

REVIEW ARTICLE

Fire, grazing and the evolution of New Zealand grasses

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Abstract: Less than 4% of the non-bamboo grasses worldwide abscise old leaves, whereas some 18% of New Zealand native grasses do so. Retention of dead or senescing leaves within grass canopies reduces biomass production and encourages fire but also protects against mammalian herbivory. Recently it has been argued that elevated rates of leaf abscission in New Zealand's native grasses are an evolutionary response to the absence of indigenous herbivorous mammals. That is, grass lineages migrating to New Zealand may have increased biomass production through leaf-shedding without suffering the penalty of increased herbivory. We show here for the Danthonioideae grasses, to which the majority (c. 74%) of New Zealand leaf-abscising species belong, that leaf abscission outside of New Zealand is almost exclusively a feature of taxa of montane and alpine environments. We suggest that the reduced frequency of fire in wet, upland areas is the key factor as montane/alpine regions also experience heavy mammalian grazing. Without frequent fire to remove dead leaves, detritus and woody competitors, evolution of leaf abscission is favoured, especially in large, long-lived tussocks with sclerophyllous leaves. As fire frequency was low in New Zealand before the arrival of humans, grass leaf-abscission was an evolutionary advantage whenever large tussock species shared habitat with tall woody plants.

Keywords: alpine; *Chionochloa*; leaf abscission; mammal; *Poa*; *Rytidosperma*; tussock

Introduction

Largely because of its long isolation, New Zealand lacks or has only a sparse and unrepresentative selection of many plant and animal groups abundant elsewhere in similar environments (Gibbs 2006). As a consequence, some functional types are missing and many traits are poorly represented (Lee 1998; McGlone 2006). On the other hand, traits unique to New Zealand or rare elsewhere have developed in response to unique pressures. For instance, as New Zealand had no terrestrial mammals (aside from three bat species) birds have expanded into niches elsewhere largely occupied by mammals. As bird herbivores browse and graze differently to mammals, some plant traits, such as divarication, are suggested as having developed as a response to herbivorous moa (Greenwood & Atkinson 1977; Atkinson & Greenwood 1980, 1989; McGlone & Clarkson 1993; Bond et al. 2004; Fadzly et al. 2009; Lee et al. 2010). Moreover, the absence of mammalian herbivores appears to have reduced the incidence of plant traits, such as spinescence, which elsewhere deter mammals but have a limited influence on birds (Greenwood & Atkinson 1977).

Antonelli et al. (2011) recently proposed an intriguing addition to the list of mammal-deterring plant traits that have been lost in New Zealand. New Zealand grasses have a high incidence (18%) of leaf abscission (versus c. 3.6% in the global non-bamboo grass flora), which they suggest arose because of relaxed selection pressure. They argue that retention of dead leaves has negative effects on grass growth via self-shading, reduction of root productivity and inhibition of N-fixation, but

that these effects are offset by the dead leaves reducing the grazing efficiency of mammals. Absence of mammalian grazers in New Zealand until its settlement by Europeans in the early 19th century may therefore explain the higher incidence of leaf abscission. A comprehensive molecular phylogeny of the subfamily Danthonioideae, to which most of the New Zealand leaf-abscising grasses belong, demonstrates a proliferation of species in New Zealand lineages possessing the leaf abscission trait, in contrast to low rates of evolution of extra-New Zealand lineages with the trait (Antonelli et al. 2011).

While this 'absence of browsing mammals' hypothesis for the evolution of leaf abscission in New Zealand is plausible, mammalian browsing has been only one of many influences on the evolution of grasses. Grassland ecosystems flourish under a wide range of climatic regimes but are extensive in the dry interiors of continents, in subtropical and tropical savannas, in the Arctic and above the alpine treeline. New Zealand, being a moist, highly oceanic archipelago in the mid-latitudes, was almost completely forest-covered before humans arrived, with the only extensive grasslands being above treeline in the alpine zone (McGlone 1989). Grassland ecosystems common elsewhere on the globe, especially those typical of fire-prone situations, were therefore rare in New Zealand (McGlone 1989, 2001; Ogden et al. 1998).

Here we critically examine Antonelli et al.'s (2011) hypothesis that the absence of mammals promoted the evolution of leaf abscission in some New Zealand grass species. We first discuss leaf abscission as a phenomenon and then document the elevational distribution and morphological attributes of

New Zealand grasses and leaf-abscising relatives elsewhere. We examine our results in the light of alternative explanations for leaf abscission.

Methods

We have used phylogeny, trait and distributional data in Antonelli et al. (2011), Edgar & Connor (2000), Linder et al. (2010) and the web-based database Ngā Tipu Aotearoa – New Zealand Plants (<http://nzflora.landcareresearch.co.nz/>) to document the habitat, distributional range, growth form and leaf abscission status of all New Zealand native grasses. For Australian species we used the web-based database AusGrass2 (<http://ausgrass2.myspecies.info/>). For leaf-abscising Danthonioideae species outside of Australasia we relied on generic descriptions in Linder et al. (2010), and a range of regional floras.

Leaf abscission in grasses

Abscission mechanisms

The position, spatial arrangement and cellular architecture of the abscission break-point differs markedly between grass species (Salim et al. 1988; Röser & Heklau 2011). We recognise the following general abscission types (regarding *absence* of abscission as one of them):

- P-type: Leaf blades persistent on entire leaf sheath (most grasses)
- L-type: Leaf blade disarticulating by a clean break at a specialised zone at the distal end of the ligule leaving an entire sheath (e.g. species of *Poa*, some *Chionochloa*, *Rytidosperma*, *Microchloa*)
- F-type: Leaf-blade falls (cadent) with part of the sheath from below ligule by fracturing of the sheath through numerous transverse weakened regions (see illustration in Antonelli et al. (2011); e.g. species of *Chionochloa*, *Cortaderia*, *Lamprothyrsus*)
- M-type: Leaf blade falls from a fracture of the blade about the ligule (*Merxmuellera* spp.; does not occur in indigenous New Zealand species)
- D-type: Leaf blades and sheaths deciduous (Bambuseae species; does not occur in indigenous New Zealand species)

Biophysical significance of abscission

Detachment of leaves via a differentiated abscission zone is a typical feature of dicotyledonous angiosperms but is rare in ferns (P. J. Brownsey, pers. comm., 2012), and monocotyledons, including the grass family (Röser & Heklau 2011). Leaf abscission is primarily a response to loss of function through aging or stress, which makes it unprofitable for a plant to retain a given leaf (Givnish 1984). Overshadowing of a leaf by newer leaves, episodic or seasonal drought or cold, or insect herbivory are the most common stresses triggering abscission (Williams & Whitham 1986; González-Carranza et al. 1998; Myneni et al. 2007; Mingo & Oesterheld 2009). However, if a plant is herbaceous or low growing, there is little need for abscission. An overtopped or stressed leaf can simply wither away without interfering with the photosynthetic gain of the remaining foliage. Low-growing herbaceous plants such as most ferns, grasses and other monocotyledons therefore usually lack a specific leaf-shedding mechanism. In contrast, a tall,

woody plant would be disadvantaged if it retained inefficient or dead leaves within its canopy because they block light from photosynthetically active foliage, and intercept wind, snow and rain thereby increasing mechanical loading. It is significant then that tall ferns and monocotyledons with complex canopies (e.g. tree ferns, bamboos and palms) often abscise their leaves. For example, five out of the eight tree ferns in New Zealand shed their massive fronds as their crown develops, possibly to increase stability through reducing the weight of the crown or to decrease the wind profile (Page & Brownsey 1986).

The typical graminoid (grass or sedge) is low-growing and herbaceous with a lightly constructed, linear leaf blade, produced by a short shoot (tiller) that performs all the functions of the canopy. As they senesce, lacking any decay-resistant woody elements, most graminoid leaves rapidly wither, rot off, hang or lie prostrate. However, when the leaf tissue is stiff and decay-resistant, dead leaves block light thereby reducing photosynthesis. New leaves formed in the shade are developmentally impaired and therefore less efficient and new foliage takes longer to get into full production (Knapp & Seastedt 1986). The disadvantages of self-shading have been quantified in a tall Andean tussock (*Festuca orthophylla*) where it has been shown that 80% of its green foliage intercepts less than 50% of the above-canopy light on average (Monteiro et al. 2011). Many graminoids build small trunks from tillers and stout leaf bases, and thus escape the consequences of accumulation of dead foliage through vertical growth, leaving the dead and senescing leaves below the photosynthetically active tissue. For instance, leaf-retaining *Poa litorosa* of the subantarctic grasslands can build thick trunks of dead leaf bases more than a metre in height. Small, low-growing stoloniferous or rhizomatous grasses avoid self-shading by developing an active horizontal front of new shoots.

We conclude that most grass species do not shed their dead leaves because there are few biophysical advantages in doing so. However, there are other ecological factors associated with dead leaf retention that must also be considered.

Knapp and Seastedt (1986) discuss the disadvantages of dead matter accumulation (amounting to two to three times greater than annual production) in a North American tallgrass prairie growing under a dry climate with warm summers and cold winters. They argue that nearly every ecosystem process in this community is adversely affected when dead tissue (necromass) accumulates within the canopy and as undecayed detritus on the surrounding ground surface. A thick overwintering ground layer of dead leaves insulates the soil from solar radiation and therefore it warms up more slowly in spring. Microbial activity in the detritus renders the inorganic nitrogen input from accompanying rainfall less available to the plant. The risk of pathogen attack is increased by the presence of slowly decaying leaves. These disadvantages are likely to be most severe in tall tussock grasses with sclerophyllous leaves and slowly decaying tissues.

Advantages of dead leaf retention

The advantages of retention of dead leaf tissue relate to climate, fire and mammalian herbivory.

Microclimate

Most grasses are shallow rooted and their leaves are held within a metre of the soil surface. They are, therefore, subject to an intensified temperature cycle with overnight lows and daytime highs more extreme than the open air above their canopies, exposing them to freezing and accelerated desiccation (Hedberg

1973). Accumulated dead tissue in the form of retained leaves, persistent leaf sheaths and thick ground detritus protects the meristems from freezing (Monteiro et al. 2011). Alpine tussocks have been shown to experience minimum temperatures in the centre of the tussock several degrees warmer than in the canopy (Hedberg & Hedberg 1979). Bare soil, being subject to high daytime temperatures, loses water faster than shaded soil, and Monteiro et al. (2011) reported less water in the soil under inter-tussock spaces than under the dense canopy of *Festuca orthophylla*. Such micro-climatic benefits are even more important in highly seasonal environments.

Fire

Fire has been a potent factor in the evolution of grasses. Osborne (2008) shows that the spread of C4 grasses occurred in the late Miocene–Pliocene under the influence of increasing climatic seasonality and fire, and suggests that similar reasoning holds for C3 grasses. Grasses are susceptible to overtopping and then exclusion by taller shrubs and trees but, because of their well-protected meristems, are also highly tolerant of fire. Grass traits that defend against grazing (tannin-like compounds, low nutrient status of tissue, sclerophylly) may also result in low decomposition rates and build-up of biomass during dry seasons, which promotes fire (Osborne 2008). Retention of dead leaves in the canopy ensures rapid spread of fire, while persistent leaf bases and densely packed tillers near or at ground level protect their meristems through insulation (Morgan 1999; Overbeck & Pfadenhauer 2007). As their competitors are seedlings and saplings of trees and shrubs that find it difficult to avoid catastrophic fire damage, this accumulation can be interpreted as a competitive strategy to resist encroachment by tall woody plants (Bond & Midgley 1995; Bond 2008). Fire can assist invading grasses. For instance, an exotic, invasive large tussock (*Ampelodesmos mauritanica*) in Catalonia has litter that decomposes 30% more slowly than that of competing shrubs, thus accumulating more quickly. The tussock and its abundant litter have been shown to be much more inflammable than any of the shrubs and thus it both promotes and is favoured by fire (Grigulis et al. 2005).

Fire is an efficient remover of dead leaf tissue and, unlike herbivores, acts as a generalised grazer because it does not preferentially single out nutrient-rich, poorly defended foliage (Bond & Keeley 2005). It may also reduce the detrital ground layer. In some grass species absence of fire leads to accumulation of necromass that restricts photosynthetic production and tillering and promotes decay, leading to slower growth (Morgan & Lunt 1999; Bond et al. 2003). Suppression of fire in the grasslands of North America has permitted expansion of shrubs and trees in some settings (Heisler et al. 2003) and endangered the persistence of some tussock grass species in Australia (Morgan & Lunt 1999). The dependence on fire of grasslands in tropical savannas is well established (Overbeck & Pfadenhauer 2007).

Mammalian herbivory

Grasses have long been suspected of having evolved with large herbivorous mammals (Osborn 1910), a supposition that is now well supported (Bouchenak-Khelladi et al. 2009). Caespitose (variously called bunch or tussock) grasses appear to be more vulnerable to grazing than rhizomatous grasses in that they place the emerging culm in a more elevated position exposed to browsing and trampling (Mack & Thompson 1982). Dead leaf retention among green foliage in the canopy of caespitose grasses may provide protection by diluting forage quality, thus

reducing green tissue consumption by large grazers. A study of *Schizahyrium scoparium* (little bluestem) in Kansas tallgrass prairie showed that this small caespitose grass resisted grazing through its small size (non-preferred by bison) and retention of dead reproductive tillers. Fire removed the dead tillers and, although the little bluestem increased its growth, increased exposure to grazing contributed to its decline relative to other grasses (Pfeiffer & Hartnett 1995). Mingo and Oesterheld (2009) showed that experimental removal of dead leaves from *Paspalum dilatatum* resulted (for large tussocks) in a higher green biomass in the absence of grazers and a smaller biomass in their presence. Small and medium-sized tussocks showed no significant change. If dead leaves were not removed, final dead biomass was identical in grazed and ungrazed trials.

Abscission in grasses (bamboos aside) removes only the lamina not the generally stiffer and densely packed sheaths and not the dead flowering culms. It follows that protection of meristems by senescing tissue or necromass is unaffected by abscission. However, this is not true for fire promotion: grasses with a low fuel bulk density with a high surface-to-volume ratio are highly flammable (Hoffmann et al. 2012). Dead leaves loosely held in the canopy or drooping as a dry fringe are drier, better aerated and therefore more flammable than densely packed sheaths and dead tillers. Shedding of lamina will therefore decrease flammability to a much greater extent than it will decrease resistance to grazing.

Global pattern of leaf abscission relative to New Zealand

Antonelli et al. (2011) estimated that only 3% of c. 11 000 grass species shed senescing leaves through abscission. However, as the c. 1500 species of bamboo (c. 13.5% of the world grass flora) abscise their leaves, and some are deciduous (Ohrnberger 1999), this value of 3% must be an underestimate. China, for instance, has c. 1795 species of grass of which 534 (29.7%) are bamboos (Bystriakova et al. 2003). If we adjust the figures given in Antonelli et al. (2011) to exclude the bamboos, around 3.6% of the world's grasses abscise leaves. The New Zealand grass flora is highly unusual in the prevalence of leaf abscission. Of the approximately 188 native New Zealand grass species, 34 (18.1%) abscise their leaves. Two genera, *Chionochloa* and *Rytidosperma*, provide 25 (74%) of these leaf-abscising species (Fig. 1a). Of the remaining 9 leaf-abscising species, 5 are in *Poa*. These three genera constitute c. 43% of the flora, but 88% of the leaf-abscising species. These three genera excluded, the remaining 57% of the grass flora has a leaf-abscission rate of 3.7%, which is nearly identical to the global average.

In Fig. 1b we present characteristics of the New Zealand grass flora in relation to abscission. Only 8% (6/72) of the stoloniferous grass species in New Zealand show leaf abscission versus 42% (21/50) of tussock species. Those species confined to the lowland/coastal zone and non-endemic species have markedly less leaf abscission than the average. In *Chionochloa*, of the 35 named species and subspecies, 22 have leaf abscission (63%); *Rytidosperma* has 20 species in New Zealand of which 60% (12/20) have leaf abscission (Fig. 1c).

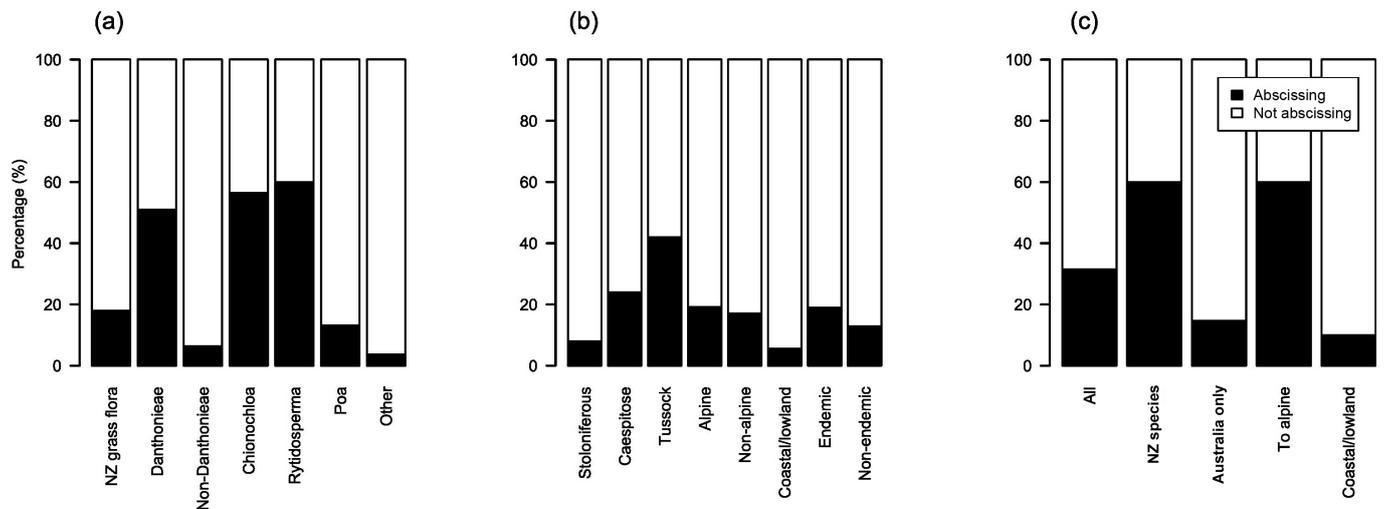


Figure 1. (a) Levels of abscission in the New Zealand (NZ) grass flora; (b) characteristics of the NZ grass flora in relation to abscission; (c) characteristics of the Australasian species of the genus *Rytidosperma* in relation to abscission. 'Other' = species not in *Chionochloa*, *Rytidosperma* or *Poa*. 'Alpine' category = species ascending above the treeline. 'Coastal/lowland' = species restricted to those zones. 'To alpine' = species ascending to the alpine zone.

Leaf abscission in the subfamily Danthoioideae

The phenomenon of leaf abscission in New Zealand is essentially confined to two genera in the Danthoioideae. If we can explain why *Chionochloa* and *Rytidosperma* have high levels of abscission, we have an answer to the question of why New Zealand has high levels of leaf abscission. Fortunately, both these genera have a modern New Zealand revision (Edgar & Connor 2010), and globally the group has a newly revised nomenclature (Linder et al. 2010) and phylogeny (Antonelli et al. 2011). *Chionochloa* has been particularly well studied over many years, has a near complete phylogeny (Pirie et al. 2010) and has had extensive observations made on a number of natural hybrids (Connor 1991). The *Rytidosperma* s.l. clade likewise has a comprehensive phylogeny (Humphreys et al. 2010).

Danthoioideae outside of New Zealand

Of the Danthoioideae outside of New Zealand, only *Chimaerochloa*, *Chionochloa*, *Cortaderia*, *Danthonia*, *Merxmuellera*, *Rytidosperma* and *Tenaxia*, have leaf-abscising species. We discuss these species below.

Chimaerochloa archboldii is the sole member of its genus. It is a tough, sclerophyllous-leaved tussock of the alpine grasslands of New Guinea.

Chionochloa frigida, a tall tussock of the Australian alpine zone, is nested within the New Zealand *Chionochloa* phylogeny and is the result of trans-Tasman dispersal.

Cortaderia spp. are large tall South American tussocks with tough, sclerophyllous leaves (New Zealand species once placed in this genus are now in *Austroderia*). Of the 20 species recognised in *Cortaderia*, almost all have leaf abscission. Both of the naturalised *Cortaderia* spp. (*C. jubata*, *C. selloana*) in New Zealand abscise their leaves (Edgar & Connor 2010), as do other close relatives of these taxa (*C. rudiusscula*, *C. atacamensis*, *C. speciosa*). *C. pilosa* is the dominant vegetation cover on the Falkland Islands where it is known as 'white grass' because of the large amount of dead leaf material

it retains as leaf bases (Davies et al. 1990). *C. araucana* is a montane (extends up to treeline) grass of higher rainfall regions in Chile (<http://www.florachilena.cl>). *C. boliviensis* is grassland species of high elevations (2500–4000 m) in the Andes. *C. nitida* grows between 2800 and 3400 m on poorly drained soils and under cool climates (DAMA: Fichas técnicas por especie).

Only one *Danthonia* (*D. parryi*) of the 25 species in the genus has leaf abscission (4%). It is a large tussock grass of montane to subalpine regions of the eastern Rocky Mountains in North America, at elevations of 1000–1800 m in the north of its range and 2400–3500 m in the south (Johnston & Dormaar 1970).

Merxmuellera species all have leaf abscission and are robust tussocks with sclerophyllous, tough leaves found in Afrotropical grasslands in areas of higher rainfall (van Oudtshoorn 1999).

Rytidosperma s.l. in Australia have a lower level of leaf abscission than in New Zealand (19%; 7/37) yet 55% (6/11) of the Australian alpine species have leaf abscission, with only 4% (1/26) of the non-alpine species showing this trait (Fig. 1c). Two out of the three species shared between the two countries have leaf abscission. A recent phylogeny of *Rytidosperma* (Humphreys et al. 2010) splits the group into an Australian clade of 40 largely lowland to montane taxa of which 10% (4/40) have leaf abscission; and a clade shared between New Zealand, southern South America and Australia that includes a substantial montane–alpine element and has 44% (20/45) with leaf abscission. None of the southern American group abscise their leaves. Two of the Australian group (*R. nitens* and *R. pauciflorum*) have variable or infrequent abscission.

Tenaxia are wiry, tussocks of the African mountains and Himalayas. Three species are recorded in Antonelli et al. (2011) as being leaf-abscising: *T. aureocephala* (Southern Africa); *T. subulata* (mountains of Ethiopia) and *T. cumminsii* (Himalayan mountains).

To summarise: leaf-abscising species of the Danthoioideae outside of New Zealand are almost exclusively species of high montane to alpine environments, and often grow under high rainfall.

Abscission in *Chionochloa*

Chionochloa is the most intensively studied of the indigenous New Zealand grass genera and provides crucial insights as to how leaf abscission has evolved. Twelve *Chionochloa* species and subspecies have L-type (disarticulating by a clean break) abscission; 10, F-type (sheath fractures below ligule via numerous transverse weakened regions); and the remaining 12 P-type (persistent) (Table 1). There is no discrimination in abscission type between species with junceous leaf-blades and those with flat, folded or U-shaped blades. There are polymorphisms within *C. pallens* where subspecies *cadens* is L-type but the other two are P-type. *C. rubra* subspecies *rubra* and subspecies *occulta* are F-type, but subspecies *cuprea* is P-type. Both subspecies of *C. conspicua* are L-type, but leaf fall is described as tardy (Connor 1991).

Naturally occurring interspecific hybrids are often encountered in *Chionochloa* and 48 are recorded (Table 2; Connor 1991). The hybrids between taxa with different abscission types reveal no general dominance of one type over another (P-type, 16 out of 28 inter-type crosses involving one P-type parent; L-type, 8/22; F-type, 10/21 although some taxa appear to confer dominance for the type they carry (*C. crassiuscula*/L-type; *C. flavescens*/F-type). Although hybrids between two species both with F-type or both with L-type retain their type, as would be expected, this is not always true of P-type crosses. Hybrids *C. australis* × *C. macra* and *C. australis* × *C. pallens* ssp. *pallens* are both L-type (but somewhat late in disarticulating) although the parents are all P-types. This is of particular interest because *C. pallens* ssp. *cadens* is of the L-type, while *C. pallens* ssp. *pallens* and *C. pallens* ssp. *pilosa* are P-type. *C. conspicua* ssp.

cunninghamii (L-type) × *C. rubra* ssp. *rubra* (F-type) has leaves of the P-type; and *C. conspicua* ssp. *conspicua* (L-type) when crossed with either *C. rubra* ssp. *rubra* or *C. rubra* ssp. *occulta* (both F-type) also has leaves of the P-type. A collection from a single site of hybrids between *C. conspicua* ssp. *cunninghamii* (L-type) and *C. pallens* ssp. *pallens* (P-type) yielded 2 L-type and 8 P-type individuals.

These hybrid studies demonstrate that inheritance of abscission traits in *Chionochloa* is complex. The genus has an abundance of natural hybrids and has evidently undergone recent reticulate evolution (Pirie et al. 2010). The five examples of a spontaneous resurgence of an abscission type in F1 hybrids whose parent species do not possess it point to a long history of acquisition and suppression of abscission traits. When abscission type is mapped onto the phylogeny of Pirie et al. (2010) a striking pattern is apparent (Fig. 2). All of the well-defined Southern / crassiuscula clade have L-type abscission; North-Western / rubra and Eastern and Southern / rigida clades have P- and F-types; and Widespread / conspicua clade has all three types (Pirie et al. 2010). Hybridisation within and between clades has most likely promoted reversion to the ancestral P-type.

If we accept that the non-abscission P-type represents a reversion and *not* a new development, quite a different interpretation to that implicit in Antonelli et al. (2011) must be placed on trait evolution in this group. Under this new interpretation, leaf abscission accompanied the initial formation of the genus and may have been universally present, but subsequently widespread reversion to P-type occurred in nearly 40% of the species and subspecies. This is likely to have occurred spontaneously during the hybridisation events

Table 1. Leaf-abscission types in *Chionochloa* species, grouped, for comparison, within the clades of Pirie et al. (2010¹).

Leaf habit	North-Western / rubra clade	Southern / crassiuscula clade	Eastern and Southern / rigida clade	Widespread / conspicua clade		
				Lowland / beddiei subclade	flavescens subclade	vireta subclade
P-type (n = 13)	<i>juncea</i>		<i>macra</i> <i>oreophila</i> <i>rubra</i> ssp. <i>cuprea</i> <i>pallens</i> ssp. <i>pilosa</i>	<i>australis</i> <i>beddiei</i> <i>bromoides</i> <i>cheesemani</i> <i>flavicans</i>	<i>pallens</i> ssp. <i>pallens</i> <i>pallens</i> ssp. <i>pilosa</i>	<i>nivifera</i>
L-type (n = 12)		<i>acicularis</i> <i>antarctica</i> <i>crassiuscula</i> ssp. <i>crassiuscula</i> ssp. <i>torta</i> <i>crassiuscula</i> ssp. <i>directa</i> <i>lanea</i> <i>ovata</i> <i>teretifolia</i>		<i>conspicua</i> ssp. <i>conspicua</i>	<i>conspicua</i> ssp. <i>cunninghamii</i>	<i>pallens</i> ssp. <i>cadens</i> <i>vireta</i>
F-type (n = 10)	<i>rubra</i> ssp. <i>rubra</i> <i>rubra</i> ssp. <i>occulta</i>		<i>rigida</i> ssp. <i>rigida</i> <i>rigida</i> ssp. <i>amara</i> <i>spiralis</i>	<i>defracta</i>	<i>flavescens</i> ssp. <i>lupeola</i> <i>flavescens</i> ssp. <i>brevis</i> <i>flavescens</i> ssp. <i>hirta</i>	<i>frigida</i>

¹Pirie et al.'s phylogeny did not include *bromoides* or ssp. *pallens* and included a second *flavescens* ssp. *brevis* in the Eastern and Southern / rigida clade.

Source: see Methods.

Table 2. Leaf-abscission type in *Chionochloa* hybrids ($n = 48$): P = persistence; L = disarticulation at ligule; F = fracturing of sheath. Data from Connor (1991).

Species	Subspecies	Type	<i>cheesemanii</i>	<i>macra</i>	<i>pallens</i> <i>pallens</i>	<i>oreophila</i>	<i>rubra</i> <i>cuprea</i>	<i>conspicua</i> <i>conspicua</i>	<i>crassiuscula</i> <i>torta</i>	<i>lanea</i>	<i>teretifolia</i>	<i>rubra</i> <i>occulta</i>	<i>rubra</i> <i>rubra</i>	<i>rigida</i> <i>amara</i>
			P	P	P	P	P	L	L	L	L	F	F	F
<i>australis</i>		P		L	L	P		L	L			P		
<i>beddei</i>		P	P											
<i>cheesemanii</i>		P						P				P		
<i>macra</i>		P				P								
<i>pallens</i> ssp. <i>pallens</i>		P				P						P	P	
<i>pallens</i> ssp. <i>pilosa</i>		P							L				P	
<i>acicularis</i>		L				P								
<i>conspicua</i> ssp.		L					P					P	P	
<i>conspicua</i> ssp.		L	P		P/L								P	
<i>cunninghamii</i>														
<i>crassiuscula</i> ssp.		L					P			L				L
<i>crassiuscula</i>														
<i>crassiuscula</i> ssp.		L									L			
<i>directa</i>														
<i>crassiuscula</i> ssp.		L				L								F
<i>torta</i>														
<i>pallen</i> ssp. <i>cadens</i>		L		P		L								L
<i>teretifolia</i>		L		P		P								F
<i>flavescens</i> ssp.		F		F		F	F						F	
<i>brevis</i>														
<i>flavescens</i> ssp.		F			F								F	
<i>flavescens</i>														
<i>flavescens</i> ssp. <i>hirta</i>		F										F		
<i>flavescens</i> ssp.		F			F							F		
<i>lupeola</i>														
<i>rigida</i> ssp. <i>rigida</i>		F		P			F							
<i>spiralis</i>		F					F				F			

that occurred during the rise of the Southern Alps and the disruptions accompanying the onset of the Plio–Pleistocene cooling (Heenan & McGlone 2013). However, those species and subspecies that reverted to retaining their leaves were clearly not disadvantaged as most are currently widespread.

We suggest that the increase in open grassland in the course of the Plio–Pleistocene may have altered selection pressure in favour of the P-type trait, at least for some species. The ecological niche and elevational range of the various species is evidence for this, although conclusions must be tentative as the numbers involved are small, and the recorded ranges and habitat types often wide. Those taxa that are recorded in Edgar & Connor (2010) as co-existing with shrubland or forest are 15% (2/13) P-type; of those only found in grassland, 35% (6/17); and cliff specialists 75% (3/4), consistent with more open habitats favouring leaf persistence. The 12 taxa that reach the high alpine zone are of particular interest, as they rarely compete with tall woody plants. Of these, 50% (6/12) are P-type in contrast to the 34% (12/35) in the genus as a whole. As discussed by Pirie et al. (2010), taxa reaching the alpine zone tend to have closest relatives in lower altitudinal zones. Of the five alpine taxa with P-type abscission all have as a closest relative a lower altitude taxon with F-type or L-type abscission. It seems improbable that the P-type trait was re-evolved in these circumstances, but rather that ancestral leaf persistence, typical of most grasses, was reasserted once selection pressure for leaf abscission was reduced. As well as being a response to reduced competition from tall woody plants, under the open cold conditions of the alpine zone leaf

retention may have been beneficial through insulating the base of the tussocks and by suppressing low-growing herbs and shrubs in inter-tussock spaces.

Leaf abscission in relation to the ‘absence of grazing mammals’ hypothesis

Leaf abscission is largely confined in New Zealand to two genera of the Danthonioideae (*Chionochloa*, *Rytidosperma*) and so this will be the focus of our discussion of the phenomenon.

Grazing and leaf abscission

The Antonellii hypothesis for leaf abscission depends on there having been no effective grazing pressure on New Zealand grasses before human settlement. The nine extinct moa species were not only browsers; some species grazed low-growing herbs and others specialised in foraging in upland tussock grasslands and herbfields (Wood et al. 2008). However, as Antonellii et al. (2011) point out, it appears that moa did not graze to any extent on grasses. They further comment that takahē (*Porphyrio mantellii*), a large flightless rail that was widespread in wetlands, tussocklands and forest and scrubland margins, feeds only on tussock bases and therefore cannot have exerted a selective pressure against leaf abscission as mature leaf tissue was not eaten. The extinct New Zealand geese (*Cnemidornis* spp.) were close relatives of the Australian Cape Barren goose (*Cereopsis novaehollandiae*), which grazes on grasses and herbs, but do not seem to have been

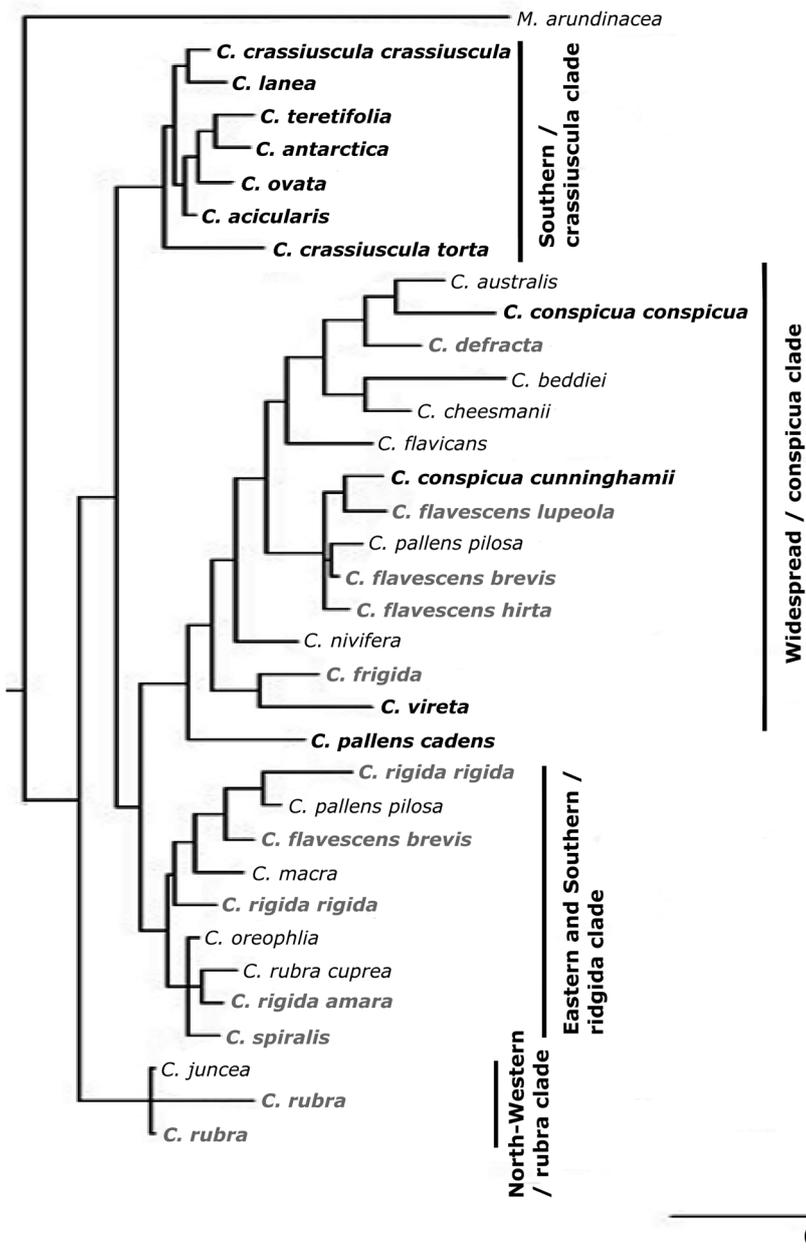


Figure 2. *Chionochloa* phylogeny from combined chloroplast DNA sequences with *Merxmuellera arundinacea* as the outgroup (derived from Pirie et al. 2010) in relation to leaf-abscission type (Bold = disarticulating L-type; grey tone = fracturing F-type; normal = persistent P-type).

common (Worthy & Holdaway 2002). The extinct Finsch’s duck (*Euryanas finschi*) was common throughout and is closely related to the Australian *Chenonetta jubata*, which eats leaves and seeds of grasses, sedges and legumes (Worthy & Holdaway 2002). Even so, it seems unlikely that these geese and ducks would have exerted anything like the grazing pressure of large mammals elsewhere. Insect herbivory, for instance by grasshoppers, which can be significant in high altitude New Zealand grasslands (White 1975), is unlikely to have promoted retention of dead tissues as a defence because insects are small and typically highly selective.

Thus, this aspect of the hypothesis appears sound: New Zealand grasses are highly unlikely to have suffered anything like the grazing pressure exerted in regions with mammalian grazers. However, for the grazing hypothesis to be tenable, those grasses in New Zealand that have acquired leaf-abscission traits should be more vulnerable to grazing by introduced mammals than those that have not. Antonelli et al. (2011) in fact make this claim. Is it substantiated?

Mammalian grazing certainly has a detrimental effect

on many New Zealand grasses and in particular the larger *Chionochloa* spp. Grazing, in combination with fire, has induced non-*Chionochloa* grasslands across large areas; and grazing alone in the subalpine–alpine zone has resulted in induced herbfields of the asterad rosette genus *Celmisia* and the apioid spiny *Aciphylla* (Mark 1994). But tussock grasslands elsewhere in the world can also be heavily impacted by intense mammalian grazing and fire, e.g. western North America (Mack & Thompson 1982). Therefore, the key question is: do leaf-abscising native grasses in New Zealand perform more poorly than leaf-retaining native grasses in the presence of grazing mammals?

The sole evidence Antonelli et al. (2011) advanced for this critical aspect of their hypothesis is a grazing exclusion study (Rose & Platt 1992), which they suggest demonstrates that leaf-abscising *Chionochloa flavescens* does better in the absence of introduced mammalian grazers than *C. macra*, a species with persistent leaves. However, Rose and Platt (1992) make no such claim: rather they show that these species dominate on sites of different aspect. As *C. flavescens* predominated

on the warmer, drier north-facing slopes where, according to Mark (1994), grazing-induced degradation begins, only eventually extending to the cooler and moister south slopes, it is highly likely it experienced more intense grazing and fire pressure. Moreover, both tussocks underwent considerable recovery when sheep were withdrawn, showing both were previously affected by sheep. After sheep exclusion, hares (*Lepus europaeus*) continued to impact these tussocks. Rose and Platt (1992) state: '*C. flavescens* [leaf-abscising] was only lightly browsed by hares...' and that '...browsing by European hares alone was capable of inhibiting *C. macra* [leaf-retaining] recovery.' While hares have a smaller bite size than sheep, and thus are likely to be more selective, their diet is largely tussock leaf blades and, in other settings, they show a variable preference for both leaf-abscising and leaf-retaining tussock species depending on availability (Norbury & Flux 2005).

Other work has shown this equivocal relationship between leaf traits and grazing vulnerability. Mark (1994) notes that *Poa colensoi*, *P. cita*, *Festuca novae-zealandiae*, *F. matthewsii*, and *Rytidosperma setifolium* are the grass species that have most commonly replaced previous *Chionochloa* grasslands (including species with and without leaf abscission) in the face of frequent fire and intensive grazing. Two of these (*P. colensoi* and *R. setifolium*) are leaf abscisers, indicating that leaf abscission is compatible with being a dominant in these fire- and grazing-induced grasslands. Investigations of palatability in New Zealand *Chionochloa* species have likewise shown no clear benefit for dead leaf retention. A cafeteria-type grazing experiment (using sheep and deer) on young plants of New Zealand *Chionochloa* tussocks (Lloyd et al. 2010) showed that leaf-abscising tussocks were as likely to have above-average biomass loss (5/8 species) as leaf-retaining tussocks (6/13). Of those species in this trial that showed much higher vulnerability to mammalian grazers and which were specifically mentioned by the authors as showing vulnerability in the field (*C. beddiei*, *C. conspicua*, *C. flavicans*, *C. macra*, *C. pallens*), only *C. conspicua* has leaf abscission. In short, field and experimental evidence do not provide any evidence of New Zealand leaf-abscising species being more susceptible to mammalian browsing than leaf-retaining species.

In the absence of evidence demonstrating New Zealand leaf-abscising grasses are more vulnerable to mammalian grazing, the hypothesis can be dismissed. Leaf abscission in all probability has very little to do with vulnerability to mammalian grazing. Palatability of the leaves and intrinsic whole-plant recovery rates after tissue loss are much more likely to be the key characteristics.

Alpine environments and leaf abscission

Apart from New Zealand, the grass species in the Danthonioideae most likely to develop leaf abscission are robust, long-lived tussocks, with sclerophyllous, tough decay-resistant leaves, in upper montane or alpine habitats. This raises the question of whether the cooler, wetter alpine environment itself could be responsible. However, in complete contrast to other regions, indigenous New Zealand grass species whose ranges extend into the upper montane or alpine zone have approximately the same level of leaf abscission (19%; 15/78) as those species that do not (17%; 19/112). Within the New Zealand Danthonioideae, species that reach the upper montane or alpine zone are no more likely to have leaf abscission (33%; 8/24) than those that do not (42%; 8/19). As we have seen, those taxa in *Chionochloa* belonging to leaf-abscising lineages recruited into the alpine zone from lower elevations

often revert to the ancestral P-type trait. We therefore argue that the strong connection between high altitude habitats and leaf abscission in non-New Zealand Danthonioideae is highly *unlikely* to be a direct consequence of the cool, moist, cloudy climatic regimes typical of those areas.

Fire and leaf abscission

Having demonstrated that birds were unlikely to have exerted much grazing pressure on grasses, Antonelli et al. (2011) make the assumption that the absence of grazing mammals is the only significant difference between New Zealand and the rest of the world as regards grass evolution. However, New Zealand has a moist, oceanic climate unlike most continental areas and, aside from the alpine zone, had a near complete forest and shrubland cover in the prehuman era (McGlone 1989). Grasslands were extensive in montane and lowland regions during the colder intervals of the Pleistocene (McGlone et al. 2010) but, unlike in most continental settings, did not persist as a permanent biome through a complete glacial–interglacial cycle. Fire was present on the New Zealand landscape, in particular in the dry eastern side of the South Island, but seems to have occurred at long intervals and thus specific fire adaptations are rare in the flora (Ogden et al. 1998; McWethy et al. 2010). Fire, an important factor in grass evolution globally, was therefore not significant in New Zealand. A case can therefore be made for the low frequency of fire as the driver for evolution of leaf abscission in New Zealand grasses.

Absence of frequent fire increases the competitive pressure from shrubs and trees (Bond & Midgley 2012). In these circumstances, avoidance of self-shading by dead foliage through leaf abscission may be a selective advantage. This evolutionary pressure should be intensified in long-lived, tall tussock grasses with tough, fibrous, decay-resistant leaves as slowly decaying dead foliage will block light interception for a considerable period. Tussocks expand slowly by radial growth and cannot escape shading by rapid lateral spread. As we have shown, there is some evidence for this in the New Zealand *Chionochloa* taxa where those recorded as regularly co-existing with shrubs or forest have less than half the incidence of leaf persistence (P-type) than those characteristic of grassland only.

The relative unimportance of fire in New Zealand suggests an answer to the conundrum discussed above where leaf-abscising non-New Zealand Danthonioideae favour montane–alpine habitats whereas leaf-abscising New Zealand species show no preference. High montane and alpine areas have more consistent cloud cover, year-round rainfall and prevailing cool temperatures and fire frequency is less (Keane et al. 2002). Krawchuk et al. (2009) found strong correlations between fire activity and productivity, and temperature and rainfall at global scales, with fire activity lowest in cool, low productivity settings such as those that characterise alpine and montane ecosystems. For instance, fire is rare in the Australian subalpine–alpine zone, major conflagrations occurring only once or twice a century (Williams et al. 2006). On the other hand, lowland grasslands in seasonally dry climates have fast-growing species that go through predictable annual cycles of biomass production, late-season curing and fire and there is little need for abscission as long as fire occurs frequently.

It can, of course, be argued that not only is fire frequency lower in the montane–alpine zone, but also grazing pressure is less. It is not obvious why this should be true. Oceanic islands aside, all montane–alpine-area plants have evolved in the presence of mammalian browsers and there are a number

of specialist alpine grazers in all continents (e.g. goats *Capra hircus*, llama *Lama glama*, hares). For instance, in Australia, the wombat (*Vombatus ursinus*) has a diet largely of tussock grasses (Evans et al. 2006). The New Zealand experience with introduced vertebrate herbivores (e.g. red deer *Cervus elaphus*; hares) is that alpine grazing was intense enough to threaten the integrity of alpine grasslands (Mark & Dickinson 2003). Some montane to subalpine tussocks elsewhere are highly browse-resistant (e.g. *Merxmuellera*) but nevertheless shed their leaves (van Oudtshoorn 1999).

Indigenous grasses reacted positively to the widespread burning that accompanied human settlement, becoming the dominant land cover in areas where rainfall was lower than c. 1000 mm per annum (McGlone 2001). The healthy state of tall tussock grassland that European settlers encountered in the 19th century shows that Māori-lit fires were frequent enough to maintain tussock grassland cover, but not so frequent as to adversely affect it. Mark (1994) has shown for *Chionochloa* that vegetative growth, flowering and seed germination increase within 2 years of burning. However, these tussocks are slow to recover, burnt plants achieving only 65% of the biomass of unburnt plants 15 years after fire, and flowering intensity takes at least 14 years to recover. Grasses in New Zealand, therefore, can tolerate infrequent fire but lack the ability to deal with the annual to triennial fire frequencies characteristic of many grasslands in seasonally dry, lowland situations.

The post-human era amounts to a giant experiment in which, first, frequent fire (with Māori settlement in the 13th century) and then mammalian grazing (European introduction in the 19th century) were introduced, reconnecting New Zealand grass lineages to these important influences. As New Zealand grass species have not lost the main features that enable grasses to persist in the presence of fire (meristems close to the ground; protective packing of persistent leaf bases; vegetative growth/flowering stimulated by fire), it would be expected that they would react positively to removal of woody competitors by fire. On the other hand, if persistent dead leaf tissue is a significant deterrent to mammalian grazing, introduction of mammalian browsers should have led to those taxa that retain dead leaves being more advantaged; clearly they are not.

Confirming the importance of fire, or the absence thereof, in the evolution of leaf-abscission traits requires carefully conceived experimental work evaluating whether necromass is a negative factor for grasses competing with shrubs and trees and a positive factor for grasses in the alpine zone. Quantifying the relative growth rate of species with differing leaf abscission would also provide further evidence with which to evaluate our hypothesis.

Conclusions

Fire and mammalian grazing are intimately linked to grass evolution and the spread of grasslands. Many grasses have effective defences against grazing in the form of tannin- and silica-enriched leaves and their well-protected meristems permit rapid recovery after grazing. However, grasses are easily overtopped and permanently eliminated by shrubs and trees. The primary threat to the persistence of most grass species is not therefore grazing, but competition from woody plants. As fire removes accumulated necromass in and around grasses, mostly without killing them, and effectively suppresses woody competitors, it is a positive factor. Before the arrival of humans c. 750 years ago, fire was not a significant influence in

New Zealand, and grassland of limited extent. Slow-growing, long-lived, large, tough-leaved Danthonioideae grasses were most affected by woody competition and growth inhibition by necromass. We suggest that they gained a selective advantage in New Zealand through evolving leaf abscission. The presence of two distinct forms of abscission in New Zealand suggests that this adaptation evolved at least twice in *Chionochloa*. Leaf-abscising Danthonioideae tussock species elsewhere in the world tend to be confined to montane and subalpine settings, which supports our hypothesis that low fire frequencies, which promotes necromass accumulation and woody competition, have been the main spur for the evolution of leaf abscission.

Absence of mammalian grazing cannot be conclusively excluded as a driver, but does not fit the facts nearly as well. In particular, the intense grazing by sheep, cattle, deer, hares and rabbits that has impacted New Zealand grasslands since the 1850s seems to have affected leaf-retaining grasses as heavily as leaf-abscising grasses. This in turn suggests that retention of dead leaves within a grass canopy has only a weak influence on resistance to grazing pressure.

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