INTRODUCTION

Loxsoma cunninghamii (R. Br.) is a disappearing member of the New Zealand fern flora; the genus is monotypic and endemic to New Zealand, its nearest relative being Loxsomopsis ( Chr.), a South American genus of four species.

This investigation deals with the ecology and distribution of Loxsoma and was carried out in the first instance not because Loxsoma is an important plant from an ecological standpoint, but rather to provide some account of the ecological relationships, abundance and distribution of a relict species.

The conclusions regarding the autecology of Loxsoma which are reached here are the result of field studies throughout the north of New Zealand. Detailed work has been done whenever Loxsoma occurred in abundance, i.e. Paremoremo (Birkdale), Parahaki (Whangarei), Great Barrier and Kaueranga Valley. Space here will permit of a detailed report from only one of these localities, Great Barrier. Points raised regarding the position and status of Loxsoma in the vegetation of Great Barrier will, however, be considered in the light of facts gleaned from observations of the plant in other areas.

AUTECOLOGY OF LOXSOMA

Loxsoma cunninghamii appears as a rare and local species in gumland country between Mangonui (35°S) and Mount Maungatautari (38°S.), ranging in altitude from sea-level (Kaiarara: Paremoremo) to 1800 ft (Mount Hobson). The plant is growing exclusively in disturbed and grossly modified
habits. This study endeavours to explain its present sporadic distribution in terms of the life cycle and growth habits of the plant (Figs. 1 and 2).

It is important to remember when considering Pteridophyte ecology, that the distribution of the sporophyte is necessarily determined and limited by the factors controlling the distribution and establishment of the gametophyte. While the adult plant may appear suited to a wide range of habitat conditions, a microclimate of a very different specialized order may be required for the establishment of prothalli.

Apart from locality names on herbarium sheets the only indication of habitats of *Loxsoma* in earlier times is that given by Cockayne (1928) who described *Loxsoma* as "confined to the lowland and lower hills"; "in the shade of *Leptospermum* to the margin of forests". Such occurrences are now rare.

The species appears to be fundamentally associated with the succession from leptospermum scrubland to kauri-dicotylous forest.

It is improbable that the contemporary distribution of *Loxsoma* is as restricted as previously thought. A rather widespread distribution throughout the Coromandel peninsula and further north on the west coast between Dargaville and Awanui is predicted. The localities specifically referred to in this work are, however, very representative habitats of *Loxsoma*, and probably include all stations in which it is growing vigorously. Localities specially studied were Parahaki (Whangarei, 794 ft); Kaiarara (sea level); Mount Hobson (2,038 ft, Great Barrier Island); Paremoremo (sea level, Waitemata) and Kaueranga Valley (sea level to 1,800 ft, Coromandel).

Great Barrier Island

*Loxsoma* has been recorded both from Great and Little Barrier; its pattern of distribution there, as on the mainland, is sporadic.

Climatic and Edaphic Factors of the Habitat

Great Barrier Island, located 55 miles north-east of Auckland, and 10 miles east of Cape Colville, is an essentially rugged island with low mountain ranges intersected by deep valleys and ravines. It is geologically and physio-
graphically similar to the Coromandel range.

Tertiary andesitic volcanics are the surface rocks in most parts of the island; the basement rocks, Mesozoic shales and greywackes, are exposed only in the north and at one eastern locality.

The erosion surface of the Miocene and second period Tertiary rocks have in turn been overlain, in two areas, by Pliocene acid rhyolites. These rhyolites cover an area 10 square miles in the centre of the island, south and east of a line from the Pinnacles, Mount Young-Mount Hobson. Similar rhyolites, with accompanying sinters, occur north and east of Okupu, and cover an area of 1,800 acres. (Description taken from the map by Hutton and Bartrum.)

Five areas of hot springs occur within 5 miles of each other, in a north-east line from Kaitoke swamp, to one mile south of Mount Hobson.

Rainfall is evenly distributed over the island, ranging in different years from 60-100 ins. The land is exposed to all winds. Kaiarara Valley, to which particular attention is given, is sheltered by Mount Hobson from all but west, north-west and south-west winds.

Occurrence of *Loxsoma*

*Loxsoma* occurs naturally only on the weathered Pliocene rhyolites. It is distributed sporadically from 800-1,800 ft throughout the chain of rhyolitic cones which stretch from Mount Hobson south-west toward Whangapara. Further small patches of *Loxsoma* are located at the hot springs in the centre of the island. In Kaiarara inlet an artificial habitat has been created by forestry workers studying kauri regeneration under kanuka canopy. All vegetation save tall kanuka, tall *Cyathea* and young kauri has been felled and removed, and under this open cover *Loxsoma* has established in one place. Further occurrences in Kaiarara are along and just behind the stream banks. Extensive clearing during 1954 has, however, largely destroyed *Loxsoma* in this habitat.

Description of the Vegetation

Only those parts of the island in which *Loxsoma* is found will be considered.
The chain of ryolitic peaks of which Mount Hobson (2,038 ft) is the highest was referred to thus by Wheetman (1889): "These mountains covered as they are from their bases to their summits with dense forest containing a large proportion of excellent kauri, form very striking objects to the eye."

The dense mixed podocarp-dicotylous and kauri-dicotylous forests of this area have been disturbed and modified since 1889 by two influences—milling of the kauri in the Kaiarara and Wairahi valleys, and the introduction of goats which have run wild over this central mountainous country.

Today, the vegetation of the Kaiarara Valley at the lower levels is manuka scrubland with some kanuka under which kauri is regenerating. Mount Hobson is covered with mixed podocarp-dicotylous forest and regenerating kauri communities. There has been no settlement in this central, mountainous area of the island.

Loxsoma on Mount Hobson occurs along the banks on either side of the track, always on the south facing slopes. The plant here is distributed regularly over a larger continuous area (900-1,800 ft) than it is in any locality on the mainland.

There are, however, no single patches of the fern comparable in area and density to those observed along the Paremoremo Stream at Birkdale, Auckland. Reports from several years ago indicated that large patches of Loxsoma were in existence at certain localities in the lower Kaiarara; these are now extinct or depleted.

Over the remainder of the area covered, Loxsoma is absent. Ferns generally are not common away from the track, save on damp rock faces or where the canopy is so dense as to exclude most undershrubs; here Asplenium bulbiferum, A. falcatum and A. lamprophyllum thrive.

Loxsoma appears suddenly along the Hobson track at an altitude of 960-1,000 ft. Below this level Paesia scaberula
occupies niches similar to those which *Loxsoma* preferentially colonized at higher levels. There is a sharp break in the cover of *Phyllocladus trichomanoides*, *Leptospermum ericoides*, *Nothopanax arboreum* and *Metrosideros robusta* and the slope falls away steeply (60°) to the south. The northern bank of the track is therefore open to the light and on this face *Loxsoma* is plentiful in association with low-growing *Blechnum fraseri*. From this point upward to approximately 1,800 ft, *Loxsoma* occurs regularly along the side of the track wherever there is a break in the canopy. Ferns which are in constant and close association with *Loxsoma* here are *Gleichenia cunninghamii*, *Cyathea dealbata*, *Blechnum procerum*, *B. fraseri* and *Dicksonia squarrosa*. Where *Loxsoma* forms dense patches there are few closely associated species. In the several patches examined, young *Lygodium articulatum* and seedlings of *Senecio kirkii*, *Metrosideros scandens*, *Knightia excelsa*, and *Geniostoma ligustrifolium* were the only plants found. No prothalli of *Loxsoma* were found within the area covered by the fern. *Loxsoma* prothalli, in fact, were found at one place only on Great Barrier Island. Along this track, below a vigorous patch of the plant, a slab of moss-covered clay had recently fallen from the bank, leaving a hollow. In this damp, well-lighted niche, *B. procerum*, *B. fraseri*, *Loxsoma* prothalli and moss protonemata were growing (Plate 5).

Where *Loxsoma*, *B. Procerum* and *B. fraseri* do not occur along this bank under the canopy gaps, the ground is covered by *Gahnia xanthocarpa*, *Schoenus tendo*, several other sedges and some grasses.

Behind and above the track cutting there are often extensive canopy gaps. The floor beneath such gaps is covered by low manuka and saplings of *Coprosma robusta*, *Nothopanax arboreum*, *Leucopogon fasciculatus*, *Weinmannia sylvicola* and *Gahnia xanthocarpa*.

Toward the track this low scrub thins out as the slope steepens, and grades in places into dense patches of *Loxsoma*. Most of the *Loxsoma* rhizomes are growing toward this open area behind. With the intense competition for space there is little or no growth towards the centres of the patches. Advance is extremely slow, however, and the *Blechnum* and *Cyathea* which are establishing in this low scrub will preclude *Loxsoma* from advancing far. No prothalli or young sporelings are present in the scrub. Approximately thirty feet from the track, the canopy is resumed and under the tall *Phyllocladus*
trichomanoides and the Weinmannia sylvicola and Nothopanax arboreum, Gleichenia cunninghamii grows in abundance. The light intensity here is much less than that in any of the stations in which Loxsoma is growing; the vegetation is also older.

Near the mouth of the Kaiarara Valley (100 ft), a very interesting habitat has been created by forestry activities. An experimental kauri nursery has been laid out by clearing all undershrubbery from beneath tall kanuka (40-50 ft). A few very tall Cyathea medullaris have been left standing. Beneath this depleted canopy young kauri seedlings alone have been encouraged to grow, the aim of the experiment being to study the natural regeneration of kauri. The forest floor is covered to a depth of 4-6 ins with kanuka branches and leaves, and through the covering very few shrubs or ferns have managed to penetrate. Doodia media is plentiful, along the track-side Oplismenius undulatifolius has established itself; occasional seedlings of Coprosma rhamnoides and Weinmannia syllicola are also present (Plate 7).

Loxsoma spreads over one small section (20 x 15 ft) within this area, and even then is sparsely distributed. Several comparable areas cleared in a similar fashion over the year 1954 show no signs of any Loxsoma. Where it occurs the plant is growing up through the litter in vigorous fashion. The fronds are in groups of 3 or 4, all from the one rhizome, indicating a steady, continuous growth rate. There are, however, no fronds higher than 20 ins, the average being approximately 9 ins (Plate 6).

Loxsoma was observed in this area in November, 1954, and again in November, 1955. On each of these occasions the number of fronds per square yard was counted in two parts of the patch. There was no significant change in the number of fronds present over this period of one year, nor had the overall area covered by the plant expanded to any extent.

Several rhizomes marked by pegs showed, on the average, 1½ ins growth over the year. This is certainly a slow rate of extension for the rhizome of a fern of habit such as that found in Loxsoma.

That young fronds of Loxsoma do not require high light conditions for their inception and vigorous growth is well shown in this locality. Places from which young fertile
fronds are springing, for example through cracks in piles of stacked logs and from beneath several inches of Leptospermum litter, are such that the growing rhizome must be existing and thriving under very low light conditions. Several cases are known of light demanding plants (e.g. Entelea arborescens, Pteridium aquilinum), which can establish in situations of low light intensity and survive on stored or translocated nutrients while growing rapidly toward the light source. This could be the case here, the young frond being nourished sufficiently by the rhizome (and its green photosynthetic petiole) to enable its rapid extension toward the light. An observation supporting this idea is that petiolar elongation is the only phase of the life cycle of this plant where growth is at all rapid.

It is evident that light, an operative and governing factor in the growth of Loxsoma, here exercises its effect at the gametophytic or young sporeling stage. At this phase of the life cycle, where the plant is small, micro-environmental differences in light intensity exert an influence which is not critical for the larger adult plant.

Reports from forestry officers in charge of this experimental plot reveal that Loxsoma first appeared in this habitat shortly after it was opened up. No one can recall the fern as present in the uncleared area beforehand. Observation on similar stations in which the regenerating vegetation as been left show a total absence of Loxsoma. In comparable positions Adiantum aethiopicum is frequent.

It seems certain that Loxsoma entered this community when the ground was first cleared of fallen debris and undershrubbery. Several sporelings became established and grew while conditions of light and competition allowed.

Further establishment of this kind is precluded now by the floor cover of Leptospermum litter, either beneath which prothalli cannot germinate, or through which young sporelings cannot rise. It is, of course, possible that ground litter exerts an influence on the plant at both of these phases of the life cycle. Neither sporelings nor prothalli have been found in this area, yet it is more probable that the greatest effect is on the young sporeling. On the relatively dark, damp floor beneath the debris would seem an ideal place for spor germination and early prothallial growth; this, however, cannot be supported by field observations. The
adult plant of Loxsoma, once established in an area, is extremely tenacious and can endure exposure, desiccation, and low light conditions; rapid spread is, however, never a feature of its growth.

This particular area is of interest because, although artificially created, it is the only place, so far as is known, in which Loxsoma grows under habitat conditions cited by Cockayne (1928) as natural for the plant: "under the shade of Leptospermum at the margins of forest". While no other strictly parallel case has been found still extant, reliable reports indicate that Cockayne's description is correct for the past occurrence of Loxsoma at Chelsea, Auckland.

Loxsoma once occurred sporadically along and above stream banks in the lower Kaiarara. As a consequence of recent road-building activities, the fern has completely disappeared from this area. Old rhizomes, do, however, remain and there is a strong possibility that Loxsoma will recolonize these banks.

Remaining Localities from which Loxsoma has been Recorded:

Very few of the distribution records and herbarium specimens of Loxsoma are accompanied by ecological notes. It is therefore difficult to gain any idea of the progress of events since collection save that which is general for the area. The following account is based on herbarium specimen records, supplemented by the writer's own field observations. Throughout the north (Whangarei to Mangonui) Loxsoma is distributed on stream banks; Keri Keri (Cunningham 1836; Dobbie, 1876); Kaitaia (P.R.B.); Waipoua (Cockayne, 1907; P.R.B.), and track cuttings: Parahaki (Dobbie, 1876; P.R.B.); Mangamuka Gorge (Thompson, 1954; P.R.B., 1955). Occasionally is said to occur on gulley slopes under tall Leptospermum (Mangonui, Dobbie, 1876). This observation I have not been able to confirm.

Parua Bay (Cranwell, 1934) and Whangarei Heads (Cranwell, 1934) were visited in July, 1955. Situations from which the plant has been recorded are now more or less completely open, and Loxsoma is absent. In all Waitemata stations habitats are essentially similar to those described for Paremoremo (Kirk, 1872; Cheeseman; P.R.B.). Loxsoma is now extinct from Chelsea (Petrie, 1919; Cheeseman). This could be due to the access of cattle to the bush, but is rather, the writer suspects, a consequence of accessibility to botanists.
Reports of small quantities of *Loxsoma* on a stream bank at Little Barrier have come from Mr. F. Holman. The location, about a quarter of a mile north-east of the homestead, is one which suffered from firing about 80 years ago.

Plants from Mount Hikurangi (not visited) are uniformly straggly and small. Mr. N. Potts of Opotiki has kindly informed me that the plant grows only along stream banks on the lower levels of the mountain where kanuka is regenerating.

Mount Maungatautari (Waikato) (Cranwell, 1931) plants are similar in all respects to those from Hikurangi and occur only along stream banks.

**GLAUCOUS VARIETIES OF LOXSOMA**

Plants of *Loxsoma* are sometimes found which have a white under-surface to the frond. They were thought by Cheeseman to be confined to the far north and to the Coromandel peninsula. It was therefore reasonable to assume that some difference in ecological preference may exist between glaucous and green varieties. This assumption is unwarranted, for in all localities visited, glaucous and green plants have been found growing in close proximity. There is a preponderance of glaucous plants at Mangonui, Kaitaia, Waipoua and Coromandel, of green at Parahaki, Auckland and the Great Barrier, Hikurangi and Maungatautari.

No differences exist in ease of establishment when both varieties are transplanted to the glasshouse, or in rate of growth and frond production under these, or natural, conditions.

Chromosome counts of the two varieties are the same. The variation must therefore be attributed to a single gene or group of genes. Existence of intermediate conditions (Parahaki, Paremoremo) could indicate that the two varieties are interfertile and that full expression of these genes can be prevented in various combinations.

Field (1890) suggests that the glaucous under-surface is a seasonal variant of the green. This postulate can be easily refuted by continued observation both in the field and in the glasshouse. Fronds which are glaucous remain so, and all fronds on a single plant are equivalent in this characteristic, regardless of season.
SEASONAL CYCLE OF LOXSOMA.

There is no observable variation with latitude in the cycle of frond production, sporangial formation and spore shedding. Parahaki, Great Barrier and Paremoremo have plants at exactly similar phases of development at the same time. Kaueranga was only visited twice during the course of this investigation, once in July and once in November. The presence there of profuse, young, light-green fronds in early November indicates a parallel cycle.

Young fronds are produced at irregular intervals throughout the whole year, but the chief burst of growth, during which all growing tips bear fronds, is from mid-September until mid-November. Over this period any patch of Loxsoma is seen to have numerous, naked petioles of a distinctive pale green colour emerging from the shade of the previously formed fronds. These petioles elongate rapidly, 14-15 ins in 14 days being the average rate of elongation. It is interesting to note here no difference in growth rate between glaucous and green plants. For a single plant with three growing apices, the average length the young fronds attain before uncurling is 28 ins.

Toward the end of October and in early November sori appear on those fronds which were produced early in the growing season. Their formation is simultaneous over the whole frond; greater numbers are formed on the large basal pinnae than on more apical ones.

When the later formed fronds reach adult shape, sporangia appear, as they do on the earlier fronds, up till the end of November. Little or no growth or frond production takes place over the hot summer months of December, January and February; over this period the fronds mature in texture and the paraphyses elongate and crowd the mouth of the indusium.

Sporangia become fully emergent in March and April and the spores are shed very shortly afterward. Culture work indicates a period of at least 4 months must elapse before spores will germinate. In the field, however, this period could be much longer. The time from germination until prothallial maturity will vary greatly with prevailing conditions, but is between 2 and 4 months. Prothalli, bearing sporophytes at the first and second leaf stages, were found in the field (Parahaki) in September and October.
Growth of the young sporeling, once the prothallus has disintegrated, is extremely slow. Leaves of mature texture, no more than 2 ins high, are found on plants two and three years old. This is probably due to the fact that gametophytes and their young sporelings can only establish in situations which prove eminently unsuited to vigorous growth and spread of the adult plant.

Observations over a period of 16 months on young plants growing in this type of situation reveal no overall increase in length of living rhizome. Growth at the tip barely compensates for decay at the proximal end. Where young plants are established in areas suitable for the continued growth, extension is far in excess of decay.

Plants growing on clay banks and cuttings (Parahaki, Kaueranga) are never vigorous. On the other hand, where colonizing stream banks, Loxsoma has, by comparison, a rapid rate of growth. Establishment in these latter habitats must have been initially by spores, but only at one critical stage it seems can Loxsoma find conditions suitable for its entry. Plants which produce a higher number of spores and have a faster rate prothallial growth (Blechnum procerum, Cyathea dealbata and Adiantum affine), are constant competitors. In every situation in which Loxsoma is thriving in the field these plants are present in greater numbers. They have, moreover, a wider tolerance of environmental extremes than Loxsoma.

The river or stream bank, being usually inaccessible to browsing animals, and often remote, soon becomes a closed habitat, especially to any slow-growing plant the establishment of which requires the access of abundant light. By comparison, clay track cuttings are kept relatively bare by artificial means and a relatively open surface is presented for colonizing plants. The individual tolerances of the species determine which will succeed and which die in this habitat.

GROWTH PATTERNS IN LOXSOMA

Few attempts have been made to study the fern ecology from a dynamic viewpoint. The studies by A.S. Watt (since 1940) on (Pteridium aquilinum) are based on fifteen years' observation of certain heathland localities. His surveys are extremely detailed and measurements on all
parts of the plant are treated statistically. From the result of this and earlier work along similar lines, Watt has formulated his hypothesis of "Pattern and Process" in vegetation. This may be expressed briefly thus: a plant community shows not only a static pattern, but also a dynamic one. In the patchy plants of the hinterland (as opposed to the solid extensive mat of the parent plant) we have a pattern in space, the components of which form a sequence in time.

Watt's experiments are designed to compare growth patterns of bracken, in isolated patches, with that forming part of the continuous bracken cover.

As Watt's work represents the only major contribution to the study of the experimental autecology of a fern of this habit type, Loxsoma communities were examined from his viewpoint. Several parallels between Pteridium aquilinum and Loxsoma have emerged and there is indeed a strong possibility that these could be found generally applicable to matforming ferns with creeping, rather than subterranean, rhizome (e.g. Paesia scaberula).

For Loxsoma no parallels can be suggested with the parent community quoted by Watt: all patches of Loxsoma are to be regarded as hinterland plants.

Fronds of Loxsoma vary in their dimensions according to their distance from the margin of the community. Young, developing and uncurling fronds at the margin, abutting on plants of other species, have a shorter, stouter petiole than do those which develop in the interior of the patch. The fronds of marginal apices, having uncurled and assumed adult form, rarely reach a height of more than 6 ins. Those apices which have become isolated from even the marginal plants by decay of the intervening rhizome, bear extremely small fronds with thin, wispy petioles.

These observations support Watt's conclusion that marginal growing apices are in a very different microenvironment from that of more central members. The effect of the stronger competition which marginal fronds meet is to reduce their extension and to make them proportionally stouter at the petiole base. The stouter petiole base is less noticeable in Loxsoma than in Pteridium, where it is largely attributable to the subterranean habit of the rhizome.
One notable difference exists here; when apices of \textit{Loxsoma} emerge any distance from the community (over 3-4 ins), the young fronds they bear are dwarfed in all respects.

In a hinterland population Watt recognizes five basic zones. These are, environmental; pioneer; building; mature; degenerate. With some slight modification, this sequence can be observed in a population of \textit{Loxsoma}.

The environmental zone is equivalent to that in which no fronds are present. In the pioneer phase, some apices, bearing marginal fronds, are growing outward and colonizing new ground. This does occur in \textit{Loxsoma}, but the rate of growth marginally is very slow and in addition biotic factors are against \textit{Loxsoma} spreading in this fashion. Internal to this zone is the building phase. Here there is more or less complete \textit{Loxsoma} coverage and fronds of internal type are produced abundantly. The mature zone can be depicted as that in which frond production per unit area, petiolar elongation, laminar size, and percentage of fertile fronds reach their maximum. A degenerate phase cannot be recognized with any accuracy. Within a clump of \textit{Loxsoma}, living rhizomes run over the dead and decaying members. These latter are not generally restricted to or concentrated in one zone. Often when the clump is verging on a stream bank where a steep face is met, old decaying rhizomes run horizontally behind the living rhizomes. These could represent the earliest point from which the plant grew and developed, and thus be a degenerate zone. In many places, this area of old rhizomes, often embedded in moss, comes abruptly. Fronds immediately adjacent to them are those of the mature zone.

Watt notes in hinterland plants an absence of any determined direction of growth. In the plants of the compact community, rhizomes are almost all in alignment, being forced to grow forward by the strong competition behind. No such alignment can be observed in hinterland plants nor in any patch of \textit{Loxsoma}, for here the rhizome pattern is an inextricable tangle with apices growing inward and outward at random.

The method used by Watt to assess the number of plants of \textit{Pteridium} per unit area is one which can well be noted. For any type of quadrat analysis or estimation of density or frequency, it is imperative to know this figure.
Plants of similar habit to *Pteridium* and *Loxsoma* cannot be counted easily. In a continuous area of *Loxsoma* the tangle of rhizomes and their mode of dying off and decaying behind makes it impossible to define the limits of one mature adult plant.

A rough estimate of the number of plants per unit area may be obtained in two ways:

(a) By comparing the length of rhizome per unit area with the average length of rhizome of an individual.

(b) By determining the number of fronds per unit length of rhizome and computing the number of individual plants from the number of fronds per unit area.

Of these methods, the second is better suited to analysis of *Loxsoma*. There is a tendency with this approach to overestimate the number of plants (Watt, 1940). An average number of plants per square yard of *Loxsoma*, on this estimate, is eight (see Table 1).

**TABLE 1**

*Calculation on Number of Plants per unit Area (1. sq. yd).*

<table>
<thead>
<tr>
<th>Frond No.</th>
<th>Rhizome Length Inches</th>
<th>Average No. Fronds per Unit Length of Rhizome</th>
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<tr>
<td>15</td>
<td>13.50</td>
<td>.856</td>
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<tr>
<td>13</td>
<td>6.75</td>
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<tr>
<td>22</td>
<td>9.25</td>
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<td>22</td>
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<tr>
<td>208</td>
<td>243</td>
<td></td>
</tr>
</tbody>
</table>

Rhizome length for one plant (22; 23; 43; 31; 28) = 28.3"
Therefore no. fronds per plant (28.3 x .856) = 24.224
Therefore no. plants per sq. yd = 200/24.2 = 8 (to nearest whole)
The fact that dense populations of *Loxsoma* show the characteristics of hinterland plants, and that isolated single shoots, with some exceptions, show the characteristics of marginal shoots of hinterland plants, provides a pointer to the status of *Loxsoma* in a regenerating community (Plate 8).

A plant of slow growth rate, *Loxsoma* does not colonize rapidly. The presence of marginal type, young fronds indicates that competition from associated plants is having a definite effect on the plant. It appears that an equilibrium is reached between competition and growth rate. Consequently, a patch of *Loxsoma* forms, over a period, a pattern in space, the components of which, form a sequence in time.

**DISCUSSION**

In all localities examined, *Loxsoma* is just maintaining itself. The one exception is at Kaiarara where roadbuilding has caused extensive damage.

Observations on the growth rates of adult plants, in the glasshouse and the field show growth to be extremely slow. Rhizome extension is never more than 3 ins per year. The gametophyte also is slow to mature ($2\frac{1}{2}-4\frac{1}{2}$ months). This slow rate of growth in both phases of the life cycle is considered to be the major factor, intrinsic in the plant, controlling the present micro- and macrodistribution of *Loxsoma*. Another factor of prime importance is the light requirement of the prothallus.

The lack of prothalli and young sporelings at Paremoremo and Kaueran and their extreme rarity on Great Barrier suggest that the plant is maintaining itself in these areas by purely vegetative means. In all of these localities the vegetational cover is more or less complete, and the amount of light reaching ground level in situations where spores may germinate is extremely small. At Parahaki where prothalli and sporelings are abundant the vegetation cover on the track side is not complete and coverage often below 50%. Incident light at ground level is approximately the same as that 18 ins above, where any adult fronds may be situated. (Plate 9).

There is here an explanation for the patchy and discontinuous distribution of *Loxsoma* within an area.
When the area was suitable for colonization by gametophytes (after fire; track cutting; clearing; giving canopy gaps) these grew; and over a period gave vigorous adult plants. Owing to the slow maturing rate of the gametophyte and the slow growth of the young sporeling, *Loxsoma* is not universally successful. Adult plants form in patches, not continuously over a whole stream bank or forest floor. As soon as the area becomes in most part covered by more rapid competitors for space under high light conditions, prothalli and sporelings can no longer establish. Neither can they do so under *Loxsoma* itself, nor on banks densely covered by bryophytes.

As new habitats are opened up, spores can germinate. Young sporelings of *Loxsoma* form about 5% of the population of such areas, for example the Parahaki track. It is obvious here, however from the extremely slow growth, impoverished appearance and lack of maturity of the plants, that this bare clay bank habitat, while suitable for establishment of gametophytes, is unsuited to the continued growth of the sporophyte. This also applies to several other ferns whose sporelings establish in association with *Loxsoma* e.g. *Cyathea dealbata*, *Lygodium articulatum* *Adiantum affine*. These plants in the sporophytic stage are not as tenacious as *Loxsoma*; sporophytes of these species die off in the early stages, while those of *Loxsoma* although dwarfed persist. *Blechnum procerum* germinates well and grows rapidly on clay bank habitats and is the prime competitor for space in all such situations. Always, when the full cycle of events in this type of community is complete, *Blechnum procerum* overshadows the banks and *Cyathea dealbata* behind it skirts the margin of the regenerating bush (*Leptospermum ericoides*). Overshadowing by *Blechnum* prevents any fresh establishment of *Loxsoma*. *Blechnum* eventually crowds *Loxsoma* out of the position it previously occupied.

Plants of *Loxsoma*, springing from old, long established rhizomes in the shaded situations described above, are often vigorous. Petiolar elongation is often marked and fronds complete their developmental cycle and mature. At Parahaki, such plants were observed to grow and thrive under conditions of low light until they are eventually choked by other plants.

Spores sown on artificially cleared shelves on stream banks at Paremoremo at the normal time of spore shedding have germinated. This supports the conclusions reached here that competition for space is a major factor controlling the
spread of *Loxsoma*.

Throughout the range of *Loxsoma* the pattern is repeated over and over again. A disturbed forest, a new track cut, patchy establishment of *Loxsoma* always with a preponderance of *B. procerum*; no sporelings or prothalli near any stand of considerable age. Finally, with the access of browsing animals to all of the described habitats, trampling is forcing *Loxsoma*, to recede into stations which are inaccessible to these animals. *B. procerum* suffers similarly. Young fronds of *Loxsoma*, being delicate, suffer severe damage from trampling of passing animals. This, rather than browsing, is the way in which these animals affect the colonizing activities of the plant. Rabbits have, however, been observed to eat the fern.

*Loxsoma* would almost certainly have been, in primitive New Zealand, a rare plant, capable of growing only in disturbed areas. There were many such areas throughout Tertiary Northland as a consequence of widespread volcanic activity, or to slumping soils on unstable slopes such as fault scarps. In Northland, there is a particularly widespread occurrence of incompetent shaly strata very prone to slumping. As these areas reverted to their primitive forest covering, *Loxsoma* would become overtopped and gradually disappear. With the arrival of man, burnt and cleared areas became even more plentiful. Felling and milling of much of Northland's kauri left large areas of broken canopy in gumland habitats. At this stage *Leptospermum* and its associated plants covered much of the north. With the increase of this type of vegetation, so *Loxsoma* would increase. Animals have gained access to many of these habitats following the opening up of adjacent areas for farmland. The overall effect of their browsing is seen in a general decline in *Loxsoma* in most habitats and its complete extinction in many others.