Is the Tussock Form of *Festuca novae-zelandiae* of Recent Origin?

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Tussock grasses are characteristic plants of much of montane Canterbury. Possible factors involved in the evolution of the tussock form include modification of the microclimate of the interior leaves resulting in reduced water-stress etc., or protection of the interior leaves from the attentions of herbivores. The tightly packed form of tussocks also means that an individual plant can better resist invasion of its 'territory'.

Modification of the microclimate of interior leaves may be an important factor in the success of tussock grasses such as *Festuca novae-zelandiae* (hard tussock) in the relatively dry, windy Canterbury high country (Wardle 1963). However, wetland sedges such as *Schoenus pauciflorus, Carex secta, Carex comans, Carex buchananii, Uncinia uncinata, Uncinia caespitosa,* and many others also form tussocks, so desiccation cannot be a primary factor in all cases.

Grazing and browsing may have played a role in the evolution of the tussock form in New Zealand. New Zealand had a number of large ground-dwelling birds such as geese, swans, ducks and rails (Holdaway 1989) that would have frequented open areas and river flood-plains. These areas would have been the pre-human habitat of short-tussocks such as *Festuca novae-zelandiae* and *Poa cita.* These birds may have attacked tussock grasses and sedges in the same way that kea, takahe and Canada geese do today.

Of course this is all assuming that the tussock habit is 'natural' for New Zealand taxa and evolved in response to conditions found within New Zealand; for genera such as *Chionochloa* this is a reasonable assumption. However, for cosmopolitan genera such as *Festuca* and *Poa,* the ancestral species may have itself been a tussock when it arrived in the country.

Alternatively the tussock form of some species may be more recent. It has been suggested by O'Connor (1986) that the tussock form of *Festuca novae-zelandiae* is a recent phenomenon resulting from the intense selection pressure of grazing by domestic stock and frequent fire. He hypothesized that in the space of 50 to 60 years of European settlement the common lowland and montane *Festuca* had gone from being a fine, highly palatable subdominant species with a slender, densely tufted habit, to the course, unpalatable dominant tussock known today as *Festuca novae-zelandiae.* Although this hypothesis sounds somewhat far-fetched it is none-the-less interesting to examine the evidence for the recent evolution of tussock *Festuca.*

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O'Connor's arguments are based on the early taxonomy of *Festuca* species, including the usage of the term 'tussock' in species description and on the pre-1880 assessments of indigenous grass palatability. Early *Festuca* taxonomy was confused and characterised by 'lumping' of taxa. Species of fescue encountered by early botanists were initially all referred to a common European pasture grass, *Festuca duriuscula*. J.D. Hooker, in his 'Handbook of the New Zealand Flora' (1867), described *Festuca duriuscula* in New Zealand as: "very slender, densely tufted, glabrous. Culms 1-3 feet high . . . Leaves slender, involute, filiform or short and setaceous. Panicle 1-6 inches long, effuse or contracted . . . Spikelets few, 4-8 flowered, 1/4 to 1/3 inch long."

Two specimens of *Festuca duriuscula* are illustrated in Buchanan's (1880) 'Manual of the Indigenous Grasses of New Zealand'. One is small and slender, with short setaceous leaves and is most probably what Buchanan refers to as the sub-alpine form that resembles *Festuca ovina*. The other is more than twice the height, with a densely tufted habit and is more like the present-day *Festuca matthewsii*. Buchanan comments that New Zealand plants grouped under *Festuca duriuscula* showed a tendency to vary.

At the turn of the century professor Edouard Hackel of Austria, described by Cheeseman as in the first rank of European agrostologists, examined New Zealand specimens of the genus *Festuca*. Plants previously referred to *Festuca duriuscula* were now divided between *Festuca ovina* and *Festuca rubra*. To *Festuca rubra* was allocated the greater part of *Festuca duriuscula*, these plants undoubtedly being the smaller, laxer types described by Hooker (1867) and Buchanan (1880). Two new entities were described under *Festuca ovina*, *Festuca ovina* var. *novae-zelandiae* and *Festuca ovina* var. *matthewsii* (Hackel 1903).

As a result of early lumping of all New Zealand species of *Festuca* into one European taxon, early assessments of grass palatability cannot be taken as necessarily referring to particular present-day species. Therefore a recent rise to dominance of the tussock habit within lowland *Festuca* cannot be argued based on taxonomy and palatability.

However, as pointed out by O'Connor (1986), the term 'tussock' was never applied to New Zealand species of *Festuca* initially grouped under *Festuca duriuscula*. This does not mean that there were no tussock *Festuca* species in New Zealand prior to 1880. The European *Festuca duriuscula* on which the New Zealand taxon was based would never have been described as a 'tussock' as this was a term peculiar to New Zealand (and Australia?). Also, as New Zealand *Festuca duriuscula* contained a range of entities the tussock growth-form would not have been a diagnostic character of the whole group.

Poa cita (known then as *Poa caespitosa* or *Poa australis* var. *laevis*) was the grass most often referred to as 'tussock' (e.g., Buchanan 1868, J.F. & J.B. Armstrong 1872, J.B. Armstrong 1880, Buchanan 1880), however *Festuca* species occurred

with *Poa cita* on the Canterbury Plains and Banks Peninsula (J.F. Armstrong 1870, J.B. Armstrong 1880).

Despite the lack of specific reference to a tussock *Festuca* in the early botanical literature, there is no reason why *Festuca novae-zelandiae* as it is today was not already present in the flora prior to European settlement. Petrie noted in 1895 that the common *Festuca*, then still referred to *Festuca duriuscula*, was being confounded by some botanical workers and most settlers with *Poa cita*. This would suggest that the common *Festuca* was also a tussock. In a situation analogous to manuka and kanuka, *Festuca novae-zelandiae* appears to have been regularly lumped with *Poa cita* during the early decades of New Zealand botany.

European settlement of New Zealand undoubtedly had an enormous impact on indigenous species. The explosion of sheep numbers in the late 19th century was supported almost solely by grazing of indigenous species (O'Connor 1986) and would have resulted in radical changes in the distribution and abundance of the more palatable species especially. It is also conceivable that this early intense grazing pressure, coupled with fire, brought about a shift in the morphological and ecological characters of species due to selective elimination of certain types. However the tussock form of *Festuca novae-zelandiae* is more likely a product of selection based on microclimate and competitive factors over thousands or years than a result of the early New Zealand farming endeavour.

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