adventitious roots pass off, which sometimes grow near the surface and attain a length of 1 m. The hanging stems almost invariably are greatly twisted, suggesting that they commenced their growth on smaller supporting trees, which they finally strangled; indeed, the climbing-stem frequently encircles a portion of some stem which has been strangled (Plate XXV, fig. 2). The condition of these decaying remains shows how intense has been the "struggle" between liane and support Both stems may be greatly compressed, and the tissues of the support between the liane-coils may be growing out and nearly surrounding the liane. But it is a significant fact that in no place has a tree been found which indicates that it has ever been tightly surrounded by one of these *Muehlenbeckia* stems.

On the top of the supporting tree the liane-shoots branch freely, the branches, interweaving and twining round each other, forming an efficient platform for the display of foliage Many shoots project beyond the support, and, continuing their growth, gradually hang down. The growing apex, however, is apogeotropic, and upon coming into contact with the hanging portion commences to twine upward round this same shoot

In the more exposed portions of the forest, where the supporting trees have numerous branches, the *Muehlenbeckia* shoots hang down in large numbers, and on their lateral branches bear large masses of foliage. The species is very abundant at the edge of the forest, where it is found growing over low shrubs. Here the liane forms large straggling masses, whose slender stems do not grow so long as in the forest, but bear numerous branches which, unable to grow erect in the absence of a support, interweave freely, and thus form cushion-like masses In these exposed situations the species is almost deciduous. A few plants lose all their leaves; others, which are more sheltered, are semi-deciduous, finally, in the shelter of the forest, the plants are evergreen

A most noticeable feature of the species is the production of adventitious shoots. These arise in autumn from almost any part of the adult, being found on the leafy stems at the top of the support, and on the adult stems trailing along the forest-floor. Although at most 0·7 cm in diameter, they can grow erect for 1–5 m, after which they bend over until they touch the ground; but if the terminal shoot be injured a lateral shoot may arise from any part of the main one, and thus finally may reach a height of 2 m. or more. At other times they project from the liane almost horizontally, and in many places finally rest on plants which are 2–3 m. distant. They thus illustrate the suitability of the term "searcher shoot," which is applied by Goebel to such organs (1905, pp. 453–54), for, in obtaining new supports for the liane, they are of immense importance. During the first metre of their growth they exhibit no nutation or torsion, but after attaining this length the shoot, even in the absence of a support, slowly commences sinistrorse spiral growth. If it comes into contact with a support the position of the latter determines the direction of the twining—*i.e.*, it may be sinistrorse or dextrorse.

A. LEAF.

(i.) *Leaf-form.*

Leaves alternate, petiolate, 4·5–6·5 cm. long; ovate, apiculate, cordate or truncate at base; membranous or subcoriaceous; glabrous, entire, margin undulate. Petioles 1–1·5 cm. long, bent in varying manner, so that the lamina usually lies facing the light. Dorsal groove along entire length. Stipules membranous, closely pressed to stem, deciduous. Shade leaves differ but slightly from sun leaves; they are slightly larger and more membranous, while the petioles are a little longer.

The above description applies to an ordinary adult leaf, but on an adult two other distinct types of leaves occur—viz., (*a*) reniform, (*b*) trilobed with acuminate apex—which arise in a definite order. The first leaf to appear on a lateral shoot is small and reniform. Either at the next node or two or three nodes distant there is borne a leaf which approaches more or less closely to the 3-lobed acuminate type, this being succeeded by the usual adult type. The same sequence is apparent in developing seedlings, and there the three types, which are very distinct, are connected by intermediate forms The series, however, is sometimes broken by the omission of any stage *except the first.* Succeeding the reniform leaf is one in which the indentation at the leaf-tip is slightly reduced, and two small incisions are present, one on each side of the tip. These incisions in later forms become more and more marked, and at the same time the leaf-tip becomes at first flat, and then produced into an acuminate apex. At this stage the leaf belongs to the 3-lobed type. In leaves succeeding this the incisions become smaller, and disappear in the final type, which has an entire undulate margin.

(ii.) *Leaf-anatomy.*

(*a.*) *Shade Leaf* (Juvenile).—Epidermis: Upper epidermis consists of large ovoid cells with thin walls; lower epidermis, smaller cells; stomata, lower surface only, slightly raised. Chlorenchyma: Palisade is poorly developed; cells in uppermost layer of mesophyll are almost isodiametrical, and are loosely packed; a collecting layer beneath this connects with a spongy tissue of about 3 layers of spherical cells loosely arranged; these cells differ from the palisade in their tendency to elongate parallel with the leaf-surface, and in their containing few chloroplasts. Leaf-margin: Outer walls of epidermal cells very convex and thickened; chlorenchmatous cells almost spherical. Vascular bundle poorly developed; no distinct sheath Calcium oxalate: A few aggregate crystals.

(*b.*) *Sun Leaf* (Adult)—Epidermis: Striated cuticle; lateral walls also thickened. Stomata level with epidermal surface. Hypoderm: Above and below midrib; one row of spherical thick-walled cells. Chlorenchyma: Palisade—3 layers of elongated cells arranged in vertical rows; tissue comprises one-half of leaf-thickness Spongy cells nearly spherical; intercellular spaces small Leaf-margin Epidermal walls thicker than in shade; chlorenchyma cells more closely packed, and showing tendency to elongate as in palisade tissue. Vascular bundle: One layered parenchymatous sheath. Calcium oxalate · Crystals in upper spongy tissue.

5. Muehlenbeckia complexa.

A. Life-form.

The members of this species are confined to the outer portions of the forest, where the plants receive a large amount of light; they are much branched and of comparatively low growth The species is most abundant in the drier, well-drained soil. The climbing-stems—at most 2 cm in diameter—are covered with a rough blackish bark and trail along the forest-floor for many metres, rooting freely at the nodes. When they reach any thin stem they twine round it, and, as in *M australis*, the twining is either sinistrorse or dextrorse, the former being the more common, and, likewise, any stem may change its direction of twining The twisting of adult stems, as well as the position of the lianes in relation to their supports, show how former supports have been strangled; but these occurrences are not so well marked as in *M. australis*. This is due partly to the small growth of *M. complexa*, which nowhere rises higher than 9 m, and partly to the nature of the supporting trees and shrubs These, as above mentioned, are much branched, and often form dense masses of the divaricating life-form. In reaching to the tops of these plants the liane *shows a tendency to scramble rather than to twine*, interlacing branches being more favourable for scramblers than for twiners; but, although twining by *M complexa* is by no means common in such places, the twining, when it does occur, prevents the liane from slipping from the support In the light at the edge of the support the stems branch freely, and the lateral branches bear large numbers of leaves, which, with the stems, form compact masses These stems, although very slender, arise in large numbers, and their tendency to twine round each other is marked By mutual support they may thus project for nearly 1 m., and by so doing come into contact with new supports, which soon become covered by the dense masses of liane-stems. These are greatest on the tops of the supports, where they grow so close that no light can penetrate the dense mass Such masses are especially characteristic of the plants of the forest-margin. Here the only supports are shrubs, which vary in height up to 3 m On these the lianes form masses which by their weight bend the shrub down to the ground. They continue their branching, and the intertwining branches soon obscure the support from view, the whole mass then resembling a rounded cushion, often from 1 m to 2 m. high, and from to 2 m to 4 m. across.

B. Leaf.*

(1) *Leaf-form.*

Leaves alternate, petiolate, varying in shape and size, 0·5–1·5 cm long, orbicular or obovate, rounded or obtuse at tip, borne singly or in pairs

* Like all the descriptions in this paper, this refers to the Riccarton Bush plant alone, Were the "species" being dealt with for the whole of its area of distribution. the differences in leaf-form would be much greater.

at ends of minute arrested branches, base cordate or truncate, slightly coriaceous, glabrous, margin entire. Petioles 3–5 mm., rounded at base, towards the lamina grooved dorsally, puberulous. Stipules membranous, closely pressed to stem, deciduous.

(ii.) *Leaf-anatomy.*

(*a.*) *Shade Leaf.*—Epidermis: Cells of upper epidermis large; walls slightly thickened, outer walls convex; lower epidermal cells smaller and outer walls straighter; stomata on lower surface only. Chlorenchyma: Palisade and spongy tissues not sharply differentiated; two upmost layers of cells isodiametrical and loosely packed; beneath these, 3–4 layers of cells loosely packed and with large intercellular spaces. Leaf-margin: Cells larger; walls more convex and more thickened. Bundle-sheath poorly developed. Calcium oxalate in aggregate crystals.

(*b.*) *Sun Leaf.*—Epidermis: Cell-walls thicker; anthocyan often in both upper and lower epidermis. Chlorenchyma: Palisade—2 layers cells slightly elongated, and more closely packed. Spongy—Intercellular spaces smaller.

6. Parsonsia heterophylla.

A. Life-form.

Although not so abundant as *Muehlenbeckia australis*, this species is quite as widely distributed. It is present in its largest numbers on trees and shrubs at the forest-margin. The stems, covered with a rough greyish bark and slightly swollen at the nodes, are at most 3–4 cm. in diameter. They reach to a height of fully 20 m., and before doing so may trail along the forest-floor for 12 m. or more, adventitious roots often arising from the trailing portions. The stems of plants in the forest-interior hang from the supports in a manner similar to those of *Muehlenbeckia australis*, and, like these, they are often twisted and encircle portions of some former support, which has been strangled. The stems differ in behaviour from those of *M. australis* in that the twining of *Parsonsia* is always sinistrorse. They are thus of less efficiency in gaining support, but they possess a marked superiority in that they can twine round much thicker supports, the climbing-stems often being found coiled round tree-trunks up to 25 cm. in diameter. The stems show a marked tendency to twine round each other, in many cases lateral shoots intertwining with the primary. By this mutual support they have a better chance of reaching higher positions. In bright light the stems bear leafy branches, which form a dense covering on the support. The stems may stand erect, but more commonly they lie horizontally on the top of the support. Others project from the latter, and gradually bend down until they hang almost vertically. The stems then commence to twine back round themselves, and should they reach any one of the many shoots which arise from these hanging stems—shoots which at first stand erect and then stretch outwards—the primary shoots may twine round one of these, and the two together thus reach some new support. In such positions on a support the tendency of stems to intertwine is very marked, and "ropes" of as many as 8 stems often project from the support for fully 2 m. These "ropes" are the chief means by which distant supports are reached, for, although adventitious shoots arise from various parts of adult plants, they are not numerous, and, unlike those of *Muehlenbeckia australis*, never attain a great length, while their growth is very slow.

B. LEAF.

(i.) *Leaf-form.*

Each adult plant may be said to have a typical leaf-form, but this is not constant. Leaves are alternate, petiolate, coriaceous, upper surface dark green and slightly glossy, under surface pale green or yellowish-green and dull, 4–7·5 cm. long, ovate, oblong-ovate, or ovate-lanceolate, acute, margin entire; petiole 1–2 cm. long. Besides any one of these forms, any individual may bear at the base of lateral shoots leaves which exhibit many juvenile leaf-forms, the most common being orbicular-ovate and lanceolate or linear with 2–6 rounded lobes on each side.

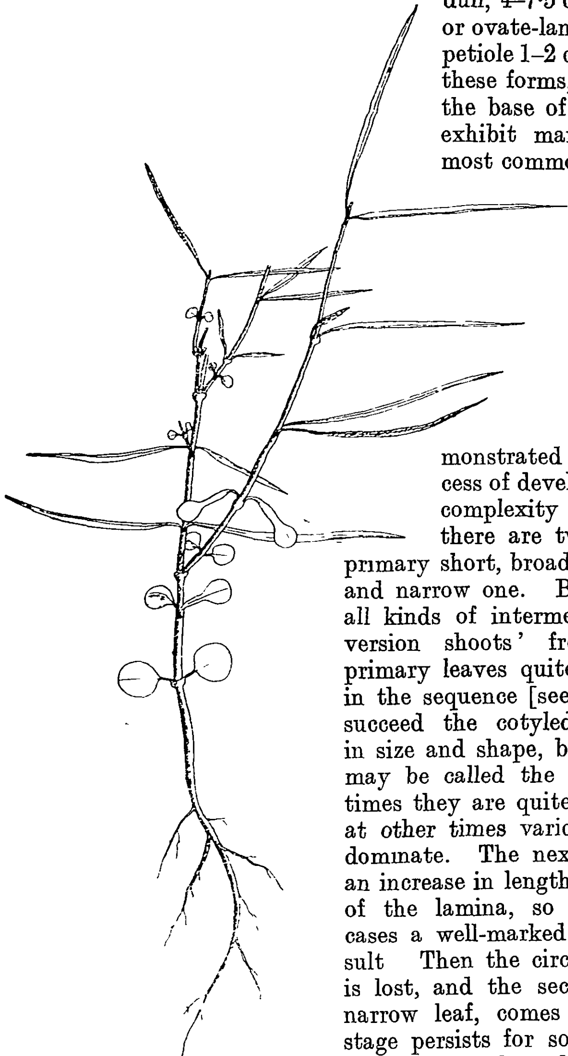


FIG. 5.—*Parsonsia heteiophylla.* Seedling.

The leaves of seedlings present a remarkable diversity in shape, and at first no connection between the forms is apparent. But in a careful study L. Cockayne demonstrated that there is a definite process of development and change: "This complexity arises from the fact that there are two distinct types of leaf—a primary short, broad leaf, and a secondary long and narrow one. Between these two there are all kinds of intermediates, and, moreover, 'reversion shoots' freely occur, thus bringing primary leaves quite out of their proper place in the sequence [see fig. 5]. The leaves which succeed the cotyledons are certainly variable in size and shape, but they are always of what may be called the short, broad type. Sometimes they are quite small and almost circular, at other times various varieties of oblong predominate. The next phase of development is an increase in length and narrowing of the base of the lamina, so that in the most extreme cases a well-marked spathulate leaf is the result Then the circular leaf-apex of this latter is lost, and the second leaf-form, a long and narrow leaf, comes into being. This second stage persists for some considerable time—*i.e.*, there is a prolonged juvenile form—but sooner or later, when by the twining of the ever-lengthening stem round its support the bright light is gained, the adult and third form appears, the leaves large and broad, and of a more or less oblong character" (Cockayne, 1908, pp. 486–87).

The direction in which seedling-leaves face exhibits to a marked extent the arrangement of leaves so as to receive a maximum amount of light.

(ii.) *Leaf-anatomy.*

(*a.*) *Shade Leaf* (Juvenile).—Epidermis: Cells in transverse section isodiametrical, outer walls slightly convex and a little thicker than lateral walls; in upper epidermis cells larger than in lower; stomata on under surface only, level with epidermal surface. A few unicellular hairs are scattered on both leaf-surfaces. Chlorenchyma: Palisade—1 layer cells cuneate, with base towards upper epidermis. Chloroplasts most numerous towards this base. Tissue occupies about one-sixth of leaf-thickness. Spongy—Beneath palisade 1 layer of fairly regular collecting-cells, with numerous chloroplasts; remainder of spongy tissue is composed of irregular cells, 5–6 cells thick, whose connections leave large intercellular spaces; chloroplasts few in number. Vascular bundle surrounded by well-developed sheath of spherical parenchymatous cells. Leaf-margin: Epidermal cells with thick cuticle; chlorenchymatous cells more or less spherical. Anthocyan often present in palisade layer. Calcium oxalate: A few aggregate crystals scattered in upper spongy tissue.

(*b.*) *Sun Leaf* (Adult).—Epidermis: Thick cuticle; lateral walls also thickened. Hypodermis: Present beneath upper epidermis in regions of vascular bundles; cells more or less spherical and thick-walled. Chlorenchyma. Palisade—Beneath hypoderm 2 layers, in other places 3 layers; cells elongated and very closely packed; chloroplasts most abundant along lateral walls; each cell contains a large oil-drop; tissue comprises about one-third of leaf-thickness. Spongy—Cells more spherical than in juvenile; intercellular spaces smaller; cells with few chloroplasts. Vascular bundle: Parenchymatous sheath thick-walled. Leaf-margin: Epidermal cells greatly thickened; beneath epidermis a mass of hypoderm composed of thick-walled cells; for a short distance from the margin the hypoderm extends in 2 layers; chlorenchymatous cells spherical or slightly elongated; intercellular spaces very small. Calcium oxalate: Crystals more numerous than in juvenile. Anthocyan: Often abundant in top palisade layer and lowest spongy layer.

7. PARSONSIA CAPSULARIS *var.* ROSEA.

A. LIFE-FORM.

This species is similar in its distribution to *P. heterophylla*, but it is present in much smaller numbers. The life-form of the two species is similar, except that *P. capsularis* var. *rosea* does not grow to such a height, being found chiefly on the dense shrubs. The young stems, brownish in colour, are very elastic, and their tendency to intertwine is even greater than in the stems of *P. heterophylla*. Groups of 4–8 stems form "ropes," and, further, a number of these "ropes" may come into contact and together form a single large "rope," which thus is fairly rigid and can project from a support for a considerable distance.

B. LEAF.

(i.) *Leaf-form.*

(*a.*) Adult.—Leaves vary in size and shape from narrow-linear, 3–10 cm. long and 0·2–0·3 cm. broad, to oblong or oblong-lanceolate, 3–7 cm. long and 1–1·5 cm. broad; obtuse or subacute, coriaceous, margins usually entire or occasionally slightly lobed.

(*b*) Juvenile.—Numerous seedlings were grown by the writer, nearly all of which were similar in their leaf-development. Seed-leaves are 1–1·5 cm. long, oblong or oblong-lanceolate; they are succeeded by a pair of leaves 2–3 cm long and 0·5–0·8 cm broad at the middle, either tapering to a point both at base and at apex or broadening out at the apex and thus being almost spathulate. The next 3 or 4 pairs of leaves which arose are narrow-linear, 4–5 cm. long and 0·2–0·3 cm. broad. In 2 or 3 plants the leaves preceding this linear stage passed through stages similar to those of *P. heterophylla.*

In connection with this heterophylly, L Cockayne writes, "At this [linear] stage, in one very distinct form of *P. capsularis*, further development always stops, and the adult leaf in this case is indentical with that of the second stage of *P. heterophylla*—i e, the adult of one species is merely a fixed juvenile form of the other" (1908, p 487)

All the leaves of the seedlings grown were variegated and this variegation is of common occurrence in wild plants Along the centre of the leaf is a white strip, while at the margin the leaf is brown or reddish-brown. The upper surface of the seed-leaves is uniformly brown, and in all the lower surface is pale green.

(ii.) *Leaf-anatomy*

(*a*) *Shade Leaf.*—Epidermis Cells slightly flattened, outer walls thickened, cells of lower epidermis smaller than upper; thin cuticle, stomata on lower surface only. Hypoderm: Well developed beneath midrib; at leaf-margin there is a single layer which extends for a short distance along both surfaces Chlorenchyma: Palisade—3 layers cells elongated, but not very closely packed; tissue comprises one-fourth of leaf-thickness; each cell with a large oil-drop. Spongy—Cells irregular, and intercellular spaces large; cells bordering on lower epidermis more regular and more closely packed Vascular bundles have a well-developed sheath of spherical cells with thickened walls Anthocyan Abundant in upmost palisade layer and lowest spongy layer. Calcium oxalate in aggregate crystals Leaf-margin: Strengthened by thicker-walled epidermis and by the layer of hypoderm

(*b.*) *Sun Leaf*—Epidermis · Cells with thicker walls; cuticle thicker Chlorenchyma Palisade—Occupies fully one-third of leaf-thickness; cells more elongated and more closely packed. Spongy—Intercellular spaces smaller. Bundle-sheath much strengthened.

8. Clematis indivisa.

A. Life-form

Growing in the interior of the forest, the species attains its greatest size in places where the smaller trees form its support. The position of the plants seems to indicate that normally the upward growth is upon shrubs, from the top of which the liane continues its growth into the branches of overhanging trees It may thus reach a height of 10 m or more, and then the frequent branching of stems expanded along the top of the supporting tree results in an effective display of leaves The ascending climbing-stem, 2–3 cm. in diameter, and covered with a buff-coloured wrinkled bark, may be close to the trunk of the support, or it may be among the leafy branches The latter is by far the more common arrangement, being associated with the best conditions of growth—*i.e.*, nearness to the underlying shrubs, from which transition is easy, and abundance of supporting branches for the climbing-organs. Branches of the liane may bridge the space between adjacent trees, and the new support be utilized for further display of foliage. Should this intervening space be small, it may be bridged by a single branch; but in many cases two or more projecting branches may intertwine and be held in position by reciprocal grasping of their petioles. By the strength thus attained these branches may reach a support at a distance of 1·5 m.

Where low shrubs form the only support for the *Clematis*, the liane grows horizontally along the tops of these shrubs. The action of the petioles prevents the displacement of the stem by the wind, and ensures the maintenance of the leaves in the favourable positions they have taken up. The primary arrangement of leaves is decussate, and in cases where the stem stands erect this position is maintained; but in stems growing along the top of a shrub, and on stems which trail along the ground, there occurs torsion of the stem, as a result of which the leaves lie in two rows. In whatever position a leaf arises, the petiole twists so that the laminae of the leaflets lie at right angles to the incident rays of light.

From stems which are lying on the ground adventitious roots arise where there is an abundance of moisture. These roots grow chiefly near the surface of the ground, and often attain a considerable length.

B. LEAF.

(i.) *Leaf-form.*

Leaves decussate, petiolate; on adult plants 3-foliate, coriaceous, glossy, upper surface dark green, under surface paler green; leaflets 4–8 cm. long,

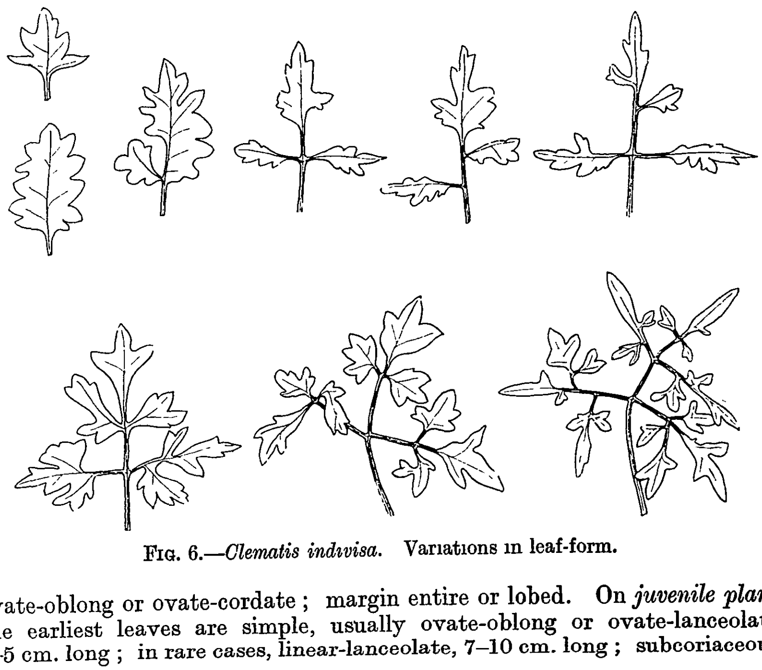


FIG. 6.—*Clematis indivisa.* Variations in leaf-form.

ovate-oblong or ovate-cordate; margin entire or lobed. On *juvenile plants* the earliest leaves are simple, usually ovate-oblong or ovate-lanceolate, 3–5 cm. long; in rare cases, linear-lanceolate, 7–10 cm. long; subcoriaceous.

Succeeding leaves show all transitions between simple and 3-foliate, and in certain plants later leaves are still more divided, many being biternate; but this form in Riccarton Bush is always followed by the 3-foliate form of the adult (fig. 6).

(ii.) *Leaf-anatomy.*

(*a.*) *Shade Leaf.*—Epidermis: Cells regular and slightly flattened; outer walls firm, with thin cuticle, stomata lower surface only, level with epidermal surface. Hypoderm: Above midrib 1 layer; below midrib forms a supporting mass, 4–5 cells in thickness. Chlorenchyma: Palisade—3 layers isodiametrical cells rather closely packed, arm-palisade cells, mentioned by Solereder (1908, p. 15), are numerous in the top layer and are present in smaller numbers in the other layers; wall-infolding is confined to the upper portion of each cell; chloroplasts irregularly scattered; tissue comprises about one-half of leaf-thickness Spongy—Cells are more irregular than palisades, but no sharp distinction between the tissues; intercellular spaces large; chloroplasts rather numerous Leaf-margin: Epidermal cells enlarged; outer walls very convex and much thickened. Vascular bundle: Well-developed parenchymatous sheath. Calcium oxalate: In aggregate crystals Anthocyan: Sometines in lower epidermis

(*b.*) *Sun Leaf* —Epidermis · Cell-walls much thickened, and well-developed cuticle, thicker on upper epidermis. Chlorenchyma: Palisade—Cells more closely packed. Spongy—Intercellular spaces smaller and cells more spherical. Leaf-margin: Strengthened by 2–3 layers of thick-walled hypoderm cells Vascular bundle: Sheath more developed.

(*c.*) *Climbing-organ* —(i) Form and Behaviour.—The pairs of leaves at first project beyond the growing apex of the stem. The petioles elongate in this position until they attain a length of 3 cm, the leaflets remaining small, being at most 1 cm. in length The leaves then bend downwards and outwards, the petioles at the same time increasing to 4 cm in length When in the horizontal position, the leaf-blades increase in size, and by curvature and torsion of the subpetioles the blades become placed at right angles to the light. If in its downward curvature a leaf-petiole comes into contact with some object the stimulus causes the petiole to coil round the object. The under surface of the petiole is most commonly in contact with the support, but curvature caused by the upper surface of the petiole being sensitive to contact is by no means uncommon. Whether the greater response of the under surface is due to its being more sensitive to contact, or whether it is due to this surface being in a position where it will most often be exposed to stimulation, has not been investigated. But it is obvious that as this results in the leaves being bent downwards it is most suitable in preventing the liane-shoots from slipping down from any support which they have reached The subpetioles are quite as sensitive, and it seems that they are equally sensitive on all sides Like the petioles, they are stimulated to curvature by contact with foreign objects, or with parts of the same plant—stem, leaf, or other petioles After their contact they become much strengthened, and the portions which are in contact with an object attain a thickness considerably greater than that of the rest of the petioles The small size of the leaf-blades during the growth of the petioles and subpetioles is of great importance in gaining supports, for a large leaf-blade would tend to become entangled in twigs, &c, and by its resistance prohibit a petiole from efficiently coiling round the support.

(ii.) Leaf-petiole: Anatomy (see fig 7).—Before the petiole attains a length of 1·5 cm. it is devoid of stereome. Four vascular bundles are at this stage well developed, and the rigidity of the petiole is further increased by abundant collenchyma. Stereome first appears between the bundles in a narrow ring, which gradually increases in thickness, and which, extending outwards, joins more masses of stereome which meanwhile have

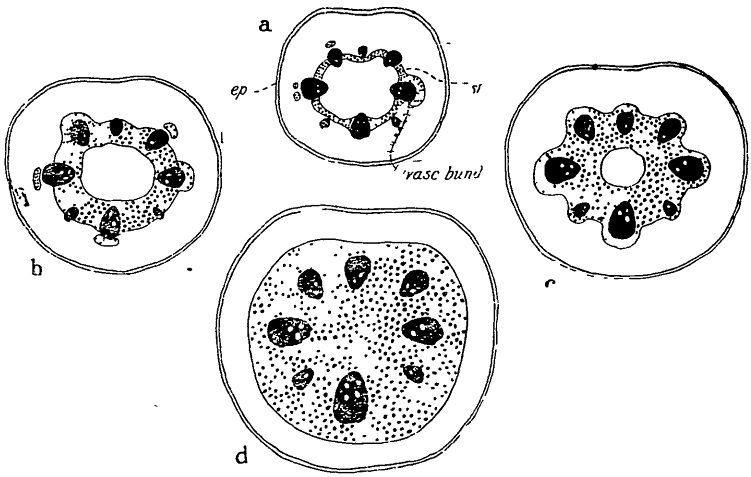


FIG. 7.—*Clematis indivisa.* Diagrams of tendril, showing development of stereome. *ep.*, epidermis; *st.*, stereome; *vasc. bund.*, vascular bundle.

developed outside the phloem. At the same time the stereome develops more and more towards the centre of the petiole, until finally all the ground-tissue except the 5 or 6 rows adjoining the epidermis becomes lignified.

These outer cells contain chlorophyll, while in a few cells anthocyan may be present. The epidermis has a thick cuticle. Stomata are sunk below the surface.

9. TETRAPATHAEA AUSTRALIS.

A. LIFE-FORM.

Although the species is found chiefly at the edge of the forest, many plants grow in the inner portions and even reach the summit of the tallest trees. The stem of the liane, growing up to 12 cm. in diameter, usually ascends close to the trunk of its support, but it sometimes trails for 10 m. along the ground before gaining the support It is evident that a tree-trunk is a poor support for a tendril-climber, but the presence of decaying stems of species of *Rubus* at the bases of trees indicates a means by which *Tetrapathaea* may have reached the lofty branches. The liane produces practically no branches in the shade, but on the exterior of the supporting tree it bends over, and ultimately gives off numerous branches, the foliage of which is often so thick as to obscure from view the supporting tree (Plate XXIV, fig. 1). Continuing their growth, these branches hang down, and the weight of the masses is frequently sufficient to break the branches of the support. The long rope-like stems may then be swung to and fro by the wind and become tangled in the branches of an adjacent tree Recommencing its upward growth on this new support, the liane may ultimately reach its greatest height. In places where shrubs form the only available support, the liane may bridge the spaces between the shrubs, and continue its growth along the tops of the shrubs for a distance of 20 m or more. As a rule, the liane forms no coiled masses at the base of a support, and it seems probable that this is due to the efficiency of the tendril as a climbing-organ. And that the tendril is not an ephemeral structure is shown by its persistence on stems which have attained a thickness of 6 cm.

Adventitious shoots are conspicuous on adult shoots in the shade. They may arise singly or in groups of 2 or 3, and, though very slight, can rise erect for about 60 cm. The first leaves are very small, being at most 4 cm. long and 2–3 cm broad, but the size of succeeding leaves gradually increases. However, on the distal portion of the stem the leaves for a long time remain quite small, thus facilitating free movement of the tendrils. The tendrils arise early on the shoots, often being present on the second node, and thus these adventitious shoots are of great value to the plant in gaining new supports.

B. LEAF

(i.) *Leaf-form.*

Leaves alternate, petiolate, 5–9 cm long, oblong-lanceolate or ovate-lanceolate, acuminate, coriaceous; upper surface very dark green and glossy, lower surface lighter green, margin entire. Petiole 0·5–1 cm, dorsal groove, often twisted Shade leaves are larger than sun leaves (sometimes 12–13 cm long), more membranous, and with longer petioles (1·5–2 cm.).

(ii.) *Leaf-anatomy*

(*a*) *Shade Leaf*—Epidermis: Slight cuticle; lateral walls also thick: stomata, lower surface only, slightly elevated. Chlorenchyma. Choroplasts large, spherical. Palisade—3 layers; cells almost as broad as long; not very tightly packed; tissue occupies slightly less than half the cell-thickness Spongy—5–7 layers, majority of cells more or less oblong, with long side parallel to leaf-surface Leaf-margin. Towards the margin the cells of palisade and spongy tissues become more and more alike, and form a homogeneous tissue which near the margin itself is composed of oblong cells resembling those of the spongy tissue, but with smaller intercellular spaces, and containing very few chloroplasts Vascular bundle: Surrounded by a parenchymatous sheath. Calcium oxalate Present in aggregate crystals

(*b*) *Sun Leaf*—Epidermis: Cuticle thicker, stomata not raised. Chlorenchyma: Palisade—Cells more elongated and more closely packed. tissue occupies fully half the leaf-thickness Spongy—Intercellular spaces smaller. Leaf-margin: Hypoderm 3–4 layers, cells of chlorenchyma spherical

(*c*) *Climbing-organ*—(i) Form and Behaviour The tendrils arise singly in the axils of leaves, and it is probable that, like those of other members of the *Passifloraceae*, they are modified inflorescence branches Lateral shoots of the plant arise from buds situated in the axils of the tendrils The tendrils at first project beyond the growing apex of the stem, and then bend outwards and downwards, at the same time increasing in size until finally they attain a length of 9–11 cm. If in this downward curvature a tendril comes into contact with some suitable support it encircles the latter, and, being thus held firmly in position, the rest of the tendril contracts into a double spiral (fig. 8). But in the absence of a support a tendril coils into a continuous spiral, and after remaining for a time in this position it again straightens, and later shrivels up. In tendrils which have obtained a hold on some support the part which is actually in contact with the latter becomes greatly thickened, often attaining a

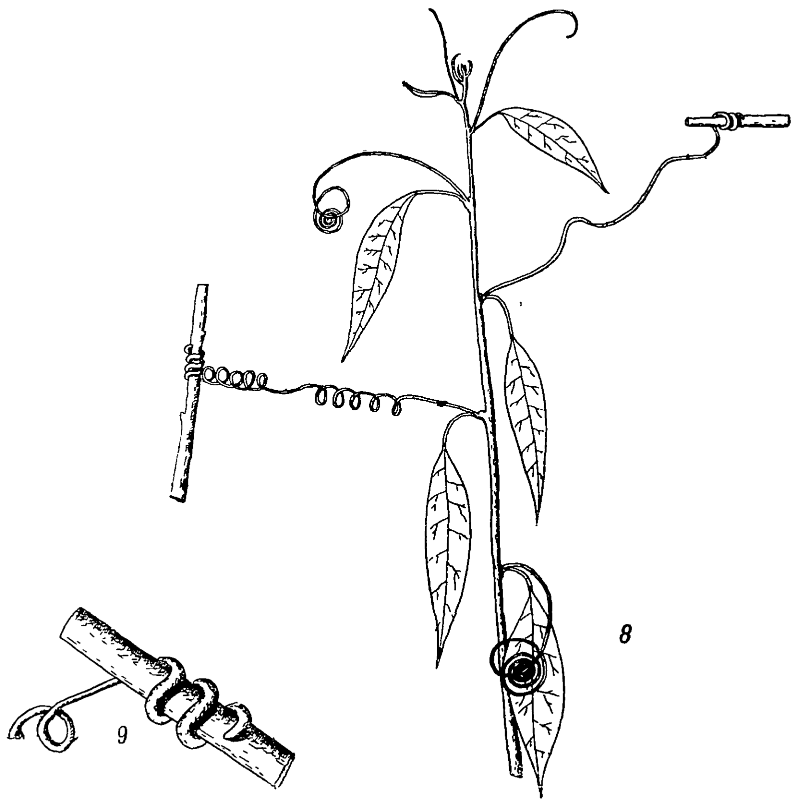


FIG. 8.—*Tetrapathaea australis.* Young shoot, with tendrils.
FIG. 9.—*Tetrapathaea australis.* Tendril, showing thickening.

diameter fully twice that of the rest of the tendril (fig. 9). By the development of mechanical tissue these tendrils persist for a great length of time, being common on stems which have grown to 6 cm. in diameter. At this age they are still extremely tough, being able to withstand a tension of 3 kg. These old tendrils are usually almost straight, and thus it is evident that, other things being equal, a younger tendril which is spirally coiled will be able to withstand a still greater strain.

As tendrils are present upon a plant in large numbers, and as they are widely distributed, the plant, in growing upwards to new positions of support, is admirably adapted for withstanding all strains—vertical strains due to the weight of the plant, and lateral strains due to the action of the wind. Further, the whole plant is thus adapted to maintain its position upon the loftiest supports in the forest.

(ii.) Tendril-anatomy: The structure of the tendril shows how in its stages of development it is admirably suited for performing its functions (fig. 10). In its earliest stages the best position is an extended one, which will increase its chances of coming into contact with a support, and the arrangement of tissues is such as to favour the maintenance of this position. The collenchyma forms a band near the periphery of the tendril, and the

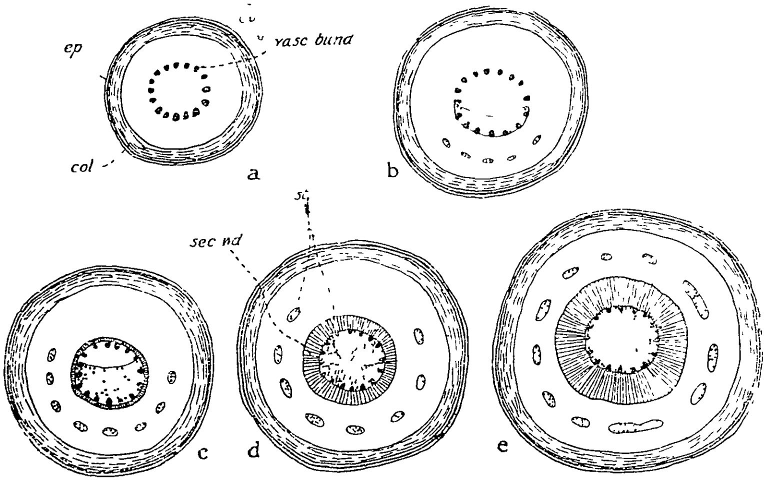


FIG. 10.—*Tetrapathaea australis.* Diagrams of tendril, showing development of mechanical tissue. *col*, collenchyma, *ep*, epidermis; *sec wd*, secondary wood; *st*, stereome; *vasc. bund.*, vascular bundle.

vascular bundles are distributed in a ring at a considerable distance from the centre. Then at a later stage the development of stereome is equally suitable. On the future convex side, where growth and expansion of the tissues is essential, stereome is at first absent, but on the concave side it develops rapidly, and thus by its resistance to tension it prevents the tendril being unrolled from the support. Finally, the injury to structures from external pressure is prevented by the ring of collenchyma, which is a constant character of the tendril-structure.

III. METHODS OF GAINING SUPPORT.

1. FUCHSIA COLENSOI.

Seedlings are numerous in the forest throughout well-drained but moist positions.

The primary shoot does not usually grow more than 35 cm. high without support, for lateral shoots are early given off and tend to drag the plant down to the ground. However, it often comes into contact with some support against which it rests. Should the support be very low, the *Fuchsia* branches, which project at right angles, soon spread over it. Shoots stand up from the top of the support, and, supporting themselves, can reach a height of fully 50 cm.; other shoots project from the sides of the support, and thus a new support is often reached

Again, if the seedling-shoot rests against the branches of some shrub, the shoot pushes its way up between the branches to the top of the shrub. The leaves, being very flexible, are of little assistance in climbing, but the sinuous growth through divaricating branches seems to afford sufficient means of keeping the plant erect, and the branches which are given off at the top of the shrub finally secure a firm anchorage.

Should a seedling not reach a support, the thin stems trail along the ground for 1–2 m., and in favourable conditions root freely. From these trailing-stems lateral shoots rise up, and thus often reach a support a considerable distance from the position where the plant emerged from the ground; in fact, it sometimes happens that a single plant reaches more than one support by means of these spreading stems. On the other hand, no support at all may be gained, and the branching stems then form a prostrate mass on the forest-floor, or else they interweave and by their mutual support the plant takes the form of a cushion-like mass, which is often as much as a metre high. Shoots projecting from the sides or from the top of such a mass may then often reach some adjacent shrub or tree, and through this rise to a greater height

2. The Species of Rubus.

The seedlings of the various species of *Rubus* show great similarity in their early behaviour. The primary shoot rises erect for 60 cm., and when the growing-point is injured a lateral shoot arises which continues the upward growth. It will be seen that this is the greatest height to which the primary shoot of any of the lianes here dealt with can stand unsupported, this being due to the relative thickness of the *Rubus* stem, seedlings 50 cm. in height having a stem 5 cm. in diameter. By resting against any near object the seedlings can reach greater heights, and in doing so the leaves are of extreme importance. Prickles are well developed at a very early stage, and, as leaves project from the stem often for 10 cm., a fairly wide area is thus in reach of the prickles. Any support is immediately held by a touching prickle, and by this means the seedlings are well suited to rapidly reach high supports. Any two shoots of a seedling rising up together support each other by the grasping of the prickles, and thus can reach to a height of nearly a metre But when there are no supports near a seedling, the shoots trail along the ground, and form low, flat, straggling growths, which are very characteristic of certain portions of the forest. They are often 3–4 m. across, and so at the circumference of such a growth there is usually some plant which is suitable for the support of *Rubus* shoots.

3. Metrosideros hypericifolia.

Young plants of this species have been observed during the course of this present investigation only in moist situations in the immediate vicinity of roots of forest-trees, which roots are present in large numbers. The *Metrosideros* plants show a marked tendency to scramble up the sides of and over these roots, applying themselves closely to the bark, and putting forth adventitious roots which fix the plants firmly. By continued growth the distal shoots extend over the tree-roots, such as those shown in Plate XXIV, fig. 2, and some of these shoots reach the base of the main tree-trunk. Here they may branch copiously, applying themselves closely to the bark, in some instances encircling the entire tree. Their climbing-roots are given off, and by this means, and by continued growth, a gradual ascent on the support is made. The growth is slow, and in the limited time at the writer's disposal a careful investigation of the species has been impossible, nor is Riccarton Bush suitable for such a study The greatest height of observed specimens is 10 m.

4. Muehlenbeckia australis.

Seedlings of this species are common throughout all parts of the forest, and in many places form more than 50 per cent of the forest-floor vegetation. They are able to grow erect for 40 cm, and if the growing-point is injured a lateral shoot arises and continues the upward growth and twines round any suitable object with which it comes into contact. The twining is usually sinistrorse, but the common occurrence of dextrorse twining seems to indicate that the direction is at least partly due to the manner of contact with the support. The stems cannot twine round any support which is more than 5 cm. in diameter.

After the seedling reaches the top of the support it continues to grow erect for a short distance, and then bends down, until finally the growing apex, which continues to point upwards, comes into contact with the more proximal hanging portion of the same shoot It then commences to twine round this, but the behaviour does not seem to aid in reaching a new support. But lateral shoots may rise from the hanging shoot, and these, by projecting out, as they do, for 40 cm, often reach an adjacent support.

In the largest number of seedlings two or more often come early into contact, and by supporting each other can reach a height of 70 cm or more, and thus have a better opportunity of coming into contact with a support. If no support is reached the seedlings sink to the ground; but yet, through their elongation, they may ultimately reach some support From the prostrate stems lateral shoots stretch up, and by their ascent in a position different from that of the primary shoot a support is often reached Many of these lateral shoots arising in autumn have vigorous growth, and unaided can reach a height of 65 cm In stations with little undergrowth the branching stems form a reticulation on the forest-floor in the same manner as those of *M complexa*, but in *M. australis* these reticulations are seldom more than 1 m. across. They are, however, far denser, and often form compact masses with an effective display of foliage

5 Muehlenbeckia complexa.

Seedlings of this species are most numerous in the vicinity of adult plants—*i e*, in the outskirts of the forest and near the forest-margin.

In the forest they grow erect for 30 cm, and upon touching a support they commence to twine In the absence of a support they bend over to the ground, and trail along the forest-floor These trailing-stems root freely at the nodes, and often attain a length of 5 m From any of the nodes lateral shoots may rise up, and should these reach no support they bend over to the ground, where they continue their growth. By a repetition of branching the plants thus soon form a loose reticulation on the forest-floor, and, unless the floor here is very bare, shoots from the network of stems will sooner or later reach a support. Indeed, it more often happens that a single liane-seedling reaches numerous supporting young plants Again, it is common for any two shoots to come into contact; these then twine round each other, and by their mutual support they grow to a greater height than can a single shoot, and thus have greater opportunity of reaching a support

At the edge of the forest there are two sets of conditions to which developing seedlings are exposed—(1) In places where the belt of introduced trees* at the forest-edge is broken the ground is partially covered by rank grasses, chief of which is *Dactylis glomerata;* (2) in the vicinity of the trees the grasses are absent, but large numbers of seedlings of oak, &c., are present, and the ground is covered with a layer of dead leaves.

In the former open situations the developing liane-seedlings upon emerging from the ground grow erect for about 30 cm., and bend over. In so doing they usually come into contact with the flowering-stalks of the grasses, which stand up for fully a metre. Round these the liane-stems twine, and after reaching the top of these supports they continue to grow up for a short distance until they are unable to support their own weight. They then cause the supporting grass-stalks to bend, and thus they are able to reach any adjacent shrub, which then forms a new support for the liane. Should the liane-seedling in such places reach no support it trails along the ground, and by the lateral shoots which arise along this stem the liane usually reaches at least one support at some distance from its original position.

But it is under the second set of conditions that the tendency for the surface trailing-shoots to elongate is most marked. The shoots become more or less covered by dead oak-leaves, and although under this covering the shoots do not branch so much as do the trailing-shoots in the forest, yet they elongate to a greater extent, and thus the area in which shoots may rise up from the plant and reach supports is greater than in the forest. By means of the rooting at the nodes the shoots are not dependent for their food-supply upon the primary root, and, as a result of this, injury to the main stem does not cause the death of lateral shoots. The oak-seedlings which surround any liane-seedling here are, on account of their small size, of little importance as supports for the lianes. Therefore the only plants which reach the adult stage are those whose growth has brought them close to the shrubs at the forest-edge, and the support obtained from these shrubs enables the lianes to reach a height from which climbing-shoots can soon reach a permanent support.

6. SPECIES OF PARSONSIA.

A young seedling at first normally grows erect, and independently can reach a height of 45 cm. In the absence of a support, further growth results in the apex gradually bending over, and, with increasing growth, bending still further, until it finally touches the ground. Then in the dense undergrowth it sooner or later reaches a support up which it twines, the twining always being sinistrorse. In seedlings whose growing-point becomes injured, a lateral shoot arises and grows erect, ultimately bending over in a manner similar to that of a primary axis. However, at an early stage a seedling is likely to come into contact with some support; especially is this the case in the interior of the forest, where in places of dense growth seedlings are often present in countless numbers. Any two seedlings may thus early come into contact, and, as the tendency to twine is soon manifested, their twining round each other gives support, which enables them to reach a height of 75 cm., after which their apices bend over in the manner

* European trees have been planted in many places on the outskirts of the Riccarton Bush for the purpose of sheltering it from the wind.

of a single seedling, but, of course, moving through a larger circle, and thus giving a better chance of touching a support. This tendency to twine round one another is not confined to the movements of any two individuals only, for very often large numbers are seen thus giving mutual support—in some cases as many as 15. These then form a rope-like mass, whose resistance to bending is very effective; and the resistance is further aided by the positions of the roots of the individuals, they being arranged round the ascending shoots in a circle, whose radius may be as much as 10 cm. By such means the seedlings often attain a height of fully 1 m.—a height at which the vegetation available as support is usually very abundant. There is no doubt that the leaf is of importance as an aid to climbing. The most common leaf-form of the seedling is the linear form. The leaves are borne in pairs, and project at right angles from the stem to a distance of 6 cm., and by torsion of the stem they point in all directions. There is thus a probability that any one of these leaves may touch a support, and by resistance to bending allow the seedling to reach a greater height From any portion of a shoot which is bending over towards the ground, lateral shoots may arise for fully 40 cm , and, as the primary shoot at the place of origin of these lateral shoots may be anything up to 20 cm from the ground, a comparatively high position is reached.

7. Clematis indivisa.

The seedlings of this species are not widespread in the forest, being confined chiefly to a small part near one of the few adult female plants. There they are well sheltered, and are surrounded by numerous supports

Without any support they can stand erect for 40 cm. The leaves, which are decussate, are at the lowest nodes simple, and project from the stem for 5–6 cm. They are thus of assistance in lessening vertical strains on the seedling. The third pair of leaves usually have petioles which upon continued contact with an object bend slightly They can thus overcome any slight lateral strain, and, as any two consecutive pairs of leaves will operate at right angles to each other, they assist in maintaining the seedling in an erect position and enabling it to reach a greater height. The petioles of leaves succeeding the third pair are more sensitive, and encircle any small branch which they touch; in doing this they become much thickened and strengthened. When a pair of leaves arise from a stem they at first project beyond the growing-point The leaf-blades for a long time remain small, but the petioles elongate to a length of 2–3 cm. The leaves then gradually bend down until they project straight out from the stem, and if in this downward movement they touch any branch they entwine it. As the leaf-blades at this stage are still small, their size does not retard the action of the petioles by their becoming arrested in the encircling movement, but they later expand, as do also the blades of leaves which have reached no support in the downward curvature. Above the anchorage secured by any of the petioles the free end portion of the seedling can rise erect for fully 30 cm., and so, on account of the numerous supports which usually surround the seedlings, the latter easily make their way into the sunlight.

However, should a seedling reach no support, and thus bend down, any lateral shoot from the primary axis will rise up in a position perhaps 20 cm from the former position of seedling, and so reach a support.

In many cases seedlings are found which, in addition to their petiole-action, ascend a support by twining, the twining being in all cases sinistrorse. The petioles entirely surround the support, one of each pair circling to the right and the other to the left, and they thus firmly grasp the support.

8. Tetrapathaea australis.

The seedlings are found chiefly in the exterior portions of the forest, where the vegetation is dense, and thus they are surrounded by numerous supports of varying nature. Without any support the seedling can stand erect for 40 cm., but a greater height can be reached near any support by means of the leaves. These are borne alternately, and project straight out from the stem for 6–8 cm.; and, being fairly rigid, they support the seedling, and maintain it in its erect position. But most assistance is gained from the tendrils which arise while the seedling is still standing erect, usually appearing first from about the 18th node. They at first project beyond the growing-point, with tip bent outwards, this bending, no doubt, assisting the tendrils to retain their hold upon any object with which they come into contact. These tendrils do not remain in this projecting position, but gradually bend down until they lie along the stem of the seedling, with the apex pointing towards the ground. And in this downward bending they may come into contact with a support. The support is firmly encircled, and by spiral contraction of the tendril the seedling is pulled towards the support. Having thus obtained an anchorage, the seedling may rise up from this point to a still greater height, and in so doing may obtain further support. Should the young seedling reach no support, it bends over to the ground, and grows for a while horizontally. In this way it may reach a support; and, further, any lateral shoots springing from the primary shoot, and rising up as they do for fully 30 cm., increase the chances of the seedling coming into contact with some shrub or other support. From the lowest branches of the shrubs the growth of the liane to the top of the shrub is easy, and thence the liane has little difficulty in reaching higher adjacent plants, and thus rising to the sunlight.

IV. THE EVOLUTION OF LIANES.

The question of the evolution of lianes cannot be gone into in much detail, for this would entail a close acquaintance with all the New Zealand lianes and with various classes of forest. However, the lianes present in the forest investigated exhibit an interesting series from non-specialized to highly specialized forms.

1. Scramblers.

Characteristics common to all the classes of lianes are the great elongation of stem and the absence of lateral branches. Now, it must be noted that in positions in the forest-interior where the liane-stems, attenuated and unbranched, elongate rapidly, this elongation is characteristic also of other plants, certain species of *Coprosma*—bushy shrubs as distinct from lianes as possible—being most noticeable in this regard.* From such observations

* Subsequent to the writing of this, Dr. L. Cockayne has drawn the writer's attention to the fact that in certain parts of the forest near Wellington stems of *Coprosma robusta*, normally a bushy shrub, are so greatly elongated that without careful attention they are easily mistaken for true liane-stems.

it is generally agreed that the chief factors determining stem-elongation are moisture and diminished light, and thus the variation in the life-form of *Fuchsia Colensoi* can be readily understood *This species, which forms a compact, much-branched shrub in the open, in the forest-shade has stems which are greatly elongated and which have few lateral branches.* These stems can rapidly push their way into vegetation above them, and by leaning against supports attain a height of fully 4 m

That this scrambling habit was at first the effect of environmental stimuli—moisture and shade—cannot, in the face of the behaviour of other plants in similar conditions, be doubted, and it is possible that races were evolved in which the scrambling habit became hereditary. On this point L Cockayne (1912, p. 21) says, "It is possible that there may be climbing and non-climbing races. This is the more likely as the 'species' is considered variable, and large forms are said to 'almost pass into *F excorticata*' (Cheeseman, 1906, p. 187), which is a small tree or shrub, but never a liane." Such a view receives support from the very great elongation of stems of *F. Colensoi* in positions in the forest where supports are abundant —positions where the stems often lie along the ground for fully 5 m

When species of *Rubus* and other plants possessing prickles commenced growth in the forest-interior they would, on account of their prickles, be better suited for reaching the light than would plants without such appendages.* They would thus be able to propagate their kind more quickly, and, with their larger number of descendants, races in which the scrambling habit was hereditary might soon arise And in comparing the relative abundance of *Rubus* plants in the forest, and the luxuriant growth of the plants there, with those in more open situations, it seems probable that natural selection would by itself result in the climbing habit being retained. In fact, it seems that in the species of *Rubus* found in the Riccarton Bush the scrambling habit is in all cases hereditary, for those plants which grow in the open do not form shrubs, but low straggling masses, which resemble somewhat the exposed forms of more specialized lianes In the forest-scramblers the importance of leaves in climbing has been pointed out above, and so *it is interesting to note how in one of the species of* Rubus, R cissoides, *the leaf has changed its rôle, or, rather, has acquired a new rôle, being now a special climbing-organ*

2 Root-climbers.

In this class of climbers the small number of representatives studied by the writer makes it difficult, using only the facts derived from the Riccarton Bush, to conceive means by which the climbing habit has been gradually adopted, but the variations in the life-form of *Metrosideros hypericifolia* may have some bearing on the question. In this species it is evident that there is no sharp distinction between climbing-roots and absorbing-roots. Both are at first similar in structure, and it seems probable that the nature of the environment determines whether the roots shall elongate and act as absorbing-organs, or whether they shall remain comparatively small and fasten the liane to the support.

It will be noticed from accounts of the life-form of the lianes that in all the species *the important fact stands out that there is a tendency to adventitious*

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* Before the scrambling growth was commenced, however, the prickles would possibly be of no use to the plants possessing them.

rooting by creeping stems in moist positions. In *M. hypericifolia* the roots arising from stems lying on the forest-floor are very numerous. Now, the surface roots of the forest-trees are often semi-exposed, and covered to a greater or less extent by debris and bryophytes, so that moisture-conditions on these roots may not be very different from those in the surrounding soil. If so, we should expect that if it is moisture which acts as a stimulus to the formation of the adventitious roots, then the rooting of *Metrosideros* stems lying over these surface roots would be a natural occurrence. And such is actually the case. It is probable that certain physiological races would arise which required a smaller amount of moisture to stimulate adventitious rooting, and so roots might be given off when stems were in contact with the moist bases of tree-trunks. By secretions the roots might easily be attached to the trunks, and thus the plants could raise themselves from the forest-floor. Greater heights would be reached by the plants whose tendency to rooting was greatest under the drier conditions which would be met at the increasing distance from the forest-floor.* And even now, as has been stated above, *M. hypericifolia* is found only in the most shaded positions of the Riccarton Bush, and these plants do not attain a very great height. But other species seem to thrive under drier conditions. For example, the writer has observed in the Botanical Gardens at Wellington a plant of *M. scandens.* This was growing in the open, and formed a much-branched dense shrub about 50 cm. high. On one side, however, a branch has come into contact with the stem of a shrub, and by means of its climbing-roots it has ascended this stem to a height of 1 m.

3. TWINING-PLANTS.

When we turn to twining we are dealing with a phenomenon which is of frequent occurrence in plants, and it is found not only in those which can at once be classed as true lianes, but also in others in which the twining is perhaps only slightly marked. It is these latter which are of importance in trying to trace the development of twining.

The fern *Pteridium esculentum* (Forst. f.) Cockayne, which usually grows in exposed stations, becomes in the shade a scrambler with elongated stems, which sometimes show a slight tendency to twine. "So, too, with the scrambling liane *Lycopodium volubile* Forst. f., which, gaining a thin support, winds freely, the winding being in this case an hereditary characteristic" (Cockayne, 1912, p. 21).

An interesting case, not hitherto reported, is that of *Carmichaelia subulata* T. Kirk, which in the open is a rigid erect xerophytic leafless shrub 0·5–1 m. high; but it has been found by the writer in the shade as a prostrate plant, with its stems hanging down over the edge of a rock and showing a marked tendency to twine round one another. From this plant a shoot rose upright for about 50 cm. Towards the distal end it was twisted and coiled into a spiral, giving the appearance of a "searcher shoot" of *Muehlenbeckia australis* which has commenced its spiral growth. Unfortunately, no opportunity arose of visiting this remarkable plant later to note the further growth of the shoot. The discovery of this plant seems to be of considerable importance. Climbing is not unknown in the genus *Carmichaelia*: it is hereditary in *C. gracilis*, a rare scrambling liane growing

* It must be remembered that the tree-trunks are kept comparatively moist by the dripping of water during atmospheric precipitations.

in damp stations in the South Island, and hereditary also in *C. exsul*, of Lord Howe Island, the only species of the genus outside New Zealand. So the presence of a scrambling form showing a tendency to twine in such a rigid species as *C. subulata* undoubtedly has close bearing on the question of liane-evolution

Another interesting case is that of *Mueklenbeckia complexa*, already noted, where, it may be remembered, the liane, having gained the uppermost twigs of a dense shrub, shows a tendency to scramble rather than to twine, interlacing branches, as pointed out, being more favourable for scramblers than they are for twiners

In connection with such cases as the above we may note Darwin's remarks: "As in many widely separated families of plants single species and single genera possess the power of revolving, and have thus become twiners, they must have independently acquired it, and cannot have inherited it from a common progenitor. Hence I was led to predict that some slight tendency to a movement of this kind would be found to be far from uncommon with plants which did not climb, and that this had afforded the basis for natural selection to work on and improve" (1878, p. 197)

In any view of the development of twining the case of *Antirrhinum majus* is of interest. In a race of this well-known garden-plant a form has been found which gives evidence of the inception of twining, the form having, too, the characteristic anatomical features of twiners. It appears to be a mutant, and it comes true to seed.

The question next arises as to whether the tendency to twine has been lost in certain plants Darwin stated that this has happened in many tendril-bearers, and in his observations on *Clematis* showed that the power of twining was in this genus poor (1865, pp 26–34) This point is brought forward here on account of the behaviour of *Clematis indivisa*.

In the section of this paper dealing with the methods of obtaining support it has been stated that the developing seedlings of *Clematis indivisa* twine round a thin support with which they come into contact; but the seedlings, being young, not one of those observed has made more than 5 spirals round the support However, the writer has found an older plant which has attained a height of 2 m, the plant having made 14 spirals and still twining regularly. Adult plants also are occasionally found which exhibit a slight twining round their supports; but the twining in these cases is so slight that it may possibly be due solely to irregular growth in the ascent of the liane.* And we may notice here *Calystegia Soldanella*, a common inhabitant of the sandy shore, where it forms a low compact mass (Cockayne, L., 1910, p 67, fig 27). This species has been seen by the writer at Day's Bay, Wellington, growing in a sandy position where a number of low shrubs have become established Here numerous shoots of the *Calystegia* rise up among the branches of the shrubs, and twine freely and regularly. Just as in *Clematis*, it is probable that we have here a species whose ancestors were twining-plants, and the capacity to twine, through inheritance from these, lies latent in the plants which now occupy the exposed places of the seashore.

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* Since this was written Dr L. Cockayne informs me that he has noted distinct twining in a large example of *C indivisa* in the forest on the southern slopes of Mount Ruapehu.

4. TENDRIL-CLIMBERS.

The evolution of tendril-climbers has been referred to by Darwin, who states, " With respect to the sensitiveness of the foot-stalks of the leaves and flowers, and of tendrils, nearly the same remarks are applicable as in the case of the revolving movements of twining-plants. As a vast number of species, belonging to widely distinct groups, are endowed with this kind of sensitiveness, it ought to be found in a nascent condition in many plants which have not become climbers " (1878, p. 197).

In support of this statement is a series of plants explained by Müller (Journ. Linn. Soc., vol. ix, p. 344)—plants which represent stages from those which climb by obtaining support from their branches stretched out at right angles, such as *Chiococca*, to those whose branches form true tendrils, as with *Strychnos*.

Transitions from leaf to tendril are also common, and so it is interesting to note the behaviour of many leaves of *Rubus cissoides*. As stated on p 326, the leaves of this species are often reduced to midribs, which, with their strong recurved hooks, form distinct climbing-organs. Many of the midribs are much curved at the distal end (Plate XXIII), and in a few cases the midribs had actually encircled a twig with which they had come into contact It may therefore rightly be asked whether such behaviour denotes the inception of tendril-formation. The plants possessing the peculiarity have a marked advantage in gaining supports, so we should expect that natural selection will preserve these plants, and that the " rudimentary tendrils " will by this means be gradually perfected.

V. GENERAL CONCLUSIONS.

The descriptions given above of the life-forms of the lianes dealt with show to a certain extent how luxuriant is their growth. Moreover, this luxuriant growth is common throughout all the New Zealand forest, to which the lianes are often said to give an appearance similar to that of tropical forests. Undoubtedly there is a Malayan element in the New Zealand forest, so that at first thought it might appear that the lianes were of tropical origin. But this is by no means the case. It is not the great heat alone of a tropical rain-forest that is the primary cause of the liane habit, but rather it is this combined with the excessive moisture of the atmosphere. In New Zealand the moisture is also great, and the climate is equable without extreme heat and cold. This condition of affairs is probably responsible for the high development of lianes in New Zealand, and this view is supported by the remarkable fact that there are here a large number of climbing *Myrtaceae*, a family without lianes in the rest of the world.*

The individual lianes studied exhibit many characters in common, of which we may first note the tendency to form adventitious roots. The formation of such roots is, of course, common with many plants, being most

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* Cheeseman (1914, pl. 50) offers as an objection to this theory, for which I am not primarily responsible, the fact that Polynesian and Malayan species of *Metrosideros* have not become lianes, although the climate they are exposed to is " even more humid and equable." I possess no exact details as to the life-forms or the exact environment, on which all depends, of each of the nine (mostly New Caledonian) Malayan and Polynesian species; but, unless some of these are shrubs, the lianoid form would not be expected. On the other hand, in New Zealand *M. scandens* (and probably *M. florida*), *M. diffusa*, and *M. albiflora* possess both shrub and lianoid forms.

noticeable in plants with creeping or underground stems It is considered probable that moisture is the chief factor determining their production, and this view is supported by the positions of the roots in the lianes observed They are of great value in obtaining food for the lianes, and by their efficiency in this respect they enable the plants to reproduce vegetatively to a marked extent. The vigorously growing shoots which may arise near these roots receive a sufficient supply of food from them, and thus can soon reach the adult stage, so that in a short time any portion of the forest may contain at least a dozen potential individuals all derived from a single plant

A point of equal interest is the striking heterophylly of many of the species These plants possess a juvenile leaf differing in form to varying extent from the adult leaf, and between the two forms there are all transitional stages. Much attention has been directed to the phenomenon by L. Cockayne, whose views in part seek to explain the different leaf-forms by reference to past changes in the environment of the plants. Thus, after dealing with *Parsonsia,* he writes, " This, taken in conjunction with the fact that about 200 species of New Zealand plants—*i.e.*, some 12 per cent. of the spermophytes—belonging to most diverse genera and natural orders, exhibit heterophylly of a more or less striking character in their life-histories, seems to distinctly point to there being some reason in New Zealand itself for this special phenomenon, and this reason, it seems to me, must be sought for in the manifold changes which the geological history of the New Zealand Archipelago has brought about " (1908, p 488) And with regard to the leaf-form of *Parsonsia* itself, " It seems clear that the possibilities of both juvenile and adult are latent in the one plant, but each requires its necessary stimulus to set it free in its entirety. If the stimulus is not sufficient, then one or the other form may persist, or there may be a combination of characters, as in the transitional forms " (1912, p 24).

In reviewing the features of the leaves of the lianes it is seen that there are many characters common to them all Also the shade leaves present many differences from the sun leaves

In shade leaves the characters are as follow: (1) The leaf-blades are relatively expanded and membranous. In *Rubus cissoides,* whose leaves are reduced to midribs, these midribs are much longer than are those in the open (2.) Petioles are elongated (3) Cuticle is not well developed (4) Lateral walls of epidermal cells are more wavy on the under leaf-surface. (5.) Palisade cells are not closely packed (6) Spongy tissue is well developed, and has irregular cells, between which are large intercellular spaces (7) Stomata are on lower surface only

In sun leaves, on the other hand : (1) Leaf-blades are smaller and more coriaceous (2) Petioles are shorter. (3) Lateral walls of epidermal cells are straighter than in shade leaves (4) There is in most cases a thick cuticle (5) Palisade tissue is well developed, with the cells elongated and very closely packed (6) Spongy tissue comprises a smaller portion of the thickness of the leaf, and has small intercellular spaces (7) Stomata are on lower surface only, but more numerous than in shade leaves

The above features appear to present the following advantages :—

The expansion of the leaf in the shade is advantageous in that a larger number of light-rays will fall upon the assimilating surface; and the utilization of light is further aided by the broad palisade cells, which give the chloroplasts a more superficial position than they occupy when the cells are narrow and elongated

The development of large intercellular spaces is more connected with transpiration. Cowles (1911, p. 554) states that it is highly probable that the feature is caused by the small transpiration which characterizes such damp shaded regions. But at the same time it cannot be doubted that the spaces are of great advantage to the plant. They necessarily result in an increase in leaf-size, and at the same time, although the transpiration-rate is low, the intercellular spaces ensure an efficient aeration of the photosynthetic tissues This view of the development of intercellular spaces explains their absence—or, rather, reduction—in the exposed sun leaves, which it is obvious must also have tissues aerated. The aeration is here aided by the greater transpiration-current, due to the dryness and warmth of the surrounding atmosphere; for, though transpiration may result in partial closure of the stomata, Cowles states that at the same time the increase of transpiration may cause an increase in the number of stomata. This view is in accord with the increase noted in all the liane sun leaves. It is further remarked by Cowles, "Stomatal structures and activities cannot stop transpiration; at best there is only retardation" (p. 567). Now, if this be correct, then the larger number of stomata on the leaves in the sunlight will, by increasing the transpiration-rate, be of advantage to the liane in aiding the conduction of water, with its contained salts, through the vessels of the stem And it is obvious that this conduction in so small a stem to so great a height is for the liane a matter of supreme importance.

The great development of cuticle in the open has also been interpreted as due to increased transpiration. While the loss in external transpiration due to cuticularization may be fully balanced by the gain caused by the increased number of stomata, the cuticle serves an important rôle in strengthening the leaf, and therefore ensuring protection from wind and storms.

The cells of the epidermis can be roughly classed into four types: Type 1, walls of cells very wavy (*e.g.*, *Fuchsia Colensoi*, shade leaf); type 2, walls wavy, but to a far less extent than in type 1 (*e.g.*, *Rubus cissoides*, shade leaf); type 3, walls straighter than in type 2, but not so straight as in type 4 (*e.g.*, *Clematis indivisa*, shade leaf); type 4, walls straight, and perhaps slightly rounded at the corners (*e.g.*, *Clematis indivisa*, sun leaf).

The importance of variation in the regularity of the lateral walls of epidermal cells is not so evident; but since they are more wavy in the lower epidermis than in the upper, and more regular in sun leaves than in shade leaves, it is probable that transpiration is a factor determining their regularity.

Finally, we must notice how the structure of the stem must be related to all questions dealing with water-conduction and transpiration. In lianes especially do the stems have to be particularly adapted for rapid water-carriage, and without knowledge of these adaptations no comprehensive conclusions can be obtained.

APPENDIX.

1. Table of Leaf-characters.

—	Number of Stomata per Square Millimetre		Percentage of Number in Shade Leaf of Sun Leaf	Type of Epidermal Cell, Lower Surface.	
	Shade Leaf.	Sun Leaf		Shade Leaf.	Sun Leaf.
1. *Fuchsia Colensoi* ..	64	80	80	1	2
2. *Rubus australis* ..	240	296	81	2	3
3. —— *schmidelioides*	216	288	75	2	3
4 —— *cissoides* ..	230	294	78	2	3
5. —— *subpauperatus* .	256	300	85	2	3
6. *Metrosideros hypericifolia* .	220	264	83	1	2
7. *Muehlenbeckia australis* .	64	88	73	1	2
8. —— *complexa* ..	96	136	71	1	2
9 *Parsonsia heterophylla* .	225	280	80	2	3
10. —— *capsularis* var. *rosea*	256	320	80	2	3
11. *Clematis indivisa* ..	96	128	75	3	4
12. *Tetrapathaea australis*	160	224	71	2	3

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