Implications of dioecy for sustainable forest management

Stan Van Uden*, Glenn H. Stewart** and Richard P. Duncan***

Abstract

The dense podocarp forests of New Zealand, and in South Westland in particular, are unusual in that they are dominated by dioecious trees. Females and males of dioecious species perform different reproductive functions and consequently may use resources in different ways. This differential resource use can result in females and males differing in growth rate, age at maturity, and life span, which in turn can result in differences between the sexes in size distribution, age distribution and number within a population. Differences in growth rate and size in particular could result in one sex being harvested at a greater rate than the other, altering the natural sex ratio — an outcome that may have important implications for the long-term sustainability of managed dioecious forests.

We review the differences between the sexes for the two species studied in New Zealand (kahikatea and rimu) and present additional rimu sex data from differently-aged landforms in Saltwater Forest, South Westland. Female dominated, male dominated, and 1:1 ratios of the sexes have all been found, and in some instances differences in growth rate reported. We discuss the implications of dioecy and differences in growth and mortality between the sexes, and suggest areas of research required, for sustainable forest management.

Introduction

The Forests Amendment Act (1993) requires management of the remaining indigenous forests of New Zealand for timber production to be based on ecologically sustainable silviculture. Sustainable harvest from indigenous forest is aimed at maintaining near-natural forest structure and composition, and emphasis is placed on forests retaining both their natural values and their regenerative capabilities in perpetuity (Ministry of Forestry 1997). In most forests there is no need to take account of gender when selecting trees for harvesting since most forests are dominated by monocious species, where both female and male reproductive structures occur together on each individual. In New Zealand, however, extensive areas of forest are dominated by dioecious conifers, where the female and male reproductive structures occur on separate individuals. Of the native conifer tree species harvested in New Zealand for timber production, eight are strictly dioecious, two are sometimes dioecious, and only one is strictly monocious (Table 1).

We searched the local and international literature and could find little published research on the implications of dioecy for production forest management, or on how harvesting may affect the population structure of dioecious species. This suggests that there is a significant gap in our understanding of dioecious forest management. In this paper we examine the possible implications of dioecy for sustainable forest management in New Zealand.

Table 1. New Zealand conifer species showing which species are dioecious, monocious or both and which species are commercially harvested.

<table>
<thead>
<tr>
<th>Family, genus, species and common name</th>
<th>Dioecious/monocious</th>
<th>Harvested</th>
</tr>
</thead>
<tbody>
<tr>
<td>Araucariaceae</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Agathis australis (katai)</td>
<td>monocious</td>
<td>small amounts</td>
</tr>
<tr>
<td>Cupressaceae</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Libocedrus bidwilli (kahikatea, cedar)</td>
<td>dioecious or monocious</td>
<td>small amounts</td>
</tr>
<tr>
<td>Libocedrus plumosa (balkiri)</td>
<td>dioecious or monocious</td>
<td>no</td>
</tr>
<tr>
<td>Podocarpaceae</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Dacrydium cupressinum (rimu)</td>
<td>dioecious</td>
<td>no</td>
</tr>
<tr>
<td>Dacrydium cupressinum (rimu)</td>
<td>dioecious</td>
<td>no</td>
</tr>
<tr>
<td>Halocarpus banksii (slender pine)</td>
<td>dioecious</td>
<td>no</td>
</tr>
<tr>
<td>Halocarpus laetus (roma pine)</td>
<td>dioecious</td>
<td>no</td>
</tr>
<tr>
<td>Halocarpus ledebourii (slender silver pine)</td>
<td>dioecious</td>
<td>no</td>
</tr>
<tr>
<td>Lepidothamnus lepidophyllus (giggy pine)</td>
<td>dioecious or monocious</td>
<td>no</td>
</tr>
<tr>
<td>Manoom colensoi (silver鄣)</td>
<td>dioecious</td>
<td>no</td>
</tr>
<tr>
<td>Phyllocladus asplenifolius var. altares (mountains manuka)</td>
<td>monocious</td>
<td>no</td>
</tr>
<tr>
<td>Phyllocladus phellolepis (romatra, silver pine)</td>
<td>dioecious or monocious</td>
<td>no</td>
</tr>
<tr>
<td>Podocarpus scandinavus</td>
<td>dioecious</td>
<td>no</td>
</tr>
<tr>
<td>Podocarpus cunninghamii (Whiffs miro)</td>
<td>dioecious</td>
<td>no</td>
</tr>
<tr>
<td>Podocarpus nivalis (new towan)</td>
<td>dioecious</td>
<td>no</td>
</tr>
<tr>
<td>Podocarpus totara (towana)</td>
<td>dioecious</td>
<td>no</td>
</tr>
<tr>
<td>Prumnopitys ferruginea (kawaka)</td>
<td>dioecious</td>
<td>no</td>
</tr>
<tr>
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<td>dioecious</td>
<td>no</td>
</tr>
</tbody>
</table>

Dioecy and population structure

In dioecious species, reproductive costs can be greater for females than males because females are required to put considerable effort into producing and maturing seeds and associated dispersal structures, a process that can span several growing seasons. If more resources are put into reproduction, fewer are available for other functions such as growth and defence, resulting in the females of many dioecious species (1) growing slower, (2) maturing later, and (3) dying earlier than males (Lloyd & Webb 1977). These differences can manifest themselves as differences in the population structure of the sexes in terms of:

(1) Size and age distributions. Because they grow slower and die earlier females may be on average smaller and younger than males (Lloyd & Webb 1977).

(2) Spatial distribution. Males may have higher survival rates and so be more common in harsher environments, such as dry or low nutrient sites, whereas females may occur more frequently in fertile or water sites (Freeman, Kilko & Harper 1976). The scale at which females and males show spatial segregation will depend on the environmental conditions that limit growth and survival and may be influenced by soil type, elevation, topography, drainage patterns, and fertility (Free- man, Kilko & Harper 1976, Lloyd & Webb 1977, Grant & Milten 1979).

(3) Sex ratios. Differential survival will result in the longer-lived sex outnumbering the other. In particular, if females die earlier then the male population will be on average older and the overall population will be male biased (Shea, Dixon & Sharitz 1993). Males have been found to exceed females in both growth rate and longevity, and consequently in both size

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and number, in many long-lived dioecious species (Lloyd & Webb 1977, Shea, Dixon & Sharitz 1993). These differences may be more obvious in harsher environments (Bierzychudek & Eckhart 1988). Nevertheless, there are studies showing no differences between males and females of dioecious species in the above attributes (Marion & Houle 1996).

Potential implications for forest management
Sustainable harvesting practices endeavour to mimic natural forest replacement cycles and maintain the regenerative capacity of the forest in perpetuity. Any harvesting practice that is biased towards removing one sex would alter the natural sex ratio of the forest. While there have been no studies examining the effects of a shift in sex ratio, such changes could potentially alter rates of pollen spread, seed set and overall seed production, and subsequently the rates of seedling establishment and forest replacement. In species producing edible fruits or seeds, a change in total seed output as a result of a shift in the sex ratio could also impact on any animal populations reliant on those food sources.

A sex bias in tree harvesting could occur if males and females consistently differed in size, age, vigour or spatial distribution. For example, in a dioecious species in which males grew faster and lived longer than females, the largest trees would be male. If a harvest of this species aimed to remove only the largest individuals, then these would be male biased, resulting in a shift in the natural sex ratio from male biased towards an even number of males and females. Alternatively, harvesting might aim to remove trees of low vigour. This could result in a female bias in tree removal if females appear less vigorous because of the greater effort they expend on reproduction at the expense of growth and maintenance. Males and females can also differ in their distribution along environmental gradients, with females dominant in one environment and males in another. Small group harvesting or heavy selection of individual trees from a particular environment could then result in a sex bias in tree removal.

If differences in the size, appearance or location of females and males did result in sex biased harvesting, then the sex of trees may need to be a criterion used in tree selection. We next examine what evidence there is that males and females of New Zealand dioecious species differ in ways that could impact on harvesting practices.

Dioecy research in New Zealand
Of all the studies on dioecious gymnosperms in New Zealand only four have examined the population structure of females and males and then in just two species: kahikatea (Dacrycarpus dacrydioides) and rimu (Dacrydium cupressinum). The results from these four studies are inconsistent. For example, Arlidge (1992) studied kahikatea at four sites and found that females were slightly larger than males and significantly so at two sites. In contrast, Molloys (1995a) found that, for the same species in Riccarton Bush (Christchurch), although there was no significant difference in the average size of the sexes in any one of eight study plots, males were significantly larger than females over the whole area. Van Uden (1997) undertook a detailed study of rimu sex structure in a 1 ha plot in Okarito Forest (South Westland).

Of 258 trees that were sexed and aged from increment cores, there were no significant differences between males and females in mean growth rate, age, age at maturity or diameter at maturity.

Similar inconsistencies have been observed in the sex ratio of trees at different sites. Arlidge (1992) found that, although sex ratios in kahikatea were both significantly female and male biased at four study sites (female to male ratios ranged from 1:0.71 to 1:2.39), overall there were more males than females. For the same species Molloys (1995a) also found female and male biased sex ratios in different plots (female to male ratios ranged from 1:0.75 to 1:1.54) but concluded that the overall sex ratio was 1:1. Powenker (1932) investigated the sex ratio of rimu in six plots near Hokitika in Westland. Although he found both female and male biased sex ratios (female to male ratios ranged from 1:0.64 to 1:1.62), none were significantly biased and he concluded that the sex ratio overall was 1:1. In contrast, while Van Uden (1997) found no differences between male and female rimu trees in growth rate, size and age distributions, the sex ratio in his 1 ha plot was significantly female biased (1:0.76 females to males).

The discrepancies in these results could have two sources. First, even if there were no differences between males and females, we would expect natural variability in the size and sex ratio of populations. The apparent inconsistencies in the above results may simply reflect this natural variability. Second, males and females may differ in important ways but these differences change with variation in site conditions. The apparent inconsistencies may then reflect our lack of understanding of the way in which males and females respond to different environments.

Variation in the sex ratio of harvested rimu trees on differently-aged landforms
Because our review of published studies was inconclusive, we were prompted to further investigate sex differences in a recently harvested 2 ha compartment (CPT 5) of rimu in Saltwater Forest, South Westland. This compartment covered two glacial terraces; terrace T4 was formed from outwash by a glacial advance c. 35,000 years ago, and T5 from an advance c. 18,000 years ago (Almond 1996).

616 trees were felled in CPT 5 by Timberlands West Coast Limited in March 1997 and at that time the diameter at breast height (dbh) of each tree was recorded and the stump permanently tagged. We sexed these 616 trees in October 1997 from foliage and reproductive parts in the tree crowns that were left in situ. The presence of seed (female) or cones (male) and foliage with reproductive characteristics in the absence of seed or cones were used for identifying the sex of each tree. Significantly curled branchlets ends and absent growing tips are a distinct characteristic of foliage that has supported female reproductive structures (Figure 1). In contrast, foliage with absent growing tips on generally straight branchlets is a distinct characteristic of foliage that has supported male reproductive structures. Of 258 trees that were sexed and aged from increment cores, there were no significant differences between males and females in mean growth rate, age, age at maturity or diameter at maturity.

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We were able to sex 290 female and 308 male rimu trees (18 trees that lacked sexually mature foliage were not sexed). The sex ratio of felled trees on the two landforms and for all the data combined were not significantly different from 1:1 (Table 2).

Table 2 Summary of the number of females, males and unsexed rimu on each landform and the entire plot, ns = not significant.

<table>
<thead>
<tr>
<th>Landform</th>
<th>Female</th>
<th>Male</th>
<th>Not sexed</th>
<th>Total</th>
<th>df</th>
<th>Sex ratio (female : male)</th>
<th>X²</th>
<th>P</th>
</tr>
</thead>
<tbody>
<tr>
<td>T4</td>
<td>78</td>
<td>91</td>
<td>4</td>
<td>173</td>
<td>1</td>
<td>0.86 : 1</td>
<td>1.000</td>
<td>ns</td>
</tr>
<tr>
<td>T5</td>
<td>212</td>
<td>217</td>
<td>14</td>
<td>443</td>
<td>1</td>
<td>0.97 : 1</td>
<td>0.058</td>
<td>ns</td>
</tr>
<tr>
<td>All trees</td>
<td>290</td>
<td>308</td>
<td>18</td>
<td>616</td>
<td>1</td>
<td>0.94 : 1</td>
<td>0.542</td>
<td>ns</td>
</tr>
</tbody>
</table>

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Figure 1. (a) female Dacrydium cupressinum foliage with cones, and (b) male foliage with fully developed cones

Note that our results do not tell us the sex ratio of the forest as a whole, only of those trees that were felled. There could be a sex bias in felling if the overall sex ratio of CPT 5 was significantly biased towards one sex, so that males or females were being preferentially harvested. There is no evidence to suggest this was the case. Trees were harvested to provide a cross-section of tree sizes from the forest and male and female trees did not differ in their size distributions for the compartment as a whole, nor on individual landforms (Figure 2).

Implications for forest management in New Zealand

The studies of New Zealand dioecious podocarp species reviewed here suggest that we have a long way to go before we understand enough about the implications of dioecy to be sure we are designing sustainable harvesting systems. We suggest an approach for extending these findings to other species, and other locations, that would:

(a) determine whether harvesting practices and forest sex ratios are selectively biased toward one sex,
(b) establish if the spatial distribution of females and males in dioecious species is random or if their distributions are related to landform and/or other environmental gradients, and more ambitiously,
(c) examine what effects any shift in sex ratio in harvested species would have on continued regeneration and growth of the forest.

Acknowledgements

We wish to acknowledge Jan Derks and Timberlands West Coast Limited for logistical support and funding for the collection of data in Saltwater Forest, and Maartje De Deugd for assistance in data collection. We also thank Kit Richards and Dr Rob Allen for reviewing the manuscript and providing many helpful comments.

References

Molloy, B. 1999b. Momoa (Podocarpaceae), a new monotypic conifer
president’s report

Collaboration with IFA
You will recall that, following the 1997 ANZIF conference and meetings in Canberra, several initiatives were raised with our colleagues in Australia to promote a closer professional relationship and some joint action between the IFA and NZIF. At its November meeting the NZIF Council discussed the very positive response which had been received from IFA President Ian Fergusson.

On the matter of professional registration and CPD, Ian advised that the IFA Council had formally decided to introduce systems for professional registration of members and he forwarded draft proposals under consideration by the IFA. There is close alignment between the IFA proposals and the recently introduced NZIF Registration scheme and this will provide a good basis for reciprocal recognition and perhaps in future a common scheme between our two professional bodies.

The IFA Council is also proposing to introduce a complementary scheme for accreditation of forestry degree providers. An NZIF Working Party is looking at whether our Institute should be involved in accreditation of degrees on this side of the Tasman too and a progress report from the IFA Education Committee on accreditation was very useful to their deliberations.

Again, the hope is that we can progress toward either a joint process or at least common criteria for accreditation.

Journal Editor
Editor Hugh Bigsby is on overseas sabbatical until August 1998, and we are very fortunate that we have an acting editor of the experience and ability of Don Mead to maintain production of our flagship during this time. Thank you Don.

Environmental Working Group update

ISO 14000
The ISO 14000 technical report on forestry has been finalised, and subject to ratification through the ISO process should be available for use in mid-1998.

NZ Forest Accord and Principles
The NZIF has been invited to attend future meetings of the NZ Forest Accord and Principles for Commercial Plantation Forestry partners on a permanent basis. The NZIF is not a signatory to either agreement and its independence on issues relating to the Accord and Principles has been noted by the partners. This independence has already proved useful in one particular instance relating to a potential land-clearing operation in North Auckland.

Position Statement on Biodiversity
No comments were received from members on the draft NZIF position statement on biodiversity published in the last issue of NZ Forestry. As a consequence, the draft will be taken to the NZIF Council for ratification, and action items further developed from it.

Environmental Report Card
ISO 14000 and Forestry Stewardship Council are two prominent forms of environmental certification. Both have their weaknesses and do not necessarily meet all market or producer expectations. The NZ Forest Industries Council (FIC) is currently looking at the development of a "report-card" for reporting on a company’s environmental performance. Developed in Canada the “report-card” format is capable of being applied to both forest and processing plant. FIC has convened a working group to pursue the idea.

Next Meeting
The next meeting of the Environmental Working Group will be held in Southland, exact venue yet to be confirmed, on March 12-13, 1998. A visit to Rayonier’s MDF plant at Mataura and discussion with Rayonier on ISO 14000 and Forestry Stewardship Council certification is on the agenda. All NZIF members who wish to attend are welcome to attend and should contact the undersigned.

Tim Thorpe