

HYBRIDISM  
IN THE FORESTS OF NEW ZEALAND

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## 1. GENERAL.

Obviously the first essential for a plant-ecologist is to be intimately acquainted with the taxonomic units with which he has to deal. Usually, up to the present, the standard flora of his country or region has been his guide. That is to say, works largely based on herbarium collections and on the Linnean conception of species have been considered adequate for dealing with the heterogeneous mixture of plant-forms encountered by an ecologist in the field. Nor must it be forgotten that large floras in general and monographs are designed for the classification of plants for herbarium purposes and that few such works, if any, attempt to deal with the individuals as they occur in free nature. Indeed, ever since the days of LINNAEUS, herbaria, large and small, have been taxonomically all in all, and it is only within the last 38 years that plant-ecology has gradually come into being with its very different demands on floristic botany. Though in my earliest plant-ecological studies during the 'nineties' of last century, as evidenced by my statement that (1900:98, 99) »it is essential for oecological work that every form treated of shall have a name of some kind, whether specific or varietal matters little«, and »ecology can assist systematic work and check its results«, I have appreciated the inadequacy of all New Zealand floras<sup>1</sup> for the plant-ecologist, yet it was not till eleven years ago (1917: 66—79), that I went at some length into the species question and expressed the opinion that »It

<sup>1</sup> Partly owing to there being even yet many undescribed species etc., but more particularly from the comprehensive view of the contents of species taken by HOOKER in his pioneer floras of New Zealand and his example being followed by T. KIRK and CHEESEMAN.

may quite well be that all 'intermediates' which are not microspecies are merely hybrids between these latter or between the hybrids themselves». Since that date this supposition has become fact and the knowledge of hybridism in the New Zealand flora has progressed by leaps and bounds, so that at the present time, taking the vascular plants only, more than 300 groups of hybrids between species are known, and there are abundant crosses between the jordanons which constitute a compound species. Obviously this recognition of hybridism on a large scale at once put a new complexion upon the classification of the flora, and its examination in the light of the new knowledge became the burning question both for the floristic and ecological botany of the New Zealand Botanical Region. Here, as a contributor to a book dedicated to a great forester and plant-ecologist, it seems fitting that I should attempt to put on record briefly what is known regarding the plant-hybrids of the New Zealand forests.

Before proceeding further it must be pointed out that H. H. ALLAN and myself have published a rather long paper on ecological taxonomy in which, *inter alia*, a number of terms not in general use are proposed which, as I am using them here, are defined in an appendix. Further, as some of the matters dealt with in this paper are the result of a research grant to ALLAN and myself from the Royal Society of London, I must call attention to our great obligation to that Society without whose aid much knowledge concerning New Zealand's wild hybrids and kindred matters would most likely have remained unknown for many years.

## 2. REASONS FOR ACCEPTING THE HYBRIDS AS VALID.

Though most geneticists look askance at all evidence concerning hybridity, unless it be based on properly-conducted breeding experiments, it seems nevertheless that evidence amounting to actual proof can be gained by field-observations. The narrowness of the main land-mass of New Zealand and the considerable number of degrees

of latitude through which it extends (34° 15' S. to 47° 30') enable one unacquainted with the Region to gain a fair idea of the main facts of distribution of species. Then there are groups of small islands lying far from the mainland, but each containing in large part species identical with those of New Zealand proper.

In what follows are cited a few clear-cut cases of almost certain hybridism in which forest species, or a forest species, and one from outside the forest, are concerned.

### (a) *Melicope simplex* × *ternata* (Rutaceae).

*Melicope simplex* (tall shrub of the divaricating<sup>1</sup> life-form with small, bicrenate, simple leaves), extends from somewhat south of latitude 46° S. as a simple species to a little south of lat. 42° S., where it meets at the base of the Seaward Kaikoura Mountains the simple species *M. ternata* (bushy-tree with moderate-sized, entire, trifoliolate leaves), and at once many forms connecting the two species appear (fig. 1), some of them intermediate in character between the parents, the latter and the connecting-forms (hybrids) continuing northwards throughout North Island.

### (b) *Myrtus bullata* × *obcordata* (Myrtaceae).

In this particularly striking case *Myrtus obcordata* (bushy-shrub or shrubby tree with smooth leaves), extends from the south of South Island and at about lat. 41° S. meets *M. bullata* (of similar life-form, but with blistered leaves), and at once, a large swarm of transitional forms (hybrids) appears (fig. 2). Both parents and hybrids continue northwards up to lat. 36° S., a little to the north of which point *M. obcordata* halts, and there are no more hybrids — *M. bullata* continuing its course to the extreme north of North Island — except in two very small areas, about 48 km. and 95 km. distant respectively from lat. 36°, where *M. obcordata* suddenly appears along with various hybrids.

<sup>1</sup> This life-form consists of a close mass of entangled slender, stiff or wiry twigs given off from the branches at a wide angle. For New Zealand the life-form occurs in 16 families, 21 genera and 51 species.

(c) *Plagianthus betulinus* × *divaricatus* (Malvaceae).

In this interesting case the two species — *P. betulinus* (low deciduous, dimorphic, canopy-tree), and *P. divaricatus* (medium-sized shrub of the divaricating life-form), — are nearly always kept far apart through their occupying very different habitats, the former forest on deep, alluvial soil, and the latter shallow salt-swamp or salt-meadow. But, where a tidal river allows *P. divaricatus* to extend for a short distance inland on its bank, and the shrub comes into an outlying part of the domain of the forest-tree, hybrids appear. In Chatham Island (717 km. east of New Zealand proper), somewhat similar conditions<sup>1</sup>, according to information generously supplied by Mr. W. MARTIN, have led to the establishment of very similar hybrids between *Plagianthus chathamicus* — a species differing from *P. betulinus* in the long-persisting juvenile form being almost wanting — and *P. divaricatus*, which is rare in the above island.

(d) *Aristotelia fruticosa* × *serrata* (Elaeocarpaceae).

In many parts of South Island the mesophytic, small tree, *Aristotelia serrata*, does not extend from the wet forest-area of the west into the contiguous tussock-grassland area, which commences at the average limit of the westerly downpour, where, however, the more or less xerophytic divaricating-shrub, *A. fruticosa*, is common and constant (a simple species), except for striking epharmonic changes of form. But the sudden alteration in climate does not in the least debar *A. fruticosa* from entering the wet area, so that the two species frequently grow side by side in company with intermediate forms (hybrids) of all grades (fig. 3). In this case a distance of merely a few metres suffices to forbid hybridization.

(e) *Corokia buddleoides* × *Cotoneaster* (Cornaceae).

In this case two species which can meet only very rarely, when

<sup>1</sup> When *P. betulinus* grows on a hillside sloping to the sea, hybrids may occur, a fact brought to my notice by Mr. E. PHILLIPS TURNER, who found one hybrid on the Miramar Peninsula, Wellington, from which place the forest was removed many years ago.

they do come together are accompanied by many intermediates (described and figured by H. H. ALLAN, 1926: 373—4).

*Corokia Cotoneaster* is mainly a plant of montane scrub in South Island, but it occasionally comes into dry *Nothofagus* forest. In North Island its distribution is more scattered, but in some places it comes to the coast-line and there it has been recorded from two localities only as meeting *C. buddleoides* (a species not found to the south of lat. 38° S), and hybrids being present in abundance.

The foregoing examples cited as proof of hybridity speak for themselves and many other striking cases could be brought forward. So far as New Zealand hybrids are concerned, apart from the ability of their parents to cross, the reason for their relative abundance lies in the degree of opportunity for crossing which the distribution of the parents (latitudinal, vertical and ecological) affords, and this I used as a basis for their classification (1923: 113—120).

If the evidence already adduced does not meet with approval, that which tells of artificially crossing the alleged parents and of producing hybrids identical with those found wild can hardly be gainsaid. Thus, H. H. ALLAN has synthesized the reputed »species» *Coprosma Cunninghamii* by crossing *C. propinqua* and *C. robusta*, and his 54 plants of the F 2 generation make a polymorphic swarm to all intents and purposes indistinguishable with what is to be seen again and again in swamps and swamp-forests, while the hybrids, almost exactly intermediate between the parents, are *Coprosma Cunninghamii* Hook. f. pure and simple. ALLAN has also reconstructed an F 1 hybrid *Rubus*, matching a natural hybrid, by crossing *Rubus parvus* with *R. schmidelioides* var. *coloratus*. In addition, he has seedlings, but yet too small for describing, between *Clianthus puniceus* and its variety *alba*, *Phormium Colensoi* and *tenax*, *Coprosma grandifolia* and *robusta*, and between the latter and *C. tenuifolia*.

Further evidence as to hybridity has been secured by sowing seeds of reputed wild hybrids. For instance, H. H. ALLAN has sown seeds of 5 berries from one individual of the so-called species *Myrtus Ralpii* and raised 26 seedlings which developed into a transitional

series of forms linking *M. bullata* and *M. obcordata*, equivalent to what occurs again and again in nature. Similar results have come about from my sowing seeds from one of the *Coprosma propinqua* × *robusta* swarm, but there were not many seedlings, as also from an alleged hybrid between a jordanon of *Acaena inermis* and one of *A. Sanguisorbae*, and from what is supposed to be the type of *Olearia macrodonta* — a species in a position of grave doubt owing to field-observations of G. SIMPSON and J. S. THOMPSON, who discovered apparently typical *O. macrodonta*<sup>1</sup> as part of a hybrid swarm between the two distinct species, *O. arborescens* and *O. ilicifolia*. Finally, in the case of supposed hybrids, polymorphic seedlings may occur in their vicinity, an outstanding example being that of × *Nothofagus cliffusca*.

### 3. DETAILS CONCERNING THE FOREST OR SEMI-FOREST HYBRIDS.

Taking into consideration all the forest communities of the New Zealand Region, the total number of species of vascular plants is 498 (Pteridophytes 121, *Coniferae* 19, Monocotyledons 70, Dicotyledons 288), and they belong to 70 families and 167 genera. But many of these species must be excluded from the standpoint of hybridism, since they belong either to genera with but one species, or are unable to cross owing to geographical or biological isolation. As for the hybrids, it is in all cases members of jordanons which cross in the first place, and such may either belong to different species, portions of a compound species, or taking the whole flora, different genera, i.e. the jordanons may be more or less distantly related or very closely related.

Taking what may be called the *species-hybrids* first, and including

<sup>1</sup> Concerning *O. macrodonta* CHEESEMAN writes (1925: 920), »A distinct species at once separated from its immediate allies by the large coarsely toothed leaves», yet of *O. ilicifolia* (loc. cit.) he says »In its ordinary state this has a very different appearance to *O. macrodonta*, but *intermediates* are not uncommon» (italics mine).

not only those which are actual members of forest but also those outside of forest, but with one of the parents a forest plant, the groups number 110 (*Filices* 19, *Coniferae* 4, Monocotyledons 16, Dicotyledons 72), which belong to 33 families and 50 genera, the largest numbers being in the following: — *Filices* 19, *Rubiaceae* 11, *Cyperaceae* and *Compositae* each 9, *Caprifoliaceae* 6, *Coprosma* 11, *Asplenium* and *Olearia* each 7, *Uncinia* and *Alseuosmia* each 6 and *Nothofagus* and *Nothopanax* each 4. Included in the above are 15 groups with one parent a non-forest species, so 95 are true forest hybrid groups.

The next question to be considered is what proportion of the species in the forest flora capable of hybridizing do hybridize. Taking the large divisions of the flora the figures are as follows: — *Filices* 98, 26.5 per cent cross, hybrid groups 19; *Lycopodiaceae* and *Psilotaceae* 5 species, none cross; *Coniferae* 15 species, 26.6 per cent cross, hybrid groups 4; Monocotyledons 42 species, 47.6 per cent cross, hybrid groups 16; Dicotyledons, 200 species, 54.5 per cent cross, hybrid groups 72. These percentages should really be higher, for not only is it certain that there must be more species unable to cross than are given, but it is almost certain that further hybrid groups will be discovered.

Coming now to the hybrids themselves, with but few exceptions they occur as polymorphic groups and in many cases such are vast swarms. Thus, there must be thousands of hybrids of *Nothofagus* (L. COCKAYNE and E. ATKINSON, 1926: 14), and hundreds of those of *Myrtus*, *Aristotelia*, *Melicope*, *Coprosma*, *Alseuosmia* and *Asplenium*. The chief factor determining the magnitude of a swarm is the relative number of the parental plants (both jordanons and hybrids), which grow in close proximity, and the size of its area of distribution. The effect of parental plants in abundance stands out clearly in those cases where man has altered the balance of nature by bringing parental species together in greater numbers than in primeval New Zealand. A striking case is the great abundance of × *Myrtus bull-obcordata* in the Whangamoia Valley in the north of South Island (lat. 41° 2' S. near the east coast of Tasman Bay), where the forest has been cut down, but with a few trees and shrubs left standing.

Though polymorphy is a fundamental characteristic of a hybrid swarm it has its limits, since there are usually not a great many noteworthy contrasting characters, and series made up of individuals having much the same combinations of characters frequently occur. For example, though the lianoid form of *Fuchsia perscandens* and the tree-form of *F. excorticata* are very different, yet the shrubby intermediates as a whole bear a general resemblance to one another, and frequently some appear almost identical. Where a hybrid group exhibits polymorphy to a comparatively feeble degree the idea arises that such is the F 1 generation, but the proof must rest upon artificial crossing. The supposition as to uniformity in the F 1 generation finds support from H. H. ALLAN's artificial hybrids between *Coprosma propinquum* and *C. robusta*, 20 in number, which (1926: 157) «are very closely similar to one another», but, as explained elsewhere in this paper, the F 2 generation is strongly polymorphic. When the polymorphy of a group is extreme — a most frequent occurrence, as when hybrid trees of all ages occur (e.g. 40 to 400 years and upwards in  $\times$  *Nothofagus cliffusca*), it seems most likely that F 2, F 3 etc. generations are represented, as also back-crosses with the parents and crosses between the hybrids themselves.

Polymorphy is not shown only by differences between individuals, but in one and the same individual striking differences in leaf-form etc. occur, e.g. in semi-juvenile  $\times$  *Nothopanax simpanomalum* (fig. 4). To understand such polymorphy that of contiguous shoots must be studied and not that of the whole tree or shrub, for epharmonic differences may be exceedingly striking, as in the peripheral leaves of the crown of  $\times$  *Nothofagus cliffusca* or  $\times$  *N. soltruncata* as compared with those from near the base of the tree — the so-called «typical» leaves as seen in herbaria and described in floras.

In some instances it seems almost certain that more than two species are represented in a hybrid, e.g. some hybrid *Coprosmae* show characters of 3 species.

The matter of fertility of hybrids is of particular importance, especially as there exists a wide-spread belief that they are mostly

sterile. Many New Zealand hybrids are fertile enough. Seedlings with hybrid characters at times occur in profusion beneath hybrid trees and shrubs. Also, in the few cases where seed from hybrids has been sown, the germination has been considerable. In fact, the only hybrid in the New Zealand flora which has shown undoubted sterility is  $\times$  *Rubus Barkeri* (= *R. australis* var. *glaber*  $\times$  *parvus*), which almost certainly belongs to the F 1 generation. But  $\times$  *R. Mackayi*, though extremely close to  $\times$  *R. Barkeri*, apparently flowers to some extent, but so far I have not had seed sufficiently mature to test its viability. As for these 2 hybrids only 1 wild plant of each has been found. Various *Hebe* hybrids frequently fail to develop seed in lowland gardens, though blossoming freely, but their pollinating insects may be wanting. But though there may be far more sterile hybrids than indicated above, the presence of so many polymorphic hybrid swarms speaks strongly in favour of hybrid fertility in abundance.

Coming next to the hybrids between the jordanons of a compound species, such are apparently extremely common and they lie at the root of the time-honoured doctrine of «variability of species». To prove the existence of such hybrids by field-observations is frequently impossible, since in a polymorphic group of individuals running into one another jordanons cannot be separated from hybrids. Indeed, in certain cases, it looks as if the jordanons were swamped by the hybrids between them, and that a so-called «species» may perhaps be composed entirely of hybrids. This appears to be generally the case in a close growth of *Leptospermum scoparium*, for flowers of many sizes etc. occur and there is no uniformity in leaf-form. Frequently dozens and dozens of bushes of this species grow side by side with no two alike. One jordanon, however, occurs with a limited distribution — the variety *incanum*, but it crosses with other jordanons or hybrids. In some cases jordanons are readily distinguishable, as in certain shrubs in which they are marked out by differently-coloured berries or drupes, but between such there are hybrids with fruits of intermediate colours, e.g. in the compound species *Cyathodes*

*acerosa*, *Corokia Coloneaster* and *Aristotelia fruticosa*. Then, there are geographical jordanons which can only cross, if they do cross, at the narrow line where they meet, e.g. *Leucopogon fasciculatus* with its broad-leaved juvenile to the north of lat. 38° (this may not be the actual limit), and the narrow-leaved jordanon for the remainder of its distribution southwards. Also, there are geographical jordanons of *Rubus australis* and *Helichrysum glomeratum*.

#### 4. THE BEARING ON TAXONOMIC BOTANY OF THE PRESENCE OF ABUNDANT HYBRID SWARMS IN A FLORA.

This part of my subject needs but little stressing here, since it has been dealt with at considerable length by H. H. ALLAN and myself in an easily accessible journal (1927: 234—77). The main feature is the severe blow which it strikes at the theory of »variability of species». On the contrary, as species are made up of invariable<sup>1</sup> jordanons — one jordanon for the simple and two or more for the compound species — variation (leaving epharmony in my sense on one side), excepting that called by De Vries »fluctuating», and possibly mutation, appears to be impossible. The variants are the inter-jordanic hybrids and the epharmones. The doctrine that species can be connected by »intermediates» which have arisen through the innate variability of the species must surely be cast aside. And with this must go also the argument that because two groups of plants, each distinct from the other, are connected by a series of intermediate forms, groups and intermediates comprise but one species. On the contrary, the presence of such intermediates (hybrids and perhaps in part epharmones), appears to be a certain proof that the groups so linked together are distinct species, and certainly the centre group of the intermediate forms can no longer be allotted that specific rank it so frequently bears.

<sup>1</sup> With LORSY (1925: 45), I hold that theoretically there are no absolutely pure cultures in nature. In practice, however, jordanons to all intents and purposes produce their like.

Although the presence of hybrids in abundance in the New Zealand flora has only been recognized within the last few years, it has led already to important taxonomic changes. Thus, taking the forest flora alone and considering the species etc. accepted in CHEESEMAN'S Manual of the New Zealand Flora edition 2 (1925), no less than 18 so-called »valid species», and 5 varieties, must be removed therefrom, since they are polymorphic groups of hybrids. On the other hand, 10 varieties supposed to run into certain species must be accorded specific rank. These changes are not based on opinion but on solid facts, the outcome of careful field-studies and, in some instances, garden experiments. These comparatively few major taxonomic alterations give but little idea of the effect which the recognition of hybrids, jordanons and epharmones has had in New Zealand floristic botany. Many so-called »variable species» stand out clearly as mixtures of jordanons, the hybrids between such, and epharmones. In some cases, some such jordanons have been defined and their distribution studied, with the result that they are seen to occupy small, but well-defined areas. Species of wide range are being studied and it seems probable that there are northern and southern jordanons or perhaps species where no »variability» has previously been suggested. New hybrid groups are frequently coming to light. In fact, it has become clear that the flora must be investigated from end to end in the light of the new knowledge and the new methods. It may, indeed, be stated with considerable truth that the more common a species is, the less is known about it.

Finally, the new outlook has stirred up an interest hitherto unknown in the taxonomy of New Zealand vascular plants. The matter is no longer a question of relying on authority and putting names to plants or making species or varieties out of mere scraps, the biological status of which is unknown. It is rather a casting aside of such authority, and turning from the herbaria with their plants of unknown status including various »types», and going forth with an open mind into the field to the plants themselves. So should arise a trustworthy knowledge of relationships, and the road be opened for a rational study of the evolution of the different taxonomic groups.

### 5. THE ROLE OF HYBRIDS IN THE FOREST.

The part played by hybrids in the forest communities is twofold, in that they may effect both their composition and their structure — the former a question of the number and relative abundance in the community of the hybrid groups, and the latter of the life-forms of the hybrid individuals which are present. To function in either of the above directions to a marked degree a great number of hybrid individuals would be required, far more, indeed, than seems possible, when the relative abundance and distribution of the parents are considered. Taking first of all the tall, dominating trees, there are only the species of *Nothofagus* and its hybrid swarms to be dealt with, unless, as seems likely, *Weinmannia racemosa* and *W. sylvicola* cross. The species of *Nothofagus* number 5, but apparently *N. Menziesii* plays little if any part (at most it lies under a slight suspicion), whereas the other species produce 4 or 5 hybrid swarms. But large areas of forest are dominated by one or other of the species, while the non-crossing *N. Menziesii* and *N. fusca* frequently occur together, and it is usually<sup>1</sup> only when the latter and one or more of the remaining species occur in proximity that hybrids occur. Generally in *Nothofagus cliffortioides* — *fusca* forest, hybrids ( $\times$  *N. cliffusca* — fig. 5), form a very small percentage of the trees, but perhaps 5—10 per cent occur with fair frequency.

In some places, however, there may be at least 50 per cent of hybrids, but such spots are small in extent. Nevertheless, it is clear that the hybrids can well hold their own, a statement substantiated by the presence of hybrid seedlings in great numbers beneath hybrid trees. After a forest fire hybrids may occur in great profusion and the reinstated forest will certainly contain more hybrid trees than did the former community. Where there are small colonies of *N. fusca*, in what is otherwise a pure forest of *N. cliffortioides*, hybrid

<sup>1</sup> One or two cases of supposed hybrids have been noted, where one of the parents is absent, but in a gradually changing community such are to be expected.

trees occur and such, of seedbearing age, I have seen on a stony riverbed, 96 km. or more below the last tree of *N. fusca*, so establishing a nucleus round which hybrids will spread into new territory and dominate.

Though in some localities  $\times$  *N. soltruncata* (fig. 6) occurs in plenty, its numbers appear to be far smaller than in the case of  $\times$  *N. cliffusca*. Both the closely-allied species cross with one another and, where *N. cliffortioides* and *N. Solandri* are in about equal numbers, there may be many individuals suggesting the combined characters of the two, yet so much alike are the two species that hybridity must be assumed rather than proved.

Coming now to the hybrid ferns, grass like plants and the smaller trees and shrubs, none are more generally present than those between various jordanons of *Asplenium*, such ranging from well-marked simple species to those which are unnamed. *Asplenium bulbiferum*, *A. laxum*, *A. tremulum* (if this be var. *tripinnatum* Hook. f. of *A. bulbiferum*), *A. Hookerianum*, *A. lucidum*, *A. Colensoi*, and the compound species *A. flaccidum*, are some of the species involved. Between these, and probably some unnamed jordanons, there is a bewildering assortment of hybrids showing dominance of certain characters of one or other of the above, and others impossible so far to place.<sup>1</sup>

Light being let [into the forest] generally favours hybridism. This is plainly to be seen in the case of hybrids of *Myrtus*, *Fuchsia* and *Aristolelia*, and in open spaces polymorphy rules among these genera.

<sup>1</sup> CHEESEMAN (1925: 51) devotes 18 lines of small print to the polymorphy of *Asplenium bulbiferum*, speaking *inter alia* of puzzling forms which «apparently connect the species with» 6 species which he cites, and he considers «it would occupy many pages to characterize them and I doubt whether it is possible to define them in language sufficiently precise to enable them to be recognized with certainty». According to the doctrine of variability this is quite true, but, in the field, let a certain jordanon absent before enter in — e.g. the very distinct *A. Hookerianum* — and its hybridizing influence is easy to estimate.



In fairly dark forest of the north of North Island the great and amazing *Alseuosmia* swarm (H. H. ALLAN 1928: figs. 16 and 17), is occasionally present and so far has defied analysis, but chiefly because no one as yet has studied it in the field in the light of hybridism, and to declare that certain of the species are »very variable« has been deemed an explanation of their variability!

As regards the effect of hybrids upon the *structure* of the community to which they belong the matter chiefly depends upon the incoming of a life-form distinct from that of either parent. The following are a few examples.

The hybrids of *Plagianthus betulinus* (small, deciduous canopy-tree), by *P. divaricatus* (dense divaricating almost deciduous shrub), are mostly small, twiggy trees — certainly not canopy-trees — which come about midway between the parents in their power of reducing the light which strikes the ground. But, as *P. divaricatus* is a plant of brackish water which does not occur in forest, the hybrids have gained their forest status by degrees, and so by degrees a new life-form and a new group of the flora have come into the forest of alluvial valleys watered by a tidal river.

The case of *Fuchsia excorticata* (low, deciduous tree with rather massive irregular trunk), crossed by *F. perscandens* (scrambling liane with a long, cord-like, naked main-stem), stands alone. Most of the hybrids are twiggy shrubs of dense habit which may occur in greater numbers than either parent. Their density cuts off much light from the ground, so that seedlings do not readily grow beneath them. On the other hand, the destruction of young trees by the liane is lessened, as its numbers decrease through the substratum being occupied by the hybrids.

In the case of *Nothopanax anomalum* var. *microphyllum* (dense, rigid divaricating-shrub), being crossed by *N. simplex* (tall bushy-shrub or low tree), the hybrids sometimes occur in great quantity, and as many are bushy-shrubs, they cut off less light from the forest-floor than does *N. anomalum* var. *microphyllum*, but, as juveniles, they are far more light-forbidding than is juvenile *N. simplex*. Somewhat

similar is the case of *Coprosma propinqua* (divaricating-shrub), by *C. robusta* (tall bushy-shrub or low bushy-tree), the hybrids generally being more open in habit than the former and denser than the latter. *Melicope simplex* × *ternata* is a similar case.

Finally, so far as the majority of hybrids are concerned, since usually similar life-forms cross, there is but little effect on the structure of a forest community.

## 6. LIST OF HYBRID GROUPS IN WHICH THE VASCULAR FOREST-PLANTS ARE CONCERNED.

### FILICES.

- Hymenophyllum flabellatum × rufescens.  
 » sanguinolentum × villosum.  
 Asplenium bulbiferum × flaccidum.  
 » » × Hookerianum.  
 » » × laxum.  
 » » × lucidum.  
 » flaccidum × Hookerianum.  
 » » × lucidum.  
 » Colensoi × Hookerianum.

(There are certainly many more *Asplenium* hybrids in which especially *A. laxum* and *A. tremulum* play a part.)

- Blechnum lanceolatum × membranaceum.  
 Pellaea falcata × rotundifolia.  
 Leptopteris hymenophylloides × superba.  
 Polystichum Richardi × vestitum.  
 » sylvaticum × vestitum.  
 Hypolepis distans × rugosula.  
 » punctata × rugosula.  
 » » × tenuifolia.  
 Pteris comans × macilenta.  
 » macilenta × pendula.

(For these *Pteris* hybrids I am indebted to information from Mr. H. CARSE, for many years a close student of ferns.)

## PODOCARPACEAE.

- Podocarpus acutifolius × nivalis.  
 »           »           × Hallii or totara.  
 »           Hallii × nivalis.  
 »           »           × totara.

## CYPERACEAE.

- Uncinia Banksii × riparia.  
 »           caespitosa × filiformis.  
 »           »           × riparia.  
 »           »           × rupestris.  
 »           ferruginea × uncinata.  
 »           filiformis × riparia.  
 Carex dissita × Lambertiana.  
 »           »           × Solandri.  
 »           ternaria × ?

## LILIACEAE.

- Astelia Cockaynei × nervosa var. sylvestris.  
 Cordyline australis × Banksii.  
 »           »           × indivisa.

## ORCHIDACEAE.

- Cyrtostylis oblonga × rotundifolia.  
 Pterostylis australis × Banksii.  
 »           »           × graminea.  
 »           Banksii × graminea.

## FAGACEAE.

- Nothofagus cliffortioides × fusca  
 »           »           × Solandri.  
 »           »           × truncata.  
 »           fusca × truncata.  
 »           Solandri × truncata.

## MORACEAE.

- Paratrophis microphylla × opaca.

## SANTALACEAE.

- Mida myrtifolia × salicifolia.

## LORANTHACEAE.

- Elytranthe flavida × tetrapetala.

## POLYGONACEAE.

- Muehlenbeckia australis × complexa.  
 »           axillaris × ephedroides.  
 »           complexa × ephedroides.

## RANUNCULACEAE.

- Clematis hexasepala × indivisa.

(Probably the other species cross, when they come together, since artificial hybrids have been raised by Mr. S. PAGE between nearly all of them.)

## SAXIFRAGACEAE.

- Quintinia acutifolia × serrata.

## WINTERACEAE.

- Wintera axillaris × colorata.

## PITTOSPORACEAE.

- Pittosporum Colensoi × fasciculatum.  
 »           »           × tenuifolium.  
 »           pimeleoides × reflexum.

(In many places *P. tenuifolium* is a polymorphic mixture of jordanons and hybrids between them.)

## ROSACEAE.

- Rubus australis var. glaber × parvus.  
 »           parvus × schmidelioides var. coloratus.  
 »           schmidelioides var. coloratus × subpauperatus.

## LEGUMINOSAE.

- Edwardsia microphylla × prostrata.

## RUTACEAE.

- Melicope simplex × ternata.

## CORIARIACEAE.

- Coriaria aborea × sarmentosa.

## ELAEOCARPACEAE.

- Aristotelia fruticosa × serrata.

## MALVACEAE.

- Plagianthus betulinus × divaricatus.  
 Hoheria angustifolia × sexstylosa.  
 »           »           × Lyallii.

## VIOLACEAE.

- Melicytus lanceolatus × ramiflorus.  
 »           micranthus var. longiusculus × microphyllus.

## MYRTACEAE.

- Leptospermum ericoides × scoparium.  
 Myrtus bullata × obcordata.  
 Metrosideros robusta × tomentosa.

## ONAGRACEAE.

- Epilobium glabellum × pubens.  
 Fuchsia excorticata × perscandens.

## ARALIACEAE.

- Nothopanax anomalum × simplex.  
 »           Colensoi × simplex.  
 »           arborescens × laetum.  
 »           »           × Pseudopanax crassifolium var. unifoliolatum.

## UMBELLIFERAE.

- Hydrocotyle elongata × ?

## CORNACEAE.

- Corokia buddleoides × Cotoneaster.

## ERICACEAE.

- Gaultheria antipoda var. erecta × oppositifolia.

## EPACRIDACEAE.

- Dracophyllum longifolium × several species.

## APOCYNACEAE.

- Parsonsia capsularis × heterophylla.

## SCROPHULARIACEAE.

- Jovellana repens × Sinclairii.  
 Hebe buxifolia × vernicosa.

## RUBIACEAE.

- Coprosma propinqua × robusta.  
 »           lucida × robusta.  
 »           »           × grandifolia.  
 »           grandifolia × tenuifolia.  
 »           Banksii × Colensoi  
 »           »           × foetidissima.  
 »           cuneata (? Astoni) × foetidissima.  
 »           Colensoi × foetidissima.  
 »           rotundifolia × ?  
 »           ramulosa × ?  
 »           pseudocuneata × ?

## CAPRIFOLIACEAE.

- Alseuosmia Banksii × linariifolia.  
 »           »           × quercifolia.  
 »           »           × macrophylla.  
 »           linariifolia × quercifolia.  
 »           »           × macrophylla.  
 »           quercifolia × macrophylla.

(Whether there are really the above species of *Alseuosmia*, I have no idea.)

## CAMPANULACEAE.

- Pratia angulata × perpusilla.

## COMPOSITAE.

- Olearia avicenniaefolia × moschata.  
 »           »           × nummularifolia.  
 »           cymbifolia × nummularifolia.  
 »           arborescens × ilicifolia.  
 »           »           × lacunosa.  
 »           »           × capillaris.  
 »           ilicifolia × lacunosa.  
 Shawia coriacea × paniculata.  
 Helichrysum bellidioides × glomeratum.

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## APPENDIX.

*Explanation of certain taxonomic terms as used in this paper.*

*Jordanon*. A true-breeding group of similar individuals distinct from any other such group.

*Epharmonie*. An unstable form of a jordanon differing markedly from the so-called «normal» form due to unusual environmental influences.

*Simple species*. A jordanon to which specific rank has been awarded not closely related to any other jordanon, e.g. *Agathis australis*.

*Compound species*. Two or more closely-related jordanons which it has been convenient to unite together under one name e.g. *Rubus australis*. Such species are abstractions and not realities.

*Variety*. Any jordanon of a compound species sufficiently distinct from any other of its jordanons to permit of a satisfactory diagnosis, e.g. the varieties *sylvestris* and *grandis* of *Astelia nervosa*.

*Linneon*. A compound species, frequently in a very wide sense, together with all the hybrids between its jordanons, and their epharmones e.g. *Cyathodes acerosa*. It may also include more than one species.

*Form*. An indefinite term applied for convenience to an individual of uncertain status.

Leonard Cockayne

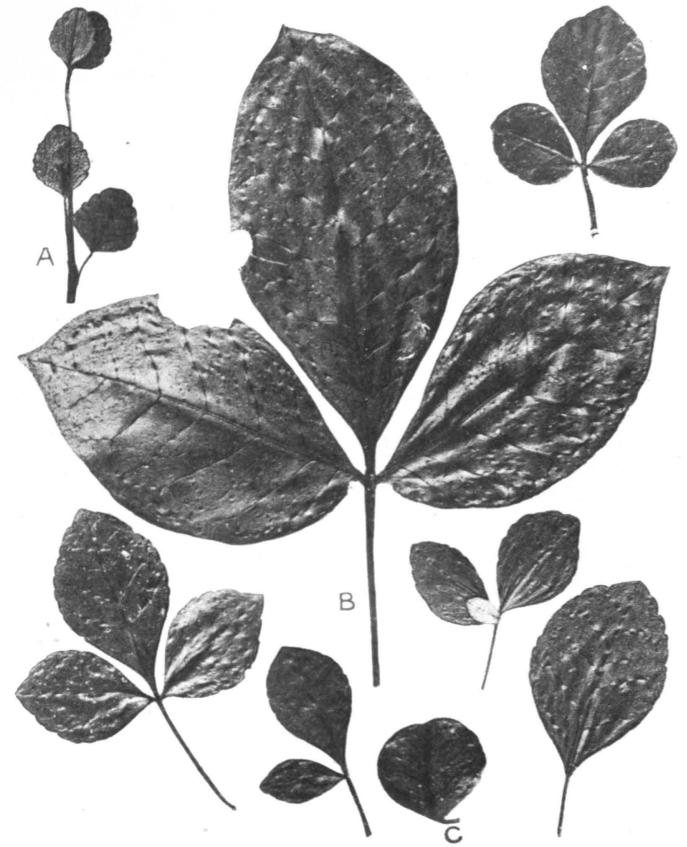


Fig. 1. *Melicope simplex* (A), *M. ternata* (B) and leaves of 6 hybrids between them, one of which (C) is similar to the leaf of *M. simplex*, but much larger. All the leaves 0.85 life-size.  
Photo S. GIBSON.



Fig. 2. *Myrtus bullata* (A), *obcordata* (B) and 9 different hybrids between them, belonging to the swarm  $\times$  *Myrtus bullobcordata*, with (C) showing leaves of „bullata“ and „obcordata“ types on the same shoot. All leaves 0.81 life-size.  
Photo S. GIBSON.



Fig. 3. A small leaf of *Aristotelia serrata* (A), a short shoot of *A. fruticosa* (B) and leaves of 6 of the hybrids between them. All 0.78 life-size.  
Photo S. GIBSON.



Fig. 4. Leaves taken from contiguous shoots of one individual of semi-juvenile  $\times$  *Nothopanax simpanomalum* (= *N. anomalum*  $\times$  *simplex*).  
About 0.68 life-size.  
Photo S. GIBSON.

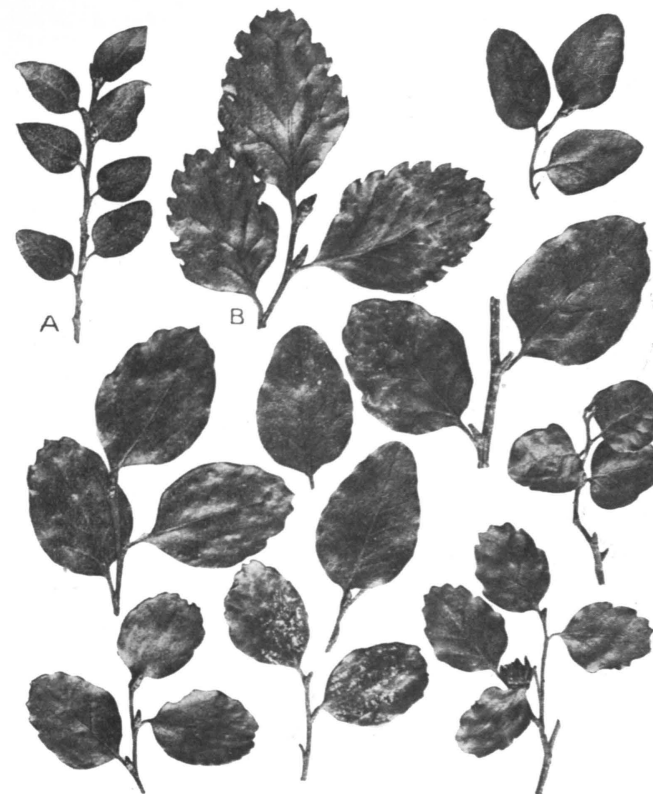


Fig. 5. *Nothofagus cliffortioides* (A), *N. fusca* (B) and 9 hybrids between them, taken from a great swarm occupying a very small area, where the hybrids equal or perhaps outnumber the parents.  
All 0.85 life-size.  
Photo S. GIBSON.

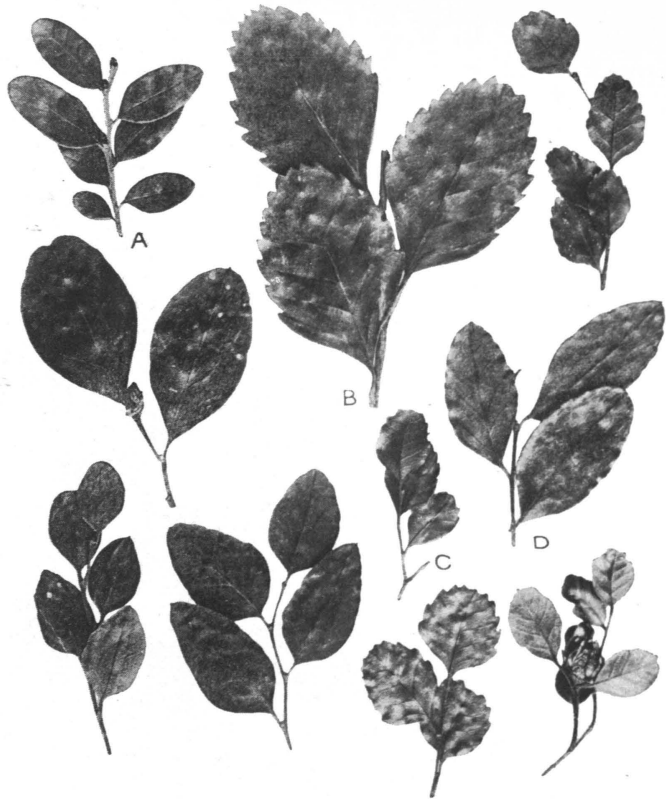


Fig. 6. *Nothofagus Solandri* (A), *N. truncata* (B) and 8 of the hybrids between them, with (C) a very small-leaved hybrid with toothed margins, and (D) of *Solandri* form, but with much larger leaves. All 0.85 life-size.

Photo S. GIBSON.