HABIT HETEROBLASTISM
OF
SOPHORA MICROPHYLLA Ait.

A thesis presented for the degree
of Master of Science and Honours in Botany,
in the University of Canterbury,
Christchurch, New Zealand
by
GILLIAN DENNY
January 1964
Acknowledgements.

The author acknowledges with gratitude the interest and guidance of Professor W. R. Philipson. She also wishes to thank other members of staff for their advice and the technical staff for their assistance. Among many others she wishes to thank particularly Mr. Sims and Mr. Palmer for help with photography.
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I. Introduction

I. 1. Statement of the Problem

Almost thirty years have elapsed since Dr. L Cockayne wrote his last comments on what he termed heteroblastism and since then little work has been done concerning what may be a very significant factor in the New Zealand vegetation. A thesis by Rumball (1961) and a paper by Wardle (1963) have re-opened the discussion. It is hoped, in this thesis, to extend the knowledge of one of the species in the New Zealand flora which shows a particular type of heteroblastism.

Divaricating shrubs and divaricating juveniles of adult trees are almost peculiar to New Zealand. Rumball (1961) reports that the only evidence he could find in the world of divaricating juvenile stages (other than in New Zealand) was in two Australian genera, and Bulmer (1958) states that the divaricating shrub is common in Tasmania but not elsewhere.

The problem can be approached experimentally from several different directions and a combination of one or more methods should offer some reasons for the prevalence in our flora of the divaricate habit.

In this thesis the genus Sophora will be studied approximately along these lines: firstly, a study of the internal and external factors which have caused the divaricate juvenile - non-divaricate adult to develop. This may be closely linked with the factors which have caused the divaricate shrub to develop.

Secondly, a study of the apices of divaricate and non
divaricate species, the apex being the determining organ of the plant and finally, a study of the factors in New Zealand which may have caused the divaricate habit to become a characteristic feature of the New Zealand flora.

I. 2. Definition of Terms

Heteroblastic.

This term was first proposed by Goebel (1896) referring to species whose early stages show juvenile characteristics which are markedly different from the later stages. It generally shows itself by different leaf forms in the juvenile and adult, but may also be characterised in other ways.

Habit Heteroblastism.

This is a particular type of heteroblastism in which the differences between juvenile and adult are characterised by a difference in habit, instead of or on occasion including, the more usual difference in leaf form (heterophylly). In this thesis this has particular reference to a divaricate juvenile which grows to a single trunked erect tree.

Divaricate.

This term is used for a wiry and intertangled habit caused by the branches or main stem diverging at a very wide angle (usually more than ninety degrees) from the main axis.

Juvenile.

The young stages of plants are often described as juvenile. It is used in a particular sense to describe young plants which are morphologically different from adult plants.
2. GENUS SOPHORA

2.1. Selection of Genus.

This genus was chosen for study because its New Zealand species form a "triad", meaning that there is a species which is a divaricate shrub, a species with a divaricate juvenile and a non-divaricate adult, and a species which shows no sign of habit heteroblastism. This "triad" nature is found only in two other New Zealand genera Pittosporum and Plagianthus. Sophora was chosen because it was familiar to the author, specimens were relatively easy to obtain and it was known to be fast growing.

2.2. Description.

This genus is a member of the Papilionaceae, (fam. Leguminosales) made up of trees or shrubs with imparipinnate leaves. Its flowers are racemose or panicled with ten free stamens; the standard is broad and the wings shorter than the keel; the style is incurved with a terminal stigma and there are numerous ovules. The pods of this species are moniliform and elongate and may be terete or four winged. The pods may also either dehisce by valves or be indehiscent. The seeds are globose and have a hard testa.

2.3. Distribution.

This genus, containing forty or more species, mostly inhabits the warmer regions of either hemisphere. Trees and shrubs of this genus are found in India, Tibet, China, Japan, Siberia, North America (Texas and California), the Caribbean and Pacific Islands, Australia, New Zealand, and South America. This thesis is particularly concerned with the section some-
times described as Edwardsia (Skottsberg 1956). The endemic species of this group are found in New Zealand, South America, Hawaii, Easter Island, Juan Fernandez, Rapa, Reunion, Tristham and Gough Islands. (see Fig. 6) Although the species are endemic they are described by many authors as having close affinities. This will be discussed at a later stage.

2.4 New Zealand Species.

Allan (1961) describes three species and two varieties.

**Sophora prostrata** Buchan. (Plate 1)

This is a prostrate densely divaricating shrub growing to a height of 2 metres. Its leaves grow to a length of 2.5 cm. with up to 8 pairs of leaflets, these less than 4 mm. long. The flowers are solitary or in threes and orange brown in colour. The standard is up to 1.5 cm. long and distinctly shorter than the wings; the keel is about 2 cm. long. The pods are 3-5 cm. long with very narrow wings - if any. The seeds are dark brown.

**Sophora microphylla** Ait. (Plates 2, 3)

A tree growing up to 10 m. tall and its juveniles show dense divarication. The leaves are found up to 15 cm. long with 20-40 pairs of leaflets each approximately 5-7 mm. long. The flowers are in racemes of 4-10 and pale to golden yellow in colour. The standard is 3 cm. long and the wings the same size or longer and the keel about 4 cm. long. The pod is broadly winged and may be up to 15 cm. long. The seeds are brownish to golden yellow.
**Sophora microphylla var longicarinata.** Allan.

Differs from the former in height, the tree growing up to 5 m. in height. The leaves are longer (10 - 20 cm.) with 20 - 40 pairs of leaflets each about 4 mm. long. The flowers are pale yellow with a long standard (3.5 cm.) and keel (4.5 cm.) while pods are winged and contain pale brown seeds.

**Sophora microphylla var fulvida.** Allan. (Plate 4)

A small tree growing up to 3 m. tall. The leaves are 8 - 10 cm. long with close set leaflets (3 - 4 mm. long) and up to 50 pairs. Fulvous hairs appear on young branches, pedicels and calyces. The standard is 3.5 cm. long; the keel is 4.5 cm. long and slightly longer than the wings. The pods are about 15 cm. long and the seeds are brown.

**Sophora tetraptera.** J. Mill. (Plate 5)

This is a large tree growing up to 12 m. tall and its juveniles show no divarication. The leaves are up to 15 cm. long with 10 - 20 pairs of leaflets, each 1.5 cm. - 3.5 cm. long. The flowers are golden yellow in racemes of 4 - 10; the standard (3 cm. long) being shorter than the wings (3.5 cm.); the keel is 4.5 cm. long. The pods are up to 2 dm. long broadly winged, the seeds are yellowish.

**2. 5. Distribution of Species in New Zealand.** (Fig. 1)

**Sophora prostrata** is found only between lat. 41° - 45° (ie. Northern part of South Island) mainly in grassy and rocky places from lowland to montane, east of the main divide.

**Sophora microphylla** is found all over New Zealand and according to Allan (1961) also in the Chatham Islands. It commonly occurs along rivers, forest outskirts and in open areas.
**Sophora microphylla var. longicarinata** is described from the Nelson district but the author has also seen small leaved forms in the south of the North Island.

**Sophora microphylla var. fulvida** is found in coastal scrub and forest around the beaches on the west coast near Auckland. It does not appear to extend inland very far nor further north than 20 miles.

**Sophora tetraptera** is found on the east coast from East Cape to lat. 40° and as far inland as Lake Taupo. Large leaf forms which may be this species also appear in the Bay of Islands. (Plate 6)

2. 6. Source of Species. (see Fig. 1)

Species for the ecological and morphological experiments were obtained from various places all over New Zealand.

**Sophora prostrata** seed and specimens were collected from the Port Hills near Christchurch.

**Sophora microphylla** seeds and specimens were collected from Titirangi, Auckland, Warkworth, North Auckland, Rakaia River, Canterbury and Murchison in the Nelson area.

**Sophora microphylla var. longicarinata** seeds were collected from near Nelson.

**Sophora microphylla var. fulvida** were collected from Piha near Auckland.

**Sophora tetraptera** seeds and specimens were collected from near Gisborne.

Seeds and specimens thought to be **Sophora tetraptera** were collected from Keri-Keri Inlet and Whangamumu in the Bay of Islands.
Sophora "chathamica" seeds were obtained from the Chatham Islands.

(facing page 7)

Figure 1. New Zealand, showing distribution of Sophora species.

Plate 1. Sophora prostrata, adult (½ natural size).

Plate 2. Sophora microphylla, adult (¼ natural size), growing in Canterbury.

Plate 3. Sophora microphylla, adult (½ natural size) growing in Auckland.

Plate 4. Sophora microphylla var. fulvida, adult, (¼ natural size).

Plate 5. Sophora tetraphylla, adult (½ natural size).

Plate 6. Sophora species, adult from the Bay of Islands, (¼ natural size).
S. microphylla (?)
North Auckland

S. microphylla var. fulvida
Piha

NORTH ISLAND

S. tetrapeta
Gisborne

S. microphylla var. longicarinata
Nelson
Murchison

S. prostrata
Christchurch

S. microphylla

SOUTH ISLAND

NEW ZEALAND SHOWING DISTRIBUTION AND PLACES OF COLLECTION OF SOPHORA SPECIES

Chatham Islands. (200 m.)
S. microphylla (?)
PLATE 2.

HERBARIUM OF
AUCKLAND UNIVERSITY COLLEGE

NAME: SOFTHAIR
FAMILY: LEGUMINOSAE
LOCALITY:

HABITAT, ETC.
RIGHT ON RIVER BED

COLL. No.: 1
DATE: 1
HERBARIUM OF AUCKLAND UNIVERSITY COLLEGE

NAME: SOPHORA

FAMILY: LEGUMINOSAE

LOCALITY: YEBORANE

HABITAT, ETC.: GUM, DYNAMITE, VERY NARROW

COLL. N. 11785.30N

DEP. 1

DATE: 30.1.37
3. **PRELIMINARY EXPERIMENTS**

3. 1. Introduction.

The experiments for this thesis were started in 1961 for the purpose of obtaining some definite information about the juvenile stages of the various species and varieties of *Sophora*. Up till then there had been no confirmation of the author's observation, that the juveniles of *Sophora microphylla* in Auckland do not divaricate under normal conditions. Allan (1961) says *Sophora microphylla* is common to the North, South and Chatham Islands, and under his description of the species describes the juvenile as divaricating. This conflicts with Cockayne (1901) who describes the juveniles of the Chatham Island *Sophora* as non-divaricate. Cockayne (1911) also comments that a form from the neighbourhood of Auckland City appears to be similar to the Chatham Island plant.

The aim of the preliminary experiments then was threefold; to grow the different species and varieties under controlled environmental conditions; to record the pattern of divarication; and to provide a source of plants of known age and environmental background for later experiments.

3. 2. Method.

Six seeds from one tree and about five trees from one area were used in the experiments. The seeds were selected from different parts of the tree and the trees chosen were as far apart as practicable in the area. This was done to try to avoid the effects of hybridization which appears to be common in this genus. The areas chosen were the Bay of
Islands (Sophora tetraptera) North Auckland (Sophora microphylla) Titirangi Auckland (Sophora microphylla) Piha, Auckland (Sophora microphylla var fulvida) Gisborne (Sophora tetraptera) Canterbury (Sophora microphylla) Canterbury (Sophora prostrata) Chatham Islands (Sophora microphylla). Later, seeds from Nelson (Sophora microphylla var longicaulis) were obtained and grown in a similar way to the experiments which are to be described.

The seeds were grown in 4" deep seed boxes using a mixture of sand and heat sterilized soil in the proportion of 1:4. The box was lined with fine shingle and then covered by the sand soil mixture. It was decided to do nothing about nodulation and see what developed.

Four types of environmental conditions were used, three in Christchurch and one in Auckland, using duplicate sets of seeds in each. In Christchurch three sets of seeds were grown, two sets in a glasshouse in the grounds of the University of Canterbury and one set outside. The seeds in the glasshouse were grown under wet and dry conditions respectively. In Auckland one set of seeds was grown outside. The seeds which were growing outside received no protection from the sun and no extra water.

The seeds were prepared for sowing late in August 1961. Germination was accelerated by cutting off a small portion of the testa opposite the micropyle and placing the seeds on wet blotting paper. They were then placed in petrie dishes and maintained at room temperature until sprouting occurred. The blotting paper was changed daily to prevent contaminat-
ion and also to get rid of the brilliant yellow stain which the testa deposited. (see Appendix I)

Following germination the seeds were planted in the boxes in rows one inch under the soil and two inches apart. The boxes were then placed under the various conditions. Temperatures over the four months varied with each set of environmental conditions. In the glasshouse the average temperature was about 78°F with a diurnal range of 20°F. Outside there was a large fluctuation ranging between 90°F and 31°F with average temperature about 59°F. In Auckland it was not possible to take readings from the actual area. The mean temperature for Auckland over the summer months is 65°F.

3.3. Results.

Germination. All species and varieties had a similar percentage of seed germination (approx 75%) except Sophora prostrata of which only about 25% germinated. The seeds from Gisborne (Sophora tetrapetala) failed to germinate probably because there was not a large number to choose from. On the average the plumule appeared above the ground about 20 days after the planting. However both Sophora prostrata and the Chatham Island species took over 30 days to germinate.

Leaf Development. There did not appear to be any significant difference between the species in the time of the appearance of the first leaf nor in the height at which the first leaf appeared (usually about 2.5 cm.).

The first leaf may be simple or ternate. In the Canterbury species it was commonly simple, in the Bay of Islands...
species it was commonly ternate and in the others it varied. However the seed leaf, which appeared later in time but earlier on the axis, was invariably simple.

**Leaflet Development.** In most species there was little difference in the pattern of leaflet development. About three or four leaves with the same number of leaflets were produced before any higher number of leaflets appeared. After six months all species had leaves with about 8 - 10 pairs of leaflets except for *Sophora microphylla* vars *longicarinata* and *fulvida* both of which had 12 - 15 pairs of leaflets.

**Pairs of leaflets on the leaves 3rd, 4th, 5th from the apex at 9 months**

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<td></td>
<td>Wet</td>
<td>Dry</td>
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<tr>
<td>Canterbury</td>
<td>5</td>
<td>3</td>
</tr>
<tr>
<td>Auckland</td>
<td>8</td>
<td>4</td>
</tr>
<tr>
<td>Nelson</td>
<td>9</td>
<td>6</td>
</tr>
<tr>
<td>Piha</td>
<td>12 - 13</td>
<td>6</td>
</tr>
<tr>
<td>North Auckland</td>
<td>9</td>
<td>-</td>
</tr>
<tr>
<td>Bay of Islands</td>
<td>10</td>
<td>6</td>
</tr>
<tr>
<td>Chatham Islands</td>
<td>4</td>
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**Fig. 2**

There were no signs of heterophylly in the first year. However in the second year after the winter had caused a trace of deciduousness, the Canterbury species tended to develop leaves with smaller leaflets and consisting of 3 - 4 pairs of leaflets. The Auckland species stayed constant at about
6 - 8 pairs of leaflets. North Auckland and Bay of Islands species lagged behind and after one year had leaves with only 6 pairs of leaflets.

The leaflet pattern of the secondary and tertiary branches followed several steps behind the primary branches. This tends to give the appearance of heterophylly, because as the shrub begins to divaricate there is a profusion of these branches, and hence a large number of leaves with fewer leaflets.

**Divarication.** Divarication did not appear in any species until the fifth node. After this point quite obvious divarication in the form of a bending of the stem at a definite angle from the axis appeared in the Canterbury species (apart from the population collected at Murchison which showed no divarication at all). Slight divarication was also evident in some of the other species under particular environmental conditions.

Species which were grown outside or in dry conditions showed more divarication than those under wet conditions or those grown outside at Titirangi.

Under all conditions the Canterbury species showed the most divarication. (Plate 7) The Bay of Islands species showed faint divarication under the dry and outside (Plate 8) conditions. The Piha and Nelson species showed no recognizable divarication. (Plate 8)

*Sophora prostrata* showed considerably less divarication in the wet conditions than it did grown outside or in dry
Branching. Secondary branches developed first in the Canterbury species. In the plants grown outside and those grown under dry conditions branches developed on lower nodes (2, 3, 4) compared with those grown under wet conditions (5, 6, 7). Tertiary branches started to show at six months in the Canterbury species. At one year tertiary branches were developed in most species. The exceptions were the Piha and Nelson species both of which showed only a few secondary branches.

Leaves. After the fifth node differences in leaf size and leaflet shape were observed. (Plate 9)

Differences were seen both in the shape of leaflets in the various species and varieties, and in the size of leaf and leaflets under different environmental conditions.

The Piha and Nelson plants (Sophora microphylla var fulvida and var longicarinata) under all conditions had longer leaves and smaller leaflets. The leaves were obovate elliptic in shape.

The Canterbury and Titirangi species were similar in shape (obovate) but under dry and outside Christchurch conditions, the leaves and leaflets on the Canterbury species were smaller.

The Bay of Islands leaflets were the same shape as the Auckland and Canterbury species but were larger under all conditions.

The Chatham Island plants had leaflets which were obcordate, and this difference persisted under all conditions.

The set of plants grown outside in Christchurch and
under dry conditions in the glasshouse had shorter leaves and smaller leaflets than those grown at Titirangi. Those grown in the glasshouse under wet conditions had the longest leaves and the largest leaflets of all. (see Plates 10, 11)

There was some differences in leaflet shape with each species or variety. This was particularly noticeable among the plants of the set of Canterbury seeds.

There was little sign of deciduousness in the first year. Leaves became sparser in the Canterbury species during the winter and were replaced by the smaller ones already mentioned. After eighteen months growth, the leaves on the Canterbury plants were still very small (corresponding to those seen on the "dry" specimen. (Plate 11)

Leaves at the nodes where branches were developing dropped off and were not replaced.

General Observations. The internode in the Canterbury Sophora microphylla was very long and this caused an increase in height. It also helped to contribute to the difference in appearance of the Canterbury species before divarication was really marked.

When the young plants were transplanted after eighteen months heavy nodulation was observed on some plants. Although it was not possible to check every plant, it appeared that the divaricate species showed less nodulation than the non-divaricate species.

The first three leaves on the Canterbury Sophora microphylla plants had large and more mesophytic leaflets than the
Figure 3. GRAPH SHOWING THE AMOUNT OF DIVARICATION
RECORDED FROM PLANTS IN THE PRELIMINARY
EXPERIMENTS.

ENVIRONMENTAL CONDITION

KEY TO VARIETIES.

Canterbury  Piha  Titirangi  Bay of Islands
Plate 7. JUVENILE PLANTS OF SOPHORA SPECIES.
(2½ years old).

Sophora microphylla from Bay of Islands (1/3rd natural size).

Sophora microphylla from Canterbury (1/3rd natural size).

Sophora microphylla from Bay of Islands (1/3rd natural size).
Plate 8. JUVENILE PLANTS OF *SOPHORA* SPECIES.
(2½ years old).

*Sophora microphylla* from Auckland (1/3rd natural size).

*Sophora microphylla* var *fulvida* (1/3rd natural size).
8th LEAF

TITIRANGI (outside) -

Canterbury Piha Chatham Is. Titirangi Bay of Is.

CANTERBURY (glasshouse) -

Canterbury Piha Chatham Is. Titirangi Bay of Is.
CANTERBURY

AUCKLAND

LEAF SUCCESSION (DRY)
rest of the leaves on the plant. (see Plates 10, 11) This confirms an observation by Cockayne (1911).

**Sophora prostrata** grown under wet conditions and outside at Titirangi showed considerably less divarication than seeds from the same plant grown outside at Canterbury and under dry conditions in the glasshouse. Also one or two plants did not "grow true". There appeared to be a considerable amount of plasticity in this species, although under drier conditions it was very different from the other young plants. (see Plate 12)

3.4. Discussion.

These experiments confirmed the observation that the juveniles of various **Sophora** species and varieties showed increased divarication under certain environmental conditions (see Fig. 3) The two environments under which more divarication was shown, were the dry environment inside the glasshouse and the outside environment in Christchurch. These two environments have in common dryness and daylength and it may be either of these or a combination of the two which is the factor responsible for divarication. The plants grown in Christchurch had approximately two hours more daylight each day over the summer than did the Auckland plants. Similarly, due to the difference in climate of the two places the Christchurch plants received less rain than the Auckland plants. Temperature might be a factor, but as it was not possible to take consecutive temperature readings in Auckland it can only be said, that taking mean temperatures for the two places, the Christchurch plants probably grew in
slightly higher temperatures.

The second observation resulting from these experiments is this; that different species and varieties of Sophora show differing degrees of divarication even under the same environment so it can be concluded that the divarication is not only phenotypic but also genotypic.

Sophora prostrata and Sophora microphylla (Canterbury) showed more divarication under all conditions than any of the other species. Both these plants inhabit dry hills or bush margins, suggesting that the divarication is in some way linked with xerophytic conditions, as has been shown by these experiments. However even under damp shady conditions in the glasshouse in Christchurch and outside at Auckland there was still some divarication in these plants. Also Sophora microphylla Canterbury found growing in shady conditions in the bush still appears to divaricate though not as densely as it does in the open. These species of Sophora appear to be genetically different from the other species and varieties, but are still capable of phenotypic alteration under various conditions. Several plants of Sophora microphylla (Canterbury) which had been grown in very dry sunny conditions for about a year were transplanted to a damp shaded place. Plate 13 shows the effect that this had on the succeeding leaves. Divarication also became less marked.

Of the other species and varieties grown the plants from Bay of Islands showed divarication under some conditions. This was not expected and unfortunately further investigation is outside the scope of this thesis. However these plants
grow in areas very close to the sea, and physiological dryness may be a factor. The Titirangi and North Auckland plants showed some divarication under drier environmental conditions but showed no trace of it at all under their normal conditions. The Piha and Nelson plants showed no discernable divarication.

One population of seeds gathered at Murchison from adults which were identified as *Sophora microphylla* showed no divarication and had a very different growth pattern from all the *Sophora microphylla* plants grown from seed collected in Canterbury. This was obviously a genetic variation but whether produced by a cross with *Sophora microphylla var longicarinata* or whether produced by isolation it is difficult to tell. The adults showed no signs of longicarinata characteristics.

It proved possible to measure the amount of divarication in terms of the angle (in degrees) at which the main axis of the plant diverged between successive internodes. The more acute the angle, the more divarication the shrub showed.

Branching was probably the most significant of the other results from these experiments. The development of branches followed very closely the divarication pattern. In the Canterbury species branching was most marked, in the Piha and Nelson species it was almost absent. This may be closely connected with divarication especially as the branches arise from the axis of the leaves at the point where the bending occurs. This will be further investigated.

The pattern of leaflet development differed both between
species and with environment. In all species three or four leaves with the same number of leaflets were produced before a higher number of leaflets were attained. This is probably a progressive developmental change. The higher number of leaflets attained by the Piha and Nelson plants was expected, because this is a characteristic feature of these varieties.

The deciduousness and consequent heterophylly in the Canterbury plants must be connected in some way with the divarication, as it was not a feature of any of the other plants under normal conditions, but showed in some plants under dry conditions. The smallness of the leaflets could be explained as a xerophytic modification.

The differences in leaflet shape were not consistent except in the Chatham Island, Piha, Nelson and Bay of Island plants and these may be variety differences. The large leaflets produced under the wet shady condition were probably etiolation effects.

The nodulation which occurred was heavy and particularly marked. (Plate 12) In view of Mothes (1931, 1932) work reported by Shields (1950) that nitrogen deficiency may contribute to xeromorphy, it was decided to try to investigate this factor in future experiments.

These experiments show quite conclusively that the separation of Sophora microphylla var longicarinata and Sophora microphylla var fulvida as varieties is quite justified. With their numerous small leaflets, lack of divarication, and lack of branching, their growth pattern is markedly different from all the other varieties and species. They are
also quite different from each other. *Sophora prostrata* too is very different from all the others and in its pure form, is a quite separate species.

The case for the remaining species and varieties is not so clear. *Sophora microphylla* from the Chatham Islands shows a very different leaf shape from the rest (see Plate 9) It is also slower to develop and it does not appear to divaricate. The *Sophora microphylla* from the Bay of Islands showed marked differences. The leaves and leaflets were longer and larger than the *Sophora microphylla* from Auckland and Canterbury. As this difference is reflected in the adult (see Plate 9) it would need further taxonomic study. The North Auckland plants appear to be intermediate between the Bay of Island plants and the Auckland plants.

Allan (1961) comments that hybridization is common in this genus and some of the above may be of hybrid origin. (Plate 14 shows a specimen of a hybrid growing on the Port Hills, Christchurch. Presumably a cross between *Sophora microphylla* and *Sophora prostrata.*) Chromosome studies which may reveal hybrid origin have been done on only three species. Rattenbury (1957) reports that *Sophora tetraptera*, *Sophora prostrata* and *Sophora microphylla* (from Auckland) have a diploid number of 18. Darlington and Wylie (1955) confirm this number, and also report it from other closely related species. Perhaps further genetic work on these other varieties would help to determine their origin.

The Auckland and Canterbury plants of *Sophora microphylla* showed marked similarities, as well as the differences of
of divarication in their pattern of growth. Because of these results it was decided in future experiments to use only these two sets of plants, and to investigate them under more controlled environmental conditions.

3.5. Description of Divarication.

Divarication begins on the main shoot with the main axis diverging at each node, this divergence becoming more acute as the plant grows older. Lateral branches, arising from the axis of the leaf develop rapidly and when the plant is about one foot high it is impossible to distinguish a main shoot. The rapid increase in length without a corresponding growth in thickness causes bending and this is followed by a rapid growth of tertiary branches. By this stage the plant is a tangled mass of branches with no obvious main shoots although a thickening in the original main axis supports the weight of the plant as well as increasing the height. There appears to be no particular point at which the plant grows out of its divarication, though it is rare to see divaricate plants higher than 2 m. A main shoot finally appears above the rest, grows in length then in thickness until the divaricate portion is left behind. At this point the plant may flower.
Plate 12. JUVENILE OF _SOPHORA PROSTRATA_ AND NODULES OF _RHIZOBIUM_.

_Sophora prostrata_ at 2½ years (1/3rd natural size).

Nodulation on the roots of _Sophora microphylla_ at 3 years (1/3rd natural size).
Plate 13. Leaves from *Sophora microphylla*, Canterbury plant, which was removed from the sun to the shade (at the point indicated by the arrow).

Plate 14. A hybrid between *Sophora microphylla* and *Sophora prostrata*. 
**Name:** Sophora  
**Family:** Leguminosae  
**Locality:** Summer, Port Hills  
**Habitat:** Dry cliff  

**Herbarium of Auckland University College**  
**Coll. G. A. J. C.**  
**Date: 20/7/19**
4. ECOLOGICAL EXPERIMENTS.

4.1. Introduction.

The purpose of these experiments was to try to isolate the factor or factors responsible for divarication, if as suggested by the previous experiments, divarication varies with environment.

Only two groups of seeds were used; *Sophora microphylla* from Auckland (one tree from Titirangi) and Canterbury (one tree from the Hurunui River). These being apparently genotypic, show no divarication and divarication respectively in their young stages. In the first group of experiments day-length was made the variable factor while in the second the variables were dryness and light conditions.

Because of the nodulation which developed on the roots of the plants in the first experiment it was decided to try to nodulate the plants in the growth room where it could be controlled under sterile conditions.

4.2. Growth Room Experiments.

The aim of these experiments (started in November 1962) was to compare the relative response of the plant to short and long days under controlled conditions of temperature and water. These experiments were carried out in a growth room in the Botany Department, University of Canterbury. The plants were grown at a constant temperature throughout of 77°F. (25°C.) under light of approximately 1,600 foot candles supplied mainly by fluorescent tubes but containing also about 24% of tungsten incandescent illumination. No attempt was made to control humidity and air changes were not less than
two per hour.

Three treatments were used. In the first plants were exposed to long-days (16 hours of light), in the second, to short-days (8 hours of light.) The third set was exposed to long-days until the fifth node then was to have been transferred to short-days. Because of the nature of the conditions it was not possible to have a control set of seeds.

Owing to the lack of space eight seeds only from each population could be used under each treatment, giving a total of twenty-four for the three treatments. The seeds were prepared for germination in the same way as in the first experiment except that the petrie dishes containing the seed were placed immediately under short and long-days in the growth room. The short-day was obtained by covering the plants with a light-proof box at 5 pm. and removing it at 9 am. The box was lightproofed by painting it black inside and ventilated by cutting a section from the top and replacing with a larger section held about 1" above the box. The temperature under the box varied by about 2° C. during the 24 hours.

After germination the seeds were planted 1" deep in plastic pots containing heat sterilized soil. As it was not possible to have completely sterile soil it was decided to inoculate all plants with Rhizobium rather than try to prevent nodulation. Cultures of Rhizobium were prepared from the nodules on the plants of the previous experiment and were used to inoculate the soil. The inoculation was done by preparing a solution of distilled water and the specific Rhizobium and pouring approximately 20 mls. of the solution over the soil
after the seeds were planted. Nodules from *Sophora microphylla* (Auckland) were used to inoculate the Auckland seeds and similarly nodules from the Canterbury plants were used to inoculate the Canterbury seeds.

The pots containing the seeds were then placed randomly in blocks under the selected environmental conditions already described. The position of the pots was changed regularly to avoid "end effects". The plants were watered once a day as evaporation in the room was high.

**Results.** The time of appearance of the plumule was twelve days on the average. The first leaves appeared at the same height as in the previous experiments in both "long-day" and "short-day". Development under both conditions proceeded as in the first group of experiments until after about a month it was noticed that the plants under the short-day conditions were wilting. Despite all efforts made to revive them, the plants died, and by the end of December there were none left.

The plants under the long-day conditions continued to grow and hence all the results that follow concern them alone.

Leaflet development proceeded faster than in the previous experiment and after three months the two populations had about 14 - 16 leaflets. Growth, after the first month was very fast - about 2 - 3 nodes a week in the Canterbury plants.

Divarication became evident in the Canterbury species about the 5th node. The Auckland species began to show some divarication about the twelfth node. (see Plate 15) As before the internode in the Canterbury species was very much long-
Branching in the two populations was not very obvious at three months. There was some secondary branching especially in the Canterbury species but no tertiary branching.

The experiment was abandoned after sixteen weeks because the remaining plants were wilting. The survivors were transferred outside and replanted. At ten months the remaining six plants were dug up and examined for nodulation but there was none to be found.

**Discussion.**

The plants probably died because of the high temperature—despite constant watering the evaporation rate was high. However probably enough information was gained to eliminate both temperature and nodulation from the factors for other experiments. The constant high temperature did not produce marked divarication as might have been expected if this had been a significant factor. The divarication which developed was slightly less than normal (140°) in the Canterbury plants and slightly abnormal in its development in the Auckland plants. The plentiful water could have been the factor which altered the Canterbury plants and the high light a factor in causing divarication in the Auckland plants. However because there were no short-day plants as a control it is difficult to reach any conclusions.

The lack of nodulation did not result in more divarication. This factor has not been sufficiently examined, because of the failure of this experiment. Owing to the lack of sterile conditions it was impossible to investigate nodulation.
Plate 15. JUVENILES OF SOPHORA MICROPHYLLA
(2 months old)

Auckland

Canterbury
4.3. Glasshouse Experiments.

These experiments were begun in April 1963 with the aim of examining differences in two seed populations (*Sophora microphylla* from Auckland and Canterbury) after growing them under a range of environmental conditions.

These conditions were the long-day and short-day already described, and a new condition of shade. There was also a group under normal conditions to provide a control. A further variable was introduced by dividing each population in two, one half being kept as dry as possible. By these means it was hoped that some significant reaction to dryness and amount of light would be produced.

The seeds were germinated as described in the previous experiments. About 10 seeds were used for each treatment, giving a total of 80 in each group of seeds, Canterbury and Auckland.

The long-day plants were grown in the day-light between 7 am. and 5 pm. and under a bank of fluorescent tubes with supplementary tungsten lamps between 5 pm. and 11 pm. (Plate 16) The reading on a cloudy day was 3,000 - 7,000 foot candles. At night the photometer reading dropped to 200 foot candles. The short-day plants were covered with a tea chest (Plate 16) for sixteen hours, giving them only eight hours of day-light. There was no light reading under this chest. The plants which were to be shaded were grown under a fine black mesh (Plate 17) which cut the daylight reading of about 5,000 foot candles to 1500 foot candles. The
plants acting as a control were grown in the open glasshouse (Plate 17).

The temperature of the glasshouse varied over about 30°F. The thermostat was set at 65°F. and the highest temperature recorded was 88°F., the lowest 57°F. The mean temperature was 67°F.

The seeds were planted in pots but were not innoculated with Rhizobium as the conditions in the glasshouse could not be kept sterile and the control plants might become inoculated. Half the plants were watered three times a week, while those which were being kept dry were watered only once a week.

The plants were left under these various conditions for three months after which time they were measured for the angle of divarication (using a protractor and taking 180° as the point of minimum divarication) on all nodes above the fifth; measured for height; and the number of branches counted.

Results: Divarication began earlier than had been the case in the previous two groups of experiments, in many cases it began below the fifth node. Divarication was most marked in the Canterbury plants which had been growing under the dry long days. The angle of divarication at the 5th, 7th and 10th node varied between 130° and 140°. The Auckland plants growing under the same conditions divaricated slightly, - the same nodes varied between 140° and 170°. The least divarication was shown by the Auckland plants under shaded wet conditions, most of the nodes were measured between 170° and 180°. Under all conditions the dry set of plants showed more div-
Figure 4. GRAPH SHOWING THE MEAN HEIGHT OF THE TWO POPULATIONS UNDER VARIOUS ENVIRONMENTAL CONDITIONS.
Figure 5. Graph showing divarication recorded from plants under various environmental conditions.

- Shaded
- Short day
- Normal
- Long day

- Canterbury - dry
- Canterbury - wet
- Auckland - dry
- Auckland - wet

Angle of divarication vs. nodes.
arication. These results can be seen more clearly in Fig. 5. Plates 18, 19, are photographs of plants selected at random from the various conditions.

More branches developed in this experiment on the Auckland plants than did in the previous experiments. The most branches were developed under the long-day conditions. The dry and wet conditions did not seem to have much effect on the amount of branching. No branches were seen on the short-day plants.

The average height was smaller than expected, about 7 cm. Heights varied considerably even within one particular environmental condition. However the short-day plants were very much shorter than the other plants, the dry set did not grow much higher than 3 cm. Pauley and Perry (1954) report that in many woody plants short days lead to a reduction in vegetative development, and this lack of height may be a reflection of this. (see Fig. 4)

Discussion. These experiments have confirmed some observations and questioned some of the previous results.

The heights of the plants were smaller than in previous experiments. This is the only experiment conducted over the winter, and though the temperatures were not low they were lower than the first experiment and very much lower than the second experiment. Height by itself is not a satisfactory measure of overall growth, but it seemed in the previous experiments to be connected in some way with divarication; where there was divarication there appeared to be a long internode (see Plate 15). Wareing (1956) Penfound (1931) report
that day length and light intensity increase the length of the internode. In these experiments the plants which divaricated most were the highest, although other plants which divaricated less were almost as high. Therefore it is possible only to say that the length of internode may be connected with divarication but until it is examined further in other species nothing positive can be stated.

The number of branches produced by the two groups of plants also raised questions about the previous results. In the last two experiments branching seemed very closely linked with divarication; where there was strong divarication there was also a profusion of branches. In this experiment branching did not bear much relationship to divarication. In most cases the Auckland plants produced as many or more branches than the Canterbury plants, and there appeared to be no greater development of branches under the dry conditions. However more branches developed during the period of long-days. These results are so very different from previous results that the question must be left open. Part of the explanation may lie in the fact that the plants yielding these results were plants three months old, whereas in the first experiment the main results were taken after six months. Also, unless branches were actually growing they were not counted as branches, and there were large numbers of branches showing as buds. Unfortunately it was not possible to check these plants after six months.

Perhaps the most significant and certainly the most in-
teresting results were in divarication patterns. Eight dif-
ferent conditions were used and some significant patterns em-
erged (see Fig. 5). As in the previous experiments the Cant-
erbury plants showed more divarication than the Auckland plants
(the only exception being in the short-day conditions where
the dry Auckland group divaricated more). In almost all cases
too, the group of plants under dry conditions divaricated more
than those under wet conditions. The third trend was between
the various light conditions. The shaded condition gave the
least divarication and there was a progression of increasing
divarication with the length of day.

These experiments confirm the observations made earlier
that there appear to be two genetic races within the \textit{Sophora}
\textit{microphylla}; the Canterbury population inherits a growth pat-
tern which includes divarication and may include a long inter-
node and early and numerous development of branches. The
Auckland population inherits a growth pattern which does not,
under normal conditions include divarication, but in xerophy-
tic conditions may develop divarication.

External environment is capable of altering the amount
of divarication. It appears that dryness and light intensity
both have the effect of increasing the amount of divarication.
The smaller and fewer leaves and leaflets (Cf. Plates 10, 11)
on the divaricate plants suggest that divarication is xero-
phytic modification in this species. What advantages a tang-
led and wiry shrub can have under hot dry conditions it is
difficult to see. Had the lack of light been a factor, the
divarication could have been explained in terms of the placing of leaves to receive the maximum amount of light. But the Canterbury plants which show divarication came from dry open habitats where the amount of sun is maximal not minimal.

The fewer and smaller leaves and leaflets can be explained in terms of xerophytic adaptations, and perhaps the wiry and much branched stems are fitted for survival in the open and exposed conditions in which it lives. Bulmer (1958) points out that where Manuka (*Leptospermum scoparium*) is growing exposed to wind or salt spray it becomes a closely branched, wind shorn mass, very similar to the truly divaricating shrubs of the same habitat. Another possibility is that constant grazing may have had some effect on the shape of these divaricate shrubs. This is a remote possibility as grazing has only been constant over the past hundred years. Before that approximately five hundred years have elapsed since the era of the Moa.

It seems most likely in this species that the divaricate habit is an adaptation partly to a dry exposed habitat and how this may have arisen will be discussed in a later chapter.

Although it was not possible to control the environmental conditions rigidly enough for a valid physiological experiment, the results in these experiments of the divarication pattern under the various light conditions is a guide to the trends which the plant shows.

The plants growing under the low light intensity (500 f.c.) showed less divarication than the other plants. The
plants growing under short days receiving 8 hours of 5,000 f.c. illumination showed less divarication than those receiving 9 hours of 5,000 f.c. (and 6 hours of 40 f.c. reflected from the long-day area of the glasshouse). The plants under 9 hours of 5,000 f.c. and 6 hours of 200 f.c. divaricated the most. Whether these light conditions react directly on the amount of photosynthate produced and so affect divarication or whether they act indirectly in affecting the production of growth substances, and thus affecting divarication is not known.

In a series of well controlled experiments on the effect of photoperiod on the growth of gorse seedlings Millener (1962) states "The influence of day length upon gorse is so profound that one may suspect this factor to operate through an integrated cell chemistry mechanism that probably affects all growth processes. It is not too difficult to imagine that processes in the hereditary material itself may be modified to different degrees by dissimilar short-day climates of different latitudes. Changes that have been induced in gorse, presumably over a long time, through these quite unknown modifications to unknown processes, have led to the production of seedlings that have essentially the qualities that tend to be impressed by the particular latitude upon any seedlings grown there. Relatively low latitudes engender the development of many juvenile leaves." (p. 127)

The trends in these experiments with Sophora seedlings have followed those first indicated by Millener. The com-
paratively low latitude plants from Auckland (37°S.) showed less divarication than the Canterbury (47°S.) plants. (The two populations which did not follow these trends, the Bay of Island and the Canterbury populations were affected by the factor of aridity; the Bay of Island plants are in an area of physiological dryness, the Chatham Island plants receive very much more rainfall than the Canterbury plants on the same latitude.) There is a difference of nearly two hours in the day-length between the two places at the height of the growing season. (see appendix II) How this affects the vegetative growth of the plant in terms of the juvenile-adult balance has received little attention from plant physiologists. Millener suggests that the differences in day length effect formative changes which can occur in sub-compensation point light, and these may be more fundamental than the flower producing photoperiodic reactions which have been studied so intensely. The nature of these formative changes is not known, but the relationship that these changes and conditions in the external environment may have with the internal condition of the plant will be discussed in the next chapter.

What is certain in the genus *Sophora* is that some environmental condition has caused fundamental internal changes which result in (a) the development of genetic variations between populations and (b) increase in divarication within any one population. These experiments have indicated that the factors concerned are probably day-length and dry-
ness, while the factors of temperature and nitrogen supply have not been studied sufficiently to be eliminated.
Plate 16. ENVIRONMENTAL CONDITIONS.

Plants growing under 'short day' condition.

Plants growing under 'long day' condition.
Plates 17. ENVIRONMENTAL CONDITIONS.

Plants growing under shaded conditions.

Plants growing under normal conditions.
Plate 18. COMPARISONS OF YOUNG SOPHORA PLANTS FROM AUCKLAND AND CANTERBURY.

Plate 19. COMPARISON OF THE EFFECT OF VARIOUS ENVIRONMENTAL CONDITIONS.

KEY:

A - Canterbury plants.
B - Auckland plants.
L.D. - Long-day
S.D. - Short-day
Sh - shaded
N - normal
D - dry
- - wet
Plate 18.

Wet conditions

Dry conditions

Wet conditions

Dry conditions
Plate 19.

Shaded conditions

Short day condition

Normal condition

Long day condition
5. MORPHOLOGY OF THE APEX.

5.1. Introduction.

The purpose of this investigation was to examine the apices of plants in the juvenile stage to see whether the bending of the stem occurred at this point, and if possible to determine the cause. If the apex is a self-determining and dominant centre of development, controlling the growth of the parts derived from it, then, unless the process of divarication is entirely physiological, morphological changes below the apex which cause the actual bending of the stem should be visible.

5.2. Description of Techniques.

The apices were taken from *Sophora microphylla*, the Auckland and Canterbury populations, which had been growing in the controlled environment of the growth room. The apices were removed when the plants were two months old before any signs of divarication were noticeable in the Auckland plants. As far as it was possible to determine, they were removed at a similar stage of plastochron. In addition 5 apices from plants grown in the preliminary experiments were collected. They were collected from plants a year old which had been growing outside in Christchurch.

Ten apices from each population were fixed, dehydrated and embedded by the tertiary-butyl alcohol method described by Johansen (1940 p. 130). Sections were then cut in longitudinal section on a rocker microtome at a thickness of 8\(\mu\). They were stained in an iron alum plus tannic acid stain.
described by Sharman (1943 p. 105) and finally mounted in "Depex".

5.3. Analysis of the Sections.

The sections proved very difficult to cut owing to an early development of wood which tended to shred them. Also a proliferation of hairs around the apex made the sections liable to split. Of the twenty apices sectioned only six were worth mounting; two from the Auckland plants and four from the Canterbury plants. This of course does not allow any definite conclusions to be drawn, though the evidence can be used to support results from other sources.

The first and obvious feature seen on the apices was the early development of the lateral branches. These branches generally developed in the axis of the fourth or fifth leaf or leaf primordia from the apex, and appeared to influence the plane of development of the apex. (see Plates 20, 21, 22.) A bending of the apex which appears to have been caused by the early development of the lateral branch was observed in almost all sections.

Due to the lack of sections it is not possible to state categorically that lateral branch development occurs earlier in the Canterbury plants. It does appear that this may be the case but until a larger number of sections, covering a range of juvenile and adult twigs, can be examined, it will not be possible to make any definite statement.

The small number of sections also precludes any definite statements about shape and organization of the apex.
However it may be worth noting that Rumball (1961) examining the apices of juvenile and adult plants in other species, noted that the juvenile apex appeared to be rather more domed than the adult apex. In these two populations the Canterbury group appears to have a higher domed apex, but this would need confirmatory work.

As it was not possible, in the time available, to refix and resection apices of adult and juveniles of the two populations, micro-dissection was attempted to find whether it was possible to confirm the early development of lateral branches. However the thick hair which covered the apex and early leaf buds, successfully prevented any dissection and prevented a sight of the young buds.

5.4. Discussion.

The early development of lateral buds which was shown in these sections also reflects the results from the earlier experiments where it appeared that the development of lateral branches was in some way connected with the amount of divarication.

Branches are formed from meristems arising in the axils of leaf primordia, and whether this potentially meristematic tissue will grow into buds and these buds produce branches depends in most cases on the stimulatory or inhibitory influence of auxin or other growth substances. The dominance of the terminal bud, first demonstrated by Thiman and Skoog (1934) was shown to depend on its production of auxin, which it was suggested, was translocated downwards to inhibit the growth of
lateral buds. This widely held view, has been questioned by Snow (1942) in a series of papers, and he postulates the hypothesis that the auxin is converted into a growth inhibitor or stimulates the production of one. Other workers have emphasised the importance of nutrition in apical dominance. Gregory and Veale (1957 quoted by Sinnott 1960) suggest that the degree of dominance is proportional to the supply of available carbohydrate and nitrogen and that competition between the various buds explains the difference in relative bud growth. They also found that high auxin concentrations limit or prevent the development of lateral vascular strands and so induce dormancy by depriving the lateral buds of nutrients.

The dominance of the terminal bud although general in woody and herbaceous plants varies in degree. In some species it extends a long way down the shoot while in others dominance is weak and lateral buds begin to grow out just below the tip and a bushy plant results.

The genus *Sophora* in New Zealand has species and varieties which exhibit all degrees of apical dominance. The *Sophora microphylla var fulvida* and *var longicarinata* plants show very little branching at all. The *Sophora microphylla* populations from Auckland and the Chatham Islands show some branching but not as much as that shown by the Bay of Islands and Canterbury plants (which showed most of all). The facts or factors responsible for this condition must be in some way connected with the production of auxin and other growth inhibitors and/or with the nutritional status of the plant.
The external factors which the experiments in this thesis indicate may be involved in the production of branches and in the subsequent divarication, are day length and dryness, with the factors of temperature and nitrogen supply (through nodulation) not definitely eliminated. It is suggested that day length (or probably more significantly) light intensity in some way affects the production of auxin or growth regulators in the apex so that the apical dominance is weakened. Sinnott (1960) says the relationship between light and auxin is not clear, sometimes light appears to destroy it, and sometimes to stimulate its production. This lack of auxin may also affect root growth (Went and other workers have shown that auxin and various natural and synthetic substances promote root formation) and in dry areas the lack of root development may lead to a xerophytic appearance.

The plants which show divarication live in an environment which includes long-days in the summer combined with, what is probably more important, a high intensity of light (because the plants grow so often in fully exposed conditions). Dryness is a factor in the area and high temperatures in summer and low temperatures in winter may also affect the internal conditions of the plant. The amount of nodulation which the plant develops may affect the nutritional balance.

As already stated photoperiod and the effect of light intensity is a factor which has been fairly extensively studied as it affects flowering but little has been done concerning other effects it may have especially on the internal con-
ditions of this plant. In addition to the work reported by Millener in the last chapter, other workers have reported the following vegetative changes which appear to be connected with photoperiod.

Garner and Allard (1923) report that as the photoperiod becomes less favorable for vegetative growth the structure of the plant becomes somewhat xerophytic, the stem tends to become more branched, underground parts to enlarge, pubescence to increase and abscission layers develop to cause leaf fall. Wareing (1956) says that as regards adaptation to habitat the primary significance of photoperiod might concern dormancy phenomena. Other workers have reported numerous other vegetative processes which appear to be affected by day-length but there appears to be no hypothesis to account for these changes. Bussell (1961) says that light may in part influence hormone production. He reports that Lockhart (1959) found that light decreases gibberillic acid synthesis in a similar way as it affects auxin synthesis and that lack of stem and leaf growth in full sunlight may be due to lack of growth substance.

As far as the factors of dryness, temperature and nitrogen supply are concerned there is also no hypothesis to explain the effects they may have on the vegetative growth of a plant. Allsop (1955) attributes heteroblastic differentiation in general to changes in the shoot apex (chiefly in size) following alteration of the water balance. Ashby (1948 b) suggests that relative xeromorphy of the upper leaves is not due to competition for water but to the influ-
ence of immature leaves which may be hormonal. Penfound (1931) found that increased water reduced xeromorphic traits, but also increased the relative amount of xylem in the stem. (this may relate to Gregory and Veale's work). The effects of temperature have produced varying vegetative results. Fisher (1954) working with Ramunculus found that at higher temperatures (20°C in the day and 15°C at night) there was a complete reversion to juvenile foliage, while at lower temperatures (10°C and 5°C) the adult form persisted. As far as nitrogen is concerned Shields and Magnum (1954) report that nitrogen content is highest in the leaves of mesophytic herbaceous species, lower in xeromorphic dicotyledons and lowest in monocotyledons with little mechanical tissue.

As before the processes which actually affect the vegetative structure are not known. In some way the influence of the external environment causes changes within the plant which produce phenotypic responses. The environment can only affect the plant within the genetically imposed limits of the plant, and until more is known of how phenotypic alteration is effected little more can be said about the factors which control divarication.
Plate 20. APICES FROM *SOPHORA MICROPHYLLA* (Canterbury).

2 months old (x 80)

1 year old (x 100)
Plate 21. APICES OF SOPHORA MICROPHYLLA (Canterbury).

2 months old (x 360)

2 months old (x 100)

2 months old (x 360)

1 year old (x 100)
6. GEOGRAPHY, ECOLOGY, AND EVOLUTION.

6.1. Introduction.

The geography, ecology, and evolution of the section Edwardsia within the genus Sophora will be discussed first in its wider aspect covering all the species involved, and then particularly with reference to New Zealand.

6.2. Section Edwardsia.

The section Edwardsia has had a varied history. It was first proposed as a genus by Salisbury (1808) to distinguish a group within the genus Sophora which was both geographically and morphologically distinct. The term was given generic rank by Hooker in 1852 but in 1856 he reverted to the original Sophora, on grounds that the 4 winged pods which had been used by Salisbury as a characteristic to separate the Edwardsia, were not found on all species within the group. Hooker said that members of the group had pods of all intermediate forms between terete, 4 angled and 4 winged. The term was not revived again until 1921 when Oliver, after examination of specimens in London Herbaria maintained the group was so distinct that it should be reinstated as a separate genus with E. chrysophylla Salis. as the genotype. However a revision of Cheeseman's flora which appeared in 1925 did not make the change and Allan (1961) has retained Sophora. Skottsberg who probably knew more about this group than any other worker, uses the generic name Sophora and distinguishes the Pacific group as sect. Edwardsia.

This group is morphologically and geographically distinct.
The morphological characters which distinguish the group are said to be 4 winged pods, short standard and exserted stamens. As has already been discussed, the 4 winged pod is not a distinguishing character as intermediates between this and the terete condition can be found. In New Zealand most of the species have pods with wings, but *Sophora prostrata* has wingless pods (see Plate 23). Examination of the *Sophora* and *Edwardsia* herbarium specimens does indicate that there are quite marked differences in the shape and position of the flower, the type of inflorescence and in the shape of the leaves. The herbarium specimens in the Museum of Natural History (London) have been annotated and in cases renamed by Tsoong in 1948, but I have been unable to find any published work on *Sophora* in English.

Geographically, the species of sect. *Edwardsia* cover a large area of the Pacific Ocean, and one species is found in the Indian Ocean and one in the Atlantic Ocean. (see Fig. 6) This group of plants has been a widely used example of transoceanic migration because it was formerly thought to show disjunct and perhaps circumpolar distribution. *Sophora tetraperta* was described as being found in New Zealand and South America (Hooker 1852) Cheeseman (1909) Andrews (1914) Oliver (1921) and consequently has been a much quoted example of phyto-geographers. But as has already been indicated in the first chapter the various species of *Sophora* around the Pacific are endemic to the island or continent on which they are found. One exception to this, *Sophora tomentosa*, (which does not fall within the sect *Edwardsia*) is a coastal species
KEY

CR - S.chrysophylla
HO - S.howinsula
MA - Maquesas sp
TE - S.tetraperta
RA - Raivavae & Rapa sp
MI - S.microphylla
PR - S.prostrata
CM - S.'chathamica'
TO - S.toromiro
FE - S.fernandeziana
MA - S.masefuerana
MC - S.macnabiana
MR - S.macrocapa
RE - Reunion sp
GO - Gough sp
Figure 6. DISTRIBUTION OF SOPHORA (sect. Edwardsia)
found on many islands of the Pacific.

Within the sect. Edwardsia *Sophora chrysophylla* is found in Hawaii, *Sophora howinsula* on Lord Howe Island, *Sophora microphylla* (and varieties), *Sophora tetraptera*, *Sophora prostrata* in New Zealand, *Sophora macrocarpa* and *Sophora macrocarpa marnabiana* from Chile, *Sophora fernandeziana*, *Sophora masafuera* from Juan Fernandez, *Sophora toromiro* from Easter Island. Gough Island has a species which is similar to *Sophora marnabiana*. Reunion Island has a species which has been given several names (*Sophora nitida*, *Sophora retusa*, *Sophora denudata*). Rapa and Raivavae in the Austral Island group have a species which is said to be like *Sophora tetraptera* (Brown 1935) Skottsberg (1956) reports species from the Marquesas and Diego Alvarez. All of these species with the exception of *Sophora macrocarpa* and *Sophora chrysophylla* were formerly described as *Sophora tetraptera*.

*Sophora tomentosa* (not sect. Edwardsia) is a common strand plant throughout Melanesia and Polynesia. It reaches as far south as Australia but does not occur in New Zealand. Guillaumin (1936, 1948) reports *Sophora tomentosa*, and *Sophora tetraptera* from New Caledonia. This is the only report of *Sophora tetraptera* from this region and unfortunately the reports do not include a description.

Most of these plants occupy similar habitats; dry open places, forest margins, beside rivers and on the shore. The exception to this is *Sophora chrysophylla* in Hawaii which is an inland tree, found usually in the forest of mountainous regions. The majority of these species are trees, the except-
ions are *Sophora prostrata* of New Zealand and the species on Juan Fernandez which can become shrub-like in exposed conditions, but which are normally small trees. There are no reports of habit heteroblastism, except from New Zealand. Guppy (1906) remarks on a *Sophora* tree which becomes very bushy when it descends to the beach, in Chile.

In view of the large number of tropical and warm temperate species of the *Sophora* it seems reasonable to postulate a tropical origin for the genus. This is Andrew's (1914) view following his postulation of a tropical origin for the Leguminosae. Andrews says that the (section) *Edwardsia* appears to have entered New Zealand from the north there establishing itself firmly, changing from a warmth-loving type to one flourishing in cold localities. He suggests that it arrived from the north-west (before the Papilionaceae were highly differentiated) by land connections between New Zealand and the warmer continents. The presence of a species of the *Edwardsia* sub-section on Lord Howe Island and reported presence of *Sophora tetraperta* in New Caledonia help to confirm this view. Oliver (1925) suggests *Sophora* may have arrived from the north by land connections and currents and from New Zealand been carried by the sea to South America and to Juan Fernandez. Cheeseman (1909) states *Sophora tetraperta*, the pods of which are adapted for floating, has doubtless been carried from New Zealand to Chile and Juan Fernandez. Guppy (1906) tested his theories about the distribution of this species by floating pods and seeds in water to record the
length of time which they remained buoyant. He found that
the pods of most species would float for about two weeks but
most (*Sophora chrysophylla* seeds did not float) of the seeds
would remain afloat for indefinite periods and would germin-
ate after removal from the water. He therefore suggested
that the *Sophora* was carried from New Zealand by the West
Wind Drift to South America and from there is spread North-
wards along the coast of South America (he reports finding
seeds in the beach drift at San Vincente 200 miles north of
Chile) from where it spread to Hawaii by currents. In Hawaii
it underwent specific differentiation and an inland mount-
ainous plant resulted which had non-buoyant seeds.

Andrews (1939) in reply to opposition to long-distance
dispersal brought forward several reasons why it was more
feasible to postulate long distance dispersal than land brid-
ges. He pointed out that the currents round the Pacific were
favourable to the spread of plants as seen and suggested that
the solitary highly speciated forms seen especially on Hawaii
were evidence of "waifs", and long periods of isolation.
The lack of gymnosperms on Hawaii was also evidence of lack
of land connection.

Skottsberg has always been an opponent of long-distance
dispersal and points out that Andrew’s currents are not al-
ways satisfactory to explain distribution. He also asks if
long-distance dispersal is a fact, why is it not now continu-
ing to reduce the number of endemic species on these islands.
He postulates an Antarctic origin for a large number of spec-
ies and from there migration north-east and north-west via land bridges.

The arguments between plant geographers are not over, and until further evidence from geology and palaeobotany is produced neither side which appear so diametrically opposed can be judged right.

Perhaps the origin of this group was in the temperate regions to the north of the equator; Andrews (1914) suggests a home in the old world tropics, but the presence of a species from Afghanistan of which there is a specimen in the Natural History Museum which appears to be of the section Edwardsia, and the large development of the genus in Asia suggests that this may be a more natural home. From its centre of origin a large-leaved form migrated south east through land bridges to the north of New Zealand, not entering Australia. (the form on Lord Howe Island is large leaved). In New Zealand the species differentiated during the Tertiary era. From New Zealand possibly via Antarctica (absence of the Sophora species on the sub-antarctic islands queries this) a migration of a smaller leaved form to South America, thence to the islands in the Pacific and Gough in the Atlantic and finally perhaps to Hawaii. Regional differentiation produced specific differences such as wingless pods, (see Plate 23) and differences in shape and size of seeds (Plate 24), (the seeds of the Chatham Island plant are similar to those illustrated by Skottsberg (1956) from Sophora macrantha and the seeds of Sophora toromiro resemble the seeds of Sophora.
microphylla var longicarinata) as well as differences in habit, leaf-shape and habitat. An alternative route to Hawaii could have been from the north of New Zealand, while the main migration was proceeding southwards, through landbridges which Campbell (1933) says may have connected Hawaii more or less directly with the Australian and Malayan region, and which broke up in the early Tertiary. Certainly the leaf morphology and the general appearance of the plant is more "tetraperta" than "microphylla". The species on Reunion could have migrated south-west instead of south-east during the original migration. The difficulty is that it is a "microphylla" type.

While this suggested migration pattern raises problems such as a migration through the tropics of a temperate species, it does not postulate a double migration south then north as would be the case if the species differentiated as part of the Antarcto-Tertiary element that Skottsberg suggests.

Although Sophora has been traditionally included within the New Zealand element in the South American flora it seems as if it should be included as a special case. The New Zealand species all have buoyant seeds with the capacity for long periods of immersion without injury and most of them are shore plants or grow by rivers. Therefore to include this species as part of New Zealand element in the South American flora is to include a species which, unlike many other species in the element, is well able to be dispersed, and thus
Plate 24. SEEDS OF VARIOUS *SOPHORA* SPECIES.

<table>
<thead>
<tr>
<th>Location</th>
<th>Seeds</th>
</tr>
</thead>
<tbody>
<tr>
<td>Pinpa</td>
<td></td>
</tr>
<tr>
<td>Canty</td>
<td></td>
</tr>
<tr>
<td>Chatham Is.</td>
<td></td>
</tr>
<tr>
<td>Nelson</td>
<td></td>
</tr>
<tr>
<td>Bay of Islands</td>
<td></td>
</tr>
<tr>
<td>Titirangi</td>
<td></td>
</tr>
</tbody>
</table>

3 months old

6 months old

1 year old
forms of the East Coast. The large leaved plants in the Bay of Islands may be connected with the large leaved *Sophora homologa* from Lord Howe Island and with the *Sophora tetrapetala* of the East coast. *Sophora prostrata* is found in a limited area east of the main divide of the South Island. The Chatham Island plant grows on one island of the Chathams two hundred miles east of Canterbury.

Most of these plants grow in similar habitats, dry open places, outskirts of bush, beside rivers, or on sea cliffs. The Chatham Island plants are reported to grow only on a limestone area on the island. The driest habitat is in the Canterbury province east of the main divide; the wettest places, the Auckland province and the Chatham Islands.

Cockayne (1911) was the first worker to attempt to explain the reason for the divaricate shrub within New Zealand. There are about 39 shrubs with divaricate habit and 11 trees with a marked shrubby juvenile stage, some of which belong to the same genera as the divaricate shrub (*Plagianthus, Sophora, Pittosporum*). Cockayne regarded the divaricate form as an adaptation to environment, but to a past environment. He suggested that there were forms in the Tertiary which lacked the divaricating juvenile (*Sophora tetrapetala*) and where the climate was wet enough these forms remained (Auckland, Chatham Islands). He regarded the divaricate shrub as having arisen on the east of the South Alps as an ephapharmonic adaptation to the dry Steppe climate of the Pleistocene. With the return of milder conditions the
adult plants resumed their normal form but the divaricate habit was impressed on the life history and thus *Sophora microphylla* was developed. In *Sophora prostrata* the stimulus was more deeply seated and so a hereditary form was developed. In 1928 (after the advent of genetics) he wrote, "the tendency to both xerophytic and mesophytic forms latent in the plant and one or other will appear as soon as the necessary intensity of stimulus is reached. Until that is the case, whichever form is the more hereditary is the more strongly fixed, will persist, even though far from being ephemamonic". (p. 26)

Cockayne because he could not see radical differences in the present day climate between New Zealand and the rest of the world which could account for divarication thus tried to explain it in terms of response to a past environment and by doing so committed himself to the view of "recapitulation of phylogeny in ontogeny", and to the idea that there was some deep-seated stimulus which caused hereditary forms to develop. As far as deep-seated stimuli are concerned he may not be far wrong except in the terms in which he describes it. If certain environmental conditions cause phenotypic alterations by unknown stimuli and if by variation and mutation plants develop which have these phenotypic changes impressed on the genotype then natural selection will enable a genetic race to develop which is adapted to its environment. But it is more likely to be adapted to a present environment than a past one and thus Cockayne's explanation of elaborate and
unlikely changes is unnecessary.

Bulmer (1958) also doubts whether Cockayne's elaborate explanation is necessary and she suggests that the strong winds experienced in the typical habitat of divaricate shrubs may cause conditions which approach the continental "steppe" climate.

Another to question Cockayne's hypothesis, in fact to reopen the whole discussion, was Wardle in 1963. He suggests that the divaricating small-leaved juvenile forms are adaptations to still existing fairly dry forest environments, and the development of mesomorphic adult forms is the result of the development of large and more efficient root systems. Thus the evolutionary species is from the tree without habit-heteroblastism, to the tree with a divaricate juvenile to the divaricate shrub which develops through an increase in neotony.

This theory of Wardle's seems an eminently reasonable solution which is confirmed by evidence presented in this thesis; that dryness and day-length bring a phenotypic response which results in more divarication, and that genotypic populations have developed in areas where the environment is dry (Canterbury Sophora prostrata, Sophora microphylla Bay of Islands) and where the plants are from a shaded or damp habitat there is little divarication (Sophora microphylla from Auckland and the Chatham Islands). It seems highly likely that these populations are adapted to a present environment.

It is questionable whether the development of a larger,
deeper, and more efficient root system is sufficient to provide the necessary stimulus for the plant to grow out of its juvenile habit. As has been shown, differing degrees of dryness can affect the divarication pattern. Thus it should follow from Wardle's suggestion, that where the plant has been able to get an abundant supply of water (e.g. under cultivated conditions) then there should be no divarication and the tree should show no xerophytic traits. But the divarication in the Canterbury population is still marked even under wet conditions, so in some way the genotype has become fixed and requires more than a change in water balance to cause a change from juvenile to adult. There may however, be some connection between the spread of the root system postulated by Wardle and the correlation between auxin and the growth of roots mentioned in the last chapter. To check this factor plants were dug up and their root systems examined. Plants of three months, six months and a year which had been growing outside in dry conditions in Canterbury were used. The results (see Plate 25) were inconclusive; on the whole there was little difference between the spread of roots in the divaricate and non-divaricate populations, and in some cases the development of roots in the Canterbury plants was greater.

The mesophytic stage which is briefly seen in the first few leaves of the Canterbury plants (see Plate 11) was explained by Cockayne as being suited to shelter by ground plants. It is more likely to be due to the plant not being fully established and still obtaining nourishment from the cotyledons. The second xerophytic stage which Cockayne felt
had been impressed on the life-history by adaptation to a past environment, is probably an adaptation to a present environment which is somewhat dry. Many of the divaricating shrubs which are found in New Zealand are found in the drier areas, eg. *Pittosporum divaricatum* - forest margins and sub-alpine scrub, *Plagianthus divaricatus* - usually inhabits coastal regions and salt swamps. *Disarla toumatou* - open rocky places. The trees with divaricating juveniles are trees mainly of forest margins and scrub, though some are found in truly forest conditions. The advantages of the divaricate habit in the open dry areas are apparently connected with xerophytic modifications but what advantage the habit can have within the sheltered environment of a forest is not known.

The adult tree which develops after an indeterminate period of divarication grows straight and tall, only reverting to the juvenile condition on very low branches or off-shoots.

The problem of the divaricate habit lies not only in how it developed, how it develops and why, but also why the tree grows from its juvenile divarication into an adult tree. The relatively sudden change in foliage and in wood structure (Rumball 1961) must reflect some physiological change.

The theory that light in some way affects the concentration of growth substances and thus affects the morphology of the plant is not sufficient explanation and the water factor appears to be connected in some way. Wardle's theory about the spread of the root system may be part of the answer. These external conditions are reflected by changes
within the plant.

Ashby (1948b, 1950a) presents evidence that the changes in leaf shape of Ipomoea are not primarily due to environmental factors (although such are operative) but to alteration of inner conditions. Whyte (1939) and Krenke (1940) suggest a theory of phasic development, postulating that changes of morphology are due to the physiological age of the plant, as contrasted with its age in time. Schaffalitzky de Muckadell (1959) suggests that the existence of developmental stages and occurrence of meristematic ageing should be regarded as two modes of expression for the same phenomena. He concludes that the ageing of the apical meristem is very common and probably universal in the woody plants. However, this theory, which is probably the most satisfactory of all theories proposed to account for differentiation, does not explain how the meristematic ageing is effected - whether it is part of the genetic pattern or whether it is controlled by internal or external factors. It appears that growth substances may be important, as may the nutritional status of the plant. As already stated how external conditions may affect these substances is not known. A series of experiments over a number of years using different environmental conditions could indicate whether or not external conditions can effect an earlier or later development of adult growth.

Why the divaricate habit should have developed solely in New Zealand is still not known. If Cockayne's theory of adaptation to a past environment is rejected then some factor or factors must be found in the present environment to account
for the presence of this habit.

New Zealand because of its relief, position and shape is characterised by a large number of regional climates. These climates often have a marked effect on plant growth and form and have formed the basis for a sub-division of New Zealand into provinces and districts. Cockayne (1928) Zotov (1938) has suggested modifications based on temperature and rainfall, and it is interesting to note that the various species and varieties of *Sophora* fall into Zotov's districts. Canterbury, east of the main divide is the home of the two species showing marked divarication in the *Sophora* and also the home of many other divaricate species. The climate of this region is the driest in New Zealand (under 25" in most of Canterbury and Central Otago) and the "northwesters" cause pronounced Fohn effects. The average range of temperature is between 17°-19°F. Whether these climatic conditions by themselves are enough to cause the distinct divaricate habit to evolve is doubtful, but combined with the fact that the typical flora of this climate elsewhere in the world (deciduous trees and annuals) is absent in New Zealand, may have caused the selection of the divaricate form to fill a vacant ecological niche. This is assuming that the dry climate has been present long enough to allow this to happen. Thus Cockayne's hypothesis that these forms rose as a response to a dry Pleistocene may be correct, but instead of adapting to the Pleistocene era the plants are adapted to a fairly dry continental-type climate which still exists. When geological evidence can indicate the time of appearance of the divaricate forms,
and give more information on the type of climate, then
more satisfactory theories can be developed.

If New Zealand is the centre of origin of the Sophora
species elsewhere in the Pacific it is likely that the spread
of species occurred in the Tertiary before the distinctive
divaricating habit was evolved. The Sophora species of Chile
and Juan Fernandez have a tendency to become bushy and scrub-
by (see page 44) but there is no report of divarication thus it
would appear to be more closely related to the Chatham Island
and Auckland plants than the Canterbury plants.

The whole problem of the evolution of the divaricate
shrub is part of a larger problem of juvenile-adult relation-
ship which in turn is only one aspect of the problem of
biological organization. As biochemists and biophysicists
discover more about organization and correlation so more
will be discovered about the nature of the divaricate shrubs.
7. IMPLICATIONS OF THE STUDY.

This study has extended the knowledge of one of the divaricate species in New Zealand, but it has also raised and left unanswered a number of problems.

It has confirmed the observation that a wide range of habit-heteroblastism exists between populations growing in different parts of New Zealand, but has also discovered that though some of these differences are phenotypic yet others have resulted in populations with genetic variations. It appears that the amount of divarication is affected by environmental conditions and although it is not possible of course to postulate one factor acting by itself it appears that the factors most concerned with divaricate response are light (light intensity and possibly length of light period) and dryness.

These factors appear to be responsible for the swift and sometimes intense phenotypic response in the form of divarication. This was a factor noted by Cockayne in 1911. However not only is there a phenotypic response but also there has been the development of genotypic populations which show varying degrees of inherited divarication. How these have developed is not easy to explain. If environmental conditions have acted to select a population then how this was effected must be explained, as well as why these forms developed.

It has been suggested that the divaricate habit might be influenced by the seemingly early development of the lateral buds, and perhaps in the phenotypic populations the environment acts on a growth substance and so early development of the laterals is effected. In the genotypic population perhaps
this early development of the lateral buds is fixed in the gene structure, and thus divarication is caused. However it has been noted that even in the genetic races the divarication pattern can be altered by altering various environmental factors, so in some way these factors are acting directly on the internal conditions in the plant causing changes which result in more divarication. The mechanism of these factors acting on the internal environment of the plant and the way the changes are effected is not known, but it is suggested that growth substances are probably involved.

Various theories have been discussed which seek to try and explain why this habit is prevalent in New Zealand, and it is likely that Wardle's theory of adaptation to a present environment is more substantially correct than Cockayne's hypothesis of adaptation to a past environment. But why this habit should have developed in New Zealand alone is still not sufficiently explained. Perhaps it was adapted to a past more rigorous climate and the forms today remain adapted to a dry environment, a high light factor, and a region where strong winds are common. The advantages of this type of habit in the climate described are obvious.

It is suggested that the Sophora in New Zealand evolved from a large-leaved non-divaricating ancestor which arrived from the north-west. Within New Zealand regional differentiation occurred leading to the evolution of new species and varieties, in the drier areas, first a species with a divaricating xerophytic juvenile, then by an entirely new species adapted for living in very dry and exposed areas. It is
postulated that the further distribution of Sophora to South America and the Pacific took place before these divaricate forms developed, because even in exposed conditions there are no reports of divarication in other species.

How the divaricate plant grows out of its divarication is not known, but it is probably part of the overall problem of juvenile-adult balance which might be best explained in terms of meristematic ageing.

Some taxonomic problems have been raised as by-products of this study. Firstly, as regards the section Edwardsia, there seems to be a case for its re-examination for claims to generic rank. Secondly, within New Zealand although the two named varieties of Sophora microphylla are distinct, there are other populations from the Bay of Islands and the Chatham Islands which need taxonomic study. Also a careful study of distribution of the species in New Zealand would help to clarify the evolutionary and taxonomic picture.

The problems raised are mainly fundamental problems of biology, the problems of correlation, differentiation and organization. Other difficulties which were raised and not answered lie in the fields of palaeobotany and plant geography and the solving of these problems is mainly a matter of time.

The author recognizes the limitations of this study, especially in regard to control of environmental conditions and the unconfirmed work on the apex. Perhaps work on other divaricate species along similar lines will substantiate these results.
SUMMARY.

1. A wide range of habit-heteroblastism exists between populations. Within the **Sophora microphylla** group it ranges from little or no divarication in the Auckland and Chatham Island plants, to a noticeable divarication in the North Auckland plants to strong divarication in the Canterbury plants.

2. Seedling populations from different sources display genetic variation.

3. The amount of divarication within any one population varies with different environmental factors. It appears that increase of light and dryness causes increase of divarication.

4. The physical cause of divarication may be the early development of lateral branches which, it is suggested, is in some way affected by growth substances produced by the apex, which in turn is affected by a genetic factor and/or by external factors.

5. The presence of the divaricate habit in the New Zealand flora is not an adaptation to a past environment, but is an adaptation to a present climate which approaches the continental climate in certain areas.

6. Geographically, **Sophora** (sect. Edwardsia) appears to have developed in Asia, spread to New Zealand and from there to South America, before the divaricate habit was evolved.

7. Taxonomically there seems to be a case for further study of the Bay of Island and Chatham Island plants. The varieties fulvida and longicarinata are distinct.
APPENDIX I.

In a series of papers since 1937, Briggs and co-workers have published the results of investigations into the chemical composition of the seeds of various *Sophora* species. Probably the brilliant yellow stain which the testa deposits (mentioned in Chapter 3) is part of the chemicals concerned. Whether or not they are germination inhibitors is not known.

They discovered that *Sophora microphylla*, *Sophora tetraperta* and *Sophora chrysophylla* (Hawaii) have a similar chemical constituents, including a new base which was named sophocystine. *Sophora "chathamica"* had similar chemical constituents but in different proportions, and Briggs remarks that the chemical evidence is not sufficient to separate *Sophora "chathamica"* from *Sophora microphylla*. The most interesting analysis was given by the seeds which Briggs described as *Sophora fulvida* (now *Sophora microphylla var. fulvida*). These had some chemicals in common with the other four but were entirely lacking in sophocystine which the others all had in varying amounts.

While chemical evidence itself is not sufficient to separate species, combined with morphological taxonomical and geographical studies it is a valuable ally.
APPENDIX II. Approximate day lengths from sunrise to sunset in hours and minutes, as at the first of each month.

<table>
<thead>
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<th>Jan</th>
<th>Feb</th>
<th>Mar</th>
<th>Apr</th>
<th>May</th>
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<th>Jul</th>
<th>Aug</th>
<th>Sep</th>
<th>Oct</th>
<th>Nov</th>
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<td>15.02</td>
<td>13.06</td>
<td>12.21</td>
<td>10.12</td>
<td>9.59</td>
<td>9.07</td>
<td>10.03</td>
<td>12.00</td>
<td>13.30</td>
<td>14.27</td>
<td>15.58</td>
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<td>Auckland</td>
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