Chapter 9

Variation in summer dormancy of cultivars of *Lolium perenne* and the cues responsible for its initiation

9.1 Introduction

Studies in Chapters 4 to 8 have shown how appropriate defoliation management in winter and spring may improve the persistence of perennial ryegrass over summer. Such defoliation practice optimises root growth through retaining higher levels of plant WSC reserves. Despite this, low WSC levels may be inevitable due to C starvation (Chapter 2, section 2.4.1). Therefore, one option for improved survival may be to either have a dormant plant over summer (Chapter 9) or have an annual plant which dies in late spring and regenerates in autumn from seed set naturally in spring (Chapter 10).

Some perennial grass species avoid summer stress by complete or near-complete cessation of growth, resuming growth in autumn when climatic conditions improve. This summer dormancy involves the death of most above-ground plant tissues, and the formation of dormant growing points close to, or below, the soil surface (Laude 1953; Hoen 1968; McWilliam 1968). Summer dormancy is thus a means of ensuring plant persistence through conditions not conducive to growth and survival. To illustrate this, Silsbury (1961) found that summer-dormant cultivars of perennial ryegrass grown in temperate Australia exhibited greater persistence than existing commercial cultivars, due to better summer survival. In the subtropics, where persistence of perennial ryegrass is closely related to summer survival (Fulkerson *et al.* 1993b), and to levels of WSC at this time (Chapter 5), summer dormancy may be one means of surviving summer.

Summer dormancy in perennial grasses appears to be initiated by a combination of temperature and moisture stress (Hoen 1968; McWilliam 1978). Moisture stress is generally accepted as being the dominant factor maintaining dormancy, as the addition of water causes dormancy to break in many lines of summer-dormant perennial ryegrass (Silsbury 1961; Biddiscombe *et al.* 1977; Arcioni *et al.* 1985c), phalaris (Hoen 1966; McWilliam 1968; Biddiscombe *et al.* 1977; Oram and Freebairn 1984) cocksfoot (Biddiscombe *et al.* 1977; Volaire 1995) and tall fescue (Biddiscombe *et al.* 1977). In a subtropical environment, where summer rainfall is a regular feature, summer dormancy of perennial ryegrass will only be useful if it is maintained primarily by high temperature. Little is known about the degree of dormancy in perennial ryegrass. Enough variation in summer dormancy exists between cultivars of phalaris (Ketellapper 1960; Hoveland 1970) and cocksfoot (Knight 1966), such that some cultivars remain dormant even when supplied with water. It is possible that similar variation exists with cultivars of perennial ryegrass. However, the shallow rooting nature of perennial ryegrass plants in the subtropics may mean that dormancy will be hard to maintain in this species, as survival of dormant growing points relies on a continued supply of water and nutrients from deep roots (McWilliam and Kramer 1968).

The present study sought to determine the variation between perennial ryegrass cultivars in temperature- and moisture-maintained dormancy. Cultivars and accessions of perennial ryegrass, including some Mediterranean cultivars which exhibit strong summer dormancy in that environment, as well as current commercial lines, were sown in field plots. When dormancy was observed, plants were transferred to a controlled-environment glasshouse, where temperature and moisture were varied to separate the effect of both on maintaining dormancy.

9.2 Materials and methods

The plots were located on river flats near Casino, on the north coast of New South Wales. For details of soil and climate see Chapter 3, section 1. The site was prepared as outlined in Chapter 4, section 2.2, and sown in June 1994 with 20 kg perennial ryegrass/ha. The 2 x 1 m plots received monthly applications of 100 kg urea/ha from July to December 1994.

Plots received 20 to 30 mm of irrigation every 10 to 14 days from sowing to November 30 1994. After November 30, plots were irrigated once in mid-December, with approximately 5 mm of water, designed to keep plants alive but not prevent dormancy. All plots were defoliated at the 3-leaf stage of regrowth.

Twenty six cultivars and accessions of perennial ryegrass were examined, of which 4 cultivars were rated as highly summer-dormant, and 3 as moderately summer-dormant when grown in temperate Australia (Lee *et al.* 1993). The summer dormancy of the other 19 cultivars and accessions was unknown. The cultivars/accessions used were:

Group 1, of Algerian origin, highly dormant: C296, 46, 49 and 59.
Group 2, of Spanish origin, moderately dormant: 123, 141 and 149.
Group 3, of European origin, level of dormancy unknown: Pamir, Tyrone, Q1808, Colmar, Chelsea, Preference, Q1734 and Jumbo.
Group 4, of New Zealand origin, level of dormancy unknown: Yatsyn, Embassy, Pacific H.E., Ellet, Banks H.E., CSLP 90-102, CSLP 92-107, CSLP 92-109, CSLP 931, CSLP 935, CSLP 936.

On December 1 1994, and again on December 30, soil cores (120 mm diameter, 100 mm deep) were taken to include the root systems of 4 plants of each perennial ryegrass cultivar, and placed into plastic pots of the same diameter, but 100 mm deeper, the difference in depth filled with coarse sand. Plants were taken to a controlled-environment glasshouse, and defoliated to a stubble height of 50 mm. Half of the plants were kept constantly at field capacity, by placing pots in trays in which water was maintained at a depth of 80 mm. Of the remaining plants, a representative sample of 10 pots were weighed, then each 3 days thereafter, were rewatered to their previous weight, and the same volume of water added to all pots. All plants were subjected to day/night temperature regimes of 38/20, 33/18, 28/15, and 23/12°C for 5 consecutive days in each regime. Day temperatures were set at 5°C intervals, and corresponding night temperatures were determined from historical weather data. After this, all plants were watered to field capacity, and kept at 23/12°C for a further 10 days, being within the temperature regime considered to be optimal for growth of ryegrass (Mitchell 1956; Evans *et al.* 1964; Spedding 1971).

Tiller regrowth was recorded at the end of each temperature interval, and expressed as a percentage of total live tillers throughout the 30-day trial period. This was used to indicate the degree of dormancy, as any tillers which had not grown during the trial period were considered dead. It was noted whether tiller growth was from existing defoliated tillers, or from growing points at the base of tillers.

9.3 Results

Cultivars in Groups 1 and 2 (of Mediterranean origin) differed from cultivars in Groups 3 and 4, in that these plants set seed earlier, and this was more extensive. Thus, these cultivars set seed in early- to mid-November, the time when those few other cultivars which did seed in this environment were just beginning the stem elongation phase. Furthermore, while the majority of tillers from Mediterranean plants became reproductive, on average less than 10% of total tillers from the other cultivars did so. The tillers of Mediterranean cultivars senesced after setting seed, leaving only a few green vegetative tillers/plant. All other cultivars remained predominantly vegetative, at no stage appearing dormant.

When plants were taken from the field to the glasshouse, all of the Mediterranean cultivars were completely dormant, as the minimal irrigation applied in mid-December did not cause extensive tiller regeneration. Mean day temperature in the weeks prior to each sampling date was 32 and 33°C, for sampling dates December 1 and December 30, respectively.

The number of live tillers/plant did not vary significantly ($P>0.05$) within cultivars or between the 2 sampling dates. Watering plants to field capacity caused regeneration of the majority of tillers, even under high temperature (38/20°C). Hence, after 5 days at 38/20°C, the highest degree of dormancy in the Mediterranean cultivars was observed in cultivars 46 and C296, with 11 and 9%, respectively, of total live tillers dormant. In all cultivars in Groups 1 and 2, tiller regeneration occurred almost exclusively from growing points at the base of dead reproductive tillers. Of the other cultivars, only Pamir and Q1808 displayed any degree of dormancy, with 14 and 11%, respectively, of total live tillers dormant after 5 days at 38/20°C. However, tiller growth in all cultivars in Groups 3 and 4 was a continuation from live vegetative tillers. As temperature decreased, all dormant plants completely regenerated.

Where temperature was decreased while maintaining moisture stress, the response of cultivars placed them into one of 4 groups as shown in Table 9.1.

Table 9.1. The mean (± s.e.) percentage of live tillers in cultivars and accessions of perennial ryegrass, in response to decreasing temperature when moisture levels were minimal. 'Highest temperature' is at the end of 5 days at 38/20°C, after transfer from field plots, while 'lowest temperature' is at the end of 5 days at 23/12°C, following 15 days of declining temperature regimes after transfer from field plots.

		Mean (± s.e.) % of green tillers	
Observed degree of dormancy	**Cultivars/accessions**	**Highest temperature**	**Lowest temperature**
High	C296, 59, 123, 141	0 ± 0	95 ± 3
Moderate	49, Pamir, Colmar, Preference, Q1734, Embassy, Pacific H.E.	41 ± 5	99 ± 0.6
Low	46, Chelsea, Jumbo	11 ± 7	62 ± 8
Nil	49, Tyrone, Q1808, Yatsyn, Ellet, Banks H.E., CSLP 90-102, CSLP 92-107, CSLP 92-109, CSLP 931, CSLP 935, CSLP 936	88 ± 6	65 ± 6

9.4 Discussion

Results from the current study indicate that although high temperature appears to maintain summer dormancy to a degree in some cultivars of perennial ryegrass, notably those of

Mediterranean origin, this is overridden by removal of moisture stress. Thus, although the number of live tillers in many cultivars increased as temperature decreased, the addition of water caused greater than 85% of total live tillers across all cultivars to regenerate, even at the highest temperature regime (38/20°C). A number of cultivars also recorded a decline in live tillers as temperature decreased (Table 9.1, 'Nil' dormancy) and this was due to death of regrowing or regenerating tillers under the initially high temperatures. As a consequence, it seems unlikely that summer dormancy in perennial ryegrass will be a beneficial trait in terms of improved persistence in the subtropics. Summer rainfall would cause dormancy to break, and since such rainfall is infrequent, under the hot, dry conditions which follow, these regenerating plants would have little chance of survival (Biddiscombe *et al.* 1977; Oram and Freebairn 1984).

Although there may be other cultivars of perennial ryegrass which are more reliant on temperature than moisture to maintain dormancy, the shallow-rooting nature of perennial ryegrass in the subtropics may mean that the dormant buds will not be supplied with adequate moisture to survive a prolonged dry period (McWilliam and Kramer 1968).

Under the minimal water regime, many of the non-dormant cultivars showed a preference to regrow at lower temperatures. This was more a short-term response by plants to heat stress and not true dormancy as exhibited by cultivars of Mediterranean origin, since regrowth was from existing tillers rather than from dormant growing points. Such a short-term response to environmental stress is termed 'relative dormancy', as it is caused by prevailing environmental conditions (Hoen 1968). In New Zealand, Korte and Chu (1983) reported that hot, dry conditions reduced leaf expansion and tillering in perennial ryegrass, and these 'dormant' plants were unresponsive to defoliation, resuming normal growth when moisture stress was removed. Similarly, it has been observed that as temperatures rise during mid- to late-summer in the subtropics, growth of many commercial perennial ryegrass cultivars slows or stops, resuming only after temperatures fall, and this may or may not be accompanied by rainfall (W.J. Fulkerson, personal communication).

The observation in the current study - that regrowth of Mediterranean cultivars of perennial ryegrass after dormancy was from growing points at the base of reproductive tillers - is consistent with results of Silsbury (1964), who found that tillers which were vegetative at the commencement of dormancy play only a minor role in summer survival of dormant perennial ryegrass cultivars. He found that less than 10% of vegetative tillers present at the commencement of summer (hence onset of dormancy) survived to the following autumn - regrowth was primarily from dormant buds which were reproductive at the commencement of summer.

Chapter 10

'Perennating' biennial ryegrass: an alternative approach to the persistence problems of perennial ryegrass

10.1 Introduction

The lack of survival of perennial ryegrass over summer in the subtropics has resulted in many farmers choosing to sow annual or biennial ryegrass pastures (see Chapter 2, section 1.1). Biennial genotypes have the advantages of being more vigorous under appropriate defoliation regimes, have significantly larger tillers, greater root DM with depth, and higher WSC levels than perennial genotypes (Fulkerson *et al.* 1994). Therefore, an alternative approach to improving persistence of perennial ryegrass may be to manage biennial genotypes to perennate, as greater persistence of grasses has been associated with higher WSC levels (Arcioni *et al.* 1980, 1985b, c; Volaire 1994b, 1995; Volaire and Gandoin 1996) and a more developed root system (Arcioni *et al.* 1980, 1985b; Fulkerson *et al.* 1993b). Biennial genotypes can persist for longer than one year under subtropical conditions (D.C. Goodenough, personal communication), but a lack of information exists regarding the conditions under which they will perennate.

The aim of this study was to determine the effect of defoliation in winter and spring, and irrigation in summer, on plant survival over summer and seedling recruitment the following year.

10.2 Materials and methods

The present study was blocked within the study on perennial ryegrass outlined in Chapter 4, with the view of allowing a valid comparison between genotypes. The pasture type examined was a mix of biennial ryegrass cv. Noble and white clover cv. Haifa. This Chapter deals predominantly with the ryegrass component of the pasture.

10.2.1 Experimental design

The site was prepared and sown as outlined in Chapter 4, section 2.2, the only differences being that the plots were 4 x 3 m, were replicated 4 times within 2 blocks, and were sown with 7 kg biennial ryegrass and 6 kg white clover/ha. Two weeks after sowing, 80 kg urea/ha urea was applied, after which plots received 100 kg urea/ha bi-monthly from May to November 1994.

Treatment details were as follows:

Defoliation interval: Period 1 (P1) from 22 March 1994 to stem elongation (13 October), plots were defoliated at the 3 *or* 1-leaf stage.

Period 2 (P2) from stem elongation to 2 regrowth cycles after stem elongation (28 December), each treatment in P1 was subjected to the same defoliation *or* was not defoliated thereafter.

Irrigation was carried out as detailed in Chapter 4, section 2.2.

10.2.2 Measurements

All measurements were as described in Chapter 4, section 2.3, with the exception that tiller density and DM/tiller were recorded between 13 October and 28 December 1994.

Approximately 15 individual tillers were marked and monitored fortnightly from 10 November 1994 to 5 January 1995. In addition, on 2 April 1995, 40 seedlings were marked with coloured wire loops along an identifiable transect in each of 2 plots, and monitored in May and June to observe seedling survival and tiller development. At each monitoring event, tillers were classed as vegetative, reproductive or dead, and the initiation of daughter tillers was also recorded. Root DM was determined on 19 November 1994.

10.2.3 Statistical analyses

Analysis of data was performed as per the procedure in Chapter 4, section 2.4, with the exception that there was no Period 3.

10.3 Results

Defoliating at the 1-leaf, as opposed to the 3-leaf, stage of regrowth from sowing to 28 December caused a significant reduction ($P < 0.001$) in ryegrass DM yield (5,683 vs. 8,638 kg/ha).

10.3.1 Impact of defoliation treatment in P1

Defoliation interval during P1 had no significant effect ($P > 0.05$) on plant density at stem elongation when there were 92 ± 2 (mean ± s.e.) ryegrass and 33 ± 2 (mean ± s.e.) tropical grass plants/m^2.

At the end of P1, tiller density was significantly greater (6,688 vs. 5,721 tillers/m^2; $P < 0.05$) but DM/tiller was significantly lower (61 vs. 86 mg/tiller; $P < 0.001$), in plots defoliated at the 1-leaf, compared to the 3-leaf, stage. However, by the end of the season on 28 December, tiller density (1,892 vs. 4,123 tillers/m^2) and DM/tiller (26 vs. 40 mg/tiller) were significantly lower ($P < 0.001$) in plots continually defoliated at the 1-leaf stage than other treatments, with no significant difference ($P > 0.05$) between the remaining treatments.

In November, root DM was significantly lower (2.2 vs. 3.0 g/plant; $P < 0.05$) in plants defoliated at 1 leaf/tiller than at 3 leaves/tiller during P1. The top 50 mm of soil contained 82 ± 2 (mean ± s.e.) % of the total root DM.

10.3.2 Impact of defoliation treatment in P2

Frequent defoliation during P2 prevented seed-head formation but not stem elongation. Plants in plots continually defoliated at 1 leaf/tiller had between 2 and 4 nodes/tiller on 28 December, with seed-heads emerging after 4 or 5 nodes/tiller. Seed germination tests indicated that only 5% of seed was dormant at high temperature (greater than 30°C). Chilling did not improve the percentage germination of seeds.

Allowing plants to set seed by cessation of defoliation in P2 severely retarded initiation of new tillers in late spring and early summer, while tiller initiation was greatest in plots which continued to be defoliated at 3 leaves/tiller over this time (Table 10.1).

Table 10.1. Mean number of daughter and dead tillers to 1 February 1995, per original ryegrass tiller marked on 26 October 1994, as affected by defoliation treatment (where 3 = 3 leaves/tiller, 1 = 1 leaf/tiller, and 0 = no further defoliation) during P1/P2 in the previous year.

Defoliation treatment	**Tiller number/original tiller**	
	Live daughter tillers	**Dead tillers**
3/3	1.21	2.21
3/0	0.23	1.23
1/1	0.81	1.81
1/0	0.03	1.03

By 22 December, all of the marked tillers had died under continual defoliation at 1 leaf/tiller, while the majority of marked tillers in undefoliated plots were still alive. All tillers had died by mid-January.

Ryegrass seedling recruitment in the autumn of year 2 was significantly higher ($P<0.05$) in plots defoliated at 3 leaves/tiller and then allowed to set seed (3/0 treatment), than the other treatments (Table 10.2).

Table 10.2. Density (plants/m^2) of ryegrass and tropical grass plants in autumn of year 2, as affected by defoliation treatment (where 3 = 3 leaves/tiller, 1 = 1 leaf/tiller, and 0 = no further defoliation) during P1/P2 in the previous year. Means with different superscripts within columns are significantly different at $P<0.05$.

Defoliation treatment	**Plant density (plants/m^2)**	
	Ryegrass	**Tropical grass**
3/3	7^b	84
3/0	81^a	72
1/1	8^b	80
1/0	21^b	82

10.3.3 Impact of summer irrigation

Although seedling recruitment in autumn was twice as high ($P<0.05$) in plots which received irrigation over summer, compared with non-irrigated plots, there was no significant interaction ($P>0.05$) with defoliation. Irrigation had no significant effect ($P>0.05$) on tropical grass plant density in the autumn of year 2.

10.3.4 Pasture productivity in year 2

In June of year 2, 79% of seedling tillers marked in April were still alive, and had produced an average of 5 new daughter tillers. The DM yield in year 2 (April to June 1995) reflected seedling recruitment, and there was a significant interaction ($P<0.001$) between irrigation and defoliation for DM yield of all pasture components, as shown in Figure 10.1.

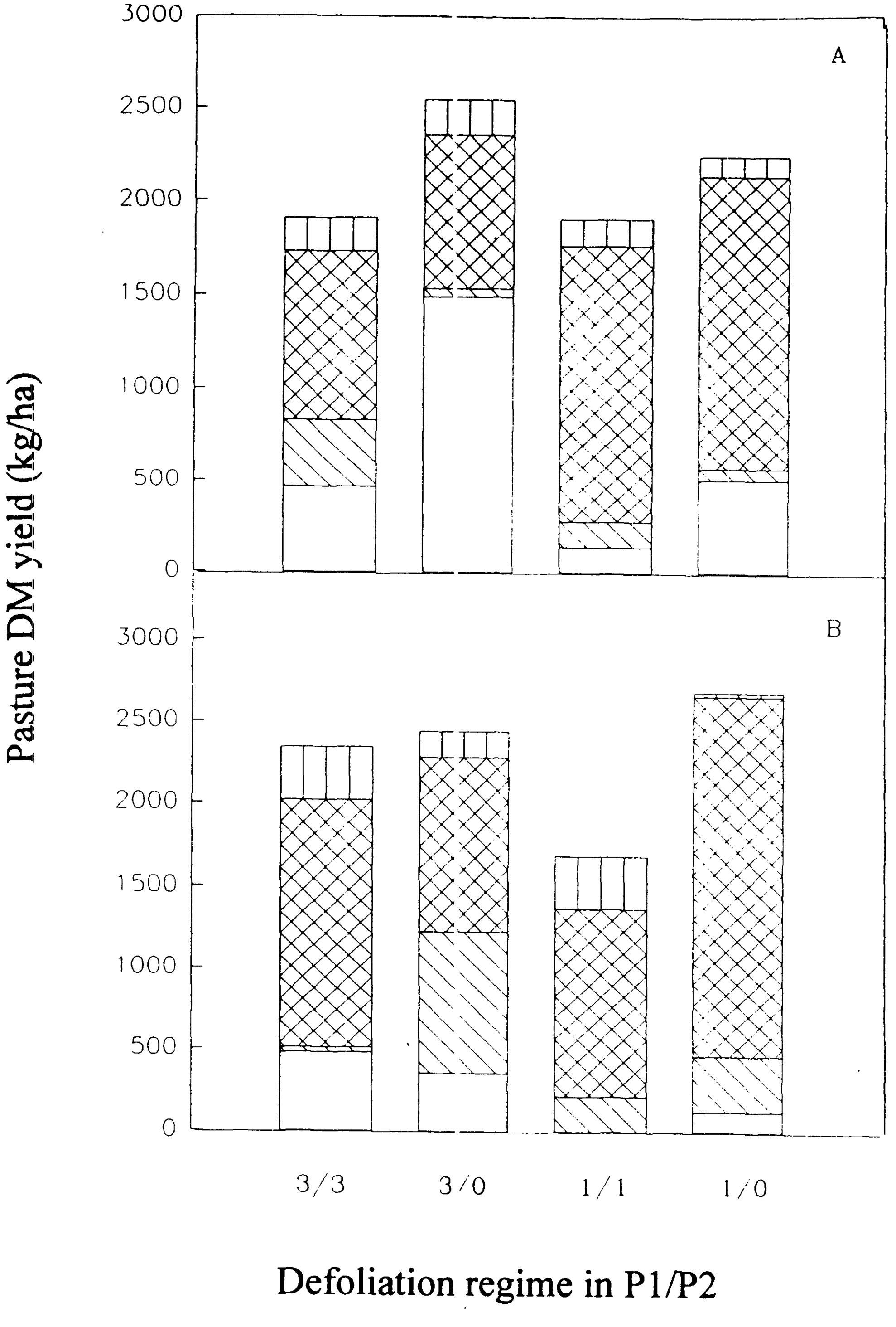

Figure 10.1. Yield (kg DM/ha) of ryegrass (□), white clover (▧), tropical grasses (▩) and weeds (▥) from April to June in year 2, in plots which were (A) irrigated or (B) not irrigated over the summer, and defoliated during P1/P2; 3 = 3 leaves/tiller, 1 = 1 leaf/tiller, and 0 = no further defoliation.

Continuing irrigation over summer increased ryegrass DM and decreased clover DM the following autumn compared to no irrigation, with the difference being more pronounced in plots where defoliation ceased after stem elongation. In irrigated plots defoliated at 1 leaf/tiller in P1, tropical grass DM was almost double that of plots defoliated at 3 leaves/tiller.

10.4 Discussion

In this study, there was no survival of ryegrass plants through the first summer after establishment and hence DM yield in the second year was dependent entirely on seedling recruitment of seed set the previous year. The variety of ryegrass used in this study, Noble, is a relatively early season variety; later seeding varieties like Concord could have been more persistent (K.F. Lowe, personal communication).

Allowing ryegrass to set seed in P2, following defoliation at 3 leaves/tiller in P1, resulted in an autumn pasture in which ryegrass plant density was only 11% lower than in the spring of the previous year. However, this treatment resulted in the loss of 3,094 kg of ryegrass and white clover DM/ha through deferred defoliation, in comparison to plots continually defoliated.

Although ryegrass seeds germinated after heavy rain in February 1995, no seedlings survived under conditions of high temperature (greater than 30°C) and waterlogging. A further germination took place in late March under cooler conditions, and over the next 2 months, 89% of these seedlings survived, even though the density of tropical grass plants was 51% greater than in perennial ryegrass pastures in the study described in Chapter 4. In a wetter summer, we would expect more false germinations, leading to a depletion of the ryegrass seedbank, to the detriment of autumn germination and subsequent pasture yield.

Over the period from sowing in late March to December, the ryegrass component of the biennial pastures was 38% more productive than perennial ryegrass pastures (7,160 ± 414 vs. 5,201 ± 292 (mean ± s.e.) kg DM/ha) for comparable treatments (defoliated continually at 1 or 3 leaves/tiller). Part of the DM production advantage in favour of the biennial would be due to increased stem, with 100% of tillers in undefoliated plots becoming reproductive compared to less than 10% of perennial ryegrass tillers. However, the biennial was also more sensitive than the perennial to defoliation frequency, with ryegrass DM yield decreased by 34% vs. 10%, respectively, when defoliation interval changed from 3 to 1 leaf/tiller. This differential response of the 2 genotypes to defoliation confirms earlier glasshouse studies by Fulkerson *et al.* (1994).

Defoliating during the reproductive phase of ryegrass development removes elevated growing points and is a means of maintaining ryegrass in the vegetative state (Reid 1959, 1962; Appadurai and Holmes 1964), hence DM is of higher quality (digestibility) than if reproduction was allowed to proceed (Smetham 1973). In the current study, the majority of biennial ryegrass tillers set seed and died by 28 December, regardless of defoliation treatment, hence defoliation presumably has no effect on the quality of biennial pasture.

Biennial ryegrass appears to be capable of regenerating a pasture in the second year with similar production to the establishment year. However, this is achieved only by deferring defoliation in late spring, with substantial loss of edible DM, and therefore the current practice of over-sowing in autumn may be a more practical option.