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A Study of *Entelea arborescens* R. Br. ("Whau").

PART I. ECOLOGY.

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SUMMARY.

Entelea arborescens (Tiliaceae), endemic monotype, is found in New Zealand from the North Cape to Nelson, near the sea-coast only.

The species is outstandingly light-demanding. It is intolerant of even moderate cold, strong wind, and a very dry or ill-drained substratum.

Even in still-primitive coastal forest occurrence is sporadic always, due to the plant's inability to live under an unbroken canopy; but in open places it is unexcelled in vigour of growth, and often plays there a vital seral rôle.

In early stages of man's interference with coastal forest (save in dry or wind-swept areas) the species spreads rapidly. With prolonged, or initially severe, interference the species is exterminated.

In lowland rain-forest *Entelea* is rare—found only, so far as is known, by streams in broadly open valleys near the coast where open ground and sufficient warmth and light are found.

Browsing animals of all kinds are destructive, but only where the normal food supply is low.

In its natural habitat the tree depends mainly for success upon its prodigious seed production, the remarkably long life of the seed, and, after germination, rapid growth. Under unnatural conditions the resistance to, and stimulation of, the seed by fire is vitally important.

INTRODUCTION.

ONLY brief general accounts of this unusual, large and delicate-leaved, monotypic, endemic genus have been published (e.g., Kirk, 1889, t. 33; Cheeseman, 1914, I, t. 22). In fact, very few New Zealand species have been treated at all fully ecologically. This paper has been written (1) to serve as introduction to Parts II and III (Dispersal; Anatomy), (2) because it gives some little detailed information about coastal forest succession in general, upon which scarcely anything has been published, and (3) because *Entelea,* in many parts, is fast becoming extinct.

Where the nomenclature is not that of Cheeseman (1925) the authority has been quoted, and Cheeseman's name added in brackets, with the first mention of the species.

AFFINITIES OF *ENTELEA.*

The genus, endemic and monotypic, is the single New Zealand member of the wide-ranging, mainly tropical and subtropical family Tiliaceae. Cockayne places it (1928, p. 414) in the Palaeotropic element of the New Zealand flora. Oliver (1925, pp. 122–3) lists it as "Palaeozelandic": but even if this view is correct the ancestors of

the genus most certainly came from the north. Oliver, again (*ibid.*), apparently arguing mainly from facts of distribution, places *Entelea* in a section "with no near relatives". But the genus is distinguished taxonomically from the South African genus *Sparmannia* only by the stamens being all fertile (Brown, 1824, t. 2480); morphologically and anatomically the two genera are remarkably similar (Part III).

LIFE FORM.

Cheeseman (1925, p. 560) describes *Entelea* as "a handsome shrub or small tree 8–20 ft. high, with a trunk 5–9 in. diameter". (Pl. 25, Fig. 1.) In favourable habitats, however (notably on islands off the North-East coast), a height of 30 ft. (extreme 48 ft.) is frequently reached, with trunk 10–15 in. diameter (extreme 21 in.). (Pl. 25, Fig. 2.)

Where bright and even light prevails throughout development, and the trees are not too crowded, the form is typically canopied (Pl. 25, Fig. 1; Pl. 27, Fig. 2) even in early stages. This is important concerning competition with other light-demanding species. Where illumination is more diffuse, or uneven, as often in forest clearings, the form is less compact (Pl. 26, Figs. 2 and 3) although leaves are larger. Under unfavourable conditions (especially in a dry or wind-swept habitat) the plant may be reduced to shrub dimensions while still retaining the tree habit. In special circumstances an unusual form may be assumed (Pl. 25, Figs. 3, 4), even that of a semi-prostrate shrub rooting all along the stem (where young plants have fallen on very moist ground).

The root system is typically shallow, 2–4 stout, almost horizontal, main roots giving off many smaller fibrous ones; but as with polydemic species in general a marked correlation with soil-water distribution is shown (p. 271).

DISTRIBUTION.

Although *Entelea* is found, here and there, in Nelson and Marlborough (Cheeseman, 1925, p. 560), occurrence is local south of Lat. 38°. The plant has never been found more than 8 km. from the sea (Waitakerei Stream, near Auckland), nor higher than 350 m. (Taranga, Map 1.) All this, doubtless, is related to temperature; but it is probably not so much the mean annual temperature (M.A.T.) of a locality which is vitally important as the *minimum* yearly temperature—for *Entelea* is very frost-tender. An analysis of the available temperature records (1919–44 inclusive) for Riverhead, near Auckland, and Cawthron, near Nelson, is significant here (Table I).

TABLE I.

Station.	Average of M.A.T.'s.	Average of Ext. Min. T's.	Ext. Min. Temp.
Riverhead (20 m. above M.S.L.)	14.1° C.	—4.0° C.	—5.1° C.
Cawthron (7.4 m. above M.S.L.)	12.7° C.	—2.2° C.	—3.5° C.

Riverhead (Lat. 37° 14′ S.) is 12 km. from the open sea, i.e., a little *beyond* the inland limit for *Entelea*: Cawthron, only 1 km. from the open sea, is in Lat. 41° 15′ S., i.e., approximately the southern

limit for *Entelea*. Although Riverhead (where *Entelea* is just unable to grow) has the higher average M.A.T., its minimum temperatures (Average and Extreme) are somewhat lower than those for Cawthron (where *Entelea* is just able to grow).

The approximation of the minimum-temperature figures for the two stations indicates that *Entelea* has spread as far south as it will.

Extreme minimum temperatures for localities where *Entelea* really thrives are always, so far as the records show, well above 0° C.

THE ROLE OF *ENTELEA* IN NEW ZEALAND VEGETATION.

The existence of the species is bound up almost exclusively with the life history of coastal forest, in which, however, it occurs only sporadically. The plant is intimately concerned with the rapidly moving successions within this forest, and the whole ecological aspect has therefore been treated developmentally.

Entelea has been investigated from the North Cape to Nelson and Marlborough along almost the whole length of both coasts; but here, for simplicity, only four areas are described in any detail, viz., Taranga, Mayor Island (islands off East Coast), Coromandel Peninsula (East Coast), Waitakerei Ranges (West Coast). These four areas, where *Entelea* is, or was, abundant, together show all the chief ecological features (for further details see unpublished thesis, 1937, Auckland University College Library).

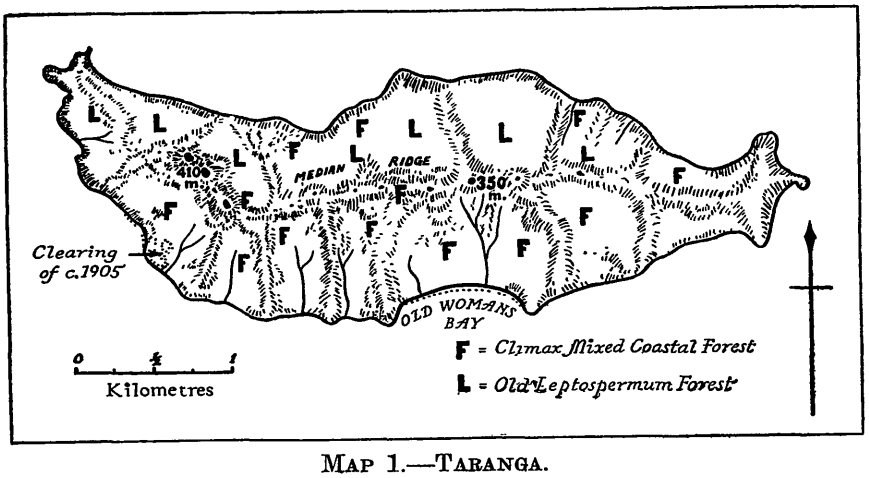
1. COASTAL FOREST.

A. VIRGIN COASTAL FOREST.

(a) *With Mixed Dominants.*

(1) *Taranga (Hen Island)* (Map 1).

Taranga (some 5 km. long and 476 hectares area) is easily the largest of the Hen and Chickens group of eight uninhabited islets lying some 17 km. E.S.E. of Whangarei Heads. The island, in most places, rises abruptly from the sea, and forest-clad slopes then sweep, at first fairly gently, but later swiftly, to the median ridge which



MAP 1.—TARANGA.
(Modified from Cranwell and Moore with kind permission.)

runs roughly E. and W. at about 300 m. to form the backbone of the island. Precipices and steep slopes abound. There are no permanent streams.

The general climatic, geological, and vegetational features have been well described by Cranwell and Moore (1935).

Taranga was chosen for the study of *Entelea* because much of the typically coastal forest cover is unquestionably virgin. Such forest falls into two main classes: (1) Mixed Coastal Forest, (2) *Metrosideros excelsa* Sol. ex Gaert. (*M. tomentosa*) (Pohutukawa) -dominated Coastal Forest.

Sharply separated from the virgin forest are considerable areas of induced forest dominated almost exclusively by tall *Leptospermum ericoides* (Map 1, L: p. 286); there is also a small area of much younger mixed regrowth (Map 1: p. 284).

The virgin mixed coastal forest forms the greater part of the primitive vegetation of Taranga, extending from the very shore at times to the base of the highest pinnacles. Podocarps are absent, epiphytes and scandent species few, tree-ferns rare. The most important species, especially over the southern face of the island, where most work was done, are *Beilschmiedia tawa, B. taraire, Dysoxylum spectabile, Vitex lucens, Corynocarpus laevigata, Melicytus ramiflorus* and *Metrosideros excelsa* (often of great size), which often occur mingled together—or the first four may form almost pure stands (especially *B. taraire*). *Rhopalostylis sapida* is locally important. On the whole, however, conditions of importance for *Entelea* are throughout fairly much the same, viz. (1) the rocky (andesite) substratum, everywhere fissured, giving excellent drainage and soil aeration; this leading to (2) comparative dryness of the subsoil, aggravated by the only moderate rainfall (Cranwell and Moore, p. 302); but (3) the presence of a rich, water-retaining, humous topsoil almost eliminates these factors in the case of the shallow-rooting *Entelea,* but not for some of the associated species; (4) the almost wind-still, but not humid, forest interior; (5) the uniformity and comparative lowness (10–15 m.) of the canopy and its density, the latter due partly to the abnormally large leaves of most of the trees (*Ibid.*, p. 306); (6) the resulting dimness of interior with poor seedling and shrub growth. The clean trunks of the trees rise, well spaced, from a densely leaf-covered floor, carpeted in most places with *Asplenium lamprophyllum* Carse (especially), *A. lucidum*, and *Polystichum richardi*. The chief shrubs are *Macropiper excelsum, Coprosma australis* (A. Rich.) Robinson (*C. grandifolia*) and *C. macrocarpa*.

Entelea occurs:

(α) *On Rocks*: Great masses of weathered rock frequently occasion an opening in the forest roof, and on their summits *Entelea,* often of large size, is usually present (Pl. 25, Fig. 3).

Almost all the other forest plants may be found also on these rocks, great trees of *Metrosideros,* or occasionally *Corynocarpus* or *Melicytus*, all of which invariably send their roots early to the ground, sometimes slowly forcing *Entelea* out of existence. The most constant and serious competitors of *Entelea,* however, are the shrubs *Macropiper, Coprosma australis,* and *C. macrocarpa,* which maintain their

rooting systems on top of the rocks where the soil layer is at best but a few centimetres thick. Where the rocks are low, *Entelea* may largely escape this severe root competition by sending to the ground cord-like roots, often 2–3 m. long, which are strikingly different in appearance from soil-growing roots (Pl. 25, Fig. 3).

These rock-growing *Entelea* are often of peculiar form owing to the unusually strong response of the plant to light. The trees grow vigorously under all circumstances directly towards the gap in the forest roof. Even when trees fall, as often happens owing to their precarious hold on the rock, they still send their shoots towards the light, either by growing upwards in a sweeping arc, or by sending up lateral branches (43 seen on one stem), the original apex often decaying away (Pl. 25, Fig. 3). The extreme, almost lianoid, example shown in Pl. 25, Fig. 4, was produced by almost horizontal growth of the young tree along the rock face in response to gradual growing in of taller plants towards the rock from left to right (in the Fig.). Eventually, nearly 7 m. from the place of germination, the tree was able to develop a leafy crown in the light.

Entelea, it should be mentioned here, has never been found as even a hemi-epiphyte.

(β) *On Steep Rock Faces*: Steep rock faces, usually quite moist and well lighted, abound on Taranga and often carry an abundant growth of *Entelea,* even where there is little soil. The root system is strikingly plastic. The tree may grow several metres high rooted only in a shallow pocket of soil; in fact, it may often be lifted, with its dense mat of rootlets, completely from the rock, unharmed. Where the seedling early outgrows its immediate resources, long, flexible roots (see above) may be sent out, snake-like, over the moist substratum. Again, where the rock is fissured, the primary root may grow almost vertically downwards.

From some rock faces seeps emerge, and there, if sufficient soil be present, *Entelea* finds optimum growth conditions. One plant had leaf blades 37–50 cm. long and up to 47·5 cm. broad, and petioles 30–60 cm. long; it grew in height 3·7 m. in 14 months.

(γ) *On Slips*: Such are common and are a favourite locality for *Entelea,* especially where very moist conditions have caused the shallow cover of rock faces to slide away. Colonies of young plants may grow so vigorously that all other species are excluded. *Entelea* may maintain itself for several generations.

(δ) *In Clearings*: In the many, usually small, clear spaces in this Taranga forest, formed either by the fall of large trees or by their death *in situ, Entelea* is easily the most striking plant. These clearings are notable for the dense growth which springs up in them. Successions are short, seral stages fairly well marked.

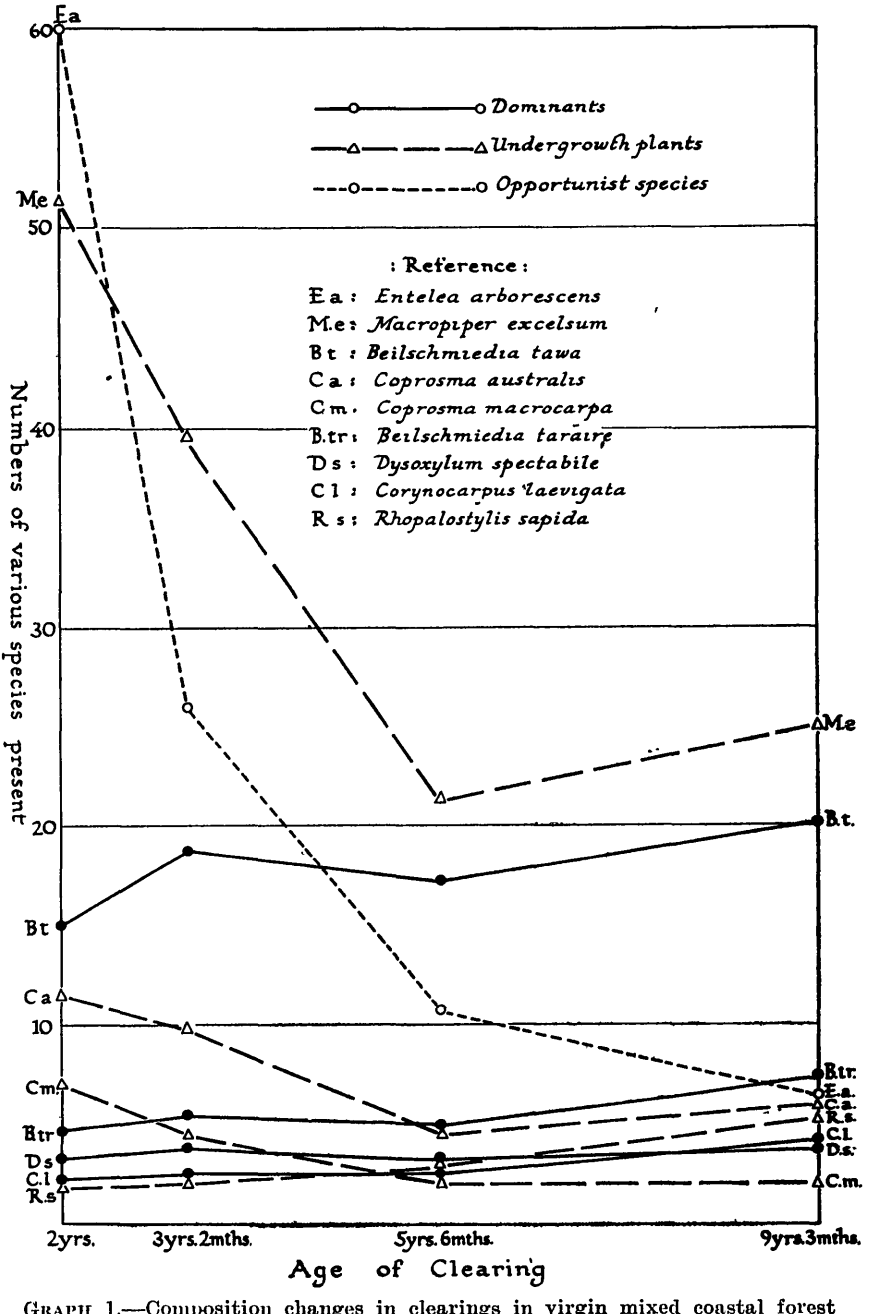
The main factors governing the success, or otherwise, of *Entelea* are: (1) The number of "viable" seeds (Part II) present in early stages relative to those of other species, especially plants of the undergrowth. (2) The initial degree of openness of the floor. If many undergrowth plants are already present the rapid growing together of their leafy parts may trap many, or all, of the young *Entelea* which spring up. *Entelea* is handicapped also by a rich floor

cover of ferns (especially *Asplenium lamprophyllum*); but the plant appears to spring from ground covered with decaying leaves as successfully as any other species. (3) The size of the clearing, a large clearing relatively favouring *Entelea.* (4) The height of the canopy, a low canopy relatively favouring *Entelea.* (5) The time elapsing before the gap in the forest roof is closed (if at all) by lateral growth of the standing trees—this connected with (3) and (4). (6) Altitude. In clearings above about 150 m. *Entelea* rarely dominates. Below this altitude the plant is seldom not dominant unless a special factor operates, e.g. (7) Aspect. At 130 m. on the S.W. face of Taranga occur two large clearings quite without *Entelea* but filled with a dense tangle of the usual undergrowth plants. These clearings are situated in a south-facing, funnel-like valley up which blows a slow, cool draught. On the warm north side of the island *Entelea* is found at 350 m., the highest altitude recorded for the species. (8) The distribution of light within the clearing (connected with 3, 4, 7, and other factors, notably topography). In a clearing behind Old Woman's Bay (Map 1), in relatively tall forest, 57 young *Entelea* were found (1937) in the southern half of the clearing, none in the northern half, where, however, occurred all the species associated with *Entelea* at the southern end.

Where conditions are initially favourable, *Entelea* is usually the first new plant to appear, followed most quickly, it seems, by *Urtica ferox* (not common), *Macropiper excelsum, Coprosma macrocarpa,* and *C. australis,* in that order. Forest dominants, in general, are slower to come in—*Corynocarpus* most quickly, followed by *Beilschmiedia tawa,* so far as could be ascertained.

Entelea establishes itself with striking rapidity. A small clearing made in December, 1935, contained several *Entelea* over 1 m. high (one with a fruit!) 14 months later. The number of *Entelea* rapidly increases until, between two and four years after the formation of the clearing, the vegetation becomes closed. This is quite the most critical stage for *Entelea.* Fortunately, it was possible to study this, and other stages, in four clearings which had been made in December, 1933, by the felling of trees. The writer visited these clearings in December, 1935, January, 1937, May, 1939, and March, 1943, and on each occasion took photographs (Plate 26), and made counts (Table 2) of all plants, except ground ferns, which remain much more constant in kind and number than other plants. Composition changes have been summarised in Graph 1 by averaging the numbers of those species common to at least three of the clearings and plotting them as shown. This is permissible, (1) since the clearings all occur in the same type of forest, (2) since they are of identical age, and (3) since all are large enough (7–16 m. across) to have allowed the establishment of a fairly representative set of species. At the same time they differ in no way save their origin (since no undergrowth was cut) from clearings made naturally by the fall of a tree, and have been treated as such.

Although the information on which Graph 1 is based is inadequate to give a really reliable picture of clearing succession as a whole, it does indicate the relation of *Entelea* to other clearing plants through most of its brief life cycle, and emphasises the surprisingly



GRAPH 1.—Composition changes in clearings in virgin mixed coastal forest on Taranga between 1935 and 1943.

rapid fluctuations which may occur in the population of a typical clearing in virgin coastal forest.

The four clearings all became closed between 1935 and 1937. The sudden drop in *Entelea* numbers, and to a lesser extent those of *Macropiper* and species of *Coprosma*, is related chiefly to the cutting

TABLE 2. *Analysis of Clearings in Virgin Mixed Coastal Forest on Taranga.*

Species	Clearing No.	'35	'37	'39	'43
Entelea arborescens	1	154	74	21	8+3
	2	54	9	6	4
	3	20	13	9	3+2
	4	12	8	7	6
Macropiper excelsum	1	79	44	17+2	12+24
	2	60	52	30+1	21+8
	3	29	28+2	17+3	10+14
	4	37	32	14+1	9+2
Coprosma australis	1	26?	20	4+1	3+7?
	2	2?	2	2	2
	3	5	2+2	1+2	1+4?
	4	13?	11+2	6+2	4+3
Coprosma macrocarpa	1	14?	8	3	3+1?
	2	10?	7	4	2
	3	3	3	1	1+1
	4	1	—	—	—
Rhopalostylis sapida	1	2	2	2+2	2+3
	2	4	4+1	4+3	4+8
	3	—	—	—	—
	4	1	1	1	1+3
Beilschmiedia tawa	1	37	33	26+5	19+28?
	2	11	24	19	13+3
	3	2	2+2	2+3	2+3
	4	10	14	12+2	9+4
Beilschmiedia taraire	1	1	1	1	1
	2	3	3+1	2+1	2+3
	3	11	6	5+2	4+3
	4	4	11	7+2?	6+11?
Corynocarpus laevigata	1	1	1+1	1+1	1+4
	2	—	—	—	—
	3	3	2+2	2+2	2+5
	4	5	4	4	4+1
Dysoxylum spectabile	1	—	—	—	—
	2	1	1	1	1
	3	5	5+2	4+2	2+3
	4	7	7	5+1	5+4
Rhabdothamnus solandri	1	—	—	—	—
	2	—	—	1	1+8
	3	—	—	—	4
	4	—	—	—	—
Nothopanax arboreum	1	—	—	—	6
	2	—	—	—	—
	3	—	—	2	2+2
	4	—	—	—	—
Hoheria populnea	1	—	—	—	3
	2	—	—	—	—
	3	1	1	1+1	1+2
	4	—	—	—	—
Edwardsia microphylla	1	—	—	—	4
	2	—	—	—	1
	3	—	—	—	—
	4	—	—	—	—
Geniostoma ligustrifolium	1	—	—	—	—
	2	1	—	—	—
	3	—	—	1	1+4
	4	—	—	—	2
Meryta sinclairii	1	—	—	—	—
	2	2	1	1+1	1+3
	3	—	—	—	—
	4	—	—	—	—
Pisonia brunoniana	1	—	—	—	—
	2	—	—	—	3
	3	—	—	—	—
	4	—	—	—	1

Note: A figure after a + sign indicates the number of plants which came in after the initial occupation by the particular species; a ? that one or more seedling identifications are doubtful, or that one or more plants were moribund.

off of light from the ground at this stage. Almost all *Entelea* that had not then grown above the "shrub" layer had perished by 1937. In Clearing 1 (Table 2; Pl. 26, Figs. 1, 2) the *Entelea* population had dropped from 154 to 74, in Clearing 2 from 54 to 9 (Table 2). Suppression of the stifled plants had been so rapid that few still dying were found. In all four clearings *Entelea* itself (many 3–5 m. high) was the plant most effective in cutting off the light from smaller seedlings (Pl. 26, Fig. 2).

Once this early critical point has been passed *Entelea* has little to fear directly from the forest undergrowth species. Plants of *Entelea* grow upwards, usually quite dominating the clearing (Pl. 26, Figs. 2, 3) until (1) they are checked by the closing or partial closing of the forest canopy above (rarely), (2) with diminished growth they are gradually overtaken by the shade-tolerating dominants which have usually been growing up steadily from below, or (3) more commonly, they reach their maximum height and die before being overtaken. At maturity they are typically 6–12 m. high, with slender, clean, smooth-barked trunks 8–15 cm. in diameter (Pl. 26, Figs. 3, 4) and relatively small crowns. They may reach the low forest roof.

The most striking feature brought out by this investigation of clearing successions is the remarkable rapidity with which *Entelea* completes its life cycle. By 1939, less than six years after the clearings were made, the species had everywhere attained its maximum dominance; in fact, in Clearings 1, 2, and 3, some trees, 6 m. or more in height, were dying of "old age" (Pl. 26, Fig. 3). By 1943, only 9¼ years after its establishment, the species had almost run its full course in these three clearings; most of the few surviving trees were senescent. In Clearing 4 alone, where competition among the *Entelea* was not so fierce, were trees still vigorous (some 12 m. high with trunks 30 cm. diameter). In Clearing 1 (Pl. 26, Fig. 4) and Clearing 3 it had become possible agan to walk about with ease, and the increase in light was so marked that light-demanding species such as *Nothopanax arboreum* and *Hoheria populnea,* even a few new *Entelea,* were again coming in, together with numerous shade-tolerating species, both undergrowth plants and dominants (Table 2).

Thus while the normal result of the invasion of a clearing by *Entelea* is early to limit, or inhibit, the activities of other colonising species, these other species will often be given a second chance to occupy the clearing, years after it first became closed, by the wholesale death of the dominating *Entelea.* A second phase of seedling competition, less intense than the first, is initiated.

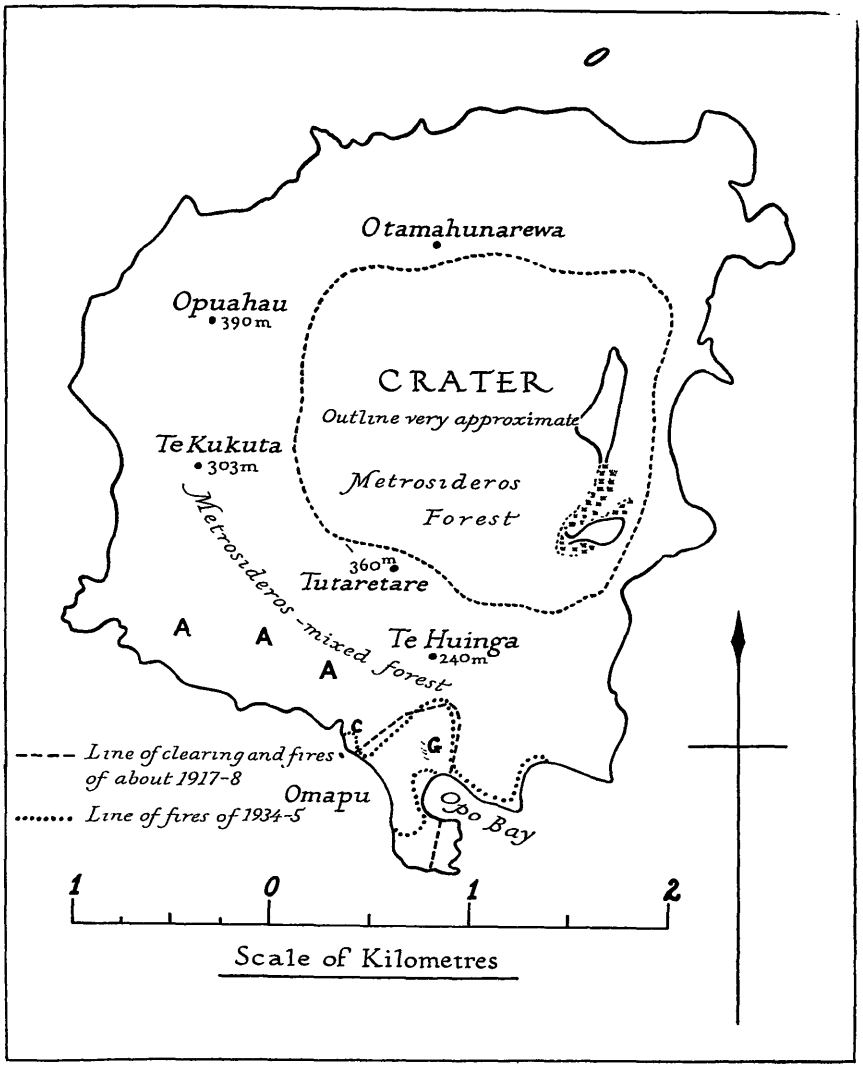
The role of Entelea, then, in virgin mixed coastal forest, under optimum conditions, is largely to control, in the first years, the course of a succession in clearings and thereafter to delay the striking of equilibrium among the other species, particularly the undergrowth plants. In 1943 such plants were more numerous, in kind and number, than in 1939—and then the frequency of all species was far above normal. Long before stabilisation has been attained in the case of any other species, *Entelea* has disappeared, not to return for a great many years. It is a noteworthy fact that *the degree of persistence of Entelea in a clearing is typically inversely proportional to its initial success, other things being equal* (above, and p. 285).

From Table 2 the following additional points, of more general interest, emerge: (1) *Macropiper,* although shade-tolerating and present in all clearings throughout the succession, is, *under the stress of severe competition,* easily the most responsive to light of all species, save *Entelea.* (2) At the other extreme, markedly shade-tolerating species such as *Rhabdothamnus solandri, Geniostoma ligustrifolium* and *Heimerliodendron brunonianum* (Endl.) Skottsberg (*Pisonia brunoniana*) are seen to have entered certain clearings relatively late —and seedlings of all dominants were still, on the whole, steadily coming in some nine years after the clearings were made. (3) By 1943 *Rhopalostylis sapida,* with the senescent *Entelea,* was the most striking plant in Clearing 1 (Pl. 26, Fig. 4), while it profoundly dominated Clearing 2. Comparison of the growth rates of *Rhopalostylis* inside and outside clearings showed that while the species is remarkably shade-tolerant the growth rate is greatly accelerated in clearings. (4) The interesting *Meryta,* usually regarded as a strong light demander, is much more shade-tolerant than *Entelea.* (5) Relative height increments of dominants (averages for three fastest-growing trees, where present, in each clearing, 1935-43) were: *Corynocarpus,* 4·1 m.; *B. taraire,* 3·8 m.; *Dysoxylum,* 2 9 m.; *B. tawa* (most crowded), 2·2 m. Cf. *Entelea.* (6) The common dominants, *Metrosideros excelsa, Vitex lucens, Knightia excelsa,* and *Melicytus ramiflorus,* are absent from all four clearings.

The history of the clearing may be somewhat different from that described above: (a) Where a single *Entelea* (more rarely two or three) gains an early ascendancy it may reach, and develop a large crown in, the forest roof and linger on, sometimes probably for twenty years or more, reaching relatively great size. The tree shown in Pl. 25, Fig. 2, probably the largest specimen recorded, was over 15 m. high with a trunk 1·7 m. circumference above the basal buttresses. In four places on Taranga the remains of solitary, very large trees were found under a closed forest canopy indicating where clearings had once existed. (b) Where the forest roof is low, and the clear space large, *Entelea* may be initially so successful that other species can gain no hold at all or are early choked out. The *Entelea,* having quickly grown in a dense mass to a height of 5–8 m., often die almost in a body, and so rapidly (cf. Pl. 27, Fig. 1) that with the influx of light to the bare ground beneath, a new generation of *Entelea* can spring up before shade-tolerating plants can occupy the area. The eventual victory of the true forest plants may be held off for some time. Nevertheless, later generations of *Entelea* are never nearly as vigorous as the first, and the conclusion is inescapable that a successful colony of *Entelea* can so impoverish the ground, from the point of view of the species itself, that long-continued success is impossible. (Cf. p. 285, and Pl. 27, Fig. 1.)

Leaf Behaviour. (For Taranga as a whole.)

There has been much speculation as to the significance of the abnormally large leaves produced by several mainland species when growing on certain coastal islands; and the matter is not always simple (Kirk, 1879, pp. 450–2; Cockayne, 1928, pp. 77–8; Cranwell and Moore, 1935, p. 310, etc.). The leaves of *Entelea* on Taranga are, on the whole, considerably above average size (see also Cheeseman,



MAP 2.—MAYOR ISLAND.

1925, p. 560), the blades being often 40 cm. long. The explanation here is simply one of epharmony. On Taranga the habitat is unusually favourable. Again, leaves of mainland plants growing under particularly good conditions may be also abnormally large; and on Taranga itself leaf size varies greatly according to conditions. Finally, trees grown by the writer at Auckland from seed taken from large-leaved Taranga specimens had leaves of only average size.

(2) *Mayor Island.* (Map 2.)

This island, which lies in the Bay of Plenty some 37 km. N.N.E. of Tauranga, was visited in the summers of 1936, 1937, 1942, and

1943. It is volcanic, probably Late Tertiary (see Part II). (Marshall, 1936, p. 344.)

Squarish in outline and of 1,277 hectares area, the island rises almost everywhere from the sea in cliffs up to 100 m. high. The forested slopes then sweep upwards, in most places fairly steeply, to the broad rim of an enormous crater, which occupies about a third the total area of the island. Rounded, forested peaks about the crater rim to west and south rise to between 300 and 400 m. The flanks of the island are furrowed by innumerable, closely-spaced, dry-floored gullies, radiating from the lip of the crater. The rocks are acidic.

The climate is comparable with that of Taranga; and here also the forest is protected from strong winds which are shot upwards by the steep cliffs.

The island has not been in permanent occupation since the Maori abandoned it nearly 60 years ago (Sladden, 1926, p. 194).

Brief general accounts of the vegetation have been given by Sladden (1926, pp. 193–205) and Allan and Dalrymple (1926, pp. 34–36).

The forest, in many places essentially virgin, from the point of view of *Entelea,* affords a most interesting transition between the pure *Metrosideros* association of seaward slopes, described under subsection (b), and mixed forest such as that on Taranga. While *Metrosideros* may be powerfully dominant over large areas, especially on the lower levels (Sladden, 1926, p. 201), all the common dominants of mixed coastal forest, save the important *Beilschmiedia,* are present also; and the warm, sheltered conditions have led to the development of an undergrowth ecologically comparable with that of a typical mixed forest. Of great interest is the presence of *Aristotelia serrata* (J. R. et G. Forst.) W. R. B. Oliver (*A. racemosa*), a species related to *Entelea* and ecologically equivalent, which is unaccountably absent from Taranga. *Suttonia australis, Geniostoma ligustrifolium, Coprosma lucida, C. robusta,* and *Brachyglottis repanda* are relatively far more important than on Taranga, *Rhopalostylis, Macropiper* and *Rhabdothamnus* less so. *Coriaria arborea* Lindsay, rare on Taranga, is quite common, but *Coprosma macrocarpa* is absent. Ground ferns are relatively rare, the absence of *Asplenium lamprophyllum* being noteworthy.

The opportunities of *Entelea* are somewhat restricted owing to the absence of rock masses in the forest, the scarcity of slips, the absence of permanent streams, and the too inhospitable nature of the numerous rock faces and cliff tops. Nevertheless, the species is frequent throughout, seizing upon newly-formed clearings with great vigour. Sufficient clearings of different ages were found to prove that the seral stages, as regards *Entelea,* are essentially similar, save often the last, to those of the Taranga clearings, so long as *Aristotelia* is absent, as is often the case. The difference in "final" stages depends on the open nature of the low forest canopy and the marked sluggishness of the dominants, notably *Metrosideros,* in reoccupying clear spaces caused by their fall. While often on Taranga only a single *Entelea* will survive to reach the forest roof (p. 276), here, nearly always, most plants which survive the early critical stages persist,

forming a grove of slender trees, until they die with age; and more than one generation may arise.

When *Entelea* and *Aristotelia* both invade a clearing, their relative success depends primarily upon the light factor. In open, sunny clearings *Entelea* often completely ousts its most dangerous competitor, (1) because of faster growth rate in early stages, and (2) because of much earlier adoption of the canopy habit. Under conditions rather less favourable to *Entelea* the two species often grow together above all the other clearing plants, *Entelea* still usually the taller, until, at a clearing age of some 8–12 years, *Aristotelia* overtops and shades out its earlier-maturing rival. Soon afterwards the light-demanding *Suttonia* and *Coriaria* are often also eliminated. *Aristotelia,* now mulberry-like in form, may finally reach the remarkable height of 10–15 m. (A, Map 2—huge specimens.) Where the clearing floor is shaded most of the day *Aristotelia* may quite replace *Entelea,* playing a role in relation to the other clearing species very similar to that of *Entelea* in the Taranga clearings. Finally, where the forest roof is hardly broken above a clearing, both *Entelea* and *Aristotelia* will be absent.

(3) *The Mainland.*

Although the writer has examined, cursorily or in detail, hundreds of kilometres of the North Island coastline where forest remnants containing *Entelea* occur, not a single forested area has been found which can be described as undoubtedly virgin. Nevertheless, it is clear that in primitive New Zealand *Entelea* played a role on the mainland essentially similar to that which it plays to-day on Taranga and Mayor Island. The following mainland variations, among many, may, however, be noted:

(α) *On Streams*: Along the lower reaches of numerous streams, on the banks, on flood-plain scrolls and other alluvium, and on slips, *Entelea* finds, and must have found, very suitable growing places of a type not available on the small islands where permanent streams do not exist. Competition, from many different types of plants, is keen. The most constant and serious rivals are, probably, *Coriaria sarmentosa* Forst. f., *Leptospermum scoparium, Coprosma robusta, Hebe salicifolia, Aristotelia serrata,* and many ferns, especially *Dicksonia squarrosa* and *Blechnum procerum* (Forst. f.) Labill. On scrolls, which are built out very slowly, succession towards forest is so condensed in space that *Entelea* occurs only, as a rule, right next the stream itself.

(β) *On Sand*: Between 1937 and 1939 a close survey of the west coast between the Manukau and Hokianga Harbours was undertaken. From the then position of *Entelea* in forest remnants on consolidated dune, it is clear that the plant once played there no mean role.

"Behind an extensive sand plain 3 km. north of Muriwai on recently consolidated dune occurs a forest which contains almost all the species of mixed coastal forest . . . In the several sheltered clearings, naturally made by the fall of large trees insecurely rooted, *Entelea* is growing with a vigour matched only (so far as is known) on Taranga. Some trees are 10 m. tall, with trunks up to 30 cm. diameter, and leaves reaching 40 cm. in length. The importance to

the plant of perfect drainage . . . is surely indicated. ''* (Thesis, 1937, p. 36.)

Whether in primitive N.Z. *Entelea* played a role in sheltered dune hollows adjacent to forest will never be determined: but a survey of the Muriwai-Woodhill coastal sector in 1945 showed that even to-day a very few *Entelea* are to be found in such places. They are growing, with a few *Cordyline australis, Macropiper,* and *Coprosma macrocarpa,* above a sea of *Ammophila arenaria* (L.) Link, *Arundo conspicua, Scirpus nodosus, Tetragonia expansa, Muehlenbeckia complexa,* and other ecologically similar species.

(γ) Neglecting *Entelea* on streams, and on sand, it is clear that even in former times *Entelea* rarely displayed on the mainland the astonishing vigour shown on Taranga and Mayor Island. The chief reasons are: (1) Generally lower, and more variable, temperatures. (2) In most places, especially on the west coast, greater exposure to wind. (3) Usually heavier rainfall. While this factor is all in favour of *Entelea* where the forest floor is bared (slips and artificial clearings) its encouragement of a denser, and floristically richer, undergrowth and, as well, a more abundant growth of shade-casting tree-ferns, climbers and epiphytes accounts, in part, for the more moderate success of *Entelea* on the mainland in naturally made clearings. (4) The presence, in some places, of umbrageous podocarps such as *Phyllocladus trichomanoides, Dacrydium cupressinum,* and *Podocarpus dacrydioides.* (5) An often taller forest roof—connected particularly with (3). (6) Imperfect drainage often—e.g., much of Waitakerei and Coromandel Ranges where the andesitic fragmentals may be strongly cemented. This is undoubtedly a factor contributing to the generally much smaller size of *Entelea* on the mainland as compared with Taranga especially. (Borne out by (β) above.)

(b) *With Metrosideros excelsa Dominant.*

(1) *Taranga, Mayor and Little Barrier Islands.*

On Taranga true *Metrosideros* forest is found only on steep, exposed, seaward slopes. Along the southern and particularly the south-western shores (Map 1) where cliffing is not marked, but where the island commonly rises in steepish slopes, for a hundred metres or more often, from the boulder beaches, an almost pure, in most places essentially virgin, *Metrosideros* forest is found. The fairly even canopy, 5–10 m. high, is relatively open owing to the wide branching of the dominants. Ample light penetrates for the growth of *Entelea;* but, except in specially sheltered places, the species is absent. It is never clean-stemmed and vigorous, as in the mixed forest immediately over the seaward slope. In fact, plant establishment in general is difficult, for the strong light, the steep slope, the much-fissured andesitic substratum, and the frequent winds have developed a dry, friable topsoil held together only by the densely-intertwining rootlets of the trees. There is usually a dry, harsh floor cover of *Metrosideros* leaves. Even hardy shrubs (*Macropiper* mostly) and ferns are not plentiful.

* A re-examination of this area in October, 1945, disclosed the forest almost destroyed and *Entelea* virtually extinct.

The Mayor Island forest, of transitional type, has already been described (p. 278). It is noteworthy, in view of the strong light demands of *Entelea,* that the species grows poorly in the magnificent *Metrosideros* forest of the enormous crater (Map 2), although the ground is relatively moist.

Hamilton (1937, p. 50) describes a unique *Metrosideros* forest on Little Barrier Island in which *Entelea* does not occur. It is most interesting, however, in the light of what has been said on p. 281 (3), that on this island, where the rainfall is much heavier than on Taranga (Hamilton, p. 31; Cranwell and Moore, 1935, p. 302), *Entelea* is more plentiful in " Pohutukawa cliff forest " than in mixed coastal forest (Hamilton, pp. 47, 50, 81).

(2) *The Mainland.*

Almost everywhere along the hundreds of kilometres of *Metrosideros*-girdled coastline, even in rainy areas like the Auckland West Coast, *Entelea* is rare. But clearing and burning have been severe, and herbivores are everywhere. The writer has not seen a single area where the past history of *Entelea* could be safely reconstructed (cf. Cockayne, 1928, p. 110).

(c) *With Corynocarpus laevigata Dominant.*

In the many remnants of *Corynocarpus* forest which the writer has investigated between Hokianga Harbour and Marlborough and Nelson *Entelea* still occurs sporadically. (See also Allan in Cockayne, 1928, p. 111.) It would be interesting to know how *Entelea* behaved in pure, virgin *Corynocarpus* forest with its dark, close roof, yet usually dry, leaf-covered floor. Again, however, interference factors have been at work too long to make surmises other than dangerous.

B. MODIFIED COASTAL FOREST.

The following classification of interference factors is arbitrary, and adopted solely to give some lucidity to an attempt to analyse an often bewildering complex series of events. Usually felling, fire, and browsing animals act together as destructive agents, and their separate effects are difficult or impossible to disentangle. As well, the fate of *Entelea* is bound up with the length of time taken by the destructive agents to produce a given effect; with many factors other than biotic; with the previous history of the area, which will largely have determined, among other things, the nearness of a seed supply and of invading exotic species; with the subsequent treatment of the area, and so on. The examples given below are some of the clearest and most significant from many hundreds investigated.

(a) *Coastal Forest With Mixed Dominants.*

(1) *Interference by Felling.*

(α) *On a Small Scale*: The behaviour of *Entelea* in small clearings made in virgin forest by the felling of dominants only has already been described in detail (pp. 272–6). Often, of course, especially on the mainland, *Entelea* may be less successful or absent.

The clearing succession may be quite different if the felling is done in already modified forest—for indigenous and exotic " weeds " may be present. A clearing (10 x 6 m.) in modified forest on the S.W. corner of Taranga (p. 284; Map 1), made like the other Taranga

clearings in 1933, and examined by the writer in 1935, 1937, 1939, and 1943, shows extremely interesting phases in the competition of *Entelea* with recognised weeds. In this clearing the three great ecological classes of plants in modified coastal forest—dominants, undergrowth species, and opportunist " invaders "—are represented. Table 3 and Graph 2 give a statistical analysis. The following notes may be added:—(1) In 1935 *Solanum, Haloragis, Parietaria,* and *Pteridium,* all vigorous " weeds," were abundant, but many *Entelea* had already far outstripped them, and by 1937, with the help of other species, especially *Macropiper,* had virtually extinguished them. (2) The phase of most intense competition among species other than the above-mentioned, and the closing of the clearing by them, came not between 1935 and 1937 (Table 2), but between 1937 and 1939. This was due mainly to the delaying effect of the " weed " growth and to the strong light admitted to the clearing (forest canopy only 5 m. high). (3) The deaths of several large *Entelea* between 1939 and 1943 initiated a second cycle of invasion, by diverse types of plants, and of competition. (4) The second generation *Entelea* were weak (cf. p. 285). (5) *Corynocarpus* will eventually strongly dominate the area.

TABLE 3. *Analysis of Clearing in Modified Mixed Coastal Forest on Taranga.*

Species.	'35	'37	'39	'43	Remarks.
Entelea arborescens	70	50	14 + 1	6 + 5	In 1935 to 2 m. high; in 1943 to 6 m., trunks to 40 cm. diameter.
Pteridium esculentum					Scores of fronds in 1935, a few, dying, in '37, none later.
Solanum nigrum	85	0	0	0	Perhaps indigenous var., Allan, 1940, p. 197.
Haloragis erecta	56	4	0	0	
Parietaria debilis	21	0	0	0	
Phytolacca octandra	0	0	0	8	Under dead *Entelea.*
Urtica ferox	0	0	0	8	To 2 m. high.
Sicyos angulata	0	0	0	2	Growing over *Entelea,* killing one and threatening to overwhelm all other plants save *Corynocarpus* and *Paratrophis.*
Muehlenbeckia australis	0	0	0	1	Growing vigorously on *Macropiper.*
Suttonia australis	0	0	2	14	In 1943 to 3 m. high.
Nothopanax arboreum	0	0	0	3	
Macropiper excelsum	42	40	23	20	In 1943 to 5 m. high, trunks to 8 cm. diameter.
Coprosma australis	9	9	5	3	In 1935 to 1 m. high; in 1943 to 2·5 m. high.
Coprosma macrocarpa	5	5	5	4 + 1?	In 1935 to 1 m. high; in 1943 to 2·5 m. high.
Corynocarpus laevigata	10	10 + 6	7 + 3	7 + 54	In 1935 to 1·5 m. high; in 1943 the most notable plant save *Entelea*—to 5 m. high—seedlings throughout clearing.
Paratrophis opaca	1	1	1	1	In 1935 2m. high; in 1943 6 m.
Beilschmiedia tawa	0	0	0	2	15 cm. and 35 cm. high.

Trees only were felled in the clearings discussed above, and the clearings were then left undisturbed. Rarely are mainland clearings not subjected to some kind of animal interference, and this has made

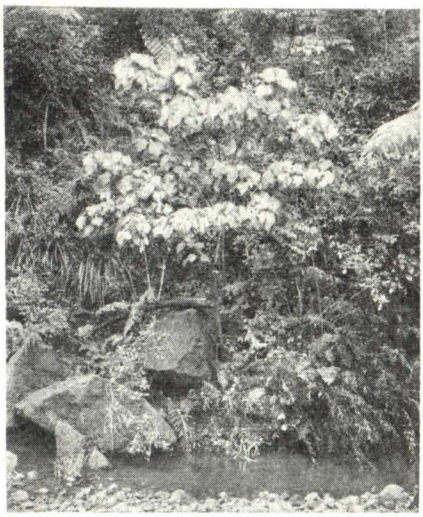


FIG. 1. Typical small tree of *Entelea* on slip on Waitakere Stream, Auckland. *Geniostoma* and *Freycinetia* at left, *Aristotelia* and *Coprosma robusta* at right, *Blechnum procerum* below.

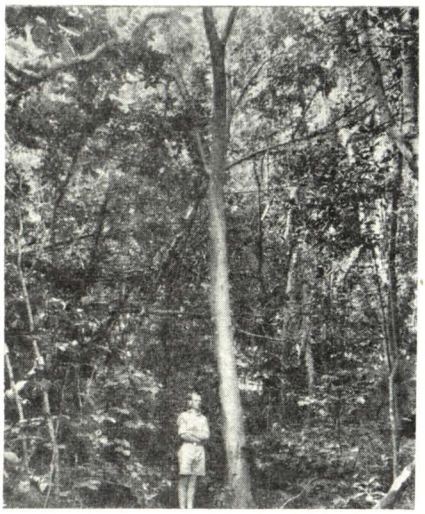


FIG. 2. Largest recorded specimen of *Entelea* (15 m. high) in virgin, mixed, coastal forest, Taranga. Other trees are *Corynocarpus*, undergrowth mainly of *Macropiper*.

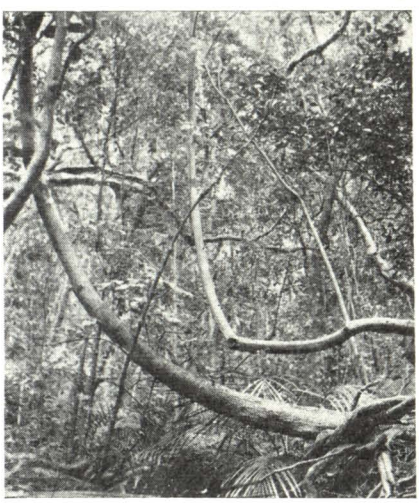


FIG. 3. Two *Entelea*, partly fallen from summit of huge rock, growing towards gap in forest roof, Taranga. Further explanation in text. Part of long cord-like root at right, quarter-way up.

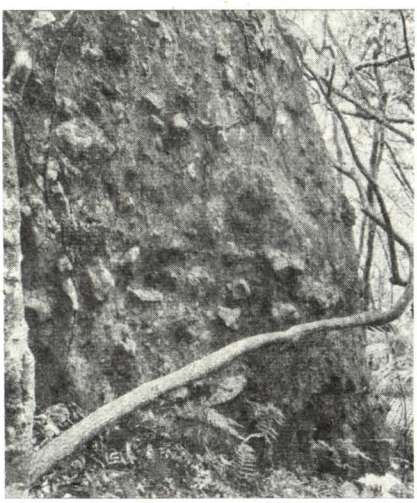


FIG. 4. "Lianoid" *Entelea* at base of andesitic rock mass in Taranga mixed forest. Explanation in text. Floor carpet of *Asplenium lucidum* (left) and *A. lamprophyllum* (centre).

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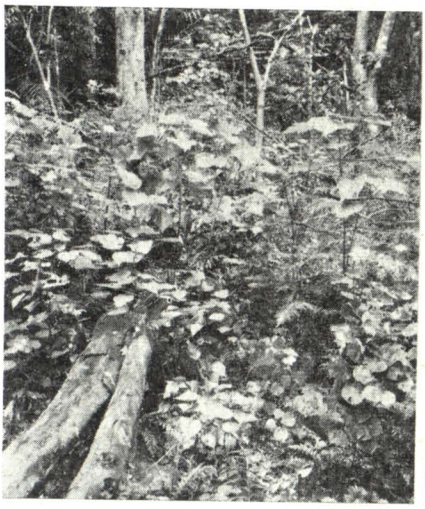


FIG. 1. Clearing No. 1, virgin, mixed, coastal forest, Taranga, December, 1935, 2 years after establishment. Note felled *Beilschmiedia tawa*. Regrowth mainly *Entelea* (centre), and *Macropiper* (left and right)—see Table I. Ground ferns are *Asplenium lucidum* and *A. lamprophyllum* (foreground) and *Polystichum richardi* (right centre).

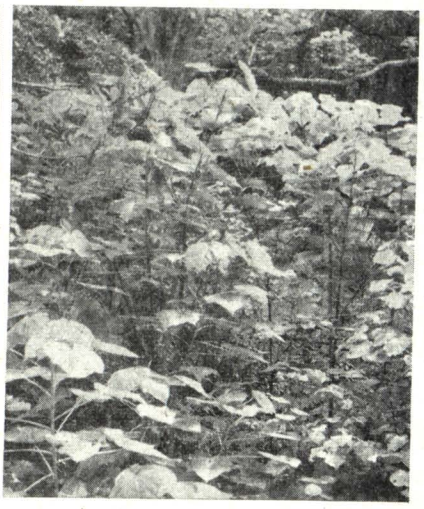


FIG. 2. The same, nearly 14 months later (January, 1937). *Entelea*, 2–4 m. high, profoundly dominant.

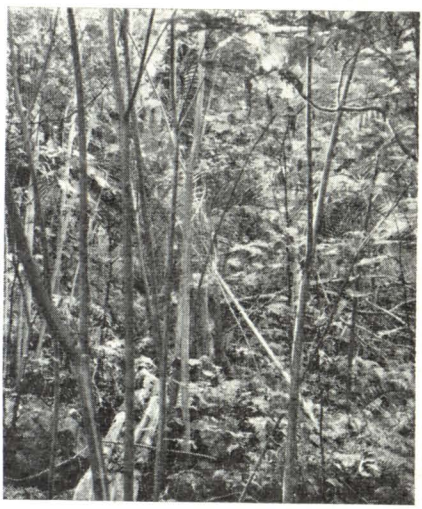


FIG. 3. The same, 3 years 6 months later (May, 1939). *Entelea* some 10 m. high, with crowns in forest roof. Note already dead trees and openness of clearing at lower levels. Slender, black stems are those of *Macropiper*.

FIG. 4. The same, 7 years 3 months later (March, 1943). Eight living *Entelea*, several moribund, alone remain. Note persisting *Macropiper*, vigorous *Rhopalostylis*, and last remains of original *Beilschmiedia tawa*.

NOTE.—These photographs were all taken from exactly the same spot, but the viewpoint in Figs. 2, 3, and 4 is necessarily a little higher than in Fig. 1.

FIG. 1. Fire clearing, approx. 50 x 30 m., above cliffs near north end of Omapu Beach, Mayor Island (Map 2, C), established in the summer of 1934–5 and photographed January, 1942. Over 2,000 dying *Entelea*, 5–7 m. high, were present in this relatively small area.

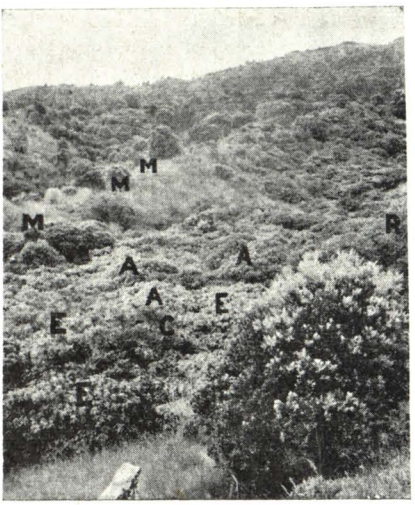


FIG. 2. Broad, shallow gully, Mayor Island (Map 2, G), filled with dense regrowth (especially *Entelea*) after fire. Photographed December, 1936. Foreground *Metrosideros excelsa* (also recolonising ridge towards l.—M), centre *Aristotelia* (A), below this *Coriaria arborea* (C), and ext r. *Melicytus ramiflorus* (R). Groundmass is *Entelea* (E).

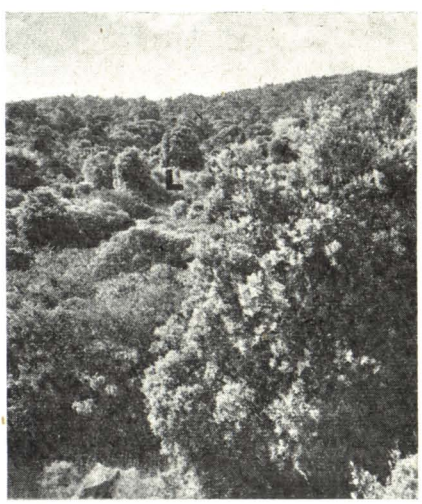
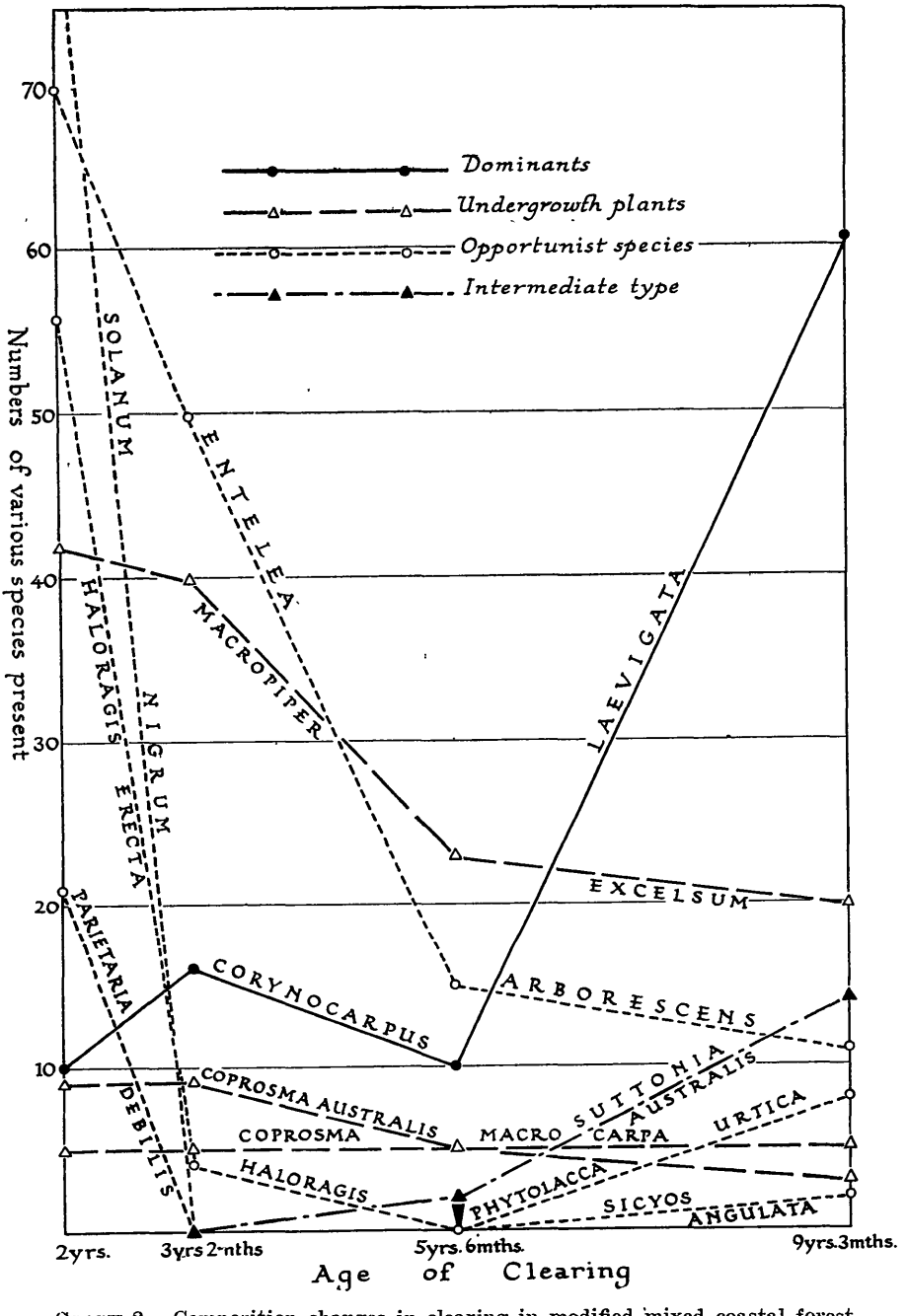


FIG. 3. The same, photographed from the same spot, 5 years later (January, 1942). Many of the trees labelled in Fig. 2 can be recognised (M and A particularly striking). At L (above and left of centre) *Leptospermum ericoides* is recolonising relatively dry, leached ridge. Note, in distance, dark spires of *Knightia excelsa*.

FIG. 4. The same, interior view. Senescent *Entelea*, and rotting remains of others, everywhere. In left foreground a small clump of young and feeble *Entelea*, in right foreground *Uncinia* sp., right centre *Erigeron canadensis*, and extreme left trunk of *Coprosma robusta*.



GRAPH 2.—Composition changes in clearing in modified mixed coastal forest on Taranga between 1935 and 1943

it impossible to study confidently numerous small clearings with all plants cut down. It is clear, however, that in forest where *Entelea* is still abundant, successions in such clearings often follow broadly the pattern outlined in Graph 2. The Coromandel Ranges, where piecemeal felling of coastal forest is nearing the end, have given particularly fine examples of the reaction of *Entelea* to this type of interference. For instance, about 1927, when a foot-track was cut through forest near Stony Bay, a dense growth of *Entelea* sprang up (settlers say) on both sides of the track, even on the thrown-out spoil. In 1937 the writer found hardly a vestige of the plant; sheep ran on the land.

(β) *On a Large Scale*: Rarely, unless the area is particularly sheltered, is *Entelea* as successful as in small clearings. Only one example has been seen where fire and animals did not complicate study. This is a few kilometres north of Muriwai, where in the summer of 1935–36, low mixed forest, fenced off from cattle, had been cut down and left. By May, 1937, *Entelea*, 1–1·5 m. high, were dotted about among a dense growth of exotic and indigenous weeds, *Macropiper, Brachyglottis, Coprosma robusta,* and *Corynocarpus.* A re-examination of the area in 1945 revealed that it had been laid down in grass.

Forest felling on a large scale, particularly where wind is strong, may act against, as well as for, *Entelea.* In March, 1937, 8 km. south of Port Charles (Coromandel), scores of small and large *Entelea* were dying of drought on the summits of rock masses exposed by forest clearing. *Coprosma* spp. and *Macropiper* were still vigorous.

(2) *Interference by Fire.*

(α) *On a Small Scale*: Destruction of small areas of forest by fire stimulates *Entelea* as nothing else can do. Unfortunately, no small fire-clearing in virgin forest has been seen. But at the S.W. corner of Taranga there is a low headland covered with a still-advancing, induced forest (4–12 m. high) of *Beilschmiedia tawa, Corynocarpus, Melicytus ramiflorus, Nothopanax arboreum,* and other species (p. 281). Cranwell and Moore (1935) do not mention this community, but according to Mr. E. Stead, who camped on Taranga in 1909-10, the headland was then clothed with grass and scattered plants of *Leptospermum ericoides. Entelea* had not then appeared. In 1935, however, there were scores of huge trees (to 12 m. high), mostly solitary and senescent, scattered among the young forest growth, especially along a line some 200 m. from the shore. Here the original clearing, made presumably by fire, stopped against the virgin forest and here the first *Entelea* would have sprung up in the protection of the rapidly-moving second growth. By 1939 hardly a large *Entelea* was left. It is clear that even under the most favourable conditions the life cycle of *Entelea* is traversed in less than 25 years, often much less (p. 275).

Where fire-clearings are made in non-virgin forest, *Entelea* usually has to compete with a variety of aggressive, ecologically similar species. All round the coasts of the North Island, north of Lat. 38°, cases of phenomenal success have been found. On Mayor Island, for instance (at C, Map 2), the fire of 1934–35 mentioned

below, had eaten three small clearings into the already somewhat modified *Metrosideros*-mixed forest behind the cliffs at the north end of Omapu Beach. When these clearings were first examined by the writer (December, 1936) a regrowth of *Entelea, Solanum aviculare,* and *Haloragis erecta* had completely taken possession of them. Great thickets of *Entelea* (to 2·5 m. high) had already almost choked out the *Haloragis.* By December, 1937, the *Solanum,* too, had gone, and the forest of *Entelea* saplings was 4–5 m. high. By January, 1942, the *Entelea* themselves, 5–7 m. high, with trunks 3–15 cm. diameter, were dying everywhere. There were over 2,000 of them in the largest clearing, 50 x 30 m. (Pl. 27, Fig. 1). Although the brilliantly lit ground was covered with innumerable *Entelea* capsules, not a single seedling was to be found. The only other plants were a few poor specimens of *Coprosma robusta, Suttonia australis, Haloragis erecta,* and *Pteridium.* This re-emphasises (p. 275; also below) how an initially great success by *Entelea* will jeopardise long-continued existence by impoverishing and drying out the ground and paving the way for the entry of a poorer type of vegetation. In the third clearing, too, events proved most interesting. In 1936 partly-burnt trees of *Metrosideros* were coming again into leaf above the tangle of weeds and *Entelea.* By 1942 the former had gone, a few *Entelea* only persisted, and the undergrowth was typically *Suttonia, Geniostoma,* and *Coprosma* species.

On the mainlaid hundreds of fire-clearings with *Entelea* have been seen. Rarely, however, does regrowth remain long undisturbed. Gradually, as a rule, periodic fires eat into the still-standing forest, animals follow, stimulating hemicryptophytic grass growth, and a vegetation arises in which *Entelea* has no place. In the Coromandels, for instance, farmers recall the occupation, 20–30 years ago, of innumerable forest clearings by dense growths of *Entelea*: numerous small induced slips were strikingly colonised by the plant. To-day *Entelea,* in many places, is becoming rare. Fires are still frequent, slips are more common than before, but the first colonisers are not *Entelea* but grasses and exotic weeds such as the drought-enduring *Verbascum thapsus.*

(β) *On a Large Scale*: About 1917–18 Wirimu Eruiti felled and burned some 25 hectares of forest on Mayor Island (Map 2). Cattle were pastured for a year or so. The island was then abandoned, two horses only being left. Regeneration went on rapidly (Sladden, 1926, p. 203) until an unfortunate fire in 1934–35 took almost the whole of the originally cleared area (Map 2). But the regrowth in the gullies largely escaped and tells the story of the succession, at least in these areas.

In 1936 (Pl. 27, Fig. 2) most gully bottoms were filled with a dense mixed growth of young trees—*Entelea, Aristotelia, Melicytus ramiflorus, Coriaria arborea,* etc. The first was easily the most conspicuous species; but the most critical point in its life history had been reached, for the trees (only 2–4 m. high in these rather dry, sunny gullies) were no longer growing, and the canopied *Melicytus,* and especially *Aristotelia* (with leaves up to 30 cm. long!), were still vigorous. By 1942 (Pl. 27, Fig. 3) most *Entelea* had been shaded out or were dying. Pl. 27, Fig. 4 shows an interior view

which once more indicates that where the growth of *Entelea* has been particularly rich, there no sturdy second generation will arise, but rather a poorer type of vegetation.

On the mainland, where conditions for plant growth are rarely as ideal as on Mayor Island, the destruction of forest by fire, with or without felling, on a relatively large scale, will often induce a heavy growth of *Leptospermum* (*scoparium*, usually). Often there must be viable seeds of *Entelea* in the altered soil after the fire (Part II); but conditions are too severe for ecesis. Sooner or later, as a rule, man will establish grassland. Where holdings are mismanaged and understocked, however, *Leptospermum* will return. In several places *Entelea*, which had vanished with the first severe fire, is reappearing, the natural cycle—grassland, scrubland, regenerating forest—having reached its final phase.

The time taken for *Entelea* to return after cleared and grazed country has been abandoned varies enormously according to circumstances. On Mayor Island (above) *Entelea* was back in a few years. On Little Barrier Island, however, a *Leptospermum* forest, which began to replace grass just before 1900, is still without *Entelea*, although numerous other forest plants are present (Hamilton, 1937, pp. 36–39). On Taranga, if the very tall *Leptospermum* forest (Map 1, L), in which *Entelea* seems a relative newcomer, has really existed since the Maori occupation (Cranwell and Moore, 1935, p. 307), it appears that there it has probably taken *Entelea* about a century to re-occupy the areas where it once occurred in forest. The sheltered conditions on Taranga, while long preventing forest from displacing the *Leptospermum*, has allowed *Entelea* to come in before true forest has regenerated, instead of after, as is the rule.

(3) *Direct Relation of Entelea to Herbivores.*

Entelea is "greedily eaten by cattle and horses, and consequently fast becoming rare on the mainland. . . ." (Cheeseman, 1925, p. 560).

Goats have virtually wiped out the species on Great King Island ("Will Watch" Expedition, 1932, unpub.). On Otata Island (Hauraki Gulf) rabbits will soon similarly account for it. Again and again, however, the writer has seen sheep, horses, and cattle browsing among young, untouched *Entelea*. Repeated observations, at different seasons, leave little doubt that herbivores are a real menace to *Entelea* only when the normal food supply runs low.

Summing up Section (a) *(page 281).*

(1) Clearing of forest by felling, or by fire, *on a relatively small scale,* where conditions favour the growth of *Entelea,* and *where the area is then left undisturbed,* involves (a) a great increase in the *Entelea* population followed by (b) a rapid fall almost to zero, and (c) a slow rise to normal frequency as the second growth trees mature and form new clearings by their fall. (2) *Continued* small-scale interference will eventually produce the same effect as destruction on an originally large and intense scale; but *Entelea* may for many years be most successful (p. 285). (3) Forest destruction *on an initially large scale* often, even where the area is then left undisturbed, involves an immediate drop in the *Entelea* population to zero and an interval of uncertain duration before the plant

slowly returns (p. 286). Finally, regarding man's activities in general, it may be said that his working is first to favour the growth and distribution of *Entelea*, since his breaking-in of forest is usually piecemeal, then to limit the plant's opportunities, and finally to extinguish it altogether.

(*b*) *Coastal Forest Dominated by Metrosideros excelsa.*

On Taranga this almost virgin association (p. 280) has been modified in several places, presumably by fire. In the more exposed places a heavy growth of *Leptospermum* spp. has been induced in which *Entelea* has no place In a few, more sheltered, places there is a low mixed growth of *Myoporum, Melicytus ramiflorus, Macropiper, Coprosma* spp., and other plants, in which *Entelea* is only occasional. Similar happenings have been common on the mainland; but animal activity has obscured the true rôle of *Entelea.*

(*c*) *Coastal Forest Dominated by Corynocarpus laevigata.*

Interference with even remotely primitive forest has nowhere been seen. It would be difficult to analyse accurately the occasional occurrence to-day of *Entelea* in this association.

II. Lowland Rain Forest.

The following account is based chiefly on an intensive investigation of the Waitakerei Ranges, where every stream valley has been explored, secondarily upon a less detailed examination of many of the remnants of lowland forest near the coasts of the remainder of the North Island and of Great Barrier Island (1939, 1941).

Entelea does not occur in the body of lowland forest even when heavy rainfall and shelter maintain this community only a few kilometres from the sea, e.g., Piha Valley, Great Barrier Island, and especially Little Barrier Island (Hamilton, 1937, pp. 52–55, 81). One cogent reason lies in the nature of the undergrowth. Light suddenly let into this forest falls, not upon ground largely ready for colonisation, as often in coastal forest, but upon a mass of struggling undergrowth (Cockayne, 1928, p. 154) which immediately springs, with intensification of competition, into renewed growth. Into such a community an opportunist invader like *Entelea* has only the remotest chance of entry.

Entelea can, however, penetrate lowland forest, up to 8 km. from the sea (Waitakerei Ranges), along sunny, sheltered, broadly open, river valleys, for there open ground is found—slips (Pl. 25, Fig. 1), scrolls, etc. (p. 279). There are many beautiful examples in the Waitakerei Ranges. Chief rivals to *Entelea* are *Aristotelia, Hoheria populnea, Coprosma robusta, Dicksonia squarrosa,* and *Blechnum procerum.* The ecological relationships of *Entelea* and *Aristotelia* are strikingly different from those on Mayor Island. Although *Aristotelia* usually eventually overtops *Entelea,* its habit is so open, and leaves relatively small and few, that the latter species often survives.

This, however, is not the whole explanation of the place of *Entelea* in lowland forest, for, even on large slips or in man-made clearings away from streams, the plant is never found, though *Aristo-*

telia is abundant. Probably *Entelea* cannot compete here with its rival because of its extreme sensitivity, under stress of competition, to even slight cold (p. 272).

THE ECOLOGICAL STATUS OF *ENTELEA.*

Entelea, in forest, is essentially an opportunist, and in a given spot a transient, species. Its importance is great only in seres, which it may dominate for a time (p. 275), modify (p. 275), even divert (p. 285). The characteristics which cause it to be an effective seral agent are, briefly: (1) Ability to seize quickly upon ground where light has been temporarily let into the forest. (2) Tremendous rate of growth (p. 271). (3) Early adoption, often, of an umbrageous canopy habit. (4) Marked powers of regeneration of lost parts. (5) Precocity in fruiting (p. 272). (6) Enormous seed production, especially when about to die. A dying tree in the garden of Mr. J. Stanton, Auckland, was estimated to have produced in 1945 some 1,100,000 seeds (Part II). (7) Seeds able to germinate as soon as capsules open *(Ibid.).* (8) Seeds shed from tree through whole year *(Ibid.).* (9) Seeds lying in, even on, the ground may remain alive for many years *(Ibid.).* (10) Surprising resistance to, and stimulation of, such seeds by fire *(Ibid.).* It will be noted that these characteristics are largely those of many successful weeds.

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