Stolons and rhizomes in tall fescue under grazing

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Abstract

The most common type of stem in perennial grasses of temperate pastures is short and erect, resulting in an upright habit such as in perennial ryegrass, cocksfoot and tall fescue. Generally these stems do not persist, and their decay results in continual fragmentation to form new plants (the process of clonal growth), which grouped tightly together, form the typical tussock habit. This is the basis of vegetative perermation in the field for these species. Other species, such as browntop, couch grass and kikuyu, rely on specialised stems that run on or under the soil surface (stolons or rhizomes respectively) rooting at the nodes. Some species may utilise more than one type of stem. Tussock-forming species like perennial ryegrass, cocksfoot and tall fescue, can elongate the main tiller axis to produce stolons that elevate the growing point to a more favourable position for survival. These may not be true stolons and their classification as pseudostolons is discussed. By contrast, rhizome formation as seen in tall fescue is concerned primarily with plant expansion. The formation of stolons and rhizomes is affected by both season and grazing management, increasing with lax, infrequent grazing.

Keywords: clonal growth, ***Festuca arundinacea,*** genetic expression, grazing management, pastures, persistence, plant habit, rhizomes, seasonal pattern, spread, stems, stolons

Introduction

In pastures, individual tufts of grass species with a tussock growth form are often mistakenly equated with the grass "plant", but is actually a close-knit group of smaller individual plants (William & Briske 1991; Wilhalm 1995). The smallest recognised agronomic unit of grass plant growth is the "tiller", consisting of a single apical bud laying down sequential nodes, each bearing a leaf, axillary bud and root initials, and separated by a short length of undifferentiated internode. These internodes persist beyond the life of the leaf, accumulating to form a condensed stem. Each axillary bud can develop a new tiller (branch), and has the capacity to form a new vegetative plant. A plant may consist of a single tiller, or a group of tillers connected by a system of branching stems. Tillering results in lateral expansion to form the tussock. Stems of perennial grass species are not long-lived and eventually senesce and decay, causing larger plants to fragment, the tussock now consisting of several smaller individuals of varying complexity (hierarchy) all genetically identical (clones), typical of many pasture species (e.g., perennial ryegrass *(Lolium perenne* L.), cocksfoot *(Dactylis glomerata* L.), and tall fescue *(Festuca arundinacea* Schreb.)). In perennial ryegrass, senescence of older branches and fragmentation can start within 6 months of germination. Such growth at the stem apex to produce new nodes, balanced by death and decay of older exhausted nodes and stem at the base, is termed clonal growth (Harper 1977).

Non-tussock-forming species have stems with elongated internodes, which, if extending laterally on the soil surface, are termed "stolons", typical of browntop *(Agrostis* spp.) and white clover (*Trifolium repens* L.), or if below the soil surface, "rhizomes", such as in kikuyu *(Pennisetum clandestinum* Chiov.).

Tussock-forming species maintain the apical bud close to or below the soil surface to avoid decapitation by grazing, and stems do not normally elongate their internodes, except to elevate the flowering culm in spring on vernalised reproductive tillers. Nevertheless, vegetative tillers can elongate. Severe base shading in over-crowded tussocks reduces tillering (Mitchell & Coles 1954), and internodes of the main tiller axis can be stimulated to elongate, much like a stolon, to elevate the apical bud to a more favourable light environment. In severely crowded situations the apical bud may be deflected horizontally towards the perimeter of the tussock, forming much longer stolons. Such stolon formation is restricted to the actively growing zone of the tiller where new leaves and roots are being produced. Not all genotypes of a population have the capacity to form vegetative stolons (Harris et *al.* 1979), indicating some degree of genetic control.

Tall fescue is an example of a pasture species that also produces rhizomes, anatomically indistinguishable from stolons (Jernstedt & Bouton 1985), and differentiated from stolons chiefly by their function in extending beyond the confines of the existing tussock.

This paper reports detailed measurements of seasonal variation in stolon and rhizome development in tall fescue, and discusses results in comparison with previous studies on plant clonal growth in perennial ryegrass and cocksfoot conducted at AgResearch Grasslands, Palmerston North over the past decade (Brock & Fletcher 1993; Brock *et* al. 1996; Hume & Brock 1997).

Methods

The pastures sampled for this study were 5-year-old mixed pastures of ‘Grasslands Advance’ tall fescue and ‘Grasslands Pitau’ white clover of an existing experiment grazed by sheep. The design included 2 frequencies of grazing, one frequency being twice that of the other varying with time of year (e.g., 2 and 4 weeks in spring, 3 and 6 weeks in summer), except in winter when all were grazed at the same frequency. There were 3 replicates.

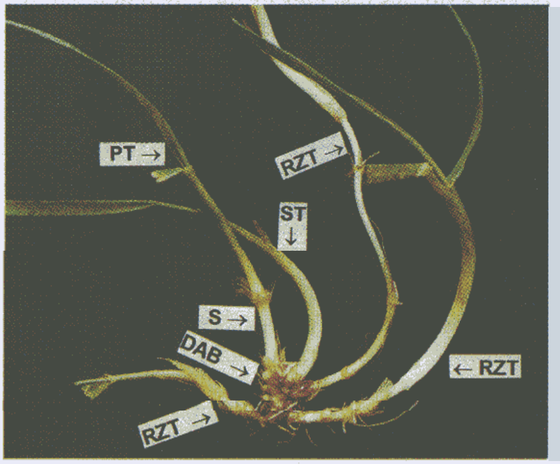
As the aim was to establish the frequency of occurrence of stolons and rhizomes in tillers of tall fescue, it was not necessary to sample intact plants as in the previous studies. Instead, IO pasture cores 100 mm in diameter and deep enough to include all rhizomes, were taken from each plot and all plant material washed out. In the laboratory, counts of stolons, rhizomes and buds were made and expressed as a proportion of the total tillers present for each core, then averaged for each plot for analysis of variance split for time. Rhizomes were differentiated into new (with soft white internodes), and old (hardened, discoloured internodes formed the previous season), and buds into dormant (spherical, yellow-brown) and elongated (showing significant outgrowth, no internodes evident).

Results

Axillary bud development, stolon or rhizome?

In tall fescue, elongation of internodes behind the apical bud of the parent tiller axis to form new stolons, was readily recognisable. However, developing axillary buds, which often arose at a high angle to the parent tiller, were difficult to distinguish as either stolon or rhizome in early development. Their propensity to develop into a tiller, with or without stolon or rhizome, appeared to be controlled by their position and orientation, and season. Axillary buds beginning development before leaf senescence were usually moulded by the leaf sheath into a flattened shape, almost invariably forming a new tiller in close orientation to the parent tiller in the normal way (Figure I). Unlike perennial ryegrass, axillary buds of tall fescue that do not develop into new tillers before the subtending leaf has senesced, can maintain viability, assuming a spherical shape and remaining dormant until required. These may develop into stolons or rhizomes, distinguishable only by their orientation and greater degree of extension. Orientation is usually at right angles to the parent stem, and on development can form directly into a tiller if near to the soil surface, or extend by stolon if deeper, or rhizome if facing downwards (Figure 2). While these spherical buds can form at any time of the year, they occur in greater numbers immediately post-flowering, numbers declining as they develop through the year. Rhizome formation clearly dominates axillary bud development in winter (Table 1), when buds that would normally be destined for tiller formation at other times of the season (those within the leaf sheath) are often diverted downwards to form rhizomes (Figure 3). These can extend several centimetres beyond the tuft to form a new tuft, or greatly expand the old.

Figure 1 A plant of Advance tall fescue (roots removed) showing tiller and stem formation. Parent (primary) tiller (PT) exhibiting stolon (S) to elevate the growing point, with normal axillary (secondary) tiller (ST) development from within the active leaf zone. Tillers developing rhizomes in various stages of extension (RZT) from lower dormant spherical axillary buds (DAB).



Seasonal effects an stolon and rhizome occurrence

In this experiment, the seasonal pattern showed that most outgrowths identified as new stolons occurred mainly in spring, presumably associated with flowering, with a smaller occurrence during the winter and none over the drier summer-autumn (Table 1). In contrast, the seasonal pattern of rhizome development showed an absence of a spring peak. During flowering there was no formation of new spherical buds and elongation of older buds began in summer and peaked in autumn,

Figure 2 An illustration of the types of buds found on the main tiller axis of Advance tall fescue in autumn (roots removed). Parent (primary) tiller (PT) showing normal axillary tiller (AT) and early developing axillary tiller bud flattened within the leaf sheath (ATB) of the active leaf zone (---), below which are dormant spherical axillary buds (DAB) and elongating buds (EAB) developing into rhizomes. Old stem (OS) could be either rhizome or stolon.

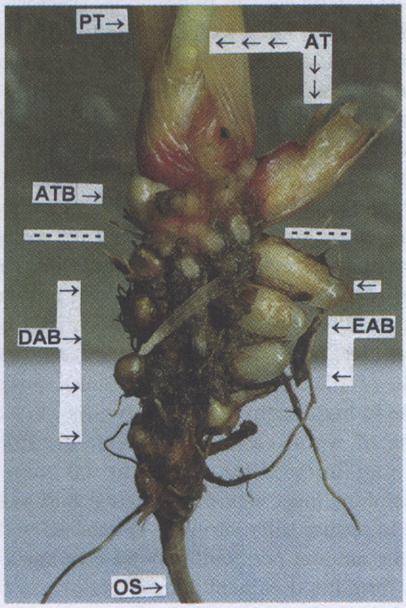


Figure 3 Rhizome formation in early winter in Advance tall fescue, illustrating both normal axillary tiller development (AT) and strong geotropic rhizome development (RAT) from axillary buds within the active leaf zone of the parent (PT) and secondary (ST) tillers.

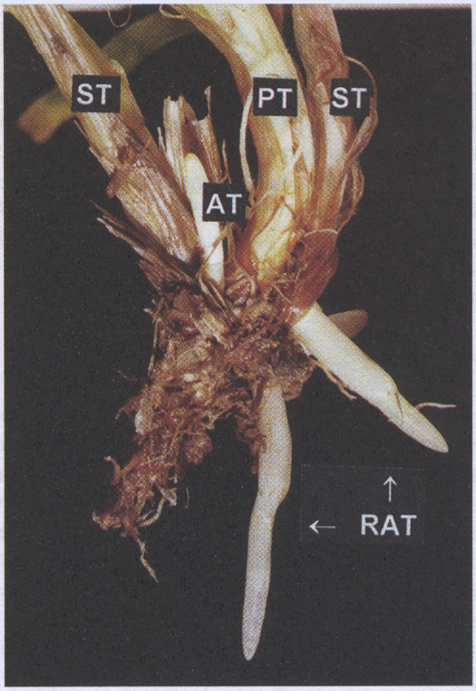


Table 1 Seasonal changes in the mean frequency of occurrence/tiller of new stolons and the various component pools of rhizome development in Advance tall fescue in pastures grazed by sheep at two frequencies (frequent = approximately twice the frequency of infrequent except winter when all grazed together).

Season / Date		Component pools of rhizome development						New stolons /tiller	
		---Dormant buds[1]/tiller---		---Elongating buds[2]/tiller---		---New rhizomes[3]/tiller---			
		Frequent	Infrequent	Frequent	Infrequent	Frequent	Infrequent	Frequent	Infrequent
Winter	8/8/95	0.029	0.090	0.037	0.051	0.045	0.060	0.033	0.111
Spring	3/10/95	0	0	0	0	0.018	0.049	0.083	0.186
Summer	13/12/95	0	0	0	0	0.006	0.023	0	0
	30/1/96	0	0	0.010	0.094	0	0	0	0
Autumn	27/3/96	0.127	0.316	0.020	0.127	0	0	0	0
	20/5/96	0.142	0.401	0.039	0.121	0.019	0.038	0	0
Winter	8/7/96	0.843	0.473	0.063	0.133	0.053	0.161	0.016	0.032
	28/8/96	0.523	0.437	0.023	0.030	0.069	0.072	0.075	0.055
Spring	10/10/96	0.257	0.109	0.003	0.002	0.048	0.048	0.258	0.165
	SED 0.05	0.2161		0.0472		0.0373		0.0500	
Mean		0.237	0.217	0.020	0.063	0.027	0.049	0.054	0.055
	SED 0.05	0.0524		0.0114		0.010		0.0177	

[1] spherical buds [2] buds elongating, no internode(s) evident [3] soft, white internode(s)

which was translated into the maximum of new rhizomes developing in winter and continuing at a declining rate into the following spring. For old rhizomes (not presented), the seasonal pattern was less distinct, suggesting higher numbers through summer to winter (0.177/tiller) maintained by continual recruitment from new rhizomes, and lower in spring (0.113/tiller) through losses from plant fragmentation.

Grazing management effects

Overall, frequency of grazing did not affect the numbers of new stolons and dormant buds formed in tall fescue, a result of the higher numbers under infrequent grazing in the first year (late winter 1995 to autumn 1996), being reversed in the second winter-spring (1996). Nevertheless, frequent grazing reduced the ability of dormant buds to develop into rhizomes (Table 1).

Discussion

The terms stolon and rhizome loosely define elongated stems running above or below ground respectively, both facilitating asexual or vegetative dispersal to new centres (Fitter 1986). Typically stolons are short-lived (usually surviving less than one growing season) while rhizomes are more perennial and suited to survive adverse seasonal conditions. Within the tussock-forming pasture grasses being discussed, it is not clear if the term stolon is strictly applicable, as they have no real function in extending the spread of the plant or establishing new centres of growth as do true stolons, as they do not project beyond the tussock boundaries. In reality, they serve only to ensure the survival of the main tiller axis. Historically, this type of stem has been called stolon (e.g., Harris et al. 1979; Korte & Harris 1987), but Minderhoud (1980) termed these stems possibly more correctly as "pseudostolons". Those turf perennial ryegrass cultivars described as "stoloniferous" where the "stolon" extends considerable distances beyond the tussock to aid expansion, may better be termed "rhizomatous".

The predominant stem type in tussock-forming grasses has short internodes (basal stem, Brock & Fletcher 1993). Pseudostolons then, although more common than is apparent, are of secondary importance, limited primarily to extension of the main tiller axis for tiller survival. In tall fescue, which can also produce rhizomes (anatomically similar to stolons (Jernstedt & Bouton 1985)), all were observed to develop from axillary buds as branches on the tiller axis, exhibiting the true rhizome function of plant expansion. The propensity for an axillary bud to develop into a new tiller or rhizome depended on its position and orientation, and was influenced by season and grazing management. Rhizome formation in tall fescue clearly appears to be under some degree of genetic control (D'uva *et* al. 1983; De Battista & Bouton 1990), and while stolon formation is also thought to have some degree of genetic control in perennial ryegrass (Harris *et* al. 1979), this is not supported by Minderhoud (1978).

While pseudostolon formation can occur throughout the year, it has a clear seasonal pattern (Table 1) similar to perennial ryegrass and cocksfoot (Brock *et al.* 1996; Hume & Brock 1997). Combining these studies, it is clear that a large portion of the strong peak in spring were reproductive stems, as the lower nodes of flowering culms are indistinguishable from stolons until the flower head is evident. Over the drier late summer–autumn, pseudostolon formation is low, and occurred in less than 10% of plants or 2% of tillers. This increased in the cooler, moister late autumn to early spring to 20–40% of plants (15–20% of tillers), possibly in response to high earthworm activity when in excess of 100 t/ha of worm casts (Matthew *et al. 1989;* Hay 1994) can bury tiller bases to 10 mm depth. Pseudostolons must elevate the apical bud to the soil surface to ensure tiller survival. Compared with white clover the amount per plant may be very small, but as grasses form the dominant component of pastures and have higher plant densities, the amount of grass pseudostolon per unit area may be considerable (Korte & Harris 1987; Brock & Fletcher 1993).

Both pseudostolon and rhizome development in these grasses was also influenced by grazing

Table 2 Size and structure of plants of temperate pasture species and their stem-stolon biomass in pastures subject to different grazing managements.

Grazing management	Species	Plant DW (mg)	Apical buds (≅ branches)	Stolon (stem) mass (g/m)
Rotational grazing (RG)	Perennial ryegrass[1,2]	106	4.5	8 (36)
	Cocksfoot'	162	4.0	2 (35)
	Tall fescue[2]	337	4.4	11 (64)
Set stocking (SS)	Perennial ryegrass	60	4.5	15 (65)
	Cocksfoot	51	4.2	2 (35)
RG with spring SS	Perennial ryegrass	102	4.4	10 (48)
	Cocksfoot	215	4.2	8 (20)
	Tall fescue	233	5.4	2 (80)

[1] Brock et al. (1996) [2] Hume & Brock (1997)

management. Rotational grazing allowed greater development in plant size compared with plants under set stocking, but had little effect on plant structure (numbers of growing points per plant) (Table 2). Compared with rotational grazing, set stocking halved the proportion of plants able to produce pseudostolons in the late autumn-early spring and greatly reduced flowering in perennial ryegrass and cocksfoot (Brock et *al.* 1996; Hume & Brock 1997). There was a similar effect of grazing frequency on rhizome formation in tall fescue (Table 1).

The relative importance of pseudostolon formation in tufted pasture grasses is not clear. While pseudostolon formation may aid the survival of individual tillers and possibly plants, its importance may be small in comparison with the major over-riding effects of grazing management on tiller size-density relationships. Hunt (1989) demonstrated the greater survival rate of smaller tillers was responsible for high tiller density in pastures continuously grazed by sheep, whereas higher tiller disappearance rates and larger tillers resulted in low tiller density in rotationally grazed pastures. Control–suppression of emerging flowering stem in spring is essential to maintain high tiller densities for summer productivity (Matthew *et al.* 1989, 1991), which can be accomplished by set stocking during the spring–early summer (Brock *et al.* 1996).

Tall fescue has long been noted for its slow, and often poor establishment compared with perennial ryegrass establishment (Rhodes 1968). A combination of slow tiller and root formation rates of Roa tall fescue seedlings, particularly once defoliation has begun, were seen as responsible (Brock 1983). With tillering rates of tall fescue one third those of perennial ryegrass (Hume & Brock 1997), young plants were particularly susceptible to overgrazing in the first summer, suffering severely from "pulling" (Brock 1982). It is not until the third winter from autumn sowing that substantial rhizome formation occurs, which may be an important agent in increasing anchorage and developing the large clump size found in older pastures. Rapid rhizome development in tall fescue may comprise an important strategy for performance and spread. Bouton *et al.* (1989) demonstrated that populations inheriting high rhizome frequency were more competitive and persistent than those with low rhizome frequency in mixtures.

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