THE FOREST FLORA OF CANTERBURY: ECOLOGICAL INFERENCES

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Species lists have been collected for forested and related scrubland areas throughout Canterbury. The total number of species involved is about 350. The patterns of distributions reflect the influence of one or a combination of several of the following factors:

1. The Pleistocene glaciation and subsequent climate amelioration.
2. The differential migration potential and length of life of beech trees and podocarp/hardwood species.
3. Climate deterioration within the last millenium.
4. Widespread fires from 500 to 800 years ago.
5. The existing climate, especially effective rainfall, with relation to topography and degree of exposure.
6. The advent of Europeans. Felling and burning. The effects of grazing animals.

Distribution patterns influenced by the post-Pleistocene mild climate are found in the presence of mosaics of podocarp and broadleaved hardwood tree species and their associated herbs, vines, shrubs and ferns throughout lowland Canterbury. These include:

PTERIDOPHYTES.

Mecodium sanguinolentum, **M. rarum*, †*M. villosum*, *M. flabellatum*, **M. flexuosum*, **Meryngium multifidum*, **Hymenophyllum peltatum*, *Polyphlebium venosum*, *Cyathea dealbata*, *C. smithii*, *Dicksonia squarrosa*, *Adiantum affine*, *Hypolepis tenuifolia*. †*H. millefolium*, *Pellaea rotundifolia*, **Paesia scaberula*, **Histiopteris incisa*, *Blechnum patersoni*, *B. discolor*, †*B. lanceolatum*, **B. procerum*, †*B. fluviatile*, **B. vulcanicum*, **Asplenium hookerianum*, *A. bulbiferum*, **A. colensoi*, **A richardi*, †*A. flaccidum*, *A. lucidum* var. *lyallii*, *Cyclosorus pennigera*, **Sticherus cunninghamii*, **Leptopteris hymenophylloides*, *Ctenopteris grammitidis*, **Microsorium diversifolium*, †*Polystichum vestitum*, *P. richardi*, *Ctenitis glabella*, *Pyrrosia serpens*, †*Lycopodium varium*, **L. volubile*, **L. scariosum*, *Tmesipteris tannensis*.

HERBS.

**Microlaena avenacea*, †*Danthonia cunninghamii*, **Gahnia pauciflora*, †*Uncinia uncinata*, *Astelia nervosa*, *Arthropodium candidum*, *Libertia ixioides*, *Dianella intermedia*, *Earina mucronata*, **Pterostylis banksii*, †*Corybas triloba*, **Gastrodia cunninghamii*, †*Urtica incisa*, *Australina pusilla*, *Chenopodium triandrum*, †*Ranunculus hirtus*, *Acaena novae-zealandiae*, **A. fissistipula*, *Linum monogynum*, *Haloragis erecta*, *Hydrocotyle moschata*, *Angelica geniculata*, †*Stellaria parviflora*, **Nertera setulosa*, *N. dichondraefolia*, †*N. depressa*, **Galium umbrosum*, **Wahlenbergia gracilis*, †*Lagenophora petiolata*, **Erechtites prenanthoides*.

VINES.

Rhipogonum scandens, **Muehlenbeckia australis*, **Clematis indivisa*, **C. forsteri*, **C. marata*, **Rubus cissioides*, *R. schmidelioides*, †*R. squarrosus*, *Metrosideros diffusa*, *Parsonsia heterophylla*, †*P. capsularis*, *Calystegia tuguriorum*.

PARASITES.

Loranthus micranthus, **Tupeia antarctica*, *Korthalsella lindsayi*.

SHRUBS.

Drimys colorata, †*Pittosporum divaricatum*, *Melicope simplex*, *Coriaria arborea*, †*Aristotelia fruticosa*, **Leptospermum ericoides*, *Myrtus obcordata*, †*M. pedunculata*, *Fuchsia colensoi*, †*Gaultheria antipoda*, **Cyathodes acerosa*, *Leucopogon fasciculatus*, †*Suttonia divaricata*, *Teucidium parvifolium*, *Solanum aviculare*, †*Hebe salicifolia*, **H. traversii*, **Coprosma lucida*, *C. robusta*, *C. rotundifolia*, *C. areolata*, **C. rhamnoides*, *C. rigida*, *C. virescens*, †*C. linariifolia*, †*Olearia arborescens*, †*O. avicenniaefolia*, *O. forsteri*, *O. fragrantissima*, **O. lineata*, *Helichrysum glomeratum*, *Notospartium torulosum*.

TREES.

Dacrydium cupressinum, *Podocarpus totara*, *P. spicatus*, *P. dacrydioides*, *Paratrophis microphylla*, †*Carpodetus serratus*, †*Pittosporum tenuifolium*, *P. eugenioides*, †*Sophora microphylla*, *Pennantia corymbosa*, **Aristotelia serrata*, **Elaeocarpus hookerianus*, *E. dentatus*, *Plagianthus betulinus*, *Hoheria angustifolia*, *Melicytus ramiflorus*, *M. micranthus*, **Fuchsia excorticata*, *Nothopanax arboreum*, *N. anomalum*, **Schefflera digitata*, †*Pseudopanax crassifolium*, †*Griselinia littoralis*, **Metrosideros umbellata*, *Nothofagus solandri sensu strictu*.

Numbers of these are also found usually between 1000 and 2500 ft. in upland Canterbury, accompanying beech forest in the basins of the large rivers. (These are indicated by an asterisk on the previous list.) Their distributions here often link with those in true lowland and foothill areas.

Other species form on upland facies of podocarp broadleaved forest, with *Libocedrus bidwillii* and *Podocarpus hallii* the dominants, growing in the heads of Rakaia and Rangitata tributaries between 2000 and 3500 ft. There are indications that the same type of forest was once well developed at high levels on Banks Peninsula, Seaward Kaikoura Range, Alford Forest and Mt. Hutt, Mt. Peel, Hunter Hills, in upper Waimakariri tributaries and widely in Tasman River, Godley River and other McKenzie country sites. The forest grades into a distinctive scrub community but many of the shrub species grow in the forest proper and attain the size of trees. Species include numbers of those already listed (marked with a dagger in the previous list) with important exceptions.

Additional species found here (many of them also in beech forest or scrub at high levels not near valley heads — marked with an asterisk) are:

FERNS.

Apteropteris malingii, **Cyathea colensoi*, **Blechnum minus*, **Asplenium trichomanes*.

HERBS.

**Astelia cockaynei*, **Enargea parviflora*, **Myosotis forsteri*, **Viola filicaulis*.

SHRUBS.

**Podocarpus nivalis*, **Phormium colensoi*, **Olearia haastii*, **O. cymbifolia*, **O. nummularifolia*, *O. colensoi*, *O. lacunosa*, *O. ilicifolia*, **Senecio bidwillii*, *S. eleagnifolius*, **S. cassinioides*, **Cassinia vauvilliersi*, **Coprosma banksii*, **C. pseudocuneata*, **C. foetidissima*, **C. colensoi*, **C. rugosa*, *C. ciliata*, **Dracophyllum longifolium*, **Hebe vernicosa*, **Nothopanax colensoi*, *Archeria traversii*.

TREES.

Dacrydium biforme, *Libocedrus bidwillii*, **Podocarpus hallii*, **Phyllocladus alpinus*, *Dracophyllum traversii*, *Nothopanax simplex*, *Hoheria glabrata*.

It will be noted that this is very similar to the forests of upper levels in Westland.

Almost the sole species in beech forest in much of Canterbury is *Nothofagus solandri* var. *cliffortioides*. The broad patterns of distribution of it and the other species *N. fusca* and *N. menziesii* are, as shown by Holloway (1954), partly determined by their differential migration rate and longevity compared with podocarp and other species, superimposed on the ancient distribution pattern after the retreat of ice from the glaciated valleys, together with effects of climate change and ancient fires. *N. fusca* appears to have contracted its area, being present only in the northern part of Canterbury with scattered outliers. *N. menziesii* and *N. cliffortioides* are found in the south and accompany *N. fusca* in the north-west. *N. menziesii* also appears to have had its area reduced as is shown by its spot distributions. This process may have occurred in part during the post-glacial optimum.

The recent deterioration in climate (Raeside 1948, Holloway 1954 and others) has resulted in reduction of members of both podocarp-broadleaved forest and beech forest to relict status in many places in Canterbury. Disjunct distributions show that these species have once been more widely and continuously distributed. The long lived *Podocarpus spicatus*, *P. dacrydioides*, *P. totara* and *Dacrydium cupressinum* are now relict throughout. *Weinmannia racemosa*, and *Melicytus lanceolatus*, extreme disjuncts, must be regarded as relict. It is probable also that species such as *Elaeocarpus dentatus*, *Plagianthus betulinus*, *Olearia lineata*, *Hebe cupressoides*, *Metrosideros umbellata*, *Rumohra hispida*, *Microlaena polynoda*, *Lindsaea cuneata* and *Gahnia pauciflora*, though able to regenerate in some places, are in general in the same state.

Beech forest has been enabled to expand at the expense of podocarp-broadleaved forest partly because of the decline in climate. Patterns of invasion by mountain beech are present in Waimakariri, Rangitata and Rakaia valleys and on the foothills. Species found normally in intact podocarp-type forest (e.g. *Carpodetus seratus*, *Nothopanax anomalum*, *Elaeocarpus hookerianus*, *Podocarpus hallii*, *Cyathea colensoi*, *Blechnum vulcanicum*, *Metrosideros umbellata*, *Myrtus pedunculata*) are found widely scattered in otherwise pure mountain beech forest. Sometimes several such species exist as an island in a sea of beech. In areas where (in rain shadow zones from both north-west and south-west rain) rainfall has become deficient, even the hardy mountain beech has failed and forest is now fragmentary or missing. This applies to a strip from the middle Clarence River through Lake Coleridge to the middle Rangitata in a line parallel to the main divide.

The main feature of the climatic change in Canterbury within the last thousand years has been a decline in rainfall of at least 20 in. Since existing lowland forest needs at least 40 in. of rain and it is known that forest formerly existed on areas now with 25 to 30 in., a further 20 in. of rain would bring these areas back to forest climate conditions (for New Zealand podocarp-broadleaved forest). This assumption is based also on the presence of fossil podsol soils in the eastern part of the Waimakariri, Waiau-uha and Rakaia catchments. The rainfall here is 40 to 50 in. and presumably podsols form on steep slopes only where rainfall is from 70 to 100 in. The degeneration of the forest has probably not been controlled chiefly by a decline in temperature, since lowland and beech forest now exist under heavy rainfall in colder climates than those in Canterbury where the forest has failed. However, a change in temperature has probably had some effect.

The ancient fires have caused complete removal of both podocarp-broadleaved and beech forests from very wide areas in Canterbury. The evidence of fallen logs, buried charcoal, other soil traces, and windfall dimpling are so widespread in Canterbury that it is certain that forest existed throughout on all land up to a treeline of about 4000 to 4500 ft. except on a few relatively small areas where rainfall was deficient, on the plains, in the McKenzie country, Hakataramea Valley, Rangitata and Rakaia Valleys, and lower Hurunui basin. This forest remained until from 500 to 1000 years ago. The distribution patterns produced by this, superimposed on patterns due to other causes are extremely complex. A few of them may be mentioned. One is the presence of an isolated tree or other plant, e.g. *Griselinia littoralis, Danthonia cunninghamii, Senecio cassinioides, Sophora microphylla, Pittosporum tenuifolium,* remote from any forest or others of its kind. Another is the development of a patch containing a few of one species, remote from any others, e.g. *Podocarpus hallii* (often surrounded by a field of large boulders), *Leptospermum ericoides, Olearia forsteri, Nothopanax arboreum, Nothofagus solandri* var. *cliffortioides.* A third involves the presence of a number of so-called scrub hardwoods, e.g. *Griselinia littoralis, Fuchsia excorticata, Melicytus ramiflorus, Nothopanax arboreum,* forming a small patch, with some ferns and shrubs underneath, in a sheltered gully. On the whole, these are the commonest tree species of the lowland forest. The ground or forest edge flora of the podocarp-broadleaved forest is often represented where forest proper no longer exists. Species such as *Blechnum lanceolatum, Asplenium flaccidum, Adiantum affine, Libertia ixioides, Urtica incisa, Haloragis erecta, Acaena novae-zealandiae, Angelica geniculata* and *Pellaea rotundifolia* are found now where a suitable microclimate is maintained under scrub or among rocks and in gorges.

A number of more complex patterns exist. In many places there is evidence that fire removed podocarps from a site, which was revegetated by the second forest tier or by combinations of the scrub hardwoods. Large areas of this type, with *Melicytus ramiflorus, Nothopanax arboreum, Griselinia littoralis, Suttonia australis* as the commonest tree species, are present in the Hunter Hills and elsewhere in the foothills. The podocarps may have died out or never have been present in some places where similar conditions exist. In the upland forests of the Rakaia and Rangitata Valleys the presence of dense pure stands of tall *Phyllocladus alpinus, Dracophyllum longifolium* and *Hoheria glabrata* are probably of this type. In some of the sites where the emergent podocarps are missing or scarce, the understorey has degenerated further until only a dense shrubbery of low trees and vines such as *Muehlenbeckia australis, Senecio sciadophilus, Calystegia tuguriorum* and *Rubus squarrosus* are present.

An interesting variant is the relatively small area of forest which contains large numbers of one or more species which are scarce in other similar areas of bush or in the podocarp-broadleaved forest as a whole.

I presume that this situation is due to the fortuitous isolation of these species in favourable sites where competition is not too great. Large populations of these species may then develop. They include *Alectryon excelsum, Paratrophis microphylla, Australina pusilla, Senecio sciadophilus, Melicytus micranthus, Myrtus obcordata, Ctenitis glabella, Coprosma rigida, C. areolata.*

The disjunction of so many species in Canterbury forests is probably also due in part to the effects of fire. Chance isolations produce situations where a species is present in the Upper Rakaia, on Banks Peninsula and Hunter Hills, or other species may be missing from one of these while present elsewhere. It is only by comparing distributions of *all* species that the ancient forest may be reconstructed.

Some invasion patterns following ancient fires may also be traced. One such was an area where pure stands of *Leptospermum ericoides* had developed after fire and were then invaded by *Metrosideros umbellata.* The invasion of *Dracophyllum* scrub by mountain beech is also noteworthy. It is important to remember that except for the podocarps and some other species, most forest species could have replaced themselves (some of them many times) in the period since the last of the major fires about 500 years ago. However, the areas of lowland type bush are confined to broken country, gullies and shady faces where extensive fire could have missed them. These are also the places of most favourable microclimate.

Distribution of soil types parallels the climatic controls, but there are some anomalies. Lewis podsolised soils near the main divide, Bealey weakly podsolised and Tekoa slightly leached soils (the latter in the central rain shadow area) form bands in succession east from the divide. On the foothills is the Hurunui soil, transitional between yellow-brown and yellow-grey earths and formed mainly under podocarp forest. Beech forest now occupies much of the same area in North Canterbury. Wherever yellow-brown earths and even some yellow-grey earths are formed below tree-line, forest probably once grew in Canterbury. It seems certain that types such as Cass and Haldon soils are degraded forest soils which have held grassland for a long period. Similarly with many of the plains and lowlands soils, e.g. Claremont and Timaru soils (Raeside 1949). Others are just as obviously soils which have only recently had forest removed: they include areas of Hurunui, Tekoa and Bealey soils. It is probable from this that contraction of forest has occurred over a long period, in many stages. The Katrine podsol is somewhat anomalous in its position in the central parts of watersheds. It is developed on rolling country and the rainfall is not especially high. I think that these represent the sites of former lowland-type podocarp-broadleaved forests. This supposition is heightened by the presence of species such as *Leptospermum ericoides* and other lowland forest associates in these areas.

Although all the above factors have contributed to the distribution of individual species and forest types, the podocarp, broadleaved and beech species are distributed where the climate (especially the effective summer rainfall) is now most suitable. For lowland podocarp forest this is in areas of 40 in. of rain or more and on south or east facing slopes or in moist ravines, chiefly on the downs and foothills. It is noticeable that there are few epiphytic species except bryophytes. *Lycopodium varium, Asplenium flaccidum* and *Earina mucronata* are about the only vascular ones. It is probable, because of this, that the climate is marginal for the lowland forest. Local very suitable places within the forest exist, however, and the vegetation becomes richer with moisture-loving ferns.

Mountain beech with its attendant species, *Chiloglottis cornuta, Phyllocladus alpinus, Elytranthe tetrapetala, Hoheria lyallii, Lagenophora pinnatifida, Gaultheria antipoda, Cyathodes acerosa, Coprosma microcarpa* and *Podocarpus nivalis,* is in equilibrium with climate in areas where rainfall also is 40 in. or over, but at higher altitudes and on more rigorous sites. Temperatures are lower and the number of frosts is greater.

The high rainfall (100 in. or more) of the valley heads near the main divide supports scrub and forest which is vigorous, although in some sites *Libocedrus* and *Podocarpus hallii* may occupy the same relict position as do the podocarps of lowland forest. In the extreme north-west silver and red beech are also regenerating vigorously.

The maritime climate of Banks Peninsula and the Kaikoura coast allows a number of species to be present which are absent elsewhere in Canterbury. Some of these are otherwise found only in the extreme north of the South Island or in the North Island. They are listed by Laing (1919) and Martin (1920) and will not be discussed further. The number of screen frosts (about 50) is low here, and the rainfall of 40 to 60 in. is relatively high.

The Europeans felled and burned extensive areas of forest, especially on Banks Peninsula, the coastal lowlands near Christchurch, at Waimate, Geraldine, Alford Forest, Kowai Bush, Oxford, Mt. Grey, Kaikoura coast, and inland in the upper reaches of the Rangitata, Rakaia, Waimakariri, Hurunui and Waiau rivers and at Lake Ohau. Complete removal of forest occurred in many areas but remnants are present elsewhere. Selective felling removed *Dacrydium cupressinum*, *Podocarpus totara*, *P. hallii*, *P. spicatus* and *P. dacryiodides* in some otherwise intact forest. Grazing animals, especially domestic stock, deer, opossums and wallabies, have eaten out or made scarce some other species. The forest floor is bare of seedlings wherever animal populations are high. Many ferns have met this fate as have species of *Nothopanax* and *Coprosma*. Numbers of fern species have disappeared from Banks Peninsula. Other species such as *Cyathodes acerosa*, *Myrtus pedunculata* and *Drimys colorata* have been favoured by selective grazing.

The facts presented above, while disagreeing in some points of detail with the theories of Holloway (1954) about the forests of Canterbury, provide support for his main concepts.

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TEMPERATURE RESPONSE OF NATIVE SHORT TUSSOCKS

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This paper reports on the response to temperature of one clone of silver tussock (*Poa caespitosa*), one clone of Otago blue tussock (*Poa colensoi* var. *intermedia*), and two clones of fescue tussock (*Festuca novae-zealandiae*). The plants were grown in control climate cabinets.

The clones of silver and fescue tussock came originally from the Godley Valley (Lake Tekapo district) and included the stouter high altitude form of fescue tussock that may well be a distinct species (Connor pers. comm.). The clone of blue tussock came from Flagstaff Hill (Dunedin district).

Growth was compared at three mean temperatures of 80°, 60° and 42° F. The growth cabinets were run on 12 hour temperature cycles with 15°F. difference between "day" and "night", the "day" temperature being the higher. The light was of approximately 3500 ft. candles intensity at pot level and of approximately daylight spectrum.

The lights were on for 16 hours a day commencing one hour before the start of "day" temperatures. Relative humidity was in the range 70-95 per cent.

Each clone was represented by at least two plants. Measurements were made of the rate of elongation of the youngest leaf of a tiller which had appeared above the sheath