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Abstract   During 1965–1984 progress in the study of biosystematics of the New Zealand flora has advanced an understanding of the monocotyledonous element more than the dicotyledonous. In *Luzula, Elymus,* and *Cortaderia* experimentally produced hybrids between New Zealand species and overseas taxa have measured gene-exchange, allowed generic realignment or confirmed taxonomic judgements. *Chionochloa,* Gramineae, lies to the forefront in experimental work at specific and infraspecific levels, ecologically, physiologically, biochemically and morphologically, and will continue to yield information needed to comprehend its evolution in New Zealand. Among dicotyledons *Epilobium,* Onagraceae, is the best documented genus because of the extent of the study of experimental hybrids, natural hybridism, gene-exchange, and cytology.

Experimental studies on economically important plants with a long lifespan e.g., *Nothofagus* are few, and even in the study of hybrid asteliads, at the end of 12–13 years there had been no flowering to allow a first assessment of pollen or seed fertility.

Experimental studies needed for the recognition of ecotypes are also few but data and responses to ultramafic soils and geothermally determined soils are available.

Wild hybrids, their frequency, their fertility or sterility, have been studied in a sporadic way, *Epilobium* excepted, and have not yielded the data needed for writing the flora of New Zealand. The Cockayne–Allan pedestal of 50 years ago awaits its column and capital.

Keywords   Biosystematics; New Zealand; natural hybrids; experimental hybrids; fertility; gene-exchange; infra-specific differentiation; ecotypy

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INTRODUCTION

This descriptive account of progress in biosystematics of the New Zealand flora is one part of a symposium to honour Dr E. J. Godley who began work in "Biosystematics' or the 'New Systematics", at Cambridge University in 1945 on *Agropyron* (Godley 1951). This review continues that of my late colleague John Bruce Hair for the period 1945–1964 (Hair 1966), a period which encompassed the post-war boom in botany to which he was a substantial contributor.

Included here are those studies which incorporate the classical biosystematic catalogue of ecotypy, transplant experiments, natural hybridism, measurement of gene-exchange in experimental and natural hybrids, fertility-sterility assessments, and infraspecific differentiation.

Of the main sustaining elements in biosystematics — cytology, genetics, experimental hybrids, morphology, and ecology — substantial contributions in New Zealand have been made in cytology and experimental hybrids.

Cytology

In his review of biosystematics of the New Zealand flora Hair (1966) indicated that the chromosome numbers of just less than 40% of the 1800 indigenous vascular plants were known. Chromosome numbers are now published in the series 'Contributions to a chromosome atlas of the New Zealand flora' for all the taxa that Hair, Beuzenberg, and Groves have examined, and these approximate to half New Zealand's indigenous flowering plants (Beuzenberg 1970, 1975, 1983; Beuzenberg & Groves 1974; Beuzenberg & Hair 1983, 1984; Groves 1977; Groves & Hair 1971; Hair 1967a, b, 1968, 1970, 1977, 1980a, b, 1983; Hair & Beuzenberg 1966, 1968; Hair, Beuzenberg & Pearson 1967; Hair & Kalin Arroyo 1984; Hair, Webb & Beuzenberg 1980; Post 1983).

Because Hair commented at length on the level of polyploidy, both primary and secondary, it is appropriate only to reinforce the generalisations of Beuzenberg (1982) that (i) in many polytypic genera there is a uniform level of polyploidy, (ii) in some genera several levels of ploidy occur, (iii) high secondary basic numbers are found in many genera, and (iv) the highest chromosome numbers yet recorded in the angiosperms are known from New Zealand plants viz. *Poa litorosa* 2n = c. 266 (Hair 1968), and *Olearia albida* (Compositae) 2n = c. 432 (Beuzenberg & Hair 1984).

Experimental hybrids

Godley (1949) in a discussion of hybridism wrote: 'The final experiment to clinch the argument is to synthesise the hybrid from the supposed parents'. The experimental hybrid *Sophora tetraptera* (n = 9) × *S. prostrata* (n = 9) has been made (Godley 1979) in part '.... to clinch the argument ...' that *S. microphylla* arose in New Zealand, and derived some of its present variation, especially its juvenile forms, from *S. prostrata* and from the older species *S. tetraptera*. The presence of juvenile forms is of considerable significance. Extensive studies on *S. microphylla* (Godley & Smith 1977, Godley 1979) showed that the possession of a juvenile form is the rule in South Island, except for *S. microphylla* var. *longicarinata* from northern Nelson. Plants from the Chatham Is, some North Auckland populations, and some central North Island populations lack the divaricating juvenile phase found elsewhere in North Island.

Godley (1979) indicated that *S. prostrata* could not be, as proposed by Cockayne (1912), a fixed or permanently juvenile (neotenous) form of *S. microphylla*, and suggested the reverse, namely, that the juvenile form of *S. microphylla* is derived from *S. prostrata*.

The F_1 *S. tetraptera* × *S. prostrata* grown by Godley (op. cit.), and probably subsequent generations, is critical to his hypothesis; flavonoid profiles should help distinguish stages in the proposed evolution of *S. microphylla* because the suggested parents have distinctive complements (Markham & Godley 1972). The outcome will be important to other parts of the Pacific basin.

The many experimental hybrids made during this twenty year period are central to this review. Any tendency to depend on barriers to crossability for species discrimination seems to have diminished in this same period.

HIGHER PLANTS

Individual taxa studied are grouped and presented under the three major headings of Gymnospermae, Dicotyledones and Monocotyledones. The level of association of taxa into other taxonomic groups is a matter of convenience.

A. GYMNOSPERMAE

The greatest activity in the study of New Zealand gymnosperms in the past two decades has been in taxonomic rearrangements. Of the 20 species in Allan (1961), distributed among five genera, these same species are now allocated to 11 genera (see Edgar & Connor 1983 for summary).

Podocarpaceae

a Natural hybridism

Two natural hybrids have been discussed in the last decade. In *Podocarpus* Wardle's report (1972)

poses the question of the time involved between initial hybridisation and the stabilisation of introgressants; in *Lepidothamnus* Quinn & Rattenbury (1972) reported a hybrid that may be the consequence of longish distance pollen or seed dispersal. Neither problem is simple in resolution.

In south Westland on alluvial valley floors totara is a uniform, stable entity distinct from *Podocarpus totara* var. *totara* in northern and eastern South Island. Wardle (1972) interpreted these south Westland plants, which he named *P. totara* var. *waihoensis*, as the result of introgression between *P. acutifolius* (2n = 34) and *P. totara* var. *totara* (2n = 34).

A very recent origin is postulated for this taxon as Wardle suggests that it was selected and stabilised from among hybrids of *P. acutifolius* × *P. totara* since the return of warmer conditions after the Otiran.

The expansion of *P. totara* var. *waihoensis* following the return to warmer conditions after the Otira glacial maximum would appropriately account for the current distribution. But for initial hybridisation and many generations of recurrent backcrossing to the long-lived, slow-maturing *P. totara*, and for the elimination of *P. totara* var. *totara* itself, the time involved is unlikely to be less than 250 000 years which would place the original hybridisation in the Pleistocene as seems quite logical.

This, so far as I can judge, is one among few recent reports in New Zealand of a hybrid giving rise to a stable and distinct taxon; *Sophora microphylla* has a similar evolutionary background (Godley 1979). In *Epilobium* Raven & Raven (1976) outlined pathways of Pleistocene interspecific hybridisation in species formation. Amphiploidy is not involved in these genera.

Time of formation may also be important in hybrids in *Lepidothamnus*. In that genus, segregated from *Dacrydium* by Quinn (1982), six isolated, uniform populations of infertile F_1 *L. laxifolius* × *L. intermedius* were found in central North Island by Quinn and Rattenbury (1972). In F_1 15_{II} is frequent, but $14_{II} + 2_I$ or $12_{II} + 4_I$ were also found; the hybrid is heterozygous for two paracentric inversions. Cytologically there is no alternative to the parentage suggested because these two species are the only indigenous species where 2n = 30. Hybrid seed was easily produced experimentally.

No plants of *L. intermedius* currently occur in the district, but may have been present in the past, or F_1 seeds on crimson, succulent receptacles could have been transported by birds from some other part of the country. This latter is the least demanding solution. Long distance pollen transport is a possibility and although pollen fertility falls off quickly with time, gymnosperm pollen is reputed to have a lag period of up to 16 h and a relatively slow rate of pollen tube growth (Hoekstra 1983). The least satisfactory solution may involve the elimination of *L. intermedius* from the district some time after hybrid formation.

b Ecotypy

In dioecious *Phyllocladus alpinus*, Wardle (1969) refers to two ecotypes — one "timberline" the other "lowland". Plants on well-drained, rocky slopes above timberline east of the Main Divide in South Island form broad, layering thickets with phylloclades 4–20 mm long; and these contrast with plants bearing phylloclades 10–50 mm long which may become erect trees up to 9 m tall and grow on poorly drained, leached soils at low altitudes in western South Island. The morphological features persisted in plants in cultivation.

Freezing resistance of phylloclades in *P. alpinus*, −10°C for lowland plants, and −18°C and −22°C for those from higher altitudes, coincided with the ecologically and morphologically differentiated lowland and subalpine ecotypes (Sakai et al. 1978, 1981).

B. DICOTYLEDONES

A wide assortment of studies is included here ranging from what Turrill (1940) called the "... simple cultivation under approximately uniform conditions ..." experiment, to the artificial production of interspecific hybrids and reports on natural hybridism.

The arrangement in this section is alphabetical by families.

1. COMPOSITAE

Two genera in the Compositae have been examined for the extent and frequency of natural hybridism, *Senecio-Brachyglottis* (Senecioneae) and *Celmisia* (Astereae). Cockayne & Allan (1934) and Allan (1961) listed c. 30 natural hybrids in *Celmisia* and c. 6 in the shrubby Senecioneae.

These two genera have contrasting taxonomic histories. *Celmisia* has a constant generic treatment, only one or two taxa having been placed in *Aster* by Forster f. The history of generic transfers between *Senecio* and *Brachyglottis* and the debate, is given in Edgar & Connor (1983) and repeated only in its essentials.

An emergent theme here is that despite uniformity of chromosome numbers in the members of both genera, gene-exchange is often limited or constrained.
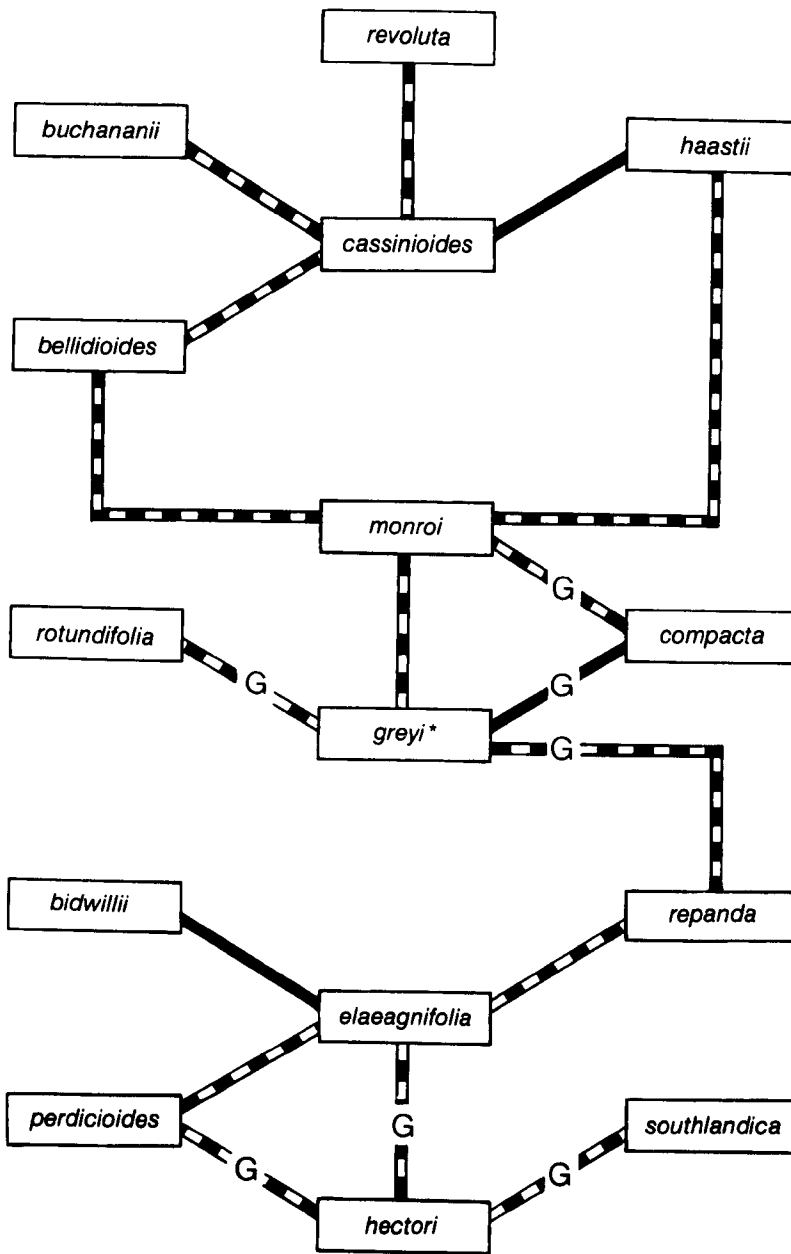
High frequency natural hybrids

Low frequency natural hybrids

G High frequency spontaneous garden hybrids

G Low frequency spontaneous garden hybrids

* includes *B. laxifolia*

Fig. 1 Crossing diagram in *Brachyglottis*; data from Drury (1973); nomenclature after Nordenstam (1978); n = 30 in all taxa (Beuzenberg 1975).

Brachyglottis

The recent taxonomy of the tribe Senecioneae in New Zealand was set in train by Drury (1973) and completed by Nordenstam (1978). The major result is the placing of all shrubby species of *Senecio* in *Brachyglottis* except *S. kirkii* which constitutes the monotypic genus *Urostemon*; the herbaceous *S. lyallii* and *S. scorzoneroides* are segregated into *Dolichoglottis*. *Senecio* s.s. is reserved for species treated by Allan (1961) as *Erechtites* and some herbaceous species.

Drury (1973) had discussed the shrubby Senecioneae and their hybrids, describing the latter in anatomic detail as well as in morphological features. Beuzenberg (1975) reported 2n = 60 for members of the complex and for four hybrids.

Half of the hybrids Drury accepts arose spontaneously in cultivation. Specimens of wild hybrids are usually few (Drury op. cit.), but there are exceptions, e.g., *B. cassinioides* × *B. revoluta*, and *B. bidwillii* × *B. elaeagnifolia*. Most natural and spontaneous hybrids are low frequency hybrids (Fig. 1).

Four species are central in the crossing diagram in Fig. 1:
(i) *B. cassinioides* occurs frequently in natural hybrid combinations;
(ii) *B. monroi* and *B. greyi* link the group composed primarily of spontaneous hybrids from cultivation with two groups of natural hybrids, and
(iii) *B. repanda–greyi* links a second group, mostly of natural hybrids, into the *monroi–greyi* complex.

There is no infrageneric treatment of the group, but as rosette herbs hybridise with trees or shrubs, boundaries separating taxa on crossability grounds may not be easily detected. Jeffrey (1979) indicated some subgroups in *Brachyglottis* (which he treats conservatively as *Senecio*); intergroup hybrids occur, e.g., *B. hectori* × *B. elaeagnifolia* and *B. perdicioides* × *B. elaeagnifolia*. It may be more important to note that *Brachyglottis* was never listed as forming hybrids with *Urostemon* or *Dolichoglottis*, though in this latter natural hybrids are said to occur (Cockayne & Allan 1934).

There may be some gene-exchange between species of *Brachyglottis*, but pollen fertility is often low although in the *B. compacta–monroi–greyi* hybrids pollen fertility exceeds 50%. There are no data on seed setting in hybrids but viable seeds are produced in some backcrosses.

Celmisia

Natural hybrids in *Celmisia* listed in Allan (1961) are based on Cockayne & Allan (1934) but with the rider "...some with good to fair field evidence, occ. supported by herbarium specimens, others more speculative." Given (1984) appended to a revision

of *Celmisia* subgenus Pelliculatae section Petiolatae an up-to-date list of (i) recognisable, (ii) very probable, and (iii) putative natural hybrids between species of that group and taxa from other subgenera. Unlike Drury he used the same techniques for hybrid identification which Cockayne & Allan (op. cit.) had used except that there is one chromosome number and one estimate of pollen fertility reported. Given's list contained two significant features (i) there is little substantive change from the list of natural interspecific hybrids in Allan (1961), (ii) free gene-exchange is probable in three hybrid combinations among 25. Chromosome number differentiation alone does not account for the extent of limited gene-exchange, the same gametic number (n ~ 54) occurring in the species studied except for some populations of *C. gracilenta* and *C. graminifolia*, which cannot at a first glance be implicated as particular parents in the hybrids.

Species of *Celmisia* subgenus Pelliculatae section Petiolatae form high and low frequency interspecific hybrids within the subgenus (Fig. 2); high frequency hybrids are *C. spectabilis* × *C. traversii*, and *C. traversii* × *C. verbascifolia*; *C. cordatifolia* × *C. spectabilis* was formed perhaps once only; *C. mackaui* and *C. hookeri* form no natural hybrids with any species of sect. Petiolatae for reasons of geographic distribution.

The hybrid *C. traversii* × *C. verbascifolia* is the only intrasectional one where, because of the variability in populations, gene-exchange is indicated; the high frequency hybrids *C. spectabilis* × *C. traversii* are interpreted as F_1 plants. Figure 2 illustrates the crossing behaviour for high frequency hybrids within the section.

This array of interspecific hybrids within section Petiolatae contrasts with the high frequency of hybrids and gene-exchange between it and other subgenera (Fig. 2).

Nine species form low frequency hybrids with *C. spectabilis*, *C. traversii* or *C. verbascifolia*, and five species form high frequency hybrids. Among the common hybrids there is evidence of gene-exchange in *C. spectabilis* × *C. lyallii* (*C.* × *pseudolyallii*), in *C. verbascifolia* × *C. lyallii*, and in *C. traversii* × *C. verbascifolia*.

Chromosome numbers for species of *Celmisia* were reported in Hair (1980a). Parent of both fertile and sterile hybrids share the common complement 2n = 108; hybrids between 2n = 108 species and those where 2n = 216 are at a low frequency.

Lee and Given (1984) demonstrated experimentally that *C. spedenii* is physiologically adapted to growth on ultramafic soils in Southland; it is the sole ultramafic endemic in southern South Island.
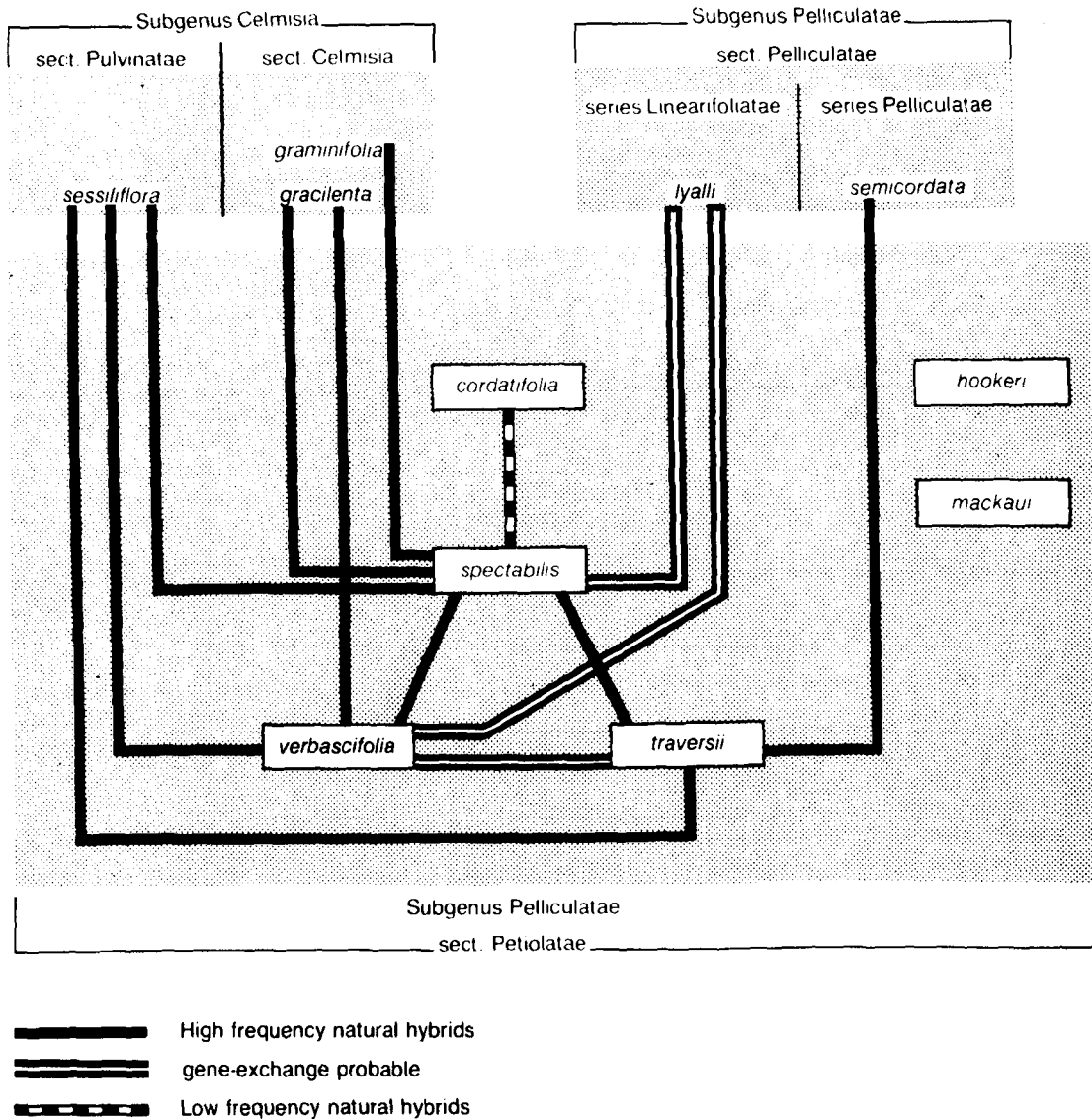
Fig. 2 Crossing diagram in *Celmisia* subgenus Pelliculatae sect. Petiolatae and of high frequency hybrids between it and other subgenera. Nine low frequency intersectional hybrids are omitted. Chromosome numbers in Hair (1980a); n = 54 in most taxa.

Cotula

In cultivation experiments to determine the growth habits of indigenous species of *Cotula*, Lloyd (1981) grew plants from Chatham Is. and the mainland. He showed (Lloyd 1982) that Chatham Is. *C. featherstonii* consists of three distinctive forms: (i) one common to much of the Chathams and its lesser islands, (ii) another, once known as *C. renwickii*, particular to the Forty Fours, a group of small islands 40 km distant and (iii) yet another particular to Pyramid Rock, south of Pitt I. Lloyd interpreted the former as the one which was common to the much larger land mass of the Chathams at the time of the last glacial maximum (c. 20 000 years BP); the others were isolated from this common stock and from each other by a deeper ocean before that glacial maximum. No taxonomic rank is accorded the three forms.

Although primarily concerned with the breeding system in dioecious species of *Cotula*, Lloyd (1975) reported that 563 plants of 163 hybrid combinations (some of them intraspecific) were raised. The hybrids were easily made — even intersectional ones — and F_1's were fertile, but the particular details were not presented. Natural hybrids occur in relatively few combinations, *C. dendyi* × *C. atrata* and *C. albida* × *C. pectinata* being the most common (Lloyd 1972).

Cotula pyrethrifolia var. *linearifolia* was shown by Lee et al. (1983) in experiments with ultramafic and contrasting soils to be an edaphic ecotype of ultramafites confirming Lloyd's earlier suggestion (1972).

Senecio

Sykes (1971) described the behaviour of the Kermadec Is. endemic *Senecio lautus* var. *esperensis* in a cultivation experiment. On the southernmost point of the Kermadec Is, L'Esperance, *S. lautus* grows on sites rich in guano. Sykes grew *S. lautus* var. *esperensis* in a glasshouse for two generations and showed it was a short-lived annual which in cultivation did not retain the height, leaf size, or succulence found in the wild. Leaf shape was fairly constant and also ".. the degree of marginal indentation". He believes that var. *esperensis* behaves as a permanent juvenile because the leaves never become deeply dissected as do mature plants of var. *lautus*.

2. FAGACEAE — *Nothofagus*

The genus *Nothofagus* has not been subject to the genetic or cultivation experiments that are warranted by its ecological and physiognomic importance in New Zealand forests. The work of Wilcox & Ledgard (1983) corrects in part this deficiency and reveals some population differentiation. Seed of the species and varieties of indigenous beeches from 50 localities were sown, and seedlings raised to 2 ½ years old at Rangiora and Rotorua.

In *N. menziesii* (silver beech) leaf size and shape differed, but there was no association between these characters and their localities. Red beech (*N. fusca*) was described as comparatively uniform, provenances not being distinctive in the nursery although some seed lots showed evidence of hybridism with *N. solandri*.

In *N. solandri* three entities were recognised:
(i) var. *cliffortioides*: mountain beech with an erect habit, green triangular, inrolled, distichous leaves in populations from high altitude sites on mountain sides, or at lower altitudes on poorly drained sites;
(ii) var. *solandri*: black beech with an interlacing branching habit, bronze oval to orbicular, flat, distant leaves in populations from ridges or spurs at low altitudes;
(iii) "Undifferentiated *N. solandri*" from sites more mesic than those typical of mountain beech and black beech and from low altitude; so far known only in South Island.

The possibility that "Undifferentiated *N. solandri*" are ancient and stable *N. solandri* × *N. fusca* hybrids is raised by Wilcox & Ledgard (op. cit.) who suggest that allozyme studies may test this hypothesis. The work of Hillis & Orman (1962) suggests that flavonoid analyses may be more easily applied, but the results of those analyses while species specific may not contain as many data as could come from the allozyme studies. The F_1 hybrid made artificially by Poole (1951), *N. solandri* var. *solandri* (n = 13) × *N. fusca* (n = 13), may still be available and would be an important datum.

Differences in *N. solandri* var. *cliffortioides* for freezing resistance of leaves relative to altitude were reported by Sakai & Wardle (1978) and Sakai et al. (1981) and although treated as ecotypic by Sakai & Wardle (1978) the results are probably better interpreted as ecoclinal because of the elevation gradient. But in experiments with plants grown in ultramafic soils and in contrasting soils, and with plants from ultramafic sites and different habitats, Lee et al. (1983) found no evidence of selection for ultramafism in *N. solandri* var. *cliffortioides*.

3. GOODENIACEAE — *Selliera*

Selliera radicans is a small herb with creeping stems and branches found on the coast in sandhills, estuaries and salt marshes, and inland on the margins of streams, lakes and tarns in flushed areas. In New Zealand 2n = 16 (Hair & Beuzenberg 1960); in Tasmania 2n = 16 and 48 (Jackson 1958).

Ogden (1974) conducted a randomised transplant experiment with plants from an estuarine salt marsh population and plants from a sand plain. The two were genetically distinct especially in leaf size and shape, and in flower width and in pedicel length. Plants from the dunes were rhizomatous with appressed leaves but those from the estuary bore erect leaves on stolons.

Ogden (loc. cit.) treats the two forms as ecotypes; there may be others among inland plants. There is no suggestion in Australia that more than one species is involved despite differences in chromosome number.

4. HALORAGACEAE — *Haloragis*

In *Haloragis erecta* (2n = 14) Forde (1964) made over 100 intraspecific crosses, 91 of which flowered in their first year. Pollen fertility was reduced to c. 50% in two families; no estimates of seed-set were possible because the fruit is indehiscent. Forde concluded that there was little evidence of sterility

between regional forms but did not estimate the extent to which gene-exchange could occur. She could not sustain *H. colensoi* as a separate species.

The experimental F_1 hybrid *H. erecta* × *H. cartilaginea* had reduced pollen fertility (52%); F_2 seed did not germinate; both qualities are indicative of some barriers to gene-exchange. Orchard (1975) treated *H. erecta* as two subspecies *H. erecta* ssp. *erecta* and *H. erecta* ssp. *cartilaginea* which appears somewhat contrary to Forde's biosystematic evidence.

5. MYRTACEAE

Leptospermum

Two major experiments with *L. scoparium* (manuka) have been reported recently, Lee et al. (1983) on response to ultramafic soils and Yin et al. (1984) on the seedling behaviour of New Zealand-wide provenances.

Leptospermum scoparium from ultramafic sites was grown in experiments on two ultramafic soils — Red Hill and Black Ridge, Southland — and in a potting mixture; these were contrasted with a population from a hill soil (Lee et al. 1983). No evidence for ecotypic differentiation was detected; and only the Black Ridge soil depressed growth significantly.

Because on Dun Mountain (Nelson) ultramafic soils manuka demonstrated a capacity for accumulating Ni, or Cr and Ni, by contrast with plants from an andesetic site on Mt Egmont, it was regarded as an ecotype by Lyon et al. (1968, 1969, 1970, 1971). As Lee et al. (1983) pointed out, and Yin et al. (1984) also noted, there was no experimental demonstration of ecotypy in *L. scoparium* by Lyon et al. (op. cit.), but all results — Lyon's and Lee's — are concordant and show that tolerance to ultramafites is within the genetic competence of that species.

The evidence that *L. scoparium* is a Cr-accumulator (Lyon et al. 1968, 1969, 1970) on ultramafic sites and without morphological differentiation (Lee et al. op. cit.), is in contrast with genetically determined prostrate forms from gley podzol soils in south western Nelson (see Wardle et al. 1973 p. 624). There is a further contrast between that Nelson genoecodeme and the response to shade and infertile soils in Fiordland which depresses manuka into a rhizomatous shrub whose habit is not genetically determined (Wardle et al. 1973).

Another physiological differentiation was revealed in a study of the relationship between manuka on waterlogged and freely drained soils (Cook et al. 1979). There is some evidence of ecotypic differentiation between populations from Central (dry) and coastal (waterlogged) Otago which

was expressed in terms of the number of layers of aerenchyma, — coast > inland. A difference in cell number, length and width in the innermost aerenchyma layer was not statistically significant.

Manuka seedlings from 17 localities lying between Kaitaia and Stewart Island were measured when 16 months old for seven morphological and habit characters (Yin et al. 1984). The populations could be segregated into four sets:
(i) a high altitude Stewart Island population from 570 m,
(ii) northern North Island populations ranging from sea-level to 330 m and occurring south to latitude 38°S,
(iii) populations from relatively moist sites at low- to mid-altitudes,
(iv) less precisely, populations from relatively dry sites of central North Island and in North Canterbury.

Yin et al. (1984) claim evidence for ecotypic differentiation associated with environmental variables, stating that altitude and distance from the coast are probably the most important in generating the responses.

Manuka is versatile in its responses, and it is improbable that all the variants have been detected in the widespread, habitat-varied species.

Kunzea

Kanuka, until recently always treated as *Leptospermum ericoides*, has been transferred to *Kunzea* as *K. ericoides* by Thompson (1983).

In an area of geothermally determined soils at Karapiti, near Wairakei, Given (1980) described heated ground covered, or almost so, with prostrate *K. ericoides* that did not exceed c. 30 cm in height — "... a habit which is retained in cultivation." In seedlings of *K. ericoides* grown in soil from their original site and in a potting mix, the branching angles indicated that the prostrate habit "... will be retained." The varietal name *microflora* attaches to these plants. Known variability would indicate that it is quite unlikely that there are only two ecotypes in *K. ericoides*, one the typical variety and the other var. *microflora*.

6. ONAGRACEAE

Two genera of the family Onagraceae occur in New Zealand — *Epilobium* and *Fuchsia*. The latter has attracted little recent attention since Godley's study of sex forms (Godley 1955, 1963). That the experimental F_1 *Fuchsia excorticata* (n = 11) × *F. procumbens* (n = 11) was made once again by Diane H. Percy, may easily escape detection, included, as it is, among a list of ornamental species of *Fuchsia* being studied for flavonoids (Williams et al. 1983); no genetic data are yet available.

Epilobium

The monumental programme of hybridisation experiments carried out by the late Walter Boa Brockie with 37 native species of *Epilobium* (Brockie 1966, 1970, and W. B. Brockie in Appendix to Raven & Raven 1976) allowed Raven & Raven (1976) to say "... the New Zealand species of *Epilobium* are probably better known in terms of their crossing relationships than any other group of plants of comparable size anywhere in the world".

Hair (1977) reported 2n = 36 in all species. New Zealand species have the BB chromosomal arrangement characteristic of Eurasian species, but some plants of *E. microphyllum* differing in one reciprocal translocation are B_1B_1.

A summary of the critical data presented by Raven & Raven (1976) on natural and artificial hybrids can be expressed in 10 points:

A Reproductive Biology

i   Self-pollination and self-fertilisation (autogamy) prevail in 33 protogynous species, with cleistogamy obtaining in eight of them; this proportion of autogamy is higher than anywhere else in the world. Three species are allogamous in an appreciable degree together with many populations of a fourth species. Autogamy is the most important constraint to natural hybridism; it is one of the most important attributes in New Zealand in that it ensures the perpetuation of adapted genotypes. Four species strictly autogamous in New Zealand have strongly outcrossing populations in Australia — *E. pallidiflorum, E. billardiereanum, E. gunnianum* and *E. hirtigerum*.

ii   Gene-exchange within natural populations is small; exchange between populations is likely to be even less. The exceptions are *E. chionanthum, E. wilsonii*, some large flowered populations of *E. glabellum* and *E. angustum* which are organised for out-crossing.

B Natural hybridism

iii   Natural hybridism in New Zealand occurs in at least 38 interspecific combinations, and there may be another 10 that could be very difficult, if not impossible, to detect in the wild because of similarity to one parent. This number is vastly in excess of the estimates of natural hybridism in *Epilobium* made by Cockayne & Allan (1934). Perhaps *E. alsinoides* and its three subspecies are more commonly involved than any other individual taxon.

iv   Natural hybridism occurs here between four (and possibly five) indigenous species and the naturalised *E. ciliatum* of North America, and one hybrid with *E. obscurum*, naturalised from Europe, is recorded.

v   High frequency and low frequency hybrids occur; ecological instability is associated with the former more often than not; habitat stability is often associated with the latter.

vi   Sympatry is relatively high. Not all sympatric taxa form natural hybrids, and ecological specialisation precludes, to a considerable extent, opportunities for sympatry.

C Experimental hybrids

vii   Experimental hybrids are easily produced, and Brockie successfully made c. 900 of them. As summarised by Raven & Raven (op. cit.) fertile F_1 which produced F_2's occurred in 75% of the hybrid combinations; 25% of the combinations produced abnormal weak plants which rarely flowered; 2 hybrids were sterile but could be backcrossed. Hair et al. (1977) reported 2n = 36 mostly as 18_{11} in the hybrids, although 16_{11} and a ring or chain of 4 was detected.

viii   (a) 27 species of the 37 in New Zealand are fully intercompatible.

(b) Some species form fertile artificial hybrids with almost all others e.g., *E. rostratum*.

(c) Four peregrinating species — *E. brunnescens, E. pernitens, E. nerterioides, E. nummularifolium* — are intercompatible but do not form hybrids with many other species.

(d) *E. pallidiflorum, E. billardiereanum* ssp. *cinereum, E. pictum, E. alsinoides* ssp. *atriplicifolium* form hybrids with several species but the frequency of abnormal weak plants is very high.

ix   (a) There are no barriers among species at the level of decreased hybrid fertility; even hybrids which are difficult to obtain are fertile.

(b) Failure to set seed is not an active barrier in interspecific hybridisation, nor is failure of seed germination.

(c) Abnormal hybrids apart, and even though reported in 25% of hybrid combinations these may not occur in all circumstances, the New Zealand species form a complex of completely interfertile taxa in contrast with other parts of the world.

x   Hybrids between Northern Hemisphere taxa and New Zealand species are often, but not invariably, of reduced pollen fertility. Seeds may arise from backcrossing to either or both parents.

Autogamy, poorly developed internal barriers to hybridisation, and rather frequent natural hybridism characterise *Epilobium* sect. Epilobium in all parts of the world. New Zealand is no different, except that adaptive radiation during the Pleistocene allowed the development of a large number of species — all 2n = 36 — compared with other countries.

The contemporary taxa here are competent to

exchange genes at a relatively high level, and it is unlikely that they were not so in the past. The contribution made by this historic gene-exchange is assessed by Raven & Raven (1976) as important in allowing recombinants to form, to become protected by prevalent autogamy and habitat preferences, and to have played an important role in the formation of the taxa that now occupy New Zealand, a country which has "... the greatest concentration of species of *Epilobium* found in any region of comparable size in the world".

7. RUBIACEAE — *Coprosma*

Coprosma was among the first genera discussed by Cockayne (1923) when natural hybridism became recognised in New Zealand. Allan (1924, 1926a, 1929b, 1931, 1938) described in morphological detail the artificial interspecific hybrid *C. propinqua*♀ × *C. robusta*♂, and its filial progenies, reporting as well sex-form segregation in F_1 (10♂, 9♀) and F_2 (18♂, 26♀). All generations up to F_3 were fertile (Allan 1940).

Flavonoid analyses by Wilson (1979) showed that plants predicted by A. P. Druce as *C. robusta* × *C. repens*, and *C. repens* × *C. crassifolia* possessed additively the flavonoid spectra of both parents. Later work by Wilson (1984) reports the flavonoid profiles of the species already recognised, and for the undescribed entities that A. P. Druce accepts. The way is clear in *Coprosma* to use these profiles in the analysis of interspecific gene-exchange.

In addition to reporting the chromosome numbers of the recognisable taxa in *Coprosma*, Beuzenberg (1983) listed the chromosome numbers of seven natural and artificial interspecific hybrids. All are regular with $2n = 44$ except *C. depressa* × *C. ciliata* where $2n = 6x = 132$; $2n = 2x = 44$ is attributed to *C. depressa*, and $2n = 4x = 88$ for *C. ciliata* . The hybrid may be an amphiploid involving doubling of the F_1 complement; its continued resemblance to an F_1 interspecific hybrid would thus be assured. Plants of *C. depressa* × *C. ciliata* were not examined by Wilson (1979).

8. SCROPHULARIACEAE

Parahebe

Garnock-Jones & Langer (1980) used multivariate analytical methods and cultivation of 35 populations under uniform glasshouse conditions to study the infraspecific taxonomy of *Parahebe catarractae*. Their analyses revealed discontinuities between four allopatric groups which were ultimately treated as (i) *P. catarractae* ssp. *diffusa* in central New Zealand, (ii) ssp. *lanceolata* in Taranaki and Coromandel, (iii) ssp. *catarractae* in Fiordland, (iv) ssp.

martinii in Marlborough. The geographic distribution can be adequately explained by changes in the land mass of New Zealand since the Otiran.

Grayer-Barkmeijer (1978) identified two flavonoid chemodemes which corresponded to ssp. *catarractae* and ssp. *martinii*, and a third for ssp. *diffusa* and ssp. *lanceolata* jointly. Flavonoid analysis of F_1 hybrids *P. hookeriana* × *P. decora* and *P. catarractae* × *P. hookeriana* showed most of the characteristic compounds of the parents, but in neither was the flavonoid profile completely additive (Grayer-Barkmeijer 1978).

Experimentally made *P. catarractae* (n = 21) × *P. hookeriana* (n = 21) and *P. catarractae* × *P. lyallii* (n = 21) were moderately fertile (Garnock-Jones & Langer 1980); no data were appended. Hybrids *P. catarractae* × *P. lyallii* have been detected in Fiordland; the other combination has been collected on the Volcanic Plateau. Garnock-Jones made intraspecific *P. catarractae* hybrids the parentages of which are not disclosed; they are reported to be "... nearly as fertile as their parents", but there are no supporting data.

Hebe

In *Hebe*, Garnock-Jones & Molloy (1982) showed that dense leaf and stem pubescence in *H. allanii* is dominant over the variable glabrousness seen in *H. amplexicaulis*. Garnock-Jones & Molloy treat the two as one species — *H. amplexicaulis*.

9. UMBELLIFERAE

a Natural hybridism

Although natural hybridism in the Umbelliferae is more frequent in New Zealand than elsewhere in the world (Webb & Druce 1984), New Zealand's umbellifers have received most attention in the last two decades in taxonomic revisions and in studies of reproductive biology (see, for example, Dawson 1967a, b, 1974; Dawson & Webb 1978; Lloyd 1973; Webb 1979, 1981). Chromosome numbers are in Hair (1980b); in *Aciphylla, Anisotome* and *Gingidia* $2n = 22$.

The natural intergeneric hybrid *Aciphylla squarrosa* × *Gingidia montana* from Marlborough is described by Webb & Druce (1984) with details of about 25 individual characters; most are intermediate between the parents. The hybrid was seed sterile and produced 3% stainable pollen. No other putative hybrid involves these two genera. But *Aciphylla* × *Anisotome* is proposed several times (see table 3 in Webb & Druce 1984) even though sometimes qualified by doubt. There is, however, no doubt about the frequency of the interspecific hybrids *Gingidia decipiens* × *G. montana*, *Anisotome haastii* × *A. pilifera*, or *A. aromatica* × *A. haastii*; all are frequent (Webb & Druce op. cit.).

In dioecious *Aciphylla*, a genus of about 40 species, Webb & Druce (op. cit.) lists 27 interspecific hybrids, one third of them involving *A. colensoi*. For once, the list of Cockayne & Allan (1934) is exceeded. Judged solely from the Webb–Druce remarks, gene-exchange between *A. poppelwellii* and *A. scott-thomsonii* is not restricted. The same may obtain in other hybrids.

b Cultivation experiments

The recognition that *Aciphylla townsonii* Cheesem. is a juvenile form of *A. hookeri* Kirk was obtained from a simple cultivation experiment (Le Comte & Webb 1981).

The two taxa were known to coexist in Nelson and Westland. Plants of both, and of a putative hybrid, were transplanted at Lauriston on the Canterbury Plains. During the next year the *townsonii* plants and the suspect hybrids "... began to resemble or exactly match plants of *A. hookeri* ..." The change involved a switch from simple 1-pinnate grasslike leaves to 2-pinnate leaves with short broad segments.

Plants raised from seed of *A. hookeri* begin life with *townsonii* leaves and during the next four years begin, and continue, to produce *hookeri* leaves. Reversion leaves in *A. hookeri* are of *townsonii* form.

10. WINTERACEAE — *Pseudowintera*
Sampson (1980) described in detail F$_1$ hybrids *Pseudowintera colorata* (n = 23) × *P. traversii* (n = 23); pollen fertility of F$_1$ and the parents is > 90%; some fruit was set in F$_1$.

It is generally asserted that *P. colorata* and *P. axillaris* hybridise freely (Allan 1961, Cockayne & Allan 1934, Vink 1970) but Sampson (op. cit.) is unconvinced. Fruits were set after experimental pollination of *P. colorata* by *P. axillaris*. Although *P. colorata* is self-incompatible (Godley & Smith 1981), Sampson is cautious enough to indicate that plants must be raised before he will be sure that he has in fact made a verifiable hybrid.

11. HYBRIDISATION WITH ALIEN FLORA
Two genera in which hybridism was studied involve species and genera now naturalised in New Zealand. Cockayne & Allan (1934) had cited seven cases of hybridism between exotic and indigenous species.

Of the world Aizoaceae only *Disphyma australe* is native to coastal New Zealand; on many parts of the coast *Carpobrotus edulis* and *C. aequilaterus* are naturalised. Chinnock (1972) found 27 chromosome, sterile, intergeneric hybrids F$_1$ *D. australe* (n = 18) × *C. edulis* (n = 9) on both coasts in North Island, and on the eastern coast of South Island. The hybrid (2n = 27) *D. australe* × *C. aequilaterus* is known from Patea only.

Ogden (1978) in a study of *Calystegia* (Convolvulaceae) in New Zealand endeavoured *inter alia* to discriminate native from introduced species and to detect natural hybrids. No experiments, cultural or genetic, were carried out.

His results are interpreted as revealing (i) indigenous *C. sepium* × naturalised *C. sepium*, with the New Zealand element dominant in the gene pool; (ii) suggestive evidence of introgression between *C. sepium* (indigenous) and *C. silvatica* (naturalised); (iii) the possibility of hybrids *C. tuguriorum* (indigenous) × *C. sepium*. Stace (1961) had synthesised the fertile hybrid *C. sepium* × *C. silvatica* in Great Britain.

C. MONOCOTYLEDONES

Genera among five orders are discussed. As with the Dicotyledones there are varied experiments to report, though experimental hybridisation has been more frequently practised than elsewhere among the native plants. Despite this clear preponderance, the range of studies is on much the same scale. Two genera deserve special mention as they were involved in experiments with overseas taxa, viz. *Luzula* and *Elymus*. *Chionochloa*, another grass genus, has an ever-increasing literature.

1. ASPARAGALES
Among the indigenous spathaceous and petalous asparagoid Monocotyledonae three genera of tall tufted herbs, *Phormium* (Phormiaceae), *Astelia* and its segregate genus *Collospermum* (Asphodeliaceae), and one, mostly trees, *Cordyline* (Asphodeliaceae) have been studied experimentally, particularly as interspecific hybrids. In *Cordyline* there are no barriers to interspecific hybridisation. *Phormium* seems equally freely open to hybridisation. Very large differences in chromosome number between *Astelia* and *Collospermum* do not deter hybridisation.

Astelia and *Collospermum*
Astelia is a dioecious genus of 13 species where the flowers are fragrant and nectar is present. It is not regarded as a genus in which hybridism is widespread, and Moore (1966) was unable to confirm the putative hybrids listed by Cockayne & Allan (1934). The chromosome numbers in *Astelia* and *Collospermum* are:
A. banksii n = 35; *A. solandri* n = 35; *A. fragrans* 2n = 70; *A. trinervia* n = 105; *A. nervosa* n = 105; *A. grandis* 2n = 140; *C. hastatum* n = 35; *C. microspermum* n = 35, 2n = 70 (Wheeler 1966; see also Moore 1980).

Wheeler (1966) judged that hybridism took place

between *A. solandri* and *A. banksii* on Rangitoto Is., Auckland Harbour. Pollen fertility of the hybrids was nil; some seed was present in fruits on female plants and may have arisen from backcrossing.

Moore (1980) reported on experimental hybrids among *Astelia* plants, some hundreds of which were in cultivation at Botany Division, Lincoln. There was one successful hybrid, *A. fragrans*♀ × *A. nervosa* S ♂ , among 11 attempts. In the F₁ family there was an evident segregation, 6 plants resembling *A. fragrans* and 3 resembling *A. nervosa*. Moore is very positive that the *A. fragrans* female plant is pure *A. fragrans*, but does not comment on the lineage of *A. nervosa*. The family was lost by misadventure when it was 5 years old and plants had not flowered.

Collospermum, also dioecious, is a generic segregate from *Astelia*. Moore (1980) reported on experimental intergeneric hybrids thus:

i a *C. microspermum*♀ × *A. nervosa* S ♂ : non-flowering; at 12 years one plant resembled *C. microspermum.*

 b *C. microspermum* ♀ × *A. nervosa* S ♂ : the progeny died, morphology unrecorded, by about the time it was 8 years old.

 c *C. microspermum* ♀ × *A. nervosa* S ♂ : at 8 years plants resembled *A. nervosa*; none flowered nor lived to 12 years.

ii *C. hastatum* ♀ × *A. nervosa* B ♂ : non-flowering and smaller than parents.

iii *C. hastatum* ♀ × *A. banksii* ♂ : the hybrids though showing characters of both parents superficially resembled the largest plants of *A. nivicola* of Fiordland! On one plant at 3½ years a female inflorescence appeared, but at 13 years no others had flowered in the then depleted family. Because of flowering time differences Moore thinks this hybrid is unlikely to occur in nature even though the two species coexist in the Auckland area.

In describing interspecific and intergeneric hybrids Moore commented very particularly on age to flowering; she had already described asteliad inflorescences and flowering (Moore 1970). *Collospermum* may flower precociously producing "reduced" inflorescences; adult plants bear well-developed spathes each subtending a simple raceme. Species of *Astelia* of similar size and habit to *Collospermum* do not flower precociously, but produce inflorescences related to their stature and habitat. In intergeneric hybrids the *Astelia* character dominates the precocity known in *Collospermum* except perhaps for one plant in *C. hastatum* × *A. banksii*.

The *Astelia–Collospermum* account contains several unresolved problems some of which were insoluble even after growing hybrids for as long as 16 years. Matrocliny and patrocliny are indicated
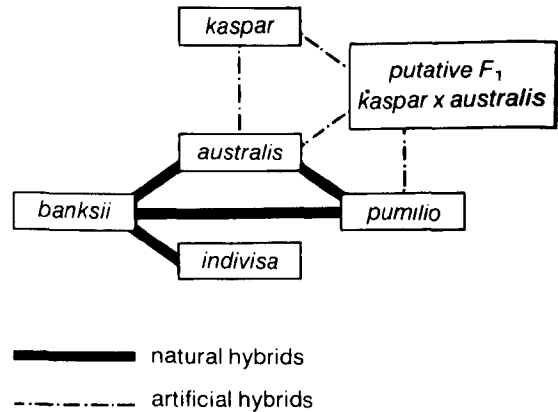

Fig. 3 Crossing polygon in *Cordyline*; n = 19 (Hair & Beuzenberg 1968).

in hybrids where chromosome imbalance would occur. Wheeler's (1966) logical conclusion that hybridism between species with n = 35 and n = 105 was unlikely, is shown not to be so by the experimental hybrids Moore (1980) described. These data Moore said "... should help to give credence to field reports of hybrid asteliads", but should also be noted for studies on the evolution of dioecism.

Field hybrids include *A. solandri* × *A. banksii* (Wheeler 1966); *A. nivicola* × *A. petriei* (Wilson 1976); and possible *A. nervosa* × *A. graminea* (Moore 1980). The hybrid *C. hastatum* × *A. solandri* which interested Skottsberg (1934), though not synthesised by Moore, may not exceed the bounds of possibility.

Cordyline

Of the cabbage trees, *Cordyline*, Moore (in Moore & Edgar 1970) recognised five endemic species; all flowers are fragrant and nectar is plentiful.

Natural hybrids are reported (Fig. 3). The only hybrids unrecorded in nature are *C. australis* × *C. indivisa* and *C. indivisa* × *C. pumilio* (Moore 1975); *C. kaspar* is the sole species on the Three Kings, and is locally endemic there. In all species n = 19 or 2n = 38 (Hair & Beuzenberg 1968).

Cordyline kaspar and *C. pumilio* are self-incompatible (Beever 1981, 1983). Experimental crosses by Beever showed that seed was formed in *C. kaspar* × *C. australis*; a putative F₁ *C. kaspar* × *C. australis* was successfully backcrossed to both species. The same presumed F₁ was interfertile with *C. pumilio*. Abundant seed was set from all pollinations.

Gene-exchange in *Cordyline*, as distinct from hybrid formation, was shown by Moore (1975)

when she grew families from seeds of two hybrid (or putative hybrid) plants. Plants were raised at Botany Division, Lincoln from seeds from a solitary open-pollinated *C. banksii* × *C. pumilio* in the Christchurch Botanic Gardens, and from *C. australis* × *C. pumilio*? seeds from one plant originally from North Cape. Moore assumed that the plant in the Botanic Gardens was either an F_1 hybrid or a segregate from *C. banksii* × *C. pumilio* because it possessed characters specific to each, and because in the families raised from seed at least one *banksii*-type plant occurred. The family from the plant of North Cape origin was not pure *C. pumilio* but contained some *C. australis* influence. It did not flower.

Beever (1981, 1983) who demonstrated self-incompatibility in *Cordyline* hybrids doubted Moore's (1975) basic assumption that the progenies she grew from single plants could take their genesis in selfing. He favoured the view that the hybrid seed parents would be pollinated by some other plants, even by other hybrids. Moore's third generation hybrids (her "second progeny") could have arisen from F_2 interpollination, or from pollination by other species or hybrids in the Lincoln collection.

Whatever their origin, pollen fertility was estimated at 90% in all plants studied by Moore and by Beever except for one plant (C) in *C. australis* × *C. pumilio*?. Seeds were set in Moore's plants just as in Beever's backcrosses. Interspecific barriers in *Cordyline* are genetically insignificant and the self-incompatibility system which operates may effectively increase the extent of gene-exchange by allowing compatible pollination between hybrids and other taxa.

Phormium

The two species of *Phormium* (Phormiaceae) in New Zealand were experimentally crossed by Allan & Zotov (1937). Allan (1940) referred to a large F_1 progeny raised by J. Swindlehurst at Moutoa; that hybrid was *P. tenax* ♀ × *P. cookianum* ♂, the reciprocal of that made by Allan & Zotov. There is no report that hybrids were fertile, but no mention to the contrary is made by Allan & Zotov (op. cit.) or by Boyce & Newhook (1953). In both species 2n = 32 (Hair & Beuzenberg 1966). Hybrids between *P. cookianum* ssp. *cookianum* and ssp. *hookeri*, are reported to occur around Wellington (Wardle 1979).

2. LILIALES — *Libertia*

In *Libertia* (Iridaceae) Moore (1967) recognised four species in New Zealand; there appear to be no hybrids among them.

All four species were grown under more or less uniform conditions at Botany Division, Lincoln.

Chromosome numbers from Hair et al. (1967) are: *L. pulchella* 2n = 2x = 38; *L. peregrinans* 2n = 6x = 114; *L. grandiflora* 2n = 6x = 114; *L. ixioides* 2n = 12x = 228. There is some conflict over chromosome counts, or identification, between Hair et al. (1967) and Kenton & Heywood (1984) who reported 2n = c. 230 in *L. grandiflora* from Nelson, and 2n = c. 72 in *L. ixioides* from Chile.

Libertia grandiflora is self-fertile; plants attributed to this hexaploid species are described by Moore as "... heterogeneous in appearance..." Flowering times are not synchronous for plants from different districts indicating some physiological differentiation. No infraspecific rank was accorded to any variant because she found it was impossible to aggregate the variation. The other hexaploid *L. peregrinans*, by contrast, is very uniform apart from colour and size differences associated with habitat. In dodecaploid *L. ixioides*, plants are strictly tufted and liable to environmental modification of size.

In diploid *L. pulchella* only could Moore (op. cit.) be reasonably sure of fairly clear-cut regional differentiation, but then only for minor characters and again not awarded infraspecific rank. Three phenodemes seem to be indicated: a Westland phenodeme with the range Fiordland to Buller, a northwest Nelson – Buller phenodeme, and a third for North Island plants which extend also south into Nelson. Perhaps the diploid alone is old enough for the evolution of such a diversification to have begun; the higher levels of ploidy may represent progressively less differentiation.

3. JUNCALES

Two genera of small herbs of world-wide distribution *Luzula* and *Juncus* have been involved in interspecific hybridisation studies. *Luzula*, through the efforts of Nordenskiöld (1966, 1969, 1971, 1977), backed by the taxonomic work of Edgar (1966, 1975), can now be seen in an international background of experimental hybrids.

Luzula

Luzula in New Zealand consists of 12 species, but infraspecific differentiation is recognised at varietal level in five of them. All belong in the *L. campestris* – *L. multiflora* complex. All are markedly protogynous. Chromosome numbers are listed in Fig. 4; there is conflict between numbers by Nordenskiöld (1966) and Hair (1967a) over the counts for some taxa.

Hybrids between New Zealand taxa
Nordenskiöld (1966) and Edgar (1966) reported on experimentally produced hybrids.

Two hybrids at the intravarietal level were fertile in F_1 but reduced fertilty and lowered vitality

New Zealand		n	*L. rufa*	*banksiana*	*picta*
New Zealand	rufa	6	3.0	—	—
	banksii	6	2.8	3.0	—
	picta	6	2.7c	3.0c	2.0c
	pumila	6	1.3	—	—
	leptophylla	6	d	d	d
Australia	meridionalis	6	1.8	0.5c	2.0c
	flaccida[1]	6	2.3c	1.7	2.0c
	australasica[2]	6	3.0	3.0	2.5
	novae-cambriae[3]	6	2.3c	2.3	2.0
	modesta[4]	12	0.8	1.0	—
	acutifolia	6	—	1.3	0
Europe	pallescens	6	1.0	0.5	2.0
	campestris	6	0	0	0
U.S.A.	macrantha[5]	6	0.4	0	0
Japan	capitata	6	1.0	0	0.8

[1] reported as *L.meridonalis* var. *flaccida*
[2] reported as *L. oldfieldii* var. *oldfieldii*
[3] reported as *L. oldfieldii* var. *angustifolia*
[4] reported as *L. australasica*
[5] *L.campestris* var. *macrantha*

scale
0 = 0-25 percent fruit set
1 = 26-50 percent fruit set
2 = 51-75 percent fruit set
3 = 76-100 percent fruit set
c = cushion-form in progeny
d = died before flowering

Fig. 4 F_1 fertility of interspecific hybrids with New Zealand species of *Luzula*. All data from Nordenskiöld (1966, 1971); F_1 *L. pumila* × *L. capitata*, and F_1 *L. pumila* × *L. campestris* var. *macrantha* were sterile.

occurred among F_2 L. rufa var. rufa and F_2 L. picta var. picta (Nordenskiöld 1966).

In intervarietal hybrids F_1 was usually fertile, but in F_2 var. rufa × var. albicomans there were chlorophyll-deficient plants, and in var. picta × var. limosa there was reduced fertilty in F_1 (Edgar 1966, Nordenskiöld 1966).

At the interspecific level (Fig. 4) plants of L. leptophylla × L. rufa, × L. banksiana, and × L. picta died; F_1 fertility was high except in L. rufa × L. pumila; chlorophyll-deficient plants occurred elsewhere in all F_2 families (Nordenskiöld 1966).

Genetic relationships between New Zealand and overseas taxa

There are 11 species of Luzula in Australia (Nordenskiöld 1969, Edgar 1975, and see the nomenclatural corrections by Jansen 1978); none is in common with New Zealand. Natural hybrids occur there (Edgar 1975). Chromosome numbers are in Fig. 4.

Interrelationships in Luzula as a whole, including Northern and Southern hemispheres, are described in the additional crossing experiments of Nordenskiöld (1971). New Zealand species crossed with Australian taxa yield relatively fertile F_1; hybrids between New Zealand taxa and Northern Hemisphere taxa are less fertile except for L. picta × L. pallescens (Europe) and L. rufa × Japanese L. capitata.

Nordenskiöld (1971) concluded that in the L. campestris – L. multiflora complex the relationships between regions, as measured by hybrid fertility, are roughly proportional to their geographic separation.

Although F_1 interspecific hybrids between mesophytic New Zealand taxa are the most fertile among all the hybrids Nordenskiöld had produced, their F_2's displayed the highest frequency of abnormalities she had encountered. The presence of cushion plants among F_2 progeny of L. rufa var. albicomans × L. picta var. picta, and in L. banksiana var. banksiana × L. picta var. pallida as well as in hybrids involving graminiform Australian species and L. picta, L. rufa, and L. banksiana, is the more remarkable because the cushion habit is not a feature of these taxa even though in New Zealand the cushion-habit occurs in both the racemosa and campestris – multiflora groups.

As well, a high level of chlorophyll-deficient seedlings occurred in New Zealand hybrids quite unlike Australian experimental hybrids, although somewhat alike to North American hybrids where about 25% of F_2 families contained albino seedlings. In New Zealand, species though self-fertile, are not exclusively self-fertilising, and Nordenskiöld detected a lack of morphological uniformity in progenies grown from seed. Northern Hemi-

sphere plants are, on the other hand, almost exclusively self-pollinating (Nordenskiöld 1966), and produce invariable families.

Natural hybridism, as reported in Edgar (1966) for New Zealand, is supported by the ease of production of fertile hybrids. Their recorded frequency in nature is not high except for L. banksiana var. banksiana × L. picta var. picta, and L. banksiana var. migrata × L. colensoi; none involves species naturalised here.

Juncus

In New Zealand Juncus is a genus with 16 native species and 31 introduced taxa (Healy & Edgar 1980). Edgar (1964a) attempted crosses among native species and achieved about half of the possible combinations. Fertile F_1 progeny was raised in J. australis × J. distegus, and J. distegus × J. gregiflorus which probably also occurs in nature. F_1 J. australis × J. pallidus was infertile — no seed was set on selfing and no pollen shed from the anthers.

Natural hybridisation in Juncus as assessed from evidence from field studies, knowledge of the reproductive systems, experimental hybrids, and a more accurate identification of specimens in herbaria, is unlikely to be a high frequency event. Cockayne & Allan (1934) had listed hybrids among most of the then recognised species.

4. CYPERALES

Two significant cyperaceous genera in New Zealand are Carex, 73 indigenous species, and Uncinia with 32 indigenous protogynous or protandrous species.

Carex

In Carex where Cockayne & Allan (1934) saw about 12 hybrid combinations, Edgar (in Moore & Edgar 1970) failed to confirm rife hybridism. Edgar (1964b) in a detailed morphometric analysis showed that F_1 C. diandra × C. secta occurred at several localities in New Zealand. Sterile pollen is present in indehiscent anthers, and seed-bearing utricles are not found. C. diandra occurs in the Northern Hemisphere as well, and Kükenthal (1909) mentioned some natural hybrids involving it.

Uncinia

Uncinia was subject to controlled cross-pollination by Edgar (in Moore & Edgar 1970). Seeds were set in just over half of those attempted — of which most were intra-series crosses. Inter-series crossing produced endospermless seeds except series Leptostachyae × series Ripariae. No details have since been published about the F_1's.

Cytological examination of 31 species showed $2n = 88$ in all except the two species of series Macrolepidae C. sinclairii ($2n = 94$, $2n = 96$), and C. elegans ($2n = 94$) (Beuzenberg 1970).

5. GRAMINALES

Among indigenous grasses the genus *Chionochloa* has been most extensively studied, as befits the importance of its ecological role in New Zealand alpine and subalpine grassland. Such studies had been urged in 1954 (Sewell et al. 1954). Lower downslope, species of *Festuca* are very abundant and often dominate the grassland landscape; two hexaploid species were involved in a biosystematic evaluation. Though never as common as *Festuca*, the New Zealand members of the tribe Triticeae are important components of several plant communities. Here experimental hybridisation and the measurement of chromosome pairing in those hybrids were used to determine the genomic constitution of the New Zealand taxa and to indicate their generic placement.

a Danthonieae
Chionochloa

Chionochloa is a danthonioid genus segregated from *Danthonia* by Zotov (1963); all 23 species in the genus are found in the New Zealand region except *C. frigida* and *C. pallida* of Australia. *Chionochloa* is one of the most important grass genera in New Zealand; it is the physiognomic dominant over millions of hectares of South Island uplands.

(i) Hybridism

Experimentally produced and spontaneously occurring hybrids between hexaploid (2n = 42) species of *Chionochloa* were reported earlier (Connor 1967); no hybrid was sterile; seed-set was relatively high in most crosses but was lower in two hybrids involving *C. cunninghamii*, and usually higher in hybrids involving *C. rigida*. Pollen stainability was invariably high.

No barriers to gene-exchange were detected except that *C. flavicans*, the rupestral species found from Coromandel and East Cape to Hawkes Bay, did not form hybrids with other species when used as a female parent although it was successful as a pollen parent. Those hybrids reputed to occur naturally were made artificially, or occurred spontaneously in the experimental gardens.

No attempts have been made to produce hybrids between 2n = 6x = 36 species and those where 2n = 6x = 42.

Triterpene methyl ether (TME) composition of the leaf-surface wax provided a methodology to help resolve problems of natural hybridism in *Chionochloa*. Triterpene methyl ethers found in *Chionochloa*, including some novel ones, are listed in Russell et al. (1976), and Pauptit et al. (1984).

On the Paparoa Range, Westland, there are plants that resemble *C. rigida* but these lie outside the expected geographic distribution of this species. Cycloartenol ME was the sole TME present in their leaf wax; *C. rigida* is not known to synthesise this compound. On the Paparoa Range with *rigida*-type plants are (i) *C. flavescens* which in that area does not synthesise TMEs, and (ii) *C. rubra* which synthesises cycloartenol ME (Connor & Purdie 1976b, 1981). We interpreted the *rigida*-type plants as hybrids between *C. rubra* and *C. flavescens*.

Chionochloa flavescens × *C. rubra* is the hybrid most frequently found: it is at least on the Tararua Range (Greenwood 1953, Druce 1957, Williams et al. 1978c), at Jacks Pass, Marlborough, (Connor 1967), in Central Otago (Williams et al. 1978a), and on the Paparoa Range (Connor & Purdie 1981).

Williams (1975) reported an increase in *C. flavescens* × *C. pallens* hybrid frequency with increasing altitude on the southern Tararuas; in South Island at various sites Williams et al. (1978b) invoke hybridism between *C. pallens* and *C. rubra*, and *C. pallens* and *C. macra*, and suggest "...obvious introgression between several taxa at ..." Temple Basin where *C. crassiuscula*, *C. flavescens*, *C. pallens* and *C. rubra* co-occur. There are no supporting data. On Mt Stokes *C. pallens* × *C. flavescens* is not infrequent (Park 1968).

Purdie and I found little or no evidence for contemporary interspecific gene-exchange as measured by TME presence, although we sampled at many sites where several species were sympatric. At the level of gene-exchange and introgression, the TME profiles of some chemodemes of *C. pallens*, and of *C. flavescens*, are suggestive of an ancient hybridisation and persistent backcrossing in one direction (Connor & Purdie 1976b, 1981). In particular, *C. pallens* from the vicinity of its *locus classicus* clearly indicates the possibility of a parkeol ME – arundoin penetration of the cycloartenol ME chemodeme at some time in the past. A possible donor is *C. rubra* from its north. From the same locality, Mt Holdsworth, *C. flavescens* was undoubtedly influenced by a species which synthesised miliacin and arundoin; no lupeol ME, characteristic of *C. flavescens* on the Rimutaka Range and in Nelson-Marlborough, was isolated from Mt Holdsworth. The miliacin-arundoin contributor to *C. flavescens* is most likely to be *C. rubra*, but a chemotype of that composition has, at present, a north Canterbury–Nelson distribution. The evident contradiction is that two distinct chemotypes of *C. rubra*, one northern and the other southern, are invoked for two events at one place. The two events need not have occurred at the same time, but there is no method of demonstrating such a possibility, no more than suggesting that *C. rubra* alone is the donor species.

(ii) Infraspecific differentiation

Some species have been studied in detail at the infraspecific level, in particular the three wide-

spread species *C. flavescens*, *C. pallens* and *C. rubra*, and, to a lesser extent because of its more restricted distribution, *C. rigida*.

Chionochloa flavescens because it is so clearly site-selective in eastern South Island, and because those plants are so ecologically, morphologically, and physiologically different from those on the Tararua Range, (type locality, Zotov 1963), has incited discussion, experiment and debate led by P. A. Williams.

Williams (1975) and Williams et al. (1976, 1977, 1978b) argued very persuasively that the ecological similarity between *C. flavescens* Tararua Range and *C. flavescens* Murchison Mountains, Fiordland, should be matched by a taxonomic similarity, and that eastern South Island phenodemes attributed to *C. flavescens* should be distinguished in some taxonomic way. Connor & Purdie (1976b, 1981) offered some taxonomic realignment by treating "Fiordland *flavescens*" as the β-amyrin methyl ether chemodeme of *C. rigida* which extends on leached soils in western South Island from Lake Kaniere to at least Doubtful Sound (Fig. 7). Veritable *C. flavescens* extends in south Westland to the Clarke River at least. For eastern South Island *C. flavescens* they did not proffer any solution; those plants do not synthesise triterpene methyl ethers and are biochemically distinct from Tararua Range plants which synthesise arundoin and miliacin.

Bell (1973), working in the Owen Range in Nelson, found what he referred to as *C.* sp. aff. *flavescens* was calcicolous, dominating on marble and on calcium-rich soils at lower altitudes. Connor & Purdie (1976b) found that it synthesises lupeol ME as do all Nelson Province plants of *C. flavescens*.

There is a good element of agreement for South Island with what Burrows (1967) recognised in *C. flavescens*: thus the western Nelson form is the lupeol ME chemodeme; plants from the Haast Pass and throughout Fiordland are the β-amyrin ME chemodeme of *C. rigida*; the central South Island form with leaves c. 14 mm wide is the phenodeme of young sites; and the Stewart Island population is differentiated by the synthesis of a mixture of miliacin and arundoin (Connor & Purdie 1981). No TME analyses were made of *C. flavescens* from Mt Stokes, Marlborough, which A. P. Druce in Park (1968) ascribed to the Tararua Range phenodeme; Purdie and I are therefore unable to comment.

Chionochloa pallens is a common enough mountain species in South Island but is restricted in North Island to the Tararua and Ruahine Ranges. Burrows (1967) distinguished North Island populations from South Island ones, but did not describe the differences. In South Island he recognised four kinds. A. P. Druce in Park (1968) considered the forms of *C. pallens* on the Tararua Range and Mt Stokes, Marlborough, to be the same.

In North Island Williams et al. (1977) recognised that *C. pallens* north of the type locality in the Tararua Range produced more robust shoots and leaves less V-shaped in section. In South Island Williams et al. (1976) identified a phenotype which extends from Fiordland to a line connecting the Godley Valley in the east and the Cook River in the west (Fig. 5); these plants are robust with broad flatter leaves, and their blades disarticulate at the ligule. In *C. pallens* north of that line blades are persistent (Williams et al. 1977). These characteristics remained in plants grown in pots. Genes controlling leaf blade abscission have no ecological or geographic coincidence with any other genes recognised to date.

Triterpene methyl ether analyses revealed infraspecific chemodemes in *C. pallens* (Connor & Purdie 1976b, 1981); chemodemes synthesising cycloartenol ME are separated by a miliacin chemodeme of central and southern South Islands (Fig. 5). Interspersed among this pattern is a sporadic distribution of arundoin, either on its own or in combination with miliacin, but never with cycloartenol ME except at Field Peak in the Tararua Range where parkeol ME intrudes as well.

In *C. crassiuscula* of higher South Island altitudes, there are two chemodemes: a northern miliacin chemodeme reaching to Fox Glacier, and an arundoin chemodeme south of there.

Red tussock, *C. rubra*, does not display triterpene methyl ether diversification to the same extent as other equally widely distributed taxa (Fig. 6). The only distinctive series of populations are (i) a cycloartenol ME chemodeme from mid-altitudes (c. 1000 m) in Westland on terraces with modestly young soils, (ii) a parkeol ME-arundoin chemodeme of the Volcanic Plateau in North Island and, less definitely, (iii) a miliacin-arundoin chemodeme from northern South Island.

Chionochloa rigida is distinguished in western South Island by the presence of a β-amyrin ME chemodeme; for the rest, non-synthesis of TMEs is characteristic (Fig. 7). In a species of even more restricted distribution — *C. cheesemanii* — two chemodemes are found. North Island populations synthesise two additional TMEs (which have not been identified to date) and these discriminate it from the South Island chemodeme (Fig. 7); lupeol ME and arundoin are common to both.

Lipid composition of leaf wax (Cowlishaw et al. 1983) showed infraspecific differentiation of much the same order as with TMEs.

These results emphasise that the geographic distribution of a number and a variety of genes, or gene complexes, in species of *Chionochloa* has become well documented, but the relationships between those genes and ecological factors remain unanswered.
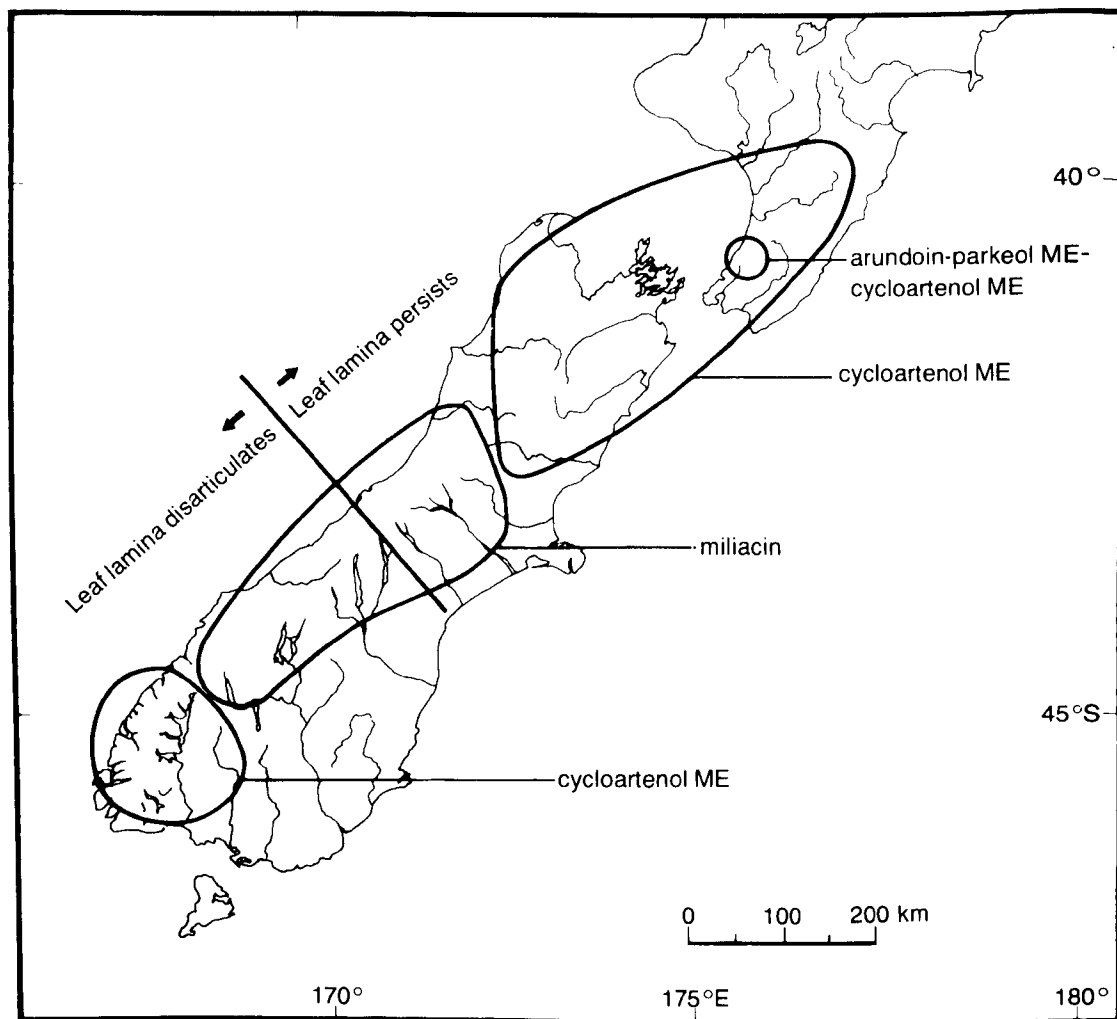
Fig. 5 Triterpene methyl ether distribution in *Chionochloa pallens*.

(iii) Cultivation and transplant experiments

I can find no evidence that I recorded of *C. macra*, that when grown under uniform conditions with other species of *Chionochloa*, it retained its characteristic slim stature, short leaves, early flowering, and non-chaffing sheath. This was, however, important in urging the formal recognition of the taxon because it could be shown that plants in culture for 5–10 years could be distinguished from a range of species. While I never acknowledged these data, neither did Zotov (1970) when he described *C. macra*, but it was a lesser concern to him; Molloy & Connor (1970) are also silent. Mark (1965) showed that in cultivation at Dunedin it retained its characters just as it did at two other sites.

Mark (1965) conducted reciprocal transplant experiments mostly with *C. rigida* in Central Otago.

Although Mark (op. cit.) identified two ecotypes in *C. rigida*, one of them from high altitudes was later recognised by Molloy & Connor (1970) as *C. macra* Zotov and thus its status as an ecotype is to be disregarded.

Growth and development was recorded in Otago populations of *C. rigida* from (i) Maungatua 870 m, (ii) Old Man Range (OM) 910 m (iii) OM 1220 m cross-transplanted, including 1590 m on OM and in the University garden, Dunedin, (Mark, 1965). Of total variance in tussock growth, about 40% was attributed to the genetic variation contributed by the populations.
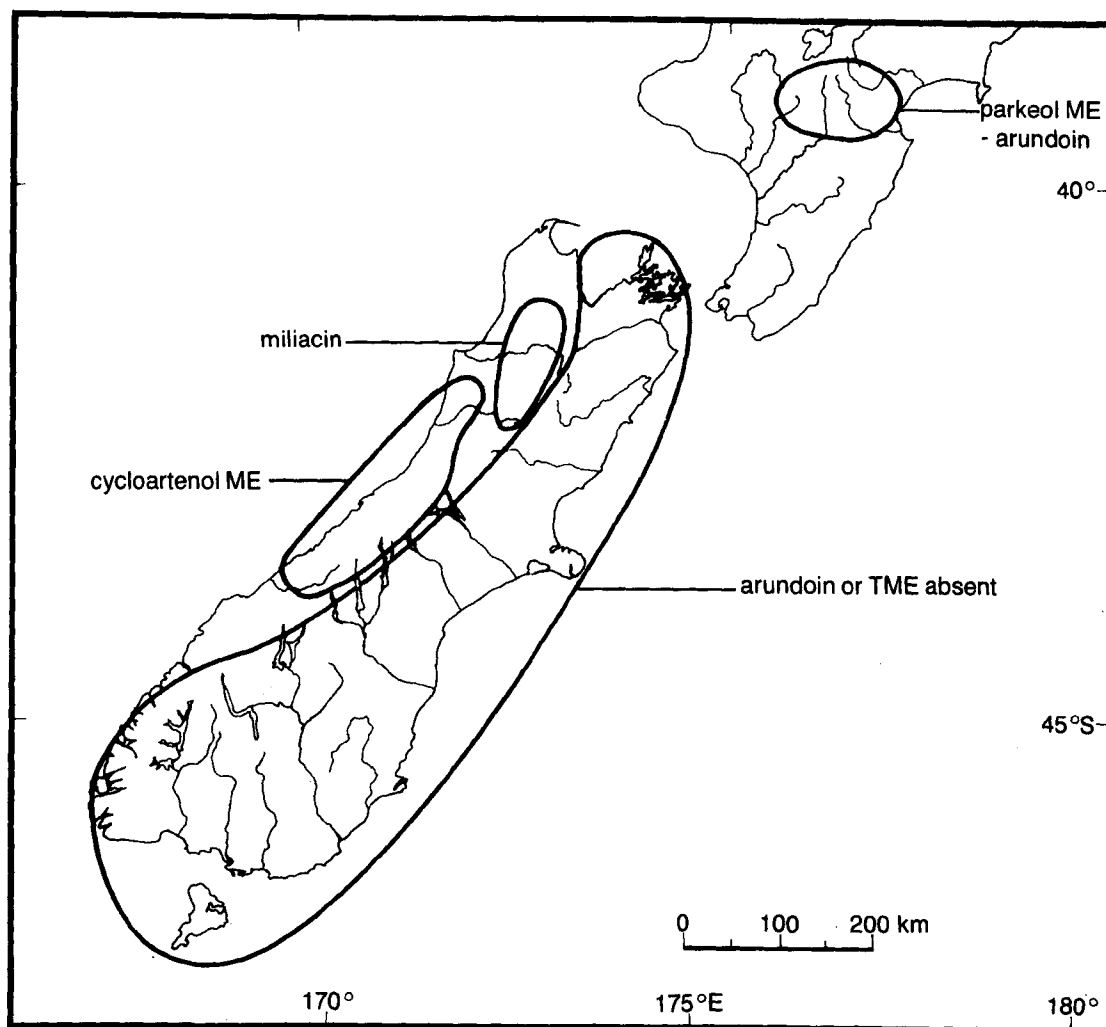
Fig. 6 Triterpene methyl ether distribution in *Chionochloa rubra*.

Mark (1965) showed that the transplants tended to become the same size as resident tussocks, but that the relative order of height was preserved, indicating genetic determination. Inflorescence height was influenced both by the environment and the genetic background.

Greer (1979) re-reciprocally transplanted clones over the same sites to determine the effect of long term (14 years) preconditioning on subsequent growth. He indicated that his results, like those of Mark, revealed a strong genetic component in differences in growth pattern associated with altitude of origin. He further recognised ecotypic differentiation in a lowland population from Shag Point, a population which he introduced into the trials but which Mark had not grown.

The results from these experiments were interpreted by Greer as revealing a high level of inherent infraspecific plasticity for leaf growth and flowering. This plasticity he attributed to post-Pleistocene selection pressures during a period when there was a very variable climate, especially during the last 5000 years. That inherent flexibility has been reinforced by, or even overtaken by, recently evolved local variants adapted to positions on the altitudinal range of the species in Otago. But no evidence for differences in photosynthetic activity was discovered by Greer (1984) which would support that particular hypothesis.

Recency in the evolution of localised biotypes is visualised by Mark (1965) and by Greer (1979) after *C. rigida* expanded its territory by occupying in
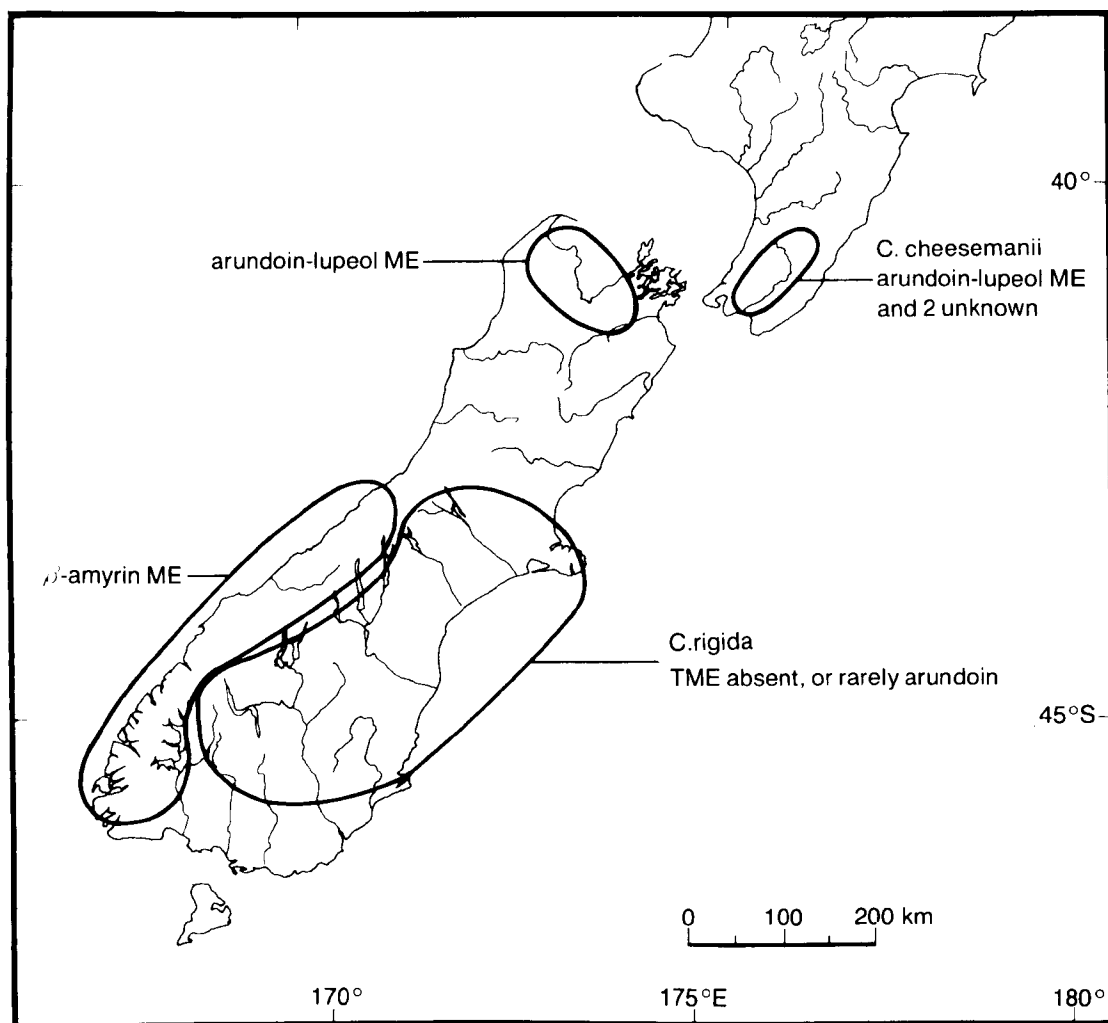
Fig. 7 Triterpene methyl ether distribution in *Chionochloa rigida* and *C. cheesemanii.*

quite recent times (c. 1000 years) land formerly under forest, (see Molloy et al. 1963; McGlone 1983).

What Mark and Greer described in *C. rigida* could adequately be identified as a combination of the alpine genotypes from upslope and the contribution made by smaller populations from subalpine and montane sites.

I had proposed earlier (Connor 1964, 1967) that gene-exchange between populations of *C. rigida*, which had become free to exchange genes after the removal of barriers separating them for long periods, would contribute to its plasticity. There was no evidence for it then, and there is none now because intraspecific gene-exchange remains unexamined.

The only inter-regional comparison of growth in *C. rigida* or *C. macra* is that of Williams (1977) who compared leaf growth and leaf death in plants in the Ashburton Catchment, Canterbury, with those of Mark (1965) and Rowley (1970) in Otago. Relative to Otago the peak of leaf elongation in both species occurred a month earlier in Canterbury; leaves did not die-back as extensively in autumn; there was no marked increase in leaf longevity with altitude. These comparisons might indicate physiological differences between *C. macra* and *C. rigida* in the two provinces but, because of

difficulties in the interpetation of growth *per se*, Williams cautioned care in their interpretation. Nevertheless, these Canterbury results and those from Otago indicate incipient ecotypy, the population from sea-level excepted.

This discussion on ecotypy has concentrated around eastern South Island *C. rigida*; there are data which allow the conclusion that western South Island and Fiordland β-amyrin ME *C. rigida* is ecotypically differentiated from that in the east, and that in *C. flavescens* ecotypy is evident. But in many widespread species, the nature of the relationship between ecological and morphological differentiation is unexplored. *Chionochloa* remains a treasure trove.

Cortaderia

Cortaderia, the first grass in which gynodioecism was recognised (Connor & Penny 1960), has been extensively studied (see Connor 1974). The four indigenous ($2n = 10x = 90$) species preserve their distinctive characteristics in cultivation at Botany Division, Lincoln.

Interspecific hybrids are easily made and were used primarily for studies on the inheritance of male sterility (Connor 1965b), and for the genetics of the synthesis and inheritance of triterpene methyl ethers (Martin-Smith et al. 1967, 1971; Connor & Purdie 1976a). F_1 fertility is very high (Connor 1983); percentage seed-set in selfed hermaphrodites of F_1 *C. richardii* × *C. fulvida* was 71.0, 71.2, 82.2, 83.8 (Connor 1983) and in F_1 *C. toetoe* × *C. richardii* was 74.0, 74.3, 87.6.

No intrinsic barriers to gene-exchange have been detected among the four indigenous species, but the opportunities for natural hybridisation are few because of differences in flowering times and geographic distribution (Connor 1965a). I know of no natural hybrids, though *C. splendens* × *C. fulvida* is a possible combination in North Island and would leave viable descendants.I indicated (Connor 1965a) that hybrids between the naturalised sexually reproducing Argentinian–Uruguayan *C. selloana* ($2n = 8x = 72$) and decaploid indigenous species were improbable because of (i) chromosome imbalance, (ii) time of flowering difference, and (iii) geographic distribution differences that would limit many combinations. The sterile ($2n = 9x = 81$) F_1 *C. toetoe* × *C. selloana* was made experimentally by using an out of season flowering *C. selloana* as male parent. In the F_1 family there are vigorous plants as well as some that are genetically inharmonious. There will be no genes exchanged between the two; there may be no genes exchanged in a parallel hybrid *Nothofagus menziesii* (New Zealand) × *N. obliqua* (Chile) which has occurred spontaneously in Britain (Wigston 1979).

In the experimental sterile F_1 hybrids *C. araucana* (Chile, n = 36) × *C. toetoe* all plants were of female sex-form (Connor 1983). This hybrid family, and the sterile *C. toetoe* × *C. selloana* family, confirm the taxonomic relationship accorded them only recently by Zotov (1963).

The other naturalised species of *Cortaderia* found in New Zealand, *C. jubata* ($2n = 12x = 108$), is autonomously aposporous (Philipson 1978); it will not be involved in genetic intrusion into the other five species found here.

b Triticeae
Elymus

The New Zealand wheatgrasses were studied extensively in the late 1940s and 1950s (Connor 1954a, b, 1956, 1957b, 1962 a, b). In *Agropyron scabrum* ($2n = 6x = 42$) where there was (i) a series of plants of different appearance; (ii) these differences were preserved in cultivation at five sites; (iii) each phenodeme occupied a geographical territory of its own; and (iv) many of these phenodemes were interfertile with each other but in some intraspecific hybrids reduction in fertility occurred at F_1 or F_2. Hair (1956) identified apomixis in some phenodemes which have since been recognised as Australian migrants (Löve & Connor 1982).

Five other indigenous species were involved: *A. enysii* ($2n = 4x = 28$), *A. kirkii* ($2n = 6x = 42$) and *A. tenue* ($2n = 8x = 56$). These were crossed experimentally; most hybrids were sterile (Connor 1956; 1962, a, b). Two species of *Cockaynea*, *C. gracilis* and *C. laevis* were also involved; in both $2n = 4x = 28$.

Classification of the Triticeae rarely satisfied taxonomists at the generic level; currently there is much redistribution of species among several genera primarily based on genome analysis (Dewey 1982, 1983a, b, 1984; Barkworth et al. 1983; Löve 1982, 1984). The level of satisfaction may not be increased.

New Zealand taxa were incorporated into a series of experimental crosses which involved a sector of the world spectrum of the Triticeae of known genomic constitution: *Critesion marinum* ($2n = 2x = 14$) genome H; *Elymus hystrix* ($2n = 4x = 28$) genome HS; *Elymus longearistatus* ($2n = 6x = 42$) genome HSS; *Elymus transhyrcanus* ($2n = 6x = 48$) genome HSS — as *E. stewartii*; *Elymus trachycaulis* ssp. *novae-angliae* ($2n = 4x = 28$) genome HS; *Elytrigia repens* ($2n = 6x = 42$) genome EJS; *Pseudoroegneria spicata* ($2n = 2x = 14$) genome S. Of these there is a difference of interpretation with Dewey (1984) over the genome for *Elytrigia*, Dewey favouring SX where X is of unknown or unspecified origin. *Critesion marinum* is included in *Hordeum* sect. *Stenostachys* by von Bothmer et al. (1983).

	n	Genome	Elymus enysii 14	E. rectisetus 21	E. tenius 28	E. laevis 14
Critesion marinum	7	H	$7_{II} + 7_I$	$7\text{-}9_{II} + 10\text{-}14_I$		
Pseudoroegneria spicta	7	S	$5_{II} + 11_I$	$3_{III} + 4_{II} + 11_I$		
Elymus enysii	14			$3_{III} + 11_{II} + 4_I$	Up to 10_{II}	$12_{II} + 1_{IV}$
E. longearistatus	14	HS	14_{II}			
E. trachycaulis	14	HS	$13_{II} + 2_I$			
E. hystrix	14	HS				$13_{II} + 2_I$
E. multiflorus	21		$3_{III} + 11_{II} + 4_I$	21_{II}		
E. transhyrcanus	21	HSS		21_{II}		
Elytrigia repens	21	EJS	4_{II}	Up to 7_{II}		

Fig. 8 Chromosome pairing in interspecific hybrids between New Zealand species of *Elymus* and overseas taxa. Data from Löve & Connor (1982); nomenclature, after Löve & Connor. See also Dewey (1984) for comment on the extent of pairing.

The results of these crosses are reported in Löve & Connor (1982). Other crosses repeated those performed earlier in New Zealand and showed that some early crosses failed through external rather than internal influences. From analyses of the chromosome pairing in hybrids, and their relationship to taxa of known genomic constitution, the overall genomic constitution of the New Zealand species was determined, and the individual haplome in each genome identified (Fig. 8). New Zealand tetraploid taxa were allocated the genomic formula HS, the hexaploids HSS, and the octoploid HHSS; HS is the basic *Elymus* genome. Dewey (1984) expressed doubt over the interpretation of the extent of pairing in some hybrids, concluding that they are impossible to reconcile with the genomic constitution of *E. repens* in particular. The genomic structure and composition of some New Zealand species are, he concluded, uncertain.

The conclusions expressed in taxonomic terms are that the New Zealand species currently placed in *Agropyron* and *Cockaynea* should be transferred to the genus *Elymus*, but in two different sections. In addition, the Central Otago, strict, wide-angled-spikeleted, blue, long-anthered plants were finally given specific rank as *Elymus apricus*.

In the *Elymus* hybrids seeds were set in F_1 *E. rectisetus* × *E. transhyrcanus* among extra-territorial crosses, 2n = 42 in both species; all the others failed, or nearly so, to set seed giving constant evidence of the failure of gene-exchange.

The most significant feature of this work was the demonstration of the relationship in internationally accepted genomic terms of the endemic genus *Cockaynea* to endemic species of *Agropyron* and to other members of the Triticeae.

c Poeae

Festuca

Two tussock grassland species of much prominence are the hexaploids (2n = 42) *Festuca novae-zelandiae* and *F. matthewsii*. Usually they are allopatric, the former at low altitudes and the latter upslope, and although they do meet at a good many sites in South Island I have no evidence of natural hybridisation between them (Connor 1968). The two species preserve their characteristic growth patterns and morphology in cultivation.

Experimental F_1 interspecific hybrids were fertile but did not set as much seed as either parent, although by F_3 seed-set was equal to parental values. Pollen fertility never fell below 90% (Connor 1968).

A high-altitude form of *F. novae-zelandiae* which occurs in north and south Canterbury was recognised some time ago (Connor 1960). It is distinctive in stature and in panicle characters both in the wild and in cultivation. Scott (1970) grew *F. novae-zelandiae* collected from 1800 m and from 700 m in the Mackenzie basin, south Canterbury, under controlled temperatures. The lower altitude collection recorded its highest relative growth rate at 18°C and the higher altitude material at 12°C; a significant difference in temperature response. The experimental results and the behaviour of the higher altitude material in cultivation are a clear indication of ecotypic differentiation. Experimentally produced F_1 hybrids between the high altitude form and lowland plants were fertile, but there was an inexplicable lowering of seed-set in F_2 (Connor 1968).

CONCLUSION

What I have discussed shows that New Zealand plant biosystematic studies have made important, if strictly conventional, advances in the last twenty years, but the investigations are heavily weighted in favour of monocotyledons — grasses, sedges, asteliads, wood-rushes. These are not unrelated to the two monocotyledonous floras which have been published in the "Flora of New Zealand" series (Moore & Edgar 1970; Healy & Edgar 1980).

Epilobium, which had the three-fold advantage of the late W. B. Brockie's abundant experimental hybrids, the international taxonomic confidence of P. H. Raven, and the cytological resolve of the late J. B. Hair, should need attention to details of reproductive biology only. *Luzula* and *Elymus*, where international co-operation was also involved, should be let rest. We know much of the interrelationships among species in those genera. *Cortaderia*, but for an adequate genetic solution on my own part to the question of the inheritance of male sterility, will yield diminishing returns.

Chionochloa (Gramineae) is the only genus of economic importance to have received significant attention. But *Nothofagus* is possibly even more important economically than the snow-tussocks. Until M. D. Wilcox and N. J. Ledgard of the New Zealand Forest Service started work on it a few years ago, it had been left where A. L. Poole laid it (Poole 1950a, b, 1952, 1958). *Weinmannia, Dacrycarpus, Podocarpus, Beilschmiedia, Kunzea, and Leptospermum* are tree genera which warrant national attention.

It is, as I write, 50 years since the publication of the list of wild hybrids in New Zealand by Cockayne & Allan (1934). That list, which has caused unease and uncertainty, developed very rapidly

from a "List of Supposed Hybrids" and the well-established record of the 15 hybrids mentioned in Cockayne (1923), and from the substantial list included in J.P. Lotsy's "Evolution considered in the light of Hybridization" (1925), itself published within four years of the discovery of widespread hybridism in *Nothofagus* (Cockayne 1921; see also Godley 1979, and Thomson 1979, 1980). Allan's final reflections on natural hybridism and the 1934 list are embodied in his "Flora of New Zealand" Vol. 1 (Allan 1961); they reveal a subdued attitude to hybridism relative to that of Cockayne. A decade earlier he foreshadowed that attitude (Allan 1951).

The study of wild hybridism has not expanded on the bases built by Cockayne and by Allan, and apart from Raven & Raven (1976) on *Epilobium*, and Fisher (1965) on alpine epirote ranunculi (see the discussion in Hair 1966) natural hybrids have either been reduced to brief sentences in taxonomic treatments, or been treated as introgressants as Orchard (1975) interpreted plants he was unable to classify in *Gonocarpus*. Gardner (1978) brought no evidence, compelling or otherwise, in favour of his conclusion that *Alseuosmia banksii* × *A. macrophylla* is a frequent hybrid which should be recognised as *A.* × *quercifolia*.

Wardle (1968) advanced reasons for the recognition of *Pseudopanax macintyrei* as a tetraploid (2n = 48) calcicolous species of the northern South Island; it had often been awarded hybrid status (Cockayne & Allan 1934, Allan 1961). Such elisions from the list of hybrids are rare.

Melville (1976) invoked novel interactions to resolve the old question of hybridism in *Parsonsia* (see Cockayne 1912, Allan 1926c). No experiments were conducted; no studies of pollen fertility made; no approximation of actual gene-exchange attempted; the solution Melville offered follows from a study of leaf polymorphism and persistent juvenility, and from his concept of the glossopterid leaf syndrome.

If ever the time was appropriate to eschew reports of natural hybridism which are based on such evidence "as apparently intermediate" or some such euphemism, that time is now. With the common availability in the 1980s of such modern techniques as thin layer chromatography, gel electrophoresis, SEM photography, computing programs, and such traditional disciplines as genetics, cytology and morphology, statements such as "putative" or "apparent" hybridism unsupported by suitable data should be unacceptable.

Allan established contemporary solutions with (i) his series "Illustrations of wild hybrids in the New Zealand flora" (Allan 1925, 1926b, c, 1927a, b, 1929a; Allan, Simpson & Thomson 1926); (ii)

detailed measurements of many character-states; (iii) artificial hybrids in *Coprosma* (Allan 1926a, 1929b, 1938), *Fuchsia* (Allan 1927b), Rubus (Allan 1927c, 1928, 1949), *Phormium* (Allan & Zotov 1937); (iv) use of the experimental garden; (v) the assessment of pollen sterility.

The onus for contemporary solutions 50 years later lies clearly with modern botanists. And if the work in the intervening 50 years has been inadequate or even antiquated, the responsibility — or fault if it is a fault — is also clear; if the work in the next half century is to be adequate, and even modern, the responsibility is equally clear. Data from plants in cultivation which at the very least reflect the different responses plants make, e.g., juvenile forms, plasticity, ecotypic differentiation, are abundant and needed, but unpublished. Flavonoid profiles could be used in assessing gene-exchange among genera such as *Coprosma* (Wilson 1984), *Carmichaelia* (Purdie 1984), and *Sophora* (Markham & Godley 1972). Divarication is common enough in all three genera.

Godley (1979) went further than positing the origin of *Sophora microphylla*; he advanced the hypothesis that the nine species in New Zealand with divaricating juvenile forms resulted from hybridisations involving species of divaricating shrubs and arborescent species. The two qualities of divarication and juvenility should be examinable in terms of the contemporary evidence of their genetic behaviour, but to be able to do so one must depend on accurate descriptions of F₁ hybrids. Allan (1925, 1926b, 1927a, 1929a) contributes most of the evidence, although there is a list of 54 species of divaricating plants in the New Zealand flora in table 1 of Greenwood & Atkinson (1977), together with an indication of interspecific hybridisation with open shrub or tree forming species.

Data on the inheritance of genes controlling juvenility are insufficient to be of much use to Godley's hypothesis (op. cit.); but the general wealth of information on juvenile forms should allow, after a complete morphological examination of hybrids, an assessment of the inheritance of this spectacular characteristic.

Divarication, an equally spectacular character and one involved in current debate (Greenwood & Atkinson 1977; Atkinson & Greenwood 1980; McGlone & Webb 1981), should be more easily assessed in terms of its inheritance. From the evidence that is available, most of it again from Allan (see above and 1924, 1937), the divaricating habit does not appear to be under the control of dominant genes by comparison with genes controlling open tree shape and form; but the same remarks about the possibility of improving our knowledge of the inheritance of juvenility apply to the inheritance of the divarication syndrome.

Biosystematics may not meet the needs or expectations of early 21st century New Zealand botany in much the way that Hagen (1983) found that there was no revolution in pre-war taxonomy. But biosystematists must find resolution to the question of interspecific gene-exchange and the taxonomy of higher plants; they could be expected to clarify whether or not natural hybridism is more important in the evolution of the New Zealand flora than it is elsewhere as Raven (1973) asked, or as Rattenbury (1962) proposed.

At the level of ecological investigation of the underlying causation of interpopulation differentiation Wardle (1969) and Sakai et al. (1978, 1981) in *Phyllocladus*, Wardle et al. (1973) in *Leptospermum scoparium* , Given (1980) in *Kunzea ericoides*, and Lee et al. (1983) in a number of genera, have demonstrated recognisable genetic components. The causes underlying the ecological selection of these gene complexes is the proper object of genecology (Turesson 1923).

Biosystematic studies are more easily carried out than genecological ones; hybrids can be made experimentally and gene-exchange measured. Genecology demands different kinds of experiments before adequate ecological explanations underpin interpopulation differentiation. Many experiments in New Zealand reveal morphological and physiological differences in populations from varied localities and from varied ecological conditions, e.g. Connor (1954a,b) in *Elymus rectisetus* (as *Agropyron scabrum*), Ornduff (1960, 1964) in the *Senecio lautus* alliance; Garnock-Jones & Langer (1980) in *Parahebe catarractae*, and Yin et al. (1984) in *Leptospermum scoparium*. Coincidence apart, none reveals genetic-ecological causation.

Much conservation effort of the 1970s and 1980s has in New Zealand been centred on forest communities especially, but not restrictively, on lowland podocarp forest; parallel ancillary action has taken place over wetlands but a basic cause here is game birds and not wetlands *per se*. With the development of the concept of Ecological Districts (see Simpson 1982) — and their misleadingly named Ecological Regions (Simpson op. cit.) — conservation must expand correctly to embrace all major members of the great plant communities — grasslands, forests, alpine fell fields, shrublands, sand dune communities, and aquatic systems. Other than by exclosure, by noxious weed and animal control, by preventive action against fire and looting, and by legislation, the conservation effort should be directed towards the understanding of the genetic differentiation in the dominant plants of those communities. Genecological — ecogenetic — investigation must become, and quite easily could become, part of conservation practice in New

Zealand. It is inconsistent to assert that the conservation of species is a safeguard against the possible loss of genes which may become valuable to man in the future without the logical investment of genetic research in those same plants which dominate forests and grasslands and shrublands and herbfields and sand dunes and lakeshore communities. The ardent conservation clamour will become credible through willingness to complete research work, or even to fund it, rather than arrogantly to demand it.

At a level of a conservation much below the protection concept, should the number of individual plants of a species locally fall, or be reduced by man or predators, below critical reproductive levels, enrichment by the addition of individual plants of the same species is a practice to be commended. That the individuals being added must be members of the same ecotype as the depleted population is a *sine qua non*.

A third level in this series from (i) widespread and abundant, to (ii) locally diminished is (iii) that group of plants described in detail by Given (1981) as rare, and/or endangered. These plants, above all, should be objects of careful and detailed genecological research, and not solely matters for legislation, or for sequestration.

In the evolution of the kind of botanical knowledge needed in New Zealand with its short history of European settlement, we have passed from the frontier days of the requirement of tree identification manuals, through the manual of useful plants phase, faster through to the weed manual phase because of the economic importance of weeds to agriculture and livestock health, to this present time where conservation competes with maximum utilisation of natural resources. The needs of the colonial phase were the more easily met than those of the late 20th century; modern methods in botanical research should allow the current needs to be satisfied rapidly. They must satisfy rapidly if no more genes are to be lost from such important plants as the beeches, kamahi, tawa, and rimu than have already been lost to attrition by axe and fire, and by domestic and wild animals.

Biosystematics in this vigesimal period was very strongly developed in monocotyledonous plants primarily because that element of the flora of New Zealand was receiving concerted attention. That most of them were herbaceous, easily propagated, of modest size, and flowered promptly in cultivation, *Astelia* excepted, and were easily manipulated for crossing experiments, were qualities to their advantage for biosystematic studies.

It is now almost twenty-five years since H. H. Allan's "Flora of New Zealand Volume 1, Indigenous Tracheophyta" was published. If the turn of the century is to see its adequate replacement — as it must — we have seen its half-life already. Biosystematics, with its obligatory tradition of experiment, must therefore make progress apace in the New Zealand Dicotyledones.

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