The botanical names of species mentioned in this paper are taken from the most comprehensive publication available, viz: Blakely's *Key to the Eucalypts*, published in 1934. In some cases they are different from those formerly in common use, and, where that is so, the older specific names have been shown in parenthesis. Blakely draws particular attention to the protean nature of the genus, and foresters requiring seed would be well advised to obtain supplies from sources, the climatic conditions of which are reasonably close to those prevailing in their own countries.

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**ECOLOGICAL INVESTIGATIONS IN THE NOTHOFAGUS FORESTS IN NEW ZEALAND**

*By J. T. HOLLOWAY.*

Within recent years there has been a growing awareness of the fundamental importance in the national economy of the *Notothofagus* forests of New Zealand, not only in connection with problems of timber production but perhaps to an even greater extent in connection with the conservation of our soil and water resources. It has been necessary, therefore, to re-examine these forests in order that, so far as possible, management and conservation policy may be based upon a sound understanding of their ecology. The problem is no simple one and will not be capable of easy resolution. The *Notothofagus* forests—and I use the plural not to stress the fact that many separate areas of forests are being dealt with but to emphasise the point that many distinct types of forest, many distinct forest associations must, be recognised—are developed in regions with an annual rainfall as high as two hundred and fifty inches, or as low as twenty-five inches. They are found as coastal forests or at the limits of tree growth in the mountains. They occur as swamp forests or on dry mountain slopes surrounded by tussock grasslands. Five species of the genus *Notothofagus* are present and the forest in any locality may contain these species in any combination or in any proportion from mixed forest in which all five are represented to areas where a single species forms a simple consociation. And again there may or may not be an admixture with podocarp species or with hardwood trees more characteristic of the podocarp forests. I might emphasise the complexity of the structure of these forests by stating that over a restricted area in the Western District of Southland upwards of fifty

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distinct types of *Nothofagus* or *Nothofagus/podocarp* forest have been recognised; and this for the purposes of timber mensuration alone and in an area where but two species of *Nothofagus* are present.

The most comprehensive account of the *Nothofagus* forests given to date is the monograph by the late Dr. Cockayne (1). This monograph described the distribution, in general terms, of the forests throughout New Zealand. In it Cockayne shed a flood of light on the vexed question of hybridism and the identity of species; but nowhere did he analyse in detail the structure of any particular forest or trace the history of any particular association. Therefore, while it serves admirably the purposes of the teaching botanist and while it provides a wholly admirable introduction to the subject, it cannot serve as a basis for the formulation of a management policy. The working forester deals with individual forests and requires a sound understanding of the structure, history and potentialities of each particular association. Investigations now in hand, therefore, are more concerned with the detailed examination of selected forests in an attempt to provide information of immediate value in the field of applied as against theoretical forestry. At the same time, however, the importance of the development of a sound over-all theoretical basis for the work is not being overlooked. In fact, phenomena revealed in the study of special areas have already required the formulation of hypotheses which, if substantiated, will have no small bearing on the conservation not only of *Nothofagus* forests but also of podocarp forests and indigenous grasslands.

**Nothofagus Forests and Forest Climates.**

I have already pointed out that *Nothofagus* forests are developed over regions with a very wide climatic range. As a simplification of the position it has been thought desirable to introduce the idea that two distinct *Nothofagus* forest formations are involved, namely "sub-continental climate" *Nothofagus* forests and, "mountain climate" *Nothofagus* forests. (2) The former are characteristic of regions where winters are cold and summers hot, where rainfall is low and periodic droughts are to be expected. The latter are developed where summers are cool, short and wet, and winters cold and wet. In the field, of course, every climatic variation between the two extremes may be experienced, but the conception has proved a useful one and, while all species of *Nothofagus* are to be found in each of the formations, yet between the two they vary in their relative abundance, growth habits and site preferences.

In this way, *N. menziesii*, the silver beech, the timber of which is at the moment the most widely employed of all, is dominant throughout New Zealand in regions possessing a mountain climate, and in many cases it may be the only species present in such areas. *N. cliffortioides*, the mountain beech, is, on the other hand, more characteristic of regions with a sub-continental climate, but it is also
widely distributed throughout the mountain climate areas particularly on steep or precipitous slopes where rapid drainage counters excessive rainfall. These two species have the lowest temperature requirements and are usually the only Nothofagus species represented in the far south or at higher altitudes. Black beech, *N. solandri*, parallels *N. cliffortioides* in its tolerance of dry conditions, but owing to its higher temperature demand, is more restricted to the lowlands and to the north. Both red beech, *N. fusca*, and hard beech, *N. truncata*, are more mesophytic and require a more equable temperature regime. Accordingly forests in which these species are dominant are frequently to be found in close proximity to coastal climate podocarp forest in mid latitudes or on special sites elsewhere. Red beech will tolerate a somewhat lower mean annual temperature than hard beech which, in turn, is slightly more xerophytic than red. In the colder south it is usually silver beech which occupies the ecotone between either of the two Nothofagus formations and the coastal climate podocarp forests, and intermingles with species of the latter forming mixed forests of very diverse types.

It will be understood that the demands of the several species overlap very considerably in respect to rainfall, humidity and temperature, and that accordingly local distribution is frequently determined by the minor factors of the site. Silver beech is particularly tolerant of a wide range of conditions and, in the absence of competition, flourishes as well in the drier sub-continental forests as in the wet mountain forests. Virgin silver beech forest produces a maximum volume per acre at lower altitudes in the mountain climate districts and along the inland fringe of the coastal podocarp forests but, at the same time, timber quality is likely to be higher inland under a decreased rainfall where also regeneration in adequate amounts can be secured most readily. In competition with mountain beech, however, it is rapidly suppressed in such areas and management units must be selected wherever, by reason of historical accident, mountain beech is absent. All species are tolerant of a wide range in edaphic conditions but black beech, hard beech, and red beech become more "fastidious" toward the south of their range. Thus in Otago red beech is restricted to the deeper colluvial soils, moist but well drained, in sheltered valleys, at the foot of the main mountain slopes. Further, although all species will grow on a wide range of soils yet there are pronounced differences in tree form, size, growth rate and timber quality from soil type to soil type.

There is an additional complication brought about by the readiness with which all Nothofagus species act as pioneers in the occupation of new ground. In this way many areas of Nothofagus forest of one or other species may exist within the climatic range of the podocarp forests or, alternatively, one Nothofagus species may pioneer an area essentially more suited to another. In this manner such apparently abnormal associations as *N. cliffortioides/Podocarpus dacrydiodes*
forest have their origin. Almost any admixture of species is theoretically possible and most have been demonstrated in the field. Thus even assuming that the forests are stable under a stable climatic regime, we must expect them to be constructed of a patchwork of distinct associations where local site factors play a disproportionate role and where local geomorphological accidents determine very largely the course of events.

The selection of forest areas for sustained yield management of any desired species is, therefore, a matter of some difficulty. In many cases optimum sites for one species are initially occupied by another. Frequently the most promising areas for sustained yield management do not carry as valuable a virgin crop as more unsuitable areas, and may even be considered unmerchantable. A fine balance must be struck between site quality, initial crop, topography and market accessibility. In no case can we expect to set aside any considerable area of uniform excellence, and Nothofagus silviculture must always remain an art to be practised and developed by the working forester conversant with all the idiosyncrasies of the forest under his control. This necessarily implies the development of a team of skilled specialist field officers who will regard such work as a full, sufficient and satisfying career.

Climatic Instability and Forest Change.

I have said that even assuming that the forests are stable under a stable climatic regime we can expect them to be constructed of an intricate patchwork of varied associations. The weight of evidence derived by careful study of the structure and distribution of the forests is against the assumption that they are, in their present condition, stable. It is not possible in this paper, to detail the many instances of instability recorded, or to develop the full argument arising from study of these facts. It is hoped to publish a more detailed paper in the near future for which this account may perhaps be read as a preliminary note.

Surveys of the forests of Western Southland suggest very strongly that major changes in species distribution are in progress. It appears that the changes in evidence are consequent upon a major climatic change in the recent past; and this change can only have been in the direction of increasing aridity inland, probably accompanied by a decrease in mean annual temperature. There followed a general retreat of the forests towards the coasts. The effect might best be pictured as comparable to that caused by casting a stone into a pool. As with the ripples so do the various vegetation zones move outwards. Near the coasts silver beech forest invades and replaces podocarp forest. Inland, the more xerophytic mountain beech forest replaces silver beech, only to be replaced in turn by scrublands and grasslands.

We can trace the migration mechanisms and the peculiar migration patterns so produced for each of these stages in the readjustment
of vegetation to climate. As silver beech and mountain beech in turn invade and occupy former podocarp forest lands, typical inversion patterns are produced where normal altitudinal distributions are reversed, the precise pattern varying according to whether the grain of the land is parallel to or lies athwart the migration path of the invading associations. In some areas these processes have followed one another so rapidly that old standards of the former podocarp forest remain even after the succeeding silver beech forest has been entirely replaced by mountain beech. At the same time many areas of forest simply stagnate. This happens wherever the logical successional stage is prevented from invading by the presence of some barrier, geographic or biotic, and also where the stagnating association covers such a large area that the interior cannot be penetrated by incoming species. In such cases the forests display all the symptoms of overmaturity and senility. There is an almost complete absence of regeneration coupled with prolonged failure of seed crops. This is outstandingly the case with hill country podocarps and to a lesser extent is evident in certain silver beech areas, although additional factors are operative in the latter case.

Now while the replacement of forest association by forest association in general proceeds gradually and, in fact, in many instances may be described as amoeboid movement on a gigantic scale, nevertheless in some cases the forest maintains itself against the climatic change for a long period of time by virtue of its own internal climates. Destruction proceeds catastrophically following the operation of such factors as fire or disease; and the forest disappears as it were in a night. There is much evidence establishing the former existence of forests throughout the present outer grassland zones, and these forests were, at least in part, inland podocarp forests comparable to those now found in central areas of the North Island. I have been able to trace remnants of these forests around the grasslands periphery for several hundred miles. I believe that they were ultimately destroyed by fire, but only after they had become unstable following the climatic change. The rate of destruction precluded the development of the expected successional type which, in many instances, should have been sub-continental Nothofagus forest. Instead, large areas developed to sub-climax grassland (notably with Danthonia ruoullii var. rubra dominant), and these grasslands persisted until biotic interference permitted the invasion of the ground by Leptospernum and other pre-forest scrub species. Such areas can be held in productive grassland only where cultivation or intensive pasture management can be practised. At the same time afforestation with exotic species is likely to be successful in such districts.

In this manner I believe that the inland Nothofagus forests were not, at the time of European colonisation, developed over their full climatic range but that much of the area which should have been under forest was occupied by various sub-climax associations.
Further destruction of the forests appears to have been the result of fires dating back to the era of the moa hunters. Thus the sub-continental *Nothofagus* forests, at the present time, are capable of extending their range both coastwards in consequence of the climatic change and inland, reoccupying damaged sub-climax grasslands. The development of grassland on the steeper mountain slopes inland, slopes graded under forest and which should now be carrying forest, has resulted in widespread accelerated erosion particularly where the barely efficient grass cover has been damaged by repeated fires and grazing. Such accelerated erosion has now, in many cases, proceeded so far that re-establishment of a suitable forest vegetation will be extremely difficult. In the central core of the present grassland area forest re-establishment is now impossible since the climatic change has taken the area outside a true forest climate and in some places, even outside a true tall grassland climate. In these latter localities destruction of the tall grass vegetation, possibly previously maintained only through its own micro-climate, because suitable indigenous short grasses had not been developed, has resulted in the deterioration of the sites to wind eroded semi-desert.

Hand in hand with the retreat of the forests to the coast, the timber limit on the mountains has been lowered, and comparable migration patterns can be traced as mountain climate *Nothofagus* forest replaces lowland and mid-slope podocarp forest. We do not yet known whether or not the present timber line has become stabilised. On certain ranges evidence of a period of intense erosion dating back a few centuries appears to indicate a fall in the timber limits at that time but the possibility that the higher altitude forests are precariously maintained only through their own inertia must be considered when studying the effects upon them of the browsing of introduced animals.

The above outline applies, of course, only to the forests of the south and particularly to those of Western Southland where most of the recent field work has been carried out. I would point out that the conclusions reached were arrived at independently of the findings of research workers in any other field. Raeside (3), in his study of the soils of South Canterbury has arrived at comparable conclusions and my findings are in complete harmony with his. The effects of a uniform climatic change will necessarily be greater in the south where the climatic limits of many important species are closely reached, but I am sufficiently certain of the correctness of the conclusions to forecast the tracing northwards of comparable vegetational readjustments, although on a diminishing scale. It is essential that these hypotheses be substantiated since, as will be realised, they have a major bearing on all problems of vegetation conservation, forest management and land utilisation policy. The impact of Western civilisation and agricultural method came at a period when the indigenous vegetation itself was in a state of flux or precarious.
balance. In many cases there may be no native species suitable to fill the gaps, and extensive reliance may have to be placed upon acclimatised exotics. As an immediate result we can delimit the area in Otago and Southland where sustained yield management of *Nothofagus menziesii*, *N. cliffortioides* and *Dacrydium cupressinum* will prove successful. We can state that there is no possibility for successful management of other major podocarp species, and that there is very little chance of successful management of *Nothofagus fusca* on any considerable scale.

Further evidence by extension of the area covered by forest survey, particularly in South Westland, North-west Nelson and Marlborough will be sought. Confirmation should come from the work of the Soil Survey, particularly by enquiry into the origins of anomalous soil types; and finally by glaciological studies with special reference to the regime and history of stagnant or semi-stagnant glaciers outside the main centres of glaciation.

**The Impact of Exotic Animals on the Forests.**

The forests, and indeed all vegetation formations in the country, can be visualised as a complex of plant associations each playing the part of one of the bits of coloured glass in a kaleidoscope. In the kaleidoscope which we are viewing at the moment one pattern falls to pieces and another begins to form. Into this rather disturbed situation a new factor has been introduced. As is well known, the indigenous vegetation developed in the complete absence of grazing, and browsing animals. The acclimatisation of deer, pigs, goats, wapiti, chamois, thar, rabbits and other animals has initiated a fresh series of changes so that over and above the readjustments now in progress as a consequence of past climatic instability are superimposed changes due to the incidence of grazing and browsing in the complete absence of normal predator control.

A paper is in preparation concerning the effects of deer upon the forests of Western Southland and I will anticipate the publication of that paper by stating here a few of the conclusions reached. We have been able to list, in approximate order of palatability, most of the forest species browsed. Unfortunately, high in the list comes the juveniles of many of the important forest trees including all species of *Nothofagus*. Few, if any, of the browsed species are browse-resistant; most are killed outright. There are very few unpalatable species although certain of these are of considerable importance. The apparent damage done varies from association to association and in accordance with the population level and population trends of the local herds. But the degree of apparent damage in evidence, that is to say the amount of destruction of secondary species of the forest interior, bears little relation to the degree of real damage which is in no case obvious to the casual observer. The real damage done rests in the complete destruction of the juveniles of the
physiognomic species. In a few instances heavy browsing appears to favour the re-establishment of the podocarps at the expense of *Nothofagus* species but these are special cases only. As yet the forest canopy is everywhere intact although the secondary vegetation has been altered beyond recognition. But in all *Nothofagus* forests in which the deer have reached a peak population no significant regeneration of the major species is present. With the decay of the present canopy, providing that the forests continue to harbour deer, a profound change in the structure and composition of the vegetation will come.

In certain cases it is possible to forecast what these changes will be; frequently a degradation to heath, fern or scrubland. In almost every case the new vegetation will be of less value than the old—non-productive of timber and of low erosion control value. In respect to forests set aside for permanent production of timber of any of the *Nothofagus* species we must face the fact that deer proof fencing of all regenerating stands will be absolutely essential. If this is done, and provided that management areas are selected within the zones of stability or advance of the desired species, then *Nothofagus* silviculture will prove relatively simple. Without the exclusion of animals it will be impossible.

The most urgent problem is the continued maintenance of the watershed protection forests. No accelerated erosion is yet in evidence *within the forests* except in a few instances where the scars left by the processes of normal erosion have been prevented from healing. But again, in no heavily populated areas is there sufficient regeneration present to replace the existing canopy. Nothing spectacular will occur until that canopy fails, which may not be for a century or more; but we must be fully prepared against that time. State killing operations in many areas have reduced the herds significantly, and in certain areas examined there are indications of a recovery in the forest vegetation. The problem requires detailed and continued study and the results of such studies must be interpreted against the background of the natural changes that are in progress, due consideration being given both to the natural and to the artificial trends in the population levels of the herds.

At the same time if killing operations prove insufficient to control the deer (and other animals), as is likely in remote mountain country, then alternative extermination measures must be devised. As a last resource experimental preparations must be made, designed to replace the natural forests by exotic browse-resistant forests. We cannot have both *Nothofagus* forests and deer.

In the meantime the most evident source of danger lies in those sub-continental type *Nothofagus* forests protecting the headwaters of the rivers flowing east from the main watersheds. Some of these forests are, in any case, of doubtful stability. In all cases they are
likely to be destroyed before the wetter forests to the west, both on account of the paucity of alternative browse (other than *Nothofagus* juveniles) and also because in these areas it would appear that the life of the canopy-formers is considerably shorter than for the same species in areas with a greater rainfall. Once destroyed such forests are most difficult to re-establish and under the climatic conditions prevailing in their locality few alternative species would be successful. Conservation of these forests implies also control of the adjacent tussock grasslands. Destruction of certain areas of forest by the downward movement of detritus from the higher slopes can already be noted.

I would again emphasise the complexity of the problem. Field studies of vegetation in relation to animal population can only be made intelligently if all the devious cross currents of events are fully appreciated. Interpretation requires skilled observation and, since so much of the original secondary vegetation has already been destroyed, the observer, in order to understand any given situation, must be able to reconstruct the virgin forest in his mind’s eye. He must know not only the species of plant which are present on a given site, but also which other species should be present. It is no suitable task for amateur or embryonic ecologists.

It may be considered that I have painted a somewhat alarming picture. The truth is that the situation contains all the elements of alarm. It may be that some unforeseen factor will operate to our advantage or that a permanent reduction in herd strengths can be achieved, a reduction such that all browsing will be restricted to species higher on the palatability lists than the juveniles of *Nothofagus*; but I do not think it possible. There can be but one objective, the extermination of all exotic animals acclimatised in the forests, coupled with preparedness to meet a difficult situation should that objective not be achieved.

This then is the field of investigation open before us. Upon the delimitation of suitable management areas and upon the devising of suitable silvicultural techniques, depends the greater part of the country’s future hardwood supplies. Upon the conservation of the *Nothofagus* forests of the mountains in face of the threat of browsing animals, depends the control of all major rivers and the preservation of our hydro-electric resources. I previously introduced the illustration of a stone cast into a pool. In effect so many stones have now been cast in with ripples criss-crossing and being deflected by rocks and shoals that it will be difficult to disentangle the true chain of events and link causes and effects with certainty. It would be a delightful hobby if it were not for its gravity and urgency.

We can pretend to no great achievement yet, but perhaps the realisation that the situation before us is not as simple as it may at first sight appear, itself marks a worth-while advance.
Summary.

A short account is given illustrative of the structural complexity of the forests with an indication of the habitat and site preferences of the various species of Nothofagus. Studies of selected forests are in progress in order to provide information of immediate value in the field of forest management and silviculture.

Arising out of these more detailed studies, it has been possible to formulate hypotheses concerning the general distribution of the forests and their inherent stability. In particular these hypotheses have reference to climatic instability and the re-distribution of the various forest associations now in progress.

Investigations are also in progress with relation to the effect upon the vegetation of populations of exotic animals. The conclusion has been reached that the only permissible objective, at least in respect to Nothofagus forests, is the complete extermination of such animals coupled with the preparation of remedial measures should extermination prove impossible.

References.


RECENT OBSERVATIONS ON THE SIREX NOCTILIO POPULATION IN PINUS RADIATA FORESTS IN NEW ZEALAND*

By G. B. RAWLINGS.

Introduction.

The last 100 years has seen the destruction of much of New Zealand's indigenous forests and their replacement by forests of exotic species. In these exotic forests *Pinus radiata* is the dominant species. From the time of their establishment the forests have been protected from fire but have received practically no silvicultural treatment.

As a result of lack of attention the forests have become overcrowded and, during periods of unfavourable climatic conditions, have suffered mortality due to attack by *Armillaria mellea*, *Diplodia pinea* and other factors consequent upon the congested and stagnant condition of the stands.

The mortality in most cases took the form of dying trees distributed throughout the stand and was regarded as normal suppression. *Sirex* was usually present but was regarded as secondary. Recently, however, the dying of all trees over areas of more than an acre has caused some concern and an investigation is now being made of the factors involved in the mortality.

During the course of this investigation some interesting details have been studied which point to *Sirex noctilio* and its associated fungus as the chief biological factors involved.

Most of the points investigated have already been discussed by various writers. *Sirex* has been dealt with by Chrystal and Hanson in England, and by Clark and Miller in New Zealand. Buckner, Cartwright, Muller, Francke-Grosman and Parkin have dealt with the question of symbiosis and the forestry principles involved have been given in numerous papers and text books.

There are certain economic, climatic and forest conditions peculiar to New Zealand which render these observations particularly pertinent at the present time and, at the risk of repetition, some account of the relationship between *Pinus radiata*, *Sirex noctilio* with its associated fungus, and possible control measures, will be given. In Europe, and particularly in England, *Sirex* species are not regarded as a serious menace to the forest, and it was largely in response to requests from New Zealand that a study of the ecology of the species of *Sirex* and their parasites was undertaken.

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