Morphological and physiological studies of prairie grass
(*Bromus willdenowii* Kunth)

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ABSTRACT

Morphological and physiological studies of prairie grass (*Bromus willdenowii* Kunth)

Doctorate Thesis, Department of Field Crops and Grassland Science, Agricultural University, Wageningen, The Netherlands, 20 March 1990.

D. E. Hume

This thesis reports the results of seven indoor and outdoor studies on the growth of prairie grass (*Bromus willdenowii* Kunth). In five studies comparisons were also made with ryegrass (*Lolium* spp.). Leaf and tiller production were quantified for undisturbed growth and growth under different cutting regimes. Water soluble carbohydrate reserves for regrowth were also determined. Particular attention was given to the effects of reproductive development on partitioning of biomass, tillering, herbage quality and yields. Field studies also investigated the effects of disease, plant populations, tillering, natural reseeding and frequency of defoliation.

Compared to ryegrass, prairie grass had a high leaf appearance rate but low site filling, which resulted in low tiller numbers. Prairie grass had large tillers with long wide leaves, resulting in high herbage production. Plants were able to tiller profusely in the field to compensate for plant death. High reproductive development occurred in prairie grass which had large effects on yields, herbage quality and tillering. Vegetative and reproductive plants performed best under infrequent defoliation regimes.

STELLINGEN

1. An important factor determining the different tillering rates of prairie grass (*Bromus willdenowii* Kunth) and ryegrass (*Lolium* spp.) during the early growth of seedlings is the capacity to develop the coleoptile and prophyll tiller buds. (this thesis)

2. Suitable management for high production of prairie grass during the vegetative and reproductive growth stages is infrequent defoliation. (this thesis)

3. The relative performance of prairie grass cultivars as identified during undisturbed growth can be highly modified under cutting, especially during reproductive growth. (this thesis)

4. Presence of the reproductive tiller in prairie grass increases the yield but decreases the herbage quality, especially at later stages of development compared to Westerwolds ryegrass. (this thesis)

5. It appears that there is an alarming and regrettable ignorance about the role and value of pasture plants throughout the (New Zealand) agricultural industry.

   Lancashire, J. A.; *Using Herbage Cultivars*, NZGA, Palmerston North, 79-87, 1985.

6. Concern for the environment is clearly lacking in the following statement. "Everyone is quite aware now that what matters is to obtain as large an amount of milk or meat as possible, not merely per animal, but also per hectare of forage crop and that at least cost."

   Loiseau, R.; Foreword, In *Latest Technical Information on Bromus catharticus*, 1982.

7. The use of pasture legumes in north west Europe is at present limited by economic constraints, but environmental considerations may prescribe their use in certain situations. Farmers, research and extension workers, however, would first need to increase their knowledge on this way of grassland farming.

8. A period of foreign study for students in any country is essential for both their personal and scientific development.

9. Even though some New Zealanders are leaving New Zealand permanently for so called 'greener pastures', the country must still have something to offer as the majority of Dutch emigrants who arrive in New Zealand settle there permanently.

10. The overall success of current political reforms in Eastern Europe may only be truly judged in the long term by economic reforms and an improved standard of living for these Europeans.

11. The declining proportion of home births in The Netherlands is a trend that the Dutch people may regret in the future.

Proefschrift D. E. Hume
Morphological and physiological studies
of prairie grass (*Bromus willdenowii* Kunth)
Wageningen, 20 maart 1990

Last but not least I must acknowledge the tremendous assistance that Karen, my wife, has given me over the last three years. Firstly for supporting my decision to travel to the other side of the world, and then assisting me with practical aspects of my projects, reading manuscripts, as well as producing two daughters.

March 1990 David Hume

CONTENTS

CHAPTER 1

GENERAL INTRODUCTION

Introduction

Over the last 20 to 30 years interest has developed in prairie grass (*Bromus willdenowii* Kunth) by research scientists, with increased farm use occurring in France (Anon., 1982) and New Zealand (Hampton and Scott, 1984; Johnson, 1985). However, use of prairie grass is still relatively small, only being used on 1 to 3 % of its potential area in New Zealand (Lancashire, 1985). Several prairie grass cultivars are now available (Anon., 1986), which have proven to be highly productive in several countries eg. France (Anon., 1982), New Zealand (Fraser, 1985) and the United Kingdom (Anon., 1986). Many of the perceived problems of establishment, management and persistency have been overcome so that we now have 'working packages' for the use of prairie grass on the farm (Anon., 1982; Clark, 1985; Fraser, 1985). Much of these 'packages' are concerned with practices that are different to those normally used for ryegrass (*Lolium* spp.), tall fescue (*Festuca arundinacea* Schreb.) and cocksfoot (*Dactylis glomerata* L.), as prairie grass has specific management requirements and a more limited environmental niche (Langer, 1973; Burgess *et al*., 1986).

In comparison to other commonly used temperate pasture species, relatively little is known about the behaviour of prairie grass, except under general farming conditions (Anon., 1982; Burgess *et al*., 1986). This study was therefore undertaken to investigate some of the morphological and physiological characters of this species, and to identify the possible implications that these may have on the value and use of prairie grass in agricultural systems. Some of this information may also be the basis for defining plant parameters for use in computer modelling of growth in prairie grass.

Features of prairie grass

Prairie grass is a true perennial originating in the Pampas of South America, and now has a very wide geographical distribution (Hafliger and Scholz, 1981). For exampie, prairie grass was first recorded in New Zealand in 1869 and soon became established as a useful pasture species (Rumball, 1967). Similar introduction occurred in France in the 1860's (Lavellee, 1865; cited by Pfitzenmeyer and Parneix, 1981). In the past, accidental introduction of prairie grass to The Netherlands occurred near sea ports and some cultivation has been practiced (Heukels, 1911; Jansen, 1951). It did not become a permanent stable species in the Dutch environment as it apparently did not survive hard winters (Jansen, 1951; Heukels and Van der Meijden, 1983).

Prairie grass has been and is known under various common names and species names. It is also known as rescue grass, brome grass, Schraders brome grass and in The Netherlands as 'paardegras'. The species is known under various botanical names; *Bromus catharticus* Vahl, *B. unioloides* H.B.K., *B. schraderi* Kunth and *B. willdenowii* Kunth, with considerable discussion over the correct species name (Hubbard, 1956; Raven, 1960). It is a tall, erect plant with wide leaves and few but large tillers. The inflorescences are large panicles with big spikelets and they are produced over a prolonged period from mid-spring to mid-autumn.

In New Zealand and France (Anon., 1982; Burgess *et al.*, 1986) prairie grass is valued for its ability to provide green forage at times when traditional pasture mixtures are low yielding. Prairie grass has the ability to grow well under the cool conditions of winter and the dry conditions of summer and early autumn. It is highly palatable at all stages with high digestibility despite large numbers of inflorescences. It also has a good level of tolerance to pests and diseases. Natural reseeding is a feature of this species and is reported to help maintain or regenerate swards. These agronomic advantages result in economic advantages to the farmer, eg. 10 to 15% higher gross margins where prairie grass is used in sheep farming systems in New Zealand (Greer and Chamberlain, 1986).

Prairie grass does have environmental and managements limits to its use. It suffers from poor persistence and production under frequent defoliation and when grown in soils susceptible to waterlogging. The prolonged, high production of reproductive tillers has caused some concern regarding quality and has therefore become a selection criterion for some plant breeders (Pfitzenmeyer, 1982). Its low tillering capacity has caused some concern (Hill and Pearson, 1985). The head smut fungus *Ustilago bullata* Berk. may infect the plant and cause reductions in plant productivity and persistence (Falloon, 1976).

Outline of this thesis

This thesis presents a number of studies that investigated several aspects of prairie grass. Chapters 1 to 5 include comparisons with ryegrass (*Lolium* spp.) in order to place prairie grass in perspective. Chapters 6 and 7 deal with aspects that are more specific to prairie grass.

Chapter 2 presents the results of a field trial at Wageningen in which prairie grass was grown for a three month period of undisturbed growth. Partitioning of biomass between all plant components and herbage quality were assessed. This was compared to a tetraploid Westerwolds ryegrass (*Lolium multiflorum* Lam.) which is reported to have similar quality and a similar upright growth habit to prairie grass.

In Chapter 3, leaf and tiller production for vegetative and reproductive prairie grass plants is quantified and compared to perennial ryegrass (*Lolium perenne* L.) and Westerwolds ryegrass under various photoperiod and temperature conditions.

Chapters 4 and 5 describe the effects of cutting on vegetative and reproductive plants with cutting frequency being a major treatment. Herbage quality and reserves for regrowth were also measured.

Chapter 6 presents the results of a two year field trial at Wageningen. Effects of cutting frequency on tillering, herbage quality and yields were measured.

Chapter 7 investigated the effects of various proportions of the head smut fungus *Ustilago bullata* Berk. in simulated prairie grass swards during a 15 month field trial in New Zealand. Plant survival, tillering and yields were assessed.

Chapter 8 presents an analysis of the relative importance of plant survival, tillering and natural reseeding in the maintenance of high producing simulated prairie grass swards in New Zealand.

Chapter 9 presents an overview and general discussion of the results of the studies presented in this thesis.

CHAPTER 2

Primary Growth and Quality Characteristics of *Bromus willdenowii* and *Lolium multiflorum*

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ABSTRACT

Prairie grass (*Bromus willdenowii* Kunth) and a tetraploid Westerwolds ryegrass (*Lolium multiflorum* Lam.) were established in a field trial in April 1987 and grown for a three month period of undisturbed growth. Leaf, tiller and plant populations were assessed on ten occasions while yields of herbage and roots, chemical composition, leaf area and light interception were determined on six occasions. Herbage was divided into leaf lamina, inflorescence, vegetative and reproductive pseudostem. Nitrogen, water soluble carbohydrates, ash, cell wall and *in vitro* digestibilities were determined.

Both species had similar light interception and leaf area index. Prairie grass had lower plant, tiller and leaf populations but larger tillers and more live leaves per tiller. Roots were distributed more evenly and to greater soil depths in prairie grass. Leaf lamina made major contributions to dry matter yields and yields of the various chemical components, but as reproductive development occurred, reproductive pseudostem became a major component of the total sward. Harvesting herbage to gain optimum yields, herbage quality and regrowth is discussed. It is concluded that prairie grass is a high yielding, high quality forage grass, comparable to Westerwolds ryegrass.

INTRODUCTION

Prairie grass also called rescue grass or Schraders brome grass (*Bromus willdenowii* Kunth; synonyms *B. catharticus* Vahl, *B. schraderi* Kunth, *B. unioloides* H.B.K.), is widely distributed through the world (Hafliger and Scholz, 1981). It has an upright growth habit, long broad leaves and few tillers many of which are reproductive over a prolonged period of the year (Langer, 1973). Over the last 25 years there has been increasing interest in prairie grass, a pasture species that is a true perennial and valued for its out of season growth (Loiseau, 1982; Hume and Fraser, 1985) and quality (Wilson and Grace, 1978; Anon., 1982).

There have been several detailed studies of seedling and primary growth of prairie grass (eg. Hill and Pearson, 1985; Hill, Pearson and Kirby, 1985; Sangakkara, Roberts and Watkin, 1985), but little is known of the partitioning of biomass and forage quality of each plant component. This could be important when the large numbers of reproductive tillers are considered. A field trial was therefore established to investigate these factors over a three month period of undisturbed growth, with Westerwolds ryegrass (*Lolium multiflorum* Lam.) as a comparison species. Westerwolds ryegrass also has an upright growth habit and produces a large number of reproductive tillers.

METHODS AND MATERIALS

Site and treatments

The trial site was at Wageningen Hoog, three km from Wageningen city, and for the previous six years had been under rotation with various crops and with high fertilizer inputs. The soil was a light free draining pleistocene sand of moderate fertility; pH-KCl 5.4, organic matter 2.6%, 25 mg P (ammonium lactate acetic acid extracted), 9 mg K (HCl extracted) and 4 mg Mg (NaCl extracted) per 100 g dry soil. A fine seedbed was prepared in late March 1987 and plots (92 m^2) were hand sown with either 'Grasslands Matua' prairie grass (*Bromus willdenowii* Kunth) or 'Caramba' tetraploid Westerwolds ryegrass (*Lolium multiflorum* Lam.) in a randomised block design replicated four times. Matua plots were sown with 505 viable seeds m^{-2} (60 kg viable seed ha^{-1}) on 13

April 1987, and Caramba plots with 925 viable seeds m^{-2} (40 kg viable seed ha^{-1}) on 21 April 1987. Spray irrigation was used to apply 20 mm of water on 28 April.

Growth of plots was then measured over a three month period of undisturbed growth until 13 July 1988. Half the area of each plot was then measured for another 21 months with treatments of frequent and infrequent cutting and these results are reported in Chapter 6 of this thesis. Root measurements were also taken in June 1988.

Measurements

The first field measurements were taken on 29 April 1987, eight days after sowing the Caramba plots. Ten randomly placed 625 cm^2 quadrats per plot were used to assess numbers of seedlings, tillers and leaves. These measurements were taken on a further three occasions, each at five day intervals after the first measurement (ie. 4, 9, 14 May).

On 24 May, the first of a series of six harvests was taken. These harvests were at successive ten day intervals, with a number of measurements being taken at each harvest. Light interception of the sward was measured in ten positions per plot using photocells situated above and below (soil surface) the leaf canopy. Root mass was estimated by randomly taking five 40 cm^2 soil cores per plot to 30 cm depth. At harvest 5, further samples were taken to assess root mass at 30-40 cm depth. One year later in June 1988, root mass was determined to a depth of 40 cm. The soil cores were separated into 10 cm depth increments and stored at -20°C until washing in winter. At washing, all roots were collected, dried at 100°C and then weighed. Root samples were then bulked to give 2 replicates, ground to 1 mm and analysed for organic matter.

To assess herbage mass, leaf and tiller numbers, plants from two 0.5 m^2 quadrats were removed from each plot by cutting the plants below ground level at the six harvests. The samples were then counted for total numbers of plants and subsamples taken for counting leaves, vegetative tillers, jointed tillers and tillers with emerged inflorescences. These components of the plant were also physically separated to give leaf lamina, vegetative pseudostem, reproductive pseudostem (culm and sheath of

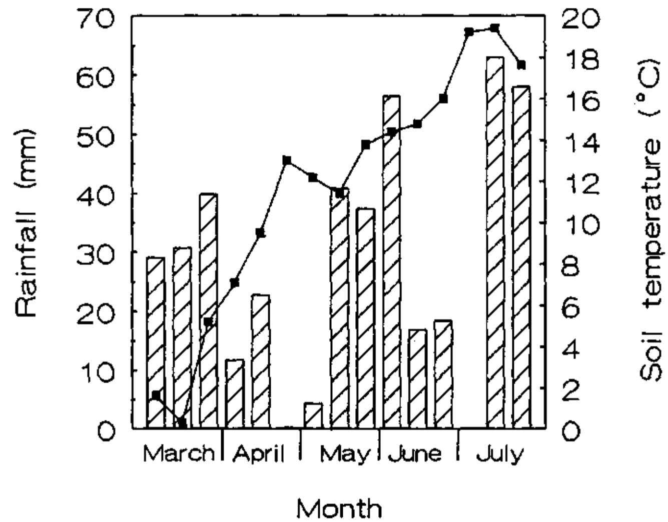


FIG. 1. Total rainfall (bars) and average soil temperatures at 5 cm depth (line) from March to July 1987 for each third of a month. Matua sown on 13 April and Caramba 21 April.

reproductive tiller) and inflorescence. Surface area of each plant component was measured with an electronic planimeter to give the total leaf area index of the sward; area of one side of leaf lamina, pseudostem and inflorescence per unit area of ground. The plant material was then dried at 70°C and weighed.

Herbage quality

Dried samples of each plant component were ground in a hammer mill (1 mm sieve) and the four replicates bulked to give two replicates for determination of herbage quality by chemical analysis. True *in vitro* digestibility of the organic matter (Van Soest, Wine and Moore, 1966) was determined and then converted to apparent digestibility of organic matter (D_{om}) by reference to a series of standard grass samples of known *in vivo* digestibility for sheep fed at maintenance. Cell wall contents (CWC), or neutral detergent fibre, were determined by Van Soest's (1977) method. Digestibility of the cell wall (D_{cwc}) was calculated from the true digestibility, cell wall content and ash content. Water soluble carbohydrates (WSC) were colourmetrically determined with an automatic analyser using ferricyanide. Nitrogen (N) was determined colourmetrically after the dry samples had been digested in a solution of salicylic and sulphuric acid with hydrogen peroxide. Ash contents of the dry material were also determined. Roots were only analysed for organic matter.

Fertilizers and herbicides

Trace elements and 90 kg N, 72 kg P_2O_5 and 144 kg K_2O ha^{-1} were applied prior to sowing. A further 100 kg N ha^{-1} as nitrolime (27% N) was applied on 13 June 1987. Broad-leaved weeds were controlled in mid-May 1987 by spraying with 4 l ha^{-1} 'Basagran P' (375 g mecoprop and 250 g bentazon l^{-1}).

Climate

Temperature and rainfall records for the trial period were obtained from the Wageningen, Haarweg meteorological station, four km from the trial site.

RESULTS

Temperature and rainfall

Soil temperature at Haarweg (5 cm depth) was 7.9°C at the time of sowing Matua plots (13 April) and 10.7°C when Caramba plots were sown 8 days later (from daily records). Soil temperature in April (9.9°C) was almost 2°C above the 30-year average [Fig. 1]. Temperatures were 2 and 1°C below the 30-year average for May and June respectively, while temperatures in July were similar to the 30-year average. Rainfall was high during March (100 mm) but immediately prior to sowing (early April) rainfall was low [Fig. 1]. For the three weeks after Matua plots were sown, rainfall was only 9 mm. Rainfall over the remainder of May was higher, and on average, rainfall was high in June and July. For an 18 day period during late June and early July no rainfall occurred. Rainfall in April, May, June and July was 68, 147, 138 and 155% of the 30-year averages for these months, respectively.

Populations

(a) Plants. Matua had the highest % emergence and plant populations [Fig. 2(a)] early in the trial. Emergence improved in Caramba plots with both species having approximately 55% emergence 32 days after sowing Matua plots. Emergence increased up until 50 days after sowing to be 70-80%. With the higher sowing rate, Caramba plots had up to 750 plants m^{-2} while there was a maximum of 375 plants m^{-2} in Matua plots. Plant populations decreased in the latter part of the trial, mostly in Caramba plots.

(b) Tillers and leaves. Tiller populations were highest in Caramba plots, reaching 4200 tillers m^{-2} 72 days after sowing, while there were only 1800 tillers m^{-2} in Matua plots [Fig. 2(b)]. Greater tiller populations in Caramba plots were on most occasions due to greater plant populations and not greater tiller numbers per plant [Fig. 2(c)]. A large rise in Caramba tiller populations 72 days after sowing [Fig. 2(b),(c)] resulted from the appearance of new vegetative tillers but these had died within 10 days. Caramba plants were faster to produce reproductive tillers (first reproductive tillers observed 61 days after sowing, Fig. 2(b)) but at later dates a greater proportion of Matua plants and tillers were reproductive. Matua had 92% and 50%, Caramba 78% and 44% reproductive tillers and reproductive plants respectively 91 days after sowing.

Matua and Caramba leaf populations were similar for the first 41 days, after which Caramba had greater leaf populations [Fig. 2(d)]. This was despite greater numbers of leaves per plant and per tiller for Matua. On average, Matua had 3.6 live leaves per tiller and Caramba 2.5 ($P<0.001$).

Biomass yields

(a) Herbage. Differences in total green herbage yields occurred from harvest 3 onwards ($P<0.01$) [Fig. 3(a)]. Caramba plots yielded 22% more than Matua plots over harvests 3, 4 and 5, but at the last harvest, Matua (9200 kg DM ha^{-1}) yielded 10% more than Caramba (8300 kg DM ha^{-1}) ($P<0.01$). Differences in yield of reproductive pseudostem between species was the primary cause of greater total yields in Caramba plots, while greater

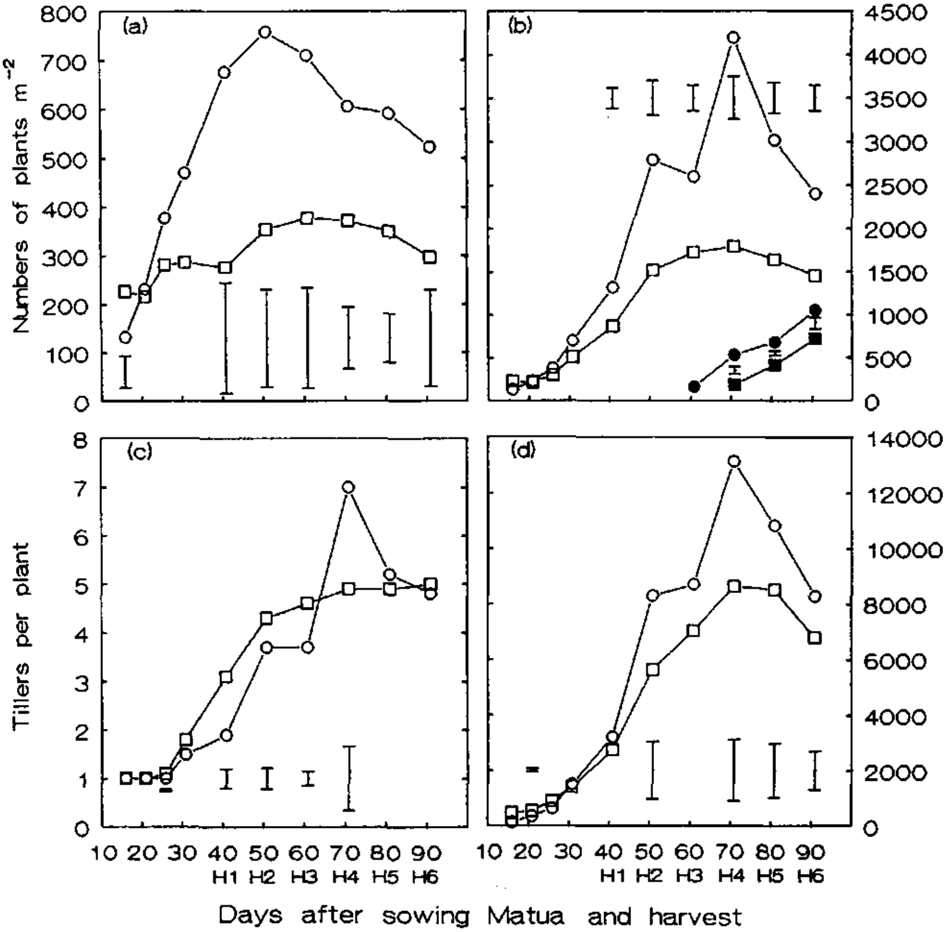


FIG. 2. Mean numbers of Matua (—□—) and Caramba (—○—) (a) plants m^{-2}, (b) total tillers and reproductive tillers (closed symbols) m^{-2}, (c) tillers per plant, (d) leaves m^{-2}, after sowing Matua plots. H1...6 indicate harvests dates 1 to 6. Vertical bars indicate LSD values ($P<0.05$) for dates where significant species differences occurred.

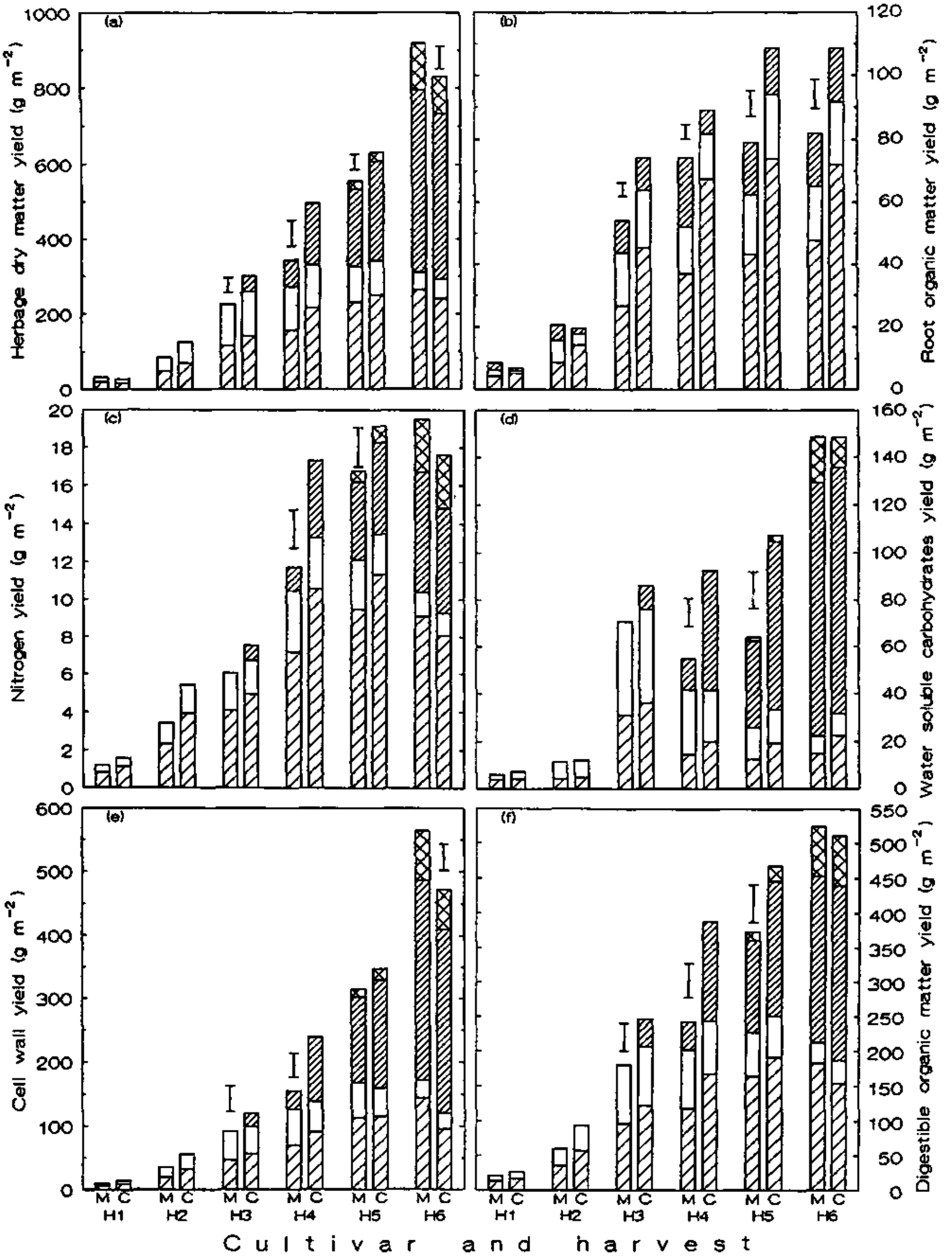


FIG. 3. Yields (g m^{-2}) of (a) herbage dry matter (b) root organic matter at soil depths of 0-10 cm ( ), 10-20 cm ( ) and 20-30 cm ( ), (c) nitrogen, (d) water soluble carbohydrates, (e) cell walls and (f) digestible organic matter, at six harvests (H1...6) for Matua (M) and Caramba (C). For (a), (c), (d), (e) and (f), leaf lamina is represented by ( ), vegetative pseudostem ( ), reproductive pseudostem ( ) and inflorescence ( ). Vertical bars indicate LSD values ($P<0.05$) for dates where significant species differences occurred for total yield.

reproductive pseudostem and inflorescence yields at the final harvest were responsible for higher Matua yields.

Leaf yield (live leaves) increased with time and reached a plateau after harvest 4 of approximately 245 g m^{-2}. Contribution of leaf to the total yield decreased with time dropping from 62 to 28%. Leaf yield was greater in Caramba plots at harvest 4 ($P<0.01$) but otherwise leaf yields were similar for the two species. Yield of vegetative pseudostem increased until harvest 3 to be 43% of total yield, but then decreased from harvest 4 as tillers showed signs of reproductive growth to be only 5% of total yield at the final harvest. Matua and Caramba did not differ in yields of vegetative pseudostem at any harvest ($P>0.05$). As reproductive tillers appeared, their rapid growth ensured a continuation of increasing total yield, contributing 53% to the total yield by the final harvest. Inflorescence yield was relatively small and only significant at the final harvest (13% of total yield). Dead matter was low reaching a maximum of 7% at the final harvest.

Growth rates measured during the later harvests were very high. For Matua, maximum growth rates of 27.5 and 36.0 g DM m^{-2} day^{-1} (275 and 360 kg DM ha^{-1} day^{-1}) were recorded for reproductive pseudostem and total yield respectively, while Caramba had maximum growth rates of 20 and 17 g DM m^{-2} day^{-1} respectively.

(b) Roots. Total root organic matter increased significantly with time, and except for the first two harvests, was greater for Caramba than Matua ($P<0.05$) [Fig. 3(b)]. Higher total root mass in Caramba was due to a greater root mass in the 0-10 cm root depth zone (mean, 46 g OM m^{-2}) than in Matua (28 g OM m^{-2}) ($P<0.01$). There were no significant differences between species for root mass in the other depth zones; means of 13 and 11 g OM m^{-2} in 10-20 cm and 20-30 cm zones respectively. Caramba had a higher percentage of total root mass in the 0-10 cm zone (68%) than Matua (52%) at all dates ($P<0.01$). In the other depth zones, Matua roots were evenly distributed in terms of mass and percentage (mean, 24%) ($P>0.05$), while 19 and 13% of Caramba roots were in the 10-20 cm and 20-30 cm zones respectively ($P<0.05$).

Shoot root ratio in Caramba was 3.2 at harvest 1, increasing to be approximately 6 at the remaining harvests. Matua had significantly lower shoot root ratios (4) over the first 4 harvests ($P<0.05$) but at harvests 5 and 6 the ratios were 7.8 and 11.7 respectively. Total biomass (organic matter of shoot and root) was 39% higher in Caramba plots at harvests 3, 4 and 5 than in Matua plots ($P<0.05$).

Sampling to 30-40 cm soil depth at harvest 5 showed small amounts of roots at this depth (6 and 3 g OM m^{-2} for Matua and Caramba respectively, $P>0.05$), representing 7 and 3% of the total root mass for Matua and Caramba respectively ($P>0.05$). Sampling one year later in June 1988, again showed significantly higher root mass (143 g OM m^{-2}) and percentages (79%) of roots in the 0-10 cm zone for Caramba compared to Matua plots (92 and 58%) ($P<0.01$). Matua had significantly greater root mass and percentage of roots at 20-30 cm (13%) and 30-40 cm (9%) than Caramba (4 and 2% respectively). Total root mass (169 g OM m^{-2}) did not differ significantly between species ($P>0.05$).

Herbage quality

Herbage quality is considered in terms of percentage of chemical components in dry matter or organic matter (eg. nitrogen content, N%) and yield of chemical components (g m^{-2}). Yield of chemical components were calculated from percentage composition and herbage yields.

(a) Nitrogen. Nitrogen content (N%) varied with each plant component and decreased with time in all components except the inflorescence [Fig. 4(a)(i)]. Leaf N% dropped from 5 to 3.5%, with Caramba having significantly higher N% at harvests 1, 4 and 6 ($P<0.01$). N content in reproductive pseudostem (mean, 1.7%), vegetative pseudostem (2.6%) and inflorescence (2.7%) was significantly greater in Matua at most harvests ($P<0.01$). The resulting N% of the total sward dropped from 4.5 to 2.1%, with significantly higher N% in Matua at harvests 2, 4 and 5, although differences were small [Fig. 4(a)(ii)]. Harvest 3 had a large drop in N% in all plant components, but with the application of 100 kg N ha^{-1}, N% had increased again by harvest 4.

Total nitrogen yield (g m^{-2}) increased with time but reached a plateau at the final 2 harvests [Fig. 3(c)]. Yields of nitrogen in Caramba plots at harvests 4 and 5 were on average 26% higher than those in Matua plots ($P<0.05$). This was due to significantly greater nitrogen yields from reproductive pseudostem and leaf in Caramba ($P<0.001$) despite greater amounts of nitrogen from vegetative pseudostem of Matua ($P<0.01$). There were few other significant differences in nitrogen yield for the other plant components. Initially, leaf nitrogen contributed 70% to the total nitrogen yield with vegetative pseudostem contributing 30%. At the final harvest almost 50% of the nitrogen yield came from reproductive pseudostem (33%) and inflorescence (15%), while leaf contributed 46% and vegetative pseudostem 6%.

(b) Water soluble carbohydrates. Contents of water soluble carbohydrates (WSC%) varied greatly with harvest, plant component and species [Fig. 4(b)]. For all plant components and the total sward, WSC% was generally significantly higher in Matua at the first 3 harvests while Caramba had higher contents at the last 3 harvests. WSC% was high at harvest 3, a harvest when N% was low. On average, leaf had a WSC content of 12%, vegetative pseudostem 20.5%, reproductive pseudostem 22%, inflorescence 12% and the total sward 17%.

Total yield of WSC was 67% higher in Caramba plots at harvests 4 and 5, primarily due to greater WSC yield from reproductive pseudostem [Fig. 3(d)]. Caramba leaf had 34% higher WSC yields than Matua leaf ($P<0.05$) at all but the first 2 harvests. Contribution of leaf WSC to total WSC yield dropped from 55% at harvest 1 to 12% at harvest 6. Reproductive pseudostem contributed significantly to WSC yield (70% at harvest 6) due to a high dry matter yield and high WSC%. Contribution from inflorescence was 11% at the final harvest while vegetative pseudostem contributed up to 60% at the initial harvests declining to 6% at the final harvest.

(c) Cell wall. Cell wall content (CWC) of inflorescence, reproductive and vegetative pseudostem was significantly higher in Matua at all harvests ($P<0.01$) [Fig. 4(c)(i)]. In the leaf this was true from harvest 3 onwards while at harvest 1 Matua had significantly lower CWC. CWC increased in all plant components with time, except for the inflorescence. Matua leaf and vegetative pseudostem had larger increases in CWC than Caramba.

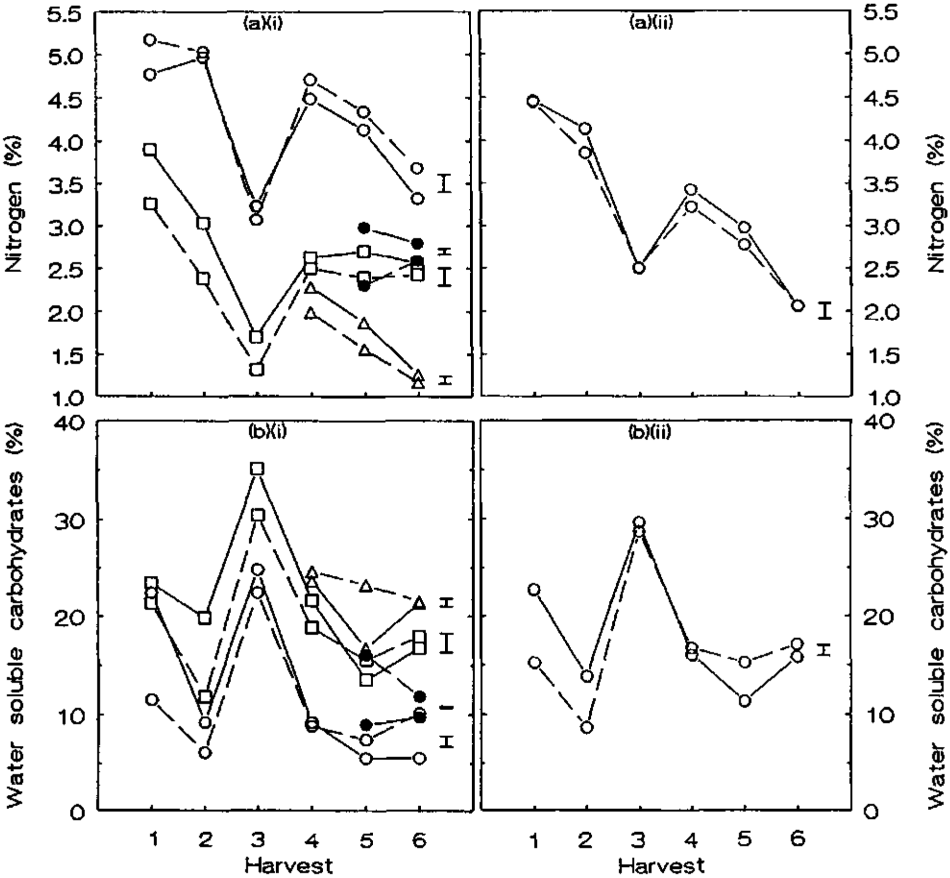
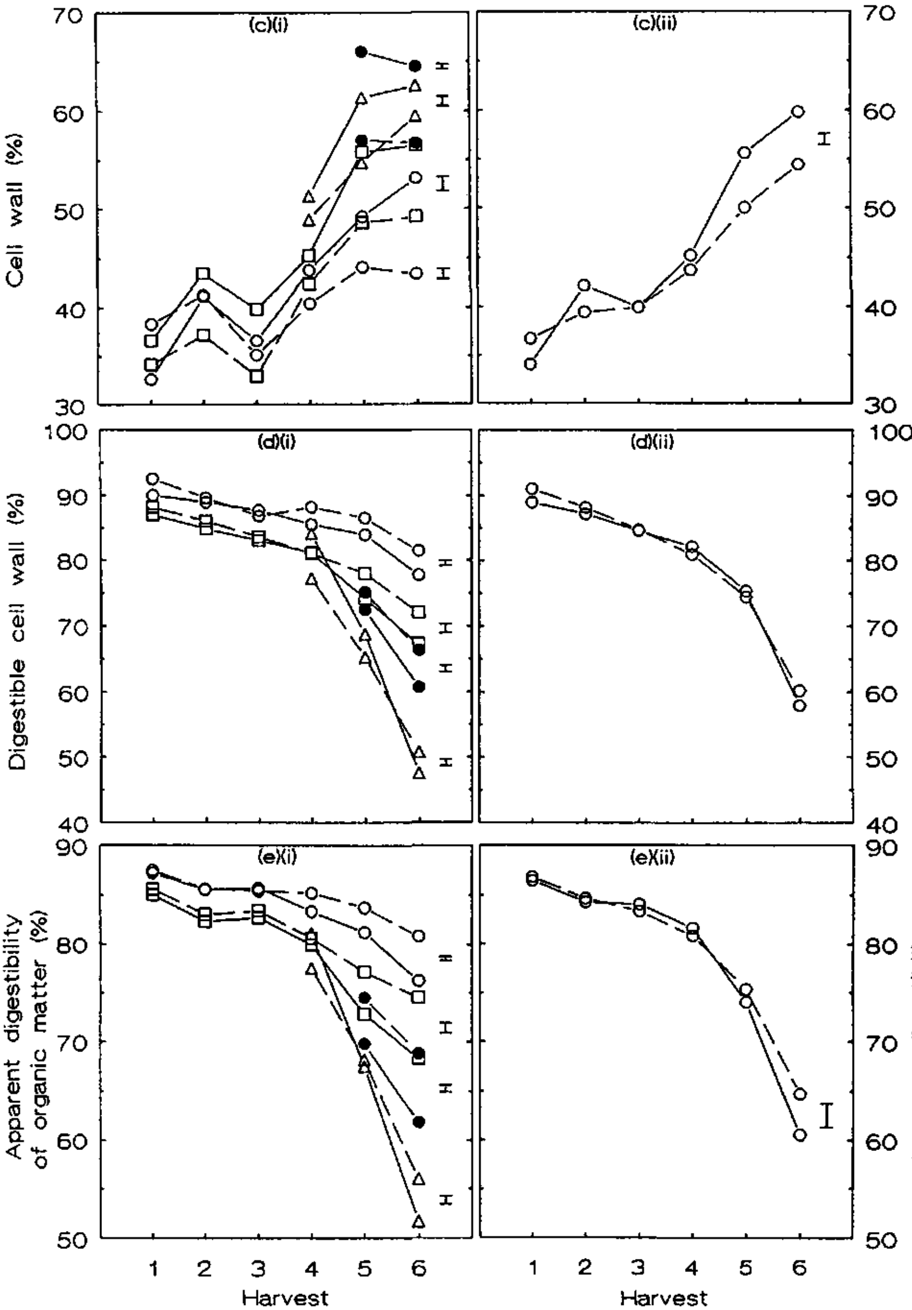


FIG. 4. Percentage composition of (a) nitrogen, (b) water soluble carbohydrates, (c) cell walls, (d) digestible cell walls, and (e) apparent digestibility of organic matter. Part (i), leaf lamina (○), vegetative pseudostem (□), reproductive pseudostem (△) and inflorescence (●); and part (ii), total sward. For six harvests (H1...6) of Matua (——) and Caramba (---). Vertical bars near each plant component indicate LSD values ($P<0.05$) for leaf lamina, vegetative pseudostem, reproductive pseudostem, inflorescence and total sward.

FIG. 4. (Continued)



For the total sward, CWC was significantly higher in Matua at harvests 2, 4, 5 and 6, while at harvest 1 Caramba had higher CWC [Fig. 4(c)(ii)].

Total yield of cell walls was significantly higher in Caramba at harvest 4 and lower at harvest 6 [Fig. 3(e)]. This was primarily due to high amounts of cell wall from reproductive pseudostem and to some extent leaf. At the final harvest, a large proportion of the total cell wall yield was from reproductive pseudostem (58%), with 23% from leaf, 14% from inflorescence and 5% from vegetative pseudostem.

Digestibility of cell wall (D_{cwc}%) decreased with time, particularly after harvest 4 and especially for Matua [Fig. 4(d)]. D_{cwc}% of leaf only decreased from 91 to 80%, while there was a steady decline in D_{cwc}% of vegetative pseudostem and sharp declines for reproductive pseudostem and inflorescence. D_{cwc}% was significantly lower in Matua at the later harvests for leaf, vegetative pseudostem and inflorescence [Fig. 4(d)(i)]. Matua had higher D_{cwc}% of reproductive pseudostem at harvests 4 and 5 while Caramba had higher D_{cwc}% at harvest 6. Resulting D_{cwc}% of the total sward showed no significant species differences ($P>0.05$) [Fig. 4(d)(ii)].

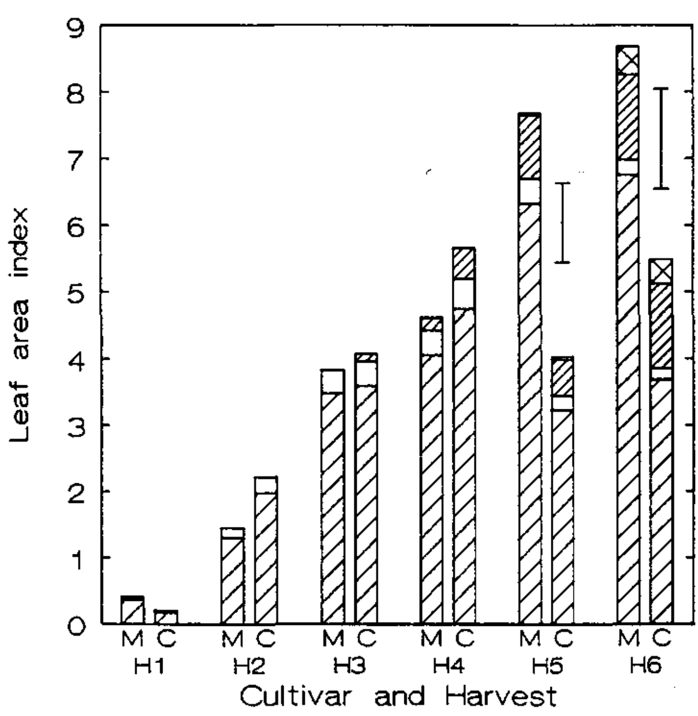
Total yield of digestible cell wall was higher in Caramba at harvest 4 and lower at harvest 6, due to differences in yields from reproductive pseudostem and leaf. These trends are similar to those shown for cell wall yield in Fig. 3(e). At harvest 1, total digestible cell wall was comprised of 64% from leaf and 36% from vegetative pseudostem. This declined to 31 and 6% respectively at harvest 6, with reproductive pseudostem contributing 49% and inflorescence 14%.

(d) Digestibility. Apparent digestibility of organic matter (D_{om}%) followed a pattern similar to that described for D_{cwc}%. Leaf D_{om}% was relatively constant over the first 3 harvests (86%) with no species differences ($P>0.05$), but then declined over the final harvests especially in Matua ($P<0.001$) [Fig. 4(e)(i)]. A similar pattern of species differences and decline occurred in vegetative pseudostem. Digestibility of reproductive pseudostem decreased rapidly, with Matua having significantly greater D_{om}% than Caramba at harvest 3 while the reverse was true at the final harvest ($P<0.001$). D_{om}% of inflorescence also declined with time with

Matua having significantly lower D_{om} (66%) than Caramba (72%) (P<0.001). D_{om}% of the total plant declined slowly from harvest 1 (86%) to harvest 4 (81%) but then declined sharply at harvests 5 and 6 [Fig. 4(e)(ii)]. Significant differences only occurred at harvest 6 when Matua had significantly lower D_{om}% (P<0.001).

Total yield of apparently digestible organic matter was significantly greater at harvests 3, 4 and 5 for Caramba [Fig. 3(f)]. This was mainly due to greater yields from reproductive pseudostem and to a lesser extent leaf. Contribution of leaf to the total yield declined from 65 to 32% and vegetative pseudostem from 35 to 6%. At the final harvest, inflorescence contributed 14% and reproductive pseudostem 48%.

FIG. 5. Leaf area index (area per unit area of ground) of leaf lamina (▨), vegetative pseudostem (□), reproductive pseudostem (▨) and inflorescence (⊠) at six harvests (H1...6) for Matua (M) and Caramba (C). Vertical bars indicate LSD values (P<0.05) for dates where significant species differences occurred for total leaf area index.



Light interception

Light interception of swards rapidly increased in both species being 17, 59, 73, 93, 99 and 100% at harvests 1 to 6 respectively. Matua had significantly greater light interception at harvest 1 ($P<0.01$) while Caramba had greater interception at harvest 2 ($P<0.001$). At subsequent harvests there were no species differences.

Total leaf area index of the sward (area per unit area of ground) as measured by electronic planimeter for each plant component, differed only at the final two harvests due to a large drop in area of leaf lamina in Caramba plots [Fig. 5]. This corresponded with severe wilting of leaf lamina in Caramba plots at these harvests. Leaf lamina made the greatest contribution (75 to 90%) to total leaf area index. Contribution from vegetative pseudostem decreased from 18 to 3%, while at the final harvest inflorescence and reproductive pseudostem contributed 6 and 15% respectively. Critical leaf area index (95% light interception) occurred at a leaf lamina area index of 4.5 and a total leaf area index of approximately 5.

DISCUSSION

The large contribution made by reproductive development in this study is similar to that described by Wilman, Ojuederie and Asare (1976) for Italian ryegrass (*Lolium multiflorum* L.). This contribution is important because reproductive tillers are produced over a major part of the growing season in both the species used in the present study. These species have no vernalization requirements, with long photoperiods being the only requirement for reproductive development (Karim, 1961; Evans, 1964). Thus the various attributes identified over the period of this study are also applicable to other times of the year. This is in contrast to some other agriculturally important temperate grass species such as perennial ryegrass (*Lolium perenne* L.), tall fescue (*Festuca arundinacea* Schreb.) and cocksfoot (*Dactylis glomerata* L.) that have reproductive development confined to a relatively short period of the year (Evans, 1964). Reproductive development is also important because it is often considered undesirable due to its detrimental effects on herbage quality and herbage intake of grazing animals. Reduction of reproductive growth in prairie grass has therefore become a selection criterion for some plant breeders (Pfitzenmeyer, 1982).

The change in tillers from the vegetative to the reproductive state affected a number of characteristics. The most obvious effect was that on yields of herbage and therefore yields of the different chemical components of the total sward. Continuation of increasing total yield at the later harvests was due in most part to reproductive development of tillers. Maximum growth rates of 360 kg DM ha^{-1} day^{-1} for the total sward and 275 kg DM ha^{-1} day^{-1} for reproductive pseudostem were very high. It is well documented that a large proportion of reproductive tillers results in high growth rates (Parsons, 1988). Large amounts of assimilates were therefore being used in the production of reproductive pseudostem at later harvests. Reproductive tillers had considerable biomass in the pseudostem (culm and sheaths) as it elongated, lesser yet still significant amounts of biomass in inflorescences, high WSC contents in the pseudostem, and leaves that are longer, appear faster and are retained on the tiller longer (Davies, 1977).

The results of this study indicate that for both species, reproductive development should not be allowed to progress too far before the herbage is defoliated. Reproductive pseudostem at an early stage of elongation had high digestibility, which is similar to that found in other species (Minson, Raymond and Harris, 1960; Wilman *et al.*, 1976). Barloy (1982) and Parneix (1982) have also found that high nutritive value and high WSC levels in prairie grass are maintained until head emergence. This rapidly changed so that digestibility was very low at the final harvest causing large reductions in digestibility of the total sward, particularly in Matua. The decision to defoliate must therefore be based on a compromise between, high dry matter yields, high yields of chemical components, availability (digestibility) and content of nutrients, and current tiller and leaf populations and recovery of these populations after defoliation. It is important that this decision is made at the correct time, as even during a short delay large changes in digestibility and nutrient contents occur rapidly when reproductive tillers are present.

For Italian and perennial ryegrass, maximum yield of digestible dry matter is reported to occur before the maximum yield of dry matter and before digestibilities have fallen to 70% (Anon., 1966), with digestibilities being maintained until the beginning of ear emergence (Minson *et al.*, 1960). The prairie grass and Westerwolds ryegrass swards in the present study appear to have similar attributes. When all these factors are taken into account, it is suggested that the optimum time for defoliation may approximate to harvests 4 or 5 in this study. At harvests 4 and 5, 11.5 and 24% of the total tillers were reproductive and 4 and 12% had emerged inflorescences, respectively. The optimum time for defoliation may also differ between the species when their different tiller dynamics are considered.

Reproductive development affected other components of the sward such as populations of tillers and leaves, and leaf area index. Reproductive tillers inhibit development of axillary tiller buds (Laidlaw and Berrie, 1974; Ong, Marshall and Sagar, 1978) thus contributing to the plateau and drop in tiller numbers at later harvests. Removal of reproductive stems is not always required to remove the suppression (Langer, 1963) as occurred in Caramba plots approximately 60-70 days after sowing when there was a flush of new vegetative tillers. A similar tillering pattern did not appear to occur for Matua although commencement of reproductive development was later in Matua. A more detailed investigation of tiller dynamics would be required to study this aspect further. Accelerated leaf appearance on reproductive tillers (Davies, 1977; Chapter 3 this thesis) also ensures a high number of leaves present to intercept light. Although area of leaf lamina was the major contributor to total leaf area index, reproductive pseudostem and inflorescence contributed up to 21% of the total leaf area at later harvests and therefore warrant inclusion in measurements of sward area (Robson and Sheehy, 1981).

Along with reproductive pseudostem, leaf lamina was the other major component of the sward particularly at early harvests and still an important component at later harvests. Leaf lamina in both species generally maintained high nutrient contents and high digestibility. Although vegetative pseudostem was a smaller component of the total sward, generally having lower herbage quality than leaf lamina, its high WSC content made significant contributions to WSC yield along with high WSC contents in reproductive pseudostem. Inflorescence generally had slightly lower levels than vegetative pseudostem for all chemical components and made a relatively small contribution to yields.

The importance placed on species differences in quality and yields at each harvest must also consider the age of the plant components and the stage of plant development. Despite an earlier sowing date, Matua was later to show signs of reproductive growth. Reproductive tissue was therefore older on average in Caramba than Matua and reproductive growth in Matua was occurring at higher temperatures. The earlier sowing date for Matua (eight days earlier than Caramba) is considered to have little influence on the results of this study. This is because temperatures and soil moisture were relatively low at the time of sowing Matua, conditions which are unfavorable for rapid establishment of prairie grass (Culleton and McCarthy, 1983; Burgess *et al.*, 1986), and would therefore minimise the effect of differences in sowing date.

Although the herbage components of the total sward were similar for the species, Caramba and Matua had different ways of forming this dry matter. Caramba swards had greater populations of plants, tillers and leaves, but Matua had bigger tillers with more leaves per tiller, due to a high leaf appearance rate, and greater area per leaf (Chapter 3 this thesis). Similar findings for prairie grass and *Lolium multiflorum* have also been gained by Hill *et al.* (1985). Westerwolds ryegrass normally has greater tiller numbers per plant than prairie grass (Hill *et al.*, 1985; Hume, unpublished data) but in the present study this varied with time. The higher number of viable seeds sown in Caramba plots may have influenced this as higher sowing rates result in lower numbers of tillers per plant (Holliday, 1953).

Westerwolds ryegrass is valued for its high forage quality (Osborne, 1980; Langer and Hill, 1982). Matua compared favorably with Caramba Westerwolds ryegrass in terms of yield of chemical components and percentage composition. These observations of high forage quality of prairie grass are similar to those of Wilson and Grace (1978) and Anon. (1982), despite considerable numbers of reproductive tillers. Reproductive herbage in prairie grass is also readily eaten by grazing animals with minimal rejection of culm or inflorescence (Pfitzenmeyer, 1982; Burgess *et al.*, 1986). Some major and trace elements are low in prairie grass (Rumball, Bulter and Jackman, 1972) but these low levels only rarely have the potential to cause problems in livestock (Burgess *et al.*, 1986). The present study considered the total herbage mass but in a grazing or cutting system the total plant is not harvested ie. a stubble remains. Caution should therefore be exercised if these results are to be used for estimating animal production. There may also be other factors to consider such as the positive effect of prairie grass sward structure on herbage intake of grazing animals (L'Huillier, Poppi and Fraser, 1986).

Root mass and distribution appeared to differ for the two species. Caramba allocated a smaller proportion of biomass to roots (higher shoot root ratio) and had a higher percentage of root mass in the top 10 cm of soil, while Matua appeared to have a better distribution of root mass to greater soil depths. Typically 70-80% of roots are in the 0-10 cm soil zone (Troughton, 1957), but species that root to greater depths and have a more even distribution of roots exhibit greater tolerance of dry soil conditions (Garwood and Sinclair, 1979). Wilting of leaves in Caramba and not in Matua plots, and death of young vegetative tillers on Caramba plants under the dry conditions in late June and early July (harvests 5 and 6), could have been the result of Matua plants having better access to soil water at greater depths. Prairie grass is known to have good tolerance to dry soil conditions (Eteve, 1982; Burgess *et al.*, 1986) and good root growth (Sangakkara *et al.*, 1985). Deeper rooting could also explain higher nitrogen yields for Matua under low soil nitrogen conditions in winter (Hume and Lucas, 1987), higher nitrogen yields for Matua in these plots in 1988 (Chapter 6 this thesis), and tolerance of grass grub (*Costelytra zealandica* White), a pest that damages roots (East, Kain and Douglas, 1980). As reproductive development occurs, root growth is reduced (Troughton, 1978) due to changes in assimilate partitioning between roots and shoot (Parsons and Robson, 1981), thus increasing shoot root ratios. This appeared to be the case for Matua (harvests 5 and 6) but not for Caramba.

Further measurements of roots would be required to confirm these observations, because although measurements had relatively low coefficients of variation (20%) they were taken over a relatively short time period and only for one soil type.

Over the period of this study, Caramba Westerwolds ryegrass and Matua prairie grass appear to have a number of similar growth characteristics and chemical compositions. Although variations will occur with different cultivars, this study has shown that prairie grass is a high yielding, high quality forage grass and warrants consideration for use in appropriate pasture situations. Although reproductive development is normally considered undesirable, this view warrants considerable thought with regards to these species due to their continual production of reproductive tillers during the growing season.

CHAPTER 3

Leaf and Tiller Production in Prairie Grass (*Bromus willdenowii* Kunth)

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ABSTRACT

A detailed morphological study of three prairie grass cultivars (*Bromus willdenowii* Kunth) was conducted under vegetative and reproductive growth conditions (short and long photoperiods) and at different temperatures. Perennial ryegrass (*Lolium perenne* L.) and Westerwolds ryegrass (*Lolium multiflorum* Lam.) were used as comparison species, although a valid comparison was limited only to vegetative growth.

Prairie grass had higher leaf appearance rates (leaves tiller^{-1} day^{-1}) and lower site filling (tillers tiller^{-1} leaf appearance interval^{-1}) than the ryegrass species. Tillering rates (tillers tiller^{-1} day^{-1}) were also lower, except under vegetative conditions at 4°C. Low tiller number in prairie grass was not due to lack of tiller sites but a result of poor filling of these sites. Lower site filling occurred because of increased delays in appearance of the youngest axillary tiller and lack of axillary tillers emerging from basal tiller buds. In prairie grass, no tillers came from coleoptile buds while only occasionally did prophyll buds develop tillers. Low tiller number in prairie grass was compensated for by greater tiller weight. Prairie grass had more live leaves per tiller, greater area per leaf and a high leaf area per plant.

Considerable cultivar variation was found in prairie grass. The cultivar 'Bellegarde' had high leaf appearance, large leaves and rapid reproductive development, but had low levels of site

filling, tillering rates, final tiller numbers and herbage quality during reproductive growth. 'Primabel' tended to have the opposite levels for these parameters, while 'Grasslands Matua' was intermediate and possibly provided the best balance of all plant parameters.

INTRODUCTION

Prairie grass (*Bromus willdenowii* Kunth; synonyms *B. catharticus* Vahl, *B. schraderi* Kunth, *B. unioloides* H.B.K.) is a highly productive forage grass, valued for its high summer production (Anon, 1982; Fraser, 1985; Anon, 1986), and also in New Zealand for high winter production (Burgess *et al.*, 1986). It is a tall plant with long broad leaves, but few, large tillers. Hill and Pearson (1985) considered that low tillering capacity in prairie grass could be a major limitation to its performance in pastures especially compared with Italian ryegrass (*Lolium multiflorum* Lam.) (Hill, Pearson and Kirby, 1985). Tillering is important during sward establishment and for regeneration of swards after apices have been removed by defoliation (Jewiss, 1972). Low tillering may also reflect poor perenniality (Cooper and Saeed, 1949).
Tiller production is controlled by rate of leaf appearance as this determines the number of tiller buds (sites), and also controlled by how many tiller buds develop (site filling) (Davies, 1974). Prairie grass has a long day requirement for reproductive growth, with no vernalization requirement (Karim, 1961; Evans, 1964), so large numbers of reproductive tillers are continually produced from mid-spring to mid-autumn (Chapter 6 this thesis). Considerable tiller losses therefore occur at cutting or grazing and there is a large suppression of tillering through apical dominance. High numbers of reproductive tillers also have a large impact on herbage production and quality (Chapter 2 this thesis).

Apart from providing tiller sites, a high leaf appearance rate is important if the plant is to intercept as much light as possible as quickly as possible, and it also provides a major part of harvested herbage. Leaf size is therefore also important but in some species this is inversely related to leaf appearance rate (Cooper and Edward, 1960; Ryle, 1964).

These plant factors are interrelated and they ultimately determine yield. For recent cultivars of prairie grass these factors have not been fully quantified. This paper therefore reports several experiments in which leaf production, tiller production and reproductive development were measured in three prairie grass cultivars compared with two ryegrass species (*Lolium* species), during undisturbed growth at different temperatures and photoperiods. Such a characterization of the species may be of value to plant breeders who are attempting to breed for a prairie grass that is better adapted to a wider range of management conditions.

METHODS AND MATERIALS

Five experiments were completed during 1987 and 1988 in temperature and photoperiod controlled glasshouses at Wageningen, The Netherlands. Experiments 1 and 2 were in short photoperiods so plants remained vegetative. Experiment 3 was conducted under a range of short and long photoperiods so that 'Caramba' tetraploid Westerwolds ryegrass (*Lolium multiflorum* Lam.) and prairie grass (*Bromus willdenowii* Kunth) could develop reproductive tillers at the long photoperiods. Experiment 4 was also conducted at a long photoperiod. Experiment 5 investigated development of the first axillary tiller buds of seedlings during a short photoperiod.

In all experiments, water was applied daily while nutrients were applied at regular intervals as modified Hoagland's nutrient solution.

Vegetative conditions

Experiment 1. During early October 1987, seedlings of 'Wendy' perennial ryegrass (*Lolium perenne* L.), 'Caramba' Westerwolds ryegrass and 'Grasslands Matua' prairie grass, were grown in white sand in a 9 h photoperiod, day/night temperatures of 20°C/12°C, with supplementary lighting from 400 W sodium lamps. When seedlings had two fully emerged leaves, they were transferred to plastic trays each containing 38 small pots (0.1 litre each) filled with a three to one mixture of yellow sand and black soil. One seedling was planted per pot and a total of twenty trays for each species. Temperatures were gradually reduced so that by early December temperature was 4°C day and night, with natural photoperiod and no supplementary lighting. Plants were cut to 6 cm height and the trays placed close together in a randomised block design to give 83 plants m^{-2}.

Eighteen plants were then randomly selected from each species and measured every 14 days for leaf appearance and tiller numbers for a period of 13 weeks. Leaf appearance rates (LAR) were obtained by marking the uppermost fully emerged leaf (ligule emerged) on a tagged tiller with an acrylic pen, then two weeks later counting the number of fully emerged leaves above this marked leaf. This procedure was then repeated for the following weeks. Leaf appearance rate was calculated by dividing the number of new fully emerged leaves appearing at each marking, by the time interval (14 days). Total tiller numbers were counted on the plants at each marking. From this, site filling, the proportion of tiller buds forming visible tillers in a single leaf appearance interval was calculated (Davies, 1974). At each marking, position of the youngest axillary tiller (number of leaf axils from the top of the tiller) was recorded for the tagged tillers. At the end of the experiment, plants were assessed for herbage yield above 6 cm height and nitrogen content.

Experiment 2. During early September 1987, seedlings of Wendy, Caramba and three prairie grass cultivars ('Grasslands Matua', 'Primabel', 'Bellegarde') were grown in white sand and then transferred to 5 litre pots (one seedling per pot) containing the sand-soil mixture. This gave forty replicates in a randomised block design. Temperatures were 18/12°C with a 9 h photoperiod during which supplementary lighting was used. When seedlings had two fully emerged leaves (23 September), weekly measurements began on the main tiller for leaf appearance, positions of the youngest and first axillary tillers (numbers of leaf axils from the top and bottom of the tiller respectively), and tiller numbers per plant. After three weeks of measurements, new young tillers with one fully emerged leaf were also monitored. Measurements finished after six weeks, and plants were cut to 6 cm height to assess herbage yields and nitrogen content. Plants from three replicates were also measured with an electronic planimeter to assess total area of leaf lamina. Older leaves marked for leaf appearance were also measured for leaf area and leaf dimensions.

After one weeks regrowth, these plants were then used in experiment 3.

Reproductive conditions

Experiment 3. The plants from experiment 2 were randomly divided into four photoperiod groups and placed in a glasshouse operating at temperatures of 18/12°C, with a 9 h photoperiod consisting of natural (winter) daylight that was supplemented by sodium lamps to ensure a minimum irradiance of 80 W m^{-2} at plant level. By means of covers and extra low intensity lighting, photoperiod was extended in three of the groups. Thus photoperiods in the four groups were 9, 11, 14 and 16 hours, with each group having the same 9 hours of full light intensity. With this design, full statistical analysis of effect of photoperiod was not possible, but within each photoperiod there were ten replicates of each species which could be statistically analysed.

The tillers tagged in experiment 2, and new tillers (one emerged leaf) tagged one week before and three weeks after the photoperiods were applied, were all measured weekly for leaf appearance and position of the youngest axillary tiller. Tiller numbers were also recorded weekly, while reproductive development of tillers was recorded daily as inflorescences emerged. Plants were measured for eight weeks and then cut to 6 cm height to assess herbage yields, nitrogen content and apparent digestibility of organic matter.

Experiment 4. Seedlings of Wendy, Caramba and Matua were grown during early April 1987, and on 17 April, transferred to 5 litre plastic pots containing the sand-soil mixture, to give four seedlings per pot. Seedlings were allowed to establish for 11 days, at which time they had two fully emerged leaves and measurements began. Pots were arranged in a randomised block design with 20 replicates. Throughout the experiment, photoperiod (14 h) and temperature (20/14°C) conditions were kept constant and no supplementary lighting was used.

Weekly measurements of leaf appearance, position of the youngest axillary tiller and tiller number, began on 28 April and continued for 11 weeks. Leaf appearance was measured on the main tiller, and also on younger tillers (one fully emerged leaf) tagged after three and six weeks of measurements. After six weeks of measurements, plants from two replicates were measured for total herbage yields.

Sites of tillering

Experiment 5. Tillering in a short photoperiod (9 h) was examined on seedlings grown in two mediums and germinated in different ways. Seeds of Wendy, Caramba, Matua, Primabel, and Bellegarde were sown in white sand, and when seedlings had two fully emerged leaves, they were transferred to either aerated nutrient solution (Steiner's solution) or to the sand-soil mixture in 5 litre pots [part (i)]. Seeds of Wendy, Caramba and Matua were also sown directly into pots containing the sand-soil mixture, or seeds were germinated on moist filter paper at 25°C for three days and then transferred to pots or nutrient solution [part (ii)]. In each case, positions were recorded for the first axillary tillers to form on the main tiller and to form on the first secondary tiller. Position of the youngest axillary tiller was also recorded.

RESULTS

Results of the five experiments are discussed for each of the measured parameters. In the photoperiod experiment (experiment 3), the two short photoperiods of 9 and 11 hours did not induce reproductive development in any cultivar. These two photoperiods therefore represent growth under vegetative conditions, and as such, can be grouped with experiments 1 and 2 on vegetative growth. Wendy had not been vernalized so it did not produce inflorescences, while Caramba apices showed signs of reproductive development at the 14 and 16 h photoperiods (dissections of apices in experiments 3 and 4), but only in experiment 4 did some inflorescences emerge.

Leaf appearance

Leaf appearance for experiments 1 to 4 is shown in Figure 1. The slopes of the lines represent the leaf appearance rates (LAR), while average LAR (leaves tiller^{-1} day^{-1}) can be calculated from the total number of leaves appeared, divided by the time in days.

(a) Vegetative. Under the vegetative conditions of experiments 1, 2 and 3 (9 and 11 h photoperiods), the prairie grass cultivars consistently had much higher LAR than the ryegrass species [Figs. 1(a),(b),(c)] ($P<0.001$). Wendy and Caramba had similar LAR in experiments 1, 2 and 3 (all photoperiods and all tagged tillers in experiment 3) ($P>0.05$) [Figs. 1(a) to 1(e)]. The only exception was a higher LAR in Wendy for the second tagged tiller in experiment 2 ($P<0.05$). For the prairie grass cultivars, Matua had higher LAR in experiment 2 ($P<0.05$), while Bellegarde had a higher LAR for all tagged tillers in experiment 3 (9 and 11 h). Primabel had significantly lower LAR than the other prairie grass cultivars, except for the second tagged tiller in experiment 2 where LAR was significantly higher.

Within each cultivar, the different tagged tillers had similar LAR ($P>0.05$), except in experiment 2 where LAR on the second tagged tiller was 7% lower for Matua and Bellegarde than on the main tiller ($P<0.05$).

(b) Reproductive. LAR of reproductive prairie grass tillers were higher than LAR in the ryegrass species [Figs. 1(d),(e),(f)] and higher than LAR of vegetative prairie grass tillers (experiment 3) [Figs. 1(c),(d),(e)]. LAR in prairie grass in the long photoperiods (14 and 16 h) of experiment 3, increased after three weeks [Figs. 1(d),(e)]. Increases were most rapid at 16 hours photoperiod, and fastest in Bellegarde and slowest in Primabel. Increases in LAR were greatest and occurred earliest on the main tiller, while increases were less and occurred later the younger the tagged tiller. LAR declined and leaves ceased to appear as the inflorescences emerged. Emergence of inflorescences occurred faster and earlier on the main tillers, earlier at 16 hours photoperiod and earlier in Bellegarde [Table 1] [Figs. 1(d),(e)]. Photoperiod appeared to have no effect on LAR in the ryegrass species.

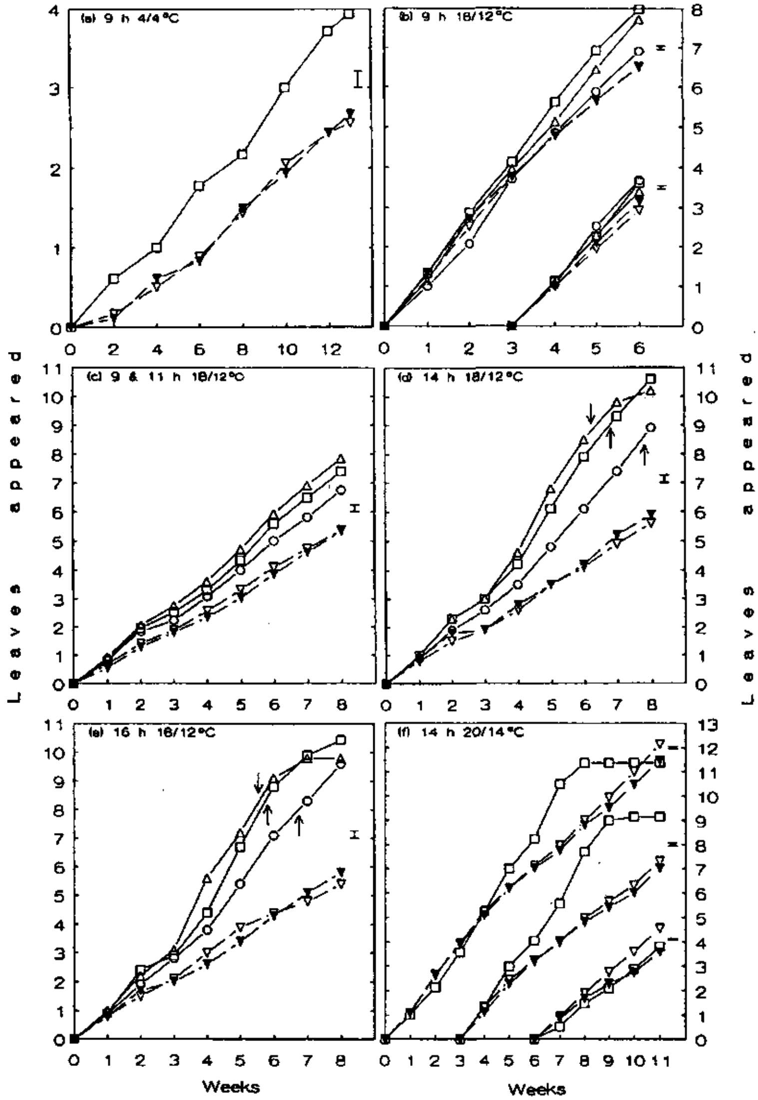

FIG. 1. Cumulative numbers of leaves appeared on tillers of Wendy (▼--▼), Caramba (▽--▽), Matua (□—□), Primabel (○—○) and Bellegarde (Δ—Δ). (a) experiment 1; (b) experiment 2, upper and lower sets of lines are main and second tagged tillers respectively; (c) experiment 3, average of three tagged tillers in the 9 and 11 h photoperiods; (d) experiment 3 (14 h), main tiller; (e) experiment 3 (16 h), main tiller; (f) experiment 4, upper, middle and lower sets of lines are main, second and third tagged tillers respectively. In experiment 3, arrows indicate for each prairie grass cultivar when 50% of the main tillers had emerged inflorescences. Temperature and photoperiod conditions are indicated in the corner of each figure. Vertical bars indicate LSD values ($P<0.05$) for significant species differences for each set of tagged tillers.

TABLE 1. Reproductive development and tiller numbers in prairie grass for experiment 3. Days taken for 50% emergence of inflorescences on the main and second tagged tillers. Total tillers per plant at the end of the experiment, and percentage of total tillers with emerged inflorescences at the 14 and 16 h photoperiods. Figures in a row that are accompanied by the same lower case letter are not significantly different (*P*>0.05).

		Cultivar	
	Matua	Primabel	Bellegarde
Days to 50% emergence of inflorescences for			
- main tiller -14 h	48_b	54_a	42_c
-16 h	40_b	46_a	38_c
-second tagged tiller -14 h	55_b	68_a	45_c
-16 h	47_b	60_a	41_c
Total tillers per plant			
- 9 h	37_a	43_a	24_b
-11 h	32_a	36_a	25_b
-14 h	27_a	30_a	17_b
-16 h	26_a	26_a	18_b
% tillers with emerged inflorescences -14 h	13_b	4_c	41_a
-16 h	24_b	7_c	44_a

Similar trends for LAR also occurred in experiment 4 for the main and second tagged tillers, but Matua showed no signs of reproductive development or accelerated LAR on the third tagged tiller [Fig. 1(f)]. LAR in Wendy and Caramba declined with time and was significantly higher on average in Caramba for all tillers (*P*<0.01). LAR of Wendy and Caramba on the second and third tagged tillers were 9 and 14% lower than on the main tiller, respectively (*P*<0.05). At the end of the experiment, 55% of Matua tillers had emerged inflorescences and 5% were jointed, while only 4% of Caramba tillers were reproductive (jointed tillers and emerged inflorescences).

Tillering and site filling

(a) Vegetative. Tillering rates were similar for all cultivars in experiment 1 (*P*>0.05) [Fig. 2(a)] [Table 2], but otherwise prairie grass had significantly lower tillering rates, lower site filling and lower tiller numbers than ryegrass under vegetative

TABLE 2. Average tillering rate (tillers tiller^{-1} day^{-1}) (x 10^{4}) and average site filling (tillers tiller^{-1} leaf appearance interval^{-1}) for all experiments. Figures in a row that are accompanied by the same lower case letter are not significantly different (*P*>0.05).

		Cultivar				
		Wendy	Caramba	Matua	Primabel	Bellegarde
Tillering rate (x 10^{4})						
Expt 1	9 h, 4/4°C	71_{a}	62_{a}	76_{a}		
Expt 2	9 h, 18/12°C	930_{a}	840_{b}	700_{c}	700_{c}	580_{d}
Expt 3	9 h, 18/12°C	155_{a}	120_{b}	86_{d}	109_{c}	112_{c}
	11 h, 18/12°C	144_{a}	137_{a}	71_{d}	79_{d}	116_{d}
	14 h, 18/12°C	138_{a}	140_{a}	26_{c}	47_{bc}	52_{b}
	16 h, 18/12°C	162_{a}	137_{b}	26_{d}	30_{d}	51_{c}
Expt 4	14 h, 20/14°C	480_{a}	460_{b}	310_{c}		
Site filling						
Expt 1	9 h, 4/4°C	0.243_{a}	0.222_{ab}	0.176_{b}		
Expt 2	9 h, 18/12°C	0.597_{a}	0.544_{b}	0.370_{d}	0.428_{c}	0.316_{e}
Expt 3	9 h, 18/12°C	0.152_{a}	0.121_{b}	0.061_{d}	0.085_{c}	0.079_{cd}
	11 h, 18/12°C	0.158_{a}	0.140_{b}	0.051_{d}	0.086_{c}	0.081_{c}
	14 h, 18/12°C	0.131_{a}	0.140_{a}	0.014_{d}	0.030_{c}	0.029_{c}
	16 h, 18/12°C	0.157_{a}	0.148_{a}	0.014_{e}	0.018_{e}	0.029_{d}
Expt 4	14 h, 20/14°C	0.298_{a}	0.276_{b}	0.172_{c}		

conditions [Figs. 2(b),(c)] [Table 2]. Increases in tiller numbers in experiments 1 and 3 were very low, and so tillering rates and site filling were also low. Tillering rates and site filling declined steadily with time in experiment 2, the greatest decline occurring in Matua and Bellegarde.

Wendy and Caramba had comparable tillering and site filling, but on average, Caramba had slightly lower tillering rates, site filling and final tiller numbers than Wendy (*P*<0.05) [Fig. 2] [Table 2]. Of the prairie grass cultivars in experiment 2, Primabel had the highest site filling, while Bellegarde had poor site filling and the lowest tiller numbers. Despite a low site filling, a good tillering rate resulted in Matua having the same tiller numbers as Primabel. In experiment 3, Bellegarde showed

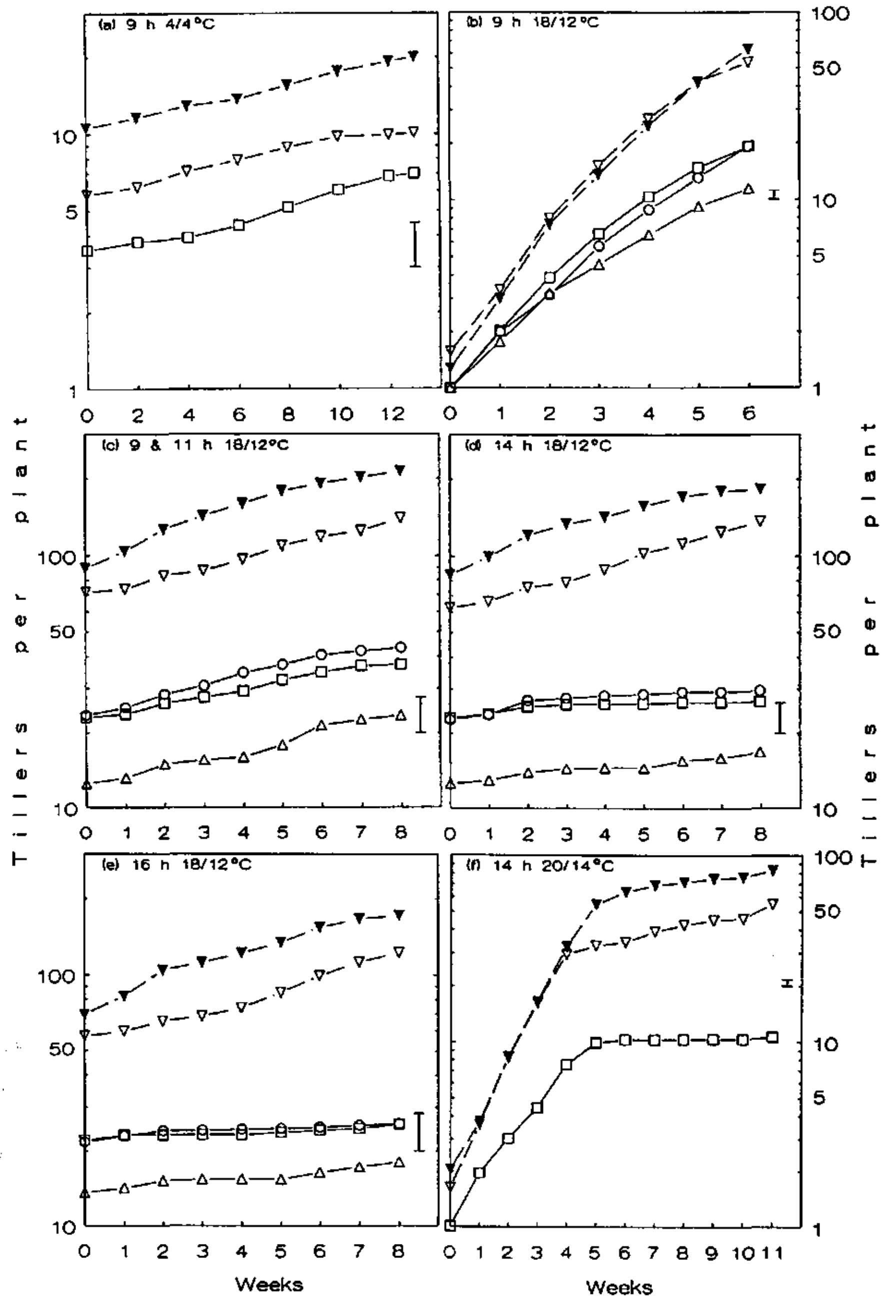

FIG. 2. Numbers of tillers per plant for Wendy (▼- -▼), Caramba (▽- -▽), Matua (□—□), Primabel (○—○) and Bellegarde (△—△). (a) experiment 1, (b) experiment 2, (c) experiment 3 (average of 9 and 11 h photoperiods), (d) experiment 3 (14 h), (e) experiment 3 (16 h), and (f) experiment 4. Temperature and photoperiod conditions are indicated in the corner of each figure. Vertical bars indicate LSD values (*P*<0.05) for significant species differences.

better tillering and site filling when compared to the other prairie grass cultivars, but increases in tiller numbers were very low in this experiment and Bellegarde still maintained a low tiller number.

(b) Reproductive. Reproductive development in the prairie grass cultivars resulted in reductions in tillering, site filling and lower final tiller numbers in the long photoperiods of experiment 3 [Figs. 2(c),(d),(e)] [Tables 1,2]. In experiment 4, tiller numbers increased in an exponential manner for Wendy and Caramba until 4 to 5 weeks of measurements [Fig. 2(f)]. Tillering rates and site filling then declined sharply, firstly in Caramba and then Wendy. This occurred at a stage when there were large numbers of tillers per pot (120-200) in Wendy and Caramba. Matua had decreasing tillering rates and site filling from an early stage, with no increase in tiller numbers after 5 weeks, and therefore site filling of zero during this later period. Average site filling was significantly higher in Wendy than Caramba, and lower in Matua [Table 2] ($P<0.001$).

Positions of axillary tillers

Position of the youngest axillary tiller (number of leaf axils from top of tiller) on the main tiller increased with time in all experiments [Fig. 3]. In some experiments, positions were similar for all cultivars at the start of the experiment, but positions soon increased so that Wendy consistently had the smallest position and the prairie grass cultivars the largest. Positions in Caramba in experiments 1 and 2 were similar to prairie grass, but in experiment 3 it was closer to that of Wendy. Of the prairie grass cultivars, Bellegarde generally had the largest position and Primabel the smallest. With the higher LAR and lower site filling associated with reproductive development, position of the youngest axillary tiller rapidly increased in experiments 3 (14 and 16 h) and 4. The increase being fastest in Bellegarde and slowest in Primabel.

In experiments 2, 3 and 4, position of the youngest axillary tiller on the second tagged tiller was similar to that of the main tiller. For Bellegarde in experiment 2, this is only based on 80% of the plants, because over the total trial period 20% of

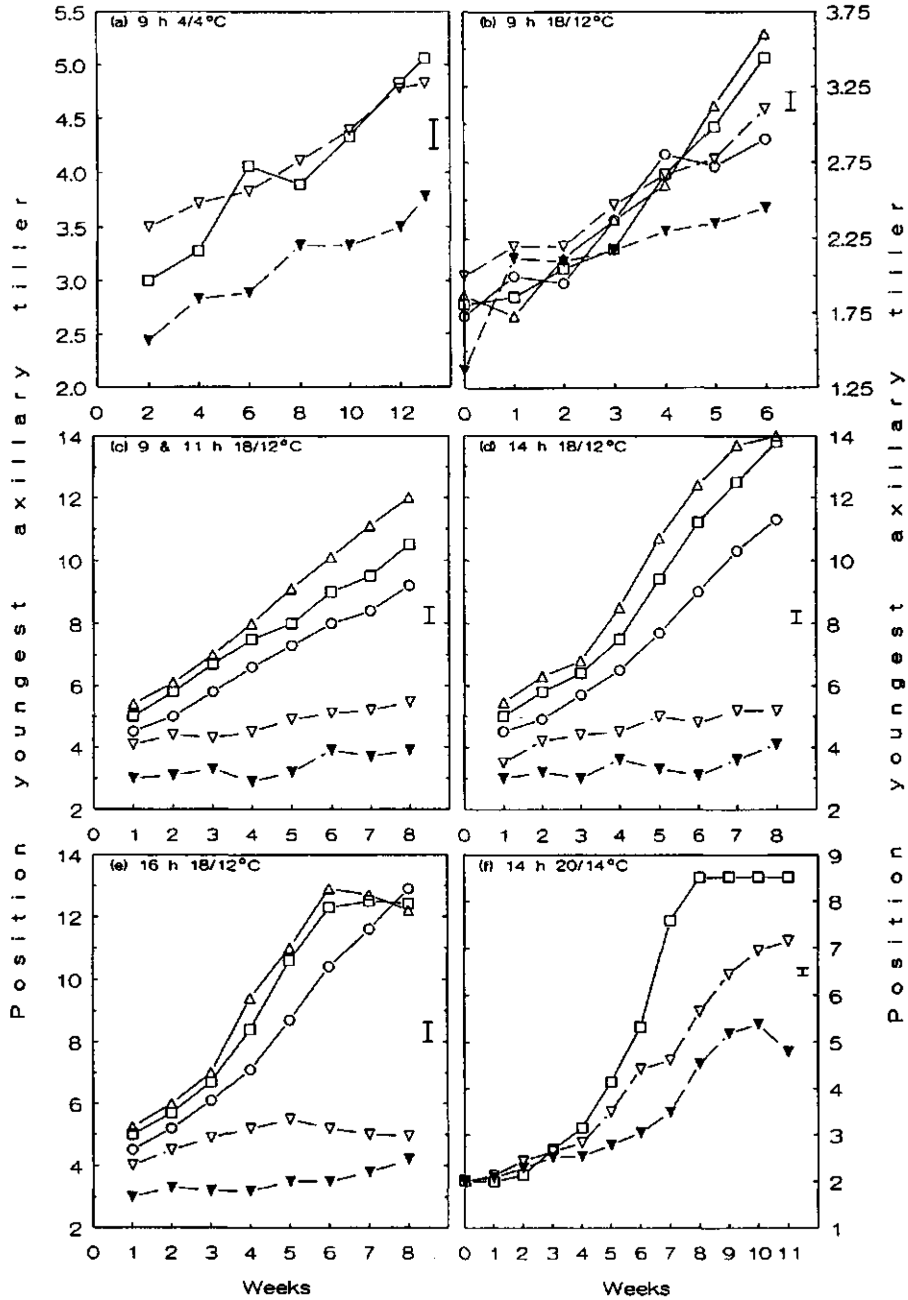

FIG. 3. Positions of the youngest axillary tillers (fully emerged leaves from the top of the tiller) on the main tillers of Wendy (▼--▼), Caramba (▽--▽), Matua (□—□), Primabel (○—○) and Bellegarde (△—△). (a) experiment 1, (b) experiment 2, (c) experiment 3 (average of 9 and 11 h photoperiods), (d) experiment 3 (14 h), (e) experiment 3 (16 h), and (f) experiment 4. Temperature and photoperiod conditions are indicated in the corner of each figure. Vertical bars indicate LSD values ($P<0.05$) for significant species differences.

the plants did not produce visible axillary tillers on the second tagged tiller. The third tagged tiller in experiment 3 produced axillary tillers in Wendy and Caramba, which were similar in position to the main tiller ($P>0.05$), but in prairie grass only 40% of these tagged tillers produced axillary tillers. No axillary tillers were produced on the fourth tagged tiller in experiment 3 or on the third tagged tiller in experiment 4.

Tillering on the main and second tagged tillers in experiment 2, and the main tiller and first secondary tiller in experiment 5, started approximately one leaf stage later in prairie grass than in ryegrass [Table 3]. For the prairie grass cultivars, tillering started later in Bellegarde. The final growing medium for the plant in experiment 5 did not affect these sites of tillering, but where no or minimal disturbance to roots occurred, ie. seed sown into soil or germinated on filter paper [experiment 5(ii)], tillering began at an earlier leaf stage.

In experiment 5(i), tiller numbers per plant when six leaves had appeared on the main tiller, were 15.3, 14.2, 5.6, 5.5 and 4.4 for Wendy, Caramba, Matua, Primabel and Bellegarde respectively ($LSD_{0.05}$=0.2, $P<0.05$). These species differences in tiller numbers were primarily due to the positions at which the first axillary tillers were produced, because at this leaf stage differences in positions of the youngest axillary tillers were small. Variation in tiller numbers between cultivars of a species corresponded with the small differences in positions of the youngest and the first axillary tillers.

Yields, herbage quality, leaves

The prairie grass cultivars had the greatest yields per tiller, being highest in Bellegarde especially at long photoperiods [Table 4(a)]. Wendy had a very low yield per tiller while Caramba was intermediate. Yield per plant [Table 4(b)] is a result of yield per tiller and tiller number. Wendy consistently had the lowest yield per plant, despite having the highest tiller number. Yield per plant for Caramba relative to prairie grass, varied with experiment, but Caramba consistently had higher yields per plant than Wendy [Table 4(b)]. Although Bellegarde had a low tiller number, a high yield per tiller gave Bellegarde the highest yield in experiment 3, particularly with

TABLE 3. Positions of the first axillary tillers to form on the main tiller, first secondary tiller and the second tagged tiller in experiments 2 and 5(i),(ii). P, C, 1, 2, etc. represent prophyll, coleoptile, first leaf, second leaf, etc. respectively. For experiment 2, figures in a column that are accompanied by the same lower case letter are not significantly different (*P*>0.05) for log transformed data.

	Position of first axillary tiller					
Experiment	2		5(i)		5(ii)	
Tiller	Main	2nd tagged	Main	Secondary	Main	Secondary
Wendy	1.6_d	P_c	1	P	C	P
Caramba	1.0_e	P_c	1	P	C	P
Matua	2.0_c	1.0_b	2	P or 1	1	P or 1
Primabel	2.1_b	1.0_b	2	P or 1		
Bellegarde	2.4_a	2.1_a	2	1 or 2		

TABLE 4. (a) Herbage yields per tiller and (b) herbage yields per plant at the end of experiments 1, 2 and 3, and yields after six weeks of measurements in experiment 4. Figures in a row that are accompanied by the same lower case letter are not significantly different (*P*>0.05).

		Cultivar				
		Wendy	Caramba	Matua	Primabel	Bellegarde
(a) Yield per tiller (g)						
Expt 1	9 h, 4/4°C	0.016_c	0.055_b	0.072_a		
Expt 2	9 h, 18/12°C	0.06_d	0.18_c	0.32_b	0.34_b	0.66_a
Expt 3	9 h, 18/12°C	0.07_e	0.14_d	0.70_b	0.63_c	1.28_a
	11 h, 18/12°C	0.08_e	0.18_d	0.85_b	0.74_c	1.20_a
	14 h, 18/12°C	0.08_e	0.24_d	1.03_b	0.83_c	2.12_a
	16 h, 18/12°C	0.09_e	0.26_d	1.34_b	1.05_c	2.16_a
Expt 4	14 h, 20/14°C	0.06_c	0.19_b	0.53_a		
(b) Yield per plant (g)						
Expt 1	9 h, 4/4°C	0.31_b	0.56_a	0.50_a		
Expt 2	9 h, 18/12°C	4.0_c	9.6_a	6.7_b	6.7_b	6.3_b
Expt 3	9 h, 18/12°C	14.5_d	19.6_c	25.6_b	26.9_{ab}	29.7_a
	11 h, 18/12°C	13.2_d	19.3_c	25.6_b	26.2_{ab}	28.6_a
	14 h, 18/12°C	14.4_d	21.8_c	27.3_b	25.1_b	34.9_a
	16 h, 18/12°C	14.8_d	22.4_c	32.0_b	24.7_c	38.8_a
Expt 4	14 h, 20/14°C	4.0_b	6.2_a	5.6_a		

TABLE 5. Numbers of leaves, area per leaf, total area of leaf lamina per plant, and leaf dimensions of six leaves of the same leaf stage from the main and second tagged tillers, at the end of experiment 2 (9 h, 18/12°C). Figures in a row that are accompanied by the same lower case letter are not significantly different (P>0.05).

	Cultivar				
	Wendy	Caramba	Matua	Primabel	Bellegarde
Live leaves - tiller^{-1}	3.1_d	3.5_d	4.9_b	4.4_c	5.5_a
- plant^{-1}	228_a	192_a	104_b	87_b	53_c
Area leaf^{-1} (cm^2)	2.7_d	9.2_c	11.5_b	12.9_b	18.4_a
Total plant leaf lamina area (cm^2)	620_c	1760_a	1190_b	1120_b	970_b
Leaves of same leaf stage					
- lamina width (cm)	0.4_c	0.7_b	1.0_a		
- lamina length (cm)	22_c	32_b	36_a		
- lamina area (cm^2)	7_c	16_b	28_a		
- sheath length (cm)	4_c	6_b	10_a		

reproductive development. Matua and Primabel had similar yields, although the long photoperiods in experiment 3 appeared to have little effect on total yield in Primabel.

Apparent digestibility of herbage organic matter in experiment 3 was consistently higher in Wendy (85%) than in Caramba (82%) and lower in prairie grass (80%) at 9 and 11 h (P<0.01). Digestibility of prairie grass at long photoperiods was less at 14 h (76%) and 16 h (74%), the greatest decrease occurring in Bellegarde (70% at 16 h) while at 16 h Primabel had 76% and Matua 74% digestibility. Nitrogen content was high (3 to 4.5%) in all cultivars in experiments 1, 2 and 3.

Wendy had high numbers of live leaves per plant but a low number of live leaves per tiller [Table 5]. Leaves were very small in Wendy, with short leaf sheaths and a low leaf area per plant. In contrast, prairie grass had high numbers of large leaves per tiller, long leaf sheaths, low numbers of leaves per plant and high leaf area per plant. Caramba was intermediate in these characters, although total leaf area was high. Of the prairie grass cultivars, Bellegarde had the highest number of leaves per tiller and the largest leaves, but a lower tiller number resulted in lower numbers of leaves per plant and lower total leaf area.

DISCUSSION

This study has characterized leaf and tiller production in prairie grass under a range of environmental conditions. Inclusion of two ryegrass species provided a good comparison as there is already considerable knowledge on the tillering and production of this genus. Only during experiments 3 (14 and 16 h) and 4, growth in long photoperiods, was this comparison not valid. In these experiments, reproductive development occurred in prairie grass but not in ryegrass. Wendy perennial ryegrass had not been vernalized and therefore could not produce reproductive tillers. Conditions were apparently suitable for reproductive development in Caramba Westerwolds ryegrass (Cooper, 1960), but very few inflorescences emerged. Although night temperatures (12-14°C) appeared to be low enough to avoid any significant inhibition of inflorescence production in Caramba (Cooper, 1958; Evans, 1960; Hill and Pearson, 1985), this could have been a possible cause of inhibition as satisfactory reproductive development has been obtained in Caramba with night temperatures of 10°C (Chapter 5 this thesis).

Under vegetative conditions, leaf appearance rate in prairie grass was consistently higher than in the ryegrass cultivars while site filling was lower. Similar results have also been found in further studies with these cultivars (Chapter 4 this thesis). Low tillering rates and low tiller numbers in vegetative prairie grass growing from mid-autumn to mid-spring, are therefore not the result of a low number of tiller sites, on the contrary, a high number of tiller sites are produced per tiller. Low filling of these sites is the cause of low tiller numbers and low tillering rates.

Low site filling in vegetative prairie grass dominated any positive effects that a high leaf appearance rate may have on tiller numbers (high number of tiller sites), so that tiller numbers were low. Despite the low tiller numbers, prairie grass yields were high, because of a high yield per tiller when compared to the ryegrass species. This was achieved through more live leaves per tiller, and bigger leaves and sheaths than for the ryegrass tillers. Similar results have also been gained by Hill, Pearson and Kirby (1985) and Hill and Pearson (1985) with Matua prairie grass and Italian ryegrass (*Lolium multiflorum* Lam.). A similar gradient for these characters also existed within the prairie grass cultivars, with Bellegarde having the lowest tiller numbers but the highest number of live leaves per tiller, greatest area per leaf and highest yield per tiller.

Under reproductive conditions, prairie grass exhibited large increases in leaf appearance and a lower site filling. It may be expected that reproductive plants of the ryegrass species would also have shown a similar pattern of accelerated leaf production and lower tiller production (Chapter 5 this thesis). Again low site filling in reproductive plants dominated any positive effects that a high leaf appearance rate may have on tiller numbers. In this case, apical dominance would appear to be the major factor limiting axillary bud activity. With the continual production of large numbers of reproductive tillers during long photoperiods, apical dominance could be expected to be a major factor in controlling tiller production from mid-spring to mid-autumn.

Length of photoperiod is reported to have various effects on tiller production in prairie grass. Eteve (1982) reported that tillering in prairie grass stops below a critical photoperiod, the length of which had not been determined with precision. Results from the present study do not support this. Karim (1961) found that long photoperiods are required for reproductive development in prairie grass and that development is accelerated by increasing photoperiod. The present study used newer cultivars of prairie grass and these exhibited a similar response to long photoperiods. There was a large range in response of the prairie grass cultivars to long photoperiods, with similar observations being noted in field trials (Hume, unpublished data). Primabel was a cultivar with a lower propensity for reproductive growth, high herbage quality and high tiller numbers, but low herbage yields during reproductive growth. On the other hand, Bellegarde had strong reproductive growth, low tiller numbers and low herbage quality, but high yields. It would appear that Matua was intermediate with regards to these characters, and with a high leaf appearance rate and high tiller numbers, Matua may be the cultivar with the best attributes to achieve high yields of quality herbage. Hill and Kirby (1985) have also suggested that Matua is well suited to agricultural use.

It should also be noted that the different photoperiods in experiment 3 appeared to have no effect on tillering and leaf production in the ryegrass species. This supports other research, as reviewed by Langer (1963) and Anslow (1966).

Neuteboom and Lantinga (1989), in a new model for leaf and tiller production in perennial ryegrass, have suggested a factor n which is a measure of axillary bud activity. Axillary tillers may show delays in appearance at the top of tillers (youngest axillary tillers) or total lack of appearance from basal buds (first axillary tillers). Much of the variation in tillering occurring between species and between cultivars within a species in the present study, was due to the position at which the first axillary tiller was produced, and at later stages, position of the youngest axillary tiller. That is to say, site filling was the major factor determining tillering.

In the ryegrass species, the first axillary tillers could come from the coleoptile or prophyll buds, while even under optimum conditions [Experiment 5(ii)], the first axillary tillers of prairie grass only came from the first leaf on the main tiller and only occasionally from the prophyll of tillers. The previous leaf and tiller production model (Davies, 1974) ignored the possibility of tillering from the coleoptile or prophyll, while the observations from the present study provide further support for the model of Neuteboom and Lantinga (1989). The prophyll and coleoptile tiller sites are of considerable importance in determining potential tillering.

Delays in appearance of the youngest axillary tiller at the top of the tiller increased (position increased) in all cases with time, with subsequent decreases in site filling. At later stages of growth, the youngest tillers on the plant did not produce any axillary tillers. This increasing delay or total lack of appearance was greatest in prairie grass and usually smaller in Caramba and consistently less in Wendy. On each tiller of prairie grass there were therefore a considerable number of potential sites for tillering, especially on reproductive tillers, many of which could develop after defoliation. These sites are particularly important in reproductive prairie grass plants because of the high tiller losses that will occur when plants are defoliated. Of the prairie grass cultivars, Matua and Primabel exhibited the greatest ability to fill all the tiller sites available. This resulted in these cultivars having high tillering rates and the highest tiller numbers for this species.

Previous findings that leaf appearance rate and leaf size are inversely related (Cooper and Edwards, 1960; Ryle, 1964), appear not to be true for the species and cultivars in the present study. Prairie grass, despite having the largest leaf size, had the highest leaf appearance rates. For the prairie grass cultivars, Bellegarde had the greatest leaf size and one of the highest leaf appearance rates. These results agree with Wilson (1963) who found significant positive correlations between leaf appearance and leaf size in prairie grass. In the present study there in fact appeared to be some negative correlation between site filling and leaf size or tiller weight.

In a review by Anslow (1966), it is suggested that age of tiller has no effect on rate of leaf appearance. From the present study, this does not always appear to be the case for vegetative plants. Lower leaf appearance appeared to be occurring on new tillers developing when there was already considerable herbage mass present. These tillers could therefore be suffering from the effects of lower light intensities (Mitchell, 1953) that occur below the leaf canopy. Also during reproductive growth there were very large differences in leaf appearance for the various tillers. These differences between tillers obviously has important implications for obtaining a true estimate of leaf appearance for the total plant, and also estimates of site filling. For site filling, this was potentially of most importance in reproductive prairie grass plants where leaf appearance ceased on tillers as inflorescences emerged. The overall effect on site filling was actually relatively small, because when the reproductive stems were elongating and inflorescences emerging, tillering rates had dropped considerably so site filling was very low or zero no matter what estimate was used for leaf appearance rate.

The various temperature and light conditions of the experiments resulted in large differences in leaf appearance, site filling and tillering rates. Due to changing plant (size, growth state) and environmental conditions, a true comparison of effects of temperature and light are not possible. It does appear though that increasing temperature and increasing total light energy resulted in higher levels of leaf appearance, site filling and tillering rates. Mitchell (1953) has also recorded similar responses although there were differences between species. In the field, Davies and Thomas (1983) have shown that temperature is the major factor determining leaf appearance rates, while light conditions appear to have little influence. Site filling appeared to be completely independent of environmental conditions and more dependent on plant size and subsequent tiller shading. The species in the present study all reacted in an approximately similar manner to the changes in temperature and light, except in experiment 1 (4°C, winter light intensity). In experiment 1, the reduction in leaf appearance was less in Matua prairie grass and so despite lower site filling in Matua, tillering rates were equal for all the cultivars. Relatively high leaf production and good tillering in such conditions could play a role in the high winter production of prairie grass.

This study has characterized leaf and tiller production in prairie grass during undisturbed growth and at high nutrient levels. A wide range of variation between cultivars was identified for the parameters measured. Future studies should further quantify the effects of cultivar variation, climate and management on these morphological features, in order to fully understand the behaviour of this species in agricultural situations.

CHAPTER 4

Effect of Cutting on Production and Tillering in Prairie Grass (*Bromus willdenowii* Kunth). 1. Vegetative plants

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ABSTRACT

Effects of cutting to 3 or 6 cm stubble height at frequencies of 1, 2 or 4 weeks were investigated in young, vegetative, spaced plants growing for eight weeks on nutrient solution at day/night temperatures of 15/10°C and in a short photoperiod. Increased cutting frequency and a lower cutting height both reduced leaf appearance, site filling and tiller numbers. Prairie grass (*Bromus willdenowii* Kunth) was affected the least by the cutting treatments while proportionally large reductions occurred in perennial ryegrass (*Lolium perenne* L.) and greater reductions in a tetraploid Westerwolds ryegrass (*Lolium multiflorum* Lam.). Relative growth rates in all species responded in a similar manner with more frequent cutting and a lower cutting height. Cutting frequency had the greatest effect on growth rates, although the effect of cutting height increased with time. A typical U-shaped curve for depletion and recovery in water soluble carbohydrates occurred after defoliation in all species, but levels remained low at frequent cutting. Water soluble carbohydrate levels in stubble and roots were higher in Matua. Regrowth at the end of the experiment was highly correlated with total stubble and root weights (r=0.84), while regrowth per tiller showed a good correlation with water soluble carbohydrate content, although the response varied between species and cutting treatments. Results confirm that general recommendations of long intervals between

defoliations will give the best yields for vegetative prairie grass, but the yield response to cutting may be no different to that of ryegrass. Stubble height was of lesser importance in determining yields.

INTRODUCTION

It is generally accepted that prairie grass (*Bromus willdenowii* Kunth) requires rotational grazing management with long intervals between grazing or cutting in order to maintain high production and persistence under intensive pastoral farming (Burgess *et al.*, 1986). Defoliation frequency, based on the height of plants when they are to be defoliated, is therefore the most important criterion on which management decisions are taken during both vegetative and reproductive (mid-spring to mid-autumn) growth (Karim, 1961; Hill and Pearson, 1985). The height plants are cut to (stubble height) appears to be of secondary importance (Karim, 1961; Hume and Lucas, 1987).

Little is known about the plant parameters that affect regrowth in prairie grass, or what is the response of the plant to different defoliation regimes. For various other grass species there has been considerable discussion about the role of various parameters such as water soluble carbohydrates, protein, residual leaf area and root and stubble weights in determining regrowth (Milthorpe and Davidson, 1966; Davies, 1988). Davies (1966) concluded that the effects of many of these factors are highly interrelated and the importance of each may vary according to the situation.

Two important growth stages exist for prairie grass; vegetative growth and reproductive growth. Both of these stages are important because reproductive growth is prolonged as long photoperiod is the only requirement for reproductive development (Karim, 1961), while prairie grass is valued for its high vegetative growth during the cool seasons of the year (Langer, 1973). Each growth stage has large effects on leaf and tiller production (Chapter 3 this thesis) but few details are known of the response of the plant to defoliation and how this differs to the response of ryegrass (*Lolium* species). This paper therefore reports a study on the effects of defoliating vegetative plants of prairie grass and ryegrass, while a further paper reports effects of defoliating reproductive plants (Chapter 5 this thesis).

METHODS AND MATERIALS

Treatments

This experiment investigated the effects of cutting height and cutting frequency on the growth of young, vegetative, spaced plants of 'Grasslands Matua' prairie grass (*Bromus willdenowii* Kunth), 'Caramba' tetraploid Westerwolds ryegrass (*Lolium multiflorum* L.) and 'Wendy' perennial ryegrass (*Lolium perenne* L.). Plants were cut to heights of 3 or 6 cm (stubble height) at frequencies of 1, 2 or 4 weeks. These treatments were replicated five times in a factorial design. Plants of each cultivar were also grown for the length of the experiment without being cut (Undisturbed Growth).

Plant material and growing conditions

Seedlings of the three cultivars were grown in a glasshouse in white sand in a nine hour photoperiod during early December 1987. On 22 December, seedlings were transferred to troughs containing Steiner's nutrient solution. The troughs were placed in a growth cabinet operating at temperatures of 15°C/10°C (day/night) and an 11 hour photoperiod. Lighting was provided by mercury and sodium lamps giving an irradiance of 115 W m^{-2} at plant level. The nutrient solution was constantly aerated and pH (5.5-6.0) was adjusted daily. Initially the solution was replaced weekly, but after four weeks it was replaced every 3-4 days.

Measurements and harvests

On 14 January 1988, plants were cut to their appropriate treatment heights and the cutting frequency and cutting height treatments were applied for the next eight weeks. Immediately prior to cutting, all plants were assessed for leaf and tiller numbers, and ten plants were measured for shoot and root weights. Throughout the experiment, five plants from each treatment were observed at weekly intervals for leaf appearance on the main tiller, tiller numbers and position of the youngest axillary tiller on the main tiller (number of leaf axils from the top of the tiller). When these plants were cut, the cut herbage was dried and weighed. Leaf appearance was assessed by marking the uppermost fully emerged leaf (ligule emerged) on the tagged tillers with an acrylic pen. One week later the number of fully emerged leaves above this marked leaf were counted. This procedure was repeated for the following weeks. From leaf appearance and total tiller numbers, site filling, the proportion of tiller buds forming visible tillers in a single leaf appearance interval was calculated (Davies, 1974). At each harvest, the cut herbage was examined for ligules of leaves that had not yet emerged but which were removed in the cut pseudostem.

Destructive harvests

Extra plants were also grown so that five plants for each cultivar and cutting treatment could be destructively harvested at various dates. Destructive harvests were taken at the beginning of the cutting treatments (14 January), and then for each treatment when cutting was due. For undisturbed growth, destructive harvests were taken 1, 2, 4, 6 and 8 weeks after the start of the cutting treatments. Plants removed for destructive harvests were separated into shoot above the 3 or 6 cm cutting heights, stubble and roots. Stubble was divided into 0-3 cm and 0-6 cm according to the appropriate cutting height, and 0-3 cm and 3-6 cm in plants growing undisturbed. These stubble fractions and roots were dried at 70°C and weighed, and then analysed for nitrogen and water soluble carbohydrates. Water soluble carbohydrates (WSC) were determined colourmetrically with an automatic analyser using ferricyanide. Nitrogen (N) was determined colourmetrically after the dry samples had been digested in a solution of salicylic and sulphuric acid with hydrogen peroxide. Nitrogen content in the cut herbage was also determined for all treatments at the final harvest.

Regrowth

After eight weeks of the cutting treatments, the remaining plants were allowed to regrow for one week after cutting. The plants were then cut to assess the amount of regrowth, and stubble and roots were dried, weighed and analysed for N and WSC contents.

RESULTS

Leaf appearance

Leaf appearance prior to the cutting treatments being applied was highest in Matua and similar in Caramba and Wendy [Table 1] ($P<0.001$). These cultivar differences also occurred during the cutting treatments [Fig. 1(a)].

Leaf appearance was approximately constant in all treatments except during the first week of the cutting treatments. At 6 cm cutting height, cutting frequency had relatively little effect on leaf appearance in Matua and Wendy, but in Caramba leaf appearance was significantly reduced by cutting every week [Fig. 1(a)]. At 3 cm cutting height, increased cutting frequency reduced leaf appearance linearly ($P<0.01$), with the greatest proportional reductions occurring in Caramba and Wendy. Cutting height had no significant effect in Matua and Caramba at the 4 week cutting frequency, while at the 1 and 2 week cutting frequencies, 3 cm cutting significantly reduced leaf appearance.

TABLE 1. Plant parameters immediately prior to applying cutting treatments. Position of the youngest axillary tiller is the number of leaf axils from the top of the tiller. Figures in a row that are accompanied by the same lower case letter are not significantly different ($P>0.05$).

	Cultivar		
	Matua	Caramba	Wendy
Leaves appeared on main tiller	5.5_a	4.9_b	4.7_b
Tillers plant^{-1}	3.5_c	7.6_a	5.9_b
Position youngest axillary tiller	3.2_a	2.4_b	2.1_c
Shoot weight mg	220_b	370_a	160_b
Root weight mg	70_b	120_a	58_b

Leaf appearance in Wendy at 6 cm was relatively low, so that at the 4 week cutting frequency leaf appearance was significantly lower at 6 cm than at 3 cm, and at the 2 week cutting frequency leaf appearance was similar for the two cutting heights. Plants growing undisturbed had similar leaf appearance to the highest leaf appearance in the cutting treatments ($P>0.05$).

The number of leaf ligules that were removed with the cut herbage before the ligules had emerged, was greater at higher cutting frequencies. At the final harvest, these leaves represented 2, 4 and 6% of the total leaves to have leaf ligules above the cutting height for the 1, 2 and 4 week cutting frequencies respectively ($P<0.01$). There were no significant effects of cultivar or cutting height.

Tiller numbers

When the cutting treatments were first applied, Caramba had the highest number of tillers per plant and Matua the lowest. [Table 1] ($P<0.001$). Significant cultivar differences occurred throughout the experiment, but were modified by cutting height and frequency. Cutting treatments affected tiller numbers at an early stage in the experiment (after one to two weeks of cutting), with tiller numbers at the final harvest illustrating the effects that occurred [Fig. 1(b)]. Calculation of tillering rates (tillers tiller^{-1} day^{-1}) removed the effect of cultivar differences in initial tiller numbers, but the trends as described below for tiller numbers were mostly unchanged.

At 6 cm cutting height, cutting frequency had relatively little effect on tiller numbers in Matua and Wendy, but tiller numbers in Caramba were reduced in a quadratic manner with greater cutting frequency ($P<0.05$) [Fig 1(b)]. Increased cutting frequency at 3 cm cutting height caused a linear reduction in tiller numbers in Matua and Caramba and a quadratic reduction in Wendy. At this cutting height, the reduction in tiller numbers was proportionally greatest in Caramba and Wendy and least in Matua. This resulted in all cultivars having similar tiller numbers for weekly cutting at 3 cm height ($P>0.05$), with tillering rates being significantly less in Caramba and Wendy, than in Matua ($P<0.001$). Tiller numbers in Caramba and Wendy in this treatment showed only slight increases after four weeks of

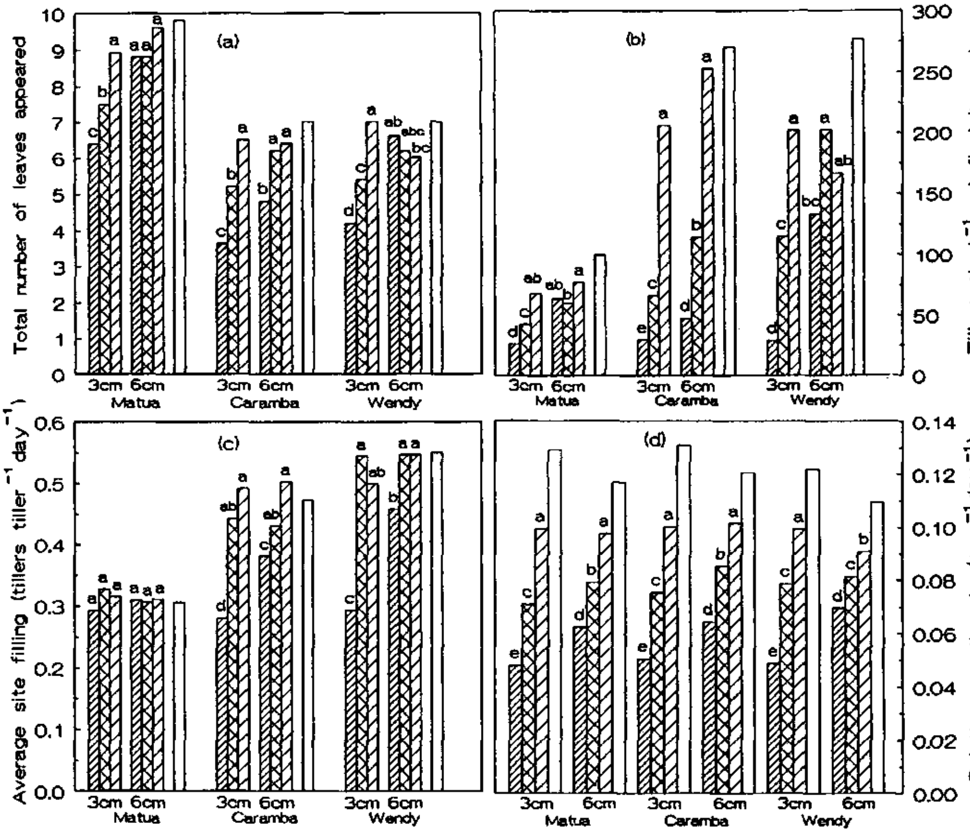

FIG. 1. After eight weeks of the cutting treatments, (a) total leaves appeared on the main tiller, (b) final numbers of tillers per plant, (c) average site filling, (d) average relative growth rates, for all cutting treatments and undisturbed growth ( ). Cutting frequency of 1 week is represented by ( ), 2 weeks ( ) and 4 weeks ( ). Within each cultivar, bars accompanied by the same letter are not significantly different ($P>0.05$). For tillers per plant, lettering is for Log_{10} transformed data.

cutting. Cutting height had no significant effect on tiller numbers in any of the cultivars at the 4 week cutting frequency ($P>0.05$), while at 1 and 2 week cutting large reductions occurred when plants were cut to 3 cm compared to 6 cm.

Matua and Caramba plants growing undisturbed had similar tiller numbers and tillering rates to the 6 cm, 4 week cutting frequency ($P>0.05$). Wendy plants growing undisturbed had higher tiller numbers and tillering rates than any of the cutting treatments ($P<0.05$).

Site filling

On average, Matua had the lowest site filling of the three cultivars, and cutting treatments had no significant effect on site filling in Matua [Fig. 1(c)]. In Caramba and Wendy, the 2 and 4 week cutting frequencies had similar site filling ($P>0.05$), while weekly cutting caused large reductions in site filling mainly at 3 cm cutting height. For these two cultivars there was a significant quadratic response occurring with increasing cutting frequency. All cultivars had similar site filling at 3 cm, weekly cutting ($P>0.05$). Site filling in plants growing undisturbed was similar to the highest site filling in the cutting treatments ($P>0.05$).

When the numbers of leaves that were removed by cutting before the ligules had emerged were included in the estimate of potential tiller sites, site filling values were only reduced on average by approximately 3% and this did not significantly alter treatment differences.

Position youngest axillary tiller

Position of the youngest axillary tiller (number of leaf axils from top of tiller) reflected to a certain extent the cultivar and treatment differences found for site filling. Matua had the largest position at the start of the cutting treatments and Wendy the smallest, with Caramba intermediate [Table 1] ($P<0.001$). After four weeks of cutting, Matua and Caramba had similar positions ($P>0.05$) for the remainder of the experiment. Position increased constantly during the experiment so that at the final harvest, position was 4 in Matua and Caramba and 2.8

in Wendy ($P<0.001$). Position increased linearly ($P<0.001$) with more frequent cutting, with mean positions at the final harvest being 4.0, 3.6 and 3.2 for the 1, 2 and 4 week cutting frequencies respectively ($LSD_{0.05}=0.3$). Position in plants growing undisturbed was similar to that in the 4 week cutting frequency ($P>0.05$). Cutting height had no significant effect on position.

Yields

(a) Cut herbage. Total yield of cut herbage was highest in Caramba (mean, 14 g), lower in Matua (mean, 8 g) and lowest in Wendy (mean, 5 g) ($P<0.001$). Yields for 1, 2 and 4 week cutting were 2, 6 and 19 g respectively ($P<0.001$) ($LSD_{0.05}=2$), and 9 and 11 g respectively for 3 and 6 cm cutting.

Due to different stubble weights for the cultivars and cutting heights at the start of the experiment (see also shoot weight Table 1) relative growth rates (g g^{-1} day^{-1}) were calculated. On this basis, growth was similar for all cultivars ($P>0.05$) but a significant interaction occurred between all treatments [Fig. 1(d)]. This interaction was primarily caused by significantly lower growth of Wendy at 4 week cutting at 6 cm height compared to 3 cm. Otherwise cutting height had no significant effect on relative growth rates at 4 weekly cutting. More frequent cutting (1 and 2 week cutting frequencies) at both cutting heights reduced growth rates in a quadratic manner ($P<0.05$). This reduction in growth was greatest at 3 cm height compared to 6 cm, except Wendy at the 2 week cutting frequency. All cultivars had similar growth rates for weekly cutting at 3 cm height and also for 4 weekly cutting at both cutting heights.

Plants growing undisturbed had significantly higher growth rates than any of the cutting treatments ($P<0.001$).

(b) Stubble and roots. Cutting treatments affected dry weights of stubble and roots in a similar manner to that described for relative growth rates of cut herbage. Weights at the final harvest were reduced by higher cutting frequency, the greatest reductions occurring at 3 cm cutting height.

Water soluble carbohydrates

(a) Stubble. Contents of water soluble carbohydrates (WSC) in

the stubble at the start of the cutting treatments were highest in Matua, lowest in Caramba and intermediate in Wendy [Fig. 2]. These differences between cultivars remained for the rest of the experiment. One week after applying the cutting treatments, WSC had decreased in all treatments especially at 3 cm cutting height and also particularly in Matua. After two weeks, WSC had started to recover in all treatments with further increases occurring after four weeks in most treatments. In plants cut weekly, WSC remained at low levels especially at 3 cm cutting height. At the 2 and 4 week cutting frequencies, WSC were higher, approaching the same levels as in the stubble of plants growing undisturbed. At the 2 week cutting frequency, WSC were generally less than or similar to those at 4 week cutting. Cutting height had relatively little effect on WSC in Matua at 2 and 4 week cutting, but in Caramba and Wendy, WSC were higher at 6 cm than 3 cm cutting height.

(b) Roots. Contents of WSC in the roots were much lower than in the stubble [Fig. 3]. Again Matua had the highest contents and Caramba the lowest. There was a similar pattern of decrease and recovery in WSC after the initial cut as occurred in the stubble. These changes though were relatively small and recovery less in Wendy and Caramba, while in Matua the changes were greater. Differences between cutting frequencies and heights in Matua were similar to those occurring in the stubble, but in Wendy and particularly Caramba, levels were generally low and relatively constant.

Nitrogen

A full analysis of nitrogen (N) contents in roots and stubble during the early part of the experiment was limited by insufficient ground plant material for determination of N content. In general, there appeared to be no consistent differences between the treatments during the course of the experiment. Plants growing undisturbed had similar or lower N contents than plants in the cutting treatments. In the stubble, N content (4.2%) was similar for all cultivars. Contents were lower in the roots of Matua and Wendy (3.6%), but in Caramba, roots and stubble had similar N contents (4.2%).

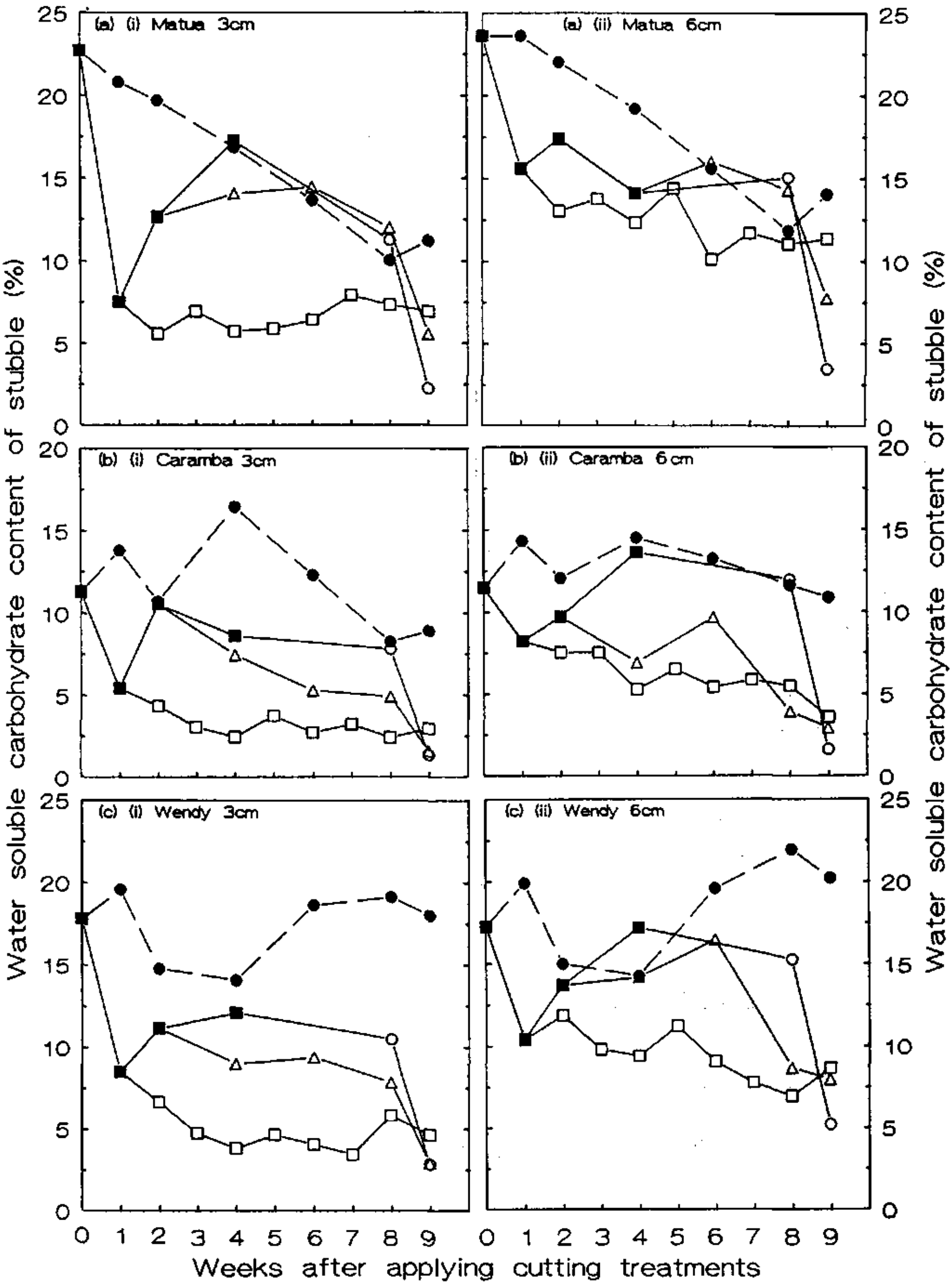

FIG. 2. Water soluble carbohydrate content (WSC) (%) of stubble for (a) Matua, (b) Caramba and (c) Wendy, for (i) 3 cm and (ii) 6 cm cutting heights. WSC content at the initial cut and the following four weeks is represented by (■—■); a cutting frequency of 1 week by (□—□), 2 weeks (△—△), 4 weeks (○—○); and 3 and 6 cm stubble heights for undisturbed growth (●--●).

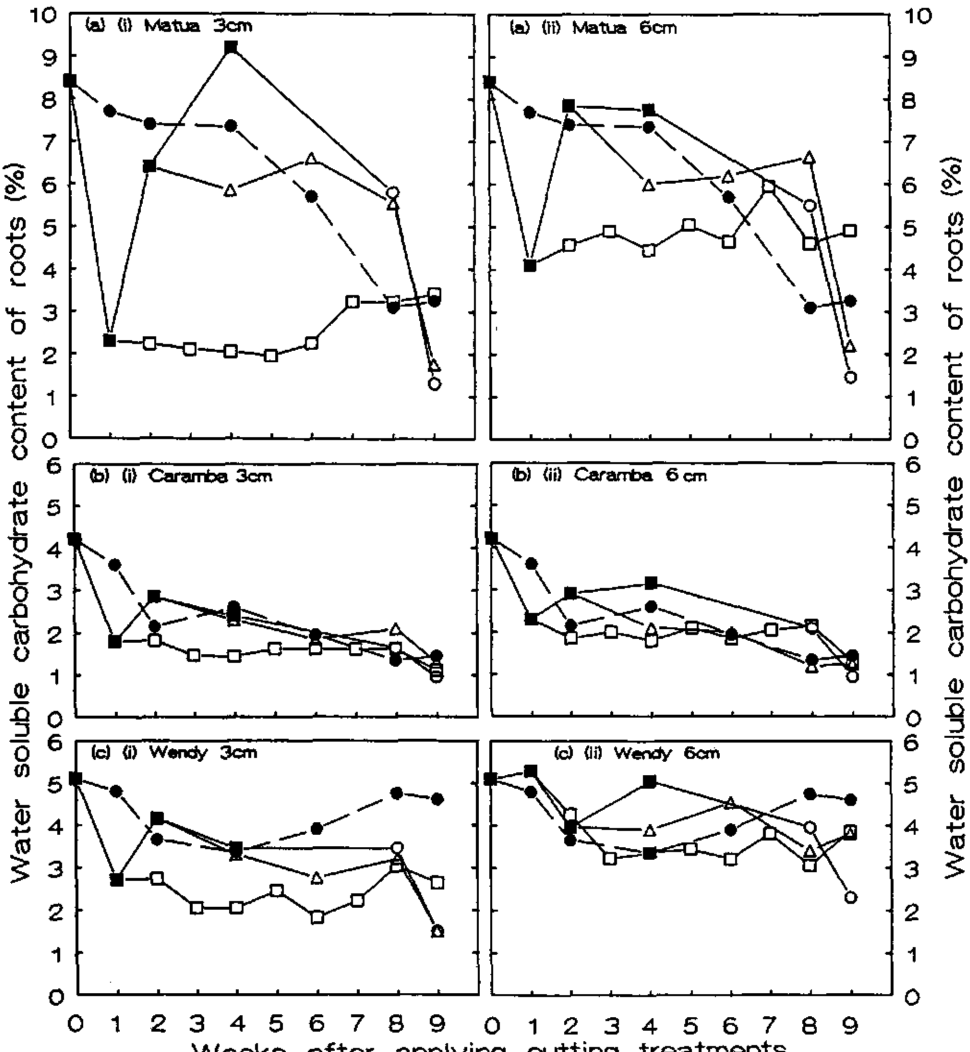

FIG. 3. Water soluble carbohydrate content (WSC) (%) of roots for (a) Matua, (b) Caramba and (c) Wendy, for (i) 3 cm and (ii) 6 cm cutting heights. WSC content at the initial cut and the following four weeks is represented by (■—■); a cutting frequency of 1 week by (□—□), 2 weeks (△—△), 4 weeks (○—○); and 3 and 6 cm stubble heights for undisturbed growth (●--●).

The cut herbage at the final harvest had high N contents (mean, 5.2%) in all cultivars (range for treatments, 4.7-5.5%).

Regrowth at the end of the experiment

After the one week of regrowth at the end of the cutting treatments, WSC and N contents in roots and stubble showed large decreases at the 4 week cutting frequency, and in most cases decreases at the 2 week cutting frequency [Figs. 2, 3]. One weekly cutting continued to have constant low levels of WSC and N. With the 4 week cutting frequency, stubble weight decreased in all cultivars while root weights only decreased in Matua, Caramba at 3 cm height and Wendy at 6 cm. Root and stubble weights decreased only in Caramba for the 2 week cutting frequency, while there were no decreases at the 1 week cutting. Yield of the regrowth was significantly higher with decreasing frequency of cutting and significantly higher with the greater cutting height [Fig. 4]. Only for Wendy at the 4 week cutting frequency was this not true, as yields were similar for both cutting heights.

Of all the variables measured, stubble weight, root weight and WSC content of stubble showed positive correlations with yield of regrowth. Regression analysis showed a high positive linear correlation between total yield of regrowth and total weight of stubble (mean for log transformed data, r=0.81) [Fig. 5]. Similar correlation coefficients also occurred for root weight and total yield of non WSC substances in the stubble. Adding WSC content or weight of WSC to the regression analysis did little to improve the percentage of variance accounted for, but this varied considerably with each treatment and cultivar as illustrated in Fig. 5. Regression analysis with only WSC content gave high correlations (r=0.9) for Matua 6 cm, Caramba 3 cm and Wendy 3 cm. When regrowth was expressed as g per tiller, stubble weight per tiller was the best indicator of regrowth for Caramba (r=0.84) but for Matua and Wendy, WSC content accounted for the greatest variation (r=0.8).

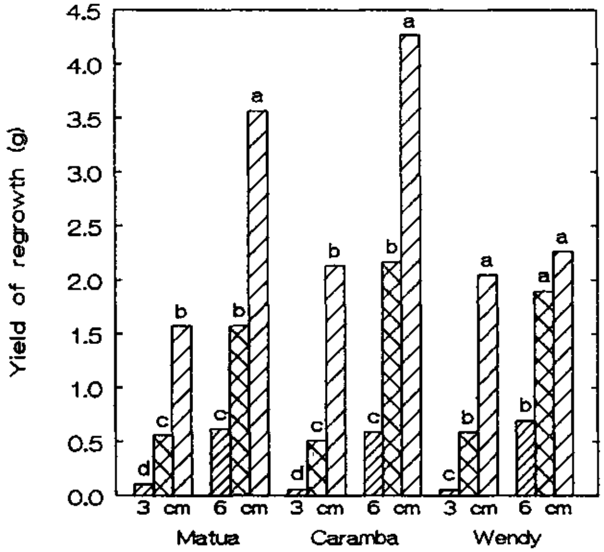

FIG. 4. Yield of regrowth one week after the end of the cutting treatments. Cutting frequency of 1 week is represented by (▨), 2 weeks (⊠), 4 weeks (▨). Within each cultivar, bars accompanied by the same letter are not significantly different for Log_{10} transformed data.($P>0.05$).

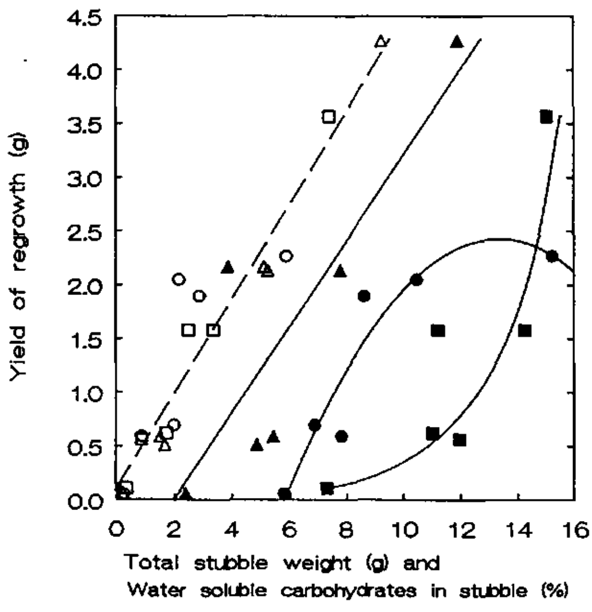

FIG. 5. Yield of regrowth one week after the end of the cutting treatments relative to total stubble weight (open symbols) and water soluble carbohydrate (WSC) content of stubble (closed symbols) at the start of regrowth. Matua is represented by (□), Caramba (△) and Wendy (○). Separate curves and lines of best fit are drawn for each cultivar for WSC content and a dotted line for all cultivars for stubble weight.

DISCUSSION

Firstly it should be noted that the Wendy perennial ryegrass plants measured in the 6 cm cutting height 4 week cutting frequency treatment appeared to have uncharacteristically low levels for total yield, regrowth yield and numbers of tillers. This was confirmed by comparison with the yields and tiller numbers of plants grown for the destructive harvests (Hume, unpublished data). It therefore appears that the poor performance of these plants was not a true indication of the effect of this defoliation treatment for Wendy. Only minor importance should therefore be placed on the relatively low tiller numbers and low yields of Wendy in this treatment.

Plant parameters

The features of high leaf appearance, low site filling and low tiller numbers in prairie grass relative to ryegrass that have already been identified during undisturbed growth (Chapter 3 this thesis), were relatively unchanged by the different defoliation treatments. Only when defoliation was very frequent at the low cutting height of 3 cm were site filling and tiller numbers reduced in the ryegrass species to the same levels as in prairie grass. Caramba and Wendy exhibited approximately similar levels for these measured parameters which is also similar to results gained in previous experiments (Chapter 3 this thesis).

There was considerable variation between species in response to the cutting treatments for leaf appearance, site filling and numbers of tillers. For these plant parameters Matua was the least affected by cutting treatment, with no effect on site filling and only at 1 and 2 week cutting at 3 cm was leaf appearance reduced and so directly reducing tiller numbers. Wendy showed some effect of cutting frequency at 6 cm height while Caramba was affected to the greatest extent at this height. At 3 cm cutting height, cutting frequency had proportionately the largest effects in Caramba and Wendy.

Herbage growth rates

Despite these species differences in response of the plant parameters to the different cutting treatments, the resulting herbage growth rates were remarkable similar for all species in each treatment. It could have been expected that under the relatively low temperature and moderate light conditions of this experiment (similar to early spring or late autumn conditions) that Matua and Caramba would have shown higher growth rates than Wendy (Langer, 1973). Langer (1970) also found no differences in growth between prairie grass and ryegrass and it was only during growth of closely spaced plants (sward conditions) that superior growth could be demonstrated for prairie grass. This was attributed to better adaptation to reduced light intensity through a more upright growth habit and better leaf distribution. Only for the plants growing undisturbed did Wendy have lower growth rates than the other cultivars, possibly because of the high herbage mass and tiller numbers in these Wendy plants. This bulk of dense herbage resulted in shading within each plant similar to the shading that may occur in swards.

The different levels of leaf appearance and tiller numbers created by the cutting treatments, did not directly result in the same response in terms of yields. This was further illustrated by significantly higher growth in plants growing undisturbed compared with those in the best cutting treatments, despite similar leaf appearance and tiller numbers. This indicated that cutting treatments were not only affecting tiller numbers and number of leaves produced per tiller, but also size of leaf lamina and sheaths. It is known that more frequent cutting and lower height of cutting leads to the production of shorter leaves and sheaths in perennial ryegrass (Davies, 1977). Defoliation frequency also has little effect on the number of green leaves per tiller (Davies, 1977). Hill and Pearson (1985) also noted large reductions in yield per tiller, weight per leaf and leaf area per tiller in Matua with frequent defoliation and smaller yet still significant reductions for these parameters for Italian ryegrass. Mitchell and Coles (1955) found that the greatest effect of repeated defoliation was on the reduction in the amount of tissue formed per tiller, mainly due to the reduction in leaf size.

Frequency of cutting had the greatest effect on growth rates, while the stubble cutting height generally had less effect especially at very infrequent cutting, ie. growth rates were unaffected by cutting height at the 4 week cutting frequency. The optimum cutting treatment in the current experiment therefore appeared to be 4 week cutting at 3 or 6 cm height for all species. This result is similar to the general recommendations that prairie grass should be defoliated infrequently, with stubble height being of secondary importance (Karim, 1961; Burgess *et al.*, 1986; Bell and Ritchie, 1989). Although cutting at 3 cm resulted in high relative growth rates (g g^{-1} day^{-1}), actual herbage yields were lower than those from 6 cm cutting, due to growth from lower stubble weights. Also cutting height was exerting a greater influence with time as illustrated by the approximately equal effects of cutting frequency and cutting height on regrowth at the end of the experiment. Differences between cutting heights for total yields were also increasing as the experiment progressed.

At the 4 week cutting frequency approximately three leaves were produced on the ryegrass tillers between each defoliation and four to five leaves in prairie grass. The production of three leaves in ryegrass has been suggested as the optimum time for defoliation, because this is the maximum number of green leaves a vegetative tiller will support and it can be the time when ceiling yield is reached (Davies, 1971, 1977). The maximum number of green leaves per tiller would appear to be higher for prairie grass, possibly being 4 to 5 leaves depending on variation between leaf appearance of different cultivars (Chapters 2 and 3 this thesis; Hume, unpublished). Species with high leaf appearance have more live leaves per tiller (Ryle, 1964). Frequency of defoliation, although set in this experiment at fixed time intervals, should therefore be based on time for herbage to reach a certain level. For prairie grass this may be 20 cm height, as recommended by Burgess *et al.* (1986), or the number of leaves per tiller. For this latter criterion, time interval between defoliations of vegetative plants is therefore determined by the leaf appearance rates, which can vary considerably with temperature (Chapter 3 this thesis).

The relatively similar yield response of all species to defoliation frequency is rather unexpected. Prairie grass and Westerwolds ryegrass with their upright growth habit, generally perform poorly under frequent defoliation while perennial ryegrass is more tolerant of defoliation (Langer and Hill, 1982). Such general statements rarely differentiate between reproductive and vegetative growth conditions for the plant. This can be important for the different species, for example, Caramba Westerwolds ryegrass defoliated frequently during reproductive growth has performed poorly compared to the other cultivars (Chapter 5 this thesis).

The temperature and photoperiod conditions in this experiment are approximately similar to those encountered during vegetative growth in early spring or late autumn. The results from this experiment therefore indicate that although increased defoliation frequency will be detrimental to growth rates in all the species, the response of prairie grass may be no different to that occurring in Westerwolds ryegrass or perennial ryegrass during vegetative growth at these times of the year. Response to defoliation may vary with different temperature and light intensities (Mitchell, 1955), and time for recovery of water soluble carbohydrate levels can be longer at lower temperatures (Davies, 1965). Further testing would therefore be required at lower temperatures, shorter photoperiods and with closely spaced, mature plants (sward conditions) in order to identify the overall response to cutting for conditions encountered during vegetative growth in the field.

Regrowth and reserves

The pattern of depletion and recovery of water soluble carbohydrate contents in stubble after the first cut, formed a characteristic U-shaped curve. Decline was greatest the higher the initial values and greater when cutting height was low. Similar results have also been obtained with perennial ryegrass (Del Pozo Ibanez, 1963; Davies, 1966). Matua differed to the ryegrass species by having higher water soluble carbohydrate contents in roots and stubble and demonstrating greater changes in water soluble carbohydrate contents in roots after the initial cut. Examination of the one week of regrowth at the end of the experiment showed that the U-shaped curve of depletion and recovery after cutting still appeared to be occurring with cutting frequencies of 2 and 4 weeks, but not for the 1 week cutting frequency.

Frequent cutting led to low constant levels of water soluble carbohydrates which is often associated with poor growth (Graber *et al.* 1927; Weinmann, 1961) and tiller death (Alberda, 1966). Levels of water soluble carbohydrates are the net result of production by photosynthesis, utilisation by respiration and transformation into structural material. With cutting every week, regular removal of leaf lamina would have been limiting photosynthate production to the extent that no net increase in water soluble carbohydrates could occur. Alberda (1966) concluded that the plant can not use stubble water soluble carbohydrates as reserves below a level of 6%, this being the minimum level for cell function. At this stage tillers will die and presumably tissue broken down and its products translocated to the remaining tillers. Levels of water soluble carbohydrates in the present study, and those recorded by Davies (1965), have gone below this level. On average, tiller numbers in Caramba and Wendy increased only slightly after four weeks of cutting at 3 cm height, with some tiller death occurring.

Although this experiment was not specifically designed to assess the major factors that determined regrowth in these species, analysis of the regrowth at the end of the experiment did reveal some differences between the species. As could have been expected (Davies, 1966) total stubble weight was a major factor in determining regrowth. High stubble weight gave high regrowth due to high tiller numbers but also high stubble weight per tiller. Higher stubble weights also had higher water soluble carbohydrate levels. Only when regrowth was expressed per tiller, or was considered for individual treatments, could water soluble carbohydrates be demonstrated to have a large influence on regrowth. This effect appeared to differ for each species for the range of water soluble carbohydrates in this study [Fig. 5]. Although a greater range of water soluble carbohydrates would be required to fully define the curves estimated in Figure 5, there at least appeared to be a maximum yield response occurring for water soluble carbohydrate content in Wendy which is similar to that described for several clones of perennial ryegrass by Davies

(1966). A similar maximum in response to water soluble carbohydrates may have occurred in Caramba at higher levels while Matua appeared to be exhibiting a different relationship, although when expressed on a per tiller basis, more linear relationships occurred for Matua and Caramba.

The overall importance of water soluble carbohydrates in regrowth appears to be on the effect it has over the first two to seven days after defoliation, until sufficient leaf area is formed to sustain plant respiration and carbohydrate utilisation for growth. Following this initial period, regrowth rates may be similar despite different initial water soluble carbohydrate levels (Del Pozo Ibanez, 1963; Davies, 1965). The initial level of water soluble carbohydrates appears to affect the length of delay before exponential increases in regrowth occur again. This influence on growth only occurs when water soluble carbohydrates are below a critical level (Davies, 1965; Davies *et al.*, 1972).

The relatively low levels of water soluble carbohydrates in roots (except for Matua), is typical of this plant organ (Davies, 1965, 1966). Root material is a consumer of photosynthate and can not supply carbon to shoots after defoliation (Marshall and Sagar, 1965). The measurements of nitrogen in the plant tissue in the current experiment revealed little change with cutting treatment. Protein can be used in regrowth (Davidson and Milthorpe, 1966; Ourry, Bigot and Boucaud, 1989), but water soluble carbohydrates are preferentially used by the plant (White, 1973). The high nitrogen status in the current experiment could have masked the effects that cutting may have had on protein levels, especially at very frequent defoliation, as only total nitrogen was measured. In high nitrogen situations, nitrate levels in the plant are high and these levels increase considerably after cutting (Alberda, 1960).

The high nutrient status in the present experiment resulted in very high levels of nitrogen in plant tissues, eg. mean 5.2% N in cut herbage. High nitrogen levels are known to reduce carbohydrate levels (Alberda, 1960) as carbohydrates are used in increased protein production (Prianishnikov, 1951). At lower levels of nitrogen that would be encountered in a field situation, it could be expected that plant nitrogen contents would be lower and so water soluble carbohydrates higher. This would give a better range of water soluble carbohydrates to determine the response curves as depicted in Figure 5. Higher levels of water soluble carbohydrates have been recorded for vegetative growth during winter or growth at low temperatures. At nitrogen contents in the cut herbage of approximately 3%, water soluble carbohydrates during growth in a glasshouse at 4°C with natural winter daylight at Wageningen were 44, 34 and 30% in the stubble (0-6 cm) of Matua, Caramba and Wendy respectively (Hume, unpublished data). Westerwolds ryegrass in New Zealand during winter is reported to have 22-47% water soluble carbohydrates in the stubble (Vartha and Bailey, 1980), while in perennial ryegrass during winter in the United Kingdom levels of 6-15% have been recorded (Baker, 1957).

Conclusions

Performance of vegetative plants of prairie grass is strongly related to defoliation frequency and less dependent on the stubble height to which plants are defoliated to. Under the spaced plant conditions of this experiment, these results confirm general recommendations for the management of prairie grass of long intervals between defoliations (Burgess *et al*, 1986). The response of prairie grass in terms of yield and changes in water soluble carbohydrate levels was similar to that occurring in ryegrass, but prairie grass demonstrated greater tolerance to defoliation for other plant parameters. Regrowth response relative to different water soluble carbohydrate contents appeared to be different for prairie grass and Westerwolds ryegrass compared to perennial ryegrass. Further investigations would be required to determine the significance of these differences.

CHAPTER 5

Effect of Cutting on Production and Tillering in Prairie Grass (*Bromus willdenowii* Kunth). 2. Reproductive plants

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ABSTRACT

Effects of time of initial cut, followed by frequency of defoliating the subsequent regrowth (1, 2 or 4 weeks) were examined in a glasshouse during summer 1988 for reproductive plants of three prairie grass cultivars (*Bromus willdenowii* Kunth), Westerwolds ryegrass (*Lolium multiflorum* Lam.) and perennial ryegrass (*Lolium perenne* L.). Measurements were made of tiller and leaf numbers, sites of tillering, reproductive development, and herbage quality and yields. Effect of time of initial cutting on regrowth appeared to be independent of stage of reproductive development, and unrelated to any of the measured plant parameters. Characteristics for each cultivar as identified during undisturbed growth prior to the initial cuts, confirmed observations from previous experiments, but these characteristics were modified by the cutting frequencies.

Perennial ryegrass had the highest yields under frequent cutting with high herbage quality. Westerwolds ryegrass and the prairie grass cultivars 'Grasslands Matua' and 'Primabel' had the highest yields with infrequent cutting, but lower quality than perennial ryegrass. At each cut, tiller death in prairie grass was determined by the number of reproductive tillers, and in Westerwolds ryegrass and perennial ryegrass also by the numbers of elongated vegetative tillers. Recovery of tiller numbers was rapid and primarily from inhibited tiller buds at the

base of reproductive tillers. Tiller numbers in prairie grass were relatively unaffected by increased cutting frequency but more axillary tillers originated from vegetative tillers rather than from inhibited tiller buds of reproductive tillers.

INTRODUCTION

Reproductive development in prairie grass (*Bromus willdenowii* Kunth) occurs during long photoperiods (Karim, 1961), and is therefore an important feature of this species as large numbers of reproductive tillers are produced from mid-spring to mid-autumn. The reproductive tiller has an inhibitory effect on the development of new axillary tillers (Langer, 1963), but this inhibition is removed when the elongating apex is decapitated, or at a late stage of flowering after elongation has finished (Langer, 1956). Regrowth after defoliation therefore depends on vegetative tillers and the development of inhibited buds. In prairie grass, where up to 70% of the tillers may be reproductive at the time of cutting (Chapter 8 this thesis), development of the inhibited buds will be important in obtaining rapid regrowth. Despite this high proportion of reproductive tillers, reproductive development in prairie grass appears to have little effect on tillering and regrowth (Eteve, 1982; Chapter 8 this thesis), but time of cutting can influence this (Eteve, 1982; Parneix, 1981, 1982).

Frequent defoliation of prairie grass is detrimental to herbage production and plant persistence (Burgess *et al.*, 1986), but such statements rarely differentiate between the response of vegetative and reproductive plants. A previous study found no significant differences in response of relative growth rates in prairie grass and two ryegrasses (*Lolium* species) to different cutting heights and cutting frequencies in vegetative plants (Chapter 4 this thesis). The present paper reports the effects of time of initial cut and frequency of cutting in reproductive plants of prairie grass and ryegrass.

METHODS AND MATERIALS

Plant material and pretreatments

During October and November 1987, seedlings of 'Grasslands Matua' prairie grass (*Bromus willdenowii* Kunth), 'Caramba' tetraploid Westerwolds ryegrass (*Lolium multiflorum* Lam.) and 'Wendy' perennial ryegrass (*Lolium perenne* L.) were grown in small pots in a glasshouse at 20°/12°C (day/night) and 12 h photoperiod at Wageningen, The Netherlands. The temperature was then reduced to 4°C with natural photoperiod for the next four months, in order to vernalize the plants. On 1 March 1988, the plants were transferred to five litre black plastic pots containing a sand-soil mixture to give one plant per pot. The temperature was increased to 18/10°C with an 11 h photoperiod, and the plants allowed to establish for one month. During early February 1988, seedlings of three prairie grass cultivars ('Grasslands Matua', 'Primabel' and 'Bellegarde') and 'Caramba' Westerwolds ryegrass were grown in five litre pots containing the sand-soil mixture, with one seedling per pot. In early March they were placed in the same glasshouse as the plants that had been vernalized.

From this material, vernalized plants of Caramba and Wendy, and plants of Matua, Primabel and Bellegarde that had not been subjected to the vernalization treatment were used in the experiment described below. Ten plants each of vernalized Matua and non-vernalized Caramba were also grown in the long photoperiod of the experiment for a period of five weeks to determine the effects of vernalization.

Experimental treatments

On 4 April 1988, the photoperiod was extended to 16 hours by the use of 400 W sodium lamps, and maintained at this length for the duration of the experiment. Temperatures remained at 18/10°C. Plants were then subjected to seven times of initial cutting, followed by three frequencies of cutting the subsequent regrowth. The first of the initial cuts was on 18 April, just prior to or at the start of stem elongation. The subsequent six times of initial cutting were at weekly intervals. After the plants had received the initial cut, the regrowth was cut at frequencies of 1, 2 or 4 weeks. These cutting frequencies were continued until 22 August, approximately four months after the first initial cut had been taken. All cutting was to a stubble height of 5 cm. The pots were placed close to one another to simulate sward conditions and the treatments were replicated four times in a randomised block design. Nutrients were applied at regular intervals as modified Hoagland's nutrient solution and water was applied daily.

Measurements

(a) Leaves, tillers and yields. Two weeks prior to applying the long photoperiod, weekly measurements of total tillers and leaf appearance were started. Leaf appearance was measured on the main tiller of the prairie grass cultivars and on a large tiller of Wendy and Caramba. When the long photoperiod was applied another tiller (1 emerged leaf) was tagged and monitored, and after 5, 8 and 12 weeks further tillers were measured. The uppermost fully emerged leaf (ligule emerged) on a tagged tiller was marked with an acrylic pen, and one week later the number of fully emerged leaves above this marked leaf were counted. This procedure was repeated for the following weeks. Leaf appearance rate (LAR) was then calculated by dividing the number of new fully emerged leaves appearing at each marking, by the time interval (7 days) (Davies, 1974). At each marking, position of the youngest axillary tiller (number of leaf axils from the top of the tiller) was recorded for the tagged tillers.

At each harvest, the cut herbage was dried and weighed, and the numbers of vegetative tillers, jointed tillers and tillers with emerged inflorescences were recorded. Three weeks before the end of the experiment, the cut herbage was also separated into vegetative and reproductive tillers.

(b) Herbage quality. Nutritive quality of the cut herbage at each initial cut and the regrowth 1, 2 and 4 weeks after each initial cut was determined by chemical analysis. The effects of the cutting frequencies on herbage quality were assessed four weeks after each of the initial cuts, and at the end of the experiment. Herbage was analysed for cell walls, digestibility and ash content, with nitrogen and water soluble carbohydrates

also being assessed for the herbage from the initial cuts.

Before analyses, the dried herbage samples were ground in a hammer mill (1 mm sieve) and the four replicates bulked to give two replicates for chemical determination. Water soluble carbohydrates (WSC) were determined colourmetrically with an automatic analyser using ferricyanide. Nitrogen (N) was determined colourmetrically after the dry samples had been digested in a solution of salicylic and sulphuric acid with hydrogen peroxide. True *in vitro* digestibility of the organic matter (Van Soest, Wine and Moore, 1966) was determined and then converted to apparent digestibility of organic matter (D_{om}) by reference to a series of standard grass samples of known *in vivo* digestibility for sheep fed at maintenance. Cell wall contents (CWC), or neutral detergent fibre, were determined by Van Soest's (1977) method. Digestibility of the cell wall (D_{cwc}) was calculated from the true digestibility, cell wall content and ash content.

Destructive harvests

Another set of pots of the five cultivars was also raised in the same way as described above. On nine occasions at weekly intervals, four replicates were destructively harvested and divided into roots, stubble (0-5 cm) and the cut herbage. Two harvests were taken prior to the first initial cut and seven harvests at the same times as the initial cuts. At each harvest, counts were made of total tillers, jointed tillers and tillers with emerged inflorescences. The stubble was further divided into reproductive and vegetative tillers. The plant material was dried, weighed and the roots and stubble fractions analysed for nitrogen and water soluble carbohydrates.

RESULTS

Results are discussed in terms of (a) growth over ten weeks from two weeks before the long photoperiod was applied until the final initial cut, and (b) growth after each of the seven initial cuts during the 1, 2 and 4 week cutting frequencies.

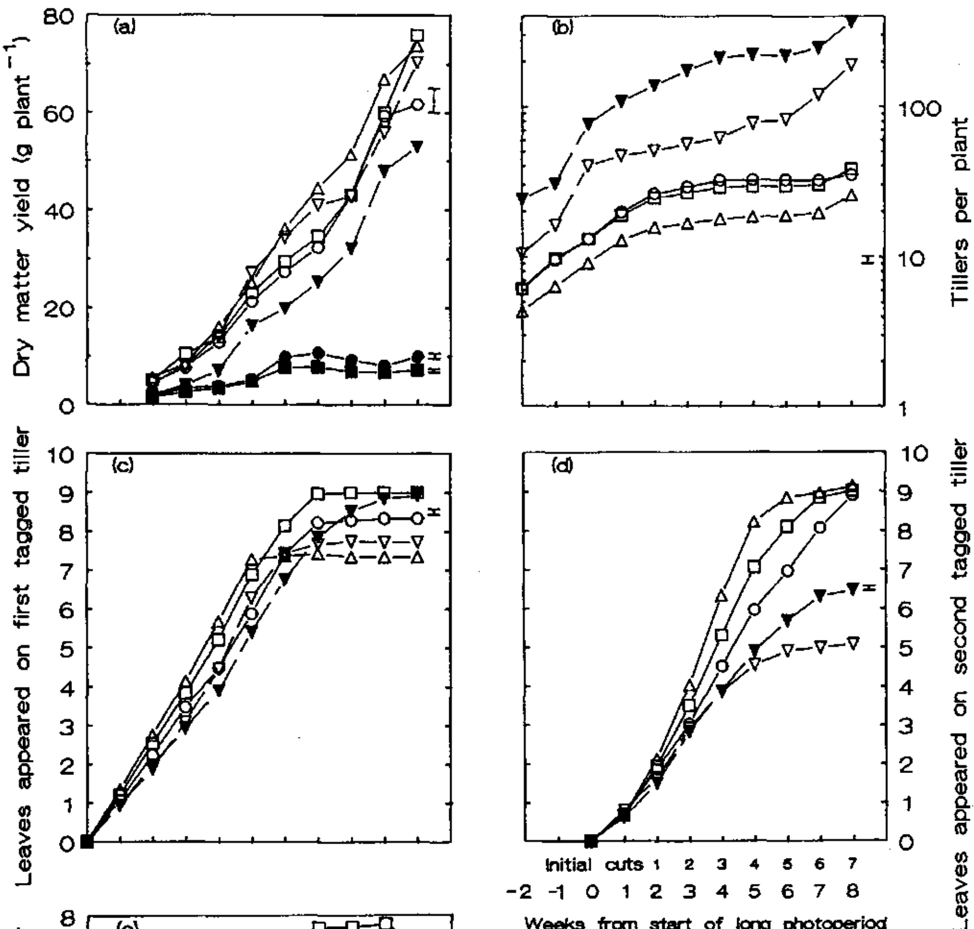
Before initial cuts

(a) Yields. Herbage dry matter yields increased in all cultivars with time [Fig. 1(a)]. Wendy consistently had the lowest yields at all dates. The other cultivars had comparable yields but higher growth rates in Caramba and Bellegarde gave higher yields at initial cuts 3 and 4. Increased growth rates did not occur in the other cultivars until initial cuts 5, 6 and 7. Yields on average were 45, 40, 40, 37 and 29 g per plant for Bellegarde, Matua, Caramba, Primabel and Wendy ($P<0.01$) ($LSD_{0.05}$= 2). The same cultivar differences and increases with time also occurred for yield of apparently digestible organic matter.

Total stubble and root weights increased until initial cut 3, then stayed approximately constant [Fig. 1(a)]. On average Primabel had the highest stubble weight (6.2 g) and Caramba the lowest (4.6 g), with no significant cultivar differences for root weight. Proportion of the total stubble that was composed of reproductive tillers increased rapidly as reproductive development occurred, reaching a maximum of 80% at initial cuts 4 to 7. Shoot root ratios increased in all cultivars from a ratio of approximately 3 to a ratio at the final initial cuts of 8 in prairie grass and 6 in Caramba and Wendy. Wendy was slow to increase the shoot root ratio with only significant increases occurring after initial cut 4.

(b) Tillers. Prior to applying the long photoperiod, tiller populations per plant were highest in Wendy and lowest in Bellegarde [Fig. 1(b)]. Tiller numbers increased rapidly in all cultivars especially in Caramba and Wendy as older tiller buds developed. Tillering then slowed as reproductive tillers developed, particularly in prairie grass where increases became negligible. Tillering then increased as old tiller buds developed at the bases of reproductive tillers in Caramba and Wendy at initial cuts 6 and 7 and in the prairie grass cultivars at initial cut 7. Tillering rates (tillers/tiller/day) prior to these new tillers emerging were 0.031 for Wendy and Caramba and 0.023 for the prairie grass cultivars ($P<0.01$).

Caramba was the first cultivar to show signs of reproductive development, one week after the long photoperiods had been applied. Reproductive development then occurred progressively



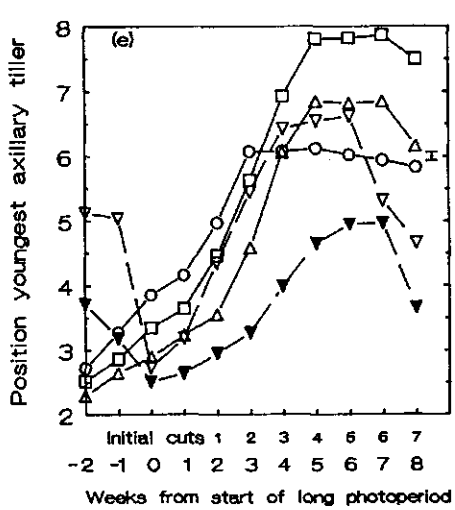


FIG. 1. Plant parameters from two weeks before the long photoperiod was applied until the final initial cut, a ten week period of undisturbed growth. Times when initial cuts were taken are indicated. (a) Herbage dry matter yields (>5 cm), root (●—●) and stubble (■—■) weights. (b) Tillers per plant. (c) Cumulative numbers of leaves appeared on first and (d) second tagged tillers. (e) Position of youngest axillary tiller on the first tagged tiller. Matua (□—□), Bellegarde (△—△), Primabel (○—○), Caramba (▽--▽) and Wendy (▼--▼). Vertical bars indicate LSD values ($P<0.05$) for significant cultivar differences, and for root and stubble weights.

TABLE 1. Reproductive tillers and tillers with emerged inflorescences as percentages of total tillers at initial cut 6 for prairie grass and for Caramba and Wendy at initial cut 5. This was prior to emergence of new tillers from the base of reproductive tillers. Figures in a row accompanied by the same lower case letter are not significantly different (*P*>0.05).

	Cultivar				
	Matua	Bellegarde	Primabel	Caramba	Wendy
% reproductive tillers	53_b	73_a	45_c	50_b	52_b
% tillers with emerged inflorescences	43_b	65_a	28_c	24_c	7_d

later in the other cultivars in the order of Bellegarde, Matua, Primabel and Wendy. Cultivar order for emergence of the first inflorescences, however, was Bellegarde, Matua, Primabel, Caramba and Wendy. For the prairie grass cultivars, Bellegarde had the highest proportion of reproductive tillers, many of which had emerged inflorescences [Table 1]. Later reproductive development in Primabel resulted in a lower proportion of reproductive tillers with fewer emerged inflorescences. Caramba and Wendy had high proportions of reproductive tillers but later inflorescence emergence resulted in lower proportions of tillers with emerged inflorescences [Table 1].

(c) Leaf appearance and reproductive development of tagged tillers. Prior to applying the long photoperiod, Matua and Bellegarde had produced more leaves on the first tagged tiller (main tiller) (6.5) than Primabel (5.9) (*P*<0.01). Leaf appearance rates (LAR) increased on the first tagged tiller (main tiller in prairie grass and a large tiller in Caramba and Wendy) in all cultivars as reproductive development occurred, firstly in Bellegarde then later in Matua, Caramba, Primabel and lastly in Wendy [Fig. 1(c)]. Leaves ceased to appear close to the time of inflorescence emergence, firstly in Bellegarde, then Caramba, Matua and Primabel, and lastly Wendy. Matua and Wendy produced the most leaves, Caramba and Bellegarde the least. This cultivar order for the cessation of leaves appearing was different to the cultivar order for inflorescence emergence (see above). Inflorescences

emerged in prairie grass before the flag leaf was fully emerged, while in ryegrass, inflorescences emerged only after the flag leaf was fully emerged.

The second tagged tiller (tagged at the stage of one emerged leaf in all cultivars) had a similar pattern of acceleration in leaf appearance and emergence of inflorescences [Fig. 1(d)]. Caramba and Wendy had lower LAR than the prairie grass cultivars even during the high LAR occurring with reproductive stem elongation. At initial cut 7, Caramba and Wendy had therefore produced 5 and 6.5 leaves respectively and the prairie grass cultivars 9 leaves. Leaves ceased to appear in both Bellegarde and Caramba at the same date but Bellegarde had produced 9 leaves and Caramba 5 leaves. The third tagged tiller showed similar trends for LAR but Caramba had much higher LAR (0.143 leaves/tiller/day), similar to that of Bellegarde, with reproductive development (visible internode elongation) occurring when the tiller was only three to four weeks old.

(d) Position of axillary tillers. Position of the youngest axillary tiller on the tagged tiller (number of leaf axils from the top of the tiller) reflected changes in tillering rates and the stage of reproductive development [Fig. 1(e)]. Position decreased in Caramba and Wendy as large increases in tiller numbers occurred during the first few weeks of measurements. As reproductive development occurred and tillering decreased, position increased and then came to a plateau as the inflorescences emerged in all cultivars. Positions decreased at the final dates as tiller buds developed on the reproductive tillers.

Positions of axillary tillers during the remainder of the experiment were not analysed because of the high numbers of tillers that had no axillary tillers, or tiller buds developed from the base of reproductive tillers and so their correct positions could not be identified.

(e) Herbage quality. Cell wall contents (CWC) of the cut herbage increased with time while apparent digestibility of organic matter (D_{om}) decreased [Figs. 2(a),(b)]. The prairie grass cultivars had similar CWC (mean, 51%) ($P>0.05$) which was significantly higher than Caramba and Wendy (mean, 48%) ($P<0.01$).

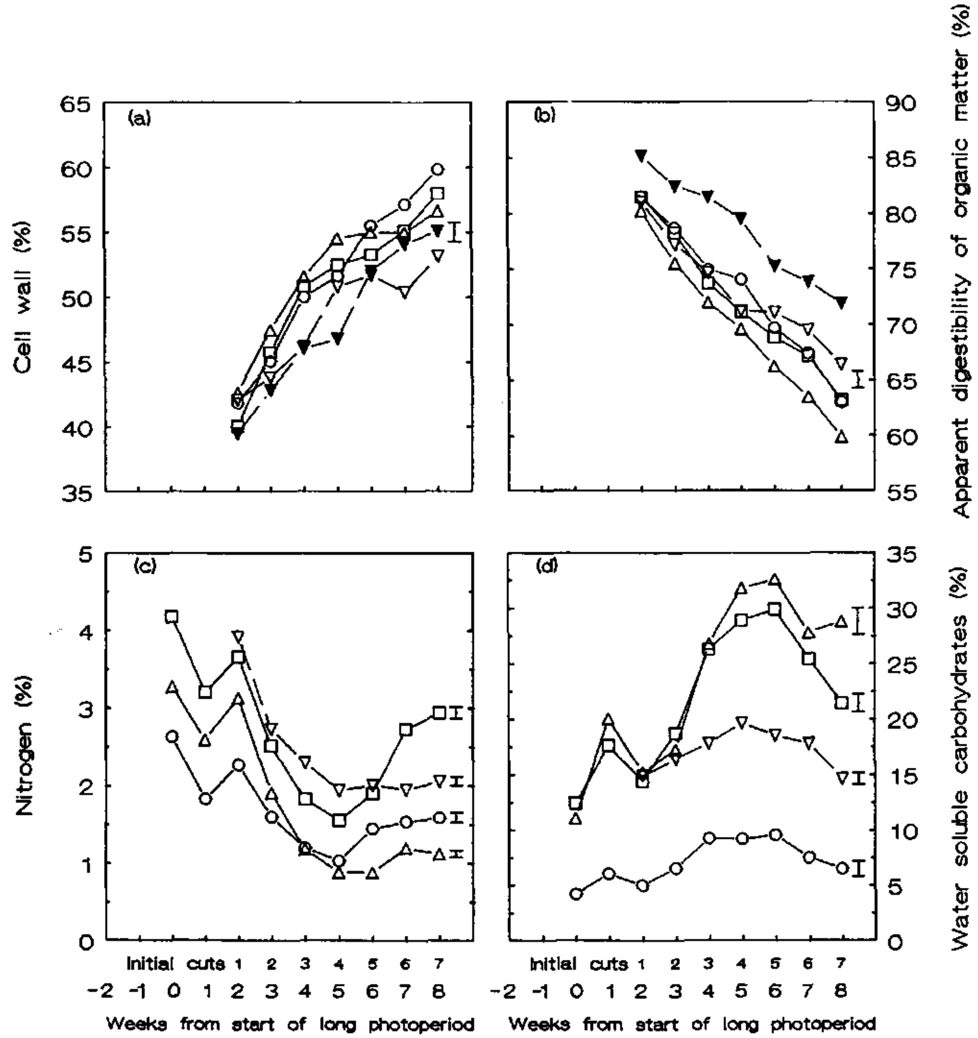


FIG. 2. Plant parameters from two weeks before the long photoperiod was applied until the final initial cut, a ten week period of undisturbed growth. Times when initial cuts were taken are indicated. (a) Cell wall contents and (b) apparent digestibility of organic matter, for Matua (□—□), Bellegarde (△—△), Primabel (○—○), Caramba (▽- -▽) and Wendy (▼- -▼). (c) Nitrogen and (d) water soluble carbohydrate contents of cut herbage (▽- -▽), roots (○—○), vegetative (□—□) and reproductive (△—△) stubble. Vertical bars indicate LSD values ($P<0.05$) for significant cultivar differences, and for each plant component in (c) and (d).

D_{om} was consistently higher in Wendy (mean, 78%) and lowest in Bellegarde (mean, 70%). Caramba and the prairie grass cultivars had similar D_{om} at initial cut 1 but the decline was greater in the prairie grass cultivars, so that at initial cut 7, digestibility was significantly higher in Caramba ($P<0.01$). Digestibility of the cell wall (D_{cwc}) followed a similar pattern of decline (81 to 59%) to that described for D_{om}.

Nitrogen (N) content in the plant decreased from relatively high levels at the start of the long photoperiod to lower levels at initial cut 4, increasing again at the final initial cuts except in cut herbage [Fig. 2(c)]. In contrast, water soluble carbohydrate (WSC) contents increased and then decreased slightly at the final initial cuts [Fig. 2(d)]. Roots had low levels of N and WSC, while reproductive stubble had low N but high WSC contents. Vegetative stubble had high contents of N and WSC. Consistent cultivar differences for N and WSC were few, but Caramba and Wendy did have significantly lower WSC contents in roots (3%), vegetative (16%) and reproductive (22%) stubble than the prairie grass cultivars (10, 25, 27% respectively). Differences between vegetative and reproductive stubble for WSC varied with each cultivar. In Caramba large differences between the stubble fractions occurred from an early stage while only from initial cuts 4, 5 and 6 did differences occur for Bellegarde, Wendy and Matua respectively, with no differences occurring in Primabel.

After initial cuts

(a) Yields. Regrowth one and two weeks after each initial cut was highest with the first initial cut (mean, 5.8 g initial cut 1, 3.2 g initial cuts 2 to 7). However, after four weeks of regrowth, yields were similar for all initial cuts (mean, 16.6 g). The time of each initial cut had no significant effect on growth rates (mean, 0.284 g day^{-1}) during the cutting frequency treatments. Total yields for the experiment were therefore higher with later initial cutting due directly to the higher yields obtained with each successive initial cut.

Cutting frequently resulted in large reductions in yields particularly in Caramba, and least in Wendy [Fig. 3]. With more infrequent cutting, yields of Bellegarde relative to the other

TABLE 2. Effect of cutting frequency and cultivar, after the initial cuts, on reproductive tillers at each cut as a percentage of total tillers, and tillers with emerged inflorescences at each cut as a percentage of total reproductive tillers. Herbage yields (>5 cm) from reproductive tillers as a percentage of the total yield at cutting, three weeks before the end of the experiment. Figures in a column accompanied by the same lower case letter are not significantly different ($P>0.05$).

	% reproductive tillers of total tillers			% emerged inflorescences of total reproductive tillers			% total yield from reproductive tillers		
Cutting frequency (weeks)	1	2	4	1	2	4	1	2	4
Matua	2_b	9_b	22_b	38_b	52_a	72_a	11_b	13_b	55_b
Bellegarde	3_b	10_b	19_b	74_a	50_a	64_b	11_b	10_b	49_b
Primabel	2_b	7_c	14_c	64_a	11_b	62_b	9_b	19_b	48_b
Caramba	23_a	34_a	44_a	1_c	2_c	38_c	42_a	57_a	78_a

cultivars declined. Thus at 4 week cutting, Bellegarde and Wendy had the lowest yields and Caramba the highest. Yields of D_{om} were similar to the trends shown for the dry matter yields in Fig. 3. The high digestibility of Caramba and Wendy increased yields of D_{om} relative to prairie grass, particularly in Wendy at 4 week cutting. This resulted in Wendy having significantly higher yields of D_{om} than Bellegarde at 4 week cutting ($P<0.01$), while dry matter yields were similar for these two cultivars [Fig. 3] ($P<0.05$).

Reproductive growth represented a high percentage of the total yield at 4 week cutting and lower percentages at more frequent cutting [Table 2]. This was closely related to the percentage of reproductive tillers at each cut [Table 2]. Caramba had relatively high percentages of yield as reproductive tillers even at frequent cutting due to the high amounts of reproductive growth.

(b) Tiller numbers. Effect of time of initial cutting on tiller numbers was variable, with no consistent effects. Therefore only

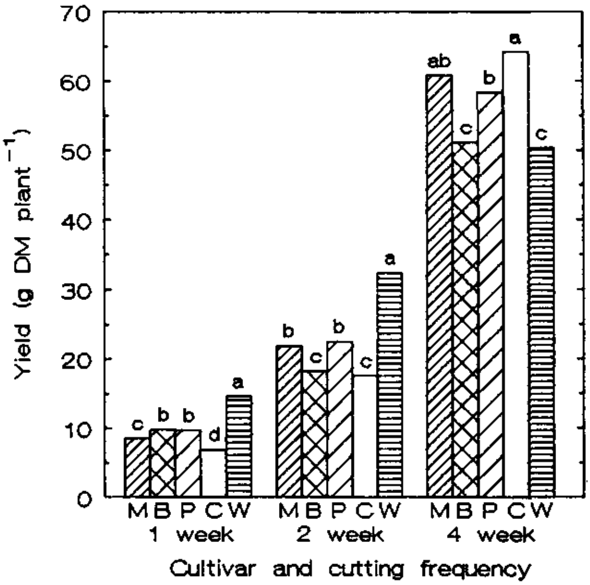


FIG. 3. Total herbage dry matter yields (>5 cm) (excluding yield at initial cuts) for 1, 2 and 4 week cutting frequencies and cultivars, Matua (M), Bellegarde (B), Primabel (P), Caramba (C) and Wendy (W). Within each cutting frequency, bars accompanied by the same lower case letter are not significantly different for log transformed data (*P*>0.05).

averages for all initial cuts are presented for each cultivar and cutting frequency treatment (Fig. 4).

Tiller numbers differed greatly between cultivars and cutting frequencies [Fig. 4]. Increased cutting frequency in Caramba and Wendy decreased tiller numbers. Similar results occurred in prairie grass during the early stages but then the 1 and 2 week cutting frequencies had a general increase in tiller numbers. In Matua and Primabel this resulted in similar tiller numbers for all cutting frequencies at later stages of the experiment, while 1 week cutting of Bellegarde resulted in consistently higher tiller numbers than the other cutting treatments.

Tiller numbers in Caramba with 4 week cutting followed a similar pattern to the other cultivars, but with 1 and 2 week cutting there were rapid declines in tiller numbers over the 4 to 6 weeks after each initial cut [Fig. 4(d)]. This resulted in all initial cutting times having similar tiller numbers (*P*>0.05) which were relatively constant for the remainder of the

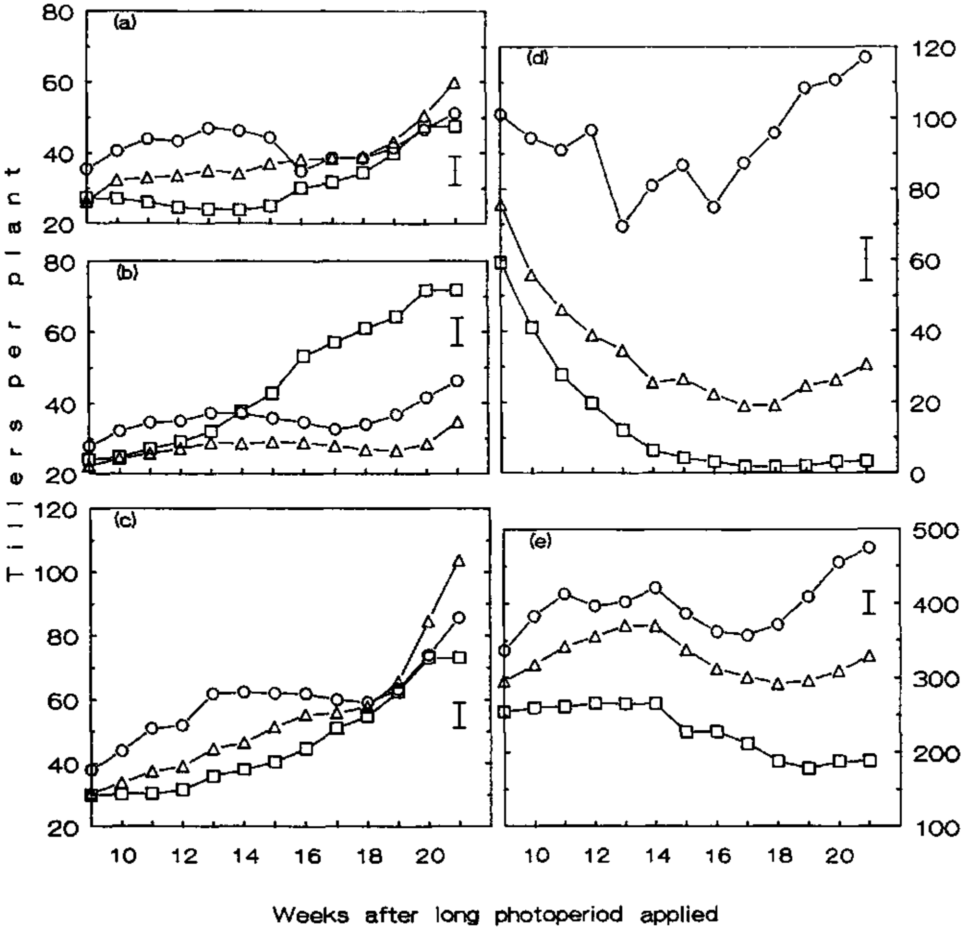


FIG. 4. Tiller numbers per plant during the cutting frequencies. Average of all initial cuts. (a) Matua, (b) Bellegarde, (c) Primabel, (d) Caramba and (e) Wendy, for 1 (□—□), 2 (Δ—Δ) and 4 (○—○) week cutting frequencies. Vertical bars indicate LSD values (*P*<0.05) for significant differences in cutting frequencies.

experiment ie. 3 and 24 tillers per plant for 1 and 2 week cutting respectively.

(c) Numbers of reproductive tillers. Reproductive tillers in Wendy had their apices removed at the initial cuts (mainly at the later initial cuts) or at the following cut after 1, 2 or 4 weeks, depending on the cutting frequency treatment. No further reproductive tillers developed in Wendy after this stage.

Proportions of tillers that were reproductive at each cut and therefore had apices removed killing the tiller, were greatest in Caramba and higher with more infrequent cutting [Table 2]. Caramba had high percentages of reproductive tillers even at 1 and 2 week cutting, but with few emerged inflorescences. Only at 4 week cutting did significant numbers of reproductive tillers have emerged inflorescences in Caramba, but still lower than prairie grass. Cutting frequency had much greater effects on percentages of reproductive tillers at each cut in prairie grass, with over 50% of these tillers having emerged inflorescences even at frequent cutting [Table 2]. Of the prairie grass cultivars, Primabel had the lowest percentages of reproductive tillers and emerged inflorescences, while Matua and Bellegarde were approximately similar in reproductive development, but with high percentages of emerged inflorescences in Bellegarde.

(d) Changes in tiller numbers with cutting and sites of tillering. At all initial cuts and subsequent cuts, tiller death in prairie grass was almost completely attributable to death of the reproductive tillers as their apices were removed. In Caramba and Wendy, vegetative stem elongation resulted in apices being carried above the cutting height and thus adding to the numbers of tillers that were killed at cutting. This was most prominent at later initial cuts with 50% of the vegetative tillers having their apices above the 5 cm cutting height at initial cut 7. Also 20 and 5% of the reproductive tillers in Caramba and Wendy, respectively, had tiller bases above 5 cm. Such large percentages did not occur during the cutting frequencies but in Caramba at 4 week cutting, tiller buds above 5 cm developed on elongated reproductive tillers and so were removed by cutting. Such vegetative stem elongation did not occur in prairie grass and all

FIG. 5. Relative tiller numbers for all cultivars immediately prior to initial cut then 1 day, 1, 2, 3 and 4 weeks after each of initial cuts 1, 3, 5 and 7. The fall in tiller numbers one day after each cut represents the tillers that died due to apices being above the 5 cm cutting height. Also see text. Initial cut 1 (▲--▲), 3 (○—○), 5 (△--△), 7 (□—□). Vertical bars indicate LSD values ($P<0.05$) for significant differences.

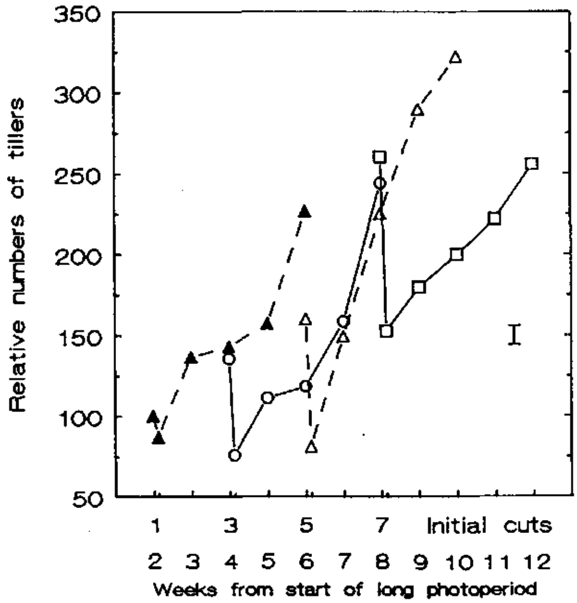


TABLE 3. Percentages of axillary tillers that could be identified as originating from the leaf axils of tagged tillers, three weeks before the end of the experiment. Figures in a row accompanied by the same lower case letter are not significantly different ($P>0.05$).

	Cultivar				
Cutting frequency	Matua	Bellegarde	Primabel	Caramba	Average
1 week	63_b	71_a	64_b	21_c	55
2 week	44_b	31_c	69_a	15_d	40
4 week	16_c	11_d	39_a	30_b	24

tiller buds developing on reproductive stems came from previously inhibited basal tiller buds and not raised on the culm.

Tiller death at each successive initial cut increased as more reproductive tillers elongated carrying the apex above the 5 cm cutting height [Fig. 5]. Within one or two weeks after cutting, tiller numbers had recovered or exceeded their previous levels [Fig. 5] due to extravaginal development of the previously inhibited tiller buds at the bases of reproductive tillers. This varied between initial cuts with initial cuts 3 and 4 taking longer to increase tiller numbers in all cultivars despite a range in stage of reproductive development. At initial cuts 6 and 7, this recovery appeared to be less, but at these cuts the previously inhibited tiller buds at the bases of reproductive tillers were starting to develop before the herbage was cut, particularly in Caramba and Wendy.

This pattern of death and recovery continued with the 4 week cutting frequency, except for Wendy, where there was no reproductive growth. The death and subsequent increase in tiller numbers was less with more frequent cutting, because of lower reproductive growth at cutting, and less in cultivars that had lower reproductive growth eg. Primabel [Table 2].

With more frequent cutting, less tillers came from inhibited reproductive tiller buds (extravaginal) and a greater number of new tillers arose from vegetative tillers (intravaginal). This is illustrated in Table 3 where greater percentages of axillary tillers could be identified as originating in the leaf axils of tillers, and so not from the base of the tiller as occurring on reproductive tillers. With infrequent cutting, few vegetative tillers had axillary tillers until they became reproductive. Tiller buds then developed either just prior to cutting (particularly in Caramba) or after cutting. In Caramba at 1 and 2 week cutting these percentages were much lower, an indication of the poor tillering in Caramba at these cutting frequencies. At 4 week cutting, Caramba had a relatively high percentage of axillary tillers than would be expected for the high degree of reproductive growth in this cultivar. This was primarily because tiller buds developed not only from the base of reproductive tillers, but also from tiller buds raised on the culm and thus were identified as coming from a leaf axil.

(e) Leaf appearance and reproductive development of tagged tillers. LAR in Wendy was similar on all tillers in all treatments (0.099 leaves/tiller/day) ($P>0.05$), while Caramba had significantly higher LAR (0.121) with no significant effect of treatment ($P>0.05$). Average LAR in Matua was 0.130, Bellegarde 0.124 and Primabel 0.139 ($P<0.01$) ($LSD_{0.05}=0.005$), with no significant effect of cutting frequency ($P>0.05$).

With later initial cuts a greater proportion of the first tagged tillers were reproductive and thus had their apices removed (mean, 80% of tillers killed by initial cuts). More of the second and third tagged tillers survived the initial cut because of later reproductive development (mean, 50% of tillers killed by initial cuts). Reproductive tillers that survived the early initial cuts, soon had their apices removed at the subsequent 1, 2 or 4 week cuts. The third tagged tiller and subsequent tagged tillers in Caramba all showed very rapid reproductive development and thus considerable tiller death occurred at each cutting making it difficult to assess LAR compared to the other cultivars. In Wendy, the third tagged tiller and subsequent tagged tillers remained vegetative for the rest of the experiment.

(f) Herbage quality. Quality of the regrowth 1, 2 and 4 weeks after each initial cut, generally increased the later the initial cut was taken. On average, CWC, D_{om} and D_{cwc} were 49, 80 and 80% respectively for the regrowth from the first three initial cuts, and 47, 82, and 84% respectively for the remaining initial cuts. Assessment of herbage quality later in the experiment showed significant effects of initial cutting time, but differences were few and not consistent.

Assessment of herbage quality (a) of regrowth one, two and four weeks after each initial cut, (b) four weeks after each initial cut for each cutting frequency, and (c) quality at the end of the experiment, all showed similar results for the effects of cultivar and cutting frequency [Fig. 6]. Herbage quality decreased in a significant quadratic manner with decreasing cutting frequency ($P<0.01$). The 1 week cutting frequency had low CWC and high digestibility. A slight decrease in quality occurred at 2 week cutting, but at 4 week cutting, CWC increased considerably and large decreases occurred in D_{cwc} and D_{om}.

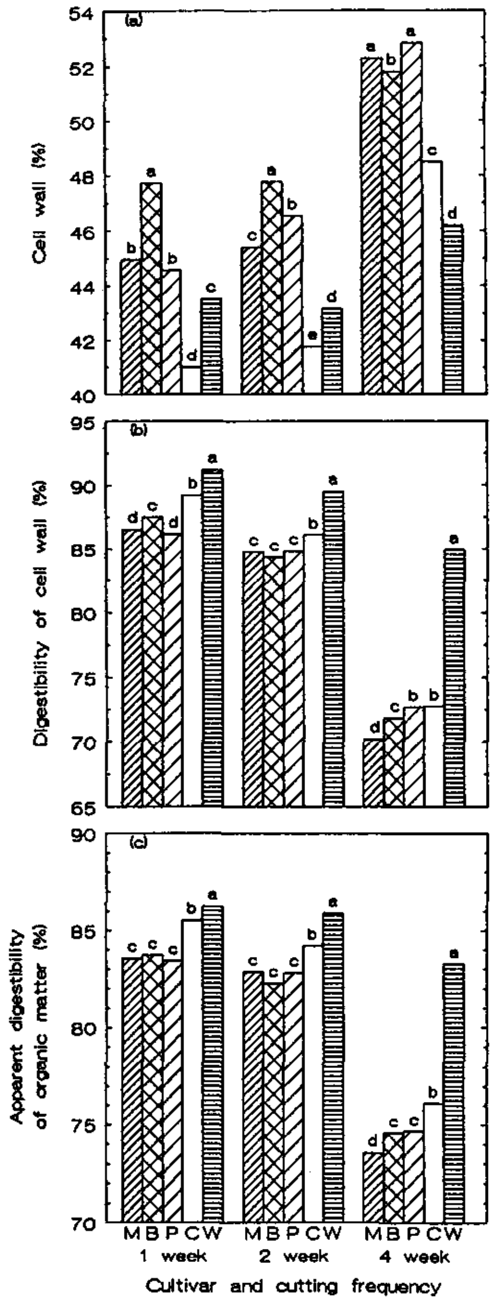


FIG. 6. Average herbage quality after the initial cuts as affected by cutting frequency and cultivar, Matua (M), Bellegarde (B), Primabel (P), Caramba (C) and Wendy (W). (a) Cell wall contents, (b) digestibility of cell wall, and (c) apparent digestibility of organic matter. Within each cutting frequency, bars accompanied by the same lower case letter are not significantly different ($P>0.05$).

The cultivars responded differently to cutting frequency. Wendy which had few reproductive tillers in the herbage, had relatively small decreases in herbage quality with increasing cutting frequency. The prairie grass cultivars and Caramba had large decreases in quality with 4 week cutting. Overall, Wendy had the highest herbage quality while prairie grass had the lowest quality. Caramba had good digestibility and low CWC at 1 and 2 week cutting, but with 4 week cutting digestibility was comparable to prairie grass. The prairie grass cultivars generally had similar herbage quality, but Bellegarde had high CWC at 1 and 2 week cutting and Matua had significantly lower digestibility at 4 week cutting.

Vernalization

The only significant effect vernalization had on Matua and Caramba was a lower number of leaves to appear in Matua at inflorescence emergence on vernalized main tillers (5.5) than on non-vernalized main tillers (9). Inflorescences on the main tiller of vernalized Matua plants therefore emerged two to three weeks before non-vernalized plants, resulting in a higher percentage of reproductive tillers in vernalized (75%) than non-vernalized (40%) plants.

DISCUSSION

Response to cutting frequency

It is generally reported that under frequent defoliation prairie grass performs poorly relative to other species (Langer and Hill, 1982; Burgess *et al.*, 1986). The results of the present study support this for reproductive plants of prairie grass. This is in contrast to defoliation of vegetative prairie grass plants (Chapter 4 this thesis), where production was reduced by frequent defoliation, but response was similar to that occurring in ryegrass. In the present experiment, prairie grass did adapt surprisingly well to frequent cutting producing high tiller numbers, but yields per tiller and per plant were low. Leaf sheaths shortened in prairie grass giving a leafy stubble with leaf lamina being the major component of the harvested herbage.

Reproductive tillers also shortened considerably so that only when inflorescences emerged were apices carried above the cutting height. This resulted in relatively high numbers of reproductive tillers with emerged inflorescences in prairie grass despite frequent cutting. So even under frequent defoliation, prairie grass may produce inflorescences which are important for natural reseeding in this species (Chapter 8 this thesis).

Caramba responded quite differently to prairie grass as cutting frequency increased. With its rapid reproductive growth, Caramba continued to produce high numbers of reproductive tillers which would start to elongate only three to four weeks after appearing in a leaf axil. Shortening of the leaf sheaths did not appear to occur to the same extent as in prairie grass, especially not in reproductive tillers of Caramba. These reproductive tillers were therefore quickly killed with frequent cutting, creating high tiller losses, and combined with lower tillering from vegetative tillers, tiller numbers declined dramatically with frequent cutting. This also resulted in some plant death.

Tiller losses at cutting were also increased in Caramba and Wendy by vegetative stem elongation and development of tiller buds raised on the culm. This did not occur in prairie grass. Minderhoud (1978) recorded similar high levels of elongation, especially at high nitrogen levels. This type of development enables some widening of the base of the plant when raised tillers are able to root to the ground. This allows ryegrass plants to spread and fill gaps in a sward (Minderhoud, 1978, 1980), but this does not occur in prairie grass (Eteve, 1982). This type of tillering can also suppress the formation of vegetative tillers at the tiller bases.

In practice, monocultures of prairie grass or Westerwolds ryegrass will be rare and these grasses will be growing with other sown species (grasses, legumes) and 'weed' species (eg. *Poa annua* L.) in the sward. Some of these species will be better adapted to frequent defoliation and will therefore be strong competitors for nutrients and light. The relatively poor performance of the prairie grass cultivars and Caramba with frequent cutting in the present experiment will therefore become more pronounced under field conditions. The relatively good performance of Wendy perennial ryegrass during frequent cutting is an example of a species that has relatively good growth under such conditions, and is a reason why mixtures of prairie grass and perennial ryegrass are usually not recommended (Burgess *et al.*, 1986).

Response to initial cutting time

Importance of time of the initial cut in relation to stage of reproductive development as it affects regrowth has been clearly demonstrated for timothy (*Phleum pratense* L.) and ryegrass (Jewiss and Powell, 1966; Davies, 1969; Davies, 1973). In the present experiment, regrowth after each initial cut appeared to be independent of the stage of reproductive development. This suggests that environmental factors or other plant parameters not measured in this study were having a greater influence.

For Bellegarde in the field, Eteve (1982) and Parneix (1981, 1982) also gained similar results to those recorded in the present study. Both researchers have noted that later initial cuts increase the yield of the initial cut, and increase the total annual yield but only due to the high yield at the initial cut. Initial cuts taken too early (plant vegetative) or very late (anthesis) were detrimental to good summer performance, but otherwise the species appeared to have a good flexibility of management and good recovery even after late cuts. Parneix (1981) also recorded similar levels and decreases in nitrogen and increases in water soluble carbohydrate contents with later initial cutting. Cabos (1985) has noted a build up in reserves (chemical composition not stated) peaking at inflorescence emergence, depleted at cutting and reserves increasing again as long as there was enough time between defoliations. The best time for defoliation could be when the levels of water soluble carbohydrates are at a peak, and may be linked with the development of inhibited tiller buds before defoliation.

Jewiss and Powell (1966) found that regrowth was most closely related to water soluble carbohydrates in the primary tillers of timothy, presumably due to higher growth of inhibited buds, and to stubble weight of primary tillers, presumably due to the direct growth that vegetative tillers produce. Water soluble carbohydrates increase in the stubble during reproductive development in late spring (Weinmann, 1952; Pollock and Jones; 1979), and it appears that these reserves are used in the formation of new tillers (Awopetu, 1979; Davies, Evans and Sant, 1981). In the present study, water soluble carbohydrates increased to high levels in reproductive stubble particularly in prairie grass, while vegetative stubble weight declined slightly with time. The results of Jewiss and Powell (1966) would suggest that in the current experiment these two factors may have been operating against each other. Whatever the factors involved in the current study, regrowth after four weeks was similar for all initial cuts.

Tillers

The pattern of tiller death (mainly reproductive tillers) at cutting followed by rapid recovery of tiller numbers as previously inhibited tiller buds developed at the base of reproductive tillers, has also been documented for other grass species (Jewiss and Powell, 1966; Awopetu, 1979; Davies, Evans and Sant, 1981). With the continual production of high numbers of reproductive tillers in prairie grass and Westerwolds ryegrass during the long photoperiods of the growing season, tiller populations are therefore completely renewed several times in the year. The greater the level of reproductive growth, either through more infrequent cutting or in cultivars with faster reproductive growth, tillering became more reliant on the development of these reproductive tiller buds with less tillering from the vegetative tillers that were present at cutting.

Observations in a field trial at Wageningen (Chapter 6 this thesis) and in other glasshouse experiments confirm this pattern of tiller death and recovery at cutting, with similar development of tiller buds at the base of reproductive tillers (Hume, unpublished data). In the field trial, the first cut in spring had the greatest tiller loss (70-80% tillers reproductive at cutting) and greatest recovery in tiller numbers, with fewer reproductive tillers at the following cuts, similar to the pattern in the present experiment. In New Zealand, high numbers of reproductive tillers (70%) have been recorded in the field in late spring, with rapid recovery in tillers within four weeks (Chapter 8 this thesis).

In some cases cutting was not required to allow inhibited tiller buds to develop. This also occurs in other species (Langer, 1956) and occurred more readily in Caramba than prairie grass. Similar results have been gained in field trials with Matua and Caramba (Chapter 2 this thesis; Hume, unpublished data) with the death of these new tillers occurring in Caramba if the sward was not cut. This indicates that Caramba may require relatively shorter regrowth intervals than prairie grass when grown in the same situation. The decision to defoliate should therefore not be based solely on period of regrowth but also on observations of new tillers developing.

Leaf appearance

Leaf appearance in prairie grass during the cutting treatments continued to be significantly higher than in Caramba and Wendy with no significant effect of cutting frequency. Of the prairie grass cultivars, leaf appearance was actually highest in Primabel and lowest in Bellegarde. To understand these results it must be recognized that different factors can be operating in different situations. In prairie grass in treatments where reproductive growth is lower (eg. 1 week cutting frequency, Primabel), there are fewer reproductive tillers present and so fewer tillers with accelerated leaf appearance, but fewer tiller deaths at cutting. In contrast, where reproductive growth is greater (4 week cutting frequency, Bellegarde), high leaf appearance rates occur during stem elongation, but as inflorescences emerge leaf appearance rates decline and become zero as leaves cease to appear. The overall result may therefore be different to what could be expected from observations of undisturbed growth. Similar observations of leaf appearance in a field trial confirm these results for the prairie grass cultivars and Caramba (Hume, unpublished data).

Other plant parameters

The important contribution made by reproductive tillers to yields of prairie grass and Caramba as identified in previous studies (Chapters 2 and 6 this thesis) was also evident in the present experiment. The proportion of yield coming from reproductive growth was approximately double the proportion of reproductive tillers present. This effect was similar for all cutting frequencies. In Wendy the role of reproductive tillers was limited to a relatively small portion of the experiment or the growing season in the field. This in part explains the lower yields and high quality of Wendy with infrequent cutting.

The analysis of plant parameters during the period of undisturbed growth prior to the final initial cut, confirms results gained in the field situation with Matua and Caramba (Chapter 2 this thesis) and in glasshouse experiments including the three prairie grass cultivars (Chapter 3 this thesis). It can be summarized that Wendy generally has high tillering and herbage quality, but leaf appearance is low even during reproductive stem elongation and yields are low partly because of later reproductive development. Prairie grass has lower herbage quality and tillering, but high leaf appearance rates and yields. Caramba is intermediate, although comparable to prairie grass in terms of yield but with rapid reproductive development and few leaves appearing by the time of inflorescence emergence. Of the prairie grass cultivars, Bellegarde has high levels of leaf appearance until inflorescence emergence, rapid reproductive development and high yields, but lower herbage quality and tillering. Primabel has lower leaf appearance rates and reproductive growth, but higher tiller numbers. Matua is generally in between the other two cultivars for these plant parameters.

These cultivar differences were modified considerably by the cutting frequencies. With no reproductive tillers, Wendy continued to have high herbage quality, but yields were relatively low with infrequent cutting and relatively high with more frequent cutting. In contrast, yields were low for frequently cut prairie grass and Caramba, but herbage quality was relatively high. Infrequent cutting allowed greater reproductive growth and thus high yields, especially in Caramba, although Bellegarde did not respond to the same degree and had low yields relative to the other prairie grass cultivars and Wendy.

Vernalization

Analysis of the effects of vernalization on Caramba

Westerwolds ryegrass and Matua prairie grass is important for the results of this study to be placed in the context of a field situation. Faster reproductive development of Matua tillers that had previously been growing at 4°C indicates a quantitative response to vernalization, though not obligatory. Karim (1961) also reported similar responses in a range of cultivars although there was considerable cultivar variation. In the field, this will result in earlier heading of tillers that have grown through the winter than spring formed tillers and so high yields earlier in spring. Field observations of heading in Matua, Bellegarde and Primabel at Wageningen confirm this (Hume, unpublished data). Eteve (1982) also reports that spring formed tillers head two to four weeks later in Bellegarde than tillers formed before winter. If vernalized prairie grass had been used in the main experiment in the present study, earlier reproductive development would have occurred in prairie grass resulting in greater yield differences relative to ryegrass. The lack of response to vernalization in Caramba is similar to results gained by Cooper and Calder (1964).

Conclusions

It could be expected from these results that in the field, perennial ryegrass would be the best species to use in situations of frequent defoliation. With infrequent defoliation, Wendy will produce the highest quality herbage but lower yields of dry matter and digestible organic matter than Matua, Primabel and Caramba. Prairie grass and Westerwolds ryegrass will perform best under infrequent cutting with Primabel and Matua being the best prairie grass cultivars. Later initial cutting will improve total yields and the yield at the first cut, but quality of the first cut will decrease. For the cultivars and conditions in this study, time of initial cutting had little influence on regrowth and very little correlation with stage of reproductive development or any of the measured plant parameters.

CHAPTER 6

Growth of prairie grass (*Bromus willdenowii* Kunth) and Westerwolds ryegrass (*Lolium multiflorum* Lam.) at Wageningen, The Netherlands

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Abstract

Herbage quality, yields, tiller and plant populations of 'Grasslands Matua' prairie grass and 'Caramba' tetraploid Westerwolds ryegrass were investigated in a two year field trial on a sandy soil. Plots were either harvested frequently (5-6 cuts per year) or infrequently (4 cuts). During the first year, herbage was separated into leaf, vegetative and reproductive pseudostem, and analysed separately.

With very mild winters and adequate water supply, swards had good persistence and production for two years. Total yield in the first year, 10.5 t DM ha^{-1}, was similar for both species. Yields in the second year were (t DM ha^{-1}) 13.4 and 18 for Matua and 11.1 and 13 for Caramba under frequent and infrequent cutting respectively. Leaf contributed 58% to yields and reproductive pseudostem 35%. Infrequently cut plots had; 23% higher dry matter yields primarily due to higher yields of reproductive pseudostem; higher yields of most chemical components and higher contents of water soluble carbohydrates and cell walls; lower digestibility and nitrogen content. Cell wall content was consistently higher in Matua but otherwise herbage quality was similar for the two species. It is suggested that prairie grass should at least be considered as a replacement for spring sown Westerwolds ryegrass on sandy soils in The Netherlands.

Introduction

Prairie grass or paardegras (*Bromus willdenowii* Kunth) is a true perennial grass originating in the Pampas of South America, and now has a very wide geographical distribution (Hafliger and Scholz, 1981). In the past, accidental introduction of prairie grass to The Netherlands occurred near sea ports and some cultivation has been practised (Jansen, 1951). It did not become a permanent stable species in the Dutch environment as it apparently did not survive hard winters (Jansen, 1951; Heukels and Van der Meijden, 1983). There are now a number of prairie grass cultivars available which have proven to be highly productive in a number of countries eg. France (Anon, 1982), New Zealand (Fraser, 1985) and the United Kingdom (Anon, 1986). No detailed studies have been published on the performance of prairie grass in The Netherlands. A field trial was therefore conducted to provide information on productivity, persistence and herbage quality of prairie grass in order to identify possible roles prairie grass may have in Dutch agriculture.

Materials and methods

Site and treatments

The trial site was at Wageningen Hoog, three km from Wageningen city, on a light free draining pleistocene sandy soil of moderate fertility; pH-KCl 5.4, organic matter 2.6%, 25 mg P (ammonium lactate acetic acid extracted), 9 mg K (HCl extracted) and 4 mg Mg (NaCl extracted) per 100 g dry soil. The trial area had been under various crops for the previous six years, with high fertilizer inputs.

Plots (11.5 x 8 m) were hand sown with either 'Grasslands Matua' prairie grass (*Bromus willdenowii* Kunth) or 'Caramba' tetraploid Westerwolds ryegrass (*Lolium multiflorum* Lam.) in a randomised block design replicated four times. Matua plots were sown with 505 viable seeds m^{-2} (60 kg viable seed ha^{-1}) on 13 April 1987 and Caramba plots with 925 viable seeds m^{-2} (40 kg viable seed ha^{-1}) on 21 April 1987. Approximately 20 mm of water was applied by spray irrigation one week after sowing the Caramba plots. Half the area of each plot (5.75 x 8 m) was used for detailed growth and quality analysis as reported in Chapter 2 of this thesis. The remaining area of each plot was used in the current study and divided into either frequent or infrequent cutting.

Along side this trial, small unreplicated plots (8 m^2) of three prairie grass cultivars, 'Grasslands Matua', 'Bellegarde' and 'Primabel', were sown at 505 viable seeds m^{-2} on 13 April 1987. These plots received the same management as the infrequent cutting treatment. Irrigation was used once in 1988, with 25 mm of water being applied to all plots in mid-June.

Measurements

At the first harvest on 3 July 1987, all treatments were cut to a height of 5 cm. Frequent plots were then harvested on four occasions and infrequent plots on three occasions during the remainder of 1987. During 1988, frequent plots were harvested on six occasions and infrequent plots on four occasions. Final harvests in both years were taken in late October.

At each harvest, total herbage yield was determined by cutting a strip of 6 x 0.88 m at 5 cm height from each plot. The cut herbage was weighed and subsampled for determination of dry matter and herbage quality. During 1987, samples were dissected to assess yields and quality of leaf lamina, vegetative pseudostem and reproductive pseudostem (culm, sheath of reproductive tillers and inflorescence). Immediately prior to each harvest, populations of vegetative tillers, jointed tillers and tillers with emerged inflorescences were determined by counting two 0.25 m^2 quadrats in each plot. Tiller populations were also determined in early April 1988 and 1989. Plant populations were assessed at the final harvests in late October 1987 and 1988, and in early April 1988 and late March 1989.

Herbage yields, tiller and plant populations for the small plots of Matua, Bellegarde and Primabel were only recorded during 1988, with tiller and plant populations also being assessed in late March 1989.

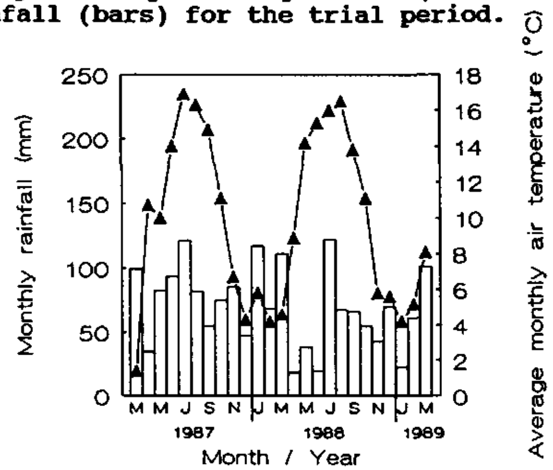
Herbage quality

Herbage samples were ground in a hammer mill with 1 mm sieves and the four replicates bulked to give two replicates for determination of herbage quality by chemical analysis. True *in vitro* digestibility of the organic matter was determined using the method of Van Soest *et al.* (1966) and then converted to apparent digestibility of organic matter (D_{om}) by reference to a series of standard grass samples with known *in vivo* digestibility for sheep. Cell wall constituents (CWC) were determined by Van Soest's (1977) method. Ash, nitrogen and water soluble carbohydrates were also measured. Digestibility of cell wall (D_{cwc}) was calculated from true digestibility, cell wall content and ash content.

Fertilizers and herbicides

Trace elements and 90 kg N, 72 kg P_2O_5 and 144 kg K_2O ha^{-1} were applied prior to sowing. A further 485 kg N, 64 kg P_2O_5 and 128 kg K_2O ha^{-1} were applied during the remainder of 1987. Total fertilizer applications in 1988 were 350 kg N, 200 kg P_2O_5 and 200 kg K_2O ha^{-1}. Last nitrogen applications were in mid-September and mid-August for 1987 and 1988 respectively. In early January 1989, 25 kg N ha^{-1} was applied to all plots as nitrogen deficiency was apparent during a mild winter. Plots were sprayed in mid-May 1987 with 4 l ha^{-1} 'Basagran P' (375 g mecoprop and 250 g bentazon l^{-1}) for control of broad-leaved weeds.

Figure 1. Average monthly air temperature (150 cm height) (line) and total rainfall (bars) for the trial period.



Climate

Temperature and rainfall records for the trial period were obtained from the Wageningen, Haarweg meteorological station, four km from the trial site.

Results

Temperature and rainfall

Mean air temperature (13.5°C) for the growing season, April to October, in both years was very similar to the 30-year average (13.4°C) (Figure 1). Temperatures in both winters (November to March) (5.2°C) were well above the 30-year average (3.5°C), being as high as 4°C above average in some months. Rainfall was greater than 50 mm per month during the growing season except for April 1987 and April, May and June 1988 when it was dry and plots were irrigated on two occasions (Figure 1). Total rainfall for the 1987 growing season (544 mm) was 18% above the 30-year average (460 mm) and in 1988 rainfall (390 mm) was 15% below average.

Tiller and plant populations

(a) 1987. Tiller populations were relatively high at the first harvest in early July 1987 (Table 1). Populations then rose by 30% in all treatments except Matua frequent, but then declined to relatively constant levels for the rest of 1987 of 1300 and 2400 tillers m^{-2} for Matua and Caramba respectively ($P<0.01$). Plant populations declined considerably from the first to the last harvest (October 1987), while plant size increased from 5 to 13 tillers $plant^{-1}$ over this time period. There were no significant differences between cutting frequencies for tiller and plant populations during 1987.

(b) 1988/89. The first measurement in early April 1988 showed a decrease in plant populations over winter (Table 1). Tiller populations also declined with the largest reduction occurring in Caramba plots. Cutting frequencies showed no significant differences at this date ($P>0.05$). During 1988, tiller populations increased the most in frequently cut plots. A peak in tiller populations occurred in late July with 2800 and 1760 tillers m^{-2} in frequently and infrequently cut plots respectively

Table 1. Numbers of tillers and plants m^{-2} for Matua and Caramba at five dates. ns indicates means that are not significantly different ($P>0.05$), * $P<0.05$, ** $P<0.01$, *** $P<0.001$.

Sward parameter Cultivar	Tillers m^{-2} Matua		 Caramba	Plants m^{-2} Matua		 Caramba
July 1987	1600	**	3000	350	**	510
October 1987	1275	***	2375	110	**	160
April 1988	745	*	850	85	***	120
October 1987	1660	ns	1990	90	ns	100
March 1989	1150	ns	920	95	ns	100

($P<0.01$). Differences between species occurred at several dates but these were always changing in terms of magnitude and species order. At the final harvest there were no significant treatment differences (Table 1) and an average of 19 tillers plant^{-1}. After winter 1988/89, there were again no significant treatment differences (Table 1).

Reproductive tillers occurred at all harvests in 1987 and 1988, with infrequently cut plots having 31% of the total tillers reproductive and frequently cut plots 17%. During 1988, Caramba frequently cut plots had a greater percentage of reproductive tillers (31%) than Matua frequently cut plots (14%) ($P<0.01$).

Herbage yields

(a) 1987. Total herbage dry matter yields during 1987 were 20% higher for infrequently cut plots (11500 kg DM ha^{-1}) than frequently cut plots (9570) (Figure 2). This was primarily due to yields of reproductive pseudostem being 54% higher in infrequently cut plots ($P<0.01$). Infrequently cut plots had an average content of 52% leaf, 8% vegetative pseudostem and 40% reproductive pseudostem compared to 60, 10 and 30% respectively for frequently cut plots ($P<0.05$ for all yield components). There were no significant species differences for total annual yield in 1987, but at five of the eight harvests significant species differences did occur, although these differences varied in

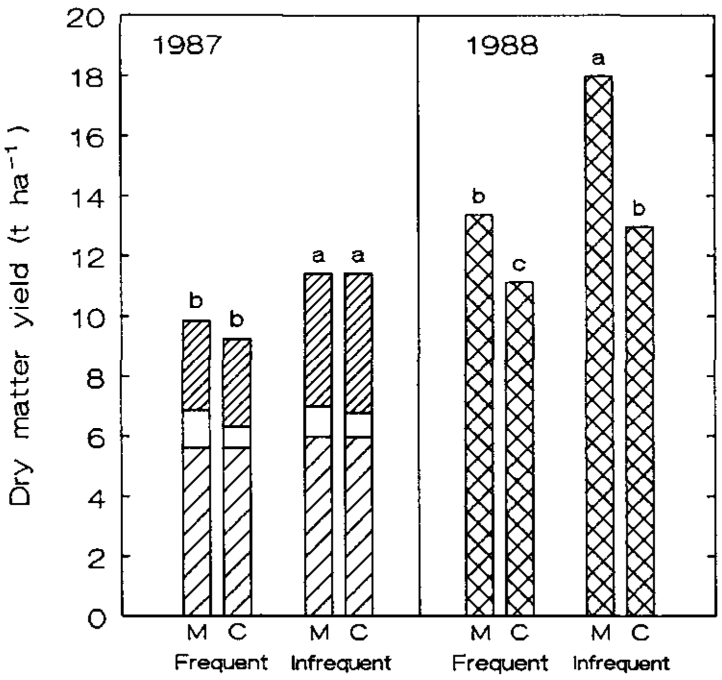


Figure 2. Total dry matter yield for frequently and infrequently cut Matua (M) and Caramba (C) plots in 1987 and 1988. For 1987 leaf is represented by (▨), vegetative pseudostem (□), reproductive pseudostem (▨), and in 1988 total yield (☒). Bars accompanied by the same letter are not significantly different (*P*>0.05) for total yield within each year.

magnitude and species order. These differences were generally due to higher yields of all plant components and not just one particular component. At each harvest there were a number of significant species differences for the yields of plant components but there was little consistency in these differences. Content of dead matter was low (<1%).

(b) 1988. A significant interaction occurred for total yield in 1988 with the greatest yield occurring in Matua plots cut infrequently (17970 kg DM ha^{-1}) and the least in Caramba plots cut frequently (11120) (Figure 2) (*P*<0.01). The interaction was due to low yields of infrequently cut Caramba plots up until 21 July (a dry period of the year), so that at this date total Caramba yield did not differ significantly between cutting treatments. It was during this first half of the growing season that the

biggest species differences in herbage yields occurred (44% higher yield in Matua than Caramba). Differences in yield for the second half of the season were considerably less (5% higher yield in Matua). Yields at the first harvest in 1988 were high (4650 kg DM ha^{-1}), being greatest in Matua infrequently cut plots (7760), representing 43% of the total annual yield for this treatment. In the other treatments, yield of the first harvest (3620 kg DM ha^{-1}) represented 29% of total annual yield.

Herbage quality

(a)1987. For the total sward in 1987, infrequently cut plots had on average significantly higher WSC% and CWC%, and lower N%, D_{om}% and D_{cwc}% than frequently cut plots (Table 2). This was also generally true for the contents in each yield component (ie. leaf, vegetative pseudostem, reproductive pseudostem). Leaf had the highest N%, D_{om}% and D_{cwc}%, and the lowest CWC% and WSC% (Table 3). In contrast, reproductive stem had low N%, D_{om}% and D_{cwc}%, and high CWC% and WSC%. Vegetative pseudostem had the highest WSC% while levels (%) of N, D_{om}, D_{cwc} and CWC were between those of leaf and reproductive pseudostem (Table 3).

Infrequently cut plots had significantly higher yields of WSC, CWC, D_{cwc} and D_{om} (Table 2). This was primarily due to infrequently cut plots having greater yields of these chemical components from reproductive pseudostem. Yields of N were approximately equal for the two cutting frequencies with 70% of N yield coming from leaf. High WSC content of pseudostem (Table 3), especially in infrequently cut plots, resulted in 57 and 66% of total WSC yield coming from pseudostem for frequent and infrequent cutting respectively. Approximately 10% of the total yields of CWC, D_{cwc} and D_{om} came from vegetative pseudostem, while 40, 35 and 30 % came from reproductive pseudostem and 50, 55 and 60% from leaf, respectively.

Species did not differ in terms of yields of chemical components but Matua had significantly lower WSC%, D_{cwc}% and D_{om}% and higher CWC% than Caramba (Table 2). This was also generally true for the contents in each yield component (ie. leaf, vegetative pseudostem, reproductive pseudostem). N% was similar for the two species. Only one significant interaction occurred and this was for D_{cwc}%. Species had similar D_{cwc}% in plots cut

Table 2. Percentage of chemical components in the total dry matter or organic matter yield for 1987, and total yields of chemical components for 1987. ns ($P>0.05$), * $P<0.05$, ** $P<0.01$, *** $P<0.001$.

Chemical Component	Cultivar			Cutting Frequency			Mean
	Matua		Caramba	Frequent		Infrequent	
N%	3.7	ns	3.7	4.1	**	3.4	3.7
N kg ha^{-1}	400	ns	380	380	ns	400	390
WSC%	8	*	10	8	*	10	9
WSC kg ha^{-1}	840	ns	1090	770	*	1160	965
CWC%	54	*	49	50	**	53	52
CWC kg ha^{-1}	5790	ns	5100	4700	*	6190	5445
D_{cwc}%	75	*	77	79	**	74	76
D_{cwc} kg ha^{-1}	4350	ns	3910	3690	*	4570	4130
D_{om}%	74	*	76	78	**	73	76
D_{om} kg ha^{-1}	7020	ns	6990	6370	*	7640	7005

Table 3. Percentage of chemical components in the total dry matter or organic matter yield of leaf, vegetative and reproductive pseudostem for 1987. Averages of all treatments. Figures in a row that are accompanied by the same lower case letters are not significantly different ($P>0.05$).

Chemical Component	Percentage content in		
	Leaf	Vegetative pseudostem	Reproductive pseudostem
N	4.8_a	3.3_b	2.3_c
WSC	6_c	16_a	12_b
CWC	46_c	50_b	62_a
D_{cwc}	84_a	79_b	67_c
D_{om}	82_a	79_b	64_c

infrequently but Caramba had significantly higher D_{cwc}% in plots cut frequently ($P<0.05$).

WSC% of pseudostem showed major changes with time. WSC% dropped from high levels at the first harvest, 15 and 19% for vegetative and reproductive pseudostem respectively, to 5-10% at the following harvests. WSC% then increased at the final harvest to 23 and 31% for vegetative pseudostem and 17 and 22% for reproductive pseudostem for Matua and Caramba respectively. WSC% of leaf also increased from 5 to 11%. Similar trends also occurred in 1988, with WSC% dropping from 28% at the first harvest to 7% and increasing to 13% at the final harvest.

(b)1988. In general, Matua herbage in 1988 had significantly (P<0.05) greater WSC%, CWC% and D_{cwc}%, with N% being higher in Caramba and D_{om}% being approximately equal (P>0.05) for the two species (Table 4). Matua had higher yields of all chemical components, primarily due to the greater herbage yields of Matua plots rather than the higher chemical composition (Table 4). Infrequent cutting decreased herbage digestibility (D_{om} and D_{cwc}), N% and N yields, while increasing CWC%. Infrequent cutting increased yields of all other chemical components for Matua, but for Caramba, only CWC yield increased with infrequent cutting.

Infrequently cut Matua plots had low N% (Table 4), especially at the first harvest when content was 1%. N% increased during the year to be 3-4% in all treatments at the final harvest. Infrequently cut Matua plots had the highest content of WSC while infrequently cut Caramba plots had the lowest content. Infrequent cutting increased CWC% in both species, especially in Caramba, with average CWC% being higher in Matua than Caramba. D_{cwc}% and D_{om}% were lower in infrequently cut plots. Herbage harvested in the middle of the growing season had higher CWC% and lower D_{cwc}% and D_{om}% than herbage harvested early or late in the season.

Small plots of prairie grass

The three prairie grass cultivars were very similar in all aspects. Herbage quality, and plant and tiller populations were similar to those in the infrequently cut Matua plots of the main trial. Yields of these plots for 1988 were 16.6, 15.2 and 15.3 t ha^{-1} for Matua, Bellegarde and Primabel respectively.

Table 4. Percentage of chemical components in the total dry matter or organic matter yield for 1988, and total yields of chemical components for 1988. Figures in a row that are accompanied by the same lower case letters are not significantly different ($P>0.05$) for the species x cutting frequency interaction and those with the same upper case letters are not significantly different ($P>0.05$) for average of the cutting frequencies.

Chemical Component	Frequent			Infrequent		
	Matua	Caramba	Mean	Matua	Caramba	Mean
N%	2.6_b	2.8_a	2.7_A	1.8_d	2.2_c	2.0_B
N kg ha^{-1}	360	310	335_A	320	270	295_B
WSC%	16_b	15_b	15.5	19_a	13_c	16.0
WSC kg ha^{-1}	2170_b	1680_c	1925_B	3570_a	1690_c	2630_A
CWC%	55_c	50_d	52.5_B	59_a	56_b	57.5_A
CWC kg ha^{-1}	7620_b	5650_d	6635_B	10940_a	7070_c	9005_A
D_{cwc} %	71	69	70.0_A	58	57	57.5_B
D_{cwc} kg ha^{-1}	5380_b	3890_c	4635_B	6380_a	4040_c	5210_A
D_{om} %	73	74	73.5_A	64	64	64.0_B
D_{om} kg ha^{-1}	9200_b	7580_c	8390_B	11060_a	7480_c	9270_A

Discussion

With good rainfall levels and irrigation when required, high levels of herbage production on this light free draining soil were achieved for both species. Adequate summer moisture and very mild winters enabled good survival of Caramba into the third year. This is unusual for this species as it is regarded as a true annual (De Haan, 1955). The very mild winter temperatures did not in any way test the tolerance of prairie grass to the cold winter conditions that may be experienced in The Netherlands or in North West Europe. It is known that Bellegarde has a low tolerance to cold temperatures (Betin, 1982) but there was no apparent decline in Bellegarde in the present study. Several prairie grass cultivars have been successfully grown in NIAB cultivar trials in England over the past ten years with *Bromus* species demonstrating good winter hardiness when given the correct management (Anon, 1986). Further years of testing with different cutting and nitrogen managements prior to winter would be needed to fully test the degree of winter survival of prairie grass in The Netherlands.

Although there was relatively little difference in 1987 between cutting frequencies, five harvests for frequent and four for infrequent, infrequent cutting increased herbage yield by 20% and yields of most chemical components were also increased. Infrequent cutting did not significantly increase N yield, but N content and digestibility decreased, and CWC% and WSC% increased. Similar results occurred in 1988 although there were several species x cutting frequency interactions. These interactions were primarily due to infrequently cut Caramba plots only having significant increases in the yields of dry matter and CWC. With reductions in digestibility and contents of chemical components, harvesting Caramba only four times in 1988 (infrequent) was a disadvantage. Although yields of dry matter and chemical components increased in Matua with infrequent cutting in 1988, decreases in digestibility, high CWC% and lower N content indicate that infrequent cutting was also detrimental to production of quality forage in Matua.

As discussed in Chapter 2 of this thesis, it is important to gain a balance between obtaining high yields and maintaining forage quality. In 1987, this was apparently controlled by the amount of reproductive pseudostem (culm, sheath, inflorescence) that was allowed to develop, as it was the extra reproductive pseudostem that contributed the most to the higher chemical and dry matter yields. Yields of vegetative pseudostem and leaf did not change significantly with infrequent cutting. Guidelines suggested for optimum timing of harvests based on proportion of reproductive tillers and emerged inflorescences (Chapter 2 this thesis), would predict in the present study that both frequencies of cutting in 1987 were optimal, but only frequent cutting in 1988 was optimal for herbage production and quality. More frequent cutting may be considered in order to gain higher forage quality, but yields will be reduced and problems of persistence may arise because neither species performs well under defoliation regimes that are too frequent.

Leaf and reproductive pseudostem were the most important components of the sward. Contribution from reproductive pseudostem was less at the end of the season when reproductive development was minimal, but on average it contributed 35% to yields whereas leaf contributed 58%. Although reproductive pseudostem decreased total sward N% and digestibility, and increased CWC, it had high WSC% and contributed to high dry matter yields and high yields of most chemical components. The importance of reproductive pseudostem in determining yields and quality of prairie grass and Westerwolds ryegrass has been emphasised in Chapter 2 of this thesis.

Species differences in terms of herbage quality varied between years with only CWC% appearing to be consistently higher in Matua. In general the two species had similar herbage quality and yields, although soil moisture and frequency of cutting had a major modifying effect on this. The dry period during the first half of the 1988 growing season demonstrated the superior herbage production that prairie grass has under dry conditions (Eteve, 1982; Burgess *et al.*, 1986). Westerwolds ryegrass is valued for its high forage production and quality (Langer and Hill, 1982), so Matua prairie grass, if managed correctly, should also be considered in a similar manner.

Lower herbage quality in 1988, especially in the middle of the growing season, could have been the result of strong winds and rain that flattened the swards immediately prior to harvesting. Harvesting was therefore difficult and leaf quality deteriorated rapidly. This occurred at two harvests of infrequently cut plots and one harvest of frequently cut plots. Both species appeared to be affected to the same degree.

It should be noted that in 1987 a high amount of nitrogen was applied (575 kg ha^{-1}) and a lower amount in 1988 (350 kg ha^{-1}). At the present time, average nitrogen use on grassland on sandy soils in The Netherlands is approximately 400 kg ha^{-1} (kg N applied in terms of equivalent fertilizer N, calculated from Aarts *et al.*, 1988). Higher nitrogen input in 1988 could have been expected to improve contents of nitrogen and improve production but decrease apparent recovery of nitrogen.

There was a decline in plant numbers but tiller populations did not decline because plant size (tillers $plant^{-1}$) increased to compensate for lower tiller populations. Compensation in prairie grass swards can occur by increased plant size (tillers $plant^{-1}$) and tiller size (weight $tiller^{-1}$) [Chapter 7 this thesis (Falloon and Hume, 1988)] and natural reseeding (Chapter 8 this thesis). Whether natural reseeding will successfully occur under the management and climatic conditions of The Netherlands is yet to be determined. Natural reseeding was observed to be occurring for both species in the present study but no measurements were taken on these seedlings. If natural reseeding is not successful, then prairie grass swards may be expected to have a shorter life than those recorded under conditions in France (Anon, 1982) and New Zealand (Fraser, 1985; Burgess *et al.*, 1986) (persistence >4 years).

It would appear that prairie grass could at least be considered as a replacement for spring sown Westerwolds ryegrass, as quality and yields are comparable for the two species, with prairie grass having the added advantage of better production and survival in dry summers and on dry soil types. Prairie grass has poor tolerance of wet soil conditions so is best suited to the sandy soils of The Netherlands. As a longer term pasture species, it can be expected to survive mild winters giving at least two years production of quality herbage when managed correctly. Further trials are required to investigate various managements to achieve maximum winter survival and to fully test the range of cultivars that are currently available.

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CHAPTER 7

Productivity and persistence of prairie grass (*Bromus willdenowii* Kunth). 1. Effects of the head smut fungus *Ustilago bullata* Berk.

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Abstract

A field trial measured effects of the head smut fungus *Ustilago bullata* Berk. on forage productivity of prairie grass (*Bromus willdenowii* Kunth). Simulated swards containing different proportions of *U. bullata* infected and non-infected plants were established in the autumn, and sward and plant parameters were measured over the following 15 months. Total herbage produced from swards containing only non-infected plants was 27·3 t ha^{-1}, while that from totally infected swards was 14·6 t ha^{-1}. Infected plants produced fewer and lighter tillers than non-infected plants when both were growing together in swards. Almost all the *U. bullata* infected plants died during an epidemic of bacterial wilt disease (caused by *Xanthomonas campestris* pv. *graminis* (Egli, Goto and Schmidt) Dye), while most of the non-infected plants survived. The deleterious effects of *U. bullata* on individual plant productivity affected sward productivity only when the proportion of infected plants in swards was greater than 50%. Plants not infected with *U. bullata* compensated for low productivity and death of infected plants by producing large numbers of tillers.

Introduction

'Grasslands Matua' prairie grass (*Bromus willdenowii* Kunth), described by Rumball (1974), is a very productive perennial forage cultivar with potential for use in high fertility, dryland and hill country pastures (Rumball, 1974; Sithamparanathan, 1979; Fraser, 1985). This cultivar has the important agronomic features of high tiller production and high individual tiller yield, characteristics that give it tolerance to defoliation (Hill and Kirby, 1985). However, it is very susceptible to the head smut fungus *Ustilago bullata* Berk. (Falloon, 1976). Plants infected by this fungus have been shown to be less productive than uninfected plants, due to decreased tillering and poor persistence (Falloon, 1976; 1979a).

Prairie grass can become infected by *U. bullata* at two stages of growth; either through the seedling coleoptile from seed-borne ustilospores (seedling infection), or through young tillers from air- or splash-borne ustilospores (shoot infection) (Falloon, 1979b). In seed crops free of head smut at the first harvest, incidence of the disease can increase at subsequent harvests due to shoot infection. However, in grazed or cut swards with heavy initial infection, disease incidence has decreased over successive years in both small plots and farm paddocks (J. A. Lancashire, personal communication). This may be due to poor persistence of infected plants, and either compensation by, or reseeding from, healthy plants.

No detailed studies of *U. bullata* epidemics in prairie grass swards have been undertaken. A field trial was therefore conducted to determine effects of *U. bullata* infection on productivity and persistence of Matua prairie grass swards, and to monitor the infection status of plants in these swards.

Materials and methods

The trial measured productivity of cut simulated

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swards of Matua prairie grass established with different proportions of *U. bullata* infected and uninfected plants.

Plants

'Infected' plants were grown from seed inoculated (Falloon, 1976) with 3·7 g kg^{-1} *U. bullata* ustilospores of high germinability (96% on potato dextrose agar after 20 h at 25°C), an inoculum level likely to infect all seedlings (Falloon, 1976). 'Healthy' plants were grown from seed treated with the fungicides triadimenol + fuberidazole ('Baytan F17') at 0·25 + 0·04 g kg^{-1} seed to ensure that no *U. bullata* infection occurred at the seedling stage (Falloon and Rolston, 1986). Seeds were sown into potting soil in seedling trays in the glasshouse. Three weeks after sowing, height and numbers of leaves and tillers of seedlings were determined. One week later in mid-autumn (1 April 1985) seedlings were planted in the field.

Site

The trial site was at DSIR Palmerston North on an imperfectly drained soil from Holocene siliceous silty alluvium. Analysis of topsoil samples (0·75 mm depth) gave: pH 5·8; Olsen P 29 ppm; and exchangeable cations (extracted with 0·72 M sulphuric acid), K 3·0 mg g^{-1} soil and Mg 1·5 mg g^{-1} soil.

A seedbed was prepared, and square metal grids with one hundred 10 × 10 cm squares were permanently positioned in each of twenty 1 × 1 m plots. The plots were arranged in four blocks of five plots each.

Treatments

Plots were planted with different numbers of healthy and infected plants to give the following treatments;

(1) 100 healthy plants (100H),
(2) 75 healthy and 25 infected plants (75H),
(3) 50 healthy and 50 infected plants (50H),
(4) 25 healthy and 75 infected plants (25H),
(5) 100 infected plants (0H).

Treatments were arranged randomly within each block. One plant was planted in each square of the metal grids to give a planting density of 100 plants m^{-2}. Healthy and infected plants were distributed evenly over plots for the 75H, 50H, and 25H treatments. Border areas (0·3 m wide) of healthy plants were planted around all plots.

Measurements

Plant and tiller populations and herbage yields were determined on ten occasions (three in late autumn–winter 1985, three in spring 1985, and two each in summer 1985–86 and autumn 1986) when green canopy heights reached about 200 mm. Tillers were counted on the plants in the central thirty-six squares in each plot. At the same time, all plants were checked for *U. bullata* infection by inspecting inflorescences for head smut symptoms. In mid-spring 1985, numbers of flowering tillers per plant were counted. After completion of tiller counts, plots were cut to 30 mm height, usually with a rotary mower, and the cut herbage from each plot was dried and weighed. On two occasions (in spring 1985 and summer 1986, 30 and 48 weeks, respectively, after planting) individual plants were harvested with electric shears, and plant dry weights were determined.

Fertilizer

A basal analysis 0% N, 6% P, 14% K and 7% S fertilizer was applied to the trial at 400 kg ha^{-1} annually as equal split applications in spring and autumn. Nitrogen removed in the cut herbage, calculated as 5% of the dry matter yield, was replaced after each cut by applying nitrolime (26% N).

Climate

Temperature and rainfall records for the trial period were obtained from the Palmerston North DSIR meteorological station (NZ Meteorological Service), 500 m from the trial site.

Results

Seedlings

Three-week-old seedlings grown from *U. bullata* inoculated seed were shorter (mean height 194 mm) than those grown from fungicide-treated seed (mean height 254 mm; $P < 0·01$). Both groups of seedlings had similar numbers of leaves (mean, 4·0). Tillering had not commenced at this stage.

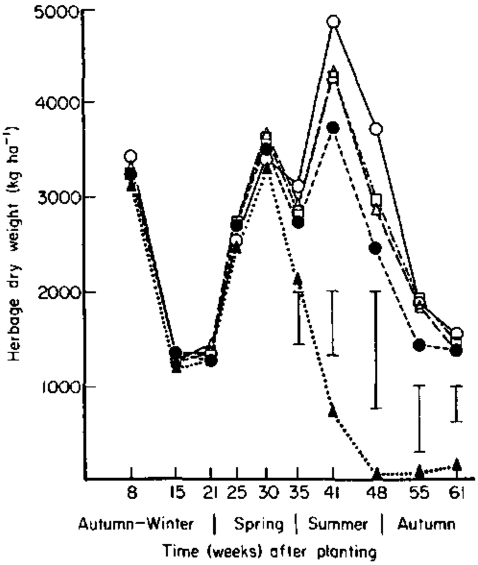

Figure 1. Mean dry weight of herbage harvested on ten occasions from plots planted with 0–100% healthy prairie grass plants and the remainder infected with *U. bullata*. LSD values ($P<0{\cdot}05$) are indicated where differences between treatments were significant. (○——○) 100H; (△ - - - △) 75H; (□ -·-·- □) 50H; (● - - - ●) 25H; (▲ . . . ▲) 0H.

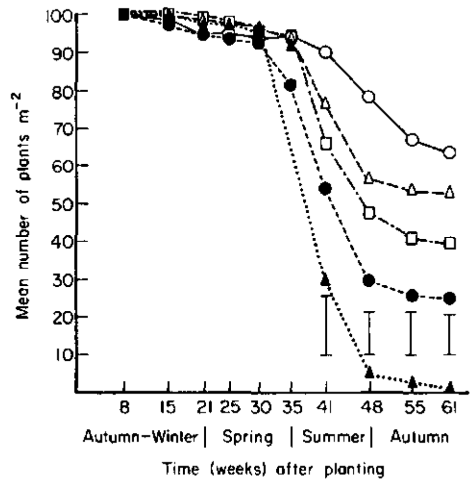

Figure 2. Mean numbers of prairie grass plants on ten occasions in plots planted with 0–100% healthy plants and the remainder infected with *U. bullata*. LSD values ($P<0{\cdot}05$) are indicated. (○——○) 100H; (△ - - - △) 75H; (□ -·-·- □) 50H; (● - - - ●) 25H; (▲ . . . ▲) 0H.

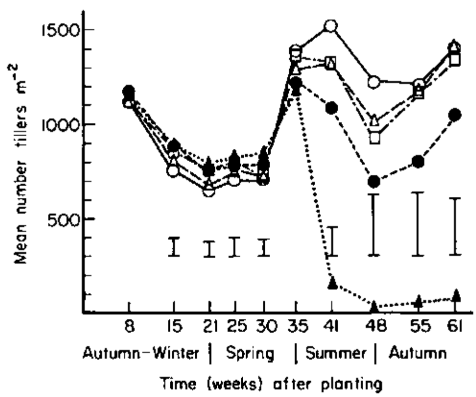

Figure 3. Mean numbers of tillers on ten occasions in plots planted with 0–100% healthy prairie grass plants and the remainder infected with *U. bullata*. LSD values ($P<0{\cdot}05$) are indicated. (○——○) 100H; (△ - - - △) 75H; (□ -·-·- □) 50H; (● - - - ●) 25H; (▲ . . . ▲) 0H.

U. bullata *infection*

In spring 1985, 98·6% of the plants grown from inoculated seed produced smutted inflorescences, while none of the plants from fungicide treated seed were infected with *U. bullata*. In autumn 1986, only three of the previously healthy plants (0·4%) produced both healthy and smutted inflorescences. Six months later (spring 1986) these three plants produced only healthy inflorescences.

Sward parameters

(a) Herbage yields. Plot yields were similar for all treatments at the first five harvests (Figure 1), but from late spring onwards, yields from 0H plots were much less than those from other treatments ($P<0{\cdot}05$). Yields from the other treatments were similar to each other, except that 25H plots yielded less ($P<0{\cdot}05$) than 100H plots at the two summer harvests (weeks 41 and 48). Total herbage yields from the ten harvests were (t DM ha^{-1}): 100H, 27·3; 75H, 25·8; 50H, 25·8; 25H, 23·8; and 0H, 14·6 (LSD 0·05 = 3·0). The 25H and 0H treatments thus gave 12·8 and 46·7% less dry herbage, respectively, than the 100H treatment.

(b) Numbers of plants. The numbers of plants in plots declined only slightly during the first 35 weeks after planting, but then decreased to a greater extent, in some treatments dramatically (Figure 2). This decrease coincided with the period of greatest inflorescence production, 53% and 74% of the tillers flowering on healthy and infected plants respectively ($P<0{\cdot}01$). Plants either failed to regrow after cutting or developed withered leaves and white seedheads before

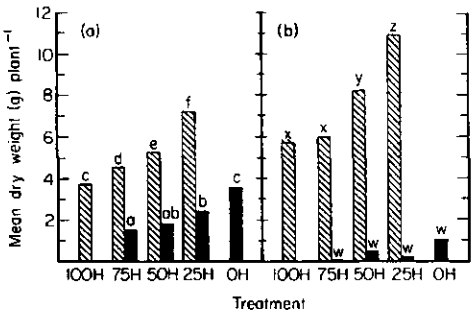

Figure 4. Mean dry weight of herbage harvested from individual prairie grass plants in plots planted with 0–100% healthy plants and the remainder infected with *U. bullata*. Harvests were carried out 30 weeks (a) and 48 weeks (b) after planting. Means accompanied by the same letter are not different ($P > 0.05$, LSD tests). (▨) healthy; (■) *U. bullata*-infected.

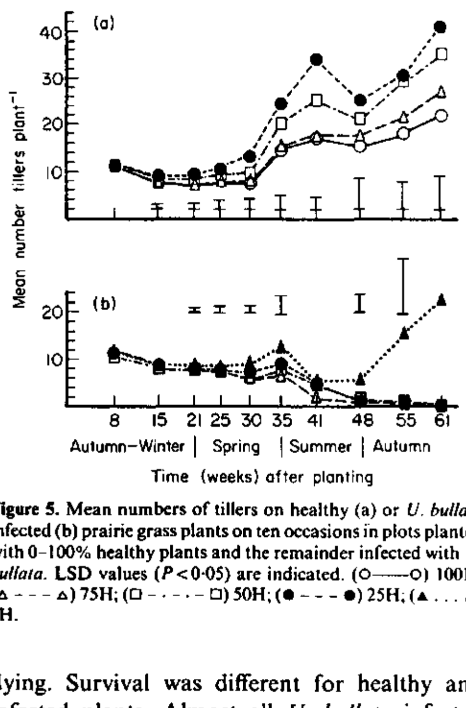

Figure 5. Mean numbers of tillers on healthy (a) or *U. bullata* infected (b) prairie grass plants on ten occasions in plots planted with 0–100% healthy plants and the remainder infected with *U. bullata*. LSD values ($P < 0.05$) are indicated. (○——○) 100H; (△ - - - △) 75H; (□ - · - · - □) 50H; (● - - - ●) 25H; (▲ . . . ▲) 0H.

dying. Survival was different for healthy and infected plants. Almost all *U. bullata* infected plants died in the summer; by 61 weeks after planting survival was 1% and unrelated to treatment. On the other hand, plants not infected with *U. bullata* died from midsummer to mid-autumn. Survival at 61 weeks was related in an inverse linear manner to the original healthy plant population ($P < 0.01$), and was 64% in 100H plots, 70% in 75H, 77% in 50H, and 93% in 25H plots.

Plant death was associated with symptoms of bacterial wilt disease, caused by *Xanthomonas campestris* pv. *graminis* (Egli, Goto and Schmidt) Dye). Subsequent investigations have shown that field-grown *U. bullata* infected plants died when infected with *X. campestris* pv. *graminis*, whereas plants free of *U. bullata* infection survived the bacterial wilt epidemic.

(c) Numbers of tillers. Different treatments had different tiller populations from 15 weeks after planting ($P < 0.05$; Figure 3); 100H plots contained fewer tillers than plots planted with mainly *U. bullata* infected plants (25H and 0H). From late spring onwards, this trend was reversed as infected plants died and numbers of tillers in 0H and 25H plots were consistently less ($P < 0.05$) than in 100H and 75H plots.

Plant parameters

(a) Yield per plant. Individual infected and healthy plants harvested in mid-spring yielded similar amounts of herbage in plots where each was grown alone (100H and 0H treatments, respectively; Figure 4a). However, healthy plants produced about three times more herbage than infected plants in plots containing both healthy and infected plants ($P < 0.05$). Healthy plants contributed 92, 78, and 57% of the total herbage from 75H, 50H, 25H treatments, respectively. In late summer, the few infected plants that still survived were very small, and contributed little to the total harvested herbage (Figure 4b).

Individual plant dry weights were affected by the different treatments. In mid-spring (Figure 4a), dry weights of both healthy and infected plants were greatest in plots containing few healthy plants (25H), and smallest in plots containing mostly healthy plants (75H; $P < 0.01$). In late summer (Figure 4b), surviving healthy plants in the 25H plots were almost twice the size of those in the 75H plots ($P < 0.01$).

(b) Tillers per plant. Infected and healthy plants had similar numbers of tillers until 25 weeks after planting (early spring; Figure 5). Thereafter, healthy plants had more tillers than infected plants ($P < 0.05$); 14%, 35%, 103%, and 513% more at weeks 25, 30, 35 and 41, respectively. Both healthy (Figure 5a) and infected (Figure 5b) plants had fewer tillers at higher than at lower healthy plant populations ($P < 0.05$). Tiller numbers increased at later assessments for

the few infected plants that survived in the 0H treatment (Figure 5b).

(c) Yield per tiller. Tiller dry weights were determined from data obtained at individual plant harvests. In mid-spring (30 weeks after planting) healthy and infected plants grown alone (100H and 0H treatments, respectively) had similar tiller dry weights (mean 0·46 g). However, in treatments where both healthy and infected plants grew together (75H, 50H and 25H), healthy plants had heavier tillers (mean 0·58 g) than infected plants (mean 0·25 g; $P<0{\cdot}01$). Healthy plants in the 100H plots had lighter tillers (mean 0·51 g) than healthy plants in other treatments (mean 0·58 g; $P<0{\cdot}05$). Infected plants in 0H plots had heavier tillers (mean 0·41 g) than infected plants in other treatments (mean 0·29 g; $P<0{\cdot}01$).

At the late summer harvest (48 weeks after planting), no differences in tiller dry weights were detected either between healthy and infected plants, or between treatments (overall mean 0·29 g per tiller).

Temperature and rainfall

Mean air temperature for the trial period was 13·8°C, 1·5°C above the 30-year average. Rainfall (1205 mm for 15 months) was similar to the 30-year average (1187 mm). Both autumns were dry (157 mm, 64% of average rainfall), winter (222 mm) and spring (290 mm) rainfall was about average, while that for summer (378 mm) was almost double the 30-year average.

Discussion

Ustilago bullata can have potentially harmful effects on forage production of prairie grass (Falloon, 1976; 1979a). The present study has demonstrated that this fungus can affect plant survival and productivity in simulated swards in the field.

The most dramatic effect of *U. bullata* was that almost all infected plants died 9 to 10 months after establishment, while most non-infected plants survived. Summer rainfall was high so moisture stress was not likely to have been a factor in plant mortality. Fischer and Holton (1957) reported that *U. bullata* infected prairie grass plants grown in a glasshouse were more susceptible to root rot pathogens than non-infected plants. In the present study, *U. bullata* infected plants died during a bacterial wilt epidemic, while most non-infected plants survived. Thus, infected plants appear to be more severely affected by other pathogens than non-infected plants. Prairie grass is also affected by several foliage diseases caused by fungi (Latch, 1965). Decline of head smut in prairie grass swards with initially high incidence may therefore be due to induced disease susceptibility, and resulting high mortality, in plants infected with *U. bullata*.

Ustilago bullata also affected growth of individual plants in the swards. Plants infected with this fungus produced less dry matter, fewer and lighter tillers, and higher proportions of flowering tillers than non-infected plants. These effects were similar to those recorded previously for field-grown spaced plants (Falloon, 1979a).

Competition effects, expressed as differences in individual plant productivity, were noted in the present trial. Healthy plants produced more and heavier tillers than plants infected with *U. bullata*, but only in swards containing both types of plants. These effects first became apparent in early spring before infected plants died, and indicate that healthy plants were more competitive than infected plants. Later in the trial, after infected plants died, the remaining healthy plants produced more tillers at low plant populations than where populations were higher, responding in a manner similar to that recorded for other grasses (Langer, 1963). Thus, high tiller production by healthy plants partially compensated for the deleterious effects of *U. bullata* on sward productivity.

Reduced dry matter production due to *U. bullata* was recorded only in swards where infected plants were predominant (25H and 0H treatments). This suggests that infection levels lower than 50% in swards may not reduce pasture production. However, as *U. bullata* can also be harmful to prairie grass establishment (Falloon 1979a; 1985), methods to control head smut should still be used routinely.

Very few of the healthy plants became infected by *U. bullata* in this trial, indicating that shoot infection occurred only rarely. Where shoot infection did occur, infected tillers on healthy plants were eliminated within 6 months. Although nearly all plants from inoculated seed produced infected inflorescences, these inflorescences were probably removed by regular harvests before ustilospores were released. Thus, shoot infection from infected plants within a sward may not readily occur in regularly grazed pastures, but is more likely to be a problem where infected inflorescences are not removed (e.g., in lightly grazed pastures, or in hay and silage crops).

This trial has demonstrated that the pathogen *U. bullata* can reduce growth and cause death of individual prairie grass plants within swards. However, this fungus is unlikely to severely reduce herbage production unless infection levels in swards are somewhat greater than 50%. Methods of head smut control in forage crops should therefore aim at preventing high initial incidence of head smut in swards. Prevention of the disease in seed crops by controlling seedling infection with fungicide seed treatments results in seed free of ustilospore contamination at harvest (Falloon and Rolston, 1986). If this seed is used for pasture establishment, adequate control of *U. bullata* should be achieved in prairie grass swards grown for forage.

CHAPTER 8

Productivity and persistence of prairie grass (*Bromus willdenowii* Kunth). 2. Effects of natural reseeding and plant compensation

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ABSTRACT

A field trial with different populations of prairie grass (*Bromus willdenowii* Kunth) plants in 1 year old simulated swards enabled changes in plant and tiller populations, and natural reseeding, to be studied. At establishment half of the plants in this trial were infected with the head smut fungus (*Ustilago bullata* Berk.), but the disease had disappeared within 2 years as all infected plants died. Where plant populations were low, plants compensated by producing more and heavier tillers than where populations were higher. There was an overall decline in plant population, mostly during the period from mid-summer to mid-autumn. Numbers of seedlings resulting from natural reseeding were greatest (1600 seedlings/m^2) in swards with the highest populations of mature plants, and lowest (650/m^2) in plots with few mature plants. Most seedlings emerged in autumn and early winter, with early emergence giving the greatest seedling survival. Seedling growth was slow so that 1 year after emergence, seedlings were still increasing in size. Seedling survival after 1 year was low (1%), but contribution to total plant and tiller populations from seedlings were 28% and 11% respectively. These results indicate that natural reseeding, plant compensation and survival of

original plants all play important roles in the persistence of prairie grass swards.

INTRODUCTION

Prairie grass (*Bromus willdenowii* Kunth) is potentially a true perennial plant (Loiseau 1972; Rumball 1974), which is capable of high forage production (Fraser 1985). However, prairie grass pasture production may decline due to poor grazing or cutting management (Alexander 1985), insect attack (East et al. 1980), summer drought, wet soil conditions in winter (Mwebaze 1986), or infection with the head smut fungus *Ustilago bullata* Berk. [Chapter 7 this thesis (Falloon & Hume, 1988)].

The mechanisms by which prairie grass pastures persist are unclear. Natural reseeding has often been suggested as a means by which declining swards can rejuvenate (eg. Langer 1973; East et al. 1980). Seedling populations of 31 to 878/m^2 have been recorded in autumn-winter from natural reseeding (Pineiro & Harris 1978; Francis 1986; Stevens & Hickey 1988; D. E. Hume unpublished data). However, the successful establishment of these seedlings, and their contribution to sward production, have not been studied. Other possible means of prairie grass persistence are the long-term survival of existing plants in the sward, and expansion of these plants to compensate for reductions in plant populations. Optimum plant populations for prairie grass swards are unknown, but plant compensation (increased tiller weight and number) can be important in maintaining sward production, at least in the short term [Chapter 7 this thesis (Falloon & Hume, 1988)].

The importance of natural reseeding, plant survival and compensation in maintenance of prairie grass pastures has not been adequately determined. A field trial, which had measured effects of *U. bullata* on sward productivity [Chapter 7 this thesis (Falloon & Hume, 1988)], gave the opportunity to study these factors in simulated prairie grass swards. The trial was therefore continued for a further 17 months, and the results obtained are reported here.

METHODS AND MATERIALS

The trial used simulated swards of 'Grasslands Matua' prairie grass established in autumn 1985 with different proportions of *U. bullata*-infected and uninfected plants. Early results have been reported and discussed in Chapter 7 of this thesis (Falloon & Hume, 1988). The present paper reports results recorded from autumn 1986 until completion of the trial in winter 1987.

Site and treatments

The trial site was at DSIR Palmerston North on an imperfectly drained fertile soil from Holocene siliceous silty alluvium. Plots measured 1 x 1 m, with 0.3 m borders around all plots. Square metal grids with one hundred 10 x 10 cm squares had been permanently positioned in each plot.

There were five treatments, replicated four times in a randomised block design. Treatments differed in the prairie grass populations per plot as follows;

(1) 78 plants (78P),
(2) 56 plants (56P),
(3) 44 plants (44P),
(4) 26 plants (26P),
(5) 5 plants (5P).

These plant populations resulted from the death of *U. bullata*-infected plants over the first summer of the trial [Chapter 7 this thesis (Falloon & Hume, 1988)]. This left the above uninfected plant populations in all but the 5P plots. All the plants in the 5P plots were infected with *U. bullata*. Full details of the site and trial establishment are outlined in Chapter 7 of this thesis (Falloon & Hume, 1988).

Measurements

When green canopy heights reached about 200 mm, the numbers of tillers on plants in the 36 central squares in each plot were counted. The plots were then cut with a rotary mower to a height of 30 mm, and the herbage dried and weighed to determine dry matter yields from each plot. Harvests were made on two occasions in both autumn and winter 1986, on three occasions in spring

1986, and on four occasions over the period of summer 1986-87 to late winter 1987. The 36 central squares in each plot were examined for prairie grass seedlings arising from natural reseeding. Newly emerged seedlings were tagged with coloured plastic triangles anchored with nails, while tags were removed from dead seedlings. Numbers of tillers were recorded for all seedlings. These measurements were taken at the same time as tiller and plant counts, and also in late autumn and early winter 1986 to coincide with emergence of new seedlings. Seedlings that emerged from natural reseeding in 1987 were not tagged but were counted in late autumn 1987.

On two occasions during late spring 1987, plants and seedlings in one replicate were examined and numbers of reproductive tillers were counted. Plants in all replicates were assessed for *U. bullata* infection.

Fertilizer

The trial was top-dressed with 400 kg superphosphate (0% N, 6% P, 14% K, 7% S) per ha annually as equal split applications in spring and autumn. Nitrolime (26% N) was applied after each harvest to replace nitrogen removed in the cut herbage. The rate of nitrogen was calculated as 5% of the dry matter yield.

Climate

Temperature and rainfall records were obtained from the Palmerston North DSIR meteorological station (N.Z. Meteorological Service), 500 m from the trial site.

RESULTS

Herbage yields

From autumn to early spring 1986, 5P plots yielded much less herbage than the other treatments ($P<0.01$; Fig. 1a), but from mid-spring to the end of the trial, all treatments had similar ($P>0.05$) dry matter yields. Total herbage yield for the 17 month trial period was 16 t DM/ha from 5P plots, lower ($P<0.01$) than from the other treatments (21 t DM/ha).

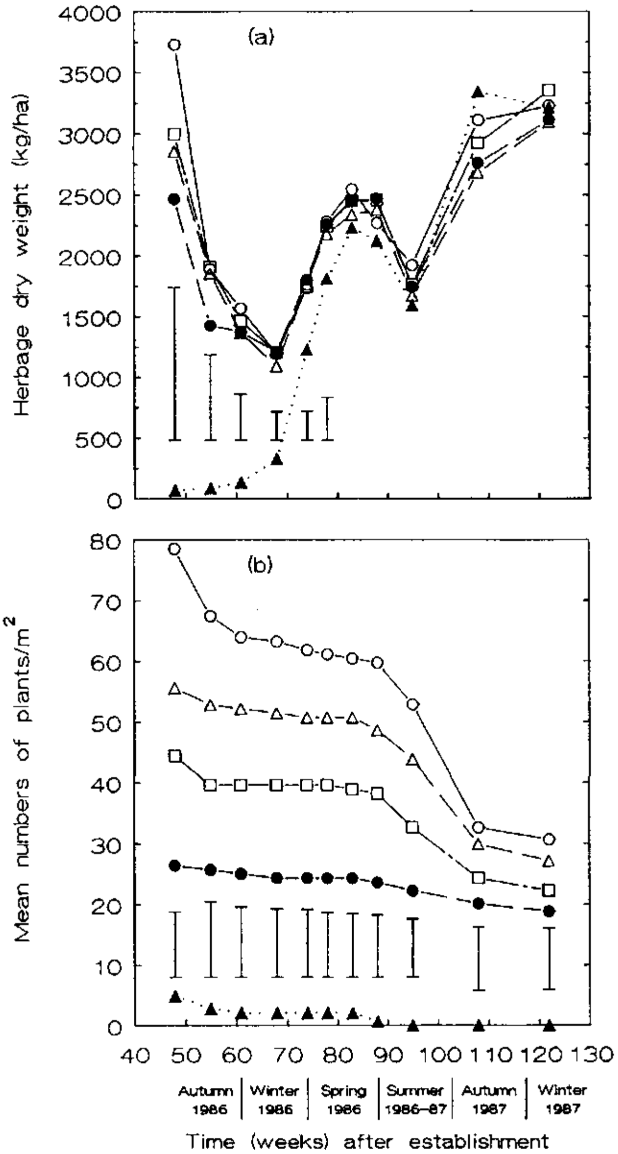

Fig. 1. Mean dry weight of herbage harvested (a) and mean numbers of prairie grass plants (b) on 11 occasions in plots originally containing different numbers of prairie grass plants. LSD values (*P*<0.05) are indicated where differences between treatments were significant. Treatments (○—○) 78P; (△--△) 56P; (□--□) 44P; (●--●) 26P; (▲···▲) 5P.

Plant parameters

(a) Numbers of plants. There was little change in numbers of plants in 5P plots (all *U. bullata*-infected plants) until early summer when they all died (Fig. 1b). Numbers of plants in the other treatments declined slightly over the first autumn, following the death of healthy plants over the period mid-summer 1985-86 to mid-autumn 1986 [Chapter 7 this thesis (Falloon & Hume, 1988)]. Numbers of plants remained approximately constant over the following winter and spring, then declined from mid-summer to mid-autumn. During this period many of the mature plants developed symptoms of bacterial wilt disease (caused by *Xanthomonas campestris* pv. *graminis* (Egli, Goto and Schmidt) Dye). For the trial period, decline in numbers of plants was 61% in 78P plots, 51% in 56P plots, 50% in 44P plots and 29% in 26P plots ($LSD_{0.05}$ = 3). At all dates mean numbers of plants in all treatments were significantly different ($P<0.01$), although the magnitude of these differences became smaller as the trial progressed (Fig. 1b).

(b) Numbers of tillers. The 44P, 56P and 78P plots had similar tiller populations (Fig. 2a), and until mid-summer, 26P plots had fewer tillers than other treatments. Later, all of these treatments had similar numbers of tillers. Populations of tillers in the 5P plots were always less than 100 tillers/m^2. Tiller populations were greatest from winter to early summer 1986, and lowest during autumn and winter 1987, but remained relatively static during both winters.

(c) Tillers per plant. Numbers of tillers on plants increased during autumn 1986, especially in 5P plots (Fig. 2b), remained almost constant through the winter and early spring, and then fluctuated until the end of the summer. For most of the trial period, tillers per plant were related to plant populations in plots in an inverse linear manner ($P<0.01$), but during autumn and winter 1987, differences between 78P, 56P, 44P and 26P plots disappeared.

Natural reseeding parameters

(a) Total numbers of emerged seedlings. Although rainfall for the summer of 1985-86 was almost double average [Chapter 7 this

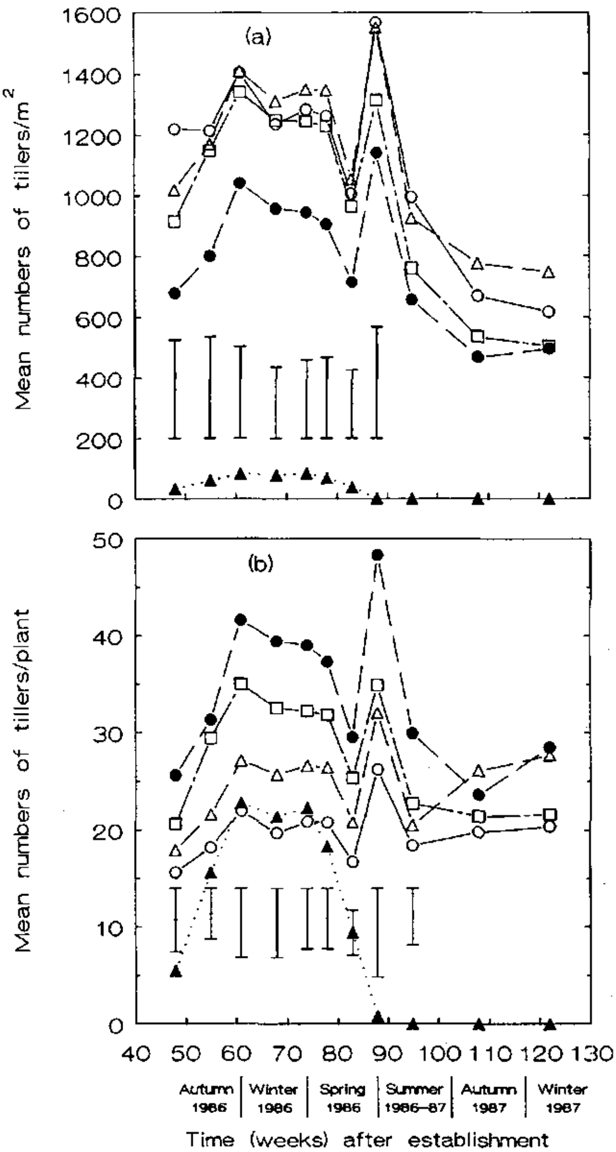

Fig. 2. Mean numbers of tillers/m² (a) and mean numbers of tillers per plant (b) for surviving original plants on 11 occasions in plots originally containing different numbers of prairie grass plants. LSD values ($P<0.05$) are indicated where differences between treatments were significant. For treatments see Fig. 1.

thesis (Falloon & Hume, 1988)], seedlings from seed shed in mid-summer did not appear until the start of autumn (Fig. 3a). Few seedlings emerged during the drier than average early autumn, and it was not until the second half of autumn that numbers of emerged seedlings increased. This coincided with more and heavier rainfall events, so that from late autumn onwards, the soil was always wet. Of the total number of seedlings to emerge, 70% appeared in the second half of autumn and the first month of winter, while only 8% emerged after this period. A total of approximately 1600 seedlings/m² emerged in 78P plots throughout the trial period, while 650 seedlings/m² emerged in 5P plots, significantly fewer (P<0.01) than for the other treatments. Seedling emergence was also later in 5P plots than in other plots (P<0.01).

(b) Numbers of live seedlings and seedling survival. Few seedlings died until the end of autumn 1986, so until that time numbers of live seedlings (Fig. 3b) followed a very similar pattern to that of total numbers of emerged seedlings. From early winter onwards numbers of live seedlings declined rapidly as many seedlings died. Of the seedlings that emerged, 50% were alive at the end of winter 1986 (510 seedlings/m²), 17% at the end of spring 1986 (180/m²), 2% in autumn 1987 (25/m²), and 1% alive in winter 1987 (16/m²). Differences between treatments for numbers of live seedlings were very similar to those for total numbers of emerged seedlings until the end of autumn 1986. Through winter and spring 1986 there were no treatment differences (P>0.05), but from early summer onwards, 5P plots had significantly (P<0.01) more seedlings and greater seedling survival than the other treatments. By winter 1987, 2.9% of emerged seedlings had survived in the 5P plots (38 seedlings/m²), while survival in the other treatments was 0.7% (10 seedlings/m²).

The first seedlings to emerge in early autumn 1986 had the best survival and growth of all seedling. These seedlings represented 14% of the total seedlings to emerge, and by winter 1987 made up 26% of the seedling population and 31% of the seedlings tillers. Seedlings that emerged in mid-autumn had good survival and growth, but relatively few of those that emerged at the end of autumn or in winter survived. The seedlings that emerged in spring survived well, but because they were so few in

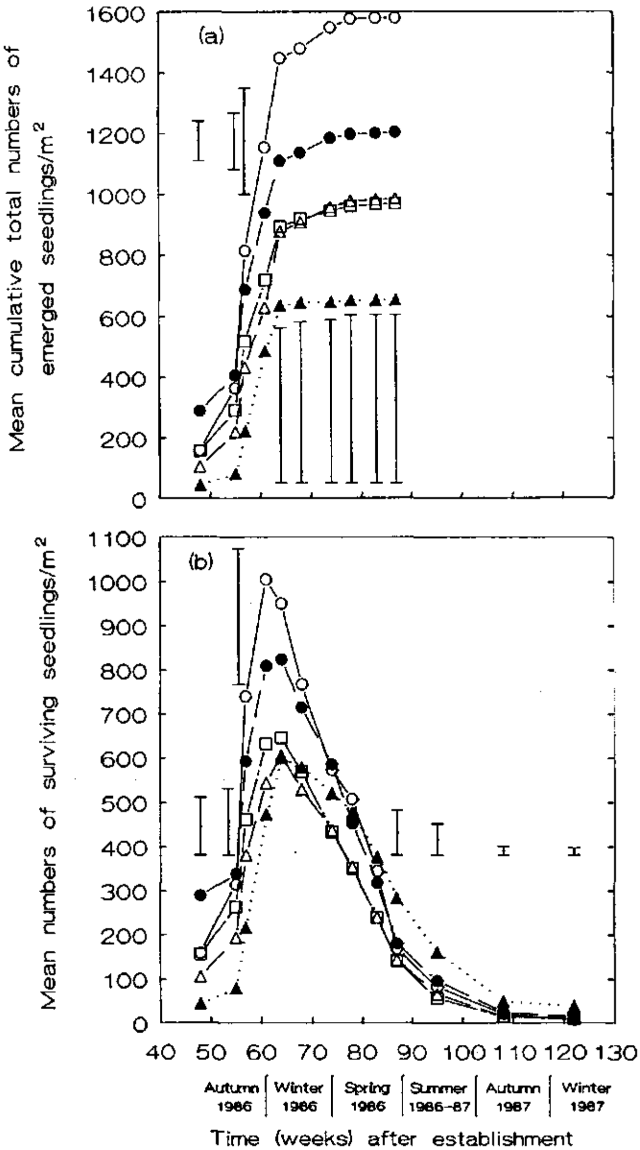

Fig. 3. Mean cumulative total numbers of emerged seedlings on ten occasions (a) and mean numbers of surviving seedlings on 13 occasions (b) in plots originally containing different numbers of prairie grass plants. LSD values (*P*<0.05) are indicated where differences between treatments were significant. For treatments see Fig. 1.

number, they contributed very little to total seedling tiller numbers.

(c) Tillers per seedling and numbers of seedling tillers. Seedlings in 5P plots increased in size much faster than seedlings in the other treatments (Fig. 4a). At the end of winter 1986, seedlings in 5P plots had an average of 3.0 tillers, while other treatments had 1.3 tillers per seedling. Only during late spring did the seedlings in these other treatments start to increase in size. At all dates, numbers of tillers per seedling were related to plant populations in an inverse linear manner ($P<0.01$).

Numbers of tillers from seedlings also differed greatly between the 5P plots and the other treatments (Fig. 4b). For all treatments except 5P, numbers of seedling tillers declined as numbers of live seedlings declined. From late winter 1986 onwards, tiller populations and patterns of change in populations with each harvest in 5P plots were similar to those occurring for mature plants in the other treatments.

Total tillers and plants

Due to the large numbers of seedlings, 95% of the total plants (seedlings plus mature plants) and 49% of the total tillers were from seedlings in winter 1986. These proportions reduced to 28% of the total plants and 11 % of the total tillers in winter 1987, due to the low level of seedling survival. In winter 1987 total numbers of tillers and total numbers of plants were related to mature plant populations in an inverse linear manner ($P<0.01$). Data from 5P plots were excluded from regression analyses because from mid-summer onwards, the only prairie grass plants in these plots were seedlings.

Other parameters

Inspection of inflorescences in spring and summer showed that apart from plants in 5P plots, no other plants were infected with *U. bullata*. In late spring a total of four seedlings were observed to be infected with *U. bullata*. These seedlings all died in early summer, at the same time as mature plants in the 5P plots (all infected with *U. bullata*).

In late spring, all the mature plants had produced

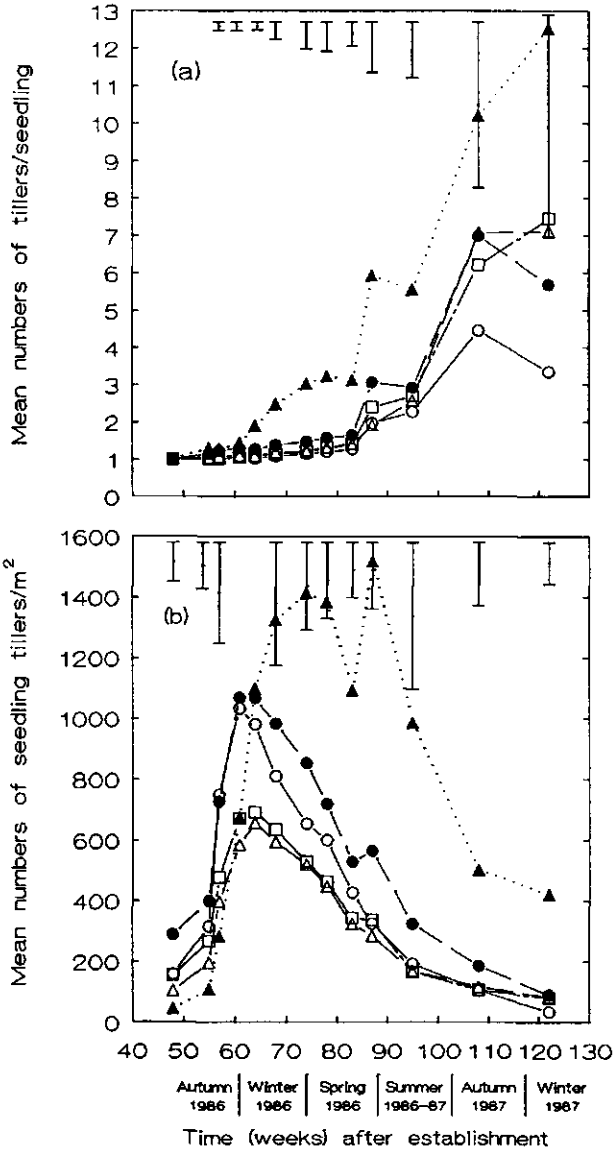

Fig. 4. Mean numbers of tillers per seedling (a) and mean numbers of seedling tillers/m² (b) on 13 occasions in plots originally containing different numbers of prairie grass plants. LSD values ($P<0.05$) are indicated where differences between treatments were significant. For treatments see Fig. 1.

reproductive tillers, while of the seedlings, 75% in 5P plots and 39% in the other treatments had developed reproductive tillers. Ninety percent of the tillers on *U. bullata* infected plants and 70% of those on non-infected plants were reproductive at this time. For seedlings that were reproductive, 97% of the tillers in 5P plots were reproductive, while 70% were reproductive in other treatments. At the next count (end of spring) there were less plants with reproductive tillers and fewer reproductive tillers on these plants and seedlings. There were also a considerable number of new vegetative tillers at the bases of plants at this time.

Temperature and rainfall

The summer of 1985-86, immediately before the trial period commenced, had almost double (378 mm) the 30 year average rainfall. For the 17 month trial period, mean air temperature was the same as the 30 year average (12.7°C), and rainfall (1233 mm) was slightly less than the 30 year average (1390 mm). Rainfall in autumn 1986, summer 1986-87 and winter 1987 was in each case about 60% of the average (245 mm). Rainfall in winter 1986 (310 mm) and spring 1986 (217 mm) was close to average, while autumn 1987 (300 mm) had 25% more rain than the 30 year average.

DISCUSSION

The present study has demonstrated that plant compensation, plant survival and natural reseeding can all play important roles in the persistence of prairie grass swards.

The ability of prairie grass plants to compensate for differences in plant populations, as identified in the first stage of this trial [Chapter 7 this thesis (Falloon & Hume, 1988)], was again evident in the results reported here. Herbage yields for the different treatments (excluding 5P plots) were similar, despite large differences in numbers of plants between treatments. At low plant populations, individual plants compensated by producing more tillers, and in 26P plots, heavier tillers. This was true during autumn, winter and early summer in 1986. Plants exhibited these compensatory features although many seedlings, collectively responsible for large tiller populations, were present in swards. However, these seedlings contributed little to plot yields because they were small and often below the 30 mm cutting height used for harvests. Seedlings growing in plots without mature plants (5P treatment) compensated in a similar manner. Seedling tiller populations in this treatment were equal to mature plant tiller populations in other treatments in late winter, and followed a pattern similar to that of mature plants from then on. As numbers of seedlings declined, numbers of tillers per seedling in the 5P treatment increased, so that tiller population was maintained.

Over the full 2.5 year period of this trial, numbers of original non-*U. bullata* infected prairie grass plants declined considerably, suggesting that plants may not survive for long periods. The decrease in plant numbers was greatest in plots with the highest plant populations (69% decrease), which indicates that the highest populations were above optimum. Even where populations were low, however, plant numbers decreased, although to a lesser extent (31% decrease in 26P plots). Plant populations were constant for most of the year, but irrespective of summer rainfall levels, mature plants died during the mid-summer to mid-autumn periods, when bacterial wilt epidemics occurred. As glasshouse experiments have shown that *X. campestris* pv. *graminis* can kill prairie grass plants (G. C. M. Latch & R. E. Falloon unpublished data), it is likely that the effects of this organism compounded plant competition effects. When this field trial was established, half of the plants were infected with *U. bullata*, but within 2 years the swards were free of head smut disease. Thus, although *U. bullata* can have deleterious effects on plant and sward productivity, previous observations (J. A. Lancashire, personal communication) that head smut disease incidence declines in heavily infected pastures have been verified by the present study.

This study has revealed a large potential for natural reseeding to occur in prairie grass swards. Prairie grass produces a high proportion of reproductive tillers, and as reproductive growth is controlled by long photoperiods (Karim 1961), inflorescences develop over a large part of the year. In the present study, inflorescences were removed by regular harvests, but in the mowing process, seed was threshed out of inflorescences so there was always a lot of seed spread over the plots. In a pasture situation, similar seed drop could occur from hay or silage crops or from grazed pastures, as inflorescences produce large amounts of seed which is freely shed (Rumball 1983). Considerable seed drop can occur when pastures are spelled in summer, management that is recommended if prairie grass populations decline (Burgess et al. 1986).

Although a large number of seedlings emerged from natural reseeding in this trial (average of 1080 seedlings/m^2), seedling survival after 1 year was only 1%, suggesting that natural reseeding contributes little to sward productivity. Low seedling survival from natural reseeding has also been recorded in extensively managed meadows (Rabotnov 1969), and intensively grazed ryegrass (L'Huillier & Aislabie 1988; D. E. Hume unpublished data) and prairie grass pastures (Francis 1986; 1987). Furthermore, success of reseeding was influenced in an inverse linear manner by plant populations, despite equal tiller populations. Thus, where plant populations are high and plant replacement is not required to maintain swards, natural reseeding is unlikely to be successful. However, when the complete sward 1 year after seedling emergence is considered, plants that arose from natural reseeding comprised 28% of the total plants and 11% of the total tillers present. With death of mature plants and continual input each year of new plants from natural reseeding, a dynamic situation is likely to develop in prairie grass pastures, with natural reseeding playing an important long-term role.

Despite almost double normal rainfall giving good moisture conditions during the 1985-86 summer, and although seed was scattered from inflorescences from late spring onwards, it was not until early autumn that the first seedlings emerged. This may have been due to seed dormancy. Although Hill and Watkin (1975) have shown that prairie grass seed can be viable as soon as 4 days after anthesis, seed dormancy is more pronounced in prairie grass than in perennial ryegrass (*Lolium perenne* L.) (Froud-Williams & Chancellor 1986; M. P. Rolston unpublished data). Late germination could also have been caused by the stage of development of seed. Late spring harvests were at 4 week intervals, so seed from these harvests may have been undeveloped and non-viable, and even very slight immaturity at harvest can extend seed dormancy considerably (Nakamura 1962). Summer harvests were at 6 week intervals, and seed scattered at these harvests may have been more fully developed.

From early autumn onwards, rainfall appeared to be a factor that controlled seedling emergence. Thus, dry conditions in early autumn may have delayed the main period for seedling emergence until later in autumn and early winter, when adequate rainfall occurred. Seed dormancy could also have affected seedling emergence at this stage, as although moisture conditions for germination became adequate from mid-autumn onwards, the main period for seedling emergence still extended over a 3 month period.

The greater survival and growth of prairie grass seedlings that emerged in early autumn and spring parallels earlier results where seed was sown into warm soils (Hare et al. 1988; Falloon & Rolston 1989). In areas or years where summers are dry and autumn rainfall comes late, natural reseeding may not be successful because soil temperatures may be too low for good seedling growth and establishment.

Without direct assessment of the yield of the seedlings and plants separately, it is difficult to determine, except in the 5P plots, the precise effect of natural reseeding on maintenance of herbage yields. Seedlings were still smaller than the original plants in plots 1 year after emergence (winter 1987), although seedlings were increasing in size while the numbers of tillers on the original plants were relatively constant. Mature plants in grazed prairie grass swards may only possess 10 tillers (Rumball 1974; Francis 1987). In the present study, over 30% of the seedling plants possessed 10 tillers or more in winter 1987, and could thus be making a considerable contribution to the sward. Also at this stage, there were no differences in numbers of plants between treatments, although there were still significant differences in numbers of original plants.

It is difficult to deduce optimum plant or tiller populations for prairie grass swards from this study, because of plant compensation effects and contributions from reseeding. Plant and tiller populations were relatively constant over the winter, but fluctuated at other times of the year, possibly due to the times of cutting and appearance of suppressed tillers (D. E. Hume unpublished data). Although numbers of tillers per plant varied with season, these remained approximately similar (15 to 35 tillers per plant) throughout the 2 years of the trial, and it was only because of death of plants that tiller populations decreased with time. Ridler (1986) reported similar plant populations (35 plants/m^2) in prairie grass swards grazed by dairy cows, but Francis (1986; 1987) found established plant populations of 100 to 200/m^2 under dairy grazing and 100 to 300/m^2 under sheep grazing. Reported tiller populations in prairie grass swards have also varied greatly from 130 to 849 tillers/m^2 (Pineiro & Harris 1978) to 4120/m^2 (Hume & Lucas 1987). The present study has demonstrated that similar variations in plant and tiller populations can occur when contributions from natural reseeding are taken into consideration. Further long-term studies that identify plant, tiller and yield components are required to fully characterise prairie grass swards. The behaviour of the *U. bullata*-infected plants reported here confirms results recorded in the previous year [Chapter 7 this thesis (Falloon & Hume, 1988)]. These plants showed little effect of the fungus during winter and early spring, and increased in size to be as big as the plants in the 78P plots. However, as was the case previously, infected plants died shortly after they produced inflorescences in early summer, probably due to the combined effects of both *U. bullata* and *X. campestris* pv. *graminis*. Furthermore, the proportion of seedlings infected with *U. bullata* was very small with only four of a total of 5400 emerged seedlings showing signs of infection in late spring. This may have been due to removal of smutted inflorescences before infective ustilospores were released, thus preventing seedling or shoot infection by *U. bullata*, or because infected seedlings have poor survival during establishment (Falloon 1979*a*; Falloon & Rolston 1989). In any event, although half of the plants originally established in plots were infected with *U. bullata*, head smut disease had completely disappeared from the swards within 2 years.

The relevance of the present study in cut swards to the situation in grazed or mixed swards should be considered. In grazed swards, animals may affect prairie grass persistence by trampling, defoliation, and dung and urine deposition. Companion plants (eg. *Trifolium* spp.) in the sward may also change the interplant environment, although competition from existing grass plants would probably be less where legumes were present, as the nitrogen status would be lower than in the present trial where nitrogen fertilizer was applied. However, changes in plant and seedling populations in the present study were similar to those recorded in swards grazed by sheep or cattle (Francis 1987). Other investigations (D. E. Hume unpublished data) have shown that sheep have little influence on early growth of naturally reseeded seedlings, because seedlings are below grazing height and are protected to some extent by mature plants in the sward. Thus, it seems likely that the dynamics of prairie grass plant and seedling populations will be similar in both cut and grazed swards.

This study has demonstrated that a dynamic situation of plant and tiller populations exists in prairie grass swards. As a sward ages, the contribution to production from originally established plants can diminish as they die of diseases such as head smut and bacterial wilt. Loss of plants can be compensated for by prolific tiller production by surviving plants and by development of new plants from natural reseeding.

CHAPTER 9

OVERVIEW AND GENERAL DISCUSSION

Prairie grass - ryegrass comparison

The inclusion of ryegrass (*Lolium* spp.) as a comparison species in five of the studies in this thesis was considered to be an essential aspect of any study on prairie grass (*Bromus willdenowii* Kunth). This is because considerable information is already available on the growth of ryegrass, while prairie grass is competing with ryegrass for use on farms. In particular, in New Zealand it is competing with perennial ryegrass (*Lolium perenne* L.) because prairie grass swards can have long term persistence (Fraser, 1985). In other regions it is also competing with perennial species such as tall fescue (*Festuca arundinacea* Schreb.) and cocksfoot (*Dactylis glomerata* L.), and short term species such as hybrid ryegrass (*Lolium x hybridum* Hausskn.), Italian and Westerwolds ryegrasses (*Lolium multiflorum* Lam.) (Anon., 1982). One of the major problems with the farm management of prairie grass is that ryegrass management practices are applied to prairie grass swards and in many situations this is unsuitable causing the demise of the species.

Westerwolds ryegrass was chosen as a comparison species because prairie grass and Westerwolds ryegrass have similar herbage quality (Wilson, 1977; Wilson and Grace, 1978), upright growth habit (Langer, 1973) and neither require vernalization treatment to flower. Long photoperiod is the only requirement for reproductive development (Evans, 1964). Chapters 2, 5 and 6 confirmed that herbage quality for these two species is similar. Prairie grass did have higher cell wall contents and high water soluble carbohydrate contents but digestibility was not markedly different between the two species. Distribution of dry matter between leaves, vegetative and reproductive pseudostem was also similar but there were considerable differences in the way this dry matter was formed. Prairie grass formed more leaves per tiller which were larger and there were more green leaves per tiller. This occurred both in the field and in the various indoor studies for vegetative and reproductive growth under different temperature and photoperiod conditions and cutting treatments. Tillering and site filling though were higher in Westerwolds ryegrass and in the field, plant densities were also higher.

Although both species performed best under infrequent cutting, and to a lesser extent at greater stubble height, increasing severity of defoliation had greater effects in Westerwolds ryegrass (Chapters 4 and 5). Much of the demise of Westerwolds ryegrass under frequent defoliation of reproductive growth was due to continued rapid reproductive development. Reproductive stem elongation occurred at an early stage in the growth of a tiller. This increased dry matter production but also resulted in many tillers being susceptible to defoliation. Also during reproductive growth, development of new tiller buds occurred earlier in Westerwolds ryegrass than in prairie grass. Applying the same cutting frequency to both species based on the development of prairie grass was actually detrimental to the production and quality of Westerwolds ryegrass under field conditions.

Another important difference between these species is that prairie grass performed well under dry soil conditions while Westerwolds ryegrass suffered leaf wilting or plants died in a dry summer at Wageningen Hoog (Chapter 2; Hume, unpublished data). This is one of the most attractive features of prairie grass which has inspired intense interest in this species by researchers and farmers (Anon., 1982; Burgess *et al.*, 1986). Root measurements taken in the field indicate that this may be due to a better distribution of root mass to greater soil depths in prairie grass (Chapter 2), and Chu (1979) has also demonstrated a lower sensitivity of cell division and cell elongation to water deficit in prairie grass.

In comparison to perennial ryegrass, prairie grass has a very contrasting morphology, period of reproductive growth and herbage quality. Comparison of these two species must be placed in the context of environmental and management conditions that occur in the field. Prairie grass in New Zealand is recommended primarily in areas where performance of ryegrass is poor, and is recommended as a special purpose pasture species (Hume and

Fraser, 1985). Relative to perennial ryegrass, prairie grass is valued for its superior winter growth and growth during dry conditions in summer and early autumn. In these cases the quality of herbage may be of secondary importance while quantity is of prime importance. Prairie grass is also useful in situations of damage from pests and diseases and in cases where animal disorders such as 'ryegrass staggers' may be a serious problem when grazing ryegrass based pastures (Fletcher and Harvey, 1981).

Implications for plant breeding in prairie grass

Inclusion of three prairie grass cultivars in some studies in this thesis has provided a good demonstration of the variation that exists within the species. This has also been demonstrated by Hill and Kirby (1985). Hill and Kirby identified two morphological groups of prairie grass, but there was an inverse relationship between high tiller numbers and high yield per plant. Both these features were considered necessary for good agronomic performance, with the cultivar 'Grasslands Matua' exhibiting these desirable characteristics. Results from this thesis indicate that the cultivar 'Primabel' also has the required attributes for good agronomic performance. Performance of 'Bellegarde' though may be limited by low tillering capacity.

Variation between cultivars in the present studies also demonstrates to plant breeders the advantages or disadvantages of selection for certain characters in prairie grass. The cultivars Bellegarde and Primabel provided extremes in the features that plant breeders may be interested in (eg. leaf appearance, tiller numbers, reproductive development). Matua was relatively intermediate, although it exhibited a good combination of high leaf appearance, moderate reproductive growth and high tiller numbers and yields. The importance of these features as identified during undisturbed growth were modified during reproductive growth in simulated cut swards in Chapter 5, reducing the differences between cultivars. This was also observed in the limited field measurements for these three cultivars during cutting (Chapter 6; Hume, unpublished data). The possible reasons for such results are discussed in Chapter 5. Cultivars such as Matua and Primabel though appear to be of greater potential overall for agronomic use (Anon., 1986).

Another feature that is of value to breeders was the occurrence of high leaf appearance rates with a large leaf size eg. Bellegarde compared with Primabel. This is contrary to findings of Cooper and Edwards (1960) and Ryle (1964) for ryegrass and other grass species showing a negative relationship between these two variables. High leaf appearance rate also has the added advantage of more live leaves per tiller (Ryle, 1964; Chapters 2 and 3). Results from Chapter 3, however, did suggest a possible negative correlation between site filling and leaf size, tiller weight or leaf appearance.

Determination of sites of tillering (ie. lack of development of basal tiller buds and delay in development of the youngest axillary tillers) and leaf appearance rates, provided a good explanation of the cultivar and species differences for final tiller numbers (Chapter 3). Site filling was the major factor determining tiller numbers. Site filling or more specifically the sites of tillering, may be considered as variables to measure in plant breeding programmes to indicate tillering capacity.

Reproductive growth

Considerable attention has been given in this thesis to the role of reproductive growth in prairie grass. While reproductive growth in perennial ryegrass, tall fescue and cocksfoot is limited to a relatively short period of the year, reproductive growth in prairie grass can occur over a prolonged period from mid-spring to mid-autumn due to long photoperiod being the only requirement for reproductive development. Although reproductive development is normally considered undesirable in pasture grasses due to its detrimental effects on tiller production, herbage quality and animal intake, this does not appear to be the case in prairie grass (Eteve, 1982; this thesis).

Concerns over the low tillering capacity in prairie grass (Pfitzenmeyer, 1982; Hill and Pearson, 1985) proved not to be a barrier to high production under the correct management conditions, even within the range of tillering of the different cultivars studied in this thesis. Prairie grass was able to tiller profusely during reproductive growth in the field to compensate for lower production from surrounding plants or when plant death occurred due to disease (Chapters 7 and 8). Although tillering was dominated by the presence of the reproductive tiller, tiller numbers in both the indoor and outdoor studies were relatively high. Rapid development of previously inhibited tillers buds after cutting, quickly compensated for the large losses of reproductive tillers that occurred at cutting. Prairie grass had a higher reliance on these inhibited tiller buds than perennial ryegrass which may place prairie grass at a greater risk to adverse environmental and management conditions during this period of growth.

The rapid increase in dry matter that is associated with reproductive development is an important feature in allowing prairie grass to achieve high yields during reproductive growth (Chapters 2, 5, 6). This large contribution to yields is an important aspect to consider in plant breeding, especially since palatability remains high and high herbage intakes of grazing animals occur in the presence of reproductive pseudostem and inflorescences (Pfitzenmeyer, 1982; Burgess *et al.*, 1986; L'Huillier, Poppi and Fraser, 1986). Reduction in reproductive development may also reduce natural reseeding in prairie grass and so reduce sward persistence.

Although infrequent cutting is recommended for prairie grass during reproductive growth, Chapter 2 has identified that it is essential that this does not occur too late in the development of reproductive tillers due to large decreases in herbage quality. Optimum defoliation time based on proportions of reproductive tillers as suggested in Chapter 2, would equate to a stage when inflorescences are beginning to emerge in the field. Up until this stage, herbage quality is maintained (Barloy, 1982; Parneix, 1982; Chapter 2). This would require further testing in field trials to determine the effects on herbage quality, dry matter yields, tillering and persistence. Other criteria (Chapters 2, 4, 5) for assessing the optimum timing of defoliation, such as development of inhibited tiller buds at the base of reproductive tillers, numbers of leaves appeared (maximum of 4 to 5 green leaves per tiller) and contribution of reserves to regrowth, all require further study.

The ability of prairie grass to maintain highly productive swards during reproductive growth in the field was well documented in Chapters 7 and 8. Prairie grass was able to maintain productivity at various plant densities through changes in tiller weight and tiller numbers per plant. Natural reseeding also contributed to the maintenance of swards and occurred even without the summer spelling that is recommended for reseeding (Burgess *et al.*, 1986). These mechanisms for maintenance of yields, tillers and plant populations are important in prairie grass swards because existing plants can not spread as can occur in ryegrass (Minderhoud, 1980). Prairie grass plants remain as relatively distinct units even in old swards (Eteve, 1982). In ryegrass, vegetative stem elongation or development of tillers raised on elongated reproductive tillers allows spreading of the plant when these tillers root to the soil. This type of tiller development does not occur in prairie grass. This prevents widening of the base of the plant or spread of plants but it does reduce tiller losses at cutting or grazing (Chapter 5; Hume, unpublished data), frost damage (Baker, 1967) and suppression of tillering (Minderhoud, 1978).

Limitations and further studies

There are several limitations to the studies in this thesis regarding the direct implications of these results for agricultural systems. Many of these limitations are discussed in each chapter. There are also discrepancies with observations made in the field. For example, prairie grass and Westerwolds ryegrass failed to show superior production to perennial ryegrass during vegetative growth in Chapter 4, while superior production is observed in the field. Prairie grass adapted to very frequent cutting during reproductive growth producing high tiller numbers (Chapter 5), while field studies show that this does not occur (Bell and Ritchie, 1989; Burgess *et al.*, 1986). Perennial ryegrass under frequent cutting in Chapter 5 had low tiller numbers while frequent defoliation in the field usually results in high tiller numbers (Langer, 1963; Davies, 1977). Such differences in experimental results may occur with indoor studies because soil, plant and other environmental conditions are highly modified to enable detailed measurements to be taken and to allow responses of the plant to specific variables to be identified while other variables are kept constant.

Further studies require the use of simulated swards, field conditions, inclusion of companion species [eg. legumes such as white and red clovers (*Trifolium repens* L., *T. pratense* L.)] and finally inclusion of the grazing animal. As has been discussed in the first section of this chapter, prairie grass has many advantages that become apparent when it is used in specific agricultural situations. Prairie grass sward conditions and the grazing animal have been shown to have large effects on plant and animal production. For example, only during growth of closely spaced plants could Langer (1970) demonstrate superior cool-season productivity of prairie grass relative to ryegrass. Langer attributed this to a better adaptation of prairie grass to reduced light intensity primarily through a more upright growth habit and better leaf arrangement in the sward. These are morphological features that are not considered in this thesis. Long leaves and upright growth habit as occurs in prairie grass are also generally associated with better light penetration and light distribution in the sward and increased yields under infrequent cutting (Rhodes, 1969, 1971). The better distribution of green leaf in prairie grass swards which increases accessibility to the animal (Allden and Whittaker, 1970), has large positive effects on animal intakes in prairie grass swards (L'Huillier, Poppi and Fraser, 1986). Prairie grass palatability is also high for horses (Hunt, Hay and Clark, 1989), deer (W. F. Hunt, personal communication), sheep, cattle (*Burgess et al.*, 1986) or even browsing rabbits (Hume, unpublished data).

With the increased interest in computer modelling of pasture growth, results from this thesis also provides some of the basic information on primary parameters used in growth models. In particular it has identified parameters which differ to those recorded in perennial ryegrass.

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SUMMARY

Introduction

Prairie grass (*Bromus willdenowii* Kunth; synonyms *B. catharticus* Vahl, *B. unioloides* H.B.K., *B. schraderi* Kunth) is a tall, erect plant with wide leaves, few but large tillers and a prolonged period of reproductive growth. Compared to other commonly used temperate grass species (eg. ryegrass, tall fescue, cocksfoot), prairie grass has several advantages. Of these can be mentioned: high yields especially during the cool conditions of winter and the dry conditions of summer and early autumn, high palatability at all growth stages, high herbage quality, good levels of tolerance to pests and diseases and good morphological characters resulting in high herbage intakes by grazing animals. However, performance is poor when it is grown in soils susceptible to waterlogging or when defoliation is frequent. It is also susceptible to the head smut fungus *Ustilago bullata* Berk., which lowers plant productivity and persistence. There is concern over the low tillering capacity and the high degree of reproductive development.

Compared to other pasture grasses, especially ryegrass, relatively little is known about the behaviour of prairie grass except under general farming conditions. This thesis therefore presents three indoor and four field studies which investigated some morphological and physiological aspects of this species. Considerable emphasis was placed on the comparison of prairie grass with ryegrass ['Wendy' perennial ryegrass (*Lolium perenne* L.) and 'Caramba' tetraploid Westerwolds ryegrass (*Lolium multiflorum* Lam.)] and to a lesser extent cultivar variation in prairie grass. Emphasis was also placed on separating the vegetative and reproductive growth stages of prairie grass. Westerwolds ryegrass was chosen as a comparison species as both species have a similar erect growth habit with long photoperiods being the only requirement for reproductive development.

Morphological and physiological features

Relative to Westerwolds ryegrass, prairie grass had similar

herbage quality during reproductive growth, although quality deteriorated quickly in prairie grass after heading. Prairie grass had higher cell wall contents and high contents of water soluble carbohydrates. The two species had similar biomass partitioning between leaf lamina and pseudostem, but prairie grass had a better distribution of root mass to greater soil depths which may explain the better performance of prairie grass under dry soil conditions.

Compared to both ryegrass species, prairie grass had higher leaf appearance rates, bigger leaves and sheaths, more live leaves per tiller, greater reproductive development, but lower site filling resulting in a lower tiller number. Low tiller number did not inhibit the potential for high yields, the ability of plants to compensate for tiller or plant death in the field, or the ability to tiller profusely after the removal of large numbers of reproductive tillers by defoliation.

Differences in site filling between species was the main reason for the different tillering rates. For the prairie grass cultivars used in the studies, tillers did not develop from the coleoptile tiller buds and only occasionally from the prophyll tiller buds, while tillers did develop from these sites in ryegrass. There was also generally a greater delay in the appearance of the youngest axillary tiller in prairie grass.

Cutting trials during vegetative and reproductive growth showed that performance of prairie grass was best under infrequent cutting, and to a lesser extent, greater cutting height. During vegetative growth, response of prairie grass to increasing cutting severity varied to the response in ryegrass for some morphological characters but relative growth rates were similar in all species. The role of reserves for regrowth (water soluble carbohydrates, protein) in prairie grass appeared to be similar to that occurring in ryegrass, although water soluble carbohydrate levels were higher in prairie grass. Identifying the precise role of reserves in prairie grass would require further study.

The prairie grass cultivars ('Bellegarde', 'Grasslands Matua' and 'Primabel') studied in this thesis provided a good range in morphological features and the implications of these in plant breeding are discussed. Bellegarde had high leaf appearance rates, large leaves, low site filling, low tiller numbers and rapid reproductive development. Primabel had relatively low leaf appearance rates, smaller leaves, less reproductive growth, but higher site filling and tiller numbers. Matua was approximately intermediate for these characters. Matua and Primabel had the best characteristics for good agronomic performance.

Maintenance of highly productive and persistent swards was dependent on a combination of changes in the numbers of tillers per plant and tiller weight of existing plants in the sward, and contributions from natural reseeding. These are important characteristics in prairie grass as plants can not spread or widen their bases by aerial tillers that root to the soil as occurs in ryegrass. Prairie grass swards were able to quickly compensate for the detrimental effects of the head smut fungus *U. bullata*. However, sward production was reduced when more than 50% of the plants were infected. Controlling seedling infection with fungicide seed treatments should prevent such high levels of infection occurring in swards.

Reproductive development resulted in high yields of dry matter and digestible organic matter, but herbage quality declined rapidly after inflorescences emerged. The necessity to gain a good balance between high yields and high quality is discussed. Tiller numbers were able to recover quickly after cutting reproductive plants, through the growth of previously inhibited tiller buds at the base of reproductive tillers.

The following morphological characters were suggested as criteria for the optimum time of defoliation to ensure high levels of herbage quality, production and persistence. Defoliation should occur when 11.5 to 24% of the total tillers are reproductive or 4 to 12% of the total tillers have emerged inflorescences, when previously inhibited tiller buds at the base of reproductive tillers start to develop, when 4 or 5 leaves have appeared per tiller, and when reserves for regrowth have increased to a high level. These all require further study in detail and under sward conditions.

In a field trial at Wageningen, prairie grass had high yields and good persistence over two years which included two mild winters. It is suggested that prairie grass should at least be considered as a replacement for spring sown Westerwolds ryegrass on sandy soils in The Netherlands.

SAMENVATTING

Inleiding

Bromus willdenowii Kunth (synonyms *B. catharticus* Vahl, *B. unioloides* H.B.K., *B. schraderi* Kunth) is een hoog opgroeiende plant met brede bladeren, weinig maar grote spruiten en een lange generatieve groeifase. Vergeleken met andere veel gebruikte grassoorten uit gematigde streken (bijv. raaigras, rietzwenkgras, kropaar) heeft *B. willdenowii* veel voordelen. Hiervan kunnen worden genoemd hoge opbrengsten, speciaal gedurende koele winterperiodes, in droge tijden gedurende de zomer en het begin van de herfst, grote smakelijkheid in alle groeifasen, hoge ruwvoederkwaliteit, goede tolerantie tegen plagen en ziekten en goede morfologische eigenschappen die leiden tot een hoge opname door weidend vee. De produktie is echter laag wanneer deze soort wordt geteeld op plaatsen die onderhevig zijn aan een hoge waterstand of wanneer vaak wordt ontbladerd. De soort is ook gevoelig voor een schimmelziekte die veroorzaakt wordt door *Ustilago bullata* Berk., waardoor de produktiviteit en standvastigheid van de soort verlaagd worden. Ook kunnen als nadeel genoemd worden de geringe uitstoelingscapaciteit en de hoge mate van generatieve ontwikkeling.

In vergelijking met andere grassen, vooral raaigras, is er relatief weinig bekend over het gedrag van *B. willdenowii*, behalve onder algemene bedrijfsomstandigheden. Dit proefschrift geeft daarom drie kas- en fytotron- en vier veldstudies weer, waarin de morfologische en fysiologische aspecten van deze soort werden onderzocht. Speciale nadruk werd gelegd op een vergelijking van *B. willdenowii* met *Lolium*-soorten (*L. perenne*, het diploide ras 'Wendy', en *L. multiflorum* het tetraploide ras 'Caramba') en in mindere mate werd aandacht besteed aan rasverschillen in *B. willdenowii*. Nadruk werd ook gelegd op een onderscheiding van de vegetatieve en generatieve groeifase in *B. willdenowii*. Westerwolds raaigras was in de vergelijking meegenomen, omdat beide soorten een vergelijkbare groeivorm hebben, met een lange daglengte als de enige voorwaarde voor generatieve ontwikkeling.

Morfologische en fysiologische eigenschappen

In vergelijking met Westerwolds raaigras had *B. willdenowii* een vergelijkbare ruwvoeder kwaliteit gedurende de reproduktieve fase, alhoewel kwaliteit bij *B. willdenowii* sneller achteruit ging na het schieten. *B. willdenowii* had hogere celwand en hogere wateroplosbare koolhydraat gehaltes. De twee soorten hadden een vergelijkbare droge stof verdeling tussen bladschijven en pseudostengels, maar *B. willdenowii* had een betere verdeling van wortelmassa over grotere bodemdieptes, waaruit wellicht de grotere droogteresistentie van *B. willdenowii* wordt verklaard.

In vergelijking met beide raaigrassoorten had *B. willdenowii* een grotere bladverschijningssnelheid, grotere bladeren en bladscheden, meer levende bladeren per spruit en grotere reproduktieve ontwikkeling, maar geringere 'site filling' waardoor een geringer spruitaantal resulteerde. Lage spruitaantallen deden niets af aan het potentieel voor hoge opbrengsten, de mogelijkheid van planten om te compenseren voor de dood van spruiten of planten in het veld en de mogelijkheid om massaal uit te stoelen na verwijdering van grote aantallen reproduktieve spruiten door ontbladering. Verschillen in 'site filling' tussen de soorten was de voornaamste reden voor verschillen in spruitvormingssnelheid. In de *B. willdenowii* rassen die gebruikt werden in deze studies ontwikkelden zich geen spruiten uit de knop van het coleoptilum en slechts zo nu en dan spruiten uit de okselknop van het prophyllum; de *Lolium*-soorten produceerden wel spruiten uit deze knoppen. In het algemeen was er een grotere vertraging in het tevoorschijn komen van de jongste axillaire spruit in *B. willdenowii*. Maaiproeven gedurende de vegetatieve en generatieve groei toonden dat de produktie van *B. willdenowii* het hoogst was bij lage maaifrequenties en in mindere mate bij grotere maaihoogte. Gedurende de vegetatieve groei verschilde *B. willdenowii* met raaigras in het effect van frequenter maaien in sommige morfologische eigenschappen, maar de relatieve groeisnelheden waren vergelijkbaar in alle soorten. De rol van reserves voor hergroei (wateroplosbare koolhydraten en eiwitten) in *B. willdenowii* waren vergelijkbaar met raaigras alhoewel het gehalte aan wateroplosbare koolhydraten hoger was in *B. willdenowii*. Het bepalen van de juiste rol van reserves in

B. willdenowii vergt verdere studie.

De *B. willdenowii* rassen 'Bellegarde', 'Grasslands Matua' en 'Primabel' die in deze studie waren betrokken toonden een goede spreiding in morfologische eigenschappen en de betekenis hiervan voor de plantenveredeling worden besproken. 'Bellegarde' had hogere bladverschijningssnelheden, grote bladeren, lage 'site filling', lage spruit aantallen en snelle reproduktieve ontwikkeling. 'Primabel' had relatief lage bladverschijningssnelheden, kleinere bladeren, minder generatieve groei, maar hogere 'site filling' en spruitaantallen. 'Matua' was ongeveer intermediair voor deze eigenschappen. 'Matua' en 'Primabel' hadden de beste eigenschappen voor landbouwkundige produktie.

Het behoud van hoog produktieve en persistente zodes was afhankelijk van een combinatie van veranderingen in de spruitaantallen per plant, het spruitgewicht van bestaande planten in de zode en uit bijdragen van natuurlijke uitzaai. Dit zijn belangrijke eigenschappen van *B. willdenowii* omdat planten zich niet kunnen verspreiden of hun basis verbreden door spruiten die boven de basis ontwikkelen en zich vestigen in de grond zoals bij raaigras gebeurt. *B. willdenowii* zodes waren in staat om snel te compenseren voor nadelige effecten van de schimmelziekte veroorzaakt door *U. bullata*, maar zodeproduktiviteit was verminderd wanneer meer dan 50% van de planten waren aangetast. De infectie bij kiemplanten kan wellicht worden voorkomen door zaadbehandeling met een fungicide.

Generatieve ontwikkeling resulteerde in hoge opbrengsten van droge stof en verteerbare organische stof, maar ruwvoederkwaliteit ging snel achteruit nadat de bloeiwijzen tevoorschijn kwamen. De noodzaak om een goed evenwicht te bereiken tussen hoge opbrengsten en hoge kwaliteit wordt besproken. Spruitaantallen konden zich snel herstellen na maaien van generatieve planten, door uitstoeling uit voorheen geremde knoppen aan de stengelbases.

De volgende morfologische eigenschappen worden gesuggereerd als criteria voor het optimale tijdstip van ontbladering om hoge niveaus van ruwvoederkwaliteit, produktie en standvastigheid te waarborgen. Ontbladering moet plaatsvinden wanneer 11,5 tot 24% van het totaal aantal spruiten reproduktief is, of 4 tot 12% van het totaal aantal spruiten zichtbare bloeiwijzen heeft, wanneer eerder geremde spruitknoppen aan de basis van de reproduktieve spruiten beginnen te ontwikkelen, wanneer 4 tot 5 bladeren per spruit aanwezig zijn en reserves voor hergroei tot een hoog niveau zijn opgelopen. Meer gedetailleerde studies in het veld zijn vereist.

In een veldproef in Wageningen had *B. willdenowii* hoge opbrengsten en goede standvastigheid over twee jaren met zachte winters. *B. willdenowii* kan in ieder geval worden beschouwd als een vervanger voor Westerwolds raaigras op zandgrond in Nederland voor inzaai in het voorjaar.

CURRICULUM VITAE

David Edward Hume was born in Christchurch, New Zealand on 20 June 1960. After finishing his secondary school education at Christchurch Boys' High School, he started a four year Bachelors degree in 1979 at Lincoln College (Agricultural and Horticultural University), Canterbury, New Zealand. In the third year of this degree course he specialised in scientific research, with further specialisation in the fourth year in soil-plant-animal interfaces. Also in the fourth year he undertook an Honours Course in the Department of Plant Science. This course involved conducting a research project on the effects of winter cutting management on the yields and tiller densities of six grass species and writing a dissertation on this work. In May 1983, he graduated as a Bachelor of Agricultural Science with First Class Honours, and Senior Scholar.

In early 1983 he accepted a scientist position as a pasture agronomist with the Department of Scientific and Industrial Research Grasslands (DSIR Grasslands) at Palmerston North, New Zealand. His work involved pasture management and ecological studies, and evaluations of grass and clover species in dry hill country and fertile moist lowland. Another aspect of his work was involvement in the New Zealand Forage Germplasm Centre at Palmerston North.

In late 1986 he was granted a study award from DSIR to conduct a research programme for a doctorate thesis at the Department of Field Crops and Grassland Science, Agricultural University at Wageningen, The Netherlands, starting in March 1987. This study was completed in March 1990 and he will now return to New Zealand to his position at DSIR Grasslands, Palmerston North.