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The effect of soil moisture content on leaf extension rate and yield of perennial ryegrass

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Three experiments are described that were designed to evaluate the relationship between soil moisture and perennial ryegrass growth and leaf extension rate (LER) in loam or silt clay loam soil. When soil moisture was maintained at a range of proportions (0.5, 0.75, 1.0, 1.25) of field capacity (FC) in a pot experiment in a glasshouse, 0.75FC had consistently higher growth and LER than 0.5FC and, to a lesser extent, 1.25FC. The quadratic relationship between herbage growth and amount of water applied to maintain target field capacity, was stronger than for that between LER and the amount of water applied, with a maximum response at an application of about 2.5 L/m^2 per day. In a microsward (soil depth of 30 cm in boxes 56 cm × 72 cm) trial inducing drought by withholding water for a range of durations resulted in a progressive decline in LER. When soil moisture content fell to about 0.4 of that of the consistently watered control LER was less than 0.1 of the control. However within one week of receiving water, even in the relatively severe drought treatment, LER was not significantly lower than the control treatment. LER was quadratically related to soil moisture content when soil was drying or after rewatering. In a further experiment on the microswards, reducing soil moisture content to about 0.18 g/g by limiting water in May-June resulted in a severe reduction in LER and growth rate and a decline in tillering rate. However, after application of the equivalent of 3 mm precipitation per day in late June, while soil moisture content remained relatively low (about 0.2 to 0.25 g/g soil), LER and herbage growth increased rapidly to as high as in consistently watered microswards. In a treatment in which soil moisture content eventually exceeded FC, LER and herbage growth declined with increase in excess above FC, concurring with findings in the steady state soil moisture experiment. Implications of the data for prediction of production from sown grass swards using temperate maritime grass-growth models are that: (1) during drought, when rainfall resumes, regrowth will be influenced more by amount of rainfall

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than soil moisture content and (2) excess soil moisture should be taken into account, including effects of reduced nutrient uptake and post-anoxia stress.

Keywords: drought; herbage production; mineral concentration; waterlogging

Introduction

Annual grass production varies widely, even under standard management conditions. In a multi-site trial carried out on perennial ryegrass swards at 21 sites in England and Wales over 4 harvest years, year-to-year variation ranged from less than 10% at some sites to over 40% at others (Morrison, Jackson and Sparrow, 1980). Rainfall from April to September and soil available water capacity were the identifiable yield determining factors. In Ireland, dry matter (DM) yield reductions of 1.4 to 4.0 t/ha have been estimated to be lost for intensively managed grassland in the driest regions, especially the south east, due to limiting soil moisture availability (Brereton and Keane, 1982). Therefore decision support systems (DSS) for managing grassland enterprises, especially for intensive dairying, have been developed (Fitzgerald, Brereton and Holden, 2005; 2008; Mayne *et al*., 2004). Grass growth models are essential components of these management aids.

Most models assume growth and/or photosynthesis to be dependent on the ratio of available soil moisture to that at which growth ceases to be adversely affected (up to a ratio of 1) or the ratio of actual to potential evapotranspiration (e.g., Topp and Doyle, 1996; Schapendonk *et al*., 1998). The model of Brereton, Danielov and Scott (1996), however, takes account of rainfall interrupting drought, and growth is predicted to resume as if soil moisture was not limiting. In studies in which soil moisture content is restored quickly to pre-drought conditions after periods of drought, grass leaf extension rates rapidly reach those of tillers under control conditions, usually within a few days of reinstatement (Volaire, Thomas and Lelievre, 1998; Clark, Newton and Barker, 1999). However, often when rainfall resumes after a period of drought in temperate maritime areas mean daily rainfall may not exceed mean daily evapotranspiration and so soil moisture content may not readily return to pre-drought levels.

In a review of studies on the effect of excess soil moisture (including drainage status) on herbage production, yield was reduced proportionately by 0.2 to 0.5, obviously depending on the severity and duration of excess (Thomasson, 1979). In Ireland, yield depression on heavy drumlin soils due to excess soil moisture, caused by raised water table, has been estimated to be on average 0.29 times potential yield (Brereton and Hope-Cawdery, 1988). This agrees well with the comparison of yield from cut plots at two contrasting sites in southwest Ireland in which the poorly drained high rainfall site with heavy soil over a plastic subsoil (Kilmaley, Co. Clare) produced proportionately 0.3 less herbage than the drier site with sandy loam-loam soil (Moorepark, Co. Cork) (Shalloo *et al*., 2004). Brereton and Hope-Cawdery (1988) quantified the relationship between water table depth and herbage growth. When depth was 250 mm below the ground surface, resulting in soil moisture content of 1 g/g dry soil, growth was only 0.4 times that when the water table depth was 450 mm (soil moisture content 0.6 g/g dry soil).

Using a modification of the model of Johnson and Thornley (1985) to predict annual DM yield of perennial ryegrass in the Recommended List trials in Northern Ireland during 1994 to 2003, the yield was predicted quite well in nine of the 10 years; the exception being 2002 in which rainfall during the growing season was exceptionally high and grass yields were over predicted (Laidlaw, 2005a). Therefore if models are to be effective grassland decision support tools for grassland management, they should take account of the effect of excess soil moisture on grass growth, even in soils which would be considered adequately drained. The effect of prolonged water logging in soils on grass growth are included in the present investigation along with evaluating the response of herbage growth and leaf extension rate to the applications of water after a drought.

In plants subjected to soil moisture stress, potassium and other minerals may play a part in osmotic regulation, a process which aids adaptation to drought conditions, while waterlogging may reduce mineral uptake (Fitter and Hay, 2002). To gain insight into whether mineral nutrition was implicated in the effects of soil moisture availability on perennial ryegrass growth, mineral content of herbage in treatments was determined in two of the experiments.

Materials and Methods

Experiment 1. Effect of maintenance of a range of constant soil moisture contents on leaf extension of perennial ryegrass

Perennial ryegrass (*Lolium perenne* L.) cv. Tivoli, a late heading tetraploid, was sown on 30 October 2002 in an undefined loam soil in 25 cm diameter × 20 cm deep pots (87 seeds/pot) in a glasshouse. Supplementary light and heat were supplied from 30 October 2002 until 18 March 2003. Light was supplied by mercury vapour lamps between 0800 and 1800, providing approximately 300 to 400 μmol m^{-2} s^{-1} photosynthetically active radiation (PAR) in addition to daylight. Supplementary heat, provided by convection heaters, resulted in a mean daily maximum temperature of 23.3 °C and minimum of 8 °C. From 18 March until 15 October 2003, no supplementary heat or light was supplied.

At sowing pots received the equivalent of 60 kg/ha N as Superbeet (170 g N, 60 g P and 240 g K/kg) at 1.33 g per pot. Thereafter the herbage was harvested at 6 to 8 week intervals to a stubble height of 4 cm after which each pot received fertiliser as described until 19 August 2003. On 4 and 8 September 2003 soil in the pots was soaked, covered to avoid evaporation from the surface, allowed to drain and each pot weighed, which was taken to be weight at field capacity (FC). Soil moisture content at FC, determined from four pots which were assigned for this purpose, was 45 g water per 100 g dry soil. Four soil moisture content treatments were established, i.e., 0.5, 0.75, 1.0 and 1.25 times field capacity, and six pots were assigned to each treatment. To prevent water draining from the 1.25FC treatment, the root ball in each pot in this treatment was eased out and the pot lined with heavy duty polythene. The target weight for each pot in the experiment was calculated. Pots remained unwatered until 19 September 2003 when the appropriate amount of water required to meet that target was applied. Pots and their contents were weighed at 2 to 3 day intervals and brought up to target weight with distilled water and the amount recorded, although some pots were required to dry out further until they achieved their target weight. Over the duration of the experiment until 1 March 2004, the mean moisture content of each treatment when water was applied was approximately, 0.42, 0.64, 0.85 and 1.0 times FC for treatments

0.5FC, 0.75FC, 1.0FC and 1.25FC, respectively. Microswards were harvested on 2 October 2003, when target soil moisture in all pots had been met, 17 November and 22 December 2003 and on 27 January and 1 March 2004. Harvested herbage was oven dried at 60 °C and weighed. Tillers were marked less than 1 week after microswards were harvested and extension growth of leaves was measured weekly for 4 weeks within each regrowth period to provide estimates of daily leaf extension rate (LER). From 15 October 2003, supplementary heat and light were supplied as in the previous winter. Mean daily maximum temperatures for each month from October to February were 24.9, 22.3, 21.0, 22.0, and 28.0 °C, respectively. Corresponding daily minimum temperatures were 9.5, 8.5, 7.2, 8.3 and 8.0 °C, respectively.

Experiment 2. The effect of severity of moisture stress on rate of recovery in response to increase in soil moisture content

Twelve microswards of perennial ryegrass cv Tivoli were established in boxes (56 cm × 72 cm and 30 cm deep) in a sandy clay loam soil (49% sand, 31% clay and 20% silt) on 2 May 2001, sowing seed at 3 cm spacing. Textural analysis of the soil indicated field capacity in the range 40 to 45% and permanent wilting point 20 to 22%. So that application of water could be controlled the swards were placed in a polytunnel rainshelter on rails so that they could be exposed to unenclosed conditions when rain was not anticipated. Prior to the harvest on 5 August 2002, when the experiment commenced, the microswards had been harvested approximately monthly during 2001 and three-weekly in 2002 during the growing season. Fertiliser (composition (g/kg) 170 N, 60 P and 240 K) equivalent to 50 kg/ha N was applied to the seed bed and after subsequent harvests in 2001, except the last in October, and on 15 March 2002. In 2002 after each harvest the equivalent of 60 kg/ha N, as calcium ammonium nitrate, was applied until the harvest on 16 July. The equivalent of 60 kg/ha N as compound fertiliser (composition (g/kg) 140 N, 140 P and 210 K) was applied after the harvests on 5 August and 3 September 2002.

Treatments were Control (W0), in which the microswards received the equivalent of 2.5 mm precipitation as distilled water per day in two applications per week on Mondays and Thursdays (3.15 litres and 4.17 litres, per microsward, respectively) from the beginning of the experiment, or unwatered until the end of the third (W3), fifth (W5) or seventh week (W7). So, after 27 August and 10 and 27 September, respectively, treatments W3, W5 and W7 were watered as for W0. Microswards were harvested to stubble height of 6 cm on 3 September and 12 October 2002 and on 18 February 2003. The microswards were arranged in 3 blocks of 4 boxes.

Twenty tillers in each microward were randomly selected, 10 cm apart within and between rows in a 5 × 4 grid, and marked with loops of PVC coated wire on 6 August. Daily leaf extension rate (LER) and leaf senescence rate (LSR) per tiller were determined by measuring length of new leaf laminae appearing and of older leaves senescing, to the nearest 1 mm using standard tissue turnover measurement procedures. After marking tillers and measuring leaves on 6 August, leaves were measured on marked tillers on 13, 20 and 27 August and 3 September during the first regrowth and, after initial (time zero) measurements on marked tillers in the second regrowth on 10 September, leaves were measured on 17, 24 and 30 September and 8 October. Mean LER for each treatment was expressed as a proportion of that of the control (0W) for each measurement period and related to soil moisture content for that week. Mean (s.d.) daily temperature (°C) and PAR (MJ m^{-2} day^{-1}) for the first growth period were 12.7 (1.39) and 6.4 (2.00), respectively, and for the second regrowth period 11.2 (1.65) and 3.2 (1.64), respectively. Between harvests on 12 October 2002 and 18 February 2003 microswards were unprotected by the shelter and received no fertilizer.

Two sets of three 15 cm time domain resonance (TDR) probes using TRIME multi-rod probe head P3-MR system (Van Walt Ltd, Preswick Lane, Grayswood, Haslemere, Surrey GU27 2DU) were inserted permanently in each microsward to monitor soil moisture content non-destructively and recorded every 2 to 3 days.

Experiment 3. Effect of progressive soil moisture stress and prolonged water excess on leaf extension rate, tillering and herbage dry matter production

The impact of increasing water deprivation and reapplication and prolonged excessive soil moisture on leaf extension and sward yield was investigated.

Treatments were applied to the microswards used in Experiment 2. To ensure that no residual effects of the treatments applied in Experiment 2 remained, all microswards were harvested approximately monthly from March 2003 until September 2003 and again on 13 May 2004, during which they received the equivalent of 50 kg ha N as a compound fertiliser (composition (g/kg) 140 N, 140 P and 210 K). So all microswards were subjected to the same management from the time they were subjected to the same watering regime from 27 September 2002 until the harvest on 13 May 2004.

Treatments were intended to simulate varying intensities of daily rainfall in late spring/early summer, and ranged from low (1 mm/day), slightly below average (2 mm/day), slightly above average (4 mm/day) to excessive (8 mm/day). On 19 May 2004 one microsward in each of three blocks was subjected to the equivalent of either 1, 2, 4 or 8 mm water per day until 28 June. So that recovery from any adverse effects due to soil moisture treatment in early summer could be evaluated, those receiving the equivalent of 1, 2 or 4 mm/day received the equivalent of 3 mm per day from 28 June (Treatments 1–3, 2–3, and 4–3); the equivalent of 8 mm/day continued to be applied to the simulated excessively high rainfall treatment (Treatment 8-8). Water was applied on Mondays, Wednesdays and Fridays. Soil moisture content was measured and total water available calculated as for Experiment 2.

After the experiment commenced on 19 May 2004, herbage was harvested to a stubble height of 4 cm on 8 and 23 June, 19 July, 12 August and 14 September (i.e., regrowth periods 1 to 5) and dried at 60 °C. LER and LSR were determined during measurement periods within each regrowth period, as in Experiment 2, except in the period 12 August to 14 September, when leaf lengths were also measured on 1 September. LER was also calculated relative to that of the control treatment which was considered to be Treatment 4–3. The number of new tillers emerging was also quantified during each regrowth period. During the five regrowth periods mean (s.d.) daily air temperatures, were 14.4, (3.49), 15.7 (2.77), 15.2 (1.58), 18.4 (1.84) and 16.9 (2.26) °C, respectively, and mean daily PAR were 8.1 (2.68), 7.2 (2.95), 6.9 (2.25), 5.2 (2.22) and 4.6 (2.06) MJ m^{-2} day^{-1}.

Chemical analyses

Dried herbage from the harvests taken on 27 January in Experiment 1 and on

12 August in Experiment 3 was milled to pass through a 1 mm sieve. Samples were analyzed for N by dry combustion using a Carlo Erba NA1500 elemental analyzer and for P, K, Ca, Mg, and S by inductively coupled plasma spectroscopy.

Statistical analysis
Variation between treatment means was compared with variance within treatments by analysis of variance by Genstat (11th Edition) to determine if differences between treatment means within a factor were significant. If so, differences between specific means were considered significant if they differed by more than the least significant difference calculated using the within treatment variance. In Experiments 1 and 2, in which measurements were taken at fixed time intervals, time was considered a factor in the analysis of variance. When Box's test for symmetry of the covariance of the time-treatment matrix was significant the repeated measures analysis of variance was run (Winer, 1971). Otherwise time was treated as a subplot effect in a split-plot design analysis of variance. Relationships between variables were quantified by fitting trend lines in MS Excel.

Results

Experiment 1
Over the four periods, 0.5FC consistently had significantly lower mean LER than 0.75FC (Table 1). Although not quite significant, LER in the first period was higher than in the subsequent three periods but response to treatments was not significantly affected by time (interaction was not significant). Mean growth rate over the four periods was significantly lower in the two extreme moisture treatments than in 0.75FC and 1.0FC (Table 2) and while not formally significant (P = 0.05), the difference between the two higher and lower growth rate means was greater at the first harvest than at the other three.

When water applied to individual pots was considered, the influence of the amount of water applied on mean LER over the duration of the experiment was weakly quadratic (Figure 1a) but had a

Table 1. Mean leaf extension rate (mm/day) in each of four consecutive regrowth periods for four soil moisture treatments (Experiment 1)

Treatment[1]	Regrowth period				Mean[2]
	1	2	3	4	
0.5FC	12.3[4]	12.2	11.5	10.9	11.7
0.75FC	15.8	15.5	15.8	16.2	15.8
1.0FC	15.8	14.2	14.4	14.5	14.7
1.25FC	14.7	12.8	13.4	13.5	13.6
Mean[3]	14.8	13.7	13.8	13.8	

[1] Soil moisture content as a proportion of field capacity (FC).
[2] s.e.d. = 0.96 for comparisons between treatment means (F test: P < 0.001).
[3] s.e.d. = 0.38 for comparisons between period means (F test: P = 0.08).
[4] s.e.d. = 1.17 for comparisons between Treatment-by-period means.

Table 2. Mean growth rate of herbage dry matter (g m^{-2} day^{-1}) harvested above 4 cm in four soil moisture treatments (Experiment 1)

Treatment[1]	Regrowth period				Mean[2]
	1	2	3	4	
0.5FC	6.83[4]	4.24	3.83	3.48	4.59
0.75FC	9.31	5.31	5.65	6.04	6.58
1.0FC	8.14	4.93	5.35	6.51	6.23
1.25FC	7.44	3.95	4.68	5.20	5.32
Mean[3]	7.93	4.61	4.88	5.30	

[1] Soil moisture content as a proportion of field capacity (FC).
[2] s.e.d. = 0.326 for comparisons between treatment means (F test: P < 0.001).
[3] s.e.d. = 0.243 for comparisons between period means (F test: P < 0.001).
[4] s.e.d. = 0.533 for comparisons between Treatment-by-period means (F test: P = 0.05).

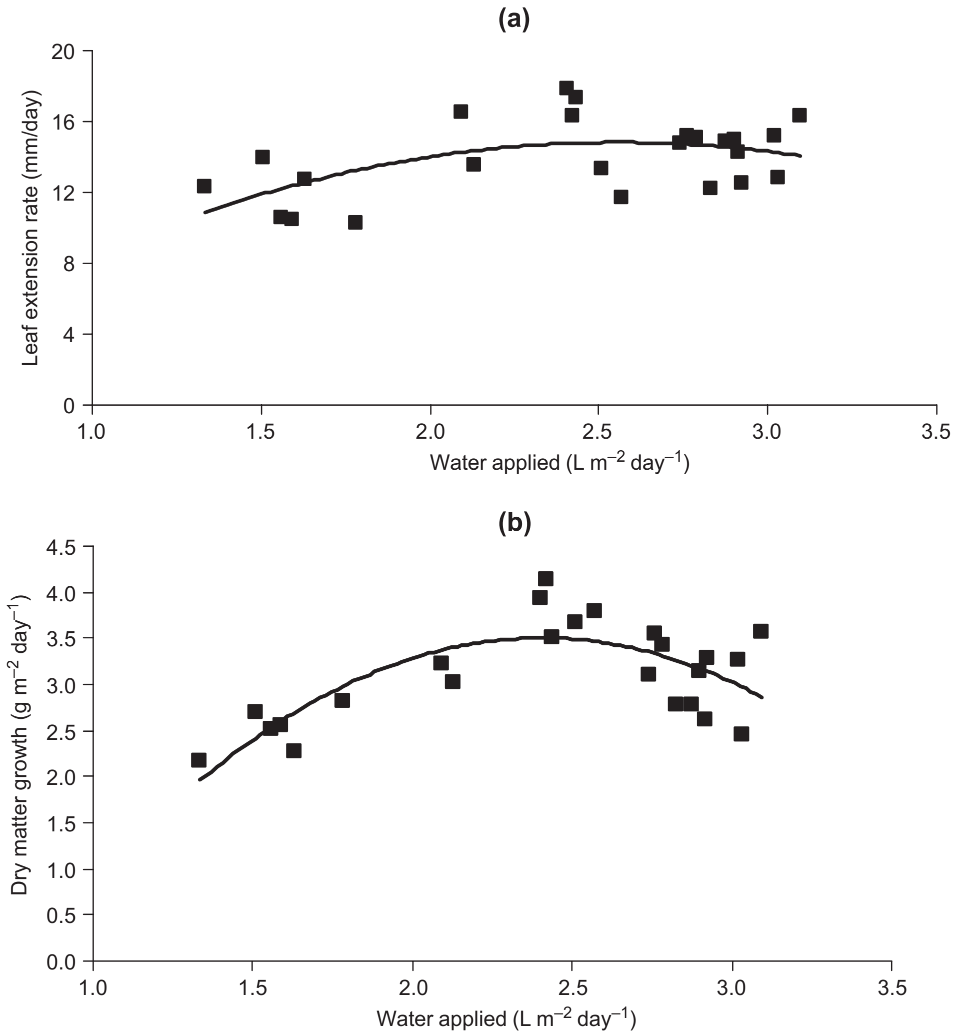

Figure 1. Relationship between rate of water applied (x) and a) mean leaf extension rate ($y = -2.63x^2 + 13.45x - 2.36$; R^2 0.27) and b) mean harvested dry matter growth rate ($y = -0.87x^2 + 5.20x - 4.32$; R^2 0.56) per pot over four regrowth periods (Experiment 1).

stronger quadratic effect on daily DM growth over the four periods (Figure 1b). Concentration of N, Ca, Mg and S in the DM was significantly lower in 0.5FC than the other treatments, with the Mg concentration in 1.25FC being significantly higher than in the other two remaining treatments (Table 3). In contrast, K concentration was significantly higher in 0.5FC and 0.75FC than the other two treatments.

Experiment 2

Soil moisture content remained relatively stable in treatment W0 over the 9 weeks of the experiment while in unwatered treat-

Table 3. Mineral concentration (g/kg) of herbage dry matter at harvest in December (Experiment 1)

Treatment[1]	Mineral					
	N	P	K	Ca	Mg	S
0.5FC	25	3.6	51	6.4	1.9	2.7
0.75FC	28	3.4	49	7.5	2.2	2.9
1.0FC	29	3.2	45	7.6	2.2	3.0
1.25FC	28	3.4	44	7.6	2.5	3.0
s.e.d.	1.12	0.20	1.09	0.37	0.07	0.02
F test	**		***	**	***	*

[1] Soil moisture content as a proportion of field capacity (FC).

ments it declined at about 0.02 to 0.04 g water per 1 g dry soil per week (Figure 2). During the first four weeks, a significant interaction between week of the experiment and treatment was due to the two unwatered treatments (W5 and W7) having significantly lower LER than the other two treatments in week 4 (Table 4). During weeks 6 to 9 (second regrowth period), the interaction between treatment and week was significant reflecting the fact that the LER in W7 for weeks 6 and 7 was only about one sixth of the mean of the other three treatments. Thereafter, LER did not differ significantly between treatments. The relationships between LER (as a proportion of the control) and estimated available soil moisture were quadratic, both for soil which was drying (moisture stress was increasing) and for soil receiving water after drying (Figure 3a).

Contrary to leaf extension rate, LSR was not significantly affected by any of

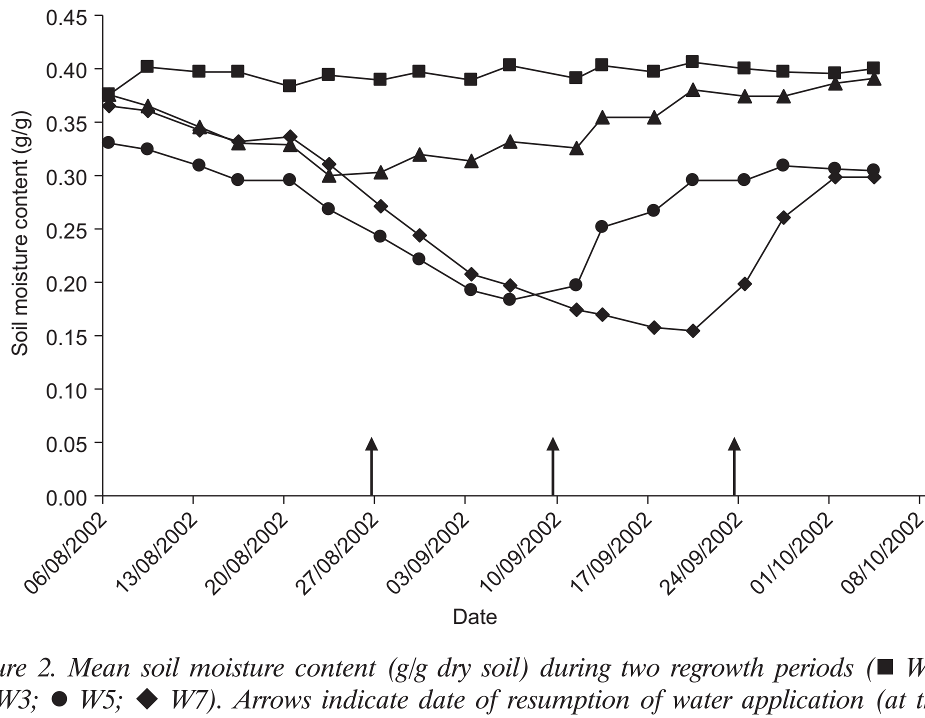

Figure 2. Mean soil moisture content (g/g dry soil) during two regrowth periods (■ W0; ▲ W3; ● W5; ◆ W7). Arrows indicate date of resumption of water application (at the equivalent of 2.5 mm precipitation per day) at the end of weeks 3, 5 and 7 to treatments (W3, W5 and W7, respectively), while W0 received equivalent of 2.5 mm precipitation/day throughout (Experiment 2).

Table 4. Mean leaf extension (mm tiller^{-1} day^{-1}) for living tillers during 1-week periods[1] from commencement of Experiment 2

Treatment[2]	Week of experiment				Mean[3]	Week of experiment				Mean[4]
	1	2	3	4		6	7	8	9	
W0	8.0[6]	7.6	9.9	8.7	8.6	8.0[7]	6.3	7.4	4.1	6.5
W3	9.6	9.5	9.4	7.1	8.9	7.4	6.2	7.2	4.9	6.4
W5	7.9	9.1	9.4	5.7	8.0	5.4	6.1	8.0	4.8	6.1
W7	7.9	8.3	9.3	5.8	7.8	1.8	0.5	6.3	4.5	3.2
Mean[5]	8.4	8.6	9.5	6.8		5.7	4.8	7.2	4.6	

[1] Plots were harvested during week 5.
[2] W0 = water at the equivalent of 2.5 mm precipitation per day throughout the experiment; W3, W5, W7 = unwatered until end of weeks 3, 5 and 7, respectively, and then watered as for W0.
[3] s.e.d. = 0.52 for comparisons between treatment means.
[4] s.e.d. = 0.70 for comparisons between treatment means (F test: $P < 0.05$).
[5] s.e.d. = 0.34 for comparisons between weeks 1 to 4 (F test: $P < 0.01$); s.e.d. = 0.26 for differences between weeks 6 to 9 (F test: $P < 0.001$).
[6] s.e.d. = 0.78 for comparisons among treatment-×-week (1 to 4) means (F test: $P < 0.001$).
[7] s.e.d. = 0.83 for comparisons among treatment-×-week (6 to 9) means (F test: $P < 0.001$).

the treatments although it was highly variable (Table 5). The rate increased significantly between weeks 7 and 9. While treatment had no effect on dry matter yield at the first harvest in Experiment 2, the two more stressed treatments had significantly lower yields than W0 and W3 at the harvest at the end of week 9 (Table 6) and yield of individual microswards at this harvest was linearly related to mean soil moisture content during the regrowth period (Figure 3b). To investigate if moisture stress had any long term effects on herbage growth, a further harvest was taken in February. Although yields differed quite widely between two of the treatments (W3 and W5), differences were not statistically significant (Table 6).

Experiment 3

During the first two periods when the treatments which eventually would receive water at a rate equivalent of 3 mm/day were receiving differential amounts of water, soil moisture declined in the 1–3 treatment to half that of the 4–3 treatment in the second period with the 2–3 treatment being intermediate (Figure 4). Thereafter, with these three treatments receiving water at the equivalent of 3 mm/day, soil moisture content in the 2–3 treatment remained higher than that of 1–3 until late August. The 8–8 treatment had a significantly higher soil moisture content than the other treatments from the second period, increasing progressively to the end of the experiment.

The difference in LER between the driest and wettest treatments in period 1 was significant, the former only proportionately 0.6 of the latter while in period 2 the two driest treatments had leaf extension rates only about 0.25 times that of the mean of the other two treatments (Table 7a). However, in the first period in which the watering regime was adjusted to provide 3 mm/day (period 3) extension rates did not differ significantly among the treatments and this prevailed until period 5 (late August) when extension in treatment 8–8 was only about half that in treatment 1–3. Senescence was variable and only in the second period did differences approach significance ($P = 0.05$) due to the higher rate in 8–8 than in 2–3 (Table 7b).

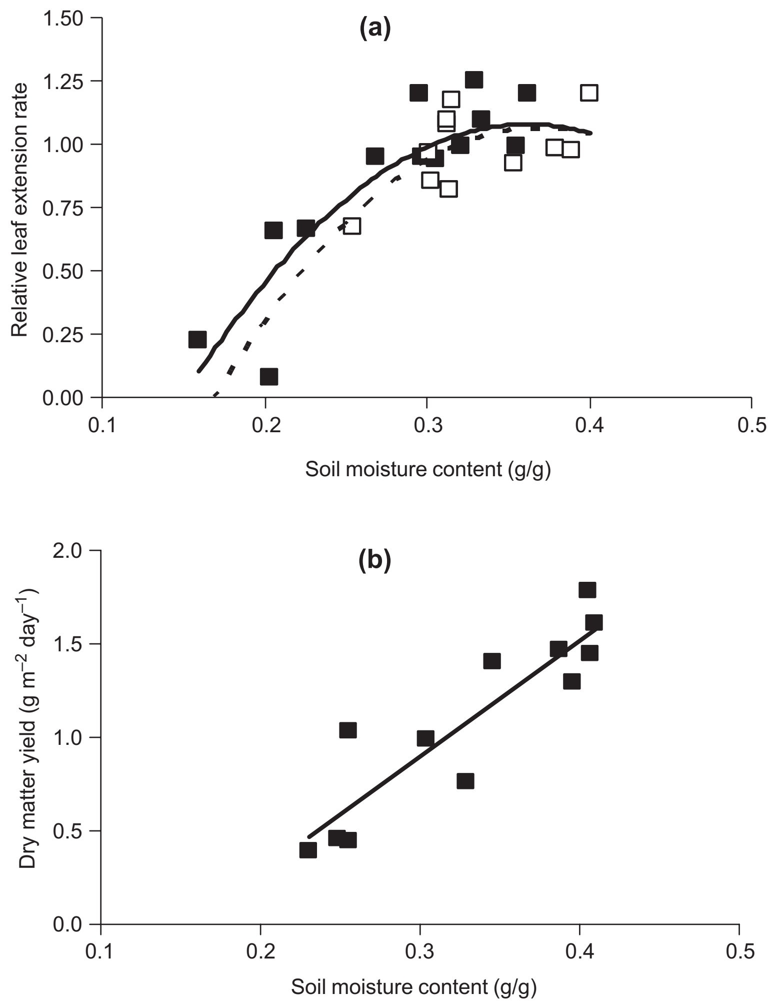

Figure 3. Relationship between estimated soil moisture content (y) and, a) leaf extension rate (x) when soil moisture stress was increasing (■)($y = -24.05x^2 + 17.38x - 2.06$, R^2 0.77) or decreasing (□) ($y = -26.67x^2 + 19.72x - 2.58$, R^2 0.39) in treatments receiving water after 5 and 7 weeks and b) harvested dry matter (x) at second harvest (in October) for each microsward ($y = 6.23x - 0.98$, R^2 0.82).

Tillering rate was affected by soil moisture only in the first two periods when the two treatments with the highest soil moisture had significantly higher tillering rates that the other two treatments (Table 8). Tiller senescence rates are not presented but did not differ significantly between any treatments; the mean rate over all treatments and sampling dates was 0.011 tillers tiller^{-1} day^{-1}.

In the first two periods, harvested yield was lower in the two driest treatments than in treatments 4–3 and 8–8 (Table 9). At the last harvest (regrowth from mid-August to

Table 5. Mean leaf senescence (mm tiller^{-1} day^{-1}) during 1-week periods[1] from commencement of Experiment 2

Treatment[2]	Week of experiment				Mean[3]	Week of experiment				Mean[4]
	1	2	3	4		6	7	8	9	
W0	1.89[6]	1.48	1.44	1.37	1.54	1.10[7]	0.94	2.59	1.70	1.58
W3	1.63	1.58	0.95	1.16	1.33	1.36	1.17	1.20	2.98	1.68
W5	1.75	1.68	2.02	2.14	1.90	1.32	1.77	1.66	1.82	1.66
W7	1.66	1.53	1.54	2.58	1.83	1.15	0.72	1.82	1.89	1.39
Mean[5]	1.73	1.57	1.49	1.81		1.23	1.15	1.82	2.12	

[1,2] See footnotes to Table 4.
[3] s.e.d. = 0.358 for comparisons between treatment means.
[4] s.e.d. = 0.407 for comparisons between treatment means.
[5] s.e.d. = 0.294 for comparisons between weeks 1–4; s.e.d. = 0.325 (F test: $P < 0.05$) for comparisons between weeks 6 to 9.
[6] s.e.d. = 0.623 for comparisons among treatment-×-week (1 to 4) means.
[7] s.e.d. = 0.694 for comparisons among treatment-×-week (6 to 9) means.

Table 6. Mean dry matter yield (g/m^2) at end of regrowth periods during which leaf extension was measured and at the subsequent (18 February) harvest (Experiment 2)

Harvest date	Treatment				s.e.d.	F test
	W0	W3	W5	W7		
3 September	41.7	48.1	32.2	31.2	9.23	
12 October	41.9	41.4	25.5	12.2	3.08	***
18 February	40.7	31.5	44.4	42.9	6.42	

mid-September) yield of 8–8 was less than one third the mean of 1–3 and 2–3.

For a given range of soil moisture content, LER was lower when soil moisture was declining than when it was increasing (Figure 5a). Further, LER in the excessively watered treatment (8–8) declined as soil moisture content exceeded estimated field capacity. These trends were reflected

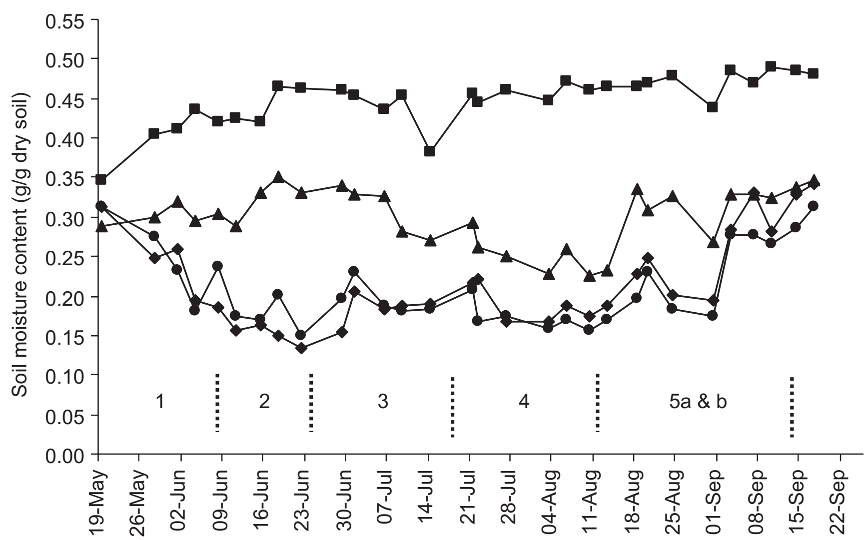

Figure 4. Mean soil moisture content on each measurement date (◆ treatment 1–3; ● treatment 2–3; ▲ treatment 4–3; ■ treatment 8–8). Numbers and arrows indicate regrowth label and date of harvest terminating each regrowth, respectively (Experiment 3).

Table 7. Mean leaf extension rate (mm/day) and leaf senescence rate (mm/day) for specific intervals within regrowth periods (Experiment 3)

Treatment[1]	Measurement interval					
	19 May to 8 June	9 to 23 June	29 June to 15 July	16 July to 5 Aug	17 Aug to 1 Sep	2 to 14 Sep
Leaf extension rate						
1–3	16.8	3.8	19.0	16.8	21.8	13.2
2–3	18.6	8.5	21.4	15.9	18.8	13.1
4–3	23.0	27.2	21.8	16.9	14.4	11.3
8–8	25.2	23.1	18.4	13.4	10.8	5.3
s.e.d.	1.78	1.70	2.06	1.71	2.83	2.16
F test	**	***			*	*
Leaf senescence rate						
1–3	1.65	4.52	1.71	0.81	2.20	5.81
2–3	0.81	1.04	1.81	1.43	2.23	4.82
4–3	0.60	1.76	2.95	1.61	1.63	5.18
8–8	1.11	2.82	2.62	0.90	2.46	5.53
s.e.d.[2]	0.325	1.207	0.902	0.602	1.530	1.940

[1] Treatment titles denote equivalent daily application of water (mm) during periods 1 and 2 (before hyphen) and during subsequent periods; application rates changed on 28 June.
[2] No significant differences except for interval 9 to 23 June when F test yielded P = 0.05.

Table 8. Mean rate of tiller production (tiller tiller^{-1} day^{-1}) within regrowth intervals (Experiment 3)

Treatment[1]	Measurement interval					
	19 May to 8 June	9 to 23 June	29 June to 15 July	16 July to 5 Aug	17 Aug to 1 Sep	2 to 14 Sep
1–3	0.026	0.006	0.071	0.008	0.007	0.013
2–3	0.050	0.021	0.054	0.007	0.000	0.005
4–3	0.077	0.082	0.044	0.006	0.001	0.006
8–8	0.088	0.059	0.045	0.019	0.001	0.009
s.e.d.	0.0156	0.0084	0.0114	0.0065	0.0031	0.0062
F test	*	***				

[1] See footnote to Table 7.

Table 9. Mean dry matter yield (g/m^2) of harvestable herbage (Experiment 3)

Treatment[1]	Harvest date				
	8 June	23 June	19 July	12 August	14 September
1–3	5	1	129	182	195
2–3	111	7	128	167	153
4–3	183	59	175	163	96
8–8	169	73	127	128	53
s.e.d.	20.1	11.0	30.7	50.5	32.8
F test	**	**			*

[1] See footnote to Table 7.

in yield of DM harvested, with growth declining linearly as soil water availability declined in drying soil. Otherwise, response of growth to soil moisture content was quadratic with maximum growth coinciding, approximately, with field capacity and declining in excessively wet soil (Figure 5b).

When measured at the harvest on 12 August N and Ca concentrations in herbage were significantly higher in 1–3 than 2–3 and 4–3, which in turn had higher concentrations than 8–8 (Table 10). Concentrations of Mg and S did not differ significantly between 1–3 and 2–3 but were significantly higher than in 8–8, as was K.

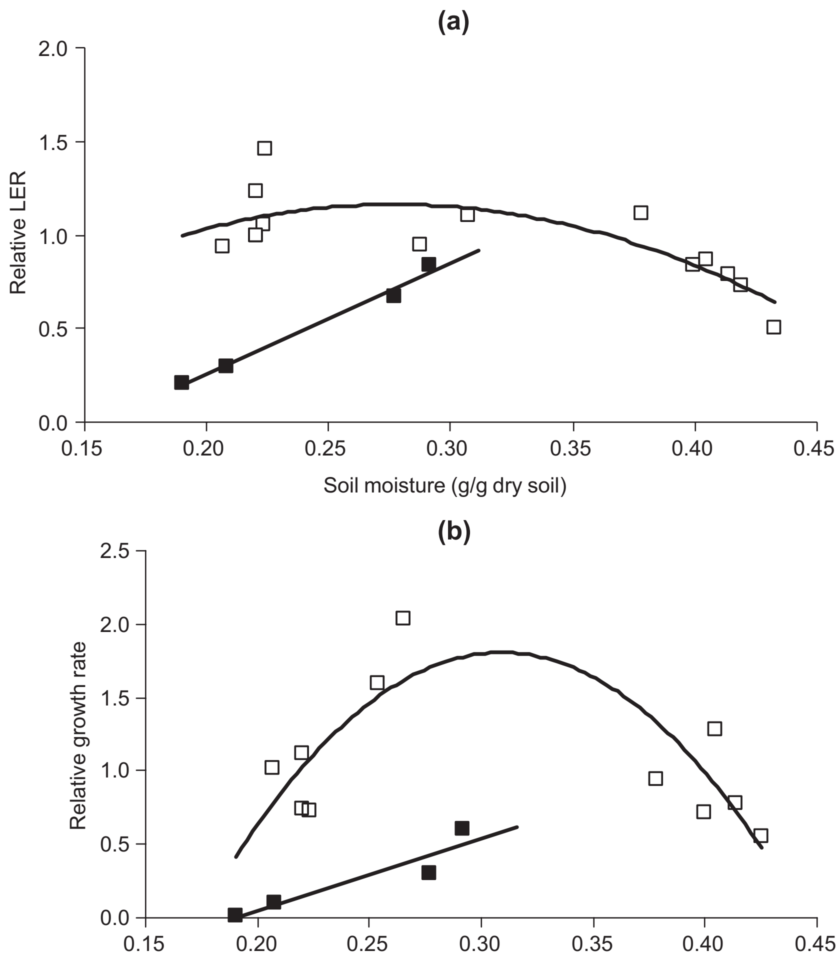

Figure 5. Means, relative to treatment 4–3, for each treatment in each period (□) except treatments 1–3 and 2–3 in first two periods (■), in response to soil moisture content for a) leaf extension rate (LER) ($y = 5.97x - 0.94$, R^2 0.99 and $y = -21.58x^2 + 11.96x - 0.49$, R^2 0.59) and b) dry matter growth rate ($y = 4.89x - 0.93$, R^2 0.87 and $y = -97.96x^2 + 60.53x - 7.55$, R^2 0.58) (Experiment 3).

Table 10. Mineral concentration (g/kg) in herbage dry matter at harvest on 12 August (Experiment 3)

Treatment[1]	Mineral					
	N	P	K	Ca	Mg	S
1–3	40	2.9	50	6.6	2.8	3.3
2–3	34	3.2	47	5.6	2.5	3.1
4–3	30	3.6	45	5.4	2.3	3.0
8–8	24	4.2	41	3.3	1.6	2.7
s.e.d.	1.84	0.20	2.18	0.38	0.24	0.18
F test	***	**	*	***	*	

[1] See footnote to Table 7.

Phosphorus concentration increased with soil moisture content, the two treatments with originally wetter soil had higher concentrations than the two drier treatments.

Discussion

All of the experiments were carried out on the one cultivar of perennial ryegrass. While genotype × environment interactions have been demonstrated in herbage grasses in the UK (Talbot, 1984), under simulated grazing management variety × year interactions are small. In variety testing trials (e.g., for the Recommended List in Northern Ireland) the impact of 'wet' and 'dry' years on differences between varieties of perennial ryegrass are relatively slight compared to the influence on the average annual yield for the species (Dr Trevor Gilliland, AFBI-Crossnacreevy, personal communication).

The experiments were carried out over a range of environments and seasons. Experiment 1 was carried out in winter in a heated glasshouse with supplementary light, Experiment 2 in the autumn (extending into winter) while in Experiment 3, extended from May to September. Variation in daily DM growth in each of the five periods of 9.7, 3.7, 7.6, 6.1 and 2.5 g m^{-2} day^{-1}, respectively, in Experiment 3 indicates the possibility of differences in the physiological state of the swards throughout the season. This will be taken into account in the following discussion.

Moisture stress

Leaf extension rate has been used as a sensitive indicator of the effect of soil moisture deficiency on grass growth and development (Keatinge, Stewart and Garrett, 1979; Jones, Leafe and Stiles, 1979a). However in Experiments 1 and 3 it was not a sensitive indicator. In Experiment 3, in which tillering rate was measured, low growth rate during drying out in the first two periods coincided with not only declining LER but also slow tillering rate. The low tiller density at the end of these two periods would have an impact on growth rate in at least the following period, even when LER had recovered rapidly.

The reduction in LER to between 0.2 to 0.4 that of optimum when soil dries out or when receiving only low rates of water relative to potential evapotranspiration, as seen in Experiments 2 and 3, is of a similar order to that found by Jones *et al.* (1979a) for both field-based swards and microswards. The importance of available water in drying soils as a determinant of growth is also clearly demonstrated and substantiates the use of this variable in models of grass growth (e.g., Topp and Doyle, 1996).

Previous studies of recovery of perennial ryegrass after drought have involved soil moisture levels being raised rapidly to close to field capacity, LER increasing to the equivalent of, or greater than, well-watered controls (Volaire *et al.*, 1998; Clark *et al.*, 1999). However, when rain returns after a period of drought in temperate maritime regions precipitation may not be in excess of evapotranspiration so soil moisture content may not increase greatly. Despite a protracted period of low soil moisture in treatments 1–3 and

2–3 of Experiment 3, LER and growth rate were similar to the 4–3 control soon after reinstatement of applied water and so the relationship between soil water availability and LER or herbage growth rate did not apply. This suggests that the applied water was readily available to the sward despite the obviously high matrix potential of the soil at that moisture content (and reflected in the growth and LER of unwatered swards).

In Experiment 2 soil moisture levels increased rapidly after watering was reinstated, while they remained low in treatments 1–3 and 2–3 for much of the summer. This was probably due to the much higher evapotranspiration in Experiment 3 as it received more than twice the solar energy and considerably higher air temperature than in Experiment 2. Data from Experiment 1 support the implication of this for the use of applied water when soil moisture content varies below that of field capacity. Water can be used with equal efficiency when applied to maintain soil moisture at a range of levels below field capacity. So even when soil has an expected matrix potential of about –1.0 MPa as in 0.5FC, in contrast to 0.01 MPa for 1.0FC, frequently applied water seems to be readily extracted by perennial ryegrass when maintained under these low soil moisture conditions. Results from Experiments 1 and 3 justify, at least partially, suspension of limitations to herbage growth in soil with low moisture content during days in which precipitation exceeds potential evapotranspiration in models such as that of Brereton *et al*. (1996). In Experiment 3, although soil moisture content in the two drier treatments in periods 1 and 2 remained low from period 3 onwards, when water application was increased to 3 mm/day, herbage growth was as high as in treatments with soil moisture closer to field capacity. As the applied water would have been mainly restricted to the surface layer of the soil, the sward could have benefited from this applied water despite it having a relatively small impact on the average moisture content to the depth soil moisture was measured. The small amount of water applied during the stress period may have been adequate to encourage growth of young roots at the surface and so swards were able to take advantage of the higher rates applied from the third period in late June.

Drought imposed during May and June reduced tillering rate in Experiment 3. Jonassen (1992) found that imposing a drought period of 3 weeks on meadow fescue (*Festuca pratensis*) starting 1 June in Norway had a particularly severe effect on tillering. As leaf extension rate (and associated leaf appearance rate) was reduced tiller sites would also be reduced. So reduced tillering due to drought would have been a combination of tiller site production and site filling (Van Loo, 1992). Drought reduced tillering in perennial ryegrass when imposed from July to September in a study in France and growth during recovery was strongly related to tiller density at the end of the drought period (Volaire *et al*., 1998). Although the most active period of tillering for late heading perennial ryegrass is May and June (Laidlaw, 2005b) and so early season drought could be predicted to have an adverse impact on yield later in summer, harvests after the drought period in treatments 1–3 and 2–3 of Experiment 3 did not reflect this. Thus, early summer droughts may not have a long term impact on yield.

Only in exceptional instances were differences in senescence rate between soil moisture treatments significant. Estimates of senescence (leaf length and proportion of tillers) had high standard errors relative to the means (i.e., had high CV) and so insufficient precision in technique may have prevented detection of differences in senescence, despite wide arithmetic differences between the means.

Nitrogen concentration increased with increase in soil moisture in Experiment 1. The higher concentration of K in soils with lowest moisture in both Experiments 1 and 3 would suggest that this may be associated with osmotic adjustment under moisture stress. However, Ca and Mg are also usually implicated in osmotic adjustment but were only higher in the moisture stressed treatment in Experiment 3, and were measured after the effect of moisture stress on yield had been overcome. Also in *Agrostis* species, subjected to drought K and Ca concentration did not increase despite other evidence of osmotic adjustment, e.g., increased proline content (DaCosta and Huang, 2006). There was no indication, after watering was reinstated, that restricted mineral uptake had been a major factor in limiting growth under low soil moisture conditions.

When canopy photosynthesis was measured at the end of the second regrowth period of Experiment 1 for a separate study, there was no relationship between soil moisture status and net canopy photosynthesis (Laidlaw, 2005b). The driest treatments had significantly lower rates of photosynthesis than FC, but the latter also had the highest leaf area index so the data are inconclusive. Jones *et al*. (1979a) concluded that when stress due to drought is imposed gradually leaves become less sensitive to, and more able to withstand, drought conditions; this adaptation possibly resulting from changes in leaf osmotic status and morphology (Jones, Leafe and Stiles, 1979b). This has relevance to the application of relationships between soil moisture and herbage growth in mathematical models as the general relationships established here may not represent the effect of gradual soil moisture loss under field conditions.

Waterlogging

In Experiment 3, it was only when soil moisture content increased to about 0.43 g/g dry soil that LER and growth rate were adversely affected, yield especially attaining only about 0.25 that of the treatment 1-3. However temperate maritime lowland grassland is unlikely to be subjected to such prolonged daily exposure to 8 mm rainfall. Just as available water determined growth when soil was drying, results from Experiment 3 also confirmed the impact of excessive soil moisture on canopy growth and LER. From the data of Brereton and Hope-Cawdery (1988) on yield suppression due to excessive soil moisture in drumlin soils in the west of Ireland, soil moisture of 1.2 times field capacity resulted in growth rate of grass of 0.83 times that in soil at field capacity. However in Experiment 1 in the first of the four growth periods, growth was reduced by about 8% due to waterlogging, becoming 20% by the fourth period. Soil moisture content above field capacity is unlikely to be quantitatively related to herbage growth as presented in the quadratic relationship in Figure 5 as drainage and overland flow usually limit the amount of moisture which can be held in soil above field capacity, which is taken to be about a 10 mm soil moisture deficit (SMD) for agricultural soils in Ireland (Schulte *et al*., 2005; Fitzgerald *et al.*, 2008). The apparent quantitative effect of soil moisture in Figure 5 is confounded with the effect of time as the highest soil moisture content was achieved in the last growth period.

Waterlogging generally reduces uptake of nutrients including N, P, K, Ca and Mg in annual crops (Huang *et al*., 1995; Gutierrez Boem, Lavado and Porcelli, 1996). Nitrogen content declined in the highly leachable conditions generated by the 8 mm/day simulated rainfall treatment in Experiment 3 suggesting that denitrification, expected to be high in the warm high moisture content soil in the 1.25FC treatment in Experiment 1 (Dobbie and Smith, 2006) was not as major a cause of N loss as leaching. Comparing the impact of high soil moisture content without and with the opportunity for leaching (Experiments 1 and 3, respectively), Ca, Mg and S concentrations in the herbage increased in the former and declined in the latter, although the decline was not significant for S. Phosphorus is a special case in relation to uptake in waterlogged soils. Phosphorus concentration increased in *Paspalum dilatatum* under waterlogging due to increased P availability, and roots became morphologically and physiologically more equipped to take up P (Rubio *et al*., 1997). Although there was no significant effect of soil moisture on P concentration in Experiment 1, the particularly high concentration of P in herbage content in the constantly high water application treatment (8–8) in Experiment 3 (almost 0.5 higher than in treatment 1–3) suggests that at least some of the factors identified by Rubio *et al*. (1997) apply to perennial ryegrass.

In waterlogged perennial ryegrass, photosynthesis was more sensitive than shoot growth to waterlogging, even in a tolerant cultivar (McFarlane, Ciavarella and Smith, 2003). The balance of the evidence is that anoxic conditions in the roots of perennial ryegrass affect photosynthesis and so will contribute to reduced leaf production and shoot growth. Post-anoxic stress is likely to be implicated as prolonged periods of saturated soils will increase the levels of oxidants and products of anaerobic fermentation (e.g., ethanol and acetaldehyde) (Fitter and Hay, 2002). Accumulation of these may account for the time dependency of the effects of waterlogging found in Experiments 1 and 3.

Application to field conditions

It is clear, especially from Experiment 3, that soil moisture is not an appropriate indicator of the limitations on sward growth of an apparently restricted water availability. The amount of water used is a more apt indicator of growth under soil water restriction. As soil moisture content was only assessed in approximately the surface 15 cm in Experiments 2 and 3 it is not possible to estimate the amount of water used per day throughout the whole soil profile in any of the treatments; so amount of water used per day can only be crudely estimated. If it is assumed that soil moisture is extracted by the sward mostly in the top 30 cm of soil and bulk density of soil is 1 this means that the rooting zone represents about 300 kg of soil per 1 m^2. So each 0.1 unit of soil water content (water:soil by weight) represents 30 L water within the rooting zone per 1 m^2. A decrease of 1 L of water per 1 m^2 is equivalent to an increase of 1 mm of SMD. In Experiment 1, at 0.5FC 1.5 L m^{-2} day^{-1} water applied produced about 0.6 times the potential growth (i.e., when about 3.5 L m^{-2} day^{-1} are applied), while in Experiment 2, when soil moisture content was below 0.4 FC, water is drawn at a rate of 1.4 L m^{-2} day^{-1} from unwatered soil and growth was about 0.3 that of well watered soil, i.e., when 2 to 2.5 L m^{-2} day^{-1} are applied. In contrast, in Experiment 3, when soil moisture stress was induced during early summer, even when water was applied at 1 L m^{-2} day^{-1}, moisture content declined at the equivalent of about 1.5 L m^{-2} day^{-1} and growth was very low by the second period. However, a further 2 L m^{-2} day^{-1} reinstated a high rate of growth. This emphasises the importance of taking account of seasonal effects when interpreting herbage growth rate responses to soil moisture.

The finding that the growth rate in the 0.75FC treatment of Experiment 1 was not significantly different from that at 1.0FC, even though it represented an SMD of 34 mm (i.e., calculated from FC of 45 g/g, soil moisture 25% below field capacity and 300 g/m soil in rooting zone per 1 m^2) is not unexpected since this is below the critical value (i.e., critical SMD, maximum SMD at which growth is not adversely affected) used by Brereton *et al.* (1996), but contradicts Schulte *et al.* (2005) who showed that moisture stress is manifest even at very low SMD. However, in the present study LER was not affected by soil moisture levels slightly below field capacity and tillering was affected only at very low soil moisture levels, so unless weight per unit length of leaf was affected at low SMD, the assumptions of Brereton *et al.* (1996) would seem to be valid in at least some systems.

In moderately or poorly drained soils, maximum moisture content in excess of field capacity is taken to be at a SMD of –10 mm (Schulte *et al*., 2005; Fitzgerald *et al*., 2008). The importance of time in the relationship between SMD above field capacity and herbage growth has been demonstrated in both Experiments 1 and 3. In the model of Fitzgerald *et al*. (2008) a growth restriction factor for poorly drained soils due to waterlogging of 0.25 times full herbage growth was introduced during calibration. While this is well in excess of the initial 8% reduction in the early stages of period 1 in Experiment 1, it is closer to that observed in period 4 and less severe than the reduction due to high moisture input in period 5 of Experiment 3. In poorly drained soils in high rainfall areas, it is possible that long periods of continuous waterlogging, in which the water table is close to the surface for long periods in the growing season, could have particularly deleterious effects on herbage growth (Brereton and Hope-Cawdery, 1988).

Two implication of the findings of this study for grass growth models are that allowance should be made for the positive effect of rainfall on grass growth during prolonged dry periods, despite soil moisture content remaining low, and the negative effect on growth of excessively high soil moisture content. The former confirms assumptions which have been made in previous models. The impact of excessive soil moisture on growth was incorporated into the model of Laidlaw (2005a) by introducing the quadratic equation relating herbage growth relative to the control treatment and soil moisture content in Figure 5. This model had previously failed to simulate the poor annual yield of herbage in a wet year (2002). Although the amended model identified yield at the mid-June cut to be the lowest of the 10 years considered, i.e., when rainfall in May and early June had been particularly high, it did not simulate the severe depression in yield at subsequent cuts to early September. Rainfall during July and August was above average but not excessively so. Therefore, further study is required to identify factors preventing rapid recovery from the adverse effects of waterlogging in intensively managed grassland.

In conclusion, due to the generally rapid response of grass to applied moisture under conditions of drought stress, predicted growth on the day of application in models should take account of the direct effect of water availability, rather than solely via the effect it has on average soil moisture content.

As a high proportion of soils on the island of Ireland are gleys (Collins, Larney and Morgan, 2004; Cruikshank, 1997) soil moisture content will exceed field capacity for parts of the growing season in some years. Account should be taken of this in grass growth models applied to intensive grassland management generally and not restricted to high rainfall on heavy clay soils with severely impeded drainage. However, further investigations are required to quantify long term effects of excess soil moisture in intensively managed grassland in temperate maritime areas.

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