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Relationship of tillering and morphological characteristics of two perennial ryegrass lines to "pulling" when grazed by dairy cows

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Abstract The morphology and sward structural characteristics of two perennial ryegrass pipeline (pre-commercial) selections that showed different "pulling" tolerances, were studied at Hamilton, New Zealand. Pulling was defined as the removal of clumps of ryegrass plants from the sward during grazing. One line, coded as NZA1, was less tolerant of pulling than was the other, coded as NZA3. NZA3 is now commercially available as the cultivar 'Bronsyn'. The ryegrass lines were established in small plots in May 1994 on a silt loam and a peaty silt loam soil. Half the area of each plot received nitrogen (N) fertiliser (30 kg N ha^{-1}) after each grazing, and tiller dynamics were monitored from September 1995 to April 1996. NZA1 had a higher leaf shear strength (6.21 versus 5.91 kg, standard error of difference (SED) = 0.087), wider leaves (3.621 versus 3.252 mm, SED = 0.0535), and a lower clump shear strength (13.4 versus 14.9 kg, SED = 0.57) than did NZA3. N fertiliser did not affect leaf shear strength, and tillering responses to N fertiliser were inconsistent. It is argued that better anchorage combined with leaves that break more easily when grazed contributed to less pulling of NZA3 than of NZA1 clumps during dry summers.

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INTRODUCTION

New Zealand plant breeders have used a perennial ryegrass (*Lolium perenne*) population located on a farm at Mangere, South Auckland, as the major source of plant material for breeding improved perennial ryegrass cultivars over the last 30 years. Examples of cultivars derived from the Mangere ecotype are 'Ellett', 'Grasslands Nui', 'Yatsyn 1', and 'Dobson'.

Variation in tolerances to "pulling", or the physical removal of clumps of ryegrass plants (plus 2–5 cm of roots) from the sward by cows during grazing, was noted during testing of recent selections from the Mangere ecotype (Thom et al. 1998). This suggests a genetic component to the ryegrass-pulling phenomenon. Ryegrass pulling has been associated with cattle grazing in summer/autumn (Hughes & Jackson 1974; Thom et al. 1986), with increased usage of nitrogen fertiliser (Mitchell & Dickens 1979; Tallowin et al. 1986), and with insect damage (Prestidge et al. 1989). Ryegrass pulling is of interest to researchers and farmers as it could potentially reduce sward productivity and persistence, and allow weed ingress.

Nitrogen (N) fertiliser applications in late spring/early summer have been promoted as a way of increasing post-flowering tillering and summer survival of perennial ryegrass (Fulkerson et al. 1993; Harris et al. 1996). However, this practice may lead to increased pulling (Bahmani et al. 2001) because of restricted root growth (Fulkerson et al. 1993). Others (Mitchell & Dickens 1979) suggested strength of underground organs (roots and rhizomes) could be reduced by applications of N fertiliser as available carbohydrate was diverted from root to shoot growth.

Leaf shear strength of grasses has been measured (Evans 1967; Easton 1989; Inoué et al. 1994; Henry et al. 1997) as a way of predicting the feeding value of herbage. Leaf shear strength also affects leaf breakage when external forces are applied during grazing, as does the structure of the root system (Ennos 1990), and hence the tolerance of the plant to pulling. Soil conditions, such as mechanical impedance and shear strength, may also affect the anchorage of plants (Hirata et al. 1994; Houlbrooke 1996).

This paper describes some plant morphological and sward structural characteristics of pipeline (pre-commercial) selections from the Mangere ecotype, and how N fertiliser and soil type modified these. The lines were coded as NZA1 and NZA3 during the experiment; NZA3 is now commercially available as the cultivar 'Bronsyn'. An earlier paper (Thom et al. 1996) confirmed the observation that NZA1 was more susceptible to pulling than was NZA3, although this did not seriously affect herbage accumulation, since NZA1 out-yielded NZA3. We also reported that ryegrass pulling was higher on the peaty silt loam than on the silt loam soil, and that pulling was highest during the driest summer/autumn. Identification of plant characteristics associated with increased pulling could provide further selection criteria for plant breeders concerned with improving ryegrass persistence in grazed pastures.

MATERIALS AND METHODS

Trial sites

The trial was conducted from May 1994 to May 1996 at the Dairying Research Corporation, (now Dexcel), Hamilton, New Zealand (37°47′S, 175°19′E; 40 m a.s.l.), on two soil types on an intensive rotationally grazed research dairy farm. The soils were a Te Kowhai silt loam and a Te Rapa peaty silt loam, a Typic Ochraqualf and a Humic Aquic Haplorthod, respectively, in soil taxonomy (Soil Survey Staff 1990). The New Zealand classification (Hewitt 1998) of these soils were Typic Orthic Gley and Humose Groundwater-Gley Podzol, respectively. Both soils had poorly drained subsoils, with root penetration limited to 20–40 cm in the Te Kowhai silt loam and 70 cm in the Te Rapa peaty silt loam (Singleton 1991). Houlbrooke (1996) demonstrated the presence of a compacted soil layer between 7.0 and 10.5 cm from the surface of both these soils, and he estimated 80% of roots (dry weight basis) were located in the top 5 cm of these soils. Sites received regular maintenance dressings of superphosphate at 600 kg ha^{-1} (54 kg P, 66 kg S) and muriate of potash at 100 kg ha^{-1} (50 kg K). Rainfall and temperature data were recorded at the Ruakura Climatological Station, c. 1 km north-west of the sites.

Establishment and trial design

Main plots (12 × 4 m) were sprayed with 1.08 kg a.i. ha^{-1} of glyphosate before cross-drilling (7 kg ha^{-1} each pass) in May 1994 with endophyte-infected perennial ryegrass lines coded NZA1 and NZA3. Three plots of each line were drilled on each soil type; Aran white clover (*Trifolium repens*) was drilled (3 kg ha^{-1}) across both lines in a third pass.

At each site, main plots were arranged in a randomised block design with three replicates. A subplot (6 × 4 m) N fertiliser treatment was introduced in October 1995. There was a 2-m border between replicate blocks and a 1-m border between main plots within blocks.

Grazing management and nitrogen fertiliser applications

During the establishment year (May 1994–May 1995), plots were grazed once over winter (August), and every 2–3 weeks over spring, lengthening to 3–4 weeks over summer/autumn. Detailed pasture measurements started in October (spring) 1995 at both sites; grazing dates and N fertiliser application dates are given in Table 1. From September 1995 to April 1996, grazing intervals ranged from 21 to 32 days on the silt loam site and from 16 to 33 days on the peaty silt loam. Thirty kg N ha^{-1} was applied as urea at each date.

The sites were grazed by different herds of Friesian cows as part of a separate experiment (Macdonald 1999). The same stocking rate of 3.2 cows ha^{-1} was used during 1994/95, increasing to 4.4 cows ha^{-1} from June 1995 until May 1998.

Tiller measurements

Parent tillers

Two representative ryegrass clumps including the 15-cm square of soil supporting each clump, were removed from each subplot on 6 May 1996. Five parent tillers per clump were randomly selected for the following measurements: (i) undisturbed tiller height (UTH)—the maximum vertical height above the soil surface to the tip of the tiller leaf; (ii) total tiller length (TTL)—length of the tiller from its attachment point at ground level to the tip of the longest leaf; and (iii) number of daughter tillers on each parent tiller. Selected parent tillers were then separated from their daughter tillers and each group was weighed after drying for 24 h at 95°C.

Tiller dynamics

Three circular (63 mm diam.) fixed frames per subplot were located over ryegrass plants in drill rows in September 1995, avoiding areas with excessively long or short herbage. To reduce labour requirements for measurements, only two of the three replicate blocks were included on the peaty silt loam.

At 3- to 4-weekly intervals from 19 September 1995 to 15 April 1996 tiller counts within each frame were made (Table 1). On 19 September all green (live) ryegrass tillers within each frame were tagged with coloured plastic tubing (2 mm diam., 3–5 mm long) that was split lengthwise to enclose the tiller base. At each measurement date, new (untagged) tillers within each frame were classified and counted as either new daughter tillers (attached to tillers from the initial population) or secondary daughter tillers (attached to previously tagged daughter tillers) (secondary tillers on existing daughter tillers) (EDST). New daughter tillers were tagged a different colour to those previously tagged, but EDST were not tagged. Aerial daughter tillers (arising from the node of an extended stem) were also counted and tagged. Dead vegetative tillers (brown and withered or with no live leaves inside the sheath) were counted and tags were removed. Vegetative tillers were re-classified as reproductive when the first node became visible above ground level. Reproductive tillers were classified as dead when defoliated stems (stubs) were brown and sapless.

Leaf measurements

Young leaves length, width, and shear strength

Five representative ryegrass clumps were removed from each subplot on 12 April 1996. The youngest fully expanded leaf blade on 10 randomly selected tillers per clump was removed. The total length (ligule to tip) of each leaf blade was measured using a ruler, and a Vernier calliper was used to measure the maximum width of each leaf blade. The groups of 10 leaf blades were formed into a bundle by aligning the ligule ends. Each bundle was sheared twice, first at 3 cm from the ligules and then at 6 cm from the ligules, using a Warner-Bratzler shear machine (Easton 1989) to estimate shear strength.

Leaf appearance rate (A_L) (leaves tiller^{-1} week^{-1})

Two ryegrass clumps per subplot (including soil to a 15-cm depth) were removed from the peaty silt loam soil (no-N treatment only) on 26 April 1996. Each clump was established in a 30-cm (surface diam.) pot using soil from its point of growth in the field. The pots were kept outdoors and the clumps were regularly watered to avoid water stress. On 7 May, when the clumps appeared to be growing normally, the herbage was clipped to a 5- to 6-cm stubble height. On 15 May the youngest fully

Table 1 Dates of grazing, nitrogen (N) fertiliser application and tiller counts on both soil types. At each date 30 kg N ha^{-1} was applied as urea.

Site 1: Silt loam soil		Site 2: Peaty silt loam soil		Sites 1 and 2
Grazing	N fertiliser	Grazing	N fertiliser	Tiller counts
1995				
25 Sep	4 Oct	29 Sep	10 Oct	19 Sep
17 Oct	24 Oct	25 Oct	30 Oct	16 Oct
7 Nov	14 Nov	15 Nov	21 Nov	14 Nov
28 Nov	6 Dec	1 Dec	14 Dec	11 Dec
21 Dec	31 Dec	22 Dec	31 Dec	
1996				
20 Jan	31 Jan	20 Jan	31 Jan	8 Jan
				30 Jan
13 Feb	20 Feb	16 Feb	20 Feb	26 Feb
16 Mar		21 Mar		18 Mar
22 Apr				15 Apr
		20 May		
28 Jul		11 Aug		

expanded leaf on 20 randomly selected tillers per clump was marked with white paint. The numbers of fully emerged leaves appearing above the marked leaves were recorded weekly until 12 June 1996.

The average number of new leaves per tiller per day for each cultivar was calculated and plotted against cumulative growing degree-days over 22 days. The slope of each graph represents the A_L of each ryegrass line. The inverse of A_L is the phyllochron (Skinner & Nelson 1995). The phyllochron is defined as the time interval between the appearance of two successive leaves, and is expressed in growing degree-days per leaf.

Clump shear strength

A clump-pulling machine with serrated steel jaws and a scissor-grab action was attached to a ryegrass clump near ground level. Steel wires running from the jaw handles were attached to a lever via clock-face scales, accurate to 0.1 kg. Force was slowly applied to the clump by pushing down on the lever, and the maximum force required to remove the clump from the sward was recorded on the scales. Subplot means were based on the force required to remove four representative clumps (each with 20–30 tillers) from each subplot on the silt loam soil in May 1996. Trial plots were maintained until March 1998 to allow these measurements to be repeated during a period when ryegrass pulling was prevalent. In this case, testing was restricted to five representative clumps from each main plot on each soil type, as the last application of the N fertiliser subplot treatment was made on 20 February 1996 (Table 1).

Statistical analysis

Data were analysed for treatment differences at each measurement date using analysis of variance (ANOVA) provided by the statistical packages Genstat 5 (Genstat 5 Committee 1993) and SAS (SAS Institute 1989). Data from each site were combined except for tiller death rates for which separate analyses were done. Tiller death rates were calculated as 1 – S where S represents tiller survival rate. The survival rate of reproductive and vegetative tillers (excluding EDST that were not tagged) was defined as the difference in the number of live tillers at successive measurement dates divided by the number of days between the dates. Assuming all tiller losses were due to death, an approximate tiller death rate can be calculated as 1 – S. Death rates between successive tiller counts were subjected to ANOVA.

RESULTS

Climate

The summer/autumn following drilling was characterised by periods of dry, warm weather. For 64 days from 23 November 1994 to 26 January 1995 only 41 mm of rain fell on 13 rain days, and from 17 December 1994 to 26 January 1995 maximum air temperature ranged from 25–28°C on 18 of the 40 days. Another dry spell occurred from 13 February to 9 March 1995 when only 21 mm of rain fell on five rain days and air temperature on 12 of the 24 days ranged from 25–27°C. Over the second summer/autumn (December 1995–May 1996) rainfall was more evenly distributed than in 1994/1995. Rainfall was 35% above the average of 241 mm over summer (December 1995 to February 1996) and 45% above the average of 295 mm over autumn (March–May 1996). Although there were 21 days in January and 15 days in February 1996 when ambient air temperature ranged from 25–29°C, regular rainfall helped reduce stress on ryegrass.

Leaf and tiller morphology

Grazing management imposed in April/May 1996 (Macdonald 1999) resulted in widely differing pasture regrowth intervals between sites when parent tiller characteristics were measured on 6 May 1996. Measurements were made 14 days post-grazing on the silt loam compared with 46 days on the peaty silt loam.

Youngest fully expanded leaves (12 April 1996)

Ryegrass line did not affect leaf length, averaging 117 mm. Leaves were longer on the silt loam than on the peaty silt loam soil (122 versus 111 mm, SED = 2.54, $P < 0.01$), possibly reflecting an extra 5 days regrowth from grazing on the former. There was no carryover effect of N on leaf length, the final application of N fertiliser being made 52 days earlier (Table 1).

The shear strength of the leaves of NZA1 was higher than for NZA3 for the tissue nearest the ligule (3 cm) and the older tissue (6 cm) (Table 2). Shear strength was also consistently highest for the leaves grown on the silt loam compared with those grown on the peaty silt loam (Table 2). The nitrogen treatment had no effect on shear strength nor were there any significant interactions.

Both ryegrass lines tended to have wider leaves when grown on the silt loam than on the peaty silt loam with the difference being greater for NZA1,

Table 2 Shear strength (kg) of youngest fully expanded leaves of the ryegrass lines NZA1 and NZA3 grown on a silt loam soil (Site 1) or a peaty silt loam soil (Site 2) on the same dairy farm. *, $P < 0.05$; **, $P < 0.01$; ***, $P < 0.001$. SED, standard error of difference.

Shearing position (from leaf ligule)	NZA1	NZA3	SED	Site 1	Site 2	SED
3 cm	6.21	5.91	0.087*	6.45	5.67	0.076***
6 cm	5.08	4.87	0.070*	5.35	4.60	0.110**

causing a significant ($P < 0.05$) interaction (Table 3). N tended to have a negative effect on leaf width but differences were not significant ($P = 0.06$).

Parent tillers (6 May 1996)

Analysis of parent tiller characteristics described by UTH and TTL showed no differences between ryegrass lines and no carryover effects of N. UTH was greater on the peaty silt loam than on the silt loam soil (198 versus 117 mm, SED = 8.5, $P < 0.001$) as was TTL (295 versus 148 mm, SED = 23.4, $P < 0.01$), probably because of the management constraints described above.

Parent tiller dry weight was greater on the peaty silt loam soil (0.489 versus 0.136 g, SED = 0.0767, $P < 0.01$), as were associated daughter tiller dry weights (0.0312 versus 0.0092 g, SED = 0.00615, $P < 0.05$) and number of daughter tillers per parent tiller (5.50 versus 3.46, SED = 0.512, $P < 0.05$). An interaction occurred for parent tiller dry weight between ryegrass line and N because NZA1 responded slightly to N (0.342 versus 0.296 g, SED = 0.047, NS) while NZA3 showed a negative response (0.259 versus 0.354 g, SED = 0.0471, $P < 0.05$).

Leaf appearance rate (A_L)

A_L of each ryegrass line was estimated over 4 weeks commencing 15 May 1996 on plants in the no-N treatment on the peaty silt loam. A_L of the ryegrass lines was similar when averaged over 4 weeks (0.233 leaves tiller^{-1} week^{-1}). Plots of A_L against growing degree-days showed no line differences in A_L, as represented by the slopes of the linear functions of 0.0013 and 0.0018 for NZA1 and NZA3, respectively. The phyllochron or number of growing degree-days required to form a leaf, defined as the inverse of these slopes, was 769 and 556 for NZA1 and NZA3, respectively. Furthermore, dividing the phyllochron by the average daily temperature (10.8°C) showed NZA1 took 71 days to form a leaf compared with 52 for NZA3, but differences were not significant.

Table 3 Effects of site on the width (mm) of the youngest fully expanded leaves of ryegrass lines NZA1 and NZA3 in April 1996. Measurements were made 3–6 cm from the leaf ligule (Thom et al. 1996). Standard error of the difference was 0.0804.

Line	Silt loam	Peaty silt loam
NZA1	3.621	3.171
NZA3	3.252	3.179

Clump shear strength

Initial clump pulling tests were carried out in May 1996 on completion of most trial measurements and after a summer/autumn that was less stressful for ryegrass than was the first (see Climate above). Ryegrass line differences in clump shear strength were not detected, nor were there any effects of N fertiliser; the average shear strength required to remove clumps was 15.8 kg.

Weather in summer 1997/1998 was adverse for ryegrass with only 16 rain days from 30 December 1997 to 21 February 1998, contributing 35 mm of rain. Total rainfall in January 1998 was only 21 mm or 30% of the long-term average and on 26 of the 59 days in January/February 1998, maximum air temperatures ranged from 25–31°C. Clump pulling was prevalent on the trial sites in March 1998. Clump shear strengths on the silt loam and peaty silt loam soils were similar, averaging 14.1 kg. The shear strength required to remove clumps from NZA3 was greater than from NZA1 plots (14.9 versus 13.4 kg, SED = 0.57, $P < 0.05$).

Tiller dynamics

Analysis of the total tiller population over time showed a significant increase in September/October 1995, followed by a general decline in total tiller population in March/April 1996 (Fig. 1). The main

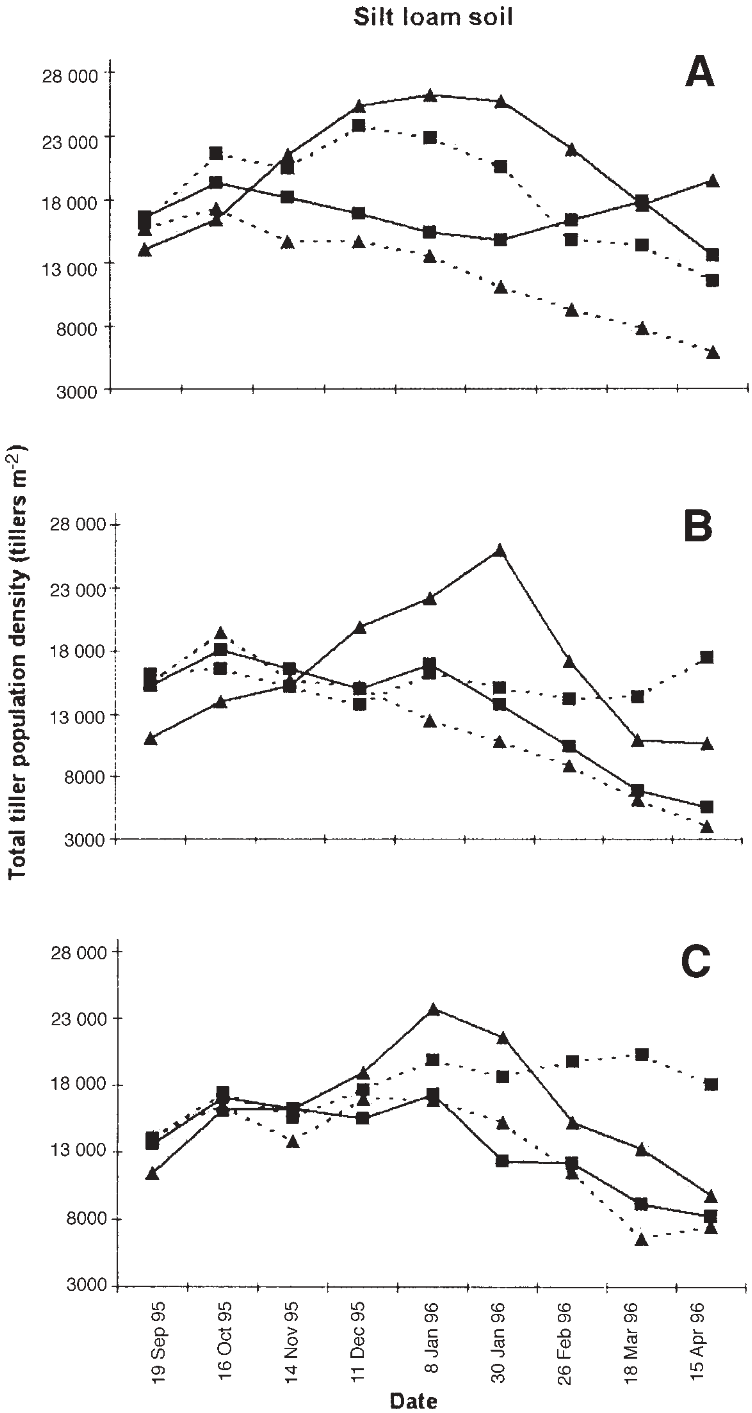
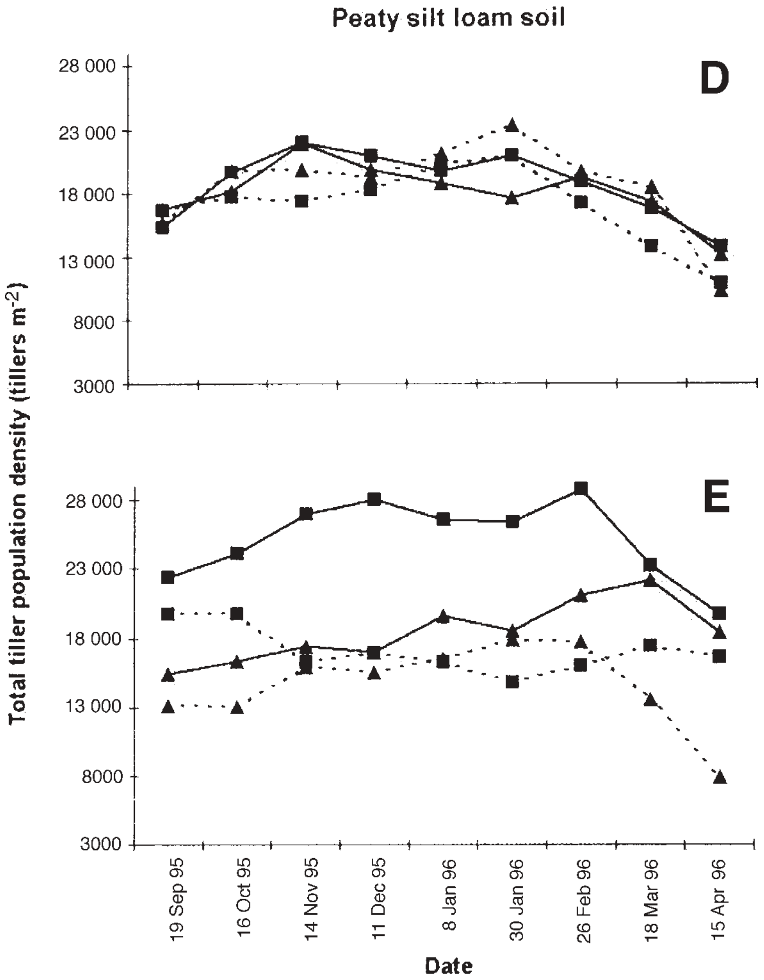


Fig. 1 Total tiller population density (tillers m^{-2}) for NZA1 and NZA3 when grown on a silt loam (replicates A, B, and C) or a peaty silt loam soil (replicates D and E), and when treated with nitrogen (N) fertiliser. ▲—▲, NZA1 +N; ▲- - -▲, NZA1 –N; ■—■, NZA3 +N; ■- - -■, NZA3 –N.

effect of ryegrass line was tested for each measurement date and differences in total tiller population for both lines were never statistically significant. N and soil type effects were only apparent from 30 January to 18 March 1996 when the average total tiller population on the peaty silt loam soil was greater than on the silt loam (19 240 versus 14 520 tillers m^{-2}). From mid December

Fig. 1 (*continued*)



1995 to February 1996 the treatment effects were expressed in a significant three-way interaction between ryegrass line, N fertiliser, and soil type. This was caused by NZA3 having a strong negative response to N on the silt loam soil (consistent over the three replicates, Fig. 1A–C) but a positive response to N on the peaty silt loam soil. On the other hand, NZA1 responded strongly to N on the silt loam soil (consistent over the three replicates, Fig. 1A–C) but with only a slight response to N on the peaty silt loam soil (Fig. 1D,E). In autumn 1996 (March and April), interactions between ryegrass line and N occurred because NZA1 produced the most tillers with N while NZA3 showed a negative response to N, regardless of soil type. A non-significant interaction in March 1996 (P = 0.09) was followed by a significant interaction ($P < 0.05$) in April.

Secondary tillers on surviving daughter tillers (EDST) were noted from December 1995. In December they represented 6% of the overall tiller population and 30% at the final measurement (April 1996). NZA1 and NZA3 produced similar numbers of EDST. Nitrogen-treated plots consistently supported more EDST than did untreated plots (Table 4).

Except between the final measurements (18 March and 15 April 1996), tiller death rates were higher on the silt loam (0.087–0.329 tillers tiller^{-1} day^{-1}) than on the peaty silt loam (0.080–0.233 tillers tiller^{-1} day^{-1}). This reflects the generally higher total tiller population on the silt loam than on the peaty silt loam (Fig. 1). From 14 November to 11 December 1995 on the silt loam, death rates of NZA3 exceeded those of NZA1 (0.249 versus 0.179 tillers tiller^{-1} day^{-1}, SED = 0.0144, $P < 0.05$).

A significant interaction between ryegrass line and N occurred from 11 December 1995 to 8 January 1996 and from 8 January to 30 January 1996; tiller death rates on the silt loam soil were highest for NZA1 in no-N plots but tended to be higher for NZA3 in N plots (only significant in January). By February/March the tiller death rate on NZA1 plots on the silt loam were higher than for NZA3 (0.420 versus 0.238 tillers tiller^{-1} day^{-1}, SED = 0.0097, $P < 0.01$). On the peaty silt loam no treatment effects were detected until March/April 1996 when NZA1 had a higher tiller death rate than NZA3 (0.522 versus 0.314 tillers tiller^{-1}day^{-1}, SED = 0.0139, $P < 0.05$).

DISCUSSION

Ryegrass pulling

In an earlier paper (Thom et al. 1996) we showed that clumps of NZA1 plants were consistently more susceptible to pulling than were those of NZA3 when grazed by cows in summer, despite both lines coming from the same ecotype. This difference in susceptibility to pulling is not surprising since a range of morphological types are usually encountered within a plant population and morphogenetic differences between ryegrass types can determine whether or not they persist in a particular environment (Hazard et al. 2001). We investigated plant morphological characteristics such as leaf shear strength, clump shear strength, and leaf width, and monitored the tiller dynamics of the ryegrass lines, to identify plant characteristics that might be manipulated in plant breeding programmes aimed at greater sward stability under intensive cow grazing. Given the importance of nitrogen to ryegrass growth and persistence (Harris et al. 1996), responses to N fertiliser were also assessed.

We found that NZA1 always had a higher leaf shear strength than NZA3, and like Easton (1989), that shear strength was lower for the older leaf tissue (further from the ligule). Another leaf feature was that, averaged over both soil types, NZA3 had narrower leaves than NZA1. The association of lower leaf strength with narrower leaves confirmed the findings of Inoué et al. (1994); these leaves also have a smaller cross-sectional area (Inoué et al. 1994). We also found the clump shear strength of NZA3 was 11% higher than NZA1, when measured during the dry 1997/98 summer and when clump pulling was prevalent. This implies that clumps of NZA3 plants were better anchored on both soil types than were those of NZA1, and that clump removal was more a function of root strength than soil strength (Ennos 1990). The superior anchorage of NZA3 clumps combined with leaves that would break more easily when grazed, contributed to less pulling of NZA3 than NZA1 clumps on both soil types (Thom et al. 1996).

N fertiliser did not affect clump shear strength or pulling (Thom et al. 1996) in this study, although Mitchell & Dickens (1979) showed it could affect root strength. However, any carryover effects of the last N fertiliser application in late February 1996 would likely be small and certainly absent by March 1998, when the second test of clump shear strength was made. Our results conflict with other research (Tallowin et al. 1986; Fulkerson et al. 1993; Bahmani et al. 2001) showing an association between ryegrass pulling and N fertiliser applications.

Leaf width was greatest when plants were grown on the silt loam soil rather than the peaty silt loam (Table 3), and thus leaf strength was higher on the silt loam than on the peaty silt loam soil (Table 2). This is an example of phenotypic plasticity or the ability of ryegrass lines to change their morphology

Table 4 Effect of ryegrass line and nitrogen (N) fertiliser on number of EDST (secondary tillers on existing daughter tillers) (tillers m^{-2}). NS, not significant; *, $P < 0.05$; SED, standard error of difference.

Measurement date	NZA1	NZA3	SED	+ N	– N	SED
1995						
11 Dec	1561	706	337^{NS}	1508	759	337^{NS}
1996						
8 Jan	2577	1722	523^{NS}	3005	1294	718*
30 Jan	2919	1636	486^{NS}	3122	1433	596*
26 Feb	2673	3005	787^{NS}	3668	2010	727^{NS}
18 Mar	3080	3112	777^{NS}	4042	2149	663*
15 Apr	3614	3700	577^{NS}	4374	2941	846^{NS}

in response to different environments (Cheplick 1991). Henry et al. (2000) also noted how the strength of plant material can vary in response to season and that shear strength of leaves was usually highest in summer when growing conditions were warmest.

It has been recognised (e.g., Ennos 1990) that the multi-branched adventitious (nodal) root systems evolved by the grasses are best at resisting external forces applied during grazing. Nevertheless, differences in root production between the ryegrass lines could have contributed to the observed pulling differences. Determination of the nodal frequency of root appearance and the nodal probability coefficient for tiller appearance on tiller axes of NZA1 and NZA3 by Matthew et al. (1998), showed values for mature nodes that were generally higher for NZA1 than NZA3. This suggests NZA1 produced more roots than NZA3, but if this were true, the effects on pulling were minimal since NZA1 pulled more than NZA3 in all situations (Thom et al. 1996). Other work in a controlled environment (Houlbrooke et al. 1997) showed that root production (root length) of NZA1 and NZA3 was similar when soil conditions (soil type, soil moisture) were similar.

An alternative interpretation of these results could be that shoot characteristics were more important determinants of susceptibility to pulling than were root characteristics (e.g., root number). The fact that NZA3 had fewer nodes on tiller axes than did NZA1 implies it has a lower leaf appearance rate and therefore lower potential tiller production (Mitchell 1953), and slower tissue turnover (Davies 1981) than does NZA1. However, line differences in leaf appearance rate were not confirmed by leaf counts made over 4 weeks in May/June 1996.

Ryegrass tillering

Seasonal fluctuations in tiller births and deaths were expressed as the total tiller population density at each tiller count from September 1995 to April 1996 (Fig. 1). The distinguishing features of the tiller population density trends for both ryegrass lines were the consistent increase in spring (September/October) and the decline in tiller density in autumn (March/April), regardless of soil type and N treatment. These trends have been reported for other New Zealand studies of ryegrass tillering under grazing (Chapman et al. 1983; Korte et al. 1984; L'Huillier 1987). In previous studies, the spring and autumn trends described were accompanied by a midsummer peak in total tiller population density that was associated with flowering, but this was not a consistent feature of our data (Fig. 1). From early (mid December) until late summer (late February), trends in total tiller population density were dominated by a significant three-way interaction, showing the ryegrass lines had different responses to N on the peaty silt loam and the silt loam soils. In autumn 1996, the ryegrass lines also showed different responses to N regardless of soil type (Fig. 1).

Perennial ryegrass usually responds strongly to N fertiliser by increasing vegetative tiller number and total herbage yield (Harris et al. 1996; McKenzie 1998; Waller & Sale 2001), although N fertiliser (Bahmani et al. 2002) can also modify reproductive tillering in some cultivars. Variations in the expected seasonal tillering pattern of the ryegrass lines may partially reflect the grazing management of the trial sites. Suppression of reproductive tillering by intensive grazing or the use of high stocking rates on perennial ryegrass swards has been reported (L'Huillier 1987; McKenzie 1998). This offers a possible explanation for the lack of a summer peak in total tiller population, as both sites were grazed at 4.4 cows ha^{-1} during the tiller measurement period, similar to the high stocking rate treatment of L'Huillier (1987) (4.28 cows ha^{-1}). This view is also supported by the fact that reproductive tillers were only 6.5 and 8.7% of the total tiller population in November 1995 for NZA3 and NZA1, respectively, compared with 18–25% for other cultivars derived from the Mangere ecotype, and when grown in Hamilton (Thom 1991; Bahmani et al. 2002).

The three-way interaction between ryegrass line, N fertiliser, and site (soil type) and the two-way interaction between ryegrass line and N fertiliser for total tiller population density, are difficult to explain. McKenzie (1998) noted that tillering responses to N fertiliser can be modified by intensive grazing, but there were no ryegrass line differences in grazing intensity as post-grazing residual dry matter (DM) yields were similar on both soil types averaging 1700 kg DM ha^{-1} (Thom et al. 1996). This residual was only slightly below the average of 1900 kg DM ha^{-1} reported by L'Huillier (1987) for his high stocking rate treatment. Small or no tillering responses to N led to a non-significant increase (+9%) in total DM yield in response to N fertiliser (Thom et al. 1996).

Daughter tiller production on tagged daughter tillers did show the expected positive increase in numbers in response to N fertiliser (Table 4). Since this secondary tiller population usually represented <30% of the total tiller population, the overall treatment responses of the total tiller population seemed to be unaffected.

Unfortunately, soil and plant N levels were not recorded. This limits somewhat the ability to interpret the tillering responses to N fertiliser. Perhaps the atypical tillering responses to N fertiliser were influenced by variable N availability from the soil (Warren & Whitehead 1988) or genotype plasticity in different environments (Cheplick 1998).

CONCLUSIONS

Plants with a low tolerance of pulling (line NZA1) had higher leaf shear strength and lower clump shear strength than plants with high tolerance (e.g., line NZA3, now marketed as 'Bronsyn'). These findings provide evidence that "plant factors" are involved in the pulling phenomenon, which plant breeders may be able to manipulate (Easton 1989). Low leaf shear strength was associated with narrow leaves, and high clump shear strength was more likely associated with higher root strength rather than with high root numbers. Applications of N fertiliser did not affect leaf shear strength or pulling.

Although ryegrass pulling may not affect total DM yield over 2–3 years from planting (Thom et al. 1996, 1998; Bahmani et al. 2001), farmers consider it detrimental to pasture persistence. Results of this study summarised here and in an earlier paper (Thom et al. 1996) confirm field observations that certain ryegrass cultivars are more susceptible to pulling than are others, and that pulling is more severe on peat soils than on silt loam soils.

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