New Zealand Ecological Society

Report of Eighth Annual Meeting

The eighth annual meeting of the New Zealand Ecological Society was held in Auckland on Thursday and Friday, 27th and 28th August, 1959, in the Biology Block of the University of Auckland. The programme followed the same pattern as in previous years, the first day being given to contributed papers, and the second day to a symposium consisting of papers by invited speakers in the morning and free discussion in the afternoon. The contributed papers had their usual wide variety, from fungus diseases of pine trees to the fauna of temporary ponds, and the birds of the Dunedin Botanical Gardens. The symposium on "The Inner Islands of the Hauraki Gulf" consisted of nine papers ranging from the geology and the soils to the birds and the marine benthos. The Annual General Meeting was held as usual on the first evening and was followed by the Presidential Address. On the Saturday an excursion by launch enabled members to see for themselves parts of the area discussed in the symposium; one party examined the vegetation and birds of Rangitoto, while another cruised round Waiheke and other islands and inspected some bird nesting areas. About 80 members attended the meeting.

PRESIDENTIAL ADDRESS

Patterns of Forest Regrowth

C. M. Smith

Last year my predecessor in office addressed you forcibly upon the subject of Observation and Deduction. He made it clear to you that observation was the basic art of the ecologist. I am venturing this year to reinforce his argument with an attempt to furnish you with examples from one particular phase of a plant community with which you are all acquainted. It is perhaps one of the most remarkable paradoxes of ecological studies that, although most students admire and even revere a forest of some size and of great reputed age, little detailed and continuous attention is paid to its younger life phases.

You will find many treatises about the incoming of a forest to bared ground by way of a long series of vegetation of lowlier stature through long periods of time. You will hear frequent references to "invasion by forest" of artificial and even of natural grasslands. You will hear of many other phenomena and stages of forest growth in great detail. But of the fundamental, natural, though far from simple, procedure of regrowth of one forest community directly after an earlier forest community you will search almost in vain through whole libraries of ecological literature.

You will find much that seems at first sight of the chapter captions to meet your needs; but seldom does it tell you what to go out and find and check in the field, in the margins, and harder still in the interiors, of

forests which you yourself have access to. Faced with a forest which you wish to study, you nearly always find that you cannot see the forest for the trees; and that, if your desired subject of study is the growth of the forest itself as a community or an organism, as distinct from an assemblage of a few dominant species of tree of a certain age and size, you are speedily lost in a maze of phenomena, if you are not indeed physically lost in the maze of the forest itself. My attempt tonight will be to direct your attention to a few key phenomena which you should look for if you do venture into forests to enquire into the mysteries of their regrowth and to warn you that you will not find all of them, or perhaps any of them, at the first time of entry.

You must train your eye to your subject; and that is the first lesson in the art of observation, which is the basis of your subject. To give you the simplest possible example; many of you are quite sure that N.Z. beech forests regenerate readily, and you are not averse to saying so in public during certain controversies which are just now much to the fore. Yet how many of you can distinguish the cotyledons of the different beech species? In how many of the numerous herbaria of this country will you find proper specimens of them, or indeed of seedling forms of most of the forest tree species of the country.

This very elementary point leads me at once to the title which I have attached to this paper. You will notice that I have not used the very common and glib term "forest regeneration". The substitution of the phrase "forest regrowth" is deliberate. The commoner and seemingly correct phrase is debased by popular use; and not once in a score of times it is written does it mean what the writer thinks it means, or the phenomenon which we are attempting to study this evening. An eminent Australian writer puts it that germination of a forest species is abundant and frequent, regeneration of the forest is difficult and rare. Elsewhere he deprecates what he terms "the glamour of natural regeneration". Of one Australian species of eucalypt, he ventures the opinion that "of 150 million seedlings germinating a single successful one is all that is neessary to carry on the forest" (Jacobs 1955).

There are other phrases frequently used in popular and technical works dealing with forests of which the forest ecologist should beware. "Over-mature forest" is one of them. It usually has a forester's economic connotation, which very seldom coincides with an ecologist's physical meaning. "Exploitation of the forest" is another. You must always remember in your ecological reading that this word has no disparaging meaning in the Romance languages. In this view, a forest is exploited as reasonably as a crop is harvested; and the harvester (or exploiter) always has an eye on the succeeding tree crop that nature will provide if left alone.

And so it goes on. The whole vocabulary of forest regrowth, though verbally it may be the one with which you are well acquainted, bespeaks a special attitude of mind that one may perhaps call a contemplative attitude. It involves a time factor that is greater than that involved when you are studying annual crop plants or even crops of short-lived perennial plants. The agriculturalist studying his pasture of "short rotation rye" may devote anything from four to seven years to the task; the forester studying the early phases of his hardwood forest in temperate Europe will allow forty years for what he terms its "regeneration period". His contemplative attitude, accompanied always by his continuous observations and deductions, will run through the whole of that period. It requires conscious and deliberate mental discipline to achieve that necessary attitude of mind, and, having achieved it, to maintain it. Every phenomenon should be viewed with an eye on the past as well as on the future; and that past should, as far as is humanly possible, be based not merely on hypothesis or conjecture, but on concrete evidence from matched examples.

Principal Families for Study

These few remarks on precision of diction must suffice as a warning that such precision both in word and thought is as necessary as precision of observation. One passes from it to a consideration of comparatively common plant families which for various reasons seem to be those on which the first studies should be focussed. Not the least of these reasons is that some at least of them are to be found in every temperate country. Perhaps a less obvious reason is that commonplace families and plants are apt to be

less attractive to students than are the more exceptional ones. All too many students of ecology finish their studies of common plants at a comparatively elementary level; the intensity of their knowledge of anything is apt to be proportionate to its obscurity and rarity.

I am therefore suggesting that, at least for students outside the tropical zones, the families in which patterns of forest growth should be carefully and continuously observed should be, in a sequence, Salicaceae, Pinaceae, Petulaceae, Fagaceae, Araucariaceae, Podocarpaceae and Myrtaceae.

At first glance these must seem a most heterogeneous group; but you will see that it has been carefully chosen; and that from it almost any student in a temperate country can select at least two families (a gymnospermous and an angiospermous one) which provide large tracts of forest land for study. The greatest initial surprise will be caused perhaps by the inclusion of the family Myrtaceae. To those who may question its selection as a sort of type family for this purpose, I would draw the attention of its importance as a forest former over the whole of the continent of Australia with the single genus *Eucalyptus* (more than 600 species); and the great significance of two other genera, *Leptospermum* in Australia and New Zealand, and *Metrosideros* in New Zealand. It so happens that these three are all Southern Hemisphere genera; and they bulk far more largely in the forest complex there than does the type genus of the family in the forest communities of the north to which it belongs.

It is perhaps worth noting that the genus *Eucalyptus* has under cultivation adapted itself more to Northern Hemisphere forest culture on a large scale than has any other southern hemisphere forest species. A hundred years ago De Candolle listed *Eucalyptus globulus* as the only southern hemisphere tree species that was adaptable to domestication in the northern hemisphere. Today the number of eucalyptus species growing abundantly and usefully in California, Portugal, Africa, Palestine, India, and even as far north as Western Scotland is far greater than that single species; but the genus is still singular amongst southern forest genera in its adaptability to northern hemisphere forest conditions. It seemed to me therefore that the family which provided this great congeries of forest species in both hemispheres must be as worthy of fundamental study as say the family Pinaceae which so dominates northern temperate forests. Its patterns of forest growth and regrowth must contain basic features from which every forest ecologist who has access to such forests must have much to deduce and observe. There is one further supporting point which makes it imperative that the serious student must give early attention to the patterns that can be discerned in great diversity, both in the life histories of eucalypt species and in the diverse forest patterns displayed by those species. There is a recent volume published by an outstanding Australian forest authority which records growth patterns of eucalypt forests of many sorts, by a treatment which has so far as I have read never before been accorded to any genus of forest trees. His treatment and findings after a lifetime of study throughout Australia must serve as a model for all who aspire to forest ecological knowledge; and should inspire systematic pattern observations and recording on a scale and with a precision seldom before attempted. Forest ecologists who have never seen a eucalyptus forest will read it with pleasure and certain profit, if only as a manual of observational technique (Jacobs, 1955). Finally, when one comes to consider the four principal patterns of forest regrowth into which I should suggest they could be classified at present, it will be seen that this enormous and immensely diversified genus can furnish examples of certainly three of the main patterns, and possibly of the fourth fundamental pattern as well. It is very doubtful whether any other genus of tree can build forest communities originating and perpetuating themselves in all of the basic patterns yet known.

Regrowth Patterns of Forests

The vegetative pattern

It is simple botanical fact to state that all plants effect their regrowth either by vegetative or sexual reproductive means; or in some cases by both. The plants which dominate the forest community are no exception, and the student of forest regrowth will very soon find that many forests utilise the

vegetative pattern of reproduction of their predominant species much more frequently and effectively than he had thought. We in New Zealand are apt to overlook this as a basic pattern of forest regrowth, because it is apparently absent from the indigenous forest communities of the country, and almost absent from the indigenous tree or shrub species whether of forest or of open heath or savannah land. The inherent power of vegetative reproduction is not however wholly absent from all native tree species, but as an effective natural pattern of forest regrowth it is known to me in only one extreme case and then is at best only a supplementary and feeble means additional to the more usual reproduction of tree species by seed.

It is largely as a precaution lest the New Zealand ecologist overlook this as a common and effective pattern of forest regrowth that the family Salicaceae was recommended as one of the principal families for study. That remarkable family has almost replaced seed reproduction of its communities by regrowth by vegetative means, though so far as I know no species has completely displaced its reproductive powers from seed. Observation alone may here fail you in your field studies in New Zealand, where many species of both its genera (*Salix* and *Populus*) have been introduced freely, and are propagated freely and economically by vegetative means only. I personally have never found field seedlings of either genus; but they have been recorded here (probably for *Salix fragilis* only) by a few collectors whose authority cannot be questioned. There are at least two explanations of this rarity of seedling regrowth. The first is that the whole family is dioecious; and when fertilisation does take place, though it may be abundant, the resultant seed has an extraordinarily brief period of viability, usually said to be of two to five days only.

The other is that since vegetative reproduction is so easy for the propagator, he has very often used one sex only for his stocks. You will consequently find in many cases that a single sex of a species dominates a whole district. This is usually the male tree, partly because its catkins are more showy and so have a better horticultural appeal; but in many cases the choice of male stocks for planting was dictated by deliberate avoidance of the free-flying cottony seed of the female tree, which had an evil reputation for causing respiratory troubles in horses and farm stock.

Whether this was the reason or not, the fact is that in this country at least you will create a record if you can collect an indubitable specimen of a female plant of the common Lombardy poplar. You must not interpret this seeming absence of female trees as being an exception to the simple rule which opened this paragraph. It is deemed to be the result of age-long selection in Europe of male stocks for vegetative propagation, a selective process which reached perfection when applied to stocks geographically isolated by transport overseas. Many recent European authorities on poplars and poplar culture doubt whether this perfection of segregation has been reached in Europe, despite centuries of male selection. Their finding is that a somewhat less common species, which had been given the distinct specific name of *P. plantierensis*, both in Britain and on the continent, is the true female plant of Lombardy poplar.

The point is of interest to us tonight as an example of the fact that all the problems you may encounter in the field are not capable of solution by local observation alone; but accepted theories are capable of a considerable degree of check. Such checking of the behaviour of tree species introduced here from overseas against the known behaviour of the same species in their native environment will sometimes provide most profitable results for the close observer. I commend for your attention in this field of forest regrowth by vegetative means the phenomenon amongst eucalypts now known as lignotuberous growth. I personally first encountered it in Invercargill many years ago—so long ago that it was not in any standard literature that I could obtain, and I was saved from pursuing a false pathological trail only by the warning of an observant old gardener there. He assured me that the "galls" never did any harm, but were always there on some eucalyptus seedlings, but not on all species that he grew. This scanty but accurate information has since been abundantly justified and amplified by Australian botanists; and the phenomenon is now accepted as a means of vegetative regrowth for certain species of *Eucalyptus*. It

is as yet far from fully known in all its detail; but it can perhaps be most readily described as a sort of early natural coppicing available to some eucalypt species when seedling regrowth is cut back on a large scale by either natural conditions or by incidents such as fire or animal grazing. Jacobs records growth from the so-called lignotubers of seedlings as long as seven years after the main shoot has been completely cut back or suppressed. It therefore is a remarkable and little known means of vegetative regrowth of whole forests that is little understood and is not recorded so far as I know for forests of any other species.

There is finally a local example which will underline my point that vegetative regrowth of forests has still secrets to yield to the ecological observer. Within the past decade a member of this society has shown that the indigenous podocarp *Dacrydium colensoi* in Westland swamps sometimes occurs in large clumps that originate from root shoots derived from a single parent stock (Moar, 1955). This was never even suspected before; and it has usually been accepted as almost a commonplace of forestry that no coniferous forest adopts this particular pattern of forest regrowth.

It will from these few examples be plain to you that though the vegetative pattern of forest regrowth is by the nature of things something of an aberrancy, yet it is well worth your attention as observant ecologists: and that there are still little known facts about it awaiting your observation.

THE PIONEER PATTERN

This term may be ill-chosen, but it is the one in most general use. It is not quite in the sense that the term is used in general ecology, where a pioneer plant is usually one that is a first coloniser of a newly exposed habitat. In this case, since the subject is forest regrowth, it follows almost by definition that the forest site has previously been occupied by forest, and that the pioneers are restoring a forest community to the forest site. The restoration may be secured by the species (or by some of them) that previously occupied the site; or it may take place by the intervention of some tree species that was inconspicuous in or absent from the original forest structure. In either case, it must be regarded as the basic pattern from which most of us derive our general ideas of renewal of a forest: and it is the pattern which non-technical popular writers picture when they so freely use the term "natural regeneration", which I deprecated earlier. It is, from one point of view, the normal, and it is certainly the simplest way by which a forest may regrow itself. Examples of it are not lacking in New Zealand. I need only refer you to the miles of young *Nothofagus* forest to be seen on margins of roads cut on either side of the Southern Alps near Arthur's Pass, or the Lewis Pass road, or to the thousands of acres of *Pinus radiata* forest which sprang up near Taupo in the North Island after the 1945/6 forest fires. Both are such dense regrowth, such monotonous tracts of sameness, that unless you are studying this particular subject, you will tend to pass them by in your field excursions. However, you will I hope not fail to note that they belong to two of the plant families that I recommended for your close attention, Pinaceae and Fagaceae. A third family is even more abundantly available for your attention, the Myrtaceae, in the still abundant manuka "scrub" (*Leptospermum* of both species) which so often succeeds as well as precedes forests of other species throughout the country. Do not be misled by the popular term "scrub". Manuka stands on forest sites can be and are true forests, although on other sites the same species may never exceed heath or scrub size.

The characteristics of species that constitute pioneer forests the world over are those I list below. They are taken in the main from Scandinavian sources: and you will not find all of them in every species. If, however, you examine every species of every pioneer stand you see, you will find some major grouping of these features.

1. The species are monoecious.
2. They set abundant seed at an early age.
3. Seed years are frequent if not annual; and the seed is light and freely shed.
4. Seedling growth is usually fast and follows a short germination period.
5. Early growth after the seedling stage is rapid for 2 or 3 years.
6. Life span of the species is usually short, i.e., short by standards of normal tree life spans.
7. Trees are strongly light-demanding, especially in early life.

8. Rooting systems are usually shallow; and root-grafting within the species is often found, at least up to the sapling stage.
9. The species is of gregarious habit; this may be thought to be a matter of tolerance only, but it seems more probably to be one of demand.

Each of these listed features is a matter for continuous field observation. It is seldom that you will be able to make up your mind on any of them at first glance. Exceptions will frequently be found, and you task will be to make, from numerous examinations, a decision as to which of the possible alternatives is the predominant trend for a species or for a particular locality. Even the seeming clean-cut feature of monoecism often resolves itself into what Cheeseman terms "polygamo-dioecism" with occasional surprising local results, detectable sometimes only after years of repeated observation.

Wherever you can in the end decide that a major tree species predominantly, throughout its range of distribution, yields an affirmative answer to most of these nine queries, you may be almost certain that you are dealing with what is potentially a pioneer species; and that, given the correct conditions, it will replace a destroyed forest with a pure stand of regrowth forest.

I recommend particularly for your study such pure stands of *Leptospermum* and *Aristotelia*. Their earliest stages are to be found soon after a forest area has been felled and burned. Many secrets of the original regrowth patterns of natural stands of the major native species are to be discerned in the dense "scrub" forests of these two genera.

Another potent reason for directing your attention to these two genera in pure stands is that each is a species of short natural life-span (see point 6 above). You have therefore a reasonable chance of finding for comparative study other stands of the same species which are at the end of their life cycle. Such stands which illustrate the death-and-decay stage of a pioneer stand are most useful for your field studies. The moribund pioneer forest if left intact naturally furnishes you with the early stages of the regrowth of its successor, which will logically be the subject of the next paragraph.

THE SUCCESSIONAL PATTERN

As students of plant ecology, you must all be aware of the phenomenon of plant succession. It is one which it is far easier to admit and understand in theory, than it is to detect in early field observation: and it is far too complex to attempt to discuss here as a general phenomenon. We are moreover discussing only that case of it which furnishes forest regrowth. There are cases where removal of a forest cover results in regrowth of a forest of the same predominant species as the preceding forest. These are the rare cases which the forester covets and usually cherishes to the utmost of his powers.

I do not propose to discuss them here; they provide the glamour of natural regeneration which I have already quoted to you. What is our concern at the moment is the procedure and conditions by which a forest of any species is succeeded, as it dies, by one or several species other than the dominant species of the original.

The variety of cases is so great that you may well be pardoned if you despair of reducing the problem to order; particularly to such a state of order that you will risk prediction with any confidence. Yet there are a few guiding rules worth remembering. The most obvious one is that the species that will enter into the successional pattern of a pioneer forest in its moribund stages depends primarily on the proximity of a seed source. You would not reasonably expect for example to find rimu seedlings or even those of abundant fruiting kahikatea in a moribund *Leptospermum* pioneer forest that is mile or more from the nearest mature podocarp tree. Do not be misled by popular anecdotes and theories of long transport of succulent fruits by birds, or of exceptional longevity of viable seeds underground. As singular records they may be interesting, and even veracious in occasional cases; but performance has to be frequent and abundant before effective regrowth of a forest community is achieved. Singular and exceptional cases do not furnish a pattern. It is better far that you should note what does *not* occur. Negative comments are frequently at least as valuable to an ecologist as positive ones.

One of the most useful observations to make systematically in matters of succes-

sional regrowth of forests is whether the successional seedlings occur marginally in the pioneer forest, or whether they extend in an erratic fashion to varying distances from the seed-source trees. In ecological language, whether the ecotone between the old and the new is narrow, wide, or indefinite. Clues about the sequence of stages in a successional pattern are most frequently to be found in or about the ecotone. The best advice to give to the novice observer therefore is to find the ecotones and observe them minutely and repeatedly. The difficulty is unfortunately to find and to recognise the ecotones, but found they can be, and when once good specimens are found in a successional forest the acute observer has an observation ground that will last him for as many decades as remain to him. Where a young ecotone of characteristic pattern is detected and well studied in a successional forest, it may and often will be possible to detect beyond it zones of growth of older ages that can be recognised and explained as of earlier ecotonal origin. You may even, if you are exceptionally fortunate, and your powers of observation have been sharpened by practice, detect series of rotting stumps which by their species and their location patterns in relation to the existing adult trees may establish beyond doubt the species that preceded the existing forest stand.

One may perhaps look on this as the other extreme of the requirements for the observational powers of the ecologist. I pointed out the necessity for ready recognition of early stages of all tree species in a forest. This now is the stage when ability to recognise dead and even half-rotted stumps from shape, location and patterning is part of the craft, and furnishes helpful evidence for deduction. Between these two stages in a forest that has regrown by successional methods, there is far more to be pieced together than can be observed in a human lifetime of observational method. As ecologists therefore you need never lack material for useful observation in a healthy and vigorous successional forest, even though it be composed of the most commonplace species or families.

THE MOSAIC PATTERN

You will recall that when I listed half a dozen families that would furnish adequate samples for ecological study of forest regrowth for any part of the globe, I mentioned that there would be a gap in the series through the tropics. It is in that gap that this pattern occurs most abundantly, if not indeed exclusively. The descriptive word "mosaic" is intended to convey the idea of a kaleidoscope, with no detectible regularity in the colour arrangement. It may not be the best descriptive word for its purpose, and you may change it if you can devise a better. I do not think it can even claim the approval of world-wide ecological convention. It is, however, the most descriptive word that I have seen during my reading: and its use seems to be spreading in its application to forests of the tropics and adjacent regions. I first noticed it some twenty years ago in d'Aubreville's works on the forests of French Equatorial Africa; it is used by Richards in his volume entitled "Tropical Rain Forests" which deals mainly with British Guiana (about 1945); I have heard it used to describe the ecological pattern of the kauri forests of Queensland.

There is not enough known about the regrowth patterns of these forests for me to attempt to list for you diagnostic features of the constituent species as I ventured to do for the pioneer pattern. It does seem certain, however, that even seedlings always appear dispersed and not clumped or zoned; and Richards testifies to the fact that counts and enumerations record as many as seventy species of full-sized adult trees to the acre. Few ecologists appear to go further than admissions of mystification when the problem of growth, origin and the regrowth of such a forest is approached. It is of interest to us because of local pride in Northland kauri forests and local conjectures as to their patterns of regrowth. I personally doubt whether the native kauri forests can be claimed as an example of the mosaic pattern of regrowth, and certainly not in its most extreme and characteristic form, as described by Richards for British Guiana.

There is however enough resemblance between what is recorded of those forests and what can be seen from place to place in New Zealand kauri forests to justify a close study of literature of the mosaic forest pattern by all who aspire to make an intensive study of the regrowth of *Agathis* forests. Much is already known: but little is quite conclusive

in its detail. Certainly some of what has been written in the past has been wrong in its conclusions, though not necessarily in its primary facts; and it is at least possible that the clue to the still concealed conclusion about the regrowth patterns of New Zealand's northern forests may be found through study of tropical rain forest, and one may hopefully say *vice versa*.

It is too late for me to pursue this topic that fascinates us all further tonight. I trust I have said enough to inspire the younger members of the Society to many years of determined, continuous observation by orderly methods, directed towards some explicit goal. I wish you all many years of good hunting and satisfying results.

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