The Reproductive Biology of the New Zealand Flora

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New Zealand's long isolation from other elements of Gondwanaland, oceanic climate, the unusual combination of ancient Gondwanic, tropical and more recently arrived elements in the flora, and its relatively depauperate pollinator and disperser fauna have set the stage for the evolution of a unique, complex and distinctive reproductive biology. This contrasts markedly with the neighbouring continent of Australia where the fauna is diverse and the flowers vivid. Recent advances in understanding New Zealand's floral biology include evidence that the ancestor to the angiosperms was, very likely, with insect pollinators receiving stigmatic nectar rewards, the discovery of ground-level bat pollination in an obligate root parasite, the finding that the greater resource sensitivity of fruit set in males than in females may account for sex ratio variation in gymnosperms, and, evidence for much more pronounced mass seeding at higher altitudes even in the absence of mammalian seed predators.

For isolated islands such as New Zealand, a relic or dispersed flora must survive with a similarly restricted suite of pollinators and dispersers. Local geomorphic and climatic history then provide a background against which the plant-animal interactions essential to most successful reproduction evolve. The reproductive biology of New Zealand plants has many unusual features: flowers are often small, simple in structure, not showy and of separate sexes, and fleshy fruit and masting are unusually common. The long proportion of annuals and high proportion of woody plants, compared with most temperate floras, may contribute to the frequency of fleshy fruited species. Constraints on the evolution of the flora, particularly those imposed by the depauperate pollinator fauna, have produced an array of more subtle mechanisms that promote pollination. This has supported a long history of reproductive biology research, already well reviewed.

Here we provide an overview of some of the distinctive features of the flora, but focus on recent research that examines the reproductive biology of one endemic retaining many primitive floral features, on pollination mechanisms that overcome the difficulties faced by New Zealand flowers, and on fleshy fruit dispersal and mass seedling.
insect pollination are probably primitive to the whole clade and arose approximately 200 million years ago. The wet stigma of angiosperms may have its origin in the pollination drop of gymnosperms, with the formation of an adaxial stigma allowing closure of the carpel.

**Infrequency of self-incompatibility**

The relative infrequency of self-incompatibility in the native flora has often been commented on, with Godley noting that it had been experimentally demonstrated for only seven species. Since then, self-incompatibility has also been reported for species of *Pseudowintera*, *Corymbia*, *Corylinea* and *Carya*, indicating that the real level of self-incompatibility in the flora is still too poorly known to allow a convincing analysis. However, the apparent low frequency is remarkable given the high proportion of long-lived perennial and woody species in the flora, and the low frequency of annuals (c. 6%). It is likely to be related to the unspecialized pollinating fauna and the long isolation of New Zealand, both of which could impose constraints on dispersal and establishment of self-incompatible taxa—termed ‘immigration selection’.

Details of the nature of the self-incompatibility systems are generally lacking but in *Pseudowintera* self- and cross-pollen enter the micropyle. Pollen-chase experiments where cross-pollen was added one or three days after self-pollen show that ovules can still be fertilized despite self-pollen having reached them. It appears that the incompatibility reaction takes place in the nucellus.

**Simple flowers and despecialization**

Several other characteristics of New Zealand flowers may also have developed as a result of immigration selection. When contrasted with other floras, New Zealand flowers are relatively inconspicuous, with a high proportion of white flowers (60%) and a paucity of blue, purple and red. This is particularly striking in genera that are mostly brightly coloured elsewhere (e.g. *Gentiana* and *Myosotis*). Small flower size and simple structure are other characteristics; the former is sometimes associated with unisexualy but not often with the evolution of selling. Both Godley and Lloyd discussed whether these features developed locally or as the result of migration selection. The absence of heterostyly may be a result of the latter, but despecialization within New Zealand may account for radially symmetric or only weakly zygomorphic flowers in families such as Orchidaceae and Scrophulariaceae, which are characterized elsewhere by strong zygomorphy.

A clear case of despecialization within New Zealand is provided by *Melicytus* (Violaceae). In most species in this Australasian and South Pacific genus, apical appendages on the anthers directly released pollen downwards in a narrow stream. In only three species, all indigenous to New Zealand, the appendages are vestigial so that pollen is released in a less-directed way.

All of these characteristics can be related to the relative paucity of specialized pollinators among all pollinating groups; for example, the relatively few bee species (c. 40) are all short-tongued and primitive.

**Specialized pollination**

Despite the rarity of specialized pollinators, some unusual and specialized pollination systems have evolved in the New Zealand flora. The most remarkable, a recent discovery, is bat pollination in the rare dioecious obligate root parasite *Daucylanthus taylorii* (Balanophoraceae). This species becomes visible only when it produces its usually dull, strongly scented, very nectariferous inflorescence on the forest floor. The flowers are pollinated by the rare endemic short-tailed bat (*Myotis robusta*), which, in a country with few indigenous terrestrial predators, often feeds at ground level. The flowers are pollinated by a variety of short-tailed bats (Myotis sp.) that visit the flowers. These small flowers are pollinated by bellbirds. Delph and Lively suggested that perianths are retained on the plant in the red phase to allow time for pollen tubes to grow down the long style past the point of perianth abscission, and that the green flowers are nectenously developed and serve to focus the birds on receptive rather than post-reproductive flowers.

**Dichogamy and herkogamy**

Less specialized but equally precise are the almost universal pollination mechanisms that separate pollen and stigma presentation in time (dichogamy) and space (herkogamy) in hermaphroditic flowers. In such flowers, pollen dispatch from anthers and its receipt by stigmas often involves contact with a restricted area of a pollinator's body, which creates the
possibility of interference between these two functions. Separation of pollen and stigma presentation enhances pollen transfer and avoids self-interference. However, except for work on vertical inflorescences, research into the selection and function of herkogamy and dichogamy has been largely neglected. Recent reviews provide a framework for studying the mechanisms (Box 1) and give many New Zealand examples.

Herkogamy and dichogamy have traditionally been regarded as outcrossing mechanisms, but their occurrence in many self-incompatible species is strong evidence that enhancing pollination efficiency and avoiding interference are also selective factors. Opportunities therefore exist for examining not only unexplored aspects of flower function, but also selective forces that influence whether plants are herkogamous or dichogamous and whether dichogamous species are protandrous or protogynous.

Herkogamy, in contrast to dichogamy, allows both pollen receipt and dispatch during a single pollinator visit; this has been suggested as the reason for the evolution of approach herkogamy in Gentiana chathamica, a species endemic to the isolated Chatham Islands, and contrasting with the protandry of most mainland New Zealand Gentiana. Dichogamous flowers generally allow greater potential for pollination precision, create the possibility of synchrony across a plant (so reducing gettromony) and allow variation at population level in maleness and femaleness that may be related to climatic factors. The degree of pollination precision may then affect the extent of pollen carryover, as shown for protogynous Myosotis colensoi, where an average 90% of pollen is retained by flies during a single flower visit. New Zealand species of Myosotis are protogynous but the stigmas remain functional during the male phase. In addition, the species may be always herkogamous, initially herkogamous but with extension of the corolla raising the anthers to the level of the stigmas and allowing self-pollination, or never herkogamous with anthers and stigmas in close proximity throughout flower life. These three types probably reflect an outcrossing-selving continuum, with the 'initially herkogamous' system warranting recognition as a separate category of herkogamy or dichogamy.

**Box 1. Dichogamy and herkogamy**

Dichogamy, the separation of pollen and stigma presentation in time, and herkogamy, the separation of these two pollination surfaces in space, are widespread pollination mechanisms in flowering plants. In New Zealand, where the frequency of self-incompatibility appears to be low, they may be particularly important in promoting outcrossing. Recent reviews provided the following classification of dichogamy and herkogamy.

**Dichogamy.** A number of criteria may be used to classify dichogamous flowers or plants:

- **Order of presentation** – protandry or protogyyn.
- **Floral units involved** – intratral or inter floral.
- **Degree of separation of presentation of pollen and stigmas** – incomplete or complete.
- **Average interval between presentation of pollen and stigmas** – a wide range of times.
- **Degree of synchrony of blossoms within one plant** – (a) asynchronous; (b) hemisynchronous; (c) synchronous.
- **Synchronous systems may be further divided as follows** – (a) multi-cyclic; (b) ½ cycle (dihydromony); (c) one-cycle; (d) heterodichogy (two morphs).

**Herkogamy.** There has been much less research on herkogamy but a number of types can be recognized:

- **Homomorphic:** all blossoms of one form, hermaphroditic.
  - (a) Unorded: pollinator contacts with pollen and stigmas within a blossom are usually rare and in no particular sequence.
  - (b) Ordered: usually a single ordered contact with pollen and stigmas – (i) Approach: stigmas placed forward in pollinator path; (ii) Reverse: pollen placed forward in pollinator path; (iii) Movement: stigmas and/or pollen moved into or out of presentation position.
  - Reciprocal: blossoms of two or more forms, all hermaphroditic but differing in presentation position of pollen and/or stigmas. Natrobyte, entomorphogy.
  - Interfarl: blossoms of two or more forms, pollen and stigmas presented in part or in whole in separate blossoms. Monoecic, andromonoecic, gynonomoneccm.

Sexual dimorphism

The high frequency of sexual dimorphism, especially dioecism, in the New Zealand floras has encouraged both experimental research and theory development on sex ratios, the evolution and maintenance of dimorphism, genetic control of sex, and secondary sex characters. The frequency of sexually dimorphic genera is estimated at 18%, higher than for most continental areas and almost as high as recently reduced estimates for Hawaii. The causes of this high frequency are not clear. The specialized pollinating fauna may have encouraged unisexual as a means of producing offspring, although many of the genera unisexual is not peculiar to New Zealand.

The evolution of dioecism from coexuality via gynodioecism has been frequent in New Zealand. Simple control of sex by nuclear genes, as hypothesized for gynodioecious Scandia geniculata, rather than complex nuclear/cytoplasmic factors in many European species, may have facilitated this evolution. The factors determining the level of seed production by the male morph (males are inconspicuous and produce some fruits) and the effect of this on sex ratios have been explored in New Zealand's largest angiosperm genus, Hebe. Clonal experiments suggest that both environment and genetics determine the level of fruit set in male plants of H. subalpina. This suggests the presence of seed-reduction modifiers in males that raise the threshold level of resources required before they set seed.

More importantly, in Hebe strigillissima, the greater plasticity of fruit set on male than on female plants may explain the equilibrium sex ratios of particular populations. Male fruit set is related to plant vigour so that at poor sites male plants produce fewer seeds. Male's relative maternal contribution is then lower explaining a negative correlation between female frequency and average plant vigour.

Recent research shows that, in Hebe subalpina, females allocate more to reproduction than males and that, in Scandia geniculata, males flower at a younger age than...
Table 1. Mast seedling species in the New Zealand flora*

<table>
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<tr>
<th>CV†</th>
<th>Species†</th>
<th>Site</th>
<th>Altitude†</th>
<th>Years*</th>
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*Ranked in order of decreasing variability of seed output.
†CV = coefficient of variation for seed output among years.
‡Other species recorded as masting but where a CV cannot be calculated include Callistemon viminalis, C. viscosus, Olearia colensoi, O. kirkii, D. laevis, Senecio bennettii, Asteraceae; Aciphylla aurita, A. hortensis, Apiaceae; Dracophyllum traversii, Euphorbiaceae; He beeria platys, Malvaceae, Pasquefloraceae colensoi, Araliaceae, Mentha australis, Myrtaceae; Cusplania parviflora, Rubiaceae; Astelia nervosa, Liaceae. The same papers list one Callistemon, two Olearia and two Dracophyllum spp which do not mast.

Altitude of site (m).

Years = length of dataset.

Prumnopitys ferruginea is arguably not variable enough to classify as masting.

Females¹, as expected in dimorphic species. The demonstration that pollen of hemaphroditic flowers is larger than that of male flowers in males of two dimorphic species is less easily explained, but may be a side-effect of sterilization of the gynoecium in male flowers.

Fleshy fruits and animal adaptation

About half the genera with separate sexes have fleshy disseminules. Indeed, many New Zealand plants have fleshy fruit (250 species in 54 families, including 70% of woody mainland forest plants). As fleshy fruits are more frequent on isolated islands, and there are well-known links between bird dispersal, fleshy fruit, dioecism and masting,¹ outside of the main island of New Zealand, pigeons appear capable of dispersing large fruits (>10 mm) between at least 11 native trees. The dispersal distances achieved by birds are rare, but New Zealand pigeons are known to feed on the fruit of a number of species native to New Zealand, including the North Island thrush (Turdus philomelos), the North Island thrush (T. philomelos) and the South Island thrush (T. chilensis).

Variance of seed output (CV)

N. solandri var. cliffortioides, N. menziesii, and N. solandri var. solandri are adapted to subalpine climate. The regression is highly significant (R² = 0.47, F = 18.8, P < 0.001, R² = 0.870 × 0.000799), indicating a strong relationship between altitude and the number of seeds produced per plant. For other species, with small (<3 mm) typically white or blue fruits, lizards may be important dispersers in dry environments.

Fig. 3. Degree of mast (CV of seed output between years) versus altitude of the study site for the data in Table 1. Masting is more pronounced at high altitudes, even though the species recorded there (e.g. Chionochloa pallens, Nothofagus solandri var. cliffortioides) are adapted to subalpine climates. The regression is highly significant (R² = 0.47, F = 18.8, P < 0.001, R² = 0.870 × 0.000799); triangles = Nothofagus circles = Podocarpaceae; squares = Phor痢um diamonds = other species.

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Their involvement is most convincing for divaricate shrubs where the fruits are inaccessible to birds (e.g., Melicytus alpinus fruit, borne under low-growing branches\textsuperscript{35}). Lizards frequently eat fruits, and although their foraging distances are small they have long gut-passage times\textsuperscript{35} (16–72 h compared with 0.5–1 h for New Zealand pigeons), perhaps increasing dispersal distances. The largest gecko known, Hoplodactylus deductivus (now extinct), may once have dispersed large fruits. Overall, the relationships are rather generalized, like fruit-frugivore associations everywhere. While seed germination is often enhanced by removal of the flesh\textsuperscript{10,11} there is no evidence for additional enhancement by passage through an animal\textsuperscript{11}. It has been suggested that the New Zealand pigeon, as almost the sole surviving disperser of seeds over 10 mm diameter, is a keystone species whose local extinction could seriously hinder forest regeneration\textsuperscript{2}. However, this may overstate the importance and effectiveness of bird dispersal of seeds.

**Frequency of mast-seeding species**

Most seeding is very common in New Zealand and is found in species with a range of growth forms, pollination and dispersal mechanisms, and habitats (Table 1), despite the total absence of native land mammals. Elsewhere, mammals like squirrels and rodents are important seed predators. Introduced rodents in New Zealand now eat much seed of native plants, and after a Nothofagus mast year, mouse numbers and then stoat numbers increase markedly, with serious consequences for native birds\textsuperscript{35}.

Masting is much more pronounced at higher altitudes (Fig. 3); this has been previously shown within a species\textsuperscript{35} but not between species. Climate is often a strong proximate factor in determining mast years\textsuperscript{11,13} but the altitude effect shows that, in the absence of any ultimate causes of masting or constant reproduction\textsuperscript{11}, plants would be expected to have somewhat more variable seed output at higher altitudes. Since some high-altitude species do not mast (e.g., Clematis spectabilis, 1200 m, Craigieburn\textsuperscript{35}), Figure 3 should focus our attention particularly on species that mast at low altitudes, or fail to mast at high altitudes.

Norton and Kelly\textsuperscript{35} showed that the ultimate cause of mast seeding is economy of scale, when large reproductive efforts are more efficient than small ones. All of their main economies are represented here. First, native birds and insects may destroy much seed\textsuperscript{33}, and predator satiation seems to favour masting in Chionochloa pallens, an alpine grass which suffers high levels of seed predation (35–94% over six years) by a specialist native choropid fly, Diplotoma similis\textsuperscript{35}. Seed losses decreased when flowering intensity increased, and vice versa. In 1980–1992 (Fig. 4), although losses were low in 1992, apparently because of limited search range of the almost-flightless insect. Secondly, wind pollination provides economies of scale in Dacrydium\textsuperscript{35} and Notholagus\textsuperscript{35,37}, and possibly other podocarps (Table I). Another economy of scale that may apply to the podocarp is attracting bird dispersers to abundant fruit crops\textsuperscript{35}. Thirdly, mastning in Phormium\textsuperscript{35} may be due to high accessory costs of reproduction (a 2–3 m tall flowering spike), combined with attraction of bird pollinators to a large floral display.

Mast years often coincide in unrelated genera such as Nothofagus, Chionochloa and Phormium\textsuperscript{32,35}. Such synchrony may be a by-product of the paucity of suitable cues to trigger mastung, so most species respond to warm summers\textsuperscript{35}. However, the same predator (Diplotoma similis) seems to attack a number of species of Chionochloa, so in this case the observed synchrony between Chionochloa species may be adaptive\textsuperscript{35}.

The wide range of masting species makes New Zealand an ideal place to study the selective advantage of mastung. The only difficulty is the extent of recent extinctions in the native fauna. Although few of the extinct birds were major granivores, changes to the native invertebrates remain largely unknown\textsuperscript{35}.

**Conclusions**

We have now reached a stage where a comprehensive analysis of the reproductive biology of the New Zealand flora, relative to that of other floras, could be attempted. This will be more difficult than for the Hawaiian flora\textsuperscript{35}, where a recent comprehensive taxonomic treatment is available, the geology is well documented and dated, and even the number of original colonizing events has been estimated. For New Zealand, 10% of the higher plants remain undescribed, the reproductive features of many are not known, and the biogeography of the flora is much more complex. However, Lloyd\textsuperscript{3} has provided a theoretical framework by which such an analysis may be approached.

As the sexual systems of many New Zealand plants are well documented, the complexity of some of the species which involve regional variation provides opportunities for testing evolutionary hypotheses on gender selection similar to recent work in Australia\textsuperscript{35}. The evolution of dioecy from hermaphroditism via gynodioecism has been examined in detail, but there are also similar opportunities to investigate the pathway via monoecism. For these plants, allocation to male and female function within individuals, particularly in many wind-pollinated monoecious and dioecious genera, should be examined.

As for most floras, relatively little is known about the evolution of fruit dispersal mechanisms or even the effective dispersal distance of seeds. In contrast a number of long-term studies of seed production continue to shed light on the origins of mast seeding. The existence of sympatric species which differ in
variability of seed output, taxonomic similarity, pollination and dispersal mechanisms, growth form and seed predation provides almost irresistible opportunities to advance theoretical understanding in this field.

Acknowledgements
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References

Human Influence on the Terrestrial Biota and Biotic Communities of New Zealand

Ian A.E. Atkinson and Ewen K. Cameron

Allen plants and animals are of major economic and conservation significance in New Zealand. Plant introductions have averaged 11 species per year since European settlement in 1840, and distinctive landscapes are being increasingly altered by weeds. Many introduced animals act as disease vectors or threaten native biota. Recent studies of introduced weeds show adverse effects on honey-eating and insectivorous birds. Introduced possums are now known to prey on eggs and nestlings of native birds in addition to their impact on native forests and transmissal of bovine tuberculosis. Research is increasingly focused on finding effective methods of biocontrol.

Following the arrival of Polynesians in New Zealand about 1000 years ago, occasional lightning-induced fires were replaced by frequent burning to clear land for crops and habitation. By 1840 this had reduced forest from 78% to 53% of the land area. Some 35 species of landbird became extinct (32% of the landbird fauna including a unique guild of large flightless herbivorous ratites called moa, many of which inhabited forests) (see A. Cooper et al., this issue). The fossil record of the 11 species now recognized terminates by 1600 AD, and archaeological evidence points to hunting by Polynesians as the primary cause.

Dogs and kōre (Rattus exulans) were the only mammals successfully introduced by Polynesians. Kōre appear to have reduced the numbers of many species of small birds, bats, tuatara (Sphenodon punctatus and S. guntheri), geckos, skinks, landsnails and large (>20 mm) flightless insects, some to extinction. The most significant food plants introduced were sweet potato (Ipomoea batatas) and taro (Colocasia esculenta).

In the much shorter period of European settlement since 1840, further native forest has been reduced to 23% of the land area, and 82 species of mammals, birds, and fishes, and more than 1600 species of plants have established (Table 1). Ten more landbird species have become extinct, bringing the total to 40% of the prehuman species.