# Regional endemism in New Zealand grasses

## H. E. Connor

# Regional endemism in New Zealand grasses

H. E. CONNOR
  Department of Geography
  University of Canterbury
  Private Bag 4800
  Christchurch, New Zealand

**Abstract**   Regional endemism is evident in 60 grass taxa among the 182 species and infraspecific taxa that comprise the New Zealand endemic grass flora. The pattern of regional endemism matches that described earlier for dicotyledons with high frequencies in Nelson-Marlborough of northern South Island, and in southern South Island in Otago, Southland, and Fiordland. Low frequencies in southern North Island and central South Island are also consistent with patterns earlier described. In northern North Island grass endemism is low, consistent with the long history of forests in that region. Habitat preference is evident for most regional endemics with rupestral and edaphic constraints dominating. Taxonomic rank is the first imperative in establishing status as a regional endemic. Disjunctions fragment species into genetically isolated populations with their own evolutionary potentialities. These populations, unadorned by taxonomic rank, are treated as simple species disjunctions unlike those supported by an infraspecific taxonomic foundation that qualify for regional endemism. This distinction seems biologically inconsistent. Regional grass endemics conform in chromosome number, reproductive biology, and habitat selection to other congeneric species except for rare departures. A comparison of the frequencies in regional distributions of endemic Gramineae and endemic herbaceous Compositae showed a high level of agreement, unlike that with endemic Cyperaceae. Among the tribes of New Zealand Gramineae, Agrostideae have a lower ratio of regional endemics:total endemics

than in tribes Poeae and Danthonieae, primarily because of the lack of coherent morphological-geographic patterns in species of wide amplitude.

## INTRODUCTION

Biogeographic analyses of the native New Zealand flora have revealed patterns of regional endemism attributed variously to the effects of glaciation, tectonism, and climatic change (Wardle 1963, 1991; Burrows 1964, 1965; McGlone 1985). The frequencies of endemic taxa in rather broadly defined regions were mapped by Wardle (1963, 1991) and McGlone (1985), and in more detailed subdivisions for South Island by Burrows (1964, 1965). Heads (1997) used the 1 degree squares of the *Fauna of New Zealand* series in mapping a selected number of genera.

The New Zealand grass flora has been recently circumscribed (Edgar & Connor 2000) and it seems opportune to compare the regional endemism of one monophyletic monocotyledonous group, with the details of the record of dicotyledons (Wardle (1963) on data compiled from Allan (1961) and as part of the "higher plants" treatment of McGlone (1985) primarily based on data from the unpublished analyses of A. P. Druce. Some examples of major disjunctions in species distribution will be discussed briefly because regional endemism studies emphasise their presence.

This paper describes the current geography of endemic New Zealand grasses especially in terms of long recognised centres of floristic richness. It is not an account of the evolution of the New Zealand grass flora nor of the pathways of dispersal to modern distribution patterns, and is therefore not of the same genre as Wardle (1963) or of McGlone et al. (2001). The current end points of evolution, dispersal, and habitat occupation are the central foci, not their

origins, nor their dispersal processes, nor the rates or times of expansion or contraction.

For the grasses, the results, which effectively partition data in McGlone (1985), and which are in part a taxonomic parallel to those of Wardle (1963), indicate conformity to the Wardle-McGlone distribution pattern of two floristically rich regions and two floristic gaps, but are not in agreement for northern North Island frequencies primarily because of the paucity there of forest grasses.

## METHODS

Distribution data for all endemic and indigenous grasses as recorded in Edgar & Connor (2000) and the preparatory *Flora* papers were examined and fitted to the mapping units of Wardle (1991). Species, subspecies, varieties, and forms occurring exclusively within the boundaries of those mapping units are interpreted as regional endemics. Disjunct distributions also derive from this analysis.

Subspecies are included here, as in Heads (1997). In species with recognised subspecies the typical subspecies, i.e., that bearing the autonym, is here treated as an independent taxon so that *Australopyrum calcis* subsp. *calcis* and subsp. *optatum* are treated as two taxa in the enumerations, and not as one species with a modest South Island disjunction. There are 37 subspecies for scrutiny.

Data for interfamily comparisons of the relative distribution of regional endemics of Cyperaceae and herbaceous Compositae were gathered from specimens in CHR, and from distribution details in recent papers. Variation in regional endemism among grass tribes was assessed from the data presented here.

## RESULTS

The New Zealand native grass flora comprises 5 endemic genera, 157 endemic species, and 23 endemic subspecies, 1 variety, and 1 form; 30 species are indigenous (Edgar & Connor 2000). Other estimates are inexact.

### Endemic taxa

Regional endemism on the Wardle-McGlone mapping bases is displayed by 44 species, 14 subspecies (three autonyms included), 1 variety, and 1 forma. Taxa included by de Lange et al. (1999) in classes of plants at various levels of risk of extinction are signified by superscripts: [1]Critically Endangered; [2]Endangered; [3]Vulnerable.

### Kermadec Islands

Two taxa are endemic: *Imperata cheesemanii*, *Poa anceps* subsp. *polyphylla*.

### North Island

Five species are endemic in the northern region: *Chionochloa bromoides*, *Cortaderia splendens*, *Festuca luciarum*, *Microlaena carsei*, *Zoysia pauciflora*.

Four taxa are southern North Island endemics: *Chionochloa beddiei*, *C. flavicans* forma *temata*[2], *C. rubra* var. *inermis*, *Rytidosperma nudum*.

### South Island

Seventeen taxa are endemic to Nelson-Marlborough. Thirteen taxa are exclusive to Nelson and western Marlborough: *Chionochloa defracta*, *C. flavescens* subsp. *lupeola*, *C. juncea*, *Deyeuxia lacustris*, *Festuca deflexa*, *F. ultramafica*, *Koeleria riguorum*, *Poa acicularifolia* subsp. *ophitalis*, *P. celsa*, *P. sudicola*, *P. xenica*, *Simplicia buchananii*, *Stenostachys deceptorix*. Four taxa are exclusive to eastern Marlborough: *Australopyrum calcis* subsp. *calcis*[1], *Dichelachne lautumia*, *Elymus sacandros*, *Festuca matthewsii* subsp. *aquilonia*.

Two taxa are endemic to Canterbury: *Australopyrum calcis* subsp. *optatum*[3], *Festuca actae*.

Fourteen taxa are endemic to Otago-Southland-Fiordland. Eight taxa are in Otago-eastern Southland: *Poa spania*[1] in North Otago, and *Deschampsia pusilla*, *Elymus apricus*, *Festuca matthewsi* subsp. *pisamontis*, *Poa pygmaea*, *P. schistacea*, *P. senex*, *Rytidosperma tenue*, all primarily of Western and Central Otago, but *Poa schistacea* and *P. pygmaea* extend into eastern Southland. Six taxa are in Fiordland-western Southland: *Chionochloa acicularis*, *C. crassiuscula* subsp. *directa*, *C. ovata*, *C. spiralis*, *C. teretifolia*, *Zotovia acicularis*.

### Stewart Island

Three taxa are endemic: *Chionochloa crassiuscula* subsp. *crassiuscula*, *C. lanea*, *Poa aucklandica* subsp. *rakiura*.

### Chatham Islands

Three species are endemic: *Cortaderia turbaria*[2], *Festuca coxii*, *Poa chathamica*.

### Subantarctic islands

Five taxa are endemic to Auckland and Campbell islands: *Agrostis subulata*, *Chionochloa antarctica*, *Poa aucklandica* subsp. *aucklandica* and subsp. *campbellensis*, *P. ramosissima*.

**Fig. 1** Numbers of regionally endemic grasses in each region; mapping after Wardle (1991).
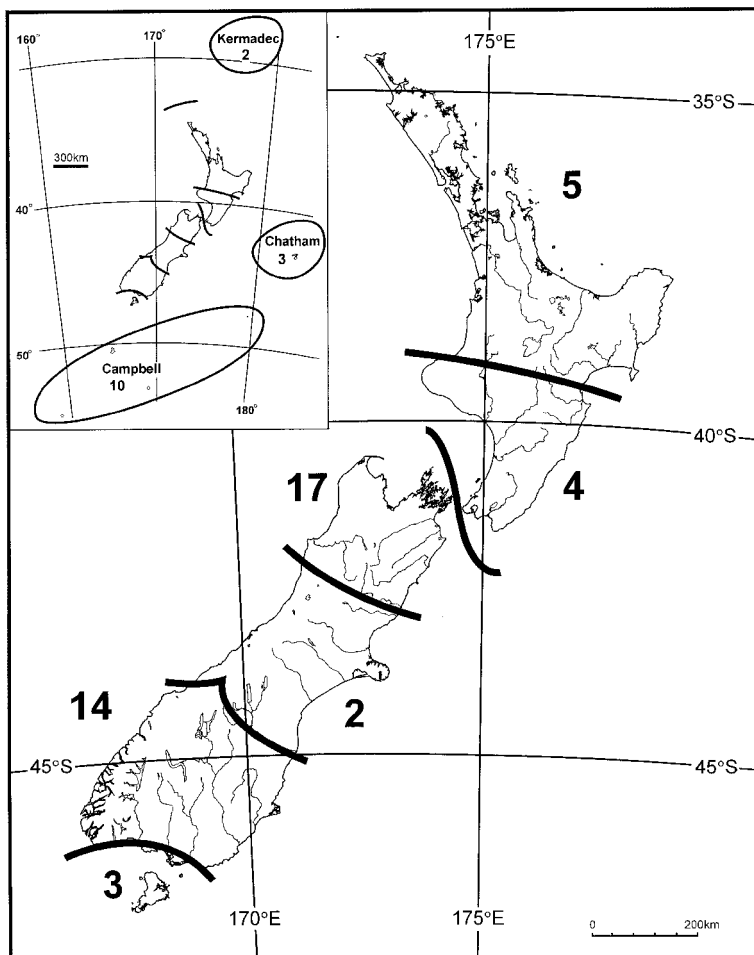


Three taxa are in an irregular pattern of endemism; in *Lachnagrostis*, *L. pilosa* subsp. *nubifera* is on the Aucklands and Antipodes, and *L. leptostachys* is on both and on Campbell Island as well; *Poa litorosa* is endemic to the Aucklands, Antipodes, Campbell, and Macquarie islands.

One taxon is endemic solely to the Antipodes Islands: *Puccinellia walkeri* subsp. *antipoda*.

One taxon is endemic solely to Macquarie Island: *Puccinellia macquariensis*.

The few taxa which seem to show some degree of regionalism but cross the geographic boundaries in Fig. 1 include: *Chionochloa flavicans* of eastern North Island rock faces; *C. australis* of Nelson-Marlborough but which extends into inland North Canterbury and into Westland; *Rytidosperma petrosum* found on both sides of Cook Strait; *R. pulchrum* of central and southern North Island

mountains; *Achnatherum petriei* and *Festuca matthewsii* subsp. *latifundii* of inland Waitaki and Central Otago basins. Boundary adjustments could accommodate some of these species but the grasses on their own are not sufficiently important to alter a pattern receiving credible support. In attempting to redefine the boundaries of the lower North Island floristic gap Rogers (1989) offered a diffuse boundary in central North Island spanning 39°20′S–39°50′S.

In New Zealand 25 grass genera have endemic species; regional endemism is detectable in 20 of them. Representation is high only in polytypic *Chionochloa*, *Poa*, and *Festuca* which together account for about 40% of regional endemics (Table 1). In other polytypic genera, e.g., *Trisetum* with seven and *Hierochloe* with six endemic species, none is regionally restricted. In *Agrostis* there is one

regional endemic among eight species. In *Rytidosperma*, of 15 endemic species, two are regional endemics: *R. nudum* of alpine bogs on the Ruahine and Tararua Ranges and *R. tenue* of Otago which sets no seeds. *Simplicia buchananii* and *Stenostachys deceptorix* both of Nelson, together with *Zotovia acicularis* of Fiordland, are the only regionally endemic species among the 10 spp. of the five endemic genera *Anemanthele*, *Pyrrhanthera*, *Simplicia*, *Stenostachys*, and *Zotovia*.

The frequencies of regional endemics among grass tribes are in Table 1. As remarked by Edgar & Connor (2000), three tribes, Poeae, Agrostideae, and

Danthonieae, have the highest numbers of endemic species, and in more or less equal numbers. Three tribes, Ehrharteae, Chlorideae, and Andropogoneae with eight endemic species among four genera, are a minor component of the endemic grass florula and contribute four taxa to regional endemism, about as many as tribe Hordeeae. None is in Stipeae of two genera and two species.

Tribe Agrostideae have most genera (nine) with endemic taxa, and in seven there are regional endemics, usually one per genus (Table 1). The ratio regional endemics:total endemics in this tribe (0.17) is very much lower than in Poeae (0.41) or Danthonieae

**Table 1**   Frequencies of regional endemic taxa in New Zealand grass flora. Tribe names and arrangement as in Flora of New Zealand V (Edgar & Connor 2000).

| Tribe and genus | No. of regional endemics recorded as | | No. of endemic | | Regional endemics:Total endemics | Reference |
|---|---|---|---|---|---|---|
| | spp. | subspp. | spp.* | subspp. | | |
| Ehrharteae | | | | | 0.40 | |
| *Microlaena* | 1 | | 2 | | | Edgar & Connor 1998, fig. 6 |
| *Zotovia* | 1 | | 3 | | | Edgar & Connor 1998, fig. 3 |
| Poeae | | | | | 0.41 | |
| *Festuca* | 5 | 2 | 9 | 3 | | Connor 1998, fig. 2, 9 |
| *Poa* | 10 | 5* | 37 | 4 | | Edgar 1986, fig. 12, 13, 16, 19, 20, 21, 22, 26 |
| *Puccinellia* | 1 | 1 | 3 | 2 | | Edgar 1996, fig. 1 |
| Agrostideae | | | | | 0.17† | |
| *Agrostis* | 1 | | 8 | | | Edgar & Forde 1991, fig. 3 |
| *Deschampsia* | 1 | | 4 | | | Edgar & Connor 2000 |
| *Deyeuxia* | 1 | | 4 | | | Edgar & Connor 1999, fig. 7 |
| *Dichelachne* | 1 | | 1 | | | Edgar & Connor 1999, fig. 2 |
| *Koeleria* | 1 | | 3 | | | Edgar & Gibb 1999, fig. 4 |
| *Lachnagrostis* | 1 | 1 | 10 | 2 | | Edgar 1995, fig. 4, 7 |
| *Simplicia* | 1 | | 2 | | | Zotov 1971a, fig. 1 |
| Hordeeae | | | | | 0.45 | |
| *Australopyrum* | | 2* | 1 | 1 | | Connor et al. 1993, fig. 3 |
| *Elymus* | 2 | | 6 | | | Connor 1994, fig. 2, 4 |
| *Stenostachys* | 1 | | 3 | | | Connor 1994, fig. 11 |
| Danthonieae | | | | | 0.34‡ | |
| *Chionochloa* | 10 | 3* | 22 | 11 | | Connor 1991, fig 1, 2, 3, 12 |
| *Cortaderia* | 2 | | 5 | | | Connor 1971, fig. 2 |
| *Rytidosperma* | 2 | | 15 | | | Connor & Edgar 1979, fig. 4, 5 |
| Chlorideae | | | | | 0.50 | |
| *Zoysia* | 1 | | 2 | | | Zotov 1971b, fig. 2 |
| Andropogoneae | | | | | 1.00 | |
| *Imperata* | 1 | | 1 | | | Edgar & Connor 2000 |

\* Autonyms included.

† In *Hierochloe* and *Trisetum*, of 13 endemic species, there are no regional endemics; total endemic taxa for the tribe is 47.

‡ Includes 1 variety and forma not listed separately in this table.

(0.34). There are no theoretical frequencies for regional endemism ratios although our data suggest something of the order of 0.30–0.40 might be realistic.

The distribution of regionally endemic grasses (Fig. 1) conforms to the pattern described by Wardle (1963) and McGlone (1985). Regional endemics are few in southern North Island and in central South Island, and at a high frequency in northern and southern South Island. The exception to the general Wardle-McGlone pattern lies in northern North Island where five species are classified as regional endemics – three of them in open coastal habitats. No specialist and localised grass has evolved in northern forests during their long history of territorial dominance except *Microlaena carsei*. On subantarctic islands 10 grass endemics are a relatively high proportion (28%) of endemic species there (Wardle 1991).

*Chionochloa* and *Poa* merit most attention because about 40% of their taxa are regional endemics. The balance of taxa displaying regional endemism mostly comprises single species in a genus, e.g., coastal *Zoysia pauciflora* in northern North Island; petrophilous *Simplicia buchananii* of Nelson; *Deyeuxia lacustris* of Nelson-Marlborough; *Deschampsia pusilla* of alpine Central Otago; *Zotovia acicularis* of Fiordland. On islands, *Imperata cheesemanii* is endemic to the Kermadecs, *Agrostis subulata* to the Auckland and Campbell islands, and *Lachnagrostis leptostachya* and *L. pilosa* subsp. *nubifera* are subantarctic islands endemics of varied distribution.

## Chionochloa

In North Island, *Chionochloa* regional endemics are on coastal cliffs, *C. bromoides* of Northland and Auckland, and *C. beddiei* in the Wairarapa. In the Nelson district there are three *Chionochloa* endemics: *C. defracta* from ultramafic soils, *C. juncea* of impoverished granitic soils on the wet Buller uplands, and *C. flavescens* subsp. *lupeola* of limestone sites. There are no *Chionochloa* endemics restricted to Marlborough, Canterbury, or Otago.

The highest concentration of species of *Chionochloa*, and of those regionally endemic, is in Southland-Fiordland. All five regional endemics occur above tree line on oligotrophic alpine acidic peats of poor drainage, except *C. spiralis*, a Fiordland limestone species of very limited distribution, and *C. ovata* of alpine gravels, rocks, and seepages (Williams et al. 1976; Lee & Fenner 1989). The most widespread is *C. teretifolia* which extends from Fiordland eastwards to the Oreti River; *C. acicularis*

and *C. ovata* are in Fiordland, and *C. crassiuscula* subsp. *directa* is endemic to the Longwoods Range and to the Takitimu and Hunter mountains in Southland.

On Stewart Island the endemics *C. crassiuscula* subsp. *crassiuscula* and *C. lanea* occur on bogs or peaty soils or in herbfields. Tussock grasslands on cushion bogs or oligotrophic blanket peat on Auckland and Campbell islands are dominated by the lowland endemic *C. antarctica*. These simple ecological correlatives of the regional endemics should not be interpreted as causal but as correspondences.

## Poa

In *Poa* with 37 species and 4 subspecies endemic, there are 15 taxa with evident regional endemism – 10 species and 5 subspecies (Edgar & Connor 2000). None is in North Island, nor in central South Island, nor in Fiordland. There are four taxa in Nelson; two are dioecious basicoles of screes, *P. sudicola* and *P. xenica*, and *P. acicularifolia* subsp. *ophitalis* is on ultramafic soils. In Otago-eastern Southland there are four species: *P. spania* is a calcicole in North Otago and classed as Critically Endangered by de Lange et al. (1999), dioecious *P. schistacea* ascends to very high altitudes on schistose screes in western Otago and north-eastern Southland, and *P. pygmaea* and *P. senex* occupy damp ground in the subalpine to alpine zones. There are no *Poa* endemics in Canterbury, not even of the prominent greywacke screes.

Seven taxa in *Poa* are on islands: *P. anceps* subsp. *polyphylla* on coastal cliffs in Kermadec Islands; *P. aucklandica* subsp. *rakiura* among rocks on Mt Anglem, Stewart Island; *P. aucklandica* subsp. *aucklandica* in upland herbfields and among rocks on Auckland Islands and subsp. *campbellensis* of Campbell Island in upland rocky herbfields; shared by both the Auckland Islands and Campbell Island, gynomonoecious *P. ramosissima* of coastal cliffs; *P. chathamica* of rocky sites but also of sand dunes and peats in Chatham Islands. All regionally endemic taxa are essentially rupestral except *P. litorosa* of tussock grasslands on subantarctic islands.

## Festuca

Species of *Festuca* are commonly physiognomic dominants in short-tussock grasslands and prominent in the tall, modified snow tussock grasslands of South Island. Twelve endemic taxa were recognised by Connor (1998); seven are interpreted as regional endemics, five species and two subspecies. Two species are basicoles, *F. luciarum* of Gisborne and Hawke's Bay mountains, and *F. deflexa* of

north-west Nelson; *F. ultramafica* is on soils developed from ultramafic rocks in Nelson; rock outcrops, and cliffs, are sites for *F. coxii* of Chatham Islands, and of *F. actae* of Banks Peninsula, Canterbury. Two subspecies in *F. matthewsii* are subalpine and alpine regional endemics, subsp. *aquilonia* of Marlborough and subsp. *pisamontis* of mountains in Central Otago.

## Indigenous taxa

Three indigenous taxa among 30 display regional endemism; two are in the Kermadec Islands. *Lepturus repens* var. *cinereus* is confined to a small area of lava rock on Chanter Islet in the Kermadecs, and *Cenchrus caliculatus* is found in open coastal places on Raoul Island. From North Cape to Auckland, *Dichelachne micrantha* grows in scrub and open sites not far from the east coast; it is the only indigenous species regionally exclusive on a main island (Edgar & Connor 1982, fig. 1).

## Disjunctions

Disjunct species distributions influence the interpretation of regional endemism, and Wardle (1963, 1991), Burrows (1964, 1965), McGlone (1985), and Rogers (1989) discussed disjunctions and regional endemism simultaneously. Some conspicuous disjunctions in 10 grass species are in Table 2; there, *Trisetum* more than any other genus is prominent. The greatest disjunction is that for the ultramafic specialist *Trisetum serpentinum* which occurs at North Cape on the Surville Cliffs and recurs several hundred kilometres south on the Nelson Mineral Belt (Edgar 1998, fig. 10). Physiological differentiation associated with the different serpentinised soils must have already evolved. *Trisetum serpentinum* does not qualify as a third ultramafic regional endemic in the Nelson-Marlborough region because of the North Cape plants.

On a lesser scale, spatial separation and genetic isolation are well illustrated by *Trisetum drucei*. In this species there are three topodemes, one extends from the Raukumara Range to Volcanic Plateau on limestone cliffs, another on eastern Marlborough and North Canterbury limestones, and the third in north-west Nelson is on marble substrates (Edgar 1998). All three are so isolated from each other that gene exchange between topodemes seems impossible now. In the absence of any infraspecific taxonomic separation *T. drucei* is not admitted to the list of regional endemics despite evident genetic isolation and substrates of different ages and origins. These populations of *T. drucei*, should any genetic effects have accumulated, may already be true ecotypes.

**Table 2** Some major disjunctions in New Zealand endemic grasses.

| Species | North Island | South Island | Reference |
|---|---|---|---|
| *Trisetum serpentinum* | North Cape | Nelson Mineral Belt | Edgar 1998, fig. 10 |
| *T. lasiorhachis* | Central and eastern mountains | Marlborough | Edgar 1998, fig. 8 |
| *T. drucei* | Eastern mountains | north-west Nelson, eastern Marlborough to North Canterbury | Edgar 1998, fig. 6 |
| *Poa maia* | Mt Egmont | Nelson and Marlborough | Edgar 1986, fig. 30 |
| *Elymus tenuis* | Central mountains | south from Nelson and Marlborough | Connor 1994, fig. 4 |
| *Festuca novae-zelandiae* | Central mountains and Mt Egmont | south from Marlborough | Connor 1998, fig. 7 |
| *F. madida* | Central mountains | inland Otago and Southland | Connor 1998, fig. 7 |
| *Koeleria cheesemanii* | Central mountains | south from Nelson and Marlborough | Edgar & Gibb 1999, fig. 2 |
| *K. novozelandica* | Central mountains | south from Nelson and Marlborough | Edgar & Gibb 1999, fig. 4 |
| *Stenostachys laevis* | Central mountains | south from Marlborough | Connor 1994, fig. 11 |

Populations of disjunct species lacking infraspecific taxonomic rank never attain the status of regional endemics because they remain members of a single taxon of wide but interrupted distribution. If I had given taxonomic recognition to the north-west Ruahine Range topodeme of *Stenostachys laevis*, or to that of *Elymus tenuis* of the Volcanic Plateau and Ruahine Range, distinguishing them somehow from South Island populations (Connor 1994), I would have included both as infraspecific regional endemics for southern North Island. It is similar, too in *Festuca novae-zealandiae* (Connor 1998). Because they lack infraspecific taxonomic rank, all are merely regarded as disjunctions. In *Festuca madida* where North Island populations of the Kaweka and Ruahine Ranges were described as more slender and graceful than plants in the widely disjunct populations in inland Otago and Southland, I made no taxonomic differentiation between them (Connor 1998); as a consequence, *F. madida* is listed as a disjunct.

Disjunctions, because they are strictly spatial, primarily ensure the genetic isolation of one population from another, usually the smaller from the larger, as in *Elymus tenuis, Stenostachys laevis,* and *Festuca madida* (Table 2). Genetic isolation, depending on its age, could promote infraspecific differentiation, especially from founder effects, which may eventually be expressed in taxonomic decisions. On its own, spatial genetic isolation does not confer taxonomic rank.

The exclusion of wide disjuncts from the units of regional endemism solely because they lack the support of an infraspecific taxonomic foundation seems biologically inconsistent. This perceived conflict between taxonomy and ecogeography is incompletely resolved and its solution may well lie in ecotypic analyses from classical experiments.

# DISCUSSION

This discussion will concentrate on the ecogeography of the regional endemics, their cytology and genetics, a comparison of their frequencies among grass tribes, and of their geographic disposition relative to that in two other plant families.

## Ecogeography

Regional endemism is recorded for 60 grass taxa among 55 species in 20 genera. Species represented more than once because subspecies are admitted in the analyses are *Australopyrum calcis*, *Chionochloa crassiuscula*, *Festuca matthewsii*, and *Poa aucklandica*. All others are present as a species or as a subspecies, variety, or forma. About a third of the species and subspecies of endemic grasses are regional endemics.

Subspecies by definition have geographic boundaries and might seem to be self-determining regional endemics, but as only 14 of the 37 subspecies (autonyms included) lie within the accepted regional boundaries, their inclusion does not seriously inflate the numbers in the analysis. Subspecies are biologically informative in *Australopyrum*, *Chionochloa*, and *Festuca*; in *Poa* they signify especially on peri-Antarctic islands.

The pattern of the distribution of regional endemism in the New Zealand grasses parallels those described for woody and herbaceous dicotyledons by Wardle (1963) and for higher plants in general by McGlone (1985) except that in northern North Island the actual frequency is relatively much lower for the grasses. Characteristically high levels of regional endemism occur in Nelson-Marlborough and in Otago-Southland-Fiordland and low levels in southern North Island and Canterbury-Westland (Fig. 1; Table 3).

Ecological or substrate preferences are clearly associated with 44 regional endemics (c. 73%); 13 are basicoles, as defined by Molloy (1994); 3 are on Nelson ultramafics; 14 occur on soils with poor drainage and in areas of high rainfall, in particular 8 taxa in *Chionochloa*; 15 taxa are associated with rock sites or cliffs, 7 in *Poa*; 2 are coastal and versatile, *Cortaderia splendens* and *Zoysia pauciflora*, which occur on rocks or sands; grasslands are indicated as the habitat of a further 5 taxa, e.g., *Poa litorosa* of subantarctic islands and *Festuca matthewsii* subspp. *aquilonia* and *pisamontis* of South Island tussock grassland. The origin of these habitat preferences and their role in speciation remains unknown but are not considered causal.

Concentrations of macro-elements in the leaf-blades of *Chionochloa* reflect the distinctive ecology of some regional endemics. Differential mineral uptake or mineral sequestration for calcium in *C. spiralis*, of sodium in *C. ovata* (Lee & Fenner 1989), and of magnesium in *C. defracta* (Williams et al. 1978) are indicative of what could be expected in species of *Poa*, *Festuca*, and *Trisetum* that are selective of limestone and ultramafic substrates unless the genetic backgrounds and physiological processes are intergenerically different.

Although grasses grow in forest no forest grass is a regional endemic except *Microlaena carsei* in

Northland. All four native species of *Microlaena* are found in forests but three of them are of widespread distribution. In *Chionochloa* two species are forest inhabiting, *C. conspicua* and *C. cheesemanii*; both are widespread, *C. cheesemanii* less so, and there are disjunctions in both main islands (Connor 1991, fig. 3, 4). Neither has the qualifications for regional endemism, nor does *Rytidosperma gracile*, a forest-occurring member of another danthonioid genus. Slender *Poa breviglumis* and *P. imbecilla*, together with *P. kirkii* and *P. pusilla*, all of light gaps in forests, do not qualify as exclusive forest species nor as regional endemics; *P. maia* of wet open forest on Mt Egmont is a disjunct in Nelson-Marlborough (Edgar 1986), a unique grass disjunction. Those species of *Poa* are found in open forests; structurally closed forests probably never allowed survival of grass immigrants and, thus, limited the opportunity for the evolution of grasses that would become specialists for these habitats. Regionally endemic grasses are plants of open places; the exception is *M. carsei*.

## Cytology and genetics

Only in *Poa litorosa* of the subantarctic islands, with the very high chromosome number $2n = c.\ 38x = 266$ (Hair & Beuzenberg 1961; Hair 1968), is absolute interspecific chromosome differentiation correlated with regional endemism. Of the 25 other known chromosome numbers for regional endemics, all lie within the range of numbers found here in other widely distributed species in those genera (Dawson 2000; de Lange & Murray 2002), e.g., diploidy ($2n = 14$) in *Australopyrum calcis*, tetraploidy ($2n = 28$) in *Poa* spp., hexaploidy ($2n = 42$) in *Chionochloa* spp., octoploidy ($2n = 56$) in *Festuca coxii*, decaploidy ($2n = 90$) in *Cortaderia splendens*, and hexadecaploidy ($2n = 116$) in *Poa chathamica*.

In terms of reproductive biology there is also conformity in behaviour between regional endemics and other taxa here: chasmogamy-cleistogamy in *Dichelachne lautumia* as in *D. crinita*; dioecism in three *Poa* spp. just as in *P. foliosa* and *P. subvestita*; inbreeding depression in *Festuca coxii* as in *F. novae-zelandiae*; self-compatibility in *Elymus apricus* as in *E. solandri*; protogyny in *Zoysia pauciflora* as in *Z. minima*. Exceptions are gyno-dioecism in *Chionochloa bromoides* in the place of characteristic hermaphroditism, and the reverse in Extinction Endangered *Cortaderia turbaria* of the Chatham Islands.

Natural hybrids which may occur between regional endemics and between them and sympatric widespread species are a feature of *Chionochloa* (Connor 1967, 1991) Fertile hybrids there could be expected to allow interspecific gene exchange because there are no operative genetic barriers preventing it, and no genetic advantage to regional endemics relative to widespread species co-occurring with them. Evolution in *Chionochloa* proceeded without the formation of interspecific genetic isolating mechanisms, just as in *Cortaderia* (Connor 1983), *Elymus* (Connor 1962; Löve & Connor 1982), and *Festuca* (Connor 1968).

**Table 3** Regional frequencies of endemic taxa in Gramineae, herbaceous Compositae, and Cyperaceae (proportions in brackets) Most herbaceous Compositae are species of *Abrotanella*, *Brachyglottis*, *Celmisia*, *Craspedia*, *Leptinella*, and *Senecio*; the number of endemic herbaceous Compositae at specific and lower rank I estimate at c. 230, somewhat in excess of the number of endemic Gramineae at all ranks ($n = 182$).

| Region | No. of endemic taxa | | | | | |
| | Gramineae | | Herbaceous Compositae | | Cyperaceae | |
| --- | --- | --- | --- | --- | --- | --- |
| Kermadec Is | 2 | (0.033) | 2 | (0.018) | 1 | (0.04) |
| Northern North I. | 5 | (0.083) | 11 | (0.096) | 7 | (0.29) |
| Southern North I. | 4 | (0.067) | 7 | (0.061) | 1 | (0.04) |
| Nelson-Marlborough | 17 | (0.283) | 42 | (0.38) | 7 | (0.29) |
| Canterbury | 2 | (0.033) | 7 | (0.061) | 0 | |
| Otago-Southland | 14 | (0.233) | 23 | (0.202) | 3 | (0.13) |
| Stewart I. | 3 | (0.050) | 8 | (0.072) | 2 | (0.08) |
| Chatham Is | 3 | (0.050) | 4 | (0.035) | 2 | (0.08) |
| Subantarctic is | 10 | (0.166) | 11 | (0.096) | 1 | (0.04) |
| *n* | 60 | (1.0) | 114 | (1.0) | 24 | (1.0) |

## Intertribal comparisons in the Gramineae

The ratios regional endemic taxa:total endemic taxa in the tribes of grasses (Table 1) indicate that the Agrostideae (0.17) are at a much lower value than Poeae (0.41) or Danthonieae (0.34). Those tribes with a small complement of taxa, Ehrharteae, Chlorideae, Andropogoneae, and the slightly larger Hordeeae, have a higher ratio than Agrostideae, but these values are open to wide fluctuation because of sample sizes. Overall, Agrostideae are a successful tribe in New Zealand with 95 species, native or naturalised, in 22 genera compared with 85 species in 12 genera in Poeae. Yet, though numerically strong, regional endemism in the Agrostideae is lower than in other tribes here.

There are some agrostidoid taxonomic difficulties but the problems of generic definition, *Koeleria-Trisetum*, *Deyeuxia-Calamagrostis*, *Agrostis-Lachnagrostis*, do not affect this discussion. Difficulties in translating the inconsistent morphological variation of several species into uniform infraspecific units with consistent geographic distributions seem the basis of this apparent low level of regional endemism, as, for example, in *Koeleria novozelandica* where "No clear morphological, geographic distinctions were found..." in a species of extreme variability (Edgar & Gibb 1999). Difficulties in invariable geographic-morphological discreteness are also present in *Agrostis* (Edgar & Forde 1991), *Deyeuxia* and *Lachnagrostis* (Edgar 1995), and in *Trisetum* (Edgar 1998).

Wide distribution is thus characteristic of most endemic species in genera of New Zealand Agrostideae; the few exceptions emerge here as the regional endemics listed in Table 1. Disjunctions in *Trisetum* (Table 2) and *Agrostis*, and on a smaller scale in *Lachnagrostis*, are one direct consequence. Another direct consequence of species of wide amplitude is the inclusion in heterotypic synonymy of species and varieties formally described earlier by Hooker, Hackel, Domin, or Petrie, which had reflected minor or trivial inconsistent differences in morphology (see Edgar & Connor 2000; Connor & Edgar 2002). A third consequence will be reflected in local clamour for taxonomic recognition of regional variants independently of a re-evaluation of species as a whole; that would reconstruct the historic past.

The low frequency of regional endemism in Agrostideae is attributed here to taxonomic problems arising from inconsistent morphological characters. Yet that same constraint did not prevent Edgar and her co-authors describing in the Agrostideae 10 new species and 2 new subspecies, and effecting 5 comb. et stat. nov. at species level, a total of 17 taxa mostly in *Lachnagrostis* and *Trisetum* (see Edgar & Connor 2000; Connor & Edgar 2002). There is no conflict between the two positions.

The Agrostideae offer an example of the possibility of a phenomenon as yet unrecorded here—endemic subspecies, or varieties, in cosmopolitan or Australasian species. Edgar (1998) showed in circumpolar and bipolar *T. spicatum* that "In the New Zealand Botanical Regions three forms are more or less recognisable (Table 1)...". For completely logical reasons she gave them no infraspecific taxonomic rank; if they had received rank, they may have qualified for the status of regional endemics.

This analysis on tribe Agrostideae relative to tribes Poeae and Danthonieae is possible only because the numbers of taxa in the three tribes are large enough to be workable data. The low numbers of taxa in most genera do not allow a similar examination except in *Poa* and *Chionochloa*, which themselves are the major contributors to the frequencies in tribes Poeae and Danthonieae.

This intertribal comparison emphasises the critical importance of taxonomic status in establishing the frequencies of regionally endemic taxa.

## Inter family comparisons

A comparison of the extent of regional endemism in the grasses with other plant families exclusively of herbaceous life-form elements, or with high frequencies of them, is opportune and may be informative. In New Zealand endemic Cyperaceae of 121 species (Wilton & Breitwieser 2000), regional endemism is present only in 24, 18 of them in *Carex*. Ecologically, the comparison is imbalanced by an excess of palustrine low-altitude species. Even so, both northern North Island and northern South Island have relatively more cyperaceous endemics than elsewhere (Table 3). Endemic Juncaceae are too few to consider in a comparison.

The relative distribution of grass regional endemics might best be compared with the endemic herbaceous element of "the grasses of the dicotyledons – the Compositae" (nom. altern. Asteraceae), but taxonomic uncertainty among some of them is of the same as once obtained in the grasses; *Craspedia* is the least precisely defined. This assessment of regional endemics (Table 3) shows, just as in the grasses, high frequencies of herbaceous Compositae in Nelson-Marlborough and in Otago-Fiordland and a low frequency in northern North Island. At two ecogeographic extremes, the

Kermadec Islands and the subantarctic islands, the numbers of grasses and herbaceous Compositae are the same but the relative frequencies differ (Table 3).

This attempt at an herbaceous Compositae-Gramineae comparison only partitions Wardle's dicotyledon data, yielding the corresponding areas of species rich northern and southern South Island mountains, and emphasising the effect of forests in northern North Island resulting in low levels of regional endemism there.

# CONCLUSIONS

Taxonomic rank is the first essential character in awarding phenodemes the status of regional endemics; the second essential is their significant spatial separation. Of these criteria, the former is liable to the change imposed by taxonomic reassessment, and the latter from land-use alteration or habitat degradation. Regional endemism such as that described here is primarily a set of taxonomic statements, which do not assure intrinsic regional physiological, biochemical, or genetic differentiation whose likelihood seems probable, and which would be shared also by wide species disjuncts. At the scale examined, regional endemism is detectable in 45 grass taxa on the main islands, and on the distant islands, particularly those in the Southern Ocean, in 15 taxa. There is a good fit to the models for dicotyledons (Wardle 1963) and for higher plants (McGlone 1985; Wardle 1991) with the highest levels of grass endemism in Nelson-Marlborough and Otago-Fiordland and low levels in southern North Island and Canterbury—the floristic gaps; the only exception to their generalisations is a low frequency of grass endemics in northern North Island. The endemic herbaceous Compositae are one group of comparable size and habit against which to test the possibility that the grass frequencies are of wider application in the flora in the New Zealand Botanical Region, and even that contains risks. There is general agreement for both that high endemism lies in the Nelson-Marlborough and Otago-Fiordland-Southland regions, that there are common pauperate floristic gaps, and that both herbaceous groups are at a low frequency in northern North Island where there is a long history of extensive forests. Nothing is novel from that comparison.

Seven of the eight grass tribes in New Zealand Gramineae have endemic taxa, but only in Poeae, Agrostideae, and Danthonieae do the numbers approach 50. In all others there are 10 or fewer taxa. Among the three large tribes the ratio regionally endemic taxa:endemic taxa in Poeae is 0.41, in Danthonieae 0.34, and in Agrostideae 0.17. This relatively low ratio in Agrostideae is attributed to problems of the recognition of consistent infra-specific morphological-geographic patterns in species of wide distribution. This phenomenon is of course not exclusive to Agrostideae but appears maximised in that tribe relative to Poeae and Danthonieae.

The regionally endemic grasses documented here in cytological, genetic, and ecological terms are taxonomic entities differentiated by morphology and spatial dimensions. For qualities such as chromosome number, reproductive strategies, absence of barriers to interspecific gene exchange, or habitat selectivity, they rarely differ from other members of the New Zealand grass flora. Because they only record the final outcomes of evolution they cannot indicate the time or the rate of the events of speciation.

## REFERENCES

Allan, H. H. 1961: Flora of New Zealand. Vol. I. Wellington, Government Printer.

Burrows, C. J. 1964: Some discontinuous distributions of plants within New Zealand and their ecological significance. Part 1. *Tuatara 12*: 125–133.

Burrows, C. J. 1965: Some discontinuous distributions of plants within New Zealand and their ecological significance. Part II: Disjunctions between Otago-Southland and Nelson-Marlborough and related distribution patterns. *Tuatara 13*: 9–29.

Connor, H. E. 1962: Studies in New Zealand *Agropyron*. Part 4. Interspecific hybrids in *A. scabrum* (R.Br.) Beauv. × *A. kirkii* Zotov. *New Zealand Journal of Science 5*: 116–119.

Connor, H. E. 1967: Interspecific hybrids in *Chionochloa* (Gramineae). *New Zealand Journal of Botany 5*: 3–16.

Connor, H. E. 1968: Interspecific hybrids in hexaploid New Zealand *Festuca*. *New Zealand Journal of Botany 6*: 295–308.

Connor, H. E. 1971: *Cortaderia splendens* Connor sp. nov. (Gramineae). *New Zealand Journal of Botany 9*: 519–525.

Connor, H. E. 1983: *Cortaderia* (Gramineae): Interspecific hybrids and the breeding system. *Heredity 51*: 395–403.

Connor, H. E. 1991: *Chionochloa* Zotov (Gramineae) in New Zealand. *New Zealand Journal of Botany 29*: 219–282.

Connor, H. E. 1994: Indigenous New Zealand Triticeae: Gramineae. *New Zealand Journal of Botany 32*: 125–154.

Connor, H. E. 1998: *Festuca* (Poeae: Gramineae) in New Zealand. I. Indigenous species. *New Zealand Journal of Botany 36*: 329–367.

Connor, H. E.; Edgar, E. 1979: *Rytidosperma* Steudel (= *Notodanthonia* Zotov) in New Zealand. *New Zealand Journal of Botany 17*: 311–337.

Connor, H. E.; Edgar, E. 2002: Historical taxonomy of the New Zealand grass flora. *Journal of the Royal Society of New Zealand 32*: 89–112.

Connor, H. E.; Molloy, B. P. J.; Dawson, M. I. 1993: *Australopyrum* (Triticeae: Gramineae) in New Zealand. *New Zealand Journal of Botany 31*: 1–10.

Dawson, M. I. 2000: Index of chromosome numbers of indigenous New Zealand Spermatophytes. *New Zealand Journal of Botany 38*: 47–149.

de Lange, P. J.; Murray, B. G. 2002: Contributions to a chromosome atlas of the New Zealand flora—37. Miscellaneous families. *New Zealand Journal of Botany 40*: 1–23.

de Lange, P. J.; Heenan, P. B.; Given, D. R.; Norton, D. A.; Ogle, C. C.; Johnson, P. N.; Cameron, E. K. 1999: Threatened and uncommon plants of New Zealand. *New Zealand Journal of Botany 37*: 603–628.

Edgar, E. 1986: *Poa* L. in New Zealand. *New Zealand Journal of Botany 24*: 425–503.

Edgar, E. 1995: New Zealand species of *Deyeuxia* P. Beauv. and *Lachnagrostis* Trin. (Gramineae:Aveneae). *New Zealand Journal of Botany 33*: 1–33.

Edgar, E. 1996: *Puccinellia* Parl. (Gramineae:Poeae) in New Zealand. *New Zealand Journal of Botany 34*: 17–32.

Edgar, E. 1998: *Trisetum* Pers. (Gramineae: Aveneae) in New Zealand. *New Zealand Journal of Botany 36*: 539–564.

Edgar, E.; Connor, H. E. 1982: *Dichelachne* (Gramineae) in New Zealand. *New Zealand Journal of Botany 20*: 303–309.

Edgar, E.; Connor, H. E. 1998: *Zotovia* and *Microlaena*: New Zealand ehrhartoid Gramineae. *New Zealand Journal of Botany 36*: 565–586.

Edgar, E.; Connor, H. E. 1999: Species novae graminum Novae-Zelandiae. I. *New Zealand Journal of Botany 37*: 63–70.

Edgar, E.; Connor, H. E. 2000: Flora of New Zealand. Vol. V. Lincoln, Maanaki Whenua Press.

Edgar, E.; Forde, M. B. 1991: *Agrostis* L. in New Zealand. *New Zealand Journal of Botany 29*: 139–161.

Edgar, E.; Gibb, E. S. 1999: *Koeleria* Pers. (Gramineae: Aveneae) in New Zealand. *New Zealand Journal of Botany 37*: 51–61.

Hair, J. B. 1968: Contributions to a chromosome atlas of the New Zealand flora—12. *Poa* (Gramineae). *New Zealand Journal of Botany 6*: 267–276.

Hair, J. B.; Beuzenberg, E. J. 1961: High polyploidy in a New Zealand *Poa*. *Nature 189*: 160.

Heads, M. 1997: Regional patterns of biodiversity in New Zealand: one degree grid analysis of plant and animal distributions. *Journal of the Royal Society of New Zealand 27*: 337–354.

Lee, W. G.; Fenner, M. 1989: Mineral nutritient allocation in seeds and shoots of twelve *Chionochloa* species in relation to soil fertility. *Journal of Ecology 77*: 704–716.

Löve, Á.; Connor, H. E. 1982: Relationships and taxonomy of New Zealand wheatgrasses. *New Zealand Journal of Botany 20*: 169–186.

McGlone, M. S. 1985: Plant biogeography and the late Cenozoic history of New Zealand. *New Zealand Journal of Botany 23*: 723–749.

McGlone, M. S.; Duncan, R. P.; Heenan, P. B. 2001: Endemism, species selection and the origins of the distribution of the vascular plant flora of New Zealand. *Journal of Biogeography 28*: 199–216.

Molloy, B. P. J. 1994: Observations on the ecology and conservation of *Australopyrum calcis* (Triticeae:Gramineae) in New Zealand. *New Zealand Journal of Botany 32*: 37–51.

Rogers, G. M. 1989: The nature of the lower North Island floristic gap. *New Zealand Journal of Botany 27*: 221–241.

Wardle, P. 1963: Evolution and distribution of the New Zealand flora, as affected by Quaternary climates. *New Zealand Journal of Botany 1*: 3–17.

Wardle, P. 1991: Vegetation of New Zealand. Cambridge, Cambridge University Press.

Williams, P. A.; Grigg, J. L.; Nes, P.; O'Connor, K. F. 1976: Vegetation/soil relationships and distribution of selected macro-elements within shoots of tall-tussocks on the Murchison Mountains, Fiordland, New Zealand. *New Zealand Journal of Botany 14*: 29–53.

Williams, P. A.; Mugambi, S.; Nes, P.; O'Connor, K. F. 1978: Macro-element composition of tall-tussocks (*Chionochloa)* in the South Island, New Zealand, and their relationship with soil chemical properties. *New Zealand Journal of Botany 16*: 479–498.

Wilton, A.; Breitwieser, I. 2000: Composition of the New Zealand seed plant flora. *New Zealand Journal of Botany 38*: 537–549.

Zotov, V. D. 1971a: *Simplicia* T. Kirk (Gramineae). *New Zealand Journal of Botany 9*: 539–544.

Zotov, V. D. 1971b: *Zoysia* Willd. (Gramineae) in New Zealand. *New Zealand Journal of Botany 9*: 639–644.