MOSAIC OR CYCLICAL REGENERATION IN NORTHERN ISLAND PODOCARP FORESTS*

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Summary

Recently it has been shown that tropical rain forest areas may possess a mosaic structure and a cyclical succession of dominants and it is probable that similar patterns and processes exist in some North Temperate forests. New Zealand podocarp forests are considered to be related to certain tropical montane rain forest formations.

It seems likely that the above concepts can be used to advantage in considering North Island mixed hardwood-podocarp forests and a tentative application of the ideas to an area of an association of this type in the Whirinaki river valley is described and discussed in this paper. This area appears to have a cyclic succession of dominants where podocarps alternate with hardwoods on individual sites. The preponderance of mature podocarps over hardwoods over quite large areas could be due to the present association being a "first rotation" crop. The various effects which could cause a cyclical succession are briefly discussed. Where extreme environmental conditions exist a monoclimax is usually found.

The values of the concepts of mosaic structure and of cyclical regeneration within the forest are discussed and tentative suggestions for working mixed hardwood podocarp forests so as to ensure their perpetuation are described.

Introduction

In a recent book entitled "The Tropical Rain Forest," P. W. Richards has given very full and most informative ecological descriptions and is to be congratulated on having made an attempt to correlate the structure of tropical forests with that of more temperate areas.

The following paper considers one or two of the more interesting of the hypotheses advanced by Richards and shows how they can be applied to North Island podocarp forests (and in particular to the forests of the Whirinaki river valley), in an attempt to clarify my own and one hopes others' ideas on the ecology of these areas.

It must be emphasized that of what follows, an overwhelming amount is either hypothesis or is based on only skeletal evidence and requires more quantitative field work for verification.

In his book Richards says that the fundamental structure of any forest may well be considered as being a variation on the pattern found in typical tropical rain forest. Here in any one area may be found one to two hundred or more tree species and overall conditions for growth and regeneration are favourable for any of these, the

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result being an intense competition among species. As one departs from the tropical rain forest areas in altitude or latitude the heterogeneity of the forest decreases and as conditions for growth become more limiting so do the number of species that can grow successfully in those areas. Thus in the northern hemisphere we have the very specialized coniferous forests growing on marginal climatic areas for tree growth and possessing only one or two component species; Richards nevertheless regards it as being only an extreme variant of the tropical rain forest theme.

He further maintains that a sound knowledge of regeneration processes and of climax stability in any forest can only be gained through a detailed study of virgin areas of forest, both tropical and temperate. No virgin areas are to be found in Europe and few elsewhere in the northern hemisphere; in fact it is believed that the tropical rain forest formation of the Amazon basin is the only large remaining area of near virgin—or at any rate of relatively undisturbed—forest. It is only in the last 150 years that New Zealand forests have been interfered with to any extent and most of the indigenous forests, if at present somewhat affected by exotic animals and exploitation, at least originated in the complete absence of these. Moreover the North Island podocarp forests possess a structure seemingly identical with a formation described by Richards, i.e. the montane rain forest as present in the mountain areas of New Guinea. Common to both are genera such as Dacrydium, Podocarpus, Phyllocladus, Libocedrus, Eugenia, Elaeocarpus, Elatostema and Dawsonia. In fact even in the montane rain forest of parts of Africa can be found genera such as Podocarpus, Sideroxylon, Pittosporum, Schefflera and Cyathea. New Zealand podocarp forests possess a structure intermediate between temperate and tropical rain forest in complexity and studies of the processes within it may give information that will be of value in interpreting forest formations elsewhere.

Mosaic Structure and Cyclical Regeneration in Tropical Forests

The tropical rain forest formation areas characteristically possess a great multiplicity of tree species, usually one to two hundred or more, and a qualitative stratification of the tree components is common. There is usually a discontinuous or emergent “A” storey, either a continuous or a discontinuous “B” storey, and a continuous “C” storey, the components of each storey differing considerably, both floristically and physiognomically. They are floristically different in that species characteristic of the “C” storey are not found in the “B” or “A,” or “B” species in the “A” storey, although immature “A” and “B” species may be found in the “C” storey and “A” species in the “B.” Physiognomically they differ in that the “A” storey component species tend to have umbrella-shaped crowns, those of the “B” storey spherical or pyriform crowns, and of the “C” storey elongated or fusiform crowns.

In forests of the above type it is common to find that there is
little correlation between the occurrence of mature trees and the seedlings of the same species — or even between mature and immature tree stages. Considering only the tree dominants it is often found that seedlings of species typically dominant may be abundant on the forest floor but are of different species to the mature trees on that particular site, the site dominants being only poorly represented. Sometimes it is possible to find an apparent correlation between this phenomenon and seeding habits, or methods of seed dispersal, but more often such an explanation seems quite irrelevant. This lack of immature stages gives the forest an appearance of overmaturity.

M. Aubréville, working in the forests of tropical Africa, and Richards, in those of British Guiana, both found that generally twenty or so species were dominant over an area of forest, but on any one small area only one to four dominants were present; the forest as a whole contained every possible combination of dominants of similar ecological requirements but considered on a smaller scale it fluctuated in composition from place to place. Over any area of forest containing a large number of species a certain amount of gregarity is bound to occur, but what Aubréville found was that the type association was made up of a mosaic of minor associations and these appear to succeed each other more or less cyclically over a unit area during a period of time; in other words, there occurs an association made up of a large number of combinations of dominants in units that are individually constant in composition but neither in space nor in time. No rigid mosaic pattern or invariable successional cycle is pictured—rather a tendency for grouping within an association, this grouping having a more recognizable measure of orderliness than would be expected from any grouping effects due to random dispersal. Nor is it claimed that this mosaic structure is of invariable occurrence for in many areas simple associations and consociations are found that are more or less stable, but these are usually the product of extreme edaphic conditions, such as high salinity or alkalinity. Thus in tropical rain forests stable edaphic consociations on sterile sands have been identified.

Some of the best evidence for Aubréville's theory of forest structure comes from temperate forest areas. In the conifer forests of the Jura Mountains of France and Switzerland there are only two dominant tree species, Silver fir and Norway spruce. Here it has been observed that Norway spruce regeneration predominates where the canopy is largely of Silver fir, and vice versa. This suggests the presence of a cyclic succession, a local association dominated by Silver fir passing in time to one dominated by Norway spruce, while the forest as a whole contains a type association of each species equally dominant — an extremely simple instance of the mosaic forest as described by Aubréville.

In the Balkans and Carpathian mountains Mauve and Iwaschkewitch have recorded sample plots in relatively undisturbed areas of spruce, fir and beech where the composition appears to be fluctu-
ating cyclically, and it is considered that these possess a mosaic structure.

It seems therefore that there is real evidence for the existence of mosaic forests, these areas having a cyclic succession of dominants. The Structure of Podocarp Forests

As mentioned earlier, New Zealand podocarp forests may well belong to a formation close to the tropical rain forest formation described by Richards, and is probably true temperate rain forest. In complexity it is intermediate between tropical rain forest and sub-temperate rain forest and genera characteristic of each can be found within it.

In past or contemporary timber-appraisal and ecological work the podocarp forests have been mapped into type areas using such criteria as proportion of hardwoods to podocarps, composite species, the merchantable volume of timber in the area, topography, accessibility and geographical location without any attempt being made to detect the existence of any other structure within each type area. In considering the regeneration processes of podocarps only superficial observations have been made, and, as in tropical areas it has been difficult to find any absolute correlation between the occurrence of regeneration and of the mature species.

That a cyclic succession may occur is an idea that has received some measure of support from New Zealand ecologists in recent years and the possibility that a cyclic climax may at times exist has also received attention. Nevertheless a predominant attitude of thought has been to consider the podocarp forests as being a sub-terminal stage in a linear succession—a pre-climax composed of light-demanding species which will in time give way to a forest dominated by more shade-tolerant species. This idea has been supported by the general “over-mature” appearance of these forests, pole and sapling stages of podocarps such as rimu and miro rarely occurring under the canopy of mature trees of the same species. In localities such as Mamuku, Te Whaiti and Pureora the appearance of the forest does, at first, sight, suggest that in these areas tawa is an invading species and is replacing the podocarps. Generally the modifying factors to this observation have been overlooked—the slowness of growth of the podocarp species, their longevity and their very poor regenerative potential. When 150 years ago large areas of the North Island were under forests of a mixed hardwood-podocarp type, it seems too easy an explanation to account for the difficulty of regenerating exploited podocarp areas by saying that the species concerned belong to a previous climax and their diminution is an inevitable and climatically governed phenomenon only hastened by our interference. There is little evidence to support the belief that any major climatic changes have occurred in recent centuries and it might well be that had the podocarp forests remained undisturbed they might still be perpetuating themselves successfully and keep on doing so for centuries to come.
With Richards' and Aubréville's work in mind an examination was made of areas of mixed hardwood-podocarp forest in the Whirinaki river valley. So far all work done must be regarded as being preliminary and precursory to more intimate studies, but nevertheless it is already possible to make one or two observations concerning the forest within the area.

Firstly, it is of interest to record that a storied structure exists, but in a double and not the treble layer recorded by Richards in tropical areas; and it is the storey corresponding to the "A" or upper storey of the latter that is absent. In most of the podocarp stands examined there appeared to be a discontinuous upper story of rimu and kahikatea, these possessing crowns that tend to be pyriform or orbicular in outline, with the individual trees from three to seven or more crown diameters apart. Below this, there is a fairly continuous storey of species such as tawa and mahoe, these having crowns varying from fusiform to broadly pyriform, the former being characteristic of immature, trees, a species such as tawa having a narrowly fusiform crown when 15 to 20 feet high which passes to a more pyriform shape as the tree matures. In hardwood dominated localities old trees with approximately pyriform crowns form an upper storey, the lower storey being either absent or else indistinctly formed by a growth of young trees. The stratification described is rather what one would expect as in New Zealand forests one has less intense environmental conditions than are found in tropical areas (cooler air and soil temperatures, lower air and soil humidities, etc.), and a less intensive aggregation of species and layering of canopy results.

In tropical forests the mosaic units detected by Richards appear to be small entities of only a few acres in extent. Similar units were found in some of the podocarp areas examined but in most stands, and particularly in the "better quality" forest carrying a large number of merchantable trees per acre the homogeneous units appear to be some hundreds of acres in extent. The tawa dominated localities are usually of smaller unit area and in association with the latter are kamahi or Quintinia dominated areas. Where podocarps are dominant the only pole stages present are those of hardwoods and mainly of tawa—and under old tawa tree groups good thickets of young tawa are not commonly found. Under the more open kamahi or Quintinia dominated areas regeneration stages of podocarps are often, although not invariably, found.

Qualitative observation indicates that the mosaic structure identified by Aubréville in the tropics probably exists in the Whirinaki podocarp forests but in a modified form and on a larger scale; a podocarp unit within the pattern may be of tens or even hundreds of acres while the hardwood dominated areas are of smaller extent. One suggestion in explanation is that the podocarps have an extremely long-lasting mature stage and therefore are to be found over a large area—possibly the hardwood species pass more rapidly through their mature stages, the regeneration phases of these species being
more prominent. It seems to me, however, that the above explanation is inadequate, for, in other podocarp areas in the Auckland province a greater number of tree species is commonly found and the large areas of what is almost a pure podocarp consociation that are found in the Whirinaki forests (and those of Pureora) are “first rotation” stands and the first high forest growth on areas denuded by heavy showers of volcanic ash, and there is other field evidence pointing to such a possibility. If this is correct the forest may not have, as yet, attained its mature structure and this could be, as some suggest, either a stable hardwood dominated forest, or equally likely, a regular mosaic-type mixed hardwood-podocarp forest, the podocarp components being of smaller unit area than those now present.

Cyclic Succession in Podocarp Forest

The concepts of a mosaic structure existing within a forest and of cyclic succession are inseparable and interdependent.

P. J. Grant has described one area of rain forest in Westland having a cyclic succession of the dominant trees species; I have long considered that similar processes are present in the North Island forests of which I have experience, namely those of the Auckland province. Species taking part in the cycle may vary somewhat with locality but in the Whirinaki forests the following cycle seems likely:

Podocarp-hardwood phase

<table>
<thead>
<tr>
<th>OPEN</th>
<th>podocarp poles</th>
</tr>
</thead>
<tbody>
<tr>
<td>mature podocarp</td>
<td>Quintinia, kamahi</td>
</tr>
<tr>
<td>(6) immature tawa</td>
<td>rewarewa</td>
</tr>
<tr>
<td>(1)</td>
<td>old podocarps</td>
</tr>
<tr>
<td></td>
<td>mature tawa</td>
</tr>
<tr>
<td></td>
<td>(rata)</td>
</tr>
<tr>
<td></td>
<td>CLOSED</td>
</tr>
</tbody>
</table>

V. OPEN podocarp poles

Quintinia, kamahi
rewarewa

(5)

(2) V. CLOSED

old tawa

(4)
kamahi
young tawa

(3)

Hardwood phase

In regard to this cycle, no one stage seems to be able to remain on an individual site indefinitely; the tendency is for a large area of forest of approximately homogeneous altitude, aspect and other general environmental conditions to be made up of a patchwork or mosaic of smaller areas each of which falls into one or other of the stages of the postulated cycle. On any one of these smaller areas the succession pictured in the schematic diagram may occur, but the sequence need not always be invariable or regular; for example, heavy wind damage causing partial or complete destruction of the canopy might short circuit a part of the cycle. Nor is there any rigid stability to the mosaic pattern, each unit being completely dynamic.
Any unusual effect could halt the cycle at some point or other—or cause deviations from the general tendency.

The causes of a cyclic succession are not well understood but it is likely that many factors contribute, all of these being effects governing the establishment or survival of the tree species.

The effect of a varying light intensity definitely plays a part. Podocarp seed, and that of rimu, in particular, can germinate and become established under a dense canopy, but the seedlings cannot grow to any size under such conditions. Thus rimu seedlings may be found under a mature tawa canopy, but rimu poles and saplings rarely, if ever. Podocarp seedlings growing under dense hardwood seem to persist for several years making little root or shoot growth, finally dying through stagnation. A rather similar condition is found in tropical rain forest, where the seedling stage of dominant tree species may last for several years or even decades, a long suppression stage being typical and there is usually a high mortality during this period. Species such as tawa, however, appear to need a fairly dense canopy for their establishment and growth, being a shade loving rather than a shade tolerant species. The mature tree seems to be able to bear full light while the young tree demands quite heavy shade.

Also important are the effects of the canopy trees upon conditions for regeneration. Podocarps give a shallow mor-type acid litter which forms a poor dry seedbed, while a hardwood species such as tawa gives a mull forming litter with a deeper humus layer. Quintinia and old kamahi generally form a mull rather than a mor and have an open canopy which allows a good light penetration to the forest floor.

Little is known concerning the rooting habits of our indigenous trees, or which species are deep rooted or which have their roots mainly in the surface layers of the soil. These are matters which can have profound effects on seedling growth and establishment, particularly in affecting the soil/water relationships of the tree species regenerating. However, so little is known concerning the requirements of the various tree species that it is impossible to say any more about these aspects at present.

Probably important are the various “toxic” effects that mature trees may have upon regeneration, and these include induced acidity effects. It is well known that certain trees form leaf litters which support a high biological activity, while other form litter layers which are extremely resistant to biological breakdown; thus the whole soil profile may, in time, be altered and conceivably the persistence of one species on a site for two or three centuries may result in the site becoming unable to support the growth of further generations of that species, and other species having different requirements, invade and become the site dominants. Less well known is the fact that some tree species either secrete or excrete substances into the soil which in time poison the soil against the growth of that species. This may be the effect observed by Mirams when, while investigating the autecology of
kauri, he found that of all soils tested, that least favourable for kauri seed germination and seedling establishment was collected from under a mature kauri tree. In some instances such toxic effects may be removed by sterilizing the soil and in such cases they are suspected to have a microbiological cause.

These aforementioned and other effects probably combine to control the successional cycles described earlier and it is likely that the controlling factors are periodic or intermittent in operation. Concerning this one prominent ecologist has said: "Climax appears to be undergoing cyclical changes, a generation of trees initiated during a favourable period of the cycle will persist through many succeeding cycles; when conditions become ripe for regeneration it might be well be for regeneration by a different species at a different phase in the cycle." This statement illustrates well the effects of the longevity of species, the continual cyclic change in environmental conditions and the haphazard nature of the processes.

There is no need at present to elaborate upon the effect that extreme soil type may have upon the site climax; for such a consideration would, at present, be of such a hypothetical nature as be of little value. It is sufficient to suggest that, as mentioned earlier, when extremes of environment are reached (say, soil poverty or deficiency, serious water-logging, extreme exposure, high altitude or similar effects), the first result is a limiting of the number of species that can successfully compete for growth on those sites, and a tendency towards the formation of consociations occurs. Examples in the Whirinaki area would be a "stable" low kamahi consociation on a high exposed ridge, or a fuchsia-wineberry-mahoe association in a wet, shaded stream gully.

Discussion

The idea of a mosaic existing in some podocarp forests may, one hopes, help us to understand more completely the ecology of such areas. Future work will, as in the past, be mainly concerned with the typing of forest areas for utilization purposes and for computing timber volumes. However, in research work, while conventional typing might be used as a means of stratifying forest areas into more homogeneous units, any more detailed study might be able to use this mosaic concept to advantage.

The concepts of a mosaic structure and of cyclical succession are inevitably connected, the one being consequential upon the other. The cyclic succession of dominant species over an area must inevitably result in a patterned structure.

The idea of a cyclical succession of dominants, as compared with any monoclimax hypothesis provides a reasonable explanation of the unstable appearance of so many podocarp areas; in the past the general appearance of overmaturity due to the preponderance of the older age classes was taken to be the sign of an outdated and disappearing species; considering the longevity of most species of podocarps it is only to be expected that immature trees would form
only a very inconspicuous part of the association and the "senile" appearance is inevitable. Similarly the apparently invading hardwood species could, in reality, be a phase in the cycle where there is a shorter lived and shade tolerant species, its regeneration and immature stages therefore being more prominent. It is unlikely that the phase dominated by the light-demanding podocarps is of more than one generation, while the phase of shade-tolerant hardwoods could be of several generations.

All things considered, it seems very probable that the mixed hardwood-podocarp forests of the North Island possess a cyclic climax. It is possible that other New Zealand forests, say, the Southland beech forests, or the kauri forests of Northland may also possess a patterned structure and undergo cyclical changes.

There is little of direct economic value in the ideas given; in fact a successful technique for regenerating podocarps has become an academic rather than a practical economic matter. It can be said that intensive regeneration of podocarp species will not be likely unless some means can be found of effectively short-circuiting the natural cycle to reduce or eliminate the closed-canopy hardwood phase. Podocarps will not regenerate to any extent under a canopy dominated by mature podocarps and when a forest is exploited the rapid growth of species that are shade tolerant but light preferring, such as rangiora, wineberry and some coprosmas, precludes the possibility of any podocarp pole-stands developing. Present evidence suggests the following sequence following logging in the Whirinaki valley:

(1) tawa-podocarp mixed forest  (2) damaged tawa and old and faulty rimu.
(3) dense wineberry, rangiora and coprosma, and imperfect drainage
(4) more open type forest with kamahi as a constituent

The broadleaved scrub stage is of indefinite duration.

What is required immediately is a means of facilitating a diversion cycle.

A possible solution would be to fell on a strip or a group system, clear felling ten to twenty-chain wide strips and leaving the alternate strips intact or felling 20 to 30 acre groups and leaving similar areas intact. Then if the felled areas were burnt as clean as possible as soon as possible after logging one or other of the two associations shown above would occur. In time, and if fire is kept out, a manuka dominated vegetation should cover the whole area and, as the manuka matures, kamahi and rewarewa should invade and an ideal nurse-crop for rimu and other podocarps result. The use of staggered fellings on a strip or group system is recommended because most podocarps have such poor regeneration
potentials that any other system, say of leaving of isolated seed trees or seed tree groups is considered inadequate to ensure an infallible seed supply. It would be difficult to give an estimate of the time that would need to elapse between the first and second fellings, but ten years is suggested as being a minimal period. There is no certainty that an area treated in the manner I have outlined would, in time, carry a hardwood-podocarp forest once more—really all that can be said is that given such a treatment an area should have a much better chance of returning to a forest containing podocarps than would a similar area under any current logging methods. The economics of the process have not been gone into but the system should not be unduly costly and is in accordance with current ideas on podocarp conservation—but support from logging and milling companies cannot be expected.

Note:
Throughout this paper “podocarps” is a term used to describe the occurrence or mixture of any of the following species:

- *Podocarpus ferrugineus*
- *Podocarpus totara*
- *Podocarpus spicatus*
- *Podocarpus dacrydioides*
- *Dacrydium cupressinum*

Other plant or tree names used and their full botanical equivalents are as follows:

- Kamahi: *Weinmannia racemosa*
- Tawa: *Beilschmiedia tawa*
- Rewarewa: *Knightia excelsa*
- Rata: *Metrosideros robusta*
- Quintinia: *Quintinia serrata*
- Mahoe: *Melicytus ramiflorus*
- Manuka: *Leptospermum scoparium*
- Wineberry: *Aristotelia racemosa*
- Rangiora: *Brachyglottis repanda*
- Fuchsia: *Fuchsia excorticata*
- Coprosma: *Coprosma lucida* and other species
- Fern: *Pteridium esculentum*

REFERENCES